A Conceptual Approach for the Application of Biological Indicators of Ecosystem Quality in the Great Lakes Basin

A Joint Effort of the International Joint Commission and the Great Lakes Fishery Commission

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Notice

This report to the Science Advisory Board was prepared by the Work Group on Indicators of Ecosystem Quality (WGIEA) of the Aquatic Ecosystem Objectives Committee (AEOC). Though the Board has reviewed and approved this report for publication, some of the specific conclusions and recommendations may not be supported by the Board.

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Prologue

A vital need exists for a pragmatic and economically viable approach towards ecosystem management within the Great Lakes Basin and elsewhere. Within this document we attempt to provide a partial solution to this need. A new and somewhat unconventional conceptual basis for ecosystem understanding is prerequisite to any level of practical application in the future by the ecosystem manager. Our contribution was not intended to be panacean in scope, but rather a logical entry into ecosystem approach concepts and an extension of them into the realm of practicality. We trust that the subsequent sequence of events will include an increasing awareness of the power and economy implicit in this approach by managers who, hopefully, will see fit to apply the concepts within their own jurisdictions.

As a final caveat, we urge managers and scientists alike to avoid a reductionist dissection of this manuscript into its component parts, but rather to read and absorb the contents from a holistic and interdisciplinary stance.

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Executive Summary

The International Joint Commission (IJC) and the Great Lakes Fishery Commission (GLFC) according to their respective mandates, have collaborated in a new initiative under the general purview of an ecosystem approach directed towards the management of the environment and resources of the Great Lakes Basin. This initiative logically followed upon the 1955 Great Lakes Fisheries Convention and the 1978 Great Lakes Water Quality Agreement between Canada and the United States, both of which were intended to provide continuing protection under rational use for fishery resources and the environment within the Great Lakes Basin ecosystem.

A prerequisite for appropriate application of an ecosystem approach is the need to determine the current state of health of the environment and its contained resources and to identify the areas where the system may be unduly stressed by cultural interventions. The task of advancing the ecosystem approach concept and subsequent application in management was assigned to a Work Group of the Aquatic Ecosystem Objectives Committee (AEOC) (Work Group on Indicators of Ecosystem Quality (WGIEQ)) which, in turn, reports to the Great Lakes Scientific Advisory Board of the International Joint Commission. The WGIEQ used as its general terms of reference the First Recommendation of the First Biennial Report (IJC 1982) under the Water Quality Agreement of 1978. The WGIEQ's more specific terms of reference were to: appraise, evaluate and critique the feasibility of using an indicator/integrator organism as a surrogate of the state-of-health of the Great Lakes; to produce an ecosystem objective and supporting rationale for inclusion into any future revisions of the 1978 Water Quality Agreement; to identify appropriate ecosystem variables for future monitoring; and to explore and develop, where appropriate, other ecosystem approaches applicable to the Great Lakes Basin.

This assignment was completed and is outlined in this document.

The WGIEQ acknowledged that there were many candidate "ecosystem approaches", but for the sake of consistency, the previous definition of the former Great Lakes Research Advisory Board (1978) was accepted as an appropriate description for the intended application. Thus, an ecosystem approach was defined as: "The view of the Great Lakes Basin as an ecosystem, in biospheric perspective; encompassing all interactions within this ecosystem, and transport of materials in and out via air as well as waters, by migratory species and by international transport". This perspective of an ecosystem approach was viewed from the position of man as an integral part of the system. .

In order to develop the indicator organism initiative further, within the concept of an ecosystem approach, an ecosystem objective was formulated using an exemplary organism, the lake trout. A realistic ecosystem objective for the Upper Great Lakes was deemed to be the attainment and maintenance of a quality oligotrophic environment ensuring the perpetuation of a cold-water community of organisms. Within this broad objective, the lake trout as a

terminal predator would be used as an ecosystem surrogate to detect any marked changes to the biota or environment. These changes would be detected within the natural community of cold-water organisms which, in turn, would reflect the state of the oligotrophic environment.

The nature of ecosystems is described with emphasis on their hierarchic attributes, integral effects, emergent properties and responses to external stresses. The qualitative difference between simulative, natural-type stresses and aberrant stresses (both of cultural origin) is shown and contrasted. It is recognized that natural communities of organisms may show more resiliency to the former type of stresses because of exposure over evolutionary time. A host of other ecosystem characteristics is identified and documented as potentially useful for quantifying change.

A determination of ecosystem stress resulting in changed conditions requires knowledge of conditions within the Great Lakes Basin ecosystem before European settlement, that is, before major cultural intervention. For this purpose, historic information from about 200 years ago seemed adequate for establishing a benchmark for a high quality environment. A description of the Great Lakes environment is provided for both an early period and currently, treating especially limnological conditions including water chemistry, nutrient loadings, epizootic outbreaks, domestic wastes and toxic substances. It is noted how land and atmospheric changes have ultimately and inexorably been expressed in terms of major limnological change to the Great Lakes. The importance of wetlands toward the maintenance of a stable, high quality environment is emphasized, despite their rather restricted extent within the watershed. Finally, contiguous systems influence one another through transport of materials, energy or organisms. Consequently, the Great Lakes were not considered as discrete basins, impervious to outside influences.

Historically, fish communities *were* substantially different from current Great Lakes' inhabitants in that they were comprised only of native, co-evolved species, were integral in nature, consisted of diverse stocks of large mean size and were generally more stable or "harmonic". In the Upper Great Lakes, fish communities tended to be dominated principally by two top predators, the lake trout (a complex of stocks) and the burbot, while the principal forage or prey species consisted of a species flock of coregonines (ciscoes and whitefishes). The sea lamprey, a selective predator, rapidly eliminated the two top predators and the largest coregonines, albeit assisted by a highly exploitive fishery. This likely resulted in introgression among many of the remaining closely related coregonines through the loss of predation refugia. It was emphasized throughout that Lake Erie and Lake Ontario are substantially different from the three Upper Great Lakes because of differences in native species composition, limnology or historical events. Development of the indicator species concept takes these factors into consideration. For example, in Lake Erie, a mesotrophic rather than an oligotrophic environment was seen to be the ideal and another set of indicator. organisms was required to reflect these differences.

In the assessment of the status of fish communities, trophic structure and particle-size density are seen as two promising avenues for further exploration, both differing substantially from the more conventional species-by-species approach.

A general set of criteria for biological indicators of ecosystem quality was devised and various organisms were classified against the standard of an ideal indicator organism. Candidate indicator organisms were divided into two categories; essentially, those intolerant of most cultural stresses and those tolerant of the same suite of stresses. The intolerant species were exemplified by lake trout and the amphipod, _Pontoporeia hoyi_ for oligotrophic systems while the walleye and the burrowing mayfly filled this role for mesotrophic systems. Carp and sludgeworms were designated as tolerant organisms for both oligotrophic and mesotrophic systems.

Generally, criteria for a useful indicator required that the organism: have broad distribution.; be indigenous and integrative in nature; have well documented and quantified niche dimensions; will exhibit a graded response to human intervention; will serve as a diagnostic tool for specific stresses; will not overlap other indicators markedly with regard to their indicative capabilities; will have historic, preferably quantified information pertaining to their abundance and other critical factors; may be easily collected; will maintain itself through natural reproduction; may be useful in laboratory experiments; responds to stresses in a manner that will be both identifiable and quantifiable; will be important to humans and readily recognized by them. The lake trout, of all organisms considered, came closest to satisfying all the prerequisites of these criteria and therefore was designated as a primary, indicator/integrator organism for oligotrophic environments; _Pontoporeia hoyi_, although falling short of measuring up to some of the criteria, will serve as a useful complementary indicator to the lake trout. Forster's tern serves as a suitable indicator for wetlands areas, although it too, falls short of fulfilling many of the requirements of an ideal indicator organism.

Having selected the lake trout as the organism about which the "indicator of ecosystem quality" concept would be further developed, the next step in the process was to document and quantify each critical niche dimension and habitat requirement of that species. In this regard, much has already been done and needs only to be synthesized from the available literature. Of particular interest is the fact that while the lake trout is usually considered to be but a single species, thirty years ago, in the Upper Lakes, the lake trout complex consisted of a multitude of stocks or races; each with specific morphological, ecological and behavioural characteristics. Recognition of this phenomenon plus the fact that limits to fundamental life requirements among the stocks were essentially the same (temperature, oxygen and metabolic considerations, for example), exemplified how useful stock diversity could be in representing various habitat dimensions including: the pelagic and demersal zones; the nearshore and distant shore littoral; and the deltaic regions and lower reaches of some-of the larger rivers. Hence the lake trout complex, which consisted of-many diverse stocks, served admirably to represent the ecologically heterogeneous environment of the Great Lakes much better than any other existing single species.

Effects of cultural impacts on ecosystems are elaborated through their effects on the key indicator species. Cultural effects on lake trout generally result in marked departures from mean harvest level, changes in mean size, changes in species ratios, loss of recruitment, increase in the incidence of deformities, changes in growth rates, aberrant behavioral patterni, changes in genetic constitution or introgression of stocks; to mention but some of the observables. Lake trout will respond in a more

specific manner to certain stresses such as: phosphorus loading; acid
precipitation; heavy metals; xenobiotic substances; or contaminant mixtures.
Various biochemical indices, as elicited within the lake trout, were
'identified as having potential value in identifying stresses of unknown
origin, particularly previously unidentified chemicals in the environment.
Those indices offering the greatest potential insight into this problem *in* the
near future are mixed function oxidases (HFO) and adenylate energy charges
(AEX). Further development of these indices is required before practical
application can be made of them. Major alteration of habitat is another
culturally induced stress which may be measured through an indicator organism.
Foremost among these are: sedimentation; cultural eutrophication; and
deforestation, all of which to a large degree, exert a similar stress syndrome
on lake trout.

Exploitation also results in serious effects on an integrated fish
community. These effects may be difficult to separate from those resulting
from other cultural perturbations. Some of these negative effects include a
reduction in mean size and stock complexity and a change in trophic
interrelations, each contributing to instability within the community.

Introduction of non-native species into an integrated, harmonic fish
community may also wreak havoc or alternatively, appear relatively benign.
Often the effects are not well defined or even known. The sea lamprey,
however, has had a major detrimental and well documented effect, especially off
lake trout and burbot, that reverberated through the remainder of the
community in the form of rapid change leading to unpredictability. Certain
other exotic species presumedly had significant effects on the indigenous
community. These include two forage species, the rainbow smelt and alewife,
the Pacific salmons and one invertebrate, <u>Eurytemora affinis</u>.

An elaboration on the effect of coho salmon on lake trout suggests that
the former species would initially be beneficial to the latter because of its
predilection for feeding on alewives. Reduction of alewives in turn, provides
a release in competition for the native coregonines, a natural food of the
lake trout. If the forage base *were* severely reduced however, the coho may
ultimately have a negative effect on the lake trout through competition for
limited forage resources. To a certain extent this scenario is already
underway in Lake Michigan.

An elaboration of the practical application of the indicator organism
approach within an ecosystem concept suggests that it should not be used
merely to complement those monitoring and management techniques already in
place. Because of the economy of the indicator approach, it has the potential
when fully operational, of reducing the need for certain other types of
information that are more costly to collect and have little real meaning to
the public. It is recommended that the indicator organism approach be applied
in conjunction with other recent initiatives for rehabilitating the Great
Lakes ecosystem.

While a practical application may not have been adequately clarified in
terms of quantification, the concept of using indicator/integrator organisms
for confirmation of the relative health of an aquatic system may be considered
as a <u>fait accompli</u>. Quantification and synthesis of the various niche

dimensions of the lake trout and complementary indicator organisms is the next logical step in the procedure towards successful application of the concept. Further development of a preliminary, dichotomous key of stress symptoms is also a desirable goal as the resulting product will provide both ecosystem managers and the public with a rapid, first approximation test of the state-of-health of an aquatic ecosytem.

The indicator/integrator organism approach has many other potential benefits, including that as an indicator of rehabilitation success and in helping to establish the proposed rehabilitation trajectory. Its versatility precludes the possibility of becoming "locked-in" to an unprofitable and expensive management approach.

Preface

The 1972 Great Lakes Water Quality Agreement between the United States and Canada affirmed the commitment of the two countries to restore and enhance the water quality of the Great Lakes. Among its provisions, this agreement included specific objectives for various properties of Great Lakes water quality and called for the development of objectives for additional significant properties. These objectives are defined as '... the concentration or quantity of a substance or level of effect that the Parties agree, after investigation, to recognize as a maximum or minimum desired limit for a defined body of water or portion thereof, taking into account the beneficial uses or level of environmental quality which the Parties desire to secure and protect . . .". The development of such objectives has been based primarily on information gathered by exposing individuals of certain species of biota to known concentrations of specific chemicals (or, in a few cases, known levels of physical properties) in the laboratory. The effects, if any, on the survival, reproduction, or other biological processes at different concentrations are observed and inferences drawn as to the effects on populations of the same or related organisms in the Great Lakes.

Use of objectives based on such toxicity testing can provide a large measure of environmental protection. However, it also has several major potential weaknesses as follows:

(1) The information on relationships between effects and concentrations of polluting substances is obtained in the controlled environment of the laboratory. To apply these results to the field, it is necessary to assume that the laboratory results are representative of what actually occurs in the natural environment. In general, this assumption is unproven. In situations where attempts at verification have been made, the laboratory results often have been found to be in rather poor agreement with the effects that actually were observed in the field.

(2) Only a limited number of species are included in the toxicity testing. It must be assumed that no species that are substantially more sensitive than those tested are- present in the environment to be protected. Although toxicity testing often attempts to concentrate on the forms that are believed to be the most sensitive to the pollutant under study, there is no assurance that this is always the case.

(3) Chemical pollutants are tested singly, yet in most natural environments, including the Great Lakes, a plethora of chemical substances in both dissolved and particulate form is found. The effects of the tested chemicals may be altered in the real world by synergistic or antagonistic relations with some of these co-occurring substances.

(4) There are many polluting substances in the Great Lakes for which
    there is not adequate toxicity information to permit development of a
    satisfactory objective. It is known that there are a number of
    pollutants present which have not, as yet, been identified and
    measured. Also, among the pollutants that have been identified, there
    are many for which no studies (or only very inadequate studies) have
    been conducted to determine effects. Further, even among the
    substances where it has been possible to develop objectives, there
    are many where the only information available relates to acute
    toxicity. Nothing is known concerning chronic toxicity or other more
    subtle effects which may be sublethal, over a long term. Thus, for
    the great majority of the Great Lakes area, no objective or only one
    that may well be inadequate can be developed, yet the substances in
    question may be having substantial organismic and environmental
    effects.

(5) Consideration is only given to the direct effects on the species
    under study. All species occurring in the Great Lakes are part of
    the complex web of trophic and other ecological interactions that are
    present in this ecosystem. Thus, relatively unimportant effects on
    the survival or some other aspect of the biology of the species under
    study could have major repercussions in the populations of other
    species and hence community integrity, or even on the ecosystem as a
    whole.

The United States and Canada signed a revised and strengthened Great Lakes
Water Quality Agreement in 1978. At that time the weaknesses in the
objectives approach *were* recognized and great emphasis was placed in this
Agreement, not just in controlling levels of chemical pollutants, but assuring
the biological integrity of the waters of the entire Great Lakes Basin
ecosystem.

To help further this goal, the IJC's Science Advisory Board established
the AEOC shortly after the Agreement was signed in 1978. Included in the
charge for this group was the directive that it develop ecosystem objectives
for the Great Lakes. The AEOC considered what form such ecosystem objectives
should take. It was concluded that these objectives should specify the level
or condition of certain biological properties that could serve as indicators
of the overall condition or health of the ecosystem.

The AEOC also concluded that to develop such indicators, it would first be
necessary *to* specify, in more detail than in the 1978 Agreement, the desired
state of the ecosystem. The 1978 Agreement reaffirmed the determination of
the two countries"... to restore and enhance the water quality of the Great
Lakes System . . .". It states the purpose of restoring and maintaining"...
the chemical, physical, and biological integrity of the waters of the Great
Lakes Basin Ecosystem . . .". The AEOC concluded that the spirit of the
Agreement could best be met by setting a general objective directed toward the'
restoration and maintenance of a Great Lakes biological community as similar
as was practical to that which was present before the influence of human
intervention. To advance this objective, the AEOC has, in fact, recommended
to the IJC that the following general objective be added as section (f) of
Article III of the Water Quality Agreement:

The waters of the Great Lakes System should be"... maintained and, as necessary, restored to a condition where a balanced and stable community of organisms is present which resembles as much as is feasible and practical the community that existed before the advent of anthropogenic intervention."

In attempting to develop indicator objectives, the AEOC quickly recognized that it would not be practical to attempt to have any one of these objectives applied to the entire Great Lakes System. Physical and chemical properties in various parts of the Great Lakes are quite different from historical values, as such the same community of organisms is not now present throughout all areas of the Lakes nor was the same community present in all areas of the lakes even before the advent of human intervention. Therefore, no one indicator objective can be expected to be appropriate everywhere. However, it was also recognized that a rather similar community is present throughout a large part of the offshore waters of the Upper Lakes and was probably also present in much of the offshore environment of the Lower Lakes before the onset of man's influences. The major exception to this is the quite distinct and separate offshore community that is believed to have always occurred in the shallow Western Basin and probably also in the Central Basin of Lake Erie. The presence of the widespread and similar offshore community everywhere but Western and possibly Central Lake Erie, was considered to present a promising situation for furthering development of a general indicator objective. Consequently, it was decided to focus initially on development of an objective for this particular community as a test of the total concept. The ubiquitous offshore community occurs in an environment that can be characterized basically as cold and nutrient-poor, that is, austere. Thus, throughout this document we shall we refer to this community as the cold-water, oligotrophic community of the Great Lakes.

To help with this task, the AEOC established a Work Group. Experts in the use of biological indicators of ecosystem quality were asked to serve on this group which was designated the Work Group on Indicators of Ecosystem Quality (WGIEQ). The WGIEQ was given the general charge of exploring the entire question of use of biological indicators for assessing ecosystem health in the Great Lakes. However, it was also given the specific charge of developing a basis for the establishment of an ecosystem objective for the cold-water oligotrophic community of the Great Lakes. This document presents the results and conclusions of the WGIEQ concerning these charges.

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1.0 INTRODUCTION

1.1 BINATIONAL TREATIES

The Great Lakes Water Quality Agreement of 1978 between the United States of America and Canada made a significant advance beyond the previous agreement of 1972 by "recognizing that restoration and enhancement of the boundary waters cannot be achieved independently of other parts of the Great Lakes Basin Ecosystem with which these waters interact" (International Joint Commission 1978). Hence, the treaty Parties, with appropriate insight, advanced the concept of an "ecosystem approach" towards the solution of a steadily deteriorating environment in the Great Lakes Basin and surrounding watershed.

The Great Lakes Science Advisory Board of the International Joint Commission (IJC), following the lead provided by the 1978 Great Lakes Water Quality Agreement, approved the formation of an Aquatic Ecosystem Objectives Committee (AEOC) which among other responsibilities, would develop and review water quality objectives and establish work groups to create position papers on which to base the development of new or altered objectives, to include an ecosystem objective. Hence, in August 1982, the Work Group on Indicators of Ecosystem Quality (WGIEQ) was created under the aegis of the AEOC. Its primary function was to develop appropriate ecosystem objectives through the utilization of biological indicators of ecosystem quality.

A parallel and mutually supportive initiative is currently sponsored by the National Research Council of Canada (Kerr, et al., 1985, in press). Moreover, many informative documents exist that purport to develop conceptual frameworks and philosophical foundations of ecosystem theory (e.g. Beanlands and Duinker 1983; Warren, et al., 1979). We have investigated several of these, but not exhaustively.

1.2 TERMS OF REFERENCE

In its First Biennial Report under the Great Lakes Water Quality Agreement of 1978, the IJC enumerated as its First Recommendation (IJC, 1982):

Note:

Scientific names of organisms are listed in Appendix I.
A glossary of terminology is included in Appendix II.

"the Parties, Jurisdictions and others foster and encourage policies, programs and institutions that:

(a) help develop and maintain a long term ecosystem perspective with respect to the pursuit of its other legitimate goals and to be more anticipatory in its actions;

(b) encourage research, monitoring and analysis of man's impact on ecosystems in order to facilitate personal and institutional actions that are consistent with ecosystem realities;

(c) help make scientific and technical information about man's place in nature more accessible, understandable and relevant to the individual citizen;

(d) encourage citizen involvement in identifying and shaping long term ecosystem goals in order to build greater community consensus and commitment; and

(e) encourage non-adversarial measures for preventing and resolving conflicts arising over the use of shared air and water resources."

The WGIEQ met under the aegis of the AEOC of the IJC's Science Advisory Board (see Appendix III for detailed terms of reference). As would be expected, the activities of the WGIEQ related to at least some of the various elements of the IJC's first set of recommendations.

The relevance of the WGIEQ activities to these recommendations may be sketched as follows, where each lettered paragraph refers to the corresponding paragraph of the IJC's recommendation (IJC, 1982). Here, the case is made with respect to lake trout, the proposed key indicator for oligotrophic parts of the Great Lakes. Quite similar statements would apply to the walleye as an indicator of mesotrophic parts of these ecosystems, or to any other proposed indicator organism or biotic community.

> (a) For at least some of the proposed "indicators of ecosystem quality", there exists a long-term historic record of relative abundance. For the most preferred indicator, lake trout, annual harvest data are available in fairly reliable quantitative form back to the 1860's; at least for Canadian waters. Less precise, but nevertheless useful data, exist before this time and trace back to the beginnings of European missions, fur trading posts and settlement in the Great Lakes Basin. The WGIEQ will take advantage of these data series by applying a long-term perspective towards developing the basis for using lake trout as an indicator of ecosystem quality. In further compliance with the recommendations of IJC, the use of the lake trout to provide symptoms of stresses yet to be identified is anticipatory indeed!

Furthermore, the WGIEQ believes that its choice of lake trout as an indicator in developing an objective for the cold-water community of the Great Lakes is anticipatory of the needs for rehabilitation of the Great Lakes Ecosystem. The binational treaty of 1955 which created the Great Lakes Fishery Commission (GLFC) has as one of its key objectives the rehabilitation of lake trout in the Great Lakes. To do this the water quality programs developed under IJC coordination must succeed so that the habitat required by this fish is maintained where it is still present and restored where it has been degraded by man's activities. Thus, the use of lake trout is anticipatory of GLFC needs and further, it aids in providing an ecosystem approach by drawing the programs of the IJC and the GLFC into closer harmony.

(b) The WGIEQ has undertaken to review the state of our understanding of man's impact on the Great Lakes ecosystems as reflected in the responses of the proposed indicators. As indicated above, the time series on lake trout populations in these lakes - monitored routinely for over 12 decades - is fully available. Intensive analysis is currently underway, fostered in part by the GLFC's Board of Technical Experts, to understand the interaction between habitat degradation (or recovery) and improper fishing practices (or the converse) on the status of the lake trout populations. Clearly, such understanding will help to inform persons and institutions on the interrelatedness of the factors that impact the Great Lakes ecosystem.

(c) Time series data on the status of environmental or resource components of direct interest to society are easily understood. Geographic maps identifying the relative status of ecosystem quality are also easy to comprehend. The data available to the Work Group lend themselves to presentation in such forms and so the rationale developed for the use of lake trout should be accessible to the general public. The Work Group believes that this is especially true, because the present state of lake trout stocks in the Great Lakes is already widely recognized and some of the causes of their collapse have been widely discussed and understood by the interested public.

(d) A recent initiative by the Joyce Foundation and the Michigan United Conservation Clubs has sought to develop a binational constituency of interested citizens, Great Lakes United, based on strong interests by anglers, environmentalists and
- naturalists concerning the well-being of the Great Lakes. For many of these activists, the state of the salmonids, including the lake trout, is a key concern. Mobilization of-citizen forces is consistent with the mandate of the IJC concerning the Water Quality Agreement of 1978 and with the mandate of the GLFC to foster rehabilitation of lake trout. The development of easily recognized and understood ecosystem indicators such as one based on lake trout, will aid these forces and should encourage increased citizen involvement. As a concrete example, "The Wild Salmonid Watch", sponsored by the International Union for the

Conservation of Nature and Natural Resources (IUCN), has
increased public participation in environmental matters through
the use of salmonids as sensitive indicator species.

(e) Some of the indicators should be species or ecosystem features
that are perceived to be desirable, in their own right, by
virtually all members of the public. Aside from questions of
tradeoffs, hardly anyone would now tolerate extinction of more
lake trout stocks or settle indefinitely for the current greatly
diminished status of this species in all the Great Lakes. On
that point it would be difficult to stage an adversarial
contest. The wide favour in which this species is held should
foster a cooperative spirit toward the rehabilitation of the
species and its habitat.

The above statements reflect the views of the Work Group (and implicitly,
its fundamental terms of reference) and demonstrate that its activities are
consistent with the purposes of both the IJC and the GLFC. That the
activities should span the mandates of the two Commissions may be seen as
meeting one of the major tests of an ecosystem perspective.

The particular example of an indicator species, i.e. lake trout, used in
this preamble demonstrates a fortunate coincidence that at least one species
is very well suited for that role. But one yardstick is not indicative of all
the important features of ecosystem quality in the Great Lakes. Thus, using
the status of the lake trout will provide only a very imperfect reflection of
the status of the ecosystem in such areas as shallow warm bays, wetlands and
small tributaries and even the whole of the relatively warm and shallow
western basin of Lake Erie. For these areas other indicators are needed.
Further, even in the cold, open waters of the Great Lakes where lake trout
naturally thrive, other indicators will also be needed to provide a broadly
reliable picture of ecosystem status.

Finally, our purpose in this section has been to demonstrate that the Work
Group activities are consistent with the IJC's first set of recommendations,
not that they are in any ultimate sense either necessary or sufficient. But as
an element of a broad program mix relevant to these recommendations, the lake.
trout indicator developed by this Work Group is an appropriate, cost efficient
aid to meeting the goals of the 1978 Great Lakes Water Quality Agreement.

1.3   THE CONCEPT OF THE ECOSYSTEM APPROACH

In a special report of the Great Lakes Research Advisory Board (forerunner
to the Science-Advisory Board of IJC), the ecosystem approach was described as
"based on a man-in-system concept rather than on the system-external-to-man
concept inherent in the 1972 Great Lakes Water Quality Agreement" (Great Lakes
Research Advisory Board 1978). In this regard; the 1978 Agreement may be
perceived as a significant advancement over that of 1972, in the
identification of the cause of degradation of the Great Lakes environment as
ecosystemic in nature. The Research Advisory Board further recognized that an
integrative framework was required for the implementation of an ecosystem
approach which would involve the various State, Provincial, Federal and
Binational Agencies with both environmental and resource interests and
responsibilities relative to the Great Lakes Basin Ecosystem.

Finally, an ecosystem approach was defined as "The view of the Great Lakes Basin as an ecosystem, in biospheric perspective; encompassing all interactions within this ecosystem and transport of materials in and out via air as well as waters, by migratory species and by international transport" (Great Lakes Research Advisory Board 1978).

1.4   THE ECOSYSTEM OBJECTIVE

Given the commitment to determine ecosystem quality through the use of one or more indicator organisms, an ecosystem objective based on these organisms would be an appropriate target for ecosystem managers of the Great Lakes and conjoining waters. Initially, this objective would be most appropriate for the three Upper Great Lakes. (A modified form of the objective for Lakes Erie and Ontario would take into account their trophic status, natural communities and inordinately high stress levels.) It is recognized that this objective sets a target to be strived for and that practical consideration for the current state of cultural development around the Great Lakes Basin may mitigate somewhat the level that may actually be attained.

Further, it is a practical first step to develop the concept of determining ecosystem quality using a single species, the lake trout, together with appropriate complementary indicator organisms. Knowledge of the fundamental life requirements of the lake trout must, of necessity, precede, the statement of the objective. However, in anticipation, an optimal, but [1] realistic ecosystem objective for each of the Upper Great Lakes within the next 50 years might be: *the attainment and sustained maintenance of an oligotrophic environment of sufficient quality over a wide geographic range, to ensure the perpetuation of a cold-water community of organisms. Naturally reproducing, genetically diverse stocks of lake trout would be major terminal predators and therefore a primary controlling component of a relatively stable community. Implicit within this objective is the understanding that optimal harvests of lake trout and other species may be taken by various user groups in proportion to their different intrinsic production rates, providing that there is no marked alteration of either the community integrity or its long-term level of steady-state yield (internally, production processes will accelerate, age structure will change and some other density-dependent factors will respond positively).*

Another major consideration of the ecosystem objective is the condition that the various vertebrate, invertebrate and plant species within the biotic community will be contaminant-free (according to the objectives established by the Great Lakes Water Quality Agreement of 1978) and the harvested segment intended for human consumption, shall constitute a palatable and safe food product.

2.0 THE ECOSYSTEM

The definition of an ecosystem is variable and the term has been applied to systems ranging from the most minute to those of near-biospheric proportions. Within the current context and according to our terms of reference, the ecosystem will encompass all of the Great Lakes Basin (Figure 1) and all that is contained therein, such as living organisms including man and non-living matter including all of the aquatic and terrestrial substrate and the enveloping atmosphere. It is recognized that each component part of an ecosystem interacts with every other part either directly or indirectly through pathways of various lengths and variable degrees of complexity. Also, each component is influenced by a variety of feedback mechanisms. In essence, an ecosystem in its most general sense, is integral and may be evaluated by measures of inputs from other contiguous systems in the form of materials and energy, as well as by its outputs to other conjoined systems. Culturally unstressed ecosystems tend to retain a steady-state, that is, their properties and outputs remain within moderately predictable, relatively narrow boundaries.

Many of the biotic outputs of culturally unstressed ecosystems, because of their moderately low levels of annual regimen variability, are readily predictable and therefore may be tractable from a management point of view in terms of a retention of sustained yields. For example, fish harvests, which are one output of an ecosystem, may be more easily managed when other cultural stresses on the system are minimal. Specifically, sustainable lake trout quotas may be more easily ascertained and at a much lower cost to management, if sea lamprey depredations were not a factor to be considered (e.g. Smith 1980). Appropriate management structures under ideal conditions ensure optimum yields, maximum prices and preferred long-term market conditions. The predictable nature of fish yields in these instances removes the uncertainty from the "gearing-up" process and ensures greater efficiency of the whole exploitation and marketing procedure.

Ecosystems subjected to inordinately high levels or various mixtures of cultural stresses, often degrade in a predictable and orderly fashion according to the particular suite and temporal order of the stresses (e.g. Smith MSb). Lake Erie provides a classic example of this type of orderly degradation of fish communities due to multiple stresses of cultural origin (Regier and Hartman 1973). Hence, populations of fish species in Lake Erie declined towards extinction starting with the lake trout and lake sturgeon and progressed through lake whitefish and lake herring, sauger, blue pike, walleye and yellow perch. By 1970, the exotic and low valued rainbow smelt was the predominant species over much of Lake Erie. Interestingly, with the advent of partial control of cultural eutrophication (e.g. Dobson 1981) plus the application of more stringent quota restrictions on the fisheries (tempered in part by a fortuitous ban on mercury-laden species from the marketplace), a reversal on the sequential loss of species from Lake Erie has taken place at least to the extent that restoration of the walleye fishery to its former level of abundance has occurred.

Figure 1   The Great Lakes Basin Ecosystem and contiguous systems
             contributing to, or receiving materials from the Great Lakes. This
           . simplified scheme shows the major pathways of materials transfer
             among the contiguous systems. Because of these exchanges, the
             Great Lakes Basin may not be regarded as a microcosm, but rather as
             an integral part of a much larger system, the Atlantic watershed.
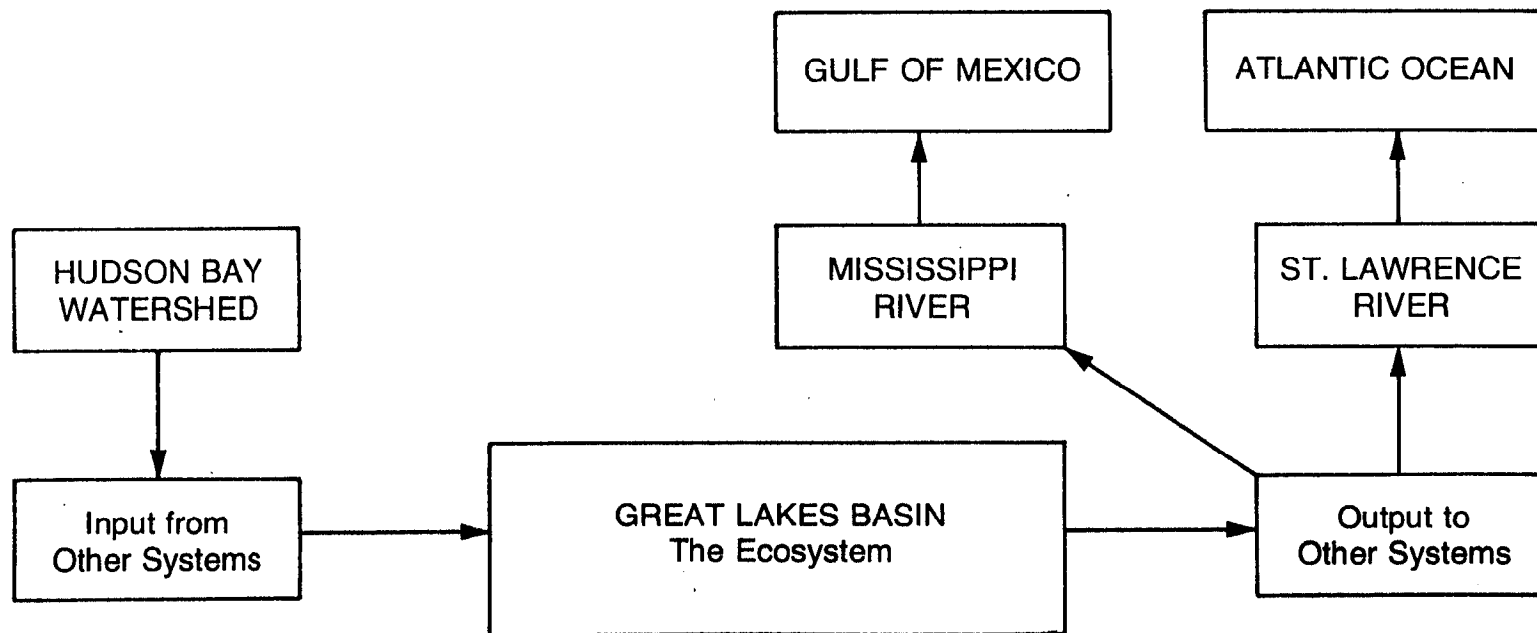
Because of the trophic-hierarchic nature of biological organization within an ecosystem, stress effects may be perceived first in specific ecosystem compartments due to stress specificity, bioconcentration of toxicants, inordinate sensitivity of an organism, or through the integral effects among component organisms, *or* between organisms and their abiotic environment. Consequently, stress effects may be most easily observed at the hierarchic level that first demonstrates readily recognizable symptoms of malaise, which may not necessarily be the level of greatest ultimate stress impact.

Culturally induced stresses such as contaminant or nutrient loading, sea lamprey predation, overexploitation and other factors, may be detected at various levels of the biological hierarchy, including those of species, stocks (genetic), populations, communities, or ecosystems (Figure 2) and measurable responses may be made practically at any of these levels. Complementary to this approach, more traditional methods of measuring environmental stresses, such as water quality assessment, provide another dimension to the identification of stresses and the response of the total ecosystem to them.

2.1   ECOSYSTEM ATTRIBUTES AND OUTPUTS

The ecosystem as defined (Section 2) may be subdivided conveniently into two major integrated realms: the biotic sector including all plants, animals and other living matter and derived organic substances; and the abiotic sector, which encompasses inorganic portions of the substrate, the water and the aeolian environment.

Ecosystem attributes and outputs, from an anthropocentric point of view, consist of properties and products of ecosystems that may be perceived by man as beneficial in a consumptive, commercial, recreational or aesthetic sense. These beneficial qualities of ecosystems, which reflect the effects of the interactions of a multitude of system and subsystem components, may be diminished both quantitatively and qualitatively by various cultural stresses.

Products of aquatic ecosystems of major importance to man include: clean water for drinking and swimming; uncontaminated fishes and waterfowl for food and recreation; and available primary resources for many commercial, industrial and transportation applications. Aesthetic perception of aquatic ecosystems or certain components of these systems such as the lake trout, is an example of a system property that is not directly consumable, but nevertheless valuable.

2.1.1   Hierarchic Levels

An ecosystem may be perceived as having many hierarchic levels (e.g. Figure 2; Allen and Starr 1982) that are closely interwoven in the biotic sector through various interdependencies such as food-web interactions and in the abiotic sector, through water exchange, nutrient leaching and energy flows (to cite but three natural processes). The biotic and abiotic sectors in turn interact at the organism-environment interfaces, where exchanges in materials and energy occur in two directions.

Often unrecognized is that the character and complexity of each hierarchic level of an ecosystem is as dependent on the observer, as it is of the system (Kerr 1982; Rosen 1978, 1979) in that an observer may interact with a system

1. BIOSPHERE
2. GREAT LAKES BASIN ECOSYSTEM
3. OLIGOTROPHIC LAKE BASIN
4. COLDWATER COMMUNITY
5. FISH POPULATIONS
6. LAKE TROUT STOCKS
7. HUMPERS

Figure 2   A hierarchy of seven levels that may be addressed in applying the ecosystem approach. The categories are incomplete and have been arbitrarily selected. The broadest category is the biosphere which includes that part of the world in which life may exist, to the narrowest category, the "humper", a phenotypically distinct stock of lake trout found in Lake Superior. The ecosystem approach may be applied at any of these seven levels. Conventional approaches are usually invoked at the populations or species levels (i.e. 5-7).

in many ways. Consequently, the hierarchic pyramid may be divided in many ways
and at various levels of complexity for convenience of analysis. One level of
the ecosystem hierarchy may be represented by an indicator organism such as
the lake trout (Figure 2). This species has been selected for system
representation not only because of its inherent physiological needs that make
it an ideal surrogate of a typical salmonid or coldwater community in an
oligotrophic environment (e.g. Loftus and Regier 1972), but also because the
public is accustomed to viewing ecosystem hierarchies in terms of familiar,
component parts such as birds and fishes. Much of the information already
available for oligotrophic ecosystems is organized in a format that relates to
individual species and the relative suitability of ambient environments to
each species. Our intention, however, is to interpret the species information
in a broader context relative to major compartments of the ecosystem, that is,
at hierarchic levels of consummate integration.

2.1.2   Integral Effects

The degree of connectedness (Margalef and Gutierrez 1983) of an ecosystem
(a measure of ecosystem integrity) is, somewhat simplistically, related to the
numbers and intensity of interactions among its component parts (both biotic
and abiotic) up to a functional optimum. At the most fundamental hierarchic
level, all ecosystem sectors merge to form the interacting subsystem of biota
and habitat. Biota and habitat may be closely interdependent or only loosely
linked, but nevertheless sustain one another in various degrees. While this"
interdependency may best be exemplified in coral reef formation, it is true of
virtually all biota-habitat interactions. Feed-back from each ecosystem
sector nurtures its complement toward some functional optimum, which in turn,
directs the total ecosystem toward steady-state (i.e. dynamic equilibrium).
The ultimate level of the steady-state may be predictable when constrained
within normally homeostatic boundaries. A closely-knit ecosystem is
integrated throughout, at each hierarchic level and between levels, such that
the total system exhibits a measurable resiliency in the face of stress. The
degree of resiliency may depend on the limits of compensation at each
hierarchic level of the system and internally, within each system
compartment. Fishes, as one ecosystem component, are dependent upon
compensatory responses to natural stresses in order to persist within the
ecosystem. Those species with maximum growth or reproduction compensation
(e.g. alewives and rainbow smelt), as but two examples, tend to have survival
advantage under stress over those species with minimal density-dependent
response flexibility such as lake trout. Consequently, the species and
community compensation characteristic sets the stage, at least in part, for
the sequential order of species and community demise in a culturally stressed
system.

In general, stresses on the abiotic sector of an ecosystem may be more
damaging and enduring to the ecosystem than those on the biotic sector alone,
which may at first respond rapidly within density-dependent limitations. The
optimal complexity within a biotic community provides an appropriate number of
pathways for interaction which, in turn, allow for maximum system integra-
tion. Moderately tight system integration leads to increased community
resilience under stress and hence, a built-in resistance to community
decomposition. The outcome of these ecosystem attributes is increased
survivability of the system as a recognizable and predictable entity. Maximum

levels of survival strategy attained for an ecosystem would seem to depend to a large extent on co-evolution of biotic components in a gradually changing abiotic milieu (e.g. Futuyma and Slatkin 1983).

The converse of this observation would seem to be the generally poor survivorship of monocultures in environments that are deliberately stressed by cultivation, for example, unless they are protected by the erection of artificial refugia, diet supplements and pathogen control.

The integral nature of an ecosystem is admirably represented by some of its components and total integrative effects may best be exemplified by terminal predators, such as the lake trout and walleye for oligotrophic and mesotrophic environments,' respectively. These two species represent a final product of the ecosystem on which people place high value and their continued presence through natural reproduction and in an uncontaminated form, will be indicative of generally healthy and desirable environments.

2.1.3   Emergent Properties

Emergent properties of ecosystems have been defined as macrosystem ecological properties (Kerr 1974) and are often not recognized by those who are more inclined to regard ecosystems from a micromechanistic point of view. In order to best utilize biological indicators as a methodology within the context of the ecosystem approach concept (e.g. Great Lakes Research Advisory; Board 1978), it is most appropriate to avoid undue dissection of the system in favor of a holistic application dealing primarily with system emergent properties. Hence many ecosystem problems may best be approached first at the biospheric level (acid precipitation) or the community level (overexploitation) before close attention is paid to effects on individual stocks or species (e.g. Figure 2).

Unfortunately, a major gap exists between the concept of an emergent property and the practical application of the concept as a means of assessing ecosystem quality. This is due primarily to the need for an appropriate measure of the latter. However, at least two practical applications of emergent property theory have been developed for the community level of an ecosystem. These include the particle-size density hypothesis (Sheldon, et al., 1972) and the morphoedaphic evaluation of fish community yield (Ryder 1965). Both of these concepts are dependent on the conservative nature of ecosystem emergent properties and both have been applied in various contexts as indicators of ecosystem status, from the standpoint of community composition, standing stocks and production, or abundance by size-class. These concepts have been widely discussed elsewhere (e.g. Borgmann and Whittle 1983; Kerr 1974, 1979; Ryder 1978, 1982; Ryder, et al 1974; Sprules and Holtby 1978) and will not be repeated here. (Sections 2.3.5, 4.3, 4.7.2).

2.1.4   Ecosystem Responses To Impacts

An ecosystem by definition, retains a recognizable identity over some prescribed evolutionary time span. Ecosystem outputs may be predictable, within the homeostatic constraints on the system, as affected by the "normal ambient environmental conditions. As an example, ecosystems experiencing thermal impacts from cultural sources that fall within the normal range of

climatic temperature variation, may be adequately buffered through the evolved resiliency of the system. Under these circumstances, the emergent properties of the system, such as fish yield, may remain relatively stable (a conservative response to changing ambience) and therefore be predictable.

Many cultural stresses imposed on an ecosystem, however, fall outside the range of the ability of the system to compensate. In such situations, the system degrades accordingly or is changed in such a manner that its original identity is lost and its emergent properties become less predictable. These cultural impacts may be conveniently grouped into two categories, that is: "simulative" stresses and "aberrant" stresses. Simulative stresses of cultural origin, to have a measurable adverse effect, need to be quantitatively greater than their corresponding natural stresses, or have different temporal regimes (see Table 1). Inordinately high levels of simulative stresses (see Section 4.2.1) may exceed the inherent compensatory ability of a system. Cultural eutrophication, a man-made magnification of a natural condition, falls into this category.

Aberrant stresses on the other hand, are those synthesized by cultural sources and do not normally occur in nature. Consequently, ecosystems may not have developed appropriate compensation mechanisms over evolutionary time by which to preserve their identities against such aberrant stresses of a qualitatively different character (e.g. Johnson 1982). Xenobiotic substances, such as PCB's and Mirex, introduced into the environment, fit readily into this category, as do many of man's physical assaults on the environment such as gravel extraction from spawning shoals.

Recognition of the differences in ecosystem response strategies to these two categories of stresses is critical. Natural background levels of the simulative stresses must be assessed before any cultural effects may be ascertained. In the case of xenobiotic substances, natural background levels do not exist and other considerations such as the qualitative nature of the impact on the system may be more important.

2.1.5   Other Considerations

Many other ecosystem attributes are important when utilizing indicator organisms as measures of integral system outputs in the assessment of ecosystem quality. For example, both structure and function of ecosystems at several hierarchic levels of organization (Figure 2) are worthy of concern. The loss of an integrating component of an ecosystem may be as vital to the structure, function and persistence of the system as would the impediment of a major pathway for nutrient or energy transfer or other critical metabolic processes. The hierarchic structure of ecosystems increases the probability of multiple interactions in many directions in a strictly stochastic sense (e.g. Patten, et al., 1982) and consequently, the potential number of changes arising from stresses.

A non-exhaustive list of important considerations of ecosystems relating to either structure, function or both, include: taxa diversity and equitability (Odum 1971); feedback controls (von Bertalanffy 1968); hysteresis . or overshoot (Kalmus 1966); recursion (Hofstadter 1979); production to biomass ratios (Margalef 1977); immigration-extinction processes (MacArthur 1972); system decomposibility, that is the resistance of an ecosystem to

TABLE 1

"SIMULATIVE" STRESSES DERIVED FROM CULTURAL SOURCES

SIMULATIVE STRESSES FROM CULTURAL SOURCES	MAJOR STRESS AGENTS	PRINCIPAL EFFECTS ON AQUATIC ENVIRONMENT AND/OR BIOTA
Accelerated Thermal Input	Heat	Water temperature increases Increased growth and production
Increased Nutrient Loadings	P	Increased growth of algae; phytoplankton "blooms"; hypolimnia1 O_2 deficits
Aeolian Fallout	SO29 NO_x	Loss of buffering capacity; decreased pH levels; release of labile Al; sequential loss of fauna through reproductive failure
Increased Loadings of Heavy Metals	Hg, Pb, Zn, Cu	Various types of tissue or organ traumas; reproductive losses; accelerated mortality; tissue residues
Forest Fires	P, N, C	Increased water temperatures; disruption of hydrologic cycles; increased water turbidity; loss of homeostasis in nutrient regime; temporary loss of stenothermic species; general rejuvenescence of system

Simulative stresses on aquatic ecosystems from cultural sources: the
additional stress from these sources tends to be additive to the natural
background levels rather than qualitatively different; restoration to natural
levels usually relieves the stress inasmuch as organisms have been genetically
adapted to their-ambient environment through eons of evolution.

disaggregation (Simon 1969); nutrient and energy transfer efficiency (Gates 1980); succession rate (Cody and Diamond 1975); non-dissipative structures (Prigogine 1978); and catastrophe (Zeeman 1977). We have avoided detailed discussion of these ecosystem attributes in order to retain our central focus, but each has been adequately dealt with in the various references above or in more generalized ecological treatises, such as Margalef (1977). Henceforth, we will deal with each ecosystem attribute as the need arises using an indicator organism of preference, but initially, we will develop the concept for oligotrophic systems using the lake trout and the cold-water community as our benchmarks.

2.2   GREAT LAKES ENVIRONMENT, NOW AND THEN

Before ecosystem quality may be judged on the basis of individual indicator organisms or representative communities of organisms for a particular environment, background information of a historical nature is necessary in order to perceive a "healthy" environment (Figure 3). The best available standard for this somewhat subjective consideration would be the quantitative evaluation of Great Lakes' environments and biota prior to any obvious or measurable impact from cultural stresses. Hence, the Great Lakes ecosystem as it probably was prior to 1800 (e.g. Loftus and Regier 1972) would be the idealistic healthy environment toward which today's ecosystem manager might strive. Even barring the possibility of precise quantification of ecosystem characteristics in 1800, the prescribed directionality for improvement of most qualitative ecosystem aspects is implicit in Figure 3.

2.2.1   Aquatic Sector

A paucity of early observations and data make it difficult to compare current environmental conditions in the Great Lakes Basin with the environment in existence before the cultural interventions of the first, non-indigenous settlers. The accounts of early European explorers, missionaries and fur traders (Agassiz 1850; Nute 1931, 1944) are naturally descriptive and provide a general picture of the pristine conditions which existed prior to 1850. For example, Hopkins (1862) was impressed with the clarity of water in the western basin of Lake Erie - "The lake water is so clear that fish can be seen from twelve to fifteen feet below the surface".

Although these descriptions portray a picture of crystal-clear water and an abundance of fishes, they offer little information about the early limnology of the Great Lakes. Ryder (1972) included the Laurentian Great Lakes in a useful comparison of early limnology and fishes in oligotrophic glacial lakes in-North America. Other historical accounts on each of the Great Lakes are included in the proceedings of the SCOL symposium (Loftus and Regier 1972): A comprehensive historical data set on chemical characteristics was compiled by Beeton (1969) for conservative ions and total dissolved solids. Beeton's curves (recently updated by Weiler 1981) indicated that in Lake Superior, concentrations of major ions have remained virtually unchanged while increases in the lower lakes began to occur about 1910 (Table 2). Major inputs of chloride and sulphate to the Great Lakes are from both point and diffuse sources, as well as from the atmosphere. Industrial inputs are an important source of chloride concentrations in Lake Erie. In Lake Ontario, industrial inputs are small compared with the. inflow from Lake Erie which contributes about 60% of the chloride (Weiler 1981).
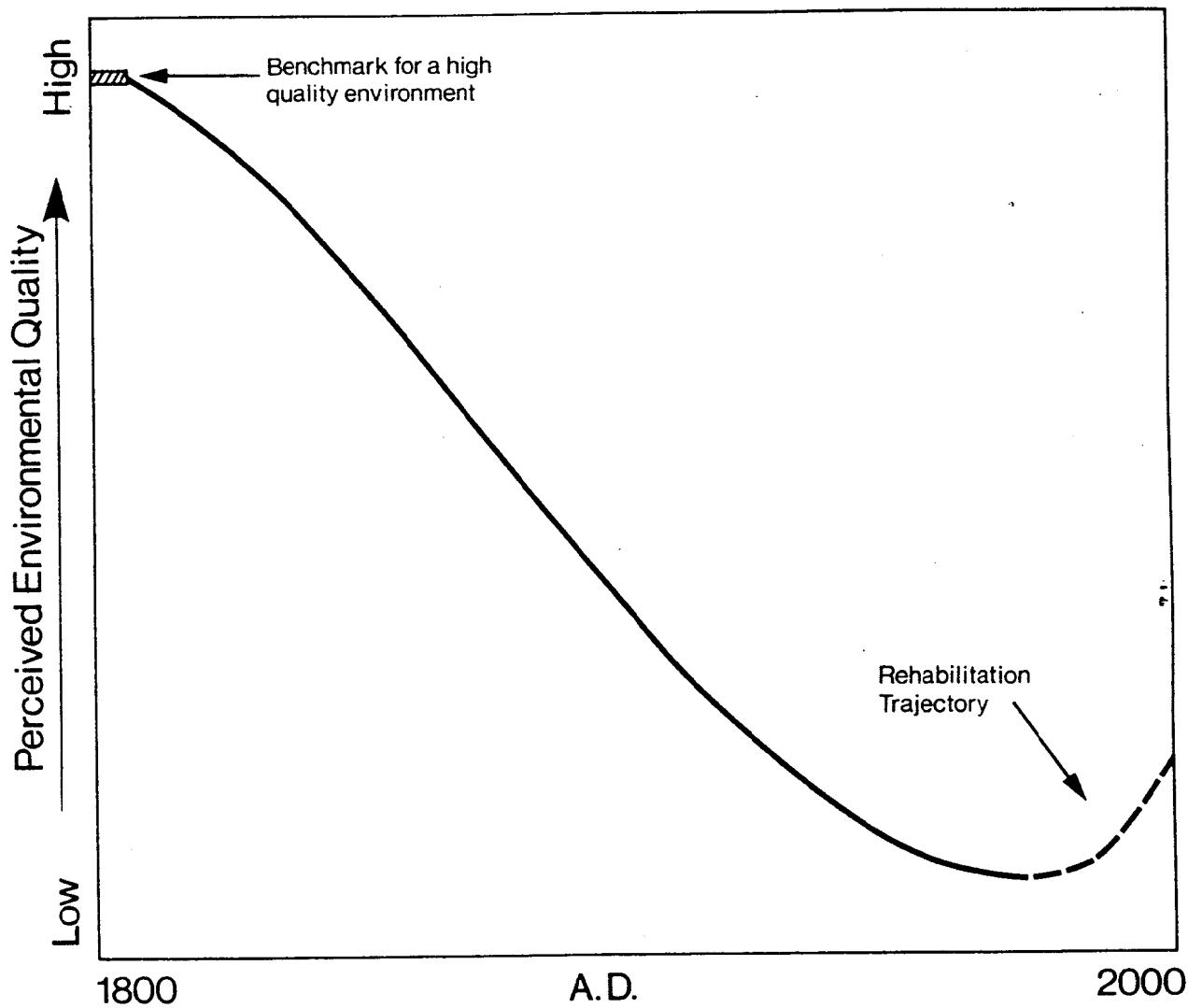
Figure 3: "Healthy" environment of 1800 A.D. provides an appropriate common known, idealistic benchmark for rehabilitation.

TABLE 2

DATES AT WHICH CONCENTRATIONS OF MAJOR IONS IN THE
GREAT LAKES BEGAN TO INCREASE (DERIVED FROM BEETON, 1969)

LAKE	SEQUENCE BEGINS	INFLECTION POINT				
		Cl	SO4	Na/K	Ca	T.D.S.
Superior	1885	NC*	NC	NC	NC	NC
Michigan	1875	1880	1880	1880	NC	1880
Huron	1900	1935	1905	NC	NC	1935
Erie	1905	1910	1910	1930	1910	1910
Ontario	1855	1905	1910	1925	1910	1910

*NC - no change.

Although trends in major ions provide an indication of man's alteration of the Great Lakes ecosystem, they do not provide a direct link with deterioration in water quality. Nutrient data, particularly total phosphorus and phosphorus loadings, have been used extensively to estimate and predict trophic status in lakes (e.g. Vollenweider 1968). Good long-term data on phosphorus in the Great Lakes are not available, partly because early analytical techniques were unreliable. Chapra (1977) modeled historical phosphorus concentrations and loadings from census data and other watershed information for the period 1800 to 1970. Major sources of phosphorus loadings to the Great Lakes prior to 1800 were assumed to be the atmosphere and runoff from forested land. Chapra's simulated loadings (Figure 4) suggest two major periods of change: (a) the clearing of forests and development of agriculture in the late 19th century; and (b) the post-World War II increase in population, accompanied by the proliferation of sewer networks and the introduction of detergents, particularly in Lakes Michigan, Erie and Ontario. The effects of increased loadings of phosphorus on historical concentrations in the Great Lakes were calculated by Chapra's model as shown in Figure 5. In the upper Great Lakes, the effects of heavy loadings on ambient concentrations have been modified favorably by lake morphology. Specifically, major point source and non-point source loadings of phosphorus have been diluted to low concentration levels by the large volume of water in the Upper Lakes. It is -impossible to verify the model historically but predictions of current phosphorus loadings and concentrations were closely related to actual measurements as determined by regression analyses (r = 0.89 and 0.94. respectively).

Vollenweider, et al., (1974) examined recent relationships in the Great Lakes among primary production, annual phosphorus loadings and mean annual surface chlorophyll a concentrations (Figure 6). The relative position of the lakes on the curves suggest a cline in their level of cultural development. This cline is expressed not only in terms of nutrients, productivity, latitude (8° span from north to south) and climate, but also in basin population, land use and energy generation. It is instructive to compare Vollenweider's trophic classification in Figure 6 with Ryder's (1972) estimate of conditions in 1800. The latter author considered that Lake Erie was probably mesotrophic, with the remaining Great Lakes being highly oligotrophic. The possibility of early enrichment in Lake Erie is also suggested by fossil ostracods (Delorme 1982) and fossil diatoms (Harris and Vollenweider 1982) in the sediments. These authors suggest that natural changes in nutrient loadings may be due to a change in the metabolism of the entire planktonic system as elicited through the diatom assemblage.

Outbreaks of typhoid fever and other diseases associated with sewage pollution afflicted nearly all major population centres on the Great Lakes in the first decade of this century (Swain 1984). This problem led to the signing of the Boundary Waters Treaty in 1909 by the United States and Canada. The first comprehensive report on pollution in the Great Lakes (International Joint Commission 1918) revealed bacterial pollution near cities, in connecting channels and in the western basin of Lake Erie.. O p e n lake waters were essentially free of pollution. Studies undertaken during 1946-48 (International Joint Commission 1950) indicated that domestic waste treatment facilities had not kept pace with population growth. Moreover, industrial and agricultural pollution were then recognized as a growing problem. In 1940, over 65% of United States industrial production occurred in
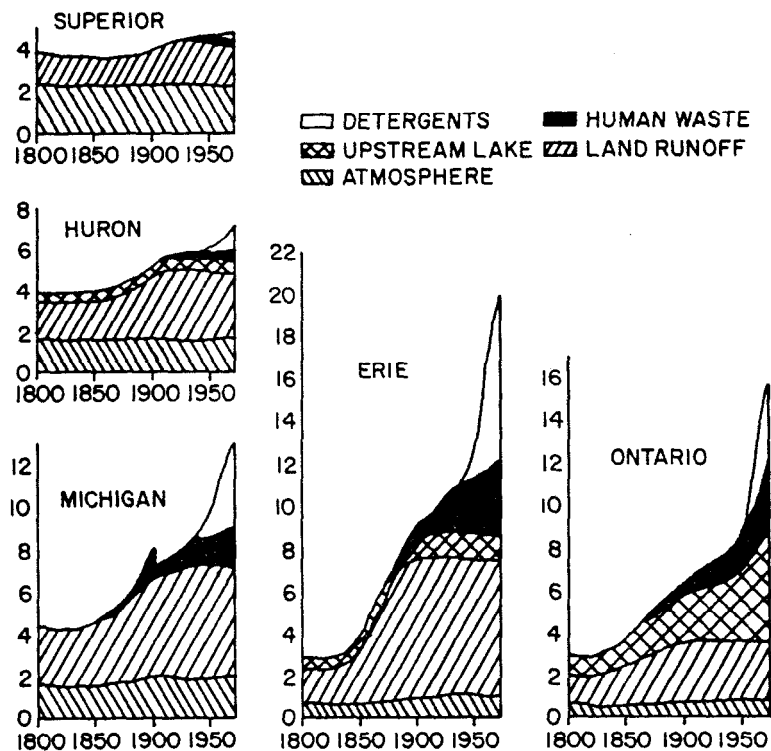
Figure 4   Historical loadings of total phosphorus (tons X 10^3 yr^{-1}) to the Great Lakes, as calculated by model (Chapra 1977).
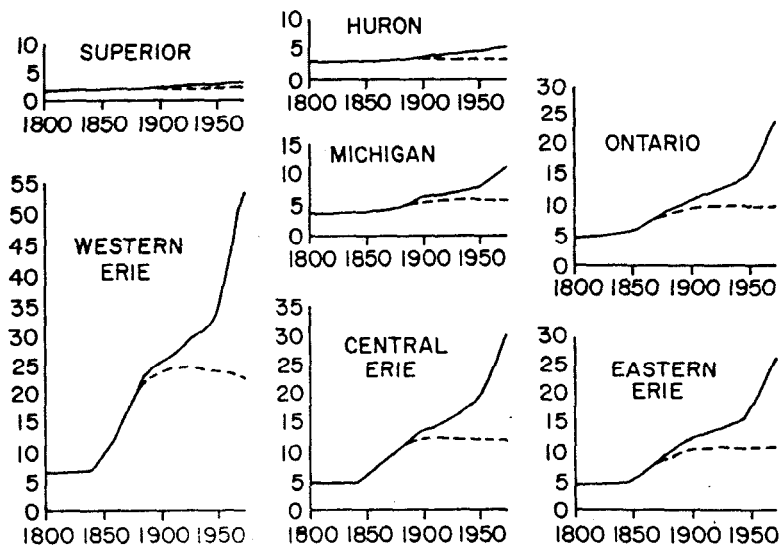
Figure 5   Historical concentrations of total phosphorus (ug L^{-1}) as calculated by model. Dashed line indicated concentration due to diffuse sources **(Chapra 1977).**

$$\Sigma a \text{ (gC/m}^2\text{y)} = 420 \frac{10\,(\text{gTP}/\text{m}^2\text{y})^{0.6}}{9 + 10\,(\text{gTP}/\text{m}^2\text{y})^{0.6}}$$

(a) — YEARLY PRIMARY PRODUCTION g C/m² y vs PHOSPHORUS LOADINGS gTP/m²y

Labels: WESTERN BASIN, L.ERIE, CENTRAL BASIN, L.ONTARIO, EASTERN BASIN, L.MICHIGAN, L.HURON, L.SUPERIOR

Axis: 400, 300, 200, 100; 0, 0.4, 0.8, 1.2, 1.6, 5.8, 6.2

$$\Sigma a \text{ (g C/m}^2\text{y)} = 420 \frac{1.15\,(\text{mg Chl } a/\text{m}^3)^{1.33}}{9 + 1.15\,(\text{mg Chl } a/\text{m}^3)^{1.33}}$$

(b) — YEARLY PRIMARY PRODUCTION g C/m² y vs YEARLY AVERAGE CHLOROPHYLL a mg/m³

Labels: WESTERN BASIN, CENTRAL BASIN, L.ONTARIO, EASTERN BASIN, L.MICHIGAN +, L.HURON, L.SUPERIOR

oligotrophic — mesotrophic — eutrophic

Axis: 400, 300, 200, 100; 0, 2, 4, 6, 8, 10, 12

Figure 6   Relations between annual primary production
and: (a) annual phosphorus loading and (b) surface
chlorophyll a in the Great Lakes (Vollenweider, et
al., 1974).

the eight Great Lakes states (Swain 1984). A report (International Joint Commission 1969) on conditions in the 1960's revealed the full severity of pollution in the lower Great Lakes. The findings and recommendations of this report as well as that of "Project Hypo" (Burns and Ross 1971), led to the development of the 1972 Great Lakes Water Quality Agreement. Efforts to reduce phosphorus loadings and the correspondingly high rate of cultural eutrophication have been successful (Great Lakes Water Quality Board 1982), although historic conditions (circa 1800) have not yet been achieved, nor are they likely to be.

Results from the 1978 Great Lakes Water Quality Agreement, which emphasized assessment and management of toxic and hazardous substances in the Great Lakes system. have not been so obvious. For the most part, the open waters of Lakes Superior, Michigan and Huron are of excellent quality in terms of nutrient loadings, but the same generalization cannot be made relative to toxic substances. In response to reduced loadings, ambient concentrations of phosphorus in the west and central basins of Lake Erie have declined 35% and 33%, respectively, between 1970 and 1980; the bulk of the decline having occurred during the past two years (Great Lakes Water Quality Board 1981). Anoxia in the bottom waters of the central basin still occurs in most years however. Lake Ontario shows some of the signs of degradation evident in Lake Erie. However, Lake Ontario has an additional problem of increasing total nitrogen and hazardous chemicals, particularly those originating from the Niagara River (Allan, et al., 1983).

Some nearshore areas, especially in Lakes Erie, Michigan and Ontario, are still plagued with persistent localized pollution problems which the Great Lakes Water Quality Board (1982) has classified as areas of concern (Table 3). From a total of 38 of these areas identified by the Water Quality Board in 1982, 10 (26%) were located in the Lake Erie basin and nine (24%) each in the Michigan and Ontario basins. The remaining 10 areas were shared by Lake Huron and Lake Superior. In most Class "A" areas of concern (Table 3). bottom sediments are contaminated with toxic and hazardous substances, volatile solids and metals. Some fish samples from these areas were contaminated with chlorinated hydrocarbons and heavy metals.

2.2.2   Terrestrial Sector

Historical changes in water quality in the Great Lakes are quite obviously related to cultural development in the watershed which, in turn, are a reflection of the exploitation of natural resources and human population growth. The historical development of the Great Lakes Basin and associated water quality problems have been reviewed recently by Bangay (1981). The total resident population within the Great Lakes Basin increased from 10 million in 1901 to almost 40 million in 1980. There has also been a general shift in population concentration from rural to urban areas and currently, about 80 percent of the basin population is classified as urban. Generally, this urbanization occurred in ecologically sensitive areas such as embayments, or near tributaries and connecting channels where the impact on water quality would be concentrated and therefore maximized, at least for that locale (Figure 7). However, as the degree of stress impact is a function of both intensity and geographic extent, intense, localized impacts may stress an ecosystem less than widespread but moderate impacts.

TABLE 3

CLASS "A" AND CLASS "B" AREAS OF CONCERN IN THE GREAT LAKES
(GREAT LAKES WATER QUALITY BOARD, 1982)

CLASS 'A" AREAS OF CONCERN	CLASS "B" AREAS OF CONCERN
Lake Superior	
None identified	St. Louis River, Minn. Thunder Bay, Ont. Nipigon Bay, Ont. Jackfish Bay, Ont. Peninsula Harbour, Ont.
Lake Michigan	
Fox R./Southern Green Bay, Wisc. Milwaukee Estuary, Wisc. Waukegan Harbor, Ill. Grand Calumet River and Indiana Harbor Canal. Ind.	Manistique River, Mich. Menominee River, Mich.-Wisc. Sheboygan, Wisc. Muskegon, Mich. White Lake, Montague, Mich.
Lake Huron	

St. Marys River, Mich.-Ont.
Saginaw River System and
  Saginaw Bay, Mich.
	Spanish River Mouth, Ont.
	Penetang Bay to Sturgeon Bay,
	  Ont.
	Collingwood, Ont.

Lake Erie	
St. Clair River, Ont.-Mich. Detroit River, Mich.-Ont. Rouge River, Mich. Raisin River, Mich. Maumee River, Ohio Black River, Ohio Cuyahoga River, Ohio Ashtabula, Ohio	Clinton River, Mich. Wheatley Harbour, Ont.
Lake Ontario	
Buffalo River, N.Y. Niagara River, N.Y. -Ont. Hamilton Harbour, Ont.	Eighteen Mile Creek, N.Y. Rochester Embayment, N.Y. Oswego River, N.Y. Toronto Waterfront, Ont. Port Hope, Ont. Bay of Quinte, Ont.
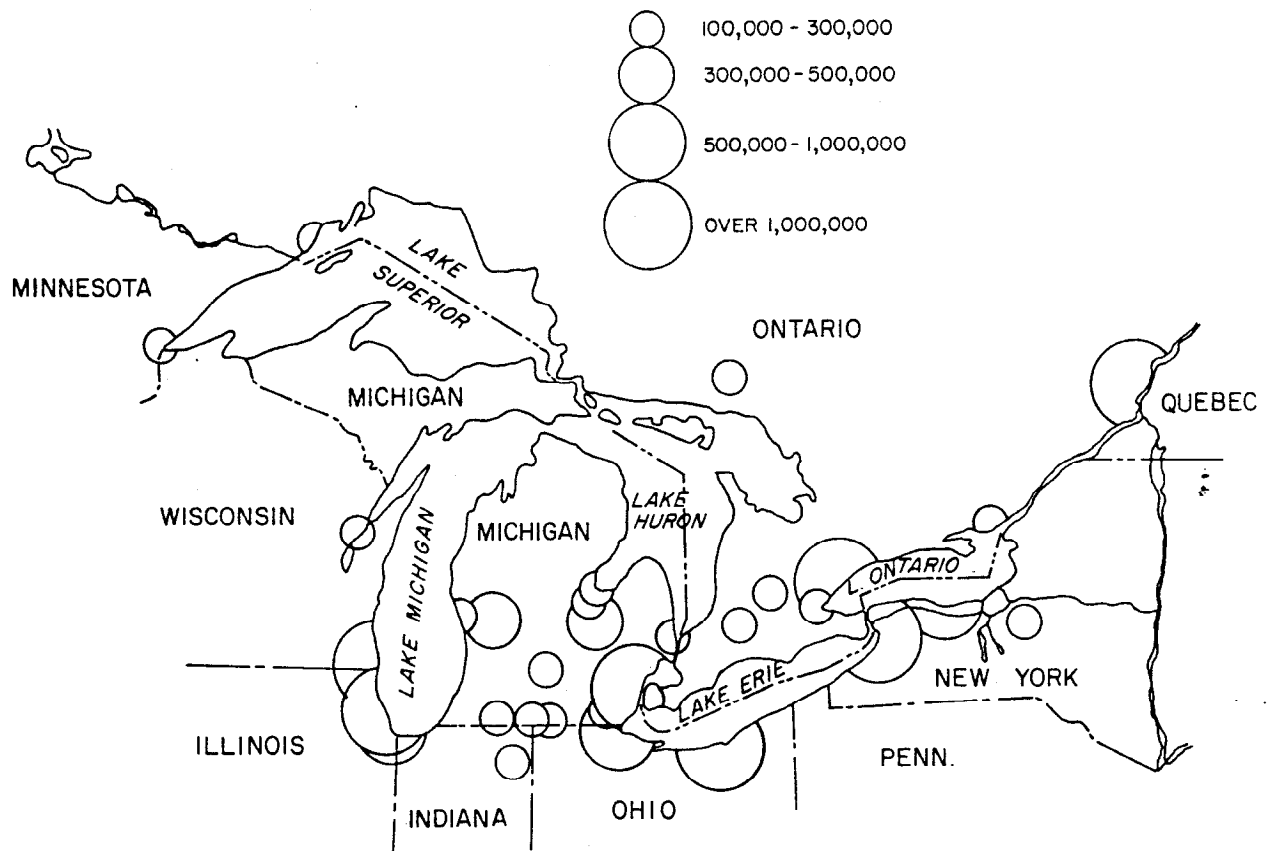
Figure 7   Major population centres in the Great Lakes Basin (International Great Lakes Diversions and Consumptive Uses Study Board, 1981).

The progression through resource exploitation - fur, timber, agriculture,
mining and the generation of energy - paralleled increasing environmental
degradation; particularly in the Lake Michigan, Erie and Ontario basins, where
population densities were the highest. Before the advent of cultural
development, most of the Great Lakes watershed was heavily forested.
Currently, virtually no virgin stands of timber remain (with some local
exceptions), although considerable forest cover still exists; especially in
the watersheds of the upper Great Lakes, where much of the land is unsuitable
for agriculture because of the generally thin soils of the Precambrian Shield
(Table 4).

    2.2.3   Aeolian Sector

    The atmosphere as a source of pollutants to the Great Lakes has recently
been recognized by the IJC (Eisenreich, et al., 1980). The Great lakes are
especially susceptible to pollution by toxic substances from the atmosphere
because of their large surface area to land ratio within the watershed and
proximity to major industrial areas of North America. For example, PCB
concentrations in the atmosphere over the Great Lakes are twice those over
global marine areas (Eisenreich, et al., 1980). The rapidly increasing ozone
content in various zones of the atmosphere is a problem not restricted to the
Great Lakes Basin and serves as another example of ecosystem degradation of a
different genre, derived from the atmosphere (Hov 1984).

    Before the development of agriculture and industry in the Great Lakes
Basin, atmospheric levels of contaminants were low. In his historical
simulation of Great Lakes phosphorus loadings, Chapra (1977) used an
atmospheric loading rate of 24 kg $km^{-2} yr^{-1}$ for the period when the
watershed was completely forested. This is equivalent to the current
atmospheric input from forested land in the Lake Superior watershed. The
contributions of the atmosphere to estimated basin loadings of phosphorus in
1980 ranged from 6% in Lake Ontario to 62% in Lake Superior (Great Lakes Water
Quality Board 1981).

    Sediment profiles (Thomas 1981; Figure 8) indicate that enhanced loadings
of trace elements such as mercury, cadmium and lead, paralleled the increased
combustion of fossil fuels in the Great Lakes Watershed. In fact, heavy metal
additions increased substantially, beginning about 1945. Recent estimated
loadings of lead from the atmosphere as a percentage of total loadings, ranged
from 36% in Lake Ontario to 87% in Lake Superior (Allen and Halley 1980).
Additions of chlorinated hydrocarbons to sediments have been recent and in
some instances are largely of atmospheric origin. For example, because of a
substantial reduction of PCBs from point sources, over 80% of PCBs now
entering Lake Michigan are estimated to be of atmospheric origin. Estimated
loadings of contaminants to the Great Lakes from atmospheric sources are
provided in Kondsewich, et al., (1978), Eisenreich, et al., (1980) and Allen
and Halley (1980).

    The role of the surface microlayer was reviewed in a recent symposium
(McNaught, et al., 1982) in which the pathways and fate of atmospheric
contaminants in the Great lakes ecosystem were examined. Atmospheric
contaminants are trapped in surface films which are rich in organic matter,
including lipids. Rice, et al., (1982) reported a 3-to 8-fold enrichment of
PCBs in surface films from Lake Michigan. Bacteria are also enriched in the

TABLE 4

MAJOR LAND USES AND LAND CAPABILITY FOR
AGRICULTURE IN GREAT LAKES BASINS
(PLUARG, 1978; BANGAY, 1981)

| | MAJOR LAND USE PER BASIN (%) | | | | |
	FOREST	AGRI-CULTURE	BARREN-BRUSH-WETLAND	URBAN	LAND CAPABILITY1 (%)
L. Superior	94.5	1.4	4.0	0.1	18
L. Michigan	49.8	23.4	23.3	3.5	68
L. Huron	65.7	22.4	10.1	1.8	35
L. Erie	17.1	59.1	14.6	9.2	86
L. Ontario	55.8	31.6	8.2	4.4	52

'Land capability for agriculture - Classes 1, 2 and 3 as a percentage of total.
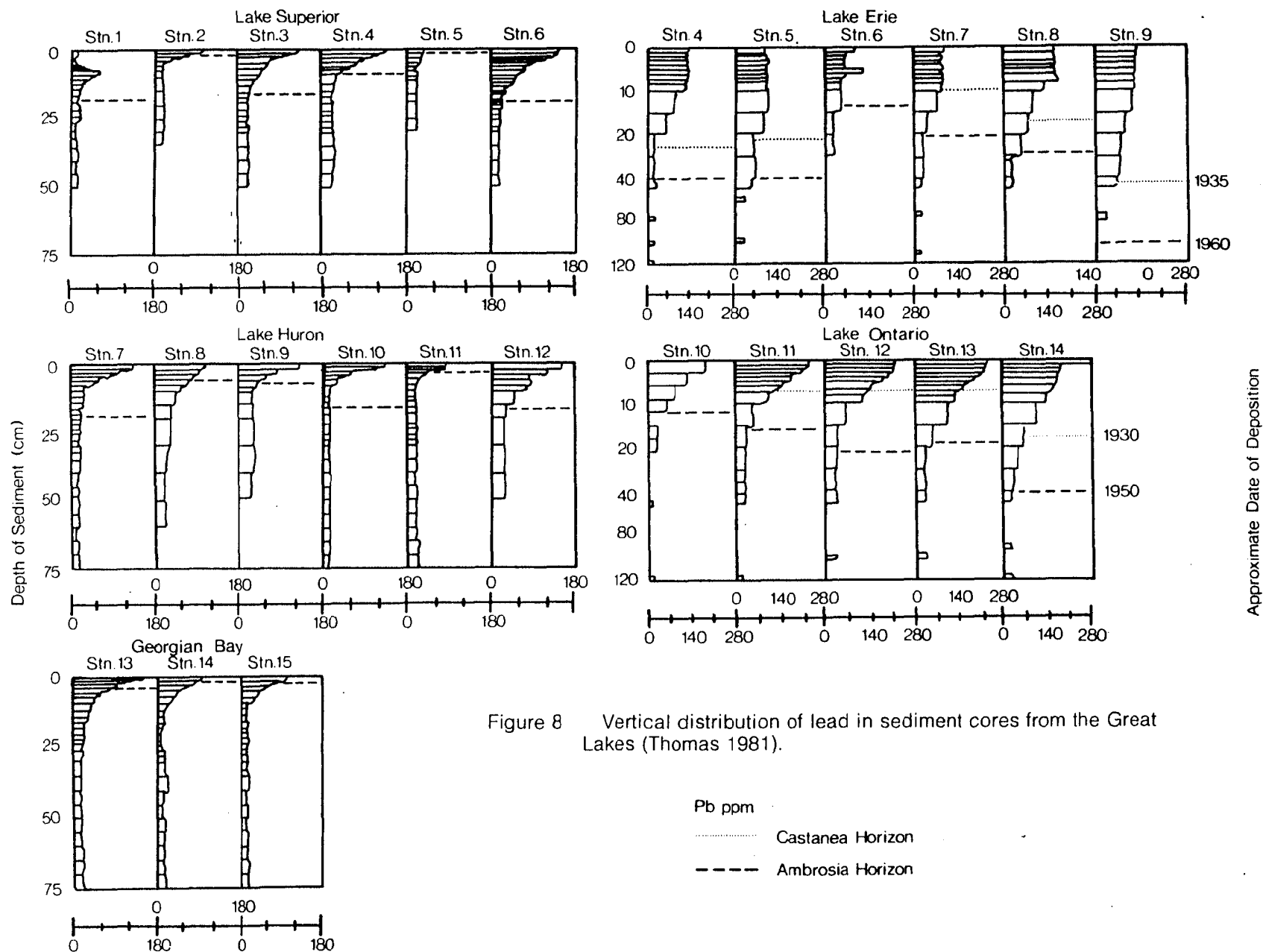
Figure 8   Vertical distribution of lead in sediment cores from the Great Lakes (Thomas 1981).

surface microlayer (Crawford, et al., 1982) and along with detritus and nannoplankton, provide a rich food supply for grazers. McNaught (1982) showed experimentally that zooplankton obtain PCBs from both particulate organic matter and nannoplankton and concluded that organic contaminants are short-cycled directly from atmospheric inputs to zooplankton through detritus. From a food-chain model, Connolly and Thomann (1982) estimated that it was possible for up to 12% of PCBs in adult Lake Michigan lake trout to be contributed from the surface microlayer.

2.2.4   Wetlands

One of the most valuable fish and wildlife habitats in the Great Lakes is the littoral zone which includes shoreline wetlands. Shoreline wetlands are important spawning and nursery areas for many fish species. The land/water interface in these zones forms an ecotone that is attractive to many vertebrates and invertebrates through the provision of food and shelter, afforded particularly by an abundance of both submergent and emergent macrophyte growth (e.g. Goodyear, et al., 1982; Herdendorf and Hartley 1980). Shoreline wetlands may also affect the limnetic, offshore zones of a lake, through: nutrient and energy transport by way of currents; or mass movements of organisms by migration; or passively, as in the case of plankton drift; and sequestering nutrients from land and lake water.

Accurate information on the pre-1800 wetland area is not available. However, based on the nature of the shorelines with their long stretches exposed to wave action, it probably was not large in relation to the total area of the Great Lakes. Protected zones where wetland habitat may develop amount to about 7% of the total shoreline length (International Great Lakes Diversions and Consumptive Uses Study Board 1981). The main locations of wetlands in the Great Lakes are: the Bay of Quinte; Long Point Bay; Rondeau Bay; western Lake Erie; Lake St. Clair; Saginaw Bay; and Green Bay, with smaller areas scattered along the shoreline. The importance of wetlands to the Great Lakes ecosystem was not formally recognized until recently and much of the original marsh area has been lost to drainage for agricultural land, dredging, dyking and development of shorelines for industrial, commercial and residential use (Herdendorf and Hartley 1980). Natural events such as water level fluctuations, erosion, storms and the accumulation of alluvium have also affected wetland areas (Whillans 1982).

Similarly, Cox (1972) estimated that the amount of clearing of original wetlands in southern Ontario bordering the Great Lakes varied from 3.6% to 93%, by county. In a more detailed study, Whillans (1982) estimated that shoreline losses of wetlands in counties bordering the Canadian shore of Lake Ontario, west of the Bay of Quinte, ranged from 6.2% to 96.6%, by county. The largest losses occurred in urban areas (Hamilton - 340 ha; Toronto - 610 ha). Jaworski and Raphael (1978[a,b]) deduced from historic maps that 50% to 77% of original wetlands have been lost in five developed shoreline areas of Lakes Huron, St. Clair and Erie. An estimated 16,835 ha of wetland have been lost in these areas due to cultural or natural causes. On the basis of these and other studies, Whillans (1982) estimated that up to 75% of the original wetlands has been lost in densely populated areas of the Great Lakes shoreline.

Although not as abundant as formerly, there are still large shoreline
areas of wetlands suitable for wildlife habitat (Table 5). About 1350 km of
the Great Lakes shoreline remain as wetlands (International Great Lakes Levels
Board 1973). Marshes along Lake Erie and Lake St. Clair are the most
extensive on the Canadian side, while Saginaw Bay, Sandusky Bay and western
Lake Erie provide the most important wetlands on the United States side.

2.2.5   Conjoined Systems

The biospheric perspective which we have assumed herein, infers the
consideration of the Great Lakes Basin as an ecosystem interacting with
conjoined ecosystems (e.g. Figure 1). For the most part, we may think of the
Laurentian Great Lakes as a moderately discrete ecosystem (but not as a
microcosm) and therefore be concerned mainly with the existing patterns and
processes occurring within the basin proper.

However, stress syndromes may be generated outside of the basin in
contiguous ecosystems and thence be transported to the Great Lakes system.
The most obvious form of inter-system stress transfer is that of wind-borne
particulate matter which may settle out in regions remote from the source of
generation. Water diversions from one watershed to another may not only
spread undesirable species into a system in which they were not indigenous,
but may also transport heavy loads of dissolved or suspended solids, including
excessive concentrations of contaminants or fertilizing agents. The Great
Lakes, in turn, contribute their contaminant loads, fauna and flora downstream
to the Gulf of St. Lawrence and the Atlantic Ocean.

Of pragmatic necessity, the remainder of this manuscript will deal
primarily with the Great Lakes as a moderately discrete ecosystem. However,
the biospheric perspective will be retained in order that all potential causes
for deviation from a quality environment may be considered.

2.3   FISH COMMUNITIES AND ASSEMBLAGES, PAST AND PRESENT

Early evidence (circa 1800) indicates that moderately integral fish
communities of that time differed substantially in the Great Lakes from those
somewhat disaggregated and relatively variable (in time) assemblages of fishes
encountered today. Typical of the differences in the fish communities of two
hundred years ago was the presence of a relatively high abundance of large,
littoral and demersal terminal predators and benthic feeders and river-run
stocks of species that now occur only in lake-spawning forms (e.g. Smith
MSa). Mean sizes of most species were markedly larger in near-pristine
environmental conditions and mean ages of mature fishes in spawning runs were
substantially greater. High levels of morphological and functional diversity
of phenotypically plastic fish stocks, such as the lake trout and cisco
complexes, allowed ready adaptation to the heterogeneous habitats of the lake
basins.

Cultural stresses about 1800 were relatively unimportant in affecting fish
abundance, except in certain local instances (e.g. Loftus and Regier 1972;
Smith MSb). The exotic or invading species of ecological and economic
importance today in the Great Lakes were not yet present in the four Upper
Lakes, although the sea lamprey and alewife may have made some early
incursions into Lake Ontario. It seems likely that even there, however, the

TABLE 5

SHORELINE WETLAND HABITAT IN THE GREAT LAKES
(MODIFIED FROM INTERNATIONAL GREAT LAKES LEVELS BOARD, 1973)

	SHORELINE WETLAND HABITAT (ha)		
	UNITED STATES	CANADA	TOTAL
Lake Superior	8240	1186	9426
St. Mary's River	2590	403	2993
Lake Huron	19982	2517	22499
Lake Michigan	13189		13189
St. Clair River and Lake St. Clair	3400	14207	17607
Detroit River	24	372	396
Lake Erie	14033	11981	26014
Lake Ontario	7444	8088	15532
TOTAL	68902	38754	107656

impact of these two species was not fully realized until such time when deforestation was sufficiently widespread in the watershed that it adversely affected mean water temperatures of influent streams (Smith MSa). The substrate was also adversely affected by deforestation and the large zones of sedimented organic materials that developed in some streams following deforestation of surrounding watersheds may have provided an abundance of preferred habitat for ammocoetes (larval sea lampreys). The most obvious conclusion to be drawn from these observations is that a pervasive environmental stress was first necessary on Lake Ontario before the impact of the sea lamprey and alewife markedly affected the indigenous community (e.g. Svardson 1976).

In summary, the early fish communities of the Great Lakes Basin may be viewed as relatively recent immigrants on a geological time scale (9000-14000 B.P.), originating, respectively, from two Pleistocene refugia; the Mississippi basin and the Atlantic drainage (Bailey and Smith 1981). These fish communities had previously become inured to a moderately austere environment similar to that found throughout most of the Great Lakes Basin, through the process of adaptive evolution over eons of time.

Today, as a generalization, the fish communities of the Great Lakes Basin may be described as of smaller mean size, comprised of species more dependent on the pelagic zone and lacking large species that formerly were abundant in rivers and near-shore zones, including large terminal predators and benthic feeders. Additionally, the communities are often dominated by opportunistic invaders such as the alewife and rainbow smelt, or top predators such as the introduced Pacific salmons and the sea lamprey. Much evidence suggests the existence of an unstable, astatic, fish association in the Great Lakes today (Ryder and Kerr 1978; Ryder, et al., 1981); that is, an assemblage of fishes that is constantly changing in response to the various stresses that are imposed upon it.

2.3.1   Oligotrophic Systems

In pristine times, the three Upper Great Lakes, Superior, Michigan and Huron, constituted a large oligotrophic subsystem that had many features in common. Lakes Erie and Ontario on the other hand were somewhat unique, particularly with respect to the composition of fish stocks and will be dealt with separately, as will the major bays of all the Great Lakes.

The species complex of prime importance from both an ecological and economic point of view in the Upper Great Lakes was undoubtedly that of the lake trout. This terminal predator occupied most of the lake basin preying on a spectrum of food- organisms, principally coregonines, sculpins and crustaceans (Eschmeyer 1964). The burbot was the only other top predator that occupied the cold, deep waters of the Upper Lakes and was at least partially partitioned from direct competition with the lake, trout in time and space through different behavioral mechanisms. A large coregonine swarm or complex, of perhaps eleven species in Lake Michigan and somewhat fewer species in Lakes Huron and Superior (Koelz 1929), constituted the bulk of the remaining fish stocks forming the cold-water community.

A unique characteristic of the early lake trout and coregonine stocks of the Upper Lakes was their diversity of form and behavior. Because of an overlap in morphological attributes among the various forms, their precise taxonomic classification remains open to speculation (e.g. Bailey and Smith 7981). Of critical importance however, is the fact that each taxon flock functioned as several separate species, exploiting unoccupied habitat rather efficiently through rapid phenotypic adaptation (e.g. Dehring, et al., 1981; Todd 1981); presumably assisted by a modicum of reproductive isolation. Hence, lake trout and several coregonines became adapted to a rather austere oligotrophic environment following glacial recession, primarily through phenotypic plasticity (Lindsey, 1981; Ryder, et al., 1981). Given a sufficiently long evolutionary time and continued reproductive isolation, the phenotypically recognizable entities of each flock may eventually have speciated and a genetic drift may have resulted in a closer adaptation to a particular habitat.

The appearance of sea lamprey in the Upper Great Lakes in the 1940's and 1950's (Lawrie 1970) selectively and sequentially reduced the various, already over-exploited, stocks of lake trout to virtual extinction in Lakes Huron and Michigan and to near-extinction in Lake Superior. Concurrently, the other top predator of the cold-water community, the burbot, was also decimated by the sea lamprey. This resulted in an explosion of various forage species and a constantly changing assemblage of fishes.

Further complications to this dynamic scene arose with the introduction and invasion of two exotic species, the rainbow smelt and the alewife and the subsequent introduction of four Pacific salmons to complement two trout species that had previously been introduced into the Upper Lakes. Currently, reproducing stocks of pink salmon exist in all three Upper Lakes in sizable numbers and a residual stock of reproducing kokanee persists in Lake Huron. Coho and chinook salmon have been intermittently introduced since the 1800's to the present, but their current reproductive status remains uncertain. Rainbow trout of several discrete origins outside the Great Lakes are now abundant throughout the Upper Lakes and brown trout are moderately common in some locations. Both retain naturally-reproducing, self-sustaining populations in the Great Lakes. Other new species of fishes may be making inroads into the Upper Great Lakes, such as the white perch which has experienced a population explosion in Lake Erie (Schaeffer, 1984) and recently has become established in Lake Huron (R. Payne, pers. comm.).

In spite of major changes in species composition of the fish assemblages of the Upper Great Lakes, the fish yield (an emergent property of a biotic community) remains about the same in terms of total biomass as it was prior to the cultural stresses (Ryder 1965; Regier and Hartman 1973). Despite this yield conservatism, predictability of the individual constituents of the yield on an annual basis is uncertain in such a dynamic situation of ever-changing fish assemblages. Unlike the early fish communities of about 200 years ago, the present astatic assemblages bear a contaminant burden perhaps sufficiently great to affect behavior and reproductive success and almost certainly, their edibility.

Lake Ontario, considered formerly to be oligotrophic for morphometric reasons (see Rawson 1952), is treated separately from the Upper Great Lakes because of its higher level of nutrient loading (Beeton 1965), its historic connection to the Atlantic Ocean, as well as the uniqueness of its former fish stocks. Perhaps its early indigenous fish community differed most from that of the Upper Great Lakes by the initial presence of Atlantic salmon and American eels in the early 1800's (Smith MSa). Neither of these species was able to gain access to Lake Erie nor to the Upper Great Lakes because of the formidable physical barrier, Niagara Falls, which emerged about 9000 years ago (Flint 1957). The Lake Ontario oligotrophic community in other respects bore at least a superficial resemblance to that of the Upper Great Lakes, but major changes in the stocks due to cultural interventions preceded that of the Upper Lakes by several decades. A chronology of major successional events occurring in the fish stocks of Lake Ontario has been outlined in detail by Christie (1972) and will not be repeated here. As a generalization, however, it should be pointed out that unlike the Upper Lakes, Lake Ontario experienced either extinction or near-extinction of several fish species, including: the Atlantic salmon; blue pike; deepwater sculpin; and three coregonines and invasion by at least three euryhaline species: the alewife; white perch; and rainbow smelt. This complex picture of ever-changing fish stocks is further complicated by the continued stocking of large numbers of chinook and coho salmon, rainbow and brown trout and other species into Lake Ontario. Currently, the fish stocks of Lake Ontario are in an unpredictable and continual state of flux. The eventual return to any semblance of its former steady-state would seem to be dependent to a large degree on: sea lamprey control; lake trout and Atlantic salmon stocking; rehabilitation of the habitat; and an improvement in water quality, in order to ensure natural reproduction of these two terminal predators.

2.3.2   Stocks and Taxon Swarms

Historically, some recently glaciated lakes, such as: the Laurentian Great Lakes and other lakes bordering the Precambrian Shield of North America; deep lakes of Fennoscandia; and mountain lakes of the European Alps, contained rich assemblages of salmonid taxa. Here "salmonid' includes the salmonines (salmon, trout, char) and grayling and the coregonines (whitefish, cisco, chub). Systematists have had great difficulty in developing an explanatory classification for these different forms or taxa. Host of the salmonid taxa recognized in these lakes early in this century have since been extirpated or have been transformed through introgressive hybridization into taxa that appear quite different from their predecessors.

In the Great Lakes, the salmonines were represented predominantly by the chars, that is, the lake trout of the lakes and large rivers and the brook trout of the streams and nearshore zones of the large rivers and lakes. Grayling occurred in some Michigan streams and some adjacent waters of the lakes proper; Atlantic salmon occurred in Lake Ontario and some inflowing streams.

Each of the chars, lake trout and brook trout, occurred in a variety of different "stocks" in different lakes. It may be that Lake Erie had only one stock of lake trout because of a low level of environmental heterogeneity. Lake Superior at the other extreme had many recognizably different stocks of lake trout (Eschmeyer 1957; Goodier 1981). The complex assortment of chars,

acted as terminal predators in the cold and most oligotrophic parts of the
Great Lakes Basin ecosystem. This swarm of char taxa was complemented in the
lakes proper by a corresponding swarm of coregonine taxa that preyed on
zooplankton and benthic invertebrates and was in turn preyed upon by the
diverse swarm of lake trout (char) stocks. In small streams, the brook trout
(char) were not complemented. by coregonines to any significant degree;
consequently brook trout food preferences were broader to include both aquatic
insects and other invertebrates and terrestrial invertebrates to a greater
extent than occurred commonly with lake trout.

A century ago, the salmonid stocks were far more diverse and consequently,
more complicated, or richer in recognizably different phenotypes, particularly
in the Upper Lakes. The assortment was simplest in Lake Erie and most complex
in Lake Superior. Although there have been many investigations of taxon
swarms, they have not yet been adequately studied by aquatic ecologists, nor
by evolutionary systematists, nor by fisheries scientists. The somewhat
comparable species swarms of cichlids (especially Haplochromis) in Lake
Victoria, have similarly been largely ignored (R. L. Welcome pers. comm.)
apparently because fisheries scientists in general, tend to work on simpler
phenomena.

Of the recognizably different stocks of lake trout to be found in the
Great Lakes a century ago, all but a few have been extirpated. This is also
the case for some of the coregonine stocks where inter-stock introgression has
further reduced their identity. Current attempts to restore lake trout
involve efforts to recreate a genetically more diverse stock structure (e.g.
Schneider, et al., 1983). Heretofore, the approach has largely been one of
trial and error, but the experience of the 1980 STOCS Symposium (Berst and
Simon 1981) promises a more informed approach.

2.3.3   Mesotrophic Systems

Lake Erie was 'distinct from the Upper Lakes in that it had a relatively
shallow basin and much higher levels of nutrient loading. In its
near-pristine state it was probably early mesotrophic or perhaps even middle
mesotrophic rather than oligotrophic sensu stricto (e.g. Beeton 1961; Ryder
1972).

The fish stocks of Lake Erie, like those of Lake Ontario, underwent major
changes due to various cultural interventions, substantially before such
changes were experienced in the Upper Great Lakes. Lake trout at one time
were moderately abundant in Lake Erie (Applegate and Van Meter 1970) and
extended throughout the eastern basin and into the central basin. Percid
species including the walleye, blue pike, sauger and yellow perch, reached
their greatest abundances in Lake Erie, particularly in the western and
central basins. The commercial fish yield from Lake Erie has generally
exceeded that from the other Great Lakes in toto. From 1879 to the early.
1970's, at least 19 different fish species have been of major significance in
the landings at one time or another (Hartman 1973; Baldwin, et al., 1979).
Other species (besides the percids and lake trout) of major importance
commercially, over the years, have included: lake herring; lake whitefish;
northern pike; suckers (including white sucker and redhorse); freshwater drum;
channel catfish; white bass; carp; goldfish; rainbow smelt; and most recently,
the white perch. It is beyond the scope of this document to list in detail

the sequential occurrences of each species in Lake Erie and its watershed, which number in total between JO6 and 125 (Ryder 1972; Bailey and Smith 1981) and are described elsewhere (Leach and Nepsy 1976). An interesting successional change that has occurred over time, however, is marked by successive losses of fish stocks, starting with lake trout and lake sturgeon and running through lake herring, lake whitefish, sauger, blue pike, walleye and yellow perch (Regier and Hartman 1973). Interestingly, despite the drastic and in some cases rapid changes in the species constituents of the total yield, a system conservatism retained the community yield over the years within predictable and only slightly fluctuating boundaries (Baldwin, et al 1979).

Currently, following a recent moratorium on commercial fishing for walleyes in the western basin of Lake Erie because of the high levels of methyl mercury in the fish and perhaps for other reasons alluded to earlier, including phosphorus control, the walleye stocks have rebounded and are once again plentiful, perhaps even exceeding their highest historic levels of abundance. The native lake trout of Lake Erie is now probably extinct, as is the blue pike, a species that constituted at one time one of the largest annual catches of a single species in the Great Lakes (Baldwin, et al 1979).

Many of the major bays of the Great Lakes were originally, at least in some respects, similar to the eastern basin of Lake Erie. Some were more oligotrophic, such as Thunder Bay and Keweenaw Bay of Lake Superior and some were likely more eutrophic, such as Saginaw Bay of Lake Huron or the Bay of Quinte on Lake Ontario. The latter two bays would probably have been classified as mesotrophic in pristine times. Fish communities in these same bays ranged from a typical coldwater salmonid community found in the Upper Lakes to a coolwater, percid community in the mesotrophic environments. Natural eutrophic conditions and their typical warmwater communities were generally unimportant in most of the Great Lakes proper except for Lake Erie tributary rivers and their deltaic regions, or along restricted lengths of shorelines in small bays such as Rondeau Bay.

Some of the larger bays of the Great Lakes are currently undergoing rehabilitation (Bay of Quinte, Green Bay) and fishes have responded favorably and with alacrity and in approximately reverse sequence to the order of their disappearance (e.g. Smith MSb).

Regier (1979) has provided an overview of general changes to fish communities in the Great Lakes. He noted that the emergence of a large biomass of rainbow smelt and alewives provided the incentive for the introduction of large pelagic salmonids, including the chinook, coho and Atlantic salmon-and the rainbow and brown trout. Consequently, the fish communities of both the oligotrophic and mesotrophic portions of the Great Lakes are now largely constituted of pelagic communities, a condition that probably did not exist 200 years ago when nearshore littoral communties were in dynamic equilibrium with pelagic, offshore communities.

Generally, small and fecund, r-selected pelagic species have now predominated over the larger, K-selected species, which were original ly more closely associated with the substrate and the coastal zone of the lakes with the exception of certain pelagic forms of lake trout. Many river-run stocks

have been decimated (Loftus 1958; Loftus and Regier 1972) to the point where the present Identity of the Great Lakes fish stocks is but faintly recognizable as being derived from the diverse communities of 200 years ago.

2.3.4.   <u>Trophic Structure</u>

Trophic structure in biotic communities not only enhances survivability at the community level through a diverse predator-prey network, but in addition, permits the community to exploit the abiotic sector of the ecosystem with optimum efficiency. Functional interactions among the different trophic levels, including feedback responses, identify a cold-water community as a responsive, integrated, structure rather than a loose assemblage of randomly interacting organisms.

Cold-water communities of organisms, in historic times, either genetically or phenotypically adapted to the oligotrophic environment provided by most of the Great Lakes waters, were undoubtedly retained at steady-state through predation by lake trout stocks. Predation occurred principally on forage fishes of the coregonine complex, but also on other fish species and at other trophic levels where lake trout feed on crustaceans and other invertebrates (Stewart, <u>et al</u>., 1981). On the basis of predation alone, the lake trout could be considered to be a key surrogate of the cold-water community. The general well-being of lake trout stocks reflect the condition of other community components. Any perturbation of lake trout stocks from whatever cause, tends to disrupt the total community and will be reflected in many ways, such as disproportionality of species numbers or biomass between trophic levels or a mean size reduction in at least some species.

The decimation of lake trout stocks in the Great Lakes by intensive fishing and sea lamprey (Lawrie 1970) for example, was strongly felt by other components of the coldwater community. The coregonine complex, in particular, generally feeding at one trophic level below that of the lake trout, radiated from their former predation refugia and spread to areas of the Upper Lakes where they did not traditionally occur in high abundance. The rather rigid boundaries between time and place of reproduction of the different coregonine stocks rapidly disintegrated and apparently resulted in introgression of formerly discrete stocks (Smith 1964). This observation should not be interpreted as a necessary cause for the original diversification of coregonine stocks. Environmental heterogeneity undoubtedly played a major role in that respect. Predation refugia from feeding lake trout, however, may have reinforced the initial diversification by reducing the probability for introgression. Undoubtedly, other effects ensued at the trophic level one step below that of the coregonines, that is, at the level of the amphipods and other invertebrates. While this effect was not studied, it might be expected that the burgeoning coregonine populations consumed substantial quantities of these invertebrates and this effect was transferred to the level of primary production. Conversely, inordinately large quantitative or qualitative changes in invertebrate stocks for whatever reason would be expected to be reflected up the trophic ladder through the coregonines, eventually to be revealed by the available food resources for the lake trout and ultimately, the well-being of that species.

While these effects on the trophic structure of the coldwater communities in the Great Lakes may be conjectural, they are nevertheless strongly supported by trophic-dynamic theory (e.g. Lindeman 1942). It is not known for certain if the loss of the lake trout complex was due to: overfishing; exotic fish introductions; sea lamprey predation; phosphorus loadings; contaminant inputs; structural changes in the environment; or a combination of some or all of these factors. The ultimate effect has been the same, however, that of destroying the integrity of the coldwater community through disruption of trophic-dynamic interactions.

2.3.5   Particle-size Density

Complementing the trophic-dynamic structure of the coldwater community in the Great Lakes is the particle-size density of the community components (Kerr 1974). Sheldon, et al., (1972) have shown that in marine pelagic communities, on a Jog0 size interval basis, organisms occur at approximately equal densities whether they are phytoplankton, zooplankton, or whales. Different, but equally characteristic size spectra have been described for the marine benthos (Schwinghamer 1981) and for the freshwater pelagic zone (Sprules and Knoechel 1984), indicating that such conservative patterns may be common to most aquatic ecosystems. The application of size-spectrum analysis to ecosystem health assessment, together with the associated theoretical background have been examined in some detail by Kerr, et al., (1985 in press) and Kerr and Dickie (1984). For present purposes, it is sufficient to note that a similarly characteristic community structure based on particle-size density apparently occurred historically in the Great Lakes (Ryder, et al., 1981) and signified in particular, healthy stocks of fishes within the coldwater community.

A conjectural scenario of particle size changes due to cultural stresses for the Great Lakes would show the large terminal predators and large benthic feeders disappearing first. Ultimate survivors would likely be the small, opportunistic, pelagic species. Intervening time would show Josses of species in an orderly sequence depending both on their size and their sensitivity to a particular stress.

Observation, as previously detailed and documented, does in fact show the lake sturgeon (a large benthic feeder) and the lake trout (a terminal predator) to be the most susceptible species to a suite of cultural stresses, while the alewife and rainbow smelt, two small pelagic species, tended to thrive under these conditions through ecological opportunism (i.e. the capability of massive spawning and short turnover times). Intermediate-sized species such as lake herring, lake whitefish, walleye and other species were drastically reduced in an orderly sequence that was consistent with the particle-size density theory. Even within species, the largest individuals tended to disappear first. This exacerbated the ability of certain species to thrive, as the largest individuals usually constituted the valuable brood stock.

Many stress effects on aquatic communities tend to reduce the mean size of organisms at any of the logarithmic intervals, but have been most obvious with the largest organisms; especially fishes which have been more or less routinely monitored through catches for the last one hundred years or more (Baldwin, et al., 1979). A disruption of the particle-size ratios of

organisms from whatever causal mechanism, may be an indicator of community malaise and perhaps indicative of a dysfunction in the ecosystem as a whole. On the other hand, production processes in lake trout exhibit a system conservatism through metabolic amelioration; that is, lake trout of different sizes feeding at different trophic levels provide similar yields (Kerr and Martin 1970).

An understanding of the conservative nature of the particle-size spectrum allows the prediction of future spectrum changes under various types of ecosystem stress. For example, the biomass size spectrum,, on a gross scale, may be predicted from relatively few variables (Borgmann, et al., 1984). Consequently, it is possible to predict changes in the shape of this spectrum following the addition of toxic chemicals (e.g. Borgmann 1985).

Rapid measurements of particle-size spectra may be easily made using any of a variety of quantitative sampling apparatus, such as image analysers (Sprules and Holtby 1979).

3.0 CRITERIA FOR BIOLOGICAL INDICATORS OF ECOSYSTEM QUALITY AND CANDIDATE ORGANISM5

3.1   <u>CRITERIA</u>

With the implicit understanding that the various biotic compartments of an ecosystem may reflect the effects of cultural stresses at several hierarchic levels, including those of: species, stocks, and populations or community (Figure 2), a major responsibility of the Work Group should be to explore these several promising avenues for developing indicators of ecosystem quality.

At the community level of organization, any observable departure from base-line conditions of steady-state or natural trends and cycles (including community production and mortality, diversity and equitability of species within the community, or changes in the community size spectrum) may provide ready foci for identifying stress effects. Within stocks and populations, density-dependent changes in response to cultural stresses, at least in some instances, would **likely** provide a suitable early measure of the latter if appropriately calibrated. That is, as compensation mechanisms are pushed towards their limits, the capability of a stock to retain homeostasis **becomes** more tenuous and identification of the stress effect becomes more facile.

Loss of particular stocks identified as either genotypically or phenotypically distinct, through the mechanisms of extinction processes or introgression, may be a symptom of more advanced environmental stresses.

Individual species fall readily into two general categories of indicator organisms that reflect ecosystem quality in quite different ways (Figure 9) and at variable levels of sensitivity.

I   <u>Specialized organisms that have narrow tolerances for most environmental properties.</u> Type I indicator organisms are stenoecious, having evolved to be specially adapted for the pristine, but somewhat austere conditions originally found in naturally occurring systems such as the oligotrophic environment of the Upper Great Lakes. They tend to diminish, either gradually or discontinuously, as cultural intrusions of the ambient environment occur. Examples of such indicator organisms for oligotrophic systems may be lake trout, deep-water sculpins and the amphipod <u>Pontoporeia</u> hoyi; walleyes, saugers and <u>Hexagenia</u> <u>limbata</u> (burrowing mayfly) that thrive in mesotrophic systems are somewhat less stenoecious yet are sufficiently sensitive to certain cultural stresses or suites of stresses. Hence, selected attributes of these Type I indicator organisms may serve as early warning indicators of a previously unperceived perturbation.

II   <u>Less specialized organisms that have relatively broad tolerances for many environmental properties.</u> Type II indicator organisms constitute a group known as euryecious organisms. They are often unable to compete with the stenoecious organisms within systems to
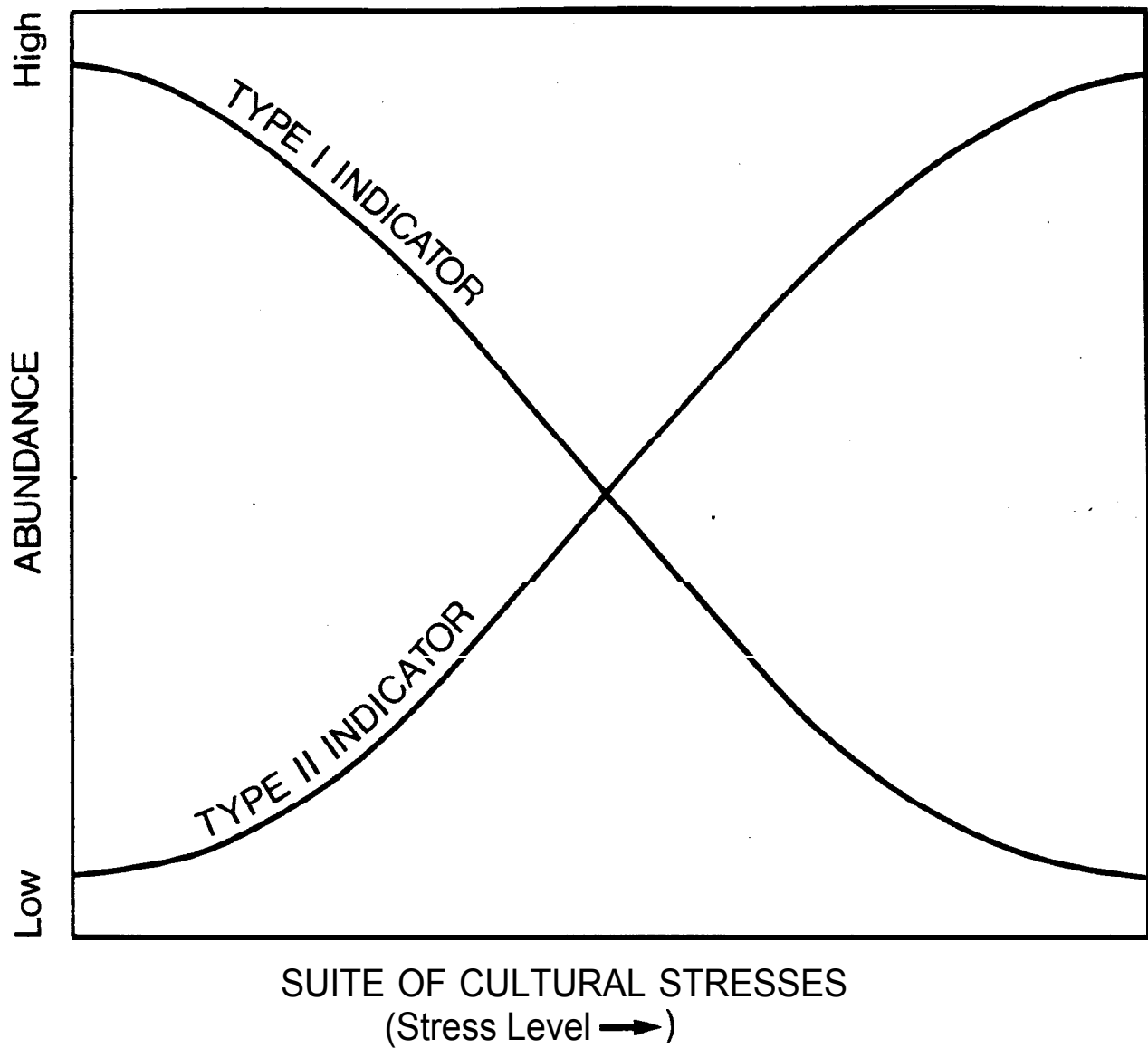
Figure 9   Indicator organisms fall into two generalized categories: Type I -specialized organisms intolerant of most culturally derived stresses: Type II -unspecialized organisms tolerant of many stresses either alone or in combination.

which the latter are especially adapted. Thus, the tolerant
organisms tend to be present only at low levels of abundances if at
all, or their distribution is narrowly restricted to unusually
enriched or otherwise exceptional parts in these systems which are
not tolerated by the more highly specialized Type I organisms.
However, tolerant organisms are better adapted to degraded features
of stressed conditions than are the specialized ones and they usually
thrive in such areas. These phenomena are quite well understood with
respect to eutrophication as a stress. Most tolerant (Type II)
organisms are especially abundant in eutrophic environments and some
may even tolerate extreme eutrophy (i.e. hypereutrophy). Some
examples of euryecious organisms include carp, <u>Limnodrilus</u>
(sludgeworms), <u>Chironomus</u> (bloodworms), <u>Cladophora</u> (a green alga),
and <u>Microcystis</u> (a blue-green alga).

For purposes of identifying the first stages of degradation of an aquatic
environment, stenoecious, Type I organisms are most useful. They also have
utility in testing the success of environmental rehabilitation measures and
may have utility as bioassay organisms. Complete absence of the sensitive and
narrowly tolerant Type I organisms in an aquatic system in which they were
once abundant, is indicative of an inordinately high level of environmental
degradation (exploitation, of course, is also an environmental stress). Early
warning indicators might include exceptionally high mortality rates and
subsequent partial loss of individual cohorts of particularly sensitive Type I
species through gradually diminishing reproductive success. In fact, any
substantive deviation from the norm by these indicators would provide cause
for environmental concern. (e.g. Successive year classes of Type I species
more than two standard deviations below mean recruitment levels might signal
reproductive stress deriving from a deteriorating environment). Confirmation
of environmental degradation would be provided by physico-chemical evidence
and by the increased abundance of Type II organisms.

Once Type II indicator organisms become abundant and widespread within an
oligotrophic or mesotrophic system, general environmental1 degradation has
already occurred. It is possible, though not common in the Great Lakes, to
degrade an ecosystem even further so that only the! most tolerant species can
be found and then only in the least degraded parts of the system. Conversely,
loss of the tolerant, Type II organisms and a corresponding resurgence of the
stenoecious types may be indicative of substantial mitigation or
rehabilitation success. High abundance of Type II organisms in a specific
locale may indicate point source loading problems.

In order to better qualify our preceding discussion for the use of
tolerant and intolerant indicator organisms, a consolidation of the rationale
into a succinct set of criteria has been prepared. The relative suitability
of each candidate indicator organism may be determined on the basis of the
criteria, but a suitable organism need not necessarily meet all of the
standards. Criteria have been developed for Type I organisms only and
proposed candidate organisms are also all of the Type I variety. This should
not be construed as a lack of utility of Type II organisms for ecosystem
evaluation (particularly during a rehabilitation phase) but rather as an
emphasis on early detection of environmental degradation.

Suitable Type I organisms:

(a) will have potentially wide distribution within the Great Lakes Basin;
    (i.e. will be a spatial indicator); this criterion may be determined
    on the basis of historic distribution for some organisms; or, if
    sedentary, occur in a well-mixed zone that allows exposure to large
    volumes of water over time; (i.e. will be a temporal indicator); or,
    if vagile, move extensively throughout large parts of the system over
    time; (i.e. will be an indicator in both time and space).

(b) will reflect at least a moderate level of system integration; (i.e.
    will interact directly with many other natural and human system
    components).

(c) will be indigenous and a structurally stable component of the
    ecosystem and therefore will reflect adaptation to relatively
    unperturbed environmental conditions.

(d) will have niche characteristics (an organismal attribute) and habitat
    requirements that are reasonably well understood and supported
    through documentation resulting from appropriate scientific studies.

(e) will thrive in water of high quality and consequently be sensitive to
    a variety of human interventions within the ecosystem (or the
    converse of this) or will exhibit a graded response to a range of
    increasing levels of each human intervention.

(f) will serve as a connective link between general measures of ecosystem
    quality and yet possess potential diagnostic capabilities for the
    determination of certain specific causes of ecosystem degradation
    (e.g. PCB's bioconcentrated in flesh samples will be indicative of
    concentrations in the water column once the appropriate scale-factor
    has been applied).

(g) will bear an orthogonal relationship to other ecosystem quality
    indicators; (i.e. different indicators will reflect divergent
    manifestations of human impact and dimensional overlap will be
    minimized insofar as possible).

(h) may be typified by one or more historic data series or capable of
    retrospective monitoring. These data series will show quantifiable
    evidence of past relative abundance of an indicator species during
    periods of relatively little human stress, or alternatively, provide
    qualitative anecdotal information by creditable observers.

(i) may be easily collected and measured for the purpose of quantifying
    standing stocks, in terms of numbers and biomass, using standard
    methods.

(j) will consist of a temporal continuum of reproducing stocks.

(k) are suitable subjects for laboratory experiments, especially those
    designed to investigate cause and effect relationships.

(1) respond to stresses in a way that will be readily identifiable and preferably, quantifiable.

(m) will be important in their own right to humans (i.e. may have inherent commercial, recreational or aesthetic value) and be readily recognized by the public; or, alternatively, may interact negatively with valued food organisms through predation or competition and thereby detract from their potential economic worth; or, may be a vital food source for a valued organism.

3.2   CANDIDATE ORGANISMS

3.2.1 Lake Trout (Salvelinus namaycush).

In consideration of the type of organism that most closely conforms to the general criteria for a biological indicator, many sensitive species preadapted to oligotrophic environments through evolutionary processes have potential Type I indicator attributes, including lake trout, deep water sculpins, Mysis relicta (Possum shrimp) and Pontoporeia hoyi (amphipod crustacean), to name but four prime candidates. Of these, the lake trout, a stenoecious organism, best conforms to the previous list of indicator criteria.. Deep water sculpins and Mysis are less well understood, have quantifiable historic data series for only some parts of the Great Lakes system or only in recent years and are not generally recognized by the public nor generally perceived to be valuable in their own right. Pontoporeia hoyi on the other hand, has been sampled quantitatively in a number of studies on the Great Lakes (e.g. Freitag, et al., 1976; Harzolf 1964; Wells 1960), is known to respond readily to some cultural stresses and consequently, may well be a complementary indicator organism to the lake trout at a different trophic level of organization in oligotrophic systems.

The qualifications for indicator status of the lake trout are as follows:

(a)   During the early days of settlement around the Great Lakes Basin, lake trout were widely distributed in the main basins of Lakes Ontario, Huron, Michigan and Superior and in the eastern and central basins of Lake Erie (e.g. Smith MSa; MSb); an area that comprised about 95% of the total surface waters of the Great Lakes Basin. In addition, river-run stocks existed in some of the large, tributary streams, where annual adfluvial spawning runs occurred (Loftus 1958). In the Upper Great Lakes, lake trout occupied almost every major habitat type, at least at certain times of the year, including the pelagic and demersal zones, the near-shore littoral zone and the lower reaches of major tributary streams (e.g. Lawrie 1978). Besides the shallow, western basin of Lake Erie, lake trout were normally absent only from some of the warm, shallow bays of the Great Lakes during the summertime.

In general, adult lake trout move extensively throughout the aquatic system of the Great Lakes Basin and consequently, are exposed to a multitude of natural stresses found in oligotrolphic systems to which they have become well adapted through evolution,.

(b) The lake trout interacts with a large variety of indigenous organisms, through the food web, as a top predator and through competition with other coldwater top predators and planktivores, particularly during its early life stanzas. The lake trout is the consummate integrator of oligotrophic biota by virtue of its function as the major terminal predator over most of the Great Lakes Basin.

(c) A variety of lake trout stocks that are indigenous to the Great Lakes Basin have coevolved first in Pleistocene refugia and more recently within the Great Lakes Basin; consequently they have been a structurally stable component of unperturbed, oligotrophic systems over an evolutionary time scale.

(d) The niche characteristics of the lake trout and its habitat requirements, including preferenda of many of its fundamental life needs (e.g. temperature and dissolved oxygen) are widely documented for the Great Lakes Basin and for a multitude of inland lakes.

(e) The lake trout thrives and reproduces abundantly in pristine, oligotrophic systems and exhibits a graded response with respect to environmental stresses such as cultural eutrophication (e.g. Loftus and Regier 1972). In general, the life requirements of the lake trout parallel those properties of greatest concern for overall lake management. In mesotrophic systems, lake trout may occur in relatively low numbers with only intermittent recruitment of cohorts" or in some cases, be moderately abundant; lake trout normally do not occur in eutrophic systems and are usually unable to reproduce successfully in them .

Lake trout are affected by many human interventions, including: loadings of toxic materials; acid precipitation; exploitation; introductions or invasions of exotic species; water level controls; dams; diking; dredging; and a variety of other physical habitat alterations.

In general, the lake trout is a stenoecious organism with respect to many of its niche dimensions such as temperature and dissolved oxygen conditions that are representative of the oligotrophic environment. 'Therefore, it is especially sensitive to stress intrusions along either of these particular dimensions. For certain other niche dimensions the lake trout shows a greater degree of tolerance. In this respect, it seems to be particularly adaptable to the rather austere habitat that is typical of ultra-oligotrophic environments. It is unlikely to be substantially affected by natural intermittent stresses of short duration or natural episodic events such as wind induced thermal upwellings (e.g. Moffett 1962) that may result in large mortalities of opportunistic, invading species such as the alewife or smelt (Ryder, et al., 1981).

Similarly, the long life and relatively low natural mortality rates of adult lake trout, make them eminently more suitable for the assessment of general environmental quality as compared with short-lived, opportunistic species. The latter species react so rapidly to both normal changes in ambient background factors as well

as to culturally induced stresses through increased mortality, that opportunity for stress evaluation may be lost in "background noise".

(f) For the reasons cited above, the lake trout is not only an excellent #indicator of general ecosystem quality for oligotrophic systems, but it also provides diagnostic capability for specific Stresses. For example, it is well known that the incidence and ratio of fresh sea lamprey wounds to healed scars provides a useful indicator to assess the effectiveness of sea lamprey control programs (Pycha 1980). Similarly, bioconcentrations of certain toxic substances, or more generally, industrial waste complexes found in lake trout, may be useful indicators of the environmental concentrations of the same substances. In general, through biomagnification of toxic organic materials within succeeding trophic compartments of the food web, sub-detectable concentrations of toxic organic substances in the environment may eventually be back-calculated on the basis of lake trout tissue analyses (e.g. Connolly and Thomann 1982; McNaught 1982; Rodgers and Swain 1983). The bioconcentration of organic contaminants in pelagic organisms may be on the order of 106 times the concentrations found in the surrounding water through equilibrium partitioning alone (Clayton, et al., 1977). Lake trout, as top predators, implicitly may be expected to further concentrate certain toxic organic substances.

The reproductive and early life history stages of the lake trout are especially vulnerable to environmental stresses. The inability of the lake trout either to produce or to sustain progeny to fishery recruitment stages provides both an early-warning and a retrospective indicator of system malfunction. A recent lack of measurable natural reproduction in lake trout observed in Lake Michigan may be indicative of high BOD's due to inordinately high organic sedimentation on the spawning grounds or of high levels of PCB's, DDT, or toxaphene in the tissues and organs of lake trout (Willford, et al., 1981); or relate to one or more of many other possible causes or combinations of effects, including insufficient brood stock (J. F. Kitchell, pers. comm.). The observation therefore, of a loss of recruitment in lake trout where abundant brood stocks are present, may provide the first clue to a degrading ecosystem. Identification of the specific effect may then proceed through a careful examination of the sequence of reproductive events and an appropriate analysis of the lake trout, its eggs or progeny (if any) and the spawning microenvironment.

(g) Because the lake trout is a terminal predator in cold-water communities, aspects or dimensions of ecosystem quality determined through its study will not likely overlap markedly with other candidate indicators at lower trophic levels.

It is the only indigenous terminal predator in the oligotrophic environment of the Great Lakes Basin that satisfies the basic requirements of an ecosystem quality indicator; the burbot falls short on several counts (especially the lack of quantifiable data), while the sea lamprey and Pacific salmons are not native and therefore do not reflect the environment that has developed over evolutionary time.

(h) Historic data series exist on the abundance of the lake trout in each
     of the Great Lakes as determined from the documentation of fishery
     harvests (Baldwin, et al 1979). Some of these data series extend
     back well into the 1800's. Prior to that time, anecdotal treatises
     (e.g. Agassiz 1850) describe lake trout stocks in the Great Lakes and
     their relative abundance (Smith MSa). Recent data series from
     commercial fisheries combine catch and effort statistics as an index
     of abundance, demographic characteristics of lake trout stocks and
     fecundity and food habits. Other studies detail reproductive
     success, location and quality of historic spawning grounds, incidence
     of sea lamprey attack, movements, stock diversity, genetic
     characteristics, contaminent burdens and many other relevant
     characteristics of lake trout stocks.

(i) The lake trout is easily sampled through existing commercial
     fisheries, during creel census of sport fisheries, or through
     purchase from wholesalers or the retail market. Independent sampling
     of lake trout stocks is ongoing through the resource agencies of the
     two federal governments, several states and the Province of Ontario,
     and coordinated by the Great Lakes Fishery Commission and the
     International Joint Commission. Many of the parallel studies that
     continue in several inland lakes in both the United States and
     Canada, have conclusions of such fundamental generality that most of
     their findings may be reasonably transferred and applied to the lake
     trout stocks of the Great Lakes (e.g. Hacker 1957; Martin 1970;
     Rawson 1961; Schumacher 1961).

(j) Abundant spawning stocks of lake trout existed until recent times in
     each of the three Upper Great Lakes, although the levels of
     reproductive success were variable over time and-among lakes.
     Increasing rates of natural reproduction from planted stocks may be a
     useful indicator of environmental improvement.

(k) In addition to the aforementioned attributes of the lake trout
     relating to its biology, historic distribution and previous studies,
     it is important to recognize that the lake trout stock complex at one
     time provided one of the largest and most valuable commercial
     fisheries in the Great Lakes Basin (Baldwin, et al 1979). It is
     also a major sport fish species in the Upper Great Lakes and
     generates- vast amounts of income through the agencies of tourist
     promotion, marinas, charter fishing, tackle sales, fishing derbies
     and other related enterprises. The lake trout is generally recognized
     by the public as a desirable species with aesthetic qualities
     indicative of a healthy environment. Because of its great demand by
     recreation and market sectors, it is USUally easily obtainable for
     study. This ready availability of the lake trout makes it a
     moderately inexpensive option for the manager to obtain a rapid
     assessment of the status of the ecosystem.

3.2.2   Amphipod (Pontoporeia hoyi)

   Pontoporeia hoyi, an amphipod crustacean, would complement the lake trout
as a second candidate indicator for oligotrophic systems. Some of our
informants, particularly P. A. Larkin, have expressed a strong preference for

Mysis relicta over Pontoporeia hoyi, as a complementary indicator for oligotrophic environments. Although we concur with their opinion that Mysis might better represent the environment, we point out that currently, easily quantifiable capture methods for Mysis are lacking.

Pontoporeia does not satisfy the criterion of appreciation by man, but in some respects this is advantageous as it is not commercially harvested, nor is it subject to sea lamprey predation. Observed stress effects may therefore be attributed to other causes. In this respect the indicator qualities of Pontoporeia are complementary, orthogonal to and non-overlapping those of the lake trout.

Pontoporeia responds to a variety of stresses such as toxic loadings, cultural eutrophication and pH and its level of response may be easily quantifiable in terms of absolute or relative abundance. For example, when cultural eutrophication occurs in an ultra-oligotrophic system, Pontoporeia first increases in abundance as a general response to increased nutrient levels and then decreases when its nutrient optimum is surpassed. This observation is readily made through the use of standardized sampling methods for Pontoporeia, which assess standing stocks in terms of numbers and biomass (e.g. Alley and Anderson 1968; Freitag, et al., 1976; Marzolf 1964).

Recent taxonomic and biogeographical studies of Pontoporeia hoyi have . indicated that it is, like the lake trout, a species complex rather than a species **per se** (E. L. Bousfield, pers. **comm.).**

Other advantages and disadvantages of using invertebrates as indicator organisms in toxicity testing are described by Maciorowski and Clarke (1980).

3.2.3   Walleye (Stizostedion vitreum)

The walleye qualifies as an indicator organism on the basis of essentially the same set of criteria that were appropriate for the Hake trout. The major difference between the two species as indicators is the type of environment that their well-being reflects. The lake trout is indicative of an oligotrophic environment which prevailed in the Great Lakes in early times and persists today in a partially degraded state. The walleye, on the other hand, best reflects, high quality mesotrophic conditions usually found in relatively shallow bays, river mouths, or the nearshore regions of the Great Lakes. In particular, historical prime walleye habitats included areas such as: the Bay of Quinte; most of Lake Erie but particularly the western basin; Lake St. Clair; Saginaw Bay; Georgian Bay; Green Bay; the North Channel; parts of Nipigon Bay and Black Bay; and most connecting waters and major tributaries of the Great Lakes; Some of these walleye stocks declined gradually between 1900 and 1940, with abrupt declines observed in seven areas between 1940-1975 (Schneider and Leach 1977; 1979). Only five of the 21 localities originally noted for prime walleye stocks, which were quantitatively assessed in the mid 1970's, remained moderately stable. These stocks occurred in the Wisconsin waters of Lake Superior, Lake St. Clair - southern Lake Huron, eastern Lake Erie, northern Lake Huron and parts of Georgian Bay (Schneider and Leach 1977). It was noted that the five stable walleye stocks were but lightly exploited in recent times and therefore better able to withstand the impact of introduced or invading species which had low to high levels of abundance in

these same areas; pollution problems were generally described as relatively minor in these same locations, although some walleye stocks in Lake St. Clair are reputed to bear high contaminant loads.

Documented losses of walleye stocks have been attributed to many causes and combinations thereof (Regier, et al., 1969). In particular, overexploitation in early years (Milner 1874), interactions with invading species (Christie 1973) and increased contaminant concentrations (Ryder 1968) or perhaps even nutrient loadings, have been shown to have dire effects on stock stability. A major secondary effect of nutrient loadings, that is, increased rates of organic sedimentation, may have adversely affected the quality of walleye spawning grounds in Lake Erie as well as the habitat of a major food organism, the burrowing mayfly (Regier, et al., 1969). Suspended solids and sedimentation have recently been identified as a major stress in Green Bay, Lake Michigan (Harris, et al., 1982).

Interestingly, the walleye does not appear to be a preferred food item of the sea lamprey (Farmer and Beamish 1973) and in this respect, walleyes are not directly stressed by them. However, indirect effects of sea lamprey predation on other species may be important to walleyes as affected through trophic interactions (e.g. Patten, et al., 1982).

Abundant, reproducing stocks of walleyes, free of contaminant burdens, will be indicative of high quality, mesotrophic environments, particularly those of the nearshore littoral and limnetic zones, river deltas and major tributary streams.

Since 1970, some walleye stocks have responded favorably to certain rehabilitation measures and have increased to near former levels of abundance. Examination of events leading to these occurrences will provide additional indications of success of rehabilitation measures taken in recent years (e.g. Francis, et al., 1979). In particular, an analysis of the efforts to rehabilitate Green Bay, Lake Michigan, provided a unique insight into the rehabilitation process (Harris, et al., 1982). In Section 5.2.4, we elaborate on the utility of the indicator organism as a measure of rehabilitation success.

   3.2.4   Forster's Tern (Sterna forsteri)

The pelagic zone of the Great Lakes is the predominant ecological division in a geographical sense. However, one subsystem associated with the littoral zone, the coastal wetlands, although relatively small in total area, is believed to be vital to the well-being of the Great Lakes as a whole. There are more than 1,000 **km²** of coastal wetlands for the five Great Lakes (Table 5; Herdendorf and Hartley 1980). Although the ecology of these subsystems is relatively poorly understood, it is generally agreed that wetlands are of critical importance to fish and wildlife resources.

The near-shore, littoral zone is subject to an array of cultural stresses (e.g. dredging and filling, shoreline development, nutrient influx, toxic discharge, etc., Harris, et al., 1982). In addition, these shallow water systems are subject to natural long- and short-term lake level fluctuations (Harris, et al., 1981). Wetlands, especially coastal marshes, are an

important component of the littoral zone and serve as a connecting link between land and water systems. As inhabitants of wetlands, the Forster's tern may be considered as an integrator of the land and Water SYStemS.

In fact, a number of colonial waterbirds, many of which are piscivorous, are tightly linked to the littoral zone. Some are highly dependent on the wetland vegetation structure for nesting habitat and some are at pinnacle positions of littoral zone food webs. As a result, colonial waterbirds may reflect changes originating in several different ecosystem components, both structural and functional.

Wading birds (herons and allies - Family Ardeidae) have been proposed as indicators of the state of estuarine ecosystems in the United States (Custer and Osborn 1977). Herring gulls have been studied intensively as monitors of contaminants in the Great Lakes (Gilman, et al., 1979), while gulls and terns have been surveyed for their usefulness as indicators of man's impact upon Lake Superior (Harris and Matteson 1975). Various species of colonial birds lend themselves as biological indicators to a greater or lesser degree, depending on how their critical habitat requirements and genetically determined niche dimensions reflect their response to cultural and natural ecosystem stresses.

To be useful in trend analysis, a species must not only be easily monitored, but the observations should be easily quantifiable for best results. Ideally, reproductive success (number of young fledged for each nesting attempt) is an integrated measure of the well-being of a given species within the habitat that it occupies and provides an index to ecosystem "health". Although most colonial species are more readily monitored than solitary nesting species, measures of reproductive success of colonial nesting birds have rarely been standardized (Erwin and Custer 1982). While ease of monitoring and quantification of observations are two requisite criteria for a useful biological indicator or integrator species, there are several other criteria that might be considered. For example, Gilman, et al., (1979) suggest the following points in favor of the herring gull as an indicator of toxic contamination of the Great Lakes:

(1) feeds at the highest trophic level of aquatic and terrestrial food chains;

(2) is a year-round resident of the Great Lakes; and

(3) has a wide Holarctic distribution.

While these attributes suggest a less specialized organism that has relatively broad tolerances for many environmental properties (and thus serves as a good indicator species), there are other compelling reasons to consider more specialized avian species that have narrower tolerances for many environmental properties. Such a species might be the Forster's tern.

We note that Forster's tern does not satisfy some of the criteria previously proposed for an ideal indicator-integrator organism (Section 3.1) but include it herein, because of the wealth of information available about its niche, habitat, food habits and reproduction (Harris and Trick 1979; Harris, et al., 1981; Trick 1982; Trick and Harris 1903). Additionally, the

Forster's tern as an indicator-integrator organism, may be regarded as a
useful adjunct for identifying ecosystem quality problems in wetlands
surrounding Green Bay of Lake Michigan and thereby play a role in the
'implementation of future rehabilitation efforts (see Harris, et al., 1982).

The Forster's tern is not widely distributed in the Great Lakes (Scharf
1979), but where it does occur its success is heavily dependent upon existing
conditions of the littoral zone. Forster's terns typically inhabit marshes
and are almost always associated with emergent marsh vegetation. The nest is
commonly situated on an accumulation of dead plant material or "mat" within
emergent marsh vegetation (Trick 1982).

The availability of these sites reflects both the quality and extent of
coastal marshes (Harris and Trick 1979; Trick 1982). Consequently, the
reproductive success of terns reflects the suitability of the emergent
vegetation of the littoral zone habitat, which may be associated with cultural
stresses that cause disturbance or loss of the marshes.

In addition to its dependency on the structural components of the littoral
zone for nesting habitat, the Forster's tern feeds primarily on small fishes
(5-8 cm) inhabiting the littoral zone waters (Baltz, et al., 1979). In Green
Bay, Lake Michigan, the Forster's tern showed wide dietary preferences, feeding-
on both forage and predator species (i.e. alewife and yellow perch) as well as
common minnows such as the spottail shiner. Thus it integrates food-chain [1]
relationships in the open waters of Green Bay. However, in comparison with the
herring gull, which is cosmopolitan in food preferences, the Forster's tern
might be considered restricted in diet (stenophagic), or at least almost
totally associated with food species of the ecotone, that is the interface
between the littoral and pelagic aquatic systems. In addition, reproductive
success of the Forster's tern is related to its foraging success, which in
turn, is linked to water quality. Trick and Harris (1983) have demonstrated
differences in foraging success and chick growth between tern colonies on
Green Bay, where water quality differences are demonstrable. Because the tern
is a sight feeder, water turbidity can readily influence foraging success.
Turbidity conditions on Green Bay are strongly linked to algal production and
cultural eutrophication (Sager, et al., 1977).

Forster's terns are almost exclusively "fish eaters" and thus should serve
well as monitors of lipophilic compounds contaminating the Great Lakes which
tend to bioaccumulate in fishes.

The rather rigorous habitat requirements and somewhat restrictive niche
dimensions of the Forster's tern may make it a better integrator species of
the littoral zone than the herring gull (this species frequents refuse dumps
which negates its value as a natural system indicator) and perhaps more
reflective of local environmental quality. This does not imply that it is a
better indicator species for the Great Lakes as a whole. It does beg the
question as to whether or not a careful selection of several avian species as
indicators for specific subsystems of particular geographic areas would be a
useful strategy for monitoring the Great Lakes.

There is substantial evidence to indicate that colonial nesting birds may
have certain advantages over fishes for monitoring purposes. Given the
disadvantages that most birds are not easily aged after the juvenile period

and that they are not confined to the lake basin Proper (the latter may also be an advantage under some circumstances), there remains a distinct advantage of birds as ecosystem monitors: many people watch birds. If one considers the number of professional and skilled amateur "bird watchers" in the Great Lakes region, it suggests a potentially powerful resource for "ecosystem surveillance". What is needed in this regard is a description of what observations to make and the establishment of a network for compiling and screening the information. It is possible to envision a professional group (such as the Colonial Water Bird Group) collaborating with federal, state or provincial government agencies, to establish monitoring priorities and procedures for colonial waterbirds. Carefully selected training sessions for both agencies and for amateur birdwatchers could lead to the establishment of a network or monitoring system which could be cost effective in providing reliable data for trend analysis. Thus, an ecologically based and citizenry supported system might provide a useful and significant monitor of the ecosystem and its relative "health" in the Great Lakes.

3.2.5   Other Candidate Species

The potential list of candidate indicator organisms is virtually endless (e.g. Warren 1971). While we have developed biological indicator criteria and the concept for indicator and integrator organisms using the lake trout, it is important to recognize that no single organism is capable of reflecting satisfactorily all of the cultural stresses to which it may have been exposed. Patrick, et al., (1968) noted that standards designed principally to protect fishes from contaminants may allow concentrations of lethal levels to persist for other community components such as invertebrates. Alternatively, nonlethal (to invertebrates) concentrations of certain substances may prove to be lethal to fishes. Consequently, an effective approach to the known dichotomous effects of contaminants on different members of the aquatic community may be to ensure that at least a few to perhaps several representative species are monitored as is practical and at various trophic levels of the food web.

We had previously classified indicator organisms as being of two types: specialized, with only narrow tolerances for environmental properties; or those species that are less specialized with broader tolerances. Both types of organisms are useful indicators but in different ways. Ideally, the most satisfactory results would be obtained through monitoring both types of organisms; the information obtained from stenoecious organisms would complement that obtained from euryecious organisms. In a practical sense, however, certain organisms stand out as prime potential indicators and this characteristic has led us to the selection of the lake trout as a representative of terminal predators (fourth trophic level of the food web) for oligotrophic environments. Similarly, the walleye has been selected as terminal predator indicative of mesotrophy and early eutrophy, while a crustacean, Pontoporeia hoyi was chosen as an invertebrate representative of the secondary trophic level of the food web for deep-water benthic and pelagic zones of oligotrophic environments. Additionally, Forster's tern has been shown to be a good indicator for wetland marshes bordering the Great Lakes and in particular, was indicative of the level of water turbidity deriving from cultural eutrophication and other sources.

Among the many candidate species, both aquatic and terrestrial, which have been proposed are: vegetation for the detection of pollutants (Jones and Heck 1981); Cladophora as an indicator of levels Of biologically available phosphorus (Auer, et al., 1982); insects, amphipods and isopods as indicators of stream quality (Hilsenhoff 1982); herring gulls representative of the highest trophic level of both aquatic and terrestrial food webs (Gilman, et al., 1979); zooplankton as indicators of PCB levels (Clayton, et al., 1977); ground beetles (Carabidae) for detection of kraft mill fallout (Freitag, et al., 1973); mussels as indicators of concentration changes in trace metals, DDEs, PCBs, hydrocarbons and artificial radionuclides (Farrington, et al., 1983); faecal bacteria in shellfish (mussels, cockles, and clams) as indicators of levels of faecal bacteria in the surrounding water (Al-Jebouri and Trollope 1984); burrowing mayflies as inverse correlates of sorbed oil in the substrate (Hiltunen and Schloesser 1983); and fish communities for multiple ecosystem stresses imposed by man (Regier 1979; Kerr and Dickie 1984). It should be noted that the latter two works were directed primarily at either the community or ecosystemic levels of the biospheric hierarchy (e.g. Regier 1977), rather than at individual species or towards individual environmental stresses per se and thus were concerned (implicitly) with the integrating characteristics of biological indicators.

4.0 INDICATOR CONCEPT DEVELOPMENT USING LAKE TROUT

We now use the concepts elaborated on in Chapter 2 to the development of the lake trout as an ecosystem indicator.

If the lake trout is to be used successfully as an indicator of a premium quality oligotrophic environment, certain quantitative information should be available a priori.

Of particular utility for establishing a baseline would be: a quantitative description of lake trout stocks (albeit of low precision) in the Great Lakes Basin, starting with the first available historic evidence (e.g. Smith MSa), at a time when cultural stresses were but slight; an account of the recognized natural constraints on the lake trout from both a hereditary and environmental perspective; and classification and grouping of stresses into those that are merely culturally amplified background or simulative stresses (e.g. cultural eutrophication), from others to which the biota have no history of genetic adaptation.

With respect to simulative stresses, niche is an important characteristic of a species in its response to environmental variability and regimen in both the biotic and abiotic compartments of the ecosystem.

Habitat constraints on the major niche dimensions of the lake trout are critical measures of survivability. Preferred habitat of the lake trout has been frequently described (e.g. Martin and Fry 1973; Martin and *Olver* 7980) and deviations from the natural condition may be measured and utilized by the ecosystem manager as indicative of habitat degradation derived from cultural sources.

Metabolic considerations, in a sense, overlap and relate to the two previous concerns of niche and habitat. The extent to which a lake provides optimum temperature conditions for lake trout, for example, may be derived from the metabolic requirements of the species. On this basis, perhaps only a relatively small portion of a lake's total volume may provide suitable habitat for lake trout-during mid-summer, while the whole lake may be suitable in winter. Recognition of this fact will be one of a number of important considerations in setting habitat objectives for lake rehabilitation.

4.1   HISTORIC ASPECTS OF STOCKS

The lake trout has been historically and continues to be, the fish species most broadly adapted to the heterogeneous natural environment of the Great Lakes. Prior to the period of cultural alterations that followed colonization of the St. Lawrence drainage Basin by immigrants from other continents, the lake trout in its various life stages, occupied virtually all of the available habitats of the Great Lakes (Lawrie and Rahrer 1972). Also, even though the Laurentian drainage is at the most southern latitude of the lake trout range in North America, because of their sheer volume and with the exception of the

western basin of Lake Erie, most of the Great Lakes appeared to be environmentally suitable for lake trout. Consequently, lake trout populations have been unusually stable, diverse and abundant in the lake system until 'recent decades.

4.1.1 Distribution

The historic lake trout stocks exhibited a high degree of adaptation to a wide variety of ecologic zones of the lakes. Observations during the early period of exploitation clearly indicate the presence of many ecologically and genetically subspecific subpopulations of lake trout (e.g. Dehring, et al., 1981). Distinct stocks were found in the many shoals and depth zones of the Great Lakes, each stock having a distinctive morphology, growth rate, size composition, spawning time and substrate preference (Brown, et al., 1981; Eschmeyer 1957; Goodier 1981). Verification of stock uniqueness occurred when intensive exploitation on an individual stock at different times usually resulted in its depletion. Stocks which were most accessible and with greatest commercial value *were* usually depleted first, often to extinction and less accessible stocks were influenced little, if at all, by exploitation (Brown, et al., 1981).

Various stocks of lake trout had evolved, some of which spawned in shallow, and some in deep areas of the open lake, on a wide variety of substrates but primarily sand, gravel and porous and fractured rock. Some stocks spawned in connecting waters and certain tributaries of the lakes (e.g. Loftus 1958). Each spawning area had its morphologically and biologically distinctive race (Brown, et al.,   1981; Goodier 1981). Some stocks appeared to spend their entire life in the vicinity of their spawning area, but others ventured across a lake as they grew larger (Rahrer 1968). All, apparently, exhibited a moderately strong homing instinct to their natal spawning area as they matured, which reduced gene flow among spawning aggregations and contributed to the genetic distinctness among stocks.

Young lake trout of certain stocks occupied the relatively shallow region close to the spawning area and moved to deeper waters as they matured (Eschmeyer 1956). Adults of some races remained primarily bottom dwellers and therefore, were more vulnerable to exploitation, while others were mostly pelagic except at spawning time and were virtually immune to exploitation. The latter stocks became increasingly vulnerable to exploitation as the benthic stocks were sequentially depleted. Some stocks in the deepwater shoals of Lake-Superior, have been little influenced by fishing in the past because of remoteness or poor food quality and because sea lampreys did not normally venture to offshore shoals in large numbers (Rahrer 1965).

4.1.2 Community Adaptations

The lake trout was historically the dominant and most abundant terminal predator in Lakes Superior, Michigan and Huron.. It became dominant in Lake Ontario after the Atlantic salmon declined and became extinct in that lake during the last half of the 1800's (Smith MSa). The lake trout may-also have been the dominant predator of the limnetic Zone Of eastern Lake Erie, at least until about 1890 (e.g. Regier and Hartman 1973). The burbot, which was less abundant than the lake trout in all lakes but Lake Erie, shared the predator

role with Take trout in the deepwater lakes. The burbot was probably the most abundant terminal predator in parts of Lake Erie, particularly in its central basin, at least until oxygen depletion disrupted the fish population of that basin in the 1960's and afterward (Smith MSb).

Although the lake trout was the major terminal predator of the Upper Great Lakes, it was not an obligate piscivore. Lake trout characteristically feed on invertebrates when available and can complete their life cycle successfully in lakes which have few or no forage fishes (Martin 1966). In the Great Lakes where there has been an abundance of both invertebrates and forage fishes, the invertebrates have constituted a major share of food consumed by lake trout prior to maturity (Van Oosten and Deason 1938) and are of moderate importance even after maturity (Stewart, et al., 1981). Food consumed by the lake trout indicates that it is an opportunistic consumer, feeding upon whatever prey may be present (e.g. Dryer, et al., 1965), with the quantity of food consumed related to the abundance of each food item available. Adult lake trout do not seem to search actively for, or rigorously select, particular sizes or kinds of food. Juvenile lake trout, however, may select for prey more easily captured such as several cladoceran species in preference to copepods which have a relatively high rate of escape (Kettle and O'Brien 1978).

Another study has indicated that food ingested by young-of-the-year lake trout consisted of 96% invertebrates and 4% fishes by volume. The conclusions of this study were that young lake trout fed heavily on planktonic organisms, sparingly on benthic organisms and essentially were opportunistic to the extent that they fed on whatever forage organisms were available in shallow nearshore waters (Swedberg and Peck 1984).

This opportunistic feeding characteristic of lake trout and their broad diet spectrum are traits which have probably contributed to their high degree of stability prior to the recent period when they have been adversely influenced by cultural stresses and non-native species. The principal food of adult lake trout, during the time of relatively little cultural disturbance, was the deepwater sculpin, the young of several species of deepwater ciscoes and at least two invertebrates, Mysis relicta and Pontoporeia hoyi. All of these species were historically abundant in the lake zones inhabited by the lake trout (Van Oosten and Deason 1938). If the abundance of any one of these food items should be depressed, the nutritional requirements of the lake trout would be adequately met by other forage fishes or invertebrates. Since food consumption of the lake trout was directly related to the availability of a particular food item, the non-selective or non-preferential feeding of lake trout would have the effect of providing stability to its forage base (e.g. Ryder and Kerr 1983).

The non-selective feeding habits of the lake trout, as opposed to the highly selective preferences of the coho, and chinook salmons, undoubtedly contributed to a characteristically slow growth and relatively late age and large size at first maturity under undisturbed historic conditions (Rahrer 1965, 1967; Sakagawa and Pycha 1971). The distinct stocks or races of lake trout from various regions of the lakes had different growth and maturity characteristics (Eschmeyer 1957; Khan and Qadri 1970; Rahrer 1965). Thus, the total lake trout biomass of a lake was a composite of many stocks, which individually and collectively represented many age cohorts and a moderate diversity of sizes within each cohort of both mature and immature fish. Such

an age structure is conservative and will give the appearance of great
stability to the lake trout population. This will be reflected in the absence
of major fluctuations in yield due to differences in year class strength, as
observed from the commercial harvest statistics which were relatively stable.
The relative stability of the fishery was maintained because it was able to
move sequentially from depleted stocks to unexploited stocks (Lawrie and
Rahrer 1973). Even when the favored local stocks were greatly reduced or
extinct and the fishery relied upon the more adaptive and wide-ranging stocks,
there was little evidence in total catch data of fluctuations which would
result from marked variations in year-class strength (e.g. Fry 1949). Although
some stocks became greatly depleted or extinct, there was no indication of
general depletion (Lawrie 1978).

4.2   NATURAL CONSTRAINTS ON STOCKS

    Even in the absence of all cultural stresses, lake trout will
nevertheless, be subjected to both temporal and spatial extremes of natural
stresses arising from their inherent phenotypic attributes (e.g. Berst and
Simon 1981). Over evolutionary time in oligotrophic environments however,
lake trout have become genetically adapted to the temporal and spatial rigours
of oligotrophy (Ryder, et al., 1981) resulting in a species that is ideally
adapted to its ambient environment.

    For the ecosystem manager, it is important to be able to recognize both
the quantitative and qualitative aspects of natural background stress levels
before an assessment of cultural intrusions may be made (Kerr, et al., 1985 in
press). Acknowledging that the lake trout is genetically adapted to an
oligotrophic environment and its cold-water community of organisms is a first
step towards the successful evaluation of the effect of aberrant stresses of
cultural derivation. Also, the oligotrophic environment by definition, is low
in nutrients and accordingly, low in food availability. This nutrient-poor
condition is exacerbated by the relatively low annual energy input, which in
turn contributes to inordinately low mean water temperatures, relatively slow
growth rates in fishes and consequently, low ichthyomass turnover rates.

    When the oligotrophic environment is compared with a eutrophic
environment, the former would seem to be austere in the extreme and
uninhabitable for many species. Yet, through evolutionary processes, a whole
suite of cold-water organisms has become adapted to oligotrophy; so much so
that survival becomes contingent on the presence of the austere conditions.
This factor permits the lake trout, as a terminal predator in a cold-water
community, to be a reasonable surrogate of both a healthy community and a high
quality oligotrophic environment.

4.2.1   Natural-Versus Aberrant Stresses

    Earlier in this-report, we noted perceived differences between natural
stresses. and aberrant stresses. It is appropriate to elaborate further on
this point to assist in understanding the ecosystem responses to different,
types of stresses, as well as to the use of biological indicators as prima
facie evidence of cultural stresses.

    Because all organisms are subjected to many natural background stresses of
varying degrees and of different durations or regimes, description and
quantification of "natural stresses" become critical to the successful

determination of incremental impacts of closely **similar,** CUlturally derived
stresses or simulative stresses. Most organisms have adapted genetically to
natural stresses at normal levels and regimens over several natural
time-frames (i.e. diurnal, lunar, annual and evolutionary). In fact, ambient
variability of many abiotic factors is a requisite to normal modes of life.
Hence circadianism (e.g. Aschoff 1960) is an endogenous organismic reaction
conditioned by diurnal light cycles (and related properties such as heat),
while photoperiodicity and reproductive cycles in contrast to daily rhythm,
may be exogenously geared to seasonal variability in the environment. The
natural phenomena of perhaps the least predictability in the Great Lakes
region are those episodic events of even greater temporal span, such as
unusual though temporary changes in climate, floods or forest fires, all of
which affect biotic cormunities either directly or through diverse paths of
the ecosystem. Communities of organisms exhibit a graded response to many
different temporal spans of natural stresses through genetic adaptation over
evolutionary time. For daily and seasonal variability, the genetic adaptation
of the organism has been such that its physiological response not only tracks
the environmental variability, but has become dependent upon it.

Episodic events of catastrophic proportions, because of their infrequent
occurrence and unpredictable nature, are the least tractable from the
perspective of organismic adaptability. Events such as forest fires and
floods may be regarded as temporarily disruptive of ecosystems as the minimal
effect, although these same systems tend to re-equilibrate in time, following
the passing of a catastrophic episode.

Consequently, the degree of genetic adaptation to natural events by an
organism or community of organisms depends, at least in part, on a relative
time scale. When episodic events are spaced sufficiently far apart, genetic
adaptation may not occur. These widely separated events should not be
considered as "natural background levels" but rather as episodic incidents
that should be of some concern to the ecosystem manager. Some of these
episodic incidents are desirable over decades or centuries, regardless of how
devastating their temporary effects on ecosystems might be. Hence, floods and
forest fires are noted by Bormann and Likens (1979) to be useful for the
release or redistribution of trapped nutrients and to produce a
"rejuvenescence" of the ecosystem.

Episodic events are important to the Great Lakes Basin relative to
Pleistocene glaciation. That event was the dominant influence on the
formation of the more resilient portions of ecosystems that persist today in
the Laurentian Great Lakes. As an event of long duration, Pleistocene
continental glaciation was not catastrophic (<u>sensu stricto</u>) and community
adaptation occurred over time through genetically controlled, phenotypic
compliance with the austere environment as exemplified by the lake trout and
much of the cold-water community (e.g. Ryder, <u>et al</u>., 1981). Alternative
adaptation occurred by migration to and survival in, glacial refugia by
species less tolerant of the ultra-oligotrophic conditions that prevailed
during glaciation (Bailey and Smith 1981).

Currently, communities of freshwater organisms utilize the same two
strategies for survival in the Great Lakes Basin; either they become

genetically adapted to the austere oligotrophic conditions, or, in the case of some warm-water species, they seek refuge in shallow bays or warm, tributary streams.

Today, many of the seemingly "natural" phenomena of the Great Lakes are in reality, secondary effects of Mn's intervention in the watershed. Intermittent, abnormally high floods are particularly suspect as man has largely eliminated the natural hydrologic dampening mechanism through the removal of forests and the drainage of marshes, swamps and bogs and channelization. Other effects attributed to Nature may be more subtle, but may often be traced indirectly to cultural intervention.

A second consideration of natural versus aberrant stresses relates to the history of exposure of an organism to the stress and the probability for genetic selection in favor of the stress. For example, eutrophication, acid precipitation and thermal pollution, are all simulative stresses or cultural amplifications of natural stresses. Organisms have long exposure histories to these stresses at natural background levels and accordingly, a marked resistance to them. The key feature of a simulative stress is quantitative rather than qualitative, exceeding substantially the levels of natural background variability, or exhibiting an atypical annual regime. Accordingly, it becomes essential to quantify the background levels of variation or the annual regimen of a simulative stress before the impact of the stress may be determined.

Rehabilitative measures for these types of stresses are usually directed at reducing the stress values back to the pre-stress levels or, alternatively, striving for the apex of an optimality curve (eutrophication, acid precipitation and thermal inputs all have optimal levels in terms of favoring community survival).

For aberrant stresses on the other hand, there is no history of exposure and adaptation. These stresses typically relate to the introduction of new substances or conditions into the environment. The effects of changed conditions and many substances on an ecosystem are virtually unknown and therefore unpredictable. Some insight may be obtained from a prolonged series of prior bioassays (this is controversial; e.g. White and Champ 1983) or other tests and studies on different taxa of diverse age structure and under varied environmental conditions. These tests may elucidate some of the synergistic or antagonistic impacts of xenobiotic mixtures, biomagnification, long-term sublethal effects or subtle genetic effects that might not surface in the affected ecosystem for many generations, providing only minimal information and hence minimal predictability.

Currently, it is probable that simulative stresses have the greatest potential for large-scale devastation of Great Lakes ecosystems because of their geographic ubiquity (e.g. forest cutting, acid precipitation and cultural eutrophication). However, over the long-term, the study of thousands of xenobiotic substances introduced into the environment at thousands of point and non-point sources would seem to be hopelessly intractable from a practical point of view, without massive new research initiatives by government agencies. In practice, this type of approach would not seem to be justified on the basis of the ultimate results. Alternatively, biological indicators

may be particularly useful to both detect and subsequently quantify the combined effects and sources of the many xenobiotic substances injected into the environment against a known background concentration of zero.

4.2.2   Major Niche Dimensions

Before we attempt to describe some of the boundary conditions of certain major niche dimensions, it would be constructive at this point to define the much misused and often misunderstood term "niche".

Niche, in the current context, will be described in the Fry-Hutchinsonian sense (Kerr and Ryder 1977), that is, within the abstract hypervolume that is generated by assigning a dimension to each factor that affects an organism's survival. Simply put, each organism has a genetically defined metabolic scope for activity along many abiotic dimensions such as heat, oxygen, light and nutrients (Figure 10) as well as a behavioral response along biotic axes such as reproduction, feeding, competition and predation (Figure 11). The inborn genetic capacity of each organism may be termed a fundamental, or "potential" niche, which is expressed phenotypically by the organism's inherent functional and metabolic capabilities along normal environmental gradients. The phenotypic response of an organism may be considered to be an "operational" or realized niche and is considerably reduced dimensionally from the potential niche, as other organisms or environmental stresses intrude along, its fundamental niche axes (Figure 11).

Niche, then, is both an inherent characteristic of an organism as well as a reflection of the environment with which it interacts. In utilizing the lake trout as an indicator organism, a rather complete understanding of its major niche characteristics becomes critical, including a quantitative description whenever possible. Much of this information has already been documented (e.g. Martin and Olver 1980) and there remains to be completed only an orderly synthesis and subsequent application of the material available. We attempt a first approximation of this approach later in this document through a computer program designed to test environmental stresses against the background niche dimensions of the lake trout. As the lake trout niche is more stenoecious (of narrower tolerance limits) than that of most other species in the cold-water community, its use will be conservative in that it will serve as an "umbrella" organism, spanning most other species in the cold-water community whose niche dimensions are wider and therefore, have physiological requirements that are less rigorous (see Appendix IV for an elaboration of these concepts).

4.2.3   Critical Limitations Of Habitat

Complementary to the organismic limitations of niche boundaries, which are genetically determined, are the constraints placed upon the organism by habitat. Habitat constraints intrude along each fundamental niche boundary, and in combination with biotic intrusions along many of the same boundaries; help shape the realized niche of an organism.

At their most fundamental levels, limits on habitat are reflected as inputs of materials and energy (Figure 11). Each organism functions optimally at appropriate ratios of energy and matter (e.g. heat and nutrients as they affect metabolic activity), which in turn, are derived from the system that
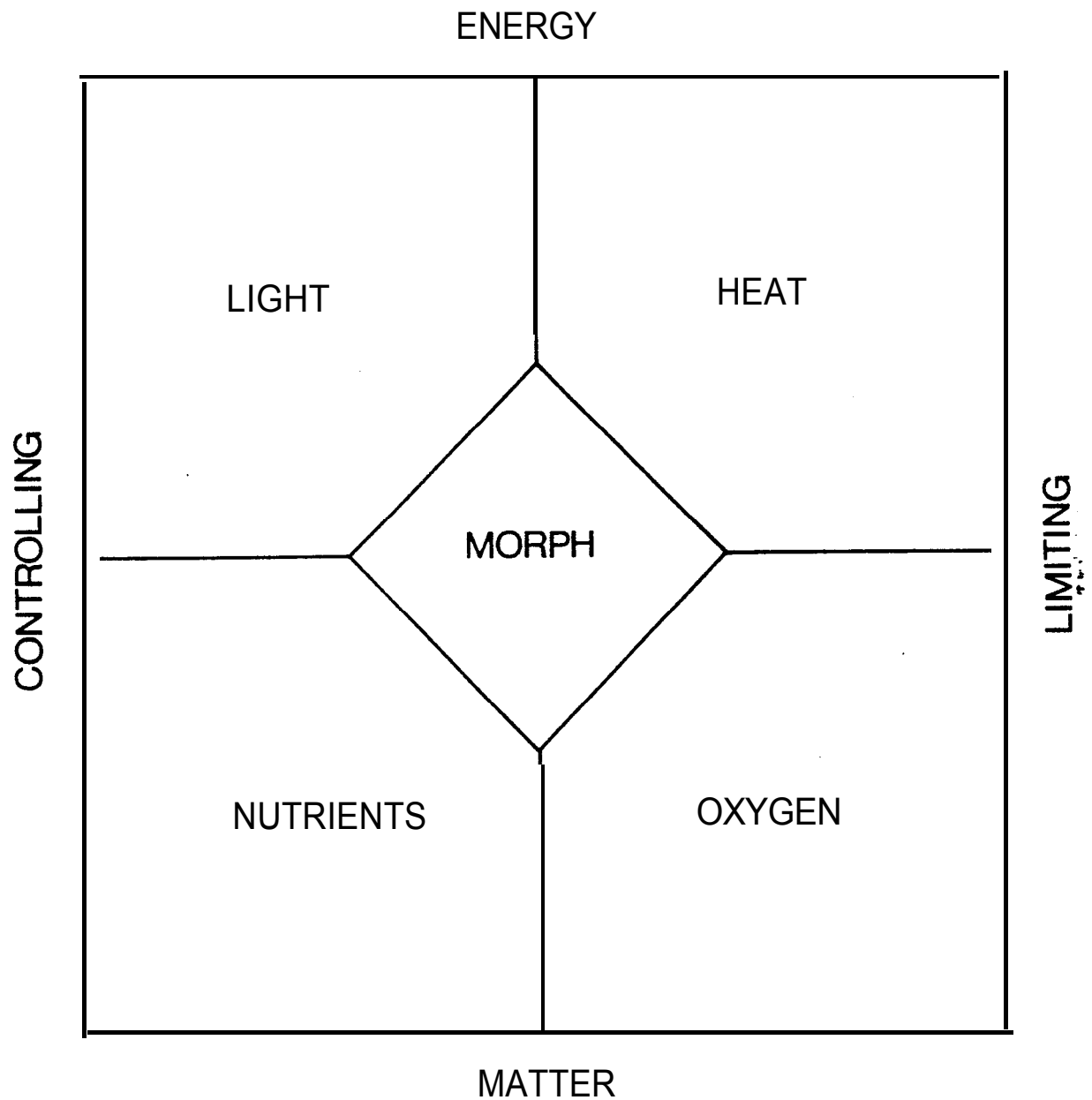
Figure 10   Fundamental controlling and limiting (potentially lethal) factors of the environment expressed in terms of energy and matter and constrained by the morphology of the system. Temperature may be, a controlling as well as a limiting factor (e.g. during spawning).
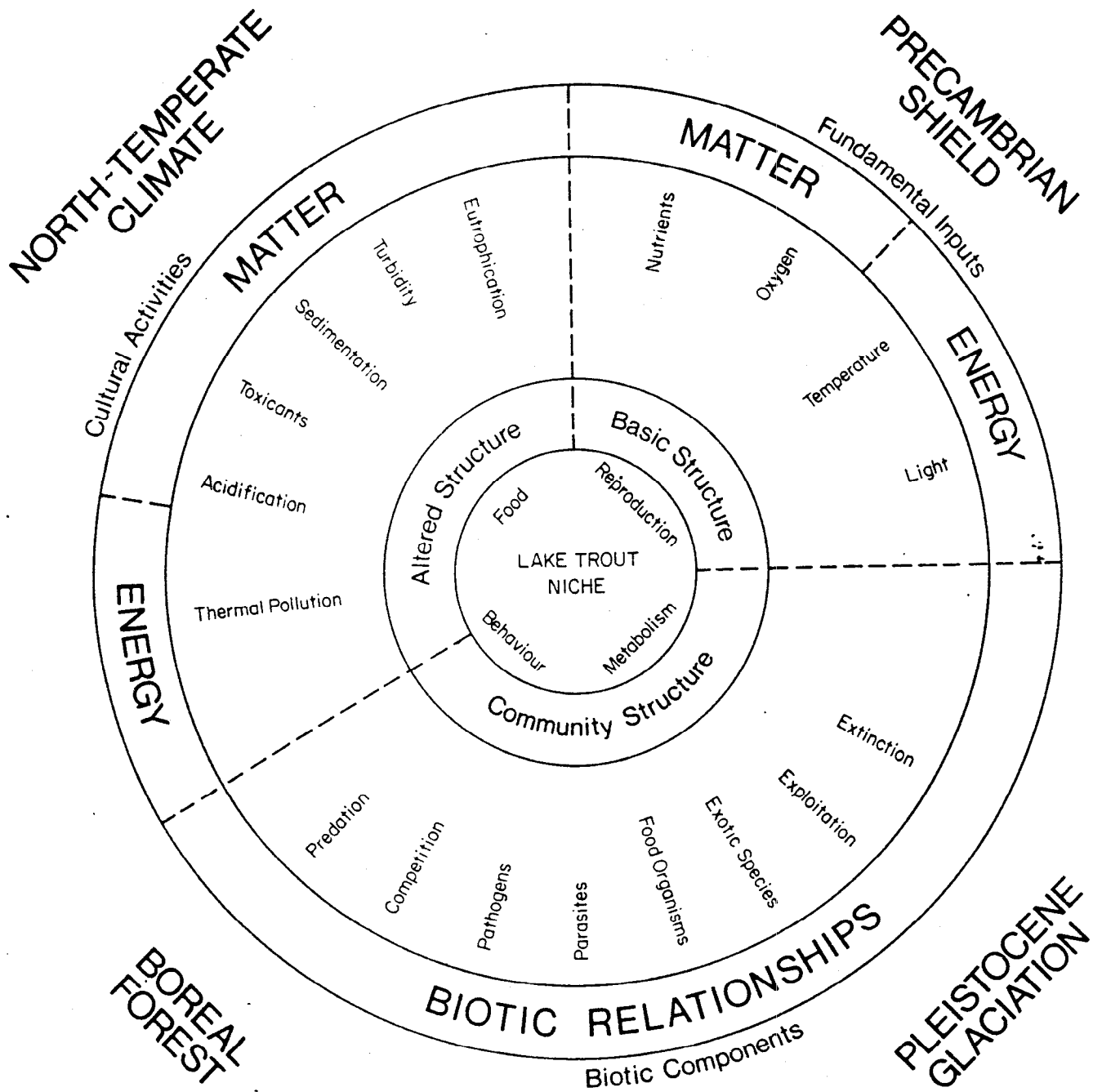
Figure 11   A two-dimensional representation of the "realized" lake trout niche pushed through time. The ecosystem attributes included in the diagram, constrain the fundamental dimensions Of niche (that which is genotypically possible) into the realized form, which is a measure of environmental suitab

approaches abiotic optimality for that particular organism or community.
Hence, the cline of oligotrophic to eutrophic aquatic systems also describes
the community types that best exploit a particular system characteristic; in
'this case, nutrients. Oligotrophic aquatic systems have been described as
optimal for salmonid communities, mesotrophic systems for percids and
eutrophic systems for centrarchids, cyprinids, ictalurids and associated
species (Ryder and Kerr 1978).

The other fundamental habitat requirement, energy, superposed on the
material (nutrient) limitations, subsumes all of the critical factors that
need to be considered at the most basic hierarchical level of an ecosystem.
The appropriate quantification of energy input into aquatic ecosystems has
been successfully applied to the estimation of global freshwater fisheries
yields by Schlesinger and Regier (1982).

At another level worthy of consideration, energy and matter may be further
subdivided into functional limiting and controlling factors of fish
communities (Fry 1947; Figure 10). Nutrients and oxygen are two key material
components commonly identified as essential to community survival.
Temperature and light are the corollary energetic components that may be most
often addressed as being important to biotic communities. Within this matrix
of four fundamental requirements of fish communities at the energetic and
material levels, it should be noted that the qualitative effects on individual,
fish species, will be different, even in a generalized sense. Hence, one
energetic factor (light) and one material factor (nutrients), while having a
strong influence on fish communities over the ambient diurnal or annual range,
are rarely lethal to fishes per se, even at the extremes of the range,
although either their surfeit or lack may induce marked behavioral changes
(Ryder 1977). Light and nutrients, therefore, may be considered as key
controlling factors of an organism or community (e.g. Fry 1947). Light
variation on a diurnal time scale, influences daily behavior patterns relating
to feeding in particular. On an annual scale, light establishes markers for
the commencement of reproduction through the photoperiod, while heat regulates
the process once initiated.

Many factors both within and external to lakes, tend to mitigate the light
influence on biological activity. These include both turbidity and internal
turbulence such as density currents, wind-induced wave action, cloud cover and
plankton blooms. These various types of light modifiers determine in a
qualitative sense-appropriate habitat conditions for different species and
tend to provide both spatial and temporal structure to the environment.

Augmenting these controlling factors, two limiting factors complete the
matrix of fundamental constraints of the habitat on the organism or community
(Figure 10). In this instance as well, one factor, dissolved oxygen, is
derived from materials input processed by aquatic plants through the agency of
photosynthesis. Dissolved oxygen, at extremely low concentrations, restricts
the extent of habitat that fishes may occupy and if chronically low, may cause
mass mortalities of fishes. A limiting factor, therefore, is similar to a
controlling factor over the middle regions of its ambient range, but becomes
lethal to fishes and other organisms at the extremes.

Heat, derived primarily from solar insolation, is also limiting in that it becomes lethal at its extremities. Again, temperature acts as a controlling factor over much of its range. Temperature regime is as important from a species or community level of concern as absolute temperature, per se.

For lake trout, the four. fundamental characteristics of habitat have been reasonably well-defined for the different life stages, but particularly for adults (e.g. Martin and Olver 1980). Lake trout are primarily sight feeders and do best in moderately to highly transparent waters. Optimum temperature for growth and other metabolic activity including the onset of reproduction, is about 10.5°C (Coutant 1977). Minimal oxygen levels for assured survival in the summer hypolimnion, of the Great Lakes is about 5.5 mg/L (Magnuson, et al., 1979), while Martin and Olver (1976) suggest that hypolimnial oxygen concentrations in excess of 4 mg/L are probably satisfactory. Optimal nutrient levels for lake trout may seem contradictory in that optimal phosphorus concentrations for maximum growth are about 10 ug/L, while this level is indicative of early mesotrophic rather than oligotrophic conditions (Chapra 1977). At 10 ug/L, however, deep, oligotrophic lakes may be expected to suffer hypolimnial oxygen deficits in the late summer (dependent upon their morphometry) and organic accumulations on potential spawning grounds through sedimentation processes may be sufficiently great to cause a marked biochemical oxygen demand. Reproduction, therefore, may be restricted geographically or possibly inhibited in its entirety. This seeming dichotomy between the conditions required for optimal growth of lake trout and optimal reproduction (Figure 12), is difficult to rationalize on an evolutionary basis. It would seem that ultra-oligotrophic conditions (extremely low nutrient concentrations) optimize lake trout reproduction, while early mesotrophic conditions (moderately high levels of nutrients) are best for growth and consequently, protoplasm elaboration or production (Figure 13). The adaptation of the lake trout to oligotrophic conditions therefore, may be an evolutionary solution to Liebig's Law of the Minimum (Odum 1971), that is; a satisfactory compromise for survival. In the Great Lakes, Lake Superior may be viewed as the lake with the best conditions for lake trout reproduction, while the Central or Eastern Basin of Lake Erie likely provided maximal growth rates.

An ecosystem manager provided with the appropriate measures of temperature, light, oxygen and nutrient levels for a lake would be in a good position to determine if that lake were potentially suited for lake trout and its attendant cold-water community. Relatively little else would have to be known in a culturally unstressed situation beyond the quality of the substrate for spawning (e.g. Sly and Widmer 1984) and the relative abundance and availability of suitable food items. The suitability of ambient habitat for lake trout may be easily established from available information (e.g. Martin and Olver 1976, 1980). This ability to determine background optima would provide the ecosystem manager with the prerequisite basis for his rehabilitation decisions in culturally stressed ecosystems, thereby yielding a goal for future habitat restoration which would be similar to that of the "ecosystem objective" (see Section 1.4).
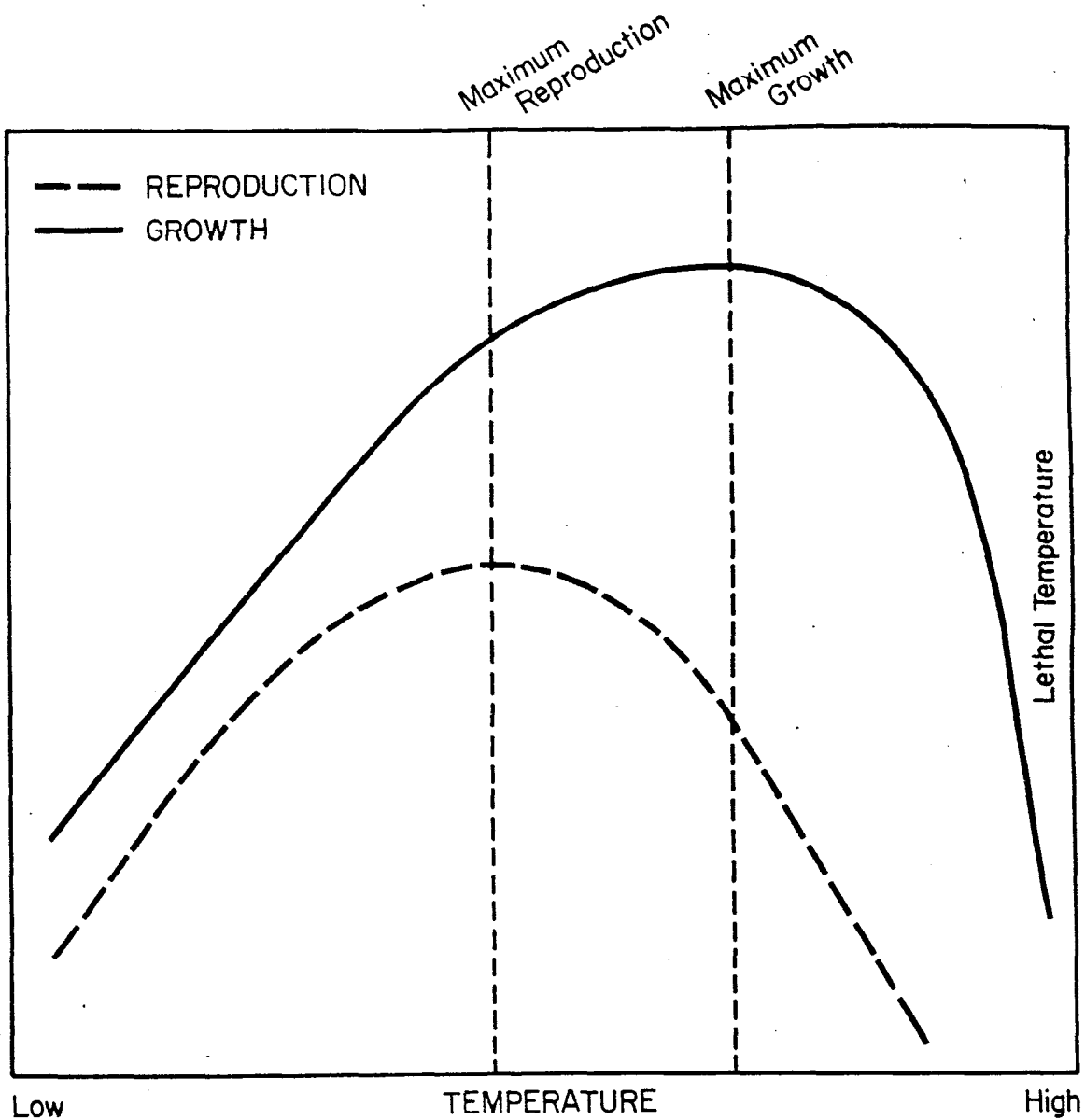
Figure 12   Growth and reproduction in lake trout peak at different environmental temperatures. Maximum growth of lake trout may not be a practical goal for ecosystem managers because of the increased risk of reaching incipient lethal temperatures. .
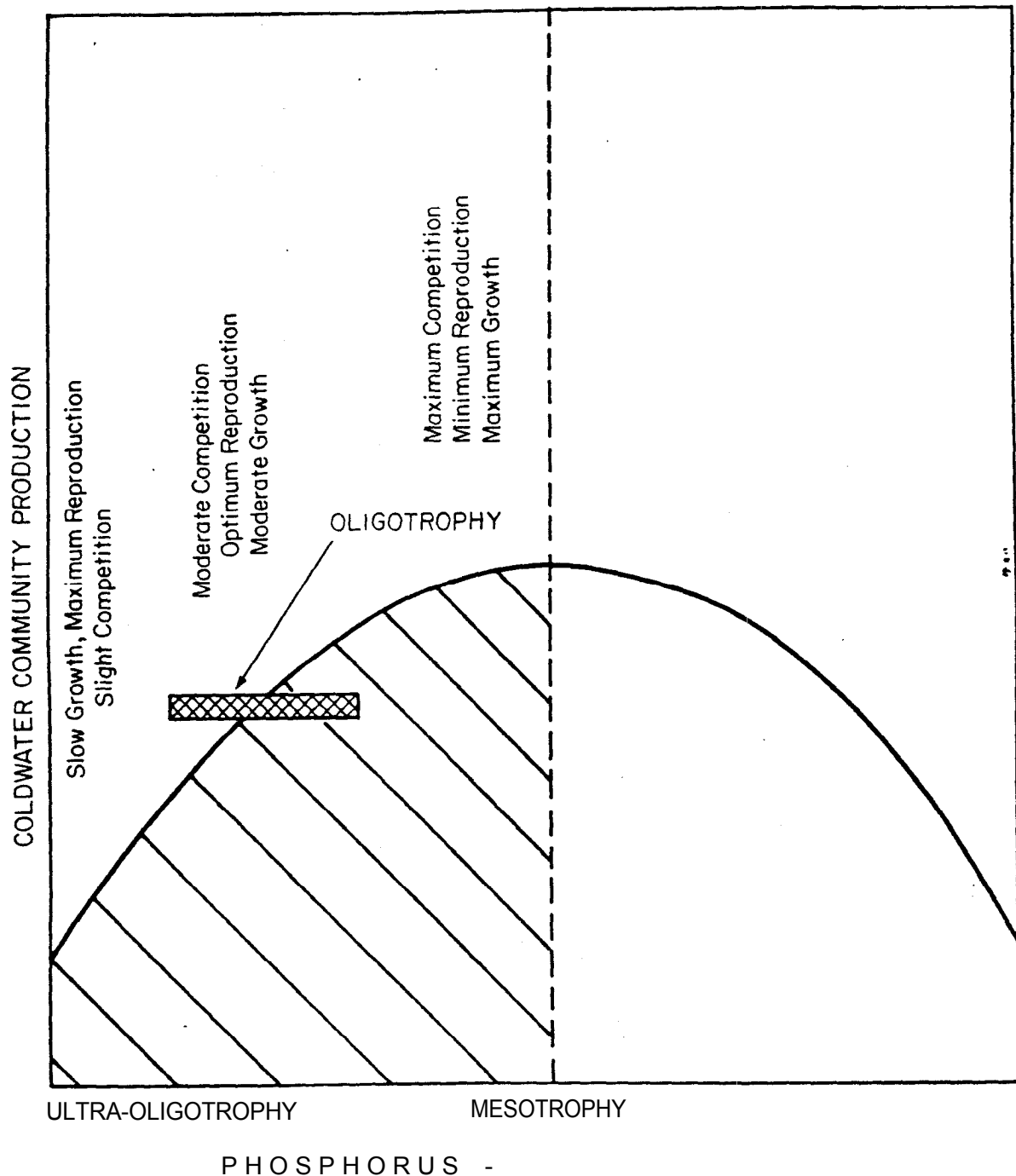
Figure 13   Oligotrophy at north-temperate latitudes is the optimal environmental condition for lake trout survival based on growth. competition and reproduction rates. The area depicted by the oblique bars represents the total inhabitable environment for lake trout. The relative level of phosphorus concentration is utilized as an indicator of the relative productivity of an aquatic system.

4.2.4   Metabolic Considerations

The innate metabolic capacities of the lake trout help to define some of the dimensional boundaries of its potential niche. The realized or operational niche is a measure of the extent to which ambient conditions of temperature, food availability and other environmental constraints, permit the potential to be reached. Quantitative measures of niche realization, that is, of the bioenergetic well-being of a cohort or population, therefore depend upon an understanding of how metabolic performance is affected by environmental factors.

The lake trout has been the object of many studies over the last few decades. Some of the pioneering work in fish metabolism by Fry and colleagues (e.g. Gibson and Fry 1954) featured lake trout and the recent size-structure analyses (Kerr 1979) and bioenergetic studies of Stewart, et a-l., (1983) have significantly augmented the previously available information on the species. The existing information on metabolism-body size relations, metabolic temperature and oxygen dependence, together with procedures for estimating maximum ingestion rates and similar variables, are adequate to support relatively detailed, quantitative analyses of the existing life support activities of the species. Additional information required to use the lake . trout as an environmental indicator would be: data on growth and fecundity performance of a given cohort, stock or population, together with measures of the major environmental factors to which they were subjected.

In essence, the reasons for such an analysis is to account for the pervasive effects of normal ambient conditions, such as temperature and food availability that so commonly affect the performance of lake trout, enabling the remaining effects due to inimical factors such as organochlorine contaminants to be examined in closer detail. For example; the performance characteristics of lake trout in Great Bear Lake are not readily comparable to the same species in say, Lake Opeongo, owing in large part to factors such as disparate thermal experience. Knowledge of the lake trout niche, however, is sufficiently fundamental to quantify the differences in thermal experience and reduce them to a metabolic common denominator, thereby allowing any residual differences to be attributed to cultural effects.

In addition to relatively complete metabolic information, there is a good choice of metabolic models for lake trout available in the recent literature, permitting analyses that are suited to the available data (e.g. Kerr 1982; Stewart, et al., 1983).

Despite the ready availability of appropriate models and metabolic data for lake trout, a detailed niche analysis of a specific stock has not yet been published, although such a study would appear to be both imminent and timely. In the interim,-the application of these analytical procedures to young-of-the-year herring by Kerr and Dickie (in press, 1985) provides an example of how the techniques might be applied to lake trout.

4.3   GENERAL EFFECTS OF CULTURAL IMPACTS

In Section 2.1.4, we sketched some general ecosystemic responses to cultural stresses as they have been applied conventially by humans. In this

instance, focus is at the species level and most specifically at the population level. The treatment of each topic in this section will be rather cursory because more critical considerations follow in Sections 4.4 to 4.8.

Effects or symptoms sketched herein tend to occur with a variety of stresses acting singly or in combination. For immediate purposes it will suffice to describe these effects or syndromes, rather than demonstrate their utility as generalized indicators of overall ecosystem quality or, conversely, as specialized indicators for diagnostic purposes. The latter aspects are discussed briefly in Section 5.1. See also Appendix V for a generalized listing of responses of an oligotrophic system under cultural stress.

4.3.1   Harked Departures From Mean Harvest Level

In the Great Lakes, most stocks of lake trout have always been valued as food and for ceremonial and recreational purposes. A few stocks of siscowets or "fats" are not a highly valued food fish because of their high fat content. Recently, some lake trout stocks have been found to have levels of contaminants judged to be excessive by resource and environmental agencies responsible for ensuring that human food be wholesome (e.g. Willford, et al., 1981). Apart from the exceptions of certain stocks of "fats" and some contaminated stocks, the remaining lake trout stocks have never lacked for market demand and fisherman attention. Declines in harvest that occurred with these valued and-wholesome stocks have apparently always been due to events (anthropogenic and otherwise) in the aquatic ecosystems that depressed the ecological production of these stocks.

4.3.2   Chancres In Mean Size And Mean Age Of Sexually Mature Fish

Stresses that act to increase the mortality rates of old and/or large fish have the effect of reducing the abundance of these age and size classes, thus reducing the mean size and mean age of sexually mature fish. It is well known that harvesting by humans and parasitism by sea lamprey have this effect and in fact, these two types of "predators" have very similar preferences with respect to stocks and sizes of lake trout. It may be that certain types of diseases, small parasites and toxic contaminants, all concomitant with ecosystem degradation, may also increase the mortality rates of older fish disproportionately, but these possibilities have not been researched in depth.

4.3.3   Ratio To Other Species

The lake trout, as terminal predator in Great Lakes' coldwater communities, may be considered as the principal factor in the retention of community stability or steady-state. Any undue stresses on lake trout that tend to reduce their numbers or biomass substantially, will likely be reflected by increased numbers or biomass in its major prey species, assuming that such a stress does not also change the trophic interrelationships within the system.

In an unstressed community, small changes in predator-prey ratios take place as a matter of course due to background environmental variability; on the other hand, large-scale or temporally persistent, unidirectional changes

should be considered as a serious concern to the ecosystem manager as they may be indicative of a persistent decline in community integrity (e.g. Ryder and Kerr 1978).

Disproportionate ratios among fish species within a coldwater community may ensue from various types of stresses on the lake trout, from over-exploitation or sea lamprey depredation, to the more subtle effects of contaminant loading and cultural eutrophication, either of which may result in partial or complete reproductive failure. Appropriate ratios for objectives of ecosystem managers may be gleaned from longterm catch records (e.g. Baldwin, et al 1979) of both predator and prey, during the period following "fishing-up", but prior to any noticeable declines in lake trout abundance. This assessment may be made for lake trout and its prey species for each of the Great Lakes and used as one quantitative indicator of a quality ecosystem (see Appendix VI for an example of species ratio quantification).

4.3.4   Loss Of Recruitment

In instances of high mortality rates of large, mature fish, the stock will gradually decline due to loss of recruitment. But recruitment may also fail if eggs carry a sufficiently high burden of contaminants (e.g. Burdick, et *al.*, 1972) so that the fry are poisoned when the egg material is metabolized (see Section 4.5 below). Further, recruitment may possibly be suppressed by predation on young lake trout by small, ubiquitous planktivores such as rainbow smelt or alewives. A variety of other cultural stresses may lead to loss of recruitment, either with respect to only occasional year classes or as a consistent phenomenon, thus leading to species extinction in extreme instances. In any event, partial *or* complete loss of recruitment with lake trout is a serious symptom of cultural stress, since it seems to occur but rarely in nature.

4.3.5   Changes In Incidence Of Deformities

During the early stages of the lake trout fishery, senile, often deformed individuals were frequently encountered. Such anomalies tend to be cropped. rather quickly and their subsequent occurrence is so rare, that few people to-day have ever encountered a senile fish.

Of more concern are deformities of juvenile fish. A variety of abiotic environmental factors emanating from cultural stresses such as toxic material, contaminant, or acid loading, act to increase the frequency of occurrence of deformities in young fish (Kennedy 1980). Few of these survive beyond their first year of life. Thus, juvenile deformities are associated with increased mortality of young stages.

Increased incidences of anomalies in otherwise healthy-appearing adult lake trout may also be indicative of, high levels of contaminant loadings in. the environment. Such anomalies may take the form of obvious external tissue lesions, lumps or papillomas, or may be internal and therefore, not overtly conspicuous; such as spinal deformities *or* testicular constrictions (e.g. Ruby and Cairns 1983). In general, lake trout may be less susceptible to anomalies derived from contaminent exposure because of their proclivity to suspend in the water column in the open, limnetic zone. In this respect, they may not be as vulnerable as persistent benthic feeders such as suckers and bullheads

which search actively in the bottom sediments. Nonetheless, lake trout do show both internal and external changes following contaminant exposure to chemicals such as dieldrin, endosulfan, 2,4D, PCB's, malathion, carbaryl, atrazine and chlordane (Meyers and Hendricks 1982). Activity of these chemicals and deformation of lake trout occurred at many body sites, including: the liver; gills; spleen; intestine; swim bladder; brain; bile; fins; eyes; skeletal muscle; fat; integument; abdomen; stomach; pyloric cecae; ureters; and urinary bladder. As adult lake trout are not normally used as bioassay organisms, the above listing should be considered only as indicative of the order of magnitude of contaminant effects in inducing anomalous conditions in lake trout. The persistance of adult lake trout, despite the occurrence of these many anomalies, makes them eminently fine indicators of general system malaise.

4.3.6   Changes In Growth Rates

With predator species such as the lake trout, cultural stresses that act directly to increase the mortality rate in a stock may have the effect of reducing intra-stock competition for food and thus lead to increased growth rates. This has often been noted for many species (e.g. Ryan and Harvey 1977).

Theoretically, culturally-triggered increases in disease, parasitism and contaminant loading should, over time, act together to reduce growth rates.. However, these possibilities have not been adequately documented.

4.3.7   Changes In Behavioral Patterns

Fairly strong circumstantial evidence and some experimental evidence support the inference that the distribution of fish in. the aquatic habitat, their migration patterns, their reaction to man-made artifacts (such as fishing gear and underwater reefs), may change quite rapidly and markedly, based on their experiences and sense perceptions (e.g. Olgivie and Anderson 1965). Recently, Arctic char were found to persist in the Bodensee (a lake on the borders of Austria, Switzerland and West Germany) only in those areas least affected by cultural intrusions (Hartmann 1983).

In the formerly pristine Great Lakes, the lake and stream chars (lake and brook trout) intermingled to some extent in stream mouths, bays and nearshore littoral and reef areas. This no longer occurs in the lower lakes and only near the occasional stream in the upper lakes with the exception of Lake Superior where such intermingling among salmonids is common. Along the lower lakes, many cities and towns have been built in areas where these chars formerly intermingled, but they no longer may be found in such degraded waters.

Currently, in the Upper Great Lakes, lake trout intermingle freely with brown and rainbow trout and the Pacific salmons, at least in some locations or at specific times of the year.

4.3.8   Changes In Genetic Constitution

Genetic phenomena within salmonids are not yet well-understood despite some major initiatives to achieve a greater understanding. The chars and also the coregonines, seem to be polyploid and this predisposes them to very complex genetic processes. Apparently, polyploidy facilitates introgression

(see Section 4.3.9) and desegregation in general, causing confusion on the question of whether taxonomic differences between stocks are of a phenotypic or genotypic nature (e.g. Ryder, et al., 1981).

Recently,, various biochemical approaches have been developed to study genetic phenomena in a direct empiric, manner. These studies may lead to biochemical-genetic indicators (e.g. electrophoresis) of stress (See especially Berst and Simon 1981).

In a general sense, any cultural stress on a taxon flock of coregonines, for example, may tend to reverse the continuing process of segregation into that of introgression. This phenomenon may provide additional survival value to a fish stock that has been decimated below its critical mass for reproduction. Introgression with other fragmented stocks may circumvent extinction while the cultural stress persists.

High stock diversity, on the other hand in the absence of cultural Stress, ensures that a taxon flock exploits its diverse environment with optimal efficiency (Ryder, et al., 1981).

4.3.9   Introgression Of Related Stocks

The recurrence of interbreeding between related stocks or species to produce a new taxon with some intermediate features, has been inferred along coregonine stocks in numerous lakes (Smith 1964; Svardson 1965). It is usually associated with intensive harvesting coupled with environmental changes such as eutrophication and physical perturbation and/or restructuring of the nearshore zone (Regier 1968; Regier, et al., 1969).

This phenomenon has not been well studied for lake trout and other char taxa. The one exception relates to the splake, a hybrid between lake trout and brook trout, which sometimes occurs naturally, but is propagated widely for stocking in lakes, including some of the Great Lakes and especially Lake Huron (see Tait 1970). It seems likely that researchers will discover that the introgression phenomenon among lake trout stocks occurs commonly whenever stocks are subjected to various kinds of cultural stresses, especially those that tend to remove either the temporal OF Spatial barriers of reproductive isolation.

4.4   RESPONSES TO CULTURAL ACCELERATION OF NATURAL LOADINGS

Lake trout exhibit a stress response to culturally accelerated loadings of many types of naturally occurring compounds and consequently, act as useful indicaters and integrators of ecosystem quality with respect to these compounds. Responses identified in lake trout may be a function of both the nature and impact of the input and subject to the specifics of the study and may occur at the biochemical, physiological; individual, stock and population levels. Regardless of the site of the impact or the nature of the response, an area of environmental concern is indicated which may be more precisely mapped following further study.

4.4.1   **Phosphorus** Loading

Until recently, each of the Great Lakes has exhibited an increase in the rate of eutrophication over the last century and a half (e.g. Loftus and Regier 1972), resulting primarily from increases in phosphorus loadings (Dobson 1981). The general response to cultural enrichment has been characterized by the proliferation of both-free-floating (and attached algae, the depletion of hypolimnia1 oxygen and marked changes in the structure of fish communities (Ryder 1981). The magnitude and severity of the response has varied greatly from lake-to-lake. In Lake Erie, for example, the entire hypolimnion of the central basin has been lost to fish production for a portion of the year as the result of cultural eutrophication (Regier, et al., 1969; Regier and Hartman 1973), while in the Upper Great Lakes, the severely impacted areas are generally restricted to the nearshore zone and certain embayments (e.g. Berst and Spangler 1973; Lawrie and Rahrer 1973; Wells and McLain 1973).

Although cultural eutrophication has been widely cited as a factor in the loss of fish stocks, it Is difficult to isolate clear-cut examples of its effects. Large increases in the phosphorus loading rate to small, previously oligotrophic, Precambrian shield lakes, have resulted (at least temporarily) in an increase in both the numbers and growth rates of lake trout, although recruitment rates to a fishery may have been reduced. An assessment of the response of Great Lakes lake trout to cultural enrichment is difficult due to concomitant changes In exploitation or predation of lake trout by both man and sea lamprey, increased toxic loadings and other simultaneous stresses. It is now **commonly** believed that over-fishing was one of the contributary causes of lake trout decline in all the Great Lakes, while the primary cause for their ultimate demise was due to sea lamprey depredations (e.g. Christie 1974). The ultimate biological extinction of lake trout populations in Lake Erie was probably related to environmental stresses, particularly to oxygen depletion in the central basin hypolimnion (Hartman 1973). The disappearance of other cold-water salmonid stocks has also been attributed to hypolimnia1 oxygen depletion (Larkin and Northcote 1970; Rubec 1975). It appears then, that excessive phosphorus Inputs indirectly result in the reduction in size of lake trout stocks by. limiting the amount of suitable habitat and in some situations at least, leads to the extinction or reduction of stocks.

4.4.2   Acid Precipitation

Dramatic changes occur in the biota at all trophic levels of lakes and rivers coincident with declining pH (Wright and Snekvik 1978; Harvey 1980; Cowling and Linthurst 1981). This is particularly true for the fish component of an aquatic ecosystem. Each fish species has a specific acid tolerance whereby a reduction in pH level below the threshold results in the loss of that species from the system (Beamish 1974). These results are further supported by the observations of Rahel and Magnuson (1983,), who found that the presence or absence of 31 fish species in 138 naturally acidified Wisconsin lakes was closely associated with the pH of those lakes.

The loss of lake trout POpulatiOnS in aquatic ecosystems experiencing a decline in pH is well-documented (Jensen and Snekvik 1972; Beamish 1974; Beamish 1975; Schofield 1975). Generally, lake trout populations cease reproduction at about pH 5.5 and become extinct at pH values below 5.0. The loss of lake trout has been attributed to a failure of recruitment in acidified waters (Beamish 1975). Anthony, et al., (1971) provide evidence that the reproductively active component of fish populations (spawners) are more susceptible to reduced pH than are the nonbreeding adults. Gunn and Keller (1984) demonstrated that pH levels in the water column less than 5.0 may not be lethal to lake trout eggs unless the latter were deposited within the interstitial waters of the spawning rubble. This was indicated by the high survival rate of test fry suspended in incubators above the substrate.

Kennedy (1980) evaluated the effects of reduced pH on reproduction and recruitment in an indigenous population of lake trout inhabiting a lake that had been experimentally acidified over a three-year period to a mean summer epilimnetic and hypolimnetic pH of 5.8 and 6.2, respectively. Although egg fertilization in the acidified lake was successful, it was followed by embryological deformation and recruitment failure. Close to 60% of the fertilized eggs in the acidified lake died or failed to gastrulate and two-thirds of the surviving embryos displayed gross anatomical malformation. Immediately prior to hatching, all surviving embryos in the acidified lake were deformed, while in a control lake 92.9% of the eggscontained normal embryos prior to hatching. Consequently, lake trout populations are unlikely-i to persist for long if the pH of their environment declines much below 6.0.

The possibility of a significant decrease in the pH of the Great Lakes as a whole over the Short or medium term is unlikely, due to their large volume and adequate buffering capacity. However, localized pH depressions are likely to occur (and indeed have already been noted; Research Advisory Board 1978) in some nearshore areas in the spring as the result of runoff generated from rapid melting of acid-laden snow. These spring depressions in pH would have a significant local impact on lake trout stocks if they occurred in the proximity of lake trout redds containing overwintering eggs or newly hatched sac fry. More significantly, perhaps, is the potential threat of acid precipitation to poorly buffered, influent streams of the Great Lakes; particularly those on the north shore of Lake Superior that formerly supported abundant river spawning stocks of lake trout (Loftus 1958). In these instances, a severe spring pH depression could all but preclude the possibility of successful rehabilitation of lake trout, river-run, stocks.

4.4.3   Thermal Input

Relative to most other fish species occurring in the Great Lakes Basin, lake trout are very stenothemric (i.e. maintain themselves over a relatively narrow temperature range). They have very specific temperature requirements for survival, growth and successful reproduction (e.g. Martin and Olver 1980). Increases in the mean temperature of the Great Lakes may lead first to reproductive and recruitment failure, increased growth and eventually, if the temperature trend persists, to subsequent reductions in growth rates and even death if the trend is prolonged (Figure 12). While there is evidence of a slight warming trend in the Great Lakes as a whole during the first half of this century (Beeton 1961) which may have adversely affected lake whitefish survival (Lawler 1965), no marked changes have taken place since that time.

Of more concern for lake trout may be the heated **effluents** discharged by electric power and industrial plants (e.g. Clark and Brownell 1973) located on the periphery of the Great Lakes. With the possible exception of Lake Michigan (Acres 1970), the impact of heated effluents is normally restricted to small areas in the vicinity of the discharge site. Nevertheless, if the location of the discharge site overlaps with "critical" lake trout habitat, such as spawning or nursery areas, the expected result could be a reduction in lake trout stocks.

Alternatively, the net effect of heated effluents into the Great Lakes may be neutral to positive (J.F. Kitchell, pers. comm.). Power plants tend to aggregate prey, provide warmer water temperatures in winter and at some sites, provide suitable spawning substrate. Further research into the effects of thermal and thermonuclear power plants on the lake trout and associated coldwater community is indicated.

4.4.4   Heavy Metals And Other Elements

More than 35 heavy metals and some Other elements with an atomic number greater than.20 have been found in lake trout from the Great Lakes Basin (Table 6; modified from Tong, et al., 1974). All these elements occur naturally in most aquatic ecosystems, although background levels in both the water and fish vary greatly, depending on the amount of the element in the soils and rocks of the lake basin and surrounding watershed (Smith, et al.,, 1975). In addition, cultural acceleration of natural loadings occurs as a result of agricultural and industrial processes (Bache, et al., 1971) and also resource extraction in the mining and forestry sectors.

Characteristic of lake trout is their ability to accumulate at least some of the heavy metals found in aquatic systems. In fact, heavy metals and other elements that are below the detection limit in water often reach concentrations that are easily detectable in lake trout tissues (Moore and Sutherland 1980). Many factors influence the degree of accumulation of heavy metals in lake trout. These factors fall into one of three categories: the geochemistry of the lake; the life history of the fish; and the trophic level at which a fish feeds.

Ultimately, the amount of a heavy metal assimilated into lake trout tissues is conditional on the concentrations available (MacCrimmon, et al., 1983). Availability is mediated not only by the loading rate but also by temperature, water chemistry (e.g. hardness, pH) and the chemical form of the metal as well as the productivity of an aquatic system. This is best illustrated for mercury, the dynamics of which are better understood than for any other heavy metal (e.g. Higgins and Burn 1975; Wright and Hamilton 1982). Clearly; lake trout are accumulators of mercury in both culturally stressed (Bache, et al., 1971) and unstressed systems (Smith, et al., 1975). While mercury in lakes is present predominantly in inorganic form, an organo-mercurial neurotoxin, methyl mercury, is the form usually identified in aquatic organisms (Fimreite, et al., 1971; Westoo 1969). As well, it is the methyl form of mercury that is most toxic (Biesinger, et al., 1982; Mason 1981).

TABLE 6

HEAVY METALS AND OTHER ELEMENTS IDENTIFIED IN
TISSUES OF LAKE TROUT FROM THE GREAT LAKES BASIN
(MODIFIED FROM TONG, ET **AL.,** 1974).

aluminum	indium	silicon
antimony	iron	silver .
arsenic	lead	strontium
barium	manganese	tellurium
boron	molybdenum	terbium
cadmium	nickel	thulium
cesium	niobium	tin
chromium	palladium	titanium
cobalt	praseodymium	tungsten
copper	rhodium	vanadium
gallium	rubidium.	yttrium
germanium	ruthenium	zinc
	zirconium	

The net production of methyl mercury is generally thought to be biologically controlled (Billen, et al., 1974; Jensen and Jernelov 1969; Spangler, et al., 1973; Wood 1974) and it is believed that an important site for mercury methylation is in the sediments (Jernelov 1972; Jernelov, et al., 1975). The net release of methyl mercury from the sediments increases as temperature rises from 4° to 20°C and with sediments enriched with nutrients (Wright and Hamilton 1982). Also, the methylation of mercury proceeds at a faster rate as the pH declines towards 6.0 (Fagerstrom and Jernelov 1972). Both the net rate of methylation and consequentially, the concentration of methyl mercury in lake trout tissues, will depend on all the above factors; however, it appears to be less dependent on the horizontal distribution of mercury in the sediments. Moore and Sutherland (1980) noted that while only 7% of the bottom of a large lake in northern Canada contained high levels of mercury (>500 ug/kg), the methyl mercury concentration in lake trout was high throughout the lake, presumably due to the movement of fish from non-contaminated to contaminated areas. Consequently, an observable increase in the amount of mercury bioaccumulated by lake trout may indicate not only a greater mercury loading, but also changes in the temperature, pH (MacCrimmon, et al., 1983) and productivity regimes of an ecosystem.

Within a given lake, the concentration of methyl mercury in lake trout generally increases with fish length (MacCrimmon, et al., 1983). weight (Smith, et al., 1975) and age, but is not correlated with the sex of a fish (Bache, et al., 1971). This occurrence probably stems from the affinity of methyl mercury for muscle tissue. Of particular interest is the observation by Bache, et al., (1971) that the ratio of methyl mercury to inorganic mercury increases with age in lake trout, perhaps due to the reduced rate of replacement of muscle tissue in old fish.

Generally, the concentration of methyl mercury in piscivores (top trophic level), including lake trout, is higher than that in either bottom feeders or planktivores (Thommes, et al., 1972). The difference is well-illustrated in lake trout that switch from a planktonic or benthic diet to one in which rainbow smelt is the predominant food and also a very efficient accumulator of methyl mercury (Akielaszek and Haines 1981; MacCrimmon, et al 1983).

Methylmercuric chloride has been shown to have adverse affects on three generations of brook trout at moderate to high concentrations (McKim, et al., 1976).

More is known about mercury, its effects and bioaccumulation than any other heavy metal. Other metals which accumulate in lake trout and have been intensively studied are few. Lead (Hodson, et al., 1982) and cadmium (Lovett, et al., 1972) concentrations in lake trout tissues and organs did not appear to be correlated with fish size. However, it has been demonstrated that lead, cadmium and chromium rapidly accumulate in the closely related brook trout until an equilibrium is reached between tissue concentration of the heavy metal and its concentration in the water column (Benoit 1976; Benoit, et al., 1976; Holcombe, et al., 1976). This equilibrium level in the fish is maintained as long as heavy metal concentrations in the water column remain approximately constant, but cadmium loss from the gill tissues was rapid for fish placed in control water (Benoit, et al 1976). Both lead and cadmium were shown to have long-term effects to at least the third generation in brook trout (Benoit, et al., 1976; Holcombe, et al., 1976).

Metabolic responses of lake trout to several heavy metals have been described by Passino and Coutant (1979), who found that inorganic cadmium, mercury and lead inhibited the liver enzyme allantOinaSe. These same three metals adversely affected the closely related brook trout. Lead exposure also resulted in marked increases in the levels of plasma sodium and chloride, with corresponding decreases in hemoglobin and glutamate dehydrogenase activity, cadmium induced increases in plasma chloride and lactic dehydrogenase activity decreased plasma glucose levels (Christensen, et al., 1977). It has been shown in a series of laboratory experiments that both cadmium (Eaton, et al., 1978) and copper (McKim, et al., 1978) can kill embryonic and larval lake trout. Furthermore, cadmium may lead to a reduction in growth rate of surviving embryos and larvae. Chronic exposure to lead is known to result in black-tail in rainbow trout, a symptom of neurotoxicity, the severity of which is determined by the growth rate of the fish (Hodson, et al., 1982). Aluminum has been shown to affect many species of fish (Baker and Schofield 1982), although the degree of the effect is strongly dependent on pH and calcium concentration (Brown 1983).

4.4.5   Naturally Occurring Organic Substances

While all bodies of water receive natural inputs of organic substances, little is known about the nature or concentration of these components or the effect of accelerating their loading on aquatic ecosystems. Generally, naturally occurring organic materials are derived from one of two sources: the biota; and soils surrounding a lake (allochthonous materials). Inputs from allochthonous sources may be classified as refractory organic compounds and include: phenols; lignins; cellulose; saponins; and humic and fulvic acids. It is likely that the concentration of the latter two compounds, which are associated with peat soils, has declined over the last century in many lakes including the Great Lakes as the result of soil drainage projects and forestry activities.

Other naturally occurring organic substances that are derived from the biota within the lake and its contained, organic matter (autochthonous substances) include: bioattractants; biorepellants; various forms of biotoxicants (e.g. derived from algae); amino acids; vitamins; organic forms of nutrients such as nitrogen and phosphorus; and nitrogenous waste products found in the excreta.

4.4.6   Radionuclides

Various radioactive elements including ^{239}Pu, ^{90}Sr, and ^{137}Cs are present in the Great Lakes (Yaguchi, et al., 1974). These materials originate primarily from nuclear weapons testing fallout, nuclear power plants and from accidental releases at fabrication, reprocessing and research locations. While relatively little is known about the response of fishes to increases in the concentration of radionuclides, the latter, have been linked to increases in the rates of tumor formation and natural mortality. All algae, zooplankters, benthic invertebrates and fishes from-Lake Michigan contain measurable quantities of radionuclides (Yaguchi, et al 1974), but there is considerable question as to whether or not fish can serve as useful quantitative indicators of such elements in aquatic systems beyond indicating their presence. Yaguchi, et al., (1974) found that there was an inverse

relationship between the concentration factors of some of the radionuclides in freshwater organisms and their position in the trophic hierarchy. Further, they-found that the concentration factor in lake trout was the lowest of eight fish species tested.

4.5   RESPONSES TO INPUTS OF XENOBIOTIC SUBSTANCES

     Earlier in this report, we have demonstrated that system response to various essential parameters (e.g. light, total dissolved solids, depth, nutrients, temperature, etc.) is dynamic but predictable within certain bounds. From a **community** perspective, each trophic level will tend to optimize productivity, barring excessive interferences from over-exploitation and other stresses such as the introduction of foreign substances (xenobiotics). A measure of ecosystem health would then, by definition, provide a gauge to judge how close the system is to reaching its maximum productive potential. We already have set the desired trophic level by identifying the lake trout as a keystone species (Paine 1966) and under these terms of reference, we need to address two major elements of concern, namely; exploitation and the introduction of toxic substances.

     We now consider inputs of xenobiotic substances. There is, quite understandably, a broad range of physiological responses of all organisms subjected to foreign substances. These are elicited in sublethal, metabolic or behavioral changes (e.g. Anderson 1971; Anderson and Peterson 7969; Anderson and Prins 1970; Ogilvie and Anderson 1965). The seemingly benign response may be of major interest because of future adverse genetic effects, for example, but seldom receives much direct attention in the literature. The ultimate response is death of the organism, which occurs when the concentration of a xenobiotic substance or combinations of substances exceeds the capacity of the organism to detoxify its body or rid its environment of the toxic material. This simple fact was exploited by early coal miners who used caged canaries as indicators to signal the presence of stale air (generally methane gas or hydrogen sulphide) and who vacated the area when the bird dropped off its perch. But the physiological response of organisms to various levels of toxic material has a breadth of ranges that encompass many changes less conspicuous than death. These changes include: (a) reproductive failure, as when mink fail to reproduce after subsisting on a diet of contaminated Great Lakes fishes (Hornshaw, et al-., 1983); (b) the incidence of external tumors or other anomalies of the integument, scales and fins of fishes, etc. (e.g. Black, 1983); and (c) the incidence of necrotic tissue or degenerative organn function, as in-testicular damage in rainbow trout (Meyers and Hendricks 1982). However, there are more subtle endogenous effects which emanate directly from enzyme or hormonal activity associated with the detoxification process that are amenable to the development of indices. These indices by implication, measure the health of the ecosystem without reference to the identity of the toxic chemical, or even necessarily to the exact levels of occurrence. As such, these types of monitoring techniques may serve as an early warning alarm or alternatively, to measure the relative health of disparate geographical areas and may even determine the trends in ecosystem health.

4.5.1   Single Contaminants

Concentrations of xenobiotic chemicals in species like lake trout have been used as a surrogate measurement for general environmental pollution, which presumably translates into ecosystem health and serves as preliminary clues to the cause for declines in stock abundance. For the chlorinated hydrocarbons or other lipophilic chemicals, understanding of the bioconcentration mechanism is essential if accurate projections of ecosystem health are to be expected. This mechanism is controlled by such factors as: initial concentration of a chemical in the environment, and partitioning and rate of uptake by the organisms; and retention and subsequent metabolism. For example, Oliver and Niimi (1983) have reported that the kinetics of various chlorobenzene congeners is influenced by an efficient, non-selective, uptake process followed by a selective elimination process that is based on the chlorine content and to a lesser degree, chlorine position.

Since fishes appear to be less capable of metabolizing PCBs than other vertebrates, the potential impact of those compounds in the Great Lakes would be more of a concern for human health resulting from consumption rather than concern for loss of stocks through direct mortality.

There is a temptation, given the profusion of research into cause and effect as determined from dose and response relationships from interactive single chemicals, to create matrices as a convenient way to stereotype the ecosystem. A thorough review of single chemical concentrations integrated through environmental compartments has yet to appear and therefore, its ultimate utility is not guaranteed. For example, if a mass balance could be derived for a chemical, using information both from the lab. and the environment, what would it tell us? We would know how much of the pollutant is in the sediments, water and biota; how it is partitioned and theoretically, how much is being added and destroyed through time. We could, with such knowledge, project the future environmental picture and presumably make recommendations as to the need for control programs. At least two realities prevent us from achieving that desired goal, namely, lack of financial resources to engage such thorough studies and the knowledge that a single chemical evaluation inherently ignores both potential synergism and antagonism of ambient chemical mixtures. An indicator approach, particularly at the aquatic community level, offers an economic first approximation of the severity of the problems through the identification of anomalous community morphology and system malfunction. Borgmann (1982) provides a mechanism for doing so, using particle-size conversion efficiency.

4.5.2   Contaminant Mixtures

Contaminant mixtures pose a special problem in aquatic systems in that sometimes the toxic effects may be more than merely additive or at other times less than additive (Alabaster, et al., 1980). In specific instances, toxic' contaminants may act quite independently of one another (Konemann 1980). Calamari and Alabaster (1980) have proposed an approach to theoretical models for evaluating the effects of contaminant mixtures on aquatic organisms. The current state of knowledge of the effects of chemical mixtures on organisms and measurement of the same is such that further research is indicated (Alabaster, et al., 1980).

The negative effects of contaminant mixtures. on fish stocks include: a
lowered resistance to disease or additional pollution; inability to complete
critical life functions, such as spawning, hatching, rearing, or the
attainment of sexual maturity; and increased incidence of deformities which
may translate into indirect and undetermined mortality through selective
predation. The mode of uptake of contaminant mixtures is another important
consideration. Where contaminant mixture concentration in the egg, for
example, is the result of transfer from the maternal body burden to the
developing egg mass, the ambient water quality may have little or no bearing
on hatching success. But if the newly hatched organism is already stressed,
then ambient water quality may bear directly in post-hatching success.
Experiments conducted by Willford, et al., (1981) between 1972 and 1977,
demonstrated that water from Lake Michigan was of such poor quality as to
impede the early life survival of lake trout carrying maternally inherited
residues. Hesselberg and Seelye (1982) also demonstrated that adult lake trout
from Lake Michigan contained some 167 identified organic chemicals as compared
to eight Identified compounds in hatchery brood fish reared in well water.
These studies are significant in that specificity of chemical toxicity may
remain undetermined, but ecosystem effects are measurable, nevertheless (e.g.
Cairns, et al., 1981). Baumann (1984) concluded that tumor incidence in some
fish species may be a sensitive indicator of carcinogenic compounds in the
environment.

4.5.3   Biochemical Indices

Aquatic populations, stocks and communities are coevolved products of
their environment and as we have already demonstrated, astatic biotic
communities often reflect unhealthy ecosystems. In this regard, indicators of
single species stress may be instructive in depicting the state of the
environment; especially when that species, as the keystone predator (e.g.
Paine 1966), is the ultimate integrator of community dynamics. Two
biochemical measures of stress that have recently received some consideration
by researchers are the mixed function oxidase system (MFO) and the adenylate
charge procedure which compares levels of ATP/ADP/AMP as indications of stress
(e.g. Hochachka and Somero 1973; Payne 1977).

Xenobiotic chemicals in the aquatic environment are biologically
transformed by certain enzymes. Of particular interest is the MFO system in
fish. The MFO enzymes are inducible by several environmental contaminants,
such as DDT, PCBs, PBBs and the polynuclear aromatic hydrocarbons (PAHs).
Experiments have shown that salmonid MFO activity increases linearly with
increasing dose levels of such chemicals (e.g. Addison, et al., 1982; Elcombe
and Lech 1978). MFO activity has also been shown to be significantly higher
in polluted areas as compared to non-polluted areas. For example, a number of
investigators have observed elevated levels of MFO relating to petroleum
spills (Spies, et al., 1982; Stegeman 1978; Walton, et al., 1978).

Experiments on lake trout have demonstrated MFO activity, suggesting that
it may be possible to use this species to indicate either local or lakewide
contamination by MFO-activated substances. However, one of the problems in
using this approach is the seasonal variation of MFO activity, which responds
to hormonal activity associated with gonadal maturity in an organism. Since
these factors are related to natural stresses, it may be difficult to
establish baseline values which are needed to develop and apply diagnostic

tests. The interactions of MFOs with the reproductive hormones, mean that
differences between sexes also need to be considered. Preliminary results of
MFO studies indicate that such variation is present in the lake trout from the
Great Lakes. Other studies have shown a similar correlation between spawning
time and lower MFO activity using species like the cunner, Pacific salmon,
sand dab, mummichog, sheepshead and mosquitofish (Chambers and Yarbrough 1979;
Trams 1969). Additional sources of variability that have been observed are:
species; size at age; temperature; feeding habits and diet; migration; and
sampling method. Thus, it will be difficult to establish with confidence a
dose/response relationship due to exposure to xenobiotic substances in the
environment.

However, results from preliminary studies suggest that there may be some
ability to use MFO activity to stereotype lakes. For example, using lake
trout from Lake Opeongo as a control, MFOs had values of 60-100 units, while
those from Lake Ontario had values between 400-600 units (V. Cairns, pers.
comm.). These values correlate well with known levels of organochlorine
pollution in the water columns of these two lakes. An advantage of MFO
activity over measures of organochlorines in a lake is the ability of the
former to reflect exposure rates and to a limited degree, some effects.
Ecosystem health determination via MFO's requires further feasibility
studies. This subject currently is too obscure to be impressive to the public
and may be considered to be too esoteric or impractical by the ecosystem
manager. Nevertheless, use of MFO's and similar biological indicators holds
substantial promise for future determinations of ecosystem quality.

Adenylate energy charge (AEC), or the ratio of energy-rich
phosphoadenylates to total adenylates in a tissue, has also been proposed as a
potentially useful indicator of stress in organisms (Atkinson, 1977). The
general theory behind AEC as a stress indicator is that any stress will result
in an increased metabolic energy demand as the organism's body defenses
respond to combat such stressors. By definition, AEC may range from 0 to 1
and generally, animals with values between 0.8 and 0.9 are indicative of
optimal environmental conditions, whereas values between 0.5 to 0.7 indicate
sub-optimal or unhealthy conditions.

Giesy, et al., (1981) and Ivanovici (1979) have demonstrated that AEC is a
sensitive indicator of stress associated with exposure to cadmium and
hydrocarbons in crayfish and molluscs, respectively. At present, because the
only published information concerning AEC and fishes has dealt with the
effects of changes in water temperature, dissolved oxygen and pH (e.g. Reinert
and Hohreiter 1984), changes in AEC may not yet provide conclusive evidence of
all types of stress-induced metabolic changes. Until such conclusive
demonstrations are made, the utility of this index remains speculative.

4.6   EFFECTS OF MAJOR HABITAT ALTERATIONS

The Great Lakes Ecosystem Rehabilitation document (Francis, et al., 1979).
has identified many culturally-induced habitat alterations in the Great Lakes
Basin that have affected fishes either directly or indirectly. We will
consider a subset of these culturally modified habitats with respect to lake
trout reproduction and subsequent survival of eggs and fry. These are the
life stages most likely to be stressed by any major environmental changes.

4.6.1 <u>Sedimentation</u>

Sedimentation has been identified by Harris, **et** al., (1982) as a stressor of paramount importance in Green Bay of Lake Michigan. Sedimentation on lake trout spawning grounds may be particularly damaging in some instances, as lake trout require clean rubble, gravel and boulders for egg survival through to hatching (see **summary** of substrate requirements in Martin and Olver 1980). Clean spawning substrate is usually ensured for shallow-water spawners through the selection of windward shoals or promontories for egg deposition (Martin 1957). Inordinately high sedimentation rates, if persistent throughout the incubation period, may smother any eggs already deposited in the redds. If the sedimentation is organic in origin, this stressful condition may be exacerbated throughout the incubation period as biochemical oxygen demand increases.

Sedimentation and inordinately high levels of turbidity may arise from several sources, particularly those that physically modify the environment (particularly inorganic sedimentation), or those that enhance productivity through the addition of nutrients (organic sedimentation). Locales of particular concern for the Great Lakes in this regard include: areas of diversion; channelization; landfill; dredging; resource extraction; or the creation of various physical structures such as dams, dikes or groynes that affect water levels or flows. In the aggregate, these physical intrusions on the environment have contributed significantly to overall rates of sedimentation of lake trout spawning grounds.

Contributions to both organic and inorganic sources of sedimentation may be a result of various agricultural practices such as: soil erosion; fertilizer applications to crops; leaching of animal wastes; and wetlands drainage, which may prevent the dampening and subsequent natural mitigation of floods. Deforestation also contributes to soil erosion, which in turn, results in accelerated sedimentation, increased turbidity and increased release of nutrients to the watershed.

4.6.2 <u>Eutrophication</u>

Cultural eutrophication has been an environmental problem in the Great Lakes for at least three decades (see Vallentyne 1974). Despite programs to reduce the use of high phosphate detergents and other nutrient inputs, continued additions of these substances from both point sources (municipalities) and non-point sources (agriculture) pose an environmental problem that has persisted to this day. For example, algal growths on lake trout spawning grounds still pose a problem in certain areas, particularly in Lake Ontario. The location of many of the traditional lake trout spawning grounds in the Great Lakes is already known (e.g. Goodyear, et al., 1982; Smith 1968); thus, periodic monitoring at the appropriate times of year should provide an adequate indication of the suitability of the substrate for spawning, incubation and subsequent fry development. The prevention of excess phosphorus entering aquatic systems has already been successfully applied to' large portions of the Great Lakes Basin with a modicum of success. The problem of <u>Cladophora</u> or other algal growths on lake trout spawning substrate has been alleviated to a marked degree. Nevertheless, cultural eutrophication remains a potential environmental threat of some concern.

4.6.3   Deforestation

The cutting of dense boreal and Laurentian forests, which once covered the major portion of the St. Lawrence drainage and subsequent development and tillage of agricultural land, have caused major changes in the hydrology of the Great Lakes drainage (e.g. Smith MSa). The process of forest removal and land clearing started in the 1700's in the Lake Ontario Basin and by the early 1900's, virtually all of the virgin timber throughout the Great Lakes Basin had been removed, with the exception of a substantial portion of the north shore of Lake Superior.

The consequences of forest removal were many. For example, the thick organic mat on the forest floor, which functioned as a sponge and absorbed the melting snow and summer rains, rapidly disappeared following forest removal. The cool springs, which maintained stream flow throughout the year, started to dry up and surface run-off from the melting snow and rains was accelerated. The consequence was a change from a relatively stable regime of stream flows to widely fluctuating flows, with many streams that had previously been nursery or spawning areas for Atlantic salmon and brook trout, becoming dry or intermittent during the summer and fall. Forest removal also allowed a greater amount of solar energy to reach the streams, warming the water enough to make them unsuitable for salmonids. This condition was exacerbated where cool springs feeding the streams had dried and summer flows were greatly reduced (Brown 1971; Brown, et al   1971).

The increased rate of runoff during the spring thaw and intermittent rain storms caused major physical changes in the already altered stream beds. In the forested situation, streams were mostly deep cut and with overhanging banks in which logs and brush formed shelter within, over and beside the streams. Rapid runoff on the other hand scoured and eroded the stream substrates, resulting in broad stream beds with open and poorly defined margins and a minimum of shelter, including a reduced number of pools which were preferred habitat of the native salmonines.

Of broader impact, forest removal and disintegration of the forest floor released vast quantities of nutrients which were ultimately washed into the Great Lakes (e.g. Bormann, et al., 1968; Bormann and Likens 1970). Following disintegration of the forest floor, particularly in areas that were subsequently cultivated for agriculture, streams carried heavy loads of silt during periods of high run-off, resulting in deposition and filling of deep areas both within the streams as well as in the deltaic regions where they entered the Great Lakes. Concomitant to these events, the development of industry along the streams usually resulted in concentrated pollution and mill dams constructed-to provide power either blocked or created serious impediments to fish migration.

The consequences of forest removal had many direct and indirect influences on lake trout. The earliest was the demise of Atlantic salmon, which had been the dominant terminal predator in Lake Ontario. The Atlantic salmon of Lake Ontario, insofar as is known, never left the basin and its tributary streams in a seaward migration (McCrimmon 1950). It's loss left the lake trout to fulfill the ecological role of top predator. The Atlantic salmon presumably became extinct because of the combined effects of mill dams blocking its spawning runs, or the spawning streams becoming dry or intermittent. In

addition, all or virtually all spawning Streams of Lake Ontario were no longer suitable habitat for young salmon because of lack of cover or warmer water due to increased insolation following deforestation (McCrimmon 1950; Nash 1908; Smith MSa).

There was a major impact from-these environmental changes on lake trout, because the substantially altered streams provided suitable habitat for the reproduction and larval development of the sea lamprey, an Atlantic invader not previously recorded in the St. Lawrence drainage prior to forest removal. Evidence indicates that streams were too cold for successful sea lamprey spawning, incubation and hatching in the forested situation, but temperatures became ideal following forest removal and the new stream conditions with wider stream beds and fertile silt areas were favorable habitat for the larval lampreys (Smith MSa).

On the positive side, the nutrients released by forest removal may have increased plankton and forage fishes consumed by lake trout in the Great Lakes, but in the long run, the increased nutrient content in the lakes contributed to accelerated eutrophication and sedimentation, which eventually led to the demise of the lake trout in both Lakes Erie and Ontario (Smith MSb).

4.7   CONSEQUENCES OF EXPLOITATION

The consequences of exploitation on co-evolved, integrated fish communities are complex and often profound. Exploitation changes not only the structural composition of the communities in terms of species, sizes and cohorts, but also the functional relationships both between and within species, size-classes or trophic levels. A synopsis of major effects is described in more detail below.

4.7.1   Effects On Stock Complex

In Section 2.3.1 we sketched the phenomenon of taxon swarms or stock complexes of lake trout in the Great Lakes. We now describe this phenomenon further as it relates to exploitation by fishermen.

The important point to note is that the Great Lakes contained many recognizably different stocks of lake trout (e.g. Eschmeyer 1957) which differed with respect to anatomical, behavioral and ecological features. The practical significance of this phenomenon has often been overlooked by scientists more interested in providing support for the existence of separate species than in the intrinsic insights stemming from empirical study.

Different lake trout stocks of the same lake, as in Lake Superior (Goodier 1981), reached sexual maturity at different ages, grew to different maximum sizes, spawned at different times of the year in diverse locations and 'occurred in many different parts of the lake. All of the above features' are important to the fishermen. In addition, different forms or taxa had markedly different qualities of flavor, flesh texture. color and other attributes that influenced the price that consumers were willing to pay. Some forms became rancid soon after death even on ice, while other forms maintained a fresh flavor. Some lake trout taxa in a lake were among the most valued of all fish species taken by fishermen, while other forms were nearly valueless and did not warrant bringing them back to the dock.

Among lake trout stocks, fishermen tended to concentrate their fishing efforts on those that were accessible spatially and seasonally, or on those of higher market value, particularly if they were easily handled without deterioration.

From the perspective of lake trout as an indicator of **ecosystem** quality, there is no evidence that the stocks preferred by the fishermen were any more or any less tolerant of the effects of other human stresses. But this does not imply that fishing was a stress acting independently of all other stresses. Generally, to limit running time and therefore, Operational costs and to reduce hazards, fishermen tended to prefer nearshore stocks. The nearshore was more heavily stressed in other respects as well, especially by the exotic sea lamprey and with respect to contaminant, thermal and nutrient loading.

For the reasons given above, relatively few of the scores of the Great Lakes' native lake trout stocks have survived into the present and apparently only on a few offshore reefs or profundal depths of Lake Superior. These stocks include some of the forms termed "fats" that never commanded high prices in the market.

4.7.2   Size-spectrum Chancres

In the near-pristine conditions of the Great Lakes prior to settlement of the basin by Europeans, some stocks of lake trout reached great age and size, but the maximum age attained or size achieved depended on the individual stock. In Lake Erie the oldest and largest lake trout may have been 20 years old and 20 kg in weight, whereas in Lake Superior, both the maximum age and size may have been twice that number. But this comparison is based on little more than informed speculation, especially with respect to the ages achieved, as firm data do not exist. As indicated in the previous section, some stocks of lake trout were neither long-lived nor of large ultimate size.

The first European fishermen found that certain stocks of lake trout contained appreciable numbers of what seemed from outward appearance, to be senile fish. In fact one reef area in Lake Superior was informally called the Hospital Reef for this reason (Goodier 1981). Fishermen worked to "weed out" these low-valued individuals and sought to maintain a fishery of younger and more valued fish.

Medium-sized fishes were also generally valued more highly in the market than were the largest fish. Lean fish were preferred over the "fats", but very lean "racers" were again low-valued.

Altogether the fishermen preferred lake trout of medium size, from about 2 to 5 kg (about 5 to 10 lb.) and typically fished the areas where these sizes made up a high proportion of the catch. Extremely large or inordinately fat lake trout were often culled from the catch as relatively worthless. ,

A second factor operated to reduce the abundance of large lake trout within the stock complex of a lake. As a fishery intensified, almost all lake trout were harvested before they could reach an old age or large size due to the rigorous selectivity of the fishing gear. Fishermen and administrators both realized, from decades or even centuries Of folk wisdom, that the stocks

needed an opportunity to reproduce if the fishery were to persist into the future. Minimum sizes were specified legally and small fish were protected; these minima were usually set so as to provide for some reasonable escapement of sexually mature fish to ensure reproductive success. For most lake trout stocks sexual maturation occurred at sizes between 2 and 3 kg.

The combination of intensive fishing and minimum size limits eventually led to a size-spectrum of the lake trout complex such that very few individuals survived to achieve a size of more than 3 kg. In contrast, circumstantial evidence indicates that, in pristine conditions, well over 50% of the total biomass of the lake trout complex was contributed by individual fish over 3 kg in size.

Other size-spectrum effects echo throughout the trophic web after the largest lake trout are harvested. In essence, an effect is felt at each trophic level as ecological disproportionality of taxa is created between interacting levels. Hence, as the largest terminal predators are harvested, forage fishes such as coregonines may grow beyond the appropriate feeding size for the next largest predators, the smaller lake trout. Species like lake herring when released from intense predation, may become superabundant and overgraze the zooplankton (e.g. Brooks and Dodson 1965). The total effect is one of an integrated community that must constantly shift its feeding preferences and strategies according to size availability. If the size shift upwards of a forage organism such as lake herring becomes sufficiently great, thereby excluding the possibility of further predation by lake trout, that organism in effect has realized a predation refugium and becomes increasingly abundant. The consequences of an overly large and superabundant forage species may be translated into a less efficient production of lake trout at the terminal predator level. Consequently, the maintenance of appropriate relative size ratios and numbers between any two trophic levels is important in ensuring a stable fishery and maintaining the community at steady-state.

4.7.3   Reproduction And Density-dependent Effects

With the normal kind of "fishing-up" process described in the preceding section, intraspecific competition within the medium to large size components of the stock complex, decreases. This often leads to more rapid growth and sexual maturation at a younger age. The inherent capability to adapt in this way appears to vary among species and the lake trout shows less resiliency than the walleye in this regard.

Some fish species have a capability to adapt reproductively to compensate for increasing or decreasing levels of abundance of older fish. A strongly domed stock-recruitment relationship (Ricker 1954) may be associated with such a capability. Lake trout apparently do not have a strong potential of this type (e.g. Martin and Fry 1973). As a fishery, or other exploitive stress such as sea lamprey predation, becomes excessive, the individual stocks appear to dwindle and disappear (Loftus and Regier 1972). The phenomenon of occasional large year-classes from low population numbers of reproducing adults, as might be expected with a domed stock-recruitment relationship, occurs seldom if ever with lake trout. This conclusion should perhaps be tempered with the following considerations. Where the lake trout occurs as a rich stock complex or taxon swarm and where the individual stock or taxon is quite adaptive phenotypically, it might be very difficult to specify and

quantify the stock-recruitment relationship for individual stocks. What does seem apparent from existing circumstantial evidence is that at the level. of the aggregated complex, the overall stock-recruitment relationship is not 'strongly domed and is thus not strongly density-dependent.

4.7.4   Effects On Trophic Interactions

Historically, the fishing effort by Europeans intensified first on preferred species, that is, lake trout, lake whitefish and walleyes. Sketchy circumstantial evidence (e.g. Regier and Hartman 1973) indicates that the most pelagic coregonines became more abundant as the preferred species were "fished-up". These relatively small coregonines, especially the bloaters, were prey for lake trout and reduced predation pressure may have been a partial cause for the spatial expansion of this species (Smith 1964). But some of the coregonines, such as the lake herring or cisco, may also have competed with the young stages of the lake whitefish, a larger, benthic coregonine; the reduced competition from lake whitefish, in turn, may have led in part to a greater abundance of the smaller coregonines. The preceding scenario, though inadequately documented, provides a useful heuristic understanding of a possible sequence of events leading to a decline of the lake whitefish and a corresponding surge of smaller coregonines. Another possible reason for early declines in lake whitefish stocks, particularly those of the more southerly portions of the Great Lakes, relates to the first stages of cultural eutrophication, a consequence of land clearing and poor forestry practices. These effects may have led to more planktonic and invertebrate food production for the small pelagic coregonines.

If in fact there was a major increase in abundance of small coregonines in all the Great Lakes much before 1900, there is no evidence available to suggest that they in turn, acted to suppress the recruitment of small lake trout through either predation of fry or through competition. There is some circumstantial evidence, however, that the exotic rainbow smelt and alewife acted on occasion to suppress recruitment of native coregonines, either through food competition (Anderson and Smith 1971) or predation on fry (Selgeby, et al., 1978).

Predation by rainbow smelt on lake herring, although common in some areas of Lake Superior, was not believed to be a significant factor in the decline of lake herring stocks (Selgeby, et al., 1978). Predation or some other density-dependent factor however, may serve to retain overexploited lake herring stocks at low levels (Selgeby 1982).

4.8   EFFECTS OF INVADING OR INTRODUCED SPECIES

4.8.1   Evaluation

The lake trout is influenced by introduced species and can be an indicator of this influence. This mechanism is elicited via the food web or simply "who eats whom". Thus, the effects may be direct as when sea lampreys eat lake trout or lake trout eat alewives, or indirect when coho salmon eat alewives and lake trout eat alewives. Many different indirect effects on lake trout from an introduced species are possible and the direction of the influence may

be either negative, such as increasing competition for food, or positive as when salmonines reduce the abundance of a particular species that competes with the other prey organisms of lake trout.

Of the many exotic species of fishes introduced into, or invading the Great Lakes, only the sea lamprey had effects so severe that the lake trout ultimately became extinct in some lakes. Other exotics may have had an identifiable influence on the lake trout but did not specifically limit the utility of the lake trout as an indicator of a multitude of other characteristics of ecosystem quality. The control of sea lampreys will likely result in the persistence of lake trout and lamprey scarring rates may be appropriately evaluated. Hence an index is provided to assess the stress on the lake trout stocks induced by the sea lamprey (e.g. Pycha 1980).

The food web among major Great Lakes' ecosystem components is provided in the matrix of Table 7. Major components of the food web are listed across the top of the table (i) and down the left side (j). Reading across a row, a (+) or (++) indicates the extent to which the jth component eats the ith component and a space indicates no known direct interaction between the ith and jth components. A single look at a row will provide the information on a direct interaction between two components. Evaluating the direction and intensity of the interaction is, of course, easier for sea lamprey or alewives for which we already have observed the effects. What is important, however, is an attempt to evaluate the potential influence of pink salmon on lake trout or of unknown species "x" on the lake trout. The intensity of the effect will be based mainly on: the biomass of the predators; their spatial and temporal overlap with their prey; the selectivity of the predators for particular prey species; and the availability of alternative prey. Information on these characteristics is important when evaluating such a matrix.

If one were using the lake trout as an indicator in a single-species (multiple stock) approach, the analysis would certainly have ended by this point, but a key feature of an ecosystem approach is the importance of indirect effects including the relative connectedness of a system (e.g. Patten, et al., 1982). A re-examination of Table 7 in greater detail reveals that, in most cases, the indirect effects may be more significant than the direct effects. An indirect effect can be identified by passing down the matrix in successive steps. For example: (step 1) coho salmon eat alewives intensively; (step 2) thus alewives provide less prey for lake trout and (probably) eat fewer eggs or larvae of rainbow smelt, bloater, lake herring and yellow perch and also eat fewer large zooplankters; (step 3) the large zooplankters provide more food for alewives, rainbow smelt and bloaters and eat more phytoplankton. Thus, alternative foods of lake trout (e.g. Eck and Wells 1983; Elrod 1983) are increased and the phytoplankton standing crop may be reduced. In this case a potential competition appears to have a positive rather than a negative effect on the lake trout. This clearly points out why an ecosystem approach is necessary if the lake trout is to be used as an indicator of environmental quality.

Similarly, an ecosystem approach, by forcing the evaluation of indirect species interactions, makes it more likely that the ecosystem objective based

TABLE 7

A MATRIX OF THE FOOD WEB IN THE UPPER LAKES: THE "j"th COMPONENT PREYS ON († OR ††) OR HAS NO DIRECT INTERACTION WITH THE "i"th COWPONENT.

"j" COMPONENT	"i" COMPONENTS																		
	Sea lamprey	Lake trout	Coho salmon	Chinook salmon	Pink salmon	Steelhead	Smelt	Alewife	Bloater	Lake herring	Sculpins	Yellow perch	Mysis	Pontoporeia	Large zooplankton	Small zooplankton	Benthos	Phytoplankton/seston	Terrestrial insects
Sea lamprey		††	††	††	†					†									
Lake trout							††	††	††	††	††	†	††	††	†				†
Coho salmon							†	††	†	††		†	†						
Chinook salmon							†	††	†	†	†	†	†						
Pink salmon							††	††					††		††				†
Steelhead*							†	††					†						†
Smelt											†	†	††	†	††	†			
Alewife											†	†	†	††	††	††			
Bloater													††	†	††		†		
Lake herring													††	†	††				
Sculpins													††	††	†		††		
Yellow perch														†	†	††	††		
Mysis																††		††	
Pontoporeia																		††	
Large zooplankton																†		††	
Small zooplankton																		††	
Benthos																		††	
Phytoplankton/seston																			
Terrestrial insects																			

* = rainbow trout

on the prosperity of the lake trout will actually be met (see Section 1.1.4). In this example, an introduction of coho salmon would initially be viewed to have a negative influence, but by step 3 in the matrix, the influence appears to be positive.

The above example is quite instructive and provides some understanding of the sequential changes that continue to occur in the fish communities of the Great Lakes. Table 7 tracks this series of interactions further. Step 5 would appear to be moving toward a modified system with rainbow smelt, bloaters and sculpins as the primary forage fishes of lake trout, while coho feed more on rainbow smelt and perhaps other inshore fishes. Reductions in rainbow smelt resulting from predation would be expected to have little influence on alewives, while similar reductions in bloaters might allow some increase in alewives. However, if stocking of coho and chinook salmon continues, alewives would likely remain low in abundance (e.g. Stewart, et al., 1981; 1983), resulting in a larger biomass of algae and a corresponding increase in abundance of large zooplankters, resulting in a more stable condition for the coldwater community dominated by lake trout. (There is some preliminary evidence that this series of interactions is occurring currently in Lake Michigan.)

A preferred alternative to this scenario might consist of a management plan that included the complete phenotypic range of diverse stocks formerly' found in the lake trout complex of the Great Lakes (e.g. Ryder, et al., 1981). In this instance; the same or closely similar objective may be achieved using native stocks of lake trout rather than Pacific salmons, with somewhat more assurance of success, as the ecosystem quality objective would have previously existed under a natural environmental regimen. In the case of the Pacific salmons, too many unknowns exist to predict accurately the future status of Great Lakes' fish communities dependent on them as one of the principal terminal predators.

4 . 8 . 2 Observations

4.8.2.1   Sea Lamprey (Petromyzon marinus)

The sea lamprey is a marine species that may have invaded the St. Lawrence drainage during the 1800's. Alternatively, the sea lamprey may have existed in Lake Ontario much earlier and may have been a relict of the last glacial retreat (Christie 1973). It has been recorded in Lake Ontario in abundance after 1880, following the virtual demise of the Atlantic salmon and subsequently spread to the Upper Great Lakes (Applegate 1950; Smith MSa). As the sea lamprey became very abundant in each lake except Lake Erie, it replaced the lake trout as the dominant terminal predator. Also, the lake trout became a primary prey of the sea lamprey, along with other large open-lake inhabitants such as burbot, lake whitefish and the largest species of deepwater ciscoes, all of which were greatly reduced by sea lamprey predation, to extinction in the case of some species.

Although sea lamprey abundance as a result of control measures declined to 10-20% of peak abundance (Smith 1972b; Smith 1973), substantial numbers of them persisted by feeding on smaller, nearshore species such as bloaters, lake herring,' suckers, walleyes and carp. Of these, the white sucker proved resistant to extreme depletion and provided a favorable enough food source to

maintain a sufficient abundance of sea lampreys to constitute a continuing threat to their prime prey species--particularly lake trout and burbot. . Thus, lake trout abundance, or alternatively, the frequency of wounds on them, has *been an extremely sensitive indicator of the abundance of sea lampreys.

Chemical lamprey control, which was initiated in Lake Superior in 1958, and has subsequently been extended to the four deepwater Great Lakes, has been successful in keeping sea lamprey abundance suppressed to moderately low levels. This degree of control has been sufficient to permit reestablishment of substantial lake trout stocks by stocking hatchery-reared juveniles, but has not restored lake trout stocks to the level of their former diversity, nor returned natural reproduction to pre-sea lamprey levels. Since the sea lamprey abundance under the present level of control is still substantial despite a significant reduction in peak abundance, lake trout stocking will likely have to be continued indefinitely to maintain their presence in the lakes as long as current circumstances persist (Smith 1973).

4.8.2.2   Rainbow Smelt (Osmerus mordax)

Although rainbow smelt were widely introduced at various times and places throughout the Great Lakes following the end of the 1800's, the only introduction to succeed was made in 1912 in Crystal Lake, a tributary to Lake Michigan. This stock spread throughout the Great Lakes above Niagara Falls, - successively colonizing each lake, where they subsequently attained high abundance, particularly in bays and shore areas of intermediate depths (Smith 1972a; Van Oosten 1937). Similar colonization occurred in Lake Ontario, but from stock presumably originating from rainbow smelt that had been introduced into the Finger Lakes of New York in the 1920's (Bergstedt 1983; Youngs and Oglesby 1972), and from there moved downstream into Lake Ontario where they were first recorded in 1931, prior to the first record of rainbow smelt in Lake Erie in 1935 (Smith 1972a).

Of the total planktivore complex, lake herring appeared to be more influenced by the presence of rainbow smelt than any other species, because both occupied the same zone of the lake to a considerable extent (Smith 1972a). Both appeared to be suitable as a secondary food source for lake trout so it is questionable whether or not the establishment of rainbow smelt had a major direct effect on adult lake trout. Indirect effects, however, may have contributed to periods of instability when rainbow smelt abundance fluctuated widely, resulting in accompanying but opposite vacillations in lake herring abundance -(Anderson and Smith 1971; Smith 1972a).

Because of the conservative nature of the planktivore complex, however, it is likely that the combined biomass of these two species retained sufficient homeostasis to provide a dependable supply of food for piscivorous lake trout. This notion is supported by the data of Anderson and Smith (1971) summarized in Figure 14. There, it is clearly shown that the combined index of abundance of the two species never dropped below 140 over a 16-year period covering the major ascendency of rainbow smelt and concomitant decline of lake herring in the Minnesota waters of Lake Superior. Individual species abundance indices for the same period (Figure 14) dropped as low as five (lake herring) and 32 (rainbow smelt). If an abundance index of 140 for planktivores (arbitrarily chosen) were the minimal requirement to ensure adequate fish forage for lake trout, then the lake herring alone would have
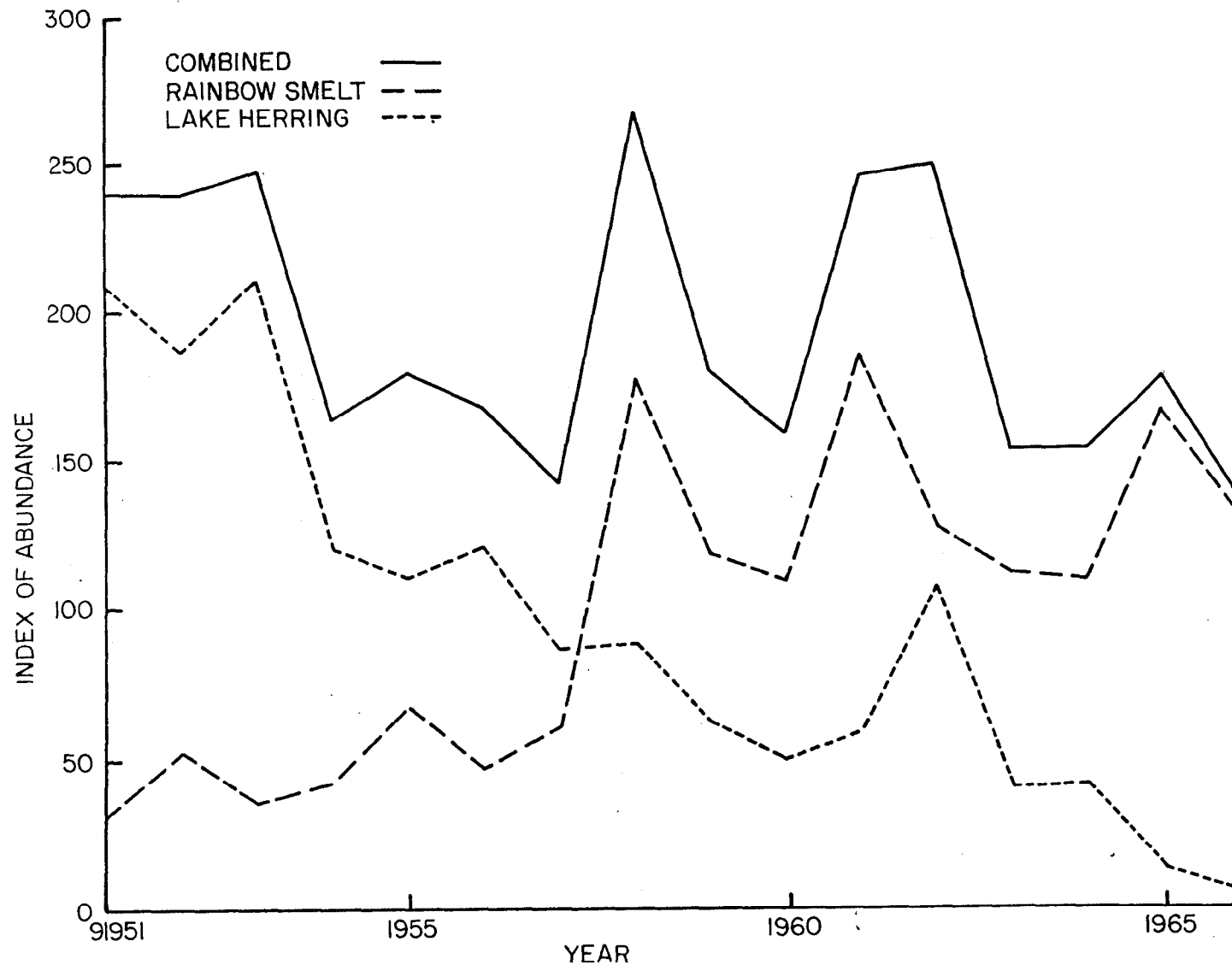
Figure 14   Index of abundance of lake herring and rainbow smelt for the Minnesota waters of Lake Superior
(from Anderson and Smith, 1971). If an index value of 140 were the critical lower limit for a suitable
lake trout forage base, then the lake herring alone would satisfy this requirement in three of the 16
years and the rainbow smelt for another three years. The two species combined however, would
provide an adequate forage base for all 16 years.

provided sufficient forage for three of the 16 years and the rainbow smelt alone for another three years, but there would have been insufficient forage for the remaining ten years based on only single species contributions to the food supply. Both species in concert, however, would have provided an adequate forage base at the arbitrary abundance index of 140 for each of the 16 years.

Availability of fish forage to be completely adequate must not only be of sufficient abundance and of the appropriate size-class, but must also be dependable from year to year. Lake herring and rainbow smelt had maximum deviations from 16-year mean indices of 119% and 86%, respectively, showing a high level of unreliability. The two species in concert, however, had maximum annual deviation from the combined index of only 37%, thus indicating a more reliable forage supply.

There was a suspected possibility of adverse influence of rainbow smelt on larval or early juvenile lake trout, because smelt were abundant on many lake trout spawning areas during incubation and hatching periods and rainbow smelt are facultative piscivores in the Great Lakes, sometimes consuming substantial quantities of small fish (Gordon 1961). If such predation were taking place when lake trout stocks were thriving (prior to destruction by the sea lamprey), it was not of sufficient impact to cause a perceivable depression of, lake trout abundance as reflected by the commercial harvest. However, because of the substantial time lag between cause and effect, it is likely that causes for substantial yield declines in lake trout were inseparable (e.g. Hile 1949).

4.8.2.3   Alewife (Alosa pseudoharengus)

The alewife, a marine invader, has been as disruptive if not more disruptive than the sea lamprey. The first confirmed observation of alewives in the Great Lakes was in Lake Ontario in 1873, when they were reported as abundant throughout the lake (Smith 1970), although what must have been an alewife spawning run was first described in 1872 (Smith MSc).

Like the rainbow smelt, the alewife was stocked in many locations throughout the Great Lakes, usually unintentionally, because young alewives were included with young American shad which were introduced in an attempt to establish a shad population. There is no evidence, however, that any of these introductions led to the establishment of reproducing populations of either the alewife or the American shad. The origin of the alewife in Lake Ontario was undoubtedly by migration from the Erie Canal or from populations of the Finger Lakes, which had previously been colonized by alewives from the Mohawk River via the Erie Canal (Smith 1970). This is also a suspected route and alternative sequence of entry of the sea lamprey (Smith MSa).

After becoming established in Lake Ontario, the alewife moved successively into the other Great Lakes and became established in the same sequence but later than the sea lamprey (Smith 1972a). The alewife attained a unique relationship with the lake trout in that its various life stages also occupied all habitat zones of the lakes in different seasons. Thus, a broad interaction between the alewife and lake trout could be expected.

Possibly three conditions existed more than 200 years ago which prevented the alewife from ascending the St. Lawrence and gaining a foothold in Lake Ontario. First, because wide-scale deforestation had not yet occurred within the watershed, temperatures were not likely amenable to spawning. Secondly, native coregonines having fundamentally similar food preferences to alewives but better adapted to the environmental milieu, offered strong competitive resistance to alewife intrusions. And finally, the two major ubiquitous predators, the lake trout and the Atlantic salmon offered additional resistance to alewife incursions through effective predation (Smith 1970; MSa). The subsequent demise of the Atlantic salmon and lake trout in Lake Ontario therefore was due to factors independent of alewife invasion and also preceded the invasion of sea lampreys into Lake Ontario (Smith MSa).

However, the demise of lake trout through exploitation and sea lamprey depredations acting in concert in the Upper Great Lakes, undoubtedly was a prerequisite to the subsequent establishment of alewives (Smith 1970; MSc). The alewife and sea lamprey appeared first in Lake Huron at about the same time in the early 1930's (Smith 1972a). However, the alewife remained rare until the 1950's (Miller 1957), long after the sea lamprey had made severe inroads into the lake trout stocks of that lake (Smith 1970).

In Lake Michigan, the alewife was not reported until 1949, a substantial time lag following the devastating effects of sea lamprey predation and exploitation.

Although alewives were first recorded in Lake Superior in 1954 (Miller 1957), they did not attain significant abundance until the early 1960's at a time when the lake trout population had already been greatly reduced (Smith 1970). Lake trout stocks had increased sharply by the late 1960's, however, as a result of intensive stocking plus the initiation of chemical sea lamprey control. Alewife abundance declined as lake trout increased in numbers until the alewife became scarce by 1970. This condition has continued and lake trout abundance has been maintained at a relatively high level, at least in some portions of the lake.

In the absence of a ubiquitous terminal piscivore, the alewife became the most abundant species in Lakes Ontario, Huron and Michigan--a position it has held in Lake Ontario since the 1870's where its extreme abundance often caused problems when massive dieoffs occurred (Smith 1970). Following intensive stocking of salmonines (mostly lake trout and Pacific salmons) and coincident with sea lamprey control, the alewife population has been suppressed in all of the Great Lakes and massive dieoffs have not occurred in recent years.

The alewife was a very efficient and selective planktivore and was capable, when abundant, of eliminating large plankters (Brooks 1968; Brooks and Dodson 1965; Wells 1970). Alewives also would consume planktonic fish larvae in both pelagic and nearshore areas. A general consequence was an extreme decline in planktivorous species as well as species with planktivorous young or those that had planktonic larvae at locations *or* times where alewives were abundant (Aron and Smith 1971). Such declines involved most of the primary and secondary forage species consumed by the lake trout, including: deepwater ciscoes; lake herring; rainbow smelt; and emerald shiners. All of these were previously among the most abundant forage species of the lakes.

The deepwater sculpin was reduced to scarcity in Lake Michigan at the peak of alewife abundance. This reduction was attributed to a near lack of . reproduction. Since the decline of alewife populations, the deepwater sculpin 'has made a spectacular comeback, although a linkage with alewife abundance has yet to be established. The yellow perch, not usually a significant lake trout forage species, was also much reduced during the period of maximum alewife abundance and has likewise had marked increases in recent years.

Thus, the consequence of the invasion and establishment of the alewife was to alter greatly the forage base of the lake trout. The apparent effect of this change was to increase the lake trout growth rate and reduce the age at maturity. Increase in lake trout growth in lakes dominated by the alewife was not because alewives constituted a greater quantity of forage, but because alewives congregated in dense schools and were more easily consumed in large quantity than the pre-alewife forage species. The native forage species differed from the alewife in that they did not usually travel in such large schools, and only seldom occurred in dense congregations. Thus, the passively feeding lake trout would consume lesser quantities of native forage species than of the tightly schooling, slower swimming alewives, which were available in larger quantities for a given feeding time, contributing to less energy expenditure and consequently a faster growth rate for the lake trout. In this instance, increased growth rate of lake trout becomes an indicator of the change in composition, but not necessarily of quantity, of the forage base.

4.8.2.4   Pacific salmons (Oncoryhnchus spp.)

Pacific salmon were first introduced to the Great Lakes by stocking chinook in Lake Ontario during the 1870's (MacKay 1963) in an attempt to establish a replacement for the rapidly declining Atlantic salmon. Chinook and coho were planted in other Great Lakes (Parsons 1973) but growth and survival to maturity was favorable only in Lake Ontario, where spawning runs subsequently developed (MacKay 1963). Few salmon were recovered from introductions in other lakes. A presumed reason for better success in Lake Ontario was the presence of the alewife, which was similar to the food of salmon in the ocean--an observation that was supported by subsequent salmon. introductions in the Upper Great Lakes in recent years (Aron and Smith 1971). Although spawning runs were developed and plantings were continued into the early 1900's, the chinook salmon did not develop a self-sustaining population, but what were conjectured to be third generation spawning fish were seen after the last introductions were made (Andrew Pritchard pers. comm.).

A recent era of salmon introduction was inaugurated in 1966 when the State of Michigan released 659,000 coho salmon in tributaries of Lake Michigan. The returns from this introduction were phenomenal, with more than 30% of these fish recovered by recreational anglers or accounted for in spawning runs. This success led to extensive introductions of coho and chinook salmon in all the 'Great Lakes by all states and the Province of Ontario during the following. years. In 1981, for example, over eight million of each species were introduced.

In general, salmon growth and survival has been excellent, with the least favorable results in Lake Superior where alewives are relatively scarce; again indicating that the presence of alewives appears to be important for successful introductions of these two highly piscivorous Pacific salmons. The

chinook and coho have also done quite **well** in Lake Erie where alewives are not extremely abundant, but where there is an abundance of many other forage species.

To a certain degree, coho and chinook salmon would compete directly with the lake trout for food (Stewart, et al., 1981). The lake trout, on the other hand, feeds more effectively on the relatively slow swimming, schooling alewives than on the pre-alewife forage species, which results in faster than normal growth for lake trout even at reduced alewife abundance. The lake trout can thrive on the pre-alewife forage species (which may become more abundant when the alewife population declines), but the coho and chinook do not do as well on non-alewife forage. Thus, the lake trout appears to have a feeding advantage when the alewife is present and has an advantage over the coho and chinook when the alewife declines.

Lake trout adults also have other food options available to them and some stocks at least, feed efficiently on deepwater sculpins or large crustaceans such as <u>Mysis</u> and <u>Pontoporeia</u> (Dryer, et al., 1965; Martin and Olver 1980), at times to the exclusion of all other food items. This facultative capability of feeding efficiently at different trophic levels gives the lake trout a distinct advantage over the piscivorous Pacific salmons. In a comparable situation (Konchina 1983), the biomass of the standing stocks of a similarly facultative species was enhanced through this opportunistic feeding advantage.

Coho and chinook salmon do not currently appear to have a strongly negative effect on lake trout, due to effective resource partitioning. Should the salmon's forage base collapse, however, we might suspect otherwise. Hungry salmon will find alternative prey, most likely those already utilized by the lake trout. Therefore, the future prospect for strong negative reactions with lake trout remain real.

Introductions of exotic species may be temporarily, or in many cases permanently, devastating to the integrity of a biotic community. Because the potential effects are often underestimated or ignored, we will treat in some detail the sequence of events that lead to an inadvertant introduction, that of the pink salmon into Lake Superior.

The pink salmon introduction while unintentional, was one of the most successful introductions of a Pacific salmon into the Great Lakes, but subsequent establishment was totally unexpected. Indeed, the pink salmon introduction into the Great Lakes Basin was one of intrigue and ecological uncertainty. Originating from the Province of British Columbia and destined for the frigid tributary streams of Hudson Bay, the pink salmon firmly established themselves first into Lake Superior during the 1960's and eventually spread to each of the other Great Lakes, where they have formed reproducing stocks.

'In late 1955, two million pink salmon eggs were imported to the Province of Ontario and incubated at the Port Arthur Fish Hatchery on the Current River, about 100 metres from the shore of Lake Superior. It was intended that these eggs would be held in the hatchery until they reached the late eyed stage in January, at which time one-half of them would be planted through the

ice in a selected tributary stream to Hudson Bay. The remainder of the eggs were to be reared to the early fingerling stage, then they would be flown to a James Bay tributary for introduction the following June (MacKay 1963).

Both plantings took place as planned and on schedule, but three unplanned incidents resulted in some pink salmon being released into Lake Superior. As the salmon fingerlings were loaded aboard aircraft for transportation to James Bay, a few escaped each day into Thunder Bay, Lake Superior. This escapement was minimal--only a few to perhaps twenty-five at most.

Secondly, some pink salmon became mixed with lake trout fingerlings at the hatchery and when the lake trout were distributed subsequently around Thunder Bay, as many as 300 pink salmon fingerlings were inadvertantly planted into Lake Superior.

Finally, following the last flight of fingerlings to James Bay in June when all pink salmon were believed to have been planted, a total of about 21,000 fingerlings remained in the hatchery troughs. This was unknown to the personnel responsible for the planting and was not disclosed until several years later, following the demise of the hatchery manager. Apparently the hatchery assistants were instructed to flush the remaining pink salmon from the troughs into the Current River where they were swiftly carried into Lake Superior.

There was little thought or concern at the time of this introduction because it was strongly believed that of the five species of North American Pacific salmons indigenous to the west coast, the pink salmon would have been the least likely to survive and reproduce in a freshwater environment. This opinion was predicated on the fact that pink salmon usually spawned in the lower reaches of west coast streams and in many instances were intertidal spawners (Scott and Crossman 1973; Morrow 1980). The residence time of pink salmon fry in the nursery stream usually lasted only a few days before they were flushed rapidly downstream into the marine environment upon loss of their yolk sac. Finally, there was not a single incidence of an established freshwater population of pink salmon on the west coast, although the sockeye salmon frequently developed lacustrine stocks secondarily (i.e. the kokanee) from formerly anadromous spawning runs (Ricker 1940). Accordingly, the advice received from west coast experts based on the best available ecological evidence at that time (1956) was that the pink salmon were not likely to become established when confined to the fresh waters of the Great Lakes.

Two mature pink salmon were first found in a stream on the north shore of Lake Superior in the fall of 1959 (Schumacher and Eddy 1960), which, because of their two-year spawning cycle, indicates that at least one pair survived from the original introductions and had spawned in 1957. Pink salmon spawning runs in Lake Superior increased steadily during the 1960's and large runs were developed in streams throughout Lake Superior by 1970 (Lawrie and Rahrer 1972). By 1981 mature pink salmon had been found in tributaries of all five Great Lakes and even-year spawning runs had been established in some areas (Wagner and Stauffer 1980).

Little is known about the pink salmon in the Great Lakes during the period between the time they leave the spawning streams as fry and their return to streams as spawning adults. Because they are not normally taken by conventional commercial impoundment or gill-nets, which are fished on the bottom from shore to the deepest waters of the lake, it is assumed that the pink salmon must live somewhere in the mid-depth, pelagic zone of the open lake. Pink salmon are obligate planktivores and hence they would most likely reside in zones where plankton is abundant, probably in the vicinity of the thermocline where there would not only be an abundance of food, but also a stratum of their preferred temperature.

The presumed area where the pink salmon grow to maturity is not inhabited by the sea lamprey which is not a free-swimming animal, being found mostly near the bottom where it is either resting or being transported by a host species. Also, the pink salmon is likely too small to be suitable prey for the sea lamprey until just shortly before it reaches maturity. There is presently no abundant large piscivore at mid-depths in the open lake which might prey on juvenile pink salmon, although in Lake Superior at least, there were substantial populations of lake trout in that region during the pre-sea lamprey period.

Thus, it appears that the adult pink salmon is virtually free from predation, at least in the four deepwater Great Lakes and occupies a limnetic region of the lake where there is an abundance of planktonic food. For these reasons it has been anticipated that the pink salmon has the potential to attain the status of the most abundant, naturally reproducing, salmonine in the Great Lakes before the end of the century (Smith 1972[b]) and may already have attained that status in Lake Superior. It appears that the primary factor that will limit how abundant pink salmon may become is the amount of suitable spawning areas available. Since the period at which the spawning adults and their eggs and progeny reside in the spawning redds is very short and spawning requirements are not highly critical, it appears that the available spawning habitat may be sufficient to support a large population of pink salmon.

The probable influence of the pink salmon on lake trout is uncertain. It is not known if pink salmon will compete for plankton to the disadvantage of any or all of the other planktivores that inhabit the mid-depth zone of the open lake (young deepwater ciscoes, lake herring, alewives, rainbow smelt and possibly, young lake trout), or if the other planktivores will compete to the disadvantage of the pink salmon.

Large pink salmon on the West Coast are known to eat small fishes occurring in the pelagic zone. Large adult pink salmon in Lake Michigan have probably expanded their diet to include young-of-the-year alewives (J.F. Kitchell, pers. comm.). If this feeding habit is widespread, a competition for a common forage base will occur and a potential for negative interaction with lake trout exists.

In any event it is apparent that the pink salmon will cause some degree of instability among the primary forage species of the lake trout and possibly the zooplankton that Take trout consume to a considerable degree, particularly as they grow to maturity. It can be expected that there will be a substantial

amount of direct and indirect interaction between the lake trout and the pink salmon and accordingly, the lake trout should be a sensitive indicator of changes that might occur.

Interestingly, despite their presence in Lake Superior for thirty years, pink salmon have not yet reached a steady-state condition with respect to the native coldwater communities. It appears that pink salmon populations are still in a state of flux and their future status seems uncertain.

4.8.2.5   Copepod (Eurytemora affinis)

Exotic species introductions are not restricted to vertebrates and invertebrate introductions or invasions may be equally devastating to the integrity of a natural community. Most generally, however, the effect of introduction or invasion is unknown, as in the case of a brackish-water copepod Eurytemora affinis, an invader from marine areas. This species was first discovered in the Great Lakes in 1958 when it was collected in Lake Ontario (Anderson and Clayton 1959). It has now been collected from all the Great Lakes (Patalas 1972) and is a commonly-found, but relatively minor, component of their zooplankton fauna.

It has been suggested that the introduction of this species is related to long-term changes in the Great Lakes environment (Great Lakes Basin Commission' 1976). It seems much more likely however, that its introduction was caused in some fashion by the construction of the St. Lawrence Seaway, since Eurytemora quickly spread throughout the lakes after the completion of this project in 1958. The species is native to the brackish parts of the Gulf of St. Lawrence and it may have been carried upstream in the bilge or ballast water of the ships using this waterway. Increases in sodium content of Great Lakes waters from human wastes, particularly sodium chloride applied to roads in winter, may provide a more favorable environment for Eurytemora than previously existed.

5.0 PRAGMATIC APPLICATIONS WITHIN THE ECOSYSTEM APPROACH

Indicator species such as lake trout, walleyes, gulls and terns and other species, used to monitor the state of ecosystem health of the Great Lakes may be justified on the grounds that they provide information that relates obviously, directly, rapidly and comprehensively, to some of the key management goals that the public have specified for these lake ecosystems. Binationally, we are firmly committed to a partial recovery of the more desirable ecosystemic features of special value to us all when we act as "sensitive users." Many of these features have become degraded by "insensitive users" acting carelessly or in ignorance, or with disregard for the undesirable ecosystemic effects.

Binational, ecosystemic goals are stated in treaties, conventions,-, agreements, diplomatic notes and minutes of meetings. Goals consistent in general with those at the binational level are specified in a myriad of policies, laws, regulations, legal precedents, or rulings at national and other levels of governance in the Great Lakes Basin. It is timely that researchers and managers provide better information on the extent of progress toward these goals, information that is directly meaningful to the public and its elected officials. This is the primary motive behind the synthesis and further development of a concise set of data on indicator species as proposed here.

The proposed indicator system is not sufficient for all management purposes--far from it. Conversely, it is not merely another information system to add to the variety already in place. The proposed system will not be costly to implement, because many of the data are already collected on a routine basis and processed to a preliminary degree. The necessary long historical data series already exist for several of the proposed indicator and integrator species so that the new information can immediately be related meaningfully to historical trends. When fully operational, the proposed indicator system may well reduce the need for some other kinds of information that are more costly to collect and have little direct meaning to the informed public.

5.1   A PRACTICAL INTEGRATIVE APPROACH TO THE DETERMINATION OF CULTURAL STRESSES

Some years ago Francis, et al., (1979) reported on the feasibility of rehabilitating Great Lakes ecosystems by reversing or mitigating the major kinds of cultural stresses that we collectively have visited on Great Lakes ecosystems. The broad spectrum of experts who collaborated in that study shared a consensus that overall rehabilitation was feasible technically, economically and institutionally with respect to each stress and with respect to the interacting mix of all the stresses. As such rehabilitation had already been mandated politically through a number of binational decisions, the consensus on feasibility was anticlimactic. The feasibility report may

have served to counter the frustrated murmurings of narrow specialists among the researchers who had contrived to hitch many specialized carts in front of the one basic policy horse.

The "cultural stresses", approximately as identified and explicated by Francis, et al., (1979), again form the background for this section. The relevance of our indicator approach to these various stresses has already been elaborated in earlier parts of the report; here some additional general points are made.

5.1.1   Quantifying Natural Backsround Factors Or "Stresses"

For several of the proposed indicator and integrator species, a great deal is known about the effects of natural phenomena. This knowledge is already shared by numerous scientists, managers and many of the informed public. This information needs to be organized in a more systematic way and then communicated in a manner that may be understood readily by the many people already informed on these matters.

Aspects of the ecological behavior of indicator species that are due to natural factors beyond our control need to be documented for species not normally harvested or otherwise disturbed by man. This can be done most directly by monitoring stocks or populations of these species that are influenced only to a minor degree by any and all of man's cultural activities (e.g. ninespine stickleback, trout-perch). Such data series provide a measure of the "background noise" or natural variation that must be taken into account in any attempt to interpret data series from indicator populations under cultural stress.

5.1.2   Assessment Of Multiple Stress Effects

Preliminary studies of the ecological inputs of a mix of cultural stresses (Francis, et al., 1979; Harris, et al., 1982; Regier, **et al.,** 1980) indicate that different stresses have seldom acted to cancel out each other's deleterious impacts. The opposite happens quite commonly. Thus, with respect to the consequences of human actions on the Great Lakes, negative effects appear to have a cumulative ecological impact.

The generalization sketched above applies strongly with respect to lake trout, but to a lesser degree to some other indicator and integrator species such as walleyes and the larids (gulls and terns). Eutrophication, singly or combined with man-caused turbidity, may act to increase the productivity of a clear, oligotrophic lake to the benefit of walleye stocks. Similarly, creation of rather barren islands or spits (say with contained dredge spoils) together with the emergence of small, pelagic, exotic fish populations may lead to an expansion of some larid populations.

The lake trout stocks of the Great Lakes have been adversely affected in many ways and this is perhaps the best single indicator and integrator species with which to assess the overall impact of a mix of stresses. But lake trout stocks are also quite sensitive to many of these individual stresses, hence they tend to be suppressed or even extinguished at levels of loading that may otherwise appear to be only moderate.

Walleyes and some larids may thrive under moderate loadings of a mix $_o$f some stresses, but they are affected adversely In time as these stresses become more substantial.

In order to use these indicators for more than just general assessment purposes, the analytical diagnostic features, as sketched in Section 4.3, must be utilized in an informed way (see Section 5.1.4).

5.1.3   Quantification Of Individual Stresses

The most direct way to quantify individual stress loadings is to measure them as they are introduced into a system. This is done routinely, though not in a coordinated manner across jurisdictions, for many stress loadings such as: fishing intensity; phosphorus loadings from sewage plants, dredgi;gieE;;i loading from electric generating plants; and other cultural impacts. approach to the assessment and quantification of stress loadings is through the use of standardized clinical methods on native fish populations (e.g. Wedemeyer and Yasutake 1977). Use of indicator species of ecosystem quality Will not replace the need to obtain direct measures of each and all of the important stress loadings, at least for the foreseeable future.

Inferring the magnitude of the effects of individual stresses, Using   - responses of indicator and integrator species for assessment purposes! will likely only be practical for parts of the Great Lakes aquatic system in which only a single stress is strongly involved. In more complicated situations, the information of Section 4.3 may be applied to judge whether various stresses are each having some effect; but it will likely be almost impossible to attribute some quantitative fraction of the overall impact to each of the stresses. To do so would likely require a very sophisticated experimental and simulation study in addition to the kind of routine monitoring associated with the indicator species concept. Currently available documents directed at objectives or criteria for various types of impacts and their effects on many other organisms, would provide useful and substantiating supplementary material to bolster a conclusion based on indicator or integrator organisms (e.g. Science Advisory Board 1983).

5.1.4   A Dichotomous Key Of Stress Symptoms

A somewhat simplistic but nevertheless pragmatic first approach to the assessment of a multiplicity of stress effects on the Great Lakes from a corresponding multitude of potential cultural sources is a dichotomous key itemizing potential stresses logically and sequentially and asking the observer to note the presence or absence of specific stress symptoms. This key would direct attention to concerns such as contaminant loadings in both the lake trout and its environment, nutrient loadings, exploitation, sea lamprey abundance as deduced from lake trout scarring and physical changes to the basin, as examples. These observations would be quantified where possible and placed in context with the current status of the lake trout in each of the Great Lakes as well as that of the cold-water communities associated with them. That is, ideally, such a key would address symptoms of malaise in lake trout, walleyes, Pontoporeia hoyi, gulls and terns or other major or complementary indicator organisms. It would also inquire about symptomatic clues observed in the habitat of these indicator organisms. A simple approach to identifying major areas of cultural stress has several advantages. Using

available data, it allows the ecosystem manager to zero in systematically and rapidly on a potentially hazardous stress that may characteristically have inconspicuous symptoms. Secondly, it leads the manager through a sequential and orderly process that considers all known possibilities for cultural stress. Normally, a harried ecosystem manager may react only to the cultural stress with the highest public profile and therefore perceived by the public to be of major concern and not to a potentially more dangerous stress with subtle symptoms.

Dichotomous keys that require only binary, "yes-no" (or "I don't know") answers, also have certain disadvantages. Symptoms arising from multiple stresses may not indicate the source of the individual stress from only a perfunctory examination of a lake trout. Consequently, examination of the lake trout's habitat may be equally as important, especially when this information is synthesized with that of other complementary indicator organisms such as <u>Pontoporeia</u>. Dichotomous keys, because of their relative simplicity and undemanding nature, may serve admirably as a means to obtain first approximation estimates of stress effects. Syndromes arising from mixtures of stresses may be ascertained by more conventional methods following initial symptomatic identification using the lake trout, the state of its, habitat and other complementary indicator organisms.

5.1.5   <u>Symptom Identification Via Computer</u>

An efficient and practical approach to the development of a dichotomous key of stress symptoms is a computerized version of the same. We have prepared a first-cut, rudimentary, program (Appendix VI) to demonstrate how a computerized dichotomous key might work. Four major areas of concern are addressed using the lake trout as the key indicator and integrator organism: (1) Contaminants Loading; (2) Abiotic and Biotic Environmental Concerns; (3) Exploitation; and (4) Sea Lamprey Depredation.

We have utilized for the dichotomous key, user-friendly, menu-driven programs in Microsoft BASIC 2.0 and 4.0, which are designed to run on two commonly used microcomputers (Commodore 64 and CBM 4032). Variations of Microsoft BASIC are available for other common microcomputers now in general use. The programs are easily convertible within the Microsoft Basic family. Conversion to other forms of BASIC is accomplished with slightly more difficulty but remains within the realm of practicality. Hence, the programs are readily transportable and are easily adaptable to many hardware systems.

The current program versions lead the ecosystem manager through a set of logically ordered questions to exact the most information for the least cost and effort expended. All questions may be answered by "yes", "no", or "I don't know". Many of the questions require quantitative data derived from monitoring lake trout stocks, other indicator organisms, or their habitat. A preliminary pass-through the sequence of questions almost invariably corrects some misconceptions. A second pass may provide new insights or focus attention on an area that previously was not seriously considered as being an ecosystem problem. Accumulations of "I don't know" answers will provide

direction for future research or monitoring by outlining the areas of research need. Ecosystem problems that formerly were unobserved or simply "fell between the slats" will be strongly emphasized by the inability of ecosystem managers to answer the key questions.

Obviously there are some disadvantages to this simplistic approach. Besides the disadvantages listed for dichotomous keys in Section 5.1.4, the binary-question computer program skirts dangerous ground by asking the manager to consider boundary numbers. It should be emphasized that quantities alluded to in the program are neither sacrosanct nor irrevocable. They are based on best information, are usually conservative in nature and may be altered easily as new information becomes available. In some cases quantities are only best guesses, but they are included to help emphasize the general areas of research needs.

Also, because many stresses act over the range of an optimality curve, two numbers, an upper and a lower one, may be necessary to describe the symptomatic response adequately. And of course, numbers ascribable to synergistic and antagonistic effects do not adequately identify nor partition the source of the effects.

Despite the obvious inadequacies of such a program, we encourage its use and request that the users provide constructive feedback in order that future-versions of the program may be expanded, improved or updated.

5.2   OVERVIEW OF INDICATOR PROPOSAL

The biological indicator approach, as herein defined, exceeds the traditional uses to which other types of indicators have-been applied in the past. We have proposed a concept and have utilized a single organism, the lake trout, to demonstrate the application of the concept. Our initiative differs in many respects from other indicator proposals in that we are suggesting a broader frontal attack in the identification of ecosystem malfunction (see Warren 1971), especially at various hierarchical levels of integration. This proposal is targeted to determine system quality for both the community and ecosystem levels, as may be determined through the observation of a single species indicator supported by appropriate complementary indicators. We consider the lake trout to be the ultimate indicator, inasmuch as it is a terminal predator and accordingly integrates much of the cold-water community in time and over space. The lake trout is also an evolutionary product of its oligotrophic environment and as such it reflects the relative quality of that environment. It responds to or retains symptoms of most environmental stresses, and in the adult stage, may persist in the face of them. In this respect it is a more suitable organism for assessing stress effects than one that responds with total lethality to the first perturbation.

5.2.1   Rates Of Response To Degradation Or Rehabilitation   .

The lake trout is not a perfect biological indicator, however--just the best for oligotrophic systems judged on the basis of a selected set of criteria (Section 3.1). The lake trout may be slow to respond to environmental rehabilitation, that is, to reach the objective of diverse, self-reproducing stocks of fish. However, because of its phenotypic

plasticity (Ryder, et al., 1981), it does perhaps have a high potential for rapidly filling all available oligotrophic habitat following rehabilitation, possibly better than any other terminal predator.

Other indicators may be used to complement lake trout for assessing the status of the coldwater community and general ecosystem quality. The selection of these indicators should be made, first of all, on the basis of the criteria previously proposed and secondly, on the basis of areas of concern not adequately covered by the lake trout.'

5.2.2   Future Initiatives Using Other Indicators

Indicators of mesotrophic environments should probably have second priority in the Great Lakes Basin. In consideration of candidate species, the walleye stands out not only because of its terminal predator status, but also because of its general ubiquity in the mesotrophic environments of the Great Lakes Basin (e.g. Schneider and Leach 1977). The walleye qualifies as an indicator and integrator organism on essentially the same set of criteria used for the lake trout, but as modified for mesotrophic environments. Interestingly, the walleye has shown rapid response to rehabilitated environments, particularly where rehabilitation has been due to regulated' harvests and possibly to phosphorus control. Their potential as an indicator of rehabilitated environments, therefore, may be better than that of the lake - trout if based only on the relative rapidity of response time.

The walleye, besides reflecting the relative health of mesotrophic waters in general, is especially useful in indicating the quality of shallow bays, deltaic regions of rivers, the nearshore littoral zone or large tributary streams. In this respect, it may be somewhat of a more cosmopolitan indicator than the lake trout.

The walleye is not normally vulnerable to attacks by the sea lamprey (e.g. Farmer and Beamish 1973) and consequently, it is not indicative of that particular stress. This may be construed as an advantage or as a disadvantage, depending on the nature of the information sought.

Use of both the lake trout and walleye as indicators in the Great Lakes Basin will provide a fast first approximation to the general assessment of the quality of the environment for most of this ecosystem. The precision of this first approximation assessment may be improved through the use of complementary organisms, representative of the oligotrophic and mesotrophic environments. As a third priority, then, we recommend the further development of the indicator approach utilizing Pontoporeia hoyi and perhaps Hexagenia limbata as complementary indicators to the lake trout and walleye, respectively, Other indicators should also be considered, particularly those representative of specialized habitats. While these specialized habitats may represent only a small portion of the total area of the Great Lakes Basin, they may be critical system components. Wetlands, for example, including marshes, swamps and bogs, may be essential for the reproduction of certain vertebrate species such as Forster's tern, for the mitigation of water level extremes in the Great Lakes, or to augment environmental heterogeneity. Indicators need to be sought, in addition to Forster's tern, that will adequately integrate and be representative of the quality of wetlands or other critical components of the Great Lakes environment.

5.2.3   Alternative Biological Indicator Approaches

Throughout this discourse we have alluded to community and ecosystem levels of approach, using indicator organisms as representative of a community or ecosystem. In fact, it is exactly this concept that distinguishes our proposal from most previous attempts to utilize indicator organisms. While we have proposed the concept of the lake trout and the walleye as biological indicator and integrator organisms, our application of this concept employs these organisms as surrogates of their respective communities, including invertebrates and plants, adapted to oligotrophic and mesotrophic environments, respectively. In this respect then, the lake trout and the walleye may be considered as indicative of output properties of a specific community at one hierarchic level, or of a particular ecosystem attribute at a higher level.

Alternative approaches to assessing ecosystem quality are available at the community and ecosystem levels of integration. By taking advantage of the conservative nature of emergent macrosystem properties, ecosystem quality assessment may be made at almost any hierarchic level. While techniques for this type of approach are not yet widely developed, opportunities exist for both creativity and rapid advancement in the direction of ecosystem assessment, utilizing whole system properties as ecosystem quality indicators. We recommend the further development of this approach through detailed analyses of both quantitative and qualitative changes in fish yields of the Great Lakes during the last century and relating these to the concomitant environmental changes (see Appendix V for an example).

Most of the lakes have responded conservatively in respect to the quantity of community annual yield during the last one hundred years of the commercial fishery (e.g. Baldwin, et al., 1979). Internally, however, certain species have ebbed and waned, some to extinction. In many instances, exotic species have made major contributions to the total fish yield of the Great Lakes. During these ever-changing species ratios within the total biomass of standing stocks, various agencies throughout the basin were introducing new species, stocks or strains into the complex. Other changes included the demographic constituency of the individual species, with the general trend being towards younger and smaller individuals in the catch, a result of harvest pressure, sea lamprey or environmental degradation.

Each of these internal changes in the composition of the catch likely related to an external stress or stresses, although the precise operational link has but rarely been made. A further detailed analysis of historical fisheries records on the Great Lakes would be desirable, especially for the last century, to be related to a corresponding detailed assessment of environmental conditions for the same period. In each instance particular attention should be directed to macrosystem properties. If the appropriate association between these two analyses is made, an ecosystem manager will be provided with a series of biotic community standards relating to general ecosystem quality which may usefully be projected into the future.

Other approaches towards ecosystem assessment at either the community or ecosystem level of integration may be equally effective.

5.2.4   <u>Use As Indicator Of Rehabilitation Success</u>

Underlying our basic <u>modus operandi</u> has been a perceived need to fill a hiatus between two existing documents directed towards the maintenance quality, rehabilitation and generally, the management of Great Lakes' fish stocks and a continued improvement in the quality of environment required to support and perpetuate them.   Hence, this document falls squarely between the policy and management recommendations of "A joint strategic plan for management of Great Lakes Fisheries" (Great Lakes Fishery Commission 1980) and the proposed rehabilitation measures of "Rehabilitating Great Lakes ecosystems" (Francis, <u>et al.</u>, 1979).   It also fulfills the needs and recommendations of the ecosystem approach concept (e.g. Great Lakes Research Advisory Board 1978) for the Great Lakes, now adopted by both the International Joint Commission and the Great Lakes Fishery Commission.

Within the new major responsibilities accepted by the various binational, federal, provincial and state agencies towards a rehabilitation of the Great Lakes Ecosystem, the current proposal provides a means, together with appropriate alternatives, of assessing the quality of the current ecosystem and providing a directionality for future rehabilitation efforts. Management initiatives progressing towards our previously stated ecosystem objective using the lake trout as an indicator/integrator species for oligotrophic systems (Section 1.4). will provide a measure of relative ecosystem quality. - Hence, the success of rehabilitation measures may be rapidly assessed and corrective actions taken wherever necessary.   At each plateau of rehabilita- tion, the status of the lake trout stocks and complementary cold-water indicator organisms will demonstrate the improved environmental milieu through: increasing numbers; optimum diversity of phenotypic and genetic stocks; wider geographic distribution; general reduction in levels of contaminant loads; increasingly successful reproduction and recruitment; and improvement in many other critical facets that reflect environmental compatibility.   (However, in terms of stock diversity, it is possible that the current gene pools of lake trout may not be sufficiently broad to establish the former level of phenotypic diversity observed more than thirty years ago).   Ultimately, if completely successful, every dimension of the ecosystem objective based on lake trout, its complementary indicators and the coldwater community, will be achieved.   Ideally, successful rehabilitation will be indicated upon attainment of each dimension of the ecosystem objective based on the fundamental life requirements of the lake trout tempered by rational cultural uses (see Section 1.4).

It should be emphasized however, that it would be irrational at the current level of cultural development to expect a complete return to pristine conditions, particularly on the Lower Great Lakes.   However, just as man's reach should exceed his grasp, the preferred state for Lakes Erie and Ontario should still be the somewhat idealistic primeval one (e.g. Schneider, et al., 1983).   It should be understood that this primeval benchmark will provide the highest quality ecosystem with the greatest long-term stability. However satisfying this concept may be philosophically, it must be coupled with the pragmatic realization that only a partial return to the pristine state may be reasonable and attainable.

On the Upper Lakes, particularly Lakes Michigan and Huron, a partial recovery to the pristine state may also provide an ecosystem of sufficiently high quality to satisfy most human expectations and needs.

In the case of Lake Superior, a higher standard may be achieved less arduously, simply by protecting the ecosystem that already exists. Because of lower human population levels (Figure 7), and less industry and agriculture in the Lake Superior watershed, ecosystem degradation generally, has not progressed as far as in Lakes Huron and Michigan. Consequently, an apposite rehabilitation scheme might concentrate initially on Class B areas of concern for Lake Superior (Table 3) where opportunities for rapid system restoration at moderately low costarely promising. A successful rehabilitation of Lake Superior might then provide a baseline standard for ecosystem managers on Lakes Michigan and Huron. Environmental restoration of Lake Superior would complement a process already underway by the Great Lakes Fishery Commission. That agency is committed to the rehabilitation of lake trout stocks in Lake Superior first, along with a necessary prerequisite, that of sea lamprey control.

In conclusion, the ecosystem objective based on the lake trout as-'an indicator/integrator organism should be a pragmatic blend of an idealistic state tempered with an attainable reality. Our recommendation proposes a pristine state of the ecosystem as the only logical known benchmark for system stability and predictability over time. For ecosystem management purposes, the primeval state indicates a direction for improvement, that is, a rehabilitation trajectory (e.g. Figure 3). A measurement of success in ecosystem rehabilitation will be based on how far we successfully move along the trajectory in the future, towards pristine conditions.

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Appendix I-A
COMMON AND SCIENTIFIC
NAMES OF FISHES [1]

Alewife[2]	Alosa pseudoharengus (Wilson)
American eel	Anguilla rostrata (Lesueur)
American shad[2]	Alosa sapidissima (Wilson)
Arctic char	Salvelinus alpinus (Linnaeus)
Atlantic herring	Clupea harengus (Linnaeus)
Atlantic salmon	Salmo salar Linnaeus
Bloater	Coregonus hoyi (Gill)
Blue pike	Stizostedion vitreum glaucum Hubbs,
Brook trout	Salvelinus fontinalis (Mitchill)
Brown trout[2]	Salmo trutta Linnaeus
Bullheads	Some members of the genus Ictalurus
Burbot	Lota lota (Linnaeus)
Carp2	See "common carp"
Centrarchid	Any member of the sunfish family
Channel catfish	Ictalurus punctatus (Rafinesque)
Char	Any member of the genus Salvelinus
Chinook salmon[2]	Oncorhynchus tshawytscha (Walbaum)
Chub	A deepwater cisco
Cichlid	Any member of the cichlid family
Cisco	Coregonus artedii Le Sueur
Cisco complex	Fishes of the genus Coregonus excluding the lake whitefish
Coho salmon[2]	Oncorhynchus kisutch (Walbaum)
Common carp[2]	Cyprinus carpio Linnaeus

Coregonine	A salmonid subfamily including the genera, <u>Coregonus</u> and <u>Prosopium</u>
Cottid	Any member of the sculpin family
Cunner	<u>Tautogolabrus adspersus</u> (Walbaum)
Cyprinid	Any member of the minnow family
Deepwater cisco	All members of the genus <u>Coregonus</u> excluding C. <u>clupeaformis</u> and C. <u>artedii</u>
Deepwater sculpin	<u>Myoxocephalus thompson</u>i (Girard)
Emerald shiner	<u>Notropis atherinoides</u> Rafinesque,
Fat	Synonym for siscowet
Freshwater drum	<u>Aplodinotus grunniens</u> Rafinesque
Goldfish[2]	<u>Carassius auratus</u> (Linnaeus)
Grayling	A member of the genus <u>Thymallus</u>
<u>Haplochromis</u>	A species swarm of cichlids found in the African rift lakes
Ictalurid	Any member of the bullhead catfish family
Killifish	Some members of the cyprinodontid family
Kokanee'	Lacustrine stocks of sockeye salmon
Lake herring.	<u>Coregonus artedii</u> Lesueur
Lake sturgeon	<u>Acipenser fulvescens</u> Rafinesque
Lake trout	<u>Salvelinus namaycush</u> (Walbaum)
Lake trout complex	Includes all phenotypic stocks of lake trout
Lake whitefish	<u>Coregonus clupeaformi</u>s (Mitchill)
Minnows	Any member of the cyprinid family

Mosquitofish[2]	<u>Gambusia affinis</u> (Baird and Girard)
Mummichog	<u>Fundulus heroclitus</u> (Linnaeus)
Ninespine stickleback	<u>Pungitius pungitius</u> (Linnaeus)
Northern pike	Esox <u>lucius</u> Linnaeus
Pacific salmons[2]	Any member of the genus <u>Oncorhynchus</u>
Percid	Any member of the perch family including walleyes, saugers and blue pike
Pink salmon[2]	<u>Oncorhynchus gorbuscha</u> (Walbaum)
Rainbow smelt[2]	<u>Osmerus mordax</u> (Mitchill)
Rainbow trout[2]	<u>Salmo gairdneri</u> Richardson
Redhorse	A sucker (catostomid) of the genus <u>Moxostoma</u>
Rock bass	<u>Ambloplites rupestris</u> (Rafinesque)
Salmon	Particularly the genus <u>Oncorhynchus</u> but also the Atlantic salmon
Salmonid	Any member of the trout family including salmon, trout, char, whitefish and ciscos
Salmonine	A salmonid subfamily including the genera <u>Salmo</u>, <u>Salvelinus</u> and <u>Oncorhynchus</u>
Sanddab	Certain members of the genus <u>Citharichthys</u>; i.e. lefteye flounders
Sauger	<u>Stizostedion canadense</u> (Smith)
Sculpin	Any members of the cottid family
Sea lamprey[2]	<u>Petromyzon marinus</u> Linnaeus
Sheepshead	<u>Archosarctus probatocephalus</u> (Walbaum)

Siscowet	A deepwater form of lake trout generally considered to be unpalatable because of its high fat content
Smelt[2]	See rainbow smelt
Sockeye salmon[2]	*Oncorhynchus nerka* (Walbaum)
Splake	*Salvelinus namaycush* x *S. fontinalis*
Spottail shiner	*Notropis hudsonius* (Clinton)
Sucker	Specifically, the genera *Catostomus* and *Moxostoma*
Trout	Usually the genus Salmo but often also used with reference to chars
Trout-perch	*Percopsis omiscomaycus* (Walbaum)
Walleye	*Stizostedion vitreum* (Mitchill)
White bass	*Morone chrysops* (Rafinesque)
Whitefish	See lake whitefish
White perch[2]	*Morone americana* (Gmelin)
White sucker	*Catostomus commersoni* (Lacepede)
Yellow perch	*Perca flavescens* (Mitchill)

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[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.

Appendix I-B

COMMON AND SCIENTIFIC
NAMES OF BIOTA (excluding fishes)

BIRDS

Canary	Serinus canarius
Forster's tern	Sterna forsteri
Gulls	Any member of the genus Larus
Herons	Wading birds of the family Ardeidae
Herring gull	Larus argentatus
Larids	Any member of the family Laridae; i.e. gulls and terns
Ring-billed gull	Larus delawarensis

MAMMALS

Man[1]	Homo sapiens
Mink	Mustela vison

INVERTEBRATES

Amphipods	Specifically Pontoporeia hoyi, a crustacean
Burrowing mayfly	Hexagenia limbata
Bloodworm	Several midges of the chironomid family
Crayfish	A decapod crustacean
Eurytemora affinis	A copepod crustacean
Ground beetles	Any member of the family Carabidae
Isopod	Aquatic sow bug, a crustacean
Molluscs	Principally snails, clams and mussels
Mussels	Molluscs of the genera Mytilus and Modiolaria

INVERTEBRATES - cont'd.

Possum shrimp	_Mysis relicta_
Sludgeworms	Genus _Limnodrilus_, aquatic earthworms

ALGAE

Cladophora sp.	A green alga
Microcystis sp.	A blue-green alga

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

Appendix II
GLOSSARY OF TERMS[1]

Aberrant stress - A culturally-derived impact on an organism for which there has been no previous evolutionary experience; consequently, no efficient defense mechanism has been developed; e.g. xenobiotic substances.

Abiotic environment - The inorganic surroundings of an organism; i.e. the inorganic constituents of the water, air and substrate.

Adenylate energy charge - A metabolic regulatory mechanism; e.g. a high energy charge that generally stimulates energy utilizing pathways.

Aeolian - Atmospheric in origin; wind related.

Allantoinase - An enzyme of the liver.

Allochthonous - Materials that are generated outside of a lake, usually in its watershed, but are deposited eventually within the lake proper.

Alluvium - Detrital material deposited by running water such as clay, silt, sand or gravel.

Ammocoete - Larval sea lamprey (<u>Petromyzon marinus</u>).

Anoxia - Severe oxygen depletion; used herein with reference to hypolimnetic waters.

Antagonism - Interaction of two or more substances (stresses) such that the combined effect is less than additive.

Anthropocentric - Interpreting the world in terms of human values.

Astatic fish assemblage - A loose association of fishes, usually created by human intervention through introductions of exotic species or through a physical or chemical modification of the environment. Such an assemblage is poorly integrated and lacks a readily identified stability domain, possibly because many of its component fish species had not coevolved.

Atmosphere - The mass of air surrounding the earth.

Autochthonous - Materials generated from within a lake.

Benthic - Relating to the substrate of a lake or stream. Hence, a "benthic feeder" ingests bottom organisms.

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1 Definitions of terms have occasionally departed from formal etymological use in order to preserve the intended ecological nuance or scientific implication.

Bioaccumulation - The aggregation and storing of compounds (usually microcontaminants) within an organism over time.

Bioattractant - A compound that attracts organisms.

Biochemical oxygen demand - The oxygen needed for the metabolism of organic materials by microorganisms; usually in water enriched with nutrients.

Bioconcentration - The accumulation of a compound in the tissues or organs of an organism over time.

Biorepellant - A compound that repells organisms.

Biosphere - That part of the globe in which life can exist.

Biotic community - Coevolved organisms, including vertebrates, invertebrates and plants. Because of coevolution, a moderately high level of integration is attained; consequently the community may be characterized by a reasonably constant identity and persistent steady-state barring cultural intervention or episodic events of large magnitude. ··

'Biotoxicants - Toxic substances derived from biotic sources.

Chlorinated hydrocarbons - A family of organic compounds such as DDT, DDE, PCB and toxaphene, as examples.

Chlorobenzene congener - Any compound closely related to chlorobenzene, a colorless, flammable, volatile, toxic liquid.

Circadian - -Internal rhythmicity in organisms characterized by approximately twenty-four hour cycles.

Coevolution - Evolving together; leads to highly integrated communities of predictable steady-state conditions because of the tightly knit web of interaction among the component organisms.

Coldwater community - A coevolved, integrated assemblage of organisms in north-temperate oligotrophic lakes, characterized principally by taxon swarms of salmonines and coregonines.

Community - A coevolved, integrated assemblage of plants and animals.

Community integrity - The output property derived from the web of interactions of organisms, that allows a community to be recognized as a persistent, identifiable entity.

Complementary indicator - A secondary indicator species that identifies concerns overlooked by, or orthogonal to, the primary indicator-integrator species; e.g. in this report, Pontoporeia hoyi has been proposed as an appropriate complementary indicator to the lake trout.

Connectedness - The number of pathways for interaction in an ecosystem or
     community. Presumably, the more pathways that exist up to an optimum
     number, the more integral is the system.

Conservative ions - Certain ions such as chloride that normally are not
     influenced by metabolism or other biotic activity.

Conservatism - Attribute of a system that retains relatively constant output,
     at steady-state, despite a reordering of internal system components. i.e.
     species composition of a coldwater community may change with cultural
     intervention, but total yield of all species remains approximately the
     same.

Controlling factor - An exogenous factor such as light that regulates the
     metabolism or behavior of organisms; i.e. a controlling factor influences
     metabolic rate by conditioning the medium in which the metabolic processes
     take place. A controlling factor is unlikely to be lethal over its normal
     ambient range.

Coolwater community - A coevolved, integrated assemblage of organisms-of
     north-temperate mesotrophic lakes characterized by percid predominance.

Cultural eutrophication - The addition of fertilizing elements derived from
     cultural activities or settlement. In freshwaters, this is essentially
     accelerated phosphorus loading.

Decomposibility - The ability of an ecosystem to resist disaggregation; i.e.
     retains a high level of integration.

Demersal zone - The zone at the bottom, or near the bottom of a lake.

Demographic characteristics - Vital statistics of populations including size,
     density, age, growth, mortality and distribution.

Density-dependent - Compensatory responses of organisms under particular
     stresses which tend to reduce their numbers without destroying the
     environment; e.g. exploitation, sea lamprey predation, etc. Compensatory
     responses include increased growth rates, decreased mortality rates and
     reduced age to maturity.

Dichotomous - Dividing into two parts.

Dynamic equilibrium - See "Steady-state".

Ecosystem - An ecological system encompassing all aspects of the abiotic
     environment as well as the biota contained therein, including mankind. An
     ecosystem in the largest sense may be the global biosphere or
     alternatively it may be a watershed, a lake or even an organism.

Ecosystem approach - One of many holistic, interdisciplinary, top-down methods
     of treating ecosystems as "black boxes". Emphasis is placed on specific
     output properties as related to quantifiable inputs without the need for
     detailing all component parts of the system nor all the intervening
     pathways. Modern ecosystem approaches regard man as an integral part of
     the system.

Ecotone - An ecological interface, often between land and water, or any other distinct physical boundaries such as mud-water interface or air-water interface. Ecotones are attractants to biota and consequently serve as zones of relatively intense interaction and exchanges of energy, nutrients and contaminants.

Emergent property - A macrosystem property that implicitly is a result of system integration. An emergent property consequently, is more than the sum of its parts, e.g. fish yield may be considered an emergent property of an aquatic biotic community.

Epilimnion - The uppermost, usually relatively warm layer of a thermally stratified lake, during the summer period of stratification in the north temperate zone.

Euryhaline species - Those species able to tolerate a wide range of salinity in water.

Euryecious - Species that are able to tolerate a broad range of ecological conditions.

Eutrophic - Lakes rich in nutrients; often characterized by an absence or depletion of dissolved oxygen in the deep waters during late summer.

Facultative species - A species that readily adapts to different environments.

Fecundity - The relative number of eggs or offspring produced by an animal.

Feedback - The return to the input of a system of part of its output, resulting in system steady-state, providing that the feedback does not reinforce the output. In the latter case, the system becomes unstable or jumps to a new stability domain.

Fish assemblage - A loose aggregation of fishes usually not integrated through coevolution but rather the result, at least in part, of introductions, invasions, or other human interventions; see "Astatic fish assemblage".

Fish community - An integral aggregation of fishes often resulting from eons of coevolution. The integration is derived from species interactions such as predator-prey relationships between two species, or various symbioses (broad sense).

Fishing-up - The removal of accumulated stock in a fishery as opposed to harvesting only the annual incremental growth. Fishing-up most often occurs during the early stages of a fishery.

Food web - The feeding interrelationships within a biotic community with particular reference to food habits.

Forage fishes - Fishes that form the usual food for piscivores. Forage fishes are normally small, pelagic planktivores, although any fish of appropriate size may serve as forage for a predator.

Fundamental niche - (Potential niche) A multidimensional response capacity of an organism relative to abiotic factors that comprise its total environment (e.g. temperature, light, dissolved oxygen, pH, etc.). Fundamental niche is genetically determined.

Gastrulate - The formation of an early embryonic stage of many organisms.

Genotype - The genetic makeup of an organism without regard for its external appearance.

Glutamate-dehydrogenase - An enzyme forming an important metabolic control site; its major regulatory function is in channelling carbon into the Krebs cycle.

Growth compensation - A density-dependent response to those stresses that remove fish from populations (e.g. harvest or predation); results in increased growth rates in remainder of population.

Harmonic community - A coevolved, integral biotic community which retains its identity over time through an innate resilience which resists change within the limits of its homeostatic boundaries.

Heterogeneous habitats - Diverse environmental conditions, often associated with faunal and floral complexity.

Hierarchic levels - The recognition that an ecosystem and its contained communities are organized into ranks, each subordinate to the one above it in terms of conservation of, or utilization of, energy and matter.

Holistic - A philosophy which regards an ecosystem as an integrated entity without the need for first dissecting it into its component parts for analysis.

Homeostasis - Operational processes within prescribed bounds by elements of an ecosystem, leading to steady-state.

Homeostatic constraints - Boundary conditions for maintenance of steady-state in an ecosystem or community.

Hypereutrophic - Lakes with a superabundance of nutrients; extreme eutrophy.

Hypolimnion - The relatively cold water of a thermally stratified, north-temperate lake, found at the bottom, below the thermocline. Temperature of the hypolimnion is relatively uniform during periods of summer stagnation.

Hysteresis - A retained attribute resulting in a retardation of an effect when forces acting upon a body are changed; lag or overshoot.

Immigration-extinction - A continuing process that determines the constituency of a biotic community. As environment changes, certain indigenous biota may be unable to survive, or to compete with recent immigrants for which the new environment may be more favorable.

Indicator organism - An organism that shows the direct effect of a cultural stress through its response to change; e.g. the observed proliferation of Cladophora with accelerated phosphorus loading.

Indigenous community - A biotic community native to a particular area or lake.

Integrator organism - An organism that mirrors indirect effects of cultural stresses as well as direct effects. Consequently, it becomes a; "system indicator" reflecting stresses at different trophic levels or different parts of the system; e.g. lake trout, as through the bioaccumulation of organochlorines.

Intraspecific - Within a single species; usually with reference to competition for a common resource.

Introgression - Inbreeding of closely related species, usually of the same genera. Ecosystem stresses that reduce brood stock numbers below critical mass requirements for successful reproduction may activate introgression. Major environmental impacts may change the site or timing for nuptial behavior of closely related species and is therefore, a second possible mechanism for introgression.

K-selected species - A species with increased competitive ability at densities' near carrying capacity. Most often these species have relatively low fecundity and a long time to maturity, are large and feed at the upper trophic levels; e.g. lake trout, walleye.

Keystone species - A major integrating species in a community of organisms, the loss of which would lead to eventual loss of steady-state or reversion to another stability domain; e.g. often a terminal predator such as the lake trout.

Limiting factor - An exogenous factor such as temperature that regulates behavior and metabolism over its intermediate range but may become lethal at extremes. A limiting factor actually enters into the chain of metabolic processes of the organism.

Limnetic - The open waters of lakes.

Lipids - A type of fat or fat-like compound found in living organisms.

Lipophilic compounds - Having an affinity for lipids. i.e. some organochlorines are accumulated in fatty compounds.

Lithosphere - The outer, solid part of the earth composed of rock.

Macrophyte - Any large, rooted aquatic plant as distinct from single-celled , . plants, such as algae and diatoms, or colonial algae.

Macrosystem properties - Attributes of an ecosystem observed at a given level of integration (i.e. emergent properties).

Mesotrophic - Lakes with moderate levels of nutrients; i.e. in the Centre of a cline between oligotrophic (depauperate in nutrients) and eutrophic (rich in nutrients).

Methylation - The impregnation or mixing of a substance with methanol.

Microcosm - Often applied to lake ecosystems in the sense that they are 'systems unto themselves" and discrete from outside influence. In actual fact, lakes interact with all their surroundings through materials and energy exchange and immigration or emigration of biota.

Micromechanistic - Concerned with the fine detail of natural processes.

Mixed function oxidase (MFO) - An enzyme system found in fishes that has the capability of metabolizing certain microcontaminants. Stress symptoms are elicited through increased MFO activity.

Morphoedaphic - Environmental contributions to lake productivity in the form of nutrient input from the surrounding watershed, the substrate or the atmosphere, channelled or constrained by the morphology of the lake basin. e.g. total dissolved solids/mean depth.

Nannoplankton - Plankton in the size range of 0.005-0.06 mm.

Necrotic tissue - Localized death of living tissue.

Neurotoxin - A toxin that acts on the nervous system.

Niche - The abstract hypervolume that is generated by assigning a dimension to each factor that affects an organism's survival. Niche is therefore, an attribute of the organism rather than of the environment.

Obligate piscivore - A predator that is best equipped functionally as an adult for feeding on fishes; i.e. requires forage fish for food.

Obligate planktivore - A predator that is functionally adapted to feed on plankton; i.e. requires plankton for food.

Oligotrophic - Lakes with low nutrient levels, usually with an abundance of dissolved oxygen in hypolimnetic waters during summer stagnation.

Operational niche - See realized niche.

Optimality curve - The range of effect of certain environmental variables on an organism; i.e. the variable may be most favorable near the mid-point of its ambient range, becoming more stressful at either end.

Particle-size density - The relative abundance in terms of biomass of size-classes of organisms grouped on a logarithmic (octave) scale (log10 basis). The particle-size theory for marine pelagic systems suggests that each size-class constitutes about the same biomass per unit volume of water over a size range covering organisms from bacteria to whales.

Pelagic - Of or pertaining to the open water of lakes (as opposed to the
    nearshore, littoral zone).

. Phenotype - The class to which an individual organism is assigned according to
    its external morphology, regardless of its genotypic make-up.

Phenotypic plasticity - The capability of an organism to adapt some of its
    phenotypic characteristics (especially morph) to its ambient environmental
    surroundings. Many coregonines and salmonines, especially the lake trout,
    seem to have the capability of being phenotypically malleable.

Photoperiodism - Physiological or behavioral response of organisms to diurnal
    or annual changes in light intensities or regimes.

Photosynthesis - The formation of carbohydrates in plants from water and
    carbon dioxide in the presence of light and chlorophyll.

Piscivores - Predators that prey principally on fishes.

Planktivores - Organisms that eat plankton.

Plankton - All organisms suspended in the water column of a lake, dependent
    mostly on water currents for locomotion rather than independent movements.-

Pleistocene refugia - Water bodies that served as sanctuaries for fauna of the
    Great Lakes Basin during the period of glaciation. With glacial
    withdrawl, these fauna reinvaded the Great Lakes Basin and tributary
    waters.

Polyploidy - A condition in which the chromosome complement of the somatic
    cells is greater than two.

Potential niche - See "Fundamental niche."

Predation refugium - Discrete lake zones within the Upper Great Lakes
    inhabited by different coregonine congeners. Reproductive isolation was
    effected by control at the periphery of the zones through predation,
    particularly by lake trout. Removal of lake trout through sea lamprey
    predation and exploitation allowed refugia boundaries to disappear and
    desegregation ensued, usually resulting in introgression of two or more
    congeners.

Production - Quantity of living protoplasm produced in a population or
    community per unit time.

Profundal zone - The deepest zone at the bottom of a lake.

Protoplasm elaboration - Equivalent to 'production" in a population or
    community, or to growth in an individual, expressed as biomass.

r-selected species - A species that has rapid population growth at low densities or in new environments. These species are usually opportunistic, fecund, with short time to maturity and rapid turnover rates; usually of small size and feeding at low trophic levels; e.g. alewife, rainbow smelt.

Radionuclides - Radio-active contaminants.

Realized niche - The fundamental niche as it is constrained by the interaction of an organism with its environment, including other organisms. Many of the environmental dimensions of the fundamental niche are reduced accordingly.

Recursion - the reiterated nesting of an ecosystem; i.e. compartments inside compartments, inside compartments.

Refractory organic compounds - Compounds resistant to breakdown; non-biodegradable.

Rehabilitation - The restoration of an ecosystem to its former, usually pristine condition.

Reproduction compensation - Increased fecundity of organisms under stress. This is a density-dependent mechanism in species with a strong stock-recruitment relationship, where brood numbers are reduced through removal, or by increased natural mortality.

Reproductive isolation - Resistance to interbreeding of two or more stocks or populations due to the establishment of barriers to desegregation. Barriers are usually geographical, ecological, temporal or behavioral in nature.

Resiliency - The ability of a system to recover under stress. Recovery usually only occurs within the boundaries of effective homeostasis.

Simulative stresses - Stresses that are only quantitatively greater than similar natural stresses. Simulative stresses include cultural eutrophication, forest fires of anthropogenic origin, acid precipitation and thermal loading.

Species swarm   A closely related group of species with a common genetic background; e.g. the coregonine complex of the Great Lakes.

Squamation - The scaly condition in most fishes.

Standing crop - See "Standing stocks".

Standing stocks - The total numbers or total biomass of a species at any point in time.

Steady-state - Open system output retained between upper and lower homeostatic boundaries; dynamic equilibrium.

Stenoecious - Tolerant of only a relatively narrow range of environmental variables.

Stenophagic - Subsisting on only a narrow range of food items.

Stenothermic - Tolerant of only a narrow range in temperature.

Stochastic - Involving chance or probability.

Stock - a reproductively isolated group of a single species showing marked phenotypic differentiation; a phenotype.

Stock complex - Various races, morphs or phenotypes of a single species; e.g. the diverse stocks of lake trout formerly occurring in Lake Superior.

Stock-recruitment - The relationship of the numbers of progeny to the numbers of brood stock that spawned them.

Succession rate - A slow, orderly progression of changes in community composition. Animal succession is dependent to a large extent on plant succession (and cultural interventions), terminating in a climax community.

Synergism - Interaction of two or more substances (stresses), such that the combined effect becomes greater than the sum of the two individual stresses.

Taxa diversity - The relationship between the number of species and the number of individuals in a community, usually expressed as an index or ratio.

Taxa equitability - The relationship among species of a community showing their evenness; usually quantified as an index.

Taxon swarm - A closely related group of genera, species or stocks with a common genetic background.

Teratogenic agents - Contaminants or toxic substances tending to cause developmental malformations and monstrosities.

Terminal predator - A piscivore in most lake systems; feeds on other piscivorous or planktivorous fishes; feeds on other occupants of the third trophic level or higher. Han, of course, is the ultimate terminal predator in many ecological systems.

Top predator - See "terminal predator."

Trophic hierarchy - A ranked structure of organisms consisting of relatively discrete levels of nutrition. In a lake, the first, or lowest level of the food web consists of autotrophic plants (phytoplankton) followed by grazing zooplankton and benthos at a secondary heterotrophic level, fishes and predatory invertebrates that feed on these at the third level and finally, piscivorous fishes, birds and mammals at a fourth trophic level.

Trophic level - A single level of a nutritional hierarchy.

Trophic-dynamic - The transfer of nutrients and energy from one part of an ecosystem to another.

Turnover time - The time required for new protoplasm to be elaborated by an organism.

Ultra-oligotrophic - Lakes with extremely low nutrient levels.

Vagile - Free to move about.

Warmwater community - A coevolved, integrated assemblage of organisms in north-temperate eutrophic lakes characterized by the presence of species flocks of centrarchids, cyprinids and ictalurids.

Xenobiotic substance - Used with reference to synthetic contaminants for which organisms have no historical experience of exposure.

Yield conservatism - The resilient nature of an aquatic ecosystem to produce moderately constant harvests of fishes in terms of total biomass, despite major temporal changes in the internal species composition.

Zooplankton - Animal plankton suspended in the water column of a lake that depend on water currents for mobility of any marked extent.

Appendix III

TERMS OF REFERENCE
for the
Aquatic Ecosystem Objectives Committee's
Work Group on Indicators of Ecosystem Quality

An ecosystem objective by definition, infers a broad scientific approach encompassing all aspects of the environment and the indigenous biota. Such an objective framed as an ultimate goal for ecosystem management in the Laurentian Great Lakes may be philosophically satisfying, but pragmatically intractable.

Alternatively, the establishment of an ecosystem objective using a single species (a seeming contradiction of terms) may be justified, provided that the niche characteristics and habitat requirements of that species can be adequately described. Comparison of these characteristics with the former environments provided by a major portion of both the biotic and abiotic subsystems of the Great Lakes, will emphasize the degree of departure from pristine conditions through recent human interventions.

With the specific task of developing an Ecosystem Objective for the Great-Lakes Basin, a designated Work Group shall proceed to investigate the following charges:

o Appraise, evaluate and critique the feasibility of using an indicator or integrator organism as a suitable surrogate for depicting a "healthy" Great Lakes;

o If feasible, produce an objective with supporting rationale applicable for inclusion into the 1978 Great Lakes Water Quality Agreement and in accordance with the Terms of Reference for the Aquatic Ecosystem Objectives Committee.

In the course of performing these specific charges the following additional charges shall be considered:

o Identify and recommend appropriate system variables for future monitoring based on these concepts; and

o Explore and develop, if appropriate, other ecosystem approaches with potential application to the Great Lakes Basin.

Appendix IV
A HIERARCHY OF RESPONSES

A fish responds to a variety of environmental factors. Its behavior is controlled by some, such as ambient subsurface illumination and severely restricted by others such as dissolved oxygen, or may be both control led and limited by the same factor as in the case of water temperature. The absolute limit of normal activity for fishes at varying levels of these environmental factors prescribes their niche boundaries, which are genetically determined. While optimality curves satisfactorily describe the behavior of controlling factors relative to the well-being of the fish, most limiting factors operate over a normal ambient range in an approximately linear fashion until a threshold (lethality) is reached. Optimum temperature for growth and other metabolic processes in some fish species, for example, may be close to incipient lethal temperature levels. Temperature, when a controlling rather than limiting factor, likely behaves as an optimality curve as in the'* regulation of spawning. Consequently, optimum stock survival usually does not occur at the temperature at which maximum growth is realized because at this level there is little slack in the system that would allow for a further temperature increase due to temporal environmental variability. See Fry (1947) and Brett (1970) for elaborations of this theme.

Controlling variables operate effectively, that is, influence the behavior of the fish only when limiting variables remain within the zone of tolerance as prescribed by the niche boundaries for a particular-species. Consequently, an array of different environmental variables regulate the operational bounds of a fish according to hierarchic priority, with all limiting variables setting the fundamental constraints on behavior or metabolic activity and the controlling variables determining the level of different types of activity within these constraints.

Because certain niche dimensions will be specific to a particular fish species, the hierarchy, or order of effect of controlling and limiting variables may not coincide in different species. In the case of the lake trout, 'an approximate order of effect is deduced of the fundamental variables as depicted in Figure 15. Here, the three primarily limiting factors, temperature, dissolved oxygen and pH are first-order effects followed by the two controlling factors, light and nutrients. However, among the controlling variables, of necessity, an internal hierarchy of priorities exists. An extension of Liebig's Law of the Minimum (Liebig 1840) to ecological systems (Watt 1973) and an expansion to include maxima during steady-state conditions (Odum 1971). is appropriate to the determination of the hierarchic order of limiting factors. Liebig's Law, thus modified, would state that only one limiting factor would be operational on the scope for activity of an organism at any one time; secondary factors, even if at near-lethal levels, could be masked by the severity of effect induced by the limiting factor of top priority. An exception to this instance (but not contrary to the order of
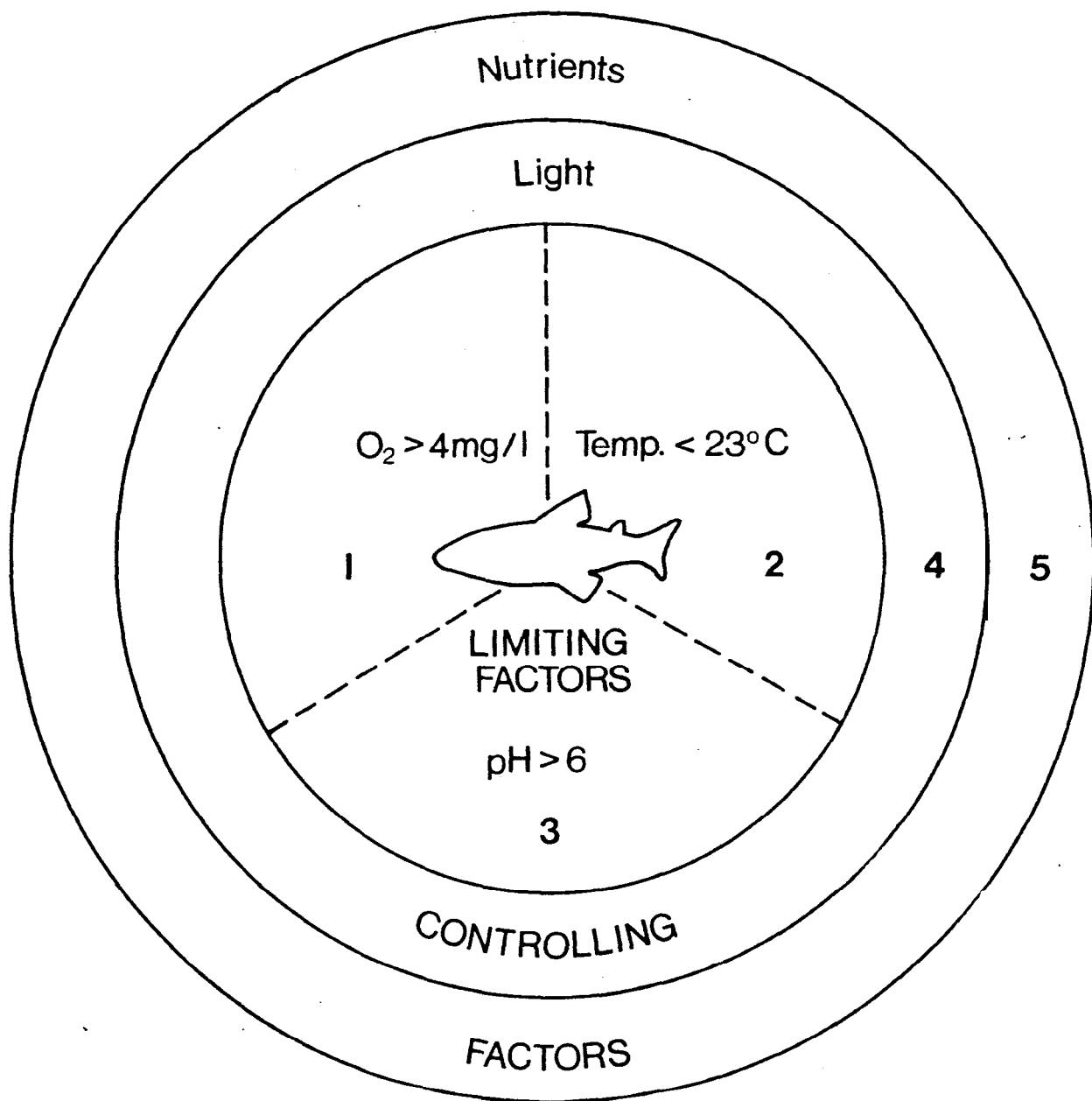
Figure 15   A proposed hierarchy of responses for the lake trout based on metabolic or behavioral necessity. Oxygen (1) has the highest priority response if limiting and nutrients (5) the lowest. All limiting (potentially lethal) factors restrict metabolism and behavior at a higher level of priority than any of the controlling factors.

priority) would occur if two or more limiting factors operated in a synergistic fashion. Adequate documentation for this latter kind of effect is difficult to obtain and instances of its occurrence are scarce in the primary scientific literature.

With regard to the lake trout in the Great Lakes, none of the limiting factors normally exceed the operational range of this species for normal behavior or metabolic activity and the establishment of a priority of effect must therefore be assumed. As most fishes can normally tolerate unfavorable temperatures for longer periods than extremely low oxygen levels, the latter effect may be of first priority, although comparative quantification of the two effects would be difficult.

A pH level which is less than six may inhibit successful reproduction, but would not necessarily stress adult lake trout unduly. The pH effect would therefore be of only tertiary importance but could have equally (as oxygen and temperature insufficiencies) drastic results on an extant population if it completely eliminated recruitment to the adult stock.

As absolute levels of all three of the limiting factors generally fall in a range favorable to the lake trout within its historical distribution in the Great Lakes, then secondary considerations relate to the rates of change of these variables or to the diurnal or annual regime. Consideration of these two factors is outside the boundaries of this Mediate discussion except to note that both concerns are again generally favorable to lake trout in the Great Lakes.

Light, as a controlling factor, becomes important only after the fundamental necessities of life are satisfied (0,, temperature, pH). Light may initiate or terminate various activities, including feeding or spawning on a diurnal basis, through its rate of change (Ryder 1977). Over an annual period, light will determine when a lake trout will spawn according to its temporal regime or photo-period.

Nutrients, for the lake trout, likely have the lowest priority in the determination of diurnal behavior or metabolic activity. North-temperate poikilotherms, because of their relatively low body temperatures and correspondingly low metabolic rates, would seem to have their behavior governed by food requirements only when all limiting variables and controlling factors of higher priority have been satisfied. Even unfavorable light levels may preclude a fish from eating (e.g. Ryder 1977), consequently, nutritional requirements must be relegated to last place in the hierarchy of priorities on a diurnal basis. However, if nutritional deficiencies are extended over substantial periods of time, then a fish will (at least temporarily) enter waters with unfavorable oxygen or temperature levels to indulge in a rapid feeding foray-(e.g. Dymond 1928; Fry 1937). This apparent contradiction to the expanded version of Liebig's Law of the Minimum as applied to ecological relationships is invalid because, when a nutritional deficiency reaches a level at which a significant stress is induced on the fish, then a departure from steady-state occurs and the application of Liebig's Law becomes inappropriate (Odum 1971).

In conclusion, implicit in the preceding discussion of the fundamental limiting and controlling factors for lake trout, is the understanding that the primary causitive agent for the demise of that species in the Great lakes was the sea lamprey, confounded by exploitation. Since the disappearance of the lake trout, however, environmental degredation has continued, and reestablishment of diverse stocks of reproducing lake trout in at least some of the Great Lakes may be dependent on more than the realization of successful sea lamprey control or fishery regulation.

Of particular concern may be the rehabilitation of former spawning grounds which have become sedimented or covered with Cladophora, or the reduction of chlorinated hydrocarbons to levels which will allow natural reproduction to take place effectively. These are only two examples of deleterious effects that may be evoked in a synthetic system, that affect neither limiting nor controlling factors in the traditional sense; that is, they do not directly influence the survival of adult lake trout.

Appendix V
COMMUNITY RESPONSES TO AN OLIGOTROPHIC SYSTEM
UNDER CULTURAL STRESS

1. Mean size of organisms decreases.
2. Life span shortens.
3. Pelagic organisms predominate.
4. Benthic organisms decline.
5. Foragers increase.
6. Top predators decrease.
7. Stenobionts replaced by eurybionts.
8. Food webs decompose or simplify.
9. Food webs shorten.
10. Introgression may occur.
11. Reproduction may cease.
12. Species ratios change.
13. Number of species reduced.
14. Mesotrophic forms increase.
15. Production declines.

Some general effects of a multitude of cultural stresses on biotic communities in north-temperate oligotrophic lakes. A specific, directed stress may elicit a different initial response, but the ultimate response will be as indicated above (e.g. acid precipitation may initially cause increased growth rates of some fish species through reduction of competitive interaction, particulary food competition. However, as the stress gradually increases to the point where metabolism is inhibited or constrained in some way, growth and therefore production, may be severely limited by the stress alone rather than through density dependent mechanisms.)

Appendix VI

DICHOTOMOUS KEY COMPUTER PROGRAM FOR
IDENTIFYING STRESS SYMPTOMS

The lake trout dichotomous key is a Basic language program designed for use with a Commodore 64 or a 4032 Pet computer. A printer is required, preferably capable of emulating Commodore graphics. The program may be modified to run on an Apple, IBM, or any microcomputer supporting Microsoft Basic by altering the printer routines and disk commands to conform with the requirements of the system. The cursor control commands, peculiar to the Commodore screen editor, must also be replaced with their appropriate equivalent.

The dichotomous key may best be envisioned as a menu-driven program which logically progresses through three key elements. Initially, a descriptive preamble is displayed on the screen, introducing and qualifying the exercise. The user is then prompted to specify one of the five Great Lakes for which he has special interest. Secondly, a series of questions is presented grouped into four areas of concern: 1) Exploitation stress; 2) Sea Lamprey predation; 3) Contaminant loading; and 4) Environmental stress (both abiotic and biotic). The user's "yes", "no", or "I don't know" responses to these questions provide the input necessary to accomplish an ecosystem quality diagnosis. Upon completion, a print-out is produced which separates the tested dimensions into three groups--those related to the lake trout as an indicator and integrator species and hence reflective of a level of ecosystem well-being; those considered probable system stressors and finally, those areas where additional data are required to effectively render an evaluation.

A sample run illustrates the subcomponents of the program, for clarity labelled I - Preamble, II - Questions & Responses, and III - Evaluation. All standard print represents computer output while the bold-face type signifies user response.

A program menu and sample run are attached, the latter including the final diagnosis of ecosystem quality based on the sample data.

DICHOTOMOUS KEY TO ECOSYSTEM WELL-BEING

This program demonstrates the use of an indicator organism to evaluate the well-being of the Great Lakes ecosystem.

The organism utilized for this purpose is lake trout, hence the key is applicable only to lakes or lake basins where lake trout currently exist, or occurred in the past. Similar keys, utilizing other appropriate indicator species are required to assess those regions which do not fit this criterion.

Respond to the questions as indicated. Upon completion a three part listing will be printed outlining those dimensions:

(1) which are suspected to be non-stressful to lake trout (indicators of a healthy ecosystem);

(2) which may possibly stress lake trout (indicators of a stressed ecosystem); and

(3) where more data are required to fully evaluate potential stressors. -

Select Area of Concern:

    1 - Lake Superior
    2 - Lake Huron
    3 - Lake Michigan
    4 - Lake Ontario
    5 - Lake Erie
    6 - Other

Input appropriate number, then "return"; 1

Please wait while Lake Superior data files are loaded.

I I - QUESTIONS & RESPONSES

DICHOTOMOUS KEY TO ECOSYSTEM WELL-BEING FOR LAKE SUPERIOR

A) Exploitation

1 - DO salmonines comprise 25% (+ or - 5%) of the total harvest of all species?

YES   ,

2 - Is the total annual harvest of all salmonines less than .24 kg/ha?

NO

3 - Do female lake trout mature at mean age 8 and total length 66 cm (+ or - 10%)?

YES

4 - Is the mean age of lake trout in the harvest >8 years?

DON'T KNOW

5 - Is the annual (conditional) fishing mortality-rate for lake trout <.36?

YES

6 - Is the rate of growth of maturing (age 6-9) lake trout 5-7 cm/yr?

NO

7 - Are diversified stocks of lake trout represented in the catch, including both river and shoal spawners and those feeding pelagically as well as in the littoral and profundal regions?

DON'T KNOW

8) Sea Lamprey

1 - Do spring catches of lake trout >53 cm in length exhibit a lamprey wounding rate <2% (unhealed wounds)?

NO

C) Contaminants

1 - Is the total DDT residue (including DDE & DDD) in whole lake trout <1.0 mg/kg wet weight?

YES

2 - Is total toxaphene residue (either singly, or in combination with all other organochlorine pesticides, excluding DDT) in whole lake trout <0.1 mg/kg wet weight?

   NO

3 - Is total PCB residue in whole lake trout <0.5 mg/kg wet weight?

   YES

4 - Is total mercury residue in whole lake trout <0.5 mg/kg wet weight?

   DON'T KNOW

D) Environmental (Biotic)

1 - Has the composition of the fish assemblage remained static for at least the past two decades with no recent introductions or invasions of exotic species?

   YES

2 - Have standing stocks of the main forage species for adult lake trout remained fairly stable over the past two decades?

   NO

3 - Are lake trout free from heavy and widespread parasite infection (other than sea lamprey)?

   YES

E) Environmental (Abiotic)

1 - During the period of late summer stratification, is the mean hypolimnetic temperature 10°C or less?

   NO

2 - Is the mean temperature on the spawning beds within the range of 6-12°C during the traditional period of spawning?

   YES

3 - Do water temperatures remain <3°C on the spawning beds during the period of egg incubation?

   YES

4 - During late summer, is the mean volume-weighted hypolimnetic dissolved oxygen concentration >5.0 mg/L?

   DON'T KNOW

5 - During egg development, does the dissolved oxygen concentration at the sediment-water interface on the spawning beds exceed 8.0 mg/L?

   DON'T KNOW

6 - Is the mean annual lake pH >6.0?

   NO

7 - Does the pH on the spawning beds remain fairly constant with no pH depressions occurring during the spring or fall pulse in runoff?

   NO

8 - Is the ratio of total spring phosphorus (ug/L) to mean depth (m) <1.0?

   YES

9 - Have the spawning shoals remained unaffected by siltation or other environmental degradation such as dredging or shoreline modification?

   NO

III - EVALUATION

DIAGNOSIS OF ECOSYSTEM WELL-BEING FOR LAKE SUPERIOR

ECOSYSTEM DIMENSIONS TESTED SUSPECTED TO BE NON-STRESSFUL TO LAKE TROUT - INDICATORS OF A HEALTHY ECOSYSTEM:

A) <u>Exploitation</u>

   1 - Salmonines comprising 25% (+ or - 5%) of the total harvest of all species is consistent with historic long term trends.

   2 - Maturity of female lake trout at mean age 8 and total length 66 cm (+ or - 10%) is consistent with that during the period of stable, long-term high yields.

   3 - An annual (conditional) fishing mortality rate <.36 would ensure an acceptable total mortality rate for lake trout of .50 or less (assuming an instantaneous natural mortality rate of .25).

B) <u>Sea Lamprey</u>

   - All answers indicate stress, or insufficient data provided.

C) <u>Contaminants</u>

   1 - Total DDT concentrations (including DDE and DDD) <1.0 mg/kg wet weight in whole lake trout are within acceptable limits.

   2 - Total PC8 concentrations <0.5 mg/kg wet weight in whole lake trout are within acceptable limits.

D) <u>Environmental (Biotic)</u>

   1 - A static fish assemblage, with no recently introduced or invaded exotics would suggest no additional predation on, or competition with young trout for zooplankton forage.

   2 - Parasite infection (other than sea lamprey) is considered light and thought to have no major deleterious effect on lake trout well-being.

E) <u>Environmental (Abiotic)</u>

   1 - The mean temperature during the traditional period of spawning is within the preferred range of 6-12°C.

   2 - Water temperatures, <3"C during incubation appear optimal for egg development.

   '3 - A total spring phosphorus (ug/L) to mean depth (m) ration <1.0 suggests that phosphorus loading is probably not excessive in terms of its effect on lake trout habitat.

ECOSYSTEM DIMENSIONS JESTED WHICH MAY STRESS LAKE TROUT -
INDICATORS OF AN UNHEALTHY ECOSYSTEM:

A) Exploitation

   1 - The total salmonine harvest is likely excessive, being greater than
       the pre-lamprey long term catch for lake trout of .24 kg/ha.

   2 - A growth rate >7 cm/yr for maturing (age 6-9) lake trout may indicate
       over-exploitation or high sea lamprey predation. A slower rate of
       growth (<5 cm/yr) may be a consequence of high contaminant loading or
       environmentally-induced stresses.

B) Sea Lamprey

   1 - A lamprey wounding rate of >2% from spring catches of lake trout
       >53cm in length reflects an annual lamprey induced mortality in
       excess of 5%.

C) Contaminants

   1 - Total toxaphene residue (either singly, or in combination with all
       other organochlorine pesticides, excluding DDT) in excess of 0.1
       mg/kg wet weight in whole lake trout may contribute to mortality.

D) Environmental (Biotic)

   1 - Decreases or fluctuations in the standing stocks of forage species
       could result in food shortages for adult trout.

E) Environmental (Abiotic)

   1 - During late summer, lake trout may be forced to occupy water
       considerably warmer than the preferred 10°C.

   2 - A mean annual lake pH <6.0 may adversely effect development of lake
       trout embryos and success of the hatch.

   3 - Spring pH depressions coincidental with the lake trout hatch may
       greatly reduce alevin emergence while fall depressions may affect
       embryonic development.

   4 - Cultural degradation of spawning shoals (through siltation, dredging,
       etc.) may impede spawning or reduce egg survival.

DATA REQUIRED TO MORE FULLY EVALUATE ALL POTENTIAL LAKE TROUT
STRESSES:

A) Exploitation

   1 - What is the mean age of lake trout in the harvest?

   2 - Are numerous, diversified lake trout stocks, if once present in the
       lake, still represented in the catch?

B) <u>Sea Lamprey</u>

   - Data adequate

C) <u>Contaminants</u>

   1 - What is the total mercury residue present in whole lake trout?

D) <u>Environmental (Biotic)</u>

   - Data adequate

E) <u>Environmental (Abiotic)</u>

   1 - What is the volume-weighted hypolimnetic dissolved oxygen concentration during late summer?

   2 - What is the dissolved oxygen concentration at the sediment-water interface during egg development?

Appendix VII

POSITION ON LAKE TROUT REHABILITATION
Great Lakes Fishery Commission
(Adopted 14 June 1976. Revised 12 May 1983.)

Article IV(A) of the Convention on Great Lakes Fisheries (Great Lakes Fishery Commission 1956) charges the Great Lakes Fishery Commission to determine measures for continued productivity of desirable fish species in the Convention area. The Commission views securing fish communities based on foundations of self-sustaining stocks as the ultimate goal of this charge, and believes that stocking with hatchery-reared lake trout is an essential step toward achieving self-sustaining lake trout populations--a major Commission objective.

The primary purpose in selecting stocking sites for lake trout should be to obtain successful reproduction. Suitability of habitat should be the major determinant. A secondary and temporary purpose for stocking site selection may reflect immediate-term social and economic considerations. The Commission emphasizes that when adequate numbers are available to accommodate stocking on secondary sites, harvest controls (refuges, seasons, quotas, etc.) are essential for these stocks in order to avoid raising user expectations to levels above those which can be met over the long term by naturally reproducing stocks. The stocking of hatchery-produced lake trout should favor areas, subject to possible designation as refuges, in which very young stages of the offspring of fish returning there to spawn, as well as spawners themselves, would likely receive greatest protection.

The Commission recognizes that in Lakes Superior, Huron and Michigan, substantial stocks of lake trout have been reestablished through stocking, controlling sea lamprey and limiting commercial exploitation. Effectual natural reproduction requires large numbers of spawning fish. Although some natural reproduction occurs in certain areas, the Commission has determined that the present stocking program as designed, combined with mortality, harvest and unknown environmental factors, has not been sufficient to establish the desired level of natural reproduction.

Hatchery-reared lake trout should be stocked in accordance with an annual stocking program developed cooperatively among fishery management agencies. Further, to increase the effectiveness of the stocking program, the Commission recommends that- a periodic review and analysis should be undertaken of the genetic constitution of hatchery broodstock, of behaviorial characteristics of their progeny and of stocking techniques and strategies. The commission has concluded that efforts to determine those factors which limit natural reproduction would continue to receive special research emphasis.

The Commission has determined that, to attain the stated objective of' . self-sustaining populations of lake trout, exploitation must be effectively controlled so that an adequate spawning stock is assured. The Commission acknowledges that allocation of the harvest among users is the responsibility of the agencies which have regulatory authority. The Commission urges that these agencies develop mutually acceptable allocation criteria; that when projecting allowable catches, including incidental captures, they ensure reasonable escapement (or set-aside) of mature fish; and that they develop and conduct the monitoring programs necessary for meeting these objectives.

Epilogue

The Great Lakes Fishery Commission holds an official position on lake trout rehabilitation (Appendix VII) based on Article IV(A) of the Binational Convention on Great Lakes Fisheries (Great Lakes Fishery Commission 1956). It provides measures for ensuring continued yields of lake trout and other desirable species based on the "foundations of self-sustaining stocks". Habitat suitability would be a major determinant in the provision of continuing natural reproduction which in turn, would ensure sustained yields for the future.

Recently, participating agencies of the Great Lakes Fishery Commission through the Lake Committee structure, are collaborating in the preparation of lake trout rehabilitation plans for each of the Great Lakes (e.g. Schneider et al. 1983). Concurrently, within the International Joint Commission and as established by the 1978 Great Lakes Water Quality Agreement, a Task Force for each of the Great Lakes is identifying areas of environmental concern and drafting plans for a strategy for allaying environmental impacts relating to water quality and perturbed physical structure.

It would be most appropriate if these individual initiatives of the two binational Commissions could be interwoven to achieve a common goal - the provision of a high quality environment and the rehabilitation of organisms adapted to such an environment. Our major thesis within this document, of assessing stresses and hence environmental deterioration through the relative well-being of native species, provides a powerful and timely solution to the stated goals of both Commissions.