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Biological Surrogates of Mesotrophic Ecosystem Health in the Laurentian Great Lakes

Great Lakes Science Advisory Board. Ecosystem Objectives Committee

United States. Department of Agriculture. Forest Service

Ontario. Ministry of Natural Resources. Fisheries Research Branch

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Report to the
Great Lakes Science Advisory Board

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DISCLAIMER

This report to the Great Lakes Science Advisory Board was carried out as part of the activities of the Ecosystem Objectives Committee (formerly, the Aquatic Ecosystem Objectives Committee). While the Board supported this work, the specific conclusions and recommendations do not necessarily represent the views or policies of the International Joint Commission, the Science Advisory Board or its committees.

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PROLOGUE

This Committee report is the second step of a lengthy process designed to assess ecosystem quality in the Great Lakes basin using biological surrogates. As with any committee effort, the final output largely represents group consensus, but minority viewpoints are also represented as viable alternative considerations. Because in one sense, we are plowing new ground, the output of this contribution is not as even-handed as we would have liked, but rather, ranges from proven fact to likely hypotheses of potential values for further development. We do not apologize for the seeming inconsistency, as timeliness in application is critical, and high precision a luxury we can ill afford.

As many of the premises, criteria and background concepts are similar to those of a previous initiative designed to find appropriate biological surrogates for oligotrophic lake ecosystems within the Great Lakes basin (Ryder and Edwards, 1985), we will not repeat them here. Accordingly, we urge you to refer to both the latter documents as well as the appendices of this document for background material lending support to the principal thesis.

1.0 INTRODUCTION

A. Charge to Work Group

The Mesotrophic Indicators Work Group has been charged by the Ecosystem Objectives Committee of the International Joint Commission's Science Advisory Board to identify appropriate surrogate organisms for mesotrophic lake ecosystems of the Great Lakes basin. This charge derives from the 1978 Great Lakes Water Quality Agreement, as amended in 1983 and 1987 (IJC 1988). The sections of the Agreement pertinent to our current charge are found in the Supplement to Annex 1, dealing with specific objectives, which states that ecosystem objectives should be developed for all of the Great Lakes basin, in addition to those which have already been applied to Lake Superior. For the latter lake, the lake trout has been accepted as a key surrogate organism and the crustacean complex typified by *Pontoporeia hoyi*, as an appropriate complementary surrogate (Ryder and Edwards, 1985). In Annex 11 of the Agreement, ecologically acceptable levels of these organisms have been proposed in order to ensure a healthy oligotrophic ecosystem. Further background information on the development and rationale for the lake trout and *Pontoporeia* as ecosystem surrogates may be found in Ryder and Edwards (1985). The current charge to the Mesotrophic Indicators Work Group calls for not only identification and development of suitable surrogate organisms for mesotrophic lake systems within the Great Lakes basin, but also for quantitative assessment of the levels of abundance required for a healthy mesotrophic ecosystem. The relevant sections of the Agreement are reprinted in Appendix A of this report.

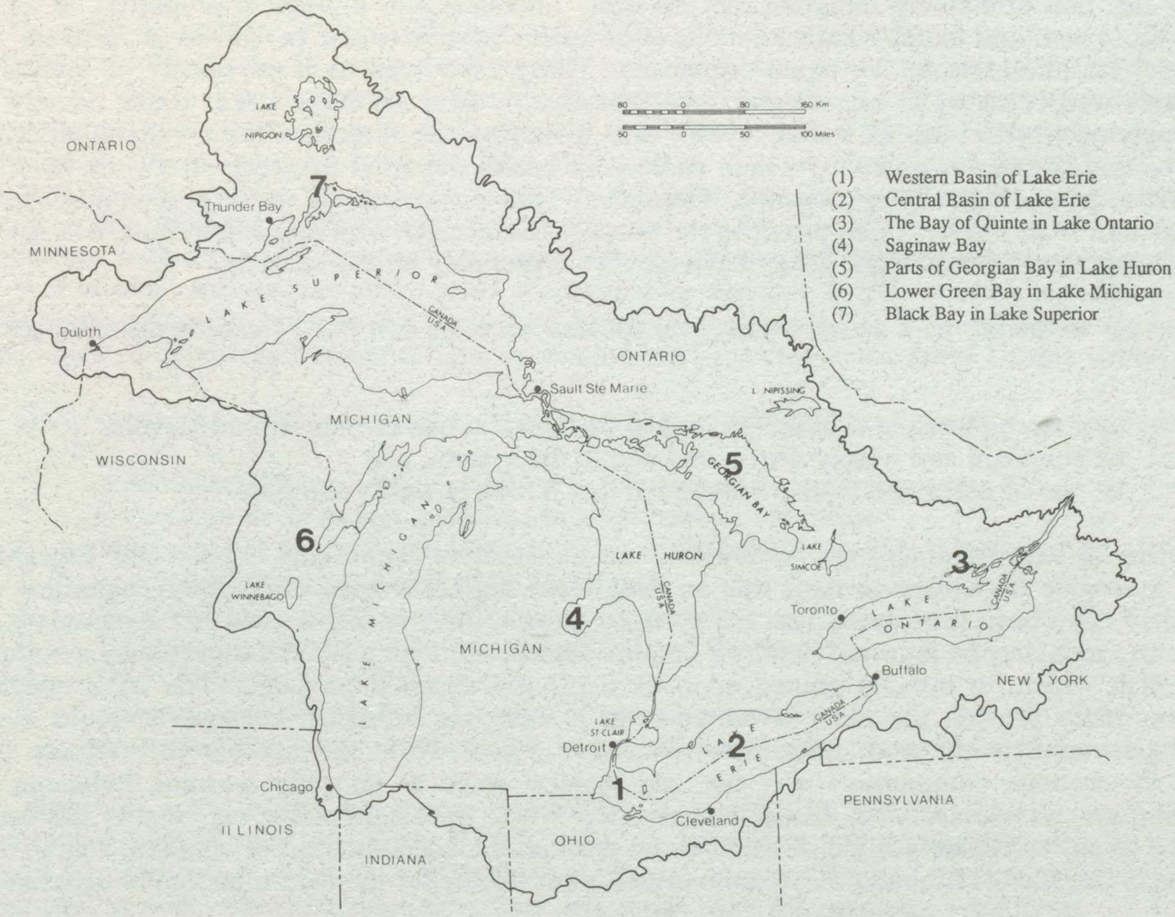

FIGURE 1. Principal geographic regions (numbered areas) of the Great Lakes that were mesotrophic historically.

B. Mesotrophic Ecosystems

In terms of most classical definitions, mesotrophy occupies the intermediate position on the oligotrophy/eutrophy scale (see Appendix B). For instance, mesotrophic ecosystems lie on a trophic cline midway between the nutrient-poor oligotrophic systems and the nutrient-rich eutrophic systems. Within the Great Lakes basin, mesotrophic waters are usually intermediate in depth, although not necessarily so, and are represented by such waters as the western and central basins of Lake Erie, the Bay of Quinte in Lake Ontario, Saginaw Bay and parts of Georgian Bay in Lake Huron, lower Green Bay in Lake Michigan and Black Bay in Lake Superior (Figure 1). Mesotrophic waters typically have fish assemblages that are qualitatively different from those in oligotrophic and eutrophic lake systems, and are usually dominated by percid communities (Hartman 1973; Leach *et al.* 1977). Benthic invertebrates also differ among oligotrophic, mesotrophic and eutrophic systems, particularly in terms of oligochaetes (Howmiller and Scott, 1977). Other benthic organisms such as the burrowing mayfly, *Hexagenia limbata*, may find optimal habitat conditions in mesotrophic systems; the organism will diminish in abundance as waters become either more oligotrophic or more eutrophic (or deeper or shallower). In fact, mesotrophy may be viewed as qualitatively different from oligotrophy and eutrophy, as determined from both its indigenous fish communities (Ryder and Kerr, 1978) and the high levels of calcium found in bottom sediments (Ryback 1965). In this sense, mesotrophy may be perceived as an ecological optimum for adapted organisms rather than only a clinal intermediary between oligotrophy and eutrophy.

C. Surrogate Organisms

Species that effectively integrate the physical, chemical and biological properties of an aquatic ecosystem and thereby indicate its level of health relative to one perceived as "pristine" or "ideal," are often termed surrogate organisms. These have been used previously, to assess the relative well-being of an oligotrophic lake ecosystem within the Great Lakes basin, namely Lake Superior (Ryder and Edwards, 1985), and to define the direction for a rehabilitation trajectory (e.g. Regier *et al.* 1980) where ecosystem health departed markedly from the level perceived to be ecologically appropriate. Germane to this process is the use of a dichotomous key (Marshall *et al.* 1987), which provides the ecosystem manager with applicable standards for which a health level determination may be made on a reasonably objective basis.

In order to qualify as a suitable surrogate species, an organism must satisfy a minimal set of criteria:

- be a strong integrator of the biological food web at one or more trophic levels;
- be abundant and widely distributed within the system; and
- be one of perceived human value such that it may be easily sampled.

Other criteria, while perhaps not as critical, are nonetheless, important (Ryder and Edwards, 1985). Surrogate organisms in their role as integrators, reflect stresses ultimately, regardless of where they have been introduced into the system. Hence, toxic contaminants that accumulate in the bottom muds may be ingested first by a benthic detritivore, which is itself ingested by a bottom feeding fish which, in turn, is preyed upon by a pelagic terminal predator. The latter species would normally provide the most information as a surrogate organism because it would most likely bioaccumulate the contaminant to detectable levels while the benthic invertebrate (or benthic invertebrate community) may not and thereby serve as an early warning indicator of impending system malaise. Yet, in another instance, where the total benthic community has been subjected to an inordinately high, directed stress through the accumulation of contaminants in the substrate, a benthic invertebrate may be the organism of choice for the determination of ecosystem health.

2.0 HISTORY OF MESOTROPHIC WATERS IN THE GREAT LAKES

Water Quality

The historical record for comprehensive water quality measurements in the Great Lakes mesotrophic waters is, with few exceptions, the contemporary record. In the western and central basins of Lake Erie, for example, acceptable data (by present standards) for selected nutrients and conservative ions began to appear in 1968 (Rathke and Edwards, 1985; Boyce *et al.* 1987). For most of the measured parameters, the data indicate an improving trend in overall water quality. An example of this improvement can be seen in the reductions to phosphorus loading and the subsequent in-lake decline in total phosphorus concentrations (Figure 2). Conversely, trends in nitrate plus nitrite concentrations have shown a consistent increase over the last twenty years throughout the Great Lakes including the mesotrophic waters (Figure 3). The source(s) and impact of these higher nitrate levels are unknown.

Clearly, one important outcome of cultural degradation of mesotrophic waters is anoxia of the hypolimnetic zone. Since 1950, numerous accounts of oxygen depletion have been documented in the western and central basins of Lake Erie. El-Shaarawi (1987) has concluded that water level, water temperature of the hypolimnion and phosphorus concentration are the controlling factors in oxygen depletion within the central basin of Lake Erie (Figure 4). On the basis of his model, it is possible to construct situations where anoxic conditions occur even with phosphorus concentrations less than current values, but these situations would require water levels to be lower and/or water temperature to be higher than long-term averages. Such combinations are entirely possible, a situation which gives credence to suggestions that hypolimnetic anoxia is not necessarily a recent phenomenon (e.g. Charlton 1987).

Bartish (1984) observed an ephemeral period of anoxia in the bottom waters of the western basin of Lake Erie and equated its cause with a brief period of meterological calm and high oxygen demand at the sediment/water interface. Again, this sequence of events is not necessarily restricted to contemporary conditions. Such events may have occurred after 1930 (or before) and would provide an explanation for the shift in year-class dominance of *Hexagenia*, identified by Chandler (unpubl.) in 1943 and described later in this chapter.

Another outcome of cultural degradation has been the accumulation of naturally occurring and anthropogenically derived chemicals at concentrations that are either directly or indirectly harmful to organisms (including humans) within the Great Lakes waters. Because a preponderance of these chemicals is present in minute quantities in the water column, their detection as represented by trend-through-time plots, has been limited by the slow development of sophisticated analytical technology. To overcome this shortcoming, scientists have taken advantage of the propensity of many of these chemicals to accumulate at detectable levels in organisms and sediments.

The use of chemical concentrations in organisms has produced results that generally denote an overall declining trend for the small selection of parameters investigated. For example, Figure 5 shows a declining trend in PCB concentrations in herring gull eggs collected from Saginaw Bay, Green Bay and western Lake Erie. Conversely, the data in Figure 6 show a static situation for dieldrin in eggs from the colonies at these same locations, even though most uses of dieldrin have been banned since 1974.

The analysis of sediment cores, which is also a relatively new approach, has the advantage of producing longer trend-through-time information through radiodating procedures (e.g. Reynoldson *et al.* 1988). This feature, combined with chemical analysis of the radiodated sediment layers, yields some rather impressive trend-through-time plots, as shown by the examples in Figures 7 and 8. These data, although limited in the number of parameters studied, unequivocally support the supposition that the chemical degradation of the Great Lakes began to accelerate after World War II and reached its zenith in the late '60s and early '70s. Whether the present levels are sufficiently low to permit an unencumbered recovery of the mesotrophic waters of the Great Lakes is unknown.

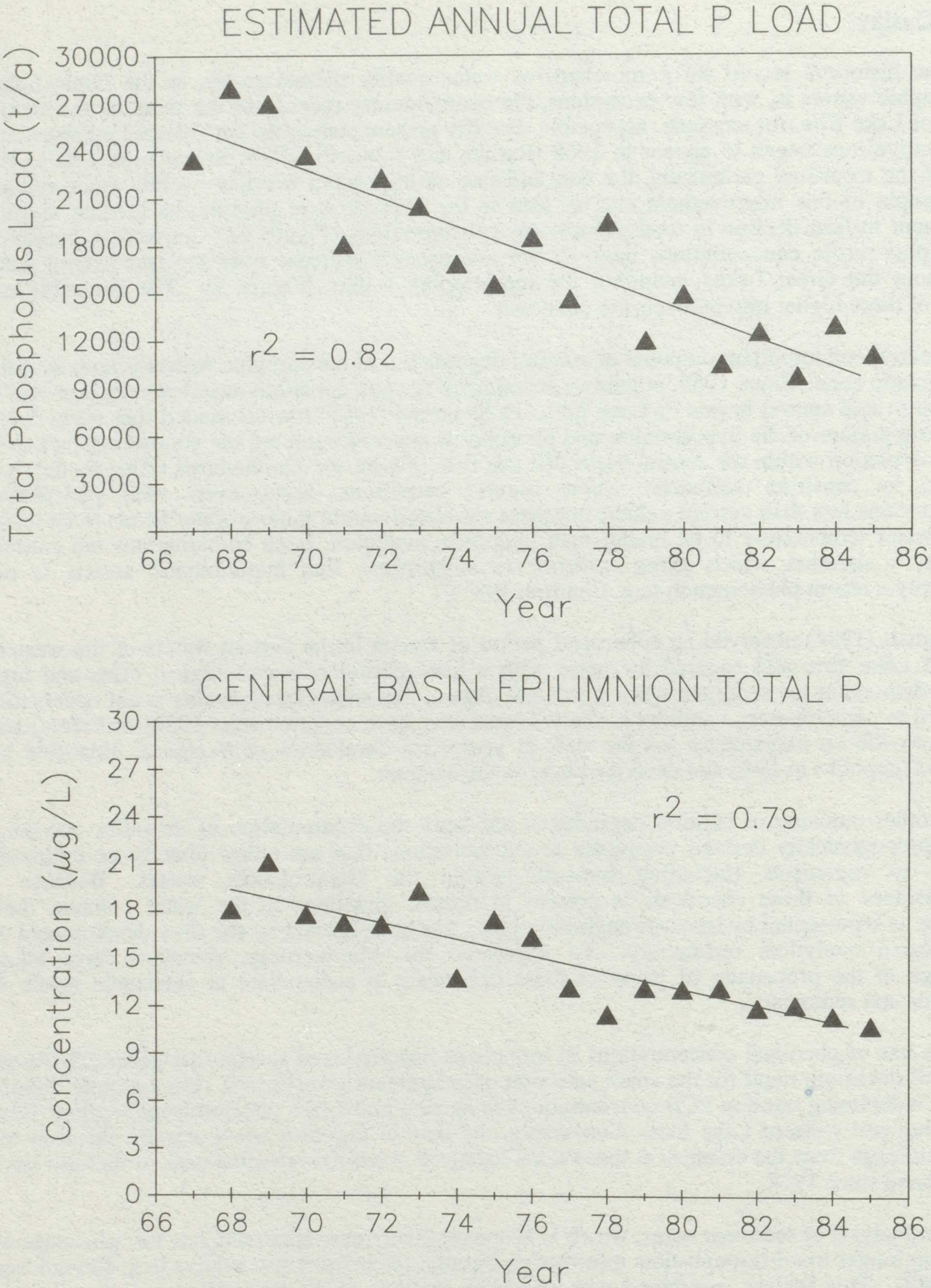

FIGURE 2. Estimated annual loading of total phosphorus to Lake Erie (top) and annual concentration of total phosphorus in the epilimnion of the central basin of Lake Erie (from IJC files)

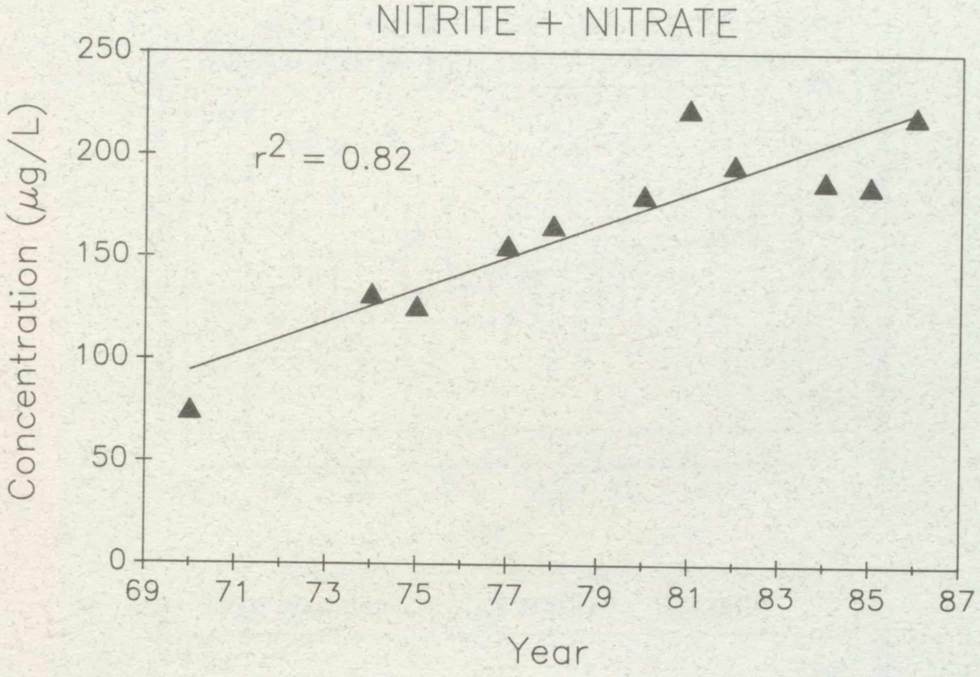

FIGURE 3. Open-lake concentrations of nitrite + nitrate in the central basin of Lake Erie, 1970-1986 (from IJC files)

