DEVELOPING RESEARCH PRIORITIES FOR LAKE WHITEFISH IN THE UPPER GREAT LAKES:

RESULTS OF A WORKSHOP SPONSORED BY THE GREAT LAKES FISHERY TRUST AND GREAT LAKES FISHERY COMMISSION

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Executive Summary

Lake whitefish stocks have declined dramatically in northern Lakes Huron and Michigan, resulting in commercial catch rates and yield that are some of the lowest in the past three decades. The exact cause(s) for these declines are uncertain, but prolonged poor recruitment seems to be a primary driver of the observed decreases in stock size. Fishery management agencies are struggling to understand why recruitment has been so poor, while also recognizing that management actions are needed. In the short term, a synthesis of existing data that explores possible mechanisms explaining observed trends in lake whitefish recruitment and where the recruitment bottleneck may be occurring is needed because some management decisions are expected to be made before new research is completed. These data are largely comprised of state, provincial, tribal, and federal agency fishery-dependent and fishery-independent assessments that provide information about lake whitefish stock dynamics and are currently used to inform catch-at-age models. The single largest question managers have right now focuses on identifying those conditions that were historically favorable for lake whitefish recruitment in the mid-1990s and understanding what role invasive species and disease, most notably dreissenid mussels, round goby, and VHS, coupled with ongoing nutrient reductions, have played in declining recruitment and year-class strength since the mid-2000s.

Workshop participants identified a series of potential management risks, management options, and information gaps that could be considered for future research to inform management, with a discussion culminating in the development of a list of short- and long-term research needs.

Workshop Proceedings

Introduction

Lake whitefish stocks in northern lakes Huron and Michigan have sustained important commercial and subsistence fisheries during the past 30 years. However, lake whitefish stocks, and, along with them lake whitefish catch and catch rates, have declined substantially since 2013. At the same time, lake whitefish recruitment and harvest from Lake Superior has been relatively stable. Increasing concern from fishers and policy makers has led managers to recognize that action options must be collectively considered. With this background in mind, fishery managers approached the Great Lakes Fishery Trust (GLFT) and the Great Lakes Fishery Commission (Commission) in fall 2017 to develop a workshop that would focus on a common set of research priorities that could then be addressed through funding by the Great Lakes Fishery Trust, and other fishery research funding sources. The research priorities developed from this workshop, and the resulting research results, will assist fishery managers to determine whether or how any management actions can assist future recovery of lake whitefish stocks.

Workshop Goals and Desired Outcomes

In February 2018, the Great Lakes Fishery Trust and the Great Lakes Fishery Commission hosted a workshop to understand recent trends in lake whitefish populations across the three upper lakes; engage fishery managers in discussion about important management risks they face; identify their needs to address those risks; determine information gaps; and develop possible priorities for research and management action.

Participants representing state, provincial, federal, and tribal managers, biologists, and researchers, along with experts from academia, were invited to participate (Appendix 1). Workshop discussions were primarily focused on needs of fishery managers, specifically lake committee and Technical Fisheries Committee members. Expertise from other participants served as a valuable resource throughout the workshop.

Presentations

The workshop ran for 1.5 days and began with a description of the problem. Three presentations followed that gave an overview of stock status and recruitment trends on lakes Huron, Michigan, and Superior, with short discussions after each presentation. The session culminated in an examination of the similarities and differences of the three upper lakes. Additional presentations provided background on changes to lower trophic levels since 2000 and their current status; a summary of recruitment and possible management implications; and a recap of ongoing research. Day one ended with facilitated discussions identifying management risks and needs; during day two participants identified information gaps, then described and prioritized short- and long-term research needs. Presenters have permitted the sharing of their respective slide decks, which are linked to each presentation title.

Impacts of Whitefish Decline on the Tribal Commercial Fishery *– Tom Gorenflo (CORA)*

Gorenflo described the urgent need to address declines in lake whitefish recruitment, recognizing that those declines impact present management and will likely impact renegotiation of the terms of the Consent Decree in 2020. Lake whitefish is the mainstay of the tribal fishery and is important to the tribes both economically and culturally. The impetus for the workshop was to focus research so as to answer several questions including:

1) What are the causes of lake whitefish recruitment declines?,

2) What is the prognosis for 'recovery' of lake whitefish?,

3) What are feasible management options to pursue?, and

4) What are priority research, funding, and synthesis items that need to be pursued in the short- and long-term to inform management options?

In 1979 a judge affirmed the right of the tribe to fish and self-regulate in the ceded waters of lakes Superior, Michigan, and Huron. In 1981 the tribes formed an inter-tribal voting body (currently known as CORA) to regulate and manage those waters. Court cases did not resolve allocation and management processes between the State of Michigan and the tribes, so in 1985 the parties negotiated a Consent Decree. A revised Consent Decree was signed in 2000, which expires in 2020.

Since 1981, lake whitefish has comprised 73% of the landings by CORA licensed commercial fishers (range – 59% - 79%), and 83% of lake whitefish harvested by CORA tribes comes from lakes Michigan and Huron. Whereas Lake Superior harvest has stayed consistent during the time series, harvest in lakes Michigan and Huron has been declining since 2012, with 2017 harvest 3 million pounds lower than the average from 1988-2012.

Presently, CORA has about 60 commercial licenses, down from a historic high of more than 200. Quotas in most management zones have been consistently reduced in recent years. Recommended annual harvest limits for the various shared and tribal-only lake whitefish management units (MUs) in 1836 Treaty waters of lakes Michigan, Huron, and Superior are generated from Statistical Catch At Age (SCAA) models by adjusting fishing mortality rates (effort, harvest etc.) to achieve MU-specific targeted total adult mortality rates. These recommendations are provided to the Technical Fisheries Committee (TFC) (shared MUs only) and tribes (non-shared MUs only). Based upon this guidance, for shared MUs, the TFC submits recommended harvest limits to the parties for approval, whereas the tribes set annual Harvest Regulation Guidelines (HRG) within MUs not shared with the state. Most recently, harvest limits (or HRGs) have been established at or below the recommended harvest limits for each of the MUs due to poor fishery performance. Additionally, tribal commercial fishers are also starting to shift effort to deeper water and new ports, which may mask the extent of declines in lake whitefish CPUE.

Policy makers are looking to biologists for answers as biologists are trying to adapt and manage the lake whitefish fishery in a rapidly changing ecosystem. A collaborative effort is needed to determine why lake whitefish numbers continue to decline and to inform possible management options.

Lake Huron Lake Whitefish Status and Trends *– Steven Lenart (USFWS), Adam Cottrill (OMNRF), and Ji He (MDNR)*

Recruitment, growth, biomass, and catch of lake whitefish has declined throughout large areas of Lake Huron. Recent CPUE values are among the lowest in the last 30 years in five of the eight Management Units, and a long-term decline in fish condition is evident in most areas. Exceptions to this trend include the North Channel and southern main basin, which show more stable recruitment.

Harvest

Commercial yield of lake whitefish peaked in the late 1990s, with 2016's yield being the lowest in the past 35 years. The majority of harvest occurs in Ontario waters of the main basin. Decreases in commercial yield have been observed in all jurisdictions, with the largest declines in the CORA fishery. Catch per unit effort has declined in CORA waters since the mid-1990s with similar patterns in all areas of the northern main basin, and Ontario's central and southern main basin fisheries.

Modeling

Model estimates of spawning stock biomass peak at different times by region. Spawning stock biomass of northern stocks is at or near historic lows but central and southern main basin and Georgian Bay stock declines aren't as precipitous. All models are developed using data, especially commercial fishery harvest and effort, from fishery-dependent assessment surveys, which are not standardized across jurisdictions. In 1836 Treaty-ceded waters for all three lakes detailed in this document, harvest limits or harvest regulation guidelines are based in part on recommendations resulting from these models.

Lake whitefish recruitment is estimated for each Management Unit from model-based absolute abundance estimates of age-5 fish. Recruitment estimates are near record lows for northern stocks, whereas Georgian Bay, and central and southern main basin stocks have shown stability.

Sampling

Fishery-independent pre-recruit surveys administered by various agencies show generally stable recruitment in the southern main basin, highly variable recruitment in Thunder Bay, and little recruitment observed after the early 2000s in southern Georgian Bay or Ontario waters of the central main basin. Surveys indicated that 2003 was a good recruitment year across Lake Huron.

Mortality estimates have declined with reduced yield, except in Ontario's North Channel waters where natural mortality is increasing.

Fish condition at age-5 declined and then leveled off with the exception of the North Channel, which is stable.

Mean age in fisheries has increased in the northern and north central main basin but young fish are still in the fishery in the southern main basin and North Channel. Fish now typically recruit to the fishery at ages 6-7, a change from the 2000s when they recruited at ages 4-5, a result of reduced growth rates.

Additional Lake Huron observations:

Zebra mussel colonization was followed by a fishery decline and a change in growth and condition, but lake whitefish seemed to be recovering until quagga mussels invaded. Georgian Bay is an anomaly because recruitment is declining but dreissenids are not present.

High mortality rates are being observed in places without high commercial effort and yield, even though spawning activity is quite evident in to the system. The number of recruits produced per spawner increased in the late 1990s and decreased in 2002-2003. Right now, fewer recruits per spawner are being produced than at any other time for which biologists can calculate these metrics.

Movement also is a confounding factor, with fish migrating from north to south in the main basin. Additionally, certain locations or stocks (Alpena, Fishing Islands) may be providing most of the recruits to the lake. Lastly, interactions with lake trout, whether through predation or displacement, have not been rigorously examined. Additional insights could come from Lake Superior where lake trout and lake whitefish co-exist.

Lake Michigan Lake Whitefish Status and Trends *– Dave Caroffino*

Recent harvest is the lowest in modern history, and recruitment declines have contributed to reduced spawning stock biomass. Regional patterns are evident in lake whitefish population dynamics, with Green Bay behaving much differently than the rest of the lake and dramatic differences in peak abundance between the northern and southern parts of the lake. Currently, SCAA models are used in conjunction with pre-established harvest control rules to guide development of harvest limits and harvest regulation guidelines for Lake Michigan Management Units. The SCAA models, however, are informed by non-standardized data collection efforts and tend to be noisy.

Harvest

Lake whitefish yield peaked in 1992 at 8.2 million pounds, with current yield less than 3 million pounds (similar to the 1970s). Harvest is typically greatest from Green Bay, with southern Lake Michigan making up a very small portion of the total harvest. Although harvest has declined substantially during the last 5 years, an earlier decline around 2000 primarily reflected changes in management strategies when commercial licenses shifted from state to tribal fishers. A recreational ice fishery has been increasing rapidly in Green Bay, with roughly 140,000 fish harvested annually since 2013. A shore fishery in Indiana and Illinois is gaining in popularity, and Indiana recently implemented a daily bag limit.

Modeling

Spawning stock biomass as estimated in Lake Michigan treaty waters (northern and central/southern), showed similar trends with abundance and biomass peaks in the late 2000s followed by declines since. Lake whitefish in northern Lake Michigan are typically five times more abundant than those in southern Lake Michigan.

Sampling

Fishery-independent surveys of age-0 Lake Michigan lake whitefish are conducted in early fall with bottom trawls and beach seines that sample water up to 30' deep in various regions. The lakewide USGS bottom trawl assessment survey showed regular recruitment from 1980s – 2010, but little recruitment since then. In Green Bay, age-0 recruitment has increased recently. A beach seine survey targeting age-0 lake whitefish has been conducted since 2013 by various agencies, however, the data is not currently incorporated into assessment models due to uncertainty about whether the survey effectively indexes recruitment.

Weight-at-age for age-6 lake whitefish has declined in all regions over time, and recent growth is low but stable. The average age at harvest is increasing across Management Units, ranging from 10-14 years. Mortality appears relatively low with fish in the population surviving to age-20. In the early 1980s, 80% of the stock was age-6 or less; currently 10% of the stock is age-10 or less.

Additional Lake Michigan observations:

Recruitment and harvest peaks observed in the 1990s may be the anomaly in the time series, with abundance seen in the 1980s and currently more indicative of system productivity.

Green Bay is becoming much less eutrophic, and lake whitefish are doing well there.

Spatial distribution of sampling is limited, and adult movement can affect the SCAA model results if not properly incorporated.

The zebra mussel infestation may have had a positive impact on structural habitat in the short-term, but quagga mussel impacts have been negative with respect to lake whitefish.

An important discussion thread explored the concern that managers do not understand where the recruitment bottleneck for lake whitefish occurs, and that there are no fishery independent pre-recruit surveys. Using existing pre-recruit surveys to develop an index of R, and better understanding how juveniles are distributed could help guide potential pre-recruit assessment survey development. Historic Green Bay data (1990s) suggested minimal correlation between age-2 relative abundance and age-3 commercial catch rates the year following, but things have changed significantly since then and this may be worth looking at more closely. The lack of information at early ages hampers managers' understanding of recruitment. A combination of looking at existing data and research could help develop a better understanding recruitment processes through time.

Lake Superior Lake Whitefish Status and Trends *– Mike Seider (USFWS)*

Since 2000, Lake Superior lake whitefish stocks have been stable. Spawning stock biomass has either increased or is stable, and mortality appears relatively low. Recruitment is stable, but density-dependent compensation is likely occurring in the Apostle Islands. No change has been observed in weight-at-age or mean age in commercial harvest.

Harvest

Lakewide commercial yield has been variable but stable at about 3 million pounds dressed taken from the lake annually since the late 1990s.

Modeling

In Lake Superior, SCAA models demonstrated consistent spawning stock biomass, recruitment, mean weight at age-8, and mean age in the fishery throughout US treaty-ceded waters from Whitefish Bay to west of the Keweenaw Peninsula. Model based estimates of recruitment (age-4 abundance) indicate stable recruitment, outside of a peak in the early-2000s west of the Keweenaw Peninsula. Mean weight at age in the fisheries has remained constant, while mean age in the harvest has slightly increased west of the Keweenaw Peninsula and remained stable east of the Keweenaw Peninsula.

Sampling

A fishery-independent pre-recruit lakewide bottom trawl assessment of age-1 lake whitefish has been conducted during the spring by USGS since 1978. Lake whitefish recruitment has been consistent throughout the time series, with several strong year classes produced between 1981 and 2007. No strong year classes have been produced since then, but recruitment has been measurable throughout the recent time series. Catch rates of age-1 lake whitefish in the Apostle Islands region far exceed those in other regions. In addition to the bottom trawl assessment, academic institutions have begun pilot beach seining assessments for age-0 lake whitefish.

Additional Lake Superior Observations:

When considering lake whitefish status in all three upper Great Lakes, Lake Superior can be considered a reference system for lakes Huron and Michigan. It is a stable system where dreissenids and round gobies have not invaded and recruitment occurs regularly throughout the lake. Lake Superior also has large numbers of lake trout, lake whitefish, and cisco that co-exist. All three species are relatively abundant in the Apostle Islands, an area that could provide insights into interactions between lake whitefish and other species. Gamble et al. (2011) did find high predation of cisco eggs by lake whitefish. Given that some locations across the upper Great Lakes likely serve as recruitment sources, establishing long-term assessments that characterize trend of lake whitefish, other fish species, and lower trophic level dynamics at these sites could provide valuable comparative insight into lake whitefish recruitment dynamics.

Lower Trophic Levels *– Steve Pothoven (NOAA)*

Phosphorus has been declining in lakes Michigan and Huron since the 1980s. In Lake Michigan, zebra mussels arrived in the mid-90s, became relatively abundant in nearshore areas through 2000, began declining in 2005, and are very rare now. Quagga mussels arrived in 2000 and rapidly colonized the entire lake. Mussel biomass has stabilized since 2010. A similar but less dramatic expansion occurred in Lake Huron, where deep water has high numbers of mussels but low biomass. Lake Huron quagga mussels may have stabilized but haven’t yet reached an equilibrium.

Spring Chlorophyll *a* blooms have declined since the early 2000s, with the spring diatom bloom now 25-30% of what is was in the 1990s. Pelagic primary production in Lake Michigan is now 1/3 of the production that occurred during the 1980s. Across the upper three Great Lakes, chlorophyll a and primary productivity have converged to similar low levels. Currently, the Lake Superior nearshore is more productive than Lake Huron or Lake Michigan.

In spite of declining lakewide phosphorus loading, harmful algal blooms and benthic algae production has increased in the nearshore, likely a function of dreissenids trapping P in nearshore areas. Models indicate that adding phosphorus in nearshore areas could bring back the spring bloom but this would exacerbate the HABs/cladophora issue.

Diporeia densities rapidly declined in lakes Michigan and Huron since 2000, and no sign of recovery is apparent. Half of the historic benthic biomass is gone in Lake Michigan, and *Diporeia* declines are associated with declines in growth or condition for a number of fish species. *Mysis* numbers are stable and similar to numbers observed in the 1980s, but as predator (bloater) abundance has decreased, *Mysis* numbers have not increased and their lipid content has declined. The data series on chironomids is relatively short, with no easily discernable trends.

Age-0 lake whitefish diets show a strong size-dependent shift from cyclopoids as they begin feeding on prey to cladocerans until they reach about 40 mm. After that, they switch to benthic prey, and in the absence of high energy food, age-0 lake whitefish are eating small mussels that have 20x less energy than mussels eaten by larger lake whitefish. In northern Lake Michigan in 2014, 39% of age-0 lake whitefish stomachs were empty, with 19% of stomachs empty near Muskegon.

Zooplankton population peaks in Saginaw Bay have shifted from June in the 1990s to September/October in the 2000s, an overall reduction in cyclopoids. Nearshore zooplankton data are largely lacking (an EPA vessel limitation) and noisy, but changes in composition are similar to offshore (later season peak, fewer cyclopoids but still dominated by cyclopoids). Invasive predatory zooplankton (*Cercopagis* and *Bythotrephes*) alter zooplankton distributions and could be competing with larval fish during the spring critical period.

Cladoceran growth is increasing, but abundance is declining. Predatory cladocerans may feed more efficiently in a quagga mussel dominated system. Production trends are very different than biomass estimates on an annual basis. Nearshore zooplankton data is very noisy, but is more cyclopoid dominated than offshore data.

Offshore surface water temperatures and ice cover have varied greatly over the past decade, but show a general warming trend, especially during winter.

Additional lower trophic level observations:

Lake Huron is mixed top to bottom all winter, so mussels have access to the entire water column and can feed more efficiently through the winter. If zooplankton rebuild over the summer during stratification, this might be one explanation for the shift in their peak. In July, the chlorophyll *a* layer is deep and is basically zero in the hypolimnion. Additionally, changes in zooplankton composition that favor more calanoids may impact foraging efficiency of larval lake whitefish because calanoids are more difficult to capture than cyclopoids and cladocerans.

Factors affecting recruitment to fisheries and management implications *– Mark Ebener*

Lake whitefish have experienced large temporal variation in recruitment, and because abundance was so high in the 1990s, the declines we're seeing may not be surprising. Lake whitefish recruitment is affected by multiple factors including: habitat, stock size, early life, growth condition, the food web, and community interactions. Within the large-scale ecosystem changes occurring, lake whitefish recruitment dynamics are established at very local scales. The effect of dreissenids and *Cladophora* on lake whitefish spawning habitat is not yet understood. Additionally, ice cover is recognized as impacting recruitment, but any links to changing water levels have not been explored.

Until about 2010, spawning stock biomass was stable at high levels in northern lakes Michigan and Huron but the number of recruits per spawner began declining around 2005 in the main basin of Lake Huron. Generally, large declines in recruitment have occurred at large stock sizes. A small change in larval survival can have a big impact on numbers of recruits. Good to stable lake whitefish recruitment can be found in several locations including Lake Superior, Green Bay, Lake Huron's North Channel, western Georgian Bay, and southern main basin of Lake Huron. The contribution of Saginaw Bay has not been explored. Populations with declining recruitment are found throughout Lake Michigan and the northern half of Lake Huron's main basin. A few river spawning stocks have re-established and are successful, specifically those in the Fox, Muskegon, Grand, and Kalamazoo rivers. Nearshore spawning might be increasing since deeper water habitat is covered with dreissenids, *Cladophora*, round gobies, and rusty crayfish.

Growth and condition are determined by multiple factors, including dreissenids; density dependence; prey quantity, quality, and composition; productivity, and local conditions. In lakes Michigan and Huron, growth has declined and many age-classes of lake whitefish are now concentrated into much narrower length and weight distributions. Invasive mussels have altered the food web such that a return to historical growth rates and condition are unlikely.

The observed food web changes indicate the carrying capacity of the lakes is reduced, resulting in increased natural mortality during early life history stages. Our understanding of early life history dynamics, such as t impacts of currents on larval distribution, or larval prey selection, is lacking.

Within the broader fish community, lake whitefish face risk of predation from sea lamprey, rainbow smelt, lake trout, and possibly burbot. Sea lamprey mortality is higher on lake whitefish than it is on lake trout in CORA waters. In Lake Superior, a significant portion of the energy that lake whitefish accumulated came from consuming cisco eggs (Gamble et al. 2011), suggesting that cisco restoration could influence lake whitefish production.

Pathogens may also have an unknown effect on recruitment. The longer-term impacts of BKD and VHS aren't well understood; clinical signs of BKD can be regularly observed. VHS arrived in 2005, and since then recruitment in northern Green Bay has not produced a strong year class. Younger fish seem to be more susceptible to this disease and mortality associated with pathogens is difficult to detect, especially at early life stages.

Stocking lake whitefish could be a viable management option; stocking is regularly conducted in European systems. However, past lake whitefish stocking in the Great Lakes was likely not effective because of low stocking numbers, and a lack of understanding of where recruitment bottlenecks for lake whitefish occur

Management recommendations to consider include protecting spawning and nursery habitat, reducing natural mortality (even if the change is small, it will matter), and altering harvest policies. Right now, lake whitefish stocks aren't accumulating biomass. The existing combination of growth changes and lower recruitment mean current fishing practices likely are not sustainable, and existing fish community objectives may not continue to be relevant.

Maintenance of long-term field studies, particularly in areas important for lake whitefish production seems important. This will require agencies to evaluate trade-offs about which assessments are most important. Integrating existing recruitment indices (larval surveys, age-0 beach seine surveys, fishery-independent surveys, onboard trap net monitoring) and use of Bayesian methods for recruitment estimation should be considered. USGS bottom trawl surveys could be improved by aging lake whitefish and developing standard indices that align spatially with either the spawning stocks or mixed stock fisheries. CLC may wish to consider modifying the MOA with USGS to include assessment and reporting of lake whitefish recruitment indices and developing assessment surveys in Lakes Michigan and Huron similar to those in Lake Superior.

The GLFC Technical Report 66 (2005), and Volume 36 Supplement 1 of the Journal of Great Lakes Research are important technical resources for managers. The GLFC report synthesized knowledge at the time about the status of lake whitefish and *Diporeia* populations, and the potential effects of dreissenid mussel proliferation. The JGLR supplement synthesized information about lake whitefish natural mortality and recruitment in lakes Michigan and Huron. Additionally, an annotated bibliography on Great Lakes lake whitefish is included here (Appendix 3), and a white paper is in production and will be posted on the GLFC website once complete.

Additional observations:

The fraction 2/3 seems to come up often when describing Lake Michigan. Phosphorus loadings, zooplankton, and lake whitefish recruitment all have been reduced by about 2/3 since the 1990s.

Lake whitefish and salmon declines seem correlated but we're not treating them the same. In the past, agencies have eliminated fisheries for recovery purposes, but now there's no other commercially viable species to switch to, so economic impacts are potentially greater.

The possible suite of options to manage salmon and lake whitefish are very different because salmon stocking is a strong management lever. That same strong management lever does not exist for lake whitefish, but understanding causes for the declines are useful for future management planning and communication. Other management options, including effort reduction strategies should be on the table for consideration as an approach to try in the name of long-term sustainability.

Lake whitefish is not an imperiled species, but the fisheries it sustains are in steep decline. If the decline does not level out, some fisheries may no longer exist, even though lake whitefish stocks are not recognized as a species of concern.

Survey of Lake Whitefish Research in the Upper Great Lakes: 2007-2017 *– So-Jung Youn (MSU), William Taylor (MSU), Tammy Newcomb (MDNR)*

Ongoing assessments and research focused on lake whitefish was identified and catalogued based on completed surveys from 32 people; a summary is available in Appendix 2. Survey participants included individuals from state, federal, and tribal governments, universities, NGOs, and industry. Most studies focused on SCAA models and early life history information, and data sharing was largely acceptable for completed projects. Published studies are described in Appendix 2.

Facilitated Discussions

Workshop participants considered biological, social, and political risks of a fishery collapse and acknowledged that one of the most challenging aspects of this problem is that management action is needed now, before much of the science is complete. The group also recognized that communication strategies are needed to manage expectations of stakeholders and leadership, and to better link stakeholders with science. It's likely that current stakeholder expectations for the lake whitefish fishery exceed the reality of what the lakes can produce, given their current trophic status.

Understanding the conditions surrounding both poor and favorable lake whitefish recruitment is essential for crafting possible management options, and managers are particularly interested in understanding the conditions that can be altered by their actions. The impacts of invasive species, disease, and nutrient reduction on recruitment and year class strength are profound, but are difficult to measure in the short term, and management options to address these causative factors may be limited. As well, sea lamprey continue to be a problematic source of lake whitefish mortality. Continued funding and social license for the use of lampricides are concerns, specifically regarding current treatment restrictions placed on control agents in the Garden and Mississagi rivers, Ontario.

Existing assessments are largely fishery dependent, making it difficult to measure recruitment success. Large information gaps exist about juvenile fish distribution and other stock parameters for age-0 to age-4 fish, and nearshore areas are undersampled. Some participants felt standardized lakewide assessments were needed that would establish and consistently sample long term monitoring sites. Others felt that more rigorous, documented estimates of harvest, effort, and age estimation would suffice. Development of a standardized assessment has been challenging, and could require agencies to shift program dollars to make it happen. If such an assessment were developed, it would ideally deploy several sampling strategies at sites to sample multiple life-history stages along with lower trophic level dynamics. Efforts like existing bottom trawl assessments or CSMI surveys could also be used to better understand lake whitefish recruitment. Lake Michigan bottom trawl assessments are conducted during the fall, but could be moved to the spring to index lake whitefish and cisco. The CSMI program is moving in the direction of evaluating broad spatial patterns driven by proximity to river mouths, but distribution of sampling effort could be driven by species concerns.

Interactions between lake whitefish and lake trout is a topic of interest, managers believe they need more information about to effectively address concerns that have been expressed. In lakes Michigan and Huron, lake trout and lake whitefish could be forced to share habitat because dreissenid mussels have altered habitat quality and food availability. In Lake Superior, Buffalo Reef is showing signs of decreasing lake whitefish recruitment, but no declines in adult abundance have been observed. Are lake trout preying on or displacing lake whitefish? Predation has been detected on occasion but diets aren’t collected systematically. The two species use the same spawning areas, but lake trout spawn earlier so it would seem that there is some separation in early life stages. Later, lake whitefish use warmer embayments whereas lake trout use sandy areas near the spawning area. Lakes Michigan and Huron have similar recruitment bottleneck patterns, but major embayments might be places to investigate for contrast because fish disappear as they move from bays to open water. Also, better understanding of lake trout distribution at early life stages would be helpful. Bottom trawl data from the Apostle Islands suggests that separation of lake trout and lake whitefish occurs gradually. Interactions with rainbow smelt and cisco were also mentioned. Lake whitefish spawning grounds are associated with rainbow smelt overwinter areas, but in the North Channel, rainbow smelt numbers are high, round goby numbers are low, and lake whitefish and cisco recruitment continues to be stable.

Stocking could be a management option, but could be a waste of money without first understanding system bottlenecks. Stocking over naturally reproducing fish is risky and difficult to get away from once it begins. Existing diversity within lake whitefish and the relative contribution of individual stocks to the fishery is not well understood. Losing within-species diversity through stocking may result in a loss of resiliency for the species.

Finally, this workshop speaks to the challenges facing fishery managers globally. Economically, socially, and culturally important fisheries are routinely managed through the use of predictive models that interpret patterns in historic data to guide decision making. As invasive species and other perturbations like climate change alter ecosystems, managers are left with tools that don't well represent future conditions. Continued vigilance to prevent the introduction of new invaders is hugely important, as is the development of management tools that can account for future ecosystem shifts.

Management Options to Consider

Workshop participants drafted the following list of management options:

- No changes to existing management
- Modify USGS-CLC MOA to include an emphasis on lake whitefish assessment and reporting
- Better manage expectations with decision makers and stakeholders
- Adjust harvest
  - Integrate mixed stock info into SCAA models
  - Establish standardized recruitment indices to improve model performance
  - Establish standardized assessment of fishery harvest and effort
  - Adjust harvest strategy or effort
- Stock to supplement existing populations
- Manage lake whitefish predators, competitors, and pathogens
- Protect or improve spawning and nursery habitat
- Shift sea lamprey control focus from lake trout to lake whitefish
- Control dreissenid mussels
- Manage round gobies
- Increase productivity
- Establish refuges
- Behavioral manipulation (train fish to enhance existing diversity)
- Transfer wild fish quotas to aquaculture production (cage culture)
- Establish long-term monitoring of the food web at selected sites

Management Option Information Gaps

Workshop participants considered the call for research included in Ludsin et al. (2014), which identified the following needs:

- Improve knowledge of physical and physically driven features important to recruitment
- Identify the role of behavior in movement patterns during early life stages
- Identify the importance of direct and indirect effects of physical processes on fish recruitment
- Identify life-history adaptations to physical processes and how they vary among populations (or stocks)
- Determine the role of physical processes in explaining population richness, stock structure, and population connectivity within a species

After considering these needs, participants drafted a list of needs that corresponded to the above list of management options:

- No information gaps exist for the status quo management option. Similarly, the option for USGS to emphasize reporting on lake whitefish does not include a knowledge gap. If a modification to the USGS-CLC MOA is desired, some information gaps around survey design and specific information needs will need to be discussed.
- Managing stakeholder expectations should include a collaborative, consensus-based approach to communication where decision makers and stakeholders are involved and managers explore information and opinions. Outside experts could be relied upon to set the tone. In cases where expectations have already been set, a focus on how to affect the situation would be useful. This is a different and interesting story that needs to get out to the broader public. Some methods for disseminating information include: information briefs, social media, infographics. An opinion statement or some other type of workshop summary would be a helpful starting place, but all products need to match managers' needs. The GLFC and GLFT collaborate to consolidate information and communicate the story through fact sheets or social media. A common session at the 2019 lake committee meetings on managing sustainable commercial fisheries in the face of dreissenid impacts that features outside experts should also be considered.
- Adjustments to harvest policy and quota management might best be undertaken through a structured decision making process. Early in the initial Consent Decree process, lake whitefish indices were calculated at the scale that trawl data was collected, but that was too coarse for agency needs. Recalculating those indices now for the upcoming Consent Decree renegotiation might be useful.
- Standardized recruitment indices are needed to improve model performance. Initially, information from existing surveys in each lake and region needs to be formally compiled and synthesized. This information might provide a reasonable unified index, developed

through Bayesian or other methods. In the future, modifications to current methods may be needed.

- Similarly, knowledge of pre-recruit life history is essential. Bottom trawl surveys (age-0), small mesh gill nets (age-1), and undersized fish in the trapnet fishery (age 2-4) could be standardized to give combined pictures across existing surveys. Such an analysis would help inform what additional life stage and spatial coverage information is needed.
- A better understanding of lake whitefish movement, stock boundaries, and harvest composition is needed to improve population models. Future stock modeling should strive to integrate mixed stock information. Understanding the stock structure of harvest (genetic, chemical, stable isotopes) through time is important.
- Stocking to supplement existing populations could be an option, but would require additional analyses, including a cost/benefit analysis of a put-grow-take fishery by jurisdiction. Identification of the benefactors of such a program would be necessary. Details to be determined include an estimate of the number of fish required to be stocked, any impacts of stocking on the structure of existing stocks, some understanding of whether the lakes would support more lake whitefish, and the value of stocking river run fish are several pieces of information necessary to evaluate.
- Management actions might include managing lake whitefish predators/competitors and pathogens. We don't currently understand the extent and significance of lake trout predation on lake whitefish stocks, but a white paper might be a good start. Past information might not be truly representative in an environment that's rapidly changing, but a diet analysis using existing data would be helpful. Michigan Sea Grant disseminates diet information to the public, and may capture lake whitefish predation their report. Understanding the impact of pathogens, especially VHS, on lake whitefish survival and fitness also would be helpful.
- Are there competitive interactions between spawning lake whitefish and lake trout at spawning and nursery habitats? Lake whitefish harvest is not prohibited in lake trout refuges, but these refuges might act as de facto refuges for them. Protecting or improving spawning and nursery habitat is important, but would require knowledge of critical habitat locations and productive capacity. Agencies also need policy tools to protect those habitats from human disturbance. Managers would need specific data (side scan/LiDAR/remote sensing) to build support for this action with stakeholders. Refuge establishment might help protect vital habitats.
- Development of a control program for dreissenid mussels was identified frequently as a management option to begin pursuing, but there are unknowns about the degree that lake whitefish stocks will rebound if dreissenid mussels are controlled, and what scale of control (basinwide, regional, or local) will be necessary to elicit a response. When dreissenids infested inland lakes, fish went through a similar abundance increase and then decline. Lakes Michigan and Huron haven't hit an equilibrium yet, but understanding where we are in that continuum and what that means for management

would be useful. Removing mussels from reefs through chemical control could have direct and indirect effects. A controlled experiment is a good place to start to understand the implications of removal. Managers also need a better understanding of the dreissenid/*Diporeia* linkage; can benthic organisms be restored through active management? A white paper focused on developing a strategy for restoring *Diporeia* would be helpful.

- Can round gobies be controlled or managed? A late winter and early spring diet study would be helpful to understand their role in lake whitefish growth, and condition changes. Some work has occurred estimating consumption of round gobies by lake whitefish, which seems to depend on the size of lake whitefish and the time of year, with larger lake whitefish consuming round gobies more frequently.
- Increasing productivity might be another management option to consider. Can localized nutrient additions meaningfully improve lake whitefish production? This is a topic for lake committees and the CLC to consider. A white paper that evaluated productivity through time and space would be helpful.
- Wild fishery quotas could be transferred to cage aquaculture. This is starting already, but has similar gaps to other cage aquaculture operations. What is the capacity, what are the effects/risks of nutrient enrichment, disease, escapement, etc.?

Prioritization

Once management options and information gaps were identified, workshop participants prioritized those information gaps and identified a series of short- and long-term needs. The highest priority needs for managers, summarized by topic, include:

Management of dreissenid mussels

Much remains unknown about how dreissenid mussels impact lake whitefish populations from habitat modification at the local scale to possible effects on lakewide population recruitment and productivity. If dreissenid mussels negatively affect lake whitefish recruitment, developing a control program for them is a management option to pursue in the long-term. Research priorities related to the development of such a program include:

- What control options for invasive mussels may be possible? (**long term**)
- What are the possible impacts of dreissenid mussel treatments (small scale progressing to large scale)?
    - What control methods could be effectively applied at smaller or larger scales that could improve productivity of lake whitefish stocks? (**long term**)
        - What is the effect of dreissenid mussel removal on the benthic community, native fish, and specifically lake whitefish recruitment? (**short term**)
    - What control methods could be effectively applied at smaller scales to improve function of spawning and nursery habitat? (**short term**)

        - How quickly do dreissenid mussels recolonize and do they recolonize at different densities than they were originally present at? (**short term**)

Management of other community factors

Other community and environmental factors may affect the status of lake whitefish stocks. Specifically, species interactions like predation, competition, or displacement by lake trout, sea lamprey, and round gobies should be investigated. Potential actions include understanding the impacts of predation or competition by lake trout on lake whitefish, continuing to control sea lampreys, developing a control strategy for round gobies and VHS, protecting spawning and nursery habitat in refuges, and finding ways to increase productivity. Research questions about managing community factors include:

- How have recent food web changes affected lake whitefish stocks? Based on that, what are the predictions for the timing of stock recovery, and at what level may they recover to? (**long term)**
- How have pre-recruit compensation factors changed from high abundance (1990s) to lower abundance periods (post-2003)? (**long term)**
    - What were growth rates and densities through time in each of the lakes and stocks? (**short term** – synthesize existing information)
- What is the impact of lake trout predation on lake whitefish?
    - Begin with a diet analysis and synthesis across jurisdictions (**short term**, collaborative)
- What are the potential impacts of lake whitefish and lake trout competition for spawning habitat? (**long term**)
- Does fish behavior change when lake trout and lake whitefish overlap spatially (other than at spawning time)? If behavior changes, does that change affect lake whitefish productivity? (**long term**)

Managing harvest

Managers identified continued declines in production and potential fishery collapse as a concern. Harvest management is one option to consider, and managers would like to know:

- Are existing harvest levels inhibiting population recovery? (**short term**)
    - Are existing harvest control strategies affecting sustainability of the fisheries because lake whitefish are growing slower and recruitment is poorer than the rates determined when existing harvest policies first went into effect? (**short term**)
    - Can the economic and cultural value system of commercial fisheries be adjusted for existing stock sizes? (**short term**)

Stocking

If the lake whitefish fishery collapses, there may be a shift of effort to other species, a loss of economic and cultural markets, and an associated loss of public, political and social support for sustainable fisheries management. Supplemental stocking was suggested as a management option to consider, with the following priority research questions:

- What is the biological feasibility of stocking? (**short term**).
- Is there a reasonable economic justification for stocking lake whitefish (agency costs to stock as compared to economic return to fishers)? (**short term**).

Next Steps

A draft list of research priorities, along with the Ludsin et al. (2014) table of suggested research, was distributed to workshop participants in April 2018, and the Great Lakes Fishery Trust incorporated those priorities into its 2018 Ecosystem Health and Sustainable Fish Populations granting cycle. A lake whitefish bibliography is included (Appendix 3) and a white paper will be posted on the GLFC website once complete.

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Compilation of Research Activities Related to Lake Whitefish (Coregonus clupeaformis) Research in the Upper Great Lakes Between the Years 2007 - 2018

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Introduction

Lake whitefish (*Coregonus clupeaformis*) has historically supported an economically and culturally valuable commercial fishery in the Great Lakes region (Fagan et al. 2017). In 2015, the state-licensed commercial harvest of lake whitefish from Lake Michigan was 766,941 round pounds with a total dockside value of $1,625,915 (MDNR, 2016). However, yields of lake whitefish have fluctuated over the past 50 years, declining to all-time lows in the 1960s and 1970s, increasing in the 1980s and 1990s, then decreasing from the mid-1990s to present (Figure 1; Baldwin et al., 2000). Declines in lake whitefish have been attributed to overfishing, reduction in primary food sources (e.g. Diporeia) due to the invasion of dreissenid mussels, increased mortality from sea lamprey (*Petromyzon marinus*), and degradation of water quality and habitat due to increasing human population density and natural resource use and landscape level changes in the Great Lakes basin (Nalepa et al., 2005).

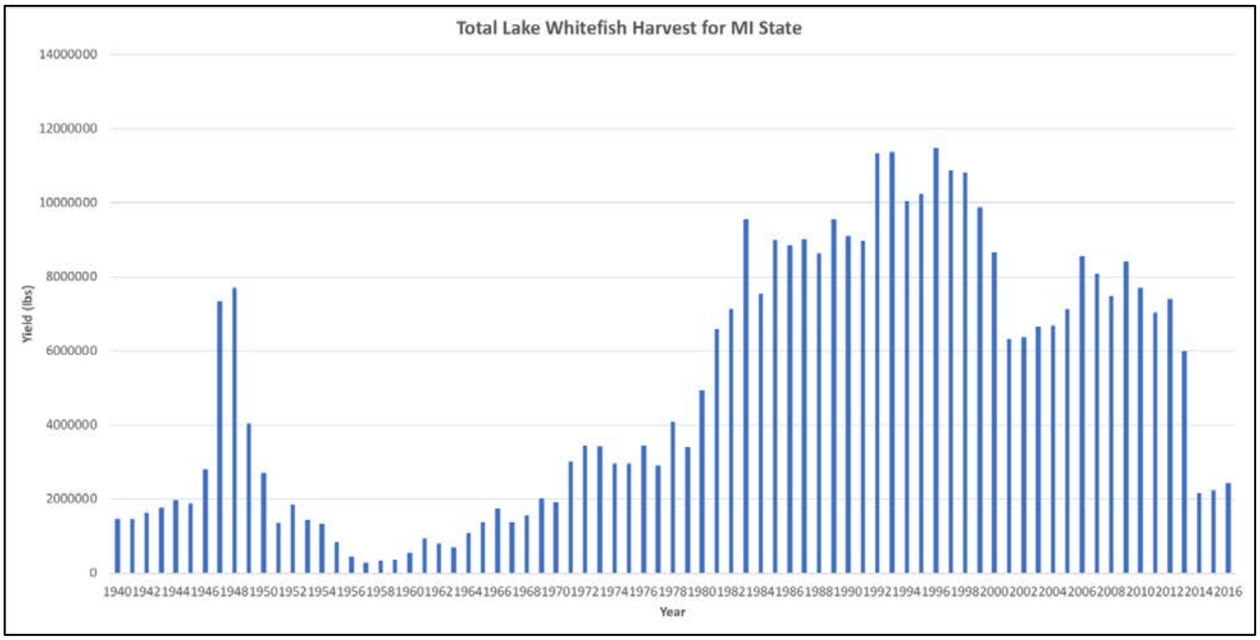

Figure 1. Yields of lake whitefish from the state of Michigan. Data were obtained from Baldwin et al. (2000) and MDNR.

Purpose of this study

The purpose of this study was to catalogue the nature, location, and timing of research on lake whitefish (*Coregonus clupeaformis*) in the upper Great Lakes over the past decade (2007 – 2018) in order to determine what research has been conducted and identify gaps in research and available data. This report identifies key investigators who have conducted lake whitefish research during this time period, the types of data they have been collecting, the data available for these fish and fisheries, and how these data may be accessed. Included in this report is a summary of investigator names, locations of study, and topic of research (e.g. the purpose for which the data were collected). The findings of this report will be shared with participants of the Lake Whitefish Management Workshop (February 27 – 28, 2018) hosted by the Great Lakes Fishery Commission (GLFC) and Great Lakes Fishery Trust (GLFT).

Methods

Identifying Participants

Emails were sent to researchers who were known to be working on lake whitefish in the upper Great Lakes at universities and state, tribal, and federal agencies (Enclosure 1). Initial survey participants were identified via recommendations from members of the Great Lakes Fisheries Trust Science Advisory Committee or because they were identified as a presenter (oral or poster) at the 2017 International Coregonid Symposium (10 – 15 September 2017 in Bayfield, WI) and whose title or abstract contained the keywords “lake whitefish” and “Huron”, “Michigan”, or “Superior”. These initial survey participants were then asked to identify additional investigators (e.g. provide name and contact information) who they knew currently were, or had been, engaged in lake whitefish research in the upper Great Lakes. This snowball sampling method enabled us to identify additional survey participants and ensure a more complete coverage of lake whitefish research programs that have been conducted in the upper Great Lakes since 2007.

Collecting Survey Responses

The survey focused on the nature, extent, and availability of information regarding lake whitefish research that survey participants were conducting in the upper Great Lakes between 2007 – 2018. The survey was developed with input from Dr. Tammy Newcomb (Michigan Department of Natural Resources; MDNR) and Dr. Bill Taylor (Michigan State University; MSU).

Potential participants were initially sent an introduction email and a copy of the survey (Enclosure 2), so that participants had an opportunity to review the survey questions before an interview was scheduled. They were informed that they had the option to complete the survey by either email or phone call. If a survey was completed via email, a follow-up phone call was scheduled, if necessary, to obtain more detailed respondent from each survey participant. If no response to the introduction email was received within 1 week of the initial email contact date, a follow-up email was sent. This follow-up email asked the participant for available dates and times in which to schedule a phone interview in order to complete the survey via phone call. A total of 3 contact attempts (including the initial email) were made for each potential participant.

Results

The results presented in this report are a compilation of the individual responses received during the survey process. All information presented are aggregated across individuals.

Survey Participants

A total of 81 people was recommended for participation in the survey (Enclosure 1). Of these 81 potential participants, complete survey responses were received from 32 participants (39.5% response rate). Of the remaining 49 people recommended for participation in the survey, we were unable to contact 9 people (no email address or phone number available), 25 people declined to participate (30.9%), and 15 people (18.5%) never responded to either the initial or follow-up emails. Most people who declined to participate in the survey cited lack of subject expertise (e.g. they did not work on lake whitefish), wrong geographical area (e.g. did not work in the upper Great Lakes), or project overlap with another respondent who we already contacted (e.g. we had already obtained a survey response from their project lead) as their reasons for declining to participate.

Lake Studied

Most studies focused on Lakes Michigan (21 studies mentioned conducting research on Lake Michigan; Enclosure 3). There were 8studies conducted on Lakes Huron and Superior, 6 studies on Lake Erie, and 3 studies on Lake Ontario.

Organization Collecting the Data

Organizations collecting data on lake whitefish (Enclosure 3) spanned federal government organizations (6 organizations total), tribal organizations (6 total), universities (6 total), state or provincial government organizations (4 total), and others (4 total). Other organizations included nongovernmental organizations (NGOs) and private industries (e.g. Consumers Energy/DTE Energy).

Topic of Research

Based on survey responses, the topic of research (e.g. what data were collected) was divided into 13 categories (Enclosure 3). Most projects focused on larval monitoring and recruitment topics (19 studies) or stock characteristics (16 studies; e.g. population abundance, adult lake whitefish indices). The stock characteristics category included data collection efforts done for biological monitoring purposes (e.g. collecting data for catch-at-age models). Some studies included more than one topic of research.

Purpose of Study

In addition to the specific topic of research, survey participants were asked to identify how the data they collected would be used (e.g. purpose of study). Based on survey responses, 12 categories were identified (Enclosure 3). Some respondents identified more than one purpose for their data. For example, participants tended to include both development of statistical catch-at-age (SCAA) models and setting management goals as uses of their data. It was rare for respondents to identify one purpose (e.g. development of SCAA model) and not the other (e.g. setting management goal). Additionally, all respondents who identified “Graduate research” as a purpose of their study also identified other uses for their data.

Accessibility of Data

Most respondents (24 out of 33; 72.7%) indicated that their data could be shared, as long as all partners who helped collect the data gave permission (Enclosure 3). Six respondents (18.2%) indicated that their data could be shared, given some limitations. These limitations included publications currently in progress (e.g. data would not be shared until paper was published), QA/QC of data not conducted, or respondent requires co-authorship recognition for sharing data. Three respondents (9.1%) indicated that their data could not be shared. Reasons for indicating that data could not be shared generally tended to be because data collection was not yet complete or data had not yet been analyzed.

Funding Source

Funding sources for lake whitefish research (Enclosure 3) spanned federal government sources (13), state/provincial sources (8), other sources of funding (5), tribal (3 sources), and universities (4 sources). Other sources of funding included nongovernmental organizations (NGOs), private industries, GLFT, and GLFC.

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Enclosures

Enclosure 1: List of People Contacted for Participation in Survey

81 participants contacted
32 complete responses
25 declined to participate (lack of expertise, did not work in upper Great Lakes, other reason)
9 unable to contact (no email address or phone number found)
15 never responded to initial or follow-up emails

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Matthew Bootsma
Hannah Schaefer
Ron Kinnunen
Gary Dawson
Tom Gorenflo
Erik Olsen
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William J. Harford
Christine Mayer
Tomas Höök
Brian Weidel
Dimitry Gorsky
Travis Brenden
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Dave Fielder
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Enclosure 2: Survey Form

Survey Questions

1. Who is collecting the data?

2. What data is being collected?

3. How long has the data been collected?

    a. What time period(s) does it cover?

4. How is the data structured?

5. Why is the data being collected?

6. How is the data being analyzed?

7. How is the information being used?

8. Can the data be shared?

    a. What are the limitations to sharing the information?

    b. Is there a publication or report that can be shared from this work?
        i. If yes, please attach a copy or provide citations

9. Who is funding this research?

10. Please list the names and contact information for others you know who are also conducting research on lake whitefish in the upper Great Lakes

Enclosure 3: Summary of Aggregated Survey Responses

Frequency denotes the number of survey responses that mentioned a given item

Lake Studied

Lake Studied	Frequency
Michigan	21
Huron	8
Superior	7
Erie	6
Ontario	3

Organization Collecting the Data

Organization	Frequency
USGS Great Lakes Science Center	8
Michigan DNR	6
Ontario MNR	5
Central Michigan University	3
University of Toledo	3
NOAA	2
University of Wisconsin – Stevens Point	2
USGS	2
Wisconsin DNR	2
Consumers Energy/DTE Energy	1
CORA	1
DFO	1
GLFC	1
GLIFWC	1
Grand Traverse Band – Natural Resources Department	1
Great Lakes Indian Fish and Wildlife Commission	1
Green Bay Fish and Wildlife Conservation Office	1
Lake Superior Technical Committee	1
LGLFWCO	1
Little River Band of Ottawa Indians	1
Little Traverse Bay Bands of Odawa Indians	1
Michigan State University	1
NYSDEC	1

Purdue University	1
The Nature Conservancy	1
University of Wisconsin – Green Bay	1

Topic of Research

Topic of Research	Frequency
Larval sampling, YOY production, and recruitment	19
Stock characteristics	16
Spawning sites, egg characteristics, and egg retention	12
Commercial catch monitoring	9
Feeding behaviors and diet analyses	8
Genetic analysis	4
Bioenergetics	4
Lake whitefish movement and stock mixing	3
Otolith microchemistry	2
Historical habitat	2
Sport harvest monitoring	1
Bycatch of lake whitefish	1
Development of lake-wide ecosystem model	1
Effectiveness of barrier net	1

Purpose of Study

Purpose of Study	Frequency
Learn more about spawning and early life history	12
Feed into SCAA models	10
Setting management actions/goals or informing managers	10
Monitoring of stock(s)	6
Graduate research	5
Determine impacts of changes in food web or *Dreissenid* invasions	2
Develop Great Lakes food webs	2
Determine historic habitat locations	2
Develop/modify lake whitefish bioenergetics model	2
Explore relationship between lake whitefish and cisco	1

Monitor barrier net performance	1

Accessibility of Data

Can the Data be Shared?	Frequency
Yes	18
With Limitations	7
No	9

Funding Source

Funding Source	Frequency
USGS Great Lakes Science Center	6
GLRI	5
Great Lakes Fish and Wildlife Restoration Act	4
Ontario MNR	4
GLFT	3
GLFC	3
MDNR	3
Central Michigan University	2
US Fish and Wildlife Service	2
NOAA	2
EPA	2
Wisconsin DNR	1
The Nature Conservancy	1
Michigan State University	1
Great Lakes Protection Fund (Canada-Ontario Agreement)	1
Office of Great Lakes – State of Wisconsin	1
Grand Traverse Band of Ottawa and Chippewa Indians	1
GLATOS	1
Little River Band of Odawa Indians	1
University of Minnesota – Duluth	1
USGS Ecosystems Mission Area	1
NYSDEC	1
Ohio DNR	1
Green Bay Fish and Wildlife Conservation Office	1
Sportfish and Restoration Act	1
NSERC grant	1

University of Windsor	1
Consumers Energy/DTE Energy	1
Great Lakes Indian Fish and Wildlife Commission	1

Enclosure 4: Individual Survey Responses, Grouped by Lake

In cases where respondents described multiple discrete projects as part of their response, each project was listed individually (e.g. some PIs have multiple, separate projects listed). Additionally, some PIs reported conducting studies in multiple lakes, so these studies appear for each lake category (e.g. a study conducted in Lakes Michigan and Superior appears under both *Lake Michigan Studies* and *Lake Superior Studies*)

Lake Michigan (21)

1. **PI:** Barry Weldon (Little River Band of Ottawa Indians; LRBOI)
   Purpose of Study: Setting management actions/goals or informing managers; Monitoring of stock(s)
   Available Data: Length, weight, sex, maturity, scales, otoliths, age, and lamprey wounding classification of lake whitefish; depth, water temperature, management unit, grid, latitude and longitude; commercial harvest. Data have been collected from 1999 – present.
   Can Data be Shared? Yes

2. **PI:** Ted Treska and Dale Hanson (FWS, Green Bay Fish & Wildlife Conservation office, native species subprogram)
   Purpose of Study: Feed into SCAA models
   Available Data: Standardized gill net surveys (spring LWAP for which FWS surveys 4 locations: Manistique, Washington Island, Sturgeon Bay, and Sheboygan; 1998 – present); Hydroacoustic and mid-water trawl survey of Green Bay pelagic community (2012 - present)
   Can Data be Shared? Yes

3. **PI:** Dan Isermann (University of Wisconsin-Stevens Point)
   Purpose of Study: Feed into SCAA models
   Available Data: stock characteristics of whitefish from Lake Michigan (estimate growth, mortality, fecundity, condition, and egg size) to compare among management zones and genetic stocks (2012 – 2013)
   Can Data be Shared? Yes

4. **PI:** Dan Isermann (University of Wisconsin-Stevens Point)
   Purpose of Study: Feed into SCAA models
   Available Data: spawning site contribution and movements (acoustic transmitters implanted into 400 lake whitefish from 4 different spawning aggregates; 2017 – 2012)
   Can Data be Shared? Not at this point (no data yet)

5. **PI**: Dave Caroffino (MDNR)
   Purpose of Study: feed into SCAA models; setting management actions/goals or informing managers; learn more about spawning and early life history; graduate research
   Available Data: commercial harvest/effort, biological monitoring, and age-0 juvenile catch

rates in nearshore seins (2013 – present); commercial biomonitoring (length, weight, age, lamprey wounds, sex, maturity, visceral fat index; 1986 – present); juvenile seining (count, length, specimens preserved for genetic analysis by UWSP; 2017 – present); maturity schedules of lake whitefish (MS research for Marissa Hammond, MSU)
Can Data be Shared? Yes

6. **PI:** Kevin Donner (Little Traverse Bay Bands of Odawa Indians)
Purpose of Study: Feed into SCAA models; Learn more about spawning and early life history; Monitoring of stocks
Available Data: YOY LWF between 25 – 60mm abundance, biodata, associated environmental data, some other species data, some otolith microchemistry data (using seines; 2013 – present); larval whitefish abundance, biodata, associated environmental data (neuston; 2012 – present); gillnetting and commercial harvest (LWF all sizes; 1998 – present)
Can Data be Shared? Yes

7. **PI:** Don Uzarski (Central Michgan University; CMU)
Purpose of Study: Graduate research; Learn more about spawning and early life history
Available Data: Seine-hauls from shore at two sites on Sand Bay of Beaver Island. All fish are identified and enumerated. These data are accompanied by YSI multiprobe - temperature (°C), dissolved oxygen (mg/L and % saturation), chlorophyll a (mg/L), oxidation-reduction potential (mV), total dissolved solids (mg/L), turbidity (Nephelometric Turbidity Units; NTU), pH (Std units), and specific conductance (µS/cm). Raw water samples are also collected for later nutrient analyses – NH_4, NO_2/NO_3, TN, SRP, TP. Data have been collected from 2015 – present.
Can Data be Shared? Yes

8. **PI:** Erik Olsen (Grand Traverse Band – Natural Resources Department)
Purpose of Study: Feed into SCAA models; Monitoring of stock(s)
Available Data: Biological data from tribal commercial fishery (both gillnet and trap net) in northern Lake Michigan (1985 - present); lake whitefish index (LWI; 2000 – present); bycatch in Lake-wide Assessment Plan survey (LWAP; 1992 – present); bycatch in Lake trout fall spawning survey (LTF; 1999 – present); bycatch in spring larval beach seining (LBS; 2017 – present)
Can Data be Shared? Yes

9. **PI:** Patrick Forsythe (University of Wisconsin Green Bay)
Purpose of Study: Learn more about spawning and early life history
Available Data: sampling for drifting larval lake whitefish from lower reaches of Menominee River: river, sampling day, time of sampling, flow rates through nets, number of larval fish collected during each net tow (2016)
Can Data be Shared? Not at the present time

10. **PI:** Patrick Forsythe (University of Wisconsin Green Bay)
Purpose of Study: Learn more about spawning and early life history
Available Data: sampling for drifting larval lake whitefish for 4 major tributaries of Green Bay (Menominee, Peshtego, Okanto, and Fox rivers): river, sampling day, time of sampling, flow rates through nets, number of larval fish collected during each net tow, otolith microchemistry (2017 – 2019)
Can Data be Shared? Not at the present time

11. **PI:** Scott Hansen (Wisconsin DNR)
Purpose of Study: Monitoring of stock(s); Feed into SCAA models; Setting management actions/goals or informing managers
Available Data: annual adult sampling in Lake Michigan and Green Bay using gill nets and boom shocking gear (late 1990s - present); sampling for juveniles in Green Bay in the spring using small-mesh gill nets; yearling indices in summer for YOY production in Green Bay (and a bit in Lake Michigan) via trawling (1997 – present); length, weight, and age information via otolith aging (1990s – present); commercial fishery harvest (1960s – present); genetic stock identification (joint with UW Stevens Point; 2005 – 2006); larval whitefish ecology production and escapement in west-shore tributaries (2009 – 2015); otolith microchemistry (identifying fish based on natal river or Green Bay area); Northern whitefish stock (Dorr County in Lake Michigan) and stocks in rivers and Green Bay; tagging whitefish in tributaries and several stocks in Green Bay to see how these stocks are mixing
Can Data be Shared? Yes

12. **PI:** Tracy Galarowicz
Purpose of Study: Learn more about spawning and early life history
Available Data: Coregonid egg deposition (2009 – 2016)
Can Data be Shared? Yes, given permission from MDNR and TNC (The Nature Conservancy)

13. **PI:** Trent Sutton (University of Alaska Fairbanks)
Purpose of Study: Learn more about spawning and early life history; Determine impacts of changes in food web or dreissenid invasions
Available Data: Female data (catch, age, size, proximate composition, fatty acid composition), egg characteristics, larval and juvenile catches and proximate composition (from subset of locations), and juvenile lake whitefish food habits for multiple stocks (fall 2004 – summer 2006)
Can Data be Shared? Yes, given permission from Co-PIs

14. **PI:** Wendylee Stott (USGS GLSC)
Purpose of Study: Setting management actions/goals or informing managers
Available Data: population genetic data (1920s, 1999 – 2001, 2005 – 2010)
Can Data be Shared? Yes

15. **PI:** Wes Larson (University of Wisconsin-Stevens Point)
Purpose of Study: Setting Management Actions/Goals or Informing Managers

Available Data: genomic data from thousands of genetic markers collected from approximately 400 lake whitefish that have acoustic tags (part of project conducted by Dan Isermann; 2017 – present)
Can Data be Shared? Yes, but data have not been collected yet

16. **PI:** Steven Pothoven (NOAA)
Purpose of Study: Learn more about spawning and early life history
Available Data: larval whitefish abundance, diets, and size and zooplankton data for Saginaw Bay (2009 – 2010) and southwestern Lake Michigan (2013 – 2017; Grand Haven, South Haven, Muskegon, Montague, Pentwater)
Can Data be Shared? Yes

17. **PI:** Scott DeBoe (Consumers Energy/DTE Energy)
Purpose of Study: Monitor barrier net performance
Available Data: gillnet catch numbers from 4 stations inside barrier net and 4 stations outside barrier net (1989 – 2017)
Can Data be Shared? Yes

18. **PI:** Randy Claramunt (MDNR)
Purpose of Study: Feed into SCAA models
Available Data: fishery survey data (commercial catch and fishery-independent data (1960s - present)); assessment data (trawls, gillnets, eggs, fry; 1960s - present); recruitment studies (2004 – present)
Can Data be Shared? Yes

19. **PI:** Charles Madenjian (USGS GLSC)
Purpose of Study: Evaluate existing model for lake whitefish bioenergetics
Available Data: feeding and growth data from lab experiment (2003); Steve Pothoven has some data on stomach contents for lake whitefish from Lake Michigan purchased from commercial fishers (also has energy density of whitefish and PCB determination of some prey species)
Can Data be Shared? Yes

20. **PI:** Ed Roseman (USGS GLSC)
Purpose of Study: Determine historic habitat; Learn more about spawning and early life history
Available Data: egg deposition; larval density and distribution; historic habitat GIS analysis of spawning and nursery areas. Data were collected for 13 years in Detroit River, 2 years for western Lake Erie and Maumee Bay, in 2017 for central and eastern Lake Erie (larvae only), in 2007 for northern Lake Huron (larvae only), and Saginaw Bay (2014 – 2016 egg deposition work with Tomas Hook and MIDNR)
Can Data be Shared? Yes

21. **PI:** Jory Jonas (MDNR)
Purpose of Study: Feed into SCAA models; determine relationship between lake whitefish and cisco in Lake Michigan
Available Data: surveys from lakewide assessment protocol (number of species, age structures, otoliths, length, and weight; 1996 or 1997 – present)
Can Data be Shared? Yes

Lake Huron (8)

1. **PI:** Trent Sutton (University of Alaska Fairbanks)
   Purpose of Study: Learn more about spawning and early life history; Determine impacts of changes in food web or dreissenid invasions
   Available Data: Female data (catch, age, size, proximate composition, fatty acid composition), egg characteristics, larval and juvenile catches and proximate composition (from subset of locations), and juvenile lake whitefish food habits for multiple stocks (fall 2004 – summer 2006)
   Can Data be Shared? Yes, given permission from Co-PIs

2. **PI:** Wendylee Stott (USGS GLSC)
   Purpose of Study: Setting management actions/goals or informing managers
   Available Data: population genetic data (1920s, 1999 – 2001, 2005 – 2010)
   Can Data be Shared? Yes

3. **PI:** Steven Pothoven (NOAA)
   Purpose of Study: Learn more about spawning and early life history
   Available Data: larval whitefish abundance, diets, and size and zooplankton data for Lake Huron (2009 – 2010)
   Can Data be Shared? Yes

4. **PI:** Steven Pothoven (NOAA)
   Purpose of Study: Develop Great Lakes food webs
   Available Data: diets of adult lake whitefish (2007 – 2011; some earlier data going back to 2002)
   Can Data be Shared? Yes

5. **PI:** Randy Claramunt (MDNR)
   Purpose of Study: Feed into SCAA models
   Available Data: fishery survey data (commercial catch and fishery-independent data (1960s - present)); assessment data (trawls, gillnets, eggs, fry; 1960s - present); recruitment studies (2004 – present)
   Can Data be Shared? Yes

6. **PI:** Ed Roseman (USGS GLSC)
   Purpose of Study: Determine historic habitat; Learn more about spawning and early life history
   Available Data: egg deposition; larval density and distribution; historic habitat GIS analysis of spawning and nursery areas. Data were collected for 13 years in Detroit River, 2 years for western Lake Erie and Maumee Bay, in 2017 for central and eastern Lake Erie (larvae only), in 2007 for northern Lake Huron (larvae only), and Saginaw Bay (2014 – 2016 egg deposition work with Tomas Hook and MIDNR)
   Can Data be Shared? Yes

7. **PI:** Michael Rennie (Lakehead University)
Purpose of Study: Determine Impacts of Changes in Food Web or *Dreissenid Invasions;* Graduate research
Available Data: lake whitefish growth and feeding behavior as estimated using stable isotopic analysis of scales (covers whole Great Lakes basin; 1947 - present); bioenergetics modelling across number of fish stocks (PhD work; variations of lake whitefish bioenergetics over concentrations of diaporeia; 2003 - 2004); nearshore and pelagic coupling spatial variations and impacts on conversion efficiency of organisms (last CSMI year on Lake Superior (2015 - 2017); MS work for Marissa)
Can Data be Shared? Yes

8. **PI:** Adam Cottrill (OMNRF)
Purpose of Study: Monitoring of stock(s); Setting management actions/goals or informing managers
Available Data: Daily catch reports filed by commercial fishers (1978 - present); fishery-independent catch data (1975 to present); Index netting program for biological characteristics and stomach contents (1984 – present)
Can Data be Shared? Yes

Lake Superior (7)

1. **PI:** Bryan Matthias (Lake Superior Technical Committee)
   Purpose of Study: Develop Great Lakes food webs; Setting management actions/goals or informing managers
   Available Data: Coordinated siscowet survey; lakewide harvest and effort data; community-wide fish survey from Ontario (2009 – present); abundance and biomass CPUE for gillnets from Wisconsin (1981 – present)
   Can Data be Shared? Yes

2. **PI:** Tim Johnson (OMNRF)
   Purpose of Study: Develop/modify lake whitefish bioenergetics model
   Available Data: samples analyzed for diets, stable isotopes (C, N), total mercury, and energy density (2016 - 2017) to inform Great Lakes basin wide analysis of trophic transfer efficiency
   Can Data be Shared? Yes, once analyses and publication have occurred

3. **PI:** Trent Sutton (University of Alaska Fairbanks)
   Purpose of Study: Learn more about spawning and early life history; Determine impacts of changes in food web or dreissenid invasions
   Available Data: Female data (catch, age, size, proximate composition, fatty acid composition), egg characteristics, larval and juvenile catches and proximate composition (from subset of locations), and juvenile lake whitefish food habits for multiple stocks (fall 2004 – summer 2006)
   Can Data be Shared? Yes, given permission from Co-PIs

4. **PI:** Wendylee Stott (USGS GLSC)
   Purpose of Study: Setting management actions/goals or informing managers
   Available Data: population genetic data (1920s, 1999 – 2001, 2005 – 2010)
   Can Data be Shared? Yes

5. **PI:** Bill Mattes (Great Lakes Indian Fish and Wildlife Commission)
   Purpose of Study: Feed into SCAA models; Setting Management Actions/Goals or Informing Managers; Monitoring of stocks
   Available Data: Commercial whitefish harvest (1985 - present); YOY whitefish beach seine in 3 locations around Keweenaw Peninsula (1996 - present); fall spawning survey on 4 major spawning reefs (1987 - present); yearly fish community survey (ciscowets) from nearshore to offshore using variable mesh (1996 - present)
   Can Data be Shared? Yes

6. **PI:** Randy Claramunt (MDNR)
   Purpose of Study: Feed into SCAA models
   Available Data: fishery survey data (commercial catch and fishery-independent data (1960s - present)); assessment data (trawls, gillnets, eggs, fry; 1960s - present);

recruitment studies (2004 – present)
Can Data be Shared? Yes

7. **PI:** Michael Rennie (Lakehead University)
   Purpose of Study: Determine Impacts of Changes in Food Web or *Dreissenid Invasions;* Graduate Research
   Available Data: lake whitefish growth and feeding behavior as estimated using stable isotopic analysis of scales (covers whole Great Lakes basin; 1947 - present); bioenergetics modelling across number of fish stocks (PhD work; variations of lake whitefish bioenergetics over concentrations of diaporeia; 2003 - 2004); nearshore and pelagic coupling spatial variations and impacts on conversion efficiency of organisms (last CSMI year on Lake Superior (2015 - 2017); MS work for Marissa)
   Can Data be Shared? Yes

Lake Erie (6)

1. **PI:** Chris Vandergoot (USGS GLSC)
   Purpose of Study: Setting management actions/goals or informing managers
   Available Data: weekly demographic information (length, weight, sex, age) for western basin reef complex (spawning grounds) via experimental gill nets (2015 – 2017); movement data via acoustic telemetry (2014 – 2017)
   Can Data be Shared? Not at this point (study is in progress)

2. **PI:** Hannah Schaefer (MS student at University of Michigan; USGS)
   Purpose of Study: Determine historic habitat locations; Graduate research
   Available Data: Historic spawning locations; non-spawning and nursery locations throughout Great Lakes basin and tributaries (1982 – present, depending on data source)
   Can Data be Shared? Yes

3. **PI:** Robin DeBruyne (USGS Great Lakes Science Center; USGS GLSC)
   Purpose of Study: Learn more about spawning and early life history
   Available Data: Larval abundance by location, larval length, otolith ages (partial), larval diets (partial) for Detroit river and northern western Lake Erie (2006 – present), St. Claire River (2010 – 2015), and Lakes Erie and Ontario (2017)
   Can Data be Shared? Yes, will be available on ScienceBase

4. **PI:** Robin DeBruyne (University of Toledo)
   Purpose of Study: Learn more about spawning and early life history; graduate research (Zachary Amidon, MS Student)
   Available Data: Egg sampling in SCDRS and western Lake Erie (2017 – 2018)
   Can Data be Shared? Yes, will be available on ScienceBase

5. **PI:** Timothy O'Brien (USGS GLSC)
   Purpose of Study: learn more about spawning and early life history
   Available Data: intermittent catch data of larval lake whitefish (2007, 2008, 2009, 2012)
   Can Data be Shared? Yes; sample size is limited as this is not targeted lake whitefish research

6. **PI:** Ed Roseman (USGS GLSC)
   Purpose of Study: Determine historic habitat; Learn more about spawning and early life history
   Available Data: egg deposition; larval density and distribution; historic habitat GIS analysis of spawning and nursery areas. Data were collected for 13 years in Detroit River, 2 years for western Lake Erie and Maumee Bay, in 2017 for central and eastern Lake Erie (larvae only), in 2007 for northern Lake Huron (larvae only), and Saginaw Bay (2014 – 2016 egg deposition work with Tomas Hook and MIDNR)
   Can Data be Shared? Yes

Lake Ontario (3)

1. **PI:** Dimitry Gorsky (FWS, Lower Great Lakes Fish and Wildlife Conservation Office; LGLFWCO)
   Purpose of Study: Learn more about spawning and early life history
   Available Data: Presence/absence of larval coregonines (spring 2017 and 2018); adult cisco abundance in Chaumont Bay (2015 – 2017)
   Can Data be Shared? Yes, given co-authorship

2. **PI:** Brian Weidel (USGS)
   Purpose of Study: Setting management actions/goals or informing managers
   Available Data: lake-wide bottom trawling for pelagic (April) and benthic (October) prey fish and lake whitefish (1978 - present)
   Can Data be Shared? Yes

3. **PI:** Michael Rennie (Lakehead University)
   Purpose of Study: Determine Impacts of Changes in Food Web or *Dreissenid Invasions*; Graduate research
   Available Data: lake whitefish growth and feeding behavior as estimated using stable isotopic analysis of scales (covers whole Great Lakes basin; 1947 - present); bioenergetics modelling across number of fish stocks (PhD work; variations of lake whitefish bioenergetics over concentrations of diaporeia; 2003 - 2004); nearshore and pelagic coupling spatial variations and impacts on conversion efficiency of organisms (last CSMI year on Lake Superior (2015 - 2017); MS work for Marissa)
   Can Data be Shared? Yes

Enclosure 5: Individual Survey Responses, Grouped by Purpose of Study

In cases where respondents described multiple discrete projects as part of their response, each project was listed individually (e.g. some PIs have multiple, separate projects listed). Additionally, some PIs reported conducting studies with multiple purposes, so these studies appear for each "Purpose of Study" category (e.g. a study conducted to feed into SCAA models and learn more about spawning and early life history appears under both *Feed into SCAA models* and *Learn more about spawning and early life history*)

Learn More about Spawning and Early Life History (12)

1. **PI**: Dave Caroffino (MDNR)
Lake Studied: Lake Michigan
Available Data: commercial harvest/effort, biological monitoring, and age-0 juvenile catch rates in nearshore seins (2013 – present); commercial biomonitoring (length, weight, age, lamprey wounds, sex, maturity, visceral fat index; 1986 – present); juvenile seining (count, length, specimens preserved for genetic analysis by UWSP; 2017 – present); maturity schedules of lake whitefish (MS research for Marissa Hammond, MSU)
Can Data be Shared? Yes

2. **PI:** Kevin Donner (Little Traverse Bay Bands of Odawa Indians)
Lake Studied: Lake Michigan
Available Data: YOY LWF between 25 – 60mm abundance, biodata, associated environmental data, some other species data, some otolith microchemistry data (using seines; 2013 – present); larval whitefish abundance, biodata, associated environmental data (neuston; 2012 – present); gillnetting and commercial harvest (LWF all sizes; 1998 – present)
Can Data be Shared? Yes

3. **PI:** Don Uzarski (Central Michgan University; CMU)
Lake Studied: Lake Michigan
Available Data: Seine-hauls from shore at two sites on Sand Bay of Beaver Island. All fish are identified and enumerated. These data are accompanied by YSI multiprobe - temperature (°C), dissolved oxygen (mg/L and % saturation), chlorophyll a (mg/L), oxidation-reduction potential (mV), total dissolved solids (mg/L), turbidity (Nephelometric Turbidity Units; NTU), pH (Std units), and specific conductance (µS/cm). Raw water samples are also collected for later nutrient analyses – NH_4, NO_2/NO_3, TN, SRP, TP. Data have been collected from 2015 – present.
Can Data be Shared? Yes

4. **PI:** Patrick Forsythe (University of Wisconsin Green Bay)
Lake Studied: Lake Michigan
Available Data: sampling for drifting larval lake whitefish from lower reaches of Menominee River: river, sampling day, time of sampling, flow rates through nets, number

of larval fish collected during each net tow (2016)
Can Data be Shared? Not at the present time

5. **PI:** Patrick Forsythe (University of Wisconsin Green Bay)
Lake Studied: Lake Michigan
Available Data: sampling for drifting larval lake whitefish for 4 major tributaries of Green Bay (Menominee, Peshtego, Okanto, and Fox rivers): river, sampling day, time of sampling, flow rates through nets, number of larval fish collected during each net tow, otolith microchemistry (2017 – 2019)
Can Data be Shared? Not at the present time

6. **PI:** Tracy Galarowicz
Lake Studied: Lake Michigan
Available Data: Coregonid egg deposition (2009 – 2016)
Can Data be Shared? Yes, given permission from MDNR and TNC (The Nature Conservancy)

7. **PI:** Trent Sutton (University of Alaska Fairbanks)
Lake Studied: Lake Michigan, Lake Huron, Lake Superior
Available Data: Female data (catch, age, size, proximate composition, fatty acid composition), egg characteristics, larval and juvenile catches and proximate composition (from subset of locations), and juvenile lake whitefish food habits for multiple stocks (fall 2004 – summer 2006)
Can Data be Shared? Yes, given permission from Co-PIs

8. **PI:** Steven Pothoven (NOAA)
Lake Studied: Lake Michigan, Lake Huron
Available Data: larval whitefish abundance, diets, and size and zooplankton data for Saginaw Bay (2009 – 2010) and southwestern Lake Michigan (2013 – 2017; Grand Haven, South Haven, Muskegon, Montague, Pentwater)
Can Data be Shared? Yes

9. **PI:** Robin DeBruyne (USGS Great Lakes Science Center; USGS GLSC)
Lake Studied: Lake Erie
Available Data: Larval abundance by location, larval length, otolith ages (partial), larval diets (partial) for Detroit river and northern western Lake Erie (2006 – present), St. Claire River (2010 – 2015), and Lakes Erie and Ontario (2017)
Can Data be Shared? Yes, will be available on ScienceBase

10. **PI:** Timothy O'Brien (USGS GLSC)
Lake Studied: Lake Erie
Available Data: intermittent catch data of larval lake whitefish (2007, 2008, 2009, 2012)
Can Data be Shared? Yes; sample size is limited as this is not targeted lake whitefish research

11. **PI:** Dimitry Gorsky (FWS, Lower Great Lakes Fish and Wildlife Conservation Office; LGLFWCO)
    Lake Studied: Lake Ontario
    Available Data: Presence/absence of larval coregonines (spring 2017 and 2018); adult cisco abundance in Chaumont Bay (2015 – 2017)
    Can Data be Shared? Yes, given co-authorship

12. **PI:** Ed Roseman (USGS GLSC)
    Lake Studied: Lake Michigan, Lake Huron, Lake Erie
    Available Data: egg deposition; larval density and distribution; historic habitat GIS analysis of spawning and nursery areas. Data were collected for 13 years in Detroit River, 2 years for western Lake Erie and Maumee Bay, in 2017 for central and eastern Lake Erie (larvae only), in 2007 for northern Lake Huron (larvae only), and Saginaw Bay (2014 – 2016 egg deposition work with Tomas Hook and MIDNR)
    Can Data be Shared? Yes

Feed into SCAA Models (10)

1. **PI:** Ted Treska and Dale Hanson (FWS, Green Bay Fish & Wildlife Conservation office, native species subprogram)
   Lake Studied: Lake Michigan
   Available Data: Standardized gill net surveys (spring LWAP for which FWS surveys 4 locations: Manistique, Washington Island, Sturgeon Bay, and Sheboygan; 1998 – present); Hydroacoustic and mid-water trawl survey of Green Bay pelagic community (2012 - present)
   Can Data be Shared? Yes

2. **PI:** Dan Isermann (University of Wisconsin-Stevens Point)
   Lake Studied: Lake Michigan
   Available Data: stock characteristics of whitefish from Lake Michigan (estimate growth, mortality, fecundity, condition, and egg size) to compare among management zones and genetic stocks (2012 – 2013)
   Can Data be Shared? Yes

3. **PI:** Dan Isermann (University of Wisconsin-Stevens Point)
   Lake Studied: Lake Michigan
   Available Data: spawning site contribution and movements (acoustic transmitters implanted into 400 lake whitefish from 4 different spawning aggregates; 2017 – 2012)
   Can Data be Shared? Not at this point (no data yet)

4. **PI**: Dave Caroffino (MDNR)
   Lake Studied: Lake Michigan
   Available Data: commercial harvest/effort, biological monitoring, and age-0 juvenile catch rates in nearshore seins (2013 – present); commercial biomonitoring (length, weight, age, lamprey wounds, sex, maturity, visceral fat index; 1986 – present); juvenile seining (count, length, specimens preserved for genetic analysis by UWSP; 2017 – present); maturity schedules of lake whitefish (MS research for Marissa Hammond, MSU)
   Can Data be Shared? Yes

5. **PI:** Kevin Donner (Little Traverse Bay Bands of Odawa Indians)
   Lake Studied: Lake Michigan
   Available Data: YOY LWF between 25 – 60mm abundance, biodata, associated environmental data, some other species data, some otolith microchemistry data (using seines; 2013 – present); larval whitefish abundance, biodata, associated environmental data (neuston; 2012 – present); gillnetting and commercial harvest (LWF all sizes; 1998 – present)
   Can Data be Shared? Yes

6. **PI:** Erik Olsen (Grand Traverse Band – Natural Resources Department)
   Lake Studied: Lake Michigan

Available Data: Biological data from tribal commercial fishery (both gillnet and trap net) in northern Lake Michigan (1985 - present); lake whitefish index (LWI; 2000 – present); bycatch in Lake-wide Assessment Plan survey (LWAP; 1992 – present); bycatch in Lake trout fall spawning survey (LTF; 1999 – present); bycatch in spring larval beach seining (LBS; 2017 – present)
Can Data be Shared? Yes

7. **PI:** Scott Hansen (Wisconsin DNR)
   Lake Studied: Lake Michigan
   Available Data: annual adult sampling in Lake Michigan and Green Bay using gill nets and boom shocking gear (late 1990s - present); sampling for juveniles in Green Bay in the spring using small-mesh gill nets; yearling indices in summer for YOY production in Green Bay (and a bit in Lake Michigan) via trawling (1997 – present); length, weight, and age information via otolith aging (1990s – present); commercial fishery harvest (1960s – present); genetic stock identification (joint with UW Stevens Point; 2005 – 2006); larval whitefish ecology production and escapement in west-shore tributaries (2009 – 2015); otolith microchemistry (identifying fish based on natal river or Green Bay area); Northern whitefish stock (Dorr County in Lake Michigan) and stocks in rivers and Green Bay; tagging whitefish in tributaries and several stocks in Green Bay to see how these stocks are mixing
   Can Data be Shared? Yes

8. **PI:** Randy Claramunt (MDNR)
   Lake Studied: Lake Michigan, Lake Huron, Lake Superior
   Available Data: fishery survey data (commercial catch and fishery-independent data (1960s - present)); assessment data (trawls, gillnets, eggs, fry; 1960s - present); recruitment studies (2004 – present)
   Can Data be Shared? Yes

9. **PI:** Jory Jonas (MDNR)
   Lake Studied: Lake Michigan
   Available Data: surveys from lakewide assessment protocol (number of species, age structures, otoliths, length, and weight; 1996 or 1997 – present)
   Can Data be Shared? Yes

10. **PI:** Bill Mattes (Great Lakes Indian Fish and Wildlife Commission)
    Lake Studied: Lake Superior
    Available Data: Commercial whitefish harvest (1985 - present); YOY whitefish beach seine in 3 locations around Keweenaw Peninsula (1996 - present); fall spawning survey on 4 major spawning reefs (1987 - present); yearly fish community survey (ciscowets) from nearshore to offshore using variable mesh (1996 - present)
    Can Data be Shared? Yes

Setting Management Actions/Goals or Informing Managers (10)

1. **PI:** Barry Weldon (Little River Band of Ottawa Indians; LRBOI)
   Lake Studied: Lake Michigan
   Available Data: Length, weight, sex, maturity, scales, otoliths, age, and lamprey wounding classification of lake whitefish; depth, water temperature, management unit, grid, latitude and longitude; commercial harvest. Data have been collected from 1999 – present.
   Can Data be Shared? Yes

2. **PI**: Dave Caroffino (MDNR)
   Lake Studied: Lake Michigan
   Available Data: commercial harvest/effort, biological monitoring, and age-0 juvenile catch rates in nearshore seins (2013 – present); commercial biomonitoring (length, weight, age, lamprey wounds, sex, maturity, visceral fat index; 1986 – present); juvenile seining (count, length, specimens preserved for genetic analysis by UWSP; 2017 – present); maturity schedules of lake whitefish (MS research for Marissa Hammond, MSU)
   Can Data be Shared? Yes

3. **PI:** Scott Hansen (Wisconsin DNR)
   Lake Studied: Lake Michigan
   Available Data: annual adult sampling in Lake Michigan and Green Bay using gill nets and boom shocking gear (late 1990s - present); sampling for juveniles in Green Bay in the spring using small-mesh gill nets; yearling indices in summer for YOY production in Green Bay (and a bit in Lake Michigan) via trawling (1997 – present); length, weight, and age information via otolith aging (1990s – present); commercial fishery harvest (1960s – present); genetic stock identification (joint with UW Stevens Point; 2005 – 2006); larval whitefish ecology production and escapement in west-shore tributaries (2009 – 2015); otolith microchemistry (identifying fish based on natal river or Green Bay area); Northern whitefish stock (Dorr County in Lake Michigan) and stocks in rivers and Green Bay; tagging whitefish in tributaries and several stocks in Green Bay to see how these stocks are mixing
   Can Data be Shared? Yes

4. **PI:** Wendylee Stott (USGS GLSC)
   Lake Studied: Lake Michigan, Lake Huron, Lake Superior
   Available Data: population genetic data (1920s, 1999 – 2001, 2005 – 2010)
   Can Data be Shared? Yes

5. **PI:** Adam Cottrill (OMNRF)
   Lake Studied: Lake Huron
   Available Data: Daily catch reports filed by commercial fishers (1978 - present); fishery-independent catch data (1975 to present); Index netting program for biological characteristics and stomach contents (1984 – present)
   Can Data be Shared? Yes

6. **PI:** Bryan Matthias (Lake Superior Technical Committee)
   Lake Studied: Lake Superior
   Available Data: Coordinated siscowet survey; lakewide harvest and effort data; community-wide fish survey from Ontario (2009 – present); abundance and biomass CPUE for gillnets from Wisconsin (1981 – present)
   Can Data be Shared? Yes

7. **PI:** Chris Vandergoot (USGS GLSC)
   Lake Studied: Lake Erie
   Available Data: weekly demographic information (length, weight, sex, age) for western basin reef complex (spawning grounds) via experimental gill nets (2015 – 2017); movement data via acoustic telemetry (2014 – 2017)
   Can Data be Shared? Not at this point (study is in progress)

8. **PI:** Brian Weidel (USGS)
   Lake Studied: Lake Ontario
   Available Data: lake-wide bottom trawling for pelagic (April) and benthic (October) prey fish and lake whitefish (1978 - present)
   Can Data be Shared? Yes

9. **PI:** Bill Mattes (Great Lakes Indian Fish and Wildlife Commission)
   Lake Studied: Lake Superior
   Available Data: Commercial whitefish harvest (1985 - present); YOY whitefish beach seine in 3 locations around Keweenaw Peninsula (1996 - present); fall spawning survey on 4 major spawning reefs (1987 - present); yearly fish community survey (ciscowets) from nearshore to offshore using variable mesh (1996 - present)
   Can Data be Shared? Yes

10. **PI:** Wes Larson (University of Wisconsin-Stevens Point)
    Lake Studied: Lake Michigan
    Available Data: genomic data from thousands of genetic markers collected from approximately 400 lake whitefish that have acoustic tags (part of project conducted by Dan Isermann; 2017 – present)
    Can Data be Shared? Yes, but data have not been collected yet

Monitoring of Stock(s) (6)

1. **PI:** Erik Olsen (Grand Traverse Band – Natural Resources Department)
   Lake Studied: Lake Michigan
   Available Data: Biological data from tribal commercial fishery (both gillnet and trap net) in northern Lake Michigan (1985 - present); lake whitefish index (LWI; 2000 – present); bycatch in Lake-wide Assessment Plan survey (LWAP; 1992 – present); bycatch in Lake trout fall spawning survey (LTF; 1999 – present); bycatch in spring larval beach seining (LBS; 2017 – present)
   Can Data be Shared? Yes

2. **PI:** Scott Hansen (Wisconsin DNR)
   Lake Studied: Lake Michigan
   Available Data: annual adult sampling in Lake Michigan and Green Bay using gill nets and boom shocking gear (late 1990s - present); sampling for juveniles in Green Bay in the spring using small-mesh gill nets; yearling indices in summer for YOY production in Green Bay (and a bit in Lake Michigan) via trawling (1997 – present); length, weight, and age information via otolith aging (1990s – present); commercial fishery harvest (1960s – present); genetic stock identification (joint with UW Stevens Point; 2005 – 2006); larval whitefish ecology production and escapement in west-shore tributaries (2009 – 2015); otolith microchemistry (identifying fish based on natal river or Green Bay area); Northern whitefish stock (Dorr County in Lake Michigan) and stocks in rivers and Green Bay; tagging whitefish in tributaries and several stocks in Green Bay to see how these stocks are mixing
   Can Data be Shared? Yes

3. **PI:** Adam Cottrill (OMNRF)
   Lake Studied: Lake Huron
   Available Data: Daily catch reports filed by commercial fishers (1978 - present); fishery-independent catch data (1975 to present); Index netting program for biological characteristics and stomach contents (1984 – present)
   Can Data be Shared? Yes

4. **PI:** Kevin Donner (Little Traverse Bay Bands of Odawa Indians)
   Lake Studied: Lake Michigan
   Available Data: YOY LWF between 25 – 60mm abundance, biodata, associated environmental data, some other species data, some otolith microchemistry data (using seines; 2013 – present); larval whitefish abundance, biodata, associated environmental data (neuston; 2012 – present); gillnetting and commercial harvest (LWF all sizes; 1998 – present)
   Can Data be Shared? Yes

5. **PI:** Bill Mattes (Great Lakes Indian Fish and Wildlife Commission)
   Lake Studied: Lake Superior
   Available Data: Commercial whitefish harvest (1985 - present); YOY whitefish beach seine

in 3 locations around Keweenaw Peninsula (1996 - present); fall spawning survey on 4 major spawning reefs (1987 - present); yearly fish community survey (ciscowets) from nearshore to offshore using variable mesh (1996 - present)
Can Data be Shared? Yes

6. **PI:** Barry Weldon (Little River Band of Ottawa Indians; LRBOI)
   Lake Studied: Lake Michigan
   Available Data: Length, weight, sex, maturity, scales, otoliths, age, and lamprey wounding classification of lake whitefish; depth, water temperature, management unit, grid, latitude and longitude; commercial harvest. Data have been collected from 1999 – present.
   Can Data be Shared? Yes

Graduate Research (5)

1. **PI:** Don Uzarski (Central Michgan University; CMU)
   Lake Studied: Lake Michigan
   Available Data: Seine-hauls from shore at two sites on Sand Bay of Beaver Island. All fish are identified and enumerated. These data are accompanied by YSI multiprobe - temperature (°C), dissolved oxygen (mg/L and % saturation), chlorophyll a (mg/L), oxidation-reduction potential (mV), total dissolved solids (mg/L), turbidity (Nephelometric Turbidity Units; NTU), pH (Std units), and specific conductance (µS/cm). Raw water samples are also collected for later nutrient analyses – NH_4, NO_2/NO_3, TN, SRP, TP. Data have been collected from 2015 – present.
   Can Data be Shared? Yes

2. **PI:** Hannah Schaefer (MS student at University of Michigan; USGS)
   Lake Studied: Lake Erie
   Available Data: Historic spawning locations; non-spawning and nursery locations throughout Great Lakes basin and tributaries (1982 – present, depending on data source)
   Can Data be Shared? Yes

3. **PI:** Robin DeBruyne (USGS Great Lakes Science Center; USGS GLSC)
   Lake Studied: Lake Erie
   Available Data: Egg sampling in SCDRS and western Lake Erie (2017 – 2018)
   Can Data be Shared? Yes, will be available on ScienceBase

4. **PI:** Michael Rennie (Lakehead University)
   Lake Studied: Lake Huron, Lake Superior, Lake Ontario
   Available Data: lake whitefish growth and feeding behavior as estimated using stable isotopic analysis of scales (covers whole Great Lakes basin; 1947 - present); bioenergetics modelling across number of fish stocks (PhD work; variations of lake whitefish bioenergetics over concentrations of diaporeia; 2003 - 2004); nearshore and pelagic coupling spatial variations and impacts on conversion efficiency of organisms (last CSMI year on Lake Superior (2015 - 2017); MS work for Marissa)
   Can Data be Shared? Yes

5. **PI**: Dave Caroffino (MDNR)
   Lake Studied: Lake Michigan
   Available Data: commercial harvest/effort, biological monitoring, and age-0 juvenile catch rates in nearshore seins (2013 – present); commercial biomonitoring (length, weight, age, lamprey wounds, sex, maturity, visceral fat index; 1986 – present); juvenile seining (count, length, specimens preserved for genetic analysis by UWSP; 2017 – present); maturity schedules of lake whitefish (MS research for Marissa Hammond, MSU)
   Can Data be Shared? Yes

Determine Impacts of Changes in Food Web or *Dreissenid Invasions* (2)

1. **PI:** Trent Sutton (University of Alaska Fairbanks)
   Lake Studied: Lake Michigan, Lake Huron, Lake Superior
   Available Data: Female data (catch, age, size, proximate composition, fatty acid composition), egg characteristics, larval and juvenile catches and proximate composition (from subset of locations), and juvenile lake whitefish food habits for multiple stocks (fall 2004 – summer 2006)
   Can Data be Shared? Yes, given permission from Co-PIs

2. **PI:** Michael Rennie (Lakehead University)
   Lake Studied: Lake Huron, Lake Superior, Lake Ontario
   Available Data: lake whitefish growth and feeding behavior as estimated using stable isotopic analysis of scales (covers whole Great Lakes basin; 1947 - present); bioenergetics modelling across number of fish stocks (PhD work; variations of lake whitefish bioenergetics over concentrations of diaporeia; 2003 - 2004); nearshore and pelagic coupling spatial variations and impacts on conversion efficiency of organisms (last CSMI year on Lake Superior (2015 - 2017); MS work for Marissa)
   Can Data be Shared? Yes

Develop Great Lakes Food Webs (2)

1. **PI:** Bryan Matthias (Lake Superior Technical Committee)
   Lake Studied: Lake Superior
   Available Data: Coordinated siscowet survey; lakewide harvest and effort data; community-wide fish survey from Ontario (2009 – present); abundance and biomass CPUE for gillnets from Wisconsin (1981 – present)
   Can Data be Shared? Yes

2. **PI:** Steven Pothoven (NOAA)
   Lake Studied: Lake Huron
   Available Data: diets of adult lake whitefish (2007 – 2011; some earlier data going back to 2002)
   Can Data be Shared? Yes

Determine Historic Habitat Locations (2)

1. **PI:** Ed Roseman (USGS GLSC)
   Lake Studied: Lake Michigan, Lake Huron, Lake Erie
   Available Data: egg deposition; larval density and distribution; historic habitat GIS analysis of spawning and nursery areas. Data were collected for 13 years in Detroit River, 2 years for western Lake Erie and Maumee Bay, in 2017 for central and eastern Lake Erie (larvae only), in 2007 for northern Lake Huron (larvae only), and Saginaw Bay (2014 – 2016 egg deposition work with Tomas Hook and MIDNR)
   Can Data be Shared? Yes

2. **PI:** Hannah Schaefer (MS student at University of Michigan; USGS)
   Lake Studied: Lake Erie
   Available Data: Historic spawning locations; non-spawning and nursery locations throughout Great Lakes basin and tributaries (1982 – present, depending on data source)
   Can Data be Shared? Yes

Develop/Modify Lake Whitefish Bioenergetics Model (2)

1. **PI:** Charles Madenjian (USGS GLSC)
   Lake Studied: Lake Michigan
   Available Data: feeding and growth data from lab experiment (2003); Steve Pothoven has some data on stomach contents for lake whitefish from Lake Michigan purchased from commercial fishers (also has energy density of whitefish and PCB determination of some prey species)
   Can Data be Shared? Yes

2. **PI:** Tim Johnson (OMNRF)
   Lake Studied: Lake Superior
   Available Data: samples analyzed for diets, stable isotopes (C, N), total mercury, and energy density (2016 - 2017) to inform Great Lakes basin wide analysis of trophic transfer efficiency
   Can Data be Shared? Yes, once analyses and publication have occurred

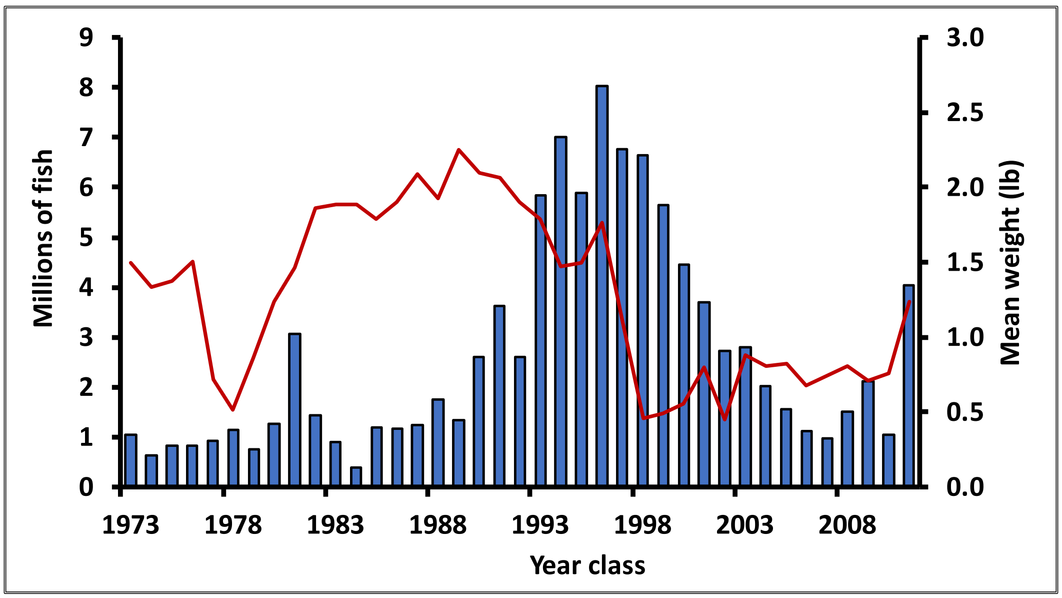
Explore Relationship Between Lake Whitefish and Cisco (1)

1. **PI:** Jory Jonas (MDNR)
   Lake Studied: Lake Michigan
   Available Data: surveys from lakewide assessment protocol (number of species, age structures, otoliths, length, and weight; 1996 or 1997 – present)
   Can Data be Shared? Yes

Monitor Barrier Net Performance (1)

1. **PI:** Scott DeBoe (Consumers Energy/DTE Energy)
   Lake Studied: Lake Michigan
   Available Data: gillnet catch numbers from 4 stations inside barrier net and 4 stations outside barrier net (1989 – 2017)
   Can Data be Shared? Yes

Annotated Bibliography for Understanding Recruitment of Lake Whitefish (*Coregonus clupeaformis*) in the Laurentian Great Lakes



Millions of age-3 lake whitefish recruits (bar) and their average weight (line) for the 1973-2011 year classes estimated through statistical catch-at-age analysis for the Big Bay de Noc spawning stock in northern Green Bay, Lake Michigan

Compiled by
Mark P. Ebener

Great Lakes Fishery Commission
2100 Commonwealth Boulevard
Ann Arbor, Michigan

Table of Contents

Habitat

Assel, R.A., Quinn, F.H., Leshkevich, G.A., and Bolsenga, S.J. 1983. NOAA Great Lakes Ice Atlas. Great Lakes Environ. Res. Lab. Contribution No. 299, Nat. Oceanic Atmosph. Admin., Ann Arbor, MI.
Over 2,800 historic Great Lakes ice charts spanning 20 winters from 1960-79 were digitized and converted to discrete 5-by-5-km grid cells. This data set was analyzed to produce a series of 46 plates, including 9 for each of the 5 Great Lakes with one extra plate for Lake Michigan. The plates portray charts of maximum, minimum, and normal ice concentrations patterns and observation density for nine semimonthly periods beginning the last half of December and ending the last half of April. The percent of the surface area covered by ice was calculated for each ice chart and summarized in tabular format. In addition, 1 10-year data set of ice thickness in the nearshore zone of the Great Lakes, i.e., primarily bays and harbors, is presented to identify ice thickness ranges and ice statigraphic patters for the Great Lakes Region. To complete the Atlas, air temperatures at 25 stations were used to classify winter severity into five severity classes, based on freezing degree-days. Winter severity trends for the pre- and post-ice concentrations climatology periods are identified on an annual and semimonthly time scale for individual stations and for lakewide averages.

Fischer, J.L., Pritt, J.J., Roseman, E.F., Prichard, C.G., Craig, J.M., Kennedy, G.W., and Manny, B.A. 2018. Lake sturgeon, lake whitefish, and walleye egg deposition patterns with response to fish spawning substrate restoration in the St. Clair-Detroit River system. Trans. Am. Fish. Soc. 147: 79-93.
Egg deposition and use of restored spawning substrates by lithophilic fishes (e.g., lake sturgeon *Acipenser fulvescens*, lake whitefish *Coregonus clupeaformis*, and walleye *Sander vitreus*) were assessed throughout the St. Clair-Detroit River system from 2005 to 2016. Bayesian models were used to quantify egg abundance and presence/absence relative to site-specific variables (e.g., depth, velocity, and artificial spawning reef presence) and temperature to evaluate fish use of restored artificial spawning reefs and assess patterns in egg deposition. Lake whitefish and walleye egg abundance, probability of detection, and probability of occupancy were assessed with detection-adjusted methods; lake sturgeon egg abundance and probability of occurrence were assessed using delta-lognormal methods. The models indicated that the probability of walleye eggs occupying a site increased with water velocity and that the rate of increase decreased with depth, whereas lake whitefish egg occupancy was not correlated with any of the attributes considered. Egg deposition by lake whitefish and walleyes was greater at sites with high water velocities and was lower over artificial spawning reefs. Lake sturgeon eggs were collected least frequently but were more likely to be collected over artificial spawning reefs and in greater abundances than elsewhere. Detection-adjusted egg abundances were not greater over artificial spawning reefs, indicating that these projects may not directly benefit spawning walleyes and lake whitefish. However, lake sturgeon eggs observed were collected over artificial spawning reefs, supporting the hypothesis that the reefs provided spawning sites for lake sturgeon and could mitigate historic losses of lake sturgeon spawning habitat.

Goodyear, C.S., Edsall, T.A., Ormsby-Dempsey, D.M., Moss, G.D., and Polanski, P.E. 1982. Atlas of the spawning and nursery areas of Great Lakes fishes. Volume one: Spawning and nursery areas of Great Lakes Fishes: A summary by geographic area. U.S. Fish and Wildlife Service, Washington, DC FWS/OBS-82/52. Library of Congress Card Number 82-600628.
Since the 1950s, intensive efforts have been mounted to reestablish stable, self-sustaining fish communities, mainly by reducing sea lamprey abundance, limiting the harvest of remnant native stocks, and stocking desirable native or exotic species to replace or supplement depleted populations. Many of the native species and some of the desirable, introduced species have responded-favorably and are now supporting valuable, productive fisheries. These successes suggest that continued judicious exercise of

established management strategies will result in further significant improvements in the fish resources and the fisheries. An emerging perspective suggests, however, that enduring, major improvements in the fish resources and the fisheries will require greater emphasis on rehabilitation efforts directed more specifically at safeguarding and improving the quality of the fish habitat in general, and on ensuring fuller utilization of the specialized habitat required by sensitive, embryonic- juvenile life stages of species that are to be included in any future, self-sustaining resource base. We prepared this atlas to provide a comprehensive information base against which past changes in the condition and use of spawning and nursery habitat of Great Lakes fishes could be viewed and evaluated and the needs of the future, self-sustaining resource base could be projected.

Hanrahan, J.L., Kravtsov, S.V., and Roebber, P.J. 2009. Quasi-periodic decadal cycle in levels of lakes Michigan and Huron. J. Great Lakes Res. 35: 30-35.
While Great Lakes' seasonal water-level variations have been previously researched and well documented, few studies thus far addressed longer-term, decadal cycles contained in the 143-yr lake-level instrumental record. Paleo-reconstructions based on Lake Michigan's coastal features, however, hinted to an approximate 30-yr quasi-periodic lake-level variability. In the present study, spectral analysis of 1865–2007 Lakes Michigan/Huron historic levels revealed 8 and 12-yr period oscillations; these time scales match those of large-scale climatic signals previously found in the North Atlantic. While the existing paleodata are inadequate to the task of asserting significance of the 30-yr signal, it is suggested here that this cycle is due to intermodulation of the two near-decadal signals. Furthermore, water budget analysis argues that the North Atlantic decadal climate modes translate to the lake levels primarily through precipitation and its associated runoff.

Hayes, D.B., Ferreri, C.P., and Taylor, W.W. 1996. Linking fish habitat to their population dynamics. Can. J. Fish. Aquat. Sci. 53(Supp. 1): 383-390.
We classify habitat features based on their effects on fish population dynamics and how fish populations affect the habitat's dynamics. We term habitat features that can be reduced in quantity or quality by fish usage as consumable resources. In general, consumable resources regulate fish populations in a density-dependent manner. In contrast, nonconsumable habitat features influence fish populations in a density-independent manner. We further classify habitat features by the influence that fish have on the supply of that resource. We designate habitat features whose supply is unaffected by fish usage (e.g., space) as being dynamically unaffected. Thus, the supply of these resources does not depend on the present or past abundance of fish. The supply of dynamically affected habitat resources (e.g., prey abundance) depends on current and past fish abundance. Using lake whitefish (*Coregonus clupeaformis*), we illustrate how changes in fish habitat can be integrated with changes in fish growth, survival, and reproduction through a stock–recruitment relationship. This example shows that single measures of population response such as carrying capacity or changes in surplus production do not fully represent the population-level changes following a habitat alteration.

Hindley, B., Speller, D., and Desjardine, R. 1977. A winter investigation of three lake trout and lake whitefish spawning shoals in Lake Simcoe, Ontario. Lake Simcoe Fish. Assess. Unit, Min. Nat. Res.
Three lake trout (*Salvelinus namaycush*) and lake whitefish (*Coregonus clupeaformis*) spawning shoals were investigated during the winter months by scuba divers on Lake Simcoe, and large inland lake in south central Ontario. Interstitial dissolved oxygen levels remained near saturation throughout the study period. Water chemical parameters did not vary appreciably from lake averages. Lake trout and lake whitefish eggs were collected using an air lift device and by hand. Seventy percent of the lake trout eggs and 63% of the lake whitefish eggs recovered by the air lift device were alive. Egg densities averaged 29 per square meter (8 – 68/m^2) for lake trout and 165/m^2 (12-322/m^2) for lake whitefish.

Mottled sculpins (*Cottus bairdi*) were identified as predators of both lake whitefish and lake trout eggs. No evidence was found for invertebrate predation on fish eggs. Rubble depth on the spawning shoals appeared to be an important factor in protecting fish eggs from predators. Quantities of lake trout and lake whitefish eggs are surviving throughout the incubation period. The exact effects of increased eutrophication on Lake Simcoe on the quality of the spawning shoals is not known.

Larsson, S., Byström, P., Berglund, J., Carlsson, U., Veneranta, L., Syliva, H., and Hudd, R. 2013. Characteristics of anadromous whitefish (*Coregonus lavaretus* (L.)) rivers in the Gulf of Bothnia. Biology and Management of Coregonid Fishes – 2011. Adv. Limnol. 64: 189-201.
In order to study anadromous whitefish spawning river requirements, we sampled 41 rivers in the Gulf of Bothnia for newly hatched whitefish larvae for one to three consecutive years. Chemical and morphological data (e.g. flow rate, topography, pH, estuary fetch and distance to coastal sandy areas) were collected for each river. Newly-hatched whitefish were caught in 19 rivers whereas whitefish were not confirmed present in 22 rivers. By applying partial least squares discriminant analysis (PLS-DA), data for rivers confirmed to support whitefish were contrasted with data for rivers in which whitefish were not found. The single most important factor was annual average water flow rate. Whitefish larvae were observed in 93% of the rivers with annual mean flow rate > 5 $m^3 s^{-1}$ (N = 14). In contrast, newly-hatched whitefish were only found in 22% of the smaller rivers (N = 27).

Li, Y., Bence, J.R., Zhang, Z., and Ebener, M.P. 2017. Why do lake whitefish move long distances in Lake Huron? Bayesian variable selection of factors explaining fish movement distance. Fish. Res. 195:169-179.
Understanding fish movement patterns is vital for stock assessment and fishery management. We used a variable selection procedure in a Bayesian framework to understand what factors most likely affect the net movement distance of individual fish based on a conventional tag-recovery study of lake whitefish populations in Lake Huron during 2003–2011, where fish of this species with spawning site fidelity were tagged during the spawning season and recovered throughout the year. We found that fish with greater total length, and those that were tagged and released from tagging sites near Cheboygan and Alpena, Michigan, moved longer net distances than fish from other tagging sites. Habitat conditions also had a profound effect on net movement distance. We found that shorter movement distances by lake whitefish can be expected if the relative density of the benthic amphipod *Diporeia* spp. was higher near the tagging site during the recovery year. We also found evidence that lake whitefish may start their annual spawning migration runs earlier during warmer years. More generally, our Bayesian framework for analysis of conventional tagging data has potential for wide applicability, and model details and our code are provided to facilitate this.

Lynch, A.J., Taylor, W.W., and Smith, K.D. 2010. The influence of changing climate on the ecology and management of selected Laurentian Great Lakes fisheries. J. Fish Biol. 77: 1764-1782.
The Laurentian Great Lakes Basin provides an ecological system to evaluate the potential effect of climate change on dynamics of fish populations and the management of their fisheries. This review describes the physical and biological mechanisms by which fish populations will be affected by changes in timing and duration of ice cover, precipitation events and temperature regimes associated with projected climate change in the Great Lakes Basin with a principal focus on the fish communities in shallower regions of the basin. Lake whitefish *Coregonus clupeaformis*, walleye *Sander vitreus* and smallmouth bass *Micropterus dolomieu* were examined to assess the potential effects of climate change on guilds of Great Lakes cold, cool and warm-water fishes, respectively. Overall, the projections for these fishes are for the increased thermally suitable habitat within the lakes, though in different regions than they currently inhabit. Colder-water fishes will seek refuge further north and deeper in the water

column and warmer-water fishes will fill the vacated habitat space in the warmer regions of the lakes. While these projections can be modified by a number of other habitat elements (e.g. anoxia, ice cover, dispersal ability and trophic productivity), it is clear that climate-change drivers will challenge the nature, flexibility and public perception of current fisheries management programmes. Fisheries agencies should develop decision support tools to provide a systematic method for incorporating ecological responses to climate change and moderating public interests to ensure a sustainable future for Great Lakes fishes and fisheries.

Mason, L.A., Riseng, C.M., Gronewold, A.D., Rutherford, E.S., Wang, J., Clites, A.H., Smith, S.D.P., and McIntyre, P.B. 2016. Fine-scale spatial variation in ice cover and surface temperature trends across the surface of the Laurentian Great Lakes. Climatic Change 138: 71-83 Available from https://www.glerl.noaa.gov/pubs/fulltext/2016/20160018.pdf.
The effects of climate change on north temperate freshwater ecosystems include increasing water temperatures and decreasing ice cover. Here we compare those trends in the Laurentian Great Lakes at three spatial scales to evaluate how warming varies across the surface of these massive inland water bodies. We compiled seasonal ice cover duration (1973–2013) and lake summer surface water temperatures (LSSWT; 1994–2013), and analyzed spatial patterns and trends at lake-wide, lake sub-basin, and fine spatial scales and compared those to reported lake- and basin-wide trends. At the lake-wide scale we found declining ice duration and warming LSSWT patterns consistent with previous studies. At the lake sub-basin scale, our statistical models identified distinct warming trends within each lake that included significant breakpoints in ice duration for 13 sub-basins, consistent linear declines in 11 sub-basins, and no trends in 4 sub-basins. At the finest scale, we found that the northern- and eastern-most portions of each Great Lake, especially in nearshore areas, have experienced faster rates of LSSWT warming and shortening ice duration than those previously reported from trends at the lake scale. We conclude that lake-level analyses mask significant spatial and temporal variation in warming patterns within the Laurentian Great Lakes. Recognizing spatial variability in rates of change can inform both mechanistic modeling of ecosystem responses and planning for long-term management of these large freshwater ecosystems.

Mills, K.H. 1985. Response of lake whitefish (*Coregonus clupeaformis*) to fertilization of lake 226, the experimental lakes area. Can. J. Fish. Aquat. Sci. 42: 129-138.
The responses of an unexploited population of lake whitefish (*Coregonus clupeaformis*) to fertilization of Lake 226 (L226), the Experimental Lakes Area, northwestern Ontario, were measured for 4 yr (1973–77). A vinyl sea curtain separated the lake into a northeast (NE) basin, which received P, N, and C additions, and a southwest (SW) basin, which received only N and C additions. Lake whitefish in the NE basin grew faster, had higher coefficients of condition, and had greater recruitment and production than those in the SW basin during the 2nd through 4th yr of fertilization. No differences between basins were detected in annual survival for fish, but survival of age 0 fish was greater in the NE basin. Whitefish production in L226NE averaged twice that in L226SW from the 2nd to the 4th yr of fertilization, though significant variations occurred between years in both the NE and SW populations.

Patrick, P.H., Chen, E., Parks, J., Powell, J., Poulton, J.S., and Fietsch, C. 2013. Effects of fixed and fluctuating temperature on hatch of round whitefish and lake whitefish eggs. N. Am. J. Fish. Manage. 33: 1091-1099.
Temperature-response information for use in evaluating thermal discharges is often over 30 years old and in the nonpeer-reviewed literature, especially for Round Whitefish *Prosopium cylindraceum* and Lake Whitefish *Coregonus clupeaformis* exposed to nonlethal, elevated, and variable temperatures. Egg incubation experiments on Round Whitefish collected in Lake Ontario and Lake Whitefish collected in

Lake Huron were carried out from December 13, 2011, to April 7, 2012. Experimental treatments included ambient baseline control conditions as well as fixed and fluctuating (variable) temperature increases of 1, 2, 3, and 5°C above ambient baseline conditions. For both species, the window for hatching for all experimental temperature treatments was variable (range, 10–38 d for Round Whitefish and 11–44 d for Lake Whitefish), and the hatching windows tended to be greater as temperatures increased. Our results indicated that both fixed and variable incremental increases in temperature above ambient baseline conditions have a statistically significant effect on 50% hatch, and hatch occurs earlier with higher incremental temperature increases. The ecological significance of advanced hatch, such as indirect mortality and food source availability, was evaluated.

Reckahn, J.C. 1986. Long-term cyclical trends in growth of lake whitefish in South Bay, Lake Huron. T. Am. Fish. Soc. 115: 787-804.
A 39-year series of samples (1947–1985) was obtained with gill nets and trawls from a discrete population of lake whitefish *Coregonus clupeaformis* within the innermost basin of South Bay, Manitoulin Island, in northern Lake Huron. Back-calculations based on scales allowed growth in weight to be estimated for 47 year classes of lake whitefish. Growth of young fish prior to entry into exploited sizes was slow in the mid-1930s, increased to a maximum in the early 1950s, declined again to a minimum in the late 1960s, and increased again during the 1970s and early 1980s. Trend analyses with Fourier transformations provided cyclic sine wave models with a 32-year period that fit growth trends better (higher r2) than either linear or polynomial models. Long-term cycles in water level and temperature correlate significantly with the observed growth cycle. These two environmental factors account for 88% of the variation in lake whitefish growth, leaving 12% to be accounted for by community interactions. Based on observations in South Bay and fishery studies in other areas of the province, a hypothesis is suggested that long-term fluctuations in the hydrological cycle and other climatic factors interact to control long-term fluctuations in fish production throughout Ontario.

Riley, S.C., and Adams, J.V. 2010. Long-term trends in habitat use of offshore demersal fishes in western Lake Huron suggest large-scale ecosystem change. T. Am. Fish. Soc. 139: 1322-1334.
We estimated mean depths of capture for offshore demersal fish species, grouped into three habitat-based guilds (shallow benthic, pelagic, and deep benthic), using fall bottom trawl data (27–73 m) in the western main basin of Lake Huron from 1976 to 2007. The mean depth of capture of the shallow and deep benthic guilds initially exhibited a trend toward capture in shallower water, switched to a trend toward capture in deeper water in 1991, and changed back to a trend toward capture in shallower water in 2001–2002. Species in the pelagic guild showed a similar pattern, but the initial change point occurred in 1981 for this guild. Individual species in these guilds showed variable patterns of depth distribution, but a feature common to all guilds and all pelagic and deep benthic species was a change to a trend toward capturing fish in shallower water that occurred nearly simultaneously (1999–2002). These common trends suggest that large-scale factors are affecting the habitat use of offshore demersal fish species in Lake Huron. The depth distributions of the three guilds have converged in recent years, indicating that the locations of suitable habitat for offshore demersal fishes may be changing. Our results indicate that the benthic ecology of the western main basin of Lake Huron is undergoing profound changes across a large spatial scale that are affecting the habitat use of offshore demersal fishes. We suggest that these changes are related to recent invasions of exotic species.

Riley, S.C., Binder, T.R., Wattrus, N.J., Faust, M.D., Janssen, J. Menzies, J., Marsden, J.E., Ebener, M.P., Bronte, C.R., He, J.X., Tucker, T.R., Hansen, M.J., Thompson, H.T., Muir, A.M., and Krueger, C.C. 2014. Lake trout in northern Lake Huron spawn on submerged drumlins. J. Great Lakes Res. 40: 415-420.

Recent observations of spawning lake trout *Salvelinus namaycush* near Drummond Island in northern Lake Huron indicate that lake trout use drumlins, landforms created in subglacial environments by the action of ice sheets, as a primary spawning habitat. From these observations, we generated a hypothesis that may in part explain locations chosen by lake trout for spawning. Most salmonines spawn in streams where they rely on streamflows to sort and clean sediments to create good spawning habitat. Flows sufficient to sort larger sediment sizes are generally lacking in lakes, but some glacial bedforms contain large pockets of sorted sediments that can provide the interstitial spaces necessary for lake trout egg incubation, particularly if these bedforms are situated such that lake currents can penetrate these sediments. We hypothesize that sediment inclusions from glacial scavenging and sediment sorting that occurred during the creation of bedforms such as drumlins, end moraines, and eskers create suitable conditions for lake trout egg incubation, particularly where these bedforms interact with lake currents to remove fine sediments. Further, these bed forms may provide high-quality lake trout spawning habitat at many locations in the Great Lakes and may be especially important along the southern edge of the range of the species. A better understanding of the role of glacially-derived bedforms in the creation of lake trout spawning habitat may help develop powerful predictors of lake trout spawning locations, provide insight into the evolution of unique spawning behaviors by lake trout, and aid in lake trout restoration in the Great Lakes.

Vanderploeg, H.A., Bolsenga, S.J., Fahnenstiel, G.L., Liebig, J.R., and Gardner, W.S. 1992. Plankton ecology in an ice-covered bay of Lake Michigan: utilization of a winter phytoplankton bloom by reproducing copepods. Hydrobiologia 243: 175-183.
Plankton ecology was examined during the 1986 winter in Grand Traverse Bay, a 190 m deep, fjord-like bay on Lake Michigan. Before ice cover, algal concentration was low and uniformly distributed with depth, as it is in open Lake Michigan. During ice cover (February and March), a bloom of a typical winter-spring phytoplankton community developed in the upper 40 m, resulting in a 4 to 7-fold increase in feeding rate of adult *Diaptomus* spp. High algal concentration and zooplankton feeding persisted after ice melt (April). During and after ice cover, lipid concentrations of *Diaptomus* dropped rapidly from 34% of dry weight to 17 % because of egg production. High incident photosynthetically active radiation (PAR), high (45–50%) PAR transmittance of the ice due to little snow on the ice, and water column stability were probably responsible for the bloom. High ice transparency may be a common feature of large lakes and bays, where strong winds blow snow cover off the ice, or at low latitudes where snowmelt due to occasional rains and warm temperature is common. Winter reproducing calanoid copepods use these blooms to increase their reproductive output.

Veneranta, L., Hudd, R., and Vanhatalo, J. 2013. Reproduction areas of sea-spawning coregonids reflect the environmental in shallow coastal waters. Mar. Ecol. Prog. Ser. 477: 231-250.
We evaluated the distribution and the extent of sea-spawning whitefish *Coregonus lavaretus* (L.) and vendace *Coregonus albula* larval areas in the Gulf of Bothnia, northern Baltic Sea, and suggest that the distribution of the reproduction areas could be an indicator of the health of the Baltic Sea shores. Our Geographic Information System (GIS) based predictive spatial model of habitat selection covers nearly the whole distribution area of both species. Extensive sampling data on larval occurrence were combined with GIS raster layers on environmental variables and used in a Gaussian process model, which predicts the spatial probability of larval occurrence. Out of 22 studied variables, shore profile, distance to sandy shallow shore, distance to 20 m depth contour line and ice break-up week were the most important for describing larval areas of both species. The earliest larval stages of sea-spawning whitefish can be found in various habitats close to the shoreline, but the highest densities of larvae were observed along gently sloping, shallow sandy shores. Vendace reproduction occurs in the northernmost and less saline areas of the Bothnian Bay and larval stages use the shallow areas. Compared to previous

studies from 1990s, the extent of whitefish larval areas has decreased. We discuss the possibility that long-term changes in the environment, such as more frequent iceless winters and increasing eutrophication, have reduced the reproductive success of sea-spawning coregonids. Larval distribution maps can be used to focus conservation measures in the most appropriate places. We propose to use this method as a monitoring tool, and produce maps to assist integrated coastal zone management and environmental protection.

Wang, J., Kessler, J., Hang, F., Hu, H. Clites, A.H., and Chu, P. 2017. Analysis of Great Lakes ice cover climatology: winters 2012-2017. NOAA Tech. Mem. GlERL-171.
This report analyzes the 2012-2017 ice cycles in the Great Lakes region through dates of first (last) ice, ice duration, ice cover distribution, ice cover anomalies, and ice cover seasonal progression. Line plots and ice charts aid the discussion of seasonal and spatial patterns of ice cover over the Great Lakes during each winter season. The data, which is in the form of digitized ice charts, was produced by the National Ice Center and are available to download from their website as ASCII files, http://www.natice.noaa.gov/products/great_lakes.html.

Stock Structure

Ames, E.P. 2011. Atlantic cod stock structure in the Gulf of Maine. Fisheries 29: 10-28.
Atlantic cod (*Gadus morhua*) in the Gulf of Maine provide an important but depleted fishery that needs to be made sustainable. However, restoring and maintaining robust population components to achieve sustainability is made difficult when their distribution and character is unknown. This study clarifies the structure of the Gulf of Maine cod grouping by deriving the distribution, movements, and behavior of population components from 1920s data and surveys of retired fishermen. These derivations are consistent with current cod populations and with the existence of localized spawning components. Nearly half the coastal spawning grounds of 50 to 70 years ago are abandoned today and their spawning components have disappeared, suggesting depletion, undetected by system-wide assessments, may have been well advanced by the 1980s.

Andvik, R.T., Sloss, B.L., VanDeHey, J.A., Claramunt, R.M., Hansen, S.P., and Isermann, D.A. 2016. Mixed stock analysis of Lake Michigan's lake whitefish *Coregonus clupeaformis* commercial fishery. J. Great Lakes Res. 42: 660-667.
Lake whitefish (*Coregonus clupeaformis*) support the primary commercial fishery in Lake Michigan. Discrete genetic stocks of lake whitefish have been identified and tagging data suggest stocks are mixed throughout much of the year. Our objectives were to determine if (1) differential stock harvest occurs in the commercial catch, (2) spatial differences in genetic composition of harvested fish were present, and (3) seasonal differences were present in the harvest by commercial fisheries that operate in management zones WI-2 and WFM-01 (Green Bay, Lake Michigan). Mixed stock analysis was conducted on 17 commercial harvest samples (n = 78–145/sample) collected from various ports lake-wide during 2009–2010. Results showed significant mixing with variability in stock composition across most samples. Samples consisted of two to four genetic stocks each accounting for ≥ 10% the catch. In 10 of 17 samples, the stock contributing the largest proportion made up < 60% of the harvest. In general, seasonal and annual differences existed in the proportional stock contribution at a single capture location. Samples from Wisconsin's primary commercial fishing management zone (WI-2) were composed predominately of fish from the Big Bay de Noc (Michigan) stock as opposed to the geographically proximate, North–Moonlight Bay (Wisconsin) stock. These findings have implications for

management and allocation of fish to various quotas. Specifically, geographic location of harvest, the current means of allocating harvest quotas, is not the best predictor of genetic stock harvest.

Anneville, O., Lasne, E., Guillard, J., Eckmann,R., Stockwell, J.D., Gillet, C., and Yule, D.L. 2015. Impact of fishing and stocking practices on coregonid diversity. Food Nutr. Sci. 6: 1045-1055.
Fish species diversity can be lost through interacting stressors including habitat loss, stocking and overfishing. Although a multitude of stressors have played a role in the global decline of coregonid (*Coregonus* spp.) diversity, a number of contemporary studies have identified habitat loss stemming from eutrophication as the primary cause. Unfortunately, reconstructing the role of fishing and stocking practices can be difficult, because these records are incomplete or appear only in hard-to-access historic grey literature. Based on an illustrative set of historic and contemporary studies, we describe how fisheries management practices may have contributed to coregonid diversity loss in European and North American lakes. We provide case studies examining how fishing and stocking may reduce coregonid diversity through demographic decline and introgressive hybridization. In some lakes, fisheries management practices may have led to a loss of coregonid diversity well before issues with habitat degradation manifested. Our review suggests that fish conservation policies could beneficially consider the relative importance of all stressors, including management practices, as potential drivers of diversity loss.

Bernard, A.M., Ferguson, M.M., Noakes, D.L.G., Morrison, B.J., and Wilson, C.C. 2009. How different is different? Defining management and conservation units for a problematic exploited species. Can. J. Fish. Aquat. Sci. 66: 1617-1630.
Discontinuous genetic structure is widely used to delineate local, regional, and phylogenetic groups within species for conservation and management purposes. We used microsatellite markers to assess the genetic distinctiveness of putative stocks and populations of lake whitefish (*Coregonus clupeaformis*) in Ontario waters. Analysis of spawning aggregations in eastern Lake Ontario showed fish from Chaumont Bay, New York, to be weakly differentiated from spawning whitefish in and near the Bay of Quinte, Ontario. No significant differences were found between lake- and bay-spawning aggregations within the Bay of Quinte. These same genetic tools were used to test the distinctiveness and evolutionary significance of Lake Simcoe lake whitefish as a designatable unit (DU) under guidelines established by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC). Although there was marked differentiation among populations from across Ontario, the Lake Simcoe population was closely allied with lake whitefish populations from Lake Ontario and Lake Huron, suggesting that a distinct status is not warranted on genetic grounds. This work demonstrates how assessing hierarchical diversity under COSEWIC's framework can provide key information of the status of exploited populations for fishery management.

Bernatchez, L., and Dodson, J.J. 1991. Phylogeographic structure in mitochondrial DNA of the lake whitefish (*Coregonus clupeaformis*) and its relation to Pleistocene glaciations. Evolution 45: 1016-1035.
Restriction-fragment length polymorphisms were employed to evaluate the phylogenetic relationships, the genetic diversity and the geographic structure in mitochondrial DNA (mtDNA) lineages of the lake whitefish, Coregonus clupeaformis. Thirteen restriction enzymes that produced 148 restriction fragments were used to assay mtDNAs of 525 specimens collected among 41 populations. The sampling covered the entire range of the species, from Alaska to Labrador. Four distinct phylogeographic assemblages were identified. The Beringian assemblage, confined to Yukon and Alaska, was phylogenetically distinct from other assemblages and exhibited the highest level of nucleotide diversity. The Acadian assemblage was confined to southeastern North America and composed of a

unique mtDNA clade. The Atlantic assemblage was confined to southern Quebec and the northeastern United States and was also observed among anadromous populations of northern Hudson Bay. This group was highly polymorphic and responsible for most of the mtDNA diversity observed outside Beringia. The Mississippian assemblage occupied most of the actual range of lake whitefish, from the Mackenzie delta to Labrador. Ninety-two percent of all whitefish of this proposed origin belonged to a single mtDNA haplotype. Overall, the diversity, the geographic structure and the times of divergence of mtDNA phylogenetic assemblages correlate with the Pleistocene glaciations classically assumed to have dramatically altered the genetic diversity of northern fishes in recent evolutionary times. Our results emphasize the dominant role of these catastrophic events in shaping the population genetic structure of lake whitefish.

Bernatchez, L. 2005. On the role of natural selection in promoting population divergence in lake whitefish (*Coregonus clupeaformis*): relevance for population management in the Great Lakes. *In* Proceedings of a workshop on the dynamics of lake whitefish (*Coregonus clupeaformis*) and the amphipod *Diporeia* spp. in the Great Lakes. *Edited* by L.C. Mohr, and T.F. Nalepa. Great Lakes Fish. Comm. Tech. Rep. 66 pp. 21-46.
The author summarizes 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 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.

Casselman, J.M., Collins, J.J., Grossman, E.J., Ihssen, P.E., and Spangler, G.R. 1981. Lake whitefish (*Coregonus clupeaformis*) stocks of the Ontario waters of Lake Huron. Can. J. Fish. Aquat. Sci. 38: 1772-1789.
Historical and contemporary data on lake whitefish (*Coregonus clupeaformis*) from the Ontario waters of Lake Huron were examined for evidence of stocks with the objective of defining population boundaries. We delineated the spatial distribution of five stocks from tag–recapture data and the general location of six additional stocks on the basis of population parameters such as growth rate, age structure, and abundance trends. Samples of fish collected (summer and fall) from 5 of the 11 potential stocks were evaluated on the basis of 11 morphometric and 7 meristic characters. We also examined osseometric features such as shape of scales and otoliths, and electrophoretic characteristics at 32 loci associated with 12 enzyme systems. The summer and fall samples for each group were generally not significantly different. For the phenotypes examined electrophoretically, each stock was in Hardy–Weinberg equilibrium; 12 of the 32 loci considered were polymorphic and 4 of the 10 possible genetic distances

differed significantly from zero. The Inner Basin stock was distinctly different from all other stocks. The Blind River stock was also found to be different by osseometrics, but not by morphometrics or electrophoresis. Osseometrics separated the stocks by basin of origin. Two stocks, Outer Basin and Burnt Island, appeared to be the most similar and could be separated from each other only on the basis of growth rate and tagging data. These two stocks are adjacent to each other in the main basin of Lake Huron, along the south shore of Manitoulin Island. Whitefish stocks of Lake Huron represent groups of fish that differ phenotypically and genotypically in varying degrees, are spatially separated, and behave as cohesive units. We conclude that they should be regarded as functional units for management purposes.

Dunlop, E.S., Eikeset, A.M., and Stenseth, N.C. 2015. From genes to populations: how fisheries-induced evolution alters stock productivity. Ecol. App. 25: 1860-1868.
By removing individuals with certain heritable characteristics such as large body size, harvesting may induce rapid evolutionary change in fish life history. There is controversy, however, as to the prevalence of fisheries-induced evolution (FIE) and to what extent it should be considered as part of sustainable resource management. Recent research has shown that FIE can be difficult to detect and its economic effects might not always be significant. Here, we show how population growth rate (r), a critical factor affecting sustainability and recovery, is affected by FIE through the analysis of a simulation model that demonstrates the link between individual-level genetic processes and stock dynamics. We examine how different levels of evolvability, fishing intensity, and density-dependence interact to influence r in three commercially harvested species: Atlantic cod (*Gadus morhua*), lake whitefish (*Coregonus clupeaformis*), and yellow perch (*Perca flavescens*). We demonstrate that at low harvest levels, evolution has minimal effect on r for all three species. However, at the harvest rates experienced by many fish stocks, evolution increases r and reduces the risk of collapse for cod and whitefish. During the initial stages of a harvest moratorium, a switch occurs, and r becomes reduced as a consequence of evolution. These results explain how evolution increases stock resilience, but also impedes recovery after periods of intense harvesting.

Ebener, M.P., and Copes, F.A. 1985. Population statistics, yield estimates, and management considerations for two lake whitefish stocks in Lake Michigan. N. Am. J. Fish. Manage. 5: 435–448.
Lake whitefish (*Coregonus clupeaformis*) were tagged at North and Moonlight bays (NMB), Wisconsin and Big Bay de Noc (BBN), Michigan, and commercial catches were sampled in 1975-1980 to determine discreteness, distribution, biological statistics, and equilibrium yield per recruit for lake whitefish stocks in Green Bay and northern Lake Michigan. Discrete stocks were associated with the spawning grounds at NMB and BBN and fish from the NMB stock were migratory, whereas fish from the BBN stock were not. Age-3 lake whitefish dominated the commercial harvest from the BBN stock, but ages 3-5 comprised the majority of the harvest from the NMB stock. The 1972 and 1975 year classes were more abundant than other year classes in the 1975-1980 harvest from the NMB stock, whereas the 1976 year class was more abundant in the 1979-1980 harvest from the BBN stock. Mortality rates were higher for fish from the BBN stock (84%) than for fish from the NMB stock (65%), and fish of Age-7 and older experienced lower mortality rates than younger ages. Fishing caused a larger proportion of the total mortality in the BBN stock than in the NMB stock. The population size of the NMB stock was roughly 3-4 times larger than the BBN stock. Estimated yield per recruit was greater for the BBN stock than for the NMB stock and indicated that increasing the minimum size limit would reduce yield per recruit for both stocks but would increase the biomass of spawners and spawning frequency - substantially so in BBN. We concluded that management steps to delay age at recruitment to the fishery and increase the biomass would benefit the BBN stock but possibly not the NMB stock. Increased fishing effort on either population would not be beneficial for the stocks.

Ebener, M.P., Brenden, T.O., Wright, G.M., Jones, M.L., and Faisal, M. 2010a. Spatial and temporal distributions of lake whitefish spawning stocks in northern lakes Michigan and Huron, 2003-2006. J. Great Lakes Res. 36(Supp. 1): 38-51.
Adult lake whitefish were tagged and released from the Big Bay de Noc (BBN) and Naubinway (NAB) stocks in northern Lake Michigan, and the Detour (DET) and Cheboygan (CHB) stocks in northern Lake Huron during 2003–2006 to describe their spatial and temporal distributions. The contemporary spatial distributions were compared with past distributions of the BBN and NAB stocks. Sixty-two percent of BBN tag recoveries occurred in Wisconsin waters during winter, spring and summer, but 83% of fall tag recoveries were made near the tagging site. Eighty-eight percent of the NAB tag recoveries were made in the management unit of tagging and 7% occurred into northern Lake Huron. Over 90% of the DET stock remained in the vicinity of the tagging sites regardless of the season, while 75% of the CHB tag recoveries were made in northwestern Lake Huron and 17% were made in Ontario. Based on regression tree analysis, there were strong stock, season, and year effects on movement distances, with weaker effects due to sex and length at tagging. Spatial distribution of the BBN stock changed from 1978–1982 to 2003–2008, but spatial distribution of the NAB stock did not. Substantial differences in movement and distribution existed among the four stocks, large seasonal differences in spatial distribution were found within some stocks, and lake whitefish exhibited strong spawning site fidelity. Present management unit boundaries are inappropriate for managing three of our four stocks, and agencies should consider developing single harvest limits for both northern Lake Huron and western Lake Michigan.

Eberts, R.L., Wissel, B., Manzon, R.G., Wilson, J.Y., Boreham, D.R., and Somers, C.M. 2016. Consistent differential resource use by sympatric lake (*Coregonus clupeaformis*) and round (*Prosopium cylindraceum*) whitefish in Lake Huron: a multi-time scale isotopic niche analysis. Can. J. Fish. Aquat. Sci. 73: 1072-1080.
Lake (*Coregonus clupeaformis*) and round (*Prosopium cylindraceum*) whitefish are sympatric benthivores in Lake Huron that are thought to coexist via niche partitioning. However, little is known about long-term resource use and niche overlap across different temporal scales. We used a multiyear (2010–2012) and multi-tissue (liver, muscle, and bone layers) isotopic niche analysis to characterize and compare resource use by lake and round whitefish across several time scales. Lake whitefish consistently used more diverse, 13C-depleted (mean δ13C = −21.9‰) and 15N-enriched (mean δ15N = +9.3‰) resources than round whitefish (mean δ13C = −18.2‰; mean δ15N = +8.3‰). Niche overlap occurred only in liver, representing the spawning period, while niche segregation was highest in juvenile life stages. Individuals of both species made variable resource shifts among time periods, suggesting that spawning aggregations are composed of individuals representing a variety of feeding strategies and locations. Our study confirms that differential resource use is an important strategy for these fish as adults and demonstrates life-long niche partitioning beginning before age-2

Eberts, R.L., Wissel, B., Simpson, G.L., Crawford, S.S., Stott, W., Hanner, R.H., Manzon, R.G., Wilson, J.Y., Boreham, D.R., and Somers, C.M. 2017. Isotopic structure of lake whitefish in Lake Huron: evidence for regional and local populations based on resource use. N. Am. J. Fish. Manage. 37: 133-148.
Lake Whitefish *Coregonus clupeaformis* is the most commercially valuable species in Lake Huron. The fishery for this species has historically been managed based on 25 management units (17 in Canada, 8 in the USA). However, congruence between the contemporary population structure of Lake Whitefish and management units is poorly understood. We used stable isotopes of carbon (δ13C) and nitrogen (δ15N), food web markers that reflect patterns in resource use (i.e., prey, location, habitat), to assess the

population structure of spawning-phase Lake Whitefish collected from 32 sites (1,474 fish) across Lake Huron. We found large isotopic variation among fish from different sites (ranges: δ13C = 10.2‰, δ15N = 5.5‰) and variable niche size and levels of overlap (standard ellipse area = 1.0–4.3‰). Lake Huron contained spawning-phase fish from four major isotopic clusters largely defined by extensive variation in δ13C, and the isotopic composition of fish sampled was spatially structured both within and between lake basins. Based on cluster compositions, we identified six putative regional groups, some of which represented sites of high diversity (three to four clusters) and others with less (one to two clusters). Analysis of isotopic values from Lake Whitefish collected from summer feeding locations and baseline prey items showed similar isotopic variation and established spatial linkage between spawning-phase and summer fish. Our results show that summer feeding location contributes strongly to the isotopic structure we observed in spawning-phase fish. One of the regional groups we identified in northern Georgian Bay is highly distinct based on isotopic composition and possibly ecologically unique within Lake Huron. Our findings are congruent with several previous studies using different markers (genetics, mark–recapture), and we conclude that current management units are generally too small and numerous to reflect the population structure of Lake Whitefish in Lake Huron.

Enberg, K., Jørgensen, C., Dunlop, E.S., Varpe, Ø., Boukal, D.S., Baulier, L. Eliassen, S., and Heino, M. 2012. Fishing-induced evolution of growth: concepts, mechanisms and the empirical evidence. Marine Ecol. 33: 1-25.
The interest in fishing-induced life-history evolution has been growing in the last decade, in part because of the increasing number of studies suggesting evolutionary changes in life-history traits, and the potential ecological and economic consequences these changes may have. Among the traits that could evolve in response to fishing, growth has lately received attention. However, critical reading of the literature on growth evolution in fish reveals conceptual confusion about the nature of 'growth' itself as an evolving trait, and about the different ways fishing can affect growth and size-at-age of fish, both on ecological and on evolutionary time-scales. It is important to separate the advantages of being big and the costs of growing to a large size, particularly when studying life-history evolution. In this review, we explore the selection pressures on growth and the resultant evolution of growth from a mechanistic viewpoint. We define important concepts and outline the processes that must be accounted for before observed phenotypic changes can be ascribed to growth evolution. When listing traits that could be traded-off with growth rate, we group the mechanisms into those affecting resource acquisition and those governing resource allocation. We summarize potential effects of fishing on traits related to growth and discuss methods for detecting evolution of growth. We also challenge the prevailing expectation that fishing-induced evolution should always lead to slower growth.

Frazin, W.G., and Clayton, J.W. 1977. A biochemical genetic study of zoogeography of lake whitefish (*Coregonus clupeaformis*) in western Canada. J. Fish. Res. Board Can. 34: 617-625.
Frequencies of alleles of the genes governing electrophoretic phenotypes of lake whitefish (*Coregonus clupeaformis*) muscle glycerol-3-phosphate dehydrogenase (G-3-PDH) and lactate dehydrogenase (LDH) enzymes, the genetics of which were determined previously, proved useful tools for characterizing populations. Malate dehydrogenase (MDH) and hemoglobin electrophoretic phenotypes, the genetics of which have not been determined, proved useful only for discerning differences among large groups of populations. Using all these characters we determined postglacial routes of gene flow among western Canadian lake whitefish populations and related the biochemical data to the glacial refugia in which lake whitefish are believed to have survived the Wisconsin glaciation. Apparently most lake whitefish populations west of the Ontario–Manitoba boundary and east of the Rocky Mountains were derived from a Mississippi refugium stock with some input from the Bering refugium. At an early stage in the mixing of the two stocks, headwaters of the Peace, Athabasca, and Mackenzie rivers and the Fraser

River system were invaded. Subsequently, these areas were cut off from mainstem rivers of the plains, and a G-3-PDH allele not found in early emigrants from the Mississippi refugium appeared and spread throughout the major river systems of central Canada. No evidence was found that any Mississippi stock lake whitefish were able to invade the upper Liard River and Yukon River system including the area of the Bering refugium. Bering stock lake whitefish probably emigrated from that refugium by way of headwater transfer from the Yukon River to the Liard River and possibly, by way of the Porcupine and Peel rivers, from the Yukon River to the lower Mackenzie River. Routes of postglacial dispersal suggested by geological information, rather than selection, appear to provide adequate explanations for the distributions of the biochemical characters in present day lake whitefish populations. This explanation of the biochemical data is also in accord with the distribution of modal gillraker counts in lake whitefish populations and also with the distribution of other freshwater fishes in western Canada.

Healey, M.C. 1975. Dynamics of exploited whitefish populations and their management with special reference to the Northwest Territories. J. Fish. Res. Board Can. 32: 427-448.
Available data on mortality, growth, reproduction, and stock size in exploited and unexploited populations of lake whitefish (*Coregonus clupeaformis*) are reviewed with a view to understanding the dynamics of exploited populations and improving their management. Natural mortality ranged from about 0.20 to 0.80 in unexploited populations. In exploited populations total mortality was as high as 0.94. Unexploited populations showed a wide range of growth rates. Growth rate increased with increasing exploitation, and growth rate in all heavily exploited populations was similar to the most rapid growth rate shown by unexploited stocks. Heavily exploited whitefish matured at a younger age and possibly also at a smaller size than those which were unexploited. Limited data on stock size suggest that although total population size declines under heavy exploitation, the vulnerable population remains of similar size. It is concluded that whitefish respond to fluctuations in population size through compensatory changes in growth rate, the difference between growth rate in a population and maximum growth rate is a measure of its scope for compensating for increased mortality. Populations with slow growth rate and low mortality should, therefore, have the best fishery potential, while those with high growth rate and high mortality have a low fishery potential. Further, it is possible to judge the fishery potential of a population or its stage of exploitation from relatively simple measurements of mortality, growth, age structure, and maturity.

Ihssen, P.E, Evans, D.O., Christie, W.J., Reckahn, J.A., and DesJardine, R.L. 1981. Life history, morphology, and electrophoretic characteristics of fi e allopatric stocks of lake whitefish (*Coregonus clupeaformis*) in the Great Lakes region. Can. J. Fish. Aquat. Sci. 38: 1790-1807.
Ecological, morphological, and electrophoretic variation among five allopatric Ontario lake whitefish (*Coregonus clupeaformis*) stocks was studied. The stocks differ in terms of diet, growth rate, movement patterns, fecundity, and egg and larval size. Morphologically, the five stocks were also different for characters such as number of gill rakers, number of pyloric ceca, and in size, adjusted for fork length, of the tail, dorsal fin, and the eye. Discriminant functions, derived from body measurements and meristic counts, classified specimens accurately into their lakes of origin. Highly significant allele frequency differences were found at 6 of the 32 electrophoretic loci examined. Standard genetic distances, derived from electrophoretic allele frequency differences, corresponded roughly to the order in which these stocks became isolated following retreat of the last continental glaciation. The genetic distance of the Opeongo stock from the other stocks is about one order of magnitude larger than the genetic distances among the other stocks. The Opeongo stock is also somewhat unusual ecologically, having different egg size and fecundity characteristics compared with the other stocks and being a member of a sympatric dwarf/normal pair. Dendrograms, derived from the Mahanalobis distances for the meristic variation and the Nei genetic distances for the electrophoretic variation, showed similar branching patterns, but the

branching patterns for the morphometric versus the biochemical variation were different. A significant part of the morphometric variation among the stocks was related to differences in growth rates of the stocks, most body measurements being negatively correlated with growth rate. The Mahanalobis distances for the meristic variation (including pyloric ceca counts) were correlated with the standard genetic distances from the electrophoretic data. The ecological, morphological, and biochemical variation among the stocks, in relation to local adaptation, is discussed.

Imhof, M., Leary, R., and Booke, H.E. 1980. Population of stock structure of lake whitefish, Coregonus clupeaformis, in northern Lake Michigan as assessed by isozyme electrophoresis. Can. J. Fish. Aquat. Sci. 37: 783-793.
Electrophoretic analysis of three polymorphic isozymes (lactate, malate, and glycerol-3-phosphate dehydrogenases) from lake whitefish, Coregonus clupeaformis, indicated that at least four populations exist in northern Lake Michigan. Cluster analysis of Nei genetic identity indices revealed much temporal and spatial overlap among population ranges. The overlap did not appear complete since the LDH A allele exhibited clinal variation with increasing frequency from south to north. Because population ranges overlap spatially and temporally, commercial catches are likely to contain fish from more than one population.

Li, Y., Bence, J.R., and Brenden, T.O. 2014. An evaluation of alternative assessment approaches for intermixing fish populations: a case study with Great Lakes lake whitefish. ICES J. Mar. Sci.; doi:10.1093/icesjms/fsu057.
We used simulation modeling to explore how three statistical catch-at-age approaches for assessing intermixed fisheries performed in terms of assessment accuracy and management performance, under differing productivity, mixing, and harvest levels. Simulations were based on intermixing lake whitefish (*Coregonus clupeaformis*) populations in the upper Laurentian Great Lakes of North America. We found that with intermixing, the “separate” assessment approach, which ignored intermixing and treated mixed populations as unit stocks, produced biased estimates of spawning stock biomass (SSB); however, the “pooled” assessment approach, which lumped populations and assessed them as a single stock, was nearly unbiased in estimating SSB. The “overlap” assessment approach, which estimated the populations in one combined assessment model by incorporating actual mixing rates, was most strongly biased in estimating SSB in the absence of mixing, with bias decreasing as mixing levels increased. With high mixing levels, the overlap method had difficulty converging on unique solutions. The pooled approach provided better management performance than the separate approach with intermixing. When the overlap method could be applied, it provided the greatest SSB with little reductions in yield and the lowest inter-annual variation in yield. Relative performances of the assessment approaches were robust to assumed harvest levels.

Nathan, L.R., Sloss, B.L., VanDeHey, J.A., Andvik, R.T., Claramunt, R.M., Hansen, S., and Sutton, T.M. 2016. Temporal stability of lake whitefish genetic stocks in Lake Michigan. J. Great Lakes Res. 42: 433-439.
Lake whitefish *Coregonus clupeaformis* are the predominant species in the Lake Michigan commercial fishing industry. Six genetic stocks were identified in Lake Michigan in 2007; however, genetic structure can fluctuate throughout time due to demographic variables and changing environments. Temporally stable genetic units have a higher probability of containing genetically adaptive traits and thus, are integral components of a sustainable stock-based management approach. The objective of this research was to determine if the genetic stock structure of lake whitefish in Lake Michigan has remained temporally stable from the 1970s through early 2007. Archived scale samples collected by state and tribal agencies during annual assessments from the 1970s, 1980s, and 1990s were used as a source of

deoxyribonucleic acid (DNA). Samples were genotyped at 11 microsatellite loci consistent with the contemporary genetic stock dataset. Tests of FST, Jost's DEST, and Nei's genetic distance were used to compare nine historical sample populations to contemporary stocks. Most stocks showed temporal stability for a majority of the three different analysis methods. The only historical samples to not support the trend of temporal stability were located in the Green Bay region, where two genetic stocks are present in close proximity and are known to have relatively high levels of gene flow between the two stocks. The prevalence of temporal stability gives support to the theory that a stock-based management plan is appropriate for lake whitefish in Lake Michigan.

Scheerer, P.D., and Taylor, W.W. 1985. Population dynamics and stock differentiation of lake whitefish in northeastern Lake Michigan with implications for their management. N. Am. J. Fish. Mange. 5: 526-536.
Lake whitefish (*Coregonus clupeaformis*) were tagged and the commercial trap-net catch was sampled in northeastern Lake Michigan to differentiate discrete stocks and determine their vital statistics. Distribution of tag returns and statistical comparisons of certain population parameters suggested the existence of at least three stocks in the study area. The stock inhabiting the North Shore area of eastern Lake Michigan was considerably larger in both numbers and biomass than the stock fished near Leland, Michigan. The Leland catch has a broader age composition and contained larger fish than the North Shore and Beaver Island samples. Exploitation and total mortality rates were similar in the North Shore and Leland fisheries. The more abundant North Shore stock showed slower back-calculated and instantaneous growth than the Leland stock. In terms of management, statistics of abundance growth, and mortality clearly varied between different lake whitefish stocks within Lake Michigan, indicating stock-by-stock management programs would be more likely to succeed than a lakewide program.

Stott, W.L., VanDeHey, J.A., and Sloss, B.L. 2010. Genetic diversity of lake whitefish in lakes Michigan and Huron; sampling standardization, and research priorities. J. Great Lakes Res. 36(Supple. 1): 59-65.
We combined data from two laboratories to increase the spatial extent of a genetic data set for lake whitefish Coregonus clupeaformis from lakes Huron and Michigan and saw that genetic diversity was greatest between lakes, but that there was also structuring within lakes. Low diversity among stocks may be a reflection of relatively recent colonization of the Great Lakes, but other factors such as recent population fluctuation and localized stresses such as lamprey predation or heavy exploitation may also have a homogenizing effect. Our data suggested that there is asymmetrical movement of lake whitefish between Lake Huron and Lake Michigan; more genotypes associated with Lake Michigan were observed in Lake Huron. Adding additional collections to the calibrated set will allow further examination of diversity in other Great Lakes, answer questions regarding movement among lakes, and estimate contributions of stocks to commercial yields. As the picture of genetic diversity and population structure of lake whitefish in the Great Lakes region emerges, we need to develop methods to combine data types to help identify important areas for biodiversity and thus conservation. Adding genetic data to existing models will increase the precision of predictions of the impacts of new stresses and changes in existing pressures on an ecologically and commercially important species.

Stott, W., Ebener, M.P., Mohr, L., Hartman, T., Johnson, J., and Roseman, E.F. 2013. Spatial and temporal genetic diversity of lake whitefish (*Coregonus clupeaformis* (Mitchell)) from Lake Huron and Lake Erie. Biology and management of coregonid fishes – 2011. Advanc. Limnol. 64: 205-222.
Lake whitefish (*Coregonus clupeaformis* (Mitchill)) are important commercially, culturally, and ecologically in the Laurentian Great Lakes. Stocks of lake whitefish in the Great Lakes have recovered from low levels of abundance in the 1960s. Reductions in abundance, loss of habitat and

environmental degradation can be accompanied by losses of genetic diversity and overall fitness that may persist even as populations recover demographically. Therefore, it is important to be able to identify stocks that have reduced levels of genetic diversity. In this study, we investigated patterns of genetic diversity at microsatellite DNA loci in lake whitefish collected between 1927 and 1929 (historical period) and between 1997 and 2005 (contemporary period) from Lake Huron and Lake Erie. Genetic analysis of lake whitefish from Lakes Huron and Erie shows that the amount of population structuring varies from lake to lake. Greater genetic divergences among collections from Lake Huron may be the result of sampling scale, migration patterns and demographic processes. Fluctuations in abundance of lake whitefish populations may have resulted in periods of increased genetic drift that have resulted in changes in allele frequencies over time, but periodic genetic drift was not severe enough to result in a significant loss of genetic diversity. Migration among stocks may have decreased levels of genetic differentiation while not completely obscuring stock boundaries. Recent changes in spatial boundaries to stocks, the number of stocks and life history characteristics of stocks further demonstrate the potential of coregonids for a swift and varied response to environmental change and emphasize the importance of incorporating both spatial and temporal considerations into management plans to ensure that diversity is preserved.

VanDeHey, J.A., Sloss, B.L., Peeters, P.J., and Sutton, T.M. 2009. Genetic structure of lake whitefish (Coregonus clupeaformis) in Lake Michigan. Can. J. Fish. Aquat. Sci. 66: 382-393.
Genetic relationships among lake whitefish (Coregonus clupeaformis) spawning aggregates in Lake Michigan were assessed and used to predict a stock or management unit (MU) model for the resource. We hypothesized that distinct spawning aggregates represented potential MUs and that differences at molecular markers underlie population differentiation. Genetic stock identification using 11 microsatellite loci indicated the presence of six genetic MUs. Resolved MUs corresponded to geographically proximate spawning aggregates clustering into genetic groups. Within MUs, analyses suggested that all but one delineated MU was a stable grouping (i.e., no between-population differences), with the exception being the Hog Island – Traverse Bay grouping. Elk Rapids was the most genetically divergent population within Lake Michigan. However, low Fst values suggested that moderate to high levels of gene flow occur or have occurred in the past between MUs. Significant tests of isolation by distance and low pairwise Fst values potentially led to conflicting results between traditional analyses and a Bayesian approach. This data set could provide baseline data from which a comprehensive mixed-stock analysis could be performed, allowing for more efficient and effective management of this economically and socially important resource.

VanDeHey, J.A., Sloss, B.L., Peeters, P.J., and Sutton, T.M. 2010. Determining the efficacy of microsatellite DNR-based mixed stock analysis of Lake Michigan's lake whitefish commercial fishery. J. Great Lakes Res. 36(Supp. 1): 52-58.
Management of commercially exploited fish should be conducted at the stock level. If a mixed stock fishery exists, a comprehensive mixed stock analysis is required for stock-based management. The lake whitefish *Coregonus clupeaformis* comprises the primary commercial fishery across the Great Lakes. Recent research resolved that six genetic stocks of lake whitefish were present in Lake Michigan, and long-term tagging data indicate that Lake Michigan's lake whitefish commercial fishery is a mixed stock fishery. The objective of this research was to determine the usefulness of microsatellite data for conducting comprehensive mixed stock analyses of the Lake Michigan lake whitefish commercial fishery. We used the individual assignment method as implemented in the program ONCOR to determine the accuracy level at which microsatellite data can reliably identify component populations or stocks. Self-assignment of lake whitefish to their population and stock of origin ranged from > 96% to 100%. Evaluation of genetic stock discreteness indicated a moderately high degree of correct assignment

(average = 75%); simulations indicated supplementing baseline data by ~ 50 to 100 individuals could increase accuracy by up to 4.5%. Simulated mixed stock commercial harvests with known stock composition showed a high degree of correct proportional assignment between observed and predicted harvest values. These data suggest that a comprehensive mixed stock analysis of Lake Michigan's lake whitefish commercial fishery is viable and would provide valuable information for improving management.

Walker, S.H., Prout, M.W., Taylor, W.W., and Winterstein, S.R. 1993. Population dynamics and management of lake whitefish stocks in Grand Traverse Bay, Lake Michigan. N. Am. J. Fish. Manage. 13: 73-85.
The population parameters and movement patterns of lake whitefish *Coregonus clupeaformis* in Grand Traverse Bay, Lake Michigan, were investigated in response to an expanding commercial fishery. Tagging data indicated that distinct spawning populations exist in West, Outer, and East bays. Little mixing was observed during the fishing season between the West Bay and East Bay populations, but both contributed to the Outer Bay fishery. The West Bay population was predominantly localized and characterized by a broad age distribution and low exploitation rates. The East Bay population was characterized by a younger age distribution and higher exploitation rates. The Outer Bay fishery mainly consisted of fish 4–6 years of age, with intermediate growth and exploitation rates. Biomass in the fishery decreased by 39%, from 439,000 kg in 1986 to 268,000 kg in 1987, because of a combination of increased exploitation and decreased recruitment. Catch quotas (total allowable catch, TAC) for Grand Traverse Bay stocks are dependent upon estimates of recruitment, which is unstable and unpredictable, Calculations of TAC that have resulted, if realized as true harvest levels, could jeopardize the integrity of these lake whitefish stocks. Calculations of TAC can be improved by including an index of the strength of the recruiting year-class.

Yule, D.L., Stockwell, J.D., Black, J.A., Cullis, K.I., Cholwek, G.A., Myers, J.T. 2008. How systematic age underestimation can impede understanding of fish population dynamics: lessons learned from a Lake Superior cisco stock. T. Am. Fish. Soc. 137: 481-485.
Systematic underestimation of fish age can impede understanding of recruitment variability and adaptive strategies (like longevity) and can bias estimates of survivorship. We suspected that previous estimates of annual survival (S; range = 0.20-0.44) for Lake Superior ciscoes *Coregonus artedi* developed from scale ages were biased low. To test this hypothesis, we estimated the total instantaneous mortality rate of adult ciscoes from the Thunder Bay, Ontario, stock by use of cohort-based catch curves developed from commercial gill-net catches and otolith-aged fish. Mean S based on otolith ages was greater for adult females (0.80) than for adult males (0.75), but these differences were not significant. Applying the results of a study of agreement between scale and otolith ages, we modeled a scale age for each otolith-aged fish to reconstruct catch curves. Using modeled scale ages, estimates of S (0.42 for females, 0.36 for males) were comparable with those reported in past studies. We conducted a November 2005 acoustic and midwater trawl survey to estimate the abundance of ciscoes when the fish were being harvested for roe. Estimated exploitation rates were 0.085 for females and 0.025 for males, and the instantaneous rates of fishing mortality were 0.089 for females and 0.025 for males. The instantaneous rates of natural mortality were 0.131 and 0.265 for females and males, respectively. Using otolith ages, we found that strong year-classes at large during November 2005 were caught in high numbers as age-1 fish in previous annual bottom trawl surveys, whereas weak or absent year-classes were not. For decades, large-scale fisheries on the Great Lakes were allowed to operate because ciscoes were assumed to be short lived and to have regular recruitment. We postulate that the collapse of these fisheries was linked in part to a misunderstanding of cisco biology driven by scale-ageing error.

Stock Recruitment

Anneville, O., Souissi, S., Molinero, J.C., and Gerdeaux, D. 2009. Influences of human activity and climate change on the stock-recruitment of whitefish, *Coregonus lavaretus*, in Lake Geneva. Fisheries Manag. Ecol. 16: 492-500.
Analysis of long-term catches from the deep peri-alpine Lake Geneva, showed a shift in the stock-recruitment relationship of *Coregonus lavaretus* (L.), a target species of commercial fishing. This change was mainly related to large-scale meteorological factors. Higher spring water temperatures may have improved larval survival and hence recruitment of whitefish via: (1) a better match between the hatching date of whitefish larvae and development of their zooplankton prey; and (2) the positive temperature effect on larval growth. In Lake Geneva, changes in regulatory mechanisms coupled with stocking and improved water-quality have led to an explosion in the C. *lavaretus* population in recent years. These results highlight the relevance of long-term changes in the stock-recruitment relationship for management of aquatic ecosystems that are sensitive to climate forcing.

Brown, E.H., Jr., and Eck, G.W. 1992. Density-dependent recruitment of the bloater (*Coregonus hoyi*) in Lake Michigan. Pol. Arch. Hydrobiol. 39:289-297.
Density-dependent recruitment of the bloater (*Coregonus hoyi*) in Lake Michigan during and afgter recovery of the population in about 1977-1983 was best reflected in the fit of the Beverton-Holt recruitment function to age -1 and -2 recruits and estimated egg of parents surveyed with trawls. A lower growth rate and lower lipid content of bloater at higher population densities and no evidence of cannibalism supported the conclusion that recruitment is resource limited when alewife (*Alosa pseudoharengus*) abundance is low. Predation on larvae by alewives was indicated in earlier studies as the probable cause of depressed recruitment of bloaters before their recovery, which coincided with declining alewife abundance. This negative interaction masked any bloater stock-recruitment relation in the earlier period.

Brown, R. W., Taylor, W.W., and Assel, R.A. 1993. Factors affecting recruitment of lake whitefish in two areas of northern Lake Michigan. J. Great Lakes Res. 19: 418-428.
Stock-recruitment and integrated recruitment models incorporating biotic and abiotic factors were developed for lake whitefish populations in northern Green Bay and the North Shore areas of Lake Michigan. Abundance and recruitment indices were calculated for the 1961-1985 year classes based on lake whitefish catch and effort data from the commercial fishery in each area. Previous research indicates that spawning stock abundance, winter ice cover, and spring temperatures are important in determining the egg and larval abundance and survival of lake whitefish. Therefore, spawning stock abundance, ice cover, winter wind velocity, and spring water and air temperature variables were used as model inputs in regression modeling. The biotic/abiotic recruitment model for northern Green Bay hindcasted lake whitefish recruitment as a function of spawning stock abundance and the number of days that ice cover exceeded 40% during egg incubation. This regression model (R^2 = 0.62) demonstrated improved hindcasting ability of historic recruitment when compared to the Beverton-Holt (R^2 = 0.37) or the Ricker (R^2 = 0.33) stock-recruitment models for the 1961-1985 cohorts. The biotic/abiotic recruitment model for the North Shore hindcasted lake whitefish recruitment as a function of average air temperature in May after larval emergence, the number of days that ice concentration exceeded 70% during egg incubation, and spawning stock abundance. The regression model (R^2 = 0.57) also demonstrated improved hindcasting ability of historical recruitment when compared with Beverton-Holt (R^2 = 0.09) or the Ricker (R^2 = 0.13) stock-recruitment models. Results of this study indicate that biotic/abiotic recruitment models were more successful in hindcasting recruitment than solely biologically based stock-recruitment relationships.

Bunnell, D B., Adams, J.V., Gorman, O.T., Madenjian, C.P., Riley, S.C., Roseman, E.F., and Schaeffer, J.S. 2010. Population synchrony of a native fish across three Laurentian Great Lakes: evaluating the effect of dispersal and climate. Oecologia 162: 641-651.
Climate and dispersal are the two most commonly cited mechanisms to explain spatial synchrony among time series of animal populations, and climate is typically most important for fishes. Using data from 1978–2006, we quantified the spatial synchrony in recruitment and population catch-per-unit-effort (CPUE) for bloater (*Coregonus hoyi*) populations across lakes Superior, Michigan, and Huron. In this natural field experiment, climate was highly synchronous across lakes but the likelihood of dispersal between lakes differed. When data from all lakes were pooled, modified correlograms revealed spatial synchrony to occur up to 800 km for long-term (data not detrended) trends and up to 600 km for short-term (data detrended by the annual rate of change) trends. This large spatial synchrony more than doubles the scale previously observed in freshwater fish populations, and exceeds the scale found in most marine or estuarine populations. When analyzing the data separately for within- and between-lake pairs, spatial synchrony was always observed within lakes, up to 400 or 600 km. Conversely, between-lake synchrony did not occur among short-term trends, and for long-term trends, the scale of synchrony was highly variable. For recruit CPUE, synchrony occurred up to 600 km between both lakes Michigan and Huron (where dispersal was most likely) and lakes Michigan and Superior (where dispersal was least likely), but failed to occur between lakes Huron and Superior (where dispersal likelihood was intermediate). When considering the scale of putative bloater dispersal and genetic information from previous studies, we concluded that dispersal was likely underlying within-lake synchrony but climate was more likely underlying between-lake synchrony. The broad scale of synchrony in Great Lakes bloater populations increases their probability of extirpation, a timely message for fishery managers given current low levels of bloater abundance.

Christie, W.J. 1963. Effects of artificial propagation and the weather on recruitment in the Lake Ontario whitefish fishery. J. Fish. Res. Board Can. 20: 597-646.
No significant relationship could be found between variations in the level of fry planting and ensuing variations in the level of catch in the long-term statistics of the Lake Ontario whitefish gill-net fishery. An alternate-year planting experiment in which fry were planted in the even-numbered years 1944 through 1954, similarly failed to show a detectable level of contribution of the hatchery fish to the fishery. The supported year-classes averaged larger than those not given hatchery support but this was judged coincidental because of a phasing with an alternate-year periodicity which characterized the catch statistics over the whole series examined, and was present in the six years prior to the start of the alternate-year plantings. Estimates of spawning stock were calculated and it was not found that the progeny-per-parent ratios were significantly affected by the fry plantings. A possible explanation for the periodicity was suggested by a significant correlation between air temperatures at the times of spawning and hatching, and the strengths of the produced year-classes. Cold Novembers followed by warm Aprils appeared to provide conditions associated with the production of larger year-classes, with the opposite combinations relating to the weaker broods. The disappearance of lake trout and ciscoes from the commercial catch resulted in increased fishing pressure directed towards the capture of the whitefish. Increases in the efficiency and intensity of the fishing were observed during the period of the study and these were likely responsible for the reduction of the average age of the fish in the catch by almost one year, and the resultant restriction of the annual catch to one year-class in recent years. Probably because most of the fish are currently caught before first spawning, a decline in spawning stock was almost continuous during the study period. The year-to-year fluctuations in the level of the catch increased both because of the reduced average age, and because of a greater variation in year-class strength. The year-classes produced in favorable years tended to increase, down to quite low levels

of stock. This gave a configuration similar to Ricker's Type C reproduction curve, and which differed chiefly in that the limiting diagonal representing minimum reproduction fell below the replacement diagonal. It was suggested that the whitefish may require more than one spawning, to achieve stock replacement. The present instability of the catch, and the potentially serious effect of any sustained break in the rhythm of the climatic conditions suggest a condition of over-exploitation in this case.

Eckmann, R. Gaedke, U. and Wetzlar, H.J. 1988. Effects of climatic and density-dependent factors on year-class strength of Coregonus lavaretus in Lake Constance. Can. J. Fish. Aquat. Sci. 45: 1088-1093.
The influences of density-dependent and density-independent factors on year-class strength (YCS) of *Coregonus lavaretus* in Lake Constance were studied by multiple linear regression analyses for the period from 1962 to 1982. Meteorological conditions that lead to early thermal stratification of the lake in April are of prime importance for YCS and account for 41% of the total YCS variance. Zooplankton concentration during spring has no significant influence on YCS. The extensive stocking program on the lake (50–200 million larvae stocked per year) significantly supports YCS, but this relationship becomes apparent only after the influence of meteorological conditions are removed from the data. Conspecifics of age-classes 1 and 2 have a negative influence on the age 0 year-class, but the nature of this intraspecific competition remains unknown. No stock–recruitment relationship could be detected in this study. The final model includes five independent variables and accounts for 84% of the total YCS variance.

Feiner, Z.S., Bunnell, D.B., Höök, T.O., Madenjian, C.P., Warner, D.M., and Collingsworth, P.D. 2015. Non-stationary recruitment dynamics of rainbow smelt: the influence of environmental variables and variation in size structure and length-at-maturation. J. Great Lakes Res. 41: 246-258.
Fish stock-recruitment dynamics may be difficult to elucidate because of nonstationary relationships resulting from shifting environmental conditions and fluctuations in important vital rates such as individual growth or maturation. The Great Lakes have experienced environmental stressors that may have changed population demographics and stock-recruitment relationships while causing the declines of several prey fish species, including rainbow smelt (*Osmerus mordax*). We investigated changes in the size and maturation of rainbow smelt in Lake Michigan and Lake Huron and recruitment dynamics of the Lake Michigan stock over the past four decades. Mean lengths and length-at-maturation of rainbow smelt generally declined over time in both lakes. To evaluate recruitment, we used both a Ricker model and a Kalman filter-random walk (KF-RW) model which incorporated nonstationarity in stock productivity by allowing the productivity term to vary over time. The KF-RW model explained nearly four times more variation in recruitment than the Ricker model, indicating the productivity of the Lake Michigan stock has increased. By accounting for this nonstationarity, we were able identify significant variations in stock productivity, evaluate its importance to rainbow smelt recruitment, and speculate on potential environmental causes for the shift. Our results suggest that investigating mechanisms driving nonstationary shifts in stock-recruit relationships can provide valuable insights into temporal variation in fish population dynamics.

Healey, M.C. 1978. Fecundity changes in exploited populations of lake whitefish (*Coregonus clupeaformis*) and lake trout (*Salvelinus namaycush*). J. Fish. Res. Board Can. 35: 945-950.
This report considers the possibility that exploited populations of lake whitefish (*Coregonus clupeaformis*) and lake trout (*Salvelinus namaycush*) may show increased individual fecundity. Average fecundity of both species in three exploited lakes varied significantly between 1972 and 1976, while fecundity in an adjacent unexploited lake did not vary. Changes in the fecundity of whitefish and trout in the exploited lakes were not clearly related to the pattern and intensity of exploitation, but fecundity of both species increased in all exploited lakes after exploitation, with trout showing the greater response.

Healey, M.C. 1980. Growth and recruitment in experimentally exploited lake whitefish (*Coregonus clupeaformis*) populations. Can. J. Fish. Aquat. Sci. 37: 255-267.
From 1971 to 1978 Healey (1980) conducted an exploitation experiment on lake whitefish (*Coregonus clupeaformis*) in four Northwest Territories lakes. The objective was to test the hypotheses that, when exploited, growth and recruitment would increase in the populations, and that the degree of increase would be proportional to the intensity of exploitation. Significant increases in size-at-age were recorded in the exploited lakes, and the degree and persistence of the increase were proportional to the intensity of exploitation. Good recruitment was stimulated in the heavily exploited lake, and to a lesser degree in the moderately exploited lake. The hypotheses were, therefore, corroborated. Analyses of growth and year-class strength in the unexploited control lake and the lightly exploited lake indicated that natural variation in growth and recruitment, on a similar scale to that stimulated by exploitation, had occurred in the past. The compensatory responses of lake whitefish populations to exploitation appear to be a logical consequence of the natural population regulating mechanisms for the species. The results of my experiment indicate that in unexploited lakes, recruitment and growth of young fish is regulated by the established population of mature fish.

Henderson, B.A., Collins, J.J., and Reckahn, J.A. 1983. Dynamics of an exploited population of lake whitefish (*Coregonus clupeaformis*) in Lake Huron. Can. J. Fish. Aquat. Sci. 40: 1556-1567.
A population of lake whitefish (*Coregonus clupeaformis*) in the waters off eastern Manitoulin Island in Lake Huron was sampled from 1950 to 1982 by an experimental pound net in the outer basin of South Bay. Year-class strength increased markedly from 1947 to 1977; the increase began with the decline of the 1943 year-class. The fork length attained by age 1–3 fish decreased during the study, but no trend was apparent for older fish. Natural mortality of year-classes varied considerably, and was probably related to the abundance of lamprey. The annual exploitation rate increased from 1 to 37% between 1960 and 1977. Year-class strength was not correlated with the thermal regime during spawning and hatching. Recruitment was a function of parental stock size, and there was evidence that survival from the egg to juvenile stage was inversely correlated with parental stock size. Instantaneous growth rates (G) during the 2nd year of growth were inversely related to year-class strength. Growth (G) in the 1st year was positively correlated with estimated surface water temperatures. The sizes attained by ages 2 and 3 were inversely related to total population abundance. Catchability coefficients in 144-mm-mesh gill nets were inversely related to estimated population sizes. An intrinsic mechanism of population regulation is proposed whereby recruitment is a function of parental stock size, juvenile survival is inversely related to stock size, and growth is inversely correlated with population abundance.

Honsey, A.E., Bunnell, D.B., Troy, C.D., Fielder, D.G., Thomas, M.V., Knight, C.T., Chong, S.C., and Hook, T.O. 2016. Recruitment synchrony of yellow perch (*Perca flavescens*, Percidae) in the Great Lakes region, 1966-2008. Fish. Res. 181: 214-221.
Population-level reproductive success (recruitment) of many fish populations is characterized by high inter-annual variation and related to annual variation in key environmental factors (e.g., climate). When such environmental factors are annually correlated across broad spatial scales, spatially separated populations may display recruitment synchrony (i.e., the Moran effect). We investigated inter-annual (1966–2008) variation in yellow perch (*Perca flavescens*, Percidae) recruitment using 16 datasets describing populations located in four of the five Laurentian Great Lakes (Erie, Huron, Michigan, and Ontario) and Lake St. Clair. We indexed relative year class strength using catch-curve residuals for each year-class across 2–4 years and compared relative year-class strength among sampling locations. Results indicate that perch recruitment is positively synchronized across the region. In addition, the spatial scale of this synchrony appears to be broader than previous estimates for both yellow perch and freshwater

fish in general. To investigate potential factors influencing relative year-class strength, we related year-class strength to regional indices of annual climatic conditions (spring-summer air temperature, winter air temperature, and spring precipitation) using data from 14 weather stations across the Great Lakes region. We found that mean spring-summer temperature is significantly positively related to recruitment success among Great Lakes yellow perch populations.

Lorenzen, K. 2008. Fish population regulation beyond "stock and recruitment": the role of density-dependent growth in the recruited stock. Bull. Mar. Sci. 83: 181-196.
Most fisheries models are based on the assumption that population regulation occurs exclusively in the prerecruit phase of the life cycle, but increasing evidence indicates that density-dependent body growth in the recruited phase and its interaction with size-dependent reproductive development can play an important role in regulation. I use comparative analyses and population modeling to explore the respective roles in regulation, and the interactions between density-dependent processes in pre- and postrecruit phases of the life cycle. Of 16 study populations, 14 show significant density dependence and therefore regulation in either (9) or both (5) phases. when standardized by habitat area, the density-dependent parameters of both phases are correlated, but the density-dependent growth parameter is a better predictor of average biomass density than the equivalent parameter of the spawner-recruit relationship. Population modeling shows that, in the absence of exploitation (i.e., near carrying capacity), 11 of the 16 populations respond most strongly to relaxation of prerecruit density dependence, whereas 5 respond most strongly to relaxation of density-dependence in postrecruit growth. Growth regulation is less important when population density is reduced below carrying capacity. Fishing erodes compensatory reserve in the recruited phase by truncating the age and size distribution. The spawner-recruit relationship therefore dominates compensation in heavily exploited populations. Growth-mediated regulation in the recruited phase is likely to be important when populations are closer to carrying capacity and therefore particularly relevant to the assessment of harvest reserves, stock rebuilding measures, and fisheries enhancements.

Lynch, A.J., Taylor, W.W., Beard, T.D. Jr., and Lofgren, B.M. 2015. Climate change projections for lake whitefish (*Coregonus clupeaformis*) recruitment in the 1836 Treaty Waters of the Upper Great Lakes. J. Great Lakes Res. 41: 415-422.
Lake whitefish (*Coregonus clupeaformis*) is an ecologically, culturally, and economically important species in the Laurentian Great Lakes. Lake whitefish have been a staple food source for thousands of years and, since 1980, have supported the most economically valuable (annual catch value ≈ US$16.6 million) and productive (annual harvest ≈ 7 million kg) commercial fishery in the upper Great Lakes (Lakes Huron, Michigan, and Superior). Climate changes, specifically changes in temperature, wind, and ice cover, are expected to impact the ecology, production dynamics, and value of this fishery because the success of recruitment to the fishery has been linked with these climatic variables. We used linear regression to determine the relationship between fall and spring air temperature indices, fall wind speed, winter ice cover, and lake whitefish recruitment in 13 management units located in the 1836 Treaty Waters of the Upper Great Lakes ceded by the Ottawa and Chippewa nations, a culturally and commercially important region for the lake whitefish fishery. In eight of the 13 management units evaluated, models including one or more climate variables (temperature, wind, ice cover) explained significantly more variation in recruitment than models with only the stock–recruitment relationship, using corrected Akaike's Information Criterion comparisons (ΔAICc > 3). Isolating the climate–recruitment relationship and projecting recruitment with the Coupled Hydrosphere-Atmosphere Research Model (CHARM) indicated the potential for increased lake whitefish recruitment in the majority of the 1836 Treaty Waters management units. These results can inform adaptive management strategies by providing anticipated implications of climate on lake whitefish recruitment.

Marshall, C.T., and Frank, K.T. 1999. The effect of interannual variation in growth and condition of haddock recruitment. Can. J. Fish. Aquat. Sci. 56: 347-355.
The relationship between recruitment and spawner biomass assumes that estimates of spawner biomass are proportional to total egg production by the stock. The validity of this assumption is in question for long-lived gadoid stocks; however, estimating total egg production independently of spawner biomass is seldom feasible. An alternative approach is to examine correlations between recruitment and variables likely to be proxies for total egg production by the stock. This indirect approach was used for haddock on the Scotian Shelf. Indices of growth (mean length at age-4) and condition (weight at 50 cm) were used as proxies for the reproductive potential of individual spawners. Both variables were positively correlated with recruitment over a 3-decade period (1964-1995). During the same time period, there was no relationship between recruitment and spawner biomass estimated by Virtual Population Analysis (VPA). This is further evidence that VPA-based spawner biomass is a poor index of the true reproductive potential of the stock. The results highlight the need to develop more accurate/precise measures of total egg production for use in recruitment research.

Myers, R.A. 2001. Stock and recruitment: generalizations about maximum reproductive rate, density dependence, and variability using meta-analytic approaches. ICES J. Mar. Sci. 58: 937-951.
The author describes the development and application of meta-analytic techniques to understand population dynamics. These methods have been applied to a compilation of over 700 populations of fish, which includes multivariate time-series of egg production, population size, natural mortality, and anthropogenic mortality. The key requirements of this approach are to make all units comparable and to make all model parameters random variables that describe the variation among populations. Parameters are then estimated using hierarchical Bayesian or classical mixed models. This approach allows patterns to be determined that are not detected otherwise. For example, the maximum annual reproductive rate is relatively constant for all species examined: between 1 and 7 replacement spawners are produced per spawner per year at low population size. Using these approaches, the author showed a 20-fold variation in carrying capacity per unit area for cod, and a decrease in carrying capacity with temperature. Recruitment variability generally increases at low population sizes, for species with higher fecundity, for populations at the edge of their range, and in regions with less oceanographic stability. The spatial scale of recruitment correlations for marine species is approximately 500 km, compared with less than 50 km for freshwater species; anadromous species fall between these two scales. Recruitment variability generally decreases with age for marine demersal fish, but often increases with age for some salmonids.

Myers, J.T., Yule, D.L., Jones, M.L., Ahrenstorff, T.D., Hrbik, T.R., Claramunt, R.M., Ebener, M.P., and Berglund, E.K. 2015. Spatial synchrony in cisco recruitment. Fish. Res. 165: 11-21.
We examined the spatial scale of recruitment variability for disparate cisco (*Coregonus artedi*) populations in the Great Lakes (n = 8) and Minnesota inland lakes (n = 4). We found that the scale of synchrony was approximately 400 km when all available data were utilized; much greater than the 50-km scale suggested for freshwater fish populations in an earlier global analysis. The presence of recruitment synchrony between Great Lakes and inland lake cisco populations supports the hypothesis that synchronicity is driven by climate and not dispersal. We also found synchrony in larval densities among three Lake Superior populations separated by 25–275 km, which further supports the hypothesis that broad-scale climatic factors are the cause of spatial synchrony. Among several candidate climate variables measured during the period of larval cisco emergence, maximum wind speeds exhibited the most similar spatial scale of synchrony to that observed for cisco. Other factors, such as average water temperatures, exhibited synchrony on broader spatial scales, which suggests they could also be

contributing to recruitment synchrony. Our results provide evidence that abiotic factors can induce synchronous patterns of recruitment for populations of cisco inhabiting waters across a broad geographic range, and show that broad-scale synchrony of recruitment can occur in freshwater fish populations as well as those from marine systems.

Rook, B J., Hansen, M.J., and Gorman, O.T. 2012. The spatial scale for cisco recruitment dynamics in Lake Superior during 1978-2007. N. Am. J. Fish. Manage. 32: 499-514.
The cisco *Coregonus artedi* was once the most abundant fish species in the Great Lakes, but currently cisco populations are greatly reduced and management agencies are attempting to restore the species throughout the basin. To increase understanding of the spatial scale at which density-independent and density-dependent factors influence cisco recruitment dynamics in the Great Lakes, we used a Ricker stock–recruitment model to identify and quantify the appropriate spatial scale for modeling age-1 cisco recruitment dynamics in Lake Superior. We found that the recruitment variation of ciscoes in Lake Superior was best described by a five-parameter regional model with separate stock–recruitment relationships for the western, southern, eastern, and northern regions. The spatial scale for modeling was about 260 km (range = 230–290 km). We also found that the density-independent recruitment rate and the rate of compensatory density dependence varied among regions at different rates. The density-independent recruitment rate was constant among regions (3.6 age-1 recruits/spawner), whereas the rate of compensatory density dependence varied 16-fold among regions (range = −0.2 to −2.9/spawner). Finally, we found that peak recruitment and the spawning stock size that produced peak recruitment varied among regions. Both peak recruitment (0.5–7.1 age-1 recruits/ha) and the spawning stock size that produced peak recruitment (0.3–5.3 spawners/ha) varied 16-fold among regions. Our findings support the hypothesis that the factors driving cisco recruitment operate within four different regions of Lake Superior, suggest that large-scale abiotic factors are more important than small-scale biotic factors in influencing cisco recruitment, and suggest that fishery managers throughout Lake Superior and the entire Great Lakes basin should address cisco restoration and management efforts on a regional scale in each lake.

Schwank-Ventling, A., and Müller, R. 1991. Survival of coregonid (*Coregonus* spp.) eggs in Lake Sempach, Switzerland. Inter. Ass. Theoret. Applied Limn. 24: 2451-2454.
The authors report on a study to understand the distribution and development of coregonid eggs laying on the lake sediment in winter 1987/88 and 1988/89 in a 14.5 km^2 lake in central Switzerland. A sled dredge was employed to gather information on preferred spawning sites and depths, and on mortality at the beginning and end of the embryogenesis. The authors used a diver-operated suction apparatus to collect eggs continually in the lake throughout the incubation period. Highest egg densities were found at 10 m of depth but eggs were found as deep as 50 m. Egg densities at 10 m decreased by 93% within 37 days in the winter and by 94% in 54 days. The highest density of egg was over 1000 eggs m-2 in mid December 1988 and reflect peak spawning period, and were consistent between the two sampling periods. Coregonid eggs captured in nylon egg bags showed similar survival for each experimental site in both years. Data from the suction dredge indicated that nearly 80% of all eggs present after peak spawning disappeared within six days possible because of wind-driven currents. Invertebrates seemed to have a negative impact on the survival of coregonid eggs. The authors concluded that naturally spawned coregonid eggs could not develop to hatching in Lake Sempach.

Straile, D., Eckmann, R., Jüngling, T., Thomas, G., and Löffler, H. 2007. Influence of climate variability on whitefish (*Coregonus lavaretus*) year class strength in a deep, warm monomictic lake. Oecologia 151: 521-529.

The year-class strength (YCS) of Blaufelchen (*Coregonus lavaretus*) in deep Upper Lake Constance was analyzed for a 52-year period, from 1947 to 1998. Despite strong anthropogenic influences on the species' population dynamics due to cultural eutrophication and oligotrophication, intense fishing, and large-scale stocking, the influence of climate variability associated with the North Atlantic Oscillation (NAO) is apparent in the data set. This influence is significant although large-scale stocking of cold-bred larvae was performed to avoid a mismatch of larvae with their food. The importance of stocking on YCS, however, is unclear and was only detectable when analyzing a subset of the data. In addition to climate variability a yet unidentified factor related to zooplankton suitability as food for fish larvae, and density-dependent mortality probably related to cannibalism do significantly influence YCS. The NAO seemed to influence YCS twofold, through temperature effects on egg development time and on larval growth rate. The first of these two mechanisms is related to the NAO via a time lag of 1 year due to the specific mixing dynamics of warm monomictic Lake Constance. Hence, a warm winter in the year before spawning results in earlier hatching of larvae, that is, hatching is decoupled from the actual meteorological conditions. This should make the larvae very prone to mismatch the dynamics of their food. However, we found no evidence for such a mismatch in this 52-year data set.

Taylor, W.W., Smale, M.A., and Freeberg, M.H. 1987. Biotic and abiotic determinants of lake whitefish (*Coregonus clupeaformis*) recruitment in northeastern Lake Michigan. Can. J. Fish. Aquat. Sci. 44(Supp. 2): 313-323.
Comparisons of lifetime average per capita reproductive rates (R0) between stocks of lake whitefish (*Coregonus clupeaformis*) in Lake Michigan found higher estimates of R0 for rapidly growing exploited stocks than for a commercially unexploited stock. Earlier maturation was the prime cause of this increase. Exploited stocks, however, were dependent on fewer age-classes for reproduction and had a greater potential for instability due to annual variation in recruitment. Overwinter whitefish egg survival in Grand Traverse Bay was nearly fourfold higher during a cold winter with prevalent ice than during the preceding mild, ice-free winter. However, the higher densities of larvae produced during the cold winter experienced greater mortality, with starvation the likely cause. Factors found to influence a stock–recruitment relationship developed for year-classes from 1958 to 1980 included spawning biomass, winter severity (ice-cover), and spring temperatures. Periods of abnormally high and low whitefish catch corresponded to periods in which cold or warm winters were more frequent, respectively. Harvest strategies that dampen naturally caused fluctuations in the spawning stock are recommended.

Zischke, M.T., Bunnell, D.B., Troy, C.D., Berglund, E.F., Caroffino, D.C., Ebener, M.P., He, J.X., Sitar, S.P., and Höök, T.O. 2017. Asynchrony in the inter-annual recruitment of lake whitefish *Coregonus clupeaformis* in the Great Lakes region. J. Great Lakes Res. 43: 359-369.
Spatially separated fish populations may display synchrony in annual recruitment if the factors that drive recruitment success, particularly abiotic factors such as temperature, are synchronized across broad spatial scales. We examined inter-annual variation in recruitment among lake whitefish (*Coregonus clupeaformis*) populations in lakes Huron, Michigan and Superior using fishery-dependent and -independent data from 1971 to 2014. Relative year-class strength (RYCS) was calculated from catch-curve residuals for each year class across multiple sampling years. Pairwise comparison of RYCS among datasets revealed no significant associations either within or between lakes, suggesting that recruitment of lake whitefish is spatially asynchronous. There was no consistent correlation between pairwise agreement and the distance between datasets, and models to estimate the spatial scale of recruitment synchrony did not fit well to these data. This suggests that inter-annual recruitment variation of lake whitefish is asynchronous across broad spatial scales in the Great Lakes. While our method primarily evaluated year-to-year recruitment variation, it is plausible that recruitment of lake whitefish varies at coarser temporal scales (e.g. decadal). Nonetheless, our findings differ from research on some other

Coregonus species and suggest that local biotic or density-dependent factors may contribute strongly to lake whitefish recruitment rather than inter-annual variability in broad-scale abiotic factors.

Early Life Stages

Berlin, W.H., Brooke, L.T., and Stone, L.J. 1977. Verification of a model for predicting the effect of inconstant temperature on embryonic development of lake whitefish (*Coregonus clupeaformis*). U.S. Fish Wildl. Serv. Tech. Paper 92.
Eggs stripped from lake whitefish (*Coregonus clupeaformis*) spawning in Lake Michigan were incubated in the laboratory at temperatures similar to those on whitefish spawning grounds in Lake Michigan during December-April. Observed times from fertilization to attainment of each of 21 developmental stages were used to test a model that predicts the rate of development at daily fluctuating temperatures; the model relates rate of development for any given stage j, expressed as the reciprocal of time (Rj), to temperature (T). The generalized equation for a developmental stage is Rj = abTcT??. Observed times agreed well (5.5% mean difference for all stages) with times predicted by the model; the observed time of 135 days from fertilization to hatching (stage 21) was only 5 days (3.7%) less than the predicted time of 140 days. The model was further verified by applying it to unpublished data supplied by the Ontario Ministry of Natural Resources, for eggs from Lake Huron whitefish incubated in the laboratory in untempered Lake Huron water. The model was used to predict the effects of small temperature increases (caused by a hypothetical waste-heat discharge) on the rate of development and time of hatching of lake whitefish eggs. According to this simulation, continuous addition of waste heat sufficient to raise the temperature 1, 2, or 3 C above ambient on the spawning grounds during December-April would advance the time of hatching 8, 16, or 21 days, respectively. Possible effects of this advancement on the reproductive success of whitefish are discussed.

Bidgood, B.F. 1974. Reproductive potential of two lake whitefish (*Coregonus clupeaformis*) populations. J. Fish. Res. Board Can. 31: 1631-1639.
The reproductive potential of two lake whitefish (*Coregonus clupeaformis*) populations with dissimilar growth rates was studied and compared. The smaller-sized Pigeon Lake females and the larger-sized Buck Lake females had similar ratios of gonad weight to body weight during the gonad development period, but the Pigeon Lake fish produced fewer but larger eggs. Spawning occurred in both lakes for a period approaching 4 mo in both open water and under ice cover in a wide range of water temperatures. Concentrated spawning occurred in shallow water over a boulder, gravel, and sand surficial lake sediment of both lakes. The incubation of whitefish eggs was retarded under ice cover but accelerated to hatching as the water warmed and the ice left the lakes in the spring. The length of the egg incubation period, not the size of the egg under incubation, governed the size of the hatching lake whitefish.

Büuttiker, B. 1986. In situ observations on coregonid egg survival in Lake Joux. Arch. Hydrobiol., Advances Limnol. 22: 353-361.
During the spawning seasons of 1981-82, 1982-83, and 1983-84, coregonid eggs were sampled by scuba diving in the eutrophic Lake Joux. Spawning takes place on the littoral platform, at a depth of 3 to 5 m. Many of the eggs are displaced later by water currents and are carried into deeper regions. Because of this fact, a direct estimation of egg mortality rates could not be done. It is concluded that a small part of eggs develop up to hatching, and that natural spawning contributes therefore to the restocking of coregonid fishes in Lake Joux. The percent of live eggs was 62% and varyed from 32 to 97% among samples and years. Egg densities ranged from 0.07 m^{-2} to 6.11 m^{-2} and averaged 1.18 m^{-2}.

Claramunt, R.M., Muir, A.M., Sutton, T.M., Peeters, P.J., Ebener, M.P., Fitzsimons, J.D., and Koops, M.A. 2010a. Measures of larval lake whitefish length and abundance as early predictors of year-class strength in Lake Michigan. J. Great Lakes Res. 36(Supp. 1): 84-91.
Many lake whitefish stocks in Lake Michigan have experienced substantial declines in growth and condition since the 1990s. Reduced growth and condition could result in reduced quality or quantity of eggs produced by spawning females, which in turn could negatively impact recruitment. We evaluated the potential for reduced recruitment by measuring early life stage density and length, and we discuss the utility of these measures as early indicators of lake whitefish year-class strength. Overall, mean larval density (number per 1000 m3±SE) in Lake Michigan was greater in 2006 (373.7±28.3) than in 2005 (16.6±24.8); whereas, mean length (mm±SE) of larval lake whitefish was smaller in 2006 (12.87±0.07) than in 2005 (14.38±0.13). The ratio of zooplankton to fish density did not show an expected relationship with larval fish density or length. Rather, variation in larval density was best explained by a multiple-regression model that included larval length, spring wind intensity, and adult stock density as predictor variables. Our results suggest that the density of larval lake whitefish is not directly regulated by temperature or zooplankton density at the time of emergence, but that a potential for density-dependent regulation exists when larval emergence rates are high. We conclude that the observed declines in growth and condition of adult lake whitefish are not resulting in substantial reductions in recruitment.

Claramunt, R.M., Muir, A.M., Johnson, J., and Sutton, T.M. 2010b. Spatio-temporal trends in the food habits of age-0 lake whitefish. J. Great Lakes Res. 36(Supp. 1): 66-72.
We compared diets of juvenile lake whitefish among six sites in Lake Michigan and one in Lake Superior during 2005 and 2006 to assess spatial and temporal patterns in food habits and evaluate if ontogenetic diet shifts occur that may influence growth and survival. A total of 262 and 496 juveniles were captured in 2005 and 2006, the majority of which were captured during June and July. Sites in southern Lake Michigan tended to have larger juveniles, and the smallest juveniles were observed at Naubinway, northern Lake Michigan, and Whitefish Point, Lake Superior. The mean number of prey items per stomach differed among sampling sites and years. Copepods were the most prevalent prey item, and were present in greater than 70% of juvenile stomachs from most sites. However, the percent by number of copepods decreased during July as chironomids and other benthic macroinvertebrates increased in number. There was a significant positive relationship between percent of benthic prey items and mean length of juvenile lake whitefish. A substantial increase in the percent of benthic prey consumed after 40 mm (total length) was observed and likely resulted from juvenile lake whitefish crossing a size threshold for benthic feeding relating to morphological changes (i.e., transition of mouth opening from terminal to sub-terminal) in addition to a potential increase in the availability of emergent macroinvertebrates. Timing of the transition to benthic feeding is likely regulated by the number of prey per juvenile and the overlap with peak emergence of important benthic aquatic invertebrates such as chironomids. A better understanding of these factors will increase our understanding of juvenile lake whitefish growth and survival, which are necessary for improving year-class strength predictions.

Eckmann, R., and Pusch, M. 1991. At what life-stage is year-class strength of coregonids (*Coregonus lavaretus* L.) in Lake Constance determined? Inter. Ass. Theort. App. Limn. 24: 2465-2469.
To understand the population dynamics of whitefish (*Coregonus lavaretus*) the authors started to investigate factors which might control year class strength (ycs) in Lake Constance, a warm monomictic pre-alpine lake of 476 km^2 surface area and 100 m depth. The authors concluded that meteorological conditions influence larval growth during April/May and that favorable growth conditions permit a larger fraction of larvae to survive, thus establishing a large year-class. The authors conclude that ycs of

C. *lavaretus* in Lake Constance is not determined shortly after hatching or at first feeding, but rather at some weeks after hatching, and that the fate of individual fish is largely determined by its size at hatching.

Faber, D.J. 1970. Ecological observations on newly hatched lake whitefish in South Bay, Lake Huron. *In* Biology of Coregonid Fishes. *Edited* by C.C. Lindsey and C.S. Woods. Univ. Manitoba Press, Winnipeg, MAN. pp. 481-500.
The distribution and general abundance of newly hatched lake whitefish, *Coregonus clupeaformis*, were studied in an inlet, South Bay, Lake Huron. They were mainly sampled along shorelines with a large fine-mesh plankton net attached to a sled and towed along the bottom by a 16 m research vessel. Towing was done during the day for four years during the months of April and May. Larval lake whitefish were captured at depths of 10 m and less, but were most abundant along certain deep shorelines ("index shorelines") for about one week each year. Maximum numbers appears to be most closely associated with a temperature of 4 ^{o}C and this date varied from the third week of April to the third week of May. Four other species of newly hatched larvae were found associated with larval whitefish along "index shorelines". They were burbot*, Lota lota, shallow water cisco, Coregonus artedi, deepwater scuplin, Myoxocephalus quadricornis*, and rainbow smelt, *Osmerus mordax*. The morphology and movements of the four species of newly hatched coregonids found in Lake Huron are discussed briefly.

Hart, J.L. 1930. The spawning and early life history of the whitefish, *Coregonus clupeaformis* (Mitchell), in the Bay of Quinte, Ontario. Contrib. Canadian Biol. Fish. 6: 167-214.
The spawning run of whitefish is described in respect to the details of the migration and sex ratio, age and size, and breeding characters of the fish. An investigation of the eggs in the spawning grounds by the use of a pump indicates that the proportion of eggs to be fertilized is high but that there is a high mortality during the development. Many whitefish eggs are eaten on the spawning grounds by the common perch (*Perca flavescens*). For the first time there is recorded the capture of a complete series of whitefish young of the year. Based on this material are descriptions of the stages of the young from twelve millimetre to eighty millimetre stages and the characters differentiating whitefish from cisco. The rate of growth of the fry is slow at first but is much accelerated in the latter part of May and until the end of July. The food from the first consists of Entomostraca, chiefly Bosmina, Daphnia and Cyclops. The first movement of the newly hatched fry is inshore close to the surface. Later they form schools and finally take to deeper water. Records of physical conditions in the habitat of young whitefish are recorded. Consideration of the food and other habits and the concentration of predaceous species where young whitefish are abnormally abundant leads to the recommendation that hatchery fry should be widely distributed in shallow water.

Hoagman, W.J. 1973. The hatching, distribution, abundance, growth and food of the larval lake whitefish (*Coregonus clupeaformis* Mitchell) of central Green Bay, Lake Michigan. Instit. Freshwater Res. Rep. No. 53.
The author provides basic information on larval whitefish distribution, development, times of hatching, movement, feeding, yolk-sac conversion, densities, growth, and interspecific relationships in Green Bay and Lake Michigan around the Door Peninsula during 1968-1970. Larval lake whitefish were captured with plankton nets towed from small boats during the day and night. The author preserved 50 larvae collected in the field for laboratory analysis of total length, size of yolk-sac, development, and stomach contents. The authors attempted to relate spatial distribution of lake whitefish larvae to water currents and movements in Green Bay.

Hoyle, J.A., Johannsson, O.E., and Bowen, K.L. 2011. Larval lake whitefish abundance, diet and growth and their zooplankton prey abundance during a period of ecosystem change on the Bay of Quinte, Lake Ontario. Aquat. Ecosyst. Health Manage. 14: 66-74.
Studies to examine larval Lake Whitefish (*Coregonus clupeaformis*) abundance, diet composition and growth, and the abundance of their zooplankton prey were conducted during eight years (1991–1993, 1995–1996 and 2003–2005) over the course of two decades that spanned a period of major ecosystem change—primarily dreissenid mussel related impacts—on the Bay of Quinte, northeastern Lake Ontario. Larval fish were captured in shallow, nearshore waters (0.2–2.0 m) from early April to mid-May each year. Larval Lake Whitefish fed primarily on cyclopoid copepods and small-bodied cladocerans. The key finding of our studies was that prey abundance declined by 89% from the earlier (1991–1993, 1995–1996) to the later (2003–2005) sampling years. Larval fish growth during spring was significantly correlated with prey availability. Recruitment to the juvenile stage in August was correlated with spring prey availability and larval fish growth. The observed decline in larval Lake Whitefish prey in the Bay of Quinte may be contributing to poor stock performance during and following a period of significant ecosystem change.

Jude, D.J., Tesar, F.J., and Tin, J.T. 1998. Spring distribution and abundance of larval fishes in the St. Marys River, with a note on potential effects of freighter traffic on survival of eggs and larvae. J. Great Lakes Res. 24: 569-581.
Larval fishes were collected at seven transects in the St. Marys River from late April to late May, 1985, to determine potential effects of extending the winter navigation season on spawning success and survival. Larval lake herring (*Coregonus artedii*) 8 to 25 mm occurred in densities of 0 to 1,450 larvae/1,000 m^3 and were most commonly found in shallow water (1 to 2 m). Most lake herring hatching occurred during late April to early May, the first 3 wk after ice break-up, but there was no distinct hatching peak. Lake whitefish (C. *clupeaformis*) larvae, 12 to 23 mm, with densities of 0 to 600/1,000 m^3, were most common at 1 m being collected at all transects, except the transect in the Edison Hydropower Canal which passes Lake Superior water into the river. Densities of the two coregonine species were similar to densities observed in important nursery areas of Lake Huron. However, the contribution of lake herring to the river population is not known. Burbot (*Lota lota*) larvae were common temporally and spatially, with higher abundances in the channel. Yellow perch (Perca flavescens) and rainbow smelt (Osmerus mordax) larvae were absent in April and early May, and abundant in late May. Lake herring, lake white-fish, and burbot have the greatest probability of being affected by the proposed extension of the navigation season through resuspension of sediments, dislodgment of eggs, and premature emergence of larvae.

McKenna, J.E. Jr., and Johnson, J.H. 2009. Spatial and temporal variation in distribution of larval lake whitefish in eastern Lake Ontario: signs of recovery? J. Great Lakes Res. 35: 94-100.
The lake whitefish (*Coregonus clupeaformis*) is one of the native Lake Ontario fishes that declined severely over the past century. Recent evidence of larval lake whitefish production in a historic spawning area (Chaumont Bay) might signal a recovery of this species in New York waters. We surveyed coastal and open water areas to evaluate densities and estimate total abundance of larval lake whitefish in Chaumont Bay. Other historic spawning areas and embayments with appropriate spawning and nursery habitat were also surveyed, but only a few larvae were found outside of Chaumont Bay. Lake whitefish larvae were found in every embayment sampled within Chaumont Bay, with larval densities of nearly 600/1000 m^2 in some samples. Greatest abundances occurred in the northern sectors and near the mouth of the bay. Open water densities were generally less than half that of nearshore sites. The total bay-wide estimate for 2005 was approximately 644,000 lake whitefish larvae, but dropped to 230,000–400,000 in 2006 and 2007, respectively. Mean larval growth rates (0.36 mm/day) did not differ

by year, but were consistently higher in early May than in late April. Lake whitefish production in Chaumont Bay is encouraging for this species, but the cause and persistence of the decline after 2005 can be determined only by continued monitoring. Other possible bottlenecks of survival may exist at juvenile and adult stages and could significantly affect recruitment dynamics. This species is sensitive to normal climatic fluctuations and increased variability associated with global climatic change could make winter nursery conditions unfavorable for this species.

Næsje, T.F., and Jonsson, B. 1988. Impacted stress: a causal agent of reduced whitefish (*Coregonus lavaretus*) egg incubation time. Can. J. Fish. Aquat. Sci. 45: 27-31.
The purpose of these experiments was to investigate whether whitefish (*Coregonus lavaretus*) eggs subjected to induced agitation had a shorter incubation period to hatching than undisturbed incubating eggs. Eyed eggs were divided into four main groups: two incubated at river temperatures and two incubated in heated water. River temperature was 2 °C at the beginning of the experiment and increased to more than 10 °C at hatching. Heated water temperatures varied between 6.5 and 8.5 °C. One sample with four replicates at each incubating water temperature was continuously agitated with flowing water, while two samples with four replicates each were incubated undisturbed. At both temperatures, eggs kept in motion by flowing water hatched at fewer degree-days (heated water: 380 ± 6.4, natural water: 417 ± 6.6) from fertilization to 50% hatching than those laying undisturbed (heated water: 513 ± 10.5, natural water: 470 ± 7.3). Eggs agitated during incubation hatched with greater synchrony than those incubated undisturbed. Larvae incubated at river temperatures were larger than those incubated in heated water. Our findings revealed that eggs can hatch at different incubation stages during the ontogeny when exposed to varying environmental stimuli.

Næsji, T.F., Sandlund, O.T., and Jonsson, B. 1986. Habitat use and growth of age-0 whitefish, *Coregonus lavaretus*, and cisco, C. *albula*. Environ. Biol. Fish. 15: 309-314.
Whitefish and cisco hatch in the River Gudbrandsdalslagen during May, and drift downstream into the Lake Mjosa where the alevins start exogenous feeding in littoral backwaters in late May and early June. Age-0 whitefish dwell in littoral areas during summer and autumn, whereas age-0 cisco abandon the littoral zone and become pelagic from August onwards. Early food of cisco and whitefish are Cyclops, and Bosmina, whereas whitefish also ate early instars of Chironomidae. Later, age-0 ciscoes feed on zooplankton (cladocerans), although surface insects are also eaten. Whitefish feed on a wider range of food items including zooplankton, surface insects, chironomid larvae and pupae, cyprinid larvae, and benthic cladocerans. Cisco grew from 1.0 to approximately 11 cm, and whitefish from 1.6 to approximately 12 cm, during the first summer and autumn.

Overdyk, L. 2011. Ecological and genetic factors in the distribution and abundance of larval lake whitefish (*Coregonus clupeaformis*) at Douglas Point, Lake Huron. PhD. Thesis, Univ. Guelph, Guelph, Ontario.
Lake Whitefish are an ecologically, economically and culturally important fish species in the Laurentian Great Lakes. Although much research has been conducted on spawning-phase adult Lake Whitefish, little research has paid attention to the ecology of larval Lake Whitefish, especially in the source waters of Bruce Nuclear Generating Station. This PhD thesis incorporates key ecological and methodological uncertainties into understanding the effects of environmental conditions on the ecology of larval Lake Whitefish at Douglas Point, Lake Huron. The result is a set of novel ideas and the development of novel methods to help answer this question. Chapter 2 investigates the effects of environmental conditions on the distribution and abundance of zooplankton as a necessary first step in understanding the ecology of larval Lake Whitefish. Chapter 3 evaluates the consistency between DNA barcoding and visual identification methods using a case study of larval fish caught in plankton tows at Stokes Bay, Lake

Huron. This evaluation strongly supports the use of DNA barcoding in combination with visual identification to improve the accuracy and precision of species identification. Chapter 4 explores genetic haplotype variation of Lake Whitefish from Lake Huron using DNA barcodes from spawning-phase Lake Whitefish collected at 28 sites around Lake Huron during Fall 2012. While this study did not detect any cryptic lineages of Lake Whitefish in Lake Huron, it did reveal the presence of rare barcode haplotypes that seem to be unique to specific sampling sites. Chapter 5 develops a novel, real-time PCR assay to specifically identify Lake Whitefish in larval fish assemblages. This technique can further increase the speed of identification of Lake Whitefish. Finally, Chapter 6 investigates the effects of environmental conditions on the distribution and abundance of larval Lake Whitefish in nearshore embayments at Douglas Point, Lake Huron. Ultimately, the new knowledge of larval Lake Whitefish ecology generated in this thesis should be seriously considered by Canada/Ontario, First Nations and Industry as they work together to evaluate effects of the existing Bruce Nuclear Generating Station, and the Deep Geologic Repository for Nuclear Waste that has been proposed for construction at Douglas Point, Lake Huron.

Pothoven, S.A., Höök, T.O., and Roswell, C.R. 2014. Feeding ecology of age-0 lake whitefish in Saginaw Bay, Lake Huron. J. Great Lakes Res. 40(Supp. 1): 148-155.
Age-0 lake whitefish Coregonus clupeaformis (11–160 mm total length) were collected from Saginaw Bay, Lake Huron during April–November 2009 and 2010 for diet analysis and for the evaluation of ontogenetic changes in feeding ecology. Lake whitefish ≤ 50 mm ate mainly zooplankton, after which their diets switched mainly to benthic macroinvertebrates. Cyclopoida were the dominant prey consumed by very small lake whitefish (< 17 mm) and the most frequently selected zooplankton type for individual small fish. Once lake whitefish reached 18–19 mm, Cyclopoida in the diet declined and cladocerans emerged as an important diet item. Daphnia were the most common cladoceran in the diets, but for fish 31–50 mm Bosminidae were also relatively important. Although the shift to Daphnia could represent an ontogenetic point when lake whitefish were large enough to effectively handle this prey, it also took place when the relative availability of Daphnia increased. Once lake whitefish were > 50 mm, Chironomidae larvae became a dominant prey item and this shift to benthivory coincided with a 55% increase in length-adjusted energy content between June and July. However, as fish grew (around 110–120 mm), Sphaeriidae and the benthic zooplankton Chydoridae became increasingly important in the diet. As these less energetically rich prey were incorporated into the diet, there were corresponding 21 and 15% decreases in length-adjusted energy content from July to August and September, respectively.

Reckahn, J. A. 1970. Ecology of young lake whitefish, *Coregonus clupeaformis*, in South Bay, Manitolin Island, Lake Huron. *In* Biology and Management of Coregonid Fishes. *Edited* by C.C. Lindsey and C.S. Woods. Univ. Manitoba Press, Winnipeg, MAN. pp. 437-460.
Young-of-year whitefish from a population restricted to South Bay, Lake Huron were sampled with small otter trawls during 1965-1969. Depth distribution. spatial distribution, growth, feeding habits, co-inhabitants and annual variations in abundance are described. The trout-perch (*Percopsis omiscomaycus*) was the most abundant coinhabitant and greatest potential competitor within the restricted zone in the metalimnion in which young whitefish were found during the months of July and August. Significant differences in growth of young whitefish were detected between years. A marked reduction in growth rate occurred near the end of August. Penetration by the fish from the metalilimion into the hypolimnion at this time was the probable direct cause of change ill growth rate but the mechanisms triggering the change in depth, temperature, light, etc., preferences are obscure. A partial check becomes apparent on the fish scales approximately a month and a half after this descent into the hypolimnion and the reduction in growth. The food habits of the fish slowly increase in scope during the first year. The diet changes I ' from primarily plankton to principally benthic organisms. Differences

in kinds and size of food organisms consumed by adult and young whitefish, in addition to differences in depth distribution, reduce intraspecific competition between these age groups.

Roseman, E.F., Kennedy, G.W., Boase, J., Manny, B.A., Todd, T.N., and Stott, W. 2007. Evidence of lake whitefish spawning in the Detroit River: implications for habitat and population recovery. J. Great Lakes Res. 33: 397-406.
Historic reports imply that the lower Detroit River was once a prolific spawning area for lake whitefish (*Coregonus clupeaformis*) prior to the construction of the Livingstone shipping channel in 1911. Large numbers of lake whitefish migrated into the river in fall where they spawned on expansive limestone bedrock and gravel bars. Lake whitefish were harvested in the river during this time by commercial fisheries and for fish culture operations. The last reported landing of lake whitefish from the Detroit River was in 1925. Loss of suitable spawning habitat during the construction of the shipping channels as well as the effects of over-fishing, sea lamprey (*Petromyzon marinus*) predation, loss of riparian wetlands, and other perturbations to riverine habitat are associated with the disappearance of lake whitefish spawning runs. Because lake whitefish are recovering in Lake Erie with substantial spawning occurring in the western basin, we suspected they may once again be using the Detroit River to spawn. We sampled in the Detroit River for lake whitefish adults and eggs in late fall of 2005 and for lake whitefish eggs and fish larvae in 2006 to assess the extent of reproduction in the river. A spawning-ready male lake whitefish was collected in gillnets and several dozen viable lake whitefish eggs were collected with a pump in the Detroit River in November and December 2005. No lake whitefish eggs were found at lower river sites in March of 2006, but viable lake whitefish eggs were found at Belle Isle in the upper river in early April. Several hundred lake whitefish larvae were collected in the river during March through early May 2006. Peak larval densities (30 fish/1,000 m3 of water) were observed during the week of 3 April. Because high numbers of lake whitefish larvae were collected from mid- and downstream sample sites in the river, we believe that production of lake whitefish in the Detroit River may be a substantial contribution to the lake whitefish population in Lake Erie.

Ryan, K.M., and Crawford, S.S. 2014. Distribution and abundance of larval lake whitefish (*Coregonus clupeaformis*) in Stokes Bay, Lake Huron. J. Great Lakes Res. 40: 755-762.
Lake whitefish (*Coregonus clupeaformis*) have been widely studied across the Laurentian Great Lakes. However, there are major gaps in our understanding of factors that affect larval distribution and abundance. The goal of this study was to investigate the distribution and abundance of larval lake whitefish in a Great Lakes embayment using Stokes Bay, Lake Huron as a case study. We collected plankton samples and environmental data from mid-spring to early summer during 2011 and 2012. Ichthyoplankton tows in 2011 revealed densities that are among the highest to be reported in Great Lakes studies. Overall there was little relationship between environmental variables (temperature, dissolved oxygen, conductivity, and depth) and larval lake whitefish distribution and abundance. Ichthyoplankton tows in 2012 revealed a virtual absence of larval lake whitefish during the entire sampling season; unseasonably warm conditions during spring 2012 likely had an important effect on larval survival.

Taylor, W.W., and Freeberg, M.H. 1984. Effect of food abundance on larval lake whitefish *Coregonus clupeaformi*s Mitchell, growth and survival. J. Fish Biol. 25: 733-741.
The effect of food ration on larval lake whitefish, *Coregonus clupeaformis*, growth and survival was determined in the laboratory using brine shrimp as the test prey. In replicate experiments, larval whitefish were fed one of seven different rations of brine shrimp over a 25 day period. Statistically significant differences were found between larval growth and survival at each feeding level. Larvae fed to excess were 1.33 times as long and 2.80 times as heavy as those on the 1.8 zooplankton/fish (z/f)

ration. No mortality was recorded until after day 15 of the experiment by which time all larvae had resorbed their yolk sac. Total mortality followed within 1 week for all feeding densities with the exception of the three highest (18 z/f, 32 z/f and excess rations) where total mortality equalled 90%, 12% and 0%, respectively.

Urpanen, O., Huuskonen, H., Marjomäki, T.J., and Karjalainen, J. 2005. Growth and size-selective mortality of vendace (*Coregonus albula* (L>)) and whitefish (C. l*avaretus* L.). Boreal Environ. Res. 10: 225-238.
Vendace (*Coregonus albula* (L.)) and whitefish (C. *lavaretus* L.) larvae were sampled by stratified random sampling design in four Finnish lakes. Otolith microstructure analysis was used to investigate individual age, hatching time and growth rate of newly hatched larvae to reveal possible size-selective mortality during early life. The majority of the larvae hatched during a short period after the ice-off. Significant differences in hatching length between the lakes were found. Growth rate decreased when larvae became larger and the growth rate was slowest in the lake with the highest density of larvae. However, larger larvae were not relatively more abundant after first weeks and thus, size-dependent mortality was not evident. Hence, we observed that mortality of these two coregonid species during the first weeks was rather random in relation to size of the larvae. Overall, the mortality of vendace larvae with smaller hatching length was higher than that of larger whitefish larvae.

Veneranta, L., Urho, L., Koho, J., and Hudd, R. 2013. Spawning and hatching temperatures of whitefish (*Coregonus lavaretus* (L.)) in the northern Baltic Sea. Adv. Limnol. 64: 39-55.
Catches of sea-spawning whitefish (*Coregonus lavaretus* (L.)) have decreased and stocks of this diverse species have become vulnerable in the Baltic Sea area. The objectives of this study were 1) to find out whether whitefish can still hatch in the wild in the Archipelago Sea of the southern Gulf of Bothnia, and 2) to define the differences in spawning and hatching times as well as hatching success between areas at different latitudes with diverging temperature loads. To estimate the spawning and hatching temperatures and times of the sea-pawning whitefish, both field and laboratory experiments were carried out in 2007 and 2008. Fertilized whitefish eggs were incubated in spawning areas and at two different temperatures in the laboratory. Naturally-spawned whitefish larvae were also sampled in the vicinity of these test areas and from a more northern reference area. The study indicated that the spawning of whitefish in the northern Baltic Sea starts in late autumn when the day length decreases to approximately 8 h 15 min and the seawater temperature decreases to a level of 7.2 to 3.5 °C, regardless of latitude. The hatching period of sea-spawning whitefish larvae is not only dependent on temperature day-degrees but also on the temperature increment. Whitefish larvae hatch in spring after the ice breakup when the water temperature reaches a level of 2 to 4 °C. The hatching experiment revealed that some natural reproduction can still take place in the southern parts of the Gulf of Bothnia in the Baltic Sea, specifically the Archipelago Sea and the Bothnian Sea, although whitefish larvae are more frequent in the northern areas.

Zawisza, J., and Backiel, T. 1970. Gonad development, fecundity, and egg survival in *Coregonus albula* L. *In* Biology of coregonid fishes. Edited by C.C. Lindsey and C.S. Woods. Univ. Manitoba Press, Winnipeg, MAN. pp. 363-394.
On the basis of histological analysis of ovaries of *Coregonus albula* L. sexual maturation has been describes. Among six maturity stages in the fish, four, tha tis III, IV, V and VI occur in annual cycles. The concur with annual changes of the relative weight of ovaries. Fecundity of C. *albula* from 94 lakes was analyzed on the background of a number of characteristics of the fish and of its environment. Fecundity was closely related to length of a fish but not its age. In several lakes fecundity showed year to year variations irrespective of growth changes. Northern populations had smaller fecundity than the

southern one in spite of minor climatic differences. The limnological type of lake did not seem to have any direct effect on the fecundity; neither did abundance of C. *albula* correlate with the characteristics. Infection by *Ergasilus sieboldin*, *Proteocephalus longicollis* and metacercaria in the eyes was investigated and only very intensive infestation with E. *sieboldin* seemed to affect fecundity and growth. Survival of eggs laid was subject to estimates on spawning grounds and to experiments in cages. Major causes of mortality were identified and their affect assessed.

Growth, Condition, and Energetics

Blukacz, E.A., Koops, M.A., Sutton, T.M., Arts, M.T., Fitzsimons, J.D., Muir, A.M., Claramunt, R.M., Johnson, T.B., Kinnunen, R.E., Ebener, M.P., Suski, C., and Burness, G. 2010. Linking lake whitefish (*Coregonus clupeaformis*) condition with male gamete quality and quantity. J. Great Lakes Res. 36(Supp. 1): 78-83.
Sexual-selection theory predicts males will increase investment in ejaculates if there is an increase in the level of sperm competition. Production of ejaculates is energetically costly, so males in better condition should be able to produce ejaculates of higher quality than individuals in poorer condition. We examined how ejaculate investment (i.e., relative testes mass) and sperm quality (i.e., sperm swimming speed) in lake whitefish (*Coregonus clupeaformis*) were related to residual soma mass, fork length, and fish age using data collected from Lake Michigan and Bay of Quinte (Lake Ontario). Populations from both lakes had positive relationships between relative testes mass and residual soma mass. Fork length was the most important predictor of sperm swimming speed with larger males from both lakes tending to have faster swimming sperm than smaller fish. Testis asymmetry, which is a commonly observed phenomenon in other animals but which has only recently been reported in fishes, was found to occur in the majority of examined lake whitefish with the left testes typically larger than the right.

Brown, R.W., and Taylor, W.W. 1992. Effects of egg composition and prey density on the larval growth and survival of lake whitefish (*Coregonus clupeaformis* Mitchell). J. Fish Biol. 40: 381-394.
Eggs were collected from two stocks of lake whitefish, *Coregonus clupeaformis*, in Lakes Michigan and Huron to assess the effect of egg composition and prey density on larval growth and survival. Egg composition parameters including wet weight (mg egg^{-1}), dry weight (mg egg^{-1}), percent water, total caloric content (cal egg^{-1}), caloric density (cal egg^{-1}), percent lipid content, and total lipid content (mg egg^{-1}) were measured. Fish hatched from six parental females in each stock were fed one of four rations (0, 18, 24, 50 brine shrimp larva^{-1} day^{-1}) after yolk sac absorption. Length at hatch, endogenous growth, exogenous growth, and survival were measured during a 42-day laboratory experiment. Length at hatch of larvae was positively related to egg caloric content (r^2=0.780). Endogenous growth for lake whitefish larvae was positively related to percent lipid content (r^2=0.896) and total egg lipid content (r^2=0.876) of parental females. Exogenous growth and survival of larval lake whitefish was positively related to prey availability. Larval fish growth was accurately modelled (r^2=0.973) as a function of prey abundance using a threshold-corrected hyperbolic equation. These results indicate that both egg composition and prey availability have the potential to influence the growth and survival dynamics of larval lake whitefish significantly.

Cook, H.A., Johnson, T.B., Locke, B., and Morrison, B.J. 2005. The status of lake whitefish (*Coregonus clupeaformis*) in Lake Erie. *In* Proceedings of a workshop on the dynamics of lake whitefish (*Coregonus clupeaformis*) and the amphipod *Diporeia* spp. in the Great Lakes. *Edited* by M.C. Mohr and T.F. Nalepa. Great Lakes Fish. Comm. Tech. Rep. 66 pp. 87-104.
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 assortment of other benthic prey remain and are consumed by lake whitefish. Lake whitefish condition for both sexes is within the historical range.

DeBruyne, R.L., Galarowicz, T.L., Claramunt, R.M., and Clapp, D.F. 2008. Lake whitefish relative abundance, length-at-age, and condition in Lake Michigan as indicated by fishery-independent surveys. J. Great Lakes Res. 34: 235-244.
In the mid 1990s, growth and condition of lake whitefish (*Coregonus clupeaformis*) declined within commercial catches in Lake Michigan. However, underlying mechanisms responsible for the declines have not been thoroughly explored. Using fishery-independent survey data, we examined growth and relative abundance of adult whitefish over historical (1980–1990) and recent (1996–2005) time periods in three regions of Lake Michigan: north, mid, and south. Relative abundance was assessed from catch-per-unit-effort (CPUE) of independent surveys, and changes in growth conditions were evaluated using size-at-age estimates. Relative abundance increased in the mid and south regions between the two time periods and decreased in the north region. Length-at-age significantly declined between the two time periods in the north, mid, and south regions; the north region consistently had the lowest length-at-age. Condition also declined between the two time periods in each region. The decline in growth and condition coupled with increases in relative abundance suggest density-dependent mechanisms are contributing to the observed population changes in the south region. The north region does not appear to be regulated by density, suggesting density-independent mechanisms, such as food web changes, are influencing stocks. Changes in the mid region are likely from a mixture of increased lake whitefish abundance and food web changes. Using fishery-independent population data, our results suggest that multiple factors are potentially contributing differentially within three Lake Michigan regions to cause similar declines in length-at-age and condition of whitefish. These factors (e.g., food web changes, lake whitefish density) should be considered when managing the commercial fishery.

Dermott, R., Munawar, M., Bonnell, R., Carou, S., Niblock, H., Nalepa, T.F., and Messick, G. 2005. Preliminary investigations for causes of the disappearance of *Diporeia* spp. from Lake Ontario. *In* Proceedings of a workshop on the dynamics of lake whitefish (*Coregonus clupeaformis*) and the amphipod *Diporeia* spp. in the Great Lakes. *Edited* by M.C. Mohr and T.F. Nalepa. Great Lakes Fish. Comm. Tech. Rep. 66 pp. 203-232.
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. 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.

Edsall, T.A. 1998. The growth-temperature relation of juvenile lake whitefish. T. Am. Fish. Soc. 128: 962-964.
The lake whitefish *Coregonus clupeaformis* supports major commercial fisheries in Lakes Superior, Huron, and Michigan, where it is managed on a sustained-yield basis; it also supports a recreational hook-and-line fishery in some Great Lakes embayments and nearshore areas. To better understand habitat use by juvenile lake whitefish in the Great Lakes, we acclimated groups of test fish in the laboratory to 5, 10, 15, 18, 21, and 24°C and fed them to excess twice daily for 55 d. The test fish increased in length and weight at all of the test temperatures and at the end of the study were heaviest and longest at 18.1°C. A curve fitted to the specific growth rate data indicated that the optimum temperature for growth was 18.5°C and, thus, that the fundamental thermal niche for juvenile lake whitefish is 15.5–19.5°C. Our results support the limited, published information on thermal ecology of wild, free-ranging juvenile lake whitefish in the Great Lakes.

Fagan, K.-A., Koops, M.A., Arts, M.T., Sutton, T.M., and Power, M. 2008. Lake whitefish feeding habits and condition in Lake Michigan. Biology and Management of Coregonid Fishes – 2008. Adv. Limnol. 63: 399-415.
Lake whitefish (*Coregonus clupeaformis*) have experienced declines in condition in some areas of the Great Lakes. The hypothesis tested was that condition—in terms of relative weight, percent lipid and docosahexaenoic acid (DHA)—was greater in regions where larger proportions of high quality prey (e.g., *Diporeia*) were included in the diet. Samples of spawning lake whitefish from four regions around Lake Michigan (northwest, Naubinway, Elk Rapids and southeast) had distinct mean carbon and nitrogen stable isotope signatures. Lake whitefish may be using a variety of prey items, especially the Naubinway population where fish occupy the largest stable isotopic niche space. However, trophic niche width inferred from stable isotopes did not vary among regions. Relative weight was highest in the southeast and lowest for all northern regions. The mean measured lipid from lake whitefish dorsal, skinless, muscle biopsies were highest for northwest fi sh. DHA was significantly different among regions, with high mean values in Elk Rapids and the northwest. No correlations were found between stable isotope measures and condition metrics. The results suggest that lake whitefish are coping with declining *Diporeia* abundances by feeding on alternate prey. Overall results do not substantiate the hypothesis of a relationship between condition and prey use, although lake whitefish from Elk Rapids and the northwest had high quality prey and good condition.

Fagan, K.-A., Koops, M.A., Arts, M.T., Sutton, T.M., Kinnunen, R.E., Muir, A.M., and Power, M. 2017. Lake whitefish (*Coregonus clupeaformis*) energy and nutrient partitioning in lakes Michigan, Erie and Superior. J. Great Lakes Res. 43: 144-154.
A concurrent decrease in lake whitefish (*Coregonus clupeaformis*) condition and *Diporeia* spp. abundance in Lake Michigan has spurred investigations into possible links between the two phenomena. We examined female lake whitefish δ13C and δ15N stable isotopes, growth, reproductive investment, dorsal muscle total lipid and docosahexaenoic acid (DHA) contents from lakes Erie, Michigan and Superior to determine whether differences in food source were correlated with measures of stock success. Stocks with higher somatic growth rates and mean reproductive potential had higher energy stores in terms of percent total lipid. Stocks with low muscle lipid concentration also had smaller egg

sizes as egg number increased. Diet varied among stocks as evidenced by δ13C and δ15N stable isotope analyses; however, muscle total lipid and DHA were not correlated to apparent *Diporeia* spp. prey use. When compared to stocks from lakes Erie and Superior, Lake Michigan stocks had lower growth, reproduction, and lipid stores. While stocks in Lake Michigan with access to declining *Diporeia* spp. populations may still feed on the amphipod, it appears that they are unable to consume the quantities necessary to maintain historical growth and reproduction. Stable isotope analyses of lakes Erie and Superior stocks, with higher growth rates and lipid values, indicated different feeding strategies with no indication of reliance on *Diporeia* spp. While differences in prey resources may have an effect on lake whitefish stocks, differences in *Diporeia* spp. abundance alone cannot explain differences in lake whitefish condition observed among the Great Lakes included in this study.

Fera, S.A., Rennie, M.D., and Dunlop, E.S. 2015. Cross-basin analysis of long-term trends in the growth of lake whitefish in the Laurentian Great Lakes. J. Great Lakes Res. 41: 1138-1149.
We conducted a basin-wide analysis of trends in the growth rate of lake whitefish (*Coregonus clupeaformis*), a commercially harvested species in the Laurentian Great Lakes. Juvenile growth (measured as the growth between ages 1 and 2 years) was back-calculated from agency archived scale collections going back as far as the 1950s. We examined trends for 11 locations within the Great Lakes, and investigated the role of multiple explanatory factors (dreissenid mussel establishment; lake whitefish relative abundance; growing degree days) in contributing to the variation observed. Juvenile growth rates declined in all but one location where dreissenid mussels have had widespread establishment. Growth of juvenile lake whitefish from Lake Ontario showed the largest decline following dreissenid establishment, decreasing by 32%. In several locations, lake whitefish growth rates declined or had breakpoints prior to dreissenid establishment and have stabilized or increased in recent years, thus indicating the contribution of other factors. One location in Lake Superior (Apostle Islands) also showed a marked decline and subsequent increase in growth, whereas the other two Lake Superior locations showed no obvious trends. Changes in relative abundance of lake whitefish and growing degree days contributed to growth patterns among locations, but the effect was inconsistent and in most cases weaker than that from the timing of dreissenid establishment. Although our study cannot identify a specific mechanism involved, the suite of changes at the base of the food web that coincided with the timeline of dreissenid establishment appear to have had a broad-scale impact on lake whitefish.

Freeberg, M.H., Taylor, W.W., and Brown, R.W. 1990. Effect of egg and larval survival on year-class strength of lake whitefish in Grand Traverse Bay, Lake Michigan. T. Am. Fish. Soc. 119: 92-100.
A study was conducted in Grand Traverse Bay, Lake Michigan, during 1983 and 1984 to identify factors that are important in determining year-class strength of lake whitefish *Coregonus clupeaformis*. The major determinants of year-class success were overwintering egg survival and the amount of food available to larval lake whitefish during the first seven weeks of life. Egg mortality was related to the timing of ice cover, with an early cold winter producing the highest survival. Larval survival was affected by the abundance of available prey, i.e. copepod zooplankton between the size of 0.7 and 1.1 mm in total length. In 1983, when zooplankton of this size were abundant relative to larval fish density, high rates of growth and survival of lake whitefish ensued. In 1984, the prey-per-fish ratio declined greatly, and poor growth and low survival were observed. Dynamics of these early life stages appear to significantly influence both lake whitefish year-class strength and eventual recruitment in Grand Traverse Bay.

Gobin, J., Lester, N.P., Cottrill, A., Fox, M.G., and Dunlop, E.S. 2015. Trends in growth and recruitment of Lake Huron lake whitefish during a period of ecosystem change, 1985-2012. J. Great Lakes Res. 41: 405-414.
We use fishery-independent survey data to describe trends in growth and recruitment for lake whitefish (*Coregonus clupeaformis*) in the southern main basin of Lake Huron. We also used a model selection approach to evaluate the potential contribution of key variables (population biomass, temperature, dreissenid mussel establishment in 1993, and the regime shift in 2003) to trends in growth and recruitment. Overall, mean growth of juvenile whitefish (i.e. back-calculated growth occurring between ages 1 and 2 years) has been reduced to approximately half of what it was before dreissenids invaded. The number of recruits per kg spawner biomass averaged 36.1 before dreissenids were established, 2.48 between dreissenid establishment and the regime shift, and 4.61 thereafter. Accounting for the timing of dreissenid establishment and the regime shift greatly improved the ability of both density-dependent growth and stock-recruitment relationships to explain the variation in growth and relative recruitment over time, providing evidence that both of these relationships have been altered by recent ecosystem changes. Current rates of growth and recruitment are much lower than before dreissenids became established, likely reducing the productivity of these populations, and in turn affecting sustainable harvest levels.

Gobin, J., Lester, N.P., Fox, M.G., and Dunlop, E.S. 2016. Effects of changes in density-dependent growth and recruitment on sustainable harvest of lake whitefish. J. Great Lakes Res. 42: 871-882.
Substantial declines in growth and recruitment of lake whitefish (*Coregonus clupeaformis*) and changes in key density-dependent relationships since the 1990s have raised concerns about the effects of these changes on valuable commercial fisheries in Lake Huron. There is evidence for lake whitefish in the southern main basin of Lake Huron that growth and recruitment rates have been reduced by up to 50%. Using a life history model parameterized from fishery-independent survey data for lake whitefish, we investigated the effects of declines in growth and recruitment rates on population dynamics and sustainable harvest. We evaluated a baseline scenario characterized by high growth and recruitment rates, an alternative scenario with a reduced growth rate, and another alternative scenario in which both growth and recruitment rates were reduced. Yield consistently declined by at least 71% in both alternative scenarios compared to the baseline scenario. Also, fishing became unsustainable when both growth and recruitment rates were reduced and the maximum instantaneous fishing mortality rate exceeded 0.5. Our results suggest that the recent reductions in growth and recruitment observed in Lake Huron are of sufficient magnitude to alter productivity and reduce how much can be sustainability harvested from these stocks.

Herbst, S.J., Marsden, J.E., and Lantry, B.F. 2013. Lake whitefish diet, condition, and energy density in Lake Champlain and the lower four Great Lakes following dreissenid invasions. T. Am. Fish. Soc. 142: 3788-398.
Lake Whitefish *Coregonus clupeaformis* support some of the most valuable commercial freshwater fisheries in North America. Recent growth and condition decreases in Lake Whitefish populations in the Great Lakes have been attributed to the invasion of the dreissenid mussels, zebra mussels *Dreissena polymorpha* and quagga mussels D. *bugensis*, and the subsequent collapse of the amphipod, *Diporeia*, a once-abundant high energy prey source. Since 1993, Lake Champlain has also experienced the invasion and proliferation of zebra mussels, but in contrast to the Great Lakes, Diporeia were not historically abundant. We compared the diet, condition, and energy density of Lake Whitefish from Lake Champlain after the dreissenid mussel invasion to values for those of Lake Whitefish from Lakes Michigan, Huron, Erie, and Ontario. Lake Whitefish were collected using gill nets and bottom trawls, and their diets were quantified seasonally. Condition was estimated using Fulton's condition factor (K) and by determining

energy density. In contrast to Lake Whitefish from some of the Great Lakes, those from Lake Champlain Lake Whitefish did not show a dietary shift towards dreissenid mussels, but instead fed primarily on fish eggs in spring, *Mysis diluviana* in summer, and gastropods and sphaeriids in fall and winter. Along with these dietary differences, the condition and energy density of Lake Whitefish from Lake Champlain were high compared with those of Lake Whitefish from Lakes Michigan, Huron, and Ontario after the dreissenid invasion, and were similar to Lake Whitefish from Lake Erie; fish from Lakes Michigan, Huron, and Ontario consumed dreissenids, whereas fish from Lake Erie did not. Our comparisons of Lake Whitefish populations in Lake Champlain to those in the Great Lakes indicate that diet and condition of Lake Champlain Lake Whitefish were not negatively affected by the dreissenid mussel invasion.

Irwin, B.J., Rudstam, L.G., Jackson, J.R., VanDeValk, A.J., and Forney, J.L. 2009. Depensatory mortality, density-dependent growth, and delayed compensation: disentangling the interplay of mortality, growth, and density during early life stages of yellow perch. Trans. Am. Fish. Soc. 138: 99-110.
We present long-term (>40-year) patterns in the density of age-0 yellow perch *Perca flavescens* in Oneida Lake at four early life stages (at egg deposition, at the attainment of a total length of 18 mm, on 1 August, and on 15 October), from which we calculated mortality and growth rates during the three intervals between these early life stages. At each of these stages, age-0 yellow perch densities have been lower in recent years than in the 1960s and 1970s. Mortality rates showed no time trend from egg to 18 mm (interval 1 [the larval stage]), increased from 18 mm to 1 August (interval 2 [the limnetic stage]), and decreased from 1 August to 15 October (interval 3 [the demersal stage]). We also tested previous hypotheses for density-dependent effects on mortality and growth using the entire long-term data set. Contrary to expectations from the 1960s, the mortality rates of age-0 yellow perch in Oneida Lake are no longer depensatory. Overall, the growth rate of age-0 yellow perch has increased over time and become density dependent. Also contrary to common expectations of size-selective mortality, greater average total length is not associated with decreased instantaneous daily mortality for two early life stage intervals. The combined effect has been a decline in age-0 yellow perch density and an increase in average total length by the end of their first year. Although increased growth has not sufficiently compensated for increased mortality during the first year of life, obtaining a larger end-of-year size should reduce subsequent mortality during the winter period, providing for a process of delayed compensation that helps stabilize density at age 1.

Jensen, A.L. 1981. Population regulation in lake whitefish, *Coregonus clupeaformis* (Mitchell). J. Fish Biol. 19: 557-573.
Mechanisms that might compensate for changes in mortality are well known but documentation of their operation and determination of their relative capacities is difficult. In this study the potential of lake whitefish to compensate for fishing mortality is quantified using a conventional fishery stock assessment model. The mechanisms examined are proportion of females, fecundity, survival of eggs and larvae, decrease in age at maturity and growth. The change in each of these parameters necessary to maintain constant recruitment with increasing fishing pressure is determined. Decrease in age of maturity and increased survival of larvae and eggs have the greatest potential for compensation. The total capacity for compensation appears large even when the mechanisms are considered alone. A review of several lake whitefish population studies indicates a large variation in the vital statistics. There is a close relation between total mortality and growth. There is also a close relation between growth and age at maturity. The analyses indicate that increased fishing results in increased growth which then results in a lower age at maturity. This feedback mechanism enables lake whitefish to respond to changes in environmental conditions and on average to maintain a birth rate in balance with mortality.

Jensen, A.L. 1985. Relations among net reproductive rate and life history parameters for lake whitefish (*Coregonus clupeaformis*). Can. J. Fish. Aquat. Sci. 42: 164-168.
An equation is derived that relates net reproductive rate to six life history parameters; the equation is applied to determine changes in the net reproductive rate of lake whitefish (Coregonus clupeaformis) that result from variation in these life history parameters. Changes in age at maturity and survival of immature fish are the only parameters that have a large effect on the net reproductive rate. Age at maturity occurs near the inflection of the growth curve, and this implies a relationship between age at maturity, length at maturity, the growth coefficient, and asymptotic length.

Johnston, T.A., Wong, D.M.-M., Moles, M.D., Weigand, M.D., Casselman, J.M., and Leggett, W.C. 2012. Reproductive allocation in exploited lake whitefish (*Coregonus clupeaformis*) and walleye (*Sander vitreus*) populations. Fish. Res. 125-126: 225-234.
We examined age-related changes in energetic status and reproductive effort of lake whitefish (*Coregonus clupeaformis*) and walleye (*Sander vitreus*) populations in Lakes Winnipeg and Ontario. We predicted, based on life history theory, that both species would exhibit declines in somatic energy stores and increases in the proportion of their energy reserves allocated to reproduction as they aged. These predicted trends were evident for walleye but not for lake whitefish, and the contrast between species was most pronounced for females. Walleye devoted an increasingly larger proportion of their body lipids to gonad development as they got older whereas lake whitefish devoted an increasingly smaller proportion. Between-species differences for some reproductive traits, particularly gonad size (GSI) and relative fecundity, were not consistent between the two lakes. Lake whitefish follow a strategy of lower relative fecundity, larger eggs, and lower egg lipid content compared to walleye. Differences between these species in the gamete quantity and quality of different age classes suggest that age-structured population models parameterized for one species should be applied to other species with caution.

Kratzer, J.F., Taylor, W.W., and Turner, M. 2007. Changes in fecundity and egg lipid content of lake whitefish (*Coregonus clupeaformis*) in the upper Laurentian Great Lakes between 1986-87 and 2003-05. J. Great Lakes Res. 34: 922-929.
Lake whitefish (*Coregonus clupeaformis* Mitchill), an important commercial species in the Laurentian Great Lakes, have experienced decreased growth and condition in regions of the upper Great Lakes over the past 20 years. Increases in lake whitefish density and decreases in the density of *Diporeia* spp., an energy rich and historically important part of the lake whitefish diet, have been implicated in the recent declines in lake whitefish growth and condition. The goal of this study was to describe lake whitefish fecundity, egg lipid content, and total ovary lipid content in selected regions of Lakes Huron, Michigan, and Superior in 1986–87 and 2003–05, two time periods with different lake whitefish and Diporeia densities. Under conditions of high lake whitefish density and low *Diporeia* density, female lake whitefish in the upper Laurentian Great Lakes generally produced fewer eggs. Egg lipid content was higher in 2003–05 than in 1986–87 at all sites, regardless of changes in lake whitefish or *Diporeia* densities. Total ovary lipid content and lake whitefish abundance were inversely related, while there was no significant relationship between total ovary lipid content and *Diporeia* density. The amount of energy that lake whitefish invested in egg production was more closely associated with lake whitefish abundance than with *Diporeia* density. This study provides evidence that recent changes in production dynamics of Great Lakes lake whitefish have not been driven solely by declines in *Diporeia* but have been significantly influenced by lake whitefish abundance.

Kratzer, J.F., Taylor, W.W., Ferreri, C.P., and Ebener, M.P. 2007. Factors affecting growth of lake whitefish in the upper Laurentian Great Lakes. Biology and Management of Coregonid Fishes – 2005, Adv. Limnol. 60: 459-470.

Lake whitefish support the single largest and most valuable commercial fishery in the Laurentian Great Lakes. Recently, fishery managers have reported declining growth and productivity of lake whitefish in the upper Great Lakes. Several causes for the declines noted in individual growth rates have been proposed. These include changes in: (1) lake whitefish density, (2) food quality and abundance, (3) population genetics, and (4) climatic conditions. We evaluated the relationships between each of these factors and lake whitefish growth in selected regions of the upper Great Lakes. Specifically, we examined the timing of the changes in the environment with lake whitefish growth to determine causal relationships. Lake whitefish growth declines began with the development of a very strong 1991 year class due to favorable climatic conditions, leading to density dependent growth dynamics, which were exacerbated by a significant decline in the high-energy, benthic prey item (*Diporeia* spp.) toward the latter part of the 1990's. It appears that declines in *Diporeia* density, which are related to the introduction of two invasive species (*Dreissena* spp.) have resulted in a lower carrying capacity for lake whitefish in the upper Great Lakes. As such, managers need to implement conservative harvest strategies that protect the viability of these stocks under lower productivity conditions.

Lorenzen, K., and Enberg, K. 2002. Density-dependent growth as a key mechanism in the regulation of fish populations: evidence from among-population comparison. Proceedings Royal Soc. B 269:
It is generally assumed that fish populations are regulated primarily in the juvenile (pre–recruit) phase of the life cycle, although density dependence in growth and reproductive parameters within the recruited phase has been widely reported. Here we present evidence to suggest that density–dependent growth in the recruited phase is a key process in the regulation of many fish populations. We analyse 16 fish populations with long–term records of size–at–age and biomass data, and detect significant density–dependent growth in nine. Among–population comparisons show a close, inverse relationship between the estimated decline in asymptotic length per unit biomass density, and the long–term average biomass density of populations. A simple population model demonstrates that regulation by density–dependent growth alone is sufficient to generate the observed relationship. Density–dependent growth should be accounted for in fisheries' assessments, and the empirical relationship established here can provide indicative estimates of the density–dependent growth parameter where population–specific data are lacking

Lozano, S.J., and Scharold, J.V. 2005. The Status of *Diporeia* in Lake Ontario, 1994-1997. *In* Proceedings of a workshop on the dynamics of lake whitefish (*Coregonus clupeaformis*) and the amphipod *Diporeia* spp. in the Great Lakes. *Edited* by M.C. Mohr and T.F. Nalepa. Great Lakes Fish. Comm. Tech. Rep. 66 pp. 233-245.
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 *Diporeia* spp. could have dramatic effects on fish production in Lake Ontario.

Lumb, C.E., Johnson, T.B., Cook, H.A., and Hoyle, J.A. 2007. Comparison of lake whitefish (*Coregonus clupeaformis*) growth, condition, and energy density between lakes Erie and Ontario. J. Great Lakes Res. 33: 314-325.

Patterns in abundance, growth, and condition of lake whitefish (*Coregonus clupeaformis*) from Lake Erie were compared with those from Lake Ontario. Discontinuous assessment data were available from 1972 to 2003 for each lake to describe abundance, growth, and condition, while a seasonally intensive field program was undertaken in 2003 to describe diet, energy density, and gonadosomatic index (GSI). Through time, abundance declined more in Lake Ontario than in Lake Erie. Length-at-age (growth) and condition both declined significantly in Lake Ontario but did not change in Lake Erie. Diet analysis revealed chironomids, dreissenid mussels and sphaeriids made up the bulk of lake whitefish diet in Lake Erie. Diet in Lake Ontario exhibited more seasonal variability with amphipods and gastropods comprising the bulk of the spring and fall diets, and dreissenid mussels dominating summer diets. Lake whitefish energy density (J/g wet mass) was significantly higher in Lake Erie than in Lake Ontario, increasing with body mass and strongly correlated with water content. Female gonadosomatic index was also significantly greater in Lake Erie than in Lake Ontario. Biological attributes of lake whitefish from Lake Erie did not change greatly from the late 1980s to 2003 while fish from Lake Ontario exhibited decreased size-at-age and condition likely due to decreased energy content of diets compared to pre-dreissenid mussel conditions, and possibly lower availability of benthic prey compared to Lake Erie.

Lumb, C.E., and Johnson, T.B. 2012. Retrospective growth analysis of lake whitefish (*Coregonus clupeaformis*) in lakes Erie and Ontario, 1954-2003. Biology and Management of Coregonid Fishes – 2008. Adv. Limnol. 63: 429-454.

Recent declines in growth and condition of lake whitefish (*Coregonus clupeaformis*) in the Laurentian Great Lakes has been attributed to ecological change largely associated with invasive species and the loss of Diporeia, an energy rich prey item. We reconstructed growth and diet for lake whitefish in Lakes Erie and Ontario over a 50-year-time period to explore the consequences of large-scale ecological change on growth rate potential for lake whitefish. Analyses were undertaken for three distinct time periods: (i) pre-phosphorous abatement, (ii) post-phosphorous abatement but pre-dreissenid invasion, and (iii) post-dreissenid colonization. Decreased growth rate in the first two years of life was observed in both lakes when comparing the post-dreissenid time period with the pre- and post-phosphorous abatement time periods. Changes in early growth persisted through adulthood. Based on bioenergetics modelling, growth was more sensitive to diet composition than differences in water temperature. Analysis of stable carbon and nitrogen isotopic ratios from archived scales showed a significant decrease in the carbon signature in the post-dreissenid period, suggesting a more pelagic carbon source than in the past. Growth of lake whitefish was limited by potential of older fish to compensate for depressed early growth following largescale changes in productivity and resource availability.

Madenjian, C.P., Pothoven, S.A., Schneeberger, P.J., O'Conner, D.V., and Brandt, S.B. 2005. Preliminary evaluation of a lake whitefish (*Coregonus clupeaformis*) bioenergetics model. *In* Proceedings of a workshop on the dynamics of lake whitefish (*Coregonus clupeaformis*) and the amphipod *Diporeia* spp. in the Great Lakes. *Edited* by M.C. Mohr and T.F. Nalepa. Great Lakes Fish. Comm. Tech. Rep. 66 pp. 189-202.

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.

Madenjian, C.P., O'Connor, D.V., Pothoven, S.A., Schneeberger, P.J., Rediske, R.R., O'Keefe, J.P., Bergstedt, R.A., Argyle, R.L., and Brandt, S.B. 2006. Evaluation of a lake whitefish bioenergetics model. T. Am. Fish. Soc. 135: 61-75.
We evaluated the Wisconsin bioenergetics model for lake whitefish *Coregonus clupeaformis* in the laboratory and in the field. For the laboratory evaluation, lake whitefish were fed rainbow smelt *Osmerus mordax* in four laboratory tanks during a 133-d experiment. Based on a comparison of bioenergetics model predictions of lake whitefish food consumption and growth with observed consumption and growth, we concluded that the bioenergetics model furnished significantly biased estimates of both food consumption and growth. On average, the model overestimated consumption by 61% and underestimated growth by 16%. The source of the bias was probably an overestimation of the respiration rate. We therefore adjusted the respiration component of the bioenergetics model to obtain a good fit of the model to the observed consumption and growth in our laboratory tanks. Based on the adjusted model, predictions of food consumption over the 133-d period fell within 5% of observed consumption in three of the four tanks and within 9% of observed consumption in the remaining tank. We used polychlorinated biphenyls (PCBs) as a tracer to evaluate model performance in the field. Based on our laboratory experiment, the efficiency with which lake whitefish retained PCBs from their food (γ) was estimated at 0.45. We applied the bioenergetics model to Lake Michigan lake whitefish and then used PCB determinations of both lake whitefish and their prey from Lake Michigan to estimate γ in the field. Application of the original model to Lake Michigan lake whitefish yielded a field estimate of 0.28, implying that the original formulation of the model overestimated consumption in Lake Michigan by 61%. Application of the bioenergetics model with the adjusted respiration component resulted in a field γ estimate of 0.56, implying that this revised model underestimated consumption by 20%.

Madenjian, C.P., Pothoven, S.A., Schneeberger, P.J., Ebener, M.P., Mohr, L.C., Nalepa, T.F., and Bence, J.R. 2010. Dreissenid mussels are not a "dead end" in Great Lakes food webs. J. Great Lakes. Res. 36(Supp. 1): 73-77.
Dreissenid mussels have been regarded as a "dead end" in Great Lakes food webs because the degree of predation on dreissenid mussels, on a lakewide basis, is believed to be low. Waterfowl predation on dreissenid mussels in the Great Lakes has primarily been confined to bays, and therefore its effects on the dreissenid mussel population have been localized rather than operating on a lakewide level. Based on results from a previous study, annual consumption of dreissenid mussels by the round goby (*Neogobius melanostomus*) population in central Lake Erie averaged only 6 kilotonnes (kt; 1 kt=one thousand metric tons) during 1995–2002. In contrast, our coupling of lake whitefish (*Coregonus clupeaformis*) population models with a lake whitefish bioenergetics model revealed that lake whitefish populations in Lakes Michigan and Huron consumed 109 and 820 kt, respectively, of dreissenid mussels each year. Our results indicated that lake whitefish can be an important predator on dreissenid mussels in the Great Lakes, and that dreissenid mussels do not represent a "dead end" in Great Lakes food webs. The Lake Michigan dreissenid mussel population has been estimated to be growing more than three times faster than the Lake Huron dreissenid mussel population during the 2000s. One plausible explanation for the higher population growth rate in Lake Michigan would be the substantially higher predation rate by lake whitefish on dreissenid mussels in Lake Huron.

Mohr, L.C., and Ebener, M.P. 2005. Status of lake whitefish (*Coregonus clupeaformis*) in Lake Huron. *In* Proceedings of a workshop on the dynamics of lake whitefish (*Coregonus clupeaformis*) and the amphipod *Diporeia* spp. in the Great Lakes. *Edited* by M.C. Mohr and T.F. Nalepa. Great Lakes Fish. Comm. Tech. Rep. 66 pp. 105-125.
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.

Mohr, L.C., and Nalepa, T.F. (*Editors*). 2005. Proceedings of a workshop on the dynamics of lake whitefish (*Coregonus clupeaformis*) and the amphipod *Diporeia* spp. in the Great Lakes. Great Lakes Fish. Comm. Tech. Rep. 66.
This technical report from the Great Lakes Fishery Commission summarizes the proceedings from a workshop held in 2002 to describe and evaluate the substantial changes in growth and condition that were being observed in lake whitefish populations in the Great Lakes after arrival of dreissenid mussels (*Dreissenia* spp.), and the subsequent almost immediate decline in abundance of the benthic amphipod *Diporeia* spp. There are papers published as part of the workshop proceedings that address status of stocks through from the 1970s through roughly 2000 in lakes Huron, Michigan, Erie, and Ontario, bioenergetics and trophic dynamics, and last exploitation and management.

Muir, A.M., Sutton, T.M., Arts, M.T., Claramunt, R.M., Ebener, M.P., Fitzsimons, J.D., Johnson, T.B., Kinnunen, R.E., Koops, M.A., and Sepulveda, M.M. 2010. Does condition of lake whitefish spawners affect physiological condition of juveniles? J. Great Lakes Res. 36(Supp. 1): 92-99.
Recent declines in growth and condition of several Great Lakes lake whitefish populations have raised concerns over potential impacts on juvenile physiological condition and ultimately recruitment. To test whether the condition of spawning adults influences juvenile condition via energy allocation dynamics, we partitioned the variation in age-0 juvenile physiological condition (i.e., growth in length and weight, whole-body moisture content, energy density, and protein content) among adult male and female (i.e., body condition, muscle moisture content, energy density, and protein content) and egg (i.e., wet and dry weight, moisture content, energy density, energy content per egg, and protein content) effects using redundancy analysis. Overall, a model that included sampling site, female condition, and egg quality explained 39% of the variation in juvenile physiological condition. After partitioning out the effects of females and eggs, site explained the most variation (23%). When other factors were accounted for, neither females (1.4%) nor eggs (2.7%) explained much variation in juvenile physiological condition. Of the variables studied, female muscle energy density, muscle moisture content, and egg moisture content were most closely associated with juvenile physiological condition. Our results suggest that parental effects, such as size, age, body condition, or body composition, may not be as important as extrinsic site-related effects or density-dependent effects in determining juvenile physiological condition.

Muir, A.M., Arts, M.T., Koops, M.A., Johnson, T.B., Krueger, C.C., and Sutton, T.M. 2014. Reproductive life-history strategies in lake whitefish (*Coregonus clupeaformis*) from the Laurentian Great Lakes. Can. J. Fish. Aquat. Sci. 71: 1256-1269.
Recent food-web changes in the Laurentian Great Lakes are affecting energy and nutrient allocation to lake whitefish (*Coregonus clupeaformis*) with potential downstream effects on egg condition and recruitment. We tested whether egg condition was conserved or varied with maternal condition in eight stocks from Lakes Erie, Michigan, and Superior. Egg condition was conserved across stocks based on (i) a lack of correlation between females and eggs for total lipid, DHA, and other essential fatty acids; (ii) higher levels of energy and long-chain polyunsaturated fatty acids (LC-PUFA) in eggs compared with females; and (iii) no among-stock differences for those same variables in eggs. Females from northern Lake Michigan generally made the greatest trade-offs between egg size and fecundity. Highly fecund females provisioned less lipid, but more n-3 LC-PUFA to their eggs. A lack of stock-level patterns in energy and nutrient allocation suggests that trade-offs occur at the level of individual females and that females in poor condition make greater trade-offs among egg size and fecundity, total lipids, and n-3 LC-PUFA than females in good condition.

Nalepa, T.C., Mohr, L.C., Henderson, B.A., Madenjian, C.P., and Schneeberger, P.J. 2005. An overview. *In* Proceedings of a workshop on the dynamics of lake whitefish (*Coregonus clupeaformis*) and the amphipod *Diporeia* spp. in the Great Lakes. *Edited* by M.C. Mohr and T.F. Nalepa. Great Lakes Fish. Comm. Tech. Rep. 66 pp. 3-19.
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.

Pothoven, S.A. 2005. Changes in lake whitefish diet in Lake Michigan, 1998-2001. *In* Proceedings of a workshop on the dynamics of lake whitefish (*Coregonus clupeaformis*) and the amphipod *Diporeia* spp. in the Great Lakes. *Edited* by M.C. Mohr and T.F. Nalepa. Great Lakes Fish. Comm. Tech. Rep. 66 pp. 127-140.
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

Pothoven, S.A., and Nalepa, T.F. 2006. Feeding ecology of lake whitefish in Lake Huron. J. Great Lakes Res. 32: 489-501.
We determined diet composition, feeding strategy, prey size, and effects of prey type on food weight and energy in stomachs for lake whitefish *Coregonus clupeaformis* in Lake Huron during 2002–04. Age-0 lake whitefish (73–149 mm TL) ate mainly large-bodied cladoceran zooplankton in the summer (July–mid September). Medium lake whitefish (≤350 mm TL excluding age-0) generally ate soft-bodied macroinvertebrates, especially Chironomidae larvae and pupae, in the spring (mid May–June). Zooplankton, if eaten, were generally most important in the summer. Molluscs were generally a minor part of medium lake whitefish diets. Large lake whitefish (> 350 mm) mainly ate molluscs, particularly quagga mussels (*Dreissena bugensis*), despite geographic differences in mussel abundance. Large-bodied crustaceans (*Diporeia* spp., *Mysis relicta*, Isopoda) were a minor part of large lake whitefish diets. Lake whitefish demonstrated a flexible feeding strategy, with individual specialization on some prey and generalized feeding on others. The size of benthic prey (*Diporeia* spp., Chironomidae, and *Dreissena* spp.) eaten increased with fish size and influenced the energetic value of prey for medium and large lake white-fish. The type of prey eaten affected the food and energy intake differently for each size class of lake whitefish. Age-0 lake whitefish that ate mainly zooplankton had more food and energy in stomachs than fish eating shelled prey or other macroinvertebrates. On the other hand, food weight in stomachs did not differ across prey groups for medium fish, but energy in stomachs was lowest for fish that ate shelled prey. For large lake whitefish, there was no difference in food weight or energy in stomachs for different prey groups.

Pothoven, S.A., Nalpea, T.F., Madenjian, C.P., Rediske, R.R., Schneeberger, P.J., and He, J.X. 2006. Energy density of lake whitefish *Coregonus clupeaformis* in lakes Huron and Michigan. Environ. Biol. Fishes 76: 151-158.
We collected lake whitefish *Coregonus clupeaformis* off Alpena and Tawas City, Michigan, USA in Lake Huron and off Muskegon, Michigan USA in Lake Michigan during 2002–2004. We determined energy density and percent dry weight for lake whitefish from both lakes and lipid content for Lake Michigan fish. Energy density increased with increasing fish weight up to 800 g, and then remained relatively constant with further increases in fish weight. Energy density, adjusted for weight, was lower in Lake Huron than in Lake Michigan for both small (≤800 g) and large fish (>800 g). Energy density did not differ seasonally for small or large lake whitefish or between adult male and female fish. Energy density was strongly correlated with percent dry weight and percent lipid content. Based on data from commercially caught lake whitefish, body condition was lower in Lake Huron than Lake Michigan during 1981–2003, indicating that the dissimilarity in body condition between the lakes could be long standing. Energy density and lipid content in 2002–2004 in Lake Michigan were lower than data for comparable sized fish collected in 1969–1971. Differences in energy density between lakes were attributed to variation in diet and prey energy content as well as factors that affect feeding rates such as lake whitefish density and prey abundance.

Pothoven, S.A., and Madenjian, C.P. 2008. Changes in consumption by alewives and lake whitefish after dreissenid mussel invasions in lakes Michigan and Huron. N. Am. J. Fish. Manage. 28: 308-320.
Growth of alewives *Alosa pseudoharengus* and lake whitefish *Coregonus clupeaformis* has declined since the arrival and spread of dreissenid mussels in Lakes Michigan and Huron. Alewives are the main forage

for the salmonids in Lake Michigan, and lake whitefish are the most important commercial species in both lakes. Bioenergetics modeling was used to determine consumption by the average individual fish before and after the dreissenid invasion and to provide insight into the invasion's effects on fish growth and food web dynamics. Alewives feed on both zooplankton and benthic macroinvertebrates, and lake whitefish are benthivores. Annual consumption of zooplankton by an average alewife in Lake Michigan was 37% lower and consumption of benthic macroinvertebrates (amphipods Diporeia spp., opossum shrimp *Mysis relicta*, and Chironomidae) was 19% lower during the postinvasion period (1995–2005) than during the preinvasion period (1983–1994). Reduced consumption by alewives corresponded with reduced alewife growth. In Lakes Michigan and Huron, consumption of nonmollusk macroinvertebrates (*Diporeia* spp., opossum shrimp, Chironomidae) by the average lake whitefish was 46–96% lower and consumption of mollusks (mainly dreissenids and gastropods) was 2–5 times greater during the postinvasion period than during the preinvasion period. Even though total food consumption by lake whitefish did not differ between the two periods in Lake Huron or the Southern Management Unit in Lake Michigan, postinvasion weight at age was at least 38% lower than preinvasion weight at age. Under the current postinvasion diet regime, consumption by lake whitefish would have to increase by up to 122% to achieve preinvasion growth rates.

Pothoven, S.A., Bunnell, D.B., Madenjian, C.P., Gorman, O.T., and Roseman, E.F. 2012. Energy density of bloaters in the upper Great Lakes. T. Am. Fish. Soc. 141: 772-780.
We evaluated the energy density of bloaters *Coregonus hoyi* as a function of fish size across Lakes Michigan, Huron, and Superior in 2008–2009 and assessed how differences in energy density are related to factors such as biomass density of bloaters and availability of prey. Additional objectives were to compare energy density between sexes and to compare energy densities of bloaters in Lake Michigan between two time periods (1998–2001 and 2008–2009). For the cross-lake comparisons in 2008, energy density increased with fish total length (TL) only in Lake Michigan. Mean energy density adjusted for fish size was 8% higher in bloaters from Lake Superior than in bloaters from Lake Huron. Relative to fish in these two lakes, small (<125 mm TL) bloaters from Lake Michigan had lower energy density, whereas large (>175 mm TL) bloaters had higher energy density. In 2009, energy density increased with bloater size, and mean energy density adjusted for fish size was about 9% higher in Lake Michigan than in Lake Huron (Lake Superior was not sampled during 2009). Energy density of bloaters in Lake Huron was generally the lowest among lakes, reflecting the relatively low densities of opossum shrimp Mysis diluviana and the relatively high biomass of bloaters reported for that lake. Other factors, such as energy content of prey, growing season, or ontogenetic differences in energy use strategies, may also influence cross-lake variation in energy density. Mean energy density adjusted for length was 7% higher for female bloaters than for male bloaters in Lakes Michigan and Huron. In Lake Superior, energy density did not differ between males and females. Finally, energy density of bloaters in Lake Michigan was similar between the periods 2008–2009 and 1998–2001, possibly due to a low population abundance of bloaters, which could offset food availability changes linked to the loss of prey such as the amphipods *Diporeia* spp.

Pothoven, S.A., and Madenjian, C.P. 2013. Increased piscivory by lake whitefish in Lake Huron. N. Am. J. Fish. Manage. 33: 1194-1202.
We evaluated the diet of Lake Whitefish Coregonus clupeaformis in Lake Huron during 2002–2011 to determine the importance of Round Goby *Neogobius melanostomus* and other fish as prey items. Lake Whitefish that had reached approximately 400 mm in length incorporated fish into their diets. The overall percentage of adult Lake Whitefish in Lake Huron that had eaten fish increased from 10% in 2002–2006 to 20% in 2007–2011, with a corresponding decrease in the frequency of Lake Whitefish that ate Dreissena spp. from 52% to 33%. During 2002–2006, Round Goby (wet mass, 38%), sculpins

(Cottidae) (34%), and Ninespine Stickleback *Pungitius pungitius* (18%) were the primary fish eaten, whereas Round Goby accounted for 92% of the fish eaten in 2007–2011. Overall, Round Goby were found in the fewest Lake Whitefish stomachs in the north region of Lake Huron (6%) and in the most in the central (23%) and south (19%) regions of the lake. In the central region, Round Goby were eaten during all seasons that were sampled (spring through fall). In the south region, Round Goby were eaten only in the winter and spring but not in the summer when *Dreissena* spp. and spiny water flea *Bythotrephes longimanus* dominated the diet. Based on the 2007–2011 diet composition, an individual Lake Whitefish would need to have increased their consumption relative to that in 1983–1994 by 6% in the north region, 12% in the central region, and 41% in the southern region in order to achieve the same growth that was observed before dreissenid mussels arrived. However, Lake Whitefish weight adjusted for length only increased by 2% between 2002–2006 and 2007–2011 in the central region, decreased by 4% in the northern region, and remained constant in the southern region. This suggests that a shift toward more frequent piscivory does not necessarily improve the condition of a generalist feeder like Lake Whitefish.

Rennie, M.D., and Verdon, R. 2008. Development and evaluation of condition indices for the lake whitefish. N. Am. J. Fish. Manage. 28: 1270-1293.
Despite frequent use of length-based condition indices by fisheries managers and scientists to describe the overall well-being of fish, these indices are rarely evaluated to determine how well they correlate with more direct measures of physiological or ecological condition. We evaluated common condition indices (Fulton's condition factor KF, Le Cren's condition index KLC, and two methods of estimating relative weight Wr) against more direct measures of physiological condition (energy density, percent lipid content, and percent dry mass) and ecological condition (prey availability) for lake whitefish *Coregonus clupeaformis* in Lake Huron. We developed four standard weight (Ws) equations using the regression length percentile (RLP) method: one for the species as a whole, and three separate equations describing immature, mature male, and mature female lake whitefish from 385 populations in North America. Species RLP-Ws showed less length-related bias and more closely matched empirical quartiles of lake-specific mean weight than did maturity- or sex-specific RLP-Ws equations. Significant length-related bias was detected in EmP-Wr. No biologically significant length-related bias was detected in KLC, but this index was specific to a single population of fish. Species RLP-Wr showed no significant length-related bias, and KF was significantly size dependent. All length-based condition indices were significantly correlated with energy density, percent lipid content, and percent dry mass. The index most strongly correlated with all three measures of physiological condition was KF, likely because both the physiological measures and KF exhibited positive relationships with body size. Across two Lake Huron sites, RLP-Wr was significantly correlated with density of prey (amphipods *Diporeia* spp.). Of the two condition indices developed in this study, RLP-Wr was consistently more strongly correlated with physiological condition indices than was EmP-Wr.

Rennie, M.D., Sprules, W.G., and Johnson, T.B. 2009. Factors affecting the growth and condition of lake whitefish (*Coregonus clupeaformis*). Can. J. Fish. Aquat. Sci. 66: 2096-2108.
Though declines in the growth and condition of Great Lakes lake whitefish (*Coregonus clupeaformis*) have been largely attributed to food web disruptions caused by invasive dreissenid mussels, a comprehensive evaluation of alternative hypotheses is currently lacking. Using various statistical approaches, we evaluated 69 years of data from the inner basin of South Bay, Lake Huron, considering the role of biological variables (food availability as *Diporeia* abundance and lake whitefish relative abundance as catch per unit effort, CPUE) versus environmental variables (climate change as growing degree days >5 °C and productive habitat capacity as percent epilimnetic volume, EV) on the condition and early growth rates of resident lake whitefish. Consistently, biological variables (*Diporeia* abundance,

CPUE) best explained changes in lake whitefish growth and condition, respectively, in years when *Diporeia* data were available. In their absence, environmental variables (EV) best explained early growth rates of lake whitefish, whereas CPUE again best explained lake whitefish condition. Our analysis revealed that environmental change contributed significantly but alone was not sufficient to explain declines in lake whitefish growth after dreissenid establishment, whereas biological variables considered here could account for the majority of growth and condition changes observed in this population.

Rennie, M.D., Sprules, W.G., and Vaillancourt, A. 2010. Changes in fish condition and mercury vary by region, not *Bythotrephes* invasion: a result of climate change? Ecography 3: 471-482.
We compared changes in body condition (relative weight) and mercury concentrations ([Hg]) in two species of coregonid fish (lake herring *Coregonus artedi*, lake whitefish C. *clupeaformis*) among discrete populations in Ontario between 1967 and 2006. Temporal comparisons among populations were made to determine whether 1) the establishment of *Bythotrephes longimanus* had affected coregonid populations, or 2) if changes in body condition or [Hg] were related to regional differences in the degree of climate change during the time period investigated. Climate data from northwestern, northeastern and southern Ontario showed a general warming trend in all regions over the period of study. However, greater temporal changes in climate were observed in the northwest where growing degree days >5°C (GDD) increased and precipitation declined over the study period compared with relatively little change in southern or northeastern Ontario. Correspondingly, northwestern Ontario coregonid populations demonstrated significantly greater declines in body condition relative to those from northeastern or southern Ontario. Declines in [Hg] of both species were also greater among northwestern populations compared with those from northeastern or southern Ontario but only significantly so for lake herring. These declines were independent of the invasion of non-native *Bythotrephes*, and declines in [Hg] were opposite predictions based on the hypothesis that *Bythotrephes* invasion lengthened aquatic food chains. Based on our findings and further evidence from the literature, we propose that warming regional climates are capable of contributing to declines in both condition and [Hg] of fishes. Because fish condition affects both reproductive success and overwinter survival, observed condition declines of the magnitude reported here could have profound implications for the structure of future aquatic ecosystems in a warming climate.

Schneeberger, P.J., Ebener, M.P., Toneys, M., and Peeters, P.J. 2005. Status of lake whitefish (*Coregonus clupeaformis*) in Lake Michigan. *In* Proceedings of a workshop on the dynamics of lake whitefish (*Coregonus clupeaformis*) and the amphipod *Diporeia* spp. in the Great Lakes. *Edited* by M.C. Mohr and T.F. Nalepa. Great Lakes Fish. Comm. Tech. Rep. 66 pp. 67-86.
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 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.

Stockwell, J.D., Yule, D.L., Hrabik, T.R., Sierszen, M.E., and Isaac, E.J. 2014. Habitat coupling in a large lake system: delivery of an energy subsidy by an offshore planktivore to the nearshore zone of Lake Superior. Freshwater Biol. 59: 1197-1212.
The authors hypothesised that the autumn spawning migration of Lake Superior cisco (*Coregonus artedi*) provides a resource subsidy, in the form of energy-rich cisco eggs, from the offshore pelagic to the nearshore benthic community over winter, when alternate prey production is likely to be low. They tested this hypothesis using fish and macroinvertebrate surveys, fish population demographics, diet and stable isotope analyses, and bioenergetics modelling. The benthic, congeneric lake whitefish (C. *clupeaformis*) was a clear beneficiary of cisco spawning. Cisco eggs represented 16% of lake whitefish annual consumption in terms of biomass, but 34% of energy (because of their high energy density: >10 kJ g wet mass^{-1}). Stable isotope analyses were consistent with these results and suggest that other nearshore fish species may also rely on cisco eggs. The lipid content of lake whitefish liver almost doubled from 26 to 49% between November and March, while that of muscle increased from 14 to 26% over the same period, suggesting lake whitefish were building, rather than depleting, lipid reserves during winter. In the other Laurentian Great Lakes, where cisco populations remain very low and rehabilitation efforts are underway, the offshore-to-nearshore ecological link apparent in Lake Superior has been replaced by non-native planktivorous species. These non-native species spawn in spring have smaller eggs and shorter incubation periods. The rehabilitation of cisco in these systems should reinstate the onshore subsidy as it has in Lake Superior.

Thomas, G., and Eckmann, R. 2007. The influence of eutrophication and population biomass on common whitefish (*Coregonus larvartus*) growth – the Lake Constance example revisited. Can. J. Fish. Aquat. Sci. 64: 402-410.
Accelerated growth of freshwater fish during anthropogenic eutrophication has been attributed almost exclusively to the increased nutrient content, while density-dependent effects have been largely neglected. We evaluated the relative importance of these factors by studying the growth of 43 consecutive year classes of common whitefish (*Coregonus lavaretus*) from Upper Lake Constance. This prealpine lake underwent eutrophication from the 1950s to 1970s, followed by reoligotrophication. Because whitefish are harvested with gill nets in a strongly size-selective way, we used back-calculated lengths of average fast-growing fish to compare growth among cohorts. Standing stock biomass was estimated based upon virtual year-class strengths. Multiple linear regression analysis revealed that growth of whitefish during their second year was most strongly related to standing stock biomass followed by PO4-P content during spring turnover and by calendar year, which was incorporated as a third independent variable (adjusted R^2 = 0.84). The negative correlation between whitefish growth rate and calendar year is interpreted as evidence of an evolutionary response to the highly size-selective fishery during at least four decades. We conclude that density-dependent effects on whitefish growth are more important than had been realized previously and that the impact of eutrophication on growth of whitefish needs to be reconsidered.

Wang, H., Höök, T.O., Ebener, M.P., Mohr, L.C., and Schneeberger, P.J. 2008. Spatial and temporal variation of maturation schedules of lake whitefish (*Coregonus clupeaformis*) in the Great Lakes. Can. J. Fish. Aquat. Sci. 65: 2157-2169.
Fish maturation schedules vary greatly among systems and over time, reflecting both plastic and adaptive responses to ecosystem structure, physical habitats, and mortality (natural and fishing). We

examined maturation schedules of commercially exploited lake whitefish (*Coregonus clupeaformis*) in the Laurentian Great Lakes (Lakes Michigan, Huron, and Superior) by estimating ages and lengths at 50% maturity, age-specific maturity ogives (age-specific probability of being mature), and probabilistic maturation reaction norms (PMRNs; a metric that accounts for effects of growth and mortality). Collectively, these estimates indicated variation in maturation schedules between sexes (i.e., males tend to mature at younger ages and shorter lengths than females) and among systems (midpoint estimates of PMRNs were smallest for Lake Michigan fish, intermediate for fish in the main basin of Lake Huron, and largest for fish in Lake Huron's Georgian Bay and Lake Superior). Temporally, recent increases in age at 50% maturity in Lakes Huron and Michigan may primarily reflect plastic responses to decreased growth rates associated with ecosystem changes (e.g., declines of the native amphipod, *Diporeia* spp.). As plastic and adaptive changes in maturation schedules of fish stocks may occur simultaneously and require different management considerations, we recommend the concomitant analysis of multiple maturation indices.

Wiegand, M.D., Johnston, T.A., Porteous, L.R., Ballevona, A.J., Casselman, J. M., and Leggett. 2014. Comparison of ovum lipids provisioning among lake whitefish walleye and northern pike co-habiting Bay of Quinte (Lake Ontario, Canada). J. Great Lakes Res. 40: 721-729.
We compared size, total lipid contents, percent of lipids as neutral lipids and fatty acid profiles of ova from Bay of Quinte (Lake Ontario) populations of lake whitefish and northern pike to previously reported data from Bay of Quinte walleye. We also assessed how the relationships between ovum lipid fatty acid composition and maternal size or age varied among these species. Ovum size, total lipid content and percent neutral lipid differed among the three species and in general were not influenced by maternal size or age. The highest percentage of neutral lipid occurred in walleye ova and the lowest in northern pike. Principal components analysis revealed significant separation of fatty acid profiles among the three species, with greater differences in the neutral lipids than in the polar lipids. Lake whitefish were more distinct from the walleye and northern pike than the walleye and northern pike were from each other in the neutral lipids. Lake whitefish ova had higher percentages of eicosapentaenoic acid (EPA) in both lipid fractions than those of the other two species. In direct contrast to the previously observed trends in walleye, percentages of arachidonic acid and docosahexaenoic acid decreased while those of EPA increased with maternal size in the lake whitefish. None of the major fatty acids in northern pike ova varied significantly with maternal size or age. Our study reveals that the Bay of Quinte populations of the three species have different patterns of allocation of fatty acids to ova as they grow and age.

Wright, G.M., Ebener, M.P., 2007. Potential effects of dietary lipid reduction on growth and reproduction of lake whitefish in northern Lake Michigan. *In* Biology and Management of Coregonid Fishes—2005. *Edited* by M. Jankun, P. Brzuzan, P. Hliwa, and Luczyski, M. Schweizerbart Science Publishers: Stuttgart, Germany, Adv. Limnol. 60 pp. 311-330.
The authors compiled information on the lipid content, growth, condition, population abundance and biomass, and recruitment of lake whitefish in Lake Michigan during 1976-2004 to evaluate whether a change in the benthic food web has reduced the amount of dietary lipids available for their consumption. Mean annual lipid content of skin-on fillets declined from 12.2% wet weight during 1977-1993 to 7.1% during 1994-1999. The lowest lipid values occurred after 1994. There was a strong seasonal and spatial effect on lipid content. Growth rate was negatively related to population abundance but only weakly. The lowest growth rates occurred when lipid levels were low and population abundance and biomass were high. Population abundance and biomass of lake whitefish, and density of the amphipod *Diporeia* spp. explained only 22% of the variability in lipid levels, and population abundance explained the largest proportion of the

variation in lipid levels. There was no evidence that recruitment was affected by reductions in lipids, growth, or condition. We suggest that the decrease in abundance of *Diporeia* spp. and the concomitant increase in colonization by dreissenid mussels may have resulted in a decrease in dietary lipid available to lake whitefish. We recommend that fishery agencies establish a dedicated program to monitor lipid content of lake whitefish. Managers must recognize that yields per recruit experienced during the 1980s and early 1990s cannot be sustained given the reduced production capacity of lake whitefish.

Food Web Effects

Barbiero, R.P., Rockwell, D.C., Warren, G.J., and Tuchman, M.L. 2006. Changes in spring phytoplankton communities and nutrient dynamics in the eastern basin of Lake Erie since the invasion of *Dreissena* spp. Can. J. Fish. Aquat. Sci. 63: 1549-1563.
Distinct changes have occurred in the size and composition of the spring phytoplankton community in the eastern basin of Lake Erie following the introduction of *Dreissena*. Since 1996, total phytoplankton biovolume has decreased to approximately 20% of pre-Dreissena levels, whereas postinvasion concentrations of spring soluble nutrients, particularly silica, have been substantially elevated compared with earlier years. Spring dominance has shifted from a mix of pennate and large centric diatoms and pyrrophytes to three centric diatoms with high silica requirements: *Aulacoseira islandica*, *Stephanodiscus hantzschii*, and *Stephanodiscus parvus*, and the overall diversity and species richness of the spring phytoplankton community has declined significantly. In addition, current April silica concentrations are approximately twice as high as historical (i.e., 1960s–1980s) winter maxima, indicating that the silica content of the lake has increased since the dreissenid invasion. These results suggest that the severe silica depletion caused by increased anthropogenic inputs of nutrients during the last century has been mitigated through a decrease in diatom production, most likely brought about by dreissenid grazing.

Barabiero, R.P., Schmude, K., Lesht, B.M., Riseng, C.M., Warren, G.J., and Tuchman, M.L. 2011. Trends in *Diporeia* populations across the Laurentian Great Lakes, 1997-2009. J. Great Lakes Res. 37: 9-17.
Benthic communities in the Laurentian Great Lakes have been in a state of flux since the arrival of dreissenid mussels, with the most dramatic changes occurring in population densities of the amphipod *Diporeia*. In response, the US EPA initiated an annual benthic macroinvertebrate monitoring program on all five Great Lakes in 1997. Although historically the dominant benthic invertebrate in all the lakes, no Diporeia have been found in Lake Erie during the first 13 years of our study, confirming that *Diporeia* is now effectively absent from that lake. Populations have almost entirely disappeared from our shallow (< 90 m) sites in lakes Ontario, Huron, and Michigan. In Lake Ontario, three of our four deep (> 90 m) sites still supported *Diporeia* populations in 2009, with densities at those sites ranging between 96 and $198/m^2$. In Lake Michigan, populations were still found at six of our seven deep sites in 2009, with densities ranging from 57 to $1409/m^2$. Densities of *Diporeia* in 2009 at the four deep sites in Lake Huron were somewhat lower than those in Lake Michigan, ranging from 191 to $720/m^2$. Interannual changes in population size in Lake Huron and Lake Michigan have shown a degree of synchrony across most sites, with periods of rapid decline (1997–2000, 2003–2004) alternating with periods of little change or even increase (2001–2002, 2005–2009). There has been no evidence of directional trends at any sites in Lake Superior, although substantial interannual variability was seen.

Dobiesz, N.E., McLeish, D.A., Eshenroder, R.L., Bence, J.R., Mohr, L.C., Ebener, M.P., Nalepa, T.F., Woldt, A.P., Johnson, J.E., Argyle, R.L., and Makarewicz, J.C. 2005. Ecology of the Lake Huron fish community, 1970-1999. Can. J. Fish. Aquat. Sci. 62: 1432-1451.
We review the status of the Lake Huron fish community between 1970 and 1999 and explore the effects of key stressors. Offshore waters changed little in terms of nutrient enrichment, while phosphorus levels declined in inner Saginaw Bay. Introduced mussels (*Dreissena* spp.) proliferated and may have caused a decline in *Diporeia* spp. This introduction could have caused a decline in lake whitefish (*Coregonus clupeaformis*) growth and condition, with serious repercussions for commercial fisheries. *Bythotrephes*, an exotic predatory cladoceran, and other new exotics may be influencing the fish community. Sea lampreys (*Petromyzon marinus*) remained prevalent, but intensive control efforts on the St. Mary's River may reduce their predation on salmonines. Overfishing was less of a problem than in the past, although fishing continued to reduce the amount of lake trout (*Salvelinus namaycush*) spawning biomass resulting from hatchery-reared fish planted to rehabilitate this species. Massive stocking programs have increased the abundance of top predators, but lake trout were rehabilitated in only one area. Successful lake trout rehabilitation may require lower densities of introduced pelagic prey fish than were seen in the 1990s, along with continued stocking of hatchery-reared lake trout and control of sea lamprey. Such reductions in prey fish could limit Pacific salmon (*Oncorhynchus* spp.) fisheries.

Bunnell, D.B., David, S.R., and Madenjian, C.P. 2009. Decline in bloater fecundity in southern Lake Michigan after decline of *Diporeia*. J. Great Lakes Res. 35: 45-49.
Population fecundity can vary through time, sometimes owing to changes in adult condition. Consideration of these fecundity changes can improve understanding of recruitment variation. Herein, we estimated fecundity of Lake Michigan bloater *Coregonus hoyi* during December 2005 and February 2006. Bloater recruitment has been highly variable from 1962 to present, and consistently poor since 1992. We compared our fecundity vs. weight regression to a previously published regression that used fish sampled in October 1969. We wanted to develop a new regression for two reasons. First, it should be more accurate because it uses fish collected closer to spawning, thus minimizing the potential for atresia (egg reabsorption) which could bias fecundity high. Second, we hypothesized that fecundity would be lower in 2006 because adult condition was 41% lower in 2006 compared to 1969, likely owing to the decline of *Diporeia* spp, a primary prey for bloater. Although the slope of the fecundity versus weight regression was similar between the years, fecundity was 24% lower in 2006 than in 1969 for bloater weighing between 70 and 240 g. Whether this was the result of the difference in sampling time prior to spawning or of differences in condition is unknown. We also found no relationship between maternal size and mature oocyte size. Incorporating our updated fecundity regression into a stock/recruit model failed to improve the model fit, indicating that the low bloater recruitment that has been observed since the early 1990s is not solely the result of reduced fecundity.

Bunnell, D.B., Madenjian, C.P., Holuszko, J.D., Adams, J.V., and French, J.R.P. III. 2009. Expansion of *Dreissena* into offshore waters of Lake Michigan and potential impacts on fish populations. J. Great Lakes Res. 35: 74-80.
Lake Michigan was invaded by zebra mussels (*Dreissena polymorpha*) in the late 1980s and then followed by quagga mussels (D. *bugensis)* around 1997. Through 2000, both species (herein *Dreissena*) were largely restricted to depths less than 50 m. Herein, we provide results of an annual lake-wide bottom trawl survey in Lake Michigan that reveal the relative biomass and depth distribution of Dreissena between 1999 and 2007 (although biomass estimates from a bottom trawl are biased low). Lake-wide mean biomass density (g/m2) and mean depth of collection revealed no trend between 1999 and 2003 (mean = 0.7 g/m2 and 37 m, respectively). Between 2004 and 2007, however, mean lake-wide biomass density increased from 0.8 g/m2 to 7.0 g/m2, because of increased density at depths between

30 and 110 m, and mean depth of collection increased from 42 to 77 m. This pattern was confirmed by a generalized additive model. Coincident with the *Dreissena* expansion that occurred beginning in 2004, fish biomass density (generally planktivores) declined 71% between 2003 and 2007. Current understanding of fish population dynamics, however, indicates that *Dreissena* expansion is not the primary explanation for the decline of fish, and we provide a species-specific account for more likely underlying factors. Nonetheless, future sampling and research may reveal a better understanding of the potential negative interactions between *Dreissena* and fish in Lake Michigan and elsewhere.

Bunnell, D.B., Davis, B.M., Warner, D.M., Chriscinske, M.C., and Roseman, E.F. 2011. Planktivory in the changing Lake Huron zooplankton community: *Bythothrephes* consumption exceeds that of *Mysis* and fish. Freshwater Biol. 56: 1365-2427.

Oligotrophic lakes are generally dominated by calanoid copepods because of their competitive advantage over cladocerans at low prey densities. Planktivory also can alter zooplankton community structure. We sought to understand the role of planktivory in driving recent changes to the zooplankton community of Lake Huron, a large oligotrophic lake on the border of Canada and the United States. We tested the hypothesis that excessive predation by fish (rainbow smelt *Osmerus mordax*, bloater *Coregonus hoyi*) and invertebrates (*Mysis relicta*, *Bythotrephes longimanus*) had driven observed declines in cladoceran and cyclopoid copepod biomass between 2002 and 2007. We used field sampling and bioenergetics modelling approach to generate estimates of daily consumption by planktivores at two 91-m depth sites in northern Lake Huron, U.S.A., for each month, May–October 2007. Daily consumption was compared to daily zooplankton production. *Bythotrephes* was the dominant planktivore and estimated to have eaten 78% of all zooplankton consumed. *Bythotrephes* consumption exceeded total zooplankton production between July and October. *Mysis* consumed 19% of all the zooplankton consumed and exceeded zooplankton production in October. Consumption by fish was relatively unimportant – eating only 3% of all zooplankton consumed. Because *Bythotrephes* was so important, we explored other consumption estimation methods that predict lower *Bythotrephes* consumption. Under this scenario, Mysis was the most important planktivore, and *Bythotrephes* consumption exceeded zooplankton production only in August. Our results provide no support for the hypothesis that excessive fish consumption directly contributed to the decline of cladocerans and cyclopoid copepods in Lake Huron. Rather, they highlight the importance of invertebrate planktivores in structuring zooplankton communities, especially for those foods webs that have both *Bythotrephes* and *Mysis*. Together, these species occupy the epi-, meta- and hypolimnion, leaving limited refuge for zooplankton prey.

Fera, S.A., Rennie, M.D., Dunlop, E.S. 2017. Broad shifts in the resource use of a commercially harvested fish following the invasion of dreissenid mussels. Ecology 98: 1681-1692.

Dreissenid mussels, including the zebra (*Dreissena polymorpha*) and quagga (*Dreissena rostiformus bugensis*) mussel, are invasive species known for their capacity to act as ecosystem engineers. They have caused significant changes in the many freshwater systems they have invaded by increasing water clarity, reducing primary productivity, and altering zooplankton and benthic invertebrate assemblages. What is less clear is how their ecosystem engineering effects manifest up the food web to impact higher trophic levels, including fish. Here, we use a biological tracer (stable isotopes of carbon and nitrogen) to analyze long-term and broad-scale trends in the resource use of benthivorous lake whitefish (*Coregonus clupeaformis*) in the Laurentian Great Lakes, where dreissenid mussels have become established in each lake except Lake Superior. We measured stable isotope ratios from archived material (fish scale samples) collected over several decades by multiple agencies and from 14 locations around the Great Lakes. In the majority of locations, the $\delta 13C$ of lake whitefish increased following the establishment of dreissenid mussels. Trends in $\delta 15N$ were less clear, but significant breakpoints in the time series occurred within 5 yr of dreissenid establishment in several locations, followed by declines in δ15N. In contrast, isotopic signatures in Lake Superior locations did not show these trends. Our results provide evidence that lake whitefish shifted toward greater reliance on nearshore benthic production, supporting the theory that fundamental energy pathways are changed when dreissenid mussels become established. Importantly, these effects were noted across multiple, large, and complex ecosystems spanning a broad geographic area. Our study underscores the potential for aquatic invasive species to alter key ecosystem services as demonstrated here through their impacts on energy pathways supporting a commercially harvested fish species.

Fernandez, R.J., Rennie, M.D., Sprules, W.G. 2009. Changes in nearshore zooplankton associated with species invasions and potential effects on larval lake whitefish. Hydrobiologia 94: 226-243.
We examined changes in the nearshore zooplankton community of South Bay, Lake Huron before (1982) and after (2002–2005) the invasions of dreissenid mussels and *Bythotrephes longimanus* and found substantial changes including lower cladoceran abundance, particularly Bosminidae, and higher copepod abundance after invasion. We also estimated changes in the energy content of zooplankton potentially available to larval lake whitefish before and after invasion using published values of energy content per unit mass. There were no differences in available zooplankton energy in May, the period when larvae feed inshore based on thermal preferences and surface temperature data. We conclude that changes in nearshore zooplankton communities following these species invasions probably do not affect larval lake whitefish.

Haffner, G.D., Johnson, T.B., Lantry, B.F., Hebert, C.H., McGoldrick, D.J., Backus, S.M., and Fish, A.T. 2014. Ecological tracers reveal resource convergence among prey fish species in a large lake ecosystem. Freshwater Biol. 59: 2150-2161.
The authors measured stable isotopes of carbon (δ13C) and nitrogen (δ15N) and fatty acid profiles in Lake Ontario alewife (*Alosa pseudoharengus*), rainbow smelt (*Osmerus mordax*), slimy sculpin (*Cottus cognatus*) and round goby (*Neogobius melanostomus*) collected from 1982 to 2008 to investigate how temporal variability in these ecological tracers can relate to ecosystem-level changes associated with the establishment of highly invasive dreissenid mussels. Prey fish δ15N values remained relatively constant, with only slimy sculpin exhibiting a temporal increase in δ15N. In contrast, δ13C values for alewife, rainbow smelt and, especially, slimy sculpin became less negative over time and were consistent with the benthification of the Lake Ontario food web associated with dreissenids. Principal components analysis revealed higher contributions of 14:0 and 16:1n-7 fatty acids and increasingly negative δ13C values in older samples in agreement with the greater historical importance of pelagic production for alewife, rainbow smelt and slimy sculpin. Temporal declines in fatty acid unsaturation indices and Σn-3/Σn-6 ratios, and also increased 24:0/14:0 ratios for alewife, rainbow smelt and slimy sculpin, indicated the increasing importance of nearshore production pathways for more recently collected fish and resulted in values more similar to those for round goby. These results indicate a temporal convergence of the food niche, whereas food partitioning has historically supported the coexistence of prey fish species in Lake Ontario. This convergence is consistent with changes in food-web processes associated with the invasion of dreissenid mussels.

Higgins, S.N., and Vander Zanden, M.J. 2017. What a difference a species makes: a meta-analysis of dreissenid mussel impacts on freshwater ecosystems. Ecol. Monogr. 80:179-196.
We performed a meta-analysis of published studies and long-term monitoring data sets to evaluate the effects of dreissenid mussels (*Dreissena polymorpha* and *D. rostriformis bugensis*), two of the world's most problematic biological invaders, on the biogeochemistry, flora, and fauna of lakes and rivers across North America and Eurasia. Dreissenid effects were structured along two distinct energy pathways. For

the pelagic–profundal pathway, large mean reductions in phytoplankton (−35% to −78%) and zooplankton (−40% to −77%) biomass occurred and were dependent on habitat type. The largest effects were found in rivers, followed by littoral and pelagic habitats in lakes. In contrast, benthic energy pathways within littoral habitats of lakes and rivers showed dramatic increases in mean benthic algal and macrophyte biomass (+170% to +180%), sediment-associated bacteria (about +2000%), non-dreissenid zoobenthic biomass (+160% to +210%), and total zoobenthic biomass, which includes dreissenid mussel soft tissues (+2000%). Our study quantifies the remarkable ability of these invasive mussels to shift aquatic food webs and energy flow from pelagic–profundal to benthic–littoral energy pathways, and it provides a basis for forecasting their impacts in diverse freshwater ecosystems. Our meta-analysis approach was a powerful tool for moving beyond the idiosyncrasies of individual case studies and may be equally powerful for assessing impacts of other biological invaders.

Hinderer, J.L., Jude, D.J., Schaeffer, J.S., Warner, D.M., and Scavia, D. 2012. Lipids and fatty acids of *Mysis diluviana* in lakes Michigan and Huron, 2008. J. Great Lakes Res. 38(Supp. 2): 93-97.
The opossum shrimp (*Mysis diluviana*) is a vital component of Great Lakes food webs. Baseline data on the nutritional condition of *Mysis* populations are necessary to evaluate potential impacts of recent, dramatic changes in the lower food webs of lakes Michigan and Huron. Information on lipid and fatty acid content can reveal patterns of health and physiological condition of mysids, including inferences on availability and quality of food. We sampled *Mysis* populations in the two lakes in spring and late summer/early fall 2008 and analyzed total lipid content and fatty acid profiles to describe Mysis nutritional condition. On average, adult *Mysis* in Lake Huron had lower total lipids and elevated concentrations of the fatty acid docosahexaenoic acid compared with Lake Michigan, although differences were not always significant. Results suggest that Lake Huron Mysis could have been starving during spring 2008.

Hoyle, J.A., Schaner, T., Casselman, J.M., and Dermott, R. 1999. Changes in lake whitefish (*Coregonus clupeaformis*) stocks in eastern Lake Ontario following *Dreissena* mussel invasion. Great Lakes Research Review 4(2): 5-10.
The authors reported that significant impacts on the eastern Lake Ontario and Bay of Quinte lake whitefish stocks were observed coincident with and following the invasion of *Dreissena* (zebra and quagga) mussels. These impacts included decreased juvenile and adult abundance, poor survival of juvenile fish, a significant decline in adult body condition, and reduced production of young of-the-year fish. A dramatic decline in *Diporeia* abundance, formerly the major lake whitefish diet item, was coincident with both historically high lake whitefish abundance and the early stages of *Dreissena* colