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Assessing the health of lake whitefish populations in the Laurentian Great Lakes: Lessons learned and research recommendations

Travis O. Brenden [a,*], Mark P. Ebener [b], Trent M. Sutton [c], Michael L. Jones [a], Michael T. Arts [d], Timothy B. Johnson [e], Marten A. Koops [f], Gregory M. Wright [g], Mohamed Faisal [h]

[a] Quantitative Fisheries Center, Department of Fisheries and Wildlife, Michigan State University, East Lansing, MI 48824, USA
[b] Inter-Tribal Fisheries and Assessment Program, Chippewa Ottawa Resource Authority, Sault Ste. Marie, MI 49783, USA
[c] School of Fisheries and Ocean Sciences, University of Alaska Fairbanks, Fairbanks, AK 99775, USA
[d] National Water Research Institute, Environment Canada, Burlington, Ontario, Canada L7R 4A6
[e] Glenora Fisheries Station, Ontario Ministry of Natural Resources, Picton, Ontario, Canada K0K 2T0
[f] Great Lakes Laboratory for Fisheries and Aquatic Sciences, Fisheries and Oceans Canada, Burlington, Ontario, Canada L7R 4A6
[g] Nunns Creek Fishery Enhancement Facility, Department of Fisheries and Wildlife, Hessel, MI 49745, USA
[h] Department of Pathobiology and Diagnostic Investigation, Department of Fisheries and Wildlife, Michigan State University, East Lansing, MI 48824, USA

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ABSTRACT

Although lake whitefish *Coregonus clupeaformis* populations in the Laurentian Great Lakes have rebounded remarkably from the low abundance levels of the 1960s and 1970s, recent declines in fish growth rates and body condition have raised concerns about the future sustainability of these populations. Because of the ecological, economic, and cultural importance of lake whitefish, a variety of research projects in the Great Lakes have recently been conducted to better understand how populations may be affected by reductions in growth and condition. Based upon our participation in projects intended to establish linkages between reductions in growth and condition and important population demographic attributes (natural mortality and recruitment potential), we offer the following recommendations for future studies meant to assess the health of Laurentian Great Lakes lake whitefish populations: (1) broaden the spatial coverage of comparative studies of demographic rates and fish health; (2) combine large-scale field studies with direct experimentation; (3) conduct multi-disciplinary evaluation of stocks; (4) conduct analyses at finer spatial and temporal scales; (5) quantify stock intermixing and examine how intermixing affects harvest policy performance on individual stocks; (6) examine the role of movement in explaining seasonal fluctuations of disease and pathogen infection and transmission; (7) evaluate sampling protocols for collecting individuals for pathological and compositional examination; (8) quantify sea lamprey-induced mortality; and (9) enact long-term monitoring programs of stock health.

Introduction

Lake whitefish *Coregonus clupeaformis* is an economically, ecologically, and culturally important species throughout the Laurentian Great Lakes. From an economic perspective, the commercial harvest of lake whitefish contributes millions of dollars annually to the gross domestic products of the United States and Canada (Ebener et al., 2008a). Ecologically, lake whitefish direct energy and nutrients from benthic to pelagic areas of the Great Lakes by feeding on a variety of benthic organisms. In terms of cultural importance, Native American tribes and First Nation communities have fished for lake whitefish for thousands of years and contemporary fishing provides a means for Native Americans and First Nation Aboriginals to maintain ties to their spiritual and traditional pasts while supporting their families (Brown et al., 1999; Ebener et al., 2008a). Many non-native fishing communities throughout the Great Lakes region also were developed around the lake whitefish fishing industry, and these communities remain strongly linked to this fishery.

Lake whitefish populations in the Great Lakes have rebounded remarkably from the low abundance levels of the 1960s and 1970s (Ebener et al., 2008a). This recovery has been attributed to sea lamprey *Petromyzon marinus* control efforts, improved environmental conditions, more restrictive and better informed harvest policies, and favorable weather conditions promoting survival of larvae (Spangler and Collins, 1980; Spangler et al., 1980; Ebener, 1997; Ebener et al., 2008a). As evidence of this recovery, lake whitefish commercial harvest in lakes Huron and Michigan has on average met or exceeded harvest goals set by fishery management agencies since the 1990s (Schneeberger et al., 2005; Ebener et al., 2008b,c). Presently, there are concerns that the recovery of Great Lakes lake whitefish stocks may be

* Corresponding author.
E-mail address: brenden@msu.edu (T.O. Brenden).