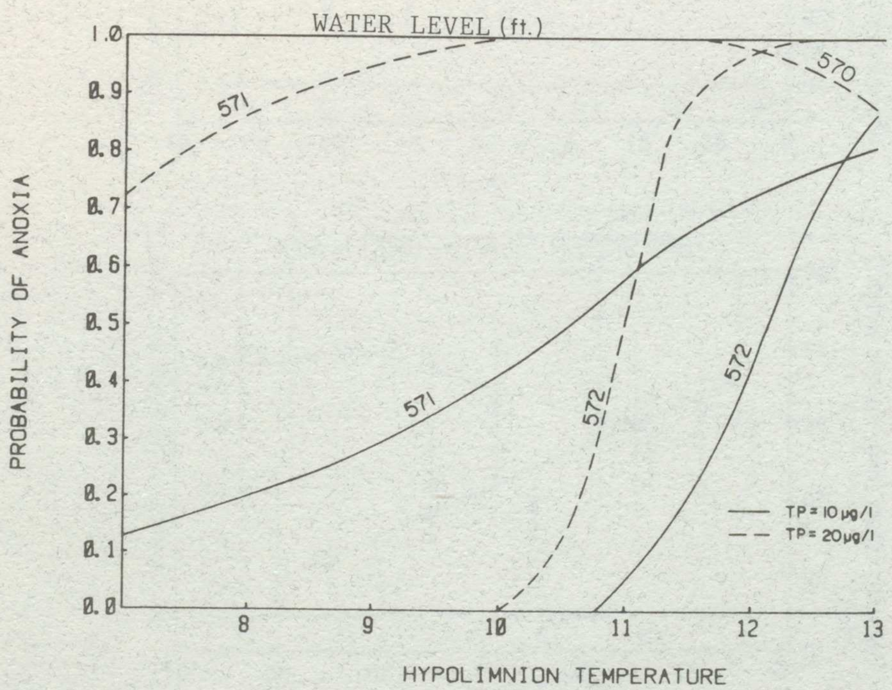

FIGURE 4. The estimated probability of anoxia in Lake Erie for a stratification period of 110 days in the central basin hypolimnion as a function of temperature, water level and total phosphorus (TP) (after El-Shaarawi 1987)

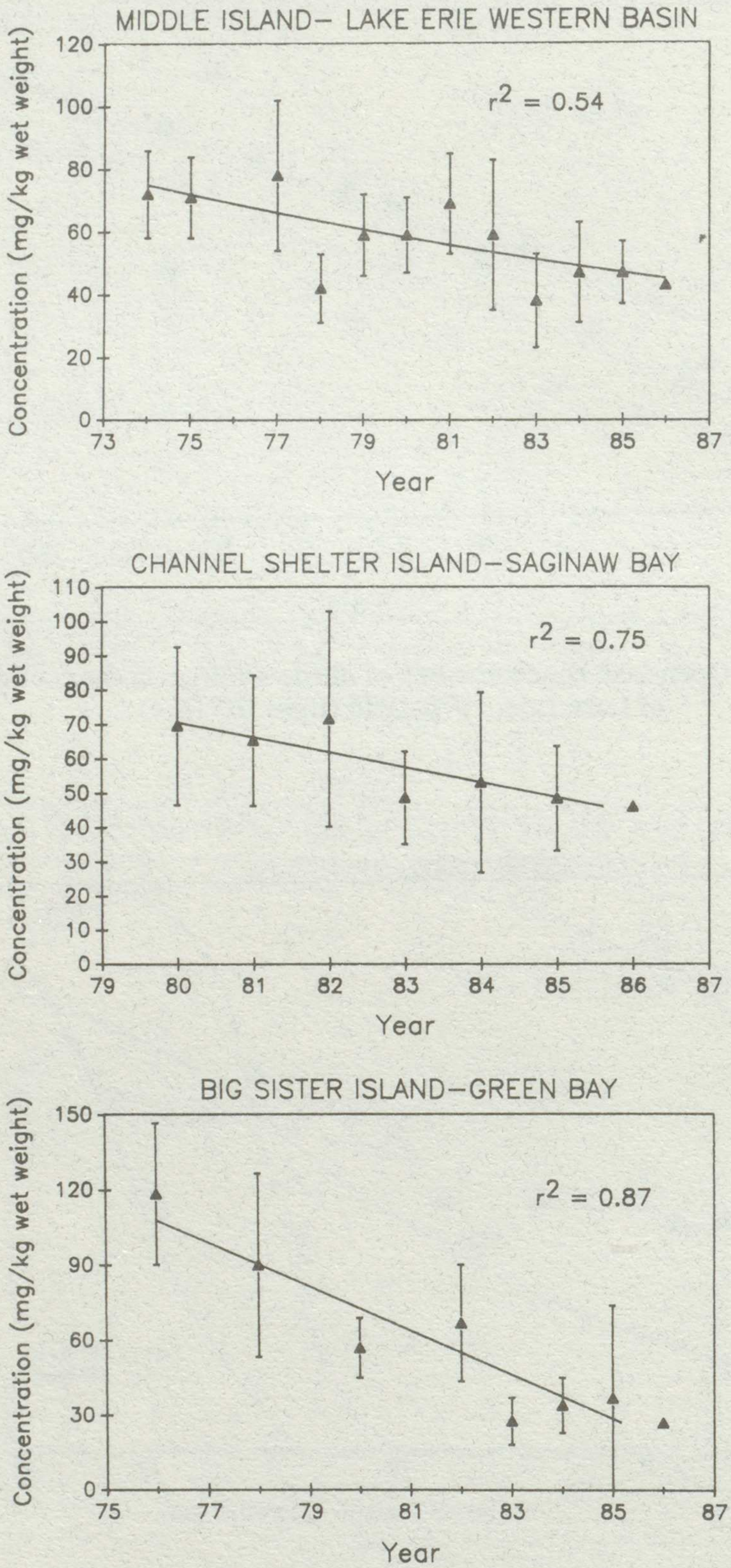

FIGURE 5. PCB concentrations in herring gull eggs taken from three colonies adjacent to mesotrophic regions of the Great Lakes (from IJC files using data provided by C. Weseloh, Canadian Wildlife Service)

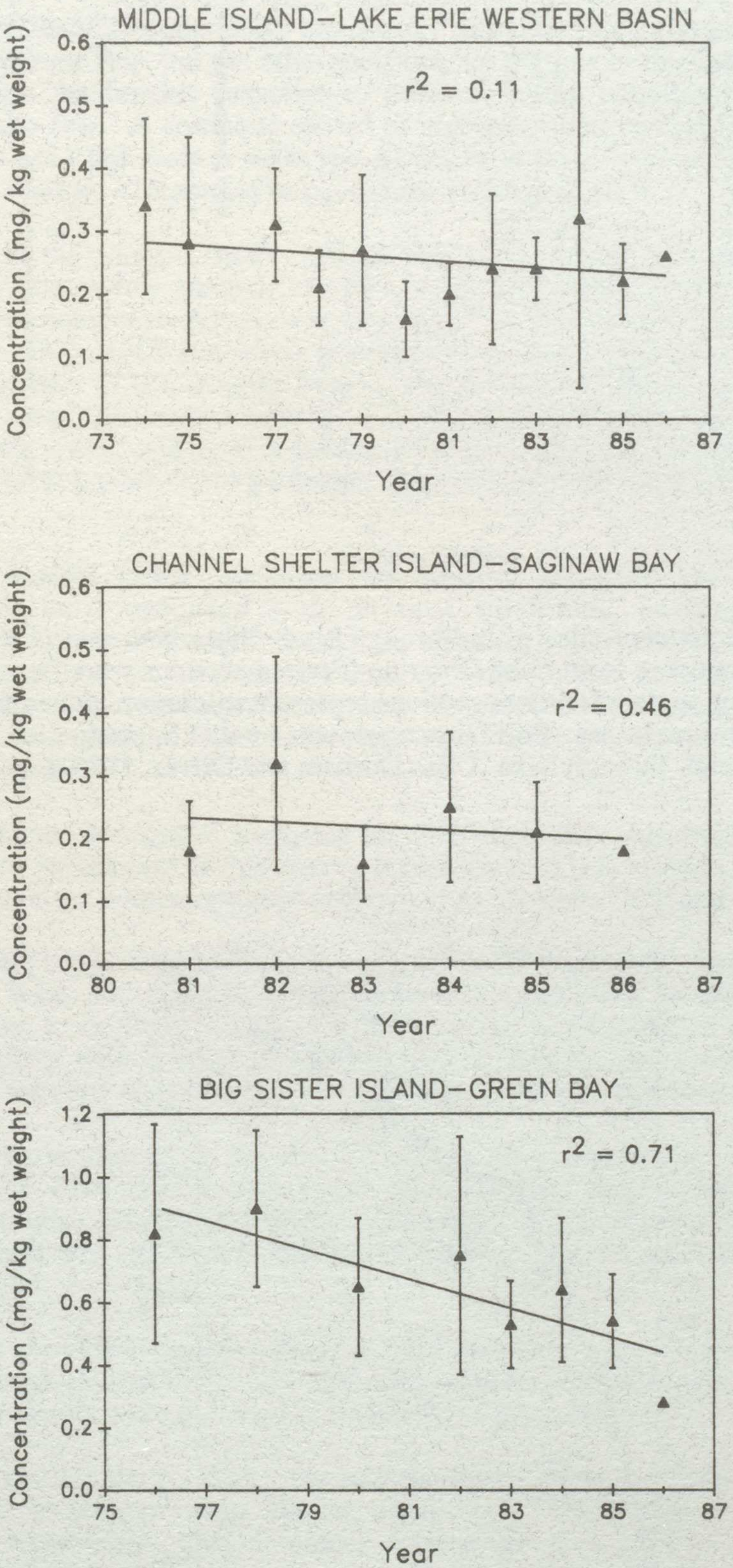

FIGURE 6. Dieldrin concentrations in herring gull eggs taken from three colonies adjacent to mesotrophic regions of the Great Lakes (from IJC files using data provided by C. Weseloh, Canadian Wildlife Service)

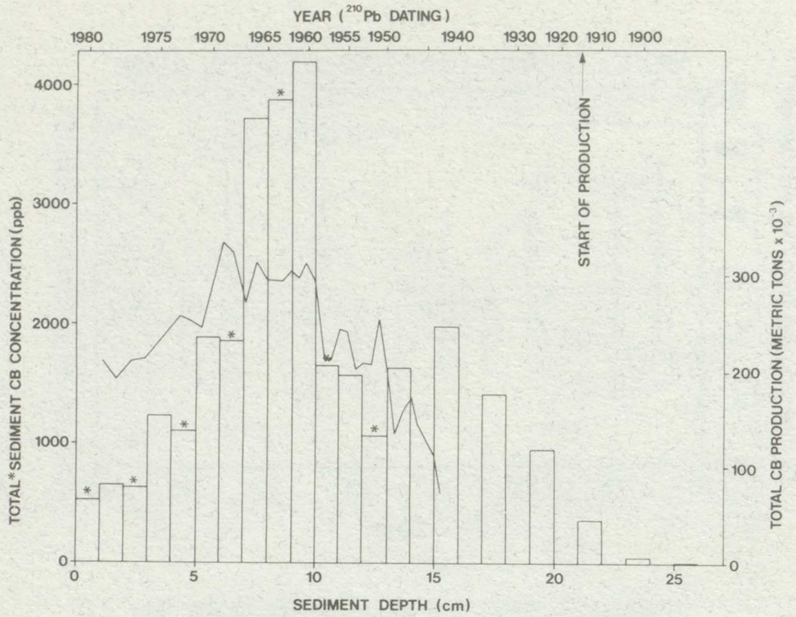

FIGURE 7. Total concentration of di- through hexa- chlorobenzenes (CBs) *versus* depth in a sediment core from Lake Ontario. [Starred sections were freeze-dried prior to analysis so data for these sections represent minimum values due to possible volatilization losses. Solid line represents total U.S. production figures for mono- through hexa- CBs (Durham and Oliver, 1983)]

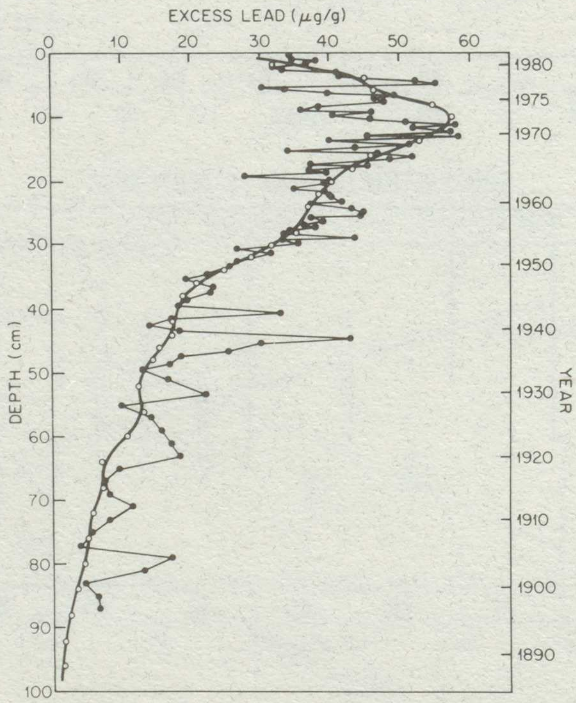

FIGURE 8. The distribution of stable lead from the eastern basin of Lake Erie (saw-tooth line) compared to the distribution of lead (solid line) based on regional use, sedimentation and mixing characteristics (Eadie and Robbins, 1987)

Benthos

The Great Lakes benthic community has clearly responded to anthropogenic changes in Lake Erie, Green Bay, Saginaw Bay and the other mesotrophic regions of the Great Lakes. A long-term data set documenting the benthic response to these changing conditions is available from the western basin of Lake Erie. A complete record of changes in the central basin, Saginaw Bay and Green Bay does not exist but there is sufficient evidence in these regions to demonstrate the onset of a general system malaise in response to environmental degradation.

Early surveys of the western basin of Lake Erie were limited in scope, encompassing but a small area and only one or two benthic taxa (Walter 1906; Osburn 1926a, b; Cutler 1929; Miller 1929). The first comprehensive survey was conducted by Wright and Tidd (1933) who sampled the western basin in 1928, 1929 and 1930, and identified 41 taxa of benthic invertebrates (Wright 1955). In the major part of the limnetic region of the western basin, nymphs of the burrowing mayfly, *Hexagenia*, were the most abundant benthic organism, more abundant than all other organisms combined, while tubificid oligochaetes were rare. At the mouths of the Maumee, Raisin and Detroit Rivers, tubificid oligochaetes were considerably more common, while *Hexagenia* was rare or absent.

Shelford and Boesel (1942) surveyed the western basin in 1937 and identified three communities, which they associated with physical conditions, turbulence and substrate. A *Goniobasis-Hydropsyche* community was found in the turbulent rocky areas, primarily in the shallow shoreline zones; a *Pleurocera-Lampsilis* community was found in the sandy zones; and a *Hexagenia-Oecetis* community was found in the less turbulent muddy zones, which constituted the greatest part of the survey area. Other taxa common to these collections were the chironomidae and tubificid oligochaetes.

Chandler conducted surveys of *Hexagenia* in 1941-43, which, unfortunately, have never been published. However, an abstract of this survey (Chandler 1963) is notable for the evidence which suggested that a year-class dominance shift had occurred between 1930 and 1940.

In 1950, Brown (1953) sampled 15 stations in western Lake Erie. Even though the sites and sampling methods were not specified, the results are noteworthy as they were the first data showing oligochaetes to be more abundant than *Hexagenia* in the benthic zone of the open lake. Wood (1953), sampling with a large dredge in 1951-52, had similar results in that oligochaetes were found in most samples and chironomids were about 50% as common as *Hexagenia*.

The most dramatic change in the benthic invertebrate community was shown in samples collected in 1953 by Britt (1955a, b). These data revealed large numbers of dead *Hexagenia* nymphs in many samples, particularly in the region north of the Bass Islands, and low densities elsewhere. This result was associated with an extended period of thermal stratification and low oxygen concentrations.

Beeton (1961) provided evidence from a 1957 survey of the western basin that *Hexagenia* numbers had declined dramatically and that oligochaetes and chironomids had increased in abundance. Similar results were obtained in their 1958-1959 surveys.

In 1961, Carr and Hiltunen (1965) repeated the initial survey of Wright and Tidd (1933) by sampling the same locations, using similar equipment. The benthic fauna was principally composed of the oligochaeta, chironomidae, sphaeriidae and gastropoda. Stations near the Maumee, Raisin and Detroit Rivers had large numbers of oligochaetes; stations with fewer oligochaetes and a more diverse fauna were furthest from the influence of these rivers. The population of *Hexagenia* had been reduced from an average of 139 m^{-2} in 1930 to less than 1 m^{-2} in 1961. From 1930 to 1961, there was an apparent nine-fold increase in oligochaetes, a four-fold increase in chironomids, a two-fold increase in sphaerids and a six-fold increase in gastopods, while *Hexagenia* was reduced to less than 1% of its former abundance.

Veal and Osmond (1968) sampled the benthos of the western basin and the nearshore areas of the eastern and central basins of Lake Erie in 1967. This study found conditions similar to those in a 1963 study by Brinkhurst *et al.* (1968) and 1963 and 1964 surveys by the Federal Water Pollution Control Administration (FWPCA 1968). In general, the eastern basin supported a wide variety of taxa, dominated by *Pontoporeia hoyi* and *Hyalella* sp. In the central basin, *P. hoyi* was predominant in the eastern zone, while *Spirosperma ferox* was common in the western zone. The western basin supported a large population of tubificids, with *Limnodrilus hoffmeisteri* and *L. cervix* as the dominant species. The formerly dominant mayflies were only recorded in the eastern basin. These results were verified by a subsequent FWPCA survey in 1967 and 1968. Additional studies by Pliodzinskas (1978) from 1973 to 1975 and Keeler (1981) confirmed the wide distribution and high densities of oligochaetes, the secondary importance of chironomidae, and the continued absence of *Hexagenia*.

An extensive survey of the western basin in 1979 by Thornley (Ontario Ministry of the Environment 1981) repeated the 1967 survey of Veal and Osmond (1968). Although the benthic community was still dominated by the oligochaetes, *Limnodrilus hoffmeisteri*, *L. cervix* and *L. maumeensis*, other tubificids such as *Spirosperma ferox* and the chironomidae accounted for a larger percentage of the organisms compared with the 1967 survey. Additionally, *Hexagenia* was found near the mouth of the Detroit River. Thus, this study identified changes in the benthic community which were indicative of improving conditions.

A survey conducted in 1982 by the U.S. Fish and Wildlife Service (unpublished) repeated the earlier studies of Wright and Tidd (1933) and Carr and Hiltunen (1961). *Hexagenia* nymphs were found in small numbers at the mouths of the Detroit, Raisin and Maumee Rivers. Numbers of oligochaetes were noticeably lower, particularly at the river mouths, and the species composition had changed significantly compared with the 1961 survey. These data provide quantitative evidence of improving conditions in the nearshore waters of the western basin of Lake Erie, including reduction in the numbers of species associated with eutrophic waters. Despite these improvements, the mayfly was not even a minor component of the benthic community.

