PROCEEDINGS OF A WORKSHOP ON THE DYNAMICS OF LAKE WHITEFISH (*COREGONUS CLUPEAFORMIS*) AND THE AMPHIPOD *DIPOREIA* SPP. IN THE GREAT LAKES

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PROCEEDINGS OF A WORKSHOP ON THE DYNAMICS OF LAKE WHITEFISH (*COREGONUS CLUPEAFORMIS*) AND THE AMPHIPOD *DIPOREIA* SPP. IN THE GREAT LAKES

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Editor's Note

Each paper in this volume referencing the amphipod *Diporeia* spp. states that diporeia will be used as a common name following its first usage, which gives the Latin name. This convention was intended to create a more-parallel usage of names between the two key players in these papers: lake whitefish *Coregonus clupeaformis*, which has an accepted common name, and diporeia, which doesn't. Diporeia is a recently evolved species complex lacking, in addition to a common name, a formal taxonomic description (see Can. J. Fish. Aquat. Sci. 46: 1714-1725). The use of *Diporeia* without the spp. was considered and rejected because this construction, although not uncommon in journals, is incorrect unless referring to the genus itself (CBE Manual for Authors, Editors, and Publishers, Sixth Edition). Readers are asked to bear with this ad hoc convention of a faunal name.

Randy L. Eshenroder, January 25, 2005

Lake Whitefish and *Diporeia* spp. in the Great Lakes: An Overview

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Abstract

Because of growing concern in the Great Lakes over declines in abundance and growth of lake whitefish (*Coregonus clupeaformis*) and declines in abundance of the benthic amphipod *Diporeia* spp., a workshop was held to examine past and current trends, to explore trophic links, and to discuss the latest research results and needs. The workshop was divided into sessions on the status of populations in each of the lakes, bioenergetics and trophic dynamics, and exploitation and management. Abundance, growth, and condition of whitefish populations in Lakes Superior and Erie are stable and within the range of historical means, but these variables are declining in Lakes Michigan and Ontario and parts of Lake Huron. The loss of *Diporeia* spp., a major food item of whitefish, has been a factor in observed declines, particularly in Lake Ontario, but density-dependent factors also likely played a role in Lakes Michigan and Huron. The loss of *Diporeia* spp. is temporally linked to the introduction and proliferation of dreissenid mussels, but a direct cause for the negative response of *Diporeia* spp. has not been established. Given changes in whitefish populations, age-structured models need to be re-evaluated. Other whitefish research needs to include a better understanding of what environmental conditions lead to strong year-classes, improved aging techniques, and better information on individual population (stock) structure. Further collaborations between assessment biologists and researchers studying the lower food web would enhance an understanding of links between trophic levels.

Introduction

As one of the most valued commercial species in the Great Lakes, lake whitefish (*Coregonus clupeaformis*, hereafter, whitefish) have long been monitored for changes in population status. Timely evaluations of trends and an understanding of factors that influence population stability are key elements in effective management of this important species. Over the past century, whitefish populations have fluctuated over a broad scale in all the lakes except Lake Superior. This species comprised a major portion of the commercial-fishery harvest in the Great Lakes until about the 1940s when their numbers began to decline. By the 1960s and early 1970s, whitefish populations were at all-time lows. Subsequently, populations began to recover, and above-average harvests were recorded in Lakes Michigan and Huron in the 1980s and 1990s. These wide population fluctuations have been attributed to various factors, depending upon the particular lake. Among the more significant factors attributed to causing declines were overexploitation, predation by and competition with invasive species (i.e., sea lamprey (*Petromyzon marinus*), rainbow smelt (*Osmerus mordax*), and alewife (*Alosa pseudoharengus*)), and degradation of water quality and habitat. These negative factors were addressed in both specific and general contexts by lake-management agencies, and the resulting recovery of whitefish populations beginning in the 1970s is considered a true success story (Ebener 1997).

From an ecosystem perspective, coregonines, in general, and whitefish, in particular, are key components of the benthic food web of the Laurentian Great Lakes. Whitefish are mainly benthivores and feed preferentially on the benthic amphipod *Diporeia* spp. (hereafter diporeia as a common name). Diporeia is the dominant component of benthic biomass and production in the colder, offshore regions of the Great Lakes (Cook and Johnson 1974). Both whitefish and diporeia are native to the Great Lakes and provide an excellent example of an evolved, efficient trophic pathway that maximizes energy flow from the lower to the upper food webs. Diporeia lives in the upper few centimeters of sediment and feeds on organic material (mostly diatoms) freshly settled from the water column. Energy fixed as primary production is thus effectively cycled through diporeia and into whitefish populations, which then serve as a harvested resource.

Recent evidence from several of the Great Lakes indicates that populations of both whitefish and diporeia are undergoing drastic changes. For instance, decreased growth and condition of whitefish have been reported in regions of Lake Michigan (Pothoven et al. 2001), and decreased abundance, growth, and condition have occurred in Lake Ontario (Hoyle et al. 1999). Similarly, populations of diporeia have declined in all the lakes except Lake Superior, and large areas are now completely devoid of this organism (Dermott and Kerec 1997; Nalepa et al. 1998; Lozano et al. 2001). Changes in whitefish and diporeia appear to coincide temporally; decreases in whitefish growth and condition in Lakes Michigan and Ontario were first observed soon after the loss of diporeia. A working hypothesis connects declines in whitefish populations to the loss of diporeia as a primary food source. Diporeia is rich in lipids and high in calories. With the loss of diporeia, whitefish have been forced to alter forage patterns and feed on benthic organisms that are of lower nutritional value, are less abundant, or are not as readily available (Pothoven et al. 2001). Besides the loss of diporeia, other direct or confounding factors that may also be contributing to the decline in whitefish growth and condition include density-dependent mechanisms, parasitism, climate/temperature changes, and/or food-web shifts other than those related to diporeia. Diporeia population declines coincided with the introduction and spread of the zebra mussel (*Dreissena polymorpha*) and the quagga mussel (*D. bugensis*). A decrease in available food as related to mussel filtering activities is suspected as a causative factor for the observed declines. This food-limitation hypothesis, however, is spatially inconsistent. Declines occur in lake areas with few or no mussels and where food is seemingly still available (Dermott 2001; Nalepa et al. 2003).

To address the many issues related to population trends in whitefish and diporeia, the Lake Whitefish-*Diporeia* Workshop was held in Ann Arbor, Michigan, in February 2002. The primary goals of the workshop were to compare and contrast trends in each of the Great Lakes so that emerging patterns might be better identified, to provide updates on recent research regarding both organisms, and to foster partnerships to address priority research. The workshop was sponsored by the Great Lakes Fishery Commission and included participants from academia; the commercial fishery industry; and federal, provincial, tribal, and state agencies. The workshop began with a keynote presentation on phenotypic differentiation in whitefish populations in response to environmental influences, such as habitat type and prey availability (Bernatchez 2005). Next in order were presentations on population status in each of the lakes, bioenergetics and trophic dynamics, and exploitation and management. Moderated discussions were held at the end of each session, and a final session focused on research, assessment, and management needs. The purpose of this overview is to summarize highlights of the presentations, ensuing discussions, and written proceedings.

Status of Populations

Historical summaries of trends in whitefish populations were presented for each of the Great Lakes. Although trends prior to recoveries, which began in the 1960s to the 1980s, were generally similar in each lake, the relative importance of influencing factors and the role of cumulative effects varied. For all lakes, the most frequently mentioned factors leading to population declines in the 1950s and 1960s were sea lamprey predation and overexploitation by the fishery. An additional factor (except in Lake Superior) was predation/competition by introduced planktivores, such as rainbow smelt and alewife. In Lake Erie, cultural eutrophication also played a significant role by causing oxygen depletion in the central basin, which limited whitefish summer habitat (Cook et al. 2005). The timing of the recovery in the upper lakes in the 1970s and in the lower lakes in the 1980s seems to confirm generalizations regarding specific causes. Control of the sea lamprey, better management of the commercial fishery, introduction of salmonids (suppression of exotic planktivores), recovery of walleye (*Stizostedion vitreum*), and phosphorus abatement were all factors contributing to the recovery (see the individual papers on the status of whitefish populations in this issue).

What are whitefish population trends in each of the lakes since the recovery? In Lake Superior, trends in catch-per-unit-effort (CPUE) in the late 1990s were, notwithstanding variation among the various management zones, similar to those in the 1980s (Ebener et al. 2005). Spatial patterns in growth and condition were often inconsistent with expectations of CPUE-derived abundance estimates, but temporal trends in both of these traits in the 1990s were consistent with historical values. Population trends in Lake Erie are difficult to interpret because of great differences in habitat within each of the lake’s three basins and the movement of fish between basins (Cook et al. 2005). Most of the commercial catch occurs in the western and central basins (52% and 47%, respectively). Catch rates in the eastern basin are low and have declined recently, but catch rates in the central basin have increased. For Lake Erie as a whole, growth and condition have remained stable, and current values are within the range of historical means. In Lake Michigan, despite varying trends in catch and effort related to different types of fishing gear, overall CPUE increased from the early 1980s and peaked in the mid-1990s (Schneeberger et al. 2005). Decreases in growth and condition were noted over the same time period. For example, between the early and late 1990s, length-at-age declined by 4-7%, weight-at-age declined by 36-47%, and condition declined by 34-60%. Declines in growth and condition were also observed in some regions of Lake Huron (Mohr and Ebener 2005). In the main basin, North Channel, and Georgian Bay, yield and CPUE increased steadily from the late 1970s through the late 1990s. Since the early 1980s, declines in growth and condition were observed throughout the main basin but were most pronounced in southern waters. Abundance in the main basin appears to have peaked in the mid-1990s and has since declined. In contrast, abundance, growth, and condition in the North Channel and Georgian Bay have remained stable in recent years. Considering all the lakes, the greatest changes have occurred in Lake Ontario. Commercial harvest in this lake increased steadily since the mid-1980s, reached a peak in the mid-1990s, but has since declined by 66% (Hoyle 2005). In addition, condition, age-at-maturity, and reproductive success all declined after the mid-1990s. Most important, these typical density-dependent attributes continued to decrease or remained low even as population abundance declined.

The status of whitefish populations in two lakes outside the Great Lakes region (Lake Nipigon and Lake Winnipeg) was examined to provide a broader perspective. The commercial harvest in Lake Nipigon has remained remarkably stable over the past 70 years (R. Salmon, Ontario Ministry of Natural Resources, P. O. Box 970, Nipigon, ON P0T 2J0, unpubl. presentation). Age-at-maturity and mean annual harvest (7700 kg; range 2,100 to 10,500 kg per yr) have been consistent over the entire period. In Lake Winnipeg, whitefish CPUE and abundance have been declining since the early 1980s (W. Lysack, Manitoba Department of Natural Resources, Fisheries Branch, 200 Saulteaux Crescent, Winnipeg, MB R3J 3W3, unpubl. presentation). Based on a long-term data set of environmental parameters, these declines were probably related to increased eutrophication. Total carbon and chlorophyll in the water column have increased significantly since the early 1980s, and recent increases in blue-green algal blooms have been documented. Diporeia have also declined in Lake Winnipeg. Because dreissenids are not present in this lake, the decline is likely related to habitat deterioration or to predation by an increasing smelt population.

Discussions following the session on the status of populations focused on two topics: variations in growth rates and changes in spatial distributions. Because of obvious implications for recruitment, variations in whitefish growth rates among the lakes were of interest. Growth rates in Lakes Michigan and Huron were generally lower after the recovery (1980s and later) than before populations reached all-time lows (1950s and 1960s). Overfishing and intensive sea lamprey predation led to low abundances and may have selected slower growing fish that now comprise populations. In contrast, whitefish growth rates in Lake Erie after the recovery appear to be similar to rates prior to the period when populations reached all-time lows. High mortality at early-life stages led to population lows in Lake Erie and was likely associated with eutrophication, which is not thought to cause size-selective mortality.

Discussions on recent changes in spatial distribution patterns focused on why whitefish are now found in deeper waters during summer in Lakes Michigan, Huron, and Ontario. Hypotheses that account for these changes include increased surface-water temperatures associated with climate warming, increased light penetration due to dreissenid filtering, and/or the loss of diporeia. Distributions in fall have also changed. In Lake Ontario, whitefish appear to move into shallower water (5-10 m) and stay there much longer than in the past.

Bioenergetics and Trophic Dynamics

The session on bioenergetics and trophic dynamics included presentations on the status of diporeia populations in the Great Lakes, efforts to define potential causes for their decline, documentation of changes in whitefish diets, and implications of these changes for bioenergetics and food-web models. The most recent data on diporeia populations in Lakes Michigan, Ontario, and Huron show that densities have continued to decline and that the areas completely devoid of diporeia are expanding (Lozano and Scharold 2005; Nalepa et al. 2005). The time from initial decline to the near total loss of diporeia populations ranged from 6 months to 4-6 years. Although the diporeia population declines in the three lakes coincided with the introduction and spread of zebra and/or quagga mussels, the exact cause is not clear. Peculiarities of amphipod life-history traits and population trends, life-history traits, and population trends in closely related species (Nalepa et al. 2005) were examined for clues to the losses in the Great Lakes. Besides food limitation, other possible causes were pathogens, oxygen deprivation, fish predation, and contaminants. The role of dreissenids as the cause was examined in a series of laboratory experiments (Dermott et al. 2005). In these studies, diporeia mortality was significantly higher in sediments from areas where mussel densities were high and diporeia were no longer found (eastern Lake Erie and western Lake Ontario), as compared to sediments from an area with no mussels and diporeia still present (Lake Superior). The Bay of Quinte, Lake Ontario, however, was an anomaly in that there was no mortality in sediments from an area where mussels were not present and diporeia were no longer found. Biodeposits from dreissenids induced only slight mortality in these studies.

Although the exact reason for the negative response of diporeia to dreissenids may never be fully understood, low densities are having a major impact on whitefish feeding. In nearshore areas of Lake Michigan where diporeia are no longer present, whitefish fed mostly on zebra mussels, gastropods, and chironomids, and whitefish fed in offshore areas on *Mysis relicta* (Pothoven 2005). Prior to their population decline, diporeia were clearly the preferred food of whitefish—the proportion of diporeia in the diet in various areas of the lake was directly related to diporeia abundance in those same areas. After the loss of diporeia from shallow areas (<60 m) in Lake Ontario, whitefish fed on quagga mussels, sphaeriids, and *Mysis relicta* (Owens et al. 2005). Whitefish abundance and condition declined sharply with this shift in prey species, likely because these items have lower nutritional value than diporeia. Also, the mean depth of capture in Lake Ontario increased from 30 m to 80 m, probably because whitefish were forced to forage in deeper waters. As noted previously, whitefish condition and growth rates in Lake Erie remain high (Cook et al. 2005). These fish fed mostly on chironomids, which are abundant in the lake's central and western basins.

Because of changes in whitefish feeding and in spatial distributions, general bioenergetic models developed for coregonines need to be re-evaluated. When a coregonine model was applied to size-at-age data for whitefish from northern Lake Michigan, it underestimated growth efficiencies when compared to efficiencies for another Lake Michigan coregonine—bloater *(Coregonus hoyi*)—and when compared to efficiencies for whitefish from inland lakes (Madenjian et al. 2005). Inserting a more realistic submodel for swimming speed gave more realistic results, but the simulation demonstrated the need for a thorough evaluation of coregonine models because of recent population changes. Three whitefish bioenergetic models (Wisconsin, Net Growth Efficiency, von Bertalanffy Growth) were compared to a contaminant (mercury) model for fish from Canadian inland lakes (M. Trudel, Department of Fisheries and Oceans, Pacific Biological Station, 3190 Hammond Bay Road, Nanaimo, BC V9R 5K6, unpubl. presentation). Consumption rates relative to growth and metabolism varied for each of the models, and assumptions for each model were discussed.

Because whitefish and diporeia are integral components of the food web in Lake Michigan, their changing roles were assessed using network analysis (D. Mason, Great Lakes Environmental Research Laboratory, NOAA, 2205 Commonwealth Blvd., Ann Arbor, MI, 48103, unpubl. presentation). Weighted energy flows through the system were constructed for conditions before and after the zebra mussel invasion. Preliminary output suggested that, although diporeia was once one of the most important organisms for transferring energy upward in the food web, it has been replaced in importance by dreissenids. More energy is now lost to upper trophic levels because feeding on dreissenids has higher metabolic costs than feeding on diporeia. Consequently, the capacity of the system to support upper trophic levels has been reduced. Among the various fishes examined in the network analysis, whitefish demonstrated the greatest energetic loss when diporeia populations declined, even though other species such as slimy sculpin (*Cottus cognatus*) were more dependent upon diporeia to meet metabolic needs prior to the decline. Because diporeia are higher in lipids than most other potential prey items, the ecological consequences of diminished numbers of diporeia are greater than simple declines in trophic efficiency expressed in mass. A 53% decline in lipid content of Lake Michigan whitefish occurring from 1983-1993 to 1996-1999 was attributed to the loss of diporeia (G.M. Wright, Nunns Creek Fishery Enhancement Facility, Chippewa/Ottawa Resource Authority, Hessel, MI, 49745, unpubl.

presentation). Low lipid levels in whitefish may depress their growth, condition, and reproduction.

Discussions following the bioenergetics and trophic-dynamics session focused on reasons for the declines in diporeia and on the extent that declines have led to reductions in whitefish growth and condition. One viewpoint (D. Honeyfield, U.S. Geological Survey, Northern Appalachian Research Laboratory, Wellsboro, PA, 16901, pers. commun.) held that ecological changes resulting from invasive species, phosphorus control, and contaminants may have led to changes in the availability of essential nutrients, thereby affecting whitefish and diporeia through food-web links. The connection between thiamine deficiency and early mortality syndrome in salmonids was offered as an example of the effects of nutrient limitation promulgated through the food web. Thiamine deficiency is caused mainly by the thiaminase carried in alewife, other clupeids, and rainbow smelt. When adult female salmonids feed on alewives, thiamine is catabolized, creating a deficiency leading ultimately to mortality in their progeny. In an analogous manner, reductions in polyunsaturated fatty acids (PUFAs) available to whitefish from diporeia can be viewed as a nutrient impairment. Because of increased light penetration resulting from dreissenid filtering, phytoplankton are exposed to higher levels of ultraviolet radiation. Under such conditions, phytoplankton decrease their production of PUFAs and levels may now be below critical thresholds for diporeia. Essential nutrients like PUFAs cannot be manufactured by higher organisms but are essential for their growth and development.

Are declines in growth and condition of whitefish a function of high population density or a result of the loss of diporeia? This question has strong implications for management. If the high-density explanation is correct, it could be argued that exploitation rates can be increased with no long-term harm to the population. Temporal trends in Lake Ontario, however, are compelling and suggest that declines in whitefish growth and condition are a result of the loss of diporeia (Hoyle 2005; Owens et al. 2005). In contrast, in Lake Michigan, the loss of diporeia occurred in the mid-1990s when whitefish populations were at record highs (Schneeberger et al. 2005). Thus, both high density and the loss of diporeia may have contributed to observed declines in whitefish growth and condition after the mid-1990s. Further, the condition of several Lake Michigan populations declined in the 1980s, prior to the loss of diporeia. Whitefish growth and condition in Lake Huron appear to be partly density-dependent. Both parameters began to decline in the 1980s, a time prior to the invasion of dreissenids and the loss of diporeia when abundance was increasing (Mohr and Ebener 2005). Even so, reductions in growth and condition in the late 1990s were most severe in southern waters where diporeia are no longer present. Based on the evidence, declines in whitefish growth and condition in both Lakes Michigan and Huron were most likely, at least initially, a function of high population densities. The loss of diporeia in both lakes is likely limiting recovery and contributing to further declines.

The decline of diporeia populations in the Great Lakes appears to be intimately associated with the introduction and proliferation of dreissenids. Thus, the continued presence and even increase in diporeia numbers in some inland lakes with dreissenids (e.g. Cayuga Lake, New York) is enigmatic (Dermott et al. 2005). Because the extirpation of diporeia can be gradual—occurring over a 5- to 6-year period—inland-lake populations need to be monitored for extended time periods.

Exploitation and Management

The session on exploitation and management examined phenotypic divergence in whitefish populations and its relevance to management; life-history characteristics of exploited vs. unexploited populations; and the development, improvement, and application of stock-assessment models. Whitefish populations can undergo rapid phenotypic divergence and reproductive isolation in response to environmental changes (Bernatchez 2005). This process, known as adaptive radiation, is relevant to current food-web changes in the Great Lakes. With a loss of benthic prey, selection would favor stocks with higher numbers of gill rakers and, thus, a better adaptation to pelagic feeding. Such populations, however, tend to be smaller bodied for a given age, younger at maturity, and have a shorter life span than populations found in benthic habitat (Bernatchez 2005). New evidence based on fin-ray aging rather than scale aging indicated that unexploited populations have slower growth, higher annual survival, and greater longevity than previously believed (Mills et al. 2005). Unexploited populations are, thus, well suited to survive periods of poor recruitment.

Comparisons of variations in life-history traits (growth, maturity, and natural mortality) of whitefish from the Great Lakes and from inland lakes showed that populations with higher growth rates matured at younger ages (K. Beauchamp, University of Toronto, Biology Department, 3359 Mississauga Road North, Mississauga, ON L5L 1C6, unpubl. presentation). Great Lakes whitefish matured at a younger age, grew faster, and achieved larger asymptotic sizes than inland-lake fish, probably due to the greater availability of prey in the Great Lakes. An age-structured model based on Georgian Bay whitefish predicted that maximum sustainable yield occurred at a mortality rate of 0.10 to 0.15 (B. Henderson, University of Toronto, Biology Department, 3359 Mississauga Road North, Mississauga, ON L5L 1C6, unpubl. presentation). At higher rates, the probability of sustaining a harvest declined dramatically and harvest became more variable. Ebener et al. (2005) summarized the development and application of catch-at-age models for whitefish in the 2000 Consent Decree waters of Lakes Superior, Michigan, and Huron. Predicted harvest limits for each management unit were based on modeled abundance and mortality and on target mortality schedules.

Discussion following the exploitation and management session addressed limitations of age-structured models and factors that may affect harvest predictions. Whitefish are managed on a population-by-population basis, and, although some life-history information for individual populations is available, a lack of understanding of stock delineation and spatial distribution patterns are major limitations. Further, some areas have mixed stocks where the development and application of multiple-population models would improve predictive consistency. Life-history information has been useful in model development, but multiple-population models are needed to develop uniform harvest policy. The bias in model outputs resulting from inaccurate aging methods is also a great concern.

Future Needs: Research, Assessment, Management

If current declines in whitefish abundance, growth, and condition are mainly a result of food-web disruptions related to invasive species, particularly dreissenids, then little can be done as long as these invasives remain abundant. Emphasis should be placed on research that enhances current management strategies. Among the most critical needs is a thorough evaluation of models and associated parameters. At the very least, parameters need to be prioritized relative to the extent they can improve management decision making. One high research priority is an understanding of natural mortality in whitefish. In particular, mortality in the first few years of life has not been adequately measured. In the upper Great Lakes, pre-recruit indices do not accurately predict recruitment. Environmental conditions that favor survival of young fish need to be identified along with conditions that favor strong year-classes, which are so vital to yields. Aging techniques also need to be improved. Because even minor misinterpretations of age structure apparently can lead to significant errors in model output, the sensitivity of catch-at-age models to aging errors needs to be examined more thoroughly.

Estimating reasonable harvest levels is currently limited by the unpredictability and rapidity by which conditions can change, making model projections inaccurate. The rather sudden loss of diporeia and its impact on whitefish growth and condition are prime examples. Future models need to be flexible and structured so that new contingencies can be readily accommodated.

Life-history attributes and environmental requirements of individual whitefish populations vary and need to be better defined. Such variability has long-term implications to management in ensuring that overfishing does not occur. A better definition of individual populations would enhance our understanding of risks associated with managing mixed-stock populations.

Although the decline of diporeia in the Great Lakes is well documented, more effort is needed to define its cause. If a causative factor can be identified, the risk of further declines can be better assessed, and the probability of recovery can be determined. Examining population trends of diporeia and dreissenids in lakes outside the Great Lakes may prove useful. Preliminary data suggest that diporeia and dreissenids co-exist in some areas. Further, knowing the cause would help define risks to other organisms that serve as alternative food for whitefish, such as *Mysis relicta.*

Finally, changes in populations of whitefish and diporeia are likely symptomatic of broader, more-extensive changes in the Great Lakes food web. Long-term data sets are needed in targeted areas to better define linkages between lower and upper tropic levels. These data can then be used to reassess energy pathways and validate new food-web models. Data collection and application can be enhanced by establishing collaborations between assessment biologists and the researchers studying lower trophic levels.

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On the Role of Natural Selection in Promoting Population Divergence in Lake Whitefish *(Coregonus clupeaformis):* Relevance for Population Management in the Great Lakes

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Abstract

In this paper, I summarize the basis for the ecological theory of adaptive radiation and illustrate how the processes implied by the theory have contributed to our understanding of population differentiation and reproductive isolation in the whitefish (*Coregonus* spp.) species complex. Finally, I discuss the relevance of acquiring such fundamental knowledge for improving the management of exploited populations. There is now sufficient information to support the hypothesis that phenotypic and ecological divergence of whitefish populations and their reproductive isolation has been driven by divergent natural selection. More specifically, the available data indicate that phenotypic differentiation and reproductive isolation between whitefish populations are caused directly by the environments they inhabit and the resources they consume. Consequently, the recent changes in the trophic environment of the Great Lakes could result in a rapid (over a few generations) evolutionary response in whitefish populations. Therefore, management of exploited whitefish populations in the Great Lakes would benefit from a better integration of fundamental concepts from the ecological theory of adaptive radiation with applied

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fisheries research. To accomplish this integration, a more comprehensive knowledge of the extent of genetic and phenotypic population structuring and differentiation and the geographic distribution of genetically distinct populations is required. A long-term population-monitoring program would also allow for a better understanding of the crucial links between changes in prey diversity and abundance and the associated evolutionary responses of whitefish populations in the Great Lakes.

Introduction

Elucidating the causes of population divergence and species diversity is a central issue in evolutionary biology. The importance of understanding evolutionary processes in conservation biology is also increasingly acknowledged (Rosenweig 2001). Progress in this field will be best achieved if studies are designed and conducted within a strong, predictive, theoretical framework. Perhaps the most comprehensive concept available to evolutionary biologists is the ecological theory of adaptive radiation. The theory holds that adaptive radiation, including both phenotypic divergence and speciation, is the outcome of divergent natural selection stemming from both environmental and resource heterogeneity and competitive interaction. Schluter (2000) has recently re-evaluated and extended this theory—making it an important theory of evolution. Members of the north-temperate freshwater-fish fauna share several attributes that corroborate the predicted effects of post-glacial ecological opportunity. This corroboration makes these members good candidates for testing the theory of adaptive radiation. Of particular interest is the occurrence of both sympatric and parapatric forms in salmonid fishes, which also occur in phylogenetically remote families (Taylor 1999). These forms share similarities in morphological, behavioral, and life-history variation, which suggests that their divergence has been partly driven by the same selective processes. Molecular genetic studies have confirmed the recent, post-glacial origin (10,000-15,000 years BP) of the forms' phenotypic divergence and revealed that genetic exchange is still occurring among most, if not all, sympatric and parapatric forms (Taylor 1999). These observations indicate that the process of reproductive isolation has been initiated but is not complete in most examples.

In this paper, I first summarize the basis of the theory of adaptive radiation, as updated by Schluter (2000). I then illustrate how the application of selected methods to evaluate the key processes implied by the theory has contributed to our understanding of population differentiation and reproductive isolation in lake whitefish (*Coregonus clupeaformis)*. Finally, I discuss the relevance of such fundamental knowledge for improving the management of exploited lake whitefish (hereafter, whitefish) populations.

Theoretical Framework of Adaptive Radiation

A major advantage of the concept of adaptive radiation is that it can be explicitly defined. Extending the basic definition of Simpson (1953), Schluter (2000) redefined adaptive radiation as "the evolution of ecological and phenotypic diversity within a rapidly multiplying lineage. It occurs when a single ancestor diverges into a host of species that uses a variety of environments and that differs in morphological or physiological traits used to exploit those environments. The process includes both speciation and phenotypic adaptation to divergent environments."

Steps involved in testing the theory of adaptive radiation all share a common objective, which is to provide evidence that divergent natural selection is the main cause for the accumulation of phenotypic differentiation and reproductive isolation. More specifically, the theory is based on three processes that drive adaptive radiation, and the role of divergent natural selection must be evidenced in each of them.

The first process implies that phenotypic differentiation between populations and species is caused directly by the environments they inhabit and the resources they consume. Thus, each environment subjects a species to unique selection pressures related to the species' particular combination of traits that allow it to efficiently exploit that environment. This process implies that individuals from different lineages experience divergent selection and that intermediate phenotypes are characterized by reduced fitness. The basic theory that underlies this principle was first presented by Simpson (1953) as the concept of selection landscapes.

The second process implies that divergence in phenotype also results from competitive interactions—broadly defined to include ecological opportunity.

Competition may drive sympatric populations or species to either exploit new resources or to utilize new environments where they will become subject to different selective pressures. Ecological opportunity, which can result in a highly reduced potential for interspecific competition for new resources or habitat, can also cause rapid divergence until new available niches are filled. In fact, ecological opportunity has been viewed as the major regulator of the rate and extent of phenotypic differentiation and speciation (Simpson 1953).

The third process is ecological speciation, by which reproductive isolation among lineages develops as a consequence of the first two processes that drive phenotypic divergence. Reproductive isolation within adaptive radiation evolves within the same time frame and results from the same processes that drive phenotypic and ecological divergence.

Divergent natural selection may affect speciation in different ways. Reproductive isolation may develop incidentally between populations that become adapted to occupy distinct habitats or utilize different resources. For instance, post-mating isolation may develop as a consequence of genetic incompatibility between allelic combinations responsible for the expression of differentially adapted phenotypes. Pre-mating isolation may develop if mating preferences are genetically correlated with phenotypic traits under the influence of divergent selection. An example is pre-mating isolation through size-assortative mating if adult body size has been differentially selected between populations. Reproductive isolation may also be favored by selection if intermediate genotypes have reduced fitness. The process is referred to as reinforcement, whereby intermediate genotypes are hybrids between populations that were previously allopatric and that had already developed partial reproductive isolation. Reinforcement also corresponds to sympatric speciation if initiated by disruptive selection within a single population.

Empirical Test of the Theory

First Process: Phenotypic Differentiation between Populations and Species Is Caused Directly by the Environments They Inhabit and the Resources They Consume

To assess the first process, evidence for a fit between the phenotypes of descendant species and their divergent environments must be provided. A statistical assessment of the correlation between genetically based phenotypic differences and the use of different environmental resources by different species is used to depict such a phenotype-environment correlation. For coregonine fishes, the number of gill rakers stands out as a key phenotypic trait for predicting such a correlation. This trait, the number of gill rakers, will be emphasized subsequently. Species or forms with large numbers of gill rakers are associated with the use of zooplankton as the primary food resource. The diets of forms with low numbers of gill rakers are mainly composed of larger prey items.

Focusing on gill-raker numbers is of particular interest because its genetic basis has been clearly demonstrated in coregonine fishes. Svärdson (1979) summarized the results of hybridization experiments that were conducted using two sympatric forms of the whitefish (*C. lavaretus)* from Lake Locknesjön in Sweden. Fig. 1 shows that the mean and variance of gill-raker counts of the pure progeny were very similar to that of their parents. In contrast, the mean number of gill rakers of the hybrid progeny was statistically different from that of either parental source and almost identical to the mean of parental sources. The variance in gill-raker counts of the hybrid progeny was also intermediate between the variance values observed in the parental sources. These observations are indicative of a strong component of additive genetic variance for gill-raker counts.

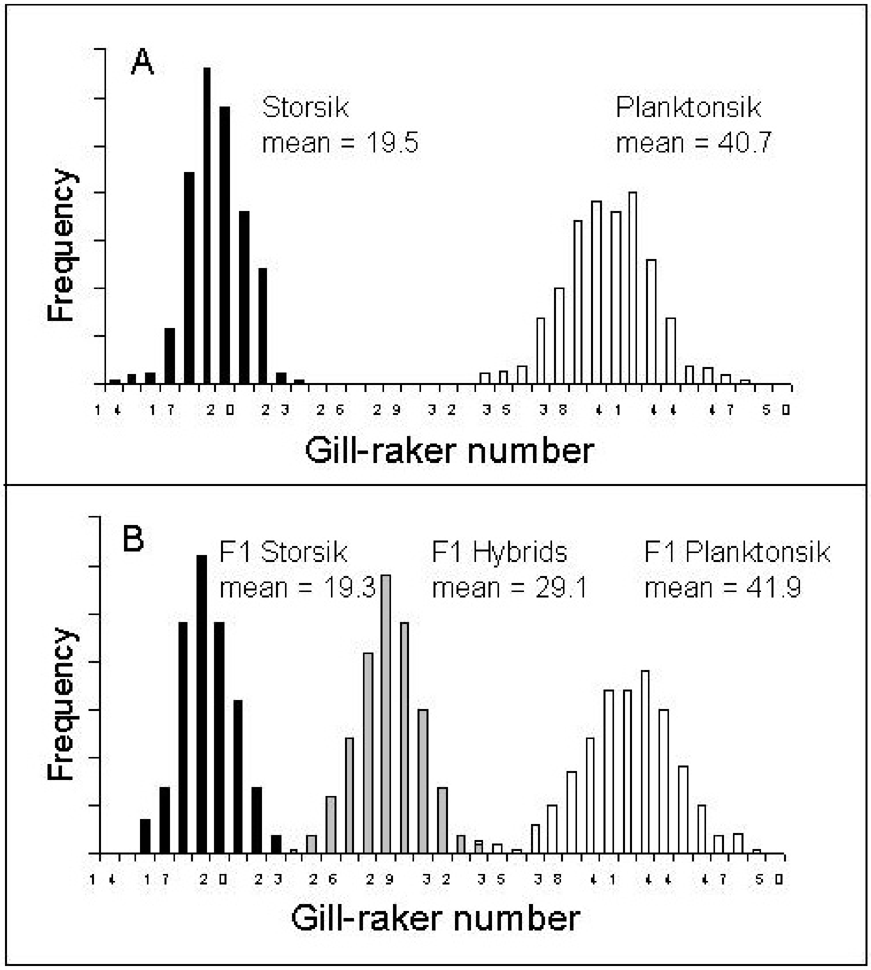

Fig. 1. Frequency distribution of gill-raker numbers for: (A) parental populations and (B) their F1 pure and hybrid progeny for the storsik and planktonsik whitefish forms from Lake Locknesjon, Sweden (Svärdson 1979).

The association between diet and number of gill rakers was assessed in four lakes in the Yukon (North America) for sympatric forms of Squanga whitefish with high numbers of gill rakers (HGR) and low numbers of gill rakers (LGR) (Bodaly 1979). These sympatric forms differ significantly in various morphometric and meristic characters, depending on the lake. The relative volume contribution of zooplankton in the diet was significantly higher in HGR (mean = 0.92, range = 0.79 − 1.0) than in LGR forms (mean = 0.37, range = 0.10 − 0.60) in all lakes. A prey diversity index ($1- \Sigma p_i^2$, where p_i = proportion of either benthic or zooplanktonic prey) also showed that the diet of the HGR form was much more specialized (mean prey diversity index = 0.13, range = 0 − 0.33) than that of the LGR form (mean = 0.40, range = 0.18 − 0.50).

A phenotype-environment correlation was also documented in a comparative analysis of diets of sympatric dwarf and normal forms of whitefish found in several lakes of the St. John River drainage in northern Maine, USA, and southeastern Québec, Canada (Bernatchez et al. 1999). If a phenotype-environment correlation exists, then the extent of trophic-niche differentiation should also vary among lakes and correlate positively with differences in gill-raker counts between forms. Because the difference in gill-raker counts between forms is more pronounced in Cliff Lake (Fig. 2A), the extent of trophic-niche partitioning should also be more pronounced. When estimated for the lakes and over all samples, the weighted importance of zooplanktonic prey was significantly higher in the dwarf form than in the normal form. The extent of overlap in diet, however, was different between the lakes (Fig. 2B). Zoobenthos and prey fishes predominated in the diet of normal adult fish in Cliff Lake at the beginning of the growing season (early June) and at the end of the growing season (late August); zooplankton prey were essentially absent from their diet. In East Lake, the diet of normal adult fish was almost exclusively composed of benthic prey (large zoobenthos including mollusks) in June.

By August, a strong shift was observed with small zoobenthos representing approximately 50% of stomach contents and the other half comprising terrestrial insects and zooplankton. A more pronounced overlap in trophic use was also observed between the dwarf normal form and the juvenile normal form. In Cliff Lake, both groups fed almost exclusively on zooplankton in June; in August, the diet of juvenile normals included, almost exclusively, small and large benthic prey. The result was a low index of trophic-niche overlap (D = 0.390) (Schoener 1970).

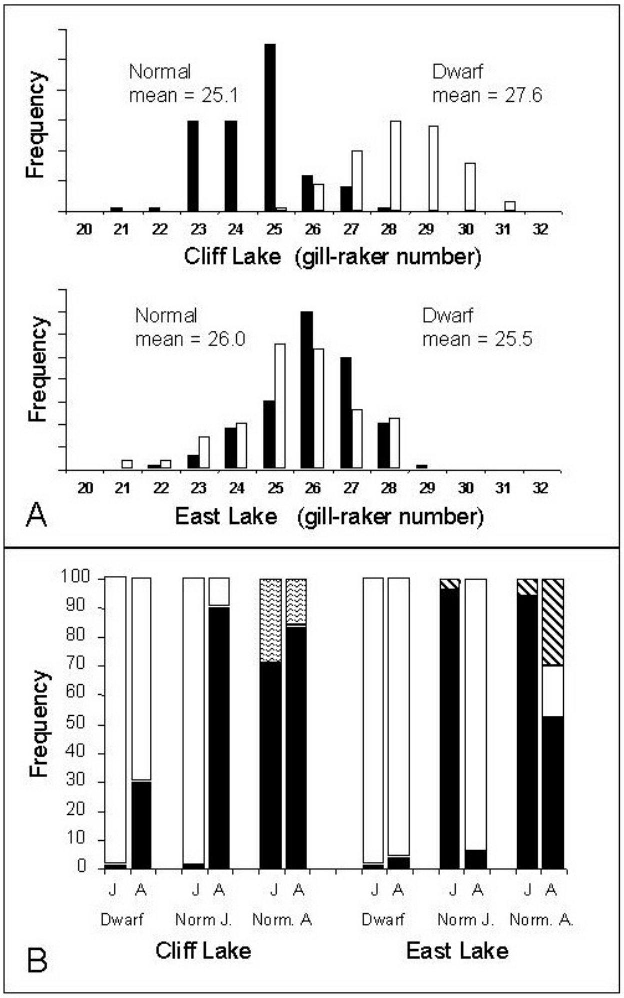

Fig. 2. (A) Frequency distribution of gill-raker numbers between dwarf (white) and normal (black) forms of whitefish from Cliff and East Lakes. (B) Diet composition expressed as the weighted frequency (percent) of prey categories for dwarf and juvenile normal (Norm J.) and adult normal (Norm A.) stages of whitefish in East and Cliff lakes for early June (J) and late August (A). White = zooplankton, black = zoobenthos, waves = terrestrial insects, cross-hatch = fish (Bernatchez et al. 1999).

In East Lake, a shift from benthos to zooplankton was observed in normal juveniles, which resulted in a very high index of trophic-niche overlap (D = 0.968) between the juvenile normal form and dwarf form. This high index indicated that, concomitant with the differential overlap in gill-raker numbers, there is generally more overlap in the diets of dwarf and juvenile forms in East Lake than in Cliff Lake, mainly due to the diet shift at the end of the growing season.

The above results support a phenotype-environment correlation between the number of gill rakers and the diet of whitefish. The next test is to provide evidence that this correlation has been shaped by divergent natural selection. Several approaches can be used. The most appropriate approach for species such as large salmonids is a comparison of population differentiation with neutral expectations (the amount of differentiation expected by mutation and genetic-drift effects only). The Qst method (Spitze 1993) has been applied most frequently and was designed for sets of conspecific populations that became differentiated while potentially exchanging migrants. In principle, the divergence in quantitative traits should be similar to that of allele frequencies at nuclear loci, if they are evolving neutrally and have a quasi-pure additive genetic basis. Under the influence of migration, mutation, and genetic drift, the among-population proportion of total genetic variance in phenotypic traits is expected to equal that of nuclear markers (Lande 1992). As an indirect method for detection of natural selection, the extent of population differentiation in quantitative traits (Qst) can be compared with that quantified at neutral molecular markers (Fst). The prediction is that divergent selection will cause Qst to be larger than expected on the basis of marker variation.

Bernatchez (2004) performed a Qst analysis using data from Lu and Bernatchez (1999), who documented phenotypic variation of 8 meristic and 18 morphometric characters, as well as molecular-genetic differentiation at 6 microsatellite loci among 6 sympatric pairs of dwarf and normal forms of whitefish. Given the evidence for a phenotype-environment association of gill-raker counts with prey types and the fact that such counts discriminate well among coregonine species, the null hypothesis is that Qst estimated from gill-raker counts will not differ significantly from either Fst derived from microsatellites or from Qst values observed for other phenotypic traits.

The analysis contrasted Qst and Fst between dwarf and normal forms from the same lake (*n* = 6 lakes in all) (Fig. 3). Mean Fst and Qst values averaged over all traits and all lakes were very similar and not significantly different. The highest Qst was observed for gill-raker counts that were also the only trait that was significantly higher than Fst, exceeding its mean value by 0.27. Rogers et al. (2002) also quantified the extent of phenotypic and molecular-genetic differentiation between populations of each form raised under the same laboratory conditions, and their conclusions were essentially the same as those of Bernatchez (2004). Together, these results strongly suggest that differences in gill-raker counts between sympatric forms are under the influence of divergent natural selection, whereas the differentiation at other traits results mainly from genetic drift. These results also corroborated the prediction that selection should primarily promote differentiation at trophic-related traits (Bernatchez 2004).

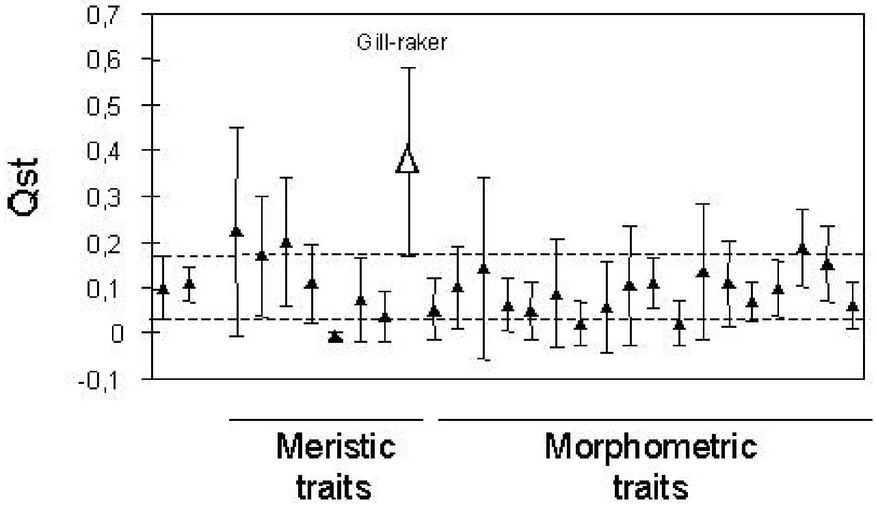

Fig. 3. Comparison of Fst and Qst values (with their 95% CI) for meristic and morphometric traits of dwarf and normal forms of whitefish from the same lake (six lakes total). Traits from left to right: (1) mean Fst values derived from microsatellite data, (2) mean Qst value over all traits, (3) scale above the lateral line, (4) suprapelvic scales, (5) lateral line scales, (6) dorsal ray counts, (7) anal ray counts, (8) pectoral ray counts, (9) pelvic ray counts, (10) gill-raker counts, (11) preorbital length, (12) orbital length, (13) post-orbital length, (14) trunk length, (15) dorsal length, (16) lumbar length, (17) anal fin length, (18) caudal peduncle length, (19) maxillary length, (20) mandible length, (21) maxillary width, (22) pectoral length, (23) pelvic length, (24) body depth, (25) head depth, (26) caudal peduncle length, (27) adipose fin length, (28) interorbital width. Horizontal dashed lines delineate 95% CI for Fst measured from molecular markers.

Second Process: Divergence in Phenotype also Results from Competitive Interaction and Ecological Opportunity

The role of interspecific competition in influencing phenotypic divergence is best shown by demonstrating ecological character displacement (Schluter 2001). Support for the role of competition in adaptive radiation has been acquired largely by observation (Schluter 2001). In whitefish, the best evidence comes from the observations of shifts in gill-raker counts in some populations when they are found in sympatry with closely related putative competitors. Lindsey (1981) compared mean gill-raker counts of allopatric populations of whitefish from Yukon lakes where the least cisco (*C. sardinella*), a zooplanktivore with an average of 45 gill rakers, was either present or absent. As predicted by the character-displacement hypothesis, populations of whitefish found in sympatry with the cisco had significantly fewer gill rakers (23.9 ± 0.83) than their conspecifics found in allopatry (26.0 ± 0.74) and were, therefore, phenotypically more divergent from *C. sardinella* than were the allopatric populations (Fig. 4A).

Phenotypic variation in gill-raker numbers within the Acadian lineage of whitefish in northeastern North America provides another example of divergence. This lineage, first identified by a phylogeographic analysis of mitochondrial DNA variation, evolved in geographic isolation from other whitefish lineages over approximately 150,000 years (Bernatchez and Dodson 1991). Allopatric populations of this group, however, are phenotypically indistinguishable from allopatric populations of other glacial lineages, all of which are of the normal phenotype. The St. John River basin is a zone of secondary contact between the Acadian and Atlantic lineages, and the occurrence of dwarf and normal sympatric whitefish pairs in lakes of this basin is typically associated with the occurrence of both lineages (Bernatchez and Dodson 1990; Pigeon et al. 1997).

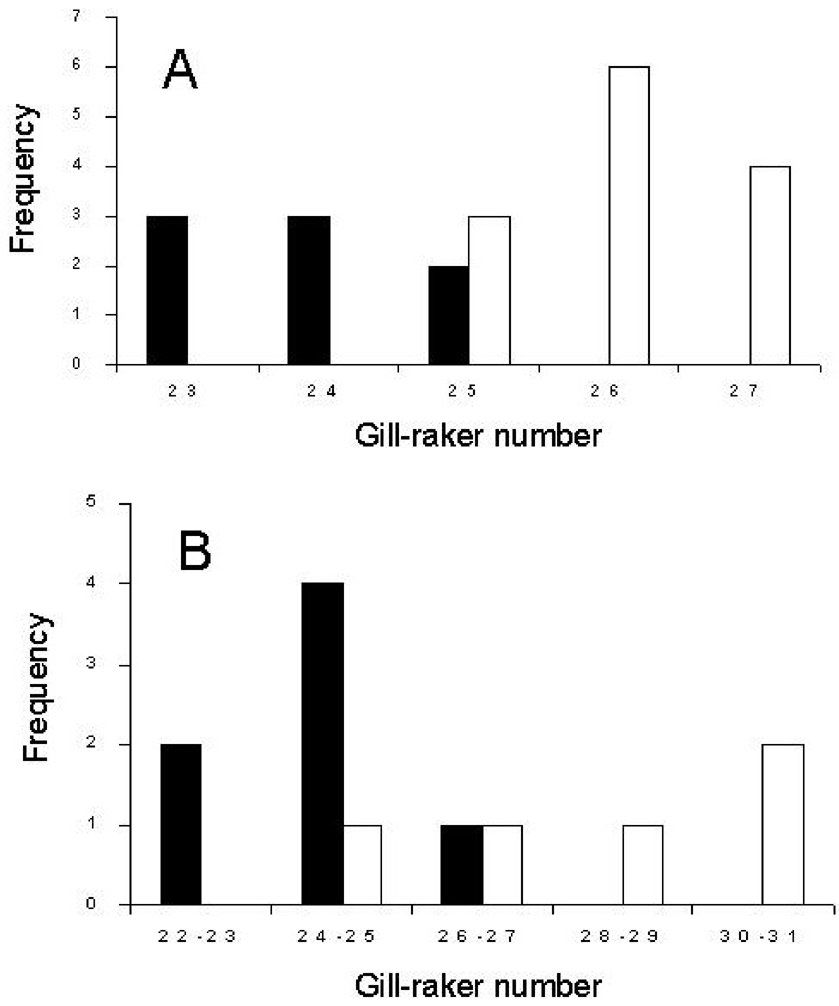

Fig. 4. Frequency distribution of gill-raker numbers between (A) 21 whitefish populations from the Bering Sea drainage found in sympatry with the least cisco (*C. sardinella*) (black) and in allopatry (white) (Lindsey (1981)), and (B) 12 whitefish populations from the Acadian lineage found in sympatry with whitefish from the Atlantic lineage (white) and in allopatry (black) (Edge et al. 1991; Lu and Bernatchez 1999).

Although introgressive hybridization has occurred between lineages, the dwarf populations remained genetically more similar to pure Acadian than to pure Atlantic populations (Lu et al. 2001). This finding indicates that the dwarf phenotype evolved post-glacially from ancestral Acadian populations of the normal phenotype after secondary contact with the Atlantic lineage. Thus, higher gill-raker counts in the planktivorous dwarf whitefish relative to those observed in other populations of pure Acadian origin would support the role of competition in causing character displacement. Lu and Bernatchez (1999) found significantly higher mean gill-raker counts (28.0 ± 2.55) in dwarf populations compared to pure Acadian populations from the Maritime Provinces of Canada studied by Edge et al. (1991) (mean: 24.9 ± 2.48) (Fig. 4B).

Further evidence that competitive interactions influence phenotypic divergence is provided by associating the increased breadth of resource use (or increased variance in correlated phenotypic traits) to situations of ecological opportunity, such as the absence of unrelated competitors. The character displacement theory predicts an increase in variance in traits when a competitor is removed. Increases in variance may be manifested either as polymorphisms within populations or be partitioned among genetically distinct sympatric populations (Robinson and Schluter 2000). Quantitative support for increased phenotypic variance in the absence of competitors is found in northern Québec whitefish (Fig. 5). Doyon et al. (1998) documented variation in size and age-at-maturity among 34 lakes of the La Grande complex where the lake cisco (*C. artedi*) is either present (western region of the basin) or absent (eastern region) (Legendre and Legendre 1984). In lakes where ciscoes were abundant, whitefish populations at sexual maturity were characterized by a unimodal distribution in size (and age), as typically observed in populations of the normal form. In contrast, whitefish populations in lakes where ciscoes were absent showed increased variance in size at sexual maturity and were characterized by the appearance of a second mode at approximately 20 cm. Both the mean and variance differed significantly between the two groups. Although a detailed analysis of morphological variation in fish for most of these lakes has not been completed, a small subsample shows that early maturing fish (dwarf form) comprise populations that are genetically distinct from sympatric late-maturing fish (Bernatchez 1996). These results support the view that the absence of cisco in the St. John River basin created an ecological opportunity that promoted the evolution of the recently derived dwarf whitefish populations as the diets of both forms differ (Doyon et al. 1998).

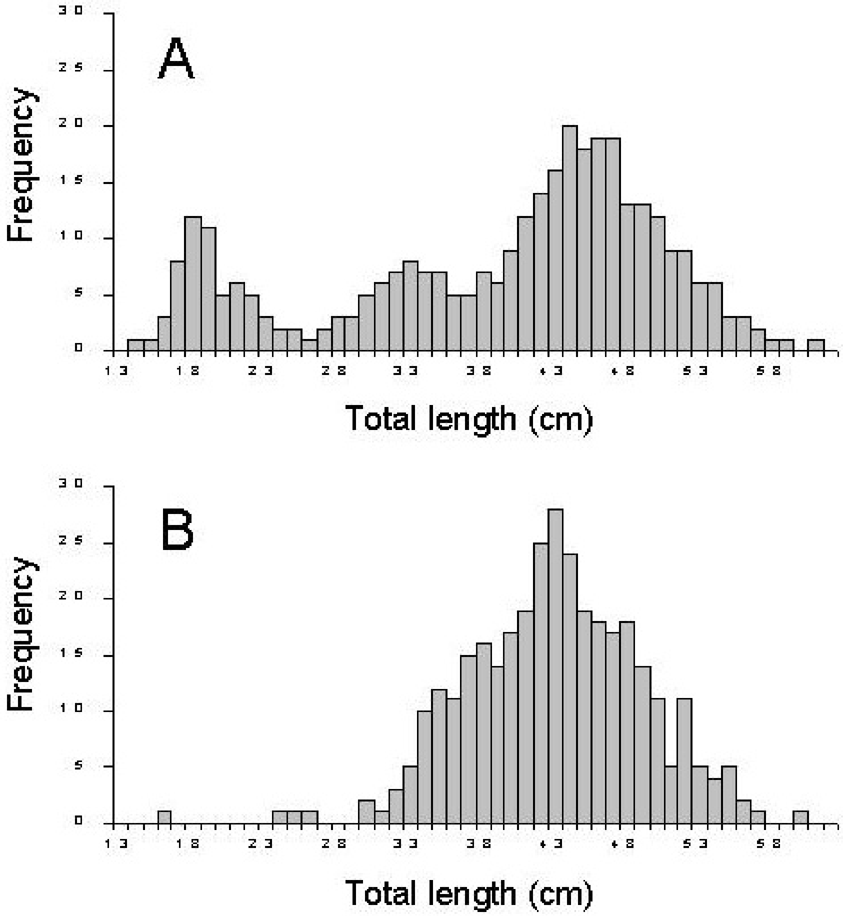

Fig. 5. Length structure of mature whitefish: (A) in the eastern part of the La Grande River drainage where lake ciscoes (*C. artedi*) are abundant (16 water bodies, *n* = 3149), and (B) in the western part of the same drainage where ciscoes are absent (18 water bodies, *n* = 23) (Doyon et al. 1998).

Third Process: Reproductive Isolation Develops as a Consequence of Divergent Natural Selection (Ecological Speciation)

Only a few studies have empirically tested the hypothesis of ecological speciation. The most straightforward test is a comparison of the rates at which reproductive isolation evolves among regions differing in the strength of natural selection (Coyne and Orr 1997). Pleistocene glaciations have had more direct impacts on fish habitats at northern rather than southern latitudes, particularly in North America. Cyclic glacial advances and retreats had two major effects. First, glacial advances were largely responsible apparently for a steep decline in fish species diversity above 50° North (Robinson and Schulter 2000). Second, a very large number of post-glacial lakes were formed following glacial retreats during which access was hampered by the limited duration of dispersal routes (Hocutt and Wiley 1986). For aquatic species that were able to gain early access, these environments offered ecological opportunities that may have promoted phenotypic divergence through divergent natural selection, as inferred by the second process described earlier. In contrast, fish species in nonglaciated regions would have had fewer opportunities because of the presumably greater stability of communities and habitats. Using the hypothesis that this same process has been responsible for the development of reproductive isolation, speciation events at northern latitudes should have occurred in more recent evolutionary times. Under the assumption that smaller divergence estimates reflect more recent speciation events, Bernatchez and Wilson (1998) quantified mitochondrial-DNA sequence divergence between coregonine and non-coregonine sister species as a function of the median latitude of their distribution. A highly significant negative relationship between sister-species divergence and latitude was observed and a stepwise linear-regression model explained 74% of the genetic divergence among species pairs. The breakpoint where the data separated into two linear relationships was at 46° North, which is approximately coincident with the median latitude of maximum Pleistocene glacial advance (44° North) in North America (Fulton and Andrews 1987).

Five coregonine sister-species pairs were included in this meta-analysis. All pairs ranked among the lowest sequence-divergence estimates observed in the study indicating that speciation events among coregonines have been recent, compared to other northern fishes. These results are consistent with the hypothesis that ecological opportunity stemming from depaurate fish diversity in new and favorable habitats has contributed to an elevated rate of speciation in freshwater fishes at northern latitudes, especially in coregonines.

