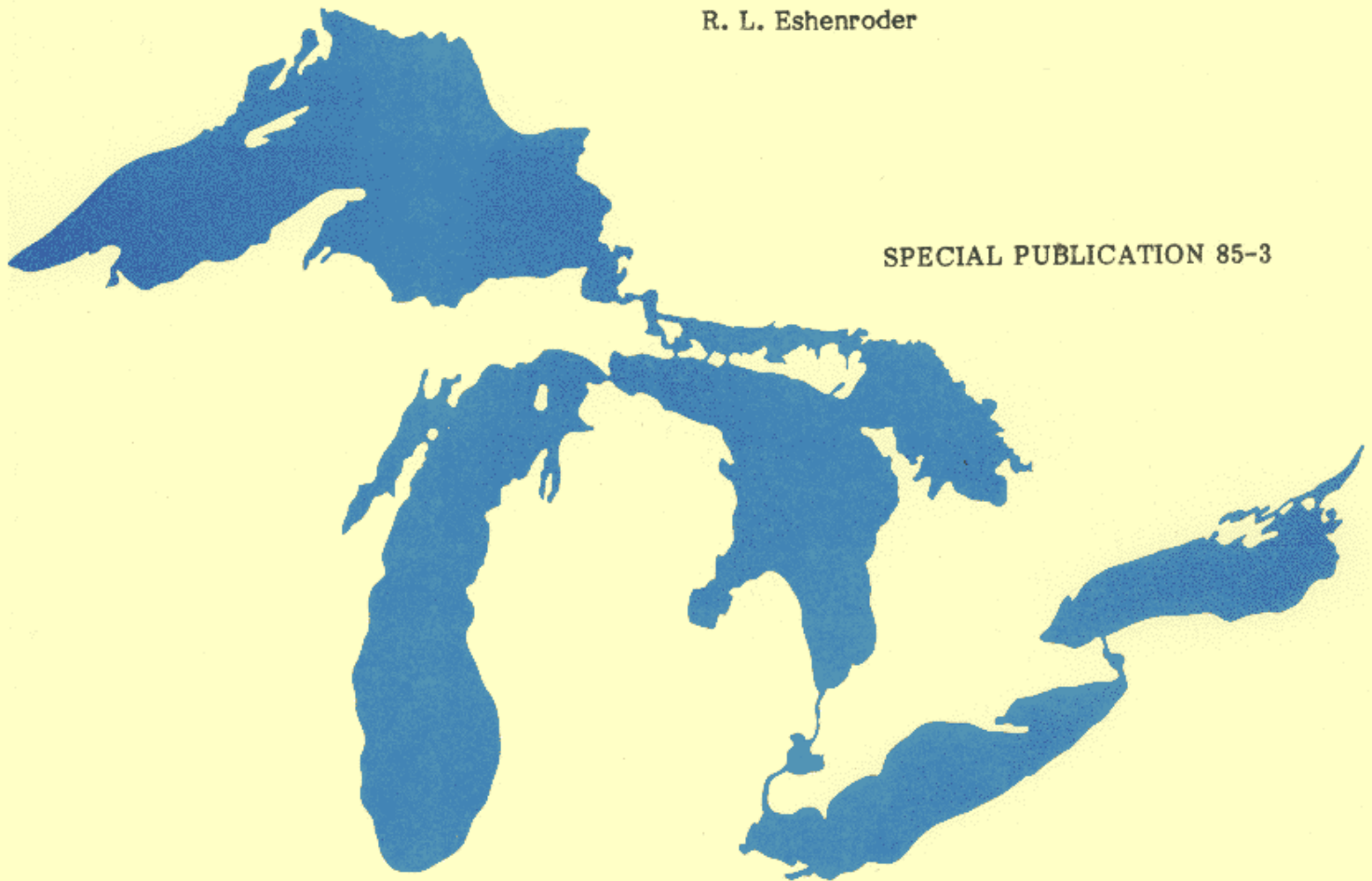


**PRESENTED PAPERS**  
**FROM THE COUNCIL OF LAKE COMMITTEES PLENARY SESSION**  
**ON GREAT LAKES PREDATOR-PREY ISSUES, MARCH 20, 1985**

edited by  
R. L. Eshenroder

SPECIAL PUBLICATION 85-3



**Great Lakes Fishery Commission**

1451 Green Road  
Ann Arbor, Michigan 48105

August 1985

The Great Lakes Fishery Commission was established by the Convention on Great Lakes Fisheries between Canada and the United States, which was ratified on October 11, 1955. It was organized in April 1956 and assumed its duties as set forth in the Convention on July 1, 1956. The Commission has two major responsibilities: first, develop coordinated programs of research in the Great Lakes and, on the basis of the findings, recommend measures which will permit the maximum sustained productivity of stocks of fish of common concern; second, formulate and implement a program to eradicate or minimize sea lamprey populations in the Great Lakes.

The Commission is also required to publish or authorize the publication of scientific or other information obtained in the performance of its duties. In fulfillment of this requirement the Commission publishes the Technical Report Series, intended for peer-reviewed scientific literature, and Special Publications, designed primarily for dissemination of reports produced by working committees of the Commission. Technical Reports are most suitable for either interdisciplinary review and synthesis papers of general interest to Great Lakes fisheries researchers, managers, and administrators or more narrowly focused material with special relevance to a single but important aspect of the Commission's program. Special Publications, being working documents, may evolve with the findings of and charges to a particular committee. Sponsorship of Technical Reports or Special Publications does not necessarily imply that the findings or conclusions contained therein are endorsed by the Commission.

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edited by

R. L. Eshenroder <sup>1</sup>

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<sup>1</sup> Great Lakes Fishery Commission  
1451 Green Road  
Ann Arbor, MI 48105

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## INTRODUCTION

Because of recent changes in populations of Great Lakes' forage fishes, the Council of Lake Committees sponsored a plenary session on predator-prey issues held at the 1985 joint meetings of the Upper Lakes and Lake Erie Committees. Ten papers covering a spectrum of topics including changes in predator and prey stocks, indicators of changes in stocks, and management implications were given and are provided here with the permission of the authors. In addition, a follow-up, overview paper on recommendations for management was presented to the Council at their 1985 meeting, and it, too, is included in this record. The Council and myself take this opportunity to thank the contributors for participating in the session and for making possible this publication.

R. L. Eshenroder  
8 August 1985

COUNCIL OF LAKE COMMITTEES PLENARY SESSION

PREDATOR-PREY ISSUES IN THE GREAT LAKES

Ann Arbor Inn  
Ann Arbor, Michigan  
20 March 1985  
8:30 a.m. to noon

(held in conjunction with the Lake Erie  
and upper Great Lakes Lake Committee Meetings)

AGENDA

- 8:30 a.m. Introduction (R. Eshenroder)
- I. Abundance of prey fish species during periods of low and high predator abundance
- 8:45 a.m. A, Cold water community
1. Lake Superior (J. Selgeby)
    - lake herring
    - b. chubs
    - c. smelt
  2. Lake Michigan (L. Wells)
    - a. chubs
    - b. alewife
    - c. smelt
    - d. shiners
    - e. sculpins
    - f. perch
- 9:15 a.m. B. Warm water community
1. Western Lake Erie (K. Muth)
    - a. shiners
    - b. alewife
    - c. gizzard shad

II. Predator responses to increased predator abundance **or** decreased prey abundance or qualitative changes in prey fish

9:30 a.m.

A. Cold water community

1. Lake Superior (T. Busiahn)

- a. lake trout
- b. Pacific salmon

2. Lake Michigan (D. Jester) (not available)

- a. lake trout
- b. Pacific salmon

10:00 a.m.

B. Warm water community

1. Western Lake Erie (**S.** Nepszy)

- a. walleye

10:15 a.m.

COFFEE

10:30 a.m. III. Implications of fish community changes for management (T. Busiahn/J. Kitchell)

A. Establishment of issues

B. Development of fish community goals

11:00 a.m.

IV. Indicators of the status of predator-prey systems

A. Cold water community (L. Crowder)

B. Warm water community (K. Muth)

11:30 a.m.

V. Effecting a policy: institutional arrangements for allocating the resource (J. Paine, R. Lange, and one other)

RLE

5 November 1984

POPULATION TRENDS OF LAKE HERRING (COREGONUS ARTEDII)  
AND RAINBOW SMELT (OSMERUS MORDAX)  
IN U.S. WATERS OF LAKE SUPERIOR, 1968-84

James H. Selgeby  
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Presented at:  
Council of Lake Committees Plenary Session  
Great Lakes Fishery Commission  
Ann Arbor, Michigan 48105  
March 20, 1985



Population trends of Lake Herring (Coregonus artedii)

and Rainbow Smelt (Osmerus mordax) in U. S.

waters of Lake Superior, 1968-84 1/ 2/

Lake herring (Coregonus artedii) once supported the largest commercial harvests of any Great Lakes species (Great Lakes Fishery Commission, 1979) and were a major forage of large lake trout in Lakes Superior and Michigan (Dryer et al. 1965, Van Ooste, and Deason 1938). Herring populations in U. S. waters of Lake Superior declined sharply in the 1940s (Minnesota), 1950s (Wisconsin), and 1960s (Michigan). Commercial harvests of herring declined from over 8 million Kg in 1941 to 140 thousand Kg in 1977 (GLFC 1979). As herring declined, rainbow smelt (Osmerus mordax) supplanted them as the major forage of salmonid predators (Dryer et al. 1965, unpublished data GLFL, Ashland).

Rainbow smelt apparently entered Lake Superior in the early 1930s (Hale 19601, but did not become commercially abundant until 1952 (GLFC 1979). Smelt abundance likely increased through the 1950s and early 1960s (Selgeby, MacCallum, and Swedberg 1973).

During the later 1970s, herring and smelt populations in U. S. waters of Lake Superior changed markedly. In this report, I document changes in herring and smelt populations in 1968-84 and examine several hypotheses that have been offered to explain those changes.

#### Methods

Estimates of abundance and year-class strength were developed from gillnet and trawl assessment surveys conducted by the GLFL, Ashland, Wisconsin. Indices of abundance are based on catch per unit of effort in assessments that have been maintained as uniform as possible. Where changes in assessment techniques or equipment were necessary, appropriate weighting factors were generated to adjust previously calculated CPEs.

#### Changes in Lake Herring Abundance

Abundance of adult lake herring declined from an index level of 3.1 in 1968 to 0.6 in 1978 and 1979, and increased sharply to 6.5 in 1984 (Fig. 1) based on gillnet catches at numerous locations in U. S. waters. Increasing abundance of herring was noted first in Wisconsin and western Minnesota waters and later in Michigan waters. In Wisconsin an 11-year-long trawl survey (1974-84) revealed that abundance of adult herring began to increase in 1978 (Fig. 2) and increased sharply in 1980-84.

Catches of young-of-the-year and yearling herring were almost nil lakewide in 1961-72 but in the fall of 1973, we caught a number of young-of-the-year herring and that year class was measurable as yearlings in 1977 (Fig. 3).

---

1/ Report to: Council of Lake Committees Plenary Session --  
Ann Arbor, Michigan  
March 20, 1985

2/ Compiled by: James H. Selgeby  
U. S. Fish and Wildlife Service  
Great Lakes Fishery Laboratory  
Ashland Biological Station, Ashland, Wisconsin

Measurable herring year classes of varying strength have been produced in the Apostle Islands region each year since 1973 of which the 1976 and 1978 were the strongest. The relatively strong 1976 year class in the Apostle Islands region was not seen outside the Island region but the 1978 year class was strong along the entire U. S. shoreline (Fig. 4) and it was that year class that led to the lakewide increase in adults in 1980 and 1981. The 1980 year class was indexed as strong lakewide and extraordinarily strong in western Wisconsin. Accumulation of adults of the 1978-81 year classes resulted in the rapidly increasing adult population seen in 1983-84. A strong 1983 and, based on preliminary observations of young-of-the-year, an unusually strong 1984 year class should lead to continuing increases in adult herring stocks.

#### Changes in Rainbow Smelt Abundance

Abundance of adult smelt declined sharply from an index level of about 4.5 in 1968-70 to 1.2 in 1975, recovered to over 3.0 in 1977-79 and declined to less than 1.0 in 1981-84 (Fig. 1). Although no single data series is available to measure the smelt population increase in the 1950s and 1960s, examination of several discontinuous series suggests that the abundance seen in 1968-70 is the highest level smelt attained in Lake Superior and abundance in 1977-79 was probably comparable to or higher than that in the mid 1960s.

Examination of 11-year-long smelt population trends in the Apostle Islands region (Fig. 5) revealed substantial changes in abundance, biomass, and average size. Abundance was high in 1974, largely due to a very strong 1973 year class. Weaker year classes in 1974-78 resulted in reduced abundance from the 1974 level but mortality rates were low (average annual mortality in 1975-79 was .64, range .62-.68) and as adult smelt accumulated, biomass and mean size increased. In 1980, abundance, biomass, and mean size plummeted as adult smelt were sharply reduced. Mortality increased to .80 in 1980-82 and year classes were relatively weak. In 1984, abundance increased sharply due to the presence of an exceptionally strong 1983 year class. Lakewide trends in abundance and biomass were similar to those seen in the Apostle Islands region (Fig. 6). The timing of smelt declines varied in the different areas of the lake. It may have occurred first in western Michigan since abundance and biomass were both very low when we first sampled there in 1978. The major declines were in 1980-81 in eastern Michigan and Minnesota and in 1979-80 in Wisconsin.

In 1984, abundance was higher than in 1978 lakewide due to sharply increased abundance in eastern Wisconsin and all of Michigan except Whitefish Bay. That increase was entirely due to the presence of a very strong 1983 year class. Abundance remained much lower than in 1978 in Whitefish Bay and western Wisconsin and somewhat lower in Minnesota. Biomass in 1984 was lower than in 1978 in all areas except western Michigan because the abundant one-year-old smelt were still small and was only four to five percent of 1978 levels in western Wisconsin and Minnesota. If the 1983 year class persists, smelt may recover from 1980-83 levels, but if high mortality continues the year class may be rapidly eliminated.

## Possible Causes for Changes in Herring and Smelt Populations

I can document no major disease or stress induced die-offs that could account for the large and rapid declines of smelt in Lake Superior. Declines occurred in all areas of U. S. waters, and although less well documented, apparently in Ontario as well, yet no reports of die-offs were received. In the Apostle Islands region of Wisconsin, an area heavily used by commercial and sport fishermen and recreational boaters, campers, and sightseers, over one million pounds of smelt disappeared between the springs of 1979 and 1980 yet no reports were made of dead smelt floating or on beaches.

Contrasting changes in smelt abundance with that of total predator abundance (Busiahn 1985) suggests that the relatively small increase in total predator abundance after 1979 cannot account for the extremely rapid decline of smelt documented in 1979-81. However, after the major declines of smelt had occurred, smelt mortality increased, probably due to continued rather intensive predation. Age composition of smelt stocks changed as high mortality persisted. Five and six year old smelt were common in 1978 and 1979 but nearly absent in 1981-83. Four, five, and six year old smelt made up 40% of total smelt biomass in 1979, 24% in 1980, 13% in 1981, and 10% in 1982-83. These changes were a result of high mortality and likely caused by continuing predation. The continuing predation on smelt, documented in a study of nearly 1,500 predator stomachs in 1981-82 and substantiated by numerous observations in U. S. and Ontario waters, despite low smelt abundance, has been one of the unusual observations during the last several years. Lake trout, in particular, have continued to eat smelt even though the smelt were very small and, in some instances, scarce. The first evidence of diet shifts from smelt to herring occurred in late 1984. Herring were found in lake trout stomachs in western Michigan waters in late summer and in western Minnesota waters in the fall.

Comparisons between trends in abundance of lake herring and smelt once again suggest some degree of interaction between the two species. Previous studies have shown that smelt prey on herring larvae (Selgeby, MacCallum, and Swedberg 1978) and changing levels of smelt predation might be presumed to affect year class strength of lake herring. However, strong year classes of herring were produced in the Apostle Islands region in 1976 and lakewide in 1978 during a period when smelt were likely at the second highest level of abundance they ever achieved and weak herring year classes were produced in 1981 and 1982 when smelt were very scarce. Changing levels of smelt abundance do not appear to explain the varying success of herring reproduction. Preliminary examinations suggest that the 1973 herring year class, which was apparently much stronger than those produced during the previous decade, initiated a process that corrected the extreme sex ratio imbalance in the adult herring population (8 or 9 females: 1 male) and sex ratios reverted toward 1:1. I believe that the succession of strong herring year classes in 1976-1983 is due to the development of increasingly effective spawning stocks. Continuing examination of lake herring data may suggest additional or different conclusions.

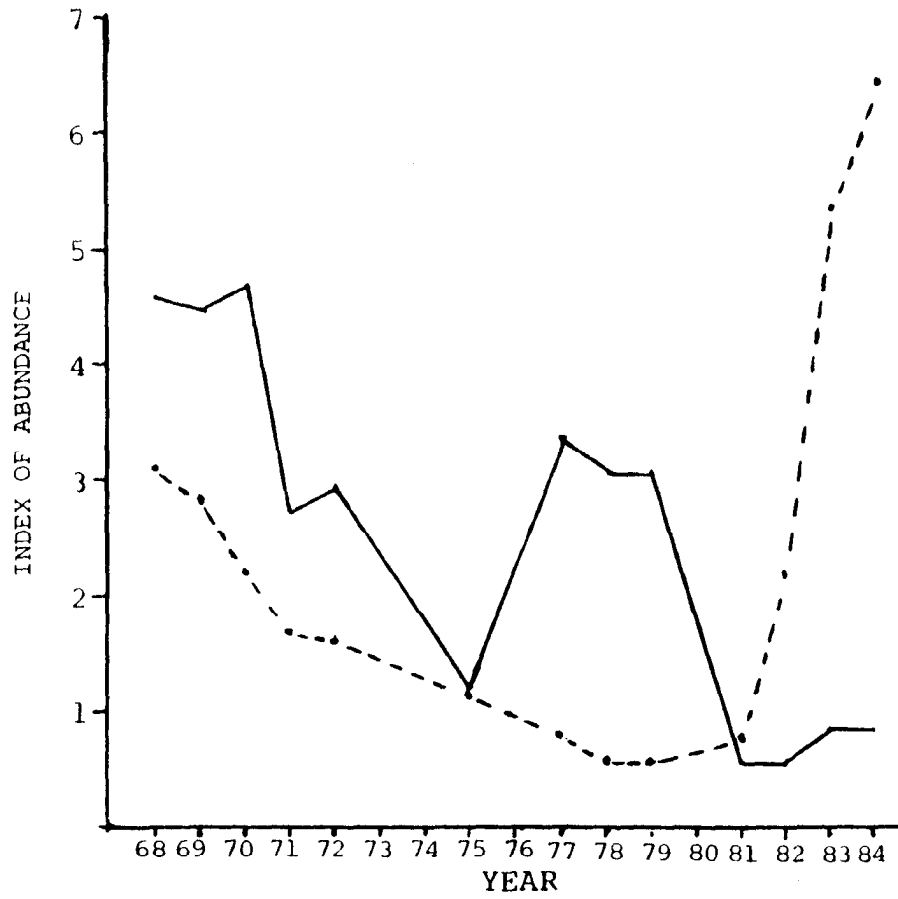
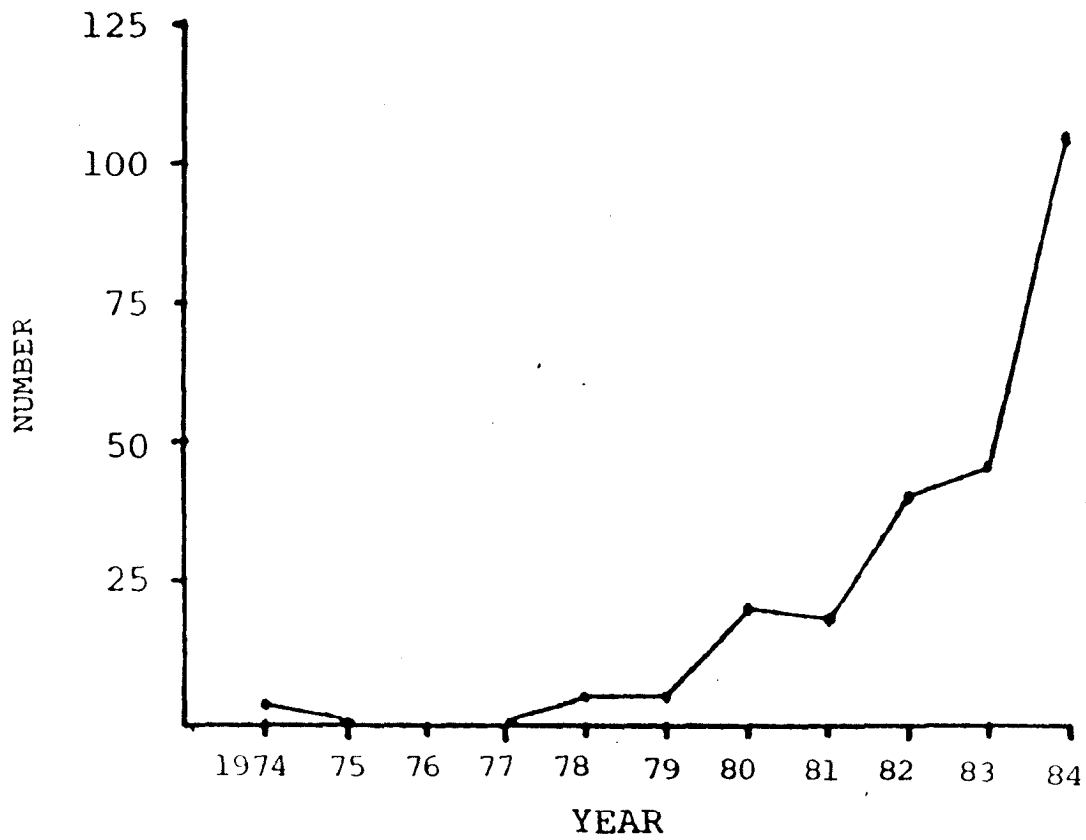


Figure 1. Index of abundance of adult smelt (solid line) and herring (broken line) in index gillnets in U. S. waters of Lake superior.



**Figure 2.** Abundance of adult herring in the Apostle Islands region 1974-84, as measured in spring cross-contour trawling assessments.

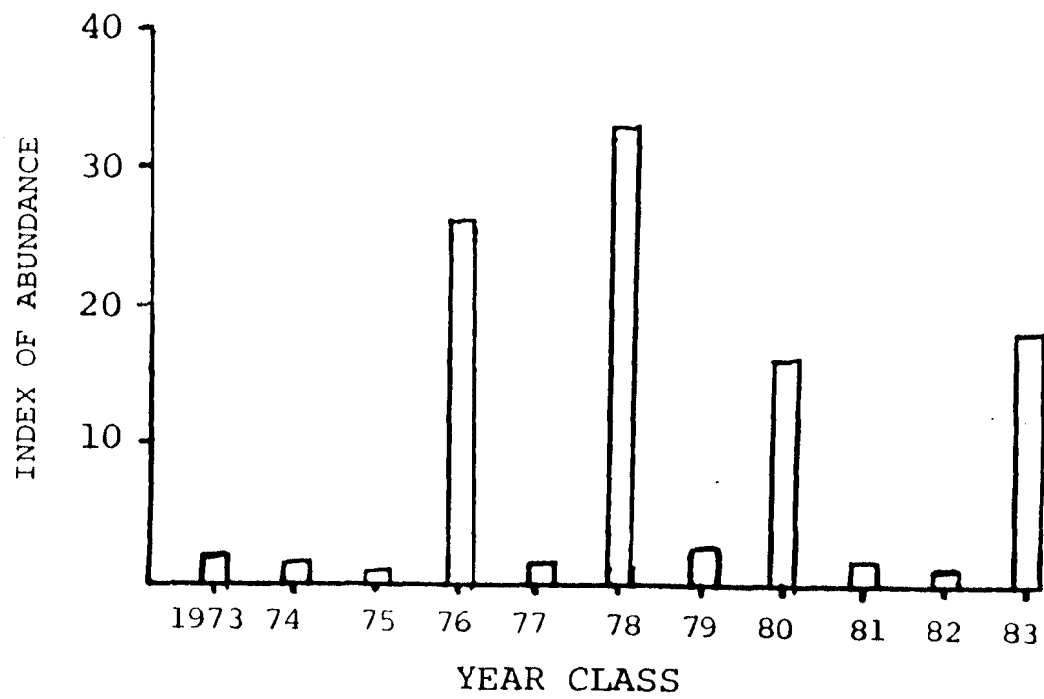
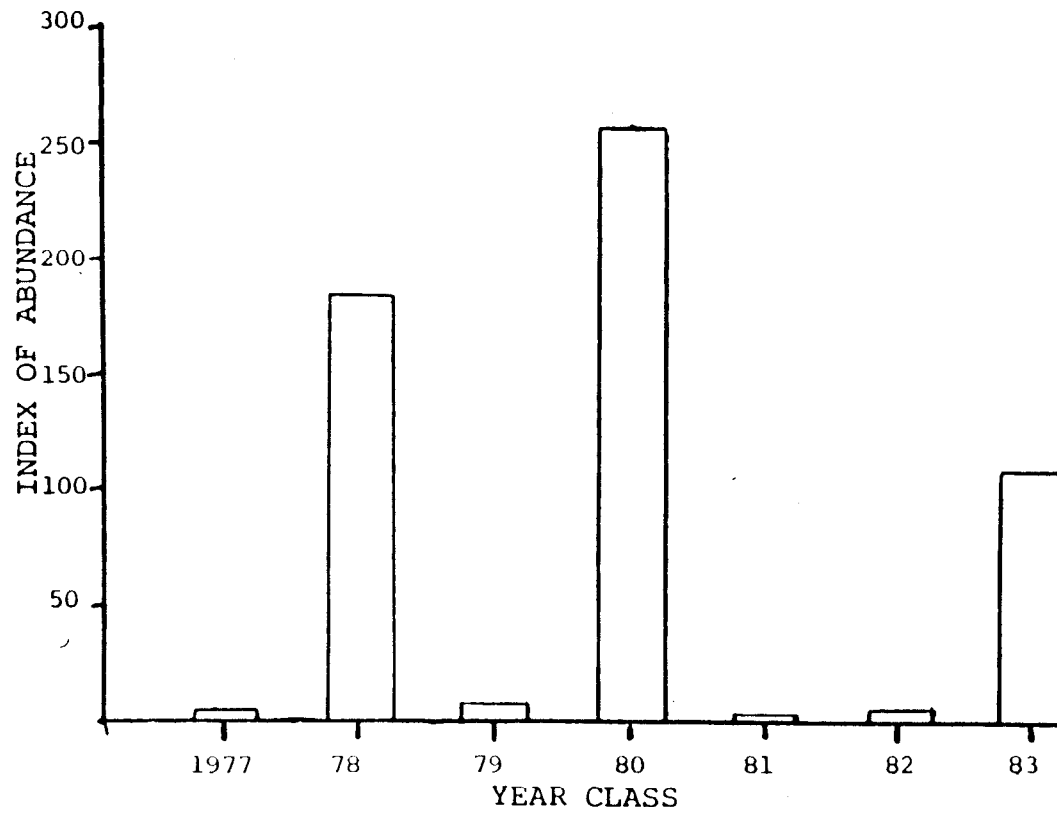


Figure 3. Index of year-class strength of lake herring in the Apostle Islands region of Lake Superior, 1973-83.