While most of the benthic data for mesotrophic regions are from the western basin of Lake Erie, surveys have also been conducted in Saginaw Bay, Green Bay and other nearshore areas. These data show a similar sequence of changes in community structure over time. In Green Bay, the abundance of oligochaetes had increased, while amphipods, leeches, gastropods, sphaeriids and *Hexagenia* had dramatically declined or disappeared between 1952 and 1969 (Surber and Cooley, 1952; Howmiller and Beeton, 1970). Howmiller and Scott (1976), using an index derived from the species composition of the tubificid oligochaetes, demonstrated a eutrophic to mesotrophic cline from the Fox River to the upper bay. Cook and Powers (1964) observed a similar trend when comparing the benthic fauna adjacent to Benton Harbor with that of a less degraded area near Little Sable Point, Lake Michigan.

In Saginaw Bay, the results of three surveys between 1955 and 1965, showed similar changes in the benthic fauna. *Hexagenia* declined from 63 m^{-2} in 1955, to 9 m^{-2} in 1956, to 1 m^{-2} in 1965. Oddly, no concomitant increase in oligochaetes was observed, a phenomenon that Schneider *et al.* (1969) considered to be a conspicuous departure from the normal pattern observed following *Hexagenia* declines, as typified not only by the Lake Erie experience but also observed in other areas outside the Great Lakes, including Oneida Lake (Jacobsen 1966) and the Mississippi River (Carlander *et al.* 1967).

In Lake Erie, Green Bay and Saginaw Bay, there is sufficient evidence to demonstrate a characteristic response to environmental degradation in each system. In part, this response is due to the inability of *Hexagenia* to tolerate extended periods of anoxia, resulting from nutrient loads that are characteristic of many perturbed regions in the Great Lakes. Thus, the disappearance of the burrowing mayfly is an indication of a stressed mesotrophic system.

With the exception of the phenomenon mentioned in Saginaw Bay, a sequential and orderly response to environmental stress has been documented in each of the mesotrophic systems described. This response is identified by the elimination of *Hexagenia* and the proliferation of a community dominated by oligochaetes and increased numbers of chironomids. Thus, the occurrence and population dynamics of *Hexagenia* make it an obvious choice as a complementary surrogate organism depicting a healthy mesotrophic system. There are disadvantages in using *Hexagenia* alone: there are no intermediate measures of system recovery; recovery may not yield a *Hexagenia* dominated community but may instead produce an alternative mesotrophic climax benthic community. In addition, the *niche* attributes of the organism are not completely known so that causal links to system degradation are difficult to make.

Obviously, an organic substrate and aerobic conditions are essential requirements for *Hexagenia*. Less obvious are the effects of contaminants, depth and predation on the maintenance of a viable population of this species, a condition which would be indicative of healthy mesotrophic ecosystems. Clearly, additional data will be required before these parameters can be factored into a quantitative approach to the ecosystem management of mesotrophic systems that utilize this species as an integrator organism.

FISHES

The commercial catch records for the Great Lakes dating back to 1867 were assembled by Baldwin *et al.* (1979). This compilation, as well as a synthesis by Hartman (1988) and reports by Smith and Snell (1891) and Hile *et al.* (1953), provide the information base for this section. While catch statistics do not necessarily reflect the actual abundance of a particular species, discrepancies are usually short-term. Such inaccuracies may be caused by: variation in effort (fishing intensity), changes in fishing gear, changes in market prices, imprecise reporting, non-reporting of illegal harvest, omission of sport-fish harvest, mixing of species (e.g. walleye and sauger), pooling or splitting catch from different zones, and other factors of lesser importance. Even with all of these qualifications, it is generally agreed that the data adequately represent the abundance of the Great Lakes fishery over the period of record. Accordingly, these data represent the only record available for tracing the long-term trends of species within the mesotrophic ecosystem.

Walleye

Historically, most of the commercial fishing for walleye in Lake Erie occurred in the western and central basins. The harvest was relatively constant at about two million pounds (900,000 kg) annually from 1915 until the mid 1930s (Figure 9), when a steady increase began, with the harvest peaking at over 15 million pounds in 1956. This was followed by a precipitous decline to less than 86,000 (39,000 kg) pounds by 1969. Speculation on the reasons for this decline included over-fishing as the foremost factor, followed by loss of the spawning habitat through siltation, summer anoxia in the central basin hypolimnion, or loss of the burrowing mayfly in the western basin and predation on walleye fry by the proliferating populations of rainbow smelt.

Mercury contamination of western basin walleye, discovered in 1970, resulted in the closure of commercial fisheries in Ontario and Ohio waters. Commercial fishing had been closed earlier in Michigan waters for other reasons. This moratorium provided an opportunity for that population to rebuild and the subsequent recovery of the walleye population has been impressive. For example, the estimated fishable stock of walleyes longer than 37 cm in the spring of 1985 was 21.8 million fish, and the total allowable catch for all fisheries combined was set at 4.9 million fish. Obviously, the environment was still able to sustain a thriving walleye population and over-exploitation must have been a leading factor in the decline of the walleye during the 1960s.

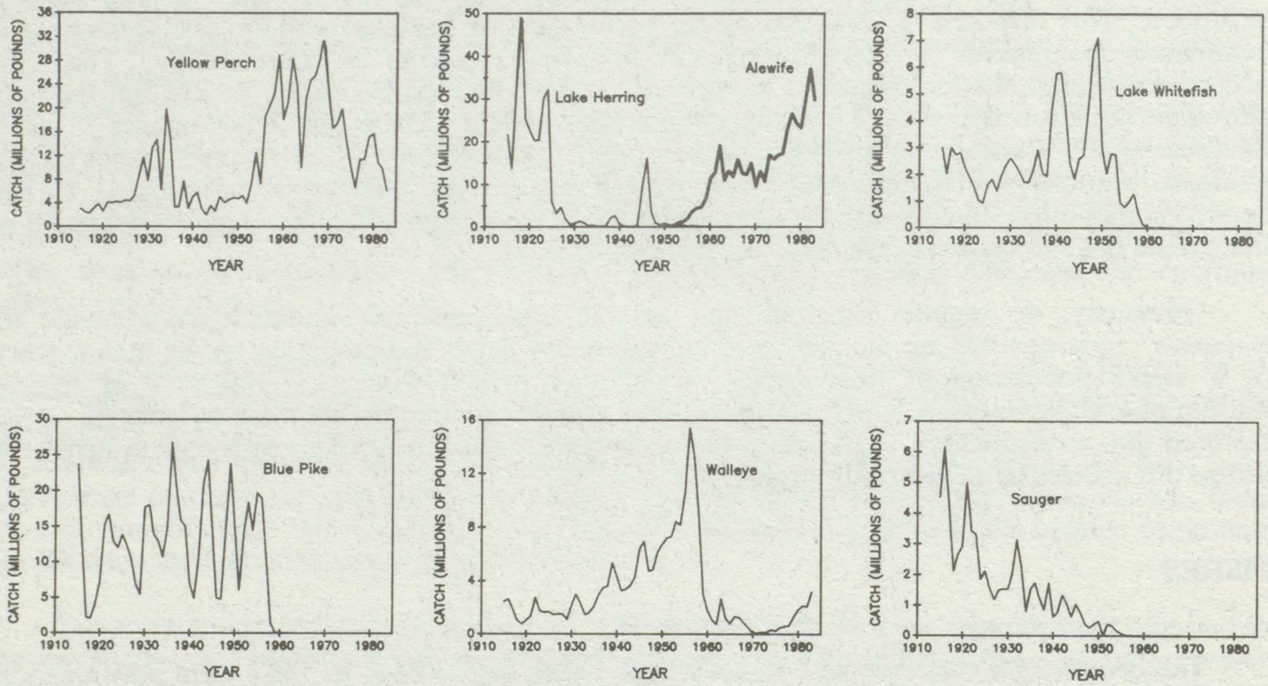

FIGURE 9. Commercial fish catch: Lake Erie (millions of pounds)

In Saginaw Bay, commercial harvests of walleye generally fluctuated between one and 1.7 million pounds (0.8 million kg) annually from 1890 into the mid 1920s. After that period, a steady, rapid increase in catches occurred, peaking at two million pounds (0.9 million kg) in 1942 (Figure 10). An abrupt and considerable decline then took place and the species became essentially "commercially" extinct by the mid 1960s (Schneider 1977). Schneider and Leach (1979) concluded that the relatively high commercial catch of walleyes from 1932 to 1943 resulted from a combination of three factors: high walleye abundance, improved somatic growth and reduced minimum size limits. They also concluded that the severe collapse of the resource was not due to sea lamprey predation and was only partly due to intensive fishing. They identified the primary cause as recruitment failure, induced by the effects of pollution and sedimentation of the critical spawning grounds. The loss of habitat hypothesis is supported by recent evidence of the survival and reasonable growth of stocked walleye, although natural reproduction has yet to be detected in the bay. Substantial reproduction does, however, occur in the Tittabawassee River.

In northern Green Bay (Figure 11a), annual catches of walleye ranged between 150,000 and 300,000 pounds (68,000 and 136,000 kg) from 1891 to 1907. The harvest then dropped to under 100,000 pounds (45,000 kg); suddenly increased in 1947, peaking at 1.3 million pounds (0.6 million kg) in 1950; steadily declined to below 100,000 pounds (45,000 kg) in 1961 and was essentially non-existent by 1969, when the commercial fishery was closed. Pycha (1961) attributes the sudden increase during the 1947-57 period to an exceptionally strong year-class in 1943, in addition to strong year-classes produced in 1950, 1951 and 1952. Reviewing all available evidence, Schneider and Leach (1979) concluded that it is unlikely that over-fishing, pollution and sea lamprey predation, alone or in concert, caused the walleye decline in Green Bay since the late 1950s. Rather, they considered poor recruitment of walleyes from predation by alewives and/or smelt on larval walleye as the cause for the decline. However, others consider that heavy commercial fishing in the late 1950s was also a significant factor. During the last decade, evidently as a result of stocking fingerling walleyes, populations are rebuilding and walleyes are now more abundant than they were 10 to 15 years ago, and natural reproduction is now occurring in the Whitefish River (Jerry Peterson, Michigan DNR, personal communication). About 30,000 pounds (14,000 kg) were landed by anglers in 1986, primarily from Little Bay de Noc.

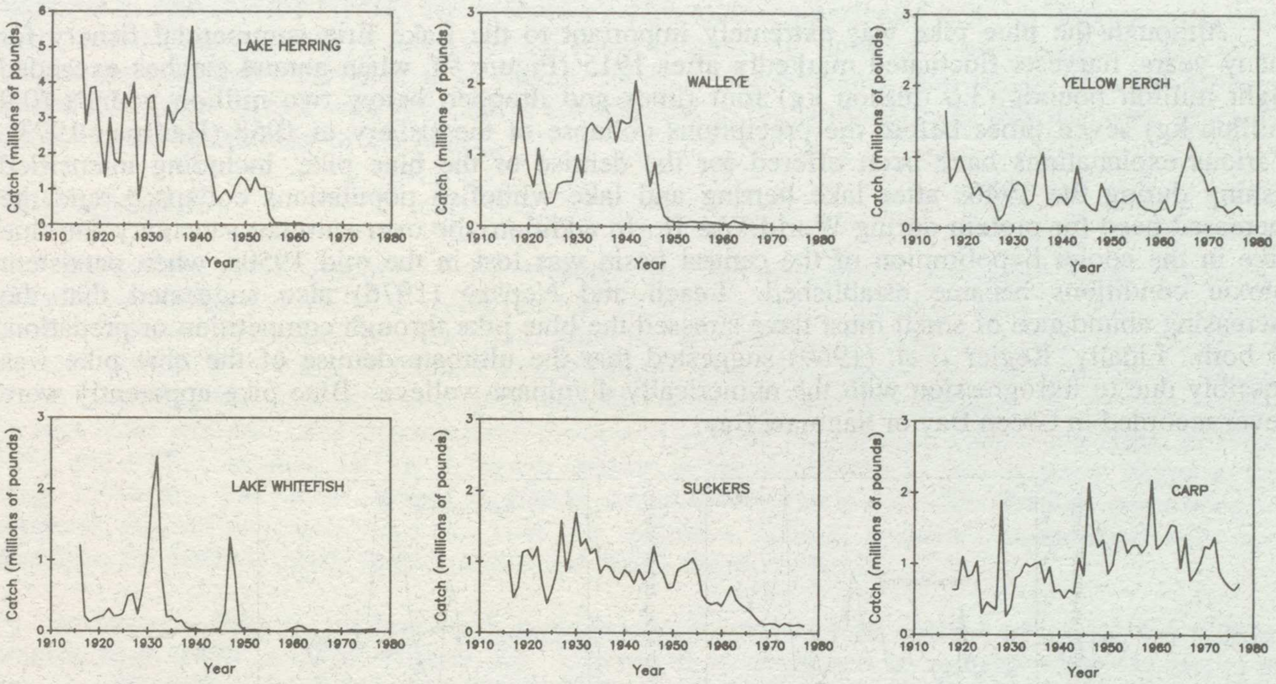

FIGURE 10. Commercial fish catch: Saginaw Bay (millions of pounds)

In southern Green Bay, catches of walleye were generally comparable to those in the northern region from 1911 to 1930. Catches gradually declined to low levels until a slight recovery in 1945, with a peak catch of 120,000 pounds (54,000 kg) in 1946. The population then collapsed and annual catches were consistently below 20,000 pounds (9,000 kg) after 1956. It is generally considered (e.g. Schneider and Leach, 1979) that the long decline was mainly due to dams being built on important spawning streams, pollutants and sediments that degraded habitat and interfered with reproduction, as well as smelt predation on walleye fry.

Stocking of young walleye has been carried on since 1977 and abundance has increased with several age classes now present. Evidently, some natural reproduction occurred in 1980 and 1982, a condition which may be the result of spawning in the Fox River, where water quality has improved substantially in recent years (Brian Boulonger, Wisconsin DNR, personal communication).

<u>Sauger</u>

Though catch records for Lake Erie are incomplete, it appears that sauger harvests between 1885 and 1924 ranged from two to six million pounds annually (Baldwin *et al.* 1979). The catch then declined steadily until the species became commercially extinct in the late 1950s. The regularity of the decline prompted Regier *et al.* (1969) to suggest that progressively deteriorating environmental conditions, including degradation by pollution, siltation and damming of spawning streams and reefs in the western basin may have seriously stressed the sauger's reproductive potential. Scott and Crossman (1973) thought that intense fishing pressure from 1930 to 1940, coupled with the inherent biological characteristics of slow growth and late sexual maturity, may have been significant factors in the population collapse. Finally, Regier *et al.* (1969) suggested that introgressive hybridization with the dominant walleye may have eliminated the pure sauger genotype. During the late 1970s, Ohio DNR attempted to reintroduce sauger into the western basin, but no self-sustaining population ever became established as a result of this program. Sauger apparently were never common in Green Bay (Becker 1983) but they did support a brief commercial fishery in Saginaw Bay between 1926 and 1936, according to Baldwin *et al.* (1975). However, Keller *et al.* (1987) did not consider sauger in their review and relegated the species to a status of minor importance.

Blue Pike

Although the blue pike was extremely important to the Lake Erie commercial fishery for many years, harvests fluctuated markedly after 1915 (Figure 9), when annual catches exceeded eight million pounds (3.6 million kg) four times and dropped below two million pounds (0.9 million kg) seven times before the precipitous collapse of the fishery in 1958 (Hartman 1973). Various explanations have been offered for the demise of the blue pike, including intensified fishing during the 1940s after lake herring and lake whitefish populations collapsed, and the increased need for protein during World War II. In addition, the over-summer sanctuary for blue pike in the cooler hypolimnion of the central basin was lost in the mid 1950s, when persistent anoxic conditions became established. Leach and Nepszy (1976) also suggested that the increasing abundance of smelt must have stressed the blue pike through competition or predation, or both. Finally, Regier *et al.* (1969) suggested that the ultimate demise of the blue pike was possibly due to introgression with the numerically dominant walleye. Blue pike apparently were never recorded in Green Bay or Saginaw Bay.

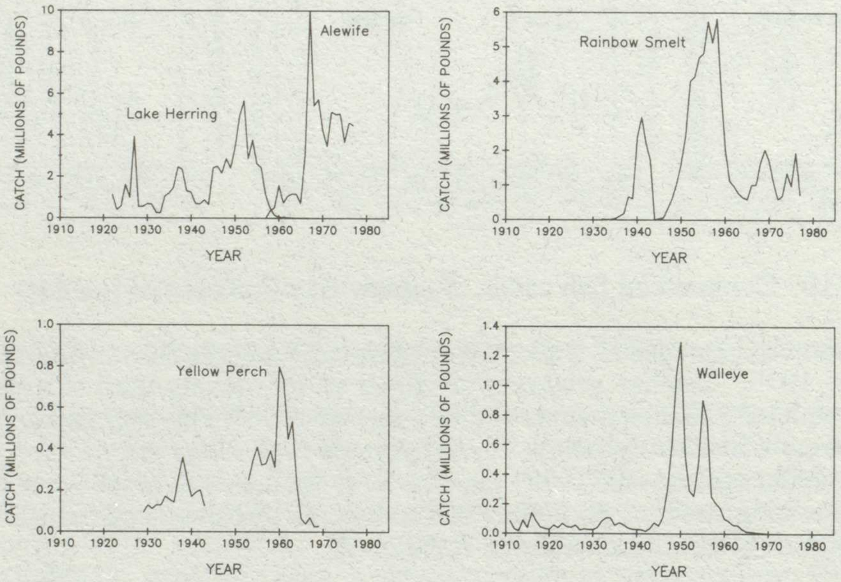

FIGURE 11a. Commercial fish catch: Northern Green Bay (millions of pounds)

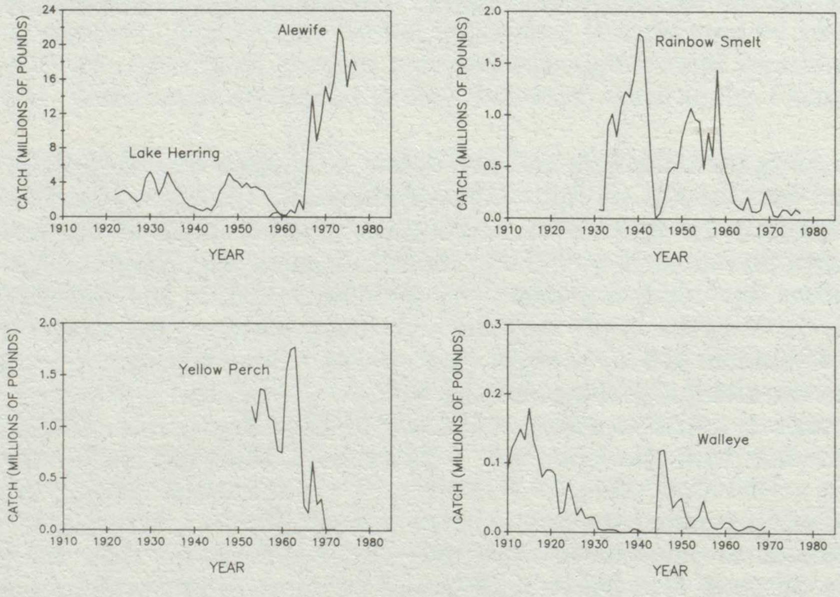

FIGURE 11b. Commercial fish catch: Southern Green Bay (millions of pounds)

The blue pike was officially declared extinct about 1965, however, this does not preclude attempts to discover the reasons for its demise. This extinct subspecies will not likely benefit from such knowledge, but fishery managers do stand to gain. If, however, the subspecies still exists within the walleye gene pool (e.g. Regier 1968) or is perchance discovered in some isolated inland lake, then further consideration of its potential in the application of the surrogate approach to ecosystem health may be warranted.