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in jeopardy because of recent declines in fish growth and condition (Hoyle et al., 1999; Hoyle, 2005; Mohr and Ebener, 2005; Schneeberger et al., 2005; Ebener et al., 2008b). Several reasons for these declines have been postulated by researchers, including density-dependent regulation due to the burgeoning abundance of lake whitefish, food web changes that have at least partly resulted from invasion and expansion of dreissenid mussels (*Dreissena polymorpha* and *D. bugensis*), and environmental change stemming from global warming (Nalepa et al., 2005; Kratzer et al., 2007; Wright and Ebener, 2007; Debruyne et al., 2008; Rennie et al., 2009). Irrespective of its exact cause, the declines in lake whitefish growth rates and condition in the Great Lakes is troubling as such declines have preceded the collapse of other high-value fisheries (Lambert and Dutil, 1997).

Concerns over the possible effects of reduced growth and condition on future sustainability of Great Lakes lake whitefish stocks were the impetus for the natural mortality and recruitment research projects from which many of the articles in this special issue were derived. These two research projects ran concurrently and were both funded by the Great Lakes Fishery Trust, which had identified lake whitefish as a priority species for research in Lake Michigan (GLFT, 2000). The purpose of the natural mortality study [Project Title: Magnitude and Potential Causes of Mortality in Four Lake Whitefish Populations in Lakes Michigan and Huron: A Multidisciplinary Approach; Principal Investigator: Michael Jones (Michigan State University)] was to relate measured differences in natural mortality rates among four lake whitefish stocks in northern lakes Huron and Michigan to various measures of fish health (e.g., fatty acid composition, percent water content, prevalence of infectious diseases). The purpose of the recruitment study [Project Title: Does Adult Body Condition Affect Recruitment Potential in Lake Whitefish?; Principal Investigator: Trent Sutton (University of Alaska - Fairbanks)] was to explore the consequences of reduced growth and body condition on factors that could govern recruitment success, such as fecundity, gamete quality, and early life-history dynamics. Although both projects yielded valuable information on lake whitefish stocks in the Great Lakes, particularly in lakes Huron and Michigan, both also encountered difficulties relating measures of individual and population health to stock demographic rates. These difficulties stemmed from several factors, most notably the limited degree of contrast in measurements among stocks (Blukacz et al., 2010; Claramunt et al., 2010; Ebener et al., 2010-a; Faisal et al., 2010-a,-b; Wagner et al., 2010). Our goal for this concluding paper of the special issue is to take what was learned during the natural mortality and recruitment studies to provide recommendations for future studies attempting to improve understanding of linkages between ecological factors affecting individual lake whitefish health and important population demographic attributes.

Recommendations

Broaden the spatial coverage for comparative studies of demographic rates and fish health

Both the natural mortality and recruitment studies involved spatial comparisons of important demographic rates as a means to evaluate how changes in health, growth, and condition might affect long-term sustainability of lake whitefish stocks. For the natural mortality study, comparisons were made among four stocks in northern lakes Huron and Michigan. For the recruitment study, comparisons were made primarily among six to ten stocks distributed throughout Lake Michigan, with additional, but less extensive, comparisons with stocks in lakes Erie and Superior. Despite the relatively large areas over which stocks were evaluated, both the natural mortality and recruitment projects found relatively little contrast in measured variables (Blukacz et al., 2010; Claramunt et al., 2010; Ebener et al., 2010-a; Faisal et al., 2010-a,-b; Wagner et al., 2010). We suggest that there were two major reasons for this lack of contrast. First, although the stocks were strongly segregated during the spawning season, there was substantial intermixing of lakes Huron and Michigan stocks during the remainder of the year (Ebener et al., 2010-b). As a result, fish from the different spawning stocks were likely experiencing similar ecological and environmental conditions during large portions of the year. We expect this to have resulted in similar physical and biological conditions of fish, even when they returned to their respective spawning areas. Second, the Laurentian Great Lakes lie at the southern end of the native range of lake whitefish (Scott and Crossman, 1973) and, as a result, contrasts in environmental conditions among Great Lakes populations may be relatively small relative to the range of conditions experienced by lake whitefish over their entire geographic range.