**Figure 4.** Index of year-class strength of lake herring in U. waters of Lake Superior, 1977-83.

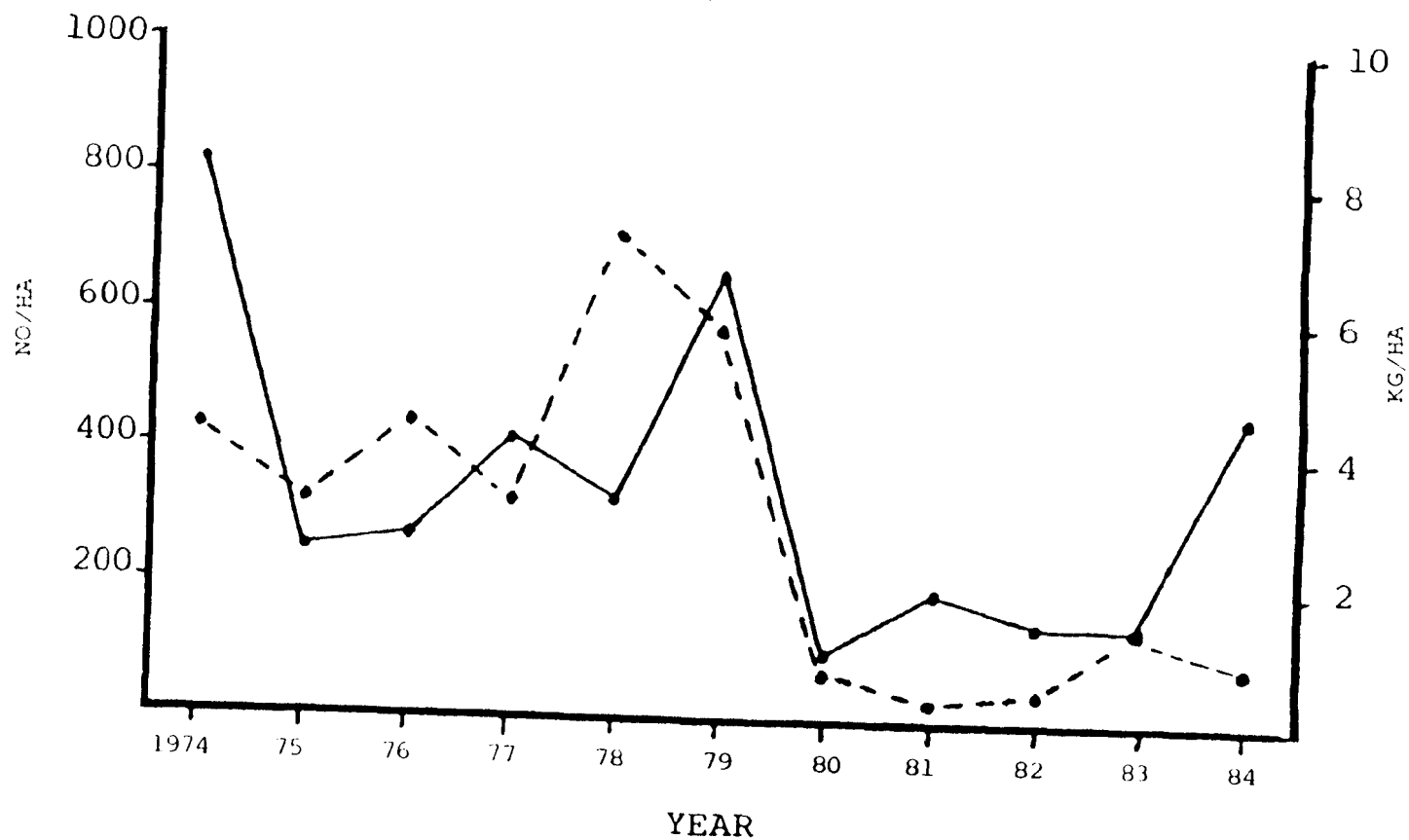


Figure 5. Abundance (NO/HA, solid line) and biomass (KG/HA, broken line) of rainbow smelt in the Apostle Islands region of Lake Superior, 1974-84, measured in spring cross-contour trawling assessment.



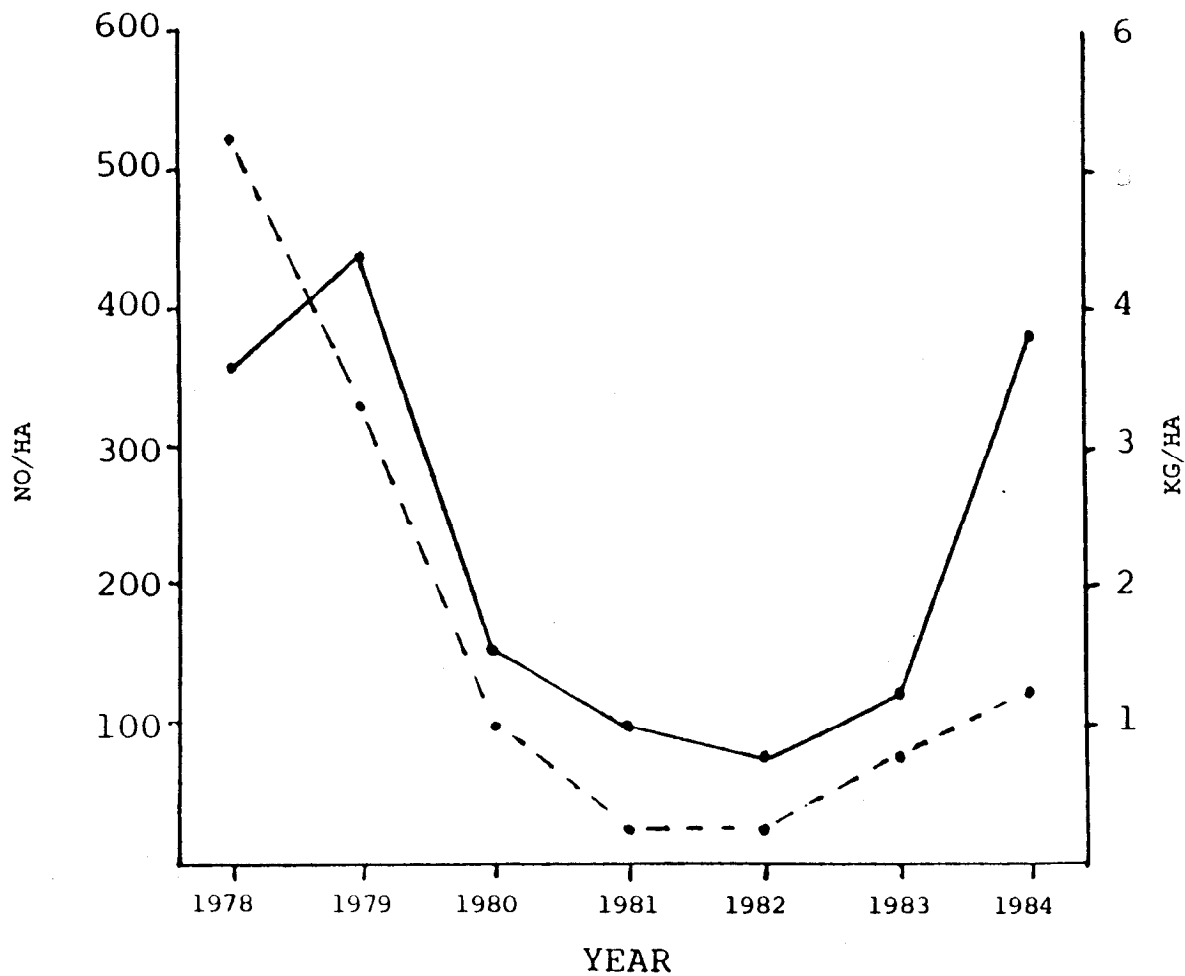


Figure 6. Abundance (NO/HA, solid line) and biomass (KG/HA, broken line) of rainbow smelt in U. S. waters of Lake Superior, as measured in spring cross-contour trawling assessment.

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CHANGES IN LAKE MICHIGAN'S PREY FISH POPULATIONS  
WITH INCREASING SALMONID ABUNDANCE, 1962 TO 1984

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Presented at:  
Council of Lake Committees Plenary Session  
Great Lakes Fishery **Commission**  
Ann Arbor, Michigan 48105  
March 20, 1985

CHANGES IN LAKE MICHIGAN'S PREY FISH POPULATIONS WITH  
INCREASING SALMONID ABUNDANCE, 1962 to 1984

LaRue Wells

Abstract

Along with dramatic increases in salmonid populations in Lake Michigan during the last two decades, striking changes in prey fish populations have occurred. Alewives increased to great abundance in the mid 1960's, suffered an enormous dieoff in 1967, recovered partly in the early 1970's, then fluctuated to low levels in 1982-84. According to some biologists the recent decline resulted from salmonid predation, but according to others it was due in considerable degree to adverse thermal conditions. Several species (smelt, chubs, deepwater sculpins, yellow perch, and emerald shiners) declined to low levels in the mid 1960's, apparently as a result of interference with their reproduction by the abundant alewife; then (except for the shiner) recovered in varying degrees as the alewife declined. Slimy sculpins decreased more or less steadily after 1971, evidently as a result of salmonid predation.

If alewives decline further and remain scarce permanently, the forage base for salmonids will probably consist mainly of abundant chubs and smelt. This forage supply should support large populations of salmonids, provided, of course, these predators substitute chubs for alewives in their diet.

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The dramatic buildup of Lake Michigan's salmonid (more accurately, salmonine) populations in the last two decades has received wide public attention. As recently as the early 1960's salmonids were virtually non-existent in Lake Michigan, but that situation began changing rapidly in the mid 1960's with large plantings of lake, steelhead, and brown trout, and coho and chinook salmon. The salmonid populations that have resulted from these plantings have generally not been measured directly, but changes in stocking rates probably provide a rough index of changes in their abundance. On that basis, the abundance of salmonids in Lake Michigan has climbed more or less steadily since 1965 (Fig. 1). Total salmonid plantings increased from an annual average of 3.4 million during 1965-68 to 8.6 million during 1969-72, 12.1 million during 1973-77, and 15.4 million during 1978-84. In all, about 215 million salmonids have been stocked in Lake Michigan in the last two decades.

Along with these increases in salmonids, striking changes have occurred in prey fish populations. Some of the changes in prey obviously were not related to the salmonids, whereas others may have been. In this report I discuss the shifts in abundance of the different forage species and present my opinions, and in some cases those of others, as to the reasons for the changes. (The discussion pertains only to Lake Michigan proper, i.e. the lake exclusive of Green Bay.) In respect to the salmonids' primary prey species, I make special reference to the possible role of predation in the changes, I used 1962 as the beginning year for my analyses because that is the first year in which data on prey species were systematically collected.

### Methods

The estimates of changes in abundances of prey species are based mainly on the results of fall bottom-trawl surveys conducted by the U.S. Fish and Wildlife Service each year 1962-84. During the surveys, samples were taken at a standard series of depths at one or more index stations. The number of index stations increased from one (Saugatuck) in 1962-66, to four, (all in the southern part of the lake and including Saugatuck) in 1967-72, and finally to eight (the four southern stations plus four in the north) in 1973-84.

The catch statistics used in this report to describe trends in abundance of prey fish differed according to species. Space limitations prevent a detailed description of those differences. Briefly, however, the trends for chubs and deepwater sculpins were derived simply from changes in average numbers in the survey catches; and for alewives, smelt, and slimy sculpins they were derived partly from changes in average numbers in the catches (earlier years) and partly from changes in estimated biomasses (as determined from the catches). Shifts in abundances of yellow perch and emerald shiners are described only in general terms.

### Changes in Abundance of Primary Prey Species

The species in this section make up the bulk of the diet of salmonids in Lake Michigan. They are discussed in order of present importance in the diet. However, the food habits of salmonids have been changing in recent years, and the order of importance of the different prey species could shift in the future.

#### Alewives

The alewife, first reported in Lake Michigan in 1949, had increased to extraordinary abundance by the mid 1960's, then declined abruptly in 1967 (Fig. 1). A partial recovery in the early 1970's was followed by a sharp decline in the mid-1970's. After another partial recovery, alewife populations descended in 1982-84 to their lowest levels since sampling began in 1962.

The decline of alewives in 1967 resulted from an enormous dieoff; salmonid numbers were still relatively small and predation on alewives must

have been minimal in relation to their population size. Increasing numbers of salmonids in the early 1970's did not prevent alewives from making a partial recovery, although they may have dampened it.

The extent to which the generally lower abundance of alewives after the mid 1970's is related to salmonid predation has become the subject of controversy. Kitchell and Crowder (in press) attributed most or all the decline, particularly that after 1981, to salmonid predation. On the other hand, Eck and Brown (in press) believed that adverse thermal conditions were the chief cause of the diminished alewife populations after the mid 1970's. Eck and Brown, whose estimates of alewife abundance and productivity were much higher than those of Kitchell and Crowder, contended that throughout the 1970's alewives were abundant enough to provide forage for more than twice the existing salmonid populations, and that therefore predation could not have been the primary factor in the decline. Using heating degree days recorded at Muskegon, Michigan, as an indirect measure of the thermal environment of Lake Michigan, they concluded that in nearly all years during 1977-83 Lake Michigan was colder than the normal for the period 1949-83, and postulated that this colder environment caused high overwinter mortality of young. Eck and Brown did, however, concede that salmonids may have hastened the decline by continuing to prey heavily on alewives while low temperatures were limiting recruitment. Even if adverse thermal conditions did trigger the decline, I think it fairly safe to assume that predation by salmonids would at least slow the progress of any future recovery of alewife populations.

#### Rainbow smelt

Rainbow smelt began a decline in 1962 (or earlier) that led to extremely low levels of abundance in the mid 1960's, then their populations gradually recovered in the late 1960's and early 1970's (Fig. 1). Their abundance did not change much from 1973 to 1980, but increased substantially in 1981 and 1982. Marked declines in 1983 and 1984 reduced populations to levels somewhat below those of 1973-80.

Salmonid predation obviously had not affected smelt populations noticeably through 1982. The sharp decline in smelt abundance in the mid 1960's started before the salmonid stocking had begun, and the increase in 1981-82 occurred at a time when salmonid populations had reached high levels. In regard to the decline in the mid 1960's, the assumption that it was a lakewide event could be questioned, because the evidence for its occurrence came from sampling in only the southern part of the lake, which usually contains only a small portion of the lake's total smelt population. However, strong evidence for the decline is provided by the commercial catch, which decreased drastically in the mid 1960's. Smith (1970) noted the drop in commercial catches and believed that the alewife was responsible for the scarcity of smelt, but thought that in general smelt are not as strongly affected by alewives as are some of the other Great Lakes species--and I agree with him on both points.

The rather substantial decrease in smelt abundance in 1983 and 1984 suggests that the recent partial substitution of smelt for alewives in the

diet of salmonids has begun to depress the smelt populations. The decline, however, was in my opinion related simply to normal fluctuations in year-class strength. Reproduction of smelt (based on catches of young-of-the-year in fall dropped 16% in 1982 and an additional 47% in 1983--decreases that would be expected to be reflected in the adult populations in 1983 and 1984, respectively. A rather heavy dieoff of smelt that occurred in the northern part of the lake in the spring of 1984 might also have contributed to the sharp decrease in abundance that year.

There is no certainty, of course, that smelt would not be affected by greatly increased predation on them, such as might result indirectly from further declines in alewives. It should be remembered, however, that smelt became established in Lake Michigan in 1923 and proliferated extremely rapidly during the next two decades, despite the presence of a considerable abundance of lake trout.

### Slimy Sculpins

Slimy sculpins populations fluctuated without trend from 1962 to 1971, but decreased more or less steadily thereafter (Fig. I). Average abundance during 1982-84 was only about 10% of that during 1962-72.

The most logical explanation for the decline in slimy sculpins seems to be predation by salmonids--specifically by lake trout, inasmuch as the other salmonids eat few sculpins. The persistence of the decline may cause concern that the slimy sculpin is in danger of disappearing from Lake Michigan, but any such fears are probably premature. Although unquestionably scarcer than they formerly were, slimy sculpins may be more abundant than the trawl data indicate. Eck and Wells (manuscript in preparation) reported that slimy sculpins were often common in stomachs of lake trout caught in areas where trout catches indicated that (at the time the trout were caught) few if any sculpins were present. This apparent anomaly **probably** relates to the low daytime vulnerability of the sculpins to the trawl. Brandt (1978) showed that in standardized trawl tows, catches of slimy sculpins may be 10 times as large at night as in daytime, presumably because these fish are more active (i.e. less tightly on bottom, and thus more vulnerable to trawls) at night than in daytime. In assessing the probability that predation will eventually exterminate the slimy sculpins in Lake Michigan, it should be borne in mind that this prey species apparently existed in at least reasonable numbers when native lake trout were abundant. No direct measurement of sculpin populations in that period were ever made, but Van Oosten and Deason (1938) reported that slimy sculpins were common in the diet of lake trout in the early 1930's.

### Changes in Abundance of Secondary Prey Species

The species discussed below, although not presently of great importance in the diet of salmonids, have the potential of becoming so. All but one of them (the emerald shiner) are consumed to some extent by salmonids and two of them (chubs and yellow perch) have recently been eaten more frequently than

before. All have undergone striking population changes that were evidently related to alewife abundance.

### Chubs

Several authors (e.g. Smith 1964, 1968; Brown 1970; Wells and McLain 1973) have described the complex changes in Lake Michigan's chub stocks before 1962. Briefly, six of the seven species included in the original chub populations had become extinct or uncommon by 1962. The smallest of the species, the bloater, became much more abundant as the others declined. Smith (1964) attributed the decreases in the six species to the commercial fishery and the sea lamprey, both of which selected larger fish; and the increase in bloaters to diminished predation on them by lake trout, (as the native trout populations collapsed), and to certain advantages gained by them as the other chubs became scarce. (Smith, based on work by Van Oosten and Deason 1938, considered the bloater the most important of the chubs as food of native lake trout.)

Bloaters (referred to as chubs hereafter) began a decline at least as early as 1962, and probably a few years earlier (Fig. 2). Although data comparable to that collected in our standard surveys are not available for years before 1962, data from other sources indicate that chubs were more abundant in the mid 1950's than in 1962 (Brown 1970). The decline continued until 1977, after which a spectacular reversal in population trend began and was still in progress in 1984.

A few words about the commercial chub fishery might be pertinent here. From 1965 to 1969 the commercial catch increased greatly despite diminishing numbers of chubs. The increase in commercial catches (which are recorded by weight) was related to the faster growth of the chubs as they became scarce, and to some increase in fishing intensity. The faster-growing chubs not only provided larger individuals to the fishery, but also were more vulnerable to the gillnets used to catch them. Commercial catches dropped off sharply after 1969, and by the mid 1970's many fishermen had discontinued operations. A chub technical committee, formed by the Great Lakes Fishery Commission and made up of biologists from the states bordering Lake Michigan and the U.S. Fish and Wildlife Service, recommended severe restrictions on the fishery. These recommendations were accepted by the different state agencies in 1976. Some restrictions are still in affect although they have been relaxed considerably in some of the states.

I believe that the changes in chub populations between 1962 and 1984 were related mainly to changes in alewife abundance. The decline in the numbers of adult chubs that took place from 1962 (or a little earlier) to 1977 resulted from poor reproduction, evidently a consequence of alewives feeding on chub fry or eggs, or competing with chub fry for planktonic food. The increase in adult chubs that began in 1978 (and was still under way in 1984) resulted from steadily improved reproduction that took place during a period of lowered alewife abundance. I do not believe that the restrictions on the chub fishery influenced the recovery significantly in the first few years. The



new regulations had been in effect too short a time to have led to much enlargement of the spawning stock. Our survey catches, in fact, show that spawning stocks were at or near their lowest levels when the first improvement in reproduction occurred. However, the restrictions may well have hastened the recovery once it was under way. In any case, the decisions by the different state agencies to give additional protection to the spawning stocks were wise ones, considering the low levels of the stocks at the time, and especially in light of earlier declines of chubs to extinction in Lake Ontario and rarity in Lake Huron.

The future of chubs in Lake Michigan depends on several factors. If alewives make a substantial comeback, chubs should decline. If alewives remain at their present population levels or decline further, trends in chub population will depend on the degree to which salmonids increase their consumption of this species. If they increase it little or none, then chubs will probably expand to the extent that their growth rate will decline and their populations may eventually resemble those of the mid 1950's, when they consisted overwhelmingly of small individuals. If, on the other hand, predation on chubs increases substantially, their populations will probably be held in check or even reduced, and should include a significant proportion of larger individuals.

#### Deepwater sculpins

In a decline that began at least as early as 1964, lakewide populations of deepwater sculpins descended to very low levels in the mid and late 1960's. Data on the abundance of deepwater sculpins were not collected systematically before 1964, but especially large catches in non-standardized trawling in 1960 as compared with the catches in 1964 suggest that the decline was well under way by the latter year. The species began a recovery in the early 1970's and had increased more than 100-fold by 1980. Successive declines of about 50% in 1981 and 1982 were followed by a 3-fold increase in 1983. Numbers changed little between 1983 and 1984.

The population trends differed somewhat according to geographical area. Recovery in the 1970's began at the start of the decade in the extreme southeastern part of the lake (judging by data from Saugatuck) but not until near the end of the decade in the extreme northwestern part. The abrupt, decline in 1981 and 1982 mentioned above did not actually extend to the extreme northwestern part, where increases occurred instead.

The decline in the 1960's resulted from poor reproduction; few small deepwater sculpins were observed in the trawl catches of those years (Wells and McLain, 1973). I believe that alewives caused the poor reproduction, probably by preying on larvae. The reason for the delayed recovery in the extreme northwestern part of the lake is not clear, but possibly the alewives in that area (near Green Bay, where the species may be more abundant than in most of the lake proper) lagged behind those in other parts in declining to levels low enough to allow good reproduction of deepwater sculpins. The decline of deepwater sculpins in most of the lake in 1981-82 resulted at least

in part from a dieoff in the winter (and perhaps spring) of 1980-81. Trawl catches in the spring of 1981 contained many dead individuals of this species. I believe the most probable cause of the dieoff was stress due to overcrowding. The absence of a decline in the extreme northwestern portion of the lake may have been simply a reflection of uncrowded populations in that area.

#### Yellow Perch

Yellow perch were once abundant almost throughout Lake Michigan but suffered a severe decline in the early and mid 1960's (perhaps beginning in the late 1950's in the northern part). By 1968 they were scarce except in the southeastern part; and even there their numbers had diminished greatly. As was true for several other native species, the decrease in perch was due to poor reproduction, almost surely a result of the very high abundance of alewives at that time. After alewives declined sharply in 1967-68, perch produced a relatively strong year class in 1969, at least in the southeastern part of the lake.

Populations of perch in the 1970's were generally larger than in the mid and late 1960's, but still not nearly so large as those before the decline. The species was still concentrated mainly in the southeastern and extreme southwestern sections of the lake, and in a few rocky-bottomed areas in the east-central part. In 1983 an immense year class was produced in at least the areas where adults were common. In 1984 another strong year class was produced, but it was not as strong as in 1983. The good reproduction of 1983 and 1984, of course, coincided with low alewife abundance.

Perch of the 1983 year class were preyed upon rather heavily by salmonids in 1984, at least in the spring. Predation on young perch by salmonids will probably be common only in spring (and perhaps winter) and during upwellings in the warm season because at most other times perch will occupy warmer water than the salmonids. Heavy predation on young perch, at least in respect to year classes as large as that of 1983, should be desirable for salmonid as well as perch populations. Presumably due to high population density, the 1983 perch have grown extremely slowly, reaching an average total length in the southeastern part of the lake of only about 100 mm at the end of two years of growth. The corresponding length of perch in the same area during the 1970's was about 160 mm. In terms of weight, the fish produced in the 1970's were four times as large as those produced in 1983 at the end of their second year of life.

#### Emerald shiners

The emerald shiner underwent a phenomenal change in abundance in Lake Michigan around 1960. Until that time it was so abundant that it occasionally clogged cooling water intake screens of power plants and was considered a nuisance when it congregated in harbors in spring and fall. However, an astonishing decline that probably began in the late 1950's reduced the emerald shiner to near extinction in the early 1960's. The species has not since recovered to any significant degree.

The sudden near-disappearance of the emerald shiner coincident with the rapid increase in alewife populations strongly suggests that the two events were related. Although confirming evidence is lacking, the shiner probably declined as a result of poor reproduction, most likely a consequence of predation on the fry by alewives.

The collapse of emerald shiner populations well before alewives had reached peak abundance suggests that the shiner is highly sensitive to the adverse effects of alewives, and that it may not be able to stage a comeback unless alewives are reduced further. Even if alewives were to become scarce enough for successful reproduction by emerald shiners, the shiner would probably recover only slowly in the beginning because its spawning stocks are exceedingly small.

#### Discussion

The striking changes in abundance of native prey fish in Lake Michigan during 1962-84 are attributable mainly to changes in abundance of the alewife, a non-native prey species (but probably also a predator on fry). Populations of several native species suffered disastrous declines as the alewife increased to extreme abundance in the mid 1960's, and most that declined (the emerald shiner being a notable exception) have staged major comebacks in recent years of lowered alewife abundance. The slimy sculpin alone among the native species seems to have been directly affected by salmonid predation. The extent to which the other native species were affected (indirectly) by salmonid predation depends, of course, on the extent to which the alewife was affected by this predation--and this point is one of considerable disagreement among biologists.

Further declines in alewife abundance, should they occur, ought to lead to even further recovery of native forage species, and perhaps even to a resurgence of the emerald shiner. Should alewife populations remain at permanently low levels, populations of native prey fish might eventually reach some semblance of stability at relatively high levels. Under such conditions the forage base might still be sufficient to support large populations of salmonids. Smelt and chubs should be available in large quantity, and some additional forage would be provided by sculpins, yellow perch, and perhaps even emerald shiners. The size of the salmonid population that this forage base could support, however, would probably ultimately depend mainly on the degree to which the salmonids substituted chubs for alewives in their diet.

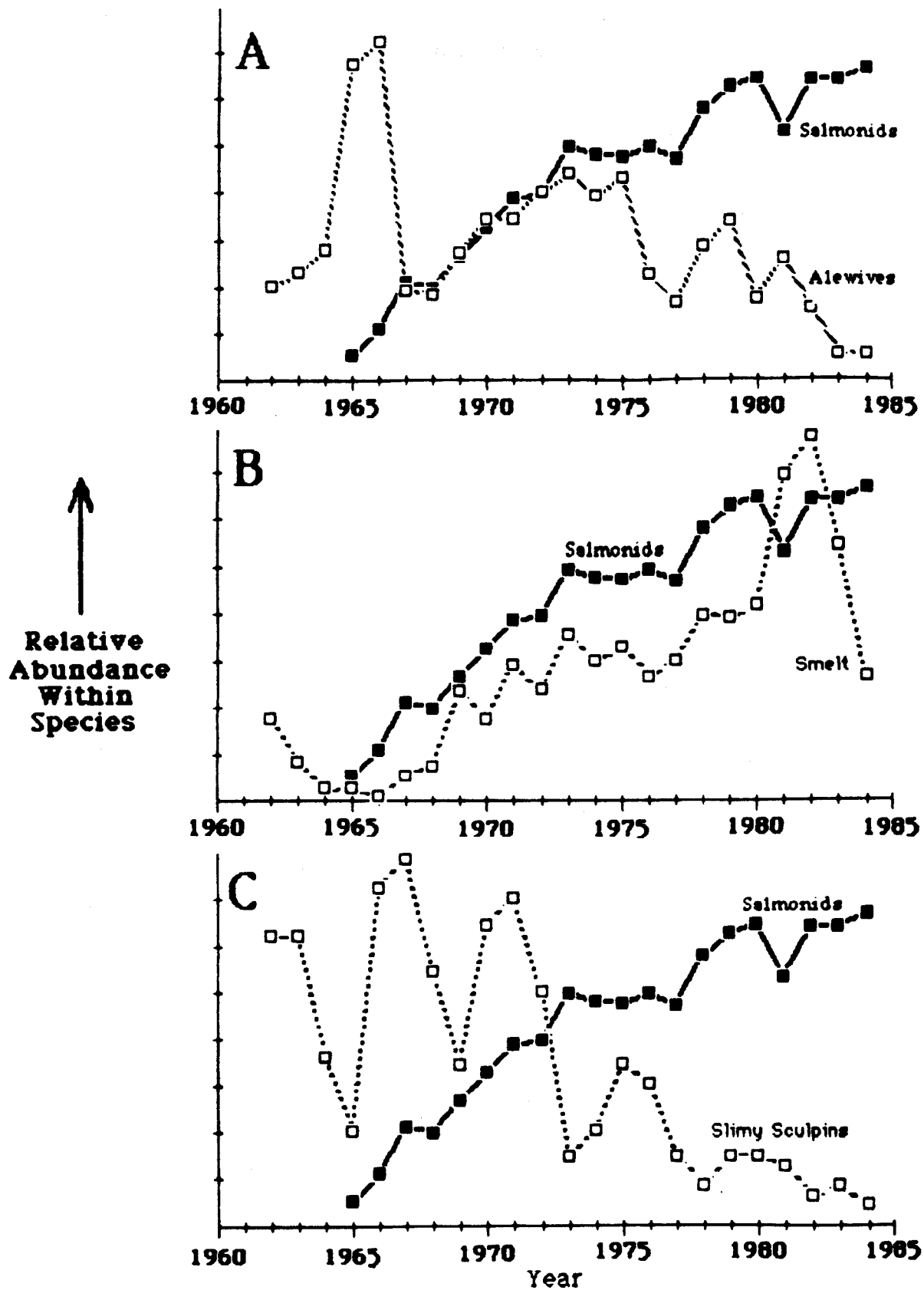


Figure 1. Trends in relative abundances of salmonids and different prey species: A-alewives; B-smelt; C-slimy sculpin. (See text for methods of determining relative abundances.)