A second test of ecological speciation in coregonine fishes compared the strength of reproductive isolation among population pairs that evolved over the same time period but that differed in the extent of trophic specialization. The hypothesis tested whether differentiation in traits related to niche occupation reflected the intensity of natural selection in different environments (Lu and Bernatchez 1999). The amount of gene flow occurring between sympatric forms should decrease as the strength of their reproductive isolation increases. Thus, the extent of genetic divergence at neutral loci can be used as a surrogate for the amount of reproductive isolation. If ecological processes are important in driving the reproductive isolation of sympatric forms, gene flow should be more restricted between sympatric populations that are more specialized for occupying distinct trophic niches. Lu and Bernatchez (1999) assessed six microsatellite loci and the morphological differentiation between sympatric dwarf and normal whitefish forms from six lakes (Fig. 6). Dwarf and normal forms in each lake differed primarily in traits related to trophic specialization (particularly gill-raker counts), but the extent of differentiation varied among lakes. Genetic divergence between forms within lakes was variable. The extent of gene flow between forms within lakes and their morphological differentiation were negatively correlated ($r = 0.78$, $P = 0.06$). This result is consistent with the prediction of ecological speciation by which the extent of reproductive isolation between sympatric whitefish forms evolved as a consequence of the intensity of local, divergent selection.

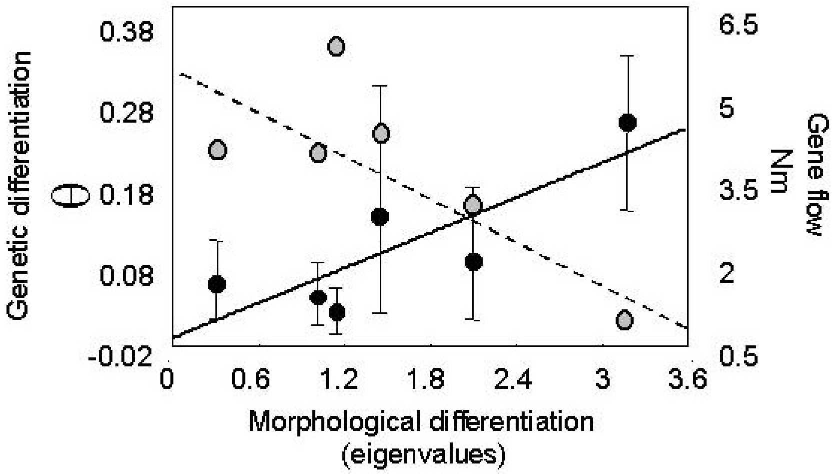

Fig. 6. Relationships between morphological differentiation (eigen values of discriminant function analysis) versus the extent of genetic differentiation (θ estimator of Fst in black) or gene flow (*Nm* values in grey) estimated from the private-allele method between sympatric dwarf and normal forms of lake whitefish. Confidence intervals (means ± 1 SE) are provided for θ values. From left to right, symbols represent East Lake, Témiscouata Lake, Crescent Pond, Webster Lake, Indian Pond, and Cliff Lake, respectively (Lu and Bernatchez 1999).

Concluding Remarks and Relevance for Whitefish Management in the Great Lakes

The state of knowledge on the ecology of adaptive radiation has progressed markedly over the last few decades (Schluter 2000). However, the number of comprehensively documented cases of this process is still relatively small. In this paper, I tried to assess the usefulness of whitefish as a model system from which the theory could be tested more broadly. Although our understanding is still fragmentary, there is now sufficiently detailed information to support the hypothesis that phenotypic and ecological divergence of whitefish populations and their reproductive isolation have been caused by divergent natural selection. More specifically, the available data indicate that phenotypic differentiation and reproductive isolation between populations are caused directly by the environments they inhabit and the resources they consume, as implied by Simpson's (1953) concept of selection landscapes. Under this concept, selection landscapes refer to surfaces that represent phenotypic traits. Fitness corresponds to the height of the surface where features of the environment shape its contours. Populations diverge when they are pulled towards different peaks (optimum phenotypes given the features of the environment) and away from the valleys of reduced fitness. The number of peaks and valleys and their shapes are generated by uneven fitness gains at different positions along gradients associated with the discreteness of environmental features. This framework predicts explicitly that phenotypic and environmental diversity will be correlated due to divergent natural selection that pulls the means of phenotypically distinct populations toward different adaptive peaks. The resulting phenotypic differentiation between populations is, therefore, caused directly by the environment and its trophic resources**.**

Most studies on whitefish have dealt with determining population differentiation between forms found in sympatry in relatively small lakes. These forms differ quite strikingly in morphology, behavior, life history, and genetic composition. In addition, there is no theoretical reason why the processes inferred to explain their divergence should not apply to the understanding of factors driving divergence among less-differentiated populations, such as whitefish "stocks" from the Great Lakes. Recent studies of other salmonids have shown that new phenotype-environment associations caused by divergent natural selection could evolve very rapidly; for example, following recent translocation to a new habitat (Stockwell et al.

2003). The theory predicts that changes in the trophic environment (such as those that have been documented in the Great Lakes following the invasion of zebra mussels (*Dreissena polymorpha*)) could potentially result in a rapid (over a few generations) evolutionary response of whitefish to these perturbations. For example, where the abundance of epibenthic prey (e.g. *Diporeia* spp. (hereafter, diporeia as a common name)) is declining, selection could favor individuals that are prone to exploit alternative and relatively more-abundant resources, such as zooplankton. The theory also predicts that exposure to this new trophic environment could favor the evolution and persistence of phenotypes (because of their higher fitness) that are more efficient at feeding on zooplankton; for example, fish with higher numbers of gill rakers. Such phenotypic changes could also be associated with changes in life-history traits. For example, numerous studies (including some on whitefish) have shown that planktivorous populations within the same species complex often differ strikingly in life-history strategies, with the planktivorous populations generally characterized by slower growth, a younger mean age-at-maturity, and a shorter life span, as compared to more benthic types (Bodaly 1979).

Life-history theory also makes specific predictions as to how trade-offs among growth, survival, and reproduction maximize the fitness of organisms (Roff 1992). Namely, selection will favor early maturation if the reproduction that can be obtained exceeds the reproduction of delayed maturation because of the risks of dying during the delay. Observed differences in age structure between planktivorous and benthic fish populations thus suggest that the probability of survival may be lower for planktivorous fish than for benthic fish. Higher mortality rates could be related to either higher predation pressure (Kahilainen and Lehtonen 2002) or, perhaps more importantly, to higher metabolic rates and reduced bioenergetic-conversion efficiency (defined as growth rate/consumption rate ratio) in planktivorous fish that may prevent them from diverting adequate energy into growth and reproduction at older ages (Trudel et al. 2001). Such changes in life-history traits associated with adaptation to a new environment could have important consequences for the exploitation of whitefish populations; for example, by reducing individual size because of early maturation and its effect on growth and by affecting distribution (for example, changes in depth associated with an increased diet of zooplankton). Of course, the possible effect of such evolutionary changes would be expected to vary geographically throughout the Great Lakes depending on local ecological conditions and alternative prey and/or habitat availability.

Consequently, a better understanding of the extent and geographic scale of whitefish population structure, connectivity, and dispersal would be important.

In summary, management of exploited whitefish populations in the Great Lakes would benefit greatly from a better integration between the concepts of the ecological theory of adaptive radiation and applied research. This approach would necessitate more knowledge about the extent of genetic and phenotypic population structuring and differentiation and the geographic distribution of genetically distinct populations. A long-term population-monitoring program would also allow for a better understanding of the crucial links between changes in prey diversity and the abundance and associated evolutionary responses of whitefish populations in the Great Lakes.

Acknowledgments

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STATUS OF WHITEFISH POPULATIONS

Status of Lake Whitefish (*Coregonus clupeaformis*) in Lake Ontario and the Response to the Disappearance of *Diporeia* spp.

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Abstract

The lake whitefish (*Coregonus clupeaformis*) is a prominent member of the eastern Lake Ontario cold-water benthic fish community. Except for a period of about two decades from the mid-1960s to the mid-1980s, lake whitefish have been the mainstay of the lake's commercial fishery. Lake whitefish stocks collapsed and remained depressed after the mid-1960s due to overexploitation, proliferation of exotic predaceous species (i.e., sea lamprey (*Petromyzon marinus*), rainbow smelt (*Osmerus mordax*), alewife (*Alosa pseudoharengus*), and white perch (*Morone americana*)), and cultural eutrophication. Reduction of these pressures and favorable weather conditions led to a recovery of stocks during the 1980s. The commercial harvest was expanded conservatively through the mid-1990s. Dreissenid mussels invaded eastern Lake Ontario in the early 1990s, and *Diporeia* spp. disappeared from the benthic food web soon thereafter. Lake whitefish stocks responded by showing signs of stress, including a die-off; diet changes; declines in body condition and growth;

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delayed mean age at maturity; very poor reproductive success; changes in seasonal, geographic, and bathymetric distribution; and changes in feeding patterns.

Introduction

The lake whitefish (*Coregonus clupeaformis,* hereafter, whitefish) is a prominent member of Lake Ontario's cold-water benthic fish community. Whitefish provide an important commercial fishery and are the focus of research. Historical commercial-fishery-harvest statistics suggest that the abundance of this species has fluctuated widely due in part to the influence of weather on recruitment (Christie 1963). During the late 1960s and 1970s, whitefish abundance declined to remnant levels due to a variety of stresses including overexploitation, predation by exotics, and eutrophication (Christie 1968; Christie 1972; Hurley and Christie 1977). Whitefish stocks showed a remarkable resurgence during the 1980s following relaxation of these pressures and weather favorable for recruitment (Casselman et al. 1996; Hoyle et al. 2003). A conservative management approach that included gear, season, and quota restrictions controlled the whitefish commercial fishery during recovery.

Whitefish are a member of the cold-water benthic food web, and their benthivorous diet, similar to that of the cohabiting slimy sculpin (*Cottus cognatus*), consists primarily of the burrowing amphipod *Diporeia* spp. (hereafter, diporeia as a common name) but also includes the opossum shrimp (*Mysis relicta)* and various gastropod and pelecypod molluscs (Hart 1931; Ihssen et al. 1981; Brandt 1986; Christie et al. 1987). The rapid disappearance of diporeia from its most productive habitat (25-60-m depth) in Lake Ontario soon after the invasion of zebra (*Dreissena polymorpha*) and quagga (*D. bugensis*) mussels during the early to mid-1990s (Dermott 2001) was a major disturbance in the benthic food web. Dermott (2001) indicated that this disturbance represented a major loss of food and, thus, a reduction in carrying capacity for cold-water fish. To date, whitefish responses to the disturbance include declines in condition and growth, delayed mean age at maturity, and decreased reproductive success (Hoyle et al. 1999). Some of these responses were also observed in Lake Huron (Mohr and Ebener 2004, this issue) and Lake Michigan (Schneeberger et al. 2005), but in Lake Erie whitefish have not shown dramatic changes attributable to the loss of diporeia (Cook et al. 2005). This report is a review of the Lake

Ontario whitefish with an emphasis on its response to the disappearance of diporeia.

Materials and Methods

Commercial harvest statistics were summarized from Baldwin et al. (1979) for the years 1867-1977 and from records maintained by the Ontario Ministry of Natural Resources (OMNR) (Lake Ontario Management Unit, Glenora Fisheries Station, Picton, Ontario, Canada, K0K 2TO, unpubl. data) for the years 1978-2001. Long-term trends (1972-2001) in whitefish abundance and year-class strength were derived from annual index gillnetting and bottom-trawling conducted by the OMNR in eastern Lake Ontario (Fig. 1), as described by Hoyle et al. (2003). Age and diet data were from whitefish sampled by index gillnetting (1992-2001) and by commercial-catch sampling (1990-2001) conducted by the OMNR (Hoyle 2001). Age interpretation used replicated otolith sections. Whitefish diet composition, expressed as frequency of occurrence, was obtained in 1998 and 2001 from index gillnetting and trawling samples.

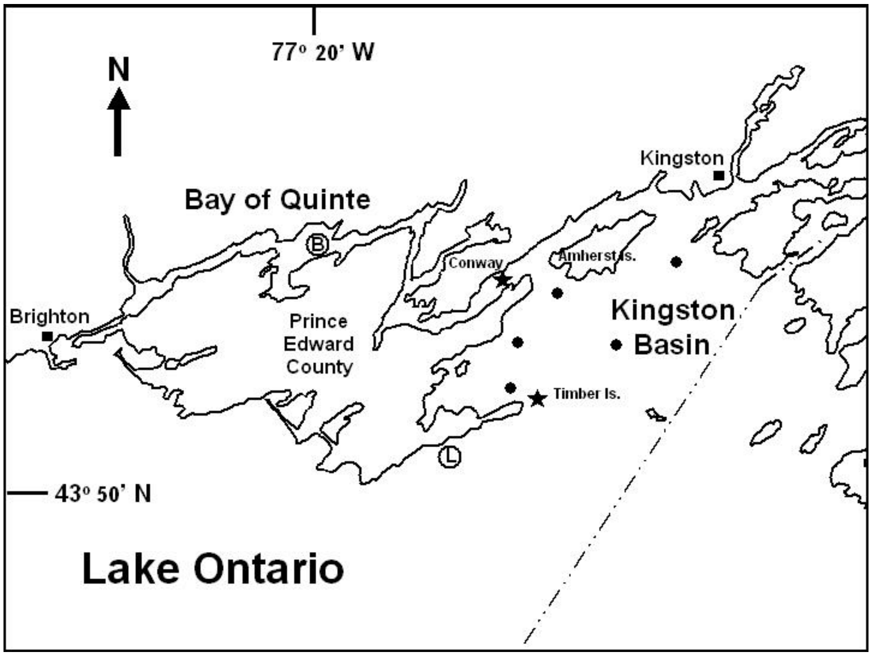

Fig. 1. Map of eastern Lake Ontario indicating lake whitefish index gillnetting (solid circles) and bottom-trawling locations at Timber Island and Conway in the Kingston Basin (stars) and commercial-harvest sampling areas on lake whitefish spawning grounds for the B = bay and L = lake stocks.

Results and Discussion

Historical commercial-harvest records (Baldwin et al. 1979) offer a picture of whitefish distribution and abundance in Lake Ontario. Although records indicate that whitefish were widely distributed in Lake Ontario from the early 1900s until stocks collapsed in the 1960s, 92% of the harvest was taken from Canadian waters. The bulk of this harvest came from waters east of Brighton (Fig. 1) where most of the gillnet fishery was located (Christie 1973). In northeastern Lake Ontario, two spawning stocks are recognized: the lake stock that spawns in November along the southern shores of Prince Edward County and Amherst Island and the bay stock that spawns in late October and early November in the Bay of Quinte (Fig. 1). During the summer months, the two spawning stocks cohabit and are found at highest densities in the Kingston Basin (Christie et al. 1987). Most of the suitable whitefish summer habitat in the Kingston Basin is found at depths of 20 to 35 m. Tagging studies, however, indicate that the distribution of these two stocks also includes areas outside of the Kingston Basin (Ontario Ministry of Natural Resources, Glenora Fisheries Station, 41 Hatchery Lane, Picton, Ontario, Canada, K0K 2TO, unpubl. data). In particular, some fish occur along the southern and western shores of Prince Edward County and along the northern shore of Lake Ontario immediately to the west of Brighton. Also, some fish from these stocks probably inhabit the New York waters of eastern Lake Ontario.

Commercial-harvest information suggests that whitefish abundance was very high in the 1920s but declined to a level that could not support the fishery by the late 1960s (Fig. 2).

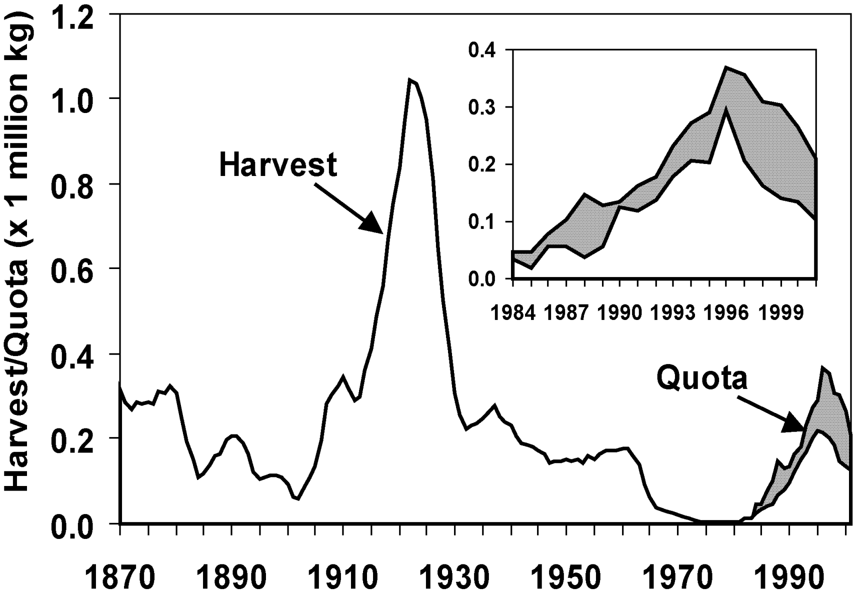

Fig. 2. Commercial harvest of lake whitefish from the Canadian waters of Lake Ontario, 1867-2001 (x 1 million kg, 5-yr moving average). Commercial quotas from 1984 to 2001 are indicated by shading. Inset shows annual quota and harvest, 1984-2001 (x 1 million kg).

As the two major stocks recovered in the 1980s, the commercial harvest was regulated with quota, season, and gear restrictions. The quota was gradually increased (Fig. 2) after index gillnetting and trawling surveys (Fig. 3) showed continued production of strong year-classes during most of the 1980s and early 1990s. Whitefish abundance peaked at historically high levels in the early 1990s (Casselman et al. 1996) and then, again, declined precipitously (Fig. 3).

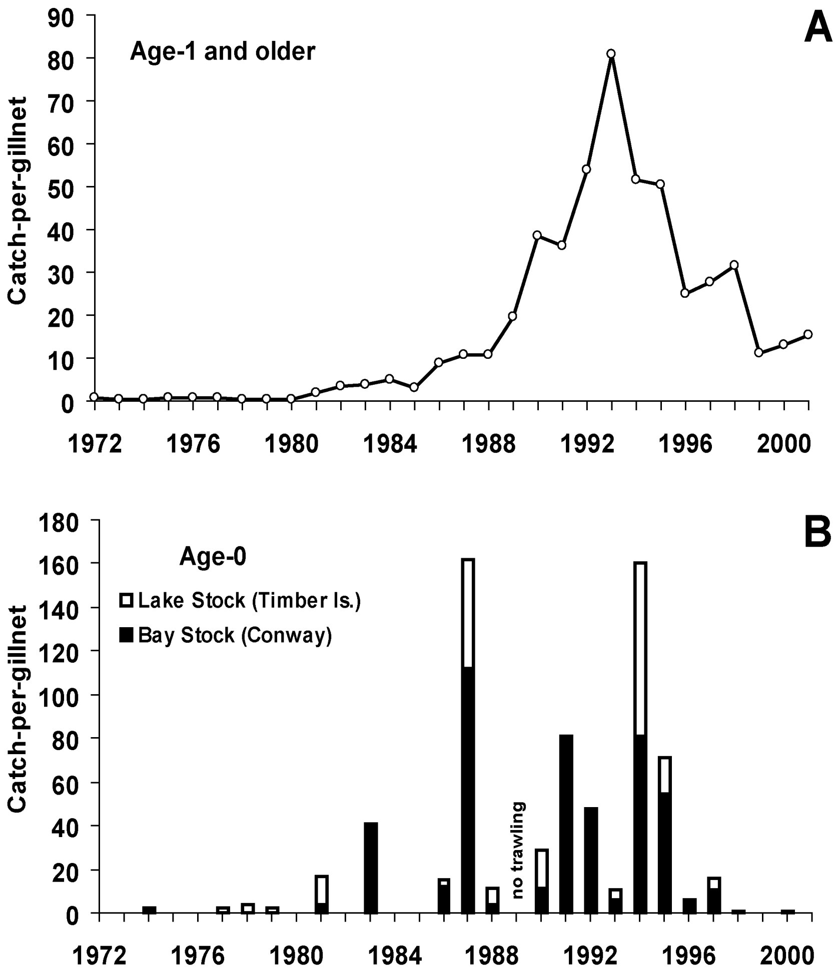

Fig. 3A. Relative abundance of age-1 and older lake whitefish (mixed stocks) caught in gillnets in the Kingston Basin of eastern Lake Ontario, 1972-2001. 3B. Relative abundance of age-0 lake whitefish caught in trawls for the lake (Timber Island, open bars) and bay (Conway, closed bars) stocks, 1972-2001 (no trawling in 1989) (see Fig. 1 for locations of Timber Island and Conway).

Factors regulating distribution and abundance of Lake Ontario whitefish have been reviewed in detail (Casselman et al. 1996; Hoyle et al. 2003) and are summarized in Table 1. Climate, specifically winter severity, plays a significant role in the population dynamics of this cold-water-adapted species living at the southern edge of its range. Other factors, including overexploitation, eutrophication, and exotic predators, have, at different times, been important. Recently, a major disturbance in the deepwater benthic food web has been a dominant factor affecting whitefish distribution and abundance.

Table 1. Summary of major factors regulating distribution and abundance of lake whitefish in Lake Ontario and the period during which each factor was considered to exert a major influence.

Factor	Period	Reference
Weather (overwinter conditions)	Ongoing	Christie 1963; Hoyle et al. 2003
Exploitation (commercial harvest)	1950s and 1960s	Christie 1968
Eutrophication (spawning substrate quality)	1960s and 1970s	Hurley and Christie 1977
Exotic species:		
Sea lamprey (*Petromyzon marinus)* (adult predator)	1960s	Christie 1973; Loftus and Hulsman 1986
Rainbow smelt *(Osmerus mordax)*, alewife *(Alosa pseudoharengus),* white perch *(Morone americana)* (larval predators)	1960s, 1970s	Casselman et al. 1996
Dreissinid mussels	1990s and current	Dermott 2001; Hoyle et al. 2003

Peak whitefish abundance coincided with the invasion of dreissenid mussels in eastern Lake Ontario. The zebra mussel was the first to become established, and it reached high densities by 1994. The quagga mussel became established during the late 1990s and largely replaced the zebra mussel. The high density of dreissenid mussels and their feeding ecology likely initiated or at least contributed to large changes in the eastern Lake Ontario ecosystem. For example, measurable impacts on water quality (e.g.

clarity, chlorophyll a, and phytoplankton) were observed in 1993 (Johannsson et al. 1998), and major impacts were reported by 1994 (Nichols 2001). The great potential for dreissenid mussels to channel energy from pelagic to benthic pathways (benthification) led to the expectation that benthic fish production might actually increase. Negative impacts on whitefish stocks were not anticipated.

Coincident with the establishment of dreissenid mussels and associated changes in water quality, the diporeia disappeared suddenly from eastern Lake Ontario sometime between 1993 and 1995 (Dermott 2001). The proliferation of dreissenid mussels and the loss of diporeia across the Great Lakes are closely linked (Nalepa et al. 2005). Hypotheses related to potential interactions have been proposed, but the precise mechanism has not been determined (Dermott and Munawar 1993; Dermott and Kerec 1997; Nalepa et al. 1998; Landrum et al. 2000; Dermott 2001). Diporeia previously accounted for 86% of the total benthic production in Lake Ontario (Dermott 2001) and was important in the diet of whitefish (Christie et al. 1987; Owens and Dittman 2003). Diporeia densities declined throughout Lake Ontario at depths <100 m, and diporeia remained abundant only in very deep waters (Dermott 2001; Lozano et al. 2001).

Whitefish condition, which had been high and stable, declined markedly in 1994 (Fig. 4) in association with the disappearance of diporeia between 1993 and 1995.

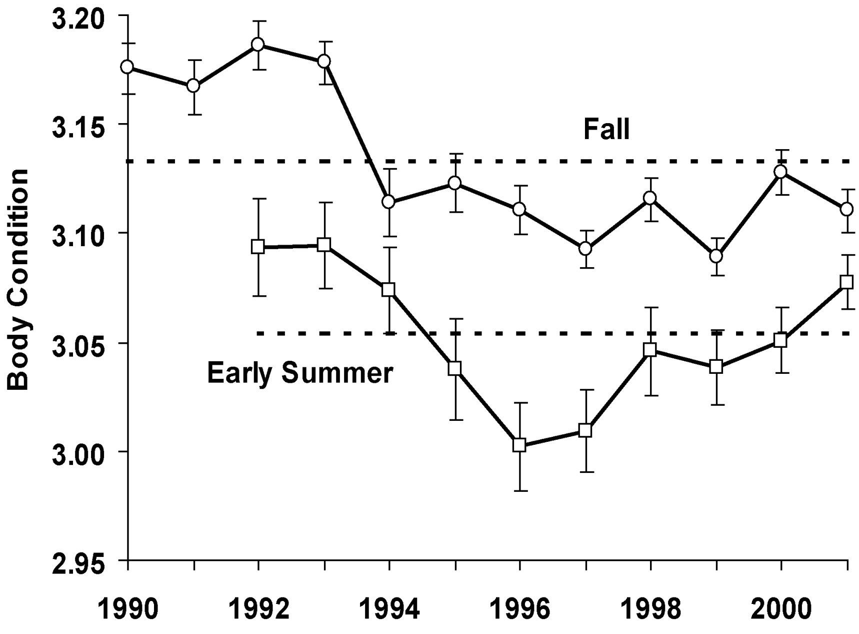

Fig. 4. Body condition ($\log_{10}$ round weight adjusted for differences in mean fork length among years, ANCOVA) for female lake whitefish sampled in the fall commercial fishery (1990-2001) and in early summer index gillnets (1992-2001). Error bars are 95% CI. Dashed lines indicate mean values for early summer and fall samples.

Declines in whitefish growth rate lagged approximately one year behind the decline in condition (Fig. 5). An increase in mean age at maturity, begun in 1996, lagged behind the decline in growth by an additional year (Fig. 6). The timing of these events suggests that, although whitefish may have been approaching the carrying capacity of eastern Lake Ontario, it was the disappearance of diporeia that most likely led to changes in whitefish condition, growth, and age at maturity. These density-dependent attributes in population density typically increase in the cases of condition and growth or decrease in the case of age at maturity with decreases. But here condition and growth decreased and age at maturity increased while whitefish density declined.

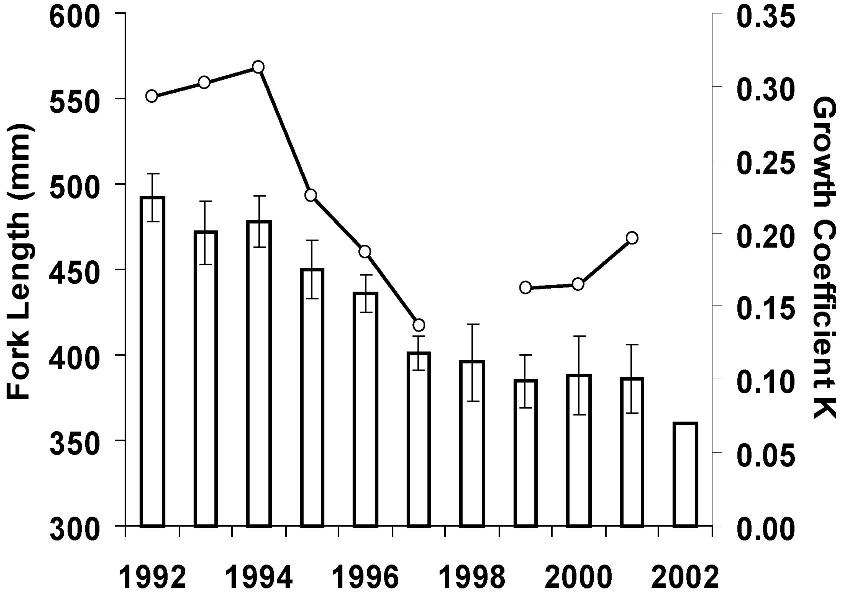

Fig. 5. Mean fork length (error bars are 95% CI) and the Brody growth coefficient K (Ricker 1975) for age-6 lake whitefish caught in summer index gillnetting in the Kingston Basin of Lake Ontario, 1992-2001.

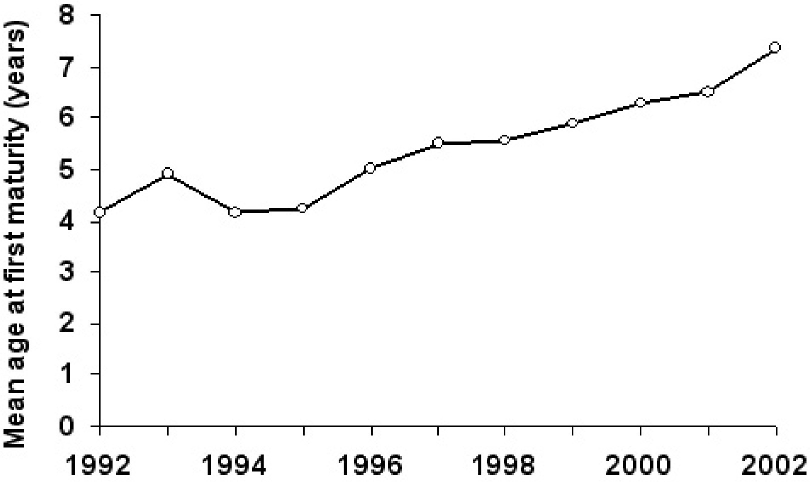

Fig. 6. Mean age at maturity (Lysak 1980) for female lake whitefish caught in summer index gillnets, 1992-2001.

Variations in whitefish condition were dependent on the time of year that samples were taken. The condition of fish sampled while spawning in the fall remained low following the large decline observed in 1994. The condition of fish sampled during early summer declined from 1993 to 1996 but condition improved gradually after 1997. The improvement, however, did not lead to the condition levels observed prior to the disappearance of diporeia (Fig. 4). Modifications in distribution and feeding patterns may account for the improvement in summer condition. During summer, whitefish typically feed below the thermocline where, since the disappearance of diporeia, benthic food resources have declined leading to losses in condition throughout the summer and into early fall. At other times of the year (fall, winter, spring), whitefish are not constrained to depths below the thermocline and can feed in shallower water where alternative prey to diporeia may be more abundant.

Whitefish may have responded to the loss of diporeia by foraging in much deeper water outside the Kingston Basin where diporeia remained abundant. In the New York waters of eastern Lake Ontario, whitefish were captured in deeper water during more recent summer bottom-trawling surveys: from about 30 to 40 m in the 1980s and early 1990s to over 80 m by 1999 (Owens et al. 2005). Foraging in such deep water may be bioenergetically costly because water temperatures at these depths are colder than midsummer temperatures at the bottom of eastern Lake Ontario.

Two other events occurred in 1997 that suggested eastern Lake Ontario whitefish stocks were stressed. First, five whitefish carcasses were observed during routine bottom trawling in the Kingston Basin (Hoyle 1998). The carcasses were observed during early summer and were not significantly decomposed. This bottom-trawling program has been conducted annually since 1972, but no whitefish carcasses had ever been observed prior to 1997. Whitefish abundance peaked in the Kingston Basin in 1993 so the likelihood of observing carcasses would have been highest at that time. Whitefish abundance had declined markedly by 1997 (Fig. 2); the appearance of the carcasses in that year suggests an increase in natural mortality. Small numbers of carcasses were also taken in early summer in subsequent years.

Also in 1997, a relatively large number of adult whitefish were observed in New York waters off Oswego where previously only very low numbers had been observed during routine bottom-trawling operations (Owens et al., 2003). This observation may represent dispersal of whitefish from their traditional range in the Kingston Basin to other areas of the lake. The observation is consistent with the hypothesis that fish were seeking better foraging opportunities.

Although whitefish condition remains in a state of flux, growth appears to have stabilized at a lower level (Fig. 5). Pothoven et al. (2001) found that decreased whitefish condition and growth in southern Lake Michigan were associated with the loss of diporeia, a high-energy prey, and the consumption of prey with lower energy content such as dreissenids. This scenario likely has occurred in eastern Lake Ontario. Diet studies in 1998 and 2001 confirmed that diporeia were absent from the diets of these fish. Shelled benthic invertebrates, primarily dreissenid mussels, gastropods, and sphaerid clams, dominated their diet (Table 2).

Table 2. Frequency of occurrence of items in the diet of whitefish in the Kingston Basin of Lake Ontario, summers of 1998 and 2001. Diet items identified to lower-level taxa in 2001.

Taxa		**1998**	**2001**
Annelids	Hirudinea		2
Arachnids	Hydracarina		3
Decapods		1	
Amphipods	Diporeia		1
	Gammarus		14
Dipterans		10	
	Chironomidae		23
	Orthocladiinae		17
Trichopterans		5	
Gastropods		5	
	Bulimidae		17
	Lymnaeidae		1
	Pleuriceridae		4
	Valvatidae		46
Pelecypods	*Dreissena*	90	
	Quagga mussel		90
	Other[1]	24	
	Sphaeriidae		19
Number of food items		5814	8482
Number of non-empty stomachs		142	107
Number of fish examined		169	115

[1] Includes mainly *Pisidium* and *Sphaerium* (fingernail clams).

Whitefish growth likely will not increase on a diet with lower energy content. Even though the growth rate stabilized at a lower level after 1997, mean age at maturity for female whitefish continued to increase thereafter, adding more than an extra year by 2001 (Fig. 6). A strong whitefish year-class has not been produced since 1995 and reproduction has virtually failed since 1998 (Fig. 3). One hypothesis for reproductive failure focuses on poor condition of adults and the consequences of low lipid reserves—reduced egg/fry viability. Egg quality, for example, is positively related to adult nutritional status. With better nutrition, fish produce offspring that have better feeding success, faster growth, greater resistance to starvation, and lower mortality (Johnston 1997).

The responses of whitefish to changes in the benthic food web have several implications for the commercial fishery. The whitefish harvest in contemporary times peaked at 295,000 kg in 1996 and comprised 50% of the total commercial harvest. Harvest declined to 100,000 kg by 2001 and comprised less than 30% of the total harvest. Poor condition affects marketability so that more fish must be harvested to reach the quota. Whitefish recruit to the fishery two years later than they did less than a decade ago because of decreased growth rate. The most severe implication for the commercial fishery, however, is that, if reproductive failure continues, the fishery will collapse as the older fish disappear completely.

Summary and Conclusions

The loss of diporeia, a formerly abundant and energy-rich benthic invertebrate, appears to have caused dramatic impacts on the ecology of eastern Lake Ontario whitefish stocks. Whitefish were forced to switch to alternative lower-energy prey, primarily dreissenid mussels. The forced diet change was linked to dramatic changes in whitefish life history, including a much slower growth rate and delayed age at maturity. Whitefish reproductive success was very poor for several years after these changes. Even given an assumption of improved reproductive success, whitefish potential yield will be lower in the future compared to that of the past.

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Status of Lake Whitefish *(Coregonus clupeaformis)* in Lake Michigan

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Abstract

The commercial lake whitefish (*Coregonus clupeaformis*) yield in Lake Michigan has fluctuated dramatically over most of the last century. Following a severe decline in the 1950s, lake whitefish abundance rebounded in the 1960s largely due to sea lamprey (*Petromyzon marinus*) control, salmonid stocking, decreased competition, and reduced fishing pressure. Annual yields have been sustained at a relatively high level since the early 1970s. Annual commercial yield targets (1,800-2,700 mt) have been either

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met or exceeded since 1979. Contemporary lake whitefish stocks are commercially harvested from Lake Michigan by state-licensed and native-American (tribal) fishermen. During 1981-2000, apportionment of the lakewide yield by gear type was 57% by trapnets, 36% by gillnets, 6% by trawls, and 1% by pound nets. Lakewide increases in lake whitefish abundance were indicated by upward catch-per-unit-effort (CPUE) trends for all four gear types aggregated over all management units during the period of sustained high yields. Biological monitoring indicated that high lake whitefish abundance, recent changes in food-web dynamics, and decreased primary production in the lake corresponded with decreasing lake whitefish size-at-age and condition. Additional research is needed in many areas of lake whitefish ecology, including diet, bioenergetics, disease, contaminants, and mortality rates.

Introduction

The lake whitefish (*Coregonus clupeaformis*, hereafter, whitefish) is currently the most important commercial fish in Lake Michigan in economic value. During the 1990s, annual commercial yields of whitefish from the lake averaged over 34 thousand mt with an average wholesale value of $6.3 million (U.S.) per year. Whitefish yield in Lake Michigan is high relative to the other Great Lakes. In the 1990s, whitefish from Lake Michigan constituted an average of 58% of the total annual whitefish yield from all the Great Lakes combined. Fish are taken in trapnets, gillnets, trawls, and pound nets. A relatively small but growing sport fishery harvested an average of 22,560 whitefish from the lake during 1985-1996 (Schorfhaar and Schneeberger 1997).

Sustained high yields of whitefish are dependent on stock stability. Effective management depends upon biological parameters being measured, estimated, and analyzed in a timely manner to determine stock trends and characteristics. Managers can exert some measure of control over exploitation by regulating harvest and/or effort, but other factors that affect stock stability (e.g., inherent biological factors, weather, and exotic species) are generally beyond managerial control.

According to Ebener (1997) there are at least 10 separate stocks of whitefish in Lake Michigan. Whitefish management is particularly complex there because the stocks intermix and are shared among tribal and state-licensed fisheries located in Michigan and Wisconsin waters. Several studies (Imhof 1977; Humphreys 1978; Leary 1979; Ebener 1980; Rowe 1984; Ebener and Copes 1985) describe the intermixing and wide geographical ranges of whitefish stocks in Lake Michigan. Stocks that are genetically separate may overlap in both time and space such that they are not distinct in terms of exploitation. Management decisions and actions must be in compliance with and consider the different regulations of, state, tribal, and federal governing authorities.

This report presents historical and baseline information relevant to whitefish in Lake Michigan and provides a context for comparison with similar information from the other Great Lakes. Most of the knowledge relating to the historical and contemporary whitefish stocks in Lake Michigan is derived from commercial-fisheries data. Assembling these data affords a depiction of the historical and contemporary (1981-2000) status of the major stocks of commercially fished whitefish in the lake and allows for cursory comparisons of relative abundance in commercial fishing gear. We also considered changes in whitefish abundance, size, and condition attributable in part to the effects of non-indigenous species and changes in the Lake Michigan benthic food web.

Methods

Commercial-fishery yield data have been collected for more than a century, and there is a 30-year record of commercial-effort data. Historical commercial-fishery yield data have been compiled by the Great Lakes Fishery Commission (Baldwin et al. 2000). Yield and economic value estimates were obtained from a web site maintained by the National Marine Fisheries Service (http://www.st.nmfs.gov/st1/commercial/index.html).

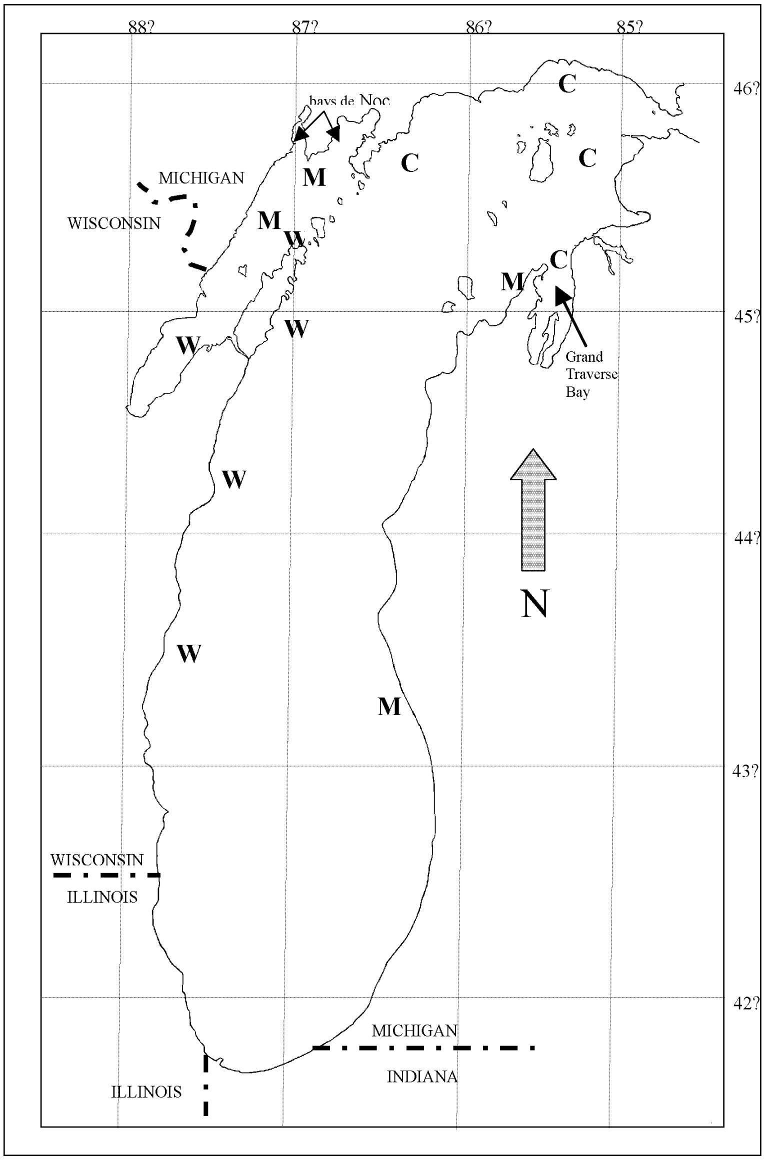

Fig. 1. Map of Lake Michigan indicating general areas where commercial whitefish fisheries are monitored by the Chippewa/Ottawa Resource Authority (C), the state of Michigan (M), and the state of Wisconsin (W).

Biological data on whitefish in commercial fisheries date back at least to the 1970s. Commercial yield, effort, and biological data have been collected by the Chippewa/Ottawa Resource Authority (CORA), the Michigan Department of Natural Resources (MDNR), and the Wisconsin Department of Natural Resources (WDNR). With some overlap, these contemporary whitefish stocks are monitored at 13 locations around the lake (Fig. 1). Whitefish length, weight, sex, and age data are used to calculate other parameters such as condition and mortality rates. Assessment netting targeting whitefish and/or other species provides additional data, and we have sport-fishing information from creel surveys. Other information pertinent to general characterizations of Lake Michigan whitefish stocks (e.g., data on parasites, diseases, and contaminants) was gleaned from the scientific literature or agency advisories.

Results and Discussion

Commercial fishing in Lake Michigan began in the early 1840s and expanded quickly thereafter (Wells and McLain 1973). Initial commercial yields of whitefish were not documented but were, by anecdotal accounts, considerably larger than anything recorded in subsequent years. The earliest commercial fishery hauled large seines along the shores (Wells and McLain 1973). This method depleted localized stocks quickly, prompting commercial fishermen to relocate their operations and develop new and increasingly efficient gear. Seines eventually gave way to gillnets, pound nets, and trapnets. Further efficiencies were gained by using smaller meshes and by changing from cotton webbing to finer linen twine in the late 1800s, flexible cotton mesh in the 1930s, multi-filament nylon beginning in the 1940s, and mono-filament nylon in the 1960s (Wells and McLain 1973). During the latter half of the 1800s, the use of engine-powered boats and adoption of subsequent mechanical and electronic innovations (e.g., hydraulic lifters and electronic navigation equipment) greatly increased fishing efficiency, capacity, and range of operations for the fleet.

The earliest quantification of a commercial yield for whitefish in Lake Michigan was also the highest ever recorded: 5457 mt in 1879 (Baldwin et al. 2000) (Fig. 2). During the 1880s, yields declined sharply, and, by 1895, commercial production had plummeted to 700 mt. The whitefish yield fluctuated during 1900-1950, averaging just over 1000 mt annually. During this period, there were two distinct, short-lived peaks: in 1928-1932 and 1947-1949. Each of these peaks was attributable to single strong year-classes moving through the fishery (Wells and McLain 1973). Between 1951 and 1960, commercial yields averaged only 250 mt per year, reaching a low of 11 mt in 1957, which is a drop of over 99% from the high value in 1879. Stocks began to recover in the 1960s, and average annual yield increased with each succeeding decade: 337 mt during the 1960s, 1402 mt during the 1970s, 2533 mt during the 1980s, and 3285 mt during the 1990s.

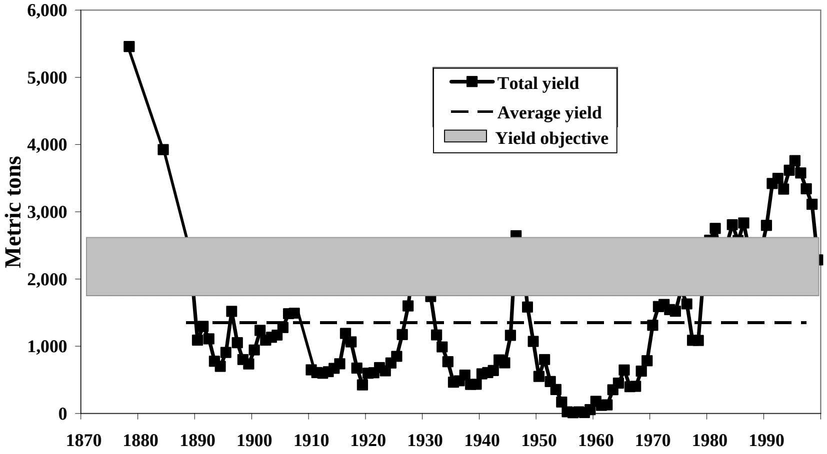

Fig. 2. Commercial yield of whitefish from Lake Michigan, 1879-2000 (data from Baldwin et al. 2000).

The sustained high annual yields during the past 30 years are unprecedented. Fish-community objectives established by the Lake Michigan Committee of the Great Lakes Fishery Commission specified that the expected annual yield of whitefish in Lake Michigan should be in the range of 1.8 to 2.7 thousand mt (Eshenroder et al. 1995). Yield has been either within or has exceeded this targeted range since 1979 (Fig. 2).

Whitefish abundance has been greatly influenced by direct and indirect effects of non-native species. Rainbow smelt (*Osmerus mordax*) was introduced relatively early (approximately 1912) and was distributed throughout Lake Michigan by the mid-1930s (Wells and McLain 1972). Rainbow smelt may have affected many native species, including whitefish, presumably by eating their fry as well as by competing with them for planktonic food. Sea lamprey (*Petromyzon marinus*) had invaded Lake Michigan by 1936, and this exotic had a very significant negative impact on several native species, including whitefish, lake trout (*Salvelinus namaycush*), and walleye (*Stizostedian vitreum*) (Shetter 1949). Wells and McLain (1972) attributed the extremely low abundance of whitefish during the 1950s to the combined negative effects of rainbow smelt and sea lamprey.

During the 1960s, sea lamprey control, introduction of salmonids, reduced competition, and reduced fishing pressure precipitated a recovery of whitefish. Sea lamprey control was initiated in the 1950s, and the most effective measures (i.e., chemical treatment of streams) were in place throughout Lake Michigan by the 1960s. As a consequence, mortality of whitefish due to sea lamprey predation declined appreciably (Eck and Wells 1987). Stocking of salmonids, especially lake trout, further reduced sea lamprey attacks on whitefish. When they are available, lake trout are the preferred sea lamprey target (Wells and McLain 1972), and the increased abundance of stocked lake trout likely deflected sea lamprey pressure away from whitefish. Stocked lake trout and Pacific salmon (*Oncorhynchus* spp.) consumed increasing numbers of rainbow smelt and alewife (*Alosa pseudoharengus*) (Wells and McLain 1972), thus reducing the potentially deleterious effects of these forage species on whitefish. The fishing industry in Lake Michigan focused on rainbow smelt and alewife during the 1960s, which reduced their effects even further and simultaneously relieved some of the fishing pressure that was previously aimed at whitefish.

Except for the bloater (*C. hoyi*), other Lake Michigan coregonines did not fare as well as whitefish. Six of the deepwater ciscoes (*C. nigripinnis*, *C. johannae*, *C. zenithicus*, *C. alpenae*, *C. reighardi,* and *C. kiyi*) that were formerly abundant and valuable members of this species complex never recovered from the combined effects of sea lamprey predation and overfishing, and these six species virtually disappeared from Lake Michigan by the early 1960s (Wells and McLain 1972). In addition, lake herring (*C.*

artedii) numbers fell and have remained very low compared with historical levels (Smith 1970). The shift in relative abundance among the various coregonine species may have resulted in more food resources being available for recovering whitefish stocks.

During 1981-2000, state-licensed fishermen from Michigan accounted for 44% of the lakewide whitefish commercial yield, tribal fishermen harvested 33%, and state-licensed fishermen from Wisconsin landed 23% (Fig. 3). Trapnets, gillnets, trawls, and pound nets took 57%, 36%, 6%, and 1%, respectively, of the total yield between 1981 and 2000 (Fig. 4).

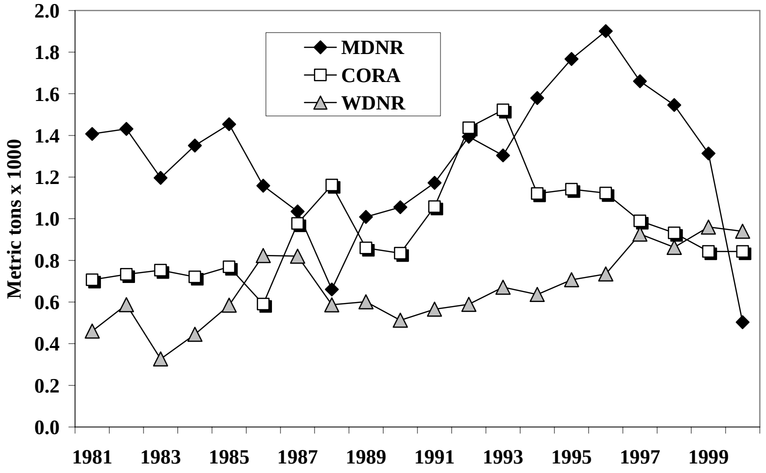

Fig. 3. Commercial yield of whitefish by management agency, 1981-2000.

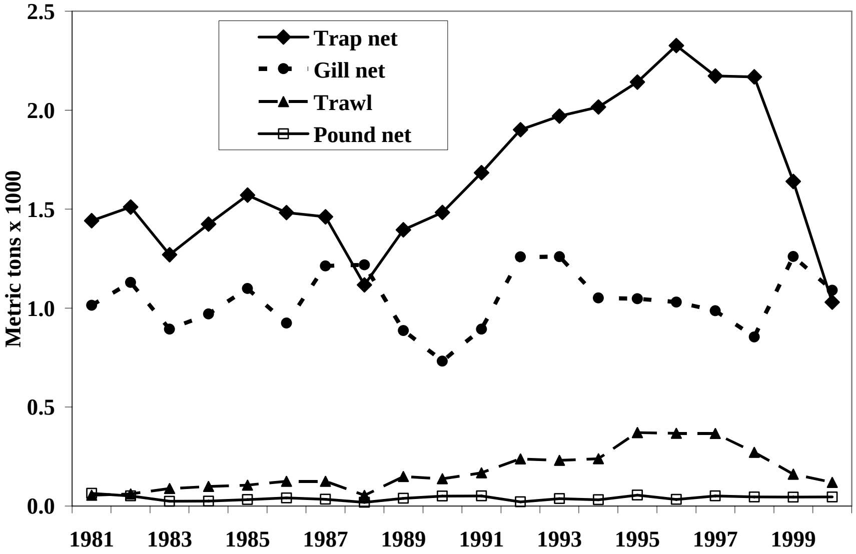

Fig. 4. Commercial yield of whitefish by gear type, 1981-2000.

Trapnet effort in Lake Michigan fluctuated without trend between 1981 and 1998 and then decreased in 1999 and 2000 (Fig. 5). Gillnet effort generally declined but increased slightly in 2000. An increase in trawl effort during 1981-1995 was followed by a decrease during 1996-2000. Pound-net effort was never high relative to other gear types, dropping to low, consistent levels after 1986. Despite varying or non-existent trends in effort, overall catch-per-unit-effort (CPUE) increased for all types of fishing gear from 1981 through the late 1990s, thus providing additional evidence for the increasing abundance of whitefish during the last 20 years (Fig. 5).

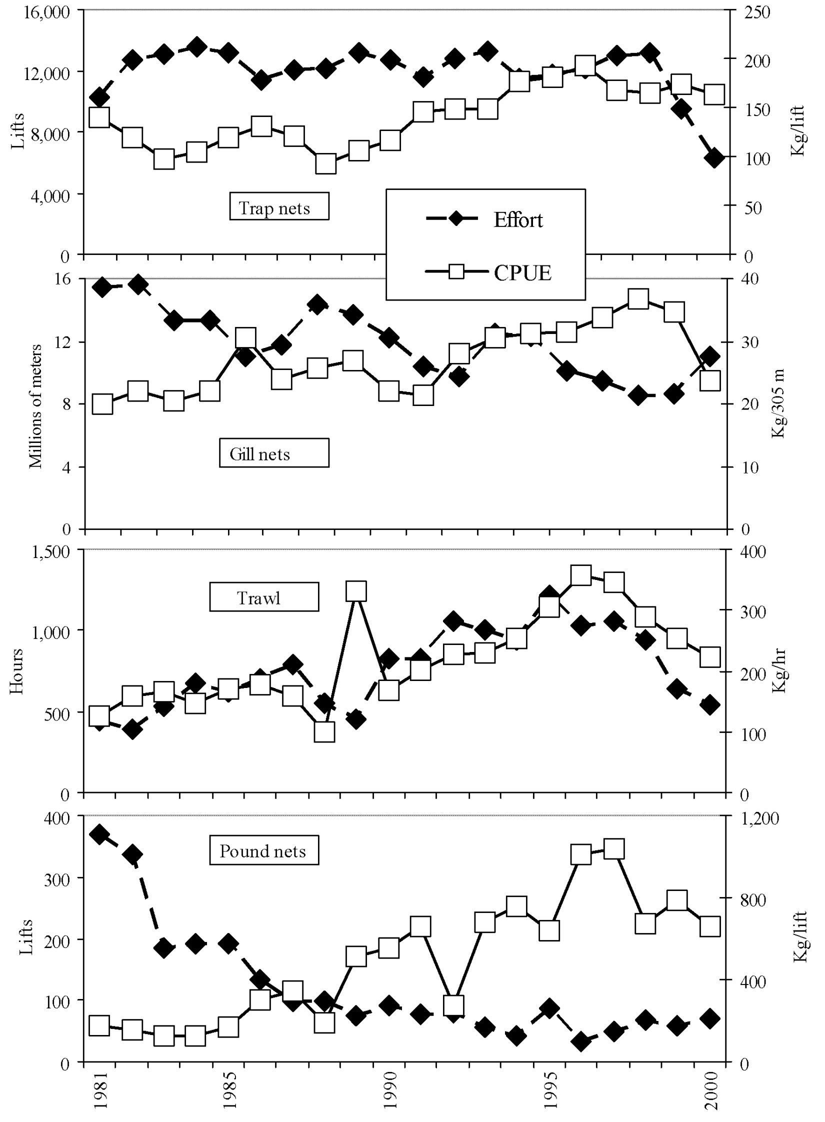

Fig. 5. Commercial effort and CPUE for whitefish fisheries by gear type, 1981-2000.

The recent drop in trapnet yield and effort is attributed to changes brought about by imposition of the 2000 Consent Decree that defined the allocation and management regulation of fisheries resources in the 1836 treaty area, which includes most of Michigan's whitefish waters in Lake Michigan (United States v. Michigan, W.D. Mich. Case No. 2:73 CV 26). Specifically, nine state-licensed fishermen from the state of Michigan agreed to turn over their bays de Noc trapnet operations to the tribes, and the tribes agreed to reduce their gillnetting effort by 4.3 million m. This agreement resulted in a redistribution of fishing effort throughout the 1836 treaty-ceded waters and less trapnet effort in the lake after mid-1999.

There were widespread anecdotal reports from commercial fishermen during the 1990s of declining whitefish girth. Fishermen sorted and returned some fish of legal length to the water because they were not of marketable weight. Investigators from each management agency began documenting reduced whitefish size-at-age during the 1990s. Changes included decreases of 4-7% in length-at-age, 36-47% in weight-at-age, and 34-40% in condition-at-age (e.g., Fig. 6). Pothoven et al. (2001) evaluated condition in whitefish aged 2-16 from southeast Lake Michigan using analysis of covariance for two time periods. They reported that the mean weight of whitefish adjusted for length was significantly lower during 1992-1999 than during 1985-1991. Pothoven et al. (2001) also performed separate *t*-tests using mean length-at-age and weight-at-age. Again, significant declines were found for most ages.