To better identify relationships between demographic rates and measures of stock health, growth, and condition, we recommend that future studies consider broadening the spatial coverage over which stocks are evaluated. Although expanding the spatial overage to include more stocks in lakes Erie, Ontario, and Superior would undoubtedly be helpful, comparisons should not be limited solely to the Great Lakes. Rather, the expanded coverage should include areas that span the native range of the species and that have not been as severely impacted by anthropogenic disturbances. Useful candidates for such comparisons include Great Slave and Great Bear lakes in the Northwest Territories of Canada. The small, relatively undisturbed lakes studied by Mills et al. (2005), where lake whitefish stocks appear to experience much lower natural mortality rates compared to lakes Huron and Michigan stocks, also may provide useful contrasts.

A common problem when conducting spatial comparisons of fish stocks is that it is often necessary to rely on information collected from several different political jurisdictions or institutions that employ different sampling procedures (e.g., gear types, temporal collection strategies, random versus fixed sampling locations, etc). Such differences can confound comparative assessment of demographic rates or stock health. So long as comparative studies rely on opportunistic sampling from multiple agencies, where sampling protocols reflect local needs as well as broader objectives, this challenge will persist. Nevertheless, the design of future comparative studies should carefully assess the limitations created by differences in sampling protocols, and, where possible, take steps to mitigate these negative effects (e.g., with a partially common sampling strategy). The high value of spatial comparisons among fish populations for creating useful recommendations for guiding future management decisions should argue in favor of comparable sampling strategies among jurisdictions.

Combine large-scale field studies with direct experimentation

Although the natural mortality and recruitment studies were beneficial in that they provided stock-level estimates of important demographic rates, such large-scale field studies may not be optimal for evaluating how changes in health, condition, and growth directly impact stock demographic rates. For one, establishing causal linkages from field studies will be difficult because of the many, potentially confounding factors that influence demographic rates and fish health in natural systems. Elucidation of causal linkages between demographic rates and measures of fish health, condition, and growth would be facilitated by controlled laboratory experiments, where fish health, growth, and condition can be manipulated under controlled settings and demographic responses are measured (Ebener and Arts, 2007). For example, laboratory experiments conducted using age-0 cisco *Coregonus artedi* allowed for the determination of the effects of body size and condition, lipid stores, and feeding history on winter survival and tolerance of rapid temperature changes (Pangle et al., 2004, 2005; Pangle and Sutton, 2005).

We recommend that future studies explicitly incorporate controlled laboratory, mesocosm, and/or whole-lake [in small lakes such as those studied by Mills et al. (2005)] experiments to complement comparative large-scale field studies. The comparative studies are valuable for elucidating hypotheses that can be examined more carefully in a controlled setting. One clear benefit of conducting controlled experimentation is that it would permit the identification of thresholds for health measures (e.g., lipid content, fatty acid concentrations, and prevalence and intensity of pathogens) that can affect factors such as fish survival, visual acuity, swimming speed, or egg/larvae viability. In other words, controlled experimentation would allow determination of levels of infection or nutrient deficiency that would need to be reached before survival, reproductive capacity, or some other aspect of fitness was affected. Establishing such thresholds from field studies can be difficult as affected individuals may not be collected during sampling events. For example, studies, such as the natural mortality study reported herein, rely on capture of surviving animals, and not the ones that succumbed as a result of poor health, to draw indirect inferences about mortality rates and deleterious tissue changes.

Conduct multi-disciplinary evaluation of stocks

Both the natural mortality and recruitment projects were multi-disciplinary studies that involved researchers with a wealth of experience in fishery population dynamics, fish diseases and pathology, and lipid dynamics. This collaboration among researchers permitted the collection of a wide variety of data on lake whitefish stocks, including aspects of life history, movement, diets, nutritional status, and disease and pathogen infection. Extensive cooperation among researchers often allowed these data to be collected from the same specimen, which strengthens our ability to examine relationships between variables. We encourage future research on Great Lakes lake whitefish to adopt a similar multi-disciplinary approach to stock evaluation. Although there can be difficulties with this type of collaboration, such as the need to develop and maintain large and complex relational databases, such multi-disciplinary studies are likely to yield the strongest evidence for linkages between lake whitefish health measures and population demographic attributes.