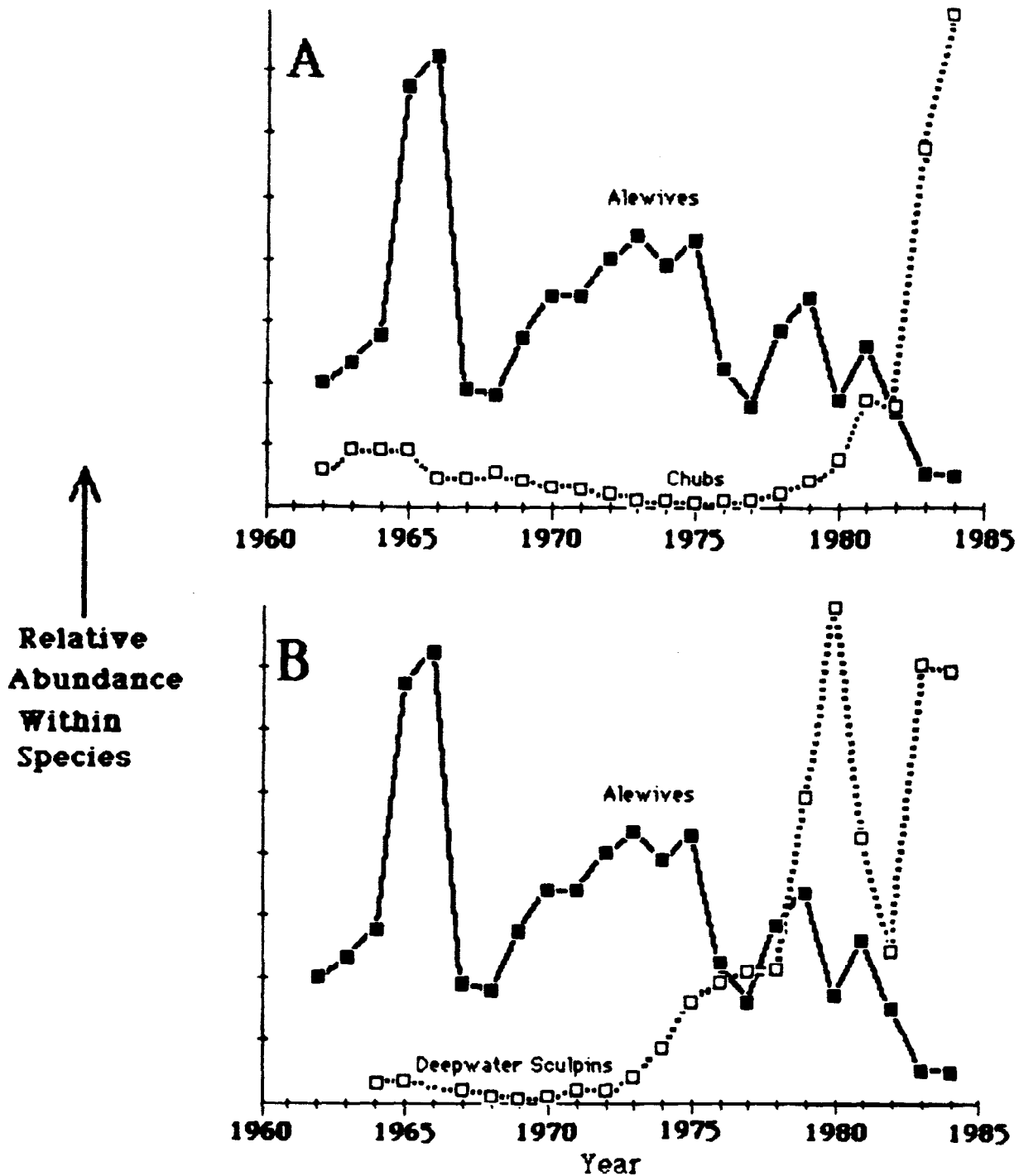


Figure 2. Trends in relative abundances of alewives and different secondary prey species: A-chubs; B-deepwater sculpins. (See text for methods of determining relative abundances.)

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CHANGES IN PREY FISH ABUNDANCE IN WESTERN LAKE ERIE  
DURING PERIODS OF HIGH AND LOW PREDATOR ABUNDANCE

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Changes in Prey Fish Abundance in Western Lake Erie  
During Periods of High and Low Predator Abundance

Predator-prey interactions in the western Lake Erie fish community are complex and difficult to understand due to the abundance and diversity of species present. However, we can develop some insight into some of these interactions by studying the population changes of a few key species that have occurred during the past two decades. Walleye *Stizostedion vitreum vitreum* was selected as the predator species for this study because it is the dominant piscivorous predator present in the fish community and it is nearly totally dependent on prey fish as a food resource. Also, the abundance of this predator has changed from very low levels in the 1960's to very high levels in the late 1970's and recent years. Emerald shiner *Notropis atherinoides* spottail shiner *Notropis hudsonius* young-of-the-year (YOY) gizzard shad *Dorosoma cepedianum* and YOY alewife *Alosa pseudoharengus* were selected as representative prey fish species because prior analyses of walleye feeding habits suggested that these species were commonly eaten. A fifth prey species, trout-perch *Percopsis omiscomaycus* was also included in our analyses of changing prey abundance because it represents a species in western Lake Erie that does not appear to be directly affected by walleye predation.

The relative abundance of the prey fish species in western Lake Erie is determined each year by the U. S. Fish and Wildlife Service by conducting bottom trawling surveys at up to 12 geographically dispersed stations that are representative of the available depth strata in the basin. Sampling occurs from May through October during most years. A semi-balloon bottom trawl having a 7.9-m head rope, a 9.4-m foot rope, and a 38- and 13-mm mesh (stretched measure) in the net body and cod end respectively, is towed at a constant speed of 3.9 km/hr. for 10 minutes along the depth contours at each station. Prey fish in the catches are sorted by species into three age categories (YOY, yearling, and age II and older) and total counts in each age category are tallied. Large catches occasionally preclude total counts, so subsamples are counted and appropriately expanded to estimate catch. Abundance indices for each age category of each species are reported as catch-per-unit-of-effort (CPUE) where effort is defined as one hour of trawling. These standardized sampling procedures have been utilized each year since 1960 so annual CPUE values for all years are comparable. However, individual CPUE values vary considerably from year to year, and the causes of this variability are unknown. Abundance values derived solely from bottom trawl catches probably underestimate true abundance and contribute to the data variability because we have no measure of the number of fish present in the upper strata, which are not sampled by the trawl. Changing light conditions, water temperatures, water currents, and a host of other unknown factors could also induce catch variability by altering fish behavior and their susceptibility to trawl sampling. Because of this unexplainable data variability, we



regard CPUE values as relative abundance indicators that suggest changing patterns of species' abundance over multiple year periods rather than considering the year to year abundance fluctuations.

The annual relative abundance index values for YOY prey fish from 1960 through 1981 are represented in Fig. 1. Emerald shiner and trout-perch abundance patterns are similar with generally high abundance levels in the early 1960's, followed by low abundance for the next 8 to 10 years, and then an apparent increasing abundance after 1975. Spottail shiner abundance remained high throughout the 1960's, but began to decline in the 1970's and low abundance persisted through 1981. The annual YOY alewife abundance has consistently been low with the exception of two years (1973-1974) when reproductive success was unexplainably good. Abundance of YOY gizzard shad has also been generally low during most years until record high abundance levels were recorded in 1980 and 1981.

Relative abundance indices for yearling prey fish are illustrated in Fig. 2. Yearling spottail and emerald shiners abundance generally remained high from 1960 to about 1974, but has been depressed to relatively low abundance levels since that time. Yearling trout-perch abundance was relatively high in the early 1960's followed by eight years of low abundance until 1977 when the abundance of this age group recovered to the 1960's level.

Relative abundance patterns of age II and older prey fish are generally similar to those demonstrated by yearling fish, but the CPUE values are usually lower (Fig. 3).

When we compare fluctuations of prey fish abundance with change in predator abundance over the 21 year period we can develop hypotheses about the predator-prey interactions. During the 1960's walleye abundance was very low in western Lake Erie and the predator pressure on prey fish populations would also be low at that time. Shiner abundance remained high during those years, even though these species are preferred food items of walleyes; so predation was probably not adversely affecting shiner populations. After efforts to rehabilitate the walleye stock were initiated in 1976, walleye abundance increased to very high levels and the effects of increased predation on the shiner populations may be reflected by the declining abundance of these species. Unlike shiners, YOY alewife and gizzard shad populations levels remained relatively low during the years when walleye abundance was low, so these prey fish species do not seem to be directly influenced by walleye predation pressure. Perhaps habitat and climatic conditions influence the spawning success of clupeids and are more important factors regulating their abundance. The high abundance levels of YOY gizzard shad during 1980 and 1981 did not seem to be adversely affected by the high Walleye predation pressure at that time even though walleye food habit studies clearly indicated that they fed extensively on this prey species. Finally, changes in trout-perch abundance in

western Lake Erie do not appear to be associated with changing walleye predation pressure. This prey species is readily consumed by walleye in some other ecosystems, but is seldom found in the Lake Erie walleye stomachs so predation does not directly influence its abundance. High abundance levels of trout-perch are indicated during both low and high walleye abundance periods.

Figure 1. Annual relative abundance of young-of-the-year (YOY) prey fish as indicated by catch-per-unit-of-effort (CPUE).

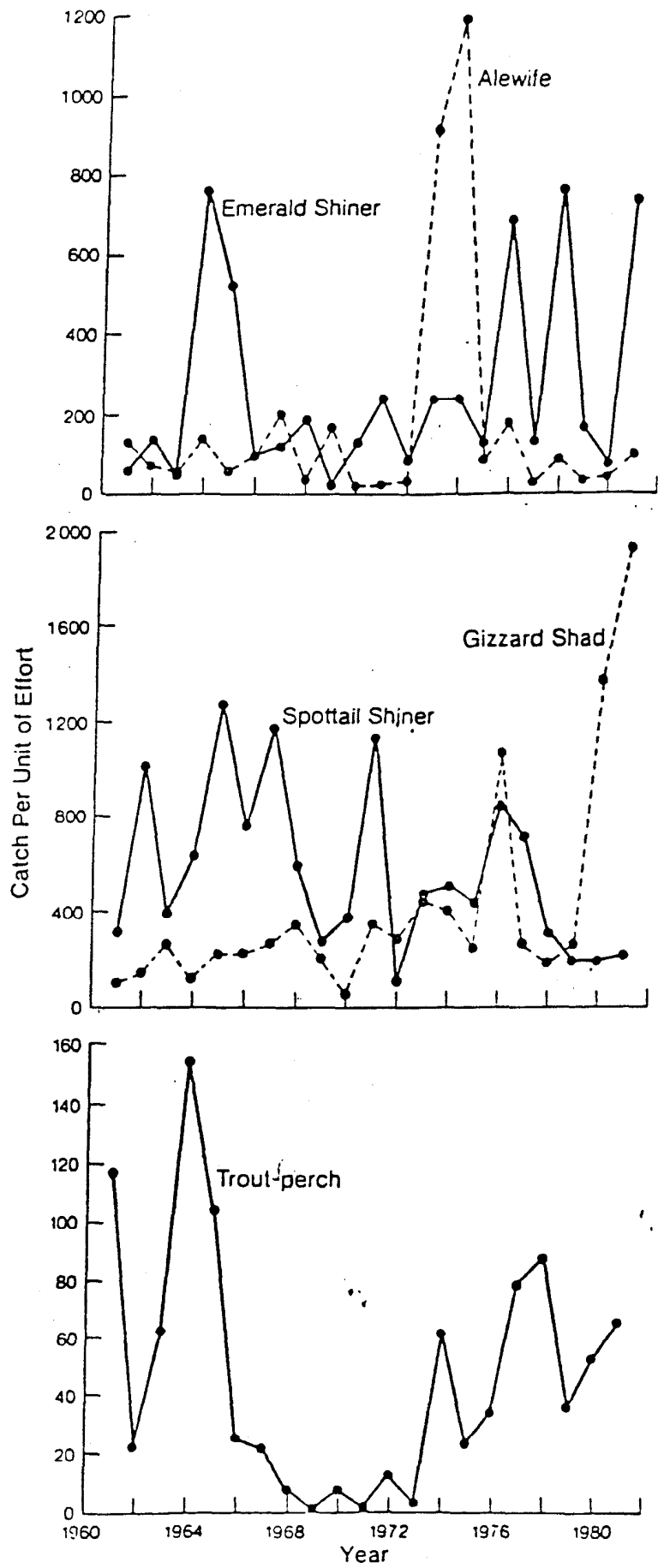


Figure 2. Annual relative abundance of yearling prey fish as indicated by catch-per-unit-of-effort (CPUE).

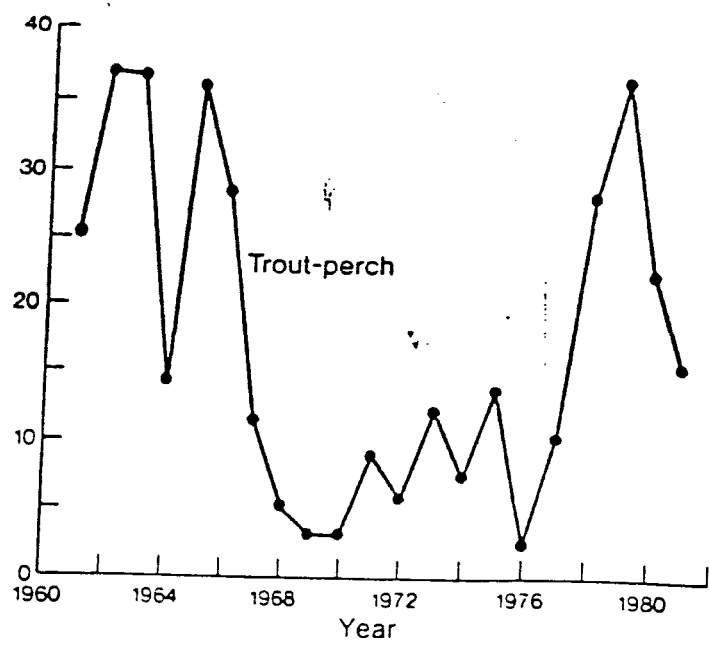
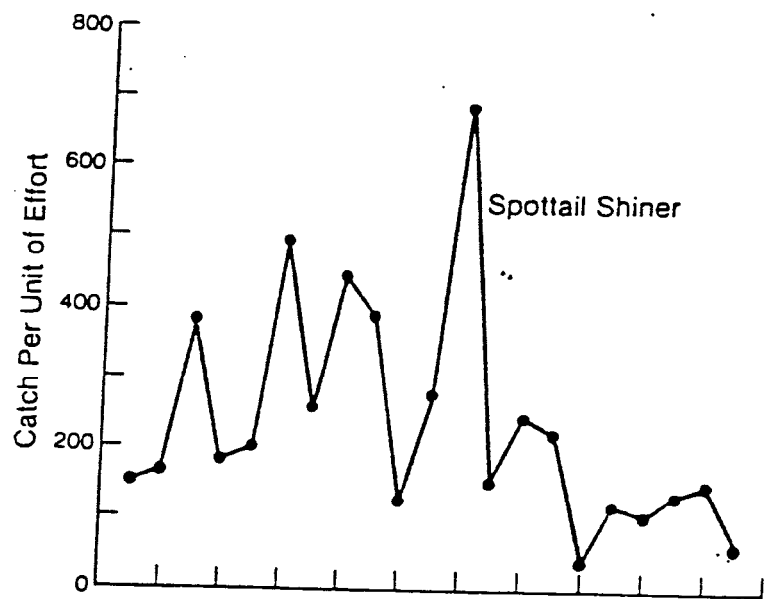
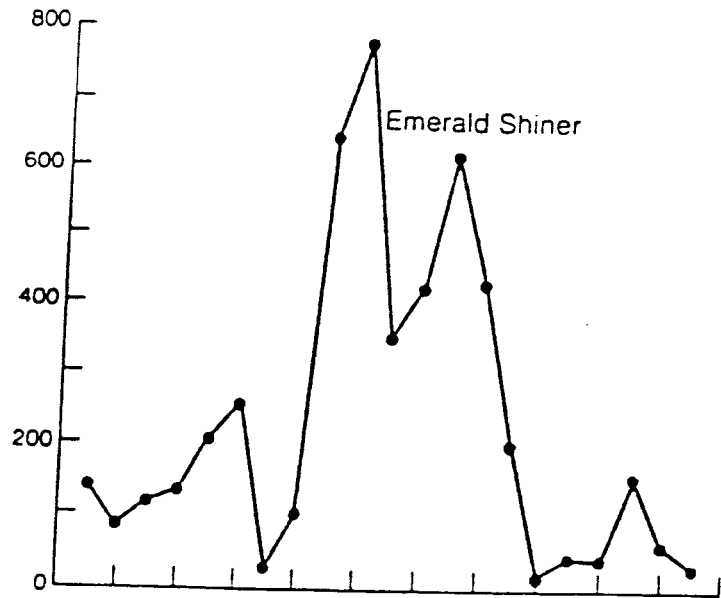
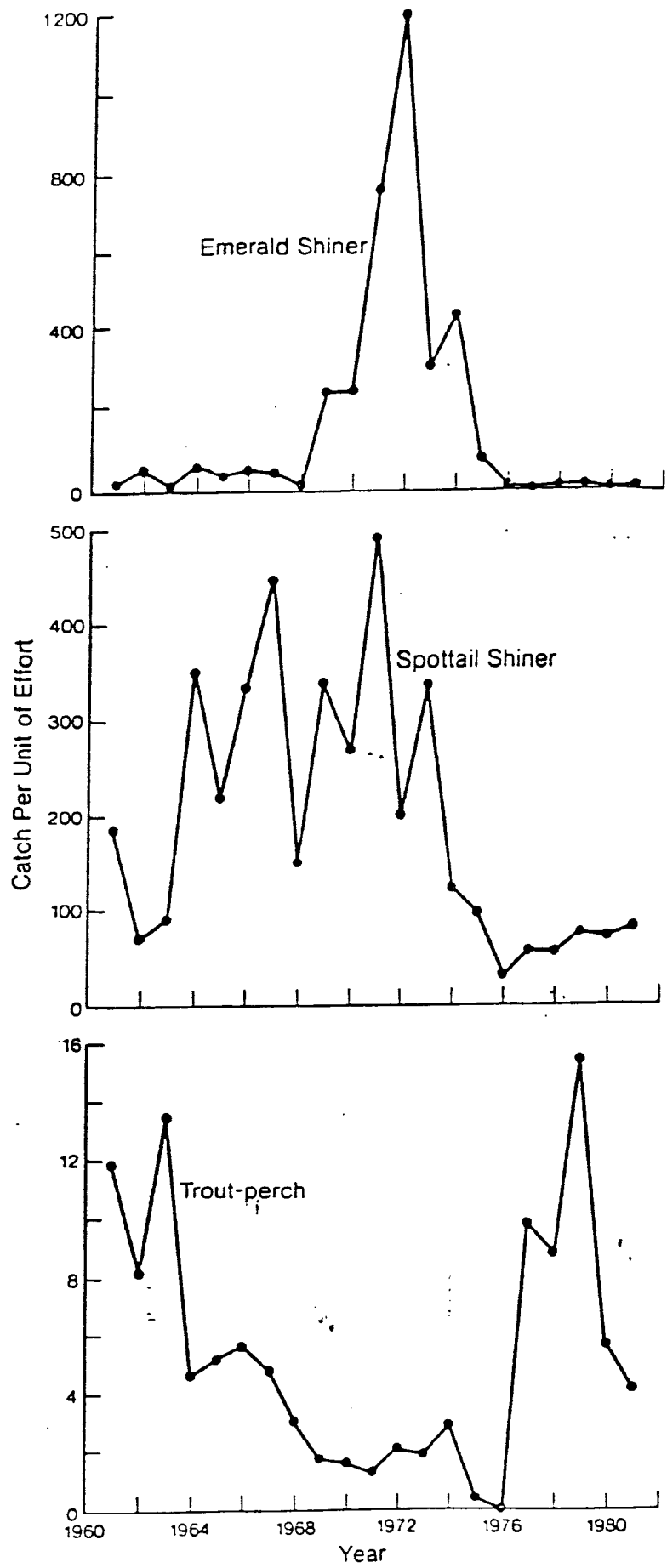


Figure 3. Annual relative abundance of age 11 and older prey fish as indicated by catch-per-unit-of-effort (CPUE).





PREDATOR RESPONSES TO FISH COMMUNITY CHANGES  
IN LAKE SUPERIOR

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Predator Responses to Fish Community Changes  
in Lake Superior

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Introduction

I have been asked to discuss responses of fish predators in Lake Superior to three changing conditions:

- 1) increased predator abundance
- 2) decreased prey abundance
- 3) qualitative changes in prey.

The first instance, which could occur through increased reproduction, increased stocking, or decreased mortality on predators, would lead to increased total consumption (C) by fish predators, or, if food availability is limited, to competition and a decreased growth rate (G) according to this relationship:

$$(1) \quad C = G * B / k$$

B = predator biomass

k = food conversion efficiency of predators.

(See Appendix for derivation of equations.)

The second instance, decreased prey abundance, could occur through increased predation (M<sub>p</sub>) or other mortality on prey species or through decreased reproduction or growth of prey. It would lead to increased predation or reduced predator growth or both according to this relationship:

$$(2) \quad M_P = G * B / (k * b)$$

M<sub>p</sub> = predation mortality

b = prey biomass.

Note that the immediate feedback from increased predation mortality can be further increased predation mortality, until consumption by predators comes into equilibrium.

The third instance is a qualitative change in prey, which I take to mean a shift in prey species composition, or changes in size or spatial distribution of prey. These changes cannot be expressed by simple equations such as (1) and (2) above. Predator responses to these conditions can be complex, such as size-dependent predator growth changes resulting from skewed prey size distribution.

## Data Sources

To begin the process of preparing this paper, I contacted the Lake Superior biologists from each of the states, the province of Ontario, and the U.S. Fish and Wildlife Service, requesting data on fish predators, specifically:

### for Lake Trout

length at age from: stock assessment nets  
spawning assessment nets  
commercial fisheries  
sport fisheries

age at maturity

### for Pacific Salmon

size composition of spawning runs  
length at age and average size in catch

### for Lake Trout and Pacific Salmon

paired length/weight data or regression equations  
stomach contents  
fecundity  
back-calculated growth

I also had access to any data developed by tribal fisheries programs. The response from the agencies was disappointing. I received little data to work with other than lake trout length at age information. There appears to be a real lack of data relevant to predator/prey studies on Lake Superior, and much potentially useful data exists in practically inaccessible form. There is a great need for a lakewide fishery database with computer access, which should include, among other items, predator growth and feeding data.

## Increased Predator Abundance in Lake Superior

The abundance of fish predators in Lake Superior is not well known. The relative abundance of lake trout in nearshore U.S. waters has been monitored with gillnets for many years (see Lake Superior Committee minutes, especially for years prior to 1982), but the data is not strictly comparable among the states, nor in some cases among years. In eastern Wisconsin and eastern Michigan, the data has been used to develop cohort models for estimating absolute lake trout abundance (Wisconsin State/Tribal Technical Committee 1984, Tri-partite Technical Working Group 1984), but these areas make up only a small percentage of the lake. Ontario has computer access to relative abundance indicators from the commercial fisheries, but has no independent estimates of lake trout abundance (W. MacCallum, pers. comm.).

Available data is inadequate to estimate either relative or absolute abundance of other predators, including coho salmon, chinook salmon, and siscowet. Stocking records for coho (beginning in 1966) and chinook (beginning in 1967) show a gradual increase in numbers. Natural reproduction of coho was noted at least as early as 1970 (Lake Superior Committee 1971, p. 36) and of chinooks in the late 1970's (Goodyear et al. 1982). The level of reproduction is probably quite significant, at least for cohos, but it has not been quantified. Siscowet abundance has been high, at least in Wisconsin waters (Pratt 1981, Red Cliff Fisheries Department 1983), but little is known about siscowet abundance lakewide. However, the diet of the deep-dwelling siscowets appears to differ substantially from lean lake trout and salmon (Pratt 1981).

As a first attempt at developing an ecologically meaningful index of near-shore and pelagic predator abundance, I derived the following figures for a series of recent years:

- 1) the number of lake trout stocked 6 years earlier,
- 2) the number of coho salmon stocked 3 years earlier, and,
- 3) the number of chinook salmon stocked 3 years earlier X 2.

The number of chinook was multiplied by 2 to account for the effect of their faster growth rate. The resulting sum is a crude indicator of the level of predatory pressure by stocked lake trout, coho, and chinook (Figure 1a). The graph indicates that there has not been much change in total predation by stocked fish since the mid-1970's. Chinook salmon make up an increasing share of the total, while lake trout make up a decreasing share.

I added an arbitrary quantity of naturally reproduced lake trout and coho as follows: I assumed that coho reproduction began in 1970 and increased linearly to equal 50% of total recruitment at present. I assumed that lake trout reproduction increased linearly from near zero in 1962 to equal 30% of total recruitment in the 1978 year class. The resulting graph (Figure 1b) indicates quite stable predatory pressure from 1974 through 1979, and an increase of about 5% per year after that. All segments of the predator community contribute to the increase under these assumptions.

I must emphasize that this is a crude indicator of predation. At this time, a lack of information on abundance and life history of salmon, and a lack of integration of agencies' lake trout data prevent very realistic analysis of predator abundance.

However, the analysis, such as it is, indicates that the first condition, increasing predator abundance, has occurred in Lake Superior in the past 5 years.

#### Decreased Prey Abundance in Lake Superior

Smelt have been an important prey of lake trout since the early 1950's, and the dominant prey since the early 1960's (Dryer et al. 1965). Smelt are also an important prey for coho and chinook salmon (Lake Superior Committee 1972, p. 32, J. Selgeby and R. Kinnunen, pers. comm.). Selgeby (1985) has documented large decreases in smelt abundance throughout U.S. waters of Lake Superior, occurring at different times in different areas between 1978 and 1981. Thus the second specified condition, decreased prey abundance, occurred in Lake Superior from 4 to 6 years ago.

#### Qualitative Changes in Prey

The first major shift in prey species dominance occurred between the early 1950's and the early 1960's, when commercial smelt landings increased from near zero to about 1 million pounds per year (Baldwin et al. 1977). During the same period, lake herring stocks were declining due to overfishing (Selgeby 1982), and possibly due to ecological interactions with smelt (Anderson and Smith 1971, Swenson and Matson 1976), leading to the extremely low abundance of herring observed in the late 1960's and 1970's. Herring had historically been the main source of nutrition for lake trout, but were replaced in this role by smelt.

A second major shift in prey species abundance began in 1978 and may still be underway (Selgeby 1985). Herring stocks have greatly increased since then, though abundance remains below historical levels. This increase coincided with the decline of smelt already referred to.

Shifts in species dominance between herring and smelt involve other qualitative changes in the availability of food for lake trout and other predators. Herring primarily inhabit the offshore pelagic zone during the growing season, and, while smelt can utilize any position in the water column, they are often associated with the bottom, and are rarely found in water deeper than 40 fathoms (73 m). The spatial distribution of lake trout changed with the distribution of prey in the 1950's such that the offshore pelagic habitat was not used to the former extent, (S. Sivertson, pers. Comm.).

Adult smelt are also smaller in size and slimmer in form than adult herring, and thus are available to a wider size range of predators. However the larger size of herring may allow more efficient feeding by large lake trout.

### Predator Responses

The first observation of a growth response by lake trout to recent fish community changes came to light in late 1982 from the Apostle Islands area (Figure 2). Lengths and weights of lake trout from samples of the Red Cliff tribal commercial catch were analyzed using a modified relative condition factor,  $K_n$  (Anderson and Guteuter 1983). The length/weight relationships of monthly samples of lake trout were compared to the relationship from samples collected in southern Lake Superior from 1948 to 1956 (Eschmeyer and Phillips 1965). The relative condition factor used here is the mean ratio of calculated weight for lengths ranging from 17 to 30 inches. A condition factor of 1.0 indicates that the condition during the sample period is the same as the base period. A factor greater than 1.0 indicates a greater weight at a given length than during the base period, and vice versa.

All but one monthly sample from the Red Cliff fishery prior to September 1982 showed a relative condition greater than 1.0. However, in September condition fell below 1.0 and remained low through May 1983. From November through April, the value averaged 0.88, indicating that trout caught during that period were about 12% lighter at a given length than during the base period. The decline appears to be an exaggeration of a normal seasonal cycle of condition. Condition recovered to apparently normal levels in the summer of 1983, but has since fluctuated over a wider range than prior to the sharp decline.

The decline in condition was probably caused by 2 factors: less food in stomachs and resorption of stored lipids for maintenance energy. The rapidity of the decline and recovery are remarkable. Unfortunately no stomach samples were collected at the time to establish a specific cause for the fluctuations.

The usefulness of body condition as an indicator of well-being is open to question (Barnes et al. 1984). There may be other indicators of nutritional status which are more sensitive, easier to interpret, or easier to collect. In order to address this question, the Great Lakes Indian Fish and Wildlife Commission and the Red Cliff Fisheries Department recently initiated a pilot study in which a suite of indicators of lake trout diet, nutrition, and growth will be examined. Measurements being taken from lake trout in this study include length, round weight, dressed weight, maximum girth, liver weight, gonad weight (where applicable), weight of stomach contents (total and by taxon) and diameter of annual rings on scales. NO summary or analysis of this data has been made yet.

There is a second piece of evidence of a lake trout growth response from Wisconsin waters. Mean length at age in the Red Cliff commercial fishery has declined overall since 1980, when the fishery was first sampled for biological data (Figure 3). The decreasing trend in length at age is not consistent over all years and

ages; however, the data may be more instructive for that very reason. Three patterns can be seen in the data. First, the 1973 year class of Stocked fish was consistently smaller than most other year classes at any given age. This is consistent with observations by Bruce Swanson (WDNR, pers. comm.) that some stocked cohorts grow slowly throughout life. This phenomenon tends to confound other inferences about growth from observed length.

Second, length at age declined for each age group from 1982 to 1983, indicating that growth during the 1982 growing season was particularly poor. This observation is consistent with and independent from the poor body condition observed after the 1982 growing season.

The third pattern is that the older age groups show the most pronounced reduction in length. This may be due to a lack of prey items of a size suitable to sustain the growth of these large fish. Selgeby (1985) has shown that the mean size of smelt has decreased markedly in recent years. The size structure of the smelt population may be sufficient to maintain growth of young lake trout, but not the older individuals.

There are two other hypotheses that could be implicated in the reduction in length at age. First, selective and intensive fishing can remove the faster growing individuals of a cohort at a young age, resulting in a remnant population of slower growing individuals. An increasingly intensive fishery may cause a pattern of decreasing apparent growth. A study of lake trout scale samples in agency files could probably determine if this is a factor.

Second, a segregation of lake trout by size and/or growth rate may have occurred. The most likely cause would be the movement of larger trout to the offshore pelagic zone to prey on the increasingly abundant lake herring stock. The result would be lower vulnerability of large trout to bottom-set gillnets. This hypothesis has little data to support it at this time, but seems to be a reasonable scenario in view of the smelt and herring population trends. Sampling the pelagic habitat may help to answer this question.

The downward trend in length at age is more distinct in samples from Michigan waters east of the Keweenaw Peninsula (Figure 4, data provided by USFWS from MDNR assessment fishery). Since 1979, lengths of ages 6 - 8 have decreased about 2 inches. Lengths at ages 5 - 10 all decreased during the 1982 growing season, when growth also appeared especially poor in the Apostle Islands.

Fishery samples from widely separated areas in Ontario also indicate a distinct downward trend in length at age after 1979 (Figure 5, data provided by OMNR), although the data series is shorter than other areas. The magnitude of decline is similar to that in Michigan waters, but it began a year later.

To alleviate some of the possible biases in length at age data, and to present a simpler, clearer picture of lake trout growth rates, I calculated instantaneous growth coefficients for cohorts at ages 6 - 8 and averaged them to obtain a single number describing population growth rate for each area for each year. I multiplied instantaneous growth in length by 3.2 (a typical length/weight regression slope in Lake Superior) to obtain instantaneous growth of biomass (Figure 6).

The plot of these points shows some similar patterns in annual growth rates in Michigan and Wisconsin. There were almost parallel fluctuations through the

1970's, **except** 1979, when growth in Wisconsin appears good, but growth in Michigan was at its lowest point. Michigan growth rates then remained low through the 1982 growing season. Growth in Wisconsin reached its lowest point in the 1982 **growing** season. Growth exceeded .40 in both ends of Ontario waters in 1979, but declined to a very low level in the Thunder Bay area in 1980. Otherwise, Ontario **growth** rates have been low to moderate in recent years ( $G = .17 - .28$ ).

Data from Rahrer (1967), from samples collected in 1953, indicates that lake trout were growing at a much higher rate at that time ( $G = .41$ , based on growth in length at age 6 - 8 during the last year of life, from Rahrer's Table 6), when lake herring were still the primary source of nutrition for lake trout (Dryer et al. 1965).

Comparisons between Wisconsin growth rates and two likely determinants of growth -- lake trout biomass (derived from a cohort model described in Wisconsin State-Tribal Technical Committee 1984) and smelt biomass (Selgeby 1985) -- indicate possible relationships, but none are statistically significant (Figure 7). The plot of lake trout biomass vs growth indicates a weak density dependence ( $r = -.36, 8df, ns$ , Table 7a). The relationship of lake trout growth to smelt biomass is stronger and more interesting ( $r = .48, 3df, ns$ , Table 7b). Although relatively good lake trout growth has occurred in years of low smelt abundance, poor growth has never occurred when smelt abundance was high. Lake trout must have made significant use of alternate food sources, especially in 1980, 1981, and perhaps 1983. A study of lake trout food in 1981 suggested that insects were an important alternate food at that time, but even then smelt dominated the diet (J. Selgeby pers. comm.).

A plot combining the predator/prey variables as a ratio (smelt biomass/lake trout biomass, Figure 7c) produces yet a stronger relationship ( $r = .53, 8df, ns$ ). This plot indicates that concern for lake trout **growth** may be in order when estimated smelt biomass is less than 1.5 times estimated lake Trout biomass in eastern Wisconsin.

### Conclusions

It appears that lake trout growth rates were lower during the 1970's, when the diet was dominated by smelt, than in the 1950's, when herring were the major food. Lake trout growth has decreased lakewide in response to the lakewide decline of smelt in recent years. Lake trout may be more opportunistic feeders in the absence of abundant prey fish, but there is as yet no data to indicate a major shift from a smelt diet.

### Acknowledgements

The following people provided data, insights, and/or advice contributing to the preparation of this paper.

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Mark Ebener	Great Lakes Indian Fish & Wildlife Commission

## APPENDIX

Equations (1) and (2) were derived using the following model, which is intended to express, as simply as practical, energy flow between prey and predator compartments of a fish community over a relatively short time period (<1 yr).

### Definitions

$B$  = mean biomass of a predator compartment during the time period  
 $G$  = instantaneous growth rate of predator biomass  
 $b$  = mean biomass of prey compartment  
 $M_p$  = instantaneous rate of predation mortality  
 $c$  = prey biomass consumed by the predator  
 $\quad = M_p * b$   
 $P$  = production of predator biomass  
 $\quad = G * B$   
 $k$  = food conversion efficiency of predator utilizing this prey  
 $\quad = P / C$

$B$ ,  $b$ ,  $C$ , and  $P$  are expressed in equivalent energy or biomass units.

#### Equation (1)

$P = G * B$             and  
 $k = P / C$             therefore  
 $P = k * C$             therefore  
 $k * C = G * B$         therefore  
 $C = G * B / k$

#### Equation (2)

$c = G * B / k$             and  
 $C = (M_p) * b$             therefore  
 $(M_p) * b = G * B / k$     therefore  
 $M_p = G * B / (k * b)$



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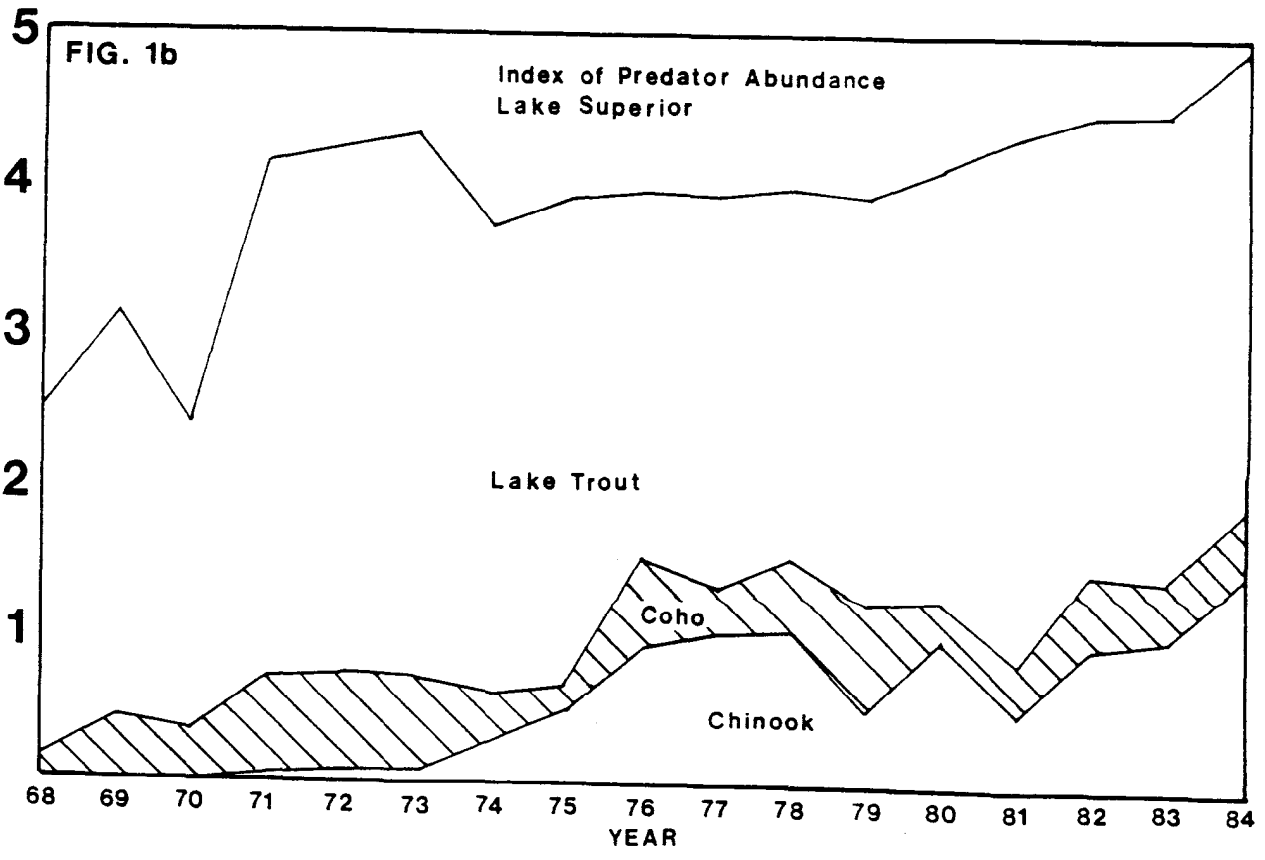
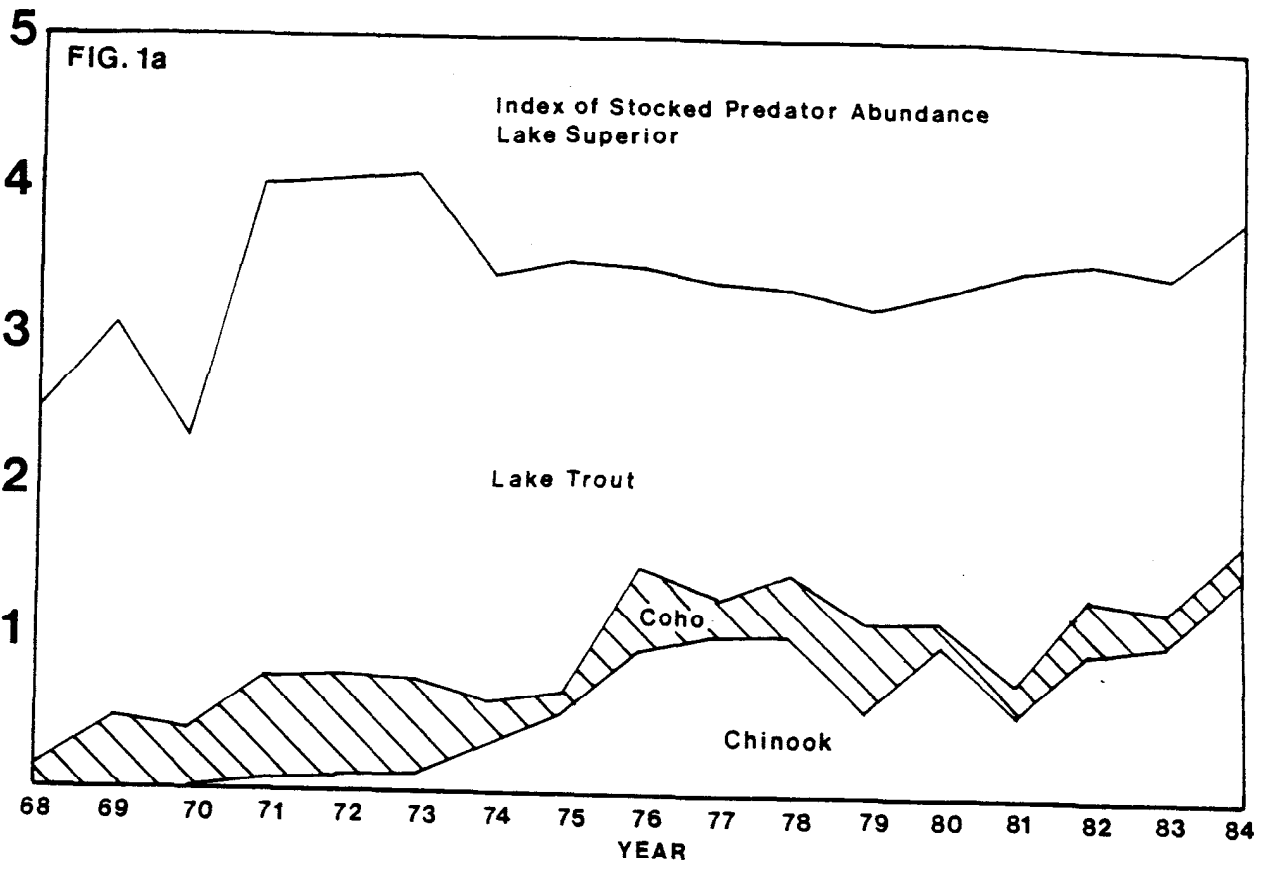


Figure 1. Index of abundance of 3 species of fish predator in Lake Superior.

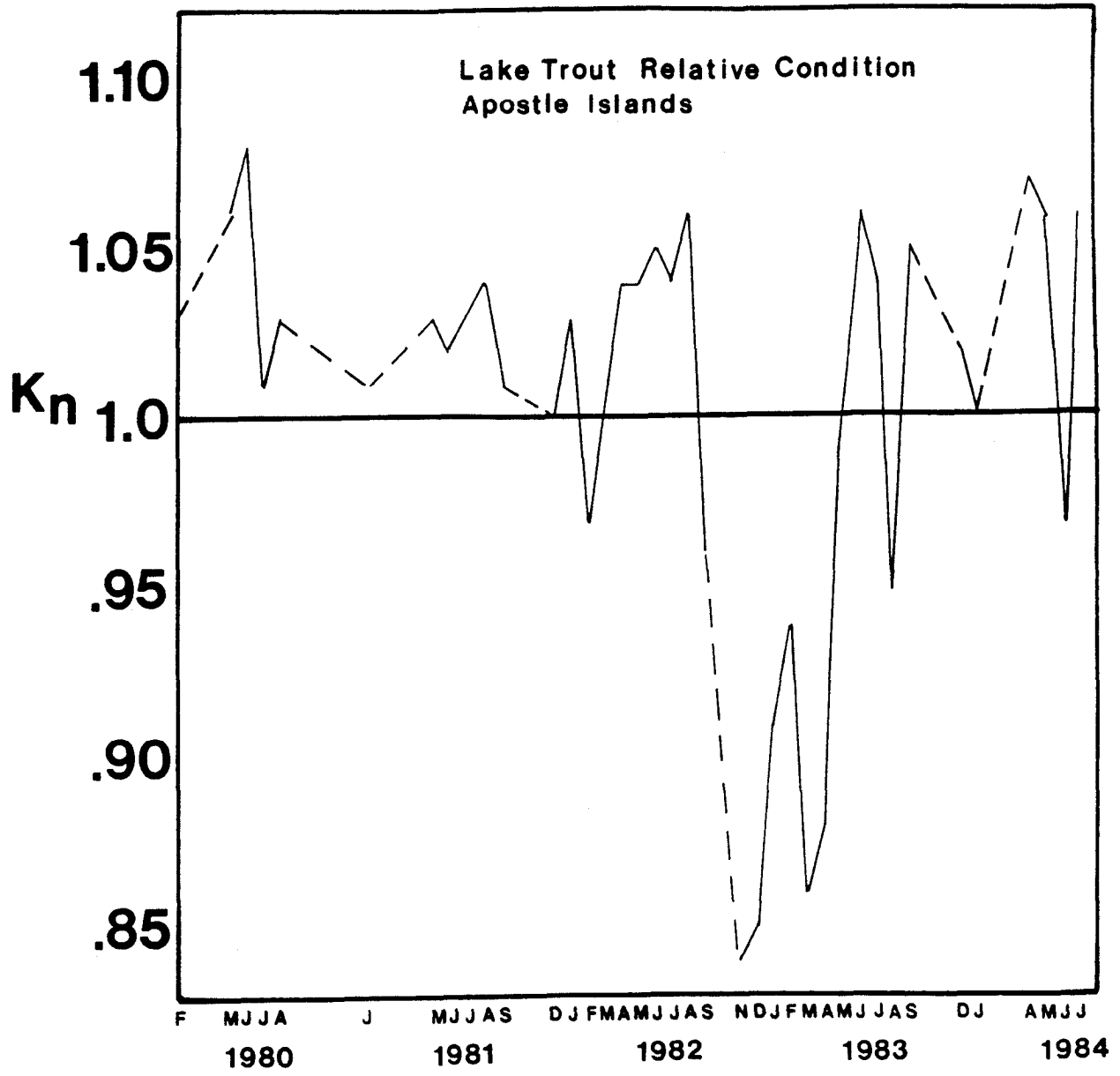


Figure 2. Relative condition factor (Kn) of lake trout in commercial fishery samples, Apostle Islands area, Lake Superior.

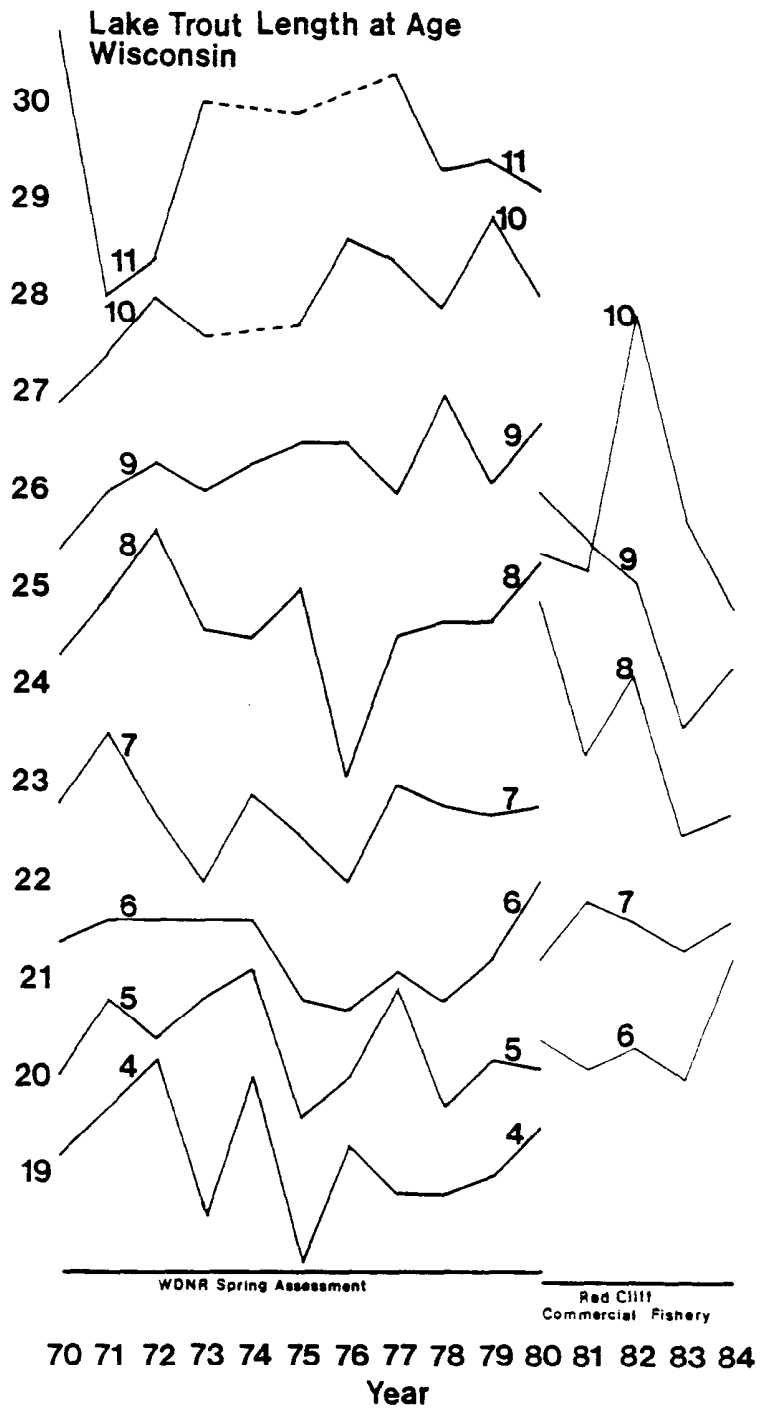


Figure 3. Length at age of lake trout in Wisconsin waters of Lake Superior.

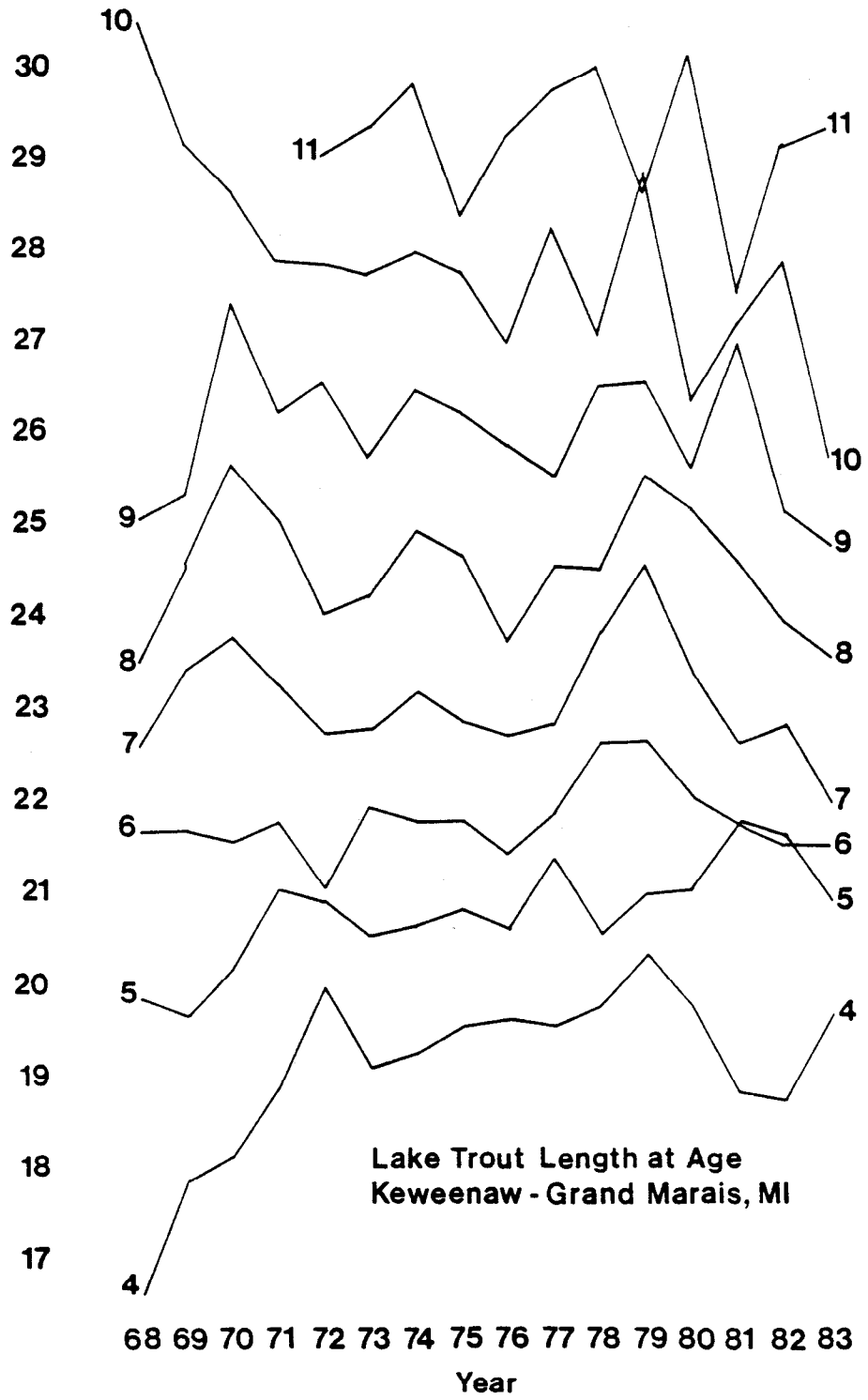


Figure 4. Length at age of lake trout in a portion of Michigan waters of Lake Superior.

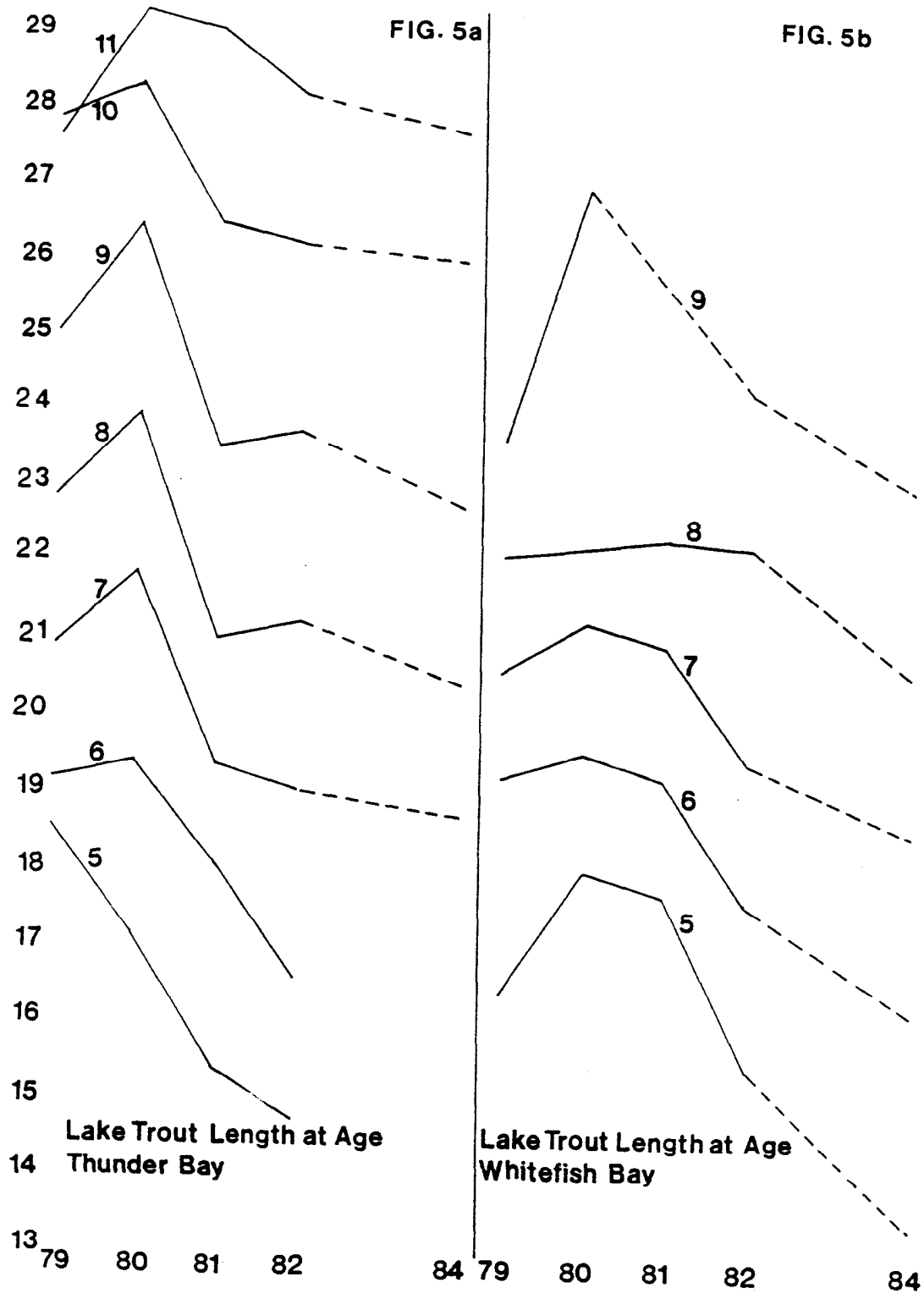


Figure 5. Length at age of lake trout in two areas of Ontario waters of Lake Superior.