Yellow Perch

The yellow perch supported a major fishery in Lake Erie during the period 1928-35, peaking at over 14 million pounds (6.4 million kg) in 1932 (Figure 9). Harvests then returned to former levels of about five million pounds (2.3 million kg) annually, until they again increased sharply in the mid 1950s. This surge in harvest was attributed to a subsequent shift of fishing to the yellow perch following the decline of blue pike and lake whitefish fisheries (Nepszy 1977). Irregularity in year-class strength later characterized the resource, with strong year-classes produced in 1962, 1965 and 1970 (Hartman 1973). A steady decline in the abundance of yellow perch began in the early 1970s and the catch dropped to barely six million pounds in 1983. Factors continuing to suppress the yellow perch in Lake Erie are intensive fishing; possible competition with and predation by rainbow smelt and for a recent invader, the white perch.

In Saginaw Bay, the yellow perch provided annual commercial catches averaging 1.5 million pounds from 1890 to 1916 (Figure 10). Catches then decreased to remain relatively stable at between 400,000 and 600,000 pounds (181,000 and 272,000 kg) annually until about 1960, when the catch began to increase and peaked at 1.23 million pounds (558,000 kg) in 1966. Catches then decreased again to under 100,000 pounds (45,000 kg) by 1986. The sport fishery became a significant factor in the 1980s, with a catch of over 700,000 pounds (318,000 kg) between June 1983 and May 1984 (Ryckman 1986). In terms of stresses on the yellow perch, Keller *et al.* (1987) summarized the evidence and concluded that colonization and establishment of smelt and alewife populations did not restrain perch recruitment. It also could not be shown that degraded water quality had a direct adverse impact. However, the burrowing mayfly populations collapsed as water quality became degraded, and yellow perch were forced to make a major shift in their diet.

In northern Green Bay, there is a dearth of early records, but during the 1930s (Figure 11a) annual commercial harvests of yellow perch were usually between 100,000 and 200,000 pounds (45,000 and 90,000 kg). During the 1950s, the fishery produced considerably larger catches, peaking at 800,000 pounds in 1960, but then the resource collapsed in the late 1960s. Reasons for the collapse have never been clearly defined, but it is most likely that predation on young perch by the large numbers of smelt and alewives was the main stress. The yellow perch population has been rebuilding over the past several years, concurrent with significant decreases in alewife abundance and substantive restrictions on the commercial fisheries. The sports catch, however, is sizeable between 300,000 and 500,000 pounds (136,000 and 227,000 kg) annually, and the winter ice fishery contributes considerably to the catch (Jerry Peterson, Michigan DNR, personal communication).

In 1953, when area-specific records for southern Green Bay were first available, commercial catches of yellow perch routinely exceeded one million pounds annually (Figure 11b) and continued to do so through 1964. The fishery then collapsed. Wells (1977) considered that the decline was due to predation on perch fry as well as direct competition for food by the expanding smelt population and was hastened by the intensive fishery. Restrictive quotas were imposed on the commercial fishery starting in 1983; alewife abundance declined during that time and yellow perch became more abundant, year-classes more stable. The sport and commercial fisheries are each now taking annual catches of roughly 400,000 pounds (181,000 kg; Brian Boulanger, Wisconsin DNR, personal communication).

Lake Herring

The lake herring was an extremely important commercial species in Lake Erie beginning in the 1880s. Hundreds of millions of pounds were harvested before the catastrophic collapse of the

3.0 MESOTROPHY: DECLINE AND RECOVERY

It is known that prior to 1920, raw sewage entered the Great Lakes in abundance; vast areas of deforestation had occurred; dammed rivers were commonplace and contaminants from the industrial revolution had begun an insidious encroachment. Such degradation was especially prevalent in Lake Erie, Green Bay and Saginaw Bay. Moreover, the lake sturgeon had been nearly extirpated and the lake herring stocks had collapsed. Nevertheless, percids and *Hexagenia* persisted and perhaps even profited, albeit temporarily, from the increasing enrichment of the waters.

From 1930 to 1950, there were signs that the ecologic fiber preserving mesotrophic integrity was weakening. Catches of sauger and yellow perch were declining and blue pike, and *Hexagenia* populations were fluctuating radically. Such instability is now accepted as a clear sign of stressed ecosystems. Additional omens of system imbalance included an increasing abundance of exotic species and the decline of aquatic macrophytes. The ultimate collapse or extinction of numerous species is a testament to the power of cultural degradation.

In retrospect, it is now obvious that after 1950, the demise of *Hexagenia*, sauger and blue pike coupled with dramatic declines in walleye and yellow perch abundance was confounded by the proliferation of fishes and benthic species characteristic of eutrophic conditions throughout most of the mesotrophic waters of the Great Lakes. These events signalled the complete transformation of mesotrophic regions towards a eutrophic condition. This transformation was undoubtedly accelerated by the increasing load of contaminants.

Results from recent surveys of benthos, fish and water quality suggest that the once degraded mesotrophic regions of the Great Lakes are recovering from eutrophication. There are still lingering problems, which are cause for concern, especially with respect to the inability of the system to achieve complete recovery. It is, therefore, instructive to evaluate, where possible, the effects of cultural degradation on mesotrophic systems, not so much from the perspective of deriving an ultimate cause (as all effects were variously responsible for the final outcome), but more from the optimistic attitude of eventual total recovery. It should be apparent by now that attempts to separate causal mechanisms with insufficient information is futile. This realization should provide the impetus to embark on a management scheme that embraces a resolution of all the candidate causes treated with equal vigour, thus striving towards an ecosystem goal.

<u>Nutrients</u>

Enrichment of lakes through nutrient loading will lead to a predictable outcome. According to Leach *et al*. (1977), percids may at first respond favourably to an increase in the loading of nutrients. Population responses are usually manifested in an increase in both growth rate and standing stocks (biomass). As the loading increases, the habitat becomes adversely affected and the productivity and biomass of percids eventually decreases as optimal conditions are exceeded (Kitchell *et al*. 1977). Some responses of percid habitats and communities to progressive enrichment are summarized in Table 1.

Many of the responses and changes in the percids can be linked to changes in physical habitat due to nutrient loading. For example, changes in feeding, spawning and distribution can be related to hypolimnetic oxygen depletion, which itself is a predictable outcome of increased nutrient loading.

The role of burrowing mayflies as an important food source for walleye (Ritchie and Colby, 1988), yellow perch (Hayward and Margraf, 1987) and saugers (Scott and Crossman, 1973) cannot be overstated. Like the percids, the mayflies may have profited at first by increased nutrient loading, however, optimal conditions were surpassed and anaerobic conditions finally extirpated the species. Another possible benefit of increased nutrient loadings to *Hexagenia* was the relaxation of predatory pressures through the collapsing lake sturgeon and lake herring stocks. Both of these species are known to feed extensively on the burrowing mayfly (Harkness and Dymond, 1961; Liston *et al*. 1986).

TABLE 1. Habitat and biotic community changes in the mesotrophic waters of the Great Lakes due to increasing enrichment (+, increase; -, decrease; [ ] response in part of indicated system; blank, no information available)

	Transparency	Hypolimnetic oxygen	TDS	ABUNDANCE Phytoplankton	Macrophytes	Zooplankton	Benthos
Bay of Quinte	-	-	+	+	-	+	+
Saginaw Bay	-	[-]	+	+			+
Lake Erie	-	[-]	+	+	-	+	+
Green Bay	-	[-]	+	+		+	+

Following the demise of *Hexagenia*, the walleye relied on alternative prey, such as gizzard shad in Lake Erie and alewives in Green Bay and Saginaw Bay, in addition to the numerous cyprinid species (e.g. spottail and emerald shiners). On the other hand, after 1975, yellow perch were forced to rely on smaller prey such as oligochaetes, chironomidae and zooplankton, which were also important prey for the burgeoning and intrusive competitor, the white perch (Hayward and Margraf, 1987; Schaeffer and Margraf, 1986). Clearly, the re-establishment of *Hexagenia* is an essential ingredient in the successful recovery of the degraded mesotrophic regions of the Great Lakes. However, *Hexagenia* recovery will not occur until aerobic conditions are restored in the bottom waters, and this situation will not occur until the oxygen demand and nutrient load of the sediments and water column are reduced. This problem is exacerbated by the process whereby nutrient loading in these systems is fueled in part by the internal cycling of resuspended sediments (e.g. Rosa 1985). The amount of nutrient reduction required to return aerobic conditions is uncertain since it involves a complex set of chemical and physical properties which are not fully understood, but are nevertheless fundamental to decisions affecting continued reductions in nutrient loading in Lake Erie, Green Bay and Saginaw Bay (*viz* Annex III, GLWQA, 1987, Rev. 1). Ironically then, the sediment, which has an inherent capacity to assimilate oxygen-demanding material as well as nutrient loads and thus, to ameliorate the impact of further nutrient loading and forestall the onset of anoxic conditions, is now a major factor in delaying the recovery process. The purging process in all probability, will likely take many years to complete, but may be accelerated by sequestering more nutrients within the percid complex.

Habitat

That discussions of habitat should cause consternation among ecologists is understandable because of what the term implies. To some, it may define a specific, physical substrate subject to quantification in form and function. To others, it is likened to the composite environmental milieu or niche and thus, conjures a vagueness that invites argument. Despite this range of perception, the difficulty in assigning a causal relationship between habitat degeneration and species extirpation or decline, can be equated with several facts. First and foremost is the dearth of quantitative historical and contemporary data (e.g. Hunt 1988). Next, the universal decline or loss of habitat quality and quantity is often a gradual event, and in the mesotrophic regions of the Great Lakes, the effects of this decline have been accruing for at least a century or more. Even abrupt events do not assure unanimity as there are the inevitable confounding factors. When not universal, habitat loss tends to be localized or directed at a particular phase of a life cycle, often irregular, or on an intermittent basis. Depending on the size of the population, its number of stocks, the longevity of the species and the relative importance of the affected habitat, impact can range from catastrophic to virtually undetectable.

That blue pike and walleye were at one time reproductively isolated in Lake Erie is a generally accepted postulate that explains the inherent genetic diversity and differences in phenotypic expression between the two subspecies. However, during the late '50s and early '60s, as cultural eutrophication and other human interventions reached an all-time high for the lake, more and more intergrades or "mules" (e.g. Trautman 1957) between the two species were captured by fishermen. It is thought that marked changes in the environment reduced the level of reproductive isolation (e.g. Nelson and Walburg, 1977) between these two subspecies resulting in introgression. Accordingly, the exclusivity of the isolating time-space dimensions so influential in maintaining reproductive separation between the two subspecies, was lost, resulting in large numbers of F1 intergrades. By the mid-sixties, virtually all captured "blue" pike in Lake Erie were, in fact, intergrades.

The erratic catch statistics from 1915 to the terminal crash (ca. 1960) suggest that the blue pike population was sustained by large periodic year classes, or conversely, was subject to frequent year class failures (Parsons 1967). Such odd behavior suggests two possibilities: their major spawning/rearing habitat was subjected to frequent disturbance, or the species was driven by density-dependent, intergenerational predation factors in the extreme (i.e. were highly cannibalistic). With respect to the former condition, the likelihood that recurring habitat disturbance, to the extent and at the frequency required to explain the consistent fluctuation in population abundance, seems remote. With regard to the density-dependent proposition, the theory becomes tenable if juvenile blue pike also preferred a cool water environment and were, therefore, sympatric with the adult cohort. There is insufficient evidence to support or refute these hypotheses, but it is important to recognize that virtually all explanations for the demise of the blue pike rely on the central basin hypolimnion anoxia as a critical precursor. In this regard, the dependence on hypolimnetic anoxia complies closely with the proposal of Svärdson (1976), that a change in a single, critical, abiotic variable may swing predominance from one species to another, or in extreme instances, completely extirpate a species.

The decline of the yellow perch is perhaps the most difficult to understand for it appears to involve a complex set of interactions that are clouded by a lack of quantitative data. Nevertheless, the abundance of yellow perch is probably more inextricably linked to habitat than previous speculations have suggested. One partial solution to the yellow perch conundrum lies perhaps in the deterioration of the once common and extensive macrophyte beds in Lake Erie (Leach and Nepszy, 1976), Saginaw Bay (Keller *et al.* 1983), Green Bay (Harris *et al.* 1982) and the Bay of Quinte (Crowder and Bristow, 1986). The loss of macrophytes was due to a combination of direct physical destruction from dredging, filling and dyking and indirect physical loss from turbidity, caused by increased soil erosion and phytoplankton blooms, resulting from eutrophication. These erstwhile macrophyte beds were clearly beneficial to the phytophilus yellow perch (e.g. Balon 1975) and their destruction, no doubt, lowered the reproductive success of this important percid. The resultant decline in recruitment was partially offset by the depletion of its major predators, namely walleye, sauger and blue pike in Lake Erie, and walleye and lake trout in Green Bay and Saginaw Bay, and resulted in increased catches of yellow perch in the early 1950s (Nepszy 1977). Moreover, with successful recruitment recorded only in 1962, 1965 and 1970 (Hartmann 1973) the level of exploitation in Lake Erie, and probably elsewhere, could not be sustained and the species began a steady decline, from which it has yet to recover fully.

The abundance of yellow perch was further affected by the decline in benthic habitat and the loss of preferential food items, as denoted by Hayward and Margraf (1987). For the percids in general, the involvement of macrophytes as rearing habitat, both as an immense source of epiphytic foodstuff (e.g. Edwards *et al.* 1989) and as a refuge from predation (Ryder 1977), has not been adequately quantified but cannot be ignored in terms of its overall importance.

The catch statistics from Lake Erie (Figure 9) indicate that the extant spawning habitat is sufficient to provide the recruitment necessary for an increasing abundance of walleye. Even with a sizeable exploitation rate (about 20%) the walleye have had several consecutive years of above average young-of-year production, a condition which suggests that reproduction is not a limiting factor at current exploitation rates and population levels. It is presumed that the offshore reefs are responsible for a significant proportion of the walleye recruitment, while the river spawning stocks are providing a minor component in its overall abundance. In the past, however, it was speculated that the major rivers, including the Maumee, Sandusky, Cuyahoga, Grand, Syndeham, Thames and especially the Detroit River, contributed a much larger share of walleyes of the overall population. Uncertainty associated with the relative contribution of these river spawning stocks to the persistence of the walleye in Lake Erie is justification for a conservative approach to the preservation of the last vestiges of the once thriving percid complex in Lake Erie.

The foregoing does not imply that the environmental requirements and niche envelope for the walleye is less rigorous than for the sauger, blue pike or yellow perch. What it demonstrates is that walleye escaped total decimation mostly through happenstance: market forces, whereby demand for other species (e.g. coregonines, blue pike and sauger) was greater and only after subsequent depletion of these species did commercial exploitation vigorously focus on the walleye; walleye spawning habitat included areas not subject to complete destruction (e.g. offshore reefs and shoals); walleye were opportunistic feeders, able to shift food preference to available prey; and their contamination with mercury provided a serendipitous respite from further exploitation of dwindling stocks. Indeed, the overall disappointing recovery of walleye in Saginaw Bay and Green Bay, due to continued poor reproductive success, reinforces the importance of extensive habitat of sufficient quality for the species to persist and proliferate.

The recovery of walleye and sauger, without an attendant return of the burrowing mayfly and macrophyte beds, would undoubtedly distort the harmonic community topologically, to the detriment of the yellow perch, and would thus not be indicative of a healthy mesotrophic environment. The likelihood that such a situation may emerge provides an impetus for the management process to adopt an ecosystem perspective. Thus one of the benefits of embracing the surrogate approach to ecosystem health lies in the resulting ability to facilitate anticipatory planning, an often sought after, but never achieved goal of ecosystem management in the Great Lakes.

<u>Exploitation</u>

At the population level, it is common knowledge that exploitation can have a measurable effect on the abundance of a target species. Indeed, exploitation is invariably listed as the top candidate for the cause of population declines throughout the Great Lakes. In the absence of confounding stresses, however, exploitation by itself seldom results in the complete elimination of a species. Moreover, when a population is composed of numerous stocks, economic forces can effectively promote the elimination of one or more of the stocks, at a rate that is probably higher than generally suspected, through sequential "fishing-up" of stocks, resulting in overfishing (e.g. Ryder and Edwards, 1985). In those instances where exploitation is the single greatest stress causing extreme stock depletion (e.g. whales), it is usually the result of recruitment overfishing, i.e. exploiting an immature cohort (Cushing 1977).

Populations subjected to exploitation tend to have well defined characteristic responses. For the percids, Spangler *et al.* (1977) identified five such responses: changes in the variability of recruitment, changes in growth rate, changes in age at first maturity, changes in the genetic composition of wild stocks and changes in biological interaction within the community. However, as Colby (1984) noted, characteristic responses to exploitation are valid only during the initial exploitation phase, i.e. "fishing-up," and other responses begin to appear after the compensatory capacity of a species is exceeded. Further, he stated that compensatory capacity is determined primarily by energy, nutrients and habitat availability, and when these factors are affected by a different stressor, additional responses begin to appear. Thus, when other stresses are acting simultaneously with exploitation as was the case in mesotrophic regions in the Great Lakes, the use of characteristic responses as diagnostic tools becomes complicated and perhaps even untenable in some instances.

The historic catch records for percids in Great Lakes mesotrophic waters do not contain sufficient detail to ascertain characteristic responses through retrospective analyses. Nevertheless, certain aspects of the fishery may be gleaned from those aspects of the database that are germane to the recovery process. For instance, Parsons' (1967) analysis of the blue pike fishery illustrates several issues that were, no doubt, operative for the other percids and that are critical in the control of the impact of exploitation. First, the data indicate that U.S. and Canadian fishermen were exploiting common stocks, a situation which, in retrospect, demonstrates the need for binational management and research to elucidate the composition of a target fishery. Furthermore, these data also point out the need to discriminate among fishable stocks with specialized techniques, such as mitochondrial DNA analysis (e.g. Billington and Hebert, 1988), to accomplish this task.

Second, the decline in blue pike abundance was occurring at the time when fishermen were switching to nylon gill nets. This new type of netting allowed fishing intensity to increase at a time of declining abundance and environmental restriction of the population to the eastern basin. While the use of gill nets in the Great Lakes is now strictly regulated, it appears that restrictions on new gear are usually not adopted until after a catastrophic impact has occurred. The prudent management of fishery resources must be able to accommodate the onset of technology, particularly the use of electronic devices to aid in fishing. This requirement offers a challenge that will, no doubt, test the ability of agencies to regulate such devices in the near future.

Third, more than half of the U.S. landings of blue pike were taken from the major spawning grounds during the spawning season. Clearly, the ability to exploit a species during a vulnerable period can impose significant mortality on the resource. Conversely, a population can withstand high levels of exploitation provided the relationship between stock and recruitment is understood and managed accordingly. This information suggests that allocations for spawning refugia will become more commonplace under future management schemes (e.g. Fogarty and Idoine, 1988).

The final point made by Parsons (1967) is that the average age of landed fish in the latter years of the blue pike fishery clearly shows that recruitment overfishing was rampant. The routine application of standard population assessment procedures, including age, growth, maturity and young-of-year surveys, should provide an adequate foundation for preventing the recurrence of over-fishing as a major stress in all mesotrophic waters of the Great Lakes.

While loss of sauger recruitment through reproductive failure resulting from habitat deterioration was singled out as the probable cause for extirpation, exploitation was not ruled out as a contributing factor. There certainly came a time when directed fishing effort on sauger was no longer economical, and the relaxation of this exploitation apparently did nothing to revitalize the population. At least three possibilities can explain the failure of the sauger to respond to decreased fishing intensity: habitat loss was the sole cause for sauger depletion; fishing concentrated on the spawning stocks at the tributary mouths during the spawning period or incidental catch of sauger in the walleye fishery was sufficiently high to cause completion of the terminal crash. Incidental catch has been blamed for the extirpation of several marine stocks and there are no data in the Great Lakes catch statistics to dissuade acceptance of incidental catch as a contributing factor in the demise of sauger in the Great Lakes. Indeed, the fact that incidental catch can cause depletion of a non-target species is sufficient impetus to guard against this form of exploitation in the future management of the percid complex in the Great Lakes.

There is every reason to suspect that the exploitation of walleye was driving the population toward severe depletion. This reasoning is supported by the impressive population resurgence following the cessation of fishing in the early 1970s, during which time other stresses were at least no less severe and possibly even greater than there had been in previous years. On the other hand, the reduction in fishing pressure on yellow perch has not resulted in an increased abundance, so logically other factors must be inhibiting the population This does not imply that yellow perch are insensitive to exploitation, but rather that the species is affected more by predation from terminal piscivores, especially of the exotic variety. Moreover, the importance of habitat (especially that which was once provided by extensive beds of macrophytes) for successful spawning or refugia for preferential prey, has been previously demonstrated to be a critical component to the effective recovery of this species, and, in general, in the entire percid complex in the Great Lakes mesotrophic waters.

While the regulation of exploitation is an important element in the recovery and maintenance of target populations, it is also beneficial to the fishing industry and ultimately to the public, who is the third-party beneficiary. Thus, an informed public is a powerful asset and an essential link in convincing the legislative branches of government to enact appropriate laws (e.g. Peyton 1987) and invoke penalties. These penalties, in turn, act as effective mechanisms for instilling a societal ecosystem ethos which, once achieved, largely negates the need for such regulations. The regulation of exploitation should also be considered an important adjunct that influences community changes as well as lakewide processes, such as nutrient cycling and plankton dynamics (e.g. Carpenter and Kitchell, 1988). Indeed, the use of exploitation to control certain undesirable species of phytoplankton, zooplankton and fish is without question an idea whose time has come. Thus, while a target population may withstand a high level of exploitation at a preordained sustainable level, decreasing exploitation to increase the population abundance may provide the predation pressure required for the control of an undesirable (exotic) species. Such management measures may not only be warranted, but may be generally acceptable to the consuming public.

Exotic Species

As a general rule, new species introduced into healthy ecosystems are seldom successful. Unfortunately, the proof of this tenet is contained in the "ghosts" of the failed attempts (e.g. Pimm and Hyman, 1987). Moreover, there are notable exceptions to this rule and the introduction of the Nile perch into Lake Victoria in 1960 is but one example. This species has had a catastrophic impact on the fish community (particularly, the endemic *Haplochromis* species flock) as well as the local economy of this once apparently healthy ecosystem (Fryer and Iles, 1972; Coulter *et al*. 1986; Huntley 1988). However, these and other examples should be reexamined carefully to ensure that the ecosystems were, in fact, healthy prior to the successful invasion. Conversely, the preponderance of successful introductions of exotic species invariably occurs in already stressed ecosystems (e.g. Elton 1958); the Great Lakes are no exception to this rule. Thus, the proliferation of non-native species can, in most cases, be used as an indicator of inherently unstable ecosystems.

From a watershed perspective, the isolation of the Great Lakes was the outcome of glaciation and tectonics; the extant drainage pattern was established some 8,000 to 12,000 years before present. Bounded by the Mississippi River, and the Arctic and Atlantic Oceans, the historical fish community of the Great Lakes Basin Ecosystem was, with few exceptions, a conglomeration of species that were also found in one or more of these neighboring watersheds (Mandrak 1989). Thus, what is indigenous to the Great Lakes is not the individual fishes *per se* but rather the total fish assemblage. Moreover, while explanations for the unplanned introduction of exotic species must account for ways to breach the physical barrier of isolation, it must also recognize that the Great Lakes Basin Ecosystem is (or was) composed of at least three identifiable trophic subsystems, namely oligotrophic, mesotrophic and eutrophic, that were created and bounded without the advantage of obvious physical barriers. This phenomenon strongly suggests that abiotic factors are critically important in the creation of an environmental milieu, that, in turn, erects the biological barriers responsible for repulsing invasion by exotic species.

Of the accidental but successful fish introductions in the upper Great Lakes and Lake Erie, rainbow smelt, alewives, sea lamprey, white perch and ruffe (from Europe), the first four have their origins in the Atlantic marine environment. The route of introduction for all five invaders can be attributed more or less to canals which were built to facilitate the transport of commerce. The two canals providing this pathway: the Welland Canal -- connecting Lake Ontario to Lake Erie, and the Erie Canal -- connecting the Hudson River to Lake Erie, were completed in 1833 and 1825, respectively. The Ohio canal system, providing a bridge from the Mississippi River watershed to the Great Lakes, was completed in 1833, yet no introductions have been attributed to this connection.

The proliferation of these five species in mesotrophic regions of the Great Lakes has been variable. The inhabitation and spawning of sea lamprey in mesotrophic areas ranged from nearly non-existent (Lake Erie) to substantial (upper Green Bay). In those areas where sea lampreys were once considered rare, recent evidence demonstrates that spawning is now occurring (i.e. the St. Louis River, the St. Marys River and various tributaries to Lake Erie). This activity has been attributed to the improving environmental quality and, ironically, may be viewed as a somewhat sinister indicator of rehabilitative success. The alewife and smelt inhabit and reproduce in all mesotrophic regions, but the alewife is not abundant in Lake Superior or in the western and central basin of Lake Erie. The white perch and the recently discovered ruffe and zebra mussel seem to prefer mesotrophic regions as they are seldom encountered in deep, oligotrophic waters.

The direct impact of these five species on the mesotrophic percid complex of the Great Lakes also has been variable. Schneider and Leach (1979) reported that sea lamprey predation was evident in 19 of the 21 mesotrophic regions of the Great Lakes which they reviewed, but considered them to be an insignificant source of mortality based on the low percentage of attachment scars (less than 3%). They also suggested that alewives were a major cause for the decline of walleye only in northern Green Bay and eastern Lake Michigan (Muskegon River) and of minor significance in the Saginaw Bay walleye decline. Smelt were implicated as a minor contributor to the walleye decline in northern Green Bay, eastern Lake Michigan and western Lake Erie. These authors also concluded that white perch were responsible for the decline of walleye in the Bay of Quinte. The impact of ruffe, which is confined to the Superior/Duluth Harbor and the contiguous nearshore zone to the Apostle Islands, is indeterminate, owing to its recent invasion (ca. 1985).

The mechanics of exotic species invasions can range from simple replacement to active displacement. In the latter situation, an exotic species is in direct competition with the indigenous species and simply wins out over time. This situation would be difficult to reverse as the exotic becomes established in an environmental milieu that is also required by the native species. In simple replacement, it is implied that under normal unstressed circumstances, an exotic species is denied access through competitive exclusion by the better adapted native species. As the native species declines in abundance, in response to overfishing or other stresses, the exotic species simply replaces the indigenous species. Such a replacement is generally explained by stating that the invader is "filling a vacant niche," a phrase which suggests that a habitat hiatus has been created by the declining native species. In reality, the fundamental niche of the invader is better adapted to the ambient suite of stresses, which allows it to gain the competitive advantage. This process implies that the environment is no longer suitable for the native species, but is reasonably fit for the facultative exotic species. Invariably, this new environment has been created by changes in nutrients and energy inputs as well as by modified habitat. The environment is often exacerbated by changes in predatory mechanisms. In other words, simple replacement is a response to a complex set of both abiotic and biological actions and reactions and may be reversible by recreating the original environmental milieu to establish a competitive advantage for the indigenous or native species.

The actual process whereby exotic species proliferate in the Great Lakes is uncertain and, therefore, controversial. This uncertainty is partly due to the time-lag between first discovery and subsequent proliferation and partly to the uncertainty regarding the importance of predation and the effects of competition for food between the exotic species and the displaced native species. In almost all cases, except perhaps for that of the sea lamprey, it appears that simple, partial or total replacement of the native species is the major effect of the invasion of exotic species into the Great Lakes, and in particular, the mesotrophic regions. Specific case histories of rainbow smelt, alewives, sea lamprey and ruffe illustrate these points.

Rainbow smelt were introduced into Crystal Lake (Michigan) in 1912, entered Lake Michigan by 1923 (Van Oosten 1937), were reported in Saginaw Bay by 1930 (Creaser 1932) and spread to the remaining Great Lakes by 1932 (Van Oosten 1937). By 1960, smelt abundance was still low in all of the Great Lakes, except Lake Erie (MacCallum and Regier, 1970) where, and perhaps not coincidentally, alewife densities were lowest (Smith 1968).

Alewives probably entered Lake Ontario by the late 1800s, reached Lake Erie by 1931 and the remaining lakes by 1954 (Dymond 1932; Smith 1970). They did not become abundant in any of the Great Lakes until the major populations of pelagic predators collapsed (Miller 1957; Smith 1970; Hartman 1972; Christie 1974; Hurley and Christie, 1977). In fact, Smith (1972) suggested that the sea lamprey contributed to the dispersal of alewives into the upper Great Lakes (i.e. Huron, Michigan and Superior) by contributing to the terminal crash of predators such as lake trout and planktivorous competitors, the coregonines.

Sea lampreys apparently became established in Lake Ontario by the mid to late 1800s (Smith 1972) and occupied all of the other Great Lakes by 1947 (Lawrie 1970). During the phase of increasing sea lamprey abundance, large deepwater species, such as lake trout, burbot and deepwater ciscos declined initially. Subsequently, there were declines in medium sized species, such as lake whitefish, lake herring, suckers and walleye (Smith 1968; 1972). During this period, alewives and smelt increased in abundance. Thus, the relationship between the sea lamprey, alewife and smelt, where they co-exist, is difficult to ignore. The simplest explanation is that sea lamprey abetted the collapse of the indigenous predators and large planktivores a situation which minimized both predation and competition in terms of the alewife and smelt. The result was a substantial population increase for these two species. The complicated explanation is that the early destruction of the lake trout, a keystone controlling organism, destroyed the integration of the co-evolved harmonic community, thus leaving the indigenous planktivorous community unstructured, whereby the two exotic species were allowed an unrestricted opportunity for exponential rates of expansion. The correct explanation does not alter the outcome; It might, however, have an important implication for the restoration programs that are now in place or being contemplated.

In all mesotrophic regions of the Great Lakes, except the western and central basins of Lake Erie, the abundance of smelt and/or alewives can be attributed to a large degree on their proliferation in the oligotrophic regions. Since these two species also utilize mesotrophic regions to spawn, rear and feed, their involvement in the decline of the percids has been suspected. The current speculation is that larval exotic species compete with larval percids for food, a situation which results in a zooplankton community that bears little resemblance to the historic assemblage. Additionally, adults feed on percid eggs and fry, a condition which, when added to the negative abiotic factors, contributes to the suppression of a percid abundance. If this speculation is correct, then control of these exotic species is important to the restoration of the Great Lakes mesotrophic regions.

The control of smelt and alewives in oligotrophic regions began with the introduction of exotic salmonids and was combined with an aggressive stocking program of lake trout. Of particular note, however, is that the planned introduction of exotic salmonids, such as coho and chinook salmon, had been attempted on numerous occasions in the Great Lakes, but apparently without success (Hubbs and Lagler, 1957). It was not until the collapse of the lake trout that such introductions in the mid 1960s, as well as the unplanned introduction of the pink salmon (1956), were successful. At present levels of salmonid stocking, there has been a dramatic decline in the abundance of alewives and smelt throughout the Great Lakes, along with a resurgence of indigenous planktivores (Christie *et al.* 1987; Brown *et al.* 1987; MacCallum and Selgeby, 1987). Moreover, there has also been a significant reduction in phosphorus loading during this period, as depicted in Figure 12. With these kinds of data, attempts to separate the effects of water quality improvement from predator abundance as each affects the restoration of Great Lakes fisheries, will be subject to contention and controversy.

Concomitant with the demise of the keystone predator, the lake trout, and major indigenous planktivorous species was the collapse of the percid terminal predators in the mesotrophic regions of the Great Lakes. In both the oligotrophic and mesotrophic regions, the abundance of smelt and alewives increased dramatically during and after the predator is demise. In the mesotrophic regions, including Lake Erie, yellow perch generally increased in abundance, presumably in response to relaxed predatory pressure. Subsequently, the perch declined, in response to the deteriorating quality of the water, food and habitat, as well as the increased competition and predation provided by the alewife, smelt and white perch. Thus far, walleye, the keystone predator in mesotrophic environments, have shown little proclivity for consuming the quantities of white perch sufficient to control the expanding population. The loss of yellow perch to the walleye diet has forced the latter to rely on alternative prey. This event may explain, in part, the recent decline of native minnows from mesotrophic regions.

The ruffe was first discovered in Duluth Harbor in Lake Superior in 1987 and is presumed to have invaded from Europe by way of ballast water from a trans-Atlantic vessel. This species has caused considerable consternation among fishery managers because one of its preferred foods may be fish eggs. Accordingly, this species may be troublesome to fishery restoration efforts. The ruffe is sexually mature within one year, and already it has been captured as far east as Marquette Harbor, Michigan. It is interesting to note that the application of terminal predator controls for exotic species have been examined, to control this newest invader to the Great Lakes mesotrophic regions. The proposed management of this species includes a reduction in the sport fishery bag-limits of walleye and northern pike in the harbor, as well as a supplemental stocking of 200,000 walleye fry in the hope that increased predation will repress the production and migration of this potentially problem species.

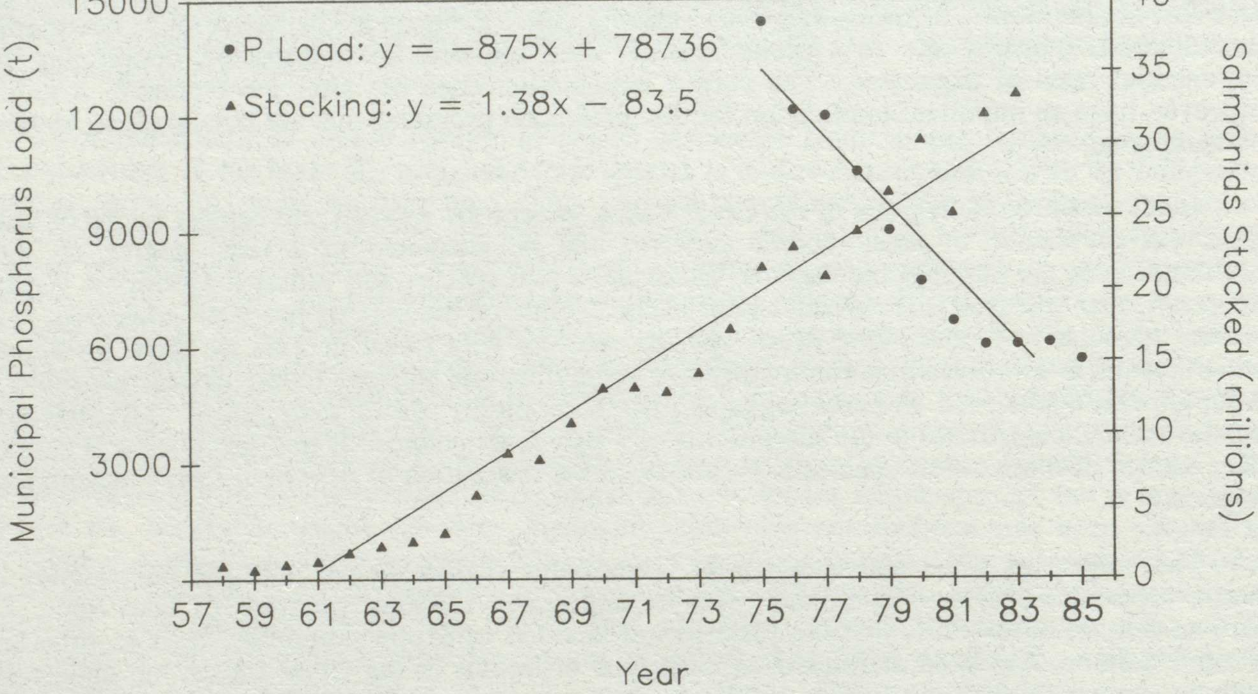

FIGURE 12. Annual summary of total phosphorus from municipal sources and total salmonid stocking (coho and chinook salmon; brown, rainbow and lake trout; splake) in all five Great Lakes (IJC files)

The restoration of the Great Lakes mesotrophic fisheries must embrace an integrated program that addresses the causes for its demise. While it is logistically feasible to control exploitation; improve mesotrophic water quality, including a reduction of toxic chemicals, restore spawning and rearing habitat, including macrophytes, the political resolve to achieve these goals may be lacking. Nevertheless, the virtual elimination of exotic species from the Great Lakes is uncertain and is the most problematic component of the recovery process. Therefore, it is prudent, no doubt, to apply the principle of Occam's Razor and suggest that the simplest solution to the problem of exotic species in the Great Lakes basin is to return the appropriate (original) environmental milieu, which should, in turn, reduce the abundance of exotic species to tractable numbers. Next, adjustments to the other components of the community could be made in response to the reaction of the percid complex, once changes in exotic species had occurred.

Contaminants

Although it is generally accepted that contaminants have had a negative impact on populations of mammals, birds and fish in the Great Lakes, the definitive study relating an environmental impact, cause and effect, to a specific chemical has yet to be published. This is not a condemnation of scientists, but rather a testimony to the rigors of proof required in scientific inquiry and the complexity of the contaminant issue. Such complexity was demonstrated by Hesselberg and Seelye (1982) in a study that identified 167 separate contaminants in Lake Michigan lake trout compared with only eight compounds isolated from a hatchery-reared stock. The combinations and permutations of such a chemical array make any attempt to isolate a causitive agent, a formidable task, even without addressing the phenomena of antagonism and synergism. Nevertheless, it has been demonstrated that the contaminant levels in Great Lakes fishes are sufficient to cause reproductive failure when fed to ranch mink (Aulerich *et al.* 1973), impairment of bald eagle reproduction (Wiemeyer *et al.* 1984) and recruitment failure in lake trout (Mac *et al.* 1985). It should also be noted that these three species are potential candidates for surrogates of ecosystem health (e.g. Ryder and Edwards, 1985).

The direct negative impact of environmental contaminants on adult fish in the Great Lakes is circumstantial. There are some studies which implicate contaminants, especially those in the PAH group, as inducers or promoters of tumors in mesotrophic waters (e.g. Black 1983; Baumann *et al.* 1982). However, most definitive studies have focused on the influence of contaminants in egg and fry development and survival. In this regard, Niimi (1983) demonstrated that a sizeable portion of maternal contaminant burden is transferred to the egg mass during oogenesis. Moreover, Mac (1988) provided data that showed eggs from fish with differing contaminant body burdens of contaminants reflected a contaminant load in a ratio consistent with the material load. In a comparative study of lake trout eggs and larva from various Great Lakes sources, Mac *et al.* (1985) showed that a differential hatching mortality was associated with water of differing contaminant concentrations, but fry survival to 139 days was apparently not influenced by the water under the same experimental conditions. More importantly, these authors demonstrated that fry mortality was significantly influenced by the maternal source of eggs, with the poorest survival being associated with the highest maternal body burden of contaminants.

Contemporary studies are attempting to identify the environmental concentrations and isolate the toxicity of trace contaminants, especially those which are isomers of generic chemical groups. Such studies have demonstrated, for example, that certain PCB isomers are differentially more toxic than others and apparently more persistent; these findings provide an explanation for past observations that equal concentrations of total PCB can impart variable toxicity effects. These findings may also be used to speculate that as chemicals such as PCB decline, as they have in the Great Lakes, their environmental impact may not decline, and may even increase as the more toxic and persistent isomers will form a larger percentage of the total environmental concentration.

There is a dearth of published results from toxicity tests on Great Lakes percids, but conclusions from existing literature would seem to indicate that lethal concentrations for yellow perch are several orders of magnitude greater than extant concentrations in the water of Lake Erie (Table 2). Thus, the direct effect of existing concentrations of contaminants on the adult percid community does not appear to be a concern. However, the body burdens of certain contaminants (e.g. PCBs) still pose a concern in terms of the consumptive uses of this species.

The differential mortality of walleye fry associated with the transfer of maternal contaminants was recently demonstrated by Hokansen (U.S. EPA, Duluth, MN, unpublished data). The results from his study indicate that the survival of walleye larvae was greater for less contaminated brood stocks from the Chippawa flowage (Wisconsin) than from brood stocks for the lower Fox River or Sturgeon Bay (Green Bay), where contaminant levels in the parental stocks were higher.

A logical extrapolation of the foregoing results would suggest that a larger quantity of maternal contaminants is transferred to the eggs and larvae as mean age at sexual maturity increases, in response to an increasing population abundance. Such a sequence of events may

TABLE 2.
Range of organic contaminant concentrations (ng/L) in Lake Erie surface waters collected in 1986 and the 95% 96 hour LC_{50} (ug/L) for yellow perch

	(1) Lake Erie surface water concentration	(2) Yellow perch 96 hour LC_{50} 95% C^2
Hexachlorobenzene	N.D. - 0.2	
a-hexachlorocyclohexane	2.2 - 5.5	
Lindane	0.5 - 2.1	60 - 76
Heptachlor epoxide	0.09 - 0.2	
cis-chlordane	N.D. - 0.09	8 - 11
DDE	N.D. - 0.2	
Dieldrin	0.02 - 0.9	
PCB (total)	0.07 - 0.9	110 - 375
1,3-dichlorobenzene	0.05 - 0.5	
1,4-dichlorobenzene	0.3 - 4.2	
1,2-dichlorobenzene	0.03 - 1.0	
1,2,4-trichlorobenzene	0.04 - 0.6	
1,2,3-trichlorobenzene	N.D. - 0.06	
1,2,3,4-tetrachlorobenzene	N.D. - 0.08	
Pentachlorobenzene	N.D. - 0.07	
trans-chlordane	N.D. - 0.08	8 - 11
1,3,5-trichlorobenzene	N.D. - 0.1	

(1) Water chemistry data from R. Stevens, Environment Canada, Burlington, Ontario (unpublished).
(2) Toxicity data from Mayer and Ellersieck (1986).

reduce reproductive success through differential mortality, and hence recruitment, thus lowering subsequent adult abundance and decreasing mean age at sexual maturity. This cause-and-effect relationship could result in recruitment oscillation in response to a varying mean age of sexual maturity, that would be driven by contaminants and not necessarily by the traditional biotic forces normally attributed to density-dependent relationships. This interpretation, while unproven, should suggest that contaminant influence on recruitment may require that the traditional assessment of population abundance, age at maturity and young-of-year surveys needs to involve a systematic assessment of maternal contaminant burdens. There is a dire need to continue and perhaps expand research on isolating the impact of trace contaminants on reproductive success, especially at the fry survival level, for the effective management of mesotrophic fish communities.

On the other hand, the indirect effects of contaminants on the percid complex may be equal or more profound than the direct effects. These indirect effects take the form of biomass alteration of the phyto- and zoo- plankton communities via shifts in the particle-size density spectrum (e.g. Borgmann 1982; 1983) and loss or suppression of preferred benthic communities, that are beneficial to long-term restoration and maintenance of healthy mesotrophic fish communities. In support of this notion, Ross and Munawar (1981) suggested that nannoplankton is the preferred food of major components of the zooplankton community. Moreover, nannoplankton has been identified by Munawar and Munawar (1982) to be highly sensitive to contaminant levels, and in the case of metals, significant mortality was observed at concentrations that are a fraction of the endorsed water quality objective levels, which are themselves considered to be ultra-conservative (*vide* GLWQA, Annex 1, Rev. 1987).

As the top-down effects of increasing the abundance of terminal predators accelerates and the quantity and quality of zooplankton improves through suppression of planktivorus fish, there is mounting evidence that more organic carbon will become available to the benthic compartment (Scavia and Fahnanstiel, 1987). Moreover, Borgmann and Whittle (1983), as cited in Christie *et al.* (1987), theorize that through this process the oligotrophic benthic communities will accumulate higher concentrations of contaminants relative to pelagic invertebrates. This accumulation will occur because the benthos are feeding to some degree on the less nutritional detritus of the seston. The benthos would, therefore, need to consume more material and thus be exposed to and accumulate higher contaminant concentrations. Clearly, a higher contaminant level in the benthic community would be transferred to an obligate demersal terminal predator or a facultative one that would be forced to switch in response to a declining pelagic forage base. However, in the Great Lakes mesotrophic system, where the extant benthic community is dominated by oligochaetes, this theory may not be wholly applicable. A switch in the benthic community to *Hexagenia*, which feeds on "detrital rain" of contemporary origin, would seem preferable to oligochaetes, which ingest sediments that also contain contaminants at higher historic levels. Unfortunately, the transition to *Hexagenia* may be forestalled by anaerobic conditions and perhaps by contaminated sediments. The suppression of *Hexagenia* in the sediments of Lake George in the St. Marys River (Hiltunen and Schloesser, 1983) may be related to contaminants. The results of contemporary studies which are evaluating the capacity of *Hexagenia* to survive and reproduce in extant sediments from Great Lakes mesotrophic regions, should clarify the role of contaminants in the demise and recolonization of *Hexagenia* .

In summary, it should be evident that contaminants have had a direct impact on the levels of consumption of adult percids and on egg and fry survival, and an indirect effect on planktonic and benthic communities. The fact that contaminants are woven into food-web dynamics should also be a sufficient impetus not only to redouble efforts to eliminate them from the environment, but to evaluate their involvement in and contribution to mesotrophic health in the context of the nutrients, habitat, exploitation and exotic species to which contaminants are inextricably linked.

4.0 CONCLUSIONS

In order to determine the relative state of health of an aquatic mesotrophic ecosystem, it is imperative to have an objective that establishes a benchmark for the ideal state. Obviously, the latter condition will be perceived differently by different people. In order to avoid the potential subjectiveness of this exercise, we propose a mesotrophic lake, ecosystem objective, based on how these systems must have been some 200 years ago (e.g. Loftus and Regier, 1972). Additional and more detailed information for Lake Erie (as one example of a mesotrophic lake) may be gleaned from Regier *et al.* (1969) and Regier and Hartman (1973). Other mesotrophic areas of the Great Lakes basin, for which we intend to set objectives, such as the Bay of Quinte, Lake St. Clair, Saginaw Bay and parts of Georgian Bay, lower Green Bay and Black Bay, have been abundantly documented, and many of these references have been used in the preparation of this report.

The common misconception of a community approach for evaluating the health of mesotrophic systems is the perceived need to monitor closely, over time, each species that is a part of the community. In fact, only key species, occupying integrative nodes need to be monitored. Hence, for mesotrophic systems, the walleye has been identified as a terminal predator that is essential to the well-being of the rest of the community (Ryder and Kerr, 1978). If the walleye maintains an ecological role as a keystone predator within the percid harmonic community, it will also retain its apposite, ecological ratio to other members of the community. It will grow at a normal rate; and reach maturity at the appropriate time and reproduce at an optimal rate. Accordingly, that particular mesotrophic ecosystem may be deduced as free from inordinately large cultural stresses with the possible exception of sub-detectable levels of toxic contaminants. If these levels are low enough that growth is not inhibited, nor reproduction or other metabolic or genetic attributes altered markedly over time, and low enough in concentration to be acceptable for human consumption, without the need for restrictive advisories, then the mesotrophic system may be said to be in a moderately healthy state.

While other factors may necessitate the monitoring of additional community species (e.g. tracking endangered species), in this instance, only a single species was used to determine the relative level of ecosystem health. The walleye was chosen from the perspective of a key community component rather than for its individual biological or demographic attributes. The walleye, therefore, was utilized as a surrogate representative of a harmonic percid community, which, in itself, is a surrogate of a healthy mesotrophic ecosystem. Ideally, complementary species may be used to add confidence to the initial assessment made on the basis of a single species. In this instance, a complementary organism, representative of community integration at a different trophic level from that occupied by the walleye, would be desirable. Following a review of several candidate species, the Work Group reached a consensus that the burrowing mayfly (*Hexagenia limbata*) was representative of a diverse benthic community and was probably the surrogate organism that best complemented the walleye, with little overlap in the system properties represented. *Hexagenia* is an important food item for both sub-adult and adult walleyes as well as for many other fishes. The burrowing mayfly is strongly indicative of healthy substrates (e.g. Hiltunen and Schloesser, 1983) with adequate levels of dissolved oxygen in the overlying water columns. *Hexagenia* abundance is easily quantified and many data exist on past levels of abundance. This organism occupies an integrative node in the ecosystem in that it tends to reflect the effects of interactions at the sediment-water interface. Since this ecotone is not addressed directly when using the walleye as a surrogate, *Hexagenia* provides additional, orthogonal information regarding the state of the mesotrophic system. As such, *Hexagenia* may be viewed as an appropriate complementary surrogate to the walleye (e.g. Ryder and Edwards, 1985).

The rationale behind the establishment of a mesotrophic ecosystem objective is not so much that it might ever be attained, but rather that it provide a trajectory for rehabilitation that has a modicum of chance for success. A partially recovered system will behave more predictably than a completely degraded one and therefore be more useful to humankind. It will consist of species that are more valuable, both in terms of economics and human values, than the changing components of astatic fish assemblages, which often are neither predictable nor indicative of any redeeming value. Accordingly, an appropriate objective for the mesotrophic portions of the Great Lakes might read:

To ensure the persistence of a high quality mesotrophic environment in the portions of the Laurentian Great Lakes where these environments existed naturally in historic times. Consistent with this approach should be the perpetuation of a cool-water community of organisms, dominated by a suite of large percids of which the walleye is the principal terminal predator. The major indigenous components of this mesotrophic community should reproduce naturally and retain a semblance of predictable steady-state over time with respect to the remainder of the community. Maintenance of this state allows for reasonable levels of harvest proportionate to individual species abundance within their limits of density-dependent compensation.

Complementary to the persistence of a cool-water percid community should be an integrated and healthy community of bottom fauna, with the burrowing mayfly (Hexagenia limbata) as the predominant benthic organism.

All vertebrate, invertebrate and plant species within the healthy mesotrophic ecosystem should be contaminant-free (Great Lakes Water Quality Agreement 1978) and the portion harvested for human consumption should constitute a palatable and safe food product.

5.0 <u>REFERENCES</u>

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APPENDIX "A"

SECTIONS OF THE 1978 (REVISED 1987) GREAT LAKES WATER QUALITY AGREEMENT RELEVANT TO MESOTROPHIC ECOSYSTEM HEALTH

The charge to identify appropriate surrogate organisms for mesotrophic lake ecosystems of the Great Lakes basin relates directly to two annexes in the 1978 Great Lakes Water Quality Agreement as amended on October 16, 1983 and on November 18, 1987. The relevant statements are:

Supplement to Annex 1, Specific Objectives

3. *Lake Ecosystem Objectives. Consistent with the purpose of this Agreement to maintain the chemical, physical and biological integrity of the [waters] of the Great Lakes Basin Ecosystem, the Parties, in consultation with State and Provincial Governments, agree to develop the following ecosystem objectives for the boundary waters of the Great Lakes System, or portions thereof, and for Lake Michigan:*

   (a) Lake Superior

   The Lake should be maintained as a balanced and stable oliogotrophic ecosystem with the lake trout as the top aquatic predator of a cold-water community and the Pontoporeia hoyi as a key organism in the food chain; and

   (b) Other Great Lakes

   Ecosystem Objectives shall be developed as the state of knowledge permits for the rest of the boundary waters of the Great Lakes System, or portions thereof, and for Lake Michigan.

Annex 11, Surveillance and Monitoring

4. *Development of Ecosystem Health Indicators for the Great Lakes. The Parties agree to develop ecosystem health indicators to assist in evaluating the achievement of the specific objectives for the ecosystem pursuant to Annex 1:*

   (a) With respect to Lakes [sic] Superior, lake trout and the crustacean Pontoporeia hoyi shall be used as indicators:

   Lake Trout

   - *productivity greater than 0.38 kilograms/hectare [/annum implied].*
   - *stable, self-producing stocks;*
   - *free from contaminants at concentrations that adversely affect the trout themselves or the quality of the harvested products.*

   Pontoporeia hoyi

   - *the abundance of the crustacean, Pontoporeia hoyi, maintained throughout the entire lake at present levels of 220-320/(metres)^2 (depths less than 100 metres) and 30-160/(metres)^2 (depths greater than 100 metres); and*

(b) *with respect to the rest of the boundary waters of the Great Lakes System or portions thereof, and for Lake Michigan, the indicators are to be developed.*

The purposes and interests to be served by ecosystem objectives (Supplement to Annex 1(3)) and ecosystem health indicators (Annex 11(4)) can be inferred from Annex 2(1c). Remedial Action Plans and Lakewide Management Plans:

Impairment of beneficial use(s)" means a change in the chemical, physical or biological integrity of the Great Lakes System sufficient to cause any of the following:

(i) *restrictions on fish and wildlife consumption;*

(ii) *tainting of fish and wildlife flavour;*

(iii) *degradation of fish and wildlife populations;*

(iv) *fish tumors or other deformities;*

(v) *bird or animal deformities or reproduction problems;*

(vi) *degradation of benthos;*

(vii) *restriction on dredging activities;*

(viii) *eutrophication or undesirable algae;*

(ix) *restrictions on drinking water consumption or taste and odour problems;*

(x) *beach closings;*

(xi) *degradation of aesthetics;*

(xii) *added costs to agriculture or industry;*

(xiii) *degradation of phytoplankton and zooplankton populations; and*

(xiv) *loss of fish and wildlife habitat.*

In the above statements, it may be seen that the November 18, 1987 Protocol has incorporated the primary recommendations of the earlier study (Ryder and Edwards, 1985) done by the Ecosystem Objectives Committee in the Supplement to Annex 1(3a), and the Supplement to Annex 11(4a). It also provided a mandate for the present study, Annex 1(3b) and 1(4b). In the definition of "impairment of beneficial use(s)," the Protocol provides guidelines for the kinds of public concerns and interests to be served by the ecosystem objectives and indicators.

APPENDIX "B"

HISTORY AND DEVELOPMENT OF THE MESOTROPHIC CLASSIFICATION

Clearly the first item to consider when attempting to describe a surrogate for a healthy mesotrophic ecosystem is to set boundary conditions (i.e. "what is a mesotrophic ecosystem?"). Mesotrophy is a Greek term for moderate nourishment and was coined out of a need by early limnologists to reduce and simplify an increasing amount of descriptive information to classify freshwater systems.

The criteria for classifying lakes are many and varied; they include geological origin, morphometry, sediments, hydro-mechanical processes, thermal regimes, trophic or chemical parameters. Since the early work of Thienemann (1918) and Naumann (1919), there has been much interest in the development of indices or typological algorithms, which indicate trophic status (Shapiro 1975; Chapra and Dobson, 1981; Vollenweider 1968b). The characteristics of lakes and their drainage basins used in these schemes are numerous, and approaches range from simple, single variables, such as mean depth (Rawson 1952), to multi-variate models (e.g. Shannon and Brezonik, 1972). Classification schemes have been proposed for virtually all of the factors involved in lake metabolism. Many models have been applied to the Great Lakes while others have been developed specifically for them.

The oligotrophic-mesotrophic-eutrophic sequence, used to characterize the trophic status of water bodies was first suggested by Weber (1907) to describe the nutrient conditions which determined the flora of German peat bogs. Thienemann (1918) characterized lakes as oligotrophic and eutrophic, depending on summer oxygen depletion in the hypolimnion and on the types of benthic organisms associated with oxygen-rich and oxygen-poor sediments. He also regarded deeper lakes as oligotrophic and shallow lakes as eutrophic. At about the same time, Naumann (1919) classified Swedish lakes as oligotrophic or eutrophic dependent upon the level of plankton biomass (Hutchinson 1973). Nutrient-deficient oligotrophic lakes supported only small amounts of algae; eutrophic lakes contained dense populations of algae, which were reflected in the colour of the water. In Naumann's classifications, mesotrophic lakes would be intermediate in phytoplankton richness.

Lundbeck (1934) incorporated depth into trophic level classification. He considered that a very deep lake with mesotrophic water would be secondarily oligotrophic, if the hypolimnion contained adequate dissolved oxygen and an oligotrophic benthic fauna. Strom (1930) also emphasized depth as an important factor in trophic status, by pointing out that the ratio of water volume to sediment surface was less in shallow lakes and, therefore, the amount of nutrients that diffuse from sediments into water would be greater than in deep lakes.

From this early work in Europe, the development of terminology, schemes, typologies and indices to describe the trophic nature of water has continued and is still of major interest to anyone concerned with surface waters, water uses and aquatic life. A selection of parameters and indices used to quantify the trophic status of lakes is shown in Table B1. In most of the indices and models, mesotrophy is placed on a cline, intermediate between oligotrophy and eutrophy.

Another approach to trophic characterization is the use of indicator organisms. Phytoplankton and zooplankton have been considered (Rawson 1956; Round 1958; Brooks 1969), but the majority of the interest in biological indicators has been expressed toward benthic organisms (Brinkhurst 1974; Cooke and Johnson, 1974; and Saether 1975). Most of the early benthic typologies were developed for European lakes, and problems with the taxonomy of groups or organisms (particularly chironomidae) have hampered efforts to relate them to lakes in North America. However, Cook and Johnson (1974) concluded that eutrophic and mesotrophic associations of oligochaetes were generally similar in both North America and Europe, except that dominant species in the oligotrophic profundal zone were different. Howmiller and Scott (1976) proposed the trophic classification of oligochaete species shown in Table B2.

TABLE B1. Suggested values of selected parameters or indices used in characterizing trophic status of lakes

Parameter or Index	Unit or Application	Oligo-trophic	Meso-trophic	Eu-trophic	References
Secchi disc transparency	m	>5	5-3	<3	Chapra and Dobson, 1981
		>6	6-3	<3	Vallentyne *et al.* 1969
Hypolimnetic oxygen deficiency	mg $cm^{-2}mo^{-1}$	<0.75	0.75-1.65	>1.65	Mortimer in Hutchinson, 1957
		<0.5	0.5-1.0	>1.0	Hutchinson 1938
Total phosphorus	mg m^{-3}	<10	10-20	>20	Chapra and Robertson, 1977
		<15	15-25	>25	Forsberg and Ryding, 1980
Total nitrogen	mg m^{-3}	<300	300-650	>650	Vollenweider 1968
		<400	400-600	>600	Forsberg and Ryding, 1980
Chlorophyll-*a*	mg m^{-3}	<3	3-7	>7	Forsberg and Ryding, 1980
		<4.3	4.3-8.8	>8.8	Dobson *et al.* 1974
Primary production rate	g C $m^{-2}yr^{-1}$	<145	145-240	>240	Chapra and Dobson, 1981
		<25	25-75	>75	Rodhe 1958
Organic matter in sediments	% D.W.	<17	17-30	>30	Entz 1977
$\frac{Na + K}{Ca + Mg}$	English lakes	>2.0	2 - .2	<.2	Pearsall 1923
Morphoedaphic index	Global lakes	<6	6-7	>7	Ryder *et al.* 1974
Trophic state index	Florida lakes	<3	3-7	>7	Shannon and Brezonik, 1972
Lake condition index	Wisconsin lakes	<5	5-10	>10	Uttormark and Wall, 1975
Naumann trophic scale	Great Lakes	<5	5-10	>10	Chapra and Dobson, 1981
Thienemann trophic scale	Great Lakes	<5	5-10	>10	Chapra and Dobson, 1981
Diatom quotient	$\frac{\textit{Chlorococcales}}{\text{Desmidiaceae}}$	<1	1	>1	Nygaard 1949
	$\frac{\textit{Araphidineae}}{\text{Centrales}}$	<1	1-2	>2	Stockner 1971

TABLE B2. Trophic classification of lakes using oligochaetes

Oligotrophic	Mesotrophic	Eutrophic
Stylodrilus heringianus	*Spirosperma ferox*	*Limnodrilus augustipenis*
Spirosperma variegatus	*Isochaetides freyi*	*L. claparedeianus*
Tasserkidrilus superiorensis	*Ilyodrilus templetoni*	*L. hoffmeisteri*
Limnodrilus profundicola	*Potamothrix moldaviensis*	*L. maumeensis*
Tasserkidrilus kessleri	*P. vejdovskyi*	*L. ukedemianus*
Rhyacodrilus coccineus	*Aulodrilus* spp.	*Quistadrilus multisetosus*
R. montana	*Arcteonais lomondi*	
	Dero digitata	
	Nais elinguis	
	Slavina appendiculata	
	Uncinais uncinata	

As indicated in Table B1, mesotrophy is usually defined as the trophic state on the cline between oligotrophy and eutrophy. Another approach is to consider mesotrophy as the apex of an optimality curve, with oligotrophy and eutrophy at either end of the curve. In this sense, mesotrophy has been considered as an optimum habitat for percid communities (Leach *et al.* 1977). In the same pattern, Ryback (1965) found that mesotrophic lakes had higher levels of calcium in their sediments than either oligotrophic or eutrophic lakes. These two examples support the view that, in some instances, mesotrophy may be an ecological optimum and not only a condition quantitatively intermediate between oligotrophy and eutrophy.

APPENDIX "C"

HARMONIC PERCID COMMUNITIES IN THE MESTROPHIC WATERS OF THE GREAT LAKES

Definition and Properties

Harmonic percid communities were first described as a practical expression of the community niche or biotope concept (e.g. Whittaker and Levin, 1975) from a data set derived from empirical observation (Ryder and Kerr, 1978). The original observations were made on a large set of boreal forest lakes, which were relatively unperturbed as a result of human intervention. Hence, the community structures were assumed to be similar to those of the Pleistocene lake epoch, which followed Wisconsin glaciation. The fishes of the subset of mesotrophic lakes were found to be highly similar in both kind and proportion from lake to lake. As most of the fishes inhabiting these boreal forest lakes had radiated from a Mississippi refugium (Bailey and Smith, 1981), it was assumed that long-term coexistence had created the moderately tight couplings or linkages observed among the most abundant species within the communities. Linkages, such as the predator-prey linkage between walleye and yellow perch, contributed to the integrative nature of the harmonic community through the optimization of niche complementarity. Germane to the harmonic community concept was the notion of a terminal, keystone predator, that, through predation, controlled to varying degrees, the lower trophic levels of the biotic system (e.g. McQueen *et al.* 1986). Hence, the predator was looked upon as beneficial to the rest of the community (especially the higher trophic levels); it retained the community at optimum diversity (e.g. Paine 1966). Presumably, optimum diversity level provided an efficient use of all available resources within the ecosystem (Ryder *et al.* 1981).

For the boreal forest-mesotrophic lake set, four fish species were found to form the nucleus of a harmonic community, and these were almost universally predominant, regardless of the composition of the rest of the community. These species included the walleye - an opportunistic, terminal predator; the northern pike - essentially a piscivore and within the community, an accessory predator; the yellow perch - a predator of moderately small organisms; and the white sucker - a feeder on benthic invertebrates. Young-of-the-year and yearling yellow perch provided the walleye and northern pike with their principal piscivorous requirements, and to a lesser extent, the young of the white sucker were preyed upon by these same two terminal predators.

This brief statement of foodweb interactions is a gross oversimplification of the true state of trophic affairs. Walleye, for example, tend to be highly opportunistic, and spend several weeks of each summer feeding upon the sub-imagos of burrowing mayflies, while adult walleyes and northern pike prey heavily upon lake herring at certain times of the year. Nonetheless, the notion of a harmonic community, aggregated about four key species, seemed to hold for other data sets, where these same four species were found to be predominant (e.g. Marshall and Ryan, 1987). Hence, the four key species form a community construct that is moderately to highly integrated, and through integrative feedback, tends to persist over time. Many other species in various combinations may be added to the mix without changing the essential features of the emergent community properties (Table B1). Hence, the term "harmonic community" implies the cybernetic properties of integration, high levels of stability, effective resilience to exogenous stresses and appropriate complexity, as well as moderately constant community composition and P/B ratios, and moderately predictable outputs (Table C1). From a management point of view, having a community of relatively constant species composition and yield, that may be accurately predicted well into the future, is a definite advantage. Subsequent planning will be simpler and more effective when the manager is able to project, within reasonable limits, the behaviour of the fish community.

TABLE C1. Ecological properties of harmonic fish communities and astatic assemblages in mesotrophic waters of the Great Lakes.

Ecological Property	Harmonic Community	Astatic Assemblage
Integration	High degree of integration among indigenous species	Random and loose linkage, particularly in the case of exotic species
Stability	Retains semblance of steady-state	Highly variable
Resilience	Rapid return to steady-state following moderate stress	Steady-state not readily attainable
Identity (persistence)	Retains species identity following topological distortion	Descriptive identity not possible over time
Species ratios	Moderately constant	Changing
P/B Community ratio	Circa 0.3	0.1 <1.0 variable
Yields	Predictable and constant	Highly variable
Resistance to invasion	Moderately resistant under natural regime	Prone to invasion
Size composition	Slight overlap of niche	High levels of space contention along some niche dimensions
Complexity	Optimal biotic complexity	Biotic complexity suboptimal or uneven
Resource utilization	Maximal	Variable and unpredictable

Species Linkages in Harmonic Communities

The walleye-yellow perch predator-prey linkage is an ecologically established coupling of species that is virtually universal, that is it is evident wherever the two species occur together (Mills *et al.* 1987). This relationship has also been observed in the two closely related Eurasian species (Deelder and Willemson, 1964; Craig 1987), the sander and the ringed perch. For all practical purposes, these congeners are ecological analogues to the two North American species. They have also established a similar predator-prey interdependency. A niche complementarity has developed that allows the walleye to feed on the yellow perch twice each day, when they are occupying the same shoals under similar and favourable conditions of sub-surface illumination (Ryder 1977). This complementary relationship arises because of the differences in visual acuity of the two species (Ali *et al.* 1977). Whether or not this symbiosis (broad sense) is a direct result of co-evolution, is an interesting and provocative question, but is not vital to the understanding of this particular species coupling. However, as both the yellow perch and the walleye are derived from a common ancestor (Svetovidov and Dorofeeva, 1963), it might reasonably be assumed that co-evolution was a strong candidate as a cause for species coupling, despite opinions to the contrary (e.g. Janzen 1980). Species linkages such as these tend to form the fundamental building blocks for a more complex and tightly integrated harmonic community. Other species pairings occur in percid communities; some of these pairings are not easily explained. For example, adult walleyes and adult white suckers quite often school together, but whether or not this behaviour provides any survival advantage for either species is unknown. Other species partition their common food resources (e.g. Schoener 1974) on either a temporal or spatial basis, such that direct confrontations for a common resource do not normally occur. In essence, then, these various species couplings, or conversely, these mutual exclusion behaviours (niche complementarity), all tend to knit species aggregations more tightly into a mosaic, that we have labelled the harmonic community. The resulting community dynamics then become more predictable in terms of species composition and ratios, and size composition and ratios, and presumably, are more efficient in the utilization and trophic transfer of available nutrient and energy resources (Ryder *et al.* 1981).

Astatic Fish Assemblages

Optimal abiotic conditions favorable to percid harmonic communities are those usually described as mesotrophic, or mid-range on the trophic scale. Hence, percid harmonic communities are clustered about some median of central tendency, representing optimum habit conditions for their respective biotope (Ryder and Kerr, 1978). These habitat optima may even be likened to an attractor region (Peterman *et al.* 1979), which provides the multidimensional milieu most favorable for thriving percid communities. Radical departure from these optima will eventually result in a disaggregated state known as an astatic assemblage (Ryder and Kerr, 1978).

An astatic assemblage of fishes has ecological properties that are essentially the antithesis of those of harmonic communities. Astatic assemblages of fishes are a bane to the fisheries manager because of their unpredictable behaviour. The most predictable property of an astatic assemblage of fishes is that it will be constantly in a state of flux, especially in terms of species composition and ratios, and yield composition and level.

Normally, astatic fish assemblages are created through one or more anthropogenic stresses, including over-exploitation, cultural eutrophication, contaminants loadings, exotic species introductions or physical modifications to the water body in question (Loftus and Regier, 1972). Often, the change of a single, abiotic, environmental variable will be found to be the underlying cause of the degradation of a harmonic community into an astatic assemblage (e.g. Svärdson 1976). A progressive change in a particular environmental variable will often move the median of a mesotrophic attractor to a markedly different level, a condition which may, in turn, be more appropriate to the life requirements of other species or species assemblages. The net result of these changes is increasing vulnerability of the harmonic community to invasion by non-indigenous species from outside the subsystem. This situation develops because of a change in the mode of interactive segregation of two or more species (Nilsson 1967). An astatic assemblage of fishes, accordingly, is vulnerable to successive waves of invaders because of a constantly fluctuating, or ill-defined attractor region. On the other hand, long-term stability of an attractor region around a new median of central tendency might result over time, in a new community aggregation, consisting of appropriate species ecologues that are specialized to exploit the new environment.

Harmonic Percid Communities in the Laurentian Great Lakes

Some of the fisheries literature of the last two decades on the Great Lakes attempts to describe what the pristine fauna might have been and how it has descended into "degraded" or astatic communities because of man's interventions (e.g. Regier 1968; Loftus and Regier, 1972). Both the pristine and the degraded states are usually described only in terms of absolute or relative abundances of individual species, rather than in the more comprehensive community context. Harmonic communities in the Laurentian Great Lakes may be qualitatively different from those observed in the inland lakes of the boreal forest zone (Ryder and Kerr, 1978; 1988). This disparity may be accounted for, almost entirely, because of differences of reinvasion patterns following deglaciation, and variability of ecological conditions between the smaller, inland lakes and the much larger Great Lakes. Hence, scale alone provides not only a much greater environmental diversity and, therefore, a much greater ecological opportunity within the Great Lakes (Barbour and Brown, 1974), but large scale also allowed greater accessibility to the Great Lakes from the various glacial refugia from which the invading stocks were derived (Radforth 1944; Bailey and Smith, 1981). Accordingly, harmonic communities within the Great Lakes may assume a different structure in terms of species composition, phenotypic stocks or other phyletic categories.

Types of Great Lakes Harmonic Communities

There are two well-defined types of harmonic communities formerly found within the Laurentian Great Lakes, namely the salmonid community (Ryder and Edwards, 1985) and the percid community (Ryder and Kerr, 1989). A third, loosely defined and less abundant category consists of the centrarchid-cyprinid-ictalurid complex, usually considered to be warm water species, inhabiting shallow eutrophic bays or the nearshore littoral and shallow demersal regions.

Our interest, herein, deals with percid harmonic communities, usually described as consisting of cool-water species, intermediate in environmental requirements between the cold-water salmonid communities and the warm-water centrarchid communities. Percid communities tend to aggregate in greatest abundance around two principal attractors, that is, moderate temperatures and intermediate levels of phosphorous loading (Ryder and Kerr, 1989). The principal areas of the Great Lakes most amenable to these conditions are some of the large bays: Black Bay (Lake Superior), lower Green Bay (Lake Michigan), Saginaw Bay and parts of Georgian Bay (Lake Huron), Lake St. Clair, the western and possibly central basins of Lake Erie and the Bay of Quinte (Lake Ontario), as well as many lesser areas. Many of the river deltas (e.g. St. Louis River delta, Lake Superior) and large connecting channels of the Great Lakes, such as the Detroit River, also provide the appropriate milieu for thriving percid communities, but generally speaking, these are special cases, not essential for the clarification of the harmonic community concept. These areas, however, are often important as spawning or nursery zones for major harmonic community components, and are often more easily degraded than the open lake areas (Ryder 1968; Edwards *et al.* in press). On the whole, each of the large bays previously noted, provided favourable living conditions for harmonic percid communities in pristine times (Hartman 1972; Ryder 1972).

The fish communities in these two mesotrophic environments reflected the levels of departure from "classic" mesotrophy, seen in most of the other bays or basins. Hence, shallow Lake St. Clair, while clearly dominated by the percid community complex, is also abundantly populated by centrarchid, cyprinid and ictalurid species. In terms of classification, an equally strong argument could be made in support of a Lake St. Clair fish community as being a warm-water, rather than a cool-water one. If phosphorus loading tends to increase in the future, in view of a gradually warming climatic trend, Lake St. Clair may well become a haven to a predominantly warm-water fish community.

The other mesotrophic extreme, the eastern basin of Lake Erie, is at the oligotrophic end of mesotrophy, particularly its outer waters. The original community there also differed from the classic percid community (Ryder and Kerr, 1988) in that it was probably dominated by the lake trout. Intermediate between the eastern basin of Lake Erie and Lake St. Clair, was the central basin of Lake Erie, in which blue pike were predominant, a sub-species of walleye particularly adapted to living in open limnetic regions of the lake, and perhaps with a preference for slightly cooler water than the walleye (Figure C1). According to Trautman (1957), the blue pike preferred the deep and clear waters; it was rarely found in the shallow, turbid sections of Lake Erie. Complementing the blue pike within the central basin community were other species normally assumed to be part of the cold-water community, namely the lake whitefish, lake herring and burbot. The latter species, not always recorded in the commercial fishery because of its low consumer value, may have been the most abundant large fish in the central basin of Lake Erie at one time (S.H. Smith, personal communication).

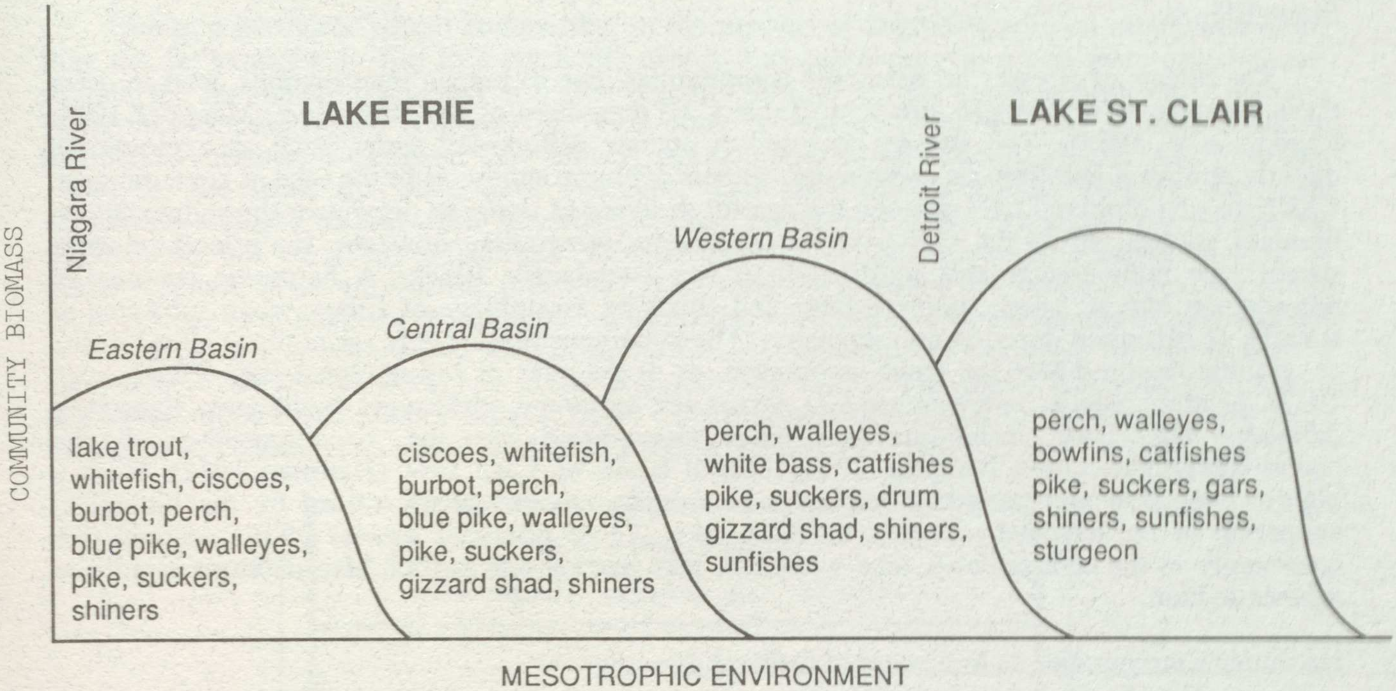

FIGURE C1. Original species composition and relative fish community biomass for the largest contiguous section of mesotrophic waters within the Great Lakes Basin Ecosystem. Some dominant species are listed for each basin as it must have been some 200 years ago.

The central basin of Lake Erie may have been unique in that most of its environmental conditions were intermediate between classic mesotrophy and classic oligotrophy. It is possible that the endemic blue pike was a phenotypic adaptation to oligotrophic-mesotrophy, and was, perhaps, in the process of genetic differentiation. The only other lake where this phenomenon was suspected to have occurred (Harkness 1936; Scott and Crossman, 1973; Anthony and Jorgensen, 1977) was Lake Nipissing in central Ontario, which is also a large mesotrophic lake with sections having strong oligotrophic tendencies (Fry 1937). Had the blue pike and associated species not been subjected to multiple anthropogenic stresses over the last one hundred years or so in the central basin of Lake Erie (Loftus and Regier, 1972), it is quite likely that a new harmonic community may have emerged over time, clustered around a different community attractor, but particularly controlled by two primary environmental variables, namely phosphorus loading and heat input. To have four distinct types of harmonic communities within the vast Great Lakes basin, despite its wide range of environmental heterogeneity, would not be unexpected. Moreover, Hartmann (1980) has described five discrete types of harmonic communities for a relatively small set of European lakes. It is quite possible that over evolutionary time, a distinctive harmonic community would develop for each lake, or each ecologically discrete section of a very large lake. Perhaps this is the condition that currently exists in the very large and very old Rift Valley Lakes of Africa. Some of these lakes, particularly Malawi and Tanganyika, contain large numbers of endemic species, some of which form very tight species linkages or specializations, such as feeding only on the eyes or scales of other fish species (Fryer and Iles, 1972).

In the Laurentian Great Lakes, on the other hand, community evolution has been disturbed intermittently by glacial advances and retreats, at sufficiently short intervals to preclude such highly obligate and specialized linkages. These glacial events serve to reset the whole ecosystem, including its indigenous fish communities. They also enrich the system by making nutrients available within the basin from outside the system proper. Glacial resets tend to distort topologically, percid harmonic communities, by favouring certain species over others with more rigorous environmental requirements. However, lacking human intervention, these communities respond to the gradually improving environments following glacial retreat, and in time, classic percid harmonic communities emerge.

Stress Effects

The effects of stresses on harmonic communities, due to human interventions, tend to drive these subsystems in a single direction (Table C2), regardless of the stress (e.g. Margalef 1974; Rapport *et al.* 1985). The stresses themselves operate differently; some, such as exploitation, directly remove a fish from its community. Others act more subtly, as in the case of contaminants, which may be observed only through the careful analyses of tissue or organs, or through extended bioassay studies. From the viewpoint of community integration, however, the effects of these stresses are both similar and equifinal (e.g. von Bertalanffy 1968). A harmonic community decomposes into an astatic, unpredictable and changing assemblage of fishes, when subjected to stresses of sufficient duration and intensity. The decomposition usually takes place either in the geographic region where the stress is greatest, as in the case of lower Green Bay (Harris *et al.* 1982), or at an astatic node (Figure C2), where the harmonic community is the least rigorously defined. The latter condition has been exemplified by the decomposition of the percid-coregonine-burbot complex in the central basin of Lake Erie (Hartman 1972), from a highly integrated and persistent harmonic community, to one characterized by the biological extinction of the terminal predator, the blue pike. Other principal species of the original fish community in the central basin, lake whitefish, lake herring and burbot, also declined rapidly to near-extinction.

Harmonic Communities as Indicators of Cultural Stresses

Harmonic communities may accurately indicate the presence of an undue cultural stress through their level of decomposition. The parts of the community most vulnerable to cultural stresses initially are the highly vulnerable, astatic nodes (Figure C2), where species linkages are weakest and where the harmonic concept may be only marginally applicable.

Most cultural stresses, at a fundamental level, tend to inject more energy and nutrients into the system rather than to decrease these levels. Hence, the general effect of cultural stress is an increase in the trophic level of the total system. However, because of the community disaggregation that results, less efficient use is made of the newly augmented nutrient and energy resources. Regardless of the stress, the system is driven more and more towards a state of disaggregation and a higher trophic state (Table C2). Since cultural interventions mostly decompose or rarely improve an ecosystem in terms of human values, a mesotrophic system will almost invariably degrade towards eutrophy. Although the phosphorus loading effect is generally accepted as clinal, increasing from ultra-oligotrophy to hyper-eutrophy (e.g. Vollenweider 1968a), a similar cline of fish communities does not exist (e.g. Ryder and Kerr, 1978; Figure B2). Rather, the communities are aggregated around abiotic optima, represented by the mean environmental conditions most appropriate to the community in question.

TABLE C2. Observed effects of five general stress categories.

STRESS	Community Disaggregation	Trophic Increase	Increased Unpredictability	Reduction of Human Values
Exploitation	x	x	x	x
Cultural Eutrophication	x	x	x	x
Contaminants Loadings	x	x	x	x
Physical Modifications	x	x	x	x
Exotic Species	x	x	x	x

Hence, a harmonic percid community, in the process of degrading into an astatic condition, may not be expected to flip to a harmonic centrarchid community in a eutrophic environment. Rather, the harmonic community will first degrade into an astatic, unpredictable state, within a hyper-mesotrophic milieu (Figure C1). This point is neither trivial, nor one of only semantic distinction. Rather, it suggests that cultural stresses tend to be aberrant (Ryder and Edwards, 1985), in the sense that they have insidious, qualitative effects beyond pushing the biotic community along a trophic cline towards increased eutrophy. These qualitative effects may be quantifiable, but are rarely quantified. Despite the lack of quantification, observation may be useful (because of the equifinality principle) in showing the presence of a cultural stress for which some corrective or remedial measures should be taken. The community symptoms usually will not be indicative of a specific stress (except in the case of contaminants loadings), but rather will be indicators of the general stress syndrome (Rapport *et al.* 1985). The percid community responses to a mesotrophic system under cultural stress will be generically similar to those previously listed for salmonid communities and oligotrophic systems (Appendix V in Ryder and Edwards, 1985).

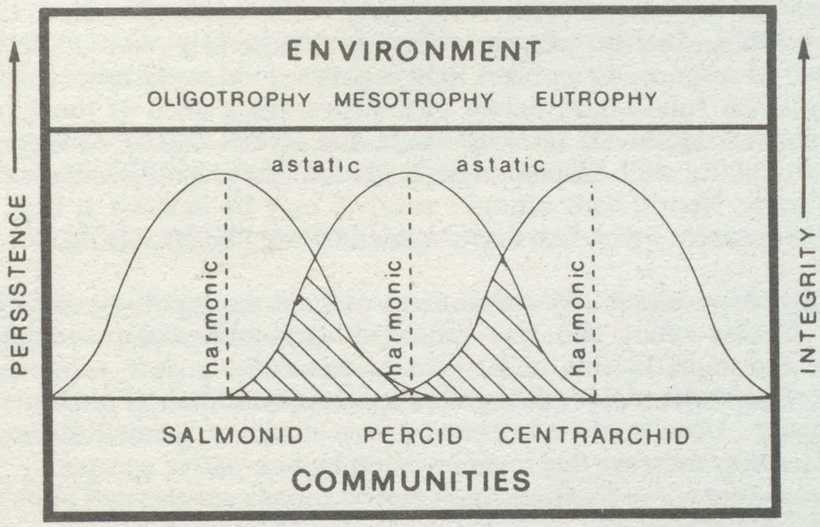

FIGURE C2. Schematic representation of three fish communities of the boreal forest zone showing the medians of central tendency (dashed vertical line) that result in harmonic species associations, complementary to prevailing environmental conditions. This association, in turn, results in high levels of community persistence and integrity. The crosshatched areas indicate astatic species associations of low persistence and variable levels of community integrity (Ryder and Kerr, 1978).

We will reiterate these community responses within the context of harmonic percid communities in mesotrophic systems. This reiteration proceeds with the understanding that, in the case of a pristine, unstressed community, there are relatively few options in terms of how that community may degrade and, regardless of the path taken, the degradation end point will be the same; equifinality, therefore, becomes a given. Accordingly, harmonic percid communities under cultural stress will inevitably degrade into an astatic assemblage of fishes, an undesirable state as measured in human values.

Among the general indications of degradation following human intervention are a reduction in the abundance of terminal predators (walleye), and therefore the loss of the principal regulator in a system primarily controlled from the top down (McQueen *et al.* 1986). Benthic organisms, especially the largest ones, tend to decline, and with them, large benthic feeders such as lake sturgeon. Pelagic prey fishes will increase because of the lack of predation control, and the mean size and mean age of the community components will decrease as a result of density-dependent growth inhibition. Food webs will shorten and simplify, but at the same time, become less predictable as the system is invaded by opportunistic exotic species, such as rainbow smelt or alewives.

Species that have relatively narrow environmental requirements (stenobionts), such as the blue pike, may be replaced by exotic eurybionts such as rainbow smelt, which have wide environmental boundaries. Introgression may contribute to the loss of species as abiotic environmental variables change, thus reducing the level of reproductive isolation between two congeners capable of interbreeding. This effect may well have contributed to the loss of the blue pike from the central basin of Lake Erie (Regier *et al.* 1969). Evidence of such an effect may have been indicated by the increased numbers of "mules" (intergrades) recorded in the commercial catches (Trautman 1957). Other species known previously to exist in the system (e.g. Scott and Smith, 1962) may also have introgressed with closely associated congeners and, for all practical purposes, became ecologically extinct.

Reproduction may be curtailed or cease altogether, in the case of some species. The mysterious disappearance of the sauger from Lake Erie and Black Bay in Lake Superior, may be indicative of a locally-degraded habitat essential for the successful reproduction of this species (e.g. tributaries). Saugers are also subject to introgression with walleyes (Stroud 1948) and would most likely introgress in accordance with a changing environmental milieu, caused by human intervention (Regier 1968). In fact, saugers coincide very closely with walleyes along several niche boundaries such as response to ambient light regimes, food preferences, and spawning times and locations. Only some subtle quantitative differences along each of these niche dimensions keeps the two species reproductively isolated (Kerr and Ryder, 1977). Saugers appear to be a Pleistocene relict, particularly well-adapted to early glacial lakes heavily laden with inorganic clay colloids or glacial flours. Hence, their ultimate survival may be tenuous at best, dependent upon the presence of an environment much like that provided by the Pleistocene lakes.

Other community responses to cultural stresses include the topological distortion of species associations. Both species ratios and size ratios of successive cohorts change under stress. Production is erratic and unpredictable under density-dependent growth responses to stress. The overall effect is a decline in the yields of desirable species, even though total integral, community production may increase. Usually, the number of native stocks of species decreases, although the total number of species may increase due to an invasion by non-native species.

COMMUNITY DESIDERATA

1. Percid component (*Perca + Stizostedion*) should be approximately 30% or more of total standing stocks in terms of biomass.

2. Harmonic components (walleye, yellow perch, northern pike and white sucker or their ecological analogues) should be about 60% by biomass of adult stocks.

3. There should be rapidly changing species ratios of four harmonic components.

4. Harmonic component should be markedly larger in terms of total biomass than exotic species.

5. Mean age of harmonic components in harvest should be one year greater than age at maturation for females.

6. The single species making the greatest contribution to the annual harvest should be one of the four harmonic community components, usually a percid.

7. Combined percid harvest (all species) should not exceed 30% of the total harvest.

8. The mayfly, *Hexagenia limbata*, should constitute a major food item for two or more of the key components of the harmonic community.

9. The mayfly should be the dominant benthic organism in terms of biomass and should number approximately 200 m^2.

10. Yields of exotic fish species should be less than one-third of the total annual fish yield.

11. The emerald shiner and the spottail shiner should constitute a major portion of the prey species standing stocks (by biomass).

12. Temporary, topological distortion of percid harmonic communities should be expected when they are subjected to a suite of light to moderate stresses, but the innate resilience of the community, derived from the integration of its component parts, should be sufficiently great to restore the community to its original state, once the stresses are alleviated.

13. Loss of reproduction and or recruitment of any of the four key components of a harmonic community is an indication of inordinate stress levels at a sensitive node in the system.

14. A persistent and inordinately slow growth rate for any of the four key components of a harmonic community represents a major cause for concern. This condition may be caused by stress at a sensitive node, such as missing or inappropriate prey species, contaminants loadings, or density-dependent effects in the case of over-abundance of the species in question.

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* These community objectives are based, for the most part, on the following publications: Abrosov (1969); Adams and Oliver (1977); Ryder and Kerr (1989). Other objectives were drawn implicitly from a vast literature on biotic communities.

APPENDIX "D"

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APPENDIX "E"

COMMON AND SCIENTIFIC NAMES OF INVERTEBRATES AND VERTEBRATES

Common and Scientific Names of Fishes (Vertebrates)[1]

Alewife[2]	*Alosa pseudoharengus* (Wilson)
Atlantic salmon	*Salmo salar* Linnaeus
Blue pike	*Stizostedion vitreum glaucum* Hubbs
Bowfin	*Amia calva* Linnaeus
Brown trout[2]	*Salmo trutta* Linnaeus
Burbot	*Lota lota* (Linnaeus)
Catfishes	Any member of the family *Ictaluridae*
Centrarchid	Any member of the sunfish family
Chinook salmon[2]	*Oncorhynchus tshawytscha* (Walbaum)
Cisco	*Coregonus artedii* LeSueur
Coho salmon[2]	*Oncorhynchus kisutch* (Walbaum)
Common carp[2]	*Cyprinus carpio* Linnaeus
Coregonine	A salmonid subfamily including the genera *Coregonus* and *Prosopium*
Cyprinid	Any member of the minnow family
Deepwater cisco	All members of the genus *Coregonus*, excluding *C. clupeaformis* and *C. artedii*
Deepwater sculpin	*Myoxocephalus thompsoni* (Girard)
Drum	See freshwater drum
Emerald shiner	*Notropis atherinoides* Rafinesque
Freshwater drum	*Aplodinotus grunniens* Rafinesque
Gar	Any member of the family *Lepisosteidae*
Gizzard shad	*Dorosoma cepedianum* (LeSueur)
Goldfish	*Carassius auratus* (Linnaeus)
Haplochromis	A species swarm of cichlids found in the African Rift Valley Lakes
Ictalurid	Any member of the bullhead or catfish family
Lake herring	*Coregonus artedii* LeSueur
Lake sturgeon	*Acipenser fulvescens* Rafinesque
Lake trout	*Salvelinus namaycush* (Walbaum)
Lake whitefish	*Coregonus clupeaformis* Mitchill
Longnose sucker	*Catostomus catostomus* Forster
Minnows	Any member of the cyprinid family
Mules	*Stizostedion* v. *vitreum* x s.v. *glaucum* (integrade)
Nile perch	*Lates niloticus* Boulenger
Ninespine stickleback	*Pungitius pungitius* (Linnaeus)
Northern pike	*Esox lucius* Linnaeus
Pacific salmon[2]	Any member of the genus *Oncorhynchus*
Perch	See yellow perch
Percid	Any member of the perch family, including walleyes, saugers and blue pike
Pike	See northern pike
Pink salmon[2]	*Oncorhynchus gorbuscha* (Walbaum)
Rainbow smelt[2]	*Osmerus mordax* (Mitchell)
Rainbow trout[2]	*Oncorhynchus mykiss* (Richardson)
Redhorse	A sucker (catostomid) of the genus *Moxostoma*
Ringed Perch	*Perca fluviatilis* Linnaeus
Rock bass	*Ambloplites rupestris* Rafinesque
Ruffe[2]	*Gymnocephalus cernuus* (Linnaeus)
Salmonid	Any member of the trout family, including salmon, trout, char, whitefish and ciscos

Common and Scientific Names of Fishes (Vertebrates)[1]

Sander	*Stizostedion lucioperca* (Linnaeus)
Sauger	*Stizostedion canadense* (Smith)
Sea lamprey[2]	*Petromyzon marinus* Linnaeus
Shiner	Any member of the genus *Notropis*
Smelt[2]	See rainbow smelt
Splake	*Salvelinus namaycush* x *S. fontinalis*
Spottail shiner	*Notropis hudsonius* (Clinton)
Sturgeon	See lake sturgeon
Sucker	Specifically, the genera *Catostomus* and *Moxostoma*
Sunfishes	Any member of the family *Centrarchidae*
Walleye	*Stizostedion vitreum* (Mitchell)
White bass	*Morone chrysops* (Rafinesque)
Whitefish	See lake whitefish
White perch	*Morone americana* (Gmelin)
White sucker	*Catostomus commersoni* (Lacepede)
Yellow perch	*Perca flavescens* (Mitchell)

1 All common names accompanied by a generic and specific name and authority are in accordance with Robins *et al*. (1980): "A list of common and scientific names of fishes from the United States and Canada." Other names are either collective terms referring to closely related taxa or common vernacular names.

2 Introduced into the Great Lakes basin and/or tributary waters, or recent invaders through the Welland Canal or other canal systems.

Common and Scientific Names of Biota

BIRDS:

Bald eagle	*Haliaeetus leucocephalus*
Herring gull	*Larus argentatus*

MAMMALS:

Man[1]	*Homo sapiens*
Mink	*Mustela vison*

INVERTEBRATES:

Amphipods	Specifically, *Pontoporeia hoyi*, a crustacean
Bloodworm	Several midges of the chironomid family
Burrowing mayfly	*Hexagenia limbata*
Chironomidae	Midge family
Dreissena polymorpha	Zebra mussel
Eurytemora affinis	A copepod crustacean
Gastropods	Snails
Glugea hertwigi	A microsporidian parasite of rainbow smelt
Goniobasis sp.	A Gastropod (snail)
Hyalella sp.	An amphipod crustacean
Hydropsyche sp.	A caddis fly
Lampsilis sp.	A Pelecypod (mussel)
Limnodrilus hoffmeisteri	A tubificid worm
Limnodrilus cervix	A tubificid worm
Limnodrilus maumeensis	A tubificid worm
Oecetis sp.	A caddis fly
Oligochaetes	Class of aquatic earthworms
Spirosperma ferox	A tubificid worm
Pleurocera sp.	A Gastropod (snail)
Pontoporeia hoyi	An amphipod crustacean
Sludgeworms	Genus *Limnodrilus*, aquatic earthworms
Sphaeriidae	A family of Pelecypods (mussels)
Tubificid	Family of oligochaetes

[1] Places emphasis on our concern for man as an integral part of an ecosystem.

EPILOGUE

The state of the environment, as always, is subject to rapid flux, both in the direction of rehabilitation as well as in that of degradation. Substantive positive changes have occurred in several mesotrophic systems over the past decade and many of these have been most obviously reflected in the fisheries of the affected areas.

Some of the events that have occurred either through willful planning or serendipity, include: substantial improvement to the fisheries as a result of environmental improvement, quota management, or sea lamprey control, noted particularly in Lake Erie, the Bay of Quinte and Green Bay; reduction of particular contaminant inputs (e.g. DDT, DDE compounds) and rapid response by biota, especially aquatic birds (e.g. in Green Bay and Black Bay); and substantial reduction in nutrient input, with corresponding improvement in water quality and favourable biotic response (e.g. Bay of Quinte, Lake Erie). These examples and many other recent events underline the value of rehabilitative measures. However, much remains to be done.

On the down side, mesotrophic systems are constantly faced with new threats, in particular, the invasion of potentially dangerous, exotic species and the introduction of a vast array of new toxic compounds. Shoreline development including the loss of adjacent spawning and nursery areas continues at a frantic pace. The possibility of further wetlands development poses an additional threat to an integrated mesotrophic system. We emphasize in this report that the use of biological surrogates for mesotrophic environments, appropriately framed within an ecosystem approach, will provide a timely and effective response to the new ecosystem inputs, that are occurring with increasing frequency.