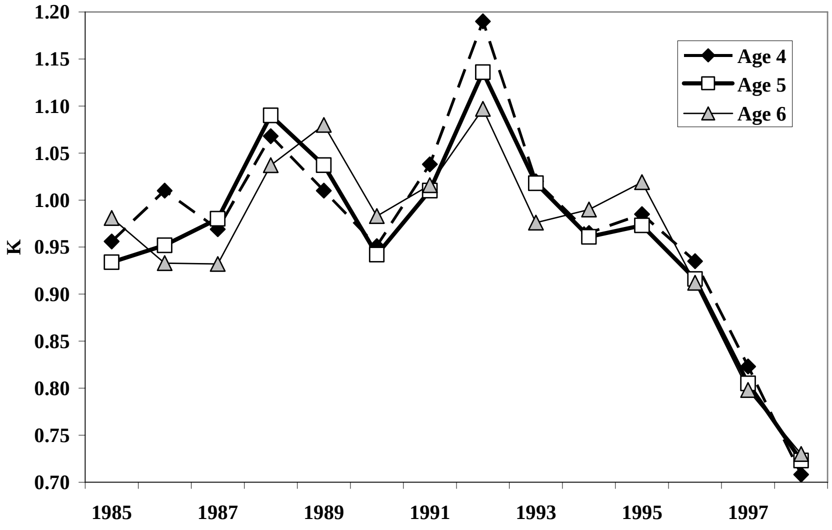

Fig. 6. Coefficients of condition (K = $Wx10^5xL^{-3}$) for whitefish in northern Lake Michigan, 1985-1998.

Some of the decrease in whitefish size and condition was attributable to density-dependent factors. Lakewide abundance of whitefish, as indicated from yield and CPUE statistics, was consistently higher in the 1990s than during any other time. Growth reductions associated with higher abundance result from increased competition for food (Henderson et al. 1983). Declines in whitefish growth seen in Lake Michigan may have been established at an early life stage, thus creating a growth deficit that carried over from that point on, or depressed growth may be cumulative and persistent over many years of a fish's life.

Important changes in the Lake Michigan ecosystem and food web have occurred during the last 20 years. Although the interconnections and implications are not thoroughly understood, these changes undoubtedly played an important role in the declining size and condition of whitefish. Madenjian et al. (2002) documented a decrease in primary production caused by reduced phosphorus loadings that were associated with decreases in *Diporeia* spp. (hereafter, diporeia as a common name), oligochaetes, and sphaeriids during the 1980s. Zebra mussels (*Dreissena polymorpha*), first reported in Lake Michigan in 1989 (Marsden et al. 1993), were associated with further declines of diporeia in Lake Michigan (Nalepa et al. 1998; Nalepa et al. 2000).

The decline of diporeia in Lake Michigan was similar to declines that occurred in other Great Lakes following the appearance, spread, and rapid increase in abundance of zebra and quagga (*Dreissena bugensis*) mussels (Dermott and Kerec 1997; Hoyle et al. 1999). However, Madenjian et al. (2002) noted that the exact ways in which diporeia are affected by zebra mussels are not known.

A recent study by Pothoven et al. (2001) analyzed diet and energy content of food items for whitefish in southeast Lake Michigan, both before and after the decline in diporeia densities. They found that the contribution of diporeia to the whitefish diet decreased, both as a proportion in weight and as a percent of occurrence, after the decline. They also found that whitefish consumed food items of lower caloric value in greater proportions and with greater frequency when diporeia were less available. The consequent loss of dietary calories contributed to the decrease in condition and growth of whitefish in the study area. Whitefish throughout the lake were likely affected by similar changes in local food webs.

Commercial fishermen and managers are concerned that the declines in growth and condition could lead to reduced fecundity or egg quality in whitefish stocks. However, these potential negative effects have not yet materialized. Strong year-classes were produced in the late 1990s, and fish in the commercial fishery appear, based on the most recent data, to be regaining their former condition.

Scott and Crossman (1973) highlighted literature that addressed parasite species affecting whitefish throughout their range in North America. Only a few investigators have reported on parasites in Great Lakes whitefish, and the latest of these reports was published in 1955. There are no reports that specifically list parasitic loads in Lake Michigan whitefish. There is a need to take an updated look at the parasites that affect Lake Michigan whitefish.

Similarly, little is known about disease organisms afflicting lake whitefish, although whitefish in Lake Michigan recently tested positive for *Renibacterium salmoninarum* (Rs), and incidence rates were similar in magnitude and trend to those of trout and salmon (Jonas et al. 2002) (Fig. 7). The Rs bacterium, which had not been documented previously in fish outside the sub-family salmoninae, causes bacterial kidney disease (BKD) and can lead to death in chinook salmon (*Oncorhynchus tschawytscha*). To date, there is no evidence that Rs has progressed to the BKD stage in whitefish, suggesting that these fish may possess resistance to Rs, and that the Rs bacterium may have infected whitefish long before it was officially documented.

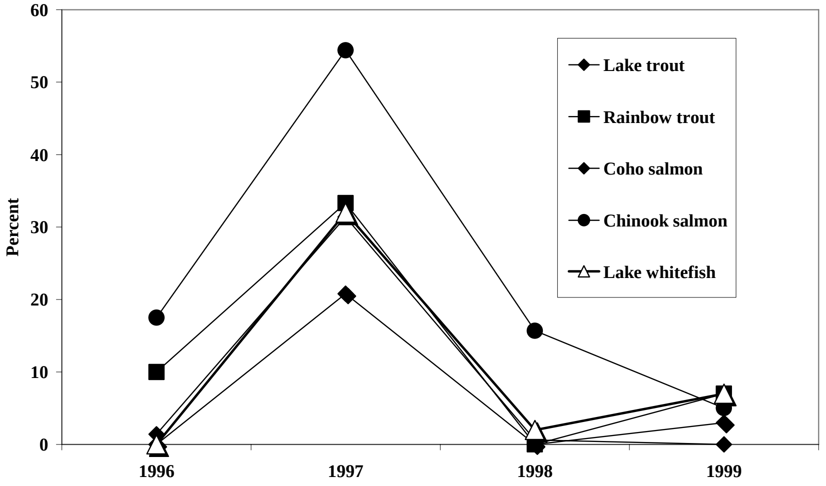

Fig. 7. Percent of assessment-sampled fish testing positive for the BKD-causing bacterium in Lake Michigan, 1996-1999.

Contaminant concentrations are generally low in whitefish from most areas of Lake Michigan, and there are currently no restrictions for human consumption based on the federal regulations that apply to commercially caught fish. However, based on more conservative trigger levels, the sport-fish consumption advisory from the Michigan Department of Community Health recommends limited or no human consumption (especially for women and children) of whitefish of a certain size and from certain areas due to PCB, chlordane, and dioxin contamination. Different trigger levels for commercial and sport-caught fish create a double standard that causes misunderstanding and confusion. This situation should be rectified.

Whitefish mortality rates in most Lake Michigan stocks are generally lower than the target maximum derived from research and established by Consent Decrees in 1985 and 2000. However, mortality rates deemed too high by managers have plagued certain whitefish stocks in northern Lake Michigan for many years. This situation is ameliorated because these northern areas are especially suited for supporting relatively consistent year-class production (Taylor et al. 1987; Brown et al. 1993). Furthermore, enforced annual yield quotas, imposed as a result of the 2000 Consent Decree, should bring mortality rates to more tolerable levels and keep them there.

Age-structured deterministic models have been developed for whitefish in eight Lake Michigan management zones. Model parameters were fitted from commercial fishery data using AD Model Builder software (Otter Research Ltd. 1996). This software has a proven track record for assessing marine stocks (Quinn and Deriso 1999) and was recently used for the first time to assess Great Lakes fish stocks (Sitar et al. 1999). For model development, a likelihood-fitting criterion was used (Fournier and Archibald 1982; Methot 1990). A Bayesian approach was adopted to determine natural mortality and uncertainty in parameter estimates. Model inputs for each year in the data set included weight-at-age, maturity schedules, von Bertalanffy growth parameters, age composition, number of fish harvested, effort, percent females in the population, and average number of eggs per kg of female biomass. Model outputs included estimates of total population size, age structure, recruitment, and mortality rates. A projection model (Ebener et al. 2005) that uses output from age-structured models is being used to calculate harvest limits for each of the eight stocks. The Technical Fisheries Committee (formed as part of the 2000 Consent Decree) created a modeling subcommittee that endorsed applying target mortality rates when determining harvest quotas. Target rates are based on the spawning-stock-biomass-per-recruit concept. That is, the spawning stock produced per recruit is targeted to be at least as high as would be achieved if survival were constant at a pre-defined level for all fish older than a specific age.

Lake Michigan has undergone substantial biological and environmental changes during the last 150 years. Whitefish stocks fluctuated over this period, then emerged in the 1970s at high levels of abundance that have been sustained for nearly 30 years. The recent declines of diporeia resulted in a loss of a very important, energy-rich diet item, likely contributing to reductions in whitefish size-at-age and condition. Recent evidence, showing a partial rebound in whitefish condition, indicates that these fish may have been able to adapt their foraging to the altered food web and provides some hope for the future regarding the resilience of the species. However, ecological changes may result in cumulative detrimental stresses. Efforts to understand and manage whitefish will benefit from increased coordination and cooperation among agencies. Maintenance of long-term data sets is critical for following trends, supporting models, generating quotas, and helping discern effects of past, present, and future perturbations to the ecosystem. Managers must remain vigilant, monitoring must continue, and strategies should be explored to ensure the continued viability of this important and valuable resource.

Additional data and research are needed in many areas, some of which (such as, parasites, diseases, diets, and contaminants) have been mentioned or alluded to in the text above. Other areas where important information is lacking include ecology, bioenergetics, behavior, recruitment dynamics, sources of mortality, gear selectivity, and movement (seasonal and age-related). Refinement and standardization of aging techniques and stock differentiation are also needed.

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Status of Lake Whitefish (*Coregonus clupeaformis*) in Lake Erie

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Abstract

Lake Erie lake whitefish (*Coregonus clupeaformis*) populations declined precipitously in 1959 due to the cumulative effects of exploitation, watershed degradation, eutrophication, and exotic species. A recovery began in the mid-1980s and was abetted by reduced nutrient loading. Also in the mid-1980s, the abundance of rainbow smelt (*Osmerus mordax*), a major predator of larval lake whitefish, was reduced as walleye (*Stizostedion vitreum*), a predator of smelt, became abundant and the trawl fishery for smelt intensified. The 1984 year-class, the first recent one to appear strongly in the fishery, gave rise to other strong year-classes. By the end of the 1990s, the harvest averaged 563 metric tonnes, most of which was taken by Ontario's gillnet fishery. The invasion of dreissenid mussels during the late 1980s was not associated with long-term reductions in growth or condition of lake whitefish. Although *Diporeia* spp. an important diet item, was nearly eliminated from the lake by the late 1990s, a diverse

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assortment of other benthic prey remain and are consumed by lake whitefish. Lake whitefish condition for both sexes is within the historical range.

Introduction

Lake Erie is the southern extent of the range for lake whitefish (*Coregonus clupeaformis,* hereafter whitefish) (Lawler 1965). Although Lake Erie is a latitudinal extreme for whitefish, sustained annual yields in excess of 1.8 million kg from 1939 to 1953 were comparable to the most productive lakes for whitefish (Christie and Regier 1988). In a study of 21 north-temperate lakes (including the Great Lakes), Lake Erie had the largest summer thermal habitat (10-14°C) by area and exceeded two-thirds of the lakes in thermal-habitat volume (Christie and Regier 1988). Although summer thermal conditions for adult whitefish are extensive, hypoxic conditions during late summer in the central basin reduce the amount of suitable whitefish habitat (Beeton 1963; Hartman 1972).

Within Lake Erie, whitefish primarily inhabit eastern waters during thermal stratification (Fig. 1). After fall turnover, adults migrate toward the western basin to spawn on rock, honeycomb limestone, gravel, or sand substrates (Goodyear et al. 1982). Some reproduction also occurs in the eastern basin, but the principal spawning stock is migratory (Ryan et al**.** 1999). Whitefish were caught commercially in the early 1800s by seining in the Maumee and Detroit Rivers (Regier et al. 1969). Pound nets and gillnets were introduced during the mid-1800s and were followed later in the 19th century by trapnets (Regier et al. 1969) (Fig. 2). Because whitefish harvests declined after 1890, hatcheries were established to propagate this valuable species (Regier et al. 1969; L. Corkum, Department of Biological Science, University of Windsor, Windsor, ON N9B 3P4, unpubl. data). Catches improved later, although whitefish disappeared from the Detroit River during the early 1900s (Regier et al. 1969; Hartman 1972; L. Corkum, Department of Biological Science, University of Windsor, Windsor, ON N9B 3P4, unpubl. data).

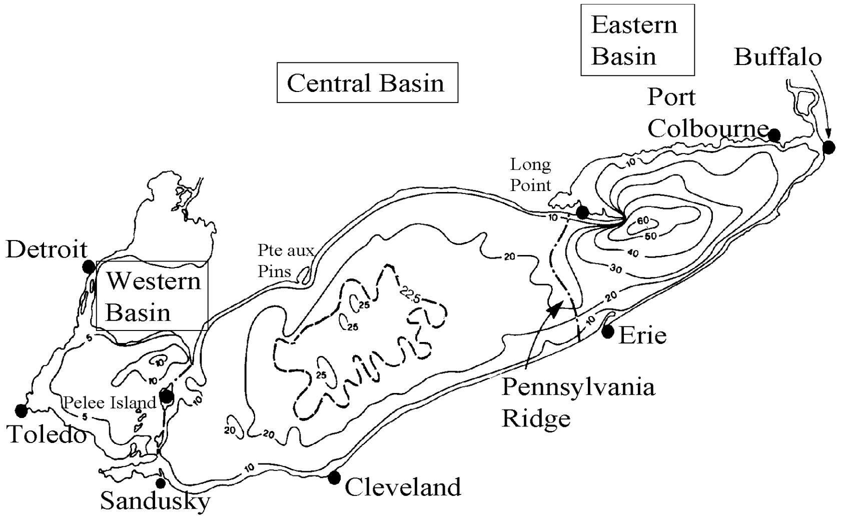


Fig. 1. Lake Erie bathymetry with bottom contours in meters (Mortimer 1987).

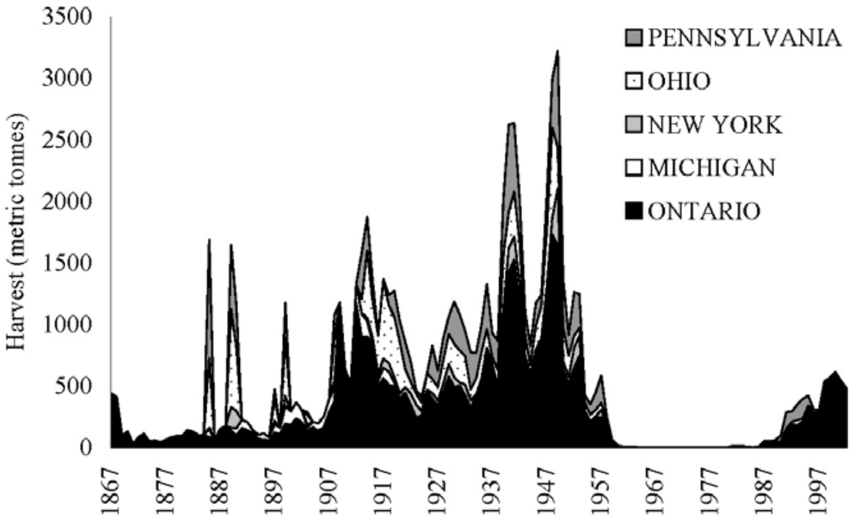


Fig. 2. Harvests (metric tonnes) of whitefish from Lake Erie (1867-2000).

The Province of Ontario's whitefish harvest achieved comparability with the United States harvest in the 1900s (Baldwin et al**.** 2002). Several exceptional year-classes supported the fishery, including those in 1926, 1936, and 1944 (Lawler 1965). Lake-wide yield peaked at 3.2 million kg in 1949, and averaged more than 1.8 million kg during the 1940s at a time when significant commercial fisheries also existed in Ohio, Pennsylvania, New York, and Michigan. Whitefish catches dropped precipitously during the 1950s and did not improve for decades (Baldwin et al. 2002).

The purpose of this paper is to review the current status and biology of whitefish, paying special attention to condition, growth, habitat constraints, diet, and spawning characteristics.

Methods

Whitefish harvest data are from Baldwin et al. (2002) and the Lake Erie Cold Water Task Group (2002). Whitefish were sampled from Canadian commercial catches (1987-2001) and index-gillnet surveys (1989-2001). The eastern basin and the region south of Long Point (Pennsylvania Ridge) were surveyed during thermal stratification, whereas the central basin was surveyed after fall turnover. Index catch rates are expressed as number per gang and include both canned and bottom sets. The proportion of index sets catching at least one whitefish includes all depths where the species was taken at least once during 1989-2001.

We compared growth and condition of whitefish captured in 1927 (Van Oosten and Hile 1947) with values based on whitefish taken in our index surveys. Non-linear least-squares regression was used to estimate the parameters of the von Bertalanffy growth curves (Pauly 1984). Condition factors (round weight (Rwt) • 10^5/total length $(TL)^3$ (Everhart et al. 1975) were estimated for males with TL >45 cm and for females >46 cm, lengths corresponding to ages 4+ (Van Oosten and Hile 1947). Condition factors for 1927 were recalculated by regressing total length on standard length using data from Van Oosten and Hile (1947). Gonadosomatic indices (GSI), where GSI = ovary weight/Rwt were calculated for female whitefish from commercial and gillnet samples taken in 2000 and 2001.

Whitefish habitat in the central basin during summer (water temperatures <16°C and dissolved oxygen (DO) >3 $\text{mg}\cdot\text{L}^{-1}$) was described from temperature and DO readings taken on August 29, 2001 with a YSI data sonde. Hypsographic data from Haltuch et al. (1998) were used to estimate habitat area and volume.

Temperature and oxygen profiles were recorded at index sites using either YSI DO/temperature probes or a YSI data sonde. These data were used to calculate the cumulative catch of whitefish over a range of temperatures and DO levels.

Linear logistic regression (maximum likelihood) was used to estimate the relationship between the proportions of spent females in western-basin commercial catches and temperature and date. Daily mean water temperatures were obtained from the Union Municipal Water Plant in Ruthven, Ontario, where the intake is approximately 7-m deep and 457-m offshore. Samples with <3 mature females and temperatures >10°C were excluded.

Results

Von Bertalanffy growth curves did not vary appreciably among samples collected in 1927-1929 (Van Oosten and Hile 1947), 1971-1974 (Kenyon 1978), 1990-1993 (Hardy 1994), 1989-1994 (our index), and 1995-2001 (our index) (Fig. 3). Parameters for our index samples are: 1989-1994, (males) $L\infty = 569$ mm, $K = 0.401$, $t_o = -0.2552$, $n = 80$ and (females) $L\infty = 634$ mm, $K = 0.280$, $t_o = -0.638$, $n = 110$; 1995-2001, (males) $L\infty = 576$ mm, $K = 0.318$, $t_o = -0.973$, $n = 282$ and (females) $L\infty = 593$ mm, $K = 0.310$, $t_o = -0.956$, $n = 283$. Variations among growth curves were greater for juveniles than for adults.

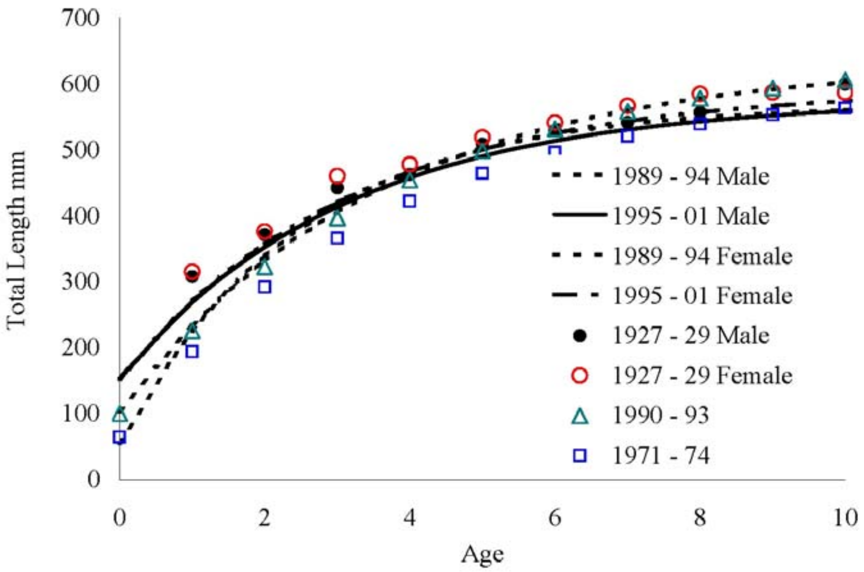


Fig. 3. Total length (mm) of whitefish in Lake Erie by age, estimated from the parameters of the von Bertalanffy growth equation.

Condition differed among ages (unbalanced ANOVA, $P < 0.001$) and whitefish younger than age 4 were significantly different from older fish (Bonferroni *t*-test, unbalanced ANOVA, $\alpha = 0.05$). Therefore, comparisons of condition were restricted to older fish. Condition was significantly different between sexes and for combinations of year and sex (unbalanced ANOVA, $P < 0.001$). Male and female condition (Fig. 4) was similar to historical values (1927-1929) derived from Van Oosten and Hile (1947).

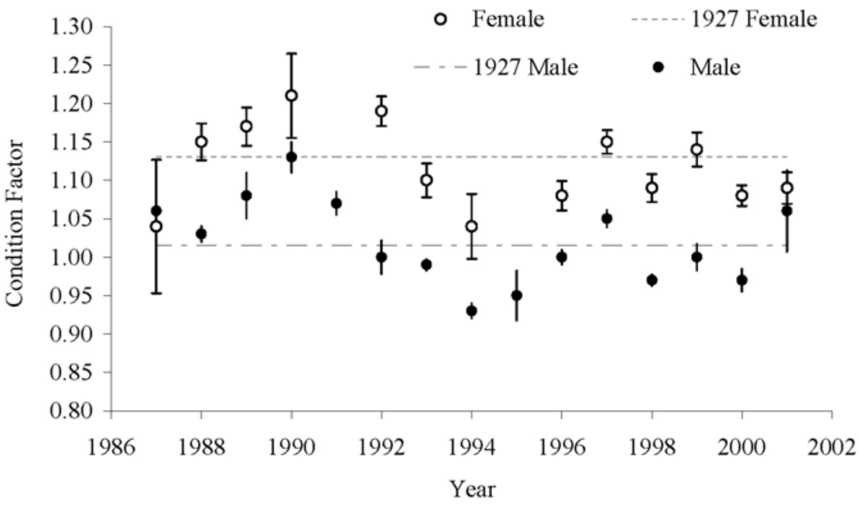


Fig. 4. Condition of male and female age-4+ whitefish in Lake Erie. Dotted and dashed lines show the average condition of females and males, respectively, in 1927.

The proportion of spent females in the commercial catch was significantly related to fall water temperatures in the western basin (Fig. 5). The model predicted that 50% of the females are spent by the time the water temperature reaches 5.7°C, which occurred by November 24. The GSI of mature females collected in 2000 and 2001 were 0.17 and 0.19, respectively.

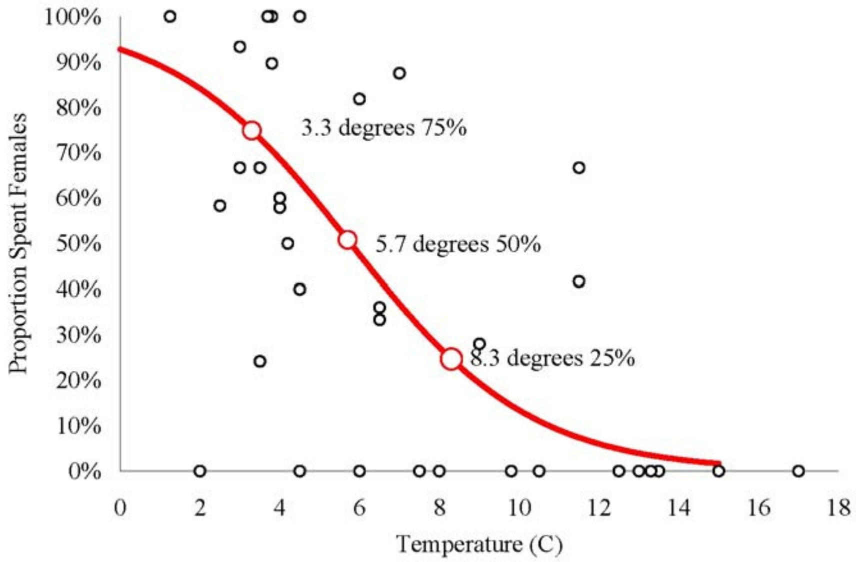


Fig. 5. Proportion of spent females in relation to water temperature in western Lake Erie (October and November).

Whitefish catch per efforts (CPE) in index gillnets were somewhat erratic during the 1990s (Fig. 6). A reasonably steady increase in CPE, however, was evident in the west-central basin. The proportion of sets containing at least one whitefish in eastern basin surveys did not correlate well with CPE (Fig. 7). Whitefish tended to be present at more netting sites in the central basin and at fewer sites in the eastern basin.

The temperatures at which whitefish were caught in gillnet surveys ranged from 5.7-21.6°C; the median temperature of capture in the eastern basin was 11.8°C, and on the Pennsylvania Ridge it was 15.3°C (Fig. 8A). The median temperature of capture after fall turnover in the central basin was 16.8°C. Whitefish were caught at DO levels from 4.3 to 13.3 mg·L^{-1} in the eastern basin and from 4.1 to 14.5 mg·L^{-1} on the Pennsylvania Ridge. Central basin catches of whitefish after fall turnover occurred at DO levels from 5.6 to 13.2 mg·L^{-1} (Fig. 8B). Median DOs for netted whitefish were 7.3, 8.2, and 8.7 mg·L^{-1} in the eastern basin, Pennsylvania Ridge, and central basin, respectively.

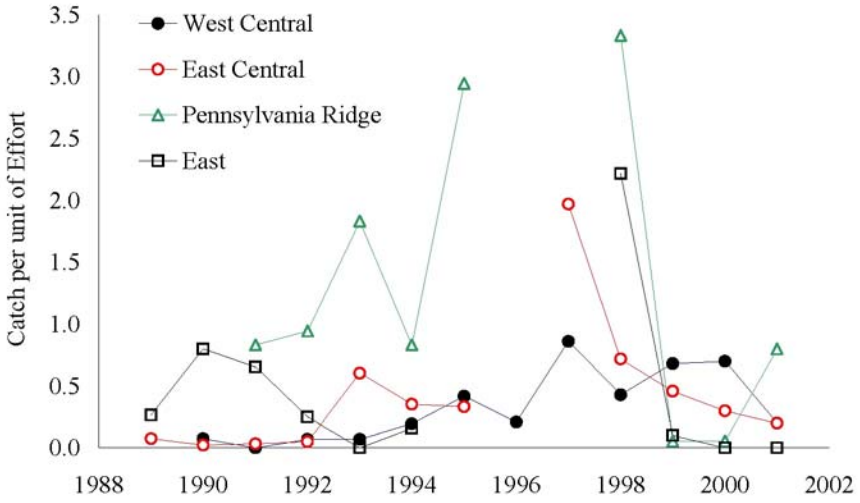


Fig. 6. CPE (arithmetic mean number per gillnet set) of whitefish in the west-central, east-central, and eastern basins and Pennsylvania Ridge in Lake Erie (1989-2001).

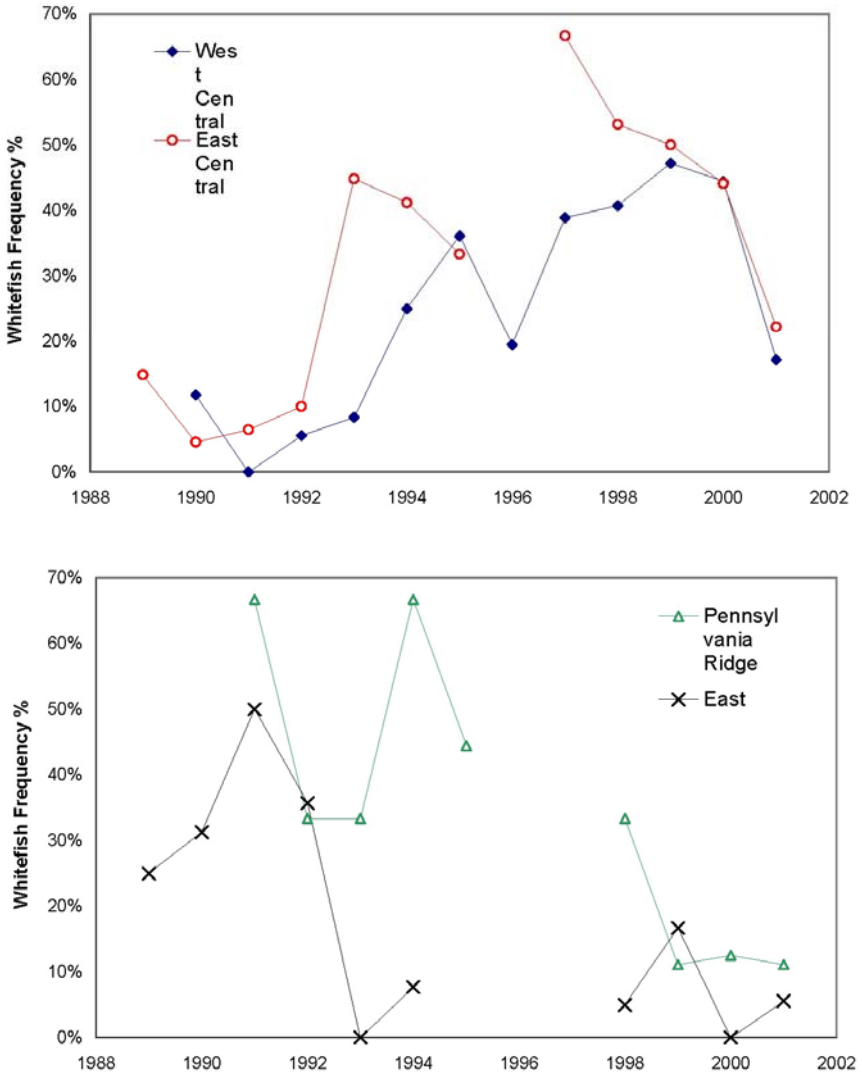
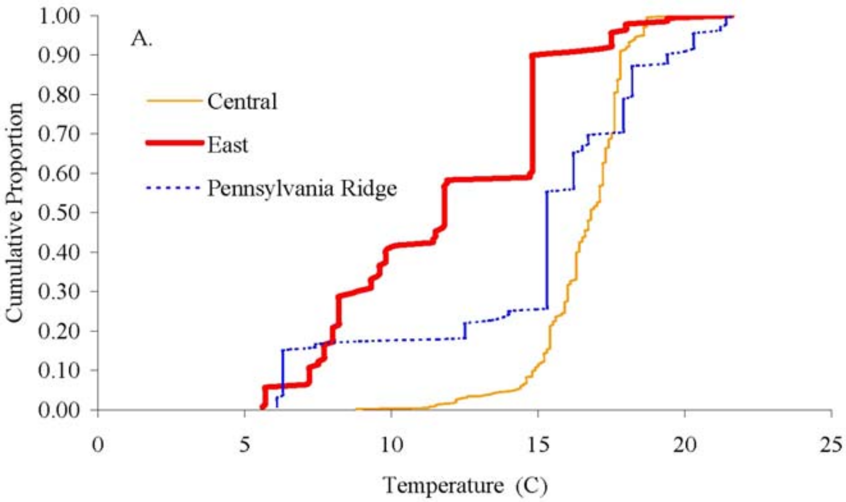


Fig. 7. Proportion of gillnet sets that captured at least one whitefish at various locations in Lake Erie (western central basin (●), eastern central basin (○), Pennsylvania Ridge (Δ), eastern basin (□)).

Temperature and oxygen profiles (Fig. 9) for the central basin were recorded on August 29, 2001. Based on criteria describing whitefish refugia (Evans 1978) and on temperature and oxygen profiles taken under conditions of thermal stratification on August 29, 2001 (Fig. 9), whitefish habitat comprises <9% of the area and <7% of the volume of the central basin. In contrast, whitefish habitat amounts to 54% of the area and 78% of the volume of the eastern basin (Fig. 9).



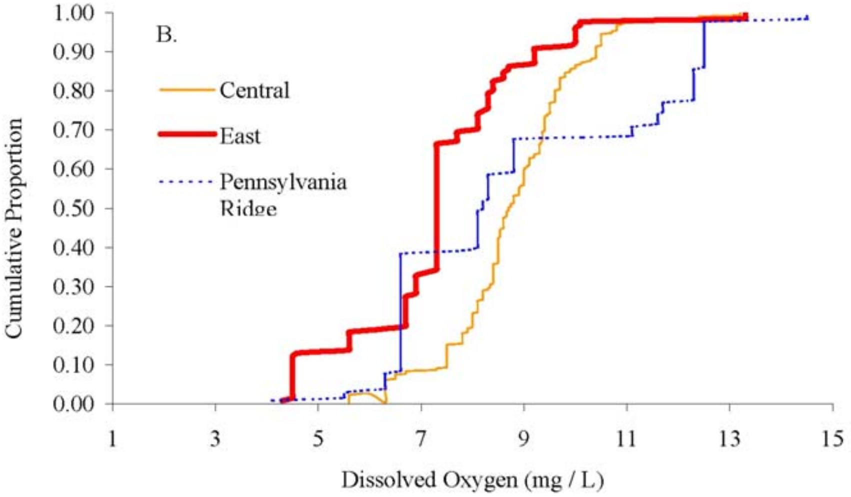


Fig. 8. Cumulative proportion of whitefish catches as a function of water temperature (A) and dissolved oxygen (B).

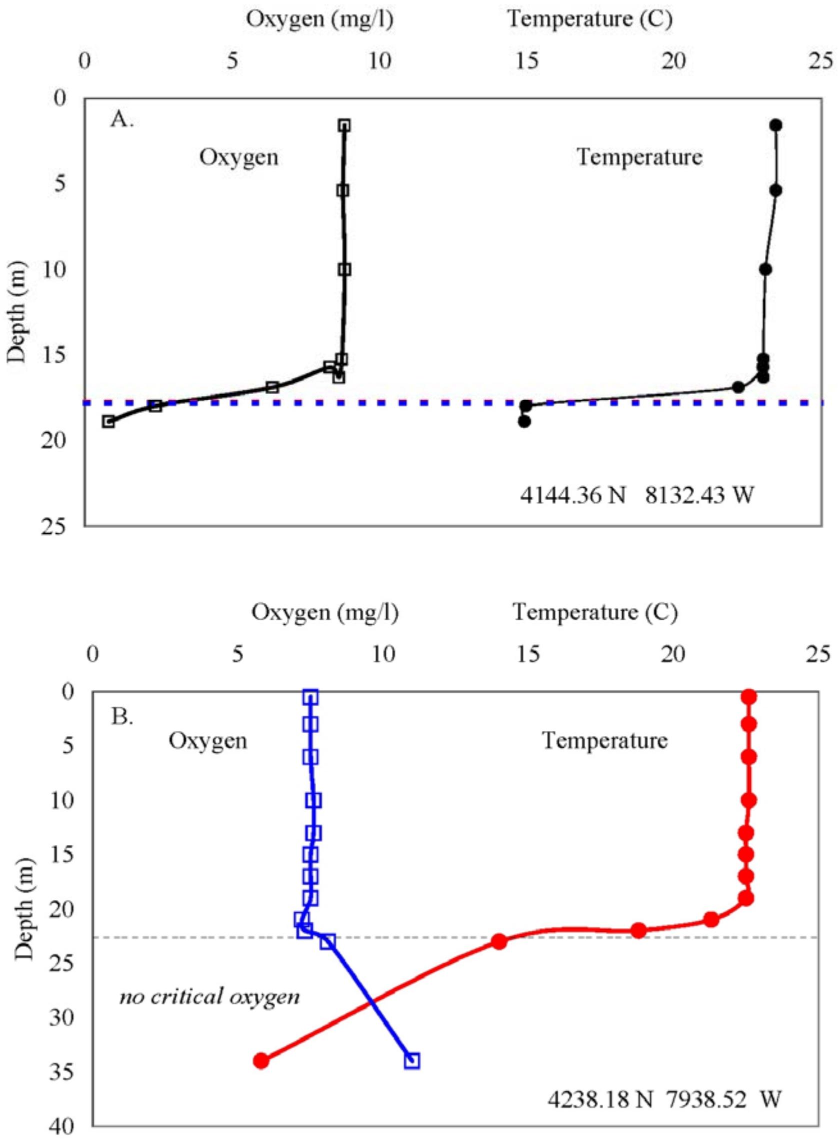


Fig. 9. Water temperature and oxygen profiles of the central (A) and eastern (B) basins of Lake Erie in late August, 2001.

Discussion

Exploitation, watershed degradation, eutrophication, and invading species all contributed to the decline of Lake Erie's whitefish population in the mid-1900s (Hartman 1972; Leach and Nepszy 1976). Eutrophication was also a major factor by 1900 in the disruption of whitefish runs into the Detroit River (Hartman 1972). Also, silt from the Maumee River smothered Maumee Bay spawning areas and led to reduced catches by 1918 (Trautman 1981). High inputs of phosphorus led to oxygen depletion and reduced summer habitat in the central basin by the mid-1950s (Hartman 1972). Reduced phosphorus loadings and more-favorable conditions for whitefish were achieved by the early 1980s (Dolan 1993) following the implementation of the Great Lakes Water Quality Agreement in 1972 (Hardy 1994; Ryan et al. 1999; Ludsin et al. 2001).

Rainbow smelt (*Osmerus mordax*), present in Lake Erie at least since 1935 (Van Oosten and Hile 1937), were considered detrimental to whitefish recruitment (Hardy 1994; Ryan et al. 1999). Ontario's trawl fishery for smelt intensified during the 1970s and 1980s, reducing the population (Ryan et al. 1999; Baldwin et al. 2002). Reductions in smelt biomass also coincided with increased predation by a growing walleye (*Stizostedion vitreum*) population and reduced pelagic productivity associated with decreased nutrient loading and zebra mussel (*Dreissena polymorpha)* colonization (Ryan et al. 1999). Whitefish recruitment has been favorable during much of the 1990s (Lake Erie Cold Water Task Group 2001) despite changes in the composition of the benthic invertebrate community (MacDougall et al. 2001).

Comparing the current population of whitefish to the historical population is difficult because historical assessment data are lacking and commercial fisheries have changed drastically. Notwithstanding these caveats, Ontario's harvest from 1909 to 1953 (707 mt) was 30% greater than from 1998 to 2001 (543 mt). Lake-wide harvest for the 1909 to 1953 period (1249 mt) was more than double the recent annual average (563 mt). Considering the persistence of the high historical harvest, one could speculate that historical conditions were more favorable than present conditions for whitefish. During the late 1990s, sea lamprey (*Petromyzon marinus*) marking rates on lake trout (*Salvelinus namaycush*) increased, reflecting increased parasitism, but sea lamprey marks on whitefish were rare (0-0.6%), suggesting a low frequency of attacks. Therefore, sea lampreys at present levels of abundance do not appear to be a threat to the whitefish population.

The deepwater amphipod *Diporeia* spp. (hereafter, diporeia as a common name), a prey of whitefish (Hardy 1994), was no longer present in benthic samples in eastern Lake Erie by 1993 (Dahl et al. 1995). With the loss of diporeia, whitefish turned to other invertebrate prey: chironomid larvae and pupae, sphaerid clams, gastropods, isopods, leeches, dreissenid mussels, amphipods, oligochaetes, and zooplankton were collected from adult whitefish stomachs. Zooplankton was more common in the diets of young-of-the-year whitefish (C. E. Lumb, Department of Biological Science, University of Windsor, Windsor, Ontario, Canada, N9B 3P4, pers. commun.).

Whitefish were harvested incidentally during the 1980s and until 1991 when they began to be targeted by the gillnet fishery (Ryan et al. 1999). The 1984 year-class was strong and gave rise to ensuing strong year-classes. Harvest increased gradually until 1997 and has averaged 563 mt from 1998 to 2001 (Lake Erie Cold Water Task Group 2001). Ontario's gillnet fishery accounted for 96% of the lake-wide catch in 2001. The remaining 4% were taken in Ohio's trapnet fishery. The mean age of whitefish harvested in the Ontario fishery in the fall and in the Ohio trapnet fishery has been >5 years since 1997. A market for whitefish eggs (caviar) was developed during the 1990s. A trawl fishery has operated on an experimental basis for several years in eastern Lake Erie, but it produces a negligible fraction of the lake-wide harvest. Pennsylvania's gillnet fishery harvested significant quantities of whitefish until gillnetting ceased in 1996.

Contemporary and historical populations of Lake Erie whitefish appear to be similar. Whitefish condition from 1987 to 2001 fluctuated around the 1927-1929 values reported by Van Oosten and Hile (1947) and were similar to those reported by (C. E. Lumb, Department of Biological Science, University of Windsor, Windsor, Ontario, Canada, N9B 3P4, pers. commun.). Further, during the last decade, von Bertalanffy growth curves for whitefish were within the historical range (Hardy 1994). Maturity schedules for the late 1920s differ little from those of today.

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Status of Lake Whitefish (*Coregonus clupeaformis*) in Lake Huron

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Abstract

The commercial harvest of lake whitefish (*Coregonus clupeaformis*) increased throughout Lake Huron during the past 25 years, peaked at 4,486 mt in 1998, and remained high compared to historical levels. Lake whitefish are now the predominant commercial species. Fishing effort shifted offshore in recent years, possibly in response to zebra mussel (*Dreissena polymorpha*) colonization. Catch-per-unit-effort (CPUE) increased steadily in most areas of the lake beginning in the late 1970s. CPUE peaked in the main basin in the mid to late 1990s. CPUE in Georgian Bay and the North Channel held steady. Growth and condition of lake whitefish have declined in the main basin, especially over the last 10 to 15 years. Size-at-age and condition for all age groups are decreasing in southern Lake Huron. In the northern region of the main basin, the older age groups grew more slowly. Declines in growth and condition were associated with a delay in maturation of lake whitefish in the main basin but not in Georgian Bay or the North Channel.

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Introduction

Lake whitefish (*Coregonus clupeaformis,* hereafter whitefish) have traditionally been one of the most important commercial fishes in the Great Lakes. First Nations' subsistence fisheries existed for the species long before Europeans arrived in the Great Lakes region (Brown et al. 1999). As the region became increasingly populated, the need for food increased, and commercial fisheries were eventually established on all of the Great Lakes. The commercial fishery in Lake Huron has changed dramatically during the past 30 years. In the mid 1960s, the state of Michigan's Department of Natural Resources (MDNR) reduced the amount and distribution of fishing activity in U.S. waters (Brown et al. 1999; Kocik and Jones 1999). In 1984, the Ontario Ministry of Natural Resources (OMNR), in conjunction with the fishing industry, introduced a modernization program that changed how fishing effort and harvest were managed in Ontario's waters. Court decisions in Canada (R. *v.* Sparrow 1990; R. *v.* Jones 1993) and the United States (U.S. v. Michigan 2000) led to further changes in the distribution and type of commercial fishing effort as Native Americans and First Nations expressed their treaty and aboriginal rights. Furthermore, recent changes in fishing technology have increased the power and efficiency of the commercial fleet in Lake Huron, which direct affect whitefish populations and population assessment (Brown et al. 1999).

The objective of this report is to document the changes that have occurred in whitefish populations and in the whitefish commercial fishery of Lake Huron over the past 100 years. We focus especially on changes during 1970-2000 for which more comprehensive data are available.

Materials and Methods

Commercial harvest records are a valuable source of information on whitefish and were used extensively in this report (Baldwin et al. 1979; Baldwin et al. 2002). Daily reports of fishing effort and harvest have been provided on a monthly basis to the MDNR by the U.S. commercial fishery since 1929. A similar reporting system was used by the Canadian commercial fishery until 1990. Since 1990, commercial fishermen in Ontario waters have been required to complete a daily catch report for each fishing trip and to submit it prior to landing any fish.

We use catch-per-unit-effort (CPUE) calculated from catch reports as a measure of the relative abundance of whitefish in Lake Huron. CPUE in this report is uncorrected for changes in gear efficiency or set duration and is simply the total annual harvest of whitefish divided by total annual targeted effort. Commercial catch reports also provide information on the type of gear used and the spatial and temporal distribution of effort.

Management agencies also collect detailed biological data to assess whitefish populations in Lake Huron. Collection is done in one of two ways. The three management agencies in Lake Huron (Chippewa/Ottawa Resource Authority, OMNR, and MDNR) sample the commercial catch for catch-at-age, mortality, growth, and condition (Mohr et al. 1997; Ebener 2002). These agencies also conduct, to various degrees, index netting designed to gather fishery-independent data. Index netting targeted at whitefish has been conducted in Canadian waters since 1977 (Mohr et al. 1997; Cottrill 2002). Community index data have been collected in U.S. waters since 1968 (Ebener 2002). Index netting provides population-specific information such as maturity, mortality, recruitment, growth and condition, relative abundance, and age composition. Condition is interpreted as changes through time in weight of fish of a fixed length. This information is generally analyzed and summarized by statistical district in Lake Huron (Fig. 1). For the purposes of this report, the data from statistical districts OH-4 and OH-5 have been combined and will be referred to as OH-4/5.

Population abundance and biomass are estimated for various whitefish populations throughout the lake using several methods. Statistical catch-at-age models have been developed for five populations in U.S. waters (Bence and Ebener 2002; Ebener et al. 2005) and six populations in Canadian waters (LCM, unpubl. data). Cohort analysis (Pope 1972) has been used to model the same populations in Canadian waters annually since 1994 (Mohr et al. 1997).

Fig. 1. Map of Lake Huron showing statistical districts used to report and summarize lake whitefish data in this report.

Results

During the first half of the last century, whitefish made up approximately 15% of the total commercial harvest from Lake Huron (Fig. 2).

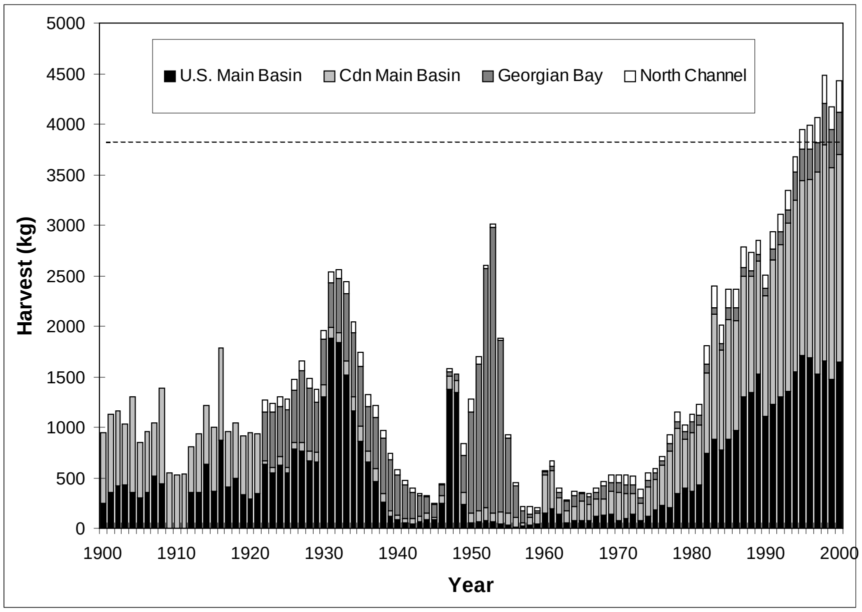

Fig. 2. Total annual commercial harvest of lake whitefish in Lake Huron, 1900-2000. Dashed line is the recommended fish-community objective yield for all coregonines.

Harvest declined by an order of magnitude from the mid-1930s to the mid-1940s. A brief resurgence was seen in U.S. waters in the late 1940s and in Georgian Bay in the early 1950s. By 1958, however, the lakewide whitefish harvest reached an all-time low of just over 200,000 kg (Fig. 3). The harvest remained very low until the mid-1970s when it began to increase steadily (Fig. 3), eventually surpassing the 3.8 million kg sustainable annual harvest target set by Desjardine et al. (1995) as a fish-community objective for all coregonines in Lake Huron. This target has been exceeded each year since 1993; since 1993, the annual harvest averaged just less than 4.2 million kg and peaked in 1998.

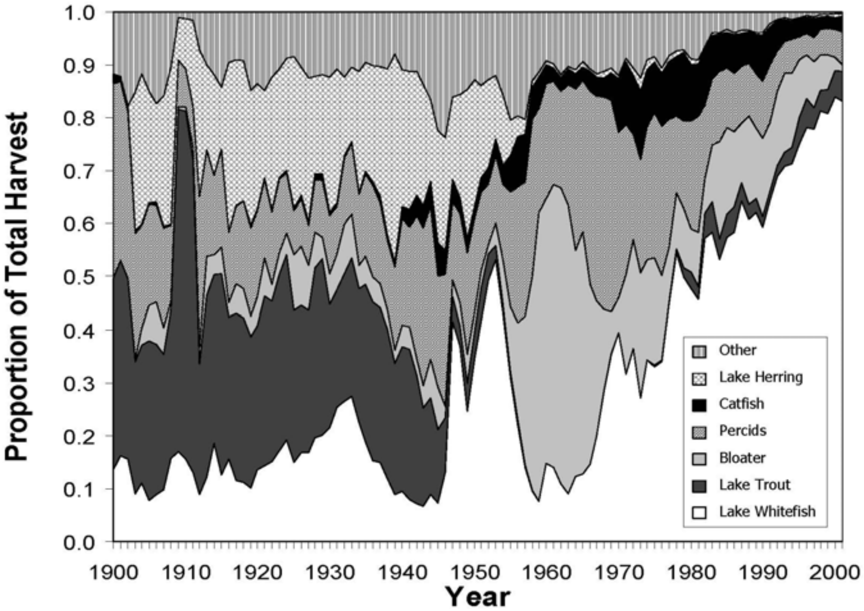

Fig. 3. Proportion of the total lakewide commercial harvest in Lake Huron by individual species, 1900-2000.

The CPUE of whitefish in the gillnet fishery was higher in the 1990s than in the 1980s in most basins of Lake Huron (Fig. 4). The targeted fishery in treaty waters of the main basin, while varying from year to year, showed no long-term trends. Recently, declining CPUE has been observed in the Canadian waters of the main basin, but values remain above those seen in the early 1980s. CPUE in Georgian Bay and the North Channel gillnet fisheries continues to increase. Abundance and biomass estimates generated from VPA models also indicate increasing numbers from the 1980s through the mid-1990s (Bence and Ebener 2002; LCM, unpubl. data). In almost all districts modeled, biomass peaked in 1996, plus or minus a year, and has decreased ever since. The only exception was district GB-4 (southern Georgian Bay) where biomass was still increasing in 2000.

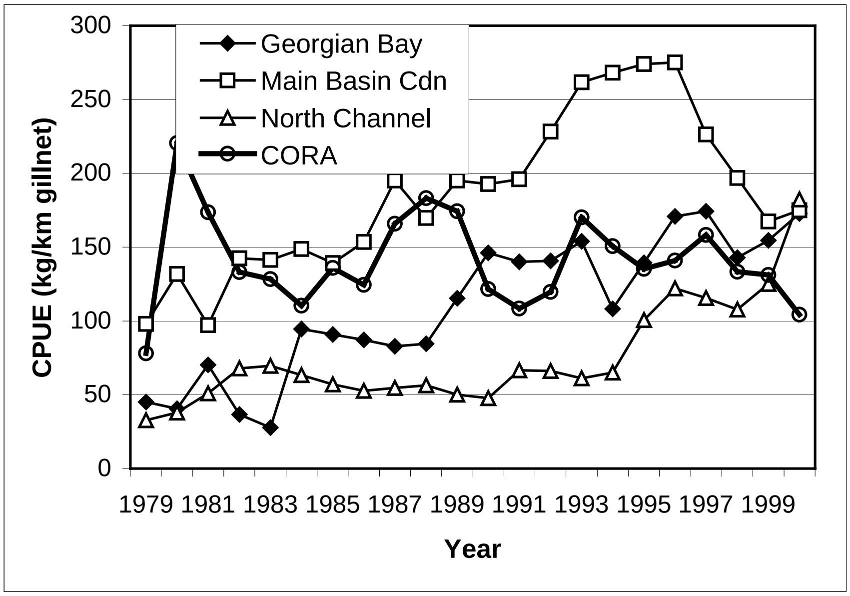

Fig. 4. Relative abundance of lake whitefish in the gillnet fishery in four regions in Lake Huron, 1975-2000.

CPUE in the trapnet fishery also suggests that whitefish populations have increased in the main basin of Lake Huron, peaking in the mid-1990s (Fig. 5). As in the gillnet fishery, CPUE has recently declined in districts OH-4/5 (southern main basin) but still remains four to five times higher than CPUE was a decade ago. CPUE in the trapnet fishery in OH-1 (southern Manitoulin Island) has never been higher since records were kept.

In the 1980s, fishermen began shifting from nylon to monofilament gillnets. The fishery has also shifted to deeper (taller) nets, especially in MH-1 (northern U.S. waters). Whereas the majority (75%) of gillnets used in the 1970s were 36-meshes tall, most fishermen (82%) in the 1990s were using nets that were 50-meshes tall, and an additional 15% were using nets that were 75-meshes tall. Similar changes and a shift to a slightly larger mesh size (from 4.5 to 4.75 inches) have taken place in Canadian waters over the past 20 years.

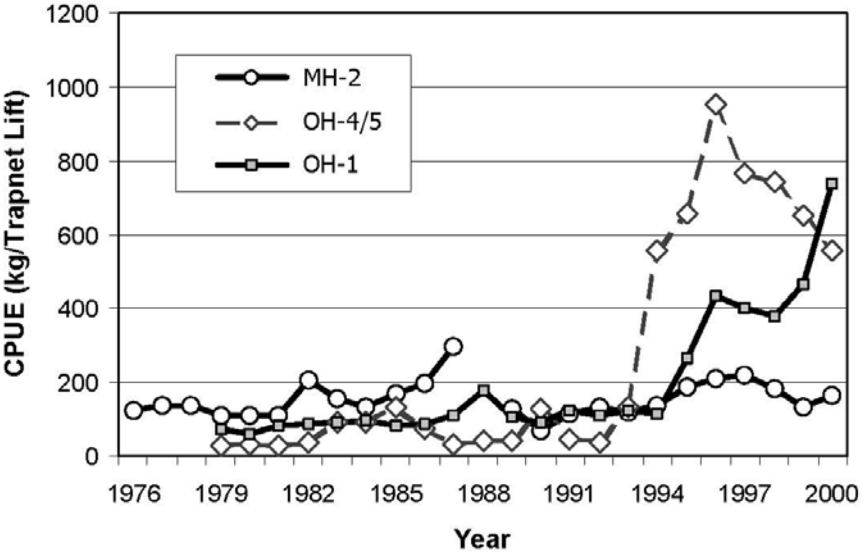

Fig. 5. CPUE of lake whitefish in the trapnet fishery in three statistical districts in Lake Huron, 1976-2000.

The distribution of commercial fishing effort shifted to offshore waters during the 1990s. The average fishing depth in OH-4/5 (southern main basin) increased from 30 m in 1992 to 61 m in 1999. Similar changes were reported in districts OH-1, OH-2, and OH-3 (central and northern main basin) and GB-4 (southern Georgian Bay). Trapnets, which were traditionally a gear for shallow nearshore areas, are now used consistently in waters deeper than 30 m (sometimes as deep as 46 m) in northern Lake Huron.

Recruitment of whitefish has been variable over the past 20 years. A pre-recruit index for age-1 to -3 whitefish in Canadian waters indicates that several strong cohorts were generated in the late 1980s and early 1990s in OH-3 (main basin) and GB-4 (southern Georgian Bay) (Fig. 6). These strong cohorts were from 1992 to 1997 followed by weaker-than-normal year-classes that are currently fully recruited to the fishery in both basins.

Cumulative CPUEs for whitefish from MH-1 (northwestern main basin, U.S.) show a similar pattern, peaking in 1989 and declining thereafter.

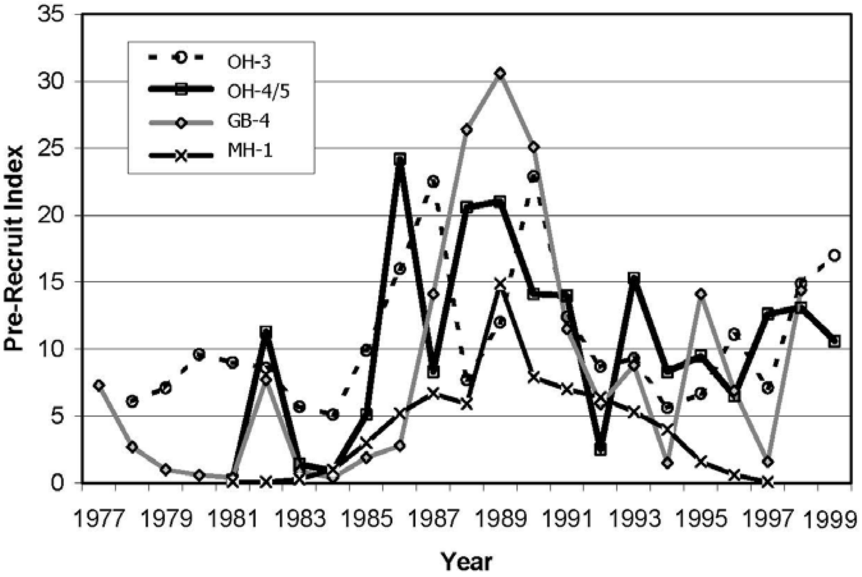

Fig. 6. Pre-recruit (ages 1-3) index for lake whitefish from four statistical districts in Lake Huron, 1977-1999.

The age structure of harvested whitefish has changed over the past 20 years. In districts OH-4/5 (southern main basin), the mean age increased steadily from 2.6 years in 1983 to 7.6 years in 2000. Since then, mean age has remained relatively stable. Whereas age 3 was the modal age in the early 1980s, age 8 was the modal age in 2000 (Table 1). In district OH-1 (northern main basin), the increase in the mean age of the harvest has been less dramatic. The mean age in this district was relatively stable averaging 4.9 years from 1975 to about 1993. Since 1997, the mean age has averaged 7.1 years. The modal age in this district was 4 or 5 years throughout the 1970s and 1980s. These two age groups generally made up 70-80% of the catch. Since 1997, the modal age in this district increased to age 7.

Table 1. Catch-per-unit-effort (number/km gillnet) by age for lake whitefish in southern waters of the main basin of Lake Huron, 1985-2000.

Age	1985	1986	1987	1988	1989	1990	1991
1	0	0	0	0	0	0	0.1
2	0.3	2.1	5.2	13.4	2.8	4	0.4
3	131.2	38.2	18.9	30.2	62.7	36.5	44.1
4	20.5	94.3	23.5	17.3	23.6	77.4	25.5
5	12.2	8.3	66.8	15.1	14.1	17.6	43.8
6	2.6	2.8	12.0	29.6	12.2	8.3	10.6
7	0.5	0.5	5.9	5.3	26.9	11.1	6.8
8	0. 9	0.5	1.7	3.6	5.9	21.7	10.3
9	0.03	0.1	1.2	1.2	3.1	7.3	12.4
10	0	0.1	0.03	0.4	1.1	4.5	2.9
11	0.1	0	0.3	0.1	0.2	1.1	0.8
12	0.03	0	0.02	0.1	0	0.6	0.1
13	0	0	0	0.1	0.1	0	0.1
>13	0	0	0	0	0.1	0.1	0.1

Table 1, continued.

Age	1992	1993	1994	1995	1996	1997	1998	1999	2000
1	0	0	0	0	0	0	0	0	0
2	0.2	0	0	0.1	0	0	0	0	0
3	15.2	4.3	1.9	0.3	0.1	0	0	0	0
4	72.8	122.1	44.1	8.5	5.5	2.4	0.9	0.2	0
5	23	55.1	110.3	73.5	41	22.1	7.7	8.5	8.1
6	33.6	13.5	43.1	93.5	104.2	75.6	23.3	32.4	45.9
7	13.2	15.1	17.1	28.8	61.7	106.5	70.4	61.5	50.1
8	8.8	6.6	10.3	12.6	24.2	48.1	93.9	88.5	58.0
9	9.5	4.5	8.6	6.8	8.3	16	44.1	60.2	61.6
10	6.9	3.9	4.3	3.7	3.7	5.1	20.0	15.7	22.3
11	1.5	2.5	2.4	2.3	2.2	2.3	3.9	4.1	6.9
12	0.3	0.2	1	0.9	0.9	0.6	1.9	1.9	1.0
13	0	0	0.4	0.4	0.2	0.2	0.4	0	0
>13	0	0.1	0	0	0	0	0	0	0

Mean age of the harvest decreased to 3.4 years from 1975 to 1985 in GB-4 (southern Georgian Bay). Since then it has been steadily increasing, reaching 6.1 years in 2000. The modal age has changed slightly from age 3 in 1985 to age 5 during the last four years.

Age-at-maturity has increased substantially in the southern districts of the main basin but not in other parts of the lake (Fig. 7). In district OH-4/5 (southern main basin), 50% of the females were mature at age 3.7 in 1989, and at age 5.9 in 1998. Meanwhile, in districts GB-4 (southern Georgian Bay) and MH-1 (northern U.S. waters), the age at which 50% of females were mature changed only marginally between 1989 and 1998 (from 3.3 to 3.6 years in GB-4 and from 4.3 to 4.8 years in MH-1).

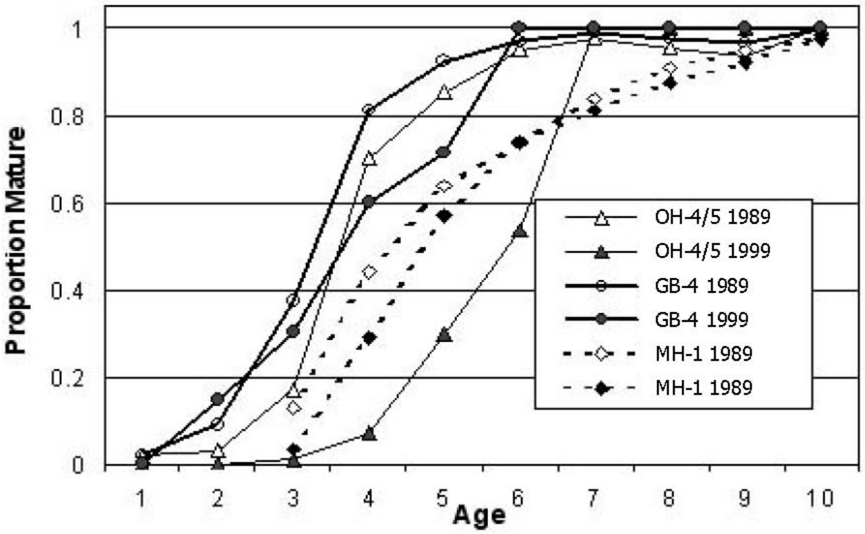

Fig. 7. The proportion of mature female lake whitefish in statistical districts MH-1 and OH-4/5 of the main basin and GB-4 (Georgian Bay), 1989-1999.

Of all the life-history traits, condition and growth of whitefish in Lake Huron changed most during the past 20 years. Condition has declined throughout the main basin with the greatest changes occurring in the southern districts (Fig. 8). The rate at which condition has declined is much faster in districts OH-4/5 (mean slope for the two districts = -21.0 $g \cdot y^{-1}$) than in MH-1 (mean slope = -6.5 $g \cdot y^{-1}$). Declining condition was more pronounced in larger fish (>500-mm fork length) than in smaller fish (430-mm fork length). A decline in condition was not evident in either Georgian Bay or the North Channel.

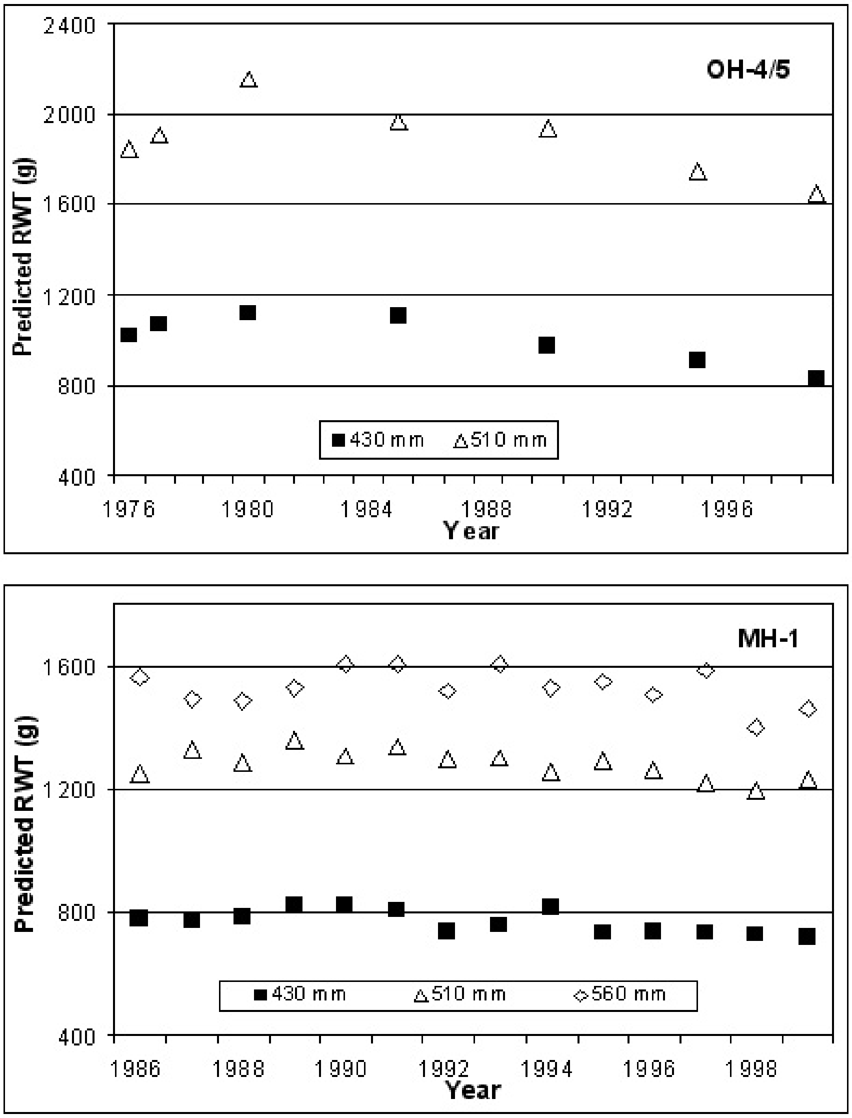

Fig. 8. Predicted (from length-weight regressions) round weight (RWT) for lake whitefish in districts MH-1 and OH-4/5 of Lake Huron. Values are from 1976-2000 for OH4/5 and from 1986-2000 for MH-1.

Whitefish growth (weight-at-age) has also declined over the past 15-20 years in both districts MH-1 and OH-4/5 (Fig. 9). Changes in weight-at-age have been more extreme in OH-4/5 (southern main basin) than in MH-1 (northern main basin). Although whitefish of all ages (3-10) are growing more slowly, the greatest declines were seen in older fish. In 1980, age-10 whitefish from districts OH-4/5 averaged 4.35 kg in weight. In 1999, the average weight for fish of the same age was only 1.69 kg. Growth has recently (1999-2000) leveled off in OH-4/5 and has increased marginally for all age groups. Similar changes in weight-at-age were not seen in the North Channel or Georgian Bay.

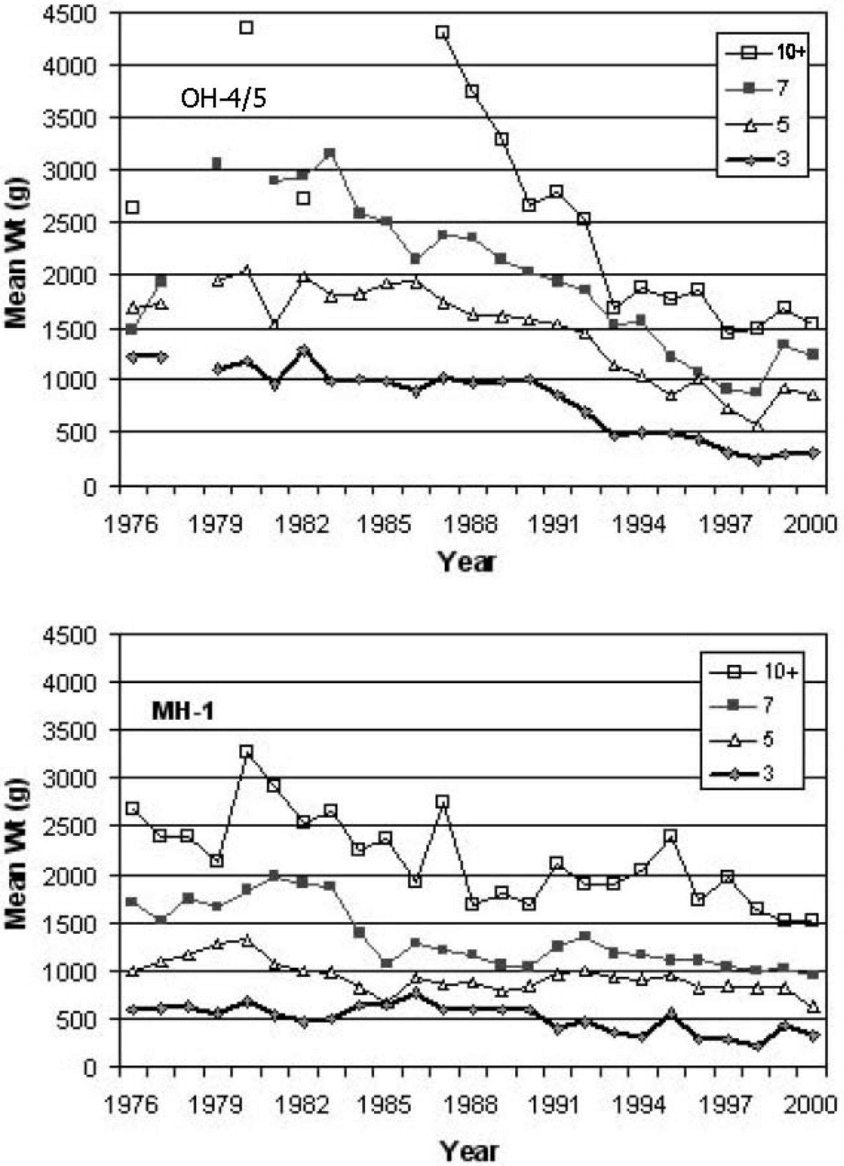

Fig. 9. Weight at ages 3, 5, 7, and 10+ for lake whitefish in districts MH-1 and OH-4/5 of Lake Huron, 1976-2000.

Discussion

Whitefish populations were large during the last 30 years of the 20th century despite large increases in harvest. Since 1993, total lakewide harvests have exceeded the fish-community objectives for the lake (Desjardine et al. 1995; Ebener 2004). However, lakewide harvests have declined since 1998. This drop is consistent with modeled biomass estimates for several districts (Bence and Ebener 2002; LCM, unpubl. data) that show biomass peaking in the mid-1990s.

What triggered the increase in whitefish biomass? Decreased predation of whitefish fry by rainbow smelt (*Osmerus mordax*) and alewife (*Alosa pseudoharengus*) and increased survival of adult whitefish due to increased sea lamprey (*Petromyzon marinus*) control begun in the 1960s probably contributed to the population resurgence. Populations of alewife and rainbow smelt have been suppressed (Fig. 10), likely by salmonines that have been stocked intensively in Lake Huron since 1968 (Kocik and Jones 1999). Large cohorts produced from the mid-1980s to the early 1990s (Fig. 6) have also contributed to the increased biomass during the past 15 years. Weaker-than-normal cohorts in the late 1990s may cause a decline in abundance in the main basin as they recruit to the commercial fishery, starting in 1998.

The whitefish population resurgence may also have been abetted by lessened competition from other coregonines whose populations were declining during the same period (1970 to present). Lake herring (*C. artedi*) dominated the coregonine catch historically while whitefish comprised only a small part (35%). The resurgence of whitefish immediately followed the near disappearance of lake herring. After 1990, the yield of deepwater ciscoes (*Coregonus* spp.) declined and is now at an all-time low. This dearth of other coregonines may have allowed whitefish to expand into new niches.

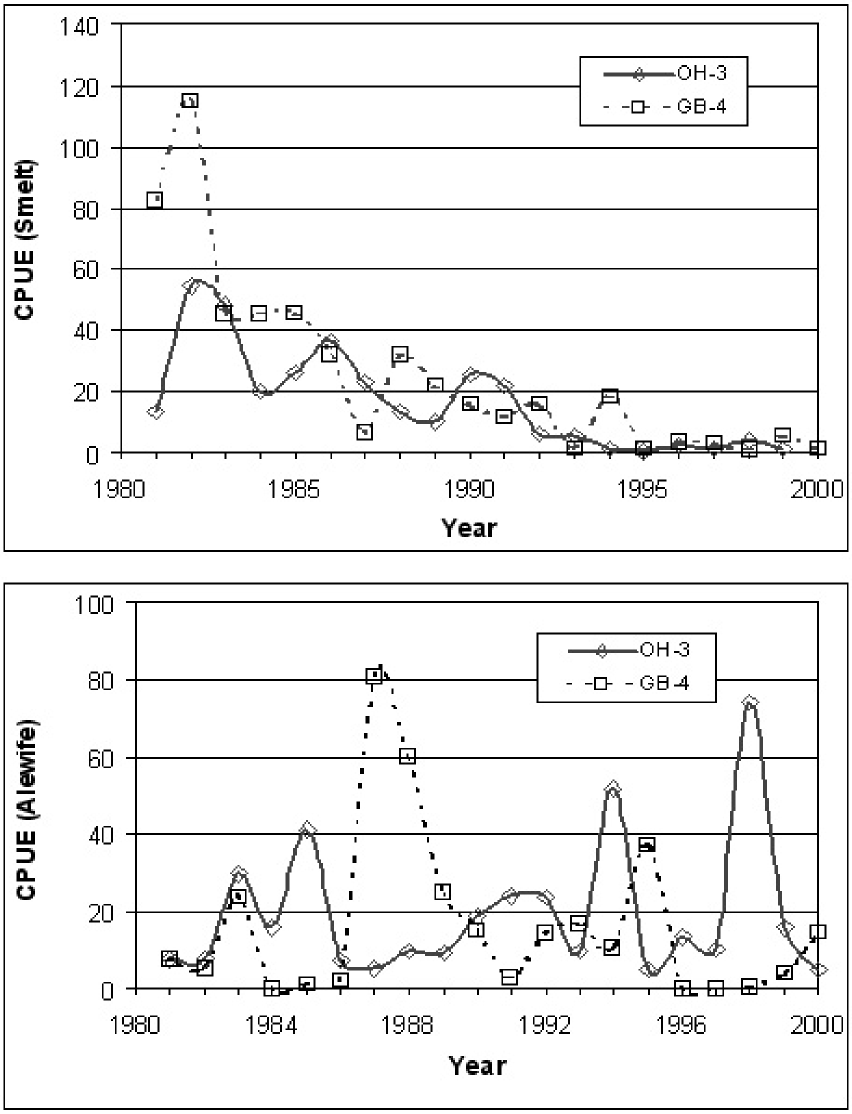

Fig. 10. Relative abundance of alewife and rainbow smelt in two statistical districts of Lake Huron, 1980-2000 (LCM, unpubl. data).

New exotic species may be a stress on whitefish populations in Lake Huron. Zebra mussels (*Dreissena polymorpha*) invaded Lake Huron in 1988 (Mills et al. 1993) and have since colonized the entire lake. Georgian Bay and the North Channel were colonized as late as the mid-1990s. Another dreissenid, the quagga mussel (*D. bugensis*), has also colonized Lake Huron beginning in 1991, and the two together have the potential to affect whitefish directly and indirectly. Reduced zooplankton production and increased light penetration could have major effects on whitefish (Nalepa et al. 1998; Bailey et al. 1999; Hoyle et al. 1999; O'Gorman et al. 2000).

Colonization by dreissenids, moreover, has been associated with population declines of the amphipod *Diporeia* spp. (hereafter, diporeia as a common name), a major whitefish prey. This phenomenon has also been reported in Lakes Ontario and Michigan (Dermott 2001; Nalepa et al. 1998). In 2000, diporeia populations declined markedly in the nearshore regions of the southern main basin, including outer Saginaw Bay. Diporeia, however, remain abundant offshore in the southern main basin, in northern regions of the main basin, and in Georgian Bay and the North Channel (T. Nalepa, National Oceanic and Atmospheric Administration, 2205 Commonwealth Blvd., Ann Arbor, MI 48103, personal communication). The loss of this high-energy food may account for the declines in growth and condition of whitefish in the main basin; similar responses occurred in Lakes Ontario and Michigan (Hoyle et al. 1999; Pothoven et al. 2001).

An offshore shift of commercial fishing effort in the main basin of Lake Huron and in southern Georgian Bay suggests a movement of whitefish into deeper waters. This shift may be an early indication of food-web changes. Further investigation of the benthos in Georgian Bay and the North Channel are urgently needed.

Increased exploitation has been shown to increase growth and reduce age-at-maturity in whitefish (Healey 1975, 1980). Conversely, increasing abundance or minimal exploitation can result in slower growth and an increase in age-at-maturity. Whitefish growth slowed in the main basin as the population was increasing, but it continued to decline as the population decreased. Determining whether a density-response occurred in the main basin is problematic.

Declining abundance, slower growth, increased age-at-maturity, and offshore movement of the whitefish population in the main basin of Lake Huron are of concern to fishery managers. Insofar as fewer or no similar changes are evident in Georgian Bay or the North Channel, the causes apparently are limited to the main basin, or possibly have been in place in the main basin for a longer time. Also important, whitefish in the southern main basin appear to be most affected, which suggests that the causes are population specific.

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BIOENERGETICS AND TROPHIC DYNAMICS

Changes in Lake Whitefish Diet in Lake Michigan, 1998-2001

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Abstract

Lake whitefish (*Coregonus clupeaformis*) were collected for diet analysis from Michigan's waters of Lake Michigan during 1998-2001. When the benthic amphipod *Diporeia* spp. was available, it was an important item in the diets of small (<430 mm) and large (>430 mm) lake whitefish. In southern Lake Michigan, the most-common prey consumed in the absence of *Diporeia* spp. included zebra mussels (*Dreissena polymorpha*), gastropods, chironomids, and *Mysis relicta*. In northern regions of the lake, alternative prey included chironomids, isopods, *Bythotrephes*, and fish. Following the decline of *Diporeia* spp. in southeastern Lake Michigan between 1998 and 2001, their contribution to the diet of small lake whitefish fell from 57% to 1% (dry weight). The contribution of *Diporeia* spp. to the diet was similar for small fish captured in nearshore (9-30 m) and offshore (31-46 m) waters. *Mysis* were more common in the diets of fish collected at offshore stations whereas

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chironomids and zebra mussels were more common in fish from nearshore stations.

Introduction

Recent declines in condition and growth of lake whitefish (*Coregonus clupeaformis,* hereafter, whitefish) in the Great Lakes have been attributed to a number of factors (Hoyle et al. 1999; Pothoven et al. 2001), including declines in the abundance of their benthic prey *Diporeia* spp. (hereafter, diporeia as a common name), increased consumption of zebra mussels (*Dreissena polymorpha*), and density-dependent factors.

There is little information on the diet of whitefish even though the species has long been a mainstay of the commercial fishery. Available information indicates that the diet of whitefish in the Great Lakes historically consisted of amphipods, chironomids, gastropods, and *Mysis* (Ihssen et al. 1981; Jude et al. 1981). More-recent data indicate that the decline of diporeia and the proliferation of zebra mussels may have resulted in changes in the diet of whitefish (Hoyle et al. 1999; Pothoven et al. 2001).

The objective of this study was to evaluate the diet of whitefish in Lake Michigan and to determine future research needs.

Methods

Whitefish were collected from 13 stations located in seven of ten Lake Michigan whitefish management zones (WFM) (Fig. 1). Whitefish were collected in water 9- to 46-m deep using monofilament gillnets (6.4- to 17.8-cm stretched mesh) and a 7.6-m semi-balloon, 4-seam bottom trawl (13-mm stretched-mesh cod-liner). Sampling took place during April-October 1999-2001, but most fish (73%) were collected in the spring (April-June). Whitefish were also collected during 1998 from WFM-08. No fish were collected for diet analysis from either WFM-00, WFM-01, or WFM-03.

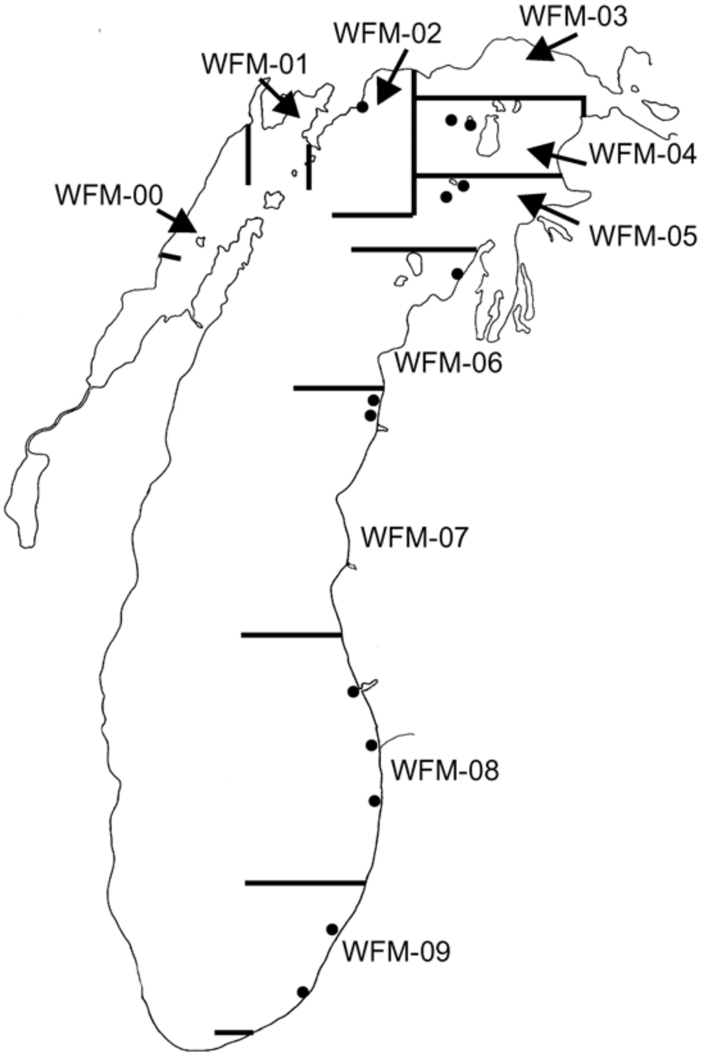

Fig. 1. Location of stations (•) and whitefish management zones (WFM) where whitefish were collected for diet analyses, 1998-2001.

All fish were weighed and measured, and stomachs (esophagus to pyloric caeca) were removed and frozen. In the laboratory, stomachs were dissected and prey items were identified and counted. Approximately 25% of stomachs were empty and were not included in subsequent analyses. Lengths of whole prey were measured using a computer image-analysis system. Length-weight regressions from the literature were used to compute the mean individual weight for each prey type (Johnson and Brinkhurst 1971; Nalepa and Quigley 1980; Smock 1980; Shea and Makarewicz 1989; Makarewicz and Jones 1990; Prejs et al. 1990; T. Nalepa, Great Lakes Environmental Research Laboratory, 2205 Commonwealth Blvd., Ann Arbor, MI, 48105, personal communication). Dry weights of partially digested prey were assumed to be equal to the mean weight of measured prey of the same species. Microzooplankton (Copepoda, Cladocera) were added to a known volume of water and subsampled with a Hensen-Stemple pipette. For species that were not measured, total counts were multiplied by representative dry weights (Hawkins and Evans 1979; Nalepa and Quigley 1980) and summed to obtain biomass.

Diets were shown as the percent of the total calculated stomach-content dry weight for fish from each management zone, year, or depth zone. Diet composition was determined separately for small (<430 mm) and large (>430 mm) whitefish. These size-classes were chosen based on the legal size limit for whitefish in the commercial fishery. Results were summarized for each management zone to detect regional differences. Stomach-content data from WFM-02, WFM-04, and WFM-05 were combined because of the small sample sizes in these northern zones. Fish from WFM-08 were used to examine temporal changes in diet during 1998-2001. Diets were also compared for fish collected from nearshore (9-30 m) stations vs. offshore (31-46 m) stations.

Results and Discussion

Based on data collected during 1998-2001, the diets of whitefish were variable throughout Lake Michigan. In some areas, the regional differences in diet reflected regional differences in the density of diporeia. The diet of large whitefish consisted mainly (95%) of age-0 alewife (*Alosa pseudoharengus*) in the northernmost zones (WFM-02, WFM-04, and WFM-05) of Lake Michigan (Table 1). The invertebrates *Bythotrephes* (3%) and diporeia (1%) were also found but were at very low levels. In WFM-06, the diet of large whitefish consisted of isopods (61%) and chironomids (37%) (Table 1). No diporeia were found in whitefish stomachs in WFM-06. The density of diporeia in the lake was relatively low ($<1{,}000 \cdot m^{-2}$) in WFM-02, WFM-04, WFM-05, and WFM-06 during this study (T. Nalepa, Great Lakes Environmental Research Laboratory, 2205 Commonwealth Blvd., Ann Arbor, MI, 48105, personal communication).

Table 1. Percent of total dry weight for diet items of small (<430-mm TL) and large (>430-mm TL) whitefish collected from WFMs in Lake Michigan, 1999-2001 (WFM-08, 1998-2001). *N* = number of whitefish used for analyses. Length = mean length (mm TL) of fish used for analyses.

	Small fish			Large fish				
Diet item	WFM -07	WFM-08	WFM-09	WFM-02, 04, 05	WFM-06	WFM-07	WFM-08	WFM-09
Diporeia	53	38	0	1	0	84	19	0
Chironomidae	9	31	38	<1	37	6	6	10
Dreissena polymorpha	1	6	17	<1	<1	<1	23	35
Mysis relicta	20	9	0	0	0	5	26	<1
Sphaeriidae	1	6	8	<1	<1	2	5	5
Gastropoda	0	4	31	<1	1	<1	13	48
Isopoda	2	<1	0	<1	61	1	<1	0
Bythotrephes	0	1	0	3	0	0	1	0
Fish	14	1	0	95	0	2	0	0
Other	<1	5	6	0	1	1	6	1
N	20	215	28	29	14	41	90	32
Length	376	349	367	629	495	492	467	455

Diporeia accounted for 53% and 84% of the diet of small and large whitefish, respectively, in WFM-07 (Table 1). Whitefish were only collected from the northern portion of WFM-07 where the density of diporeia was 2,000-3,000$\cdot$m^{-2} in 2000. The density of diporeia in WFM-07 had not been particularly high (3,000-4,000$\cdot$m^{-2}) relative to other regions in the lake in 1994-1995 (Nalepa et al. 2000). Zebra mussels were not an important component of the diet of whitefish in either the northern or central management zones.

In WFM-08, the diet of whitefish consisted of several prey items including diporeia, chironomids, *Mysis*, zebra mussels, and gastropods (Table 1). Drastic declines of diporeia occurred in WFM-08 during 1998-99, although the species persisted at densities of 5,500$\cdot$m^{-2} in the northern portion of this management zone (Pothoven et al. 2001). Sufficient numbers of whitefish were caught in WFM-08 to examine temporal changes in diet relative to the declines of diporeia between 1998 and 2001. By 2000, the densities of diporeia ranged from near zero to 1,000$\cdot$m^{-2} (Pothoven et al. 2001). In 1998, the diet of small whitefish in WFM-08 consisted mainly of diporeia (57%) and chironomids (20%) (Table 2). Following the decline of diporeia in 1999, the diet of small whitefish consisted mainly of chironomids (66%). The percentage of diporeia in the diet increased from 7% in 1999 to 33% in 2000. The contribution of *Mysis* increased from 0-3% to 30% between 1998-99 and 2000. Diporeia had declined to very low densities in WFM-08 in 2001. In that year, chironomids (34%) and *Mysis* (35%) were the main prey consumed by small whitefish, while diporeia comprised 1% of the diet.

Table 2. Percent of total dry weight for diet items of small (<430-mm TL) and large (>430-mm TL) whitefish collected from WFM-08 in Lake Michigan, 1998-2001. *N* = number of whitefish used for analyses.

	Small fish				Large fish	
Diet item	1998	1999	2000	2001	2000	2001
Diporeia	57	7	33	1	31	<1
Chironomidae	20	66	15	34	5	3
Dreissena polymorpha	9	2	1	3	5	47
Mysis relicta	3	0	30	35	42	1
Sphaeriidae	4	2	12	13	7	1
Gastropoda	3	7	<1	7	<1	39
Ostracoda	0	6	<1	<1	<1	< 1
Bythotrephes	<1	0	6	0	2	0
Zooplankton	<1	8	<1	0	0	<1
Other	2	1	3	5	6	9
N	78	62	42	33	45	38
Mean length	355	290	397	387	465	471

Information on the diet of large whitefish in WFM-08 was available only for 2000-2001. In 2000, the diet of large whitefish was similar to that of small whitefish and comprised mainly diporeia (31%) and *Mysis* (42%) (Table 2). In 2001, the diet of large whitefish consisted mostly of zebra mussels (47%) and gastropods (39%).

The increases in diporeia and *Mysis* in the diet in 2000 in WFM-08 could reflect differences in sampling depths among years. In 2000, 42% of the fish in WFM-08 were collected from a 45-m depth, whereas fish were collected from shallower depths (<35 m) in other years. Diporeia and *Mysis* are generally more abundant offshore (Nalepa et al. 2000; Pothoven et al. 2000). *Mysis,* however, were found in stomachs of fish collected from water as shallow as 15 m in April 2000. *Mysis* continued to be an important prey for small whitefish in 2001.

In the southernmost management zone (WFM-09), diets consisted mainly of gastropods and chironomids (for small fish) and zebra mussels and gastropods (for large fish) (Table 1). Diporeia began to decline in WFM-09 in 1992 and were virtually absent by 1997 (Nalepa et al. 2005).

Whitefish may be adapted to consume hard-shelled prey items such as zebra mussels because they historically have consumed molluscs such as gastropods. In the absence of a high-energy prey source (for example, diporeia*)*, however, the consumption of mainly hard-shelled prey could have detrimental bioenergetic consequences for whitefish (Ihssen et al. 1981; French and Bur 1996; Pothoven et al. 2001). Additionally, alternative prey (for example, chironomids) may not be sufficiently abundant to sustain whitefish (Pothoven et al. 2001).

One could expect that the diet of whitefish in northern Lake Michigan will become similar to that in southern regions as diporeia continues to decline and zebra and quagga (*D. bugensis*) mussels increase throughout the lake. On the other hand, diet patterns in the northern regions may not become similar to those observed in the southern regions if prey other than zebra mussels are available. For example, in this study, large whitefish were observed to become piscivorous and/or consume isopods in northern regions of the lake where diporeia were already scarce.

Diets of whitefish collected from nearshore (<30 m) and offshore (31-46 m) areas differed (Table 3). The contribution of diporeia was generally similar between depth zones for small whitefish. Chironomids and zebra mussels were more common in the diets of whitefish from nearshore stations relative to offshore stations, while the contribution of *Mysis* to the diet was much higher offshore. Studies of whitefish diets need to account for differences in depth distribution. Seasonal movements of whitefish between nearshore and offshore areas further complicate such analyses. Additionally, whitefish may be moving farther offshore in the Great Lakes. Although diporeia and other large prey such as *Mysis* are more abundant offshore, bioenergetic costs associated with feeding in deeper, colder water may be high (O'Gorman et al. 2000).

Table 3. Percent of total dry weight for diet items of small (<430-m TL) and large (>430-mm TL) whitefish collected from nearshore (<30 m) and offshore (31-46 m) zones in Lake Michigan, 1998-2001. *N* = number of lake whitefish used for analyses.

Diet item	Small fish		Large fish	
	Nearshore	Offshore	Nearshore	Offshore
Diporeia	38	35	5	35
Chrionomidae	34	9	16	1
Dreissena polymorpha	8	<1	22	<1
Mysis relicta	4	29	<1	58
Sphaeriidae	4	7	2	3
Gastropoda	4	0	4	<1
Bythotrephes	<1	4	<1	2
Fish	0	14	46	0
Other	7	2	4	<1
N	165	39	35	25

There was little correlation between the length of whitefish and the lengths of diporeia ($r^2 = 0.02$) and zebra mussels ($r^2 = 0.10$) that were consumed. The modal length of diporeia in the diet of whitefish was 6-8 mm, indicating that whitefish consumed mostly adults. In contrast, the modal length of zebra mussels (2-4 mm) in the diet of whitefish indicated that the smallest zebra mussels were consumed.

Our data indicate that if diporeia are available, they are an important prey item for both small and large whitefish. *Diporeia* were already beginning to decline at the start of this study (1998), so the species historically may have been an even more important prey. On the other hand, the importance of diporeia in this study could also be somewhat inflated because most fish were collected in the spring. Other fish (for example, bloater (*Coregonus hoyi)* and alewife) are also dependent upon diporeia as a food source during the spring (Rand et al. 1995).

Future research is needed in several areas to understand how changes in the food web of the Great Lakes might affect the diet of whitefish. First, researchers need to have a better understanding of the age-specific and seasonal patterns in diets. Second, researchers need to conduct bioenergetics analyses to understand how the ration of whitefish could be changing. Studies on feeding behavior are needed to understand how prey type, density, and predator size affect foraging patterns and success. Information on diets of whitefish from areas where diporeia remain abundant would provide better insight into the importance of this species as a prey resource.

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Recovery and Decline of Lake Whitefish in U.S. Waters of Eastern Lake Ontario, 1980-2001

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Abstract

The lake whitefish (*Coregonus clupeaformis*) was an important member of the native fish community and a valued commercial species in Lake Ontario. Lake whitefish were common in U.S. waters of the lake until 1965 and very abundant in Canadian waters through the early 1970s, although their numbers declined shortly thereafter. During 1975-1985, lake whitefish stocks remained depressed throughout the lake as a result of the combined effects of degraded water quality, overfishing, and predation. Rainbow smelt (*Osmerus mordax)* probably preyed on whitefish fry, and sea lamprey (*Petromyzon marinus*) preyed on adults. During 1985-1987, lake whitefish stocks began to recover in eastern Lake Ontario, and their buildup continued into the mid-1990s. Reasons for the recovery likely included control of the sea lamprey population and a reduction in the number of piscivorous rainbow smelt. By 1997, lake whitefish abundance had declined severely again; some fish appeared to have dispersed from the northeastern to the southeastern regions of the lake, and the depth of capture increased. We believe that the collapse of *Diporeia* spp. populations during 1992-1999 was responsible for the decline in the lake whitefish populations and the shifts in geographic and bathymetric distribution because lake whitefish fed primarily on *Diporeia* spp. After the collapse of *Diporeia* spp. populations, lake whitefish in southeastern Lake Ontario fed on *Mysis relicta* and quagga mussels (*Dreissena bugensis)*. Changing from a diet of high-lipid *Diporeia* spp. to low-lipid dreissenids and foraging on *Mysis relicta* at lower temperatures are apparently hampering the rebuilding of lake whitefish stocks.

Introduction

Historically, lake whitefish (*Coregonus clupeaformis*, hereafter, whitefish) were an abundant and important commercial species throughout Lake Ontario (Rathbun and Wakeham 1897; Koelz 1926). Commercial landings of whitefish in U.S. waters between 1885 and 1965 ranged from 9-91 mt per year and were roughly 10 times that amount in Canadian waters. By 1966, annual whitefish landings had dropped to <1 mt from U.S. waters. By 1975, the U.S. commercial fishery no longer existed, and whitefish landings had plummeted to 4.5 mt in Canadian waters (Baldwin et al. 1979). The reasons for the decline of whitefish stocks in Lake Ontario likely included predation by sea lamprey (*Petromyzon marinus*) (Christie 1973), overfishing, predation on young-of-the-year (YOY) whitefish by the exotic rainbow smelt (*Osmerus mordax*, hereafter, smelt) (Warner and Fenderson 1963; Bergstedt 1983; Evans and Loftus 1987), and perhaps degradation of water quality (Christie 1973; Hoyle et al., 2003; Owens et al., 2003).

During 1980-1986, whitefish were conspicuously absent in bottom trawl surveys conducted jointly by the U.S. Geological Survey (USGS) and the New York State Department of Environmental Conservation (NYSDEC) in U.S. waters of Lake Ontario (Owens et al., 2003). Whitefish stocks began to recover in eastern Lake Ontario during 1985-1987, and recovery was well under way by 1995 (Hoyle et al., 2003; Owens et al., 2003). In June of 1997, however, off Prince Edward County, Ontario, Canada, emaciated and dead whitefish were observed (suggestive of starvation), and whitefish recruitment declined, which eventually led to a decline in abundance (Hoyle et al. in press). In 1996, whitefish abundance declined near Henderson Harbor, New York, located about 50-km southeast of Prince Edward County. In 1997, an unusually large number of whitefish (about 70) were caught approximately 50 km southwest of Henderson Harbor near Oswego, New York, suggesting that whitefish might have been dispersing from the shallow northeastern basin of the lake.

These recent changes in abundance, bathymetric distribution, and length-weight relationships of whitefish were likely the result of the collapse of the burrowing amphipod *Diporeia* spp., (hereafter diporeia as a common name) population, which began as early as 1992 in eastern Lake Ontario (Owens and Dittman 2003) and spread lakewide thereafter (Dermott 2001; Lozano et al. 2001). Diporeia was the staple item in the diet of whitefish (Hart 1931; Hoyle et al., 2003; Owens and Dittman 2003). Its population collapse coincided with the establishment and expansion of the exotic zebra mussel (*Dreissena polymorpha*) and quagga mussel (*D. bugensis*), first noted in Lake Ontario in 1989 (Mills et al. 1999). In this paper, we describe the rise and fall in whitefish abundance, dispersion from the Henderson Harbor area, changes in bathymetric distribution, and changes in their length-weight regressions in U.S. waters of eastern Lake Ontario during 1980-2001. We also discuss the events that were likely responsible for the changes.

Methods

Determination of whitefish abundance in 1980-2001 followed procedures outlined in Owens et al. (2003). Briefly, abundance was the total number caught each year during four separate bottom-trawl surveys adjusted to a standard effort of 350 tows, which is very close to the average number of tows conducted annually since 1980. Trawl surveys were conducted from mid-April to early November in U.S. waters. The number of locations fished in each survey varied from 6-13, depending on the targeted species. Trawl locations were spaced at about 25-km intervals along the southern and eastern shores of Lake Ontario, starting near Olcott and finishing near the head of the St. Lawrence River (Fig. 1). Because the abundance of whitefish varied geographically, we divided the lake into two regions: eastern and western. The eastern region was further divided into two areas: Henderson Harbor (1, Fig. 1), an area encompassing historically important whitefish grounds where whitefish were most abundant during this study, and Oswego (2, Fig. 1), a transition area where whitefish abundance spiked temporarily in 1997. The western and largest region (3, Fig. 1), where whitefish abundance was uniformly low during 1980-2001, extended from Sodus westward to the Niagara River. Four to eight locations were fished within the western region, depending on the targeted species. About nine tows were made at each location covering depths from 8-150 m with the exception of the Henderson Harbor area where the maximum depth is about 55 m.

Fig. 1. Map of Lake Ontario depicting three geographic areas of varying whitefish abundance. The eastern region comprises two areas: Henderson Harbor (1) and Oswego (2). The western region (3) extends from Sodus westward to the Niagara River.

The trawls used by the USGS and NYSDEC are constructed identically, as are the trawl doors and harness riggings. After 1995, with the exception of the autumn survey that targeted slimy sculpins *(Cottus cognatus),* the USGS 12-m bottom trawl was replaced with a three-seam bottom trawl featuring small rollers to counteract heavy fouling by the rapidly increasing population of dreissenids. Trawling depths remained the same as in previous surveys. The new trawl was calibrated against the old trawl by making over 100 side-by-side tows. In theory, whitefish should be more vulnerable to the three-seam bottom trawl because the three-seam bottom trawl's opening is twice as high as that of the 12-m trawl, although its spread is similar. The three-seam trawl was towed at the same speed as the old trawl. During our calibration trials, 17 whitefish were caught in the three-seam trawl compared with 10 whitefish in the 12-m bottom trawl. We did not attempt to calculate a conversion factor because no whitefish were taken in either net in over 95% of the paired tows. Therefore, we assumed that whitefish were similarly vulnerable to the old and new gear. All whitefish were measured (total length, mm) and weighed (nearest g) shortly after capture.

We used analysis of covariance (ANCOVA) to test for differences in length-weight regressions for mature whitefish (≥300 mm) during two time periods: pre-dreissenid colonization (1983-1990) and post-dreissenid colonization (1992-1999). We used a $\log_{10}$ transformation to linearize the data. If the ANCOVA indicated that the slopes were equal, we used least-squares means to test for differences in elevation of regression lines. The first dreissenids were caught in our trawls in 1991, which is the year we used to separate the two time periods (pre- and post-colonization).

The recovery of whitefish may be related to the reduction of large smelt through predation by salmonines. To determine if the resurgence of whitefish followed or preceded the decline in abundance of smelt, we calculated the abundance of large (≥150-mm) smelt from the average number caught per 10-min tow during our joint bottom-trawl surveys conducted annually in June, 1980-2001. To obtain the total catch of large smelt, the number of all smelt caught in one tow was multiplied by the proportion of smelt ≥150 mm from length-frequencies for smelt from nearly all trawl tows.

We correlated the total number of all six species of salmonids stocked two years before (after two years in the lake, these fish should have been of sufficient size to eat all sizes of smelt) with the abundance of large smelt in U.S. waters during 1980-1991. For example, the number of trout and salmon stocked in 1978 (1.53 million) was paired with the number of large smelt caught per trawl tow in 1980 (141). We limited the correlation of smelt and salmonines to 1980-1991 to eliminate any effects on smelt due to dreissenid colonization (when dreissenid became abundant after 1992, water clarity increased and the bathymetric distribution of smelt shifted, potentially increasing the vulnerability of smelt to predation).

Results

Whitefish were uncommon near Henderson Harbor during 1980-1986, but their abundance increased during 1987-1995 (Fig. 2). About 97% of all whitefish caught in U.S. waters came from Henderson Harbor even though effort in this area was only about 15% of the total. This increase in whitefish numbers followed a decline in abundance of large smelt (Fig. 2). The decline in the abundance of large smelt during 1980-1991 was significantly correlated ($r = -0.802$, $P = 0.001$) with the number of trout and salmon stocked two years prior in U.S. waters (Fig. 2). Abundance of whitefish began to decline sharply near Henderson Harbor beginning in 1996. Between 1995 and 2001, the number of whitefish caught in this area dropped by more than 95%.

Seventy whitefish were caught near Oswego in the autumn of 1997 whereas whitefish were rarely caught there during 1980-1995. Abundance of whitefish near Oswego declined sharply after 1997 (Fig. 2).

Catches of whitefish in the western region were low during 1980-2001 even though 65% of all trawling effort occurred in this large area. Contrary to the trend toward increasing abundance in the Henderson Harbor region during 1987-1995, the trend in southwestern Lake Ontario was low catches, averaging <1% of the total.

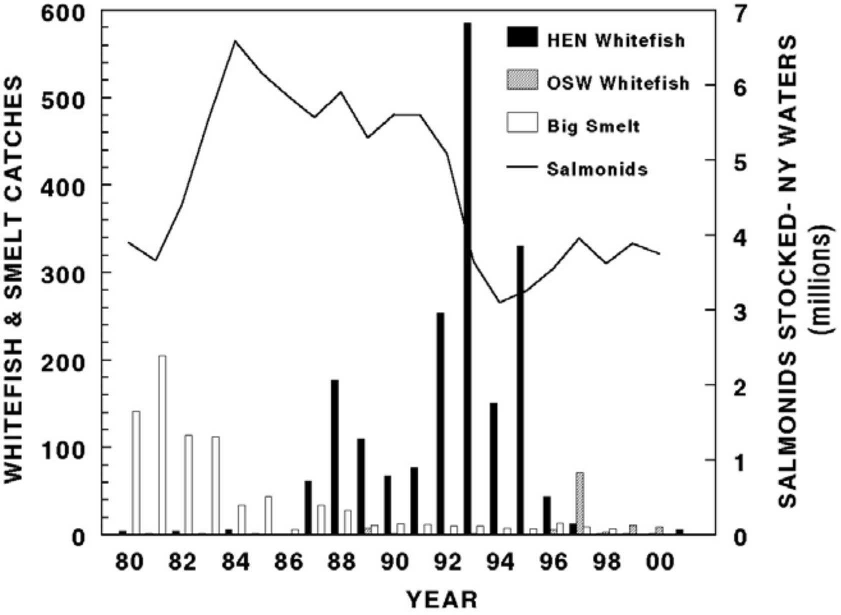

Fig. 2. Total number of whitefish caught per 350 bottom-trawl tows. HEN = Henderson Harbor area (black bars), OSW = Oswego area (cross-hatched bars), Big Smelt = mean number of large (≥150 mm) rainbow smelt (white bars) per tow in U.S. waters of Lake Ontario, and Salmonids = the number stocked (other than fry) two-years before in U.S. waters of Lake Ontario.

Our ANCOVA indicated that the slopes for the length-weight regressions for whitefish were not different (*P* = >0.05). The least-squares means were significantly different, indicating that the regression line from post-dreissenid colonization was below that of the pre-dreissenid time period (*P* = 0.006) (Fig. 3). For example, the predicted weight of a 500-mm whitefish declined by nearly 20%: from 1216 g during 1983-1990 ($\log_{10} W = -5.541 + 3.196\log_{10}L$) to 973 g during 1992-1999 ($\log_{10} W = -5.166 + 3.021\log_{10}L$).

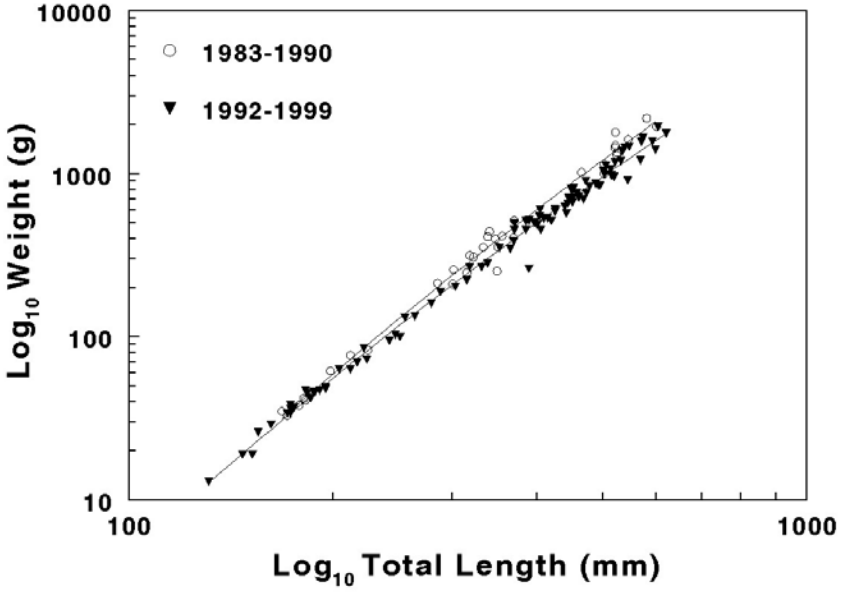

Fig. 3. Length-weight regressions for whitefish in Lake Ontario prior to dreissenid establishment (1983-1990, open circles with regression line) and after dreissenid establishment (1992-1999, solid triangles with regression line).

Discussion

Although whitefish were probably common throughout Lake Ontario prior to 1900, they were likely most abundant in the northeastern region of the lake (Rathbun and Wakeham 1897; Koelz 1926). This region, especially from Henderson Harbor northwards toward Prince Edward County, is shallow (<60 m) with an extensive area between the 20- and 50-m depth contours, has suitable temperature regimes for whitefish, and the region has numerous islands that protect whitefish spawning shoals from intense wave action. Whitefish were much more abundant in Canadian than in U.S. waters, where landings were one-tenth lower (Baldwin et al. 1979). Landings were essentially nil after 1965 in U.S. waters and after 1974 in Canadian waters, suggesting that the lakewide population had nearly vanished. Our assessment fishing showed that whitefish stocks in U.S. waters remained depressed during 1980-1986. The stocks near Henderson Harbor began to recover around 1987 shortly after recovery began off Prince Edward County (Hoyle et al. 2003), and whitefish abundance in these areas was high by 1995. Possible reasons for this recovery include sea lamprey control, which began in the late 1970s (Schneider et al. 1996), and a reduction in the abundance of large smelt because of increased predation by the expanding lake trout (*Salvelinus namaycush*) and salmon (*Oncorhynchus* spp.) populations. Hatchery-reared trout and salmon consume smelt (Brandt 1986; Elrod and O'Gorman 1991; J. R. Lantry 2001). Some studies suggest a negative relation between smelt abundance and whitefish reproductive success—a result of smelt preying on YOY whitefish (Warner and Fenderson 1963; Evans and Loftus 1987). Yearling smelt are able to consume fish larvae but piscivory on advanced fry or small juveniles (40-75 mm) is generally greatest among smelt >150 mm (O'Gorman 1974; Evans and Loftus 1987). Casselman et al. (1996) attributed the population recovery of whitefish near Prince Edward County to a decline in the numbers of large smelt and to temperatures more favorable for whitefish egg incubation.

By 1997, however, whitefish stocks in U.S. waters were showing signs of stress. Whitefish were scarcer near Henderson Harbor where they had been historically abundant, and part of the population may have dispersed southward along the eastern shore, as suggested by a sharp increase in abundance near Oswego in 1997. After 1997, whitefish were again uncommon in U.S. waters. Length-weight regressions for whitefish indicated that, for a given length, they were 20% lighter after 1992. Hoyle et al. (2003) also noted a decline in growth of whitefish off Prince Edward County after 1996.

Diporeia was formerly the principal prey in whitefish diet (Hart 1931) and the most abundant benthic macroinvertebrate in the open waters of the lake (Golini 1979). Diporeia is much higher in lipid content than many other macroinvertebrates, including dreissenids (Gardner et al. 1985; Nalepa et al. 1993). The decline in diporeia was first detected near Oswego in southeastern Lake Ontario in autumn 1992 at depths beyond 60 m (Owens and Dittman 2003). By 1995, diporeia had disappeared, or nearly disappeared, from a wide area off of Prince Edward County and the Bay of Quinte (Dermott 2001), the same area where Hoyle et al. (2003) observed dead and emaciated whitefish in 1997. By 1999, the diporeia population had collapsed along the southern and eastern shores of the lake at depths <100 m and in some areas at depths >100 m (Dermott 2001; Lozano et al. 2001; Owens and Dittman 2003). In 1992, near Olcott, diporeia densities were as high as 8000 m^{-2} at depths of 55 and 75 m; by 1999, densities had declined to or near zero (Owens and Dittman 2003).

Whitefish collected from deep (>70 m) U.S. waters consumed mostly *Mysis relicta*, sphaeriids (fingernail clams), and quagga mussels (Owens and Dittman 2003). During 1998, about 75% of the whitefish collected for diet analysis had *Mysis relicta* in the gut, about 95% had fingernail clams, and about 15% had quagga mussels. Only a few whitefish consumed diporeia in 1998, and none were found during 1999-2000. During 1999-2000, more than 90% of the whitefish consumed *Mysis relicta,* about 95% consumed fingernail clams, and about 40% consumed quagga mussels.