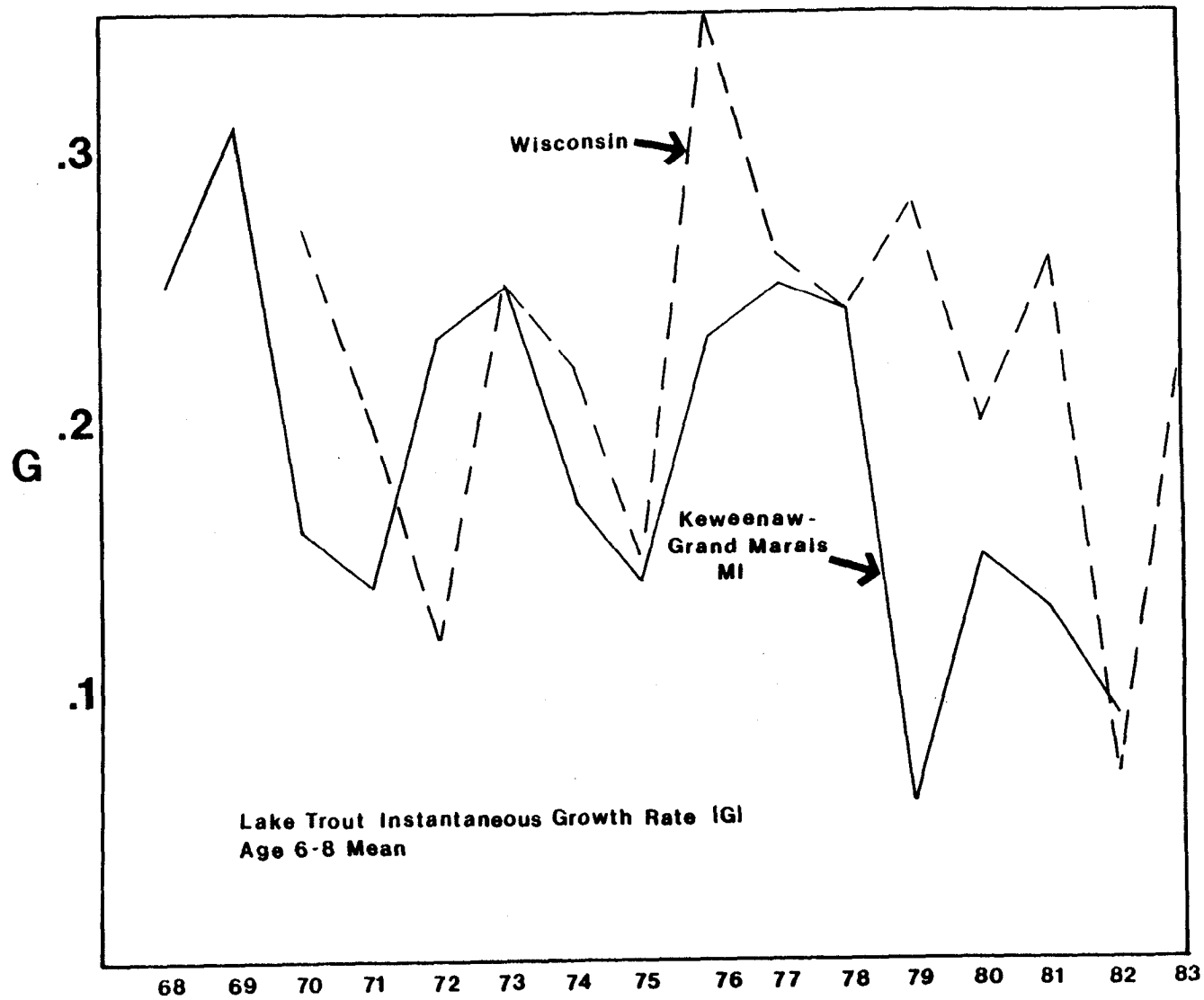


Table 6. Instantaneous growth rates of lake trout biomass in Wisconsin and Michigan waters of Lake Superior, calculated from length at age.



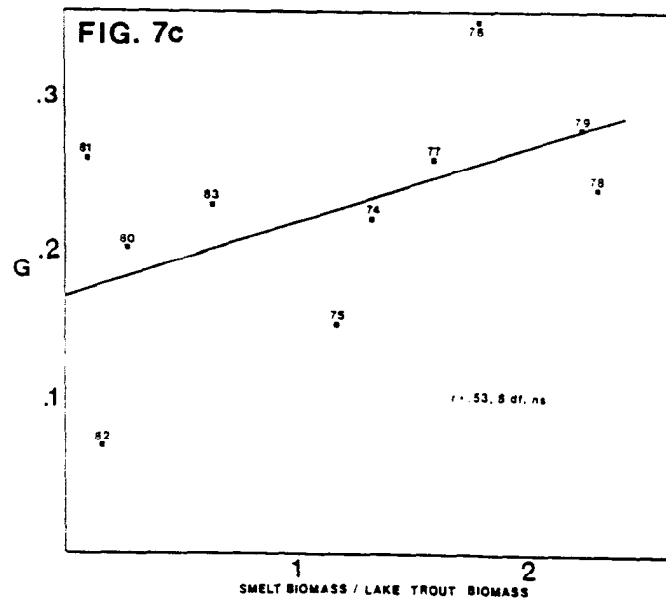
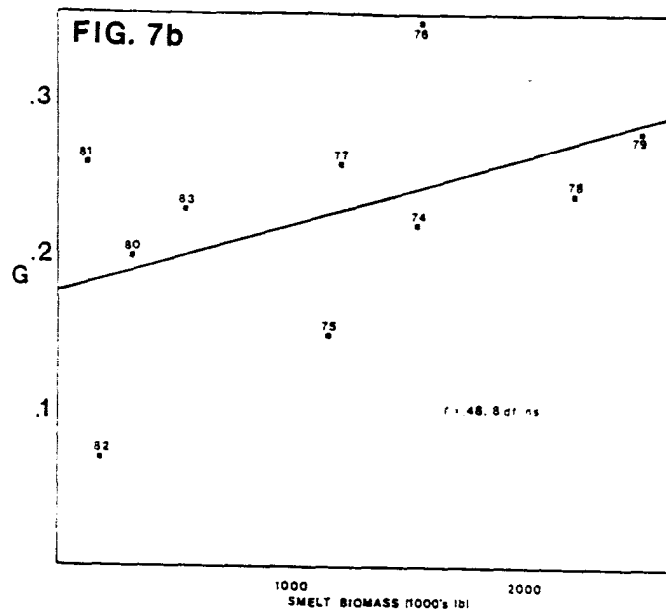
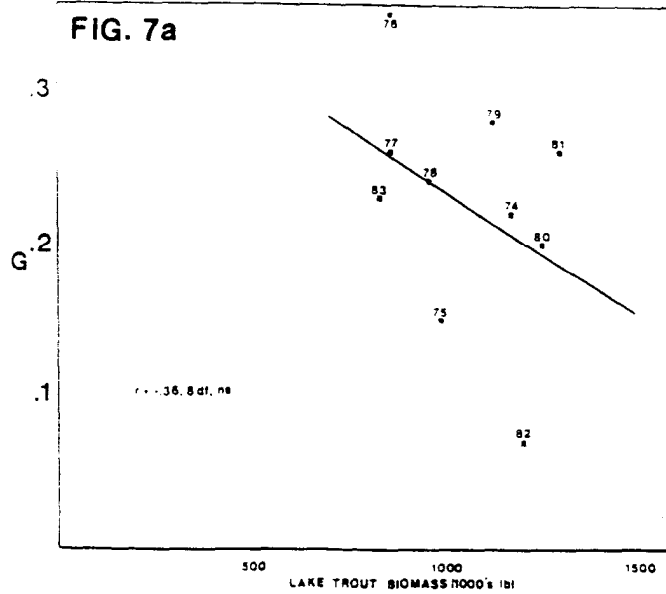


Figure 7. Relationships between instantaneous growth of lake trout biomass (G) and abundance of lake trout and smelt in eastern Wisconsin waters of Lake Superior.

WALLEYE IN WESTERN LAKE ERIE:  
RESPONSES TO CHANGE IN PREDATORS AND PREY

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*"But answer came there none -  
And that was scarcely odd, because  
They'd eaten every one"*

from Lewis Carroll's  
"The Walrus and the Carpenter"

Walleyes have been and continue to be an important fishery resource in western Lake Erie. They were and are an important and integral component of the fish community. They are also a very important human resource - having been accessed by commercial fishermen as well as recreational fishermen.

Annual commercial landings of walleyes fluctuated narrowly about a mean of 825 tonnes from 1915 to 1936 and then increased steadily to 7000t in 1956 before declining precipitously. From 1915 to 1956 greatest production was from central and western basin U.S. waters, particularly by Ohio trapnetters. Ontario had a small fishery with most landings also from these basins, reaching a peak in 1956. The stocks then collapsed and production dropped to only 317t by 1962 and to a record low of less than 229t in 1969 (Fig. 1).

After a closure in 1970 because of the mercury crisis and with a subsequent formation of an Interagency Walleye Scientific Protocol Committee to develop the technical basis for coordinated scientific management of this valuable resource, the current status of the walleye population is very encouraging. However, this status needs to be viewed with cautious optimism. The increased population has been the result of:

- (1) good young-of-the-year (YOY) recruitment in recent years, in fact, recruitment during the past decade has been exceptionally high when compared to recruitment levels in the 1960s;
- (2) the closure of the commercial fishery in 1970 by Ontario, Ohio and Michigan because of the concentrations of mercury in walleye;
- (3) international management approaches to control

sport and commercial harvests. A catch quota system was implemented in 1976 and has continued to the present. Estimates of the standing stock of yearling and older walleyes in western Lake Erie was only 14.6 million fish in 1976 but both fishable and standing stocks have increased substantially over the past number of years (Fig. 2).

There have also been some evident changes in the biomass of preyfish. Some recent information prepared by Muth (in press) indicates that forage fish biomass generally decreased as walleye abundance increased and an apparent decline in the biomass of emerald shiners, a preferred prey of walleyes was seemingly evident (?). However, this has been partly alleviated by the presence of large numbers of YOY gizzard shad produced in various years (Table 1). But YOY gizzard shad are suitable prey only during the summer and fall when they are small enough to be eaten. Therefore, they may not meet the walleye forage requirements throughout the year. Although there have been changes in recruitment for gizzard shad they more than likely fall within natural variations. Other forage fishes have also fluctuated but also likely within natural variations. Available evidence suggests that emerald shiner populations also fluctuate widely in abundance from year to year. Concern is sometimes generated over the relative scarcity of emerald shiners in Lake Erie, but experience seems to indicate that periods of scarcity followed by abundance have been characteristic of these populations for more than 50 years.

In order to describe some of the changes that have occurred to the predators or prey, it might be informative to

present some of the interactions that are evident in Lake Erie and those that deal with walleye in particular. Some of the more evident species interactions are shown in Figure 3. Walleyes are an important part of this system and their more specific interactions are illustrated in Figure 4.

Some of the more obvious changes that have occurred in the populations of predators and prey in the system are:

- . that walleyes as a main predator have increased
- . that some of the forage base has changed and maybe decreased (but recruitment has been variable)
- . that there have been other community changes
  - white perch have increased in abundance and have extended their range in Lake Erie
  - yellow perch populations have decreased
- . that walleyes have extended their "normal range" and are now present in central basin areas.

The intent of this presentation is to address the responses of predators (walleye in particular) to changes in predators or prey abundances. Some of the possible responses are shown in Table 2.

Undoubtedly, changes in growth and age at maturity are important indices of stress or measures of compensatory reserve. Although there are some changes in growth in length and weight of walleye, most particularly for age groups 1 and 2 from 1974-1983, it appears that the changes during this period were not statistically significant until very recently. (Fig. 5). Some recent unpublished data by Muth and Wolfert suggests very evident growth changes for YOY, yearling and 2 year old walleyes. But careful examination of the data shows that there may indeed have been a decrease in growth in the early 1970s but that growth in recent years may not really have

been very significantly different.

There has also been some evidence for a change in **size** and age of walleye at the onset of maturity. Muth and Wolfert (unpublished) have recently compared the age at maturity of walleyes during three periods: 1964-66; 1974-80 and 1981-83. They found that usually 80% or more of the age 2 females were mature each fall during the 1960s and early 1970s but that this percentage dropped significantly to 7% by the fall of 1983. During 1964-66, age 3 females were 86% mature in the spring, but age 2 females in the fall decreased to 57% in 1974-80 and to 38% in 1981-83. The maturity of age 2 females dropped from 90% in 1976 to 45% in 1977 and then reached a steady level until the 1980s when it decreased from 37% in 1981 to 7% in 1983 (Fig. 6). Delayed maturity presumably reflects an increase in stock biomass.

Competition for food is undoubtedly an important factor in controlling numbers. Most feeding by walleyes occurs during the summer and autumn and is reduced during the winter, perhaps due to non-availability of forage species in areas frequented by walleyes during this time. Adult and juvenile walleyes are largely piscivorous, feeding on a variety of prey species, namely, emerald shiners, trout perch, alewife, gizzard shad. If forage species are available at preferred lengths, walleyes may tend to feed on the most abundant species. If so, then in western Lake Erie the gizzard shad are still quite abundant because that is what walleye have been actively feeding on in more recent years.

Diet selection by walleyes has apparently changed since

the 1950s. Since walleye are size selective feeders, changes in size selection reflect changes in the diet. A comparison of size selection between walleyes from 1981 and 1959-60 distinctly shows that walleyes were less selective in 1981. The decline in size selection is attributed to the greater density of walleyes in 1981 than in 1959-60 (Knight et al. 1984).

However, electivity indices show that walleye prefer shiners and YOY gizzard shad when other forage species were also available. Yearling and older walleye fed almost exclusively on yearling shiners in the spring, but shifted to the very abundant gizzard shad in late July. Walleye diet in the fall was mainly YOY clupeids and shiners. Walleyes did not usually consume great quantities of spiny-rayed fish even when they were abundant (Knight et al, 1984).

In the absence of its "regular prey" (whether that is considered to be emerald shiners or gizzard shad in WLE), walleye will turn to something else. To be sure, growth and survival of the predator may change, but these may be only minor changes. I think the moral is not to expect big changes for the predator that loses a species of prey.

Also, the fisheries for one predator commonly take other predators during the exercise so that increased fishing effort may be synonymous with an overall decrease in predation.

Predatory fish are not normally considered active "prey switchers" and it is usually quite reasonable to expect that there might be some delayed response to the presence of an invading or new species or reduced abundance of a prey species.



White perch, the new increasingly abundant predator/competitor in this system is not presently part of the diet of walleye. Although gizzard shad may be the preferred diet and/or the most accessible at this time, their status is variable and questionable. Subsequently, there may in time be an active shift to other species that are present and abundant in the system (Knight et al, 1984). And we thought for certain that walleye would take advantage of the abundant white perch and be a controlling mechanism on this species. However, this has not occurred and indicates that walleye will not switch to white perch or yellow perch and conversely that there appear to be sufficient numbers of "preferred" prey in the vicinity.

Walleyes in western Lake Erie are still growing much faster and maturing earlier than walleyes in many inland lakes. Although there are some changes in growth and an apparent delay in the onset of sexual maturity, concerns about these changes, about the condition of walleyes and possible increases in natural mortality may be premature. The declining trend of the onset of sexual maturity for female walleyes has not apparently affected the reproductive potential of this species in western Lake Erie. Delayed maturity, if it is really significant, is offset by the presence of increasing numbers of larger, older spawners in the population. Perhaps a more immediate concern should be the effect of increased walleye biomass on walleye production. If the biomass continues to increase, it may be expedient to increase the fishing mortality but at the risk of producing an unacceptably low survival.

In summary then, the responses by walleye to various changes in predator or prey abundance are summarized in Table 3.

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Table 1. Young-of-the-year per trawling hour, Ohio's western Lake Erie and Sandusky Bay (summer trawling June through August).

Year	Walleye	Yellow perch	White bass	Freshwater drum	Spottail shiner	Gizzard shad	Alewife	White Perch
1970	44	1,038	2,180	207	511	788	350	--
1971	3	499	713	163	1,145	6,607	2,744	--
1972	<b>15</b>	764	938	244	320	1,825	586	--
1973	<b>81</b>	312	1,097	274	571	9,313	6,165	--
1974		2,507	1,504	172	586	11,013	5,192	--
1975	<b>7</b>	238	2,907	994	270	2,252	142	--
1976	<b>270</b>	242	1,746	286	387	3,880	<b>54</b>	--
1977		1,777	3,548	716	866	5,049	<b>1,584</b>	--
1978	<b>67</b>	<b>67</b>	1,314	530	573	11,512		--
1979	<b>200</b>	<b>548</b>	781	4,088	1,051	10,770	591	--
1980		1,870	6,788	876	179	7,632	193	--
1981	<b>60</b>	624	7,754	417	398	16,146	<b>5</b>	--
1982	<b>260</b>	1,365	1,270	207	329	2,554	<b>356</b>	606
1983	<b>&lt;1</b>	28	671	301	114	6,540		276
1984	71	1,780	4,516	91	61	10,305	361	3,360

(from ODNR, 1985)

Table 2. Possible responses of predators to changes in predators and/or prey abundance.

Action	Predator Responses
Increase in predators	Growth rate Delay in onset of sexual maturity Range extension (change in distribution)
Decreased prey abundance	Growth rate Prey switching Active searching (change in distribution)
Qualitative change in prey	Selective or opportunistic feeding Active searching Condition change (growth) Reduced competition

Table 3. Evident responses of walleye in Western Lake Erie to changes in predators and/or prey abundances.

Action	Predator Responses
Increase in predators	<p>Growth Rate+(?)</p> <p>Delay in onset of sexual maturity</p> <p>Range extension (change in distribution)</p>
Decreased prey abundance	<p>Growth Rate+(?)</p> <p>Prey switching?</p> <p>Active searching (change in distribution)</p>
Qualitative change in prey	<p>Selective or opportunistic feeding</p> <p>Active searching</p> <p>Condition change (growth)</p> <p>Reduced competition</p>

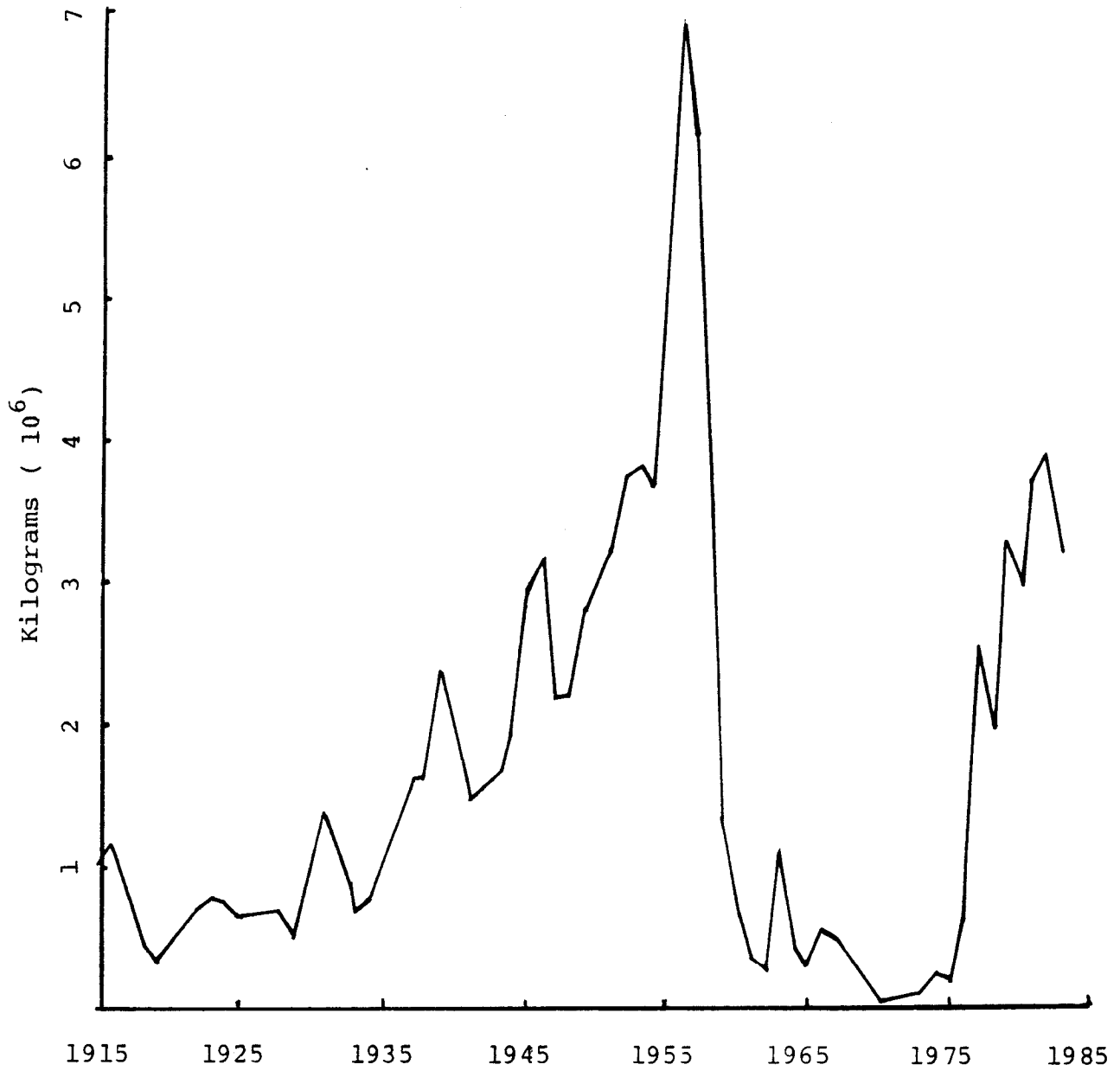


Figure 1. REPORTED LANDINGS OF WALLEYE FROM THE WESTERN BASIN OF LAKE ERIE, 1915-1984

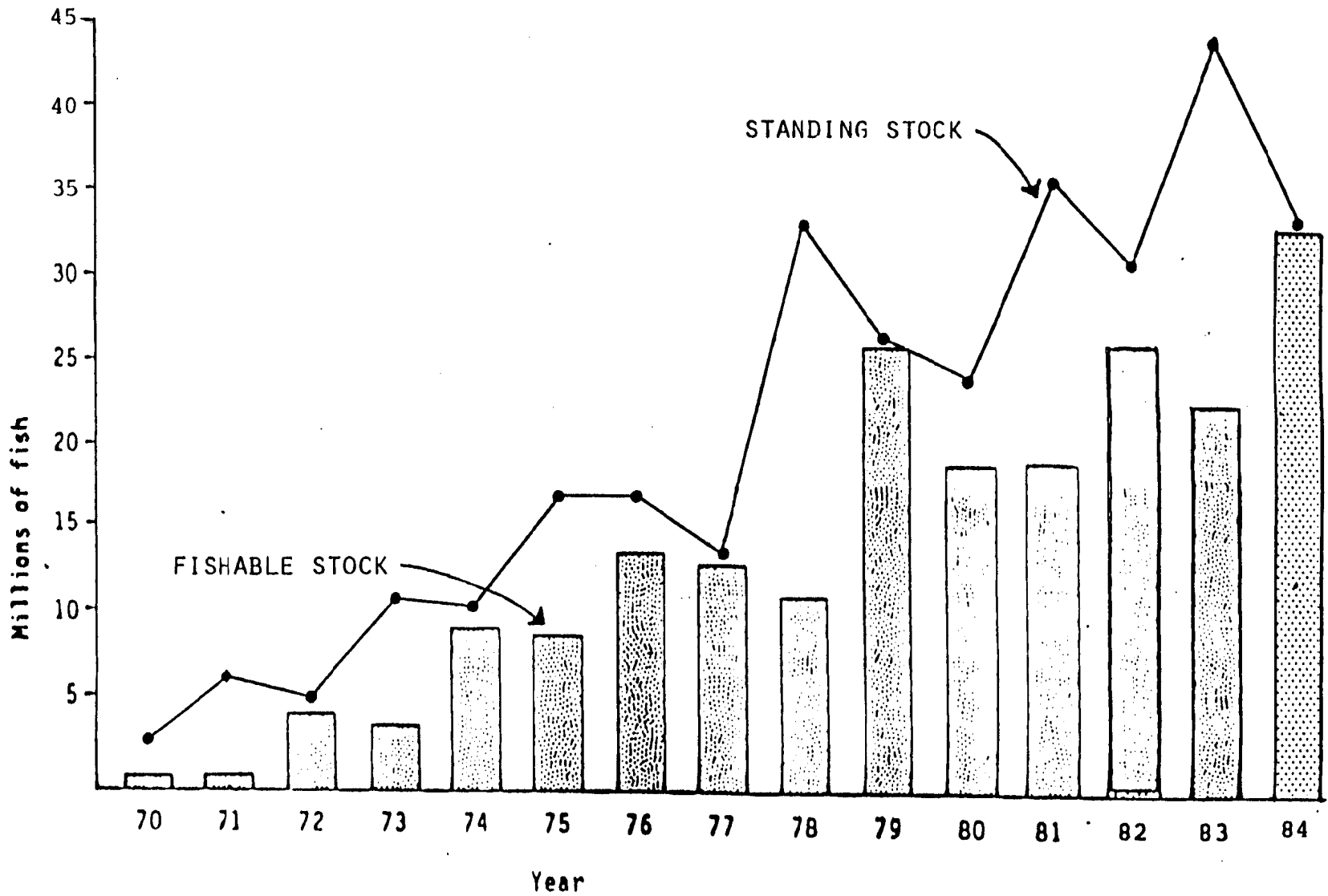


Figure 2. Estimates of standing stock and fishable stock of walleye in western Lake Erie, 1970-1984



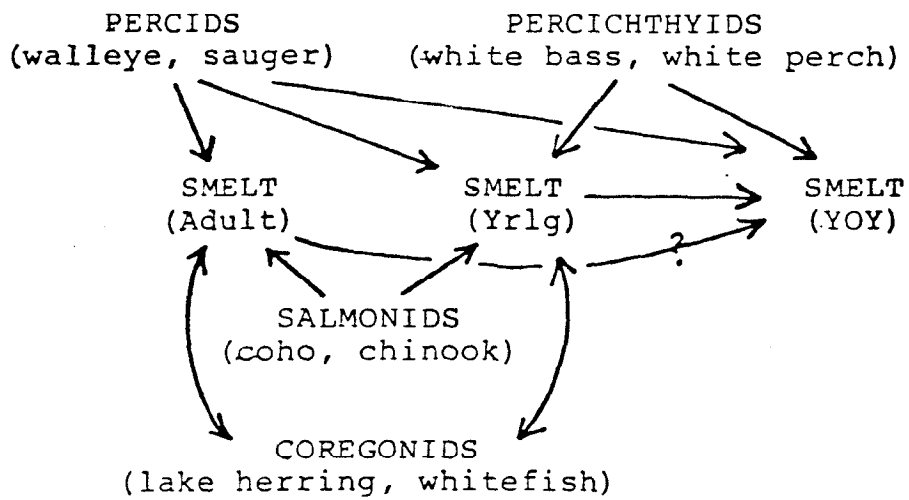


Figure 3. Interactions among the major fish species in Lake Erie.

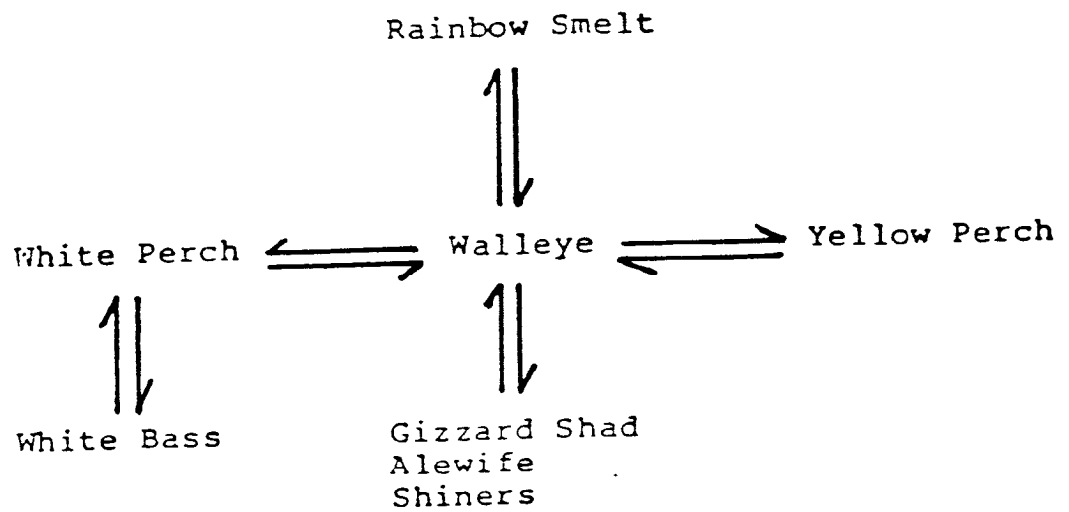
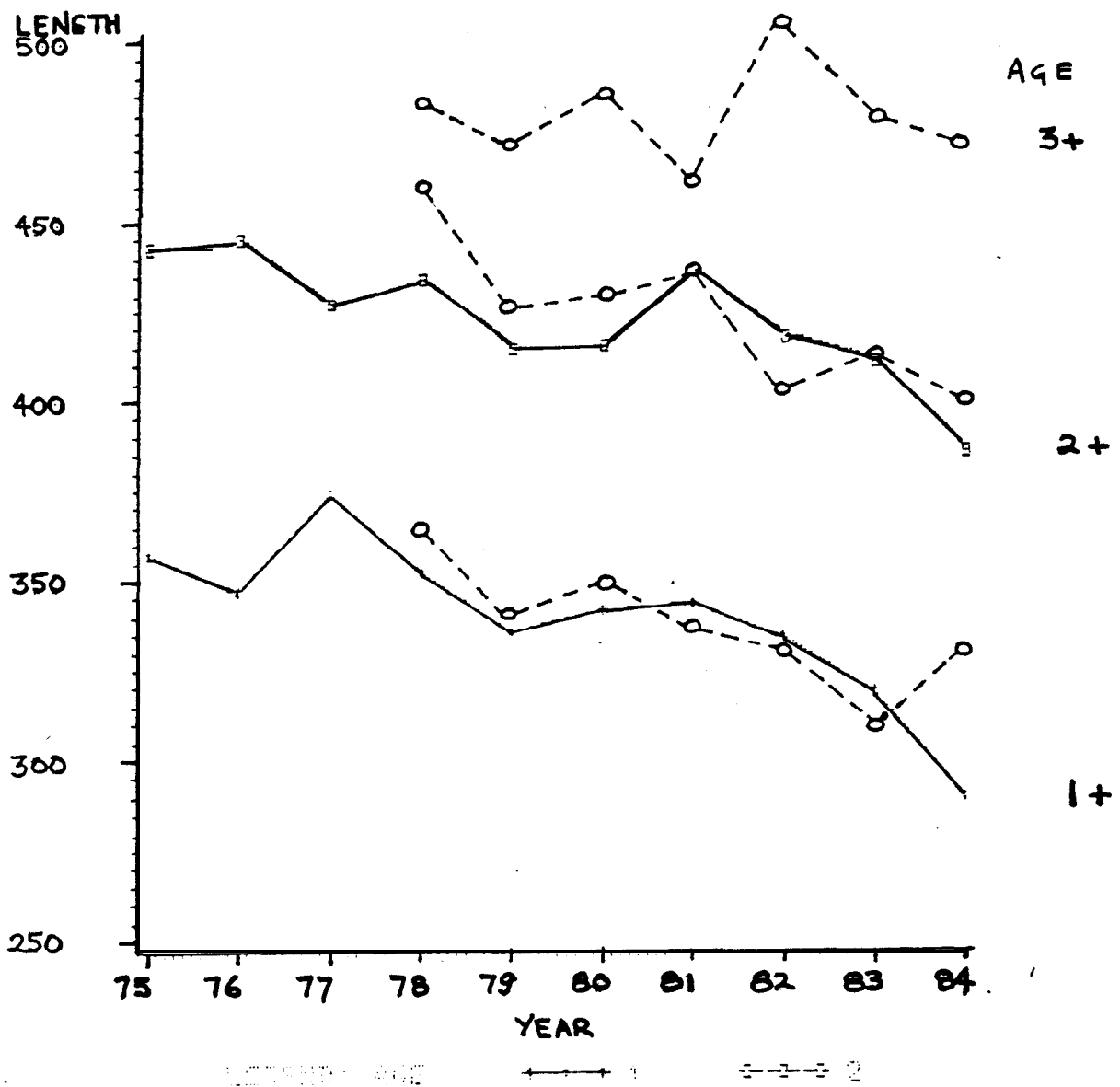


Figure 4. Specific interactions of walleye in western Lake Erie.



Figure' 5. Length at age of walleye sampled from experimental gillnets in western Lake Erie: Ohio Division of Wildlife (—), 1975-1984; Ontario Ministry of Natural Resources (---), 1978-1984.

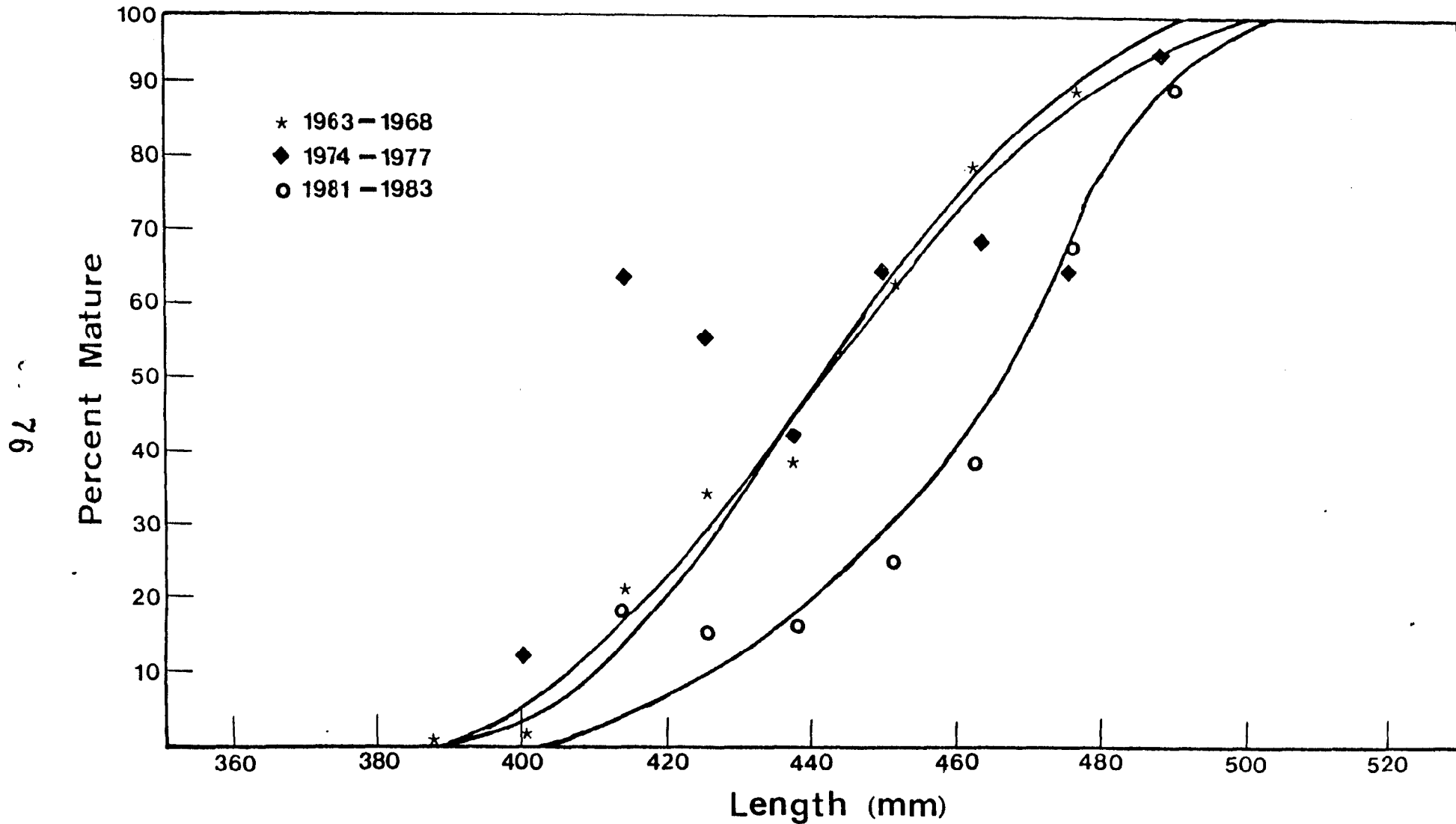


Figure 6. Percent maturity vs. total length (mm) of female walleyes taken in trap nets from western Lake Erie during three periods of stock abundances, 1963-1983. Data for 1963-68 from Wolfert (1969). (Courtesy of K. Muth and D. Wolfert).

IMPLICATIONS OF FISH COMMUNITY CHANGES  
FOR FISHERY MANAGEMENT ON THE GREAT LAKES

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Presented at:  
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Great Lakes Fishery Commission  
Ann Arbor, Michigan 48105  
March 20, 1985

Presented at GLFC Council  
of Lake Committees Plenary  
Session on "Predator-Prey  
Issues in the Great Lakes"  
Ann Arbor, MI  
March 20, 1985

Implications of Fish Community Changes for Fishery Management  
on the Great Lakes

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Fish community changes in the Great Lakes and elsewhere indicate that total fish biomass remains relatively constant as the magnitude of components of the biomass fluctuate widely due to human influences or natural causes. Certain fish populations exhibit great vigor in expanding to utilize available food and space after other populations are reduced. For example, as populations of pelagic planktivores are reduced by intensive fishing or predation, the offshore biological production which they formerly consumed presumably sinks to the profundal zone to the benefit of deep-dwelling invertebrates and chubs, and in Lake Superior, siscowets. This phenomenon has apparently occurred in each of the three upper lakes.

The extreme environmental conditions encountered by fishes in Lake Superior, and to a lesser degree the other Great Lakes, may amplify fluctuations of species which are marginally adapted to those conditions. For example, smelt have been very successful in colonizing Lake Superior, but they are incapable of utilizing areas deeper than about 40 fathoms (about 78% of the lake). They have been most successful in the shallow areas. The extreme and rapid decline of smelt in 1978-81 apparently cannot be accounted for by predation and fishery harvest, and some unexplained environmental stress may be implicated. Fluctuations in temperature over time periods of a few years to a few decades may do more to determine the future of smelt in Lake Superior than any management measures. Fortunately, USFWS has thousands of temperature profile measurements on file, so that temperature could be accounted for if the data were accessible on computer and analytical methods were available.

Lake Superior is near the low end of the range of primary productivity of freshwaters (about 400 kg C/sq m/yr). It is also extremely low in trophic efficiency, or the rate at which primary production is converted to fishery harvest. Currently about 0.01% of primary production in Lake Superior is harvested as fish biomass for human use. It is likely that a rehabilitated, well-managed Lake Superior ecosystem could yield a trophic efficiency of 0.03%, for a total harvest approaching 10 million kg/yr (Upper Lakes Reference Group 1976, Matuszek 1978). By comparison, Oglesby (1977) found trophic efficiency of freshwater fishery ecosystem to range up to 1.49%, although most were less than 0.21%. The trophic efficiency of marine fisheries worldwide was about 0.25% in 1970, with a maximum potential of 0.45% (yield data from Gulland 1974; primary production from Whittaker 1970). In general, trophic efficiency is inversely related to surface area and depth, and directly related to dissolved solids.

These three situations are examples of fish community problems or opportunities which are not being adequately addressed by existing fishery management programs. Others have previously recognized this shortcoming on the Great Lakes. Claude VerDuin, long-time Commissioner on the Great Lakes Fishery Commission, has said:

"We have to have a complete inventory of stocks. We must know the complete composition of the biomass... *YOU* can't regulate a fishery without knowing all the component parts. We know there is an interaction between species... In the future management of the fisheries, we have to manage the total biomass." (Kuchenberg 1978).

I suspect everyone would agree with these statements in principle, but how can they be put into practice?

Implementing a community approach toward fishery management **ON** the Great Lakes will require that management be done with a view toward whole-lake systems. Inputs and outputs from the lake system must be quantified so that managers can adequately assess their own actions, as well as the realized and potential benefit of fish harvest. Species and life stages should be grouped into ecologically relevant compartments, so that accumulation of energy (as biomass) and flow of energy (as predation and fishery catch) can be understood at several levels of resolution.

It is not feasible to implement a fish community management approach solely with traditional single-species management tools. For example, it will never be feasible to physically measure the biomass of every important species in any of the Great Lakes. Management of the total biomass will require the formulation of fishery ecosystem models to provide a framework for a coordinated whole-lake system of information storage and analysis. The models must be accessible and usable by fish managers at the inter-agency technical committee level.

Greater emphasis must be placed on the dynamic aspects of populations and the fish community. Measurements of rates of growth, food consumption, predation mortality, and food conversion efficiency are just as important in fish community management as measures of population abundance and catch. Missing data can usually be estimated indirectly, often with two or more independent methods, if a practical model of the fish community is available. Factors external to fish populations, but which vitally affect them (such as water temperature and zooplankton density and size distribution), should be explicitly factored into fishery ecosystem models.

Briefly, what I am describing and advocating is a new conceptual approach to the planning and evaluation of fishery management on the Great Lakes. This approach is consistent with, and a logical extension of, much past work, including SCOL (Regier and Loftus 1972) and GLFC-sponsored adaptive management workshops (Koonce et al. 1982). My thinking has been influenced by the work of Laevastu and Larkins (1981) in fishery ecosystem modelling, and the concepts of Odum (1983) in systems ecology.

This approach to fish community management would facilitate communication among field managers, administrators, and researchers, and among agencies, by providing a common format for planning and reporting work on a Great Lake. Each level of the fishery management community views system inputs and outputs at a different level of resolution, and a model providing a common format would help to ensure that the various levels are connected in a useful way. I propose that the concept of energy flow through the ecosystem could be a practical basis for the models. Using energy flow as the "currency" in ecosystem models would allow fisheries scientists to utilize analogous experience gained in other fields (Odum 1983). Some of the thorniest Great Lakes fishery problems, including sea lampreys and mortality due to contaminants, can be considered analogous to short circuits

in the energy flow model. This may not alter our immediate reaction to these problems, but it may alter our perception of them, and allow them to be placed in a more complete fish community context.

At the whole-lake level of resolution, the energy flow can be diagrammed as in Figure 1, where the inputs are sunlight, water and nutrients from the watershed, fishing effort, and fishery management. The output is fish biomass harvested. The ecosystem at this resolution is a "black box" without information as to its internal mechanisms; however, an agency administrator, with responsibility for management budgets and for satisfying the public's demand for fish harvest, is not immediately concerned with these internal biological mechanisms. This level of resolution may also be interesting to a researcher investigating the overall efficiency of the systems in producing products of value to humans (Oglesby 1977).

A second level of resolution of the whole-lake system is illustrated in Figure 2, where major biomass compartments and routes of energy flow have been filled in. Various aspects of predator/prey issues can be investigated by using different combinations of predator and prey compartments. The flow of energy from prey to predator can be calculated for the most part with existing or easily obtainable data (i.e. stomach contents, predator growth rates, etc.). This level of resolution is useful for examining whole-lake predator/prey status for determining stocking and harvest strategies. There are still some rather large "black boxes" in the system, but this level of resolution should be most useful for program administrators and lakewide technical committees, who are not immediately concerned with the mechanics of predation.

Finer levels of resolution can be observed by delving into the black boxes, where the mechanics of predation and growth can be studied. This is the level of energetics research, which should include objectives of defining ecologically sound biomass compartments, and describing the mechanisms which result in the observed rates of energy flow between compartments.

The existing institutional context in which fishery management occurs on the Great Lakes may be the greatest barrier to the establishment of a fish community management approach on the Great Lakes. This is certainly not a new problem for fishery managers, and major steps have been taken to solve it. The Strategic Great Lakes Fishery Management Plan (which regrettably does not include all governments with management authority on the upper lakes) provides an institutional framework which could help to make fish community management a success.

Recent advances in microcomputer technology have removed another barrier to managing complicated systems. Technology has advanced to the point that lakewide databases, with computer access from every fishery agency office, can easily be established. The major problem in establishing such databases would be the design of data formats; this process should be guided by lakewide fishery ecosystem models. Microcomputers are now being sold with enough memory to run complex ecosystem models. Every inter-agency technical committee meeting should include at least a transportable microcomputer for use in data retrieval and fish population and community simulation. This is a major, even revolutionary, change from the past, when access to data and analytical procedures was a major limiting factor.

I am not naive enough to think that there will be immediate changes along the lines that I am suggesting. Even if these are recognized as good ideas, the inertia of people and institutions will make change a slow process. However the time is



now to start thinking about fish populations in their proper perspective: populations are only parts of larger systems. Fishery management, to be successful, must operate on all relevant levels, which certainly include the ecosystem. Fishery ecosystem management will require changes in planning and evaluation procedures, and eventually changes in agency operations, but the first essential change is one of attitude and perception on the part of individuals. Fishery managers and administrators with responsibility for Great Lakes fisheries must begin to view their actions in the context of the fish community and to commit themselves to the success of fish community management. There is a tremendous challenge awaiting us.

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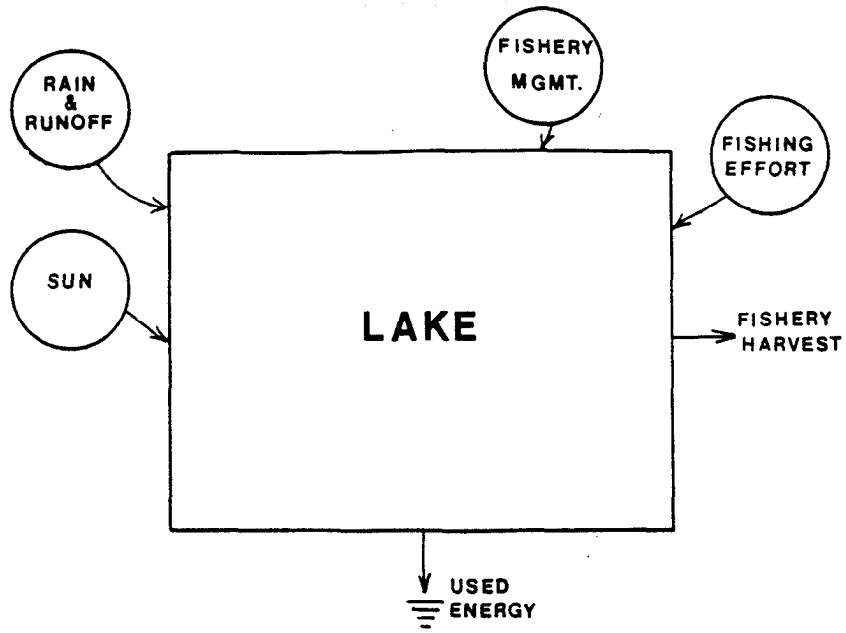


Figure 1.

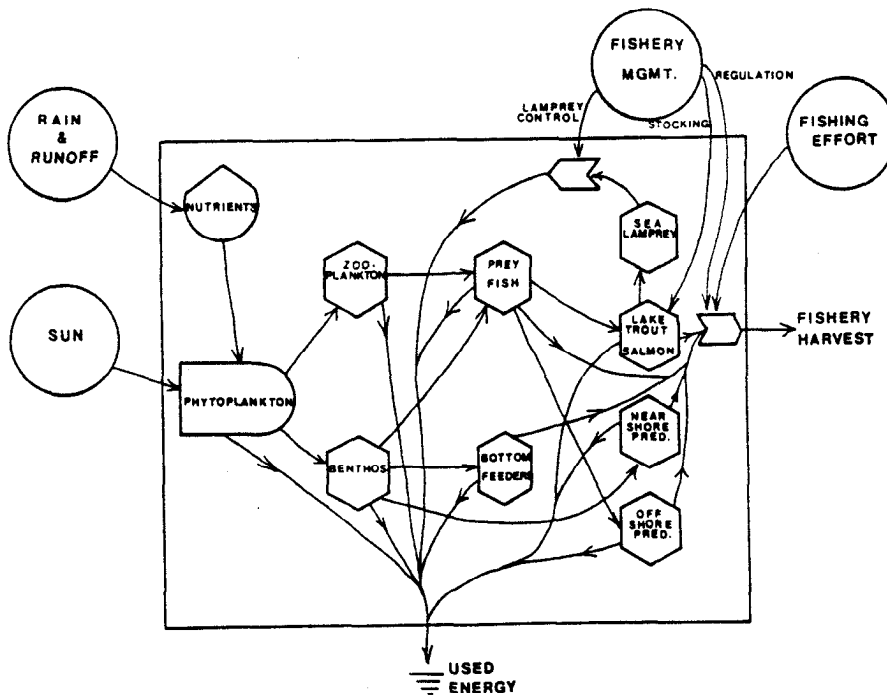


Figure 2.

(Energy circuit symbols after Odum, 1983)

AN ECOLOGICAL RATIONALE FOR MANAGING PREDATOR-PREY SYSTEMS  
IN THE GREAT LAKES

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Great Lakes Fishery Commission  
Ann Arbor, Michigan 48105  
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# An Ecological Rationale for Managing Predator-prey Systems in the Great Lakes

by

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## Introduction

An ecological rationale for development of salmonid stocking policies is a requisite of the overall objectives and major strategic procedures outlined in the Joint Strategic Plan for management of Great Lakes Fisheries (GLFC, 1980). Planning by some agencies, such as Wisconsin DNR, now includes initial recognition of the need for development of stocking policies predicated on a stable and/or sustainable forage base. Although these goals are reasonable and desirable what remains is the substantive task of developing the research perspective, the analytical tools and the practical guidelines to management that are required to put the strategic planning into tactical practice. The initial focus of our work to date has emphasized applications to Lake Michigan. Principles derived from that effort can be modified as appropriate to the unique characteristics of the other four lakes (Smith, 1970).

## Alternative Hypotheses

The status of the forage base for salmonid predators in Lake Michigan is the subject of some contention. On one hand, predictions based on bioenergetics modeling and ecological reasoning are being borne out: (1) populations of fishes suppressed by alewife competition are now increasing (Crowder and Magnuson 1982), (2) large zooplankton are more common (Gitter 1982), (3) growth rates of salmon and lake trout are declining, and (4) salmon diet diversity has increased. Crowder (MS) details those predictions and the recent evidence from Lake Michigan. These tend to substantiate the argument that current levels of predation are exerting a strong impact on the alewife population, at least in the southern basin of Lake Michigan. Eck and Brown (In Press) argue that alewife abundance is oscillating about an equilibrium level without trend and that increased predation on alewife could be substituted for other agents of natural mortality. If a significant portion of natural mortality is weather-related, or if year class failures are related to climatic fluctuations, the latter assumption may not be true. As developed by Stewart et al. (1981) the "predator inertia" brought about by increased stocking of long-lived predators could severely hamper the ability of alewife to recover from a population crash.

The arguments advanced from an ecological perspective are based on the assumption that species interactions, notably predation and competition, have become a major component of alewife population dynamics in Lake Michigan. An important alternative view is advanced by Eck and Brown (In Press)), who assert that the variability in alewife is largely determined by weather-related mortality. In a related paper, Eck and Wells (1983) conclude that predation by salmonids is a minor component of alewife mortality and that Lake Michigan could support several-fold increases in salmonid stocking. We (Stewart et al., 1981; Kitchell and Crowder ms 1984) disagree but feel that the alternatives need to be effectively evaluated. Toward that end I have attempted a simple analysis which follows from the assertion that density-

independent (i.e. weather) effects are the major source of variation in forage stocks.

Based on assessment catches reported by Wells and Hatch (1984) and Argyle (1984) I conducted a simple comparison of forage stocks in Lake Michigan and in Lake Huron during the period of 1973-1983. A simple correlation matrix was constructed to evaluate co-variation in alewife and smelt populations in both lakes. The assumptions made in the analysis are:

1. Variability in weather effects are regional In other words, a year of below average winter temperatures in Lake Michigan should be a below average year in Lake Huron.
2. Weather-related effects on mortality are expressed in densities of adult fishes.

I used this approach to test several simple hypotheses:

- A. Adult stocks of alewife and smelt vary independently in response to weather-related effects.
- B. Alewife and smelt populations express density-dependent interaction by varying inversely due to strong biological interactions.
- c. Predation rate by stocked salmonids is a major cause of alewife and/or smelt mortality.

The resulting correlation matrix (Table 1) demonstrates that significant changes in several variables have occurred over the past eleven years. Smelt have increased in both lakes. Alewife have decreased in Lake Michigan and salmonid predation has increased strongly there. Smelt populations in both lakes show positive covariation; alewife do not. The alewife decline in Lake Michigan is highly correlated ( $r^2 = 69\%$ ) with increased salmonid predation rate.

This analysis, albeit simplistic. in that no time lags are included offers little support for the ideas that interactions between alewife and smelt are direct and important components of variability. There is modest evidence that regional<sub>2</sub> weather-related effects play some role in population dynamics of smelt ( $r = 44\%$ ) but no evidence of significant covariation in alewife populations. The strongest inference of cause and effect is that increased salmonid predation has caused decreased adult alewife abundance in Lake Michigan. My conclusion is that although weather-related effects have been a major component of alewife population dynamics in the past and may continue to play a role, the primary component of change in the Lake Michigan alewife population over the recent past has been predation by stocked salmon and trout.

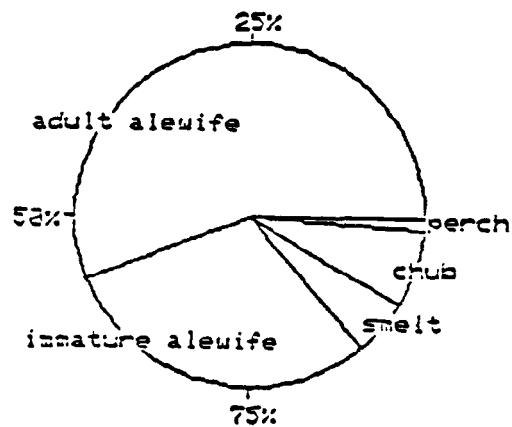
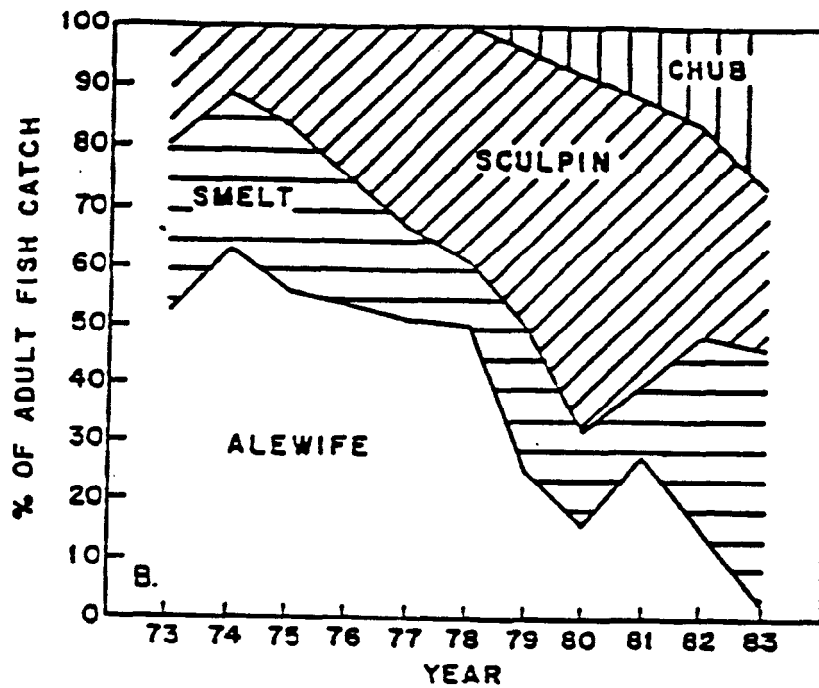
Due to the "keystone predator" effect of stocked salmonids, the species composition of the forage base in Lake Michigan has shifted (Hagar 1984, Wells and Hatch 1984, Crowder and Magnuson 1982). For example, USFWS surveys at Port Washington, Wisconsin show continuous change in relative abundance of alewife (Figure 1) yet the summer diets of coho and chinook salmon sampled

Table 1.

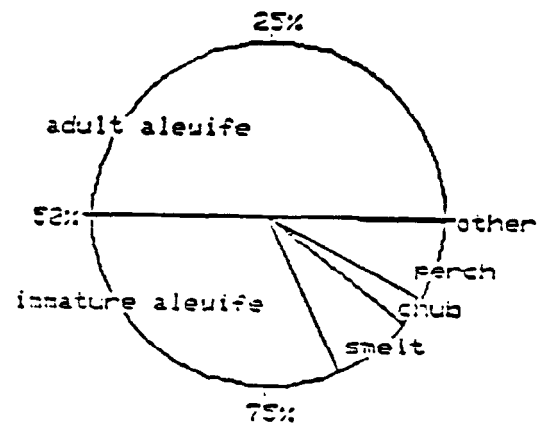
Correlation matrix (r) of Lake Michigan and Lake Huron adult alewife and adult smelt populations during 1973-83. Data are from Hatch and Wells (1984) and Argyle (1984). The estimate of predation by salmonids in Lake Michigan is from Stewart et al. (1981) as modified by Kitchell and Crowder (MS). Those marked with an asterisk (\*) are statistically significant (two tailed test,  $p < .05$ ).

Dependent Variable	Year	Huron		Michigan	
		Alewife	Smelt	Alewife	Smelt
Huron Alewife	-.37	-			
Huron Smelt	0.69*	-.01	-		
Michigan Alewife	-.75*	0.57	-		
Michigan Smelt	0.77*	-	0.66*	-.38	-
Salmonid Predation Rate	0.86*	-		-.83*	0.48

Figure 1.



chinook 83 data



coho 83 data

Fig. 1. Changes in relative abundance of forage fishes in USFWS fall trawl surveys off Port Washington, Wisconsin (upper panel) compared with relative diet components of coho and chinook salmon sampled at Port Washington during summer 1983. Diet data are from Hagar (1984).

there continue to be dominated by alewife prey (Hagar, 1984). It is uncertain how increased numbers of perch, bloaters, and smelt will affect the resiliency of the alewife population, currently at a low level.

Superimposed on this uncertainty are trends at the predator level that can only lead to even greater impact on alewife stocks. These include public pressure to increase stocking and to shift management emphasis to trophy species (rainbow trout and chinook salmon) at the expense of coho salmon. In addition, improvements in hatchery and stocking procedures lead to greater survival to stocked fish. Although current policy calls for no increase in stocking rate, it is unlikely that surplus fish will be discarded, as evidenced by recent experience in Wisconsin where a 15% surplus was distributed and stocked. We should expect the same in other states. Our ability to directly control predation through manipulation of salmonid stocking rates may be greatly eroded if successful natural reproduction by lake trout is realized, if stream-run salmonids (e.g., rainbow trout) increase recruitment from natural reproduction, and if the invasion of the pink salmon results in a permanent addition to the fauna.

Predator-prey problems are not confined to Lake Michigan. For example, a recent decline in the condition of lake trout in western Lake Superior may be attributable to a decline in smelt, the principal prey of both trout and stocked salmon in that lake. The trout and salmon apparently have not switched to consumption of lake herring, which are currently increasing in numbers.

#### A Need for Prediction

The future of predator-prey systems in Great Lakes ecosystems will be difficult to predict because the dominant member of fish communities are non-native species with little or no co-evolutionary history. In addition, there is lessened prospect that natural regulators of predation effects will operate effectively because recruitment to salmonid populations is largely dictated by economic, social, and political processes governing hatchery production and stocking rates rather than through natural ecological processes. That control over predator populations is of tremendous potential advantage if an ecological rationale can be developed.

The literature of ecology and fisheries provides abundant examples of calamitous changes in natural systems due to the instability and unpredictability of effects caused by introduced predators (Ursin, 1982). How then, can we estimate the carrying capacity of salmon and trout stocked in these systems? There is of course, no single answer to that question. As described by Busiahn in this volume, one can estimate the likely boundaries dictated by thermo-dynamic constraints. Within those limits the species interactions involved plus a large element of stochasticity can be evaluated to narrow the realm of possibilities. A more appropriate question is: What are the boundary conditions of natural variation that provide for stable co-existence of the species involved in these trophic systems? There are two general ways to answer these questions. One approach is to continue expanding stocking rates until major community transformations are effected. This is an undesirable approach because of the political and economic instabilities that will result. If major changes are forced by predator stocking, the predatory inertia may be so great that many years may be required before



steady state conditions can be re-established.

The second approach involves a combination of modeling and ecological reasoning. The modeling studies and components of the ecological approach are detailed in Stewart et al., (1981, 1983) and Kitchell and Crowder (MS). A new component to be developed is that offered through the paleoecological approach. The basis for this work is the argument that the sediments of these lakes are archives that contain zooplankton remains indicative of the predator-prey systems operating in the overlying water column. The dynamics and composition of the zooplankton community are widely recognized as highly responsive to predator effects and have been successfully used as indirect and integrative source of insights for the whole ecosystem (Kitchell and Kitchell 1980, Kerfoot 1981).

As a preliminary study, we analyzed samples of sediments taken in box cores from a deep-water station in the southern basin of Lake Michigan. This coring program was conducted in 1981-82 by the NOAA Great Lakes Environmental Research Laboratory and the samples plus background analyses were provided through the courtesy of Dr. Brian Eadie. A complete description of the analysis is forthcoming (Kitchell and Carpenter in prep. ) but the salient features are stated here as evidence of the potential of this approach.

Cladoceran remains in Lake Michigan sediments were sparse. Only the head shields and carapaces of *Bosmina longirostris* occurred in sufficient abundance for quantitative evaluation. *B. longirostris* is a major component of Lake Michigan zooplankton, and is preyed upon by both fishes (Wells 1970) and predaceous invertebrates such as *Mysis* and the large copepods (Gitter 1982, Evans et al 1980). In fact, 90% or more of the organic remains found in deep-water sediment traps in Lake Michigan are derived from fecal pellets (*B. Eadie, pers. Comm.*) indicating that, as in the marine environment, deep-water sediments are an archive of predation processes, (Levinton, 1982).

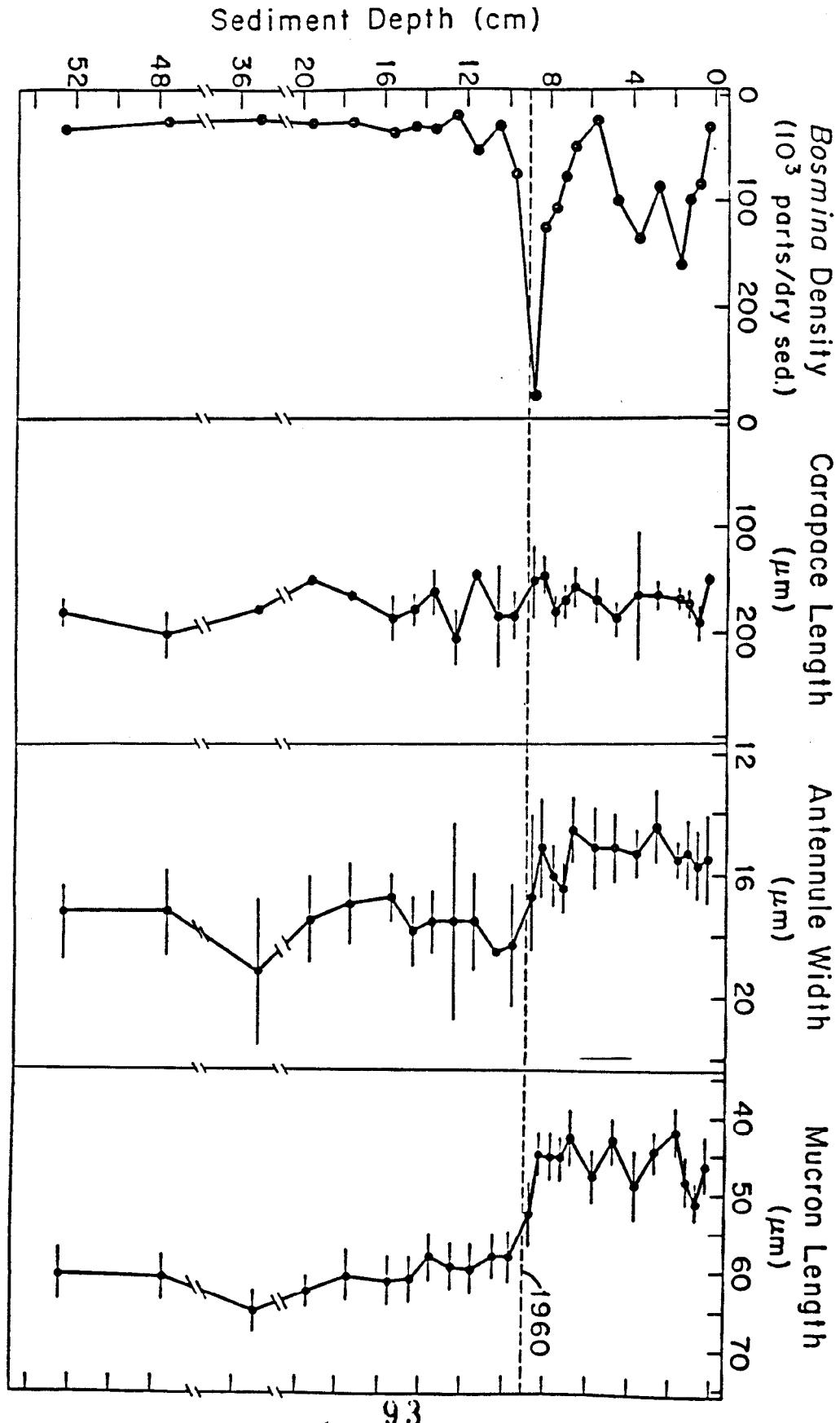
Our preliminary analyses involved counts and measurements of *Bosmina* remains found in one-half to one centimeter thick subsamples from segments of the top 20 cm of a core which has been age-dated using lead and cesium isotopes. Linear sedimentation rate at this site is approximately 0.3 cm/yr. Thus the core represents material deposited over the past 150-175 years. A mixing depth, due primarily to bioturbation, of about 1 cm is estimated by the NOAA team (Eadie, pers. Comm.). We made morphological measurements on at least 50 *Bosmina* carapaces from each subsample. Our results revealed:

1. Deposition rates of fossil parts (based on added known amounts of *Eucalyptus* pollen) are highly variable but within the ranges reported by others (Kerfoot 1981). Deposition rate increased sharply at depths of 8-10 cm.

2. *Bosmina* carapace sizes showed no apparent trend over core depth.

3. Length of the mucron (the posterior spine of *Bosmina* carapaces) exhibited dramatic changes as did width of the antennule at its base. Antennules are usually broken in these samples but the basal width is correlated with length. Together, mucron length and antennule width are taken as evidence of adaptive, anti-predatory morphology. Means and their 95% confidence intervals are presented in Figure 2.

Figure 2. *Bosmina longirostris* densities, carapace sizes, antennule width at the base and mucron length derived from a sediment core taken by NOAA-GLFRL personnel in Lake Michigan during 1981. Means and 95% confidence intervals are given for morphometric measurements.



Based on the analyses and interpretation of changes in *Bosmina* morphology reported by Kerfoot (1981), we interpret the significant changes observed at 8-10 cm depth and depth as responses in this clonal species to major shifts in the balance of selection pressures indicative of community changes.

Assuming a mixing depth of 1 cm, *Bosmina* mucron lengths changed dramatically from long-featured morphs to short-featured morphs during a period some 20-25 years before the core was taken: i.e. during the late 1950's and early 1960's. This corresponds with the period when alewife abundance was rapidly increasing in southern Lake Michigan (Wells, 1970) and large-bodied zooplankton (cladocerans and copepods) were substantially reduced through heavy size-selective predation by alewife. An estimate of depth is given for 1960 in Fig. 1. The long-spined Bosmina morph dominant before the alewife invasion was presumably evidence of anti-predator morphology selected for as defense against copepods. *Bosmina* spine length has little or no effect on Mysis or on fishes as predators (G. Warren, Ctr. Great Lakes Res. Milwaukee pers. Comm.; Kerfoot, 1981). Alewife reduced the populations of predaceous copepods (e.g. *Mesocyclops*, *Cyclops*, *Limnocalanus* and) to very low levels (Evans et al., 1980) thereby reducing selection pressure for anti-copepod morphology and a short-featured morph dominated until very recently (Figure 2).

In other words, *Bosmina* morphology can be used to document the advent, dominance and--most importantly--recent decline in the impact of alewife on L. Michigan zooplankton. Thus it can also serve as an indirect indicator of alewife populations which we argue elsewhere have been recently depressed through intense predation by stocked salmonids (Stewart et al. 1981). In that paper, we also argued that the dynamics of zooplankton would be among the best indicators of predator-prey systems operating in Lake Michigan. Crowder's contribution to these proceedings further amplifies that conclusion.

Two prospects for research follow from this result:

1. In each of the Great Lakes there exists an archive of predation effects. As in the Lake Michigan core, the timing and magnitude of major dynamics of the predator-prey systems may be reconstructed through analysis of core material. As the alewife invasion is less-well documented in Lakes Huron, Erie and Ontario and never occurred in Lake Superior, cores from each of those lakes can be analyzed to deduce their histories.

2. The second research perspective derives from examination of the data presented in Figure 2. *Bosmina* morphology appears to exhibit strong prospect as an indicator of alternate steady-state behavior in the predator-prey system. The responses are neither gradational nor linearly related to alewife effects suggesting the combination of switching and compensatory mechanisms often observed as systems change state (Holling, 1978; Walters et al 1980). Since we do not know the carrying capacity of these systems as currently populated by non-native species, we might derive insights from the kinds of evidence offered through a paleoecological approach. The zooplankton of Lake Michigan appear now to be exhibiting a reversal of the alewife effect.

Comparing the paleoecological evidence with open water collections and with recent sediments provides a basis for developing an integrated indicator

of the extent to which current predator-prey systems are displaced from their ancestral condition. This, then, will also lead to comparisons within and among the other lakes. Although we cannot expect to predict carrying capacities or conditions for stable co-existence for these systems, we can develop a more realistic expectation of the likelihood and possible magnitude of change that may be affected through manipulation.

Bioenergetics modeling can be used to investigate current Salmonid-forage interactions. It now seems necessary, however, to consider the northern and southern basins of Lake Michigan separately. The southern basin is most subject to changes in the composition and intensity of salmonid stocking; the northern basin is most subject to changes in natural recruitment, especially by stream-spawning species. Moreover, changes in the forage fishes appear to occur sooner in the southern basin, and alewife stocks in the southern basin may be subject to greater fluctuations (Hatch et al 1981). Current stocking and sport fishing mortality rates for model input must be updated by the best estimates that can be provided by the various state and federal agencies and can be combined with the results of the ongoing studies such as the Sea Grant-sponsored salmonid diet survey. Information on diet composition and prey sizes can be used to decompose model estimates of total biomass consumed during a period into estimates of the number of each prey type eaten, providing estimates of predation-induced mortality rates (Rice and Cochran 1984). Relationships between salmonid growth rates and alewife abundance can be used to develop functional response curves relating consumption of alewives to their abundance. There now exists sufficient change in alewife abundance and salmonid growth rates to allow this functional response analysis.

Modeling can be extended to simulations of possible future scenarios. These include changes in management policy, shifts in the forage base, natural reproduction by lake trout, and the prospect of stocking sterile chinook salmon which do not mature sexually thereby providing a new trophy fishery as they continue to grow. Answers should be sought for such questions as: What combinations of salmonid predators will result in an equal impact on the alewife, and what trade-offs are involved? What effect would a switch to consumption of perch and bloater by salmonids in lieu of alewife have on the commercial and recreational fisheries? How are species interactions among the zooplanktivorous forage fishes expressed in the zooplankton community? How may the recent changes in alewife abundance, salmonid growth rates and zooplankton community structure be used as a basis for estimating predator carrying capacity?

Unfortunately, we cannot rely on the traditional tools of fishery population dynamics for adequate answers to these questions. Those approaches yield post hoc answers and serve only as a basis for reactive management. We can develop forecasting techniques and conduct bona fide hypothesis testing if fisheries data, ecological reasoning and modeling techniques are developed for the pertinent questions. The history of Great Lakes fish communities have been dominated by surprises and calamitous change. We can only expect more of the same unless we are willing to take the risks and initiatives required to develop predictive tools based on an ecological perspective.

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INDICATORS OF THE STATUS OF COLD WATER PREDATOR-PREY SYSTEMS

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## Indicators of the Status of Cold Water Predator-Prey Systems

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The recent and historical dynamics of Great Lakes fish communities have indicated that these systems can change rapidly based on dynamics of predator-prey systems. The recent decline in the Lake Michigan alewife population could be due to increases in salmonid stocking rates (Stewart et al. 1981), but Eck and Brown (1985) have argued that the alewife decline is more likely due to a series of cold winters beginning in 1976. Regardless of the mechanism(s) causing the initial decline of the alewife population, if the salmonid predators do not switch from feeding predominantly on the alewife, compensatory mortality will result. In this paper, I will review the projections of Stewart et al. (1981) regarding indicators of change in the salmonid-alewife system and suggest which, if any, might be useful for indicating future dynamics.

Size selective predators can have a profound impact on the structure of aquatic ecosystems (Brooks and Dodson 1965). Manipulative experiments on fish predator-prey interactions in small, cold water, oligotrophic lakes in Sweden (Stenson et al. 1976, Henrikson et al. 1980) suggest strong functional linkages in these systems. When the planktivores were removed experimentally, the zooplankton increased in size due to both competition and predation interactions within the zooplankton. Other changes further down the food chain (reduced primary productivity, reduced pH and nutrients, increased water clarity) were associated with the observed changes in the fish-zooplankton predator prey system. Though these experiments were performed in small lakes (1-2 ha) the expectations should be more general.

In Lake Michigan, one might expect similar system-wide changes in response to the elimination of the pelagic planktivores. But we have only reduced, not eliminated the alewife in Lake Michigan. Thus, the effects which appear so obvious in the experimental lakes in Sweden will be more difficult to interpret in Lake Michigan. Those variables which underwent step-function shifts in the experimental lakes might be expected to change gradually if the planktivores are reduced more gradually. Forecasting imminent changes in the structure of the Lake Michigan fish community is difficult because these structural changes may be based on threshold phenomena which are currently poorly understood.

### Indicator variables

We suggested a number of ecological variables which might be expected to indicate or accompany a decline in the alewife population (Stewart et al. 1981). Obviously, we would like to isolate those indicators which might forecast a change in the forage base rather depend upon those which tell us a change is already underway. The original forecasts included:

1. Increase in the abundance of large zooplankton.
2. Reduced growth rates of salmon, particularly coho. Increased growth rates in alewife.
3. Increased diet breadth of salmon and lake trout.
4. Increased recruitment of fishes suppressed by alewife.



### Zooplankton size changes

Larger zooplankton have increased in abundance in Lake Michigan since the mid to late 1970s. In particular, size shifts have been apparent in the cladoceran community of the offshore zone (30-55m) in southeastern Lake Michigan (Gitter 1982, Evans pers. comm. 1. **From** 1979 to 1981, cladocerans increased in mean body size by **22-35%** (Gitter 1982). This size increase reflected declines in the abundance of Bosmina and increases in the abundance of larger D. retrocurva and D. galeata. An even larger Daphnia (D. pulicaria) first appeared in our samples in 1979-80 but was still rare in the 1961 samples. D. pulicaria became extremely common by late summer **1982**. Evans (pers. comm. ) has similar results showing increases in large zooplankton, especially offshore copepods, dating back to the mid 1970s for southeastern Lake Michigan and has documented a dramatic increase of D. pulicaria in the summer of 1983. Over all, zooplankton densities increased by a factor of 5 in the offshore zone from 1979-1981 (Gitter 1982).

One might expect zooplankton size to better integrate total planktivory and be a more sensitive indicator of changes in planktivore abundance than zooplankton abundance which can vary by a factor of 2-3 in the offshore zone from year to year (Evans et al. **1980**). Kitchell (pers. Comm.) has examined paleolimnological cores from Lake Michigan and found morphological indicators of changes in planktivory (Bosmina mucron length) which may also be helpful indicators.

### Growth Rates

Salmon growth rates have declined steadily since the early 1970s; coho growth rates have declined more than chinook (Hagar **1984**). Lake trout growth rates have also declined since the early 1970s. Growth rates are easy to monitor, but generally serve as poor indicators of potential system change because they integrate ups and downs in the forage base, particularly in long lived species such as lake trout. Shorter lived species, such as coho salmon should be much more sensitive to reduced ration levels. Because growth rates change smoothly, it is difficult to use them to predict step changes in the forage community. Growth rates will likely reflect a change already underway and are not generally useful to forecast changes in the forage community. **Alewife** growth rates appear to have increased in recent years though I am unaware of any comprehensive data to test this idea. Hagar (1984) noted that the alewives which appeared in salmonid diets showed better "condition" in 1983 than in 1982.

Growth rates seem a poor indicator of imminent system change. Unless we experience a number of ups and downs in the forage base, we will not know when salmon growth rates have fallen far enough to suggest forage deficiency. This is somewhat analogous to titration in chemistry-- as we approach a color endpoint, the sample is clear, but suddenly changes color. If we know from previous experience about how much titrant will get us close to the endpoint, we can add titrant rapidly until we are near that point and then titrate slowly. But if we have no idea how much titrant might be necessary, we often overrun the endpoint. If we know from salmon growth rates that we are nearing a forage decline, growth rates could perhaps be a useful indicator.

### Predator Diet Diversity

Once the alewife decline became apparent in 1982 and 1983, many of us expected the salmon and lake trout to rapidly switch to alternate forage, especially smelt, bloaters and yellow perch. Because of the expected behavioral flexibility in diet selection, shifts in diet diversity seemed to have good potential as an early warning indicator. Lake trout diets and growth have been closely monitored, but until recently, no routine monitoring of salmon diets was being done. Hagar (1984) recently completed two years of sampling from sport caught fish in Wisconsin waters of Lake Michigan. He found that coho and chinook are still primarily eating alewife (in 1983, 71% and 81% respectively) and that diet diversity increased only slightly ~~from~~ 1982 to 1983. In late summer, when the bioenergetic **demands** of the salmon are highest, diet diversity was great est. Chinook salmon added yellow perch; sculpins and even ninespine sticklebacks to their diets in late summer 1983! Both chinook and coho had a higher percent empty stomachs in 1983 and mean stomach fullness declined 35% in chinook and 42% in coho. Further, both chinook and coho were eating smaller alewives in 1983 than in 1982. In 1982, the average alewife in the chinook diets was 110 mm. In 1983, alewife mean size in the stomachs declined to **87mm. Alewives** in coho diets declined from 114mm to 94mm over this same period. This suggests that the salmon are eating a substantial number of pre-reproductive alewives which could reduce alewife recruitment further. Along with the reductions in growth rates, the diet data suggest a strong reduction in available forage, but much less switching than one might expect.

Why don't the salmon readily switch to alternate prey? I think habitat constraints may be important. Salmon forage most readily on pelagic schooling prey such as alewife. Furthermore, salmon are most likely to forage in or below the thermocline (13-15 C). Smelt seem the most obvious alternate prey and account for 8-10% of diets in both salmon in 1982-83. Though smelt have been increasing in recent years, the biomass of alewife and smelt in 1983 was only 42% of their average biomass in the five previous years (1978-82, Wells and Hatch 1984). In 1984, adult alewife and smelt biomass was reduced 35% from 1383 (Wells and Hatch 1985). Bloaters have increased several orders of magnitude since 1977, but are still rare in salmon diets (<5%. except in the very southern end of Lake Michigan, see Hagar 1984). Perhaps this is due to the fact that bloaters appear to shift to the bottom as yearlings (Crowder and Crawford 1984) and are thus less available to salmon. Yellow perch are distributed in the nearshore zone in much warmer water than one might expect salmon to forage though they were taken in late summer 1983 by both coho and chinook.

### Recruitment of Native Fishes

Bloaters have increased several orders of magnitude since 1977. Our field data suggest that larval and young-of-year bloaters feed in the plankton-- for the first ten days or so in the hypolimnion and for the rest of their first summer near the surface of the lake (Crowder and Crawford 1984). They recruit to the benthos as Yearlings, so the zooplankton feeding period of the life history could constitute a "bottleneck" constraining year class strength. When bloaters declined in the late 1960s they experienced recruitment problems and zooplankton

were small. In the late 1970s, strong recruitment was associated with abundant large zooplankton in the offshore zone. Rice (1985) has suggested that bloater year class strength may be improved when larvae grow rapidly and thus are available to larval predators for a shorter period of time. Growth rates of larval bloaters in Lake Michigan in 1982-83 were extremely rapid (Rice 1985).

Yellow perch declined dramatically in the mid 1960s in response to the alewife increase, perhaps due to predation by alewives on larvae (Wells 1977). In 1982 and 1983, extremely large year classes of perch were formed, perhaps the largest since the 1950s (Wells and Hatch 1984). The mechanisms underlying these strong year classes are unclear, but zooplankton abundance in the nearshore zone in 1982-1983 was low relative to that in previous years (Evans, pers. comm.) though the zooplankton available were fairly large. The shortage of nearshore zooplankton in 1982-83 correlates with strong year classes which suggests that whatever mechanism limits perch recruitment was reduced in 1982-83. Perhaps the availability of large zooplankton in the larval stage or reduced predation by alewife on perch larvae may have been important in the formation of these large year classes (Wells 1977).

The general constraints on recruitment of alewife and other fishes in Lake Michigan and their relation to zooplankton prey available, predators and environmental variables needs much more research if we are to relate the formation of strong and weak year classes to these variables.

### Discussion

If we are to search for indicators of change in the forage base in Lake Michigan, even with the benefit of hindsight, we need to decide when the recent decline of alewife began. Is it true that the alewife population was oscillating without trend from 1973-1980 (Eck and Brown 1985), which might indicate some sort of equilibrium? Or was the alewife population, in fact, increasing after the 1967 population crash to some maximum only to decrease later? To explore these questions, I fitted the alewife biomass estimate for the period 1967-1983 (Wells and Hatch 1984) to a quadratic regression. This produced a significant fit ( $p < .025$ ), though the  $r^2$  value was relatively poor (46%) and highly dependent on the 1967 and 1983 points (though 1984 is similar to 1983). I then took the derivative of the regression equation to estimate the year in which the post 1967 alewife increase levelled off and the decline began. The "equilibrium year" was 1974. Given the lags due to predator inertia, the stocking level which appeared to reverse the pattern of alewife population increase were fish stocked in 1970-71. What this suggests is that the alewife decline is not a recent phenomenon, but may have been underway for 10 years! And if a major contributing factor to the decline was predation by stocked salmonids, the stocking rate at "equilibrium" (1974) is only half of the current stocking rate. Of course this analysis requires large, perhaps indefensible, assumptions. But we do need to decide if the weight of the evidence suggests the alewife decline is a recent phenomenon, beginning in 1983 or if, in fact the decline has been underway for as long as 10 years. If the decline has been underway for a relatively long period, we might have been able to anticipate the recent severe declines-- if we had known what to look for.

Of the indicator variables I have discussed, only offshore zooplankton community structure (especially size) and perhaps recruitment

of native fishes appear to be indicators by which one might have forecast the alewife decline, Changes in zooplankton size structure appear to have been underway since the mid to late 1970s. Strong bloater recruitment began in 1977. Weather may have influenced alewife survival and thus have contributed to the alewife decline (Eck and Brown 1985), but the mechanisms underlying this correlation are poorly known. Other "indicators" correlate with the alewife decline and provide additional evidence that food chain effects are important, but these variables hold little promise for forecasting system change. Growth declines in the salmonids have been continuous and relating a particular salmon growth rate to forage deficiency seems nebulous. alewife growth changes are also continuous and integrative and thus are difficult to interpret. Diet shifts have lagged, perhaps due to habitat differences **between** alewife and the native fishes we had hoped would compensate for their decline. We may expect to have to use a suite of indicators- it is too much to hope for that one indicator would do the job.

In order to be useful to managers, any indicator variables to be used must be apparent early enough to overcome the time lags inherent in the salmonid stocking process. From egg collection to maximum impact on **the** forage base, the lags are 3-6 years. Thus, if institutional response times were immediate (which they are not!), we would need to have indicators which will at least suggest the trends in the forage populations 3-6 years in the future. The appearance of D. pulicaria might be considered an indicator, but it first appeared in 1978- only 4-5 years before the alewife decline became obvious. Changes in size structure and species composition of the zooplankton associated with the alewife decline may have cued strong recruitment in bloater in 1977, but the recruitment process is too poorly understood to make this assumption. In order to document indicators which meet the requirements of predictability and overcome the long time lags in the stocking process, we will have to understand the zooplankton dynamics and recruitment processes better than we do now. The alternative is to consider control policies which have shorter time lags such as the management of fishing mortality on predatory salmonids.

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INDICATORS OF CHANGES IN PREDATOR AND PREY POPULATIONS  
IN WESTERN LAKE ERIE

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## Indicators of Changes in Predator and Prey Populations in Western Lake Erie

While many species of fish in western Lake Erie could be considered as either predator or prey at various stages of their life history, and to varying degrees, it is not possible to consider or even understand all the existing interactions that occur among this multi-species complex. For purposes of this discussion, we will use walleye *Stizostedion vitreum* as a representative predator species and emerald shiner *Notropis atherinoides*, spottail shiner *Notropis hudsonius*, young-of-the-year (YOY) gizzard shad *Dorosoma cepedianum*, and YOY alewife *Alosa pseudoharengus* as representative prey species. These species were selected because walleye become piscivorous predators while they are still small YOY fish, and are almost totally dependent on prey fish as a food resource thereafter, and because these prey species are the ones that constitute the bulk of the walleye diet in western Lake Erie.

The indicators of changes in the predator and prey fish populations in western Lake Erie, that are most evident at the present time, can be categorized as: 1) changes in the abundance of both predator and prey species, and 2) changes in the growth and maturity of the walleye population. These indicators are subject to yearly fluctuations which are caused by climatic factors that affect spawning success, individual species responses to the predator-prey interactions, and perhaps other unknown factors. Furthermore, yearly fluctuations in indicator values can be large and readily apparent or small and less obvious, so the interpretation of short term fluctuations can be misleading with respect to the future conditions of a given population. Therefore, we evaluate changes in indicators over a number of years to establish trend changes in the status of predator-prey populations and consider this procedure to be more reliable.

### Abundance Indicators

More than 20 years of (bottom trawling survey data from western Lake Erie are available to assess the changing status of the prey fish populations. We use catch-per-unit-of-effort (CPUE) as the indicator of annual relative abundance of each species where the catch is reported as numbers of fish and effort is one hour of trawling. Trawling surveys have been conducted at a number of sampling stations each year from May through October and standardized procedures and gear have been consistently utilized so all relative abundance indices are directly comparable.

Changing trends in prey fish abundance (already presented at this seminar) suggest that emerald and spottail shiner abundance levels were high from 1960 through approximately 1974, when annual CPUE values (all age groups combined) frequently exceeded 500. After 1975, annual CPUE values for shiner populations were

usually below the 500 index level and a declining trend in shiner abundance is indicated. The abundance of YOY alewife has remained fairly constant over the 21 year period with low annual CPUE index values usually ranging between 50 and 200. Unusually high index values of approximately 900 and 1,000 were recorded in 1973 and 1974, but the abundance of this species in subsequent years returned to lower levels. Abundance levels of YOY gizzard shad are usually higher than those of alewife with annual index values commonly ranging between 150 and 400. Exceptionally high CPUE index values of 1,057, 1,353, and 1,917 were recorded in 1976, 1980, and 1981 respectively for gizzard shad but these values do not seem to indicate a sustained trend of increasing abundance for this species.

Two indicators are used to assess changing abundance trends for walleye. The first indicator is the annual commercial fishery catch reports for the period from 1960 until 1970 when the walleye fishery was closed because of mercury contamination. There are no walleye population estimates for that period, but fishing effort was high and any changes in catch would be indicative of changes in abundance. Using reported walleye catches from Ohio and Michigan waters of Lake Erie, catches decline by nearly 85% from approximately 1.1 million pounds in 1960, to 186,000 pounds in 1969. - This indicates a declining trend of walleye abundance to very low levels. The second indicator of walleye abundance change is the annual total stock estimate derived by the Walleye Task Group of the Lake Erie Committee from the total allowable catch quota model. The estimated walleye total stock in western Lake Erie in 1976 (the first year of catch quota management) was nearly 15 million fish, and this total stock estimate has increased nearly three-fold, to approximately 44 million fish in 1983. This trend indicated that recent walleye abundance levels in western Lake Erie are increasing to high levels.

### Changing Walleye Growth and Maturity Indicators

The Changing status of the western Lake Erie walleye population may be indicated by changes in growth if growth rate is density dependent. Examination of YOY walleye total length attained each fall from 1951 to 1983 indicates that average length had decreased approximately 50 mm during that time (Figure 1), while walleye abundance increased. Data for growth of older age groups are available from 1974 to 1983 as the walleye population was increasing. Annual changes in total length of both males and females were usually small with both increases and decreases in total length occurring from year to year (Figures 2 and 3). However, the 10-year growth trend demonstrated a declining growth rate associated with increasing abundance.

A secondary indicator of the changing status of the walleye population is the increasing delayed onset of sexual maturity (Table 1). During the 1964-1966 period when walleye abundance was low 96% of the age II males were mature, while 86% and 99% of the age II and age III females were mature and spawning each



spring. During the 1974-1980 period when walleye abundance was increasing the onset of sexual maturity began to be delayed and this was most apparent for the females. Fall samples of age I females were nearly all immature suggesting that they would not spawn the following spring as age II fish. Only 57% of the age II females collected during the fall were sexually mature and would spawn at age III. Increasing delayed sexual maturity for both sexes was evident during the 1981-1985 period, when walleye abundance was very high. Fall samples indicated that only 45% of the age I males and none of the age I females would spawn the following spring, while only 38% of the age II females would be sexually mature.

## Discussion

Trend analyses? using more than 20 years of predator and prey abundance, growth, and maturity data, suggests the abundance of important prey fish populations in western Lake Erie was higher in the 1960's and early 1970's when the abundance of the primary predator (walleye) was low. Conversely, prey abundance decreased as the predator abundance increased after the mid-1970's. A simultaneous decrease in walleye growth and delayed maturity coincide closely with decreased prey abundance, and we believe this is a cause-and-effect relationship. Walleye abundance and the associated predator pressure on the primary prey fish populations may be excessively high in recent years and the predator food requirements are no longer being met by available prey. Declining growth rate and delayed maturity are two indicators supporting this hypothesis.

Figure 1. Changes in average total length of young-of-the-year walleyes collected in fall from waters off of East Harbor, Ohio, 1961-1983 (numbers show sample size).

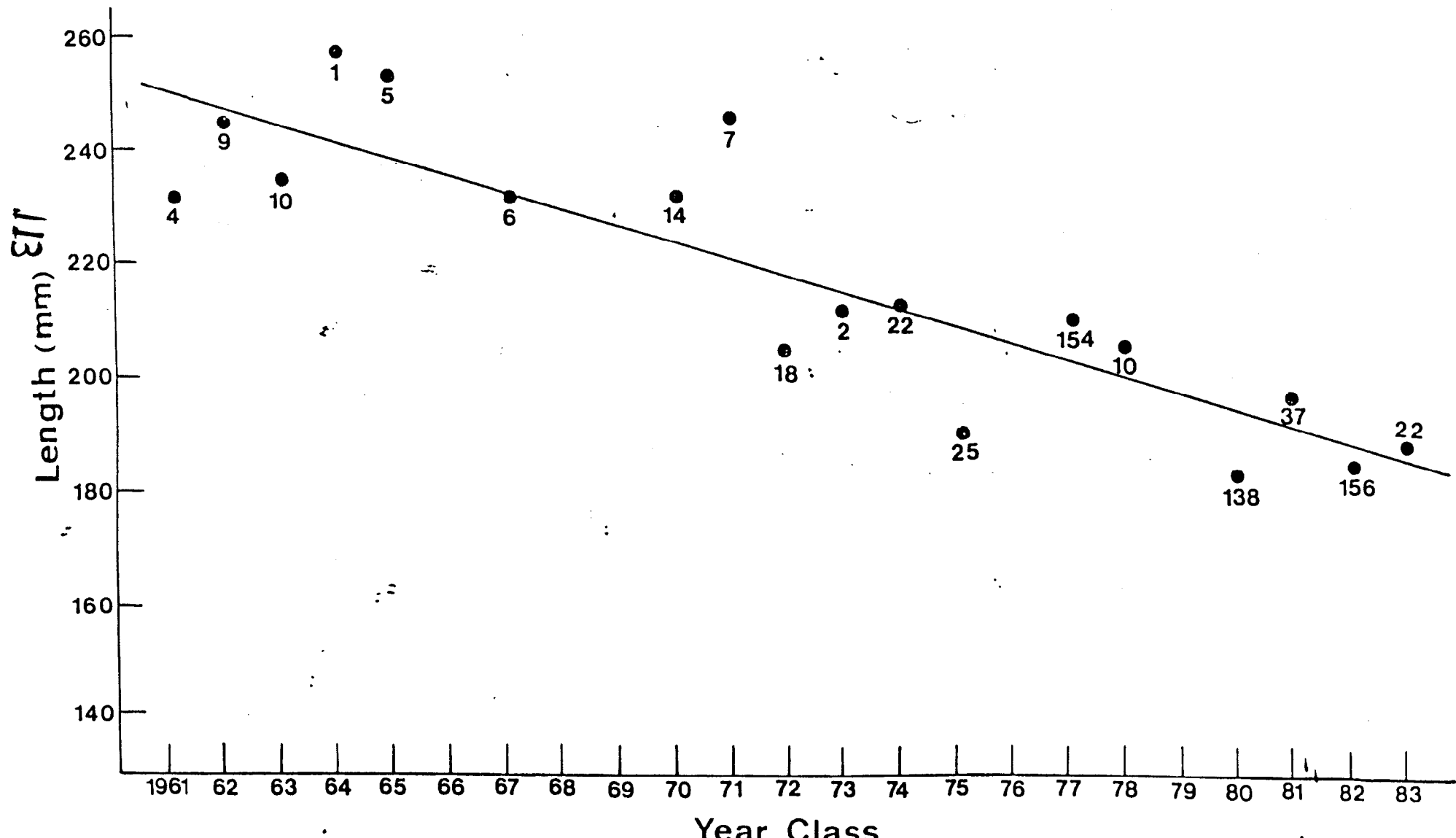


Figure 2. Changes in the average length of age I, II, and III net-run male walleyes taken from trap nets from western Lake Erie in fall, 1974-2983 (numbers show sample size).

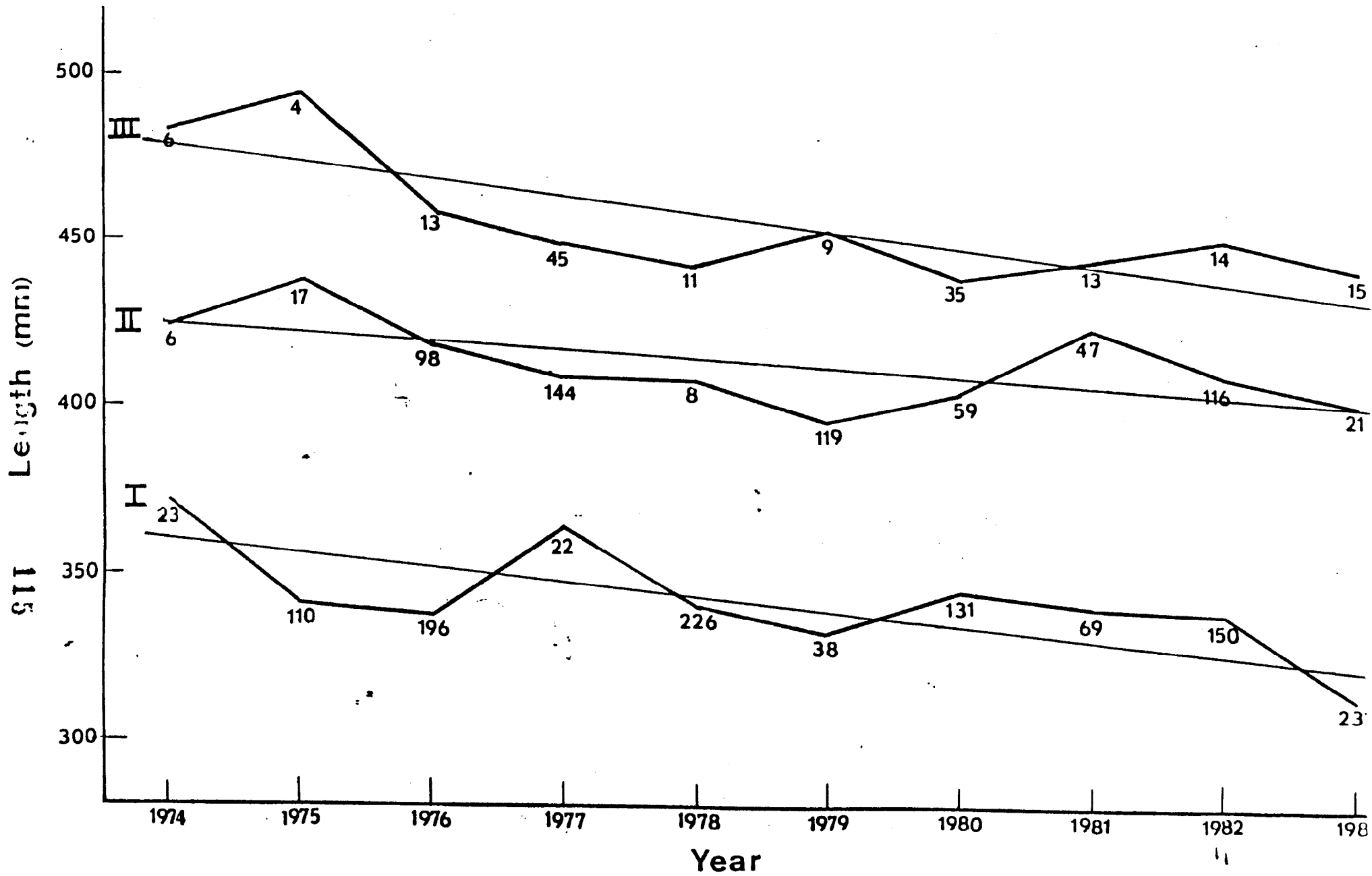


Figure 3. Changes in the average length of age I, II, and III net-run female walleyes taken in trap nets from western Lake Erie in fall, 1974-1983 (numbers show sample size).

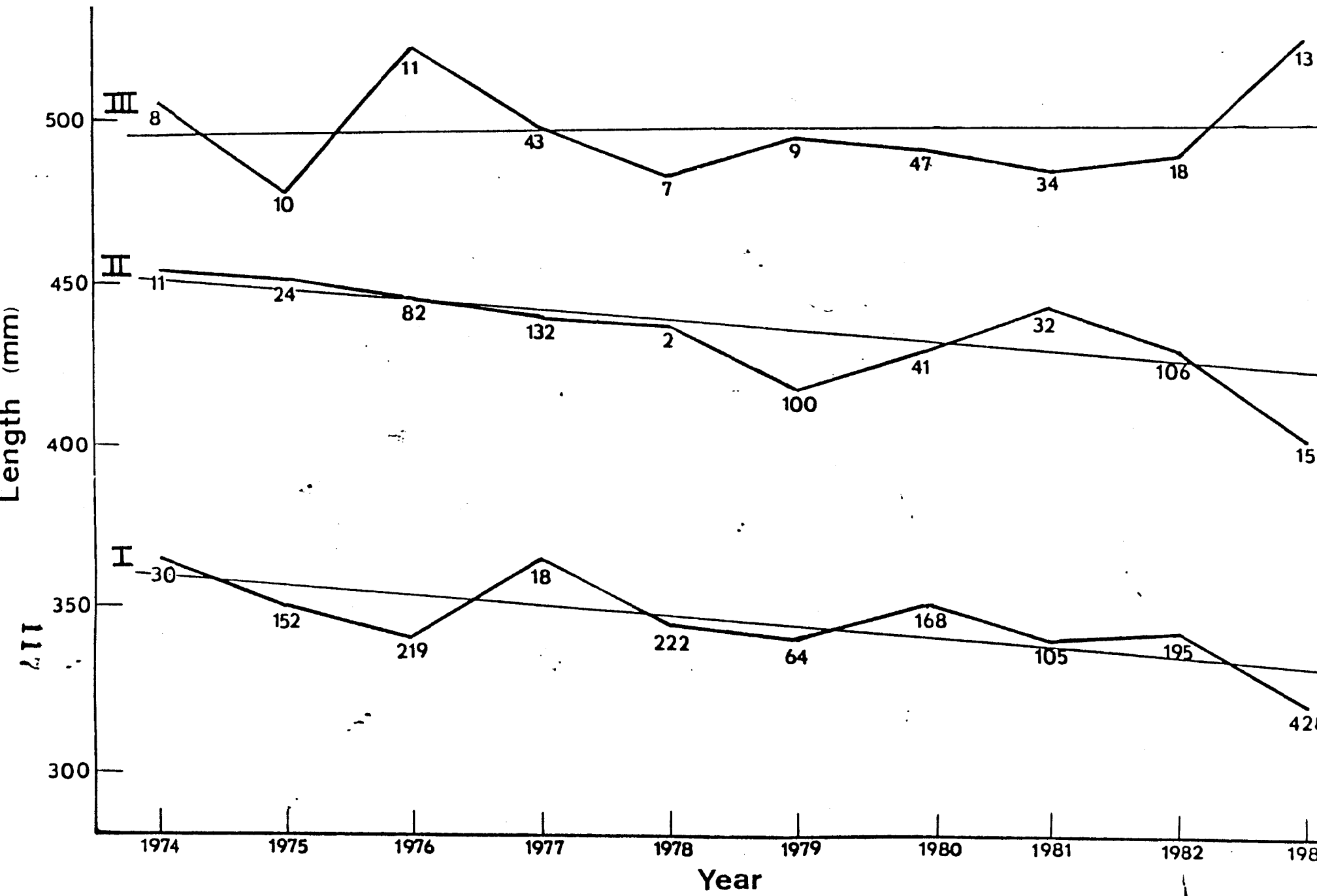


Table 1. Maturity, by age group, of net-run male and female walleyes taken in trap nets in western Lake Erie during three periods of differing population abundance.

Period and Age Group	Males		Females	
	Number	Mature (%)	Number	Mature (%)
<b>1964-1966 <sup>a/</sup></b>				
II	364	96.2		
III			161	86.3
IV			74	98.6
<b>1974-1980 <sup>b/</sup></b>				
I	746	88.9	873	0.3
II	451	99.6	392	56.6
III	123	100.0	135	99.3
IV			59	100.0
<b>1981-1983 <sup>b/</sup></b>				
I	459	43.1	728	0.0
II	184	98.4	53	37.8
III	42	100.0	65	98.5
IV			40	100.0

<sup>a/</sup> Fish samples collected during spring spawning (Wolfert 1969).

<sup>b/</sup> Fish samples collected in fall. Age groups designated as I, II, and III would be expected to spawn the following spring, at age II, III, and IV.



EFFECTING A POLICY: INSTITUTIONAL ARRANGEMENTS  
FOR ALLOCATING THE RESOURCE

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## Effecting A Policy: Institutional Arrangements For Allocating the Resource

In developing a direction for co-operative management of Great Lakes fisheries resources, agencies with responsibility for fisheries management will be required to take a number of steps prior to reaching agreement on the manner in which the resource will be divided among jurisdictions. In this paper, we will suggest possible steps which agencies can take which will lead to resource allocation and point out optional allocation criteria for managerial consideration.

Within the mandates of agencies responsible for management of fisheries resources, guiding principles may be identified and applied in any given management area. Those principles range from rehabilitation through maintenance to enhancement of the resource, each carried out in the best interest of the people with direct benefits normally realized by the users of the resource.

Given these guiding principles, agencies with jurisdiction over common fisheries resources must reach agreement on the fish community structure which satisfies their collective needs.

Having achieved agreement on a target fish community, objectives for management can be developed and will serve as source material in policy formulation for co-operating agencies. These objectives will pertain to particular species or groups of species which are perceived to meet some need of the user groups. While it may be relatively easy to achieve consensus that certain species be included in the fish community, consensus on the priority of objectives pertaining to these species may be more difficult as the requirements of users in the various jurisdictions will differ.

After placing priorities on the array of objectives, strategies for achieving objectives may be developed. For the most part, strategies employed by fisheries management agencies will involve altering mortality rates, supplementing the fish community or promoting the alteration of habitat as deemed necessary for the achievement of fish community objectives. Habitat modifications, while fundamental in reaching certain objectives, are seldom achievable in the short term; effort directed at habitat modifications is ongoing. In the short term, fisheries management agencies generally concentrate their efforts on control of mortality rates or on supplementing the fish community.

To be effective in the manipulation of species of common concern, both control of mortality and supplementing of the fish community require that allocation of the resources be considered on a multi,-jurisdictional basis. It is assumed here that allocation is made only to the level of jurisdiction as the manner in which an agency allocates the resource within its jurisdiction is not in itself a matter of common concern. An

allocation may be used directly i.e., harvested by man or indirectly i.e., harvested by a top predator used to supplement the fish community or a combination of the two.

### Direct Use

Allowing that a reduction in fishing mortality of a species is the strategy chosen, the manner in which allocation of harvest among co-operating agencies can be based on a variety of criteria. Agreement must be gained on the choice of criteria or combination of criteria employed.

Traditional - Where fisheries have exploited common stocks, historical sharing patterns can be used to apportion a total allowable harvest.

Areal - The allowable harvest is divided based on the proportion of water area in each jurisdiction. This approach may be further refined to reflect area of suitable habitat.

Distribution - Information on distribution if available may be used in the allocation process. Differences in habitat or available prey may influence the distribution of target species at a given point in time and over time distribution may change in response to both prey and behavioural patterns. Also the utilization of prey may be a consideration if cycles of movement are identified.

Origin - When predators are introduced into the fish community, jurisdiction of origin may be considered. It is unlikely that origin would be used in isolation as a criteria for allocation as the distribution through jurisdictions other than that of origin would be linked to use of prey in those areas.

### Indirect Use

This category recognizes the finite nature of prey species and should be considered when the management strategy includes supplementing the fish community with predators. The allocation process might make use of some of the same criteria described earlier for direct use but the allocation would be translated not into harvest for man but an allowable input of predators. Of the criteria listed, those considered might include area of waters within jurisdictions and distribution of prey. The manner in which predators would distribute themselves would also be of concern.

### Direct and Indirect Use Combined

The combination of direct and indirect *use* of prey species exists in some instances. Prey species may be allocated to jurisdictions in accord with selected criteria presented earlier. The manner in which a management agency chooses to impose mortality on a prey species either directly through

exploitation by man or indirectly through controlled levels of supplemental predators is not at issue; however, issues may surface. For instance, direct use of prey species by man limits access to jurisdictional waters. In contrast, supplemental predators introduced into the system range freely among jurisdictions not only taking advantage of prey in jurisdictions other than that of their origin but congregating in areas where they are subject to direct exploitation either intentionally or as by-catch. This type of problem is not likely to be totally resolved in the process of allocating prey but would extend into the process of allocating supplemental predators.

### Summary

Consistent with the complexity of fish communities and the differing priorities of co-operating agencies, the allocation of species among jurisdictions will not be simple and will require compromise by co-operating agencies at each step leading up to final allocation.

Finally, the steps suggested as leading to final allocation of the resource are as follows:

- Define the fish community.
- Set clear fish community objectives.
- Develop strategies for achieving objectives.
- Select criteria for allocating the resource.
- Resolve issues arising from criteria selected.

revised March 11, 1985

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REPORT TO THE COUNCIL OF LAKE COMMITTEES

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Great Lakes Fishery Commission  
Ann Arbor, Michigan 48105  
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A Plenary Session About  
PREDATOR-PREY ISSUES OF THE GREAT LAKES

Report to the Council of Lake Committees

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Introduction

In March 1985, a-plenary session about predator-prey issues was held at the Lake Committee meetings in Ann Arbor, Michigan. The session participants first historically reviewed information about the predator and prey abundance in cold and warmwater Great Lakes communities, and then examined management related goals, problems, information needs, and potential management actions in relation to these communities. A total of ten presentations were made by state, federal, tribal, and university biologists. The purpose of this report is to relate our general observations about the material presented at the plenary session, to propose a process for implementation of ecosystem management, and to recommend specific actions for the Council of Lake Committees to take in order to foster the proposed process.

## Session Observations

Below are listed and discussed our three main observations about the reports presented at the plenary session.

1. Forage is something that needs to be managed in the Great Lakes. The occurrence of this plenary session draws attention to the slow but steady change of management focus from species orientation to community based concerns.
2. There is a state of change in Great Lakes forage species and abundance. Forage communities are changing markedly in Lake Superior and Lake Michigan. The causes for these changes appears to vary among the lakes. In Lake Superior, variation in the forage communities appear to be unrelated to predation; however, in Lake Michigan, forage consumption by salmonid predators is implicated as the mechanism for change. In Lake Erie, the white perch, first reported in 1953, is now expanding lakewide. The impact by this species (as either predator or prey) on predator prey systems is unknown. White perch could also colonize other areas in the upper Great Lakes such as Green Bay.
3. Management discussions appeared to be based on the implied assumption that **stability** is good within forage communities and predator-prey system. Adoption of this assumption by biologists may be related to a concern about our inability to control or predict the impacts on Great Lakes communities that result from changes in forage

species and abundance. Uncontrolled change is not thought to be good management. Community changes (either predators or prey) can cause conflicts with users' expectations (e.g., anglers) that are based on recent past experiences. In this case, agencies are then placed in the awkward position of responding to user group concerns about fishery issues that are difficult to control (manage) or predict.

Community stability, however, may not be **"good"** but rather may be a rigid unnatural condition that could lead to system fragility (based on work by C.S. Hollings). Management agencies should instead focus on understanding the sources and levels of natural system variability and accept variability as a desirable natural characteristic of ecosystems. Consideration should be given to educating users that some ecosystem components are not controllable, and therefore, variability should be expected.

#### Process for Implementation of Ecosystem Management

At the conclusion of the session, there was agreement in favor of ecosystem based, as opposed to species based, management; however, probably most everyone prior to the session had already agreed conceptually with this idea. The problem with implementation has been the inability to translate ecosystem concepts into functional management practices. Listed below are what we view



as the steps in a transition process between these management approaches. We recommend that the Lake Committees begin to address these steps for their respective lakes.

1. Define the ecological boundaries of each Great Lake in terms of community structure and function (energy flow), Specifically answers to the questions of, "what forage species assemblages do we want" and "how will different forage species assemblages functionally respond to various levels of predator consumption and/or commercial harvest" should be sought. Predation impacts on forage species assemblages may be by a direct process through mortality, for example, "lake trout eat sculpins", or they may be indirect, such as 'salmonids affect yellow perch populations by predating on alewives which interact with yellow perch (through predation, food competition)".
2. By understanding the ecological boundaries of each system (as described above), different options should then be identifiable for forage structure and abundance at different predator densities. These options will then form the basis for community level management goals for each lake.
3. After the ecologically based management alternatives are identified, then these options would be evaluated in terms of maximizing economic and social benefits. Each management authority will have to determine the economic and social benefits within their respective

jurisdictions. These management options will need to be evaluated at an interagency level (such as by the Lake Committees) in order that benefits may be maximized among jurisdictions. This last step could be enormously difficult due to the institutional complex of management agencies on the Great Lakes.

#### Recommended Actions for the Council of Lake Committees

There are a number of actions that the Council of Lake Committees could immediately initiate in order to aid implementation of the process identified above. These actions are as follows:

1. Predatory impacts on the forage base caused by stocking and/or commercial harvest should be controlled in relation to forage abundance. If forage consumption by stocked salmonid predators is a force for change in community structure, then management agencies currently have the capability to control much of this impact by the regulation of the predator numbers stocked. For example, Wisconsin has been working on a stocking policy that regulates stocking numbers based on indicators of forage abundance. In the past year, Wisconsin has refused to stock surplus hatchery production of chinook salmon into Lake Michigan. In some locations, regulations may be necessary to control the commercial harvest of forage species. These efforts to control forage utilization levels in order to control predatory impacts (including man) on forage species

should be coordinated by the Lake Committees. We recommend that new working groups be established within each Lake Committee to address this issue. We suspect that a transfer of this responsibility to the Lake Trout Technical Committees would not be wise because committee member composition, although appropriate for lake trout management, may not contain the expertise required to begin this first step towards community level management. The intent of this first action is to reduce the rate of change that is being observed in Great Lakes forage communities in order to preserve the maximum number of management options available for later ecological, economic, and social evaluation.

2. **A data base management system for data sets about forage and predator species should be established for each Great Lake.** Establishment of this system will require standardized data collection among agencies. One agency should be given the responsibility for compilation and updating of data files. It is recommended that a central data base be maintained for each Great Lake and that access to the data base be decentralized to assure ease of availability to participating agencies. A protocol must be developed to determine "rights" for data analysis and subsequent publishing of common access files. Data quality control and security of files will also have to be addressed by the Council of Lake Committees.

Establishment of a data base management system will not be an easy task since data collection procedures are not standardized among districts or regions within some agencies.

3. There are a number of key information needs that must be addressed about community structure, function, and interaction, for example:
  - a. About some issues there may be a lack of ecosystem theory available in order to implement community based fish management. The upcoming ASPY symposium may serve to fill some of these theoretical gaps.
  - b. There is a need for the identification of community level indicators that can be used to measure ecosystem dynamics. Such indicators could then serve as parameters to be stated within management objectives. These indicators would probably focus on energetic or structural measures of communities.
  - c. There is a need to evaluate the feasibility (political, sociological) of adjusting fishing regulations and stocking in order to manage fish community structure and function.
  - d. We have a need to better understand the amount of forage recruitment variability that is a function of abiotic (climatic) and biotic (predation, competition) processes. There is a current controversy between the University of Wisconsin (Kitchell) and the Great

Lakes Fishery Laboratory (Eck, Brown) about the roles of these processes. This information will also help in understanding the natural level of variability that should be anticipated in these ecosystems.

- e. If stocking is to be used as a management tool to affect Great Lakes communities, then there is a need to understand the amount of variation in forage consumption that will be caused by natural recruitment processes (for example, the amount of natural reproduction of Pacific salmon in Michigan tributaries) and by the stocking of different genetic strains of a species (for example, Skamania versus Shasta rainbow trout). This information is essential in order to determine the level of control over predation that is possible by the regulation of stocking.
- f. There is also a need to document and understand the impact of white perch on Lake Erie. This information could help to predict future impacts in other locations such as Green Bay. The Council of Lake Committees should advise the Commission to encourage research about this species.

AVAILABLE PUBLICATIONS  
GREAT LAKES FISHERY COMMISSION  
1451 Green Road  
AM Arbor, MI 48105

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- 79-1 KING, E. L., Jr. and T. A. EDSALL. 1979. Illustrated field guide for the classification of sea lamprey attack marks on Great Lakes lake trout. Great Lakes Fish. Comm. Spec. Pub. 79-1. 41 p.
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- 85-2 SPANGLER, G. R., and L. D. JACOBSON (**ed.**). A workshop concerning the application of integrated pest management (IPM) to sea lamprey control in the Great Lakes. Great Lakes Fish. Comm. Spec. Pub. 85-2. 97 p.

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**Other**

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Contaminant research needs in the Great Lakes. June 28, 1979. 55 p.

Report of the audit of the Great Lakes Fishery Commission's program of sea lamprey control and research. 1980. 157 p.

The effect of environmental issues and programs on Great Lakes fisheries: Directions for the future. 1980. 55 p.

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**Brochures**

Sea lamprey management program  
Lake trout rehabilitation in the Great Lakes

August 1965