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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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