In U.S. waters, the mean depth of capture increased from about 30 m to nearly 80 m, reflecting perhaps a search for alternative prey (Owens et al. 2003). Whitefish are now foraging where temperatures are much colder (Owens et al. 2003). This change in foraging strategy was apparently not sufficient to stave off a further decline in abundance in eastern Lake Ontario.

The demise of the whitefish populations in Lake Ontario may be indirectly linked to colonization by dreissenids. The diporeia population collapsed following the rapid expansion of the dreissenid population during 1990-1999 (Dermott 2001; Lozano et al. 2001). Although no cause-and-effect relationship has been identified between dreissenids and diporeia, one hypothesis points to competition between dreissenids and diporeia for algae, especially diatoms (Dermott and Kerec 1997; Nalepa et al. 1998). Diatoms and bacteria have been identified as important components of the diet of diporeia (Marzolf 1965). The collapse of the diporeia population could be unrelated to dreissenid establishment and perhaps is due to an exotic pathogen, climate change, or other factors.

We do not expect the whitefish populations to recover unless the diporeia population either recovers or is replaced by another suitable prey. Also, the establishment of another exotic species, the round goby (*Neogobius melanostomus*), may further impede a whitefish recovery. Gobies were found to suppress the recruitment of the mottled sculpin (*Cottus bairdi*) in

Lake Michigan (Janssen and Jude 2001) and to prey on small fishes in the St. Clair River, Michigan (French and Jude 2001).

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Characteristics and Potential Causes of Declining *Diporeia* spp. Populations in Southern Lake Michigan and Saginaw Bay, Lake Huron

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Abstract

Populations of the amphipods *Diporeia* spp. are declining in all of the Great Lakes except Lake Superior. We examine characteristics and potential causes of declines in southern Lake Michigan and outer Saginaw Bay, Lake Huron. Amphipod populations began to decline within 3-4 years after zebra mussels (*Dreissena polymorpha*) colonized both areas. In Lake Michigan, which was better studied, the decline occurred first in shallow waters (<30 m) and then progressed deeper (51-90 m). Between 1980-1981 (pre-*Dreissena*) and 1998-1999 (post-*Dreissena*), densities at sites in these two depth intervals declined 92%

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and 58%, respectively. At a 45-m site in southeastern Lake Michigan, densities of *Diporeia* spp. declined to near zero within six months even though mussels were never collected at the site itself. At a nearby 45-m site, densities declined gradually to zero over a six-year period and correlated with increased mussel densities. Although mussels are likely outcompeting *Diporeia* spp. populations for food, and food limitation is probably a contributing factor to population declines, populations show no physiological signs of starvation; lipid content is at a maximum as densities approach zero. Pathogens, fish predation, contaminants, and low dissolved oxygen do not appear to be the sole causes of population declines. The decline of *Diporeia* spp. is likely to continue as dreissenid populations expand.

Introduction

The benthic amphipod *Diporeia* spp. (hereafter diporeia as a common name) is part of a deepwater fauna that inhabit cold, proglaciated lakes, brackish estuaries, and coastal margins in the Holarctic region. This organism was the most abundant benthic macroinvertebrate in the deeper regions of the Great Lakes, comprising >70% of all benthic biomass at depths >30 m (Cook and Johnson 1974; Nalepa 1989). Diporeia populations are present but less dominant in open, nearshore regions and naturally absent from shallow, warm bays and basins (i.e., inner Green Bay, inner Saginaw Bay, and western and central Lake Erie). As a detritivore, the amphipod burrows in the upper 1-2 cm of sediment and feeds on organic material settled from the water column. In turn, diporeia populations are fed upon by many fish species, including yellow perch (*Perca flavescens*), alewife (*Alosa pseudoharengus*), bloater (*Coregonus hoyi*), rainbow smelt (*Osmerus mordax*), slimy sculpin (*Cottus cognatus*), deepwater sculpin (*Myoxocephalus thompsoni*), and lake whitefish (*Coregonus clupeaformis,* hereafter whitefish) (Anderson and Smith 1971; Scott and Crossman 1973; Wells 1980). As an important diet item, the amphipod plays a key role in the cycling of energy between lower and upper trophic levels in the offshore region. Because the amphipod has a high lipid content and is rich in calories, it assumes a greater role in the trophic transfer of energy than might be assumed strictly from biomass or production estimates alone.

Diporeia populations are currently in a state of decline in portions of all the Great Lakes except Lake Superior (Dermott and Kerec 1997; Nalepa et al. 1998; Dermott 2001; Lozano et al. 2001; Nalepa et al. 2003). While population declines are evident over wide areas, the amphipod is rare or completely gone from the southeastern and far northern portions of Lake Michigan, outer Saginaw Bay, the eastern basin of Lake Erie, and the eastern portion of Lake Ontario. In each of these areas, diporeia populations have disappeared to water depths of at least 50 m. Population declines were first noted in the late 1980s and early 1990s and coincided with the introduction and spread of the zebra mussel (*Dreissena polymorpha*) and the quagga mussel (*D. bugensis*). In each lake area where diporeia populations are no longer found, populations disappeared within six years after mussels were first reported. Diporeia populations appear to be negatively impacted by dreissenids but resolving the exact mechanism for the negative response is difficult. Regardless of cause, however, the population declines are having an adverse impact on fish species that feed heavily on *Diporeia* spp., particularly the commercially important whitefish (Hoyle et al. 1999, Pothoven et al. 2001). In this paper, we examine characteristics of the declines in diporeia populations based on our studies in Lake Michigan and outer Saginaw Bay and explore various hypotheses for these declines. A better understanding of potential causes for the loss of diporeia populations may indicate what other lake areas are at risk and what the potential is for recovery.

Characteristics of Declining Populations in Southern Lake Michigan and Outer Saginaw Bay

As part of a long-term monitoring program of benthic macroinvertebrate populations in southern Lake Michigan, benthic samples have been collected at 40 sites in the southern basin since 1980 (Nalepa 1987; Nalepa et al. 1998) (Fig. 1). At each of the sites, samples were taken in triplicate with a Ponar grab in spring, summer, and fall in 1980-1981, 1986-1987, 1992-1993, and 1998-1999. Bottom substrates at these sites range from coarse sand and gravel to silt, and sampling depths range from 16-154 m. Further details of the sampling design and procedures are given in Nalepa et al. (1985).

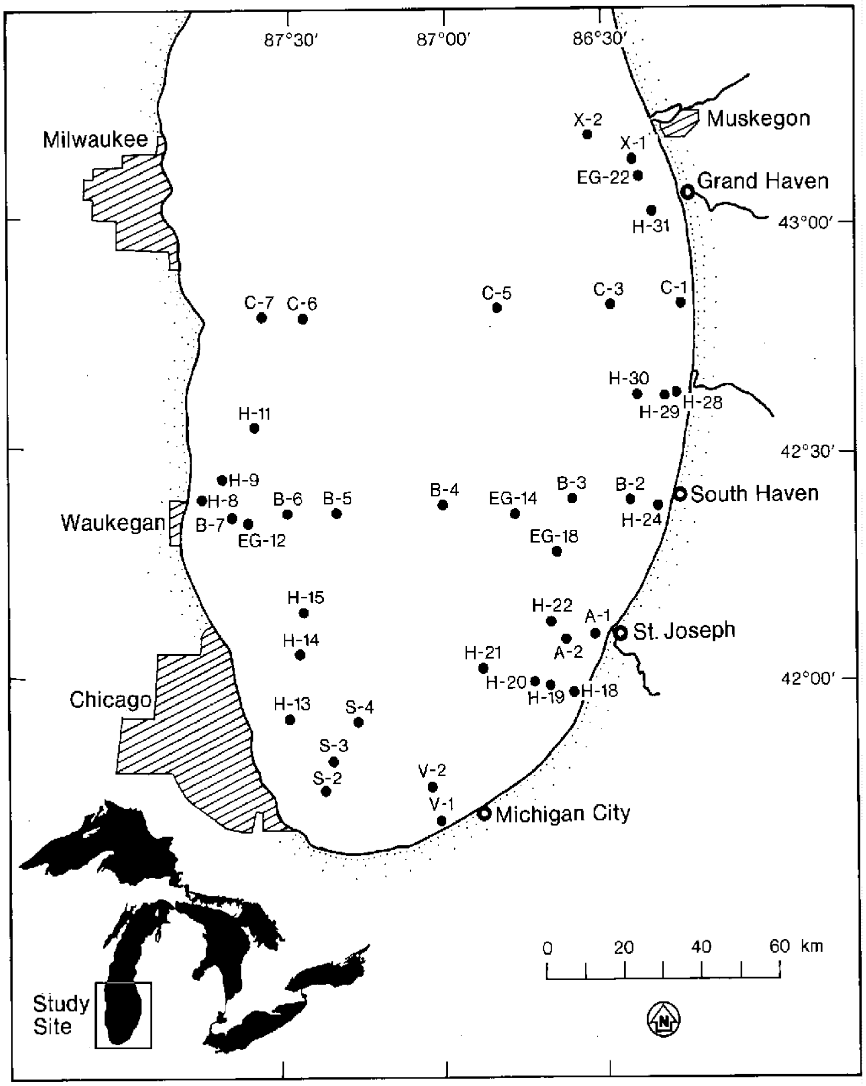

Fig. 1. Location of sampling sites in southern Lake Michigan.

For analysis, the sites were divided into four depth intervals: <30 m, 31-50 m, 51-90 m, and >90 m. These depth intervals are consistent with prior depth-macroinvertebrate associations in Lake Michigan (Alley and Mozley 1975). Over the 20-year sampling period (1980-1999), there were significant declines (Ln +1 transformed; ANOVA; $P < 0.05$) in diporeia population densities at sites at the three shallowest depth intervals (>90 m). Mean densities declined from 7,821 m^{-2} in 1980-1981 to 659 m^{-2} in 1998-1999 at the <30-m interval, from 10,892 m^{-2} to 2,184 m^{-2} at the 31- to 50-m interval, and from 5,769 m^{-2} to 3,405 m^{-2} at the 51- to 90-m interval (Fig. 2). These changes represent declines of 92%, 80%, and 58%, respectively. These population declines occurred mostly after 1986-1987 and showed two distinct spatial patterns: densities declined progressively from shallow to deep water, and declines were more marked on the east side of the basin as compared to the west side. Declines in population density first became evident at sites in the <30-m interval in 1992-1993; mean densities in these two years were significantly lower compared to mean densities in 1986-1987 (ANOVA, Tukey's HSD; $P < 0.05$). Significant declines were not apparent at sites in the 31-50-m and 51-90-m intervals until 1998-1999 (ANOVA, Tukey's HSD; $P < 0.05$). When sites were divided into east and west within the three shallowest depth intervals, declines were more apparent on the east side of the lake than the west for the 31-50-m and 51-90-m intervals (Table 1).

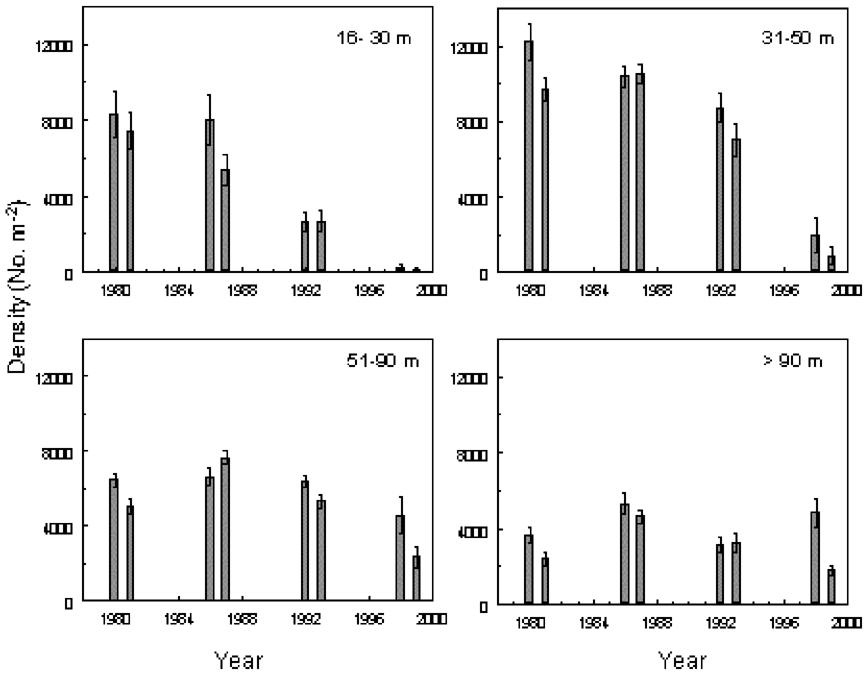

Fig. 2. Mean (+ SE) density of diporeia populations at each of four depth intervals in southern Lake Michigan between 1980 and 1999: <30 m; 31-50 m; 51-90 m; >90 m. The number of stations in each depth interval were 11, 12, 11, and 6, respectively.

Table 1. Percent decline (mean ± SE) of diporeia populations on the east and west sides of the southern basin of Lake Michigan between 1980-1981 and 1998-1999. The number of stations is given in parentheses. West Side Stations: B-6, B-7, C-7, EG-12, H-8, H-9, H-11, H-13, H-14, and H-15; East Side Stations: A-1, A-2, B-2, B-3, C-1, C-3, EG-18, H-18, H-19, H-20, H-21, H-22, H-24, H-28, H-29, and H-30 (for locations, see Fig. 1).

Depth Interval (m)	**East Side**	**West Side**
< 30	84.4 ± 13.5 (5)	87.0 ± 13.0 (2)
31-50	87.4 ± 7.0 (5)	66.1 ± 17.9 (3)
51-90	78.5 ± 12.2 (6)	30.0 ± 11.1 (5)

Although patterns of decline appeared gradual and systematic on a broad spatial scale, rates of decline were often highly variable even at sites of similar depth along the same side of the lake. For example, at Station H-22, located at a 45-m depth off St. Joseph, MI, diporeia populations declined from a mean density of 10,595 m^{-2} in spring 1992 to 193 m^{-2} in fall 1992, a decline of 98% in just six months. Diporeia samples were not collected at this site in 1997, 1998, or 1999. In contrast, at Station H-31, located at a 45-m depth off Grand Haven, MI, the decline took longer; mean density declined gradually from 11,340 m^{-2} in 1992 to 98 m^{-2} in 1999 (Fig. 3).

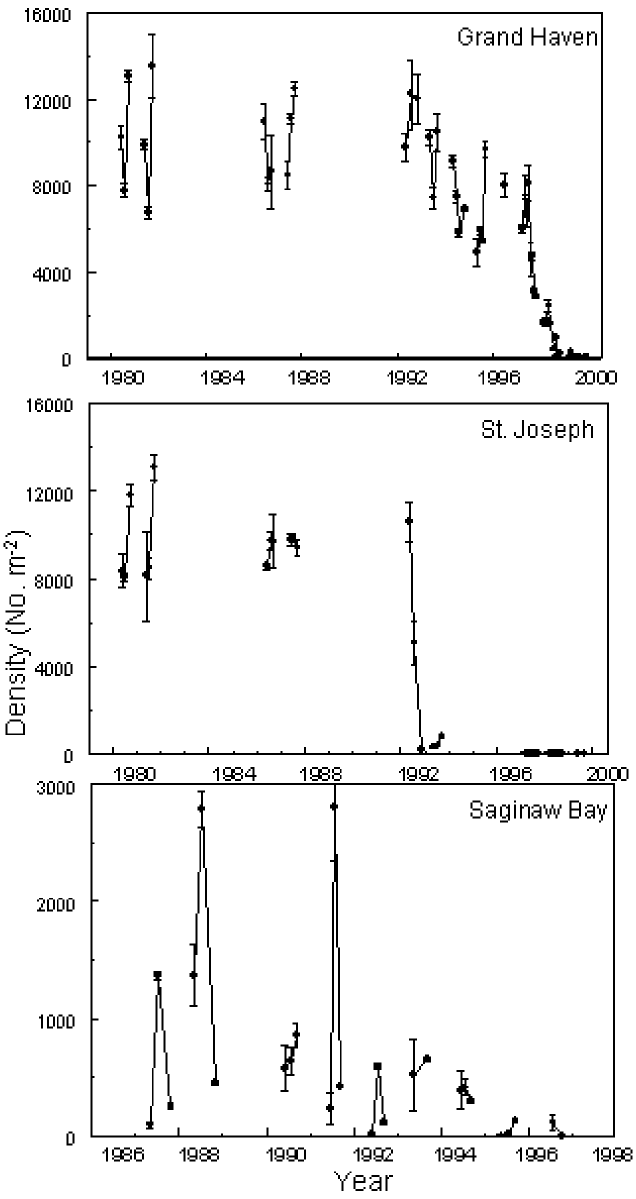

Fig 3. Mean (± SE) density of diporeia populations at two 45-m stations in southern Lake Michigan (Grand Haven: H-31; St. Joseph: H-22) between 1980 and 1999 and at a 23-m station in outer Saginaw Bay between 1987 and 1996.

Declines in diporeia populations appear to coincide with the introduction and spread of dreissenids. In southern Lake Michigan, dreissenids were first reported in 1989 along shallow reef areas off Chicago (Marsden et al. 1993). Mussels rapidly spread eastward and then northward along the eastern shore most likely because their veligers were carried by the counterclockwise current patterns typically found in this region (Beletsky et al. 1999). During 1992-1993, the greatest densities of dreissenids and the most dramatic and consistent declines in diporeia populations were found at shallow-water sites (<30 m) in the southeastern portion of the lake (Nalepa et al. 1998). Despite the high correlation between declines in diporeia populations and increased numbers of dreissenids in this area, the rapid decline of diporeia populations at Station H-22 in 1992 (Fig. 3) occurred even though no mussels were collected at this site in 1992. The lack of mussels at this site and in the immediate surrounding area was confirmed in film footage taken with an ROV in 1998. Although mussels were present at depths <30 m, no mussels were observed in deeper water. In contrast, the decline of diporeia populations at Station H-31 was closely related to an increase in dreissenids over a period of six years (Table 2). Hence, population declines at these two 45-m sites are paradoxical.

Table 2. Mean (± SE) lipid content (% dry weight) of diporeia at a 45-m site (Station H-31) in Lake Michigan near Grand Haven, MI. The number of individuals is given in parentheses. Also given are mean annual population densities (no. m^{-2}) of diporeia and dreissenids.

Year	**Lipid Content**	**Mean Density**	
		Diporeia	**Driessenids**
1980	–	10,363	0
1981	–	10,048	0
1984	31.6 (67)[1]	–	–
1986	32.2 (30)[2]	9,355	0
1987	–	10,687	0
1988	26.8 (≈70)[3]	–	–
1989	25.8 (≈40)[3]	–	–
1992	–	11,340	2
1993	–	9,375	14
1994	15.2 ± 1.0 (59)	7,349	39
1995	17.8 ± 0.9 (42)	6,484	50
1996	24.9 ± 1.3 (43)	7,996	143
1997	23.9 ± 0.6 (121)	6,285	669
1998	30.2 ± 0.7 (123)	1,154	2561
1999	34.7 ± 2.1 (5)	98	258

[1] Data from Gardner et al. (1985)
[2] Data from Gauvin et.al. (1989)
[3] Data from Cavaletto et al. (1996)

Population trends in Saginaw Bay provide another example of diporeia declines that were spatially distant from dreissenids. Dreissenids were first found in Saginaw Bay in 1991, peaked in shallow-water areas in 1992, and then declined to stable levels during 1993-1996 (Nalepa et al. 2003). At a 23-m site in the outer bay, diporeia populations began to decline in 1992 and by 1996 had fallen 93% compared to 1987-1990 (Fig. 3). Although mussels were found at shallower sites in the outer bay, no mussels were ever collected at the 23-m site itself. Neither amphipods nor mussels were collected in subsequent sampling at this site in 2000 (TFN, unpubl. data).

Historical and Geographical Perspective

A sufficient number of benthic surveys have been conducted in the Great Lakes over the past 70 years to conclude that the current large-scale disappearance of diporeia populations appears to be unprecedented. Studies of temporal changes have documented long-term (decades) (Robertson and Alley 1966; Johnson and McNeil 1986; Nalepa et al. 1987; Nalepa et al. 1998; Dermott 2001) and short-term (seasonal, year-to-year) (Alley and Mozley 1975; Winnell 1984) population trends. Although studies of spatial distributions have documented local areas lacking diporeia because of anthropogenic inputs (Nalepa and Thomas 1976; Vander Wal 1977; Kraft 1979), the systematic loss of a population over widely separated areas over such short time periods is unique. One record exists of an apparent diporeia population die-off from unknown causes near the St. Joseph site (H-22) in 1971, but many individuals survived, and the population soon recovered (Mozley and Howmiller 1977). Outside of the Great Lakes region, there are records of rapid and extended population declines of another deepwater amphipod, *Monoporeia affinis*. This species is closely related to diporeia and is endemic to the Palearctic region of Europe. In the Baltic Sea, the *M. affinis* population declined from 7,000-8,000 m^{-2} to 88 m^{-2} from 1929 to 1933 and then recovered to 500 m^{-2} two years later (Segarstrale 1960). No reason for the sudden decline was given although a pathogenic disease was suspected. A 30-year record of *M. affinis* at several deep sites (47-50 m) in Lake Malaren, Sweden, showed that the population declined to near zero for extended periods on several occasions (Goedkoop and Johnson 2001). Densities exceeded 15,000 m^{-2} in 1971 and 1980 but were less than 100 m^{-2} in 1973-1976 and 1992-1997. The authors suggested reduced dissolved oxygen (DO) concentrations as a plausible explanation for low densities.

The total disappearance of *M. affinis* in other European lakes over several decades has been attributed to increased eutrophication and reduced DO (Kansanen and Aho 1981; Zmudzinski 1995), and declines in the Baltic Sea in the 1990s have been attributed to both reduced DO and food competition with the invading polychaete *Marenzelleria viridis* (Cederwall et al. 1999; Kotta and Olafsson 2003).

Although dreissenids have just recently become established in North America, they have been naturalized in European waters for nearly a century. Unfortunately, there are no studies that examine temporal trends in deepwater amphipods relative to population expansions of dreissenids. Perhaps the best data set is from Lake Malaren, Sweden. Dreissenids became established in this lake in the 1920s, and the highest densities occurred in the 1960s (Josefsson and Andersson 2001). Dreissenids are presently found in the littoral and sublittoral regions of the deeper, oligotrophic basins but quantitative estimates are lacking (W. Goedkoop, Swedish University of Agricultural Sciences, SE-750 07, Uppsala, Sweden, pers. commun.). *M. affinis* is still present and quite abundant in these basins, although, as indicated earlier, populations fluctuate widely. Of relevance here is that the two species seem to co-occur in the deeper basins of the lake.

Potential Reasons for the Decline of Diporeia Populations in the Great Lakes

Were declines in diporeia populations caused by decreased food availability resulting from the filtering activities of dreissenids? Diporeia populations feed in the upper sediments layers, whereas dreissenids filter-feed at the sediment surface. Thus, food settling to the bottom is likely intercepted and utilized by dreissenids before it actually reaches the upper sediments and becomes available to diporeia. Similar to other benthic organisms found in deep lakes, diporeia abundance is directly related to water-column productivity and the amount of food settling to the bottom (Saether 1980; Siegfried 1985; Johnson 1988). A similar strong relationship has also been found for *M. affinis* in European lakes (Johnson and Wiederholm 1992) and in the Baltic Sea (Andersin et al. 1978). In southern Lake Michigan, mean abundances of diporeia increased 1.5-fold between the mid-1930s and the mid-1960s (Robertson and Alley 1966) and 2- to 5-fold between the 1960s and 1980-1981 (Nalepa 1987). These increases were attributed to increased phosphorus loads and higher water-column productivity. With dreissenids now present and filtering at the sediment-water interface, food materials settling from the water column are diverted, and a direct relationship between water-column productivity and standing stocks of diporeia can no longer be assumed. In nearshore southeastern Lake Michigan, phytoplankton biomass (as measured by chlorophyll) has declined 50% since the 1970s (Madenjian et al. 2002); in eastern Lake Ontario, diatom biomass declined by 80% (Dermott 2001). Under previous assumptions and with other factors being equal, diporeia populations should have declined by 50% and 80%, respectively. Yet, in both lake areas, diporeia populations have completely disappeared at depths <50 m.

The food-limitation hypothesis is most convincing in areas where mussel populations co-occur directly with diporeia because mussels can severely deplete food resources just above the bottom (Ackerman et al. 2001). In the eastern basin of Lake Erie, quagga mussels became widespread and abundant to the basin's maximum depth of 60 m, and diporeia populations were extirpated within three years (Dermott and Kerec 1997). Over this period, there was a direct inverse relationship in individual grab samples between densities of diporeia and mussels. The food-limitation hypothesis is less convincing in areas such as Station H-22 in Lake Michigan where, as noted, mussels did not spatially overlap with diporeia and yet diporeia population densities declined 98% in six months. At Station H-22, biogenic silica was present in material collected in sedimentation traps in spring 1997 indicating at least some food material (i.e., diatoms) was still settling to the bottom (TFN, unpubl. data). At the previously mentioned outer Saginaw Bay site, water-column chlorophyll and diatom biovolumes did not change during the period when the diporeia population declined (Johengen et al. 2000; H. A. Vanderploeg, NOAA, Great Lakes Environmental Research Laboratory, 2205 Commonwealth Blvd., Ann Arbor, MI 48105-2945, unpubl. data).

If food limitation is the major cause of the decline in diporeia populations, individuals should logically show physiological signs of starvation before and/or during the period in which populations decrease. In diporeia and *M. affinis,* lipid levels are a good indicator of food availability; levels increase during seasonal periods of high benthic-food inputs and decline when food is scarce (Gardner et al. 1985; Gauvin et al. 1989; Hill et al.1992; Lehtonen 1995, 1996). In Lake Michigan, lipid levels generally peak in late spring/early summer just after the spring diatom bloom (Gardner et al.

1985). During this event, large diatoms such as *Aulacoseira* spp. (*Melosira*), which typically dominate the unstratified spring period, sink rapidly from the water column and reach the sediments virtually intact. Also, diatom decomposition during settlement is minimized in the spring because of cold water temperatures and the lack of zooplankton grazers. Diporeia populations feed most intensively in the spring, likely in response to this fresh food source (Dermott and Corning 1988; Quigley 1988). A recent study using stable isotopes has confirmed that diporeia uses freshly settled material during the nonstratified period in the spring (Leggett et al. 1999).

Just as lipid levels in diporeia increase after periods of high food availability, lipid levels decrease during periods of food deprivation, as during summer stratification when less algal food settles to the bottom (Scavia and Fahnenstiel 1987). During these periods, diporeia utilizes accumulated lipid reserves as a source of energy. Gauvin et al. (1989) showed that diporeia can live without food for 217 days and that lipid levels gradually decreased over this period. For diporeia, rapid accumulation of lipids during periods of high food availability and use of lipids during periods of food shortage are considered a life-history strategy for survival in cold, deep lakes where benthic food inputs are highly seasonal.

At Station H-31 (Grand Haven, Lake Michigan), mean annual lipid levels for April to November varied from 26% to 32% in larger animals (>5-mm body length (BL)) in the 1980s prior to colonization by dreissenids populations (Table 2). In 1994, after mussels had become widespread in the southern basin, mean lipid level was only 15.2% (Table 2), which is near the low of 12% found in animals starved in the laboratory for 120 days (Gauvin et al. 1989). Levels of at least 20% are considered necessary for successful reproduction in deepwater amphipods (Hill et al. 1992). Densities at Station H-31 began to decline in 1994 (Fig. 3). After 1994-1995, lipid levels increased unexpectedly, and by 1998-1999 were as high as or higher than levels found in the 1980s prior to dreissenid colonization. Reasons for these lipid increases remain unclear. Declining densities may have resulted in greater amounts of food for the remaining diporeia leading to an increase in lipids. Yet, if higher lipids reflect greater amounts of food, then food would not be limiting, and densities should have stabilized rather than continuing to decline in 1998-1999 (Table 2). Also, the increase in mussel densities after 1994-1995 (Table 2) would likely have led to declines in available food, regardless of changes in diporeia densities.

Because lipids are reported on a weight-specific basis, an increase in lipids may be related to selective catabolism of non-lipid materials during periods of severe starvation. Gauvin et al. (1989) attributed an increase in lipid content of diporeia after 191 days without food to the catabolism of non-lipid material. To explore this possibility, we examined the relationship between BL and non-lipid dry weight (NLDW) at Station H-31 from 1994 and 1998. The relationship was described by $NLDW = aBL^b$, and each year's linear regression (based on log-transformed values) was significant ($P < 0.05$). The calculated weight of a standard 5-mm animal from 1994 to 1998 was 0.69, 0.41, 0.45, 0.58, and 0.60, respectively. Thus, non-lipid dry weight did not appear to decrease but tended to increase along with lipid levels, a finding that seems to refute the possibility that lipid increases resulted from selective catabolism of non-lipid material. To examine further the possibility that diporeia were no longer able to metabolize lipids, individuals collected from Station H-31 were placed in filtered lake water and kept without food for 66 days (TFN, unpubl. data). Lipid content gradually decreased over this time period indicating that the animals were still able to use lipids as a source of energy. If the food-limitation hypothesis is correct, the reason why lipids increased as diporeia populations disappeared remains unresolved.

When examining the food-limitation hypothesis, food quality as well as food quantity must be considered. Most food settling to the benthic region occurs during the spring diatom bloom (Scavia and Fahnenstiel 1987). Diatoms are high in long-chain polyunsaturated fatty acids (PUFAs) that serve as precursors to a number of hormones critical to a host of physiological processes in invertebrates including maturation, egg production, egg development, and immunological responses to infection (Brett and Muller-Navarra 1997). Invertebrates can only obtain PUFA from the algal component of their diet, so the PUFA content of settled algal material likely plays a key role in diporeia growth, development, and physiological well being. The amount of PUFA available to diporeia populations may have decreased not only because of lowered numbers of diatoms resulting from filtering activities of dreissenids, but also because of reduced PUFA content of those diatoms remaining. In southern Lake Michigan, water clarity has increased 2-fold since mussels became established (Marsden et al. 1993), allowing for greater light penetration and increased exposure of phytoplankton to ultraviolet radiation. The latter leads to a number of biochemical and physiological changes in phytoplankton, including a reduction in PUFA content (Hessen et al. 1997). The rapid decline of diporeia populations at Station H-22 likely was not caused by changes in algal PUFA. However, the unexplained increase in lipid content of diporeia at Station H-31 during the gradual decline in population density indicated that physiological/biochemical changes were occurring that potentially could have been related to shifts in food quality.

Members of diporeia populations may be actively avoiding areas influenced by mussels either because of lack of food or because of a negative response to mussel biodeposits (i.e., bacteria/mucus in feces and pseudofeces). Diporeia reside in the upper sediments but are not confined to the benthic region. Nocturnal migrations into the water column have been well documented (Marzolf 1965a; McNaught and Hasler 1966; Wells 1968; Mozley 1974). Most movement into the water column likely is related to mating behavior, but juveniles are also commonly found in the water column at night indicating that swimming behavior may also be a response to changing environmental conditions. Mass horizontal migrations to and from inshore areas in response to seasonal changes in water temperatures have frequently been reported or suspected (Winnell and White 1984, Siegfried 1985, Johnson 1988). In addition, diporeia can be selective in their choice of habitat. When offered a choice of different sediments in laboratory experiments, diporeia overwhelmingly selected sediments from offshore, open-lake areas for burrowing as compared to sediments from harbors and river mouths (Gannon and Beeton 1969). In similar experiments, Marzolf (1965b) found that diporeia burrowed more frequently in sediments where algal food was presented as a light layer over the sediment surface rather than as mixed into the sediment.

Given its swimming behavior and propensity for substrate selection, diporeia were subjected to preference/avoidance experiments to determine their response to sediments collected from sites where populations had disappeared (i.e., Station H-22) and were still present (Landrum et al. 2000). There were significantly fewer animals burrowed in sediments from the site where diporeia had disappeared. When the experiments were repeated with diatoms added to the sediments, there were no significant differences in burrowing between the two types of sediments. This finding suggests that the animals likely were responding to food availability and not to some component of dreissenid biodeposits.

Could diporeia populations be actively swimming away from mussel colonies in search of better food? If so, field collections should show a negative relationship between the two organisms. Ponar grabs at Station H-31 in 1997-1998 did not show a negative relationship between diporeia and dreissenid densities on this small spatial scale (Fig. 4). Most grab samples contained few if any mussels because of patchy dreissenid distributions, but samples with large numbers of dreissenids also contained diporeia, indicating that diporeia did not appear to be actively avoiding mussel clusters.

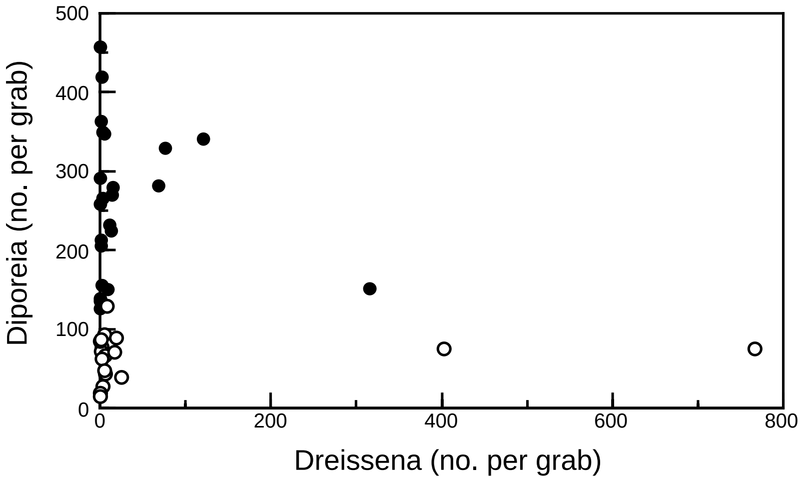

Fig. 4. Numbers of diporeia and dreissenids collected in individual grab samples at Station H-31 in Lake Michigan off Grand Haven, MI. Three replicate samples were taken monthly from April to November (solid circle, 1997; open circle, 1998).

Diporeia are fed upon by many fish species, and some population declines have been attributed to increased predation pressure. For instance, in Lake Michigan, declines in diporeia populations over a four-year period were attributed to increased numbers of yellow perch and bloaters (McDonald et al. 1990). In the Bay of Quinte, Lake Ontario, low abundance of diporeia was attributed to a large population of stunted white perch (*Morona americana*), and abundances increased after the white perch population crashed (Johnson and McNeil 1986). While predation pressure may play a role in population fluctuations, it is unlikely that such pressure would systematically lead to a loss of all diporeia. In southern Lake Michigan, trends in populations of fish that feed heavily on diporeia (such as sculpins, yellow perch, and bloater) could not account for observed decreases in diporeia populations in the early 1990s (Nalepa et al. 1998). While not the sole cause, fish predation may still play some role in population declines. Animals subjected to food declines become more active in search of food and more susceptible to predation (Lomnicki 1978).

Pathogens and diseases are common in amphipods and are known to reduce or limit populations (Pixell-Goodrich 1929; Johnson 1985). A dramatic decline of the amphipod *Corophium volutator* in nearshore waters of the Baltic Sea in 1928-1930 was attributed to the yeast pathogen *Micrococcus* (Segarstrale 1960). The previously mentioned decline in *M. affinis* in the Baltic Sea occurred over the same period but in deeper waters. Given these observations, a pathogen introduced with dreissenids could be affecting diporeia. Alternatively, new stressors related to the establishment of dreissenids (i.e., decrease in quantity and quality of available food) may have made diporeia more susceptible to endemic pathogens. A wide survey of parasites and diseases in diporeia throughout Lakes Michigan and Huron indicated that individuals were infected with various pathogens, including virus-like infections, rickettsia-like organisms, fungi, haplosporidian-like organisms, microsporidian-like organisms, putative epibiotic ciliates, gregarines, cestodes, and acanthacephalan worms (Messick et al. 2004). Incidence rates at 12 sites in southern Lake Michigan, however, were uniformly low (Table 3). Diporeia populations at these sites were in various stages of decline from 1992-1993 to 1998-1999 likely suggesting that pathogens were not a direct cause of decreased populations.

Table 3. The incidence rate (%) of disease and pathogens found in diporeia populations from sites in southern Lake Michigan in 2000. Station locations are given in Fig. 1. Decline is given as the percent decrease in density from 1992-1993 to 1998-1999; *n* = number of animals examined.

Station	**Depth Interval**	**Decline**	**n**	**nod**	**cil**	**mic**	**gre**	**hap**	**ric**	**yea**	**fun**	**vir**
C-5	>90	0.0	20	0.0	35.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
C-6	>90	9.8	15	6.7	26.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0
B-5	>90	10.9	16	0.0	43.8	6.3	0.0	0.0	0.0	0.0	0.0	0.0
B-6	51-90	13.0	17	0.0	17.7	29.4	0.0	0.0	0.0	0.0	0.0	0.0
B-7	30-50	25.1	23	8.7	17.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0
C-7	51-90	23.2	19	15.8	31.6	5.3	0.0	0.0	5.3	0.0	5.3	0.0
H-15	51-90	31.9	14	7.1	28.6	0.0	0.0	7.1	0.0	0.0	0.0	0.0
H-9	30-50	33.5	19	5.3	15.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0
EG-12	51-90	40.8	19	5.3	42.1	0.0	0.0	0.0	5.3	0.0	0.0	0.0
H-21	51-90	62.8	19	5.3	63.2	0.0	5.3	0.0	0.0	0.0	0.0	0.0
EG-14	>90	63.5	18	0.0	55.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0
H-30	51-90	80.2	17	17.7	32.3	0.0	5.9	5.9	0.0	0.0	0.0	0.0

nod = nodules; hemocyte encapsulation of tissue debris, injurious agent, or foreign material
cil = ciliates (externally attached symbionts not considered harmful)
mic = microsporidians (intracellular parasite)
gre = gregarines (sporozoan parasite)
hap = haplosporidia (parasitic protist)
ric = rickettsia-like organism (intracellular, prokaryotic parasite)
yea = yeast
fun = fungus
vir = virus

Diporeia are considered pollution-sensitive and are generally not present or occur in low numbers in areas influenced heavily by contaminants (Nalepa and Thomas 1976; Vander Wal 1977; Kraft 1979). The sensitivity of diporeia was confirmed in laboratory assays with contaminated sediments from various harbors around the Great Lakes; after 48-h exposures, mortality was 70% in diporeia but only 9% in the more tolerant amphipod *Gammarus* (Gannon and Beeton 1969). Could dreissenid biodeposits have an acute toxic effect on diporeia populations, or could dreissenids modify sediment-associated contaminants to increase their toxicity to diporeia populations? Landrum et al. (2000) examined these possibilities by exposing diporeia to sediments from several 45-m sites in southeastern Lake Michigan, including Stations H-22 and H-31. After a 28-d exposure, no mortality was observed in any of the sediments indicating that acute toxicity was not the likely reason for population declines. The bioassays were later repeated with a 66-d exposure, and, again, significant mortality was not observed (TFN, unpubl. data).

Deepwater amphipods such as diporeia and *M. affinis* are generally sensitive to low DO concentrations. As noted earlier, the elimination of *M. affinis* from European lakes and extended periods of low densities in Lake Malaren, Sweden, were attributed to reduced DO. In laboratory experiments, DO concentrations of 2-5 mg·L^{-1} affected the swimming behavior of *M. affinis* (Johansson 1997), and similar concentrations led to a higher frequency of unfertilized females and a greater number of females carrying dead broods (Ericksson-Wiklund and Sundelin 2001). Although most regions in the Great Lakes with hypoxia (i.e., central basin of Lake Erie) are too warm and shallow for diporeia to be present naturally, diporeia distribution seems to be related to the oxidative state of the sediment surface (Sly and Christie 1992). Could dreissenids have reduced DO at the sediment-water interface to the point of adversely affecting diporeia populations? Within mussel beds, microbial decomposition of mussel biodeposits and/or dead mussel tissue may lead to areas of reduced DO. This reduced DO would mostly be a local effect and not likely in deep, hypolimnetic areas where mussels are not abundant, such as at Station H-22. On the other hand, dreissenid biodeposits from shallow, nearshore regions may resuspend during spring storm events; settle into offshore, depositional zones; and create periods of reduced DO. In nearshore areas with large numbers of mussels, sediment particle-size distributions decreased from 125-200 µm to 4-7 µm because of mussel biodeposits (Howell et al. 1996). Over 80% of mussel pseudofeces can be

<10 µm in size (Reeders and Bij de Vaate 1992). These fine particles are easily resuspended and have a high DO demand when re-deposited. Depositional areas may experience brief periods of reduced DO after sedimentation events (Graf 1987; Hansen and Leppanen 1994). Station H-22 is located in the area of highest sedimentation in Lake Michigan, and most sediment deposition occurs in the spring (Eadie et al. 2002). The decline of diporeia populations at this site was first observed after spring.

Summary and Conclusions

The complete loss of diporeia populations from large areas in Lakes Michigan, Huron, Erie, and Ontario appears to be unprecedented and caused either directly or indirectly by the establishment and spread of zebra and quagga mussels. The only feature common to these areas is that initial declines occurred within 3-4 years after mussels established. Declines typically occur first in shallow waters and then progress deeper. Although several theories have been suggested, field observations and laboratory studies have not established a clear, causative mechanism for the population declines. Inconsistencies in the commonly suggested food-limitation hypothesis are apparent and cannot be readily explained. Diporeia populations declined to near zero very rapidly (months to several years) in areas where mussels were far removed and food was seemingly available. Diporeia lipid levels were low when populations initially began their decline, which is consistent with a food-limitation hypothesis. Yet, as the population decline continued, lipid levels increased and were near maximum levels as numbers approached zero. Increased lipids suggest that physiological changes are occurring, but the cause and meaning of such changes are not clear. Future investigations should examine other indicators of physiological well being, such as respiration rates and nutrient excretion. Investigations at the biochemical or cellular level also may prove informative. Conceivably, a decline in food had an indirect impact on abundances by making the animals more susceptible to other factors, such as lowered DO or predation by fish. Although diporeia are active in the water column, animals from areas where they are still present are not recolonizing areas from which they have long disappeared, indicating that conditions that led to the declines are still present and/or are re-occurring.

The loss of diporeia from extensive areas is having an impact on the food web, particularly on fish that rely heavily on diporeia as a food source. The loss of diporeia populations has been implicated in the decline of rainbow smelt in eastern Lake Erie (Dermott and Munawar 1993), the decline of sculpins in Lake Ontario (Lozano et al. 2001), and the decline in condition of whitefish (Pothoven et al. 2001) and alewife in Lake Michigan (Madenjian et al. 2003). Moreover, simulation models predict cascading impacts across several trophic levels (Kitchell et al. 2000). For whitefish, specifically, the loss of diporeia has led to increased consumption of dreissenid mussels, which provide less nutrition than diporeia, and to shifts in distribution patterns as fish search for alternate food (Owens et al. 2000; Hoyle 2005).

As dreissenid populations expand (Fleischer et al. 2001; Nalepa et al. 2001), the continued decline of diporeia populations seems inevitable. Long-term field studies should examine changes in diporeia recruitment, growth, and survival before and after the invasion of dreissenids, and laboratory studies should further explore the negative relationship between these two organisms (Dermott et al. 2005). Without fully understanding the cause, predicting the eventual extent of the population loss and the potential for recovery cannot be meaningfully attempted.

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Preliminary Evaluation of a Lake Whitefish (*Coregonus clupeaformis*) Bioenergetics Model

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Abstract

We conducted a preliminary evaluation of a lake whitefish (*Coregonus clupeaformis*) bioenergetics model by applying the model to size-at-age data for lake whitefish from northern Lake Michigan. We then compared estimates of gross growth efficiency (GGE) from our bioenergetics model with previously published estimates of GGE for bloater (*C. hoyi*) in Lake Michigan and for lake whitefish in Quebec. According to our model, the GGE of Lake Michigan lake whitefish decreased from 0.075 to 0.02 as age increased from 2 to 5 years. In contrast, the GGE of lake whitefish in Quebec inland waters decreased from 0.12 to 0.05 for the same ages. When our swimming-speed submodel was replaced with a submodel that had been used for lake trout (*Salvelinus namaycush*) in Lake Michigan and an observed predator energy density for Lake Michigan lake whitefish was employed, our model predicted that the GGE of Lake Michigan lake whitefish decreased from 0.12 to 0.04 as age increased from 2 to 5 years.

Introduction

Since 1980, the lake whitefish (*Coregonus clupeaformis,* hereafter, whitefish) has been the most commercially valuable fish in the upper Great Lakes (S. Nelson, United States Geological Survey, Great Lakes Science Center, COMCAT database, Ann Arbor, MI 48105, U.S.A.). Whitefish populations in the Great Lakes have shown a strong recovery since the 1960s with the commercial harvest increasing more than tenfold from 1959 to 1995 (Ebener 1997). This remarkable recovery has been attributed, in part, to effective control of sea lamprey (*Petromyzon marinus*), a program that began in the 1960s (Wells and McLain 1973; Ebener 1997; Madenjian et al. 2002). Sea lampreys invaded the upper Great Lakes during the 1940s and preyed heavily on whitefish during the 1950s.

The condition of whitefish at several locations in Lake Michigan has declined since 1995 (Pothoven et al. 2001; Madenjian et al. 2002). This decline has been partially attributed to a decrease in the abundance of *Diporeia* spp. (hereafter, diporeia as a common name) in nearshore waters and to the relatively high densities of whitefish in the lake. Diporeia has the highest lipid content of the major benthic macroinvertebrates in the lake and has been a favored prey item for Lake Michigan whitefish (Pothoven et al. 2001). The continued decrease in diporeia abundance during the 1990s has been associated with the zebra mussel (*Dreissena polymorpha*) invasion, but the specific mechanism by which zebra mussels could negatively affect diporeia remains unidentified (Nalepa et al. 2000; Madenjian et al. 2002).

Bioenergetics modeling has played a key role in the study of the feeding ecology and growth of fishes (Hayward and Margraf 1987; Madenjian et al. 1998). The Wisconsin bioenergetics models—a suite of fish bioenergetics models developed by researchers associated with the University of Wisconsin Center for Limnology—have been widely applied in fisheries science (Hansen et al. 1993; Ney 1993). Hanson et al. (1997) offered a generalized coregonine bioenergetics model (GCBM) in the latest versions of the Wisconsin bioenergetics models. This model was based largely on the bioenergetics model developed by Rudstam et al. (1994) for bloater (*C. hoyi*) in Lake Michigan. However, neither the GCBM nor the bloater model has been evaluated. A validated bioenergetics model for whitefish should be a useful tool to evaluate its energetic requirements and the impact of changing prey resources on its growth and condition.

The objective of this study was to conduct a preliminary evaluation of the GCBM proposed by Hanson et al. (1997) by applying the model to Lake Michigan whitefish. We then compared the model's predictions of gross growth efficiency (GGE) for whitefish with published estimates of GGE for Lake Michigan bloater and for whitefish from inland waters in Quebec. The GGE is equal to the increase in fish weight divided by the amount of food consumed by the fish to achieve its weight increase. Although whitefish typically attain much larger sizes than bloater, GGE estimates for Lake Michigan bloater were similar to GGE estimates for whitefish from Quebec's inland waters (Rudstam et al. 1994; Trudel et al. 2001). Therefore, a comparison of the model's predictions of GGE for Lake Michigan whitefish with previously published estimates for North American coregonines would serve as an initial check on the model's predictions.

We also determined the sensitivity of the generalized coregonine model predictions of food consumption for Lake Michigan whitefish to alterations in the submodel for fish activity. Activity can be an important contributor to the overall energy budget of a fish (Boisclair and Leggett 1989). To the best of our knowledge, direct measurements of swimming speeds of whitefish in lakes were not available. Therefore, an examination of the sensitivity of the model's predictions of GGE to changes in fish activity was warranted.

In addition, we investigated the sensitivity of the GCBM's predictions of food consumption for Lake Michigan whitefish to perturbations in predator energy density. Rudstam et al. (1994) developed a regression model for predicting coregonine energy density based on fish weight. We compared the energy density predicted by the regression equation with an actual measurement in 2000 of the energy density of Lake Michigan whitefish. We then compared estimates of food consumption by Lake Michigan whitefish from the Rudstam et al. (1994) regression equation with the actual measurements of energy density.

Methods

The Hanson et al. (1997) version of the Rudstam et al. bioenergetics model for bloater (1994) contained only one modification: the exponent for fish weight in the consumption submodel was changed from -0.538 to -0.32. This change was made to adapt the model to larger coregonine. Interestingly, the respiration component of the bloater bioenergetics model was based on laboratory observations of whitefish. The most-detailed respiration measurements on coregonines were performed by Bernatchez and Dodson (1985). They measured respiration rates of whitefish at three different water temperatures (5, 12, and 17°C) and at swimming speeds ranging from 20 $\text{cm}\cdot\text{s}^{-1}$ to 80 $\text{cm}\cdot\text{s}^{-1}$. These measurements were used to build the regression equations representing the respiration component of the bloater bioenergetics model (Rudstam et al. 1994). Direct observations of the swimming speeds of bloater in Lake Michigan were unavailable; however, volitional swimming speeds of bloaters were observed in large laboratory tanks (Rudstam et al. 1984). From these laboratory measurements, Rudstam et al. (1994) developed a regression equation relating swimming speed to bloater weight. According to this equation, a 300-g bloater would swim at 30 $\text{cm}\cdot\text{s}^{-1}$. Swimming speed was assumed to be independent of water temperature (Rudstam et al. 1994). The generalized coregonine bioenergetics model's respiration and swimming-speed submodels are identical to those in the bloater bioenergetics model (Hanson et al. 1997).

Rudstam et al. (1994) described energy density of bloaters as a function of bloater weight. According to this function, bloater energy density was equal to 13 050 $J \cdot g^{-1}$ on a wet-weight basis for bloater weights ≥155 g. The predator energy-density function used in the bloater bioenergetics model was identical to that used in the GCBM.

To estimate food consumption, we fitted the generalized coregonine model to observed weight-at-age data for Lake Michigan whitefish. Whitefish were captured in commercial trapnets in northern Lake Michigan during May 1991-2000. Fish were weighed to the nearest gram and aged by scales. Averaging mean weight-at-age across all years during 1991-2000, we obtained mean weights of 0.18 kg, 0.53 kg, 0.79 kg, 0.95 kg, and 1.16 kg for whitefish of ages 2, 3, 4, 5, and 6, respectively. The starting date for each model simulation was 1 May and the ending date was 30 April of the following year. For each simulation run, the appropriate starting and ending weights were chosen from the mean weights presented above, and consumption during the simulation year was estimated from the model.

According to Christie and Regier (1988), the optimal temperature range for subadult and adult whitefish is 10 to 14°C. To bound the effect of water temperature on consumption estimates, we performed simulations under four summer maximum water temperatures: 8, 10, 12, and 15°C. For the 10°C summer-maximum-water-temperature regime, we used the temperature schedule used by Stewart et al. (1983) for modeling Lake Michigan lake trout (*Salvelinus namaycush*). Stewart et al. (1983), using an annual cycle of water temperature for the surface waters of Lake Michigan in the middle of the lake, assumed that lake trout would occupy 10°C water for as long as that water temperature was available. We used this same annual cycle of water temperature to develop temperature regimes under the 8, 12, and 15°C summer-maximum scenarios. In each scenario, we assumed that whitefish would occupy waters of the summer-maximum temperature for as long as that temperature was available.

We performed a set of simulations for each of the four water-temperature scenarios outlined above. Each set of simulations consisted of four runs—

one run for each of the four age groups bounded between ages 2 and 6. Because the diet of whitefish in Lake Michigan is similar to that of adult bloater (Rudstam et al. 1994; Pothoven et al. 2001), we used the diet schedule for adult bloater in our whitefish bioenergetics simulations. Rudstam et al. (1994) assumed that adult bloater fed exclusively on benthic prey—primarily *Mysis* and diporeia—and that their caloric density was 4000 $J \cdot g^{-1}$ on a wet-weight basis. We used the predator energy-density function developed of Rudstam et al. (1994) in these four sets of simulations.

To explore the sensitivity of the model predictions to swimming speed, we conducted an additional set of simulations in which the swimming-speed submodel by Rudstam et al. (1994) was replaced with the swimming-speed submodel used for Lake Michigan lake trout by Stewart et al. (1983). The swimming-speed submodel developed by Rudstam et al. (1994) yielded a swimming-speed estimate of 45 $cm \cdot s^{-1}$ for a 1.5-kg whitefish. This speed appeared to be excessively high because it substantially exceeded swimming speeds predicted by Stewart and Ibarra (1991) for similarly sized coho (*Oncorhynchus kisutch*) and chinook (*O. tshawytscha*) salmon in Lake Michigan. Underwater observations of both whitefish and lake trout swimming in trapnets in Hammond Bay, Lake Huron, by PJS suggested that whitefish are no more active than lake trout. Furthermore, Stewart et al. (1983) predicted that lake trout were less active than salmon in Lake Michigan. Therefore, we replaced the Rudstam et al. (1994) swimming-speed submodel with the submodel developed by Stewart et al. (1983) for Lake Michigan lake trout, and we performed a set of four—one simulation for each of the four whitefish age groups—simulations with a summer-maximum water temperature of 10°C.

To explore the sensitivity of model predictions to predator energy density, we conducted a final set of simulations in which the Rudstam et al. (1994) predator energy-density function was replaced with a mean energy density based on a recent determination of energy density of Lake Michigan whitefish.

Using bomb calorimetry, we determined that the mean energy density of five whitefish from Lake Michigan, captured near Muskegon, Michigan, in 2000 was 6531 $J \cdot g^{-1}$ on a wet-weight basis. In contrast, the Rudstam et al. (1994) predator energy-density function yielded an estimate of 13 050 $J \cdot g^{-1}$ on a wet-weight basis for fish with weights ≥155 g. Therefore, we replaced the Rudstam et al. (1994) predator energy-density function with the mean energy-density value of 6531 $J \cdot g^{-1}$ and performed a set of four—one simulation for each of the four whitefish age groups—simulations using the lake trout swimming-speed submodel and a summer-maximum water temperature of 10°C.

Results

According to our bioenergetics-model simulations, the GGE of whitefish decreased slightly as the summer-maximum water temperature increased from 8 to 15°C (Fig. 1). Averaging across all four water-temperature regimes, the GGE of whitefish during their third year in the lake was 0.075, and the GGE of whitefish during their fifth year was 0.02.

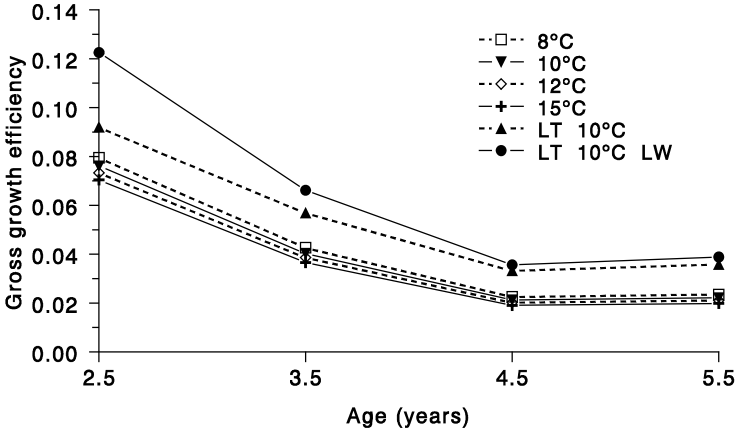

Fig. 1. The GGE of lake whitefish in northern Lake Michigan during 1991-2000 was estimated as follows: four lower curves—unmodified generalized coregonine bioenergetics model of Hanson et al. (1997) using summer-maximum water temperatures of 8, 10, 12, and 15ºC; second curve from top—as above with original swimming-speed submodel replaced with the swimming-speed submodel of Stewart et al. (1983) for Lake Michigan lake trout and a summer-maximum water temperature of 10ºC; and top curve—as above with the lake trout swimming-speed submodel, the predator energy-density function replaced by a value of 6531 J·g^{-1} (wet-weight basis), and a summer-maximum water temperature of 10ºC.

Replacing the Rudstam et al. (1994) swimming-speed submodel with the Stewart et al. (1983) swimming-speed submodel for lake trout led to a substantial increase in the GGE at all ages (Fig. 1). Whitefish GGEs during their third and fifth years in the lake were 0.09 and 0.035, respectively.

Using the lake trout swimming-speed submodel and replacing the Rudstam et al. (1994) predator energy-density function with an actual caloric density for Lake Michigan whitefish led to a considerable increase in GGE for younger fish but only a slight increase for older fish (Fig. 1). Whitefish GGEs during their third and fifth years in the lake were 0.12 and 0.04, respectively.

Discussion

Estimates of the GGE from the unmodified version of the generalized coregonine bioenergetics model applied to Lake Michigan whitefish were relatively low compared with published estimates for Lake Michigan bloater by Rudstam et al. (1994) or with published estimates for whitefish from inland waters in northern Quebec (Trudel et al. 2001; M. Trudel, Department of Fisheries and Oceans, Nanaimo, British Columbia, V9R 5K6, Canada, personal communication). Rudstam et al. (1994) generated estimates of bloater GGE of 0.10 and 0.05 for their third and fifth years in Lake Michigan, respectively. Trudel et al. (2001) developed their own bioenergetics model using mercury as a tracer for whitefish in Quebec. Their model predicted that whitefish GGEs during their third and fifth years in inland waters of northern Quebec were 0.12 and 0.05, respectively. In contrast, the unmodified version of the GCBM by Hanson et al. (1997) predicted that whitefish GGEs during their third and fifth years in Lake Michigan would be 0.075 and 0.02, respectively.

The Rudstam et al. (1994) swimming-speed submodel may have overestimated swimming speeds of whitefish in Lake Michigan. As mentioned above, the estimated swimming speed of 45 $cm \cdot s^{-1}$ appeared to be too high. Stewart and Ibarra (1991) commented that Pacific salmon would be expected to exhibit relatively high swimming speeds because they evolved to swim long distances searching for active, pelagic prey. Yet, the average annual swimming speed predicted by the submodel developed by Stewart and Ibarra (1991) for 1.5-kg chinook and coho salmon in Lake Michigan was 35 $cm \cdot s^{-1}$.

The predator energy-density function developed by Rudstam et al. (1994) substantially overestimated the energy density of Lake Michigan whitefish. Energy density estimated by the unmodified GCBM was 13 050 $J \cdot g^{-1}$, whereas the actual energy density for Lake Michigan whitefish was measured at 6531 $J \cdot g^{-1}$. Interestingly, when the lake trout swimming-speed submodel was incorporated into the generalized coregonine bioenergetics model and a more realistic value of energy density of whitefish in Lake Michigan was used, the modified bioenergetics model yielded estimates of GGE for Lake Michigan whitefish that were in accord with previously published estimates of GGE for Lake Michigan bloater and for whitefish in inland waters of northern Quebec.

Our study did not show that the unmodified version of the GCBM was providing inaccurate estimates of food consumption by whitefish in Lake Michigan. Nevertheless, the disagreement between the predictions of GGE for Lake Michigan whitefish and the estimates of GGE for Lake Michigan bloater and whitefish in northern Quebec suggested that the unmodified version of the GCBM was substantially overestimating food consumption by whitefish in Lake Michigan. Clearly, the GCBM needs to be thoroughly evaluated. The approach recommended by Madenjian et al. (2000) would not only provide a plan for a reasonably thorough evaluation of the generalized coregonine bioenergetics model but would also serve as a framework to improve the model performance should the evaluation indicate model deficiencies. In the Madenjian et al. (2000) approach, consumption and growth of whitefish in laboratory tanks would be compared to model predictions of consumption and growth.

A comparison of field and laboratory estimates of PCB net-trophic-transfer efficiency would also serve as a field evaluation of the GCBM. In the laboratory, the efficiency of the net trophic transfer of PCBs to whitefish could be measured by determining PCB concentrations in the whitefish at the start and end of the experiment and by determining PCB concentrations in their food. A field estimate of PCB net-trophic-transfer efficiency to whitefish from their prey could be generated by applying the GCBM to Lake Michigan whitefish to estimate food consumption and by determining PCB concentrations in both whitefish and their prey. Because the respiration component of the bioenergetics model is based on detailed respiration measurements over a range of swimming speeds and water temperatures, we suspect that the model performance in the laboratory would be reasonably good. Because the swimming speeds predicted in the field by the model appear to be unrealistically high and the model estimate of predator energy density is biased high, we suspect that the model substantially overestimates food consumption. Should a thorough evaluation of the model confirm our suspicions, the swimming-speed submodel and the predator energy-density function of the GCBM should be modified, and the modified model should be applied to several Lake Michigan whitefish data sets to test the accuracy of its predictions.

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Preliminary Investigations for Causes of the Disappearance of *Diporeia* spp. from Lake Ontario

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Abstract

The amphipod *Diporeia* spp. comprised 60-80% of the benthos in offshore Lake Ontario and was an important food for fish. In eastern Lake Ontario, *Diporeia* spp. began disappearing in 1993 just after the arrival of dreissenid mussels. We compared survival of *Diporeia* spp. and *Hyalella azteca* in sediments from areas where *Diporeia* spp. populations had vanished with survival in sediments still inhabited. Survival was also examined in the presence of zebra mussel (*Dreissena polymorpha*) pseudofeces, filtered water from mussel cultures, and added bacteria. The Microtox® test indicated that sediment pore water was not toxic. Sediments from sites with large *Dreissena* spp.

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populations (Lake Erie and western Lake Ontario) lowered *Diporeia* spp. survival. *Diporeia* spp. and *H. azteca* responded differently to test sediments and zebra mussel pseudofeces. Pseudofeces added to Lake Superior sediment greatly reduced *H. azteca* survival but had less effect on *Diporeia* spp. survival. Added bacteria had little effect on the survival of either species. Sediments exposed to dying *Diporeia* spp. caused significant mortality suggesting the presence of a pathogen. *Diporeia* spp. remained common in two inland lakes containing dreissenids indicating that the amphipod can co-exist with the mussels.

Introduction

The biota of the Great Lakes has changed greatly since the arrival of several exotic species over the last two decades. Following the arrival of the zebra mussel (*Dreissena polymorpha)* and quagga mussel (*D. bugensis)*, the deepwater amphipod *Diporeia* spp. (hereafter, diporeia as a common name), formerly *Pontoporeia hoyi,* has declined in all of the Great Lakes except Lake Superior. Since 1992, diporeia has disappeared from suitable habitats in Lakes Michigan, Huron, Erie, and Ontario at depths <70 m where they had been abundant (>3000/m^2) (Dermott and Kerec 1997; Nalepa et al. 1998; Dermott 2001). Maximum densities had occurred at depths of 30-60 m (Nalepa 1989; Sly and Christie 1992) where temperatures remain cold and organic matter accumulates on fine sediments. Settling diatoms and sediment bacteria are the main food of diporeia, and their lipid levels peak after the spring diatom bloom (Gardner et al.1985). This amphipod provided over 20% of the food energy (Flint 1986) for the offshore Lake Ontario fish community (lake whitefish (*Coregonus clupeaformis*, hereafter, whitefish), alewife (*Alosa pseudoharengus*), smelt (*Osmerus mordax*), and Pacific salmon (*Oncorhynchus* spp.)). Commercial catches and reproduction rates of whitefish and smelt have decreased in Lakes Erie and Ontario following the decline in diporeia populations (Dermott et al. 1999; Hoyle et al. 1999; Owens and Dittman 2002). Proposed hypotheses for the loss of diporeia include a decrease in available food due to competition with mussels, increased sediment toxicity due to changing contaminant cycling, biological toxicants associated with zebra mussel pseudofeces or excretions, and pathological bacteria or viruses.

Nutrient levels and algal biomass have declined in the Great Lakes since the 1970s. Between 1981 and 1995, there were significant reductions in phosphorus, algal biomass, and chlorophyll in eastern Lake Ontario, but chlorophyll and algal biomass did not change significantly in the middle of the lake (Johannsson et al. 1998). Since 1990, large mussel populations on shoals and in nearshore regions have further increased water clarity, reduced nutrients and phytoplankton density (Leach 1993; Markarewicz et al. 1999; Millard et al. 1999), and removed a large portion of the algae that had previously settled offshore in diporeia habitat (Dermott and Kerec 1997; Nalepa et al. 1998).

The absence of diporeia near the Niagara River was considered to be a result of high levels of persistent organic compounds in the area (Nalepa 1991) because diporeia are sensitive to sediment contaminants (Gossiaux et al. 1993). Concentrations of the most persistent organic pollutants have declined in the Great Lakes since 1980 (Pierce et al. 1998), but residues of newer compounds such as brominated flame retardants and herbicides have been increasing in the Great Lakes basin (Alaee et al. 1999; Thurman and Cromwell 2000). If these newer compounds are becoming toxic to Great Lakes populations of diporeia, their widespread use likely would also impact diporeia populations in smaller lakes within the Great Lakes basin.

Dreissenids produce large quantities of pseudofeces that accumulate on the bottom near the colonies. During storms, this material is transported offshore and could affect diporeia populations far removed from nearshore colonies. In Lake Erie, a reduction in sediment particle size increased total organic content, and the presence of polycyclic aromatic hydrocarbons in sediments has been associated with biodeposits from the large mussel population (Howell et al. 1996). Blooms of the cyanobacteria *Microcystis* have increased in Lake Erie and Saginaw Bay due to selective rejection of cyanobacteria by filtering dreissenids (Vanderploeg et al. 2001). The toxicant microcystin is known to cause mortality in crustaceans (DeMott et al. 1991) and could be transferred to diporeia via deposited pseudofeces. Biological toxicants and viral, bacterial, or ciliate pathogens may be associated with the mussels or their pseudofeces. There has been a recent increase in botulism in Lake Erie (Getchell et al. 2002) possibly due to biomagnification of the *Clostridium* toxin by dreissenids or increased spore abundance among the decomposing mussels and pseudofeces in the sediments. In the Bay of Quinte, benthic mats of the filamentous bacterium

Thioploca ingrica appeared in the sediment following the disappearance of diporeia (Dermott and Legner 2002).

The purposes of this study were to determine if sediments from locations where diporeia have disappeared or the presence of mussel pseudofeces, their excretions, or added bacteria would reduce diporeia survival; to determine if the amphipod *Hyalella azteca* also had reduced survival when exposed to such sediments, added pseudofeces, or bacteria; to determine if the Microtox® test exhibited any inhibition when exposed to pore water from these sediments; and to examine trends in diporeia populations in the Bay of Quinte and in two smaller lakes that also have zebra mussel populations.

Methods

Sediments were collected from nine sites in the Great Lakes (Fig. 1, Table 1) mostly in the spring (April-June) and again in the autumn (August-October). Diporeia populations were still present at the Lake Superior, Batchawana Bay, Colpoy's Bay, and mid-Lake Ontario sites but had disappeared at the Lake Erie, western and eastern Lake Ontario, and Bay of Quinte sites (Table 1).

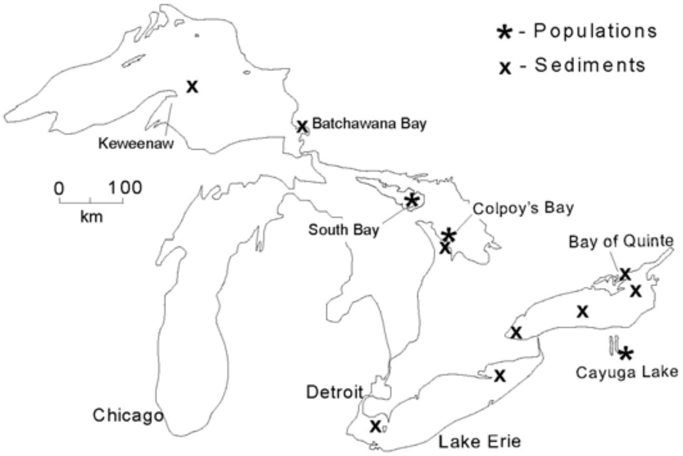

Fig. 1. Location of sediment collections and sampled *Diporeia* spp. populations.

Table 1. Depth, density of *Diporeia* spp. and dreissenid mussels, and relative abundance of *Thioploca ingrica* at sites where sediments were collected. Also given are percent sand, mean particle size (µm), and percent organics (loss on ignition) in sediments.

Sediment source	**Depth (m)**	***Diporeia* spp. (no./m^2)**	**Dreissenids (no./m^2)**	***Thioploca ingrica****	**Sand (%)**	**Size (µm)**	**Organics (%)**
Lake Superior							
Lake Superior (composite)	104/ 164	96	0	-	66	65.6	1.7
Batchawana Bay	32	548	0	+	1	7.3	4.3
Lake Huron							
Colpoy’s Bay	33	2000	+	-	19	5.8	2.4
Lake Erie							
Western	10	0	500	-	5	7.1	6.2
Eastern	38	0	4590	+	0	3.2	3.4
Lake Ontario							
Western	45	0	2320	-	22	21.8	3.2
Mid-lake	125	987	0	-	0	3.9	7.9
Eastern	35	0	0	+	2	9.7	10.6
Bay of Quinte	32	0	420	+++	0	5.3	9.7

*Degree of abundance: - absent; + low; +++ high

Diporeia were collected during cold epilimnion conditions in spring and autumn from Colpoy's Bay on Georgian Bay. The amphipods were maintained at 5ºC in the dark for up to four months in large plastic bags with native sediments and 12 L of water. Initially, each bag contained a minimum of 100 amphipods. Every month, half of the water in each bag was replaced with cooled, dechlorinated tap water, and the amphipods were fed about 0.25 g of freeze-dried diatoms. Assays were conducted for up to 90 days to allow chronic effects to appear during this short part of their two-year generation time. Methods were adapted from Jackson et al. (1995) and Munawar et al.

(1999). Five adult-sized diporeia (4-7 mm) were added to 40 mL of sediment in 250-mL jars (6-cm ID x 7-cm high) resulting in a density of about 1800 m^{-2} and a dry biomass of 1.7 g m^{-2}. The amphipods were captured and transferred to the jars using 6-mm ID pipettes to reduce exposure to air. Each jar was filled with water and covered with a 1-mm-mesh screen held on by an elastic band. Six replicate jars were placed in a 12-L aquarium containing 3 L of water. Aquaria were transferred to an incubator set at 10ºC with a 12-h light/dark photoperiod to match the August to October conditions at a 35-m depth in Lake Ontario. A bubbler was placed in each aquarium, and the water level was gently adjusted to leave the jars 1 cm below the water surface. The sediment surfaces in the jars were monitored at 24 and 48 h after setup, and any dead or injured diporeia seen on the surface during the first 48 hours were replaced. Once per week, the water in the aquarium was drained, 2 mg of freeze-dried diatoms were added to each jar, and fresh 10ºC dechlorinated water was added to each aquarium to bring the final volume back up to 3 L. This feeding provided slightly more than the consumption rate of diporeia in Lake Ontario (0.03 mg organics individual^{-1}day^{-1}) (Dermott and Corning 1988). At 30 and 60 days, the sediment in each jar was screened through a 1-mm-mesh sieve, and the surviving amphipods were counted and placed back into the original sediment in the same jar. At the end of 90 days, the surviving amphipods were counted, and specimens were either frozen for lipid analysis or preserved for pathological analysis. For most sediments, two replicated trials were conducted, and each trial was run within three months of the month of sample collection (Table 2).

Table 2. Sediments assayed for *Diporeia spp.* and *Hyalella azteca* survival and for Microtox® tests. N = number of replicates in all trials. nt = not tested.

Sediment source	**Collection month**	***Diporeia* spp. replicates N**	***Hyalella azteca* N**	**Microtox® test N**
Lake Superior				
Lake Superior (composite)	May	6	8	2
Batchawana Bay	July	12	16	2
Lake Huron				
Colpoy's Bay	June	6	8	nt
Lake Erie				
Western Lake Erie	April	6	8	2
Eastern Lake Erie	April	6	8	2
	October	6	8	2
Lake Ontario				
Western	June	6	8	nt
	October	6	8	2
Mid-lake	April	6	8	nt
	October	6	8	2
Eastern	April	12	12	2
Bay of Quinte	April	6	8	2
	October	6	8	2

Selected diporeia were measured, placed into Durham tubes (6 x 50 mm), dried under nitrogen for 24 hours at 60ºC, and frozen at -80ºC in preparation for total lipid analysis. In some assays, diporeia were sampled for lipids after only 60 days exposure. For comparison, lipids were also determined for diporeia (4-7 mm) collected in field samples from Colpoy's Bay and mid-Lake Ontario. Lipids were determined on a per dry-weight basis using lipid extraction with chloroform:methanol (2:1, v/v) and quantified gravimetrically (Cavaletto et al. 1996).

In addition to conducting assays on sediments collected from various regions of the Great Lakes, test assays were also conducted where either dreissenid pseudofeces, filtered water from dreissenid cultures, dead or paralyzed diporeia, or the bacterium *Bacillus thuringiensis* (commercially *B.t.*) were added to a control sediment (Table 3). The sediments used as controls were from the Lake Superior composite, Batchawana Bay, or Colpoy's Bay (Georgian Bay), and mid-Lake Ontario (for *H. azteca*), all of which supported stable diporeia populations. The *B.t.* was used as a surrogate for bacteria that could colonize pseudofeces and interfere with either the gut flora or gut enzymes of diporeia. To each jar, 0.2 mg of *B.t.* was added in weeks 1 and 3.

In the pseudofeces assays each week, 0.3 or 0.4 mL of pseudofeces slurry, a food source in place of diatoms or TetraMin® flakes, was added to each replicate jar or cone. Assuming pseudofeces were much less nutritional than diatoms, the volume of added pseudofeces was adjusted to provide double the organic matter in the regular weekly diet (2 mg of diatoms for diporeia or 2.5 mg TetraMin® for *H. azteca*). Pseudofeces were collected from laboratory cultures of dreissenids held in 30-L aquaria and fed frozen diatoms collected from Lake Ontario during the spring bloom (March-April). The pseudofeces were siphoned onto a 28-µ mesh, placed in centrifuge tubes, and allowed to settle for 24 h. The ratio of water was then adjusted to 12 mL pseudofeces:8 mL water. Replicate, 1-mL aliquots of this pseudofeces slurry were dried and ashed to estimate organic content. From these calculations, we calculated the required feeding volume of slurry that had double the organic content of the diatom diet. The pseudofeces were stored for a minimum of two weeks at 5ºC before use to represent a transport time from nearshore to below the thermocline.

Table 3. Number of test assays in all trials for *Diporeia* spp. and *Hyalella azteca* survival using dreissenid pseudofeces, filtered water, or added *Thioploca ingrica* or *(B.t.)* bacteria. Control sediments for *Diporeia* spp. were from Lake Superior or Batchawana Bay. Control substrates for *H. azteca* were mid-Lake Ontario sediment and gauze only. nt = not tested.

Assay	***Diporeia* spp. replicates**	***Hyalella azteca* replicates**
Batchawana Bay	12	12
Mid-Lake Ontario	6	8
Pseudofeces		
Superior	6	8
Batchawana Bay	12	8
Filtered water/Batchawana Bay	12	nt
Zebra mussels		
Batchawana Bay	6	nt
Colpoy's Bay	6	nt
Thioploca ingrica/Bay of Quinte	6	nt
Bacillus thuringiensis (B.t.)		
Batchawana Bay	6	nt
Colpoy's Bay	nt	4
Bay of Quinte	nt	4
Dying amphipods/Batchawana Bay	12	nt
Pseudofeces/gauze	nt	8
Filtered water/gauze	nt	8
TetraMin®/gauze	nt	12

Water from dreissenid cultures was put through a 0.45-µ filter to remove all but viral-sized particles and dissolved chemicals. The 3 L of water in each assay aquarium or 1 L in each Imhoff cone (*H. azteca*) was replaced every week with freshly filtered water at the appropriate temperature. Diporeia were also exposed to clean control sediment (Batchawana Bay) on which dying diporeia were left for 48 h. We exposed diporeia directly to competition with dreissenids by adding two mussels (17-mm length) to each jar containing the control sediment (Batchawana Bay). The feeding regime for this assay was 6 mg diatoms/week (standard diet plus 2 mg for each mussel).

We also measured survival of diporeia and the sulfur bacterium *T. ingrica* in one experiment. *T. ingrica* filaments were collected from Bay of Quinte sediment by screening them through a 0.5-mm mesh. Approximately 0.12 g of bacteria was added to jars containing screened Bay of Quinte sediment, resulting in a biomass of bacteria about one-third that at the collection site. Five diporeia were added to each of five jars; one jar had no diporeia. At 30 and 60 days the jars were screened on a 0.5-mm mesh and the number of surviving diporeia and the wet weight of surviving *T. ingrica* filaments were tallied.

Assays using *H. azteca* were conducted for 28 days (four weeks) following the procedure of Borgmann and Norwood (1999) who used Imhoff settling cones with 1 L of water overlying 15 mL of sediment. Young amphipods (0-10 days old; <0.01 mg ind^{-1}) were obtained from laboratory cultures grown at room temperature with a 16-h-light:8-h-dark photoperiod. Fifteen young amphipods were added to each cone and fed 2.5 mg TetraMin® fish flakes weekly. The amphipods were exposed to nine different sediments and five treatments including sediment with either added pseudofeces or the insecticidal bacterium *B.t.* In addition, amphipods were exposed to three treatments using cotton gauze as a substrate instead of sediment. They were exposed to either gauze alone (control), filtered water from an aquarium containing zebra mussels, or zebra mussel pseudofeces (food source) in place of the TetraMin® (Table 3). Two trial runs of four replicates were conducted for each treatment with sediments from Lakes Erie and Ontario collected in spring and autumn. Sediment was sieved through a 1-mm mesh prior to use to remove macroinvertebrates, mussels, shell fragments, and coarse particles.

Dissolved oxygen, ammonia concentration, pH, and temperature were measured prior to adding the amphipods and at the end of the 28-day period. After 28 days, animals were counted and then allowed to clear their guts in a 50-µM solution of the chelator ethylenediamine tetraacetic acid (EDTA) for 24 hours. After gut clearing and drying for 48 hours at 60ºC, dry weights of *H. azteca* were measured. The animals were then frozen for future calculations of body burdens and lipid levels. Statistical comparisons were done on the average number surviving in each test using one-way analysis of variance (ANOVA) and treatment comparisons were made using the *F*-test.

The Microtox® liquid-phase acute-toxicity test was conducted using pore water extracted from sediments (Table 1). Pore water was isolated by centrifuging approximately 240 mL of sediment at 6000 rpm for 60 min at 4ºC (Giesy et al. 1988) and filtering the supernatant through glass-microfiber filters (GF/C) under a 10-psi vacuum. Pore water was stored at 4ºC and used within three days. Two replicate tests were performed using the Beckman Microtox® model 500 analyzer following the standard 100% test protocol (Microtox Omni Software, Azur Environmental, Strategic Diagnostics, 111 Pencader Dr., Newark, Delaware, 19702-3322). Control standards of saline were prepared to measure the photo-luminescence of the bacteria. As a positive test of toxicity, solutions of phenol and $ZnSO_4$ were prepared to measure photo-inhibition of the photobacterium after 5-min and 15-min exposures.

Changes in diporeia populations in the lower Bay of Quinte were examined using published and unpublished data from 1967-2000. Trends in diporeia populations in two lakes with dreissenid populations were also examined: Cayuga Lake (upper New York State) and South Bay (Manitoulin Island, Lake Huron). In Cayuga Lake, two sites at 43- and 63-m depths (42º 28.93'N: 076º 31.30'W and 42º 29.31'N: 76º 31.41'W, respectively) were sampled, and these data were compared to data from 1994 (E. L. Mills, Cornell University Biological Field Station, 900 Shackelton Point Road, Bridgeport, New York, 13030, unpubl. data). Data from five sites in South Bay were compared to the data of Cooper (1964) and Johnson (1988). At each site, a 22-cm Ekman grab was used to collect five replicate samples, which were sieved through a 0.58-mm screen (#30 mesh) and preserved in 10% formalin following the methods of Johnson (1988). The diporeia and dreissenids were later removed, identified, enumerated, and weighed (blotted wet biomass).

Results

Diporeia had significantly lower survival (ANOVA, $P < .005$) in sediments from eastern Lake Erie and western Lake Ontario than in Lake Superior sediment (Fig. 2). Both the eastern Lake Erie and western Lake Ontario sites had high *D. bugensis* densities (>2300 m^{-2}; Table 1). Survival in sediments from western Lake Erie and eastern Lake Ontario was not significantly less than in Lake Superior sediment ($P > 0.5$). Survival was less variable in the Lake Superior composite sediment than in sediment from Batchawana, Colpoy's Bay, or mid-Lake Ontario. Survival in Bay of Quinte sediment was the same as in Lake Superior sediment despite the absence of diporeia in the bay.

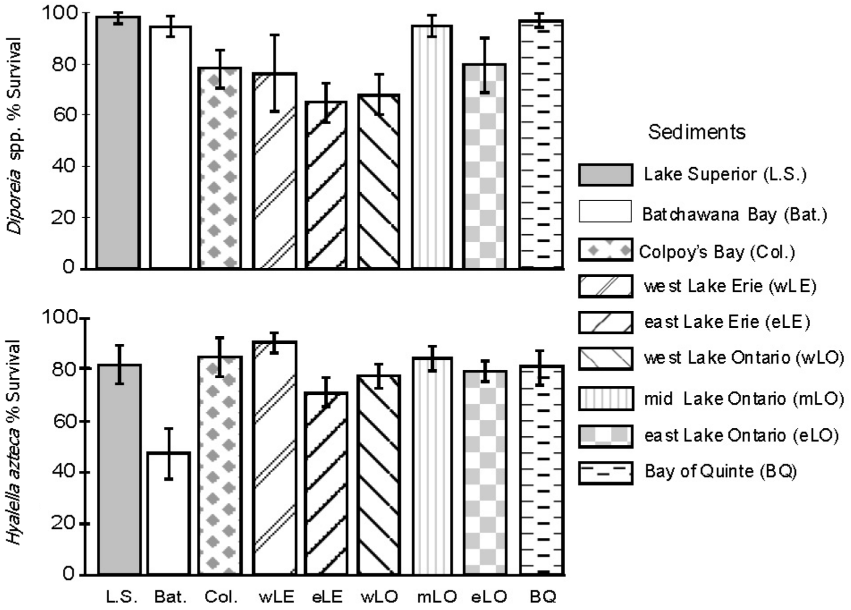

Fig. 2. Average percent survival and standard error bars for *Diporeia* spp. (upper panel) and *Hyalella azteca* (lower panel) when exposed to Great Lakes sediments. Data from all trials; *Diporeia* spp. experiments lasted 90 days, and *H. azteca* experiments lasted 28 days.

Diporeia survival was significantly lower (ANOVA, $P < 0005$) in the control sediment to which zebra mussel pseudofeces were added than in Lake Superior sediment (Fig. 3). Addition of pseudofeces reduced survival 24%

below that in the control sediment. Diporeia survived better in Batchawana Bay sediment when exposed directly to zebra mussels in the same jar than when exposed to either pseudofeces ($P < 0.5$) or filtered water from mussel aquaria ($P > 0.5$). Mussel density in the jars was about 600 m^{-2} with a dry shell-free biomass of 10.0 g m^{-2}, almost six times the biomass of the added amphipods. Diporeia was not sensitive to the bacterium *B.t.* added to the control sediment ($P > 0.1$). They were, however, very sensitive to Batchawana Bay sediment onto which paralyzed and dying diporeia had been placed for 48 hours and then removed ($P < 0.001$) (Fig. 3). Dead animals from this assay were preserved for pathological examination to identify causes. Microsporidian and a rickettsia-like parasite were found in amphipods from some of the assays.

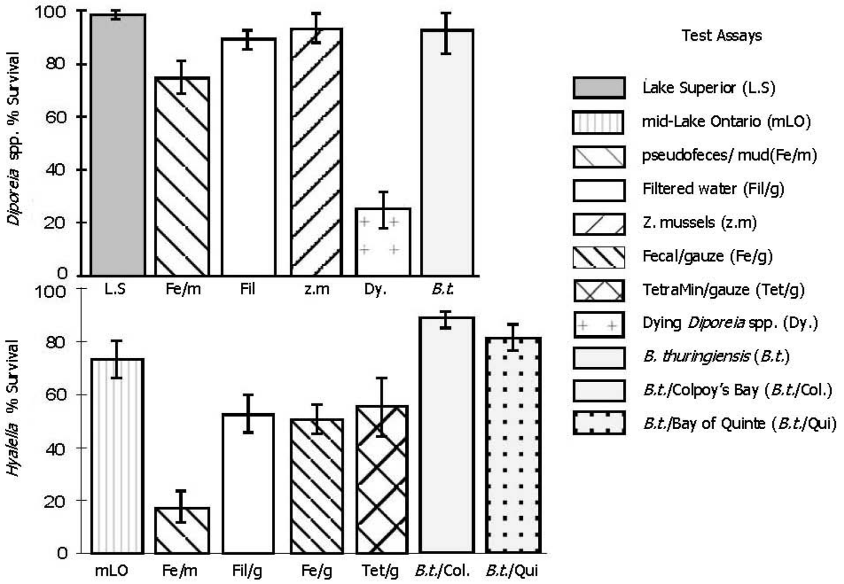

Fig. 3. Average percent survival of *Diporeia* spp. and *Hyalella azteca* in various test assays. Bars are ±1 standard error.

The addition of the bacterium *T. ingrica* to the Bay of Quinte sediment had no effect on diporeia survival (97%) when compared to either Lake Superior or mid-Lake Ontario sediments ($P > 0.7$). The amount of *T. ingrica* in the sediment was reduced by the presence of diporeia due to burrowing or grazing on the bacterial filaments (Fig. 4).

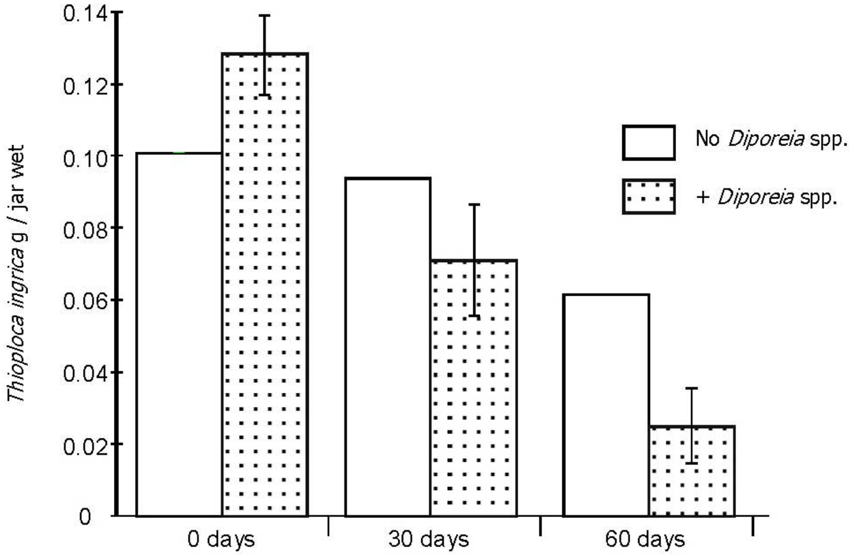

Fig. 4. Wet weight of *Thioploca ingrica* filaments after 30 and 60 days in sediment with or without *Diporeia* spp. Bars are ±1 standard error.

Sediment surfaces in jars with healthy diporeia were well tilled, typically having no visible burrows. Only when a few amphipods remained in the jar was the sediment surface smooth with visible burrow openings. Dead or moribund amphipods were often seen on top of such sediments. Active amphipods burrowed into the sediment and fed on algal remains, bacteria, and detritus, which appeared as a dark band in their guts. However, when diatoms were added, the amphipods would often orient vertically in the sediment with only their eyes and antennae exposed. Then the diporeia would sweep the sediment surface with their antenna, drawing the recently settled diatoms toward their mouths. After a few minutes of sweeping, they would burrow to re-emerge about one to two body-lengths away and then begin sweeping the surface again.

Lipid levels were highest in diporeia collected from mid-Lake Ontario in June but were not significantly higher in amphipods collected from Colpoy's Bay (Table 4). For most assays, there was no difference in lipids after 90-days exposure compared to 60 days, indicating that the feeding regime of 2 mg per week was sufficient. Lipid levels were highest in diporeia exposed to *T. ingrica* or in direct competition with zebra mussels in the same jars, indicating that the added *T. ingrica* filaments and increased ration (6 mg) for jars with mussels provided diporeia with more calories. Lipid levels in diporeia fed only pseudofeces were equal to those fed diatoms on Lake Superior sediment (Table 4).

Survival of *H. azteca* was high when exposed to the Lake Superior composite, Colpoy's Bay, western Lake Erie, and mid-Lake Ontario sediments (Fig. 2). Low survival was observed after exposure to sediment from Batchawana Bay (ANOVA, $P > 0.01$). Survival of *H. azteca* was not significantly less ($P > 0.3$) in sediments from sites with high densities of dreissenids (eastern Lake Erie and western Lake Ontario, Table 1). Survival in western Lake Erie sediments was the highest of all assays and was significantly higher than in eastern Lake Erie sediment ($P > 0.02$). The survival of *H. azteca* tended to be high in sediments with higher organic content (Table 1).

Table 4. Mean length and percent lipid of *Diporeia* spp. from collection sites in Lake Ontario and Colpoy's Bay during 2001 and values for *Diporeia* spp. exposed to various control/test sediments and assays. S.E. given in parentheses.

Sediment/assay	**N (repl.)**	**Exposure (days)**	**Length (mm)**	**Total lipid (% dry mass)**
Sediment*				
Mid-Lake Ontario				
April	15	0	5.15 (0.42)	12.33 (2.59)
June	14	0	6.05 (0.30)	20.34 (2.41)
Oct	14	0	5.39 (0.16)	13.76 (1.83)
Colpoy's Bay (June)	30	0	5.39 (0.16)	15.53 (2.06)
Assays				
Lake Superior (composite)	14	60	6.32 (0.31)	12.05 (1.04)
	14	90	6.33 (0.23)	10.57 (1.42)
Eastern Lake Erie	14	90	6.29 (0.32)	8.64 (0.91)
Western Lake Ontario	14	60	6.83 (0.08)	15.02 (1.86)
	22	90	5.75 (0.20)	5.06 (1.10)
Mid-Lake Ontario	15	60	6.95 (0.15)	8.58 (1.33)
	12	90	6.55 (0.24)	8.36 (1.87)
Bay of Quinte	14	90	6.64 (0.23)	10.28 (1.42)
Bay of Quinte + *Thioploca ingrica*	14	90	5.83 (0.15)	16.11 (1.19)
Filtered water + control	12	60	6.71 (0.18)	12.18 (1.79)
	33	90	5.97 (0.12)	14.87 (1.13)
Z. mussels + control	8	60	6.59 (0.29)	17.57 (0.89)
	18	90	5.96 (0.16)	18.35 (1.31)
Pseudofeces + control	19	60	6.60 (0.19)	11.39 (1.21)
	26	90	6.11 (0.18)	10.57 (1.55)

* Lipids prepared within one week of collection.

Survival of *H. azteca* on cotton gauze as a sediment-free control with TetraMin® as food (Tet/g in Fig. 3) was lower in all but one of the sediments (ANOVA, $P < 0.05$; Fig. 3). The *H. azteca* survival on gauze exposed to either filtered water (Fil/g) from the mussel cultures or pseudofeces (Fe/g) was similar to survival on gauze alone (Tet/g; $P > 0.5$). Pseudofeces clearly had a negative effect on *H. azteca* survival when added to Lake Superior composite sediment (Fe/m; $P < 0.001$), in which only 17% of the *H. azteca* survived the 28-day exposure (Fig. 3). In all 16 trials of pseudofeces added onto sediment, survival was less than in any other treatment. Presence of the bacterium *B.t.* had no effect on *H. azteca* survival in either Colpoy's Bay or Bay of Quinte sediments ($P > 0.5$; Fig. 3). Survival in these two *B.t.* treatments was better than in mid-Lake Ontario sediment ($P > 0.7$).

Average individual dry weights of *H. azteca* on sediments or gauze was related to observed survival rates (Fig. 5). Body weight after 28 days was greatest on mid-Lake Ontario or Bay of Quinte sediments and was lowest on Batchawana Bay sediment or Lake Superior sediment with added pseudofeces. Although *H. azteca* in treatments with gauze and pseudofeces (Fe/g) or gauze and filtered water (Fil/g) had much better survival than the treatment with pseudofeces added to the sediment (Fe/m), their final average body weights (as growth) in the gauze treatments were very low (<1.5 mg) and similar to final body weight in pseudofeces on sediment (Fe/m; Figs. 3 and 5). Final weights of *H. azteca* exposed to the gauze alone as a control were double the final weight in the other gauze treatments and more similar to that in the sediment treatments.

Levels of neutral herbicides, including atrazine, were below detection limits in all the sediments tested ($<18\ \mu g\ kg^{-1}$). Metal levels were greatest in sediments from mid- and eastern Lake Ontario (Table 5), both of which had higher amphipod survival than the Lake Erie sediments. Metal levels in Batchawana Bay (Lake Superior) sediments were higher than eastern Lake Erie sediments. Metal levels in the Lake Ontario sediments were well below the estimated Severe Effect Levels (SEL) which are levels above which acute toxicity to biota are likely (Persaud et al. 1992) (Table 5). However, the chelating ability of the higher Ca, Fe, and organic content (Table 1) in the Lake Ontario sediment may make its metals less available to aquatic organisms compared to levels in the Batchawana Bay sediment.

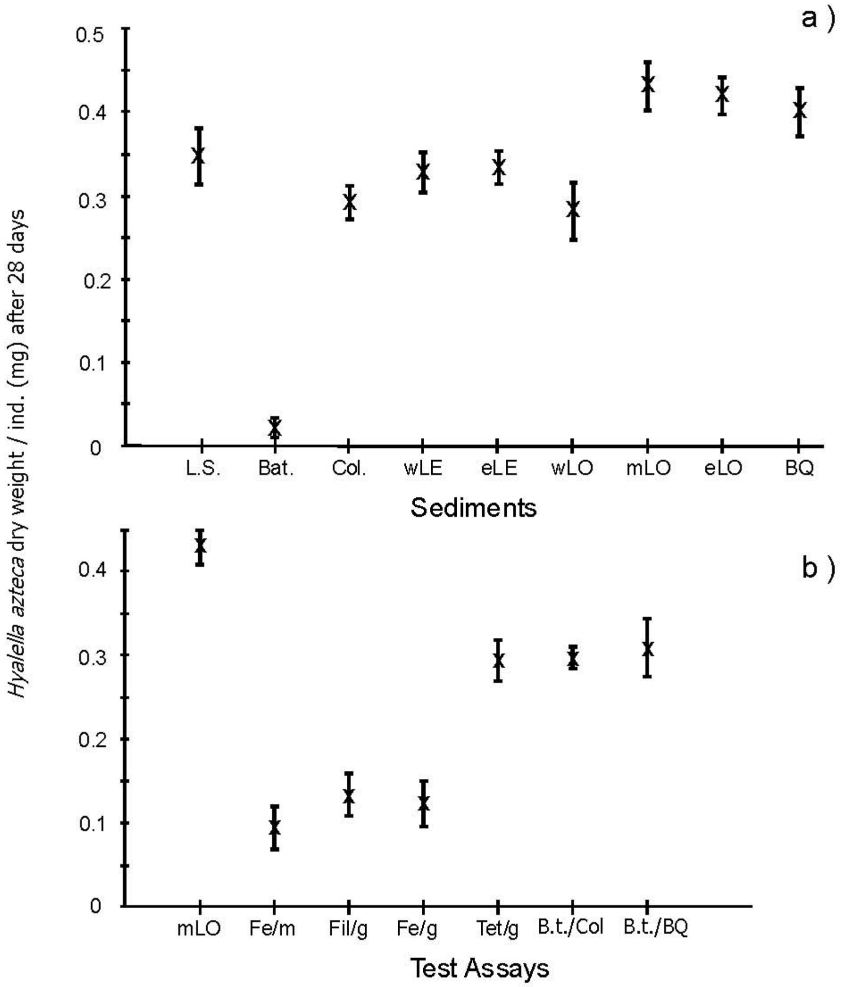

Fig. 5. Average individual dry weight (mg) and standard errors of *Hyalella azteca* after 28-day exposures to: (a) sediments or (b) various test assays. Abbreviations as in Figs. 2 and 3.

Table 5. Metal values as mg/kg in tested sediments. Also given is the Ontario Ministry of Environment's Severe Effect Levels (SEL), which are considered levels that acutely affect the health of sediment-dwelling organisms (Persaud et al. 1992).

Sediment Source	**Ca**	**Cd**	**Cr**	**Cu**	**Fe**	**Ni**	**Pb**	**Zn**
Lake Superior								
Lake Superior (composite)	23800	0.3	25	25	16400	19.7	12.5	40
Batchawana Bay	7660	1.5	65	38	13713	31.7	30.5	111
Lake Huron								
Colpoy's Bay	n.a.	1.9	48	25	25917	51.8	40.6	69
Lake Erie								
Western	35600	1.8	62	40	28900	46.9	48.8	159
Eastern	81300	0.4	49	26	32700	38.2	18.3	95
Lake Ontario								
Western	15600	0.4	38	27	27200	28.9	22.6	95
Mid-lake	16900	2.1	74	75	46200	61.9	88.1	293
Eastern	64100	1.2	42	47	20600	38.1	41.3	141
Bay of Quinte	8440	1.0	63	42	43700	50.4	27.6	143
SEL	-	10	110	110	-	75	250	820

None of the sediments caused a sufficient response in the Microtox® test to allow calculation of an EC_{50} (effective concentration) from a pore-water dilution series. The test with 90% pore water indicated that only sediment from eastern Lake Ontario caused a response (Table 6). A negative percent-effect indicated stimulation rather than inhibition as shown by the 32 to 70% inhibition in the standard solutions of phenol and $ZnS0_4$. The Lake Superior composite sediment caused the second greatest inhibition of the photobacteria (14.8%) in the sediment pore-waters tested. Western Lake Ontario sediment caused the greatest photoactivity (-39%) compared to the saline control. Thus, the absence of diporeia at the eastern Lake Erie and Ontario sites was apparently not due to acute toxicity of a chemical pollutant in their sediments.

We compared diporeia densities from two sites in the Bay of Quinte (Glenora at 21-m depth and Conway at 32-m depth) with chlorophyll *a* levels (Fig. 6). Following improvements in sewage treatment during 1977, chlorophyll decreased steadily between 1985 and 1998 to about 40% of 1977 levels (Fig. 6). A large die-off of white perch (*Morone americana*), a winter predator of diporeia, occurred in the bay during the winter of 1977-1978 (marked as W.P. in Fig. 6). As water quality improved and chlorophyll decreased in the bay, the diporeia population increased until 1990, especially at the shallow 21-m site. Dreissenid mussels became common in the lower bay during 1993 (marked Z.m. in Fig. 6), after which diporeia disappeared at the 32-m site. The population persisted until 1998 at the less favorable 21-m site, which experiences temperatures above its optimum.

Table 6. Average percent effect in Microtox® tests on various sediments using a concentration of 90% pore-water plus saline. Two trials were done with measurements of percent-effect taken at 5 and 15 minutes. nt = not tested.

Sediment source	**% effect @ 5 min.**	**% effect @ 15 min.**
Controls		
Saline	0.0	0.0
Phenol (5 mg/L)	68.8	66.2
$ZnSO_4$ (5 mg/L)	32.0	70.0
Lake Superior		
Lake Superior (composite)	9.5	14.8
Batchawana Bay	8.5	4.8
Lake Huron		
Colpoy’s Bay	nt	nt
Lake Erie		
Western Lake Erie	-16.3	-24.9
Eastern Lake Erie	-22.5	-30.8
Lake Ontario		
Western	-26.1	-38.5
Mid-lake	-32.5	-25.9
Eastern	43.7	29.3
Bay of Quinte	0.3	-14.5

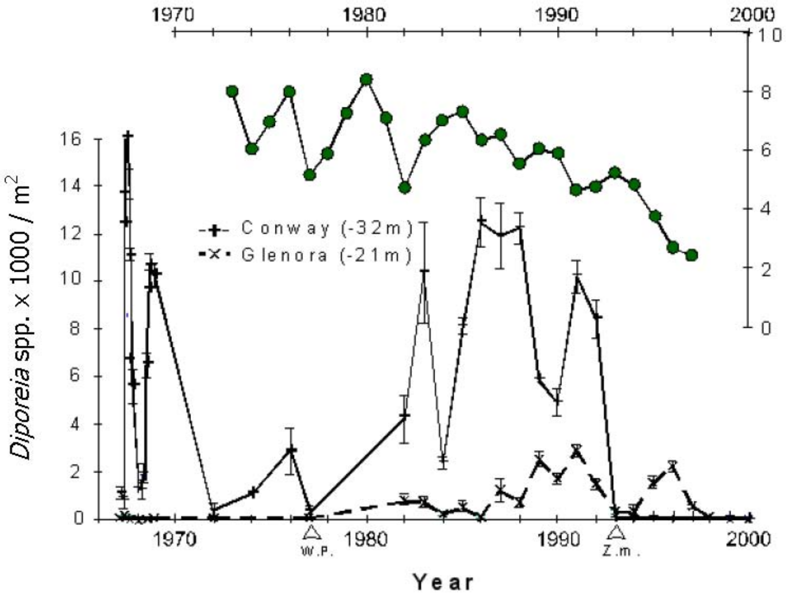

Fig. 6. Density of *Diporeia* spp. at two sites in the lower Bay of Quinte (1967-2000) and chlorophyll *a* levels at the 32-m site (1973-1997) (K. Nichols, Ontario Ministry of Environment and Energy, RR #2, Sutton West, ON L0E 1R0, Canada, unpubl. data). Bars are ±1 standard error. W.P. marks date of a white perch die-off and the start of phosphate controls. Z.m. marks when zebra mussels became common in the bay.

Diporeia remained common in South Bay, Lake Huron, and in Cayuga Lake, NY (Fig. 7), in the presence of moderate zebra mussel populations. In South Bay, zebra mussel density was 766 m^{-2} (SE = 344.6) above a 20-m depth and 7.5 m^{-2} (SE = 5.2) between 30 and 37 m. In Cayuga Lake, zebra mussel density in 2000 averaged 1452 m^{-2} (SE = 456) at 43-m depth and 200 m^{-2} (SE = 120) at 64-m depth. Mussel densities were 1640 m^{-2} (SE = 646) and 700 m^{-2} (SE = 588), respectively, at these depths in 2001. The diporeia population decreased in South Bay but increased in Cayuga Lake after the arrival of zebra mussels (Fig. 7).

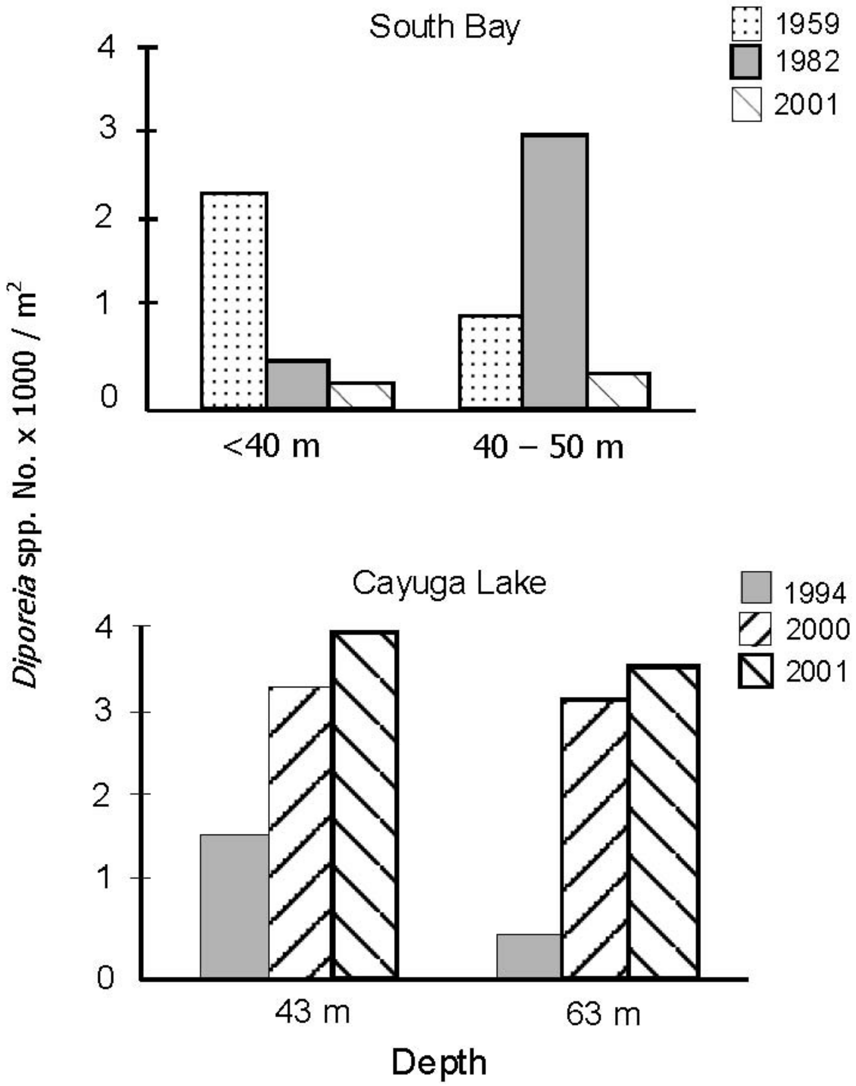

Fig. 7. Trends in *Diporeia* spp. density in South Bay, Lake Huron, and Cayuga Lake, upper New York State.

Discussion

Nalepa et al. (1998) theorized that the diporeia population decline in offshore regions of the Great Lakes was due to food scarcity caused by the filtering of large nearshore dreissenid populations. Direct competition for settling algae had occurred in eastern Lake Erie where *D. bugensis* density averaged over 4000 m^{-2} at depths between 30 and 64 m (Dermott et al. 1998). At mussel densities >1000 m^{-2}, diporeia and dreissenids rarely occurred together in the same samples from Lake Erie (Dermott and Kerec 1997) and Lakes Ontario and Michigan (Nalepa et al. 2005). The extended mussel siphons intercept settling detritus 1-2 cm above the sediment surface before it can settle onto the sediment where the diporeia feed. This direct competition for space and food may have been the cause of the disappearance of diporeia from Lake Erie after the mussels had colonized most of the bottom of the eastern basin (Dermott et. al. 1998). The extant diporeia population in Cayuga Lake is an exception to this concept.

A few amphipods were always present in the Bay of Quinte during the 1970s when diporeia densities were kept low by poor water quality and high fish predation (Johnson and McNeil 1986). As water quality improved, the diporeia population increased as the density of algae in the Bay of Quinte declined from 30-50% prior to 1990. Dreissenids were only established for one summer in the lower Bay of Quinte before diporeia disappeared at the 32-m site in 1993 (Dermott 2001). The persistence of diporeia among a moderate zebra mussel population in Cayuga Lake weakens our argument that food competition is the sole cause of the decline. At many locations in the Great Lakes where diporeia are disappearing, dreissenids are rare or limited to a narrow depth zone along the shore. In other areas, mussel clumps occur sporadically at depths of 40-70 m (Lozano et al. 2001; Nalepa et al. 2005). Algal production in nearshore areas can be greatly reduced by dreissenids (Millard et al. 1999). Dense dreissenid populations on the slopes of lakes can reduce the amount of suspended food before it moves offshore to the depositional zones inhabited by diporeia. Total lipid levels in diporeia collected from mid-Lake Ontario in 1989 (32-37%) (Cavaletto et al. 1996) were greater than the mid-lake average of 11-20% during 2001, which may reflect a declining food supply. We estimate that the decline in algal biomass in the Great Lakes since the start of phosphate control and the arrival of dreissenids can account for a reduction between 40% to as much as 70% of the diporeia population. If reduced algal production were the only cause, a slow decline to densities typical of ultra-oligotrophic lakes (Superior, Great Bear) would be expected. Instead, a rapid and complete elimination of diporeia occurred across large areas of the Great Lakes within 2-5 years after the arrival of zebra mussels.

The Microtox® tests failed to show that any of the tested sediments were acutely toxic indicating that chemical toxicity in the sediments is not the cause of the diporeia decline. Likewise, Landrum et al. (2000) found no acute toxicity to diporeia in Lake Michigan sediments that are now devoid of diporeia. Concentrations of most persistent organic chemicals, including most agricultural chemicals, have decreased in the Lake Ontario drainage basin (Pierce et al. 1998; J. Struger, Environmental Conservation Branch, Environment Canada, 867 Lakeshore Rd., Burlington, ON L7R 4A6, Canada, personal communication). Exceptions are increased use of glyphosate on modified soya and corn crops, increased residues of atrazine and brominated compounds, and the occurrence of endocrine disrupters in nearshore waters (Alaee et al. 1999; Thurman and Cromwell, 2000). It is unknown if these compounds, at the levels reported, affect diporeia survival and reproduction. Other substances, such as cadmium and dump wastes, have been shown to create reproductive disorders and asynchronous maturation in the Baltic amphipod *Monoporeia affinis* (Breitholtz et al. 2001).

Diporeia survival in sediments from areas with high dreissenid populations was consistently lower in our 90-day experiments. We do not know whether exposure to these sediments over the two-year lifespan of diporeia would also reduce reproductive success. The high survival and lipid levels in the diporeia in water filtered from mussel cultures suggests that mussel excretory products are not detrimental. Pseudofeces added to the Lake Superior composite or Batchawana Bay (Lake Superior) sediment caused very low survival and growth of *H. azteca* but reduced diporeia survival by only 24%. Feeding on pseudofeces may reduce amphipod fitness, as shown by the low growth of *H. azteca* when exposed to pseudofeces, as pseudofeces would be less nutritional than the same amount of diatoms or green algae. Landrum et al. (2000) suggested that sediments that had lost their diporeia populations may now be nutritionally limited to diporeia. In their experiments, diporeia were attracted to sediments following the addition of diatoms but avoided the same sediments without added diatoms. In our experiments, lipid levels in amphipods exposed to sediments that had lost their populations were not lower than in amphipods exposed to control sediments suggesting that the nutritional quality was adequate.

An unknown agent was found to be transmissible to diporeia when dying amphipods were left on Batchawana Bay sediment for 48 h and then removed. The dying amphipods were originally isolated from assays of western Lake Ontario sediment. Also, during the same time period, our diporeia cultures from Colpoy's Bay also had high mortality. This mortality could be the result of a pathogen that came from the amphipods collected from Colpoy's Bay or from the western Lake Ontario sediments. Additional work to identify the pathogen causing the mortality and the role these agents play in the decline of diporeia is ongoing. Messick et al. (2004) identified a rickettsia-like organism and a haplosporidian in diporeia from Lakes Huron and Michigan.

Conclusions

This study indicated that the loss of diporeia from suitable habitats is not due to the presence of toxic chemicals or the bacterium *T. ingrica* in sediments. Mussel pseudofeces significantly reduced diporeia survival compared to those fed diatoms, although *H. azteca* was more sensitive to the pseudofeces. Tests with the bacterium *B.t.* showed no effect on the survival of either diporeia or *H. azteca*. This study was unable to rule out bacterial, viral, or ciliate pathogens associated with dreissenids or their pseudofeces as factors in the diporeia population decline. Pseudofeces apparently reduce the fitness of diporeia, perhaps by interfering with metabolism, or they are a source for a protozoan infection. The high survival in our filtered water assay (0.45-μ filter) indicates the agent is not a chemical or virus which would pass through the filter. If a pathogen is the cause of the demise of diporeia, the coevolution of dreissenids and *Echinogammarus ischnus*, a recently introduced shallow-water amphipod, opens the possibility that dreissenids act as a secondary host in transmitting a parasite to diporeia.