Conduct analyses at finer spatial and temporal scales

Future investigations into the consequences of declining growth and condition of lake whitefish would likely benefit from attempting to incorporate finer-scale measurements of demographic rates. As part of the natural mortality study, substantial seasonal differences in *Cystidicola farionis* and *Renibacterium salmoninarum* infection were observed in several of the stocks, with stocks often fluctuating between 1ow and high levels of infection intensity and prevalence from one season to the next (Faisal et al., 2010-a,-b). An obvious hypothesis for why these seasonal fluctuations occurred is that heavily infected individuals died as a result of the infection. However, seasonal estimation of natural mortality rates was not possible because of the tag-recovery protocol that was implemented as part of the natural mortality study. As a result, it was not possible to determine whether higher mortality rates were associated with seasonally elevated infection rates. Seasonal estimates of natural mortality can be obtained through alternative tag-recovery protocols (Hightower et al., 2001; Thompson et al., 2007), and we encourage future research to consider protocols that will permit seasonal or annual estimation of natural mortality rates.

We anticipate that research conducted at finer spatial scales would also prove beneficial for investigations into lake whitefish recruitment potential. As part of the recruitment study, only small differences in measures of recruitment potential were detected among the Lake Michigan stocks. Within an individual sampling site, however, there was substantial variability in relative abundance of captured recruits as well as fish size, growth rate, water temperature, and zooplankton composition and abundance. This suggests that at particular spawning locations there may be smaller-scale differences in habitat affecting recruitment success, and examination of how recruitment success varies based on factors such as depth at spawning or available larval habitat may help improve understanding of recruitment processes in lake whitefish.

Quantify stock intermixing and examine how intermixing affects harvest policy performance on individual stocks

Currently, lake whitefish stocks in the Great Lakes are managed on a unit-by-unit basis, with the stock assessments and harvest rules explicitly treating each unit as consisting of a single, distinct stock. If stocks with differing levels of vulnerability to overharvest actually mix during periods of commercial fishing, as our findings suggest, the weaker stocks could be vulnerable to overharvest in these mixed-stock fisheries. For admixed fisheries, knowing the relative productivity or recruitment of individual spawning stocks is critical for ensuring long-term sustainability of the mixed fisheries. Knowing the recruitment levels of individual stocks and how they vary in time helps to establish regulations that protect less productive stocks from overharvest and possible extinction while maximizing harvests of numerically abundant stocks. It is a common occurrence in mixed-stock fisheries for less productive stocks to be severely overexploited if harvest rates do not account for differences in stock productivity (Hilborn and Walters, 1992). Preservation of less productive stocks, even at the expense of some yield from more productive stocks, may be critical to conserving genetic diversity of the species within a region, and thus the species' ability to adapt to future environmental change. Alternative harvest policies could be comparing using simulation methods (e.g., Cooke, 1999, Butterworth, 2007) that explicitly allow consideration of trade-offs between yield and conservation objectives (Deroba and Bence, 2008).

Although the degree of stock intermixing of lake whitefish in lakes Michigan and Huron has been demonstrated through both tagging (Ebener and Copes, 1985; Ebener et al., 2010-b) and genetic studies (Van de Hey et al., 2009), the degree to which stocks mix in some of the other Great Lakes is currently unknown. Most notably, there is a very poor understanding of the distribution and habitat utilization of lake whitefish during non-spawning periods in both lakes Erie and Ontario. Because the degree of stock intermixing can be critically important to management, particularly in systems where the admixed stocks are exploited by fishing, we recommend that research be conducted in those systems where the degree of stock intermixing is presently unknown.

Examine the role of movement in explaining seasonal fluctuations of disease and pathogen infection and transmission

As mentioned previously, substantial seasonal differences in *C. farionis* and *R. salmoninarum* infection were observed in several of the lake whitefish stocks studied for the natural mortality project (Faisal et al., 2010-a,-b). It is possible that sharp declines in infection prevalence resulted from high mortality rates for infected fish, but evidence to support this conclusion, such as large die-offs of fish, is not readily apparent. Another factor that could contribute to the seasonal fluctuations in infection prevalence observed at our sampling locations is movement of lake whitefish aggregations with contrasting infection levels into and out of these sampling areas. Increased knowledge of smaller-scale seasonal movement patterns of lake whitefish, and the local heterogeneity of health measures, would greatly assist in interpretation of the seasonal patterns we observed in both infection prevalence and fatty acid composition (Wagner et al., 2010).

The intermixing of stocks outside of the spawning period also raises the possibility that a few lake whitefish spawning areas could be serving as disease sources and the dispersal of fish from these spawning areas to other parts of the lake could be spreading disease. Research into whether there are habitat-specific sources for viruses and bacteria such as *R. salmoninarum* (Faisal et al., 2010-b) and *Aeromonas* spp. (Loch and Faisal, 2010-a,-b), or local populations of infected intermediate hosts for parasites such as *C. farionis* (Faisal et al., 2010-a), would greatly enhance our understanding of the epidemiology of these diseases.

Evaluate sampling protocols for collecting individuals for pathological and compositional examination

Given the schooling behavior of lake whitefish (Scott and Crossman, 1973), an evaluation of an appropriate sampling protocol for collecting individuals for pathological or compositional examination is warranted to ensure that fish health measures are representative of the stock being studied. It is often the case that when collecting individuals for pathological and compositional examination, a sample size of between 30 and 60 individuals is established as a target and sampling continues until this target has been met. In cases of schooling individuals, this target can be reached in a single net lift or haul. However, given the aggregate behavior of the school, it seems reasonable to expect that individuals from the school will have experienced similar conditions and possibly exposed one another to infectious pathogens or diseases. Thus, the independence of observations from the school is questionable, as is the representativeness of the sample to the spawning stock.

We recommend that future investigations into the status of lake whitefish stocks consider adopting a sampling protocol that accounts for the life-history characteristics of the species. One possible sampling protocol that may be appropriate for assessing the health of lake whitefish stocks would be a two-stage cluster sampling design in which lake whitefish spawning areas or stocks are subdivided into smaller regions or groups of fish and a sample of these regions or fish groups are selected as primary units for measurements. From these primary units, subsamples of fish are selected for actual measurement. The advantages of such a sampling design are that it can provide more accurate measures of stock health compared to that of opportunistic sampling while reducing costs associated with sampling and pathological and composition examination (Thompson, 1992).

Quantify sea lamprey-induced mortality

Sea lampreys continue to be a significant source of mortality for lake whitefish in the Great Lakes, particularly in Lake Huron where sea lamprey abundance is greater than in the other lakes (Mullett et al., 2003). Estimates of lake whitefish natural mortality rates were greater for northern Lake Huron stocks compared to northern Lake Michigan stocks, and it appeared that sea lamprey mortality accounted for at least some of these differences (Ebener et al., 2010-a). Sea lamprey-induced mortality rates are estimated annually for lake whitefish stocks in northern Lake Huron for the purpose of estimating stock-specific commercial fishery harvest limits. Sea lamprey-induced mortality rates are treated as known quantities in the assessment models and are calculated based on annual estimates of age-specific sea lamprey marking rates and an estimate of the probability (P) that a lake whitefish survives an attack (Bence et al., 2003; Ebener et al., 2005). The probability of surviving a sea lamprey attack is critical for determining sea lamprey-induced mortality. Unfortunately, the only estimate of P comes from a study conducted in northern Lake Huron at a time when sea lamprey were extremely abundant (Spangler, 1970). No laboratory or other independent evaluation of P has been conducted for lake whitefish. Ebener et al. (2010-a) concluded that latent mortality of lake whitefish from sea lamprey attacks was minimal, and that mark type was not a good indicator of the severity of an attack, which suggests that the current estimate of P may not be appropriate. We recommend that a combined large-scale field study/direct experimentation project be conducted to determine the probability of a lake whitefish surviving a sea lamprey attach. Swink (2003) and Patrick et al. (2009) provide useful guides for how laboratory experiments might be conducted on lake whitefish. A field study similar to what was conducted by Spangler (1970), but carried out across a much greater range of sea lamprey densities, would be beneficial for providing empirical estimates of P that either validated or refuted laboratory estimates.

Enact long-term monitoring programs of stock health

Although substantial efforts were extended for both the natural mortality and recruitment studies, these projects provided mere glimpses into the current status of lake whitefish stocks in the Great Lakes. Changes affecting Great Lakes food webs are ongoing and are likely to accelerate in the immediate future given impending threats such as global climate change and additional invasion of non-indigenous species. Understanding how lake whitefish stocks are responding to these changes will require long-term monitoring of stock health as well as the status and health of the species' principle food items. In conducting such monitoring programs, it is important to consider that different ages of lake whitefish may be more vulnerable to declines in health, growth, and condition. As a result, monitoring programs that are stratified by age and collect specimens across a wide range of ages will likely be of greatest use to researchers. It would also likely be of benefit to include as part of these monitoring programs a tagging aspect as this can yield a wealth of information on mortality, exploitation rates, and intermixing of lake whitefish stocks.

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