Acknowledgements

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The Status of *Diporeia* spp. in Lake Ontario, 1994-1997

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Abstract

Surveys of benthic macroinvertebrates conducted in Lake Ontario between 1994 and 1997 revealed a recent decline in *Diporeia* spp. (Amphipoda) abundance. The lowest population densities and summer biomass are in the eastern basin of the lake at all depths. Densities and biomass declined in the shallowest (10-50 m) depth zone between 1994 and 1997. Mean *Diporeia* spp. densities declined from 1412 m^{-2} to 1 m^{-2}, and the total mean biomass declined from 0.66-g DW m^{-2} to 0.001 g-DW m^{-2}. The latter represents an overall loss of about 5100 mt of biomass in the shallowest depth zone. In contrast, biomass at the deepest zone (>90 m) did not change from 1994 to 1997 and has actually increased over twofold since 1972. This shift of total biomass from shallow to deeper sediments will have a profound effect on organisms that depend upon *Diporeia* spp. for food. Because of the importance of benthic macroinvertebrates, and particularly *Diporeia* spp. in fish diets, changes in the status of

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Diporeia spp. could have dramatic effects on fish production in Lake Ontario.

Introduction

The abundance of the deep-water amphipod, *Diporeia* spp. (hereafter, diporeia as a common name), in Lake Ontario has undergone dramatic changes since the early 1990s. Prior to 1990, diporeia (formerly *Pontoporeia hoyi*) was the most abundant macroinvertebrate in the lake (Mozley and Howmiller 1977; Nalepa 1991). In deeper habitats, it accounted for 40-70% of the total density of benthic organisms (Nalepa 1991), reaching the greatest densities at depths below the summer thermocline in waters 30-60-m deep. After 1994, benthic-macroinvertebrate populations declined in many areas of Lake Ontario (Lozano et al. 2001; Dermott 2001). In the eastern basin, the densities of diporeia averaged 8200 m^{-2} between 1982 and 1993. After 1995, no amphipods were found at three stations in the eastern basin. At a mid-lake station, diporeia increased from 1100 to 5200 m^{-2} (Dermott 2001). Lake-wide surveys in 1994 and 1997 showed that densities of diporeia were highest at depths >42 m but that diporeia was absent at shallower depths (Lozano et al. 2001). At depths between 41 and 100 m, densities of diporeia averaged 5200 m^2 in 1994 and 2400 m^{-2} in 1997. At depths <40 m, the percentage of stations where very few or no diporeia (<6 m^{-2}) were found doubled from 40% in 1994 to 84% in 1997. A zone of very low diporeia density (<6 m^{-2}) extended in 1997 as far as 26-km offshore and as deep as 200 m, encompassing over 29% of the total surface area of Lake Ontario (Lozano et al. 2001).

In this paper, we examined the status of diporeia from 1994 to 1997 and compared our findings to earlier research studies conducted prior to the invasion of dreissenids. We present evidence that, although the total biomass of amphipods did not decline between 1972 and 1997, the current distributional patterns of diporeia biomass may have a major impact on nearshore trophic dynamics.

Methods

Benthic-macroinvertebrate data were obtained from two sources. The benthic invertebrate data from Nalepa and Thomas (1976) were used to describe densities and biomass of diporeia in Lake Ontario in 1972 prior to the invasion by *Dreissena polymorpha* and *D. bugensis.* They collected triplicate sediment samples with a Ponar grab at 55 stations throughout the lake. Sampling depths ranged from 14 to 223 m.

The second source was the 1994 and 1997 data from Lozano et al. (2001) and Dermott (2001) whose work followed the invasion of dreissenids. Benthic samples were collected at 51 stations in 1994 and 68 stations in 1997. Sampling depths ranged from 10 to 213 m. Methods in Nalepa and Thomas (1976) were similar to those of Lozano et al. (2001) with one exception. To estimate site densities, Nalepa and Thomas (1976) averaged individual grab samples; Lozano et al. (2001) pooled three grab samples.

Sampling sites for diporeia were divided into a western, central, and eastern basin based on Thomas et al. (1972). Sites were also divided into three depth intervals (10-50 m, 51-90 m, and >90 m) similar to prior characterizations of depth-macroinvertebrate associations in Lake Ontario (Nalepa and Thomas 1976; Lozano et al. 2001). These depth intervals also approximate sediment depositional areas within the lake (Thomas et al. 1972) and sediment types (Lozano et al. 2001).

The main effects of year and/or basin were tested with a one- or two-way ANOVA for mean population densities within each depth zone (numbers of individuals m^{-2}). Tukey's pairwise comparison test ($P < 0.05$) was used to test for differences between mean densities (Wilkinson 1996). A log transformation was used to stabilize the variance prior to data analysis. Diporeia densities were converted to dry biomass using average weight (1.3 mg) reported by Cavaletto et al. (1996) for diporeia collected in Lake Ontario. Total biomass of diporeia was calculated for each depth interval within each of the three basins. Bathymetry measurements for calculation of sediment surface area were taken from Schwab and Sellers (1996).

Results

The spatial distribution of diporeia differed between 1994 and 1997, especially in the 10- to 50-m zone. In 1994, the highest population densities were found at stations located along the north shore and at the eastern end of the lake (Fig. 1). Along the north shore, there was only a single site (42-m deep) with density equal to zero. At the other nine locations along the north shore, densities reached levels between 5900 and 7900 m^{-2} at depths ranging from 48 to 82 m. A contiguous zone with stations with population densities of <6 individuals m^{-2} was found along the southeastern shore between the Genesee River outlet and Mexico Bay (Fig.1). The number of stations with population densities of <6 individuals m^{-2} increased to 30 of 68 in 1997 compared to 8 of 51 in 1994, and these stations extended all around the lake. The depauperate zone in 1997 extended as far as 26-km offshore to a depth of 160 m and encompassed more than 29% of the total lake area. The most-severe decline in diporeia was found along the southern and eastern shores from the outlet of the Niagara River to Point Petre (Fig. 1) where diporeia was completely absent from samples collected in waters ≤140-m deep.

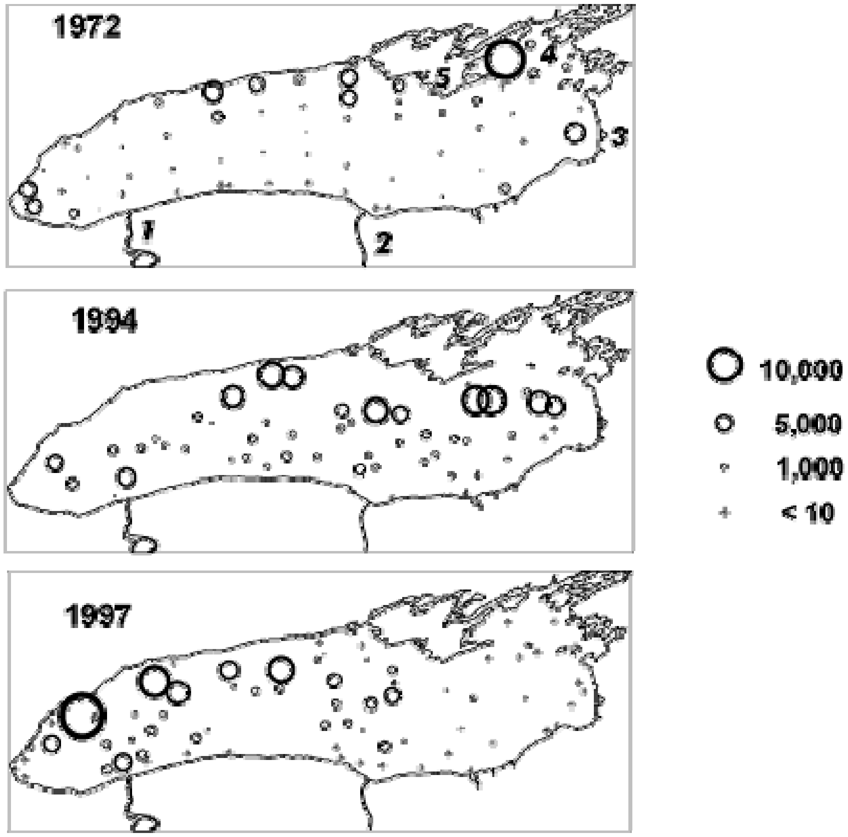

Fig. 1. Distribution and density (no.m^{-2}) of diporeia in 1972, 1994, and 1997. Kingston basin was not sample in 1994. A cross marks sites with very-low densities (<6 m^{-2}). Geographical locations mentioned in text are given in the top panel, where 1 = Niagara River, 2 = Rochester (mouth of the Genessee River), 3 = Mexico Bay, 4 = Kingston Basin, and 5 = Point Petre.

Table 1. Mean density and standard error (#/m^2) of diporeia at three depth intervals for three basins of Lake Ontario, 1972-1997.

		1972			1994			1997		
Depth interval (m)		West	Central	East	West	Central	East	West	Central	East
10-50	Mean	1,701	1,932	3,226	203	2,131	2[a]	34[a]	1[a]	0[a]
	SE	816	671	1,621	–	2,131	2	33	1	0
	N	7	11	6	1	2	3	6	6	9
51-90	Mean	986	2,427	2,536	3,266	6,575	5,581	5,725	1,791	11[b]
	SE	564	2,060	837	–	573	1,263	1,853	845	5
	N	3	2	5	1	4	6	6	10	3
>90	Mean	773	938	521	2,388	2,064	1,811	2,524	2,279	596
	SE	188	246	202	756	200	572	605	306	232
	N	5	10	5	6	20	8	8	14	6

[a] Represents mean densities within the depth interval 10-50 m that were significantly smaller compared to densities in 1972.

[b] Represents mean densities within the depth interval 51-90 m that were significantly smaller compared to 1972.

The patterns of diporeia distribution shifted away from the eastern basin and away from shallower waters from 1972 to 1997. In the shallowest depth interval (10-50 m), densities of diporeia in 1994 and 1997 were significantly lower compared to densities found in 1972 within the eastern basin of the lake (Table 1). At depths of 10-50 m in the central and western basins, densities of diporeia in 1997 were significantly lower compared to densities found in 1972. In the shallowest depth interval, lake-wide mean density of *Diporeia* in 1972 was 2188 m^{-2} compared to lake-wide mean densities of 1412 and 10 m^{-2} in 1994 and 1997, respectively. Both values were significantly lower than the density in 1972. At depths of 51-90 m, densities of diporeia were significantly lower in the eastern basin in 1997 (11 m^{-2}) compared to densities there in 1972 and 1994 (2536 and 5581 m^{-2}, respectively). In the mid-depth (51-90 m) interval, lake-wide mean density of diporeia in 1972 was 2049 m^{-2} compared to lake-wide mean densities of 6167 and 3266 m^{-2} in 1994 and 1997, respectively. There were no statistical differences between lake-wide densities between years. In the >90-m depth interval, the densities of diporeia in 1972 ranged between 521 and 938 m^{-2} and were generally lower compared to densities in 1994 and 1997 (combined range of 596 to 2524 m^{-2}). Lake-wide mean densities at depths >90 m were 793, 2060, and 1920 m^{-2} for 1972, 1994, and 1997, respectively.

The biomass of diporeia also shifted away from the eastern basin and from shallower waters from 1972 to 1997 (Fig. 2). Within the 10- to 50-m-depth zone, total biomass in 1972 was 17.1 kilotons (1 kiloton = 1000 metric tonnes). At similar depths, total biomass was 0.04 kilotons in 1997. This biomass represents a substantial loss (99.8%) of benthic biomass that could have been available for fish consumption. In 1997, total biomass was reduced in the 51- to 90-m-depth interval compared to biomass in 1994 but was generally similar to biomass in 1972. From 1994 to 1997, there were no losses or increases in total biomass at depths >90 m, but values then were greater than those found in 1972.

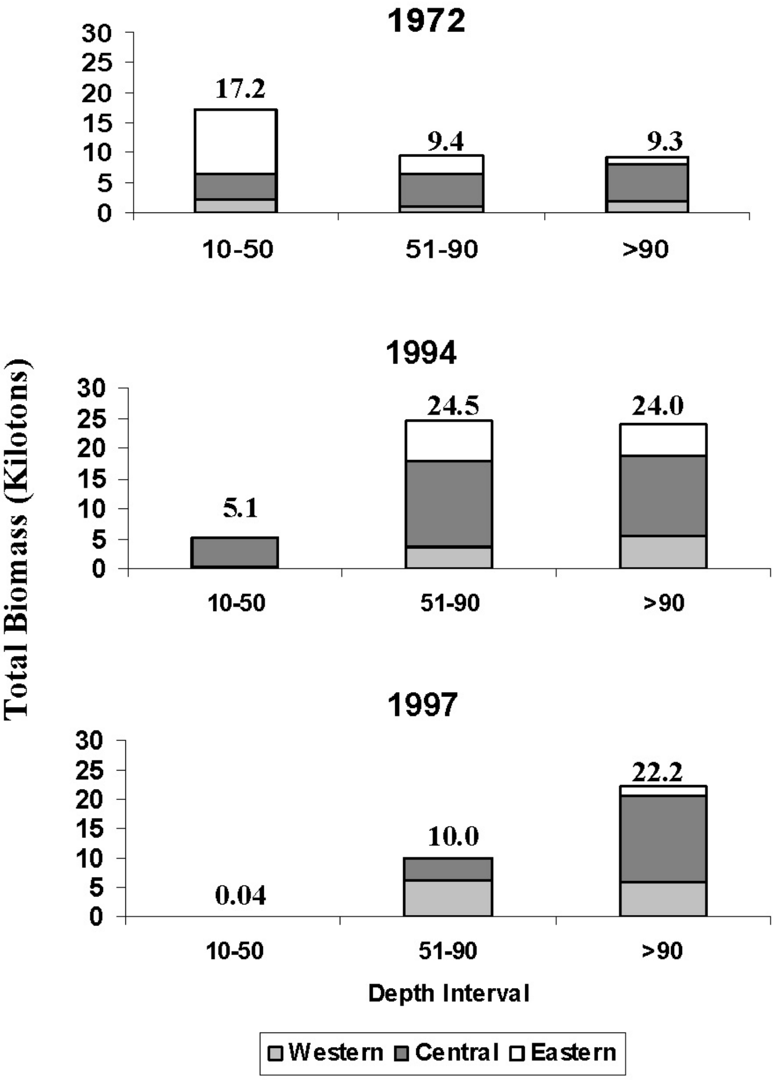

Fig. 2. Total biomass (kilotons) of diporeia in 1972, 1994, and 1997 within three depth intervals and three basins of Lake Ontario. The total biomass for each depth interval is displayed above the bar.

Discussion

Our data indicate a major decline in diporeia densities at depths <50 m from 1972 to 1994-1997 with the greatest decline in the eastern and central basins (Table 1). At depths between 51 and 90 m, the densities of diporeia also declined over the same years but only in the eastern basin of the lake. There were no trends in the densities of diporeia at depths >90 m.

Diporeia populations at deeper sites in Lake Ontario were either stable and/or increased during the past decade and appear unaffected by the causes of the declines at shallower depths. Dermott (2001) reported an increase from 1050 to 5239 m^{-2} at a mid-lake station (110-m deep) between 1992 and 1995. Nalepa (1991) reported diporeia densities of 1400 to 2400 m^{-2} between 1964 and 1987 at the same mid-lake station. At a similar location, we found diporeia density to be 4730 m^{-2} in 1997.

The area where diporeia was collected in very low numbers (<6 m^{-2}) was smallest in 1972 and greatest in 1997. In 1972, diporeia was absent in an area extending along the south shore from the Niagara River eastward to Rochester, New York (Nalepa and Thomas 1976). The loss of diporeia in Lake Ontario sediments has accelerated since 1994. In 1997, the area at depths between 10 and 50 m where diporeia was absent expanded all around the lake. The loss was greatest in the eastern basin. Diporeia was found at only nine of 40 stations in 1997 and all of these stations were deeper than 75 m.

At three sites where diporeia was sampled in the eastern basin between 1982 and 1996 (Dermott 2001), diporeia populations declined from >6000 m^{-2} to zero. Dermott (2001) suggested that with the elimination of diporeia between the 10- to 60-m contours, 29% of the lake-wide amphipod production was lost. Our calculations did not support this conclusion because total biomass in 1997 was around 32 kilotons, similar to the 36 kilotons found in 1972. Our data, however, did show a shift of production from shallow to deep water.

Prior to the invasion of dreissenids, 48% of the total biomass was found in shallow depths (<50 m). In 1997 the production of diporeia in shallow waters approached zero, but, in the same year, 69% of the total biomass of diporeia was produced in waters deeper than 90 m (Fig. 2).

The shift of production from shallow to deeper sediments will have a profound effect on diporeia consumers. Great Lakes benthic-community biomass, especially in deeper waters, is driven by pelagic primary production. An important food source for diporeia arrives in the spring and fall when water conditions favor diatom blooms and subsequent settling of diatoms (Gardner et al. 1990; Scavia et al. 1986). Diporeia requires these algae for growth and reproduction, storing the assimilated energy as lipid. Lipid levels of diporeia are high and can account for up to 50% of amphipod dry weight after the spring diatom bloom (Gardner et al. 1985). Flint (1986) estimated that 23% of the total annual carbon production from pelagic phytoplankton is consumed by diporeia. A large portion of diporeia biomass is transferred up the food chain to forage fish. Diporeia is the dominant food organism of the slimy sculpin (*Cottus cognatus*) in Lake Ontario (Owens and Weber 1995), and many fish species feed on diporeia at some stage in their life cycle (Mozley and Howmiller 1977). Therefore, changes in the status of diporeia could have dramatic effects on fish production in Lake Ontario. For example, slimy sculpin populations began to increase from 1984 to 1991, abruptly declined in 1992, and remained low through 1998 (Mills et al. 2003). Owens et al. (2003) suggest that reductions in populations of diporeia, an important food item for slimy sculpin, were the cause of the decline.

In Lake Ontario, the loss of diporeia coincided with the appearance of dreissenid mussels, *Dreissena polymorpha* and *D. bugensis*. Since their invasion, dreissenids have been collected from sand/silt substrates to depths of 140 m (Lozano et al. 2001; Mills et al. 1993). Densities reached 37,000 m^{-2} at depths between 10 and 27 m (Lozano et al. 2001). High densities, widespread distribution, and high filtering rates enable *Dreissena* populations to filter large volumes of water and thereby decrease algal biomass (Holland 1993; Fahnenstiel et al. 1995). The diversion of algal production into dreissenid tissue and biodeposits may deprive diporeia of food settling from the water column (Dermott 2001), but competition for food does not fully explain the complete collapse of diporeia populations in eastern Lake Ontario.

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EXPLOITATION AND MANAGEMENT

The Population Dynamics of Unexploited Lake Whitefish (C*oregonus clupeaformis*) Populations and Their Responses to Stresses

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Abstract

We reviewed growth, annual survival, length frequency, age frequency, and annual recruitment of unexploited lake whitefish (*Coregonus clupeaformis*) populations. We compared estimates of growth curves, annual survival, and age frequencies using scale and fin-ray ages. Growth was slower, annual survival higher, and there were many more age groups in unexploited populations when these estimates were based on fin-ray ages. We believe that unexploited lake whitefish populations have slower growth, higher annual survival, and more age groups present in the population than previously thought. These populations are characterized by many individuals of large, uniform size and by widely varying yearly recruitment.

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Introduction

The lake whitefish (*Coregonus clupeaformis*, hereafter, whitefish) was historically one of the most important commercial species in the Laurentian Great Lakes. Populations were exploited starting with the first human settlements along each lake, and exploitation increased when European immigrants arrived. Unfortunately, there are no data for the initial phases of this exploitation. The earliest scientific studies of these populations occurred at a time when populations in the lower Great Lakes were already heavily exploited, and those of Lake Superior were lightly to moderately exploited (Regier and Applegate 1972; Smith 1972). Therefore, to gain insight into what the characteristics of these Great Lakes populations might have been, unexploited populations in other lakes must be examined.

Johnson (1972, 1976) was one of the first researchers to describe the characteristics of unexploited whitefish populations, and he has contributed greatly to our current understanding of their population regulation. He showed that these populations were characterized by a large number of individuals of a similar, large size. Although uniform in size, however, the populations were composed of individuals of many ages. Moreover, if the abundance of an unexploited population was reduced, the size structure of the population returned quickly to its original state. Johnson also showed that the size structure of these unexploited populations changed little when studied for many years.

Healey (1975) summarized the then-current knowledge of mortality, growth, age-at-maturity, and abundance of unexploited and exploited whitefish populations. At the time of his review, he did not find any published studies where the abundance of unexploited populations was described. Published estimates of mortality for the unexploited populations were derived exclusively from catch-curves based on scale ages. These data and mortality estimates that he calculated for a few other populations varied widely, from 18-74% per year. Often these mortality estimates were based on the same data that were used to produce growth curves for the population. Growth of these unexploited populations varied from very slow to as fast as that in highly exploited populations. Although Healey (1975) recognized that scale ages might be underestimates of true ages for a few individuals in some populations, he believed that such errors would not seriously bias mortality and growth estimates.

Scales are the traditional structures used to age whitefish. The basis for the scale aging of whitefish can be traced to the early research of Van Oosten (1923) on fish held in the New York aquarium for a known number of years. He thoroughly described the criteria for scale aging in coregonines (Van Oosten 1929) using Great Lakes cisco (*C. artedi*). Ages determined from scales are usually considered accurate for highly exploited or fast growing populations of whitefish (Hoagman 1968; Mills and Beamish 1980). If individuals grow slowly, circuli may not form on the scale edge or resorption may occur, and annuli may not be discernable (Mills and Beamish 1980).

Power (1978) challenged the validity of scale ages for unexploited whitefish populations in northern Canada. He found that ages determined from otolith sections of whitefish from northern Quebec populations were much older than ages read from their scales. He had small sample sizes, less than 38 individuals from three populations, but believed similar errors when using scales were common for many northern whitefish populations. Mills and Beamish (1980) challenged the validity of scale ages for southern as well as northern unexploited whitefish populations. They found that ages for seven unexploited populations determined from sectioned pelvic fin-rays were frequently older than those determined from scales.

Fin-ray aging of whitefish can be traced to the early research of Cuerrier (1951), which was expanded by Mills and Beamish (1980) and Mills and Chalanchuk (2004), who validated annuli on fin rays using mark-recapture methods. In three-year mark-recapture studies, Mills and Beamish (1980) found that distinct annuli were formed on both the fin rays and scales of fast-growing individuals, but that annuli were more readily distinguishable on fin-ray sections than on scales for slower-growing individuals. Mills and Chalanchuk (2004) extended this three-year validation to 14 years in one of the lakes used in the original study. During this 14-year period, annual growth varied from as fast as that in highly exploited populations to as slow as that in the slowest growing unexploited population. They confirmed the validity of fin-ray ages for this longer time period and also found no significant difference between ages determined from otolith and fin-ray sections.

The primary purpose of this study is to present an updated analysis of growth, annual survival, length frequency, age frequency, and annual recruitment of unexploited whitefish populations. A secondary purpose is to demonstrate the differences in such estimates that can occur when they are based on scale rather than fin-ray ages.

Methods

We used the data for unexploited populations summarized in Healey (1975) as well as our own data for the analyses of growth, annual survival, length frequency, age frequency, and recruitment (Table 1). For his analyses, Healey (1975) summarized growth for 31 unexploited populations and mortality for 13 populations from data collected from 1926-1973. We decided to exclude the growth data used by Healey for the Lake La Marte population (Bond 1973) from our analysis. This population was significantly exploited when Bond (1973) collected his data. Healey used the mortality estimate for this population in his synopsis for exploited populations, but we believe he erroneously included the growth data in his synopsis for unexploited populations. All of Healey's estimates were based on scale ages.

Table 1. Lake names, locations, dates of sampling, method of calculating annual survival, aging structures used to calculate growth curves, and data source.

Lake	**State or province**	**Year of data collection**	**Survival**	**Aging structure**	**Original source**
Cliff	ME	1959-62		Scales	Fenderson 1964
Second Musquacook	ME	1959-62		Scales	Fenderson 1964
Webster	ME	1959-62		Scales	Fenderson 1964
Neso	MB	1968-69		Scales	Kliewer 1970
Payuk	MB	1968-69		Scales	Kliewer 1970
Mink Narrows	MB	1968-69		Scales	Kliewer 1970
Big Athapapuskow	MB	1968-69		Scales	Kliewer 1970
Little Athapapuskow	MB	1968-69		Scales	Kliewar 1970
Big Twin	MB	1968-69		Scales	Kliewer 1970
Little Twin	MB	1968-69		Scales	Kliewer 1970
George	MB	1967		Scales	Gibson and Johnson 1969

Table 1, continued.

Lake	State or province	Year of data collection	Survival	Aging structure	Original source
Munising Bay	MI	1953	Catch curve*	Scales	Edsall 1960
Long Lake	NT	1971		Scales	Healey and Woodall 1973
Grace Lake	NT	1971		Scales	Healey and Woodall 1973
Kam Lake	NT	1971		Scales	Healey and Woodall 1973
Trout Lake	NT	1971		Scales	Healey and Woodall 1973
Michel Lake	NT	1971		Scales	Healey and Woodall 1973
Dunnet Lake	NT	1971		Scales	Healey and Woodall 1973
Nueltin	NT	1948-49	Catch curve	Scales	Kennedy 1963
MacDonald	NT	1953	Catch curve	Scales	Kennedy 1963
MacEwan	NT	1960	Catch curve	Scales	Kennedy 1963
Great Bear Lake	NT	1945	Catch curve*	Scales	Kennedy 1949
Great Slave lake	NT	1944-46	Catch curve*	Scales	Rawson 1949; Kennedy 1953
Hottah	NT	1971	Catch curve*	Scales	Wong and Williams 1973
Drygeese Lake	NT	1971-73	Catch curve	Scales	Healey 1975
Alexie Lake	NT	1971-73	Catch curve	Scales	Healey 1975
		1980-85	Catch curve	Scales	This study
		1980-85	Catch curve	Fin rays	This study
Baptiste Lake	NT	1971-73	Catch curve	Scales	Healey 1975
		1980-85	Catch curve	Scales	This study
		1980-91	Catch curve	Fin rays	This study

Table 1, continued.

Lake	State or province	Year of data collection	Survival	Aging structure	Original source
Shakespeare Island	ON	1926	Catch curve	Scales	Hart 1932
Opeongo	ON	1936-40	Catch curve		Kennedy 1943
		1973	Catch curve	Scales	Mills and Beamish 1980
		1973	Catch curve	Fin rays	This study
Lake 305	ON	1973-74	Catch curve	Scales	Mills and Beamish 1980
		1980-81	Catch curve	Fin rays	This study
Lake 302	ON	1975	Catch curve	Scales	Mills and Beamish 1980
		1975-81	Catch curve	Fin rays	This study
		1981-1991**	Mark-recapture		This study
Lake 226	ON	1973-74	Catch curve	Scales	Mills and Beamish 1980
			Catch curve	Fin rays	This study
		1973-74, 1984-94	Mark-recapture		This study
Lake 258	ON	1986-94		Scales	Mills and Beamish 1980
Lake 259	ON	1972, 1975		Fin rays	Mills and Beamish 1980
Lake 310	ON	1973, 1975	Catch curve	Scales	Mills and Beamish 1980

Table 1, continued.

Lake	State or province	Year of data collection	Survival	Aging structure	Original source
Lake 468	ON	1973, 1975	Catch curve	Scales	Mills and Beamish 1980
		1973, 1975, 1981-99	Catch curve	Fin rays	This study
Trout Lake	WI	1927-32		Scales	Hile and Deason 1934
Dezadeash Lake	YK	1975	Catch curve	Scales	Mills and Beamish 1980
		1975	Catch curve	Fin rays	Mills and Beamish 1980

* Healey (1975) calculated mortality using data from these studies

** North basin

We collected data from 12 unexploited populations. Three of these (Alexie, Baptiste, and Chitty) were the same populations first sampled by Healey ten years earlier (Table 1). We collected fin-rays for aging individuals from all 12 populations, and collected scales from 11 populations. No scales were collected from Lake 258 whitefish. Some of the ages were reported previously in Mills and Beamish (1980), but we added more data for some of these populations in this study. Fin-ray and scale ages for each population were read by individuals who had many years of experience using each method.

Four of the lakes were used for pulse-exploitation experiments (Healey 1980; Mills et al. 1995). Populations were exploited for one or two years and then were allowed to recover. Pulse experiments occurred in Alexie, Baptiste, and Chitty lakes in 1973 and 1974, Lake 305 in 1982, and Lake 258 in 1983. Healey (1980) believed that the populations in Alexie and Chitty Lakes had recovered three years after the exploitation. We used data from Alexie and Chitty lakes collected 5-10 years after Healey's pulse exploitation (Table 1). Because we found no evidence of changes in growth for these populations for these years, we believe they had recovered from exploitation prior to our study. Based on a combination of growth, age-structure, and length-frequency analyses, the Drygeese Lake population had not recovered from the exploitation at the time of the data collection for this study. Therefore, we excluded the recent data for this population from our analyses. The data used in this study for Lakes 305 and 258 were collected prior to exploitation.

Additional experiments were conducted in Lakes 226 and 302. A nutrient-addition experiment was conducted from 1973-1980 (Mills 1981, 1985; Mills and Chalanchuk 1987; Mills et al. 1998), and a drawdown study was conducted from 1994-1996 (Mills et al. 2002b). Acidification experiments were conducted in Lake 302 (Mills et al. 1992, 2002a). We used data collected before the experiments in each lake and data collected in Lake 226 from 1984-1994, three years after the nutrient additions had ended and prior to the drawdown experiment that started in winter 1994. Whitefish were captured in these lakes using trapnets and small-mesh gillnets as described in Mills (1985) and Mills et al. (1995). Whitefish were captured in all the other lakes with gillnets.

We fitted the von Bertalanffy growth model (Ricker 1975; Haddon 2001) to mean length-at-age data for each unexploited whitefish population. We fitted Healey's (1975) scale-age data to this model, and, after plotting all of the curves, eye-fitted upper and lower limits to the curves to define a range of growth. We believe that Healey (1975) eye-fitted curves and growth limits to his data. We used the youngest age in each data set as the starting age for our von Bertalanffy analyses. We generated von Bertalanffy growth curves using fin-ray and scale ages for each population. When we had data for more than one year for a population, we combined the data prior to growth analysis. Healey (1975) calculated growth curves based on scales for Alexie, Baptiste, Chitty, and Drygeese Lakes collected before the 1974-1975 pulse-exploitation experiments started. We had scale-age data from 1980-1985 for the same populations, so we compared our more recent scale-growth curves to Healey's (1975) curves for the first three populations.

We used the Robson-Chapman (1961) method to calculate catch-curve annual survival rates for our populations using the combined data for each population, as described above, for growth. We calculated estimates using fin-ray ages for 12 populations and scale ages for nine populations. Our sample sizes were not large enough to form scale estimates for three populations. In addition, we calculated separate estimates for the 1971-1973 data Healey used for the Alexie, Baptiste, Chitty, and Drygeese populations and compared his estimates for the first three lakes to the estimates from the more recent (1980-1985) scale data. Although Healey (1975) stated he used methods from Ricker (1975) to calculate mortality estimates for these populations, we were not sure which method he used. We converted the average mortality estimates in Healey (1975) to survival estimates by taking the inverses of each estimate (Ricker 1975) and compared these numbers to our estimates.

Robson-Chapman estimates are usually calculated with data from one year of sampling. Our estimates were almost always based on data collected over many years, so we used the data for Baptiste Lake where 12 successive years of estimates (1980-1991) could be calculated using fin-ray ages to examine the differences that could occur between the overall estimate and estimates for individual years. The 12 annual estimates varied from 0.67 ± 0.07 (95% C.I.) to 0.85 ± 0.04, with a mean of 0.73 ± 0.05. This mean was almost identical to our combined data estimate, 0.72 ± 0.02. Therefore, we combined all data to produce composite estimates.

We conducted mark-recapture experiments in Lakes 226 and 302, and calculated mark-recapture survival estimates for each population using the Jolly-Seber full model (Mills 1985; Mills and Chalanchuk 1987; Mills et al. 1998, 2002a, 2000b). We used the mean of these estimates calculated for consecutive years 1984-1994 for the Lake 226 population and 1981-1991 for the Lake 302 population to compare to the analogous catch-curve estimates.

We constructed age- and length-frequency distributions for our 12 unexploited whitefish populations based on fin-ray and scale ages. We combined data for all years for a population prior to analysis. For populations where we had sufficient samples from five or more consecutive years (Lakes 226, 259, 302, and 468; Alexie, Baptiste, and Chitty Lakes, respectively), we constructed age- and length-frequency distributions for each year. We excluded data for Lakes 226 and 302 when experiments were conducted or populations were recovering from experiments.

We constructed age-frequency distributions for each year of data collection to evaluate year-class recruitment for each of our 12 populations. We converted the annual catches to percent composition to normalize for differences in sample sizes each year. We used ages based on fin-ray sections for these analyses.

Results

We found that growth curves based on scale ages for our 12 unexploited populations (Fig. 1, Lake 258 excluded) were in the range of growth reported by Healey (1975) for his 32 populations (Fig. 2). We included more recent data for four of the populations reported by Healey: Opeongo, Alexie, Baptiste, Chitty, and Drygeese Lakes. Our scale-based growth curves for these populations using 1980-1985 data were almost identical to the curves reported by Healey using 1971-1973 data. For 11 of our 12 populations, the growth curves based on fin-ray ages indicated slower growth than those based on scale ages (Fig. 1). Growth for six of the populations, when based on fin-ray ages, was slower than the lower growth limit reported by Healey (1975). The differences in mean lengths-at-age between the two methods started at relatively early ages. For example, there was a 10-20-mm difference in mean lengths between methods starting at age 2 for the fish from Lakes 259, 302, 305, 310, Dezadeash, and Opeongo. The magnitude of this difference increased progressively at older ages. For the other populations, differences occurred first at ages 3-5 and then increased at older ages.

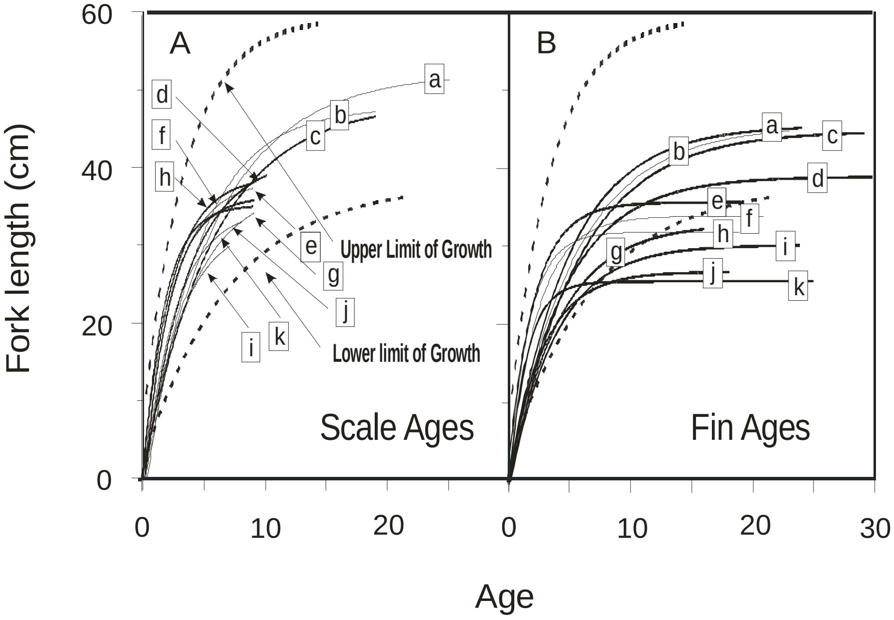

Figure 1. Growth curves for 11 unexploited lake whitefish populations based on (A) scale and (B) fin-ray ages. Individual populations were from (a) Alexie Lake, (b) Chitty Lake, (c) Baptiste Lake, (d) Lake 305, (e) Lake 302, (f) Lake 226, (g) Dezadeash Lake, (h) Lake Opeongo, (i) Lake 259, (j) Lake 310, and (k) Lake 468. The dotted lines show the upper and lower limits of whitefish growth for unexploited populations reported in Healey (1975).

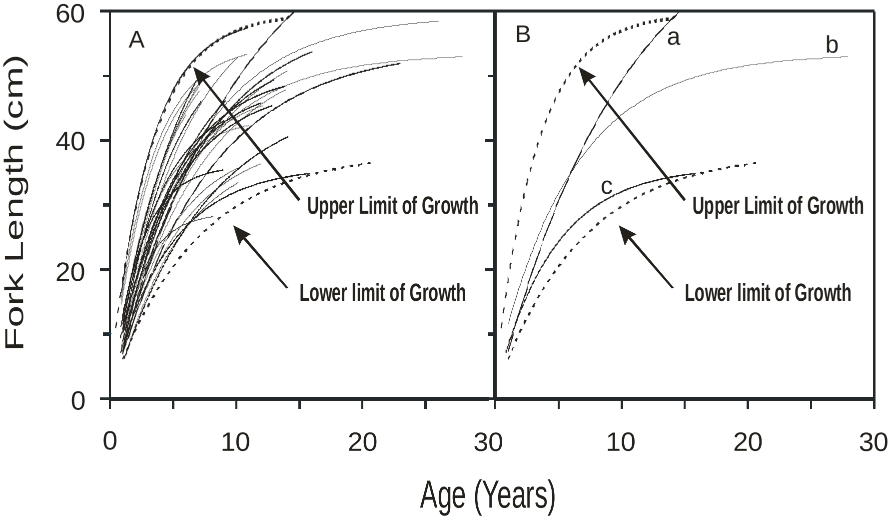

Figure 2. Growth curves for 32 unexploited lake whitefish populations listed in Healey (1975) based on scale ages for (A) all populations and (B) Great Lakes of North America populations. Individual curves in (B) are for (a) Great Bear Lake; (b) Great Slave Lake; and (c) Munising Bay, Lake Superior. The dotted lines are the same upper and lower limits of lake whitefish growth for unexploited populations reported in Fig. 1.

The catch-curve annual survival for our populations was higher, averaging 77% per year when based on fin-ray ages, than when based on scale ages, 48% per year (Table 2). There was much greater variability in scale estimates (38-59%) than fin-ray estimates (74-81%). When based on scale ages, our Robson-Chapman (1961) survival rates for Alexie, Baptiste, and Chitty Lake populations for the 1971-1973 data (49, 48, 49%, respectively) were similar to the estimates reported by Healey for the same years (52, 44, 46%, respectively). The 1971-1973 estimates were lower than the estimates we calculated for the 1980-1985 scale data for the same populations (59, 58, 50%, respectively) (Table 2), but the confidence intervals for the 1971-1973 and 1980-1985 estimates overlapped for Baptiste and Chitty Lakes. The two averages of mark-recapture survival (Table 2) were very similar to the fin-ray estimates for Lakes 226 and 302, but 33 and 50% higher, respectively, than the scale estimates.

Table 2. Catch-curve annual survival rates (S) based on scale and fin-ray ages, and the average Jolly-Seber mark-recapture annual survival for two populations. Sample sizes for catch curve analyses and number of age groups used for each Chapman-Robson rate are indicated.

Lake	**Scale Catch curve**				**Fin-ray Catch curve**				**Mark recapture**	
	Sample size	**N ages**	**S (%)**	**95% C.I.**	**Sample size**	**N ages**	**S (%)**	**95% C.I.**	**S (%)**	**95% C.I.**
226	510	6	59	0.04	2723	24	74	0.01	79	0.02
258					220	16	81	0.02		
259					661	16	78	0.02		
305					312	18	85	0.02		
468	145	6	37	0.05	1123	14	77	0.02		
310	135	7	45	0.03	133	12	78	0.04		
302	130	7	35	0.11	719	16	76	0.02	70	0.14
Dezadeash	213	6	44	0.08	218	9	79	0.03		
Opeongo	108	6	49	0.07	164	8	75	0.05		
Alexie	324	6	59	0.04	515	18	74	0.02		
Baptiste	410	10	58	0.04	1514	19	76	0.02		
Chitty	164	11	50	0.06	654	13	75	0.03		

The length-frequency distributions for each population were characterized by two or four modes as described previously by Johnson (1972, 1976) for unexploited populations. Each population had a large number of individuals of uniform, large size (four examples in Fig. 3). The smallest size mode for each of the 12 populations was usually about 10-17 cm, the length of age-0 to age-1 fish. The second mode was usually 18-28 cm, and the third mode varied from 24-46 cm. The modal length of the large size group was usually longer in the larger lakes than in the smaller lakes (for example, it was 33 cm for 16-ha Lake 226 and 43 cm for 346-ha Baptiste Lake, Fig. 3). There were instances, such as Lake 226, where a fourth mode was present. For all populations, the mode for the largest individuals comprised many age-classes.

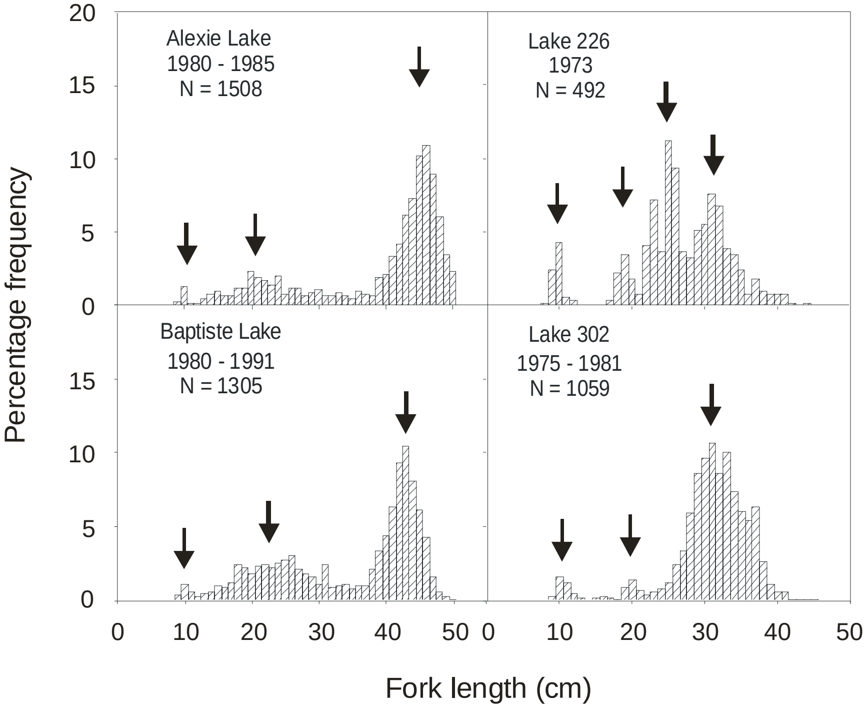

Figure 3. Length-frequency distributions for four lake whitefish populations. Length increments are 1 cm, and modes for the distributions are indicated by arrows.

More age groups were present in each population based on fin-ray ages than when based on scales (two examples in Fig. 4). For Lake 226, less than 5% of the 1973-1974 sample had ages greater than five based on scale ages, whereas more than 50% of the individuals had ages greater than five based on fin-ray ages. The differences in age frequencies were less pronounced in Baptiste Lake although there were still more than twice as many fish with ages greater than 11 based on fin-ray ages than when based on scale ages. When fin-ray ages were used, distributions for the other populations were similar to those from Baptiste Lake and Lake 226 (four examples in Fig. 5). In some populations, the composite distributions for many years followed the typical catch-curve pattern such as that for Lakes 468 and 302 (Fig. 5), whereas others, such as Alexie and Chitty Lakes, showed a much greater influence of variable yearly cohorts. In most populations, 25-30 age-classes were present based on fin-ray ages.

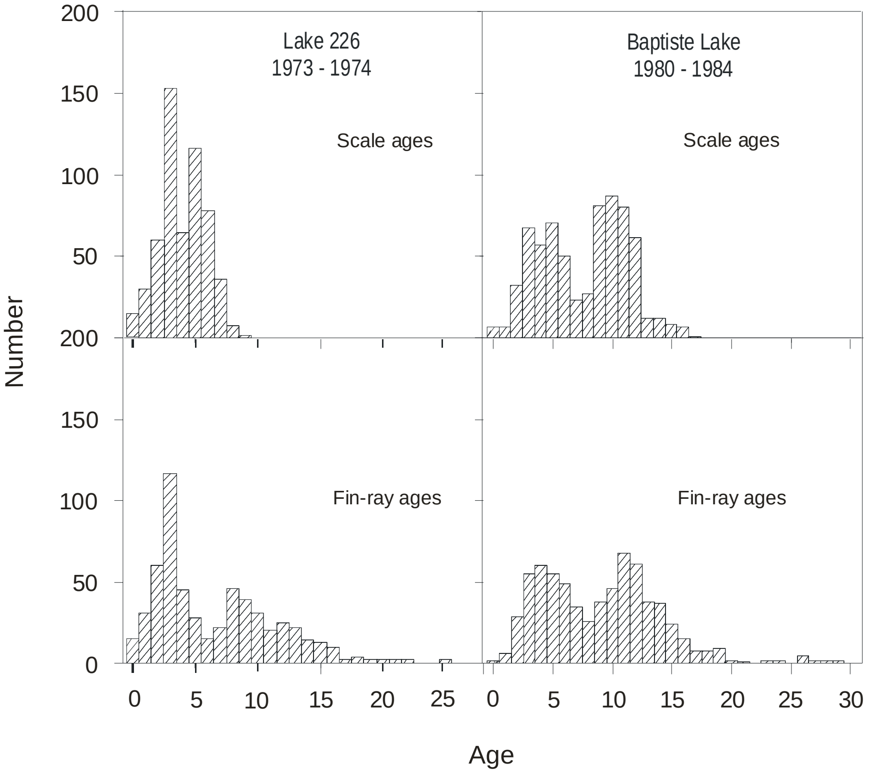

Figure 4. Age-frequency distributions based on scales and fin-ray sections for Lake 226 and Baptiste Lake.

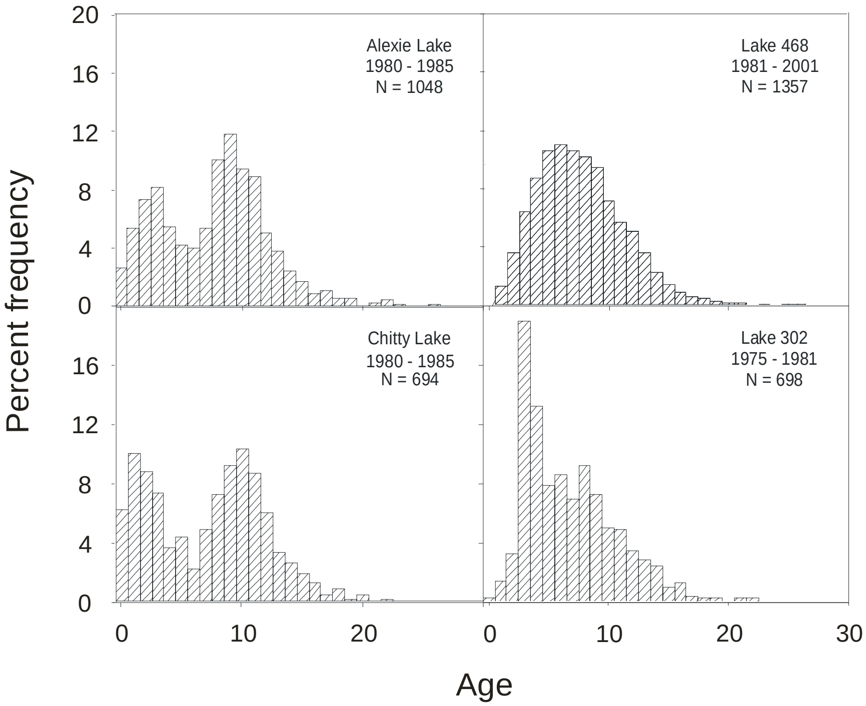

Figure 5. Age-frequency distributions for lake whitefish populations for Alexie, Chitty, 302, and 468 Lakes.

The whitefish populations we examined had widely variable recruitment. This variation was clearly evident in populations where yearly sampling occurred (example in Fig. 6). We found no evidence of year-class failures in any of the populations, but years of sparse and high recruitment occurred frequently. In each population, a series of weak year-classes was usually followed by a series of strong year-classes.

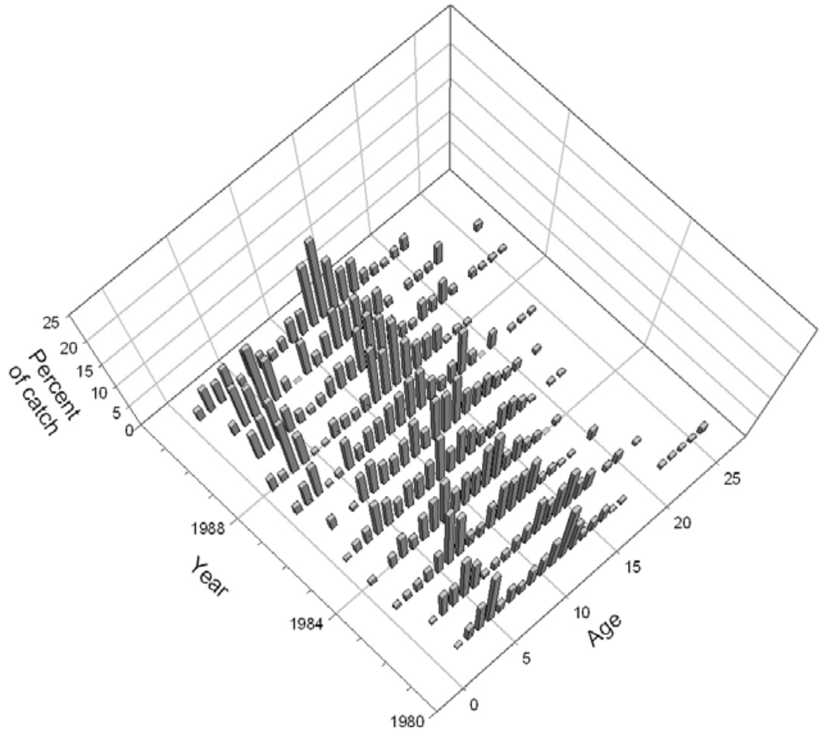

Figure 6. Age composition of lake whitefish catches for Baptiste Lake, 1981-1991.

Discussion

Unexploited whitefish populations are characterized by slow growth, higher annual survival, many individuals of uniform size, many age groups in the population, and highly variable recruitment. Healey (1975) found that the range of growth of unexploited populations based on scale ages was as wide as the range for exploited populations. Using fin-ray ages, we found that the range of growth of unexploited populations was well below what had been previously described for exploited and unexploited populations based on scale ages. We also found a much higher and narrower range of annual survival, 71-85%, for unexploited populations based on fin-ray catch curves than those based on scale ages, 35-59% in our study (Table 2) and 26-82%

from Healey (1975). The close agreement between the average mark-recapture survival estimates and the fin-ray catch-curve estimates gives greater confidence for the catch-curve fin-ray estimates. Healey (1975) discussed the implications of aging errors for estimates of survival and growth, but, based on our analyses, the potential for biases caused by aging errors is much higher than he believed. The great danger, as shown in our data, is that overestimated growth is associated with underestimated catch-curve survival.

Johnson (1972, 1976) presented length-frequency distributions that were very similar to those for the populations in our study. He has been criticized because these distributions could be artifacts caused by gillnet selectivity. We relied extensively on trapnet catches in Lakes 226 and 302, and, although we caught a higher proportion of smaller fish in trapnets than in gillnets, the overall modes for the smaller fish in the length-frequency distributions were similar to those for populations where only experimental gillnets were used (Fig. 3). Modal groups were definitely present in all of the populations that we studied, but it is not clear why there were differences in the length of the largest-sized group among populations. We noted in our analysis of growth that variance in length increased with fish age, and this relationship could be a part of the explanation for the buildup in each population of a large number of fish of uniform, large size.

We were surprised that annual survival of whitefish was relatively uniform and high in all the unexploited populations (Table 2). An obvious weakness in all catch-curve estimates is they are based on data for the descending portion of the curve (Ricker 1975) and do not include the youngest age groups in the population. Mills (1985) and Mills and Chalanchuk (1987) presented data for age-0 and age-1 lake whitefish that showed that survival can vary among years and with trophic conditions. Further, Healey (1980) and Mills et al. (1995) showed that annual survival of age-0 fish increased if adults were removed from a population. Survival of older juveniles, prior to the age where catch-curve analysis usually begins, may be less variable. In an intensive mark-recapture study of lake whitefish age-1 and older, Mills (1981) was able to stratify data according to age or length of individuals. He found no significant difference in annual survival between the younger (1-3, 4-6) and older age groups and no difference in survival of the smallest (17-25 cm) and larger length groups. Therefore, we believe that annual survival of very young fish can vary extensively, but it varies little after individuals are beyond age 1. This finding is slightly different from Johnson (1972, 1976) who suggested that mortality was much higher in juveniles than adults in unexploited populations. Johnson captured few individuals younger than age 3 in his studies, so the difference in our two views is primarily when the mortality in juveniles begins. Johnson believed that behavioral segregation of the smaller individuals from the rest of the population was responsible for the higher mortality of young individuals. This may be the explanation for the differences Mills and Chalanchuk (1987) found in survival of age-0 and age-1 lake whitefish in Lake 226. They felt that food resources were the limiting factor in the survival of very young fish. Our analyses clearly show that annual survival of older whitefish is high, so population regulation must occur very early in life.

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Application of Statistical Catch-at-Age Models to Assess Lake Whitefish Stocks in the 1836 Treaty-Ceded Waters of the Upper Great Lakes

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Abstract

Commercial-fishery statistics were integrated with biological data from the fishery to develop statistical catch-at-age models of lake whitefish (*Coregonus clupeaformis*) in the 1836 treaty-ceded waters of the upper Great Lakes. Fishery yield and effort were adjusted to account for underreporting and increases in height of gillnets. Biological inputs to models included maturity, age composition, mean weight of fish, and sex ratio of spawners. Sea lamprey (*Petromyzon marinus*) mortality was estimated separately from the modeling process and

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input as an age- and year-specific matrix for stocks showing measurable levels of predation. Natural mortality was calculated as a function of L_∞, the Brody growth coefficient, and water temperature. Models were composed of a population-dynamics submodel and an observation submodel that predicted observed data given the estimated population for each year. Agreement between the model predictions and observed data was measured through negative log likelihood. A double-logistic function of age was used to estimate time-varying selectivity of gillnets and trapnets. We adjusted fishing mortality to achieve an annual mortality target of 65% on the most fully vulnerable age while maintaining spawning-stock biomass at 20% or more of the unfished state. Harvest limits were predicted using abundance and mortality rates from the models in conjunction with the target mortality and spawning potential reduction.

Introduction

In 1979, in what is known as the Fox Decision, U.S. federal courts re-affirmed the existence of treaty-reserved fishing rights in Michigan waters of Lakes Superior, Huron, and Michigan. These waters were ceded to the U.S. government by Native American bands whose predecessors were signatory to the Treaty of Washington, 1836 (Fig. 1). Subsequent to the 1979 court decision, the Sault Ste. Marie Tribe of Chippewa Indians, the Bay Mills Indian Community, and the Grand Traverse Band of Ottawa and Chippewa Indians formed the Chippewa/Ottawa Treaty Fishery Management Authority (COTFMA) and developed regulations to govern commercial and subsistence fishing activities by their members in Great Lakes waters of the 1836-ceded territory (Brown et al. 1999). These regulations were approved by the federal district court in 1982 with the stipulation that total allowable catches (TACs) be developed for all fish species important to the fishery and adopted as a way to prevent overharvest.

Cooperative technical working groups had been established to assess the status of fish species important to tribal and state commercial and sport fisheries prior to creation of COTFMA. These ad hoc working groups composed of federal, state, and tribal biologists produced stock assessments and projected annual TACs for lake whitefish (*Coregonus clupeaformis*, hereafter whitefish) and lake trout (*Salvelinus namaycush*) from 1979 to 1982 (Ad Hoc Working Group 1979; Tripartite Technical Working Group 1981). Stock assessments were typically updated annually, and TACs were projected one year into the future.

In 1985 COTFMA-member tribes, the Michigan Department of Natural Resources (MDNR), and the U.S. Department of the Interior negotiated a 15-year agreement regarding the exercise of treaty rights in 1836-ceded waters. The agreement known as the 1985 Consent Decree created a Technical Fisheries Review Committee (TFRC) that was charged to assess the status of important fish stocks in 1836-ceded waters and to submit reports to the parties (i.e., the state, tribes, and federal government) that described the status of whitefish and recommended TACs for the stocks (Technical Fisheries Review Committee 1985). Various ad hoc technical working groups were established under the TFRC structure; these groups were typically responsible for data analysis, report writing, and making TAC recommendations to the TFRC.

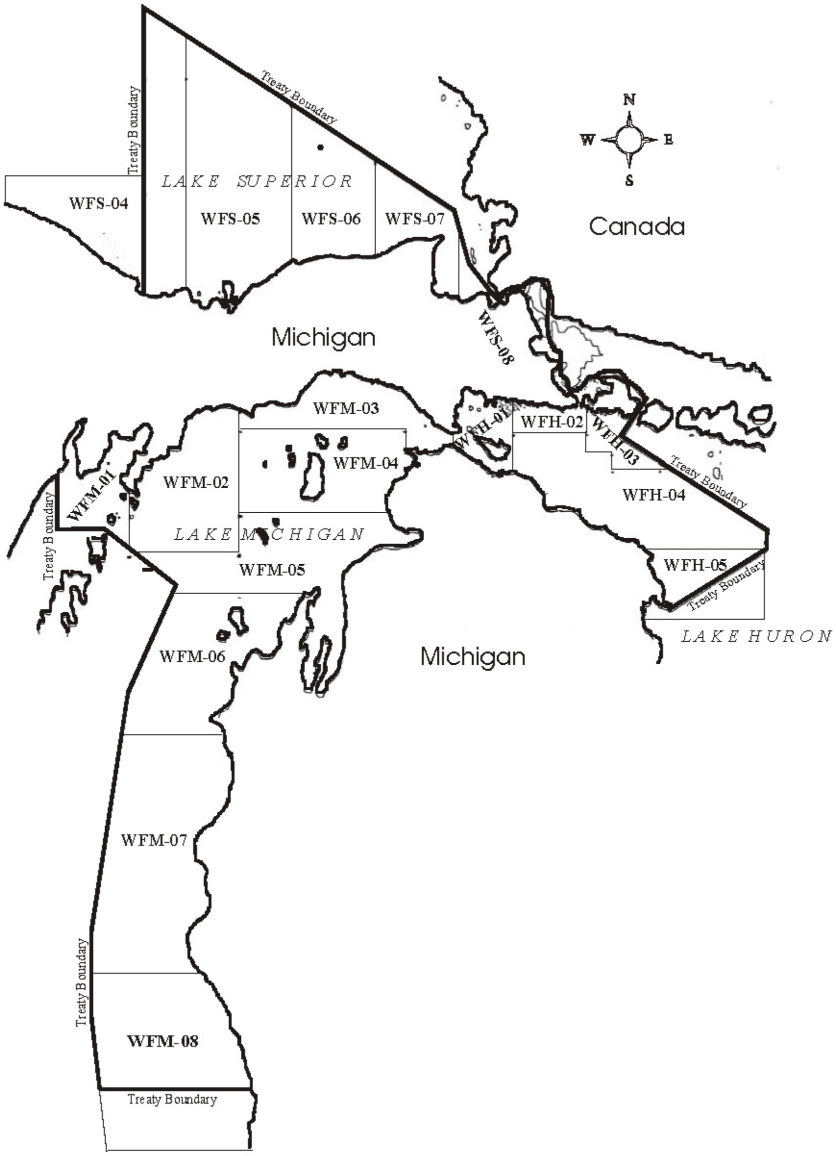


Fig. 1. 1836-ceded waters and lake whitefish management units in Lakes Superior, Huron, and Michigan.

A 20-year negotiated settlement among the parties was achieved in 2000 as the 1985 Consent Decree expired. The 2000 Consent Decree allocated fishery resources among the parties, but, unlike the 1985 Consent Decree, it outlined how whitefish stocks would be managed. The 2000 Consent Decree specifically states that "whitefish harvest shall be regulated by the parties in accordance with whitefish harvest limits developed as provided in subsection 1" (U.S. *v.* Michigan 2000) using time frames, mortality rates, size limits, allocations, and management aspects addressed within the decree. COTFMA was reorganized into the Chippewa/Ottawa Resource Authority (CORA) as part of the 2000 Consent Decree, and the TFRC was replaced with the Technical Fisheries Committee (TFC) that was to be the primary body for consultation on biological issues.

In 1998, prior to the 2000 Consent Decree, biologists from each of the parties formed an ad hoc working group. It was created to develop population models for whitefish and lake trout that would be needed to allocate stocks of these species among the state and tribes and provide for estimating future harvest limits. This working group was formally recognized by the parties in 1999 as the Modeling Technical Subcommittee (MSC), and the 2000 Consent Decree mandated that the MSC develop and annually update fish-population models to be used for setting harvest levels. In 2002, the TFC created terms of reference for the MSC that formally defined how the subcommittee operates.

Our objective in this paper is to provide an overview of the assessments and projections of TACs used to advise management in 2001, the first full year covered by the 2000 Consent Decree. We believe this new approach is a substantial improvement over previous methods and makes better use of the richer and longer-term data sets now available but not available prior to 1984. We also provide an overview of the recent status of the whitefish stocks in 1836-treaty ceded waters and suggest ways that assessments could be improved.

Methods and Results

Objectives for developing whitefish TACs prior to 1984 were inconsistent. The pre-COTFMA ad hoc working group believed that data were not always sufficient to assess stock size and mortality rates for whitefish (Ad Hoc

Working Group 1979). At that time, TACs were based on temporal patterns in catch-per-unit-effort (CPUE) and recent yields. At times, surplus production models based on yield and effort were used to estimate standing stocks of whitefish (Ad Hoc Working Group 1979). At other times, an equilibrium approach was used: total mortality rate was estimated by catch curve, and recruitment and the corresponding stock size were determined assuming a value for natural mortality and an equilibrium stock. TACs were determined either as a proportion of the standing-stock estimate or by an assumed level of recruitment. During 1984-1991, stock assessments were typically updated annually, and TACs were projected one year into the future. These assessments followed an equilibrium approach using the Beverton and Holt dynamic-pool model and were implemented using software developed by the MDNR (Clark and Smith 1984).

The TFRC's ad hoc working group developed maximum target mortality rates to set TACs and guide management of whitefish stocks in 1836-ceded waters. The ad hoc working group originally did not use a specified target mortality rate to set TACs; instead, fishing mortality rates were set to maximize yield per recruit. Maximum target mortality rates were first introduced in 1984 (Tripartite Technical Working Group 1984) when the ad hoc working group proposed to use rates of 60-65%, which were based on whitefish stocks outside the Great Lakes. A substantial proportion of the whitefish stocks with mortality rates in excess of 70% have been described as depleted or precarious, whereas stocks with rates below 65% fared better (Healey 1975). The ad hoc working group stated that mortality rates should not exceed 70%. To estimate TACs, total mortality rates for stocks were either reduced to or increased to 65%, as appropriate in Lake Michigan, 60% in Lake Huron, and 45-60% in Lake Superior (Tripartite Technical Working Group 1984).

After implementation of the 1985 Consent Decree, the TFRC adopted a maximum target-mortality-rate strategy. The Decree, however, contained no specific provisions about target mortality rates for whitefish. In 1985, the long-term-maximum target rate for whitefish remained 65% in Lake Michigan and was increased to 65% in Lake Huron. The long-term targets for whitefish in Lake Superior varied among areas: 50% in WFS-04 and 55% in WFS-05 and -06 as a way to keep fishing effort and the incidental harvest of lake trout down. The TFRC also indicated that target mortality rates in Lake Superior were subject to change as additional data became available. Mortality rates of whitefish were estimated during 1985-1991 from combinations of commercial trapnet and gillnet age compositions, depending on area.

In 1998, as the 2000 Consent Decree began to be negotiated, new methods were developed and implemented to assess whitefish and calculate TACs. The TFRC's ad hoc technical working group decided to apply statistical catch-at-age analysis (SCAA) and a non-linear-estimation software package called AD Model Builder® (Otter Research Ltd. 2001) to estimate abundance and mortality as well as fishery and population parameters for each whitefish stock. The output from these models was to be used to project stock abundance, mortality, and TACs based on management options provided by policy makers involved in the negotiation process. These SCAA assessments and TACs took into account differences in life-history characteristics among stocks through calculations of spawning-stock biomass per recruit (SSBR).

Stock assessments of whitefish in 1836-ceded waters have always been conducted on spatially defined stocks (Fig. 1). Stock boundaries, in general, are supposed to represent the entire spatial distribution of reproductively isolated spawning populations. Stock boundaries were originally based on statistical-district boundaries (Rybicki and Schneeberger 1990), but stock boundaries were later realigned based on published mark-recapture studies (Ebener and Copes 1985; Scheerer and Taylor 1985; Prout 1989); unpublished mark-recapture studies (MPE, file data); knowledge of the locations of spawning populations; and fishing patterns of the commercial fishery (Rakoczy 1983). Several reproductively isolated populations likely occur within some management units such as WFM-03, -04, and -05 (Scheerer and Taylor 1985; Walker et al. 1993) in northern Lake Michigan.

Management units in the 1836-ceded waters represent 18 virtual stocks of whitefish. An additional stock (WFM-00) bordering the ceded waters was also assessed. These management units range from 19,000 to 733,000 ha in surface area and total 5.8 million ha. Locations where bottom depths were <73-m deep were considered potential whitefish habitat, which, within individual management units, ranged from 16,000-234,000 ha of surface area. The area within the 73-m contour comprised 9-100% of the total area within individual units and averaged 35% over all management units. One stock in each of the upper lakes has boundaries that straddle the 1836-ceded waters. Harvest limits for these stocks apply to the entire management unit not just to 1836-ceded waters.

Tribal and state-licensed commercial-fishery catch and effort data are the primary inputs to the SCAA models. Monofilament large-mesh gillnets of ≥114-mm stretched mesh and 6- to 14-m-tall deep trapnets account for nearly 100% of the whitefish commercial harvest from 1836-ceded waters. All licensed fisheries submit monthly reports that describe for each day of the month the weight of fish landed, the amount of gear lifted, the 10-minute by 10-minute statistical grid where fishing took place, and other information. These monthly catch reports are compiled to produce a single annual estimate of yield (kg) and effort (length of gillnet and number of trapnet lifts) in each management unit for input into the SCAA models. Recreational fisheries also harvest substantial numbers of whitefish from certain management units (Schorfhaar and Schneeberger 1997), but these harvests are not included in the SCAA models.

Commercial-fishery yields in our SCAA models are adjusted to account for underreporting because not all fish landed and sold are reported. To estimate underreporting, we compared the commercial whitefish harvest reported by tribal fisheries with the weight of whitefish reported bought by wholesalers from tribal licensed fishermen during 1981, 1986, 1992, and 1998. The ratio of the reported harvest to the wholesale purchases of whitefish was always greater than 1.0, and this ratio was then multiplied by the reported harvest for all subsequent years. We assumed that the amount of underreporting was greater for the gillnet fishery than the trapnet fishery during the early years in the time series because the small-boat gillnet fishery was notorious for underreporting landed catch. We also assumed that the amount of underreporting by the state-licensed trapnet fishery was the same as for the tribal trapnet fishery, and that the underreporting was the same in every management unit. These underreporting values (Table 1) were incorporated into gear-specific vectors in the SCAA models and then divided into the reported yield to produce an adjusted yield value in the SCAA models.

Commercial large-mesh gillnet effort was also adjusted upward to account for increases in the height of gillnets (Collins 1987; Brown et al. 1999) used by the tribal fishery. A multiplier for adjusting gillnet effort was estimated separately for the small-boat and large-boat gillnet fisheries because they use different amounts of each size of gillnet (Fig. 2). The CPUE of whitefish caught in monofilament gillnets of 114-mm stretched mesh and 0.20 mm diameter (i.e., the standard commercial gillnet) that were 28-36, 36-50, 50, and 50-75 meshes deep was estimated from a study conducted in Lakes Michigan, Huron, and Superior during 1992-1994 (MPE, unpubl. data). The CPUE of whitefish in the 28-36 mesh-deep gillnets (the standard of the gillnet fishery prior to 1978) was divided into the CPUE of the 36-50, 50, and 50-75 mesh-deep nets to yield CPUE ratios of 1.19, 1.26, and 1.38, respectively, for each group of nets. These ratios were multiplied by the amount of tribal large- and small-boat gillnet effort made up of nets 28-36, 36-50, 50, and 50-75 meshes deep each year (Fig. 2) to estimate a weighted average gillnet multiplier for each fishery type during 1977-1999 (Table 1). A year-specific gillnet multiplier for each management unit was estimated by weighting the large- and small-boat multipliers in Table 1 by the amount of effort expended by each fishery. Total gillnet effort reported by the tribal fishery in each management unit was then increased by the amount of the year-specific multiplier.

Table 1. Proportion of the lake whitefish harvest actually reported by the commercial fishery, and gillnet effort multipliers used as year- and gear-specific vectors in the SCAA models.

	Proportion reported		**Gillnet multiplier**	
Year	**Trapnet**	**Gillnet**	**Large boat**	**Small boat**
1976	0.85	0.70	1.00	1.00
1977	0.85	0.70	1.00	1.00
1978	0.85	0.70	1.19	1.00
1979	0.85	0.70	1.19	1.00
1980	0.85	0.75	1.19	1.00
1981	0.85	0.85	1.24	1.00
1982	0.85	0.85	1.24	1.19
1983	0.85	0.85	1.24	1.19
1984	0.85	0.85	1.24	1.19
1985	0.85	0.85	1.24	1.19
1986	0.90	0.90	1.24	1.23
1987	0.90	0.90	1.24	1.23
1988	0.90	0.90	1.24	1.23
1989	0.90	0.90	1.24	1.23
1990	0.90	0.90	1.24	1.23
1991	0.90	0.90	1.24	1.23
1992	0.94	0.94	1.24	1.23
1993	0.94	0.94	1.24	1.23
1994	0.94	0.94	1.24	1.23
1995	0.94	0.94	1.26	1.26
1996	0.94	0.94	1.30	1.26
1997	0.94	0.94	1.30	1.26
1998	0.94	0.94	1.34	1.26
1999	0.94	0.94	1.34	1.26

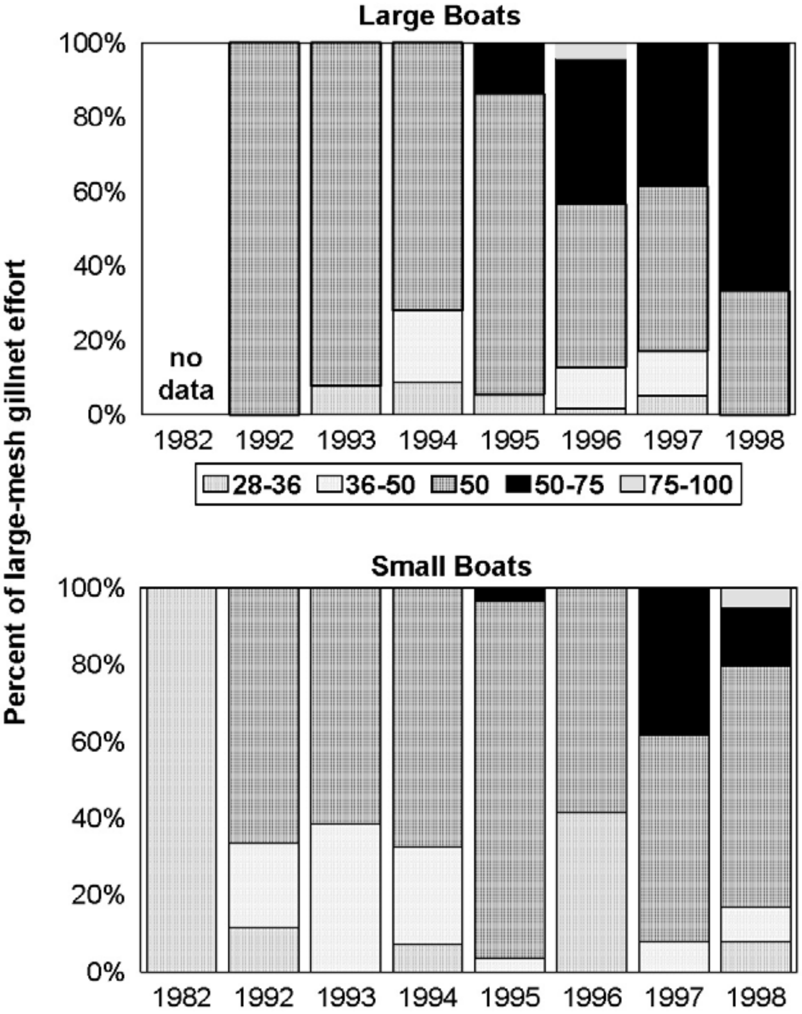


Fig. 2. Percent of gillnets of different heights (in meshes) in the tribal small- and large-boat fisheries during 1982 and 1992-1998.

Since 1991, the objective of the CORA sampling program has been to sample at least 0.25-0.5% of the total landed harvest from each gear in each management unit. Sampling occurs throughout the fishing season and is weighted by the seasonal proportion of the harvest from each gear type. CORA sampling takes place on board fishing vessels and on shore and consists of measuring length and weight, collecting scales, enumerating the number of sea lamprey (*Petromyzon marinus*) marks, and, at times, identifying sex and stage of sexual maturity. Monitoring of state-licensed trapnet fisheries varies by lake but consists of sampling 200 net-run whitefish caught in a single day in each management unit, although some management units are sampled more frequently. The MDNR sampling protocol has been described by Rakoczy (1983) and Rybicki and Schneeberger (1990) and is similar to the CORA process described above.

Age composition of the harvest, mean weight of a harvested fish, mean weight-at-age in the harvest, von Bertalanffy growth coefficients, and weight-at-age of the stock was input to the SCAA models. The proportion of each age-class harvested annually is input to the model as a matrix specific to each gear type. Year- and age-specific matrices start with either age-3 or age-4 fish depending upon management unit. All fish older than a specific age are combined together into a single age-class. Combined age-classes included fish from 9+ to 12+ depending upon management unit. The mean weight of a harvested fish in a gear type is input as a vector and is divided into the annual biomass caught to estimate the number of fish caught by that gear in a year.

Mean weight-at-age harvested for each gear is calculated and input as a constant across years and is used in the model to estimate a matrix of age-specific harvested biomass in each year. In units where mean weight-at-age changed through time, only data averaged for the most recent years were used in the model.

Observed weight-at-age for the stock was typically calculated from samples of the commercial harvest supplemented by samples from graded-mesh gillnet surveys, which better capture the smallest and largest fish. Undersized whitefish, typically released from trapnets, were also included in the calculation of observed weight-at-age for each stock but not in the calculation of mean weight-at-age in the harvest. The observed weight-at-age in the stocks and in harvests were assumed to be mid-year weights. Weight-at-age in the stocks at other times of the year (beginning of the year and at spawning) were calculated from mid-year weights assuming exponential growth rates.

Asymptotic mean length (L_∞) and the Brody growth coefficient (K) were estimated by fitting a von Bertalanffy growth model to calculated length-at-age by non-linear regression. These parameter estimates were used in calculating natural mortality (see below). Mean length-at-age was calculated by combining individual lengths of whitefish caught in commercial fisheries and in graded-mesh gillnet surveys either during the last three years or during all years depending on management unit and growth of whitefish.

The maturity schedule for female whitefish was input to the SCAA models as an age- and year-specific matrix. The proportion of sexually mature females within the 20- or 25-mm length-classes was estimated for each management unit and aggregated across years. A single length-at-maturity schedule was developed instead of an annual schedule because we believe that length at maturity does not change appreciably through time although age at sexual maturity changes as growth changes. In addition, data on sexual maturity were scant in most management units, which precludes estimation of year-specific maturity-at-length schedules. In management units without maturity data, the maturity schedule from an adjacent unit in the same lake was used in our models.

The length-based maturity schedule for a management unit was projected on an age-length distribution for the same unit to estimate an age-specific maturity schedule for female whitefish. We assumed there was no difference in the length distributions of male and female whitefish. Age-specific sexual maturity of female lake whitefish was estimated as

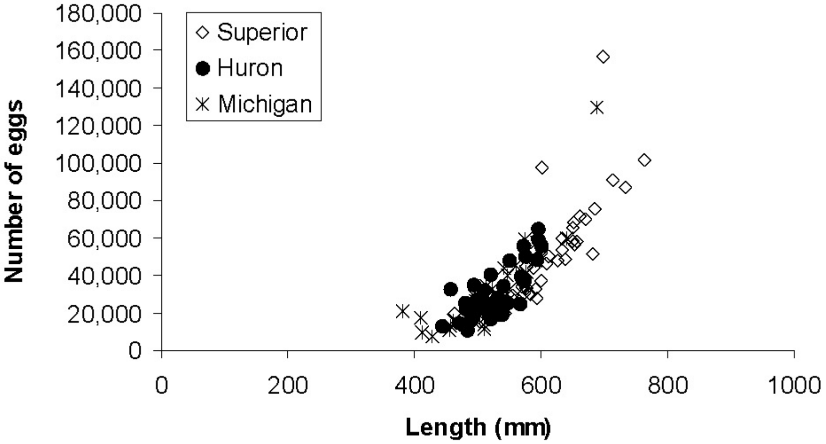
$$FM_{a,y} = \sum_{l} p_l pm_{l,a,y}$$

where pm is the proportion of age (a) in length-class (l) for that year (y) and p is the proportion of females that are sexually mature in the same length-class. A single length distribution at age was calculated for each of the following five-year periods: 1976-1980, 1981-1985, 1986-1990, 1991-1995, and 1996-1999. We used five-year time periods as a compromise between limited sample sizes for some ages in some years, which accounts for the fact that size-at-age clearly changed over the assessment period.

We estimated the proportion of females in the spawning population because Patriarche (1977) reported that it did vary by year and management unit, and the sex ratio of whitefish was not 1:1 in northern Lake Michigan. The proportion of female whitefish in each spawning stock was input as a single value to the SCAA models and assumed constant across all ages.

The time of year at spawning was input to the SCAA models and used to estimate weight-at-age of spawning whitefish as described previously. We elected to use the mid-point of the spawning season for the time of year of spawning in each management unit on that Julian Day divided by 365. In most units, November 15 was used as the mid-point of the spawning season, but, in some Lake Huron management units, time of spawning was set to October 15.

Fecundity in the SCAA models was expressed as the number of eggs per kilogram of female whitefish and was assumed to be the same in all management units. Fecundity was estimated from samples collected in Whitefish Bay, Lake Superior, in 1983 and in numerous management units during October and November of 1996. Although there appeared to be differences in fecundity among lakes (Fig. 3), these differences were not statistically significant so we used an average weight-specific fecundity of 19,937 eggs$\cdot$kg^{-1}.



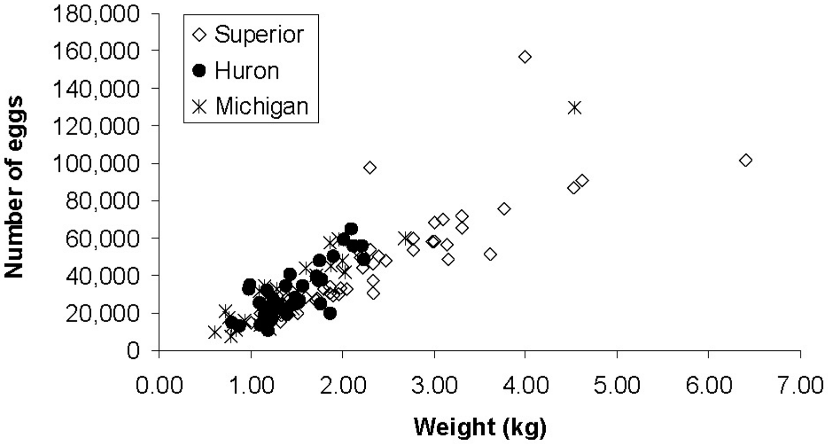


Fig. 3. Relationship between length and weight and the number of eggs per female lake whitefish from Lakes Superior, Huron, and Michigan in 1983 and 1996.

We assumed the background natural mortality rate (*M*, not due to sea lamprey) was constant over ages and over time and was known *a priori* (i.e., not estimated when models were fit to data). Values were calculated based on a relationship between *M*, L_∞, and *K* and *T* (temperature) as described by Pauly (1980)

$$\ln(M) = -0.0238 - 0.277(L_\infty) + 0.655\ln(K) + 0.465\ln(T)$$

with length measured in mm and temperature in ^{o}C. We obtained the parameters and other regression diagnostics (Table 2) for this equation by refitting Pauly's (1980) relationship to his original data to ensure correct interpretation of units and transformations. We used natural logs instead of $\log_{10}$ as Pauly apparently did, and accordingly our estimates of the model's parameters differ slightly from those reported by Pauly, although careful checking did not reveal any discrepancy between the data we used and Pauly's published data. Note that to estimate *M*, the temperature is intended (according to Pauly) to be the mean annual temperature at the location where samples are collected. These temperatures were set to 6^{o}C in Lakes Huron and Michigan and 4-5^{o}C (depending on unit) in Lake Superior based on the temperature occupied by whitefish in the Great Lakes. Although catch-curve estimates of mortality for unexploited or lightly exploited whitefish stocks are available for the Great Lakes, these estimates appear to have substantial measurement error (partly because of time-varying recruitment) and relatively little contrast in the values of L_∞, *K*, and *T*. Therefore, a useful test of the Pauly equation for Great Lakes whitefish is not feasible.

Table 2. Parameter estimates obtained by fitting Pauly's (1980) regression model of asymptote length ($L\infty$), temperature (*T*), and Brody growth coefficient (*K*) to natural mortality rate of fishes. RMSE is the root mean square error.

Parameter	Estimate	SE
Intercept	-0.0238	0.264
Slope for $\log_e(L_\infty)$	-0.277	0.0665
Slope for $\log_e(T)$	0.465	0.0819
RMSE	0.563	-

Under current conditions, most stocks of whitefish in treaty waters exhibit little or no wounding or scarring due to sea lampreys. Because high levels of scarring and wounding were observed (Spangler et al. 1980) when sea lampreys were clearly more abundant, we believe this observation reflects generally low mortality due to sea lamprey. Thus, for most stocks we assumed that sea lamprey-induced mortality was zero. An exception was stocks in Lake Huron. We observed similar sea lamprey marking rates across management units and time in the ceded waters of Lake Huron. Because marking rates did not appear to vary spatially or temporally, we combined marking data from all management units and years and estimated a single set of constant age-specific sea lamprey-induced mortality rates. These mortality rates were based on spring samples and counts of type AI, AII, and AIII marks following the King (1980) classification system. Henceforth, we will refer to these types of marks as wounds.

Not all sampled whitefish had been aged, so we first estimated wounding rates by 50-mm length categories but pooled all fish $\geq$650-mm total length. We then converted these rates to age-specific rates using an age-length distribution. That is, we calculated for each age the proportion of fish falling into each length category ($pm_{l,a}$) and calculated the age-specific wounding rates as

$$W_a = \sum_l W_l pm_{l,a}$$

which is a weighted average of the length-specific rates (W_l) with weights equal to the proportion of the specified age in a particular length category.

Sea lamprey-induced mortality rates were calculated by transforming the wounding rates by

$$M_{L,a} = W_a \frac{(1-P)}{P}$$

where W is the mean wounds per fish for an age-class (a) and P is an estimate of the probability of surviving an attack. This equation assumes that fish with wounds observed in the spring represent survivors of potentially lethal attacks the previous year (Eshenroder and Koonce 1984; Sitar et al. 1999). Bence et al. (2003) and Ebener et al. (2003) discuss in depth the assumptions underlying this approach and the properties of wounding data. We used the value of 0.25 from Spangler et al. (1980) for *P*.

We used age-structured population models, first, to generate estimates of whitefish abundance and mortality and to describe how they have changed over time and, second, to project TAC, harvest, and associated effort that met established criteria for the next fishing year (e.g., mortality-rate targets). The first of these tasks was accomplished by constructing SCAA models that are widely regarded as a state-of-the-art approach (Hilborn and Walters 1992). These catch-at-age models operated with annual time steps and age-specific abundances, and mortality rates were estimated for each year of model runs. In WFH-02 and –03, we were unable to obtain reliable parameter estimates because the data from these areas were apparently inadequate to support modeling.

We estimated TACs by projecting the estimated whitefish populations forward through the next fishing season, accounting for fishing and expected natural mortality and projecting the associated harvest and yield. The fishing mortality rates in these projections were adjusted to match upper bounds on fishing effort, fishery harvest, or total mortality while satisfying desired state and tribal allocations.

Catch-at-age models consist of two submodels (Methot 1990; Schnute 1994). The first submodel describes the population dynamics of the stock. The second predicts observed data given the estimated stock numbers for each year. In our applications, the agreement between model predictions and observed data was measured using a likelihood function. Both the population and observation submodels include adjustable parameters that correspond to a specific sequence of stock abundances, mortality rates, and predicted data. The set of such parameters and associated stock dynamics and mortality rates that maximize the likelihood (the maximum likelihood estimates) is taken as the best estimate.

The basic population model describes the survival of each cohort. Except for the first age and first modeled year, abundance-at-age at the start of each year is calculated as the proportion of the cohort surviving from the start of the previous year.

$$N_{a+1,y+1} = N_{a,y} P_{a,y}$$

The proportion surviving is modeled as

$$P_{a,y} = e^{-Z_{a,y}}$$

where $Z_{a,y}$ is the total instantaneous mortality rate for age-a and year-y.

The total instantaneous mortality rate needs to be broken into components that can be calculated from a suite of parameters that are estimated from available data. All the models include fishing mortality (F) and background natural mortality (M). For Lake Huron, an additional source of natural mortality due to sea lamprey (M_L) was added. Fishing mortality was often broken into two subcomponents representing different fishery types. Typically these two components were trapnet and gillnet, although a trawl fishery operates in WFM-00 (Table 3).

Table 3. Components of fishing mortality (*F*) considered for each management unit where the status of whitefish stocks was assessed for 1999.

Lake	Mgt unit	Gillnet fishery	Trapnet fishery	Trawl fishery	Model estimated?
Superior	WFS-04	Yes	Yes	No	Yes
	WFS-05	Yes	Yes	No	Yes
	WFS-06	Yes	No	No	Yes
	WFS-07	Yes	Yes	No	Yes
	WFS-08	Yes	Yes	No	Yes
Huron	WFH-01	Yes	Yes	No	Yes
	WFH-02	Yes	Yes	No	No
	WFH-03	Yes	Yes	No	No
	WFH-05	No	Yes	No	Yes
Michigan	WFM-00	No	Yes	Yes	Yes
	WFM-01	No	Yes	No	Yes
	WFM-02	Yes	Yes	No	Yes
	WFM-03	Yes	Yes	No	Yes
	WFM-04	Yes	Yes	No	Yes
	WFM-05	Yes	Yes	No	Yes
	WFM-06	Yes	Yes	No	Yes
	WFM-07	No	No	No	No
	WFM-08	No	Yes	No	Yes

Thus, in an area with gillnet and trapnet fisheries and where we included sea lamprey-induced mortality, total instantaneous mortality was modeled as

$$Z_{a,y} = F_{G,a,y} + F_{T,a,y} + M + M_{L,a,y}$$

where F_G and F_T represent the gillnet and trapnet fishery components. As detailed above, background and sea lamprey-induced mortality rates were calculated and assumed known prior to fitting the catch-at-age models. To further reduce the number of parameters, for each fishery component, the age- and year-specific fishing mortality rates are products of age-specific "selectivity" (*S*) and year-specific fishing intensity (*f*). In a purely separable model, selectivity is constant for fish of a given age; thus, for each fishing mortality component (*i*), the fishing mortality rate is the product of an age (*S*) and year (*f*) effect.

$$F_{i,a,y} = S_{i,a} f_{i,y}$$

Our assessment models relax the separability assumption to account for changing selectivity resulting from changes in size-at-age (Schneeberger et al. 2005), fishery behavior, or other causes. To accomplish this departure, we modeled the relationship between selectivity and age as a function, and we allowed one of the parameters of the function to vary over time. Our basic age-specific selectivity function was the double logistic, which allows a flexible, dome-shaped selectivity relationship to age and includes an asymptotic pattern as a special case (Methot 1990)

$$S_{a,y} = \frac{\left[\dfrac{1}{1+e^{-\alpha_1(a-\beta_{1,y})}}\right] \times \left[1 - \dfrac{1}{1+e^{-\alpha_2(a-\beta_2)}}\right]}{K}$$

where the numerator is the product of a logistic function and a second logistic function subtracted from one. The denominator (*K*) is a normalizing constant that is set equal to the value obtained for the numerator for a reference age (thought to be nearly fully selected by the fisheries) in the first year. This sets the selectivity for the reference age in the first year to 1.0. This normalization is necessary to obtain a unique parameterization of the model. The results, in terms of estimated fishing mortality rates or management parameters, do not depend upon which age is selected. The parameters α_1, α_2, β_1, and β_2 determine the shape of the function. Note that β_1 is subscripted by year. Time-varying selectivity was allowed by letting this parameter follow a quadratic function in time

$$\beta_{1,y} = \beta_{1,y_0} + b_1(y - y_0) + b_2(y - y_0)^2$$

where y_0 is the first year included in the model. Thus, for this general model, we needed to estimate six parameters, the four basic parameters of the logistic (α_1, α_2, B_{1,y_0}, and β_2) and two additional parameters (b_1 and b_2) to allow selectivity to vary over time. The number of parameters was reduced for trapnet fisheries by assuming a logistic relationship so that α_2 and β_2 did not need to be estimated. In WFM-03, reliable estimates could not be obtained for the quadratic function so a linear function was used instead by fixing b_2 to zero.

Fishing intensity is the fishing mortality rate associated with each component (i) for ages that have a selectivity of 1.0. Fishing intensities were not estimated freely but instead were assumed to be proportional to effort, up to a multiplicative deviation

$$f_{i,y} = q_{i,y} E_{i,y_y} \zeta_{i,y}$$

where q is catchability (the proportionality constant), E is observed effort, and ζ is the deviation. During model fitting, large estimated deviations were penalized (see below).

In summary, from three to six parameters were estimated during the fitting of the SCAA models to describe each fishery's selectivity pattern, and a year-specific parameter associated with each fishery's fishing intensity was estimated. No additional parameters to describe background natural mortality or sea lamprey-induced mortality were estimated during model fitting.

To complete the population model and describe stock dynamics over time, it was necessary to specify the initial numbers at age in the first year and the recruitment of the youngest age in each subsequent year. The initial numbers at each age were estimated as parameters just as were the values for gear selectivity. In the simplest cases, recruitment to the youngest age each year was also estimated as a parameter during model fitting. Although we estimated recruitment (N_{y,a_0}, where a_0 is the first age in the model) for each year, large deviations from the recruitment expected on the basis of a Ricker stock recruitment model were penalized for those years for which predictions could be generated. These predicted recruitments

$$N_{y,a_0} = \alpha E_{y-a_0-1} e^{-\beta E_{y-a_0-1}}$$

were based on the numbers of eggs produced by spawners in the late fall a_0-1 years prior to the year of recruitment (E_{y-a0-1}). Numbers of eggs were based on the model estimate of the number of fish alive at each age adjusted for the estimated instantaneous mortality rate over the proportion of the year prior to spawning. To obtain the stock size in terms of eggs, these numbers were sequentially multiplied by the proportion of the population that was estimated to be female, the estimated proportion of females at that age that were mature, the weight of a mature female of the given age at the time of spawning, and an estimate of the weight-specific fecundity of a mature female. The weight-at-age at the time of spawning was based on observed weight-at-age in the population adjusted for expected growth up to the time of spawning. This adjustment was based on age- and year-specific instantaneous growth rates calculated from observed weight-at-age.

The observation submodel predicts by age the numbers of whitefish killed by each fishing component. Fishery kill is then converted into proportions-at-age and total number killed for comparison with empirical data. Fishery kill is predicted using Baranov's catch equation

$$C_{i,a,y} = \frac{F_{i,a,y}}{Z_{a,y}} N_{a,y} A_{a,y}$$

where the total mortality rate $A = 1\text{-}e^{-Z}$. Note that no additional parameters, beyond those already needed for the population submodel, need to be estimated.

For numerical and coding reasons it is convenient to maximize the likelihood by minimizing the negative log likelihood. Let L stand for the total log-likelihood. This is calculated as the sum of a set of K-independent components:

$$L = L_1 + L_2 + L_3 + \ldots + L_K$$

Each component represents a data source or penalty, and the number of these components varied among stocks. For each fishery that was included in the model there were three components for each year: one for the total fishery kill, one for the fishery age-composition, and one for the effort deviations. These likelihood components were calculated under the assumption that total fishery kill and effort deviations were log-normal and that the proportions-at-age were determined by a multinomial distribution. An additional component came from variation about stock-recruit functions. In the calculation of this penalty term, the deviations were treated as log-normal (Table 4).

These various components were automatically weighted by either the inverse of the variance associated with them (log-normal components) or the effective sample size (multinomial components). Here, if X is log-normally distributed, variance refers to the variance of ln (X). The square root of the log-scale variances for the log-normal variables is approximately equal to the coefficient of variation (CV) on an arithmetic scale. In the case of a multinomial variable, the CV for a proportion (p) is:

$$CV(p) = \sqrt{\frac{p(1-p)}{N}}$$

Table 4. Log-likelihood components (excluding some additive constants) used during model fitting. The first term on the right-hand side of the log likelihood components (-*n*lnσ) is a constant when the variances (σ^2) are not estimated, which was our situation. We included it in this table for completeness, in case these equations are used as a basis for other applications where the variances are estimated. To represent observed quantities, as distinct from model predictions, ~ is placed over the symbol.

Description of likelihood components	**Equation for the log-likelihood component L_k, k = 1 to number of components**
For fish killed by a specific component *j* (e.g., gillnets), based on log-normal assumption.	$L_k = -n \ln \sigma_{C_j} - \frac{1}{2\sigma_{C_j}^2} \sum_y [\ln(\widetilde{C}_{j,y} / C_{j,y})]^2$
For age composition associated with a specific fishery component *j*, based on multinomial assumption. The effective sample size is *J* and $p_{j,a,y}$ is the proportion at age in a year in the j^{th} fishery component's catch.	$L_k = \sum_y \left[J_{j,y} \sum_a \widetilde{p}_{j,a,y} \ln(p_{j,a,y}) \right]$
For fishery effort deviations for a specific fishery component *j*.	$L_k = -n \ln \sigma_{\zeta_j} - \frac{1}{2\sigma_{\zeta_j}^2} \sum_y [\ln(\zeta_{j,y})]^2$
For deviations in recruitment about stock-recruitment function, based on a log-normal assumption and prediction of recruitment by a Ricker function of stock size (*E*, calculated as the number of eggs produced by the modeled abundance-at-age). The Ricker parameters (α, β) as well as recruitments of either age 3 or 4 (the $N_{r,y}$) were estimated during model fitting.	$L_k = -n \ln \sigma_R - \frac{1}{2\sigma_R^2} \sum_y [\ln(N_{r,y} / f(E_{y-r-1}))]^2$ $f(E) = \alpha E e^{-\beta E}$

With these relationships in mind, the modeling subcommittee considered the measurement error associated with the various data sources and then specified default variances or effective sample sizes for each type of data, which were adjusted where additional information was available on data quality.

When variations of recruitment were expected on the stock-recruit function, an iterative approach was followed during model fitting. An initial value for the standard deviation for variations about expected values was specified, and the model was fit. Then the standard deviation of the resulting deviations was calculated. The model was refit, adjusting the value of the input standard deviation until the deviation between the standard-deviation value specified prior to model fitting and the value calculated after model fitting was minimized. A minimum deviation was defined when the ratio of pre- to post-standard deviation was closest to 1.0.

The resulting maximum-likelihood parameter estimates were checked in several ways to help ensure that the results were reliable and that the model had converged to a global solution. These checks included examination of model output including the asymptotic variance-covariance matrix and the gradient at the solution (which should be near zero). In addition, we refit models starting from different initial values to determine whether the same solution was obtained.

Our stock assessment results need to be compared with the target mortality rate specified in the 2000 Consent Decree (U.S. *v.* Michigan 2000) at 65% per year. The Consent Decree, however, did not specify which ages or categories of fish were applicable to the target. Substantially different results are obtained if the 65% is assumed to be the maximum that can be applied to any given age rather than an average over all age groups. We developed an approach that considered different age-specific mortality schedules as equivalent if they produced the same SSBR. SSBR can be calculated by applying the estimated or assumed mortality schedule over the life span of a recruit and summing up the amount of spawning biomass present each year at the time of spawning. We had used this concept with lake trout using a target schedule that assumed a natural mortality rate up to the age at 50% maturity and then assumed the target mortality rate for older ages. This scheme did not have desirable properties when applied to whitefish because of the diversity of life histories and growth rates among different stocks. In particular, this scheme, when modeled, greatly depleted spawning stocks in some units and appeared to be conservative in others.

We, therefore, adopted a two-stage approach for defining a target-mortality schedule for whitefish. First, SSBR was calculated for a scenario where overall fishing-mortality rates were adjusted (proportionally for all ages) so that, during the projection period, total mortality on the age experiencing the highest projected fishing-mortality rate was equal to 65%. Spawning potential reduction (SPR) is calculated by dividing SSBR by the spawning-stock biomass per recruit calculated assuming only background natural mortality. The SSBR target was defined as either the lower of the SSBR calculated above and or as associated with an SPR of 0.2. We developed this approach by examining various different rules and ascertaining that this approach generally ensured that more than one age-class was contributing substantially to spawning. An SPR of 0.2 is aggressive by standards applied in other fisheries (Quinn and Deriso 1999) and reflects our perception that whitefish stocks are generally robust even when subjected to fairly high fishing rates. Most of the whitefish stocks in 1836-ceded waters had an SPR over 0.2 when ages fully recruited to the fishery experienced a total mortality rate of 65%. The SSBR values and total mortality rates projected for 2001 vary substantially among management units (Table 5) because of the stock-specific rates of fishing, growth, and maturity.

Table 5. Spawning stock biomass per recruit (SSBR) in unexploited (base), current (1999), and projected (2001) states; estimated average instantaneous mortality rates (M = natural mortality, F_T = trapnet fishing mortality, F_G = gillnet fishing mortality, M_L = sea lamprey mortality) during 1997-1999, and total-mortality-rate target (Z) estimated for 2001.

Lake	**Mgt unit**	**SSBR**			**Instantaneous mortality rate 1997-1999**					
		Base	**1999**	**2001**	**Ages**	**M**	**F_T**	**F_G**	**M_L**	**Z_{2001}**
Superior	WFS-04	0.93	0.41	0.22	4+	0.22	0.12	0.04	0.00	0.73
	WFS-05	0.82	0.43	0.18	4+	0.23	0.08	0.02	0.00	0.59
	WFS-06	3.96	1.10	0.26	5+	0.22	0.00	0.24	0.00	0.53
	WFS-07	5.72	0.92	0.59	5+	0.15	0.21	0.18	0.00	0.46
	WFS-08	3.43	0.66	0.64	5+	0.17	0.36	0.31	0.00	.079
Huron	WFH-01	0.89	0.31	0.26	4+	0.27	0.09	0.25	0.06	0.74
	WFH-02				No SCAA model					
	WFH-03				No SCAA model					
	WFH-04	0.48	0.16	0.10	4+	0.32	0.06	0.16	0.05	0.80
	WFH-05	0.71	0.34	0.17	4+	0.32	0.14	0.01	0.05	0.84
Michigan	WFM-00	0.25	0.07	0.06	4+	0.38	0.23	0.22[1]	0.00	0.92
	WFM-01	0.24	0.02	0.04	4+	0.38	0.80	0.00	0.00	0.87
	WFM-02	1.64	0.34	0.39	4+	0.25	0.25	0.51	0.00	0.74
	WFM-03	0.94	0.49	0.40	4+	0.34	0.20	0.12	0.00	0.84
	WFM-04	1.42	0.54	0.38	4+	0.25	0.09	0.21	0.00	0.82
	WFM-05	1.97	0.71	0.34	4+	0.27	0.16	0.12	0.00	0.87
	WFM-06	0.69	0.30	0.17	4+	0.31	0.18	0.08	0.00	0.95
	WFM-07				No SCAA model					
	WFM-08	0.60	0.47	0.20	4+	0.37	0.06	0.00	0.00	0.94

[1] Represents fishing mortality rate for the trawl fishery

One use of our stock-assessment models is to determine the amount of yield that is consistent with target-mortality rates. To project yield at target mortality rates, age-specific abundance estimated for the last year in the SCAA model was projected forward to the next year by accounting for age-specific mortality rates by source using the same equations described above for the SCAA models. Numbers harvested-at-age were calculated by application of the Baranov catch equation. Harvest-at-age was converted to yield by multiplying numbers harvested-at-age by weight-at-age for the fishery and summing over ages. In these calculations, *M* was left at the same value used or estimated in the SCAA assessments. Although *M* is calculated as the average rate in recent years in most of the projections, it is currently assumed constant in our assessment models. For Lake Huron stocks, projected sea lamprey-induced mortality was set as the average of the values for the last three years used in the SCAA models. Recruitment of the youngest age was assumed to equal the average recruitment over the previous ten years (Table 6).

Our first task was to obtain abundance-at-age for the start of the projection year because there is usually a one-year lag between the last year included in a SCAA model and the harvest projection. For example, consider the task of projecting harvest for 2002 based on an assessment that included data through 2000. The assessment provides estimates of stock numbers and mortality rates that allow calculating abundance-at-age for the start of 2001. Those numbers are then projected forward one year by applying the average total-mortality rate estimated in the assessment for the last three years (1998-2000). The only missing age group, the youngest, which comprises recruits, is assumed to equal in numbers the average recruitment over the previous ten years.

Table 6. Surface area of water <73 m deep, mean annual yield, average recruitment, fishable biomass, spawning biomass for whitefish during 1990-1999 from SCAA models, and recommended yield at the target mortality rate in 2001 (Z_{2001}). Management units as per Fig. 1.

Lake	**Mgt unit**	**Area <73 m (ha)**	**Mean yield (kg)**	**Mean recruitment**		**Mean biomass (kg)**			**Yield at Z_{2001} (kg)**
				Age	**No. fish**	**Ages**	**Fishable**	**Spawning**	
Superior (WFS)	04	86,926	43,526	4	201,000	4+	357,431	241,311	199,581
	05	75,202	64,961	4	161,000	4+	807,394	538,414	220,899
	06	35,896	38,152	4	29,600	4+	174,633	136,531	28,576
	07	150,516	265,025	4	267,000	4+	977,945	909,453	185,519
	08	64,933	51,933	4	85,000	4+	196,859	204,570	79,832
Huron (WFH)	01	94,071	237,698	3	805,000	3+	1,477,350	936,215	148,325
	02	16.012	238,428				No SCAA model		
	03	36.607	27,193				No SCAA model		
	04	152,915	365,202	3	1,496,000	3+	3,455,466	2,214,438	119,295
	05	84,464	196,376	3	874,000	3+	2,847,653	2,188,583	103,873
Michigan (WFM)	00	78,830	574,884	3	2,183,000	3+	3,065,831	1,008,789	791,993
	01	135,783	796,550	3	1,813,000	3+	3,187,847	1,015,140	361,059
	02	156,919	162,319	3	308,000	3+	640,472	521,631	53,070
	03	195,744	537,284	3	1,750,000	3+	1,451,495	1,406,136	432,273
	04	233,776	280,009	3	596,000	3+	1,426,094	1,369,395	267,619
	05	197,749	93,482	3	184,000	3+	566,083	460,396	106,594
	06	111,684	22,550	3	88,000	3+	316,607	287,578	68,492
	07	195,190					No SCAA model		
	08	161,322	116,223	3	1,547,000	3+	2,847,199	2,658,505	1,499,123

Baseline fishing mortality rates by fishery component (e.g., trapnet or gillnet) are average rates for the most recent three years included in the SCAA models. These average rates were adjusted to the baseline age-specific rates to account for changes stipulated in the 2000 Consent Decree, or for known changes in fishing activity. For example, if a gillnet fishery existed in an area prior to 2001 but not in 2002, the projection of yield for 2002 uses a gillnet fishing-mortality rate of zero. If gillnet effort was expected to decrease by 50% due to gear conversion, the baseline gillnet fishing-mortality rate would be multiplied by 0.5. When fishing mortality was adjusted to account for a specified change in fishing effort or when fishing effort was calculated to correspond to a specified level of fishing mortality, effort and fishing mortality were treated as being directly proportional. This approach assumes that selectivity and catchability for each component will remain, on average, as it was in recent years.

Baseline fishing-mortality rates were then adjusted to achieve desired targets. Where there was no specified allocation among gear types, an overall multiplier (that applied to the baseline fishing-mortality rates for each fishery component) was adjusted until the target mortality rate (expressed in terms of SSBR) was reached. When an allocation among parties was specified, the separate multipliers for the two gear types were adjusted simultaneously to achieve mortality and allocation targets.

The process of finding the correct multipliers was expedited by making use of the Solver utility within Excel® spreadsheets. The multipliers were treated as variables that change until deviations between the target and projected SSBR, and between the target and projected allocation, approached zero. Projected SSBR was based on a projected mortality schedule.

The modeling subcommittee's projected yields corresponding to the target mortality (and SSBR) were generally recommended as upper bounds on yield. These yields were adjusted downward from model output to account for estimated underreporting (Table 1). This adjustment is necessary because the reported harvest during model fitting was assumed to be less than the actual harvest, and estimated fishing mortality rates accounted for whitefish that were assumed to have been killed but not reported.

During 1997-1999, the most recent years with actual data relevant to yield projections, only four of 16 assessed whitefish stocks (WFM-01 and -02, WFS-07 and -08) were being overfished relative to the target mortality schedule (Table 5). In WFS-07, total annual mortality on the fully vulnerable ages was less than 65%, but SSBR was less than 20% of the unfished level. In the other three overfished units, total mortality on the fully vulnerable ages exceeded 65%. In the other 12 units, our projections for 2001 incorporated increases in fishing mortality rates to either increase total mortality on fully vulnerable ages to 65% or reduce SSBR to 20% of the unfished level (Table 5). Despite these increases in fishing mortality rates, the projected yields were frequently less than seen in recent years. In nine of 16 assessed units, the projected yield for 2001 was less than the average yield during the 1990s (Table 6), and six of these nine projected decreases occurred even though fishing mortality rates were increased (Table 5). Projected yields were substantially below the 1990s average in some units in every lake, and, in Lake Huron, this was true in every assessed unit. These declines were caused by declines in recruitment and declines in individual growth in the mid- to late 1990s.

Discussion

In this paper, we have provided an overview of how the MSC is currently assessing whitefish stocks in the 1836-ceded waters. In the late 1970s and early 1980s, the challenge was to find, given limited information, any reasonable way to assess the stocks. Biologists turned to surplus-production models and then to equilibrium assumptions coupled with yield-per-recruit analyses. They rejected the possibility of developing full age-structured assessments because of the limited data (Ad Hoc Working Group 1979). This was a reasonable strategy given the information available at that time.

Our shift to age-structured models is reasonable because we now have more than 20 years of age-composition information from some management units. We believe our assessments are substantial improvements over what could be accomplished with the earlier methods. The surplus production models assumed deterministic population growth with population biomass following a logistic model. This approach is better suited to populations where recruitment is not highly variable and growth compensation dominates biomass dynamics. The equilibrium approach requires making even stronger assumptions of constant recruitment and mortality rates. In contrast, our SCAA models allow for year-to-year variations in recruitment and mortality.

Some uncertainties faced in the late 1970s still remain—nearly all our data on whitefish are fishery dependent. Consequently, we assume that fishery CPUE is proportional to stock abundance. The dangers associated with this untested assumption and the great value of fishery-independent surveys of abundance are well known (National Research Council 1998). Throughout the 1836 treaty-ceded waters, fishery-independent surveys are being initiated. These will improve the assessments and should lead to better estimates of catch rates of whitefish in the Great Lakes.

Estimates of recruitment to the fishery remain uncertain in most management units. The lack of long-term fishery-independent surveys has precluded estimating year-class relative abundance that could be used to refine estimates of recruitment in SCAA model runs for the current year and for the next year. These last two year-classes contribute substantial numbers to the fishable population and many times have a substantial influence on projected harvest limits. To deal with this problem, we arbitrarily chose to use average recruitment during the previous ten years to project harvest limits.

The assumed level of natural mortality has a strong influence on estimates of stock size and yield (Vetter 1988). During the 1980s, the same *M* (0.45) was assumed across the 1836-ceded management units based on survey catches from an unexploited population of whitefish in WFM-05. Clearly, the appropriateness of this *M* for other units was questionable. We now calculate *M* for each management unit based on Pauly's (1980) relationship between *M*, growth parameters, and temperature. Our revised natural-mortality rates are substantially lower than 0.45 and appear to better match other estimates of mortality for unfished or lightly fished whitefish stocks (Mills et al. 2005). Nevertheless, substantial quantitative and qualitative uncertainty remains. Our assumption that natural mortality remains constant over time could be in error, and we lack an independent check on Pauly's approach. We believe that declines in growth and condition of some whitefish stocks (Hoyle 2005; Schneeberger et al. 2005) caused a concurrent increase in *M*. We believe the most practical way to develop better information on natural mortality is through tagging. Such studies would need to be done on a broad-enough spatial scale to account for migration and with sufficient investment in the recovery effort so that the total recovery of tagged fish could be determined. Ideally, estimates of *M* would be developed for stocks experiencing a range of different growth conditions. Such tagging studies would also better identify stock distributions.

The maximum total-annual-mortality rate of 65% called for in the 2000 Consent Decree is not based on any clearly defined biological protocol and remains problematic because it does not specify how the rate should be calculated. Moreover, the MSC requirement that the SSBR be at least 20% of the unfished level is arbitrary and not especially conservative (Quinn and Deriso 1999). We suggest taking into account variations in life history among stocks to help prevent depletion of spawning stocks where maturity occurs after the age of substantial recruitment. The dynamics of whitefish throughout the Great Lakes and over a range of fishing levels and stock sizes should be used to evaluate the current treaty-fishery policy and its alternatives. Such alternatives should include different fishing-rate policies that adjust fishing rates to account for the life-history parameters of a stock and that allow fishing rates to vary in response to stock size. Such a policy analysis would likely take the form of stochastic simulations to assess the probabilities of different outcomes on whitefish populations for each policy implemented (Quinn and Deriso 1999).

Our SCAA models assume that catchability remains constant. We accounted for known changes in fishing power (e.g., changes in the height of gillnets) by adjusting fishing effort. Other unknown but continuing changes in catchability have likely occurred in some management units. Variants of the existing assessment models could be developed to evaluate and perhaps replace the current assumption of constant catchability. One possibility is to allow catchability to be a function of fish abundance (Henderson et al. 1983). A second option is to allow catchability to vary over time in a less structured way, perhaps by allowing it to follow a random walk or other time-series model. Ultimately, fishery-independent surveys are needed to fully address this assumption, but consideration of alternative models provides an approach that could provide benefits in the near term.

In contrast to catchability, age-specific selectivity in our models is allowed to vary over time. This is done by allowing one parameter of the double-logistic selectivity function to vary as a quadratic function with time. Although this approach appears to capture much of the complexity involved in how changing growth and other factors influence selectivity, other modeling approaches are possible. These include allowing selectivity parameters to vary following time-series models, or, alternatively, combining a time-varying growth model with a model that makes selectivity an explicit function of fish size instead of age. Although these approaches have not been evaluated here, they have been successful elsewhere.

The trend in statistical catch-at-age modeling for the past twenty years has been toward greater flexibility with models tailored for a specific application. Such models are of particular value for a species such as whitefish for which biological attributes and fisheries vary greatly from place to place. We expect that the assessments in the 1836-ceded waters will lead to improved recommendations regarding fishery-yield limits and to a better understanding of the population dynamics of this species in the Great Lakes.

The equations, methods, and analyses presented in this paper do not reflect the cooperative relationship developed among biologists from many agencies that produced the SCAA models. The cooperation among biologists involved in numerous ad hoc working groups and in the MSC and their willingness to exchange information freely have made possible the development of SCAA models for the 1836-ceded waters. The real success here is that biologists working for agencies with divergent views on fishery management and commercial fishing have been able to put aside their differences and keep a biological perspective in an at-times contentious atmosphere over treaty rights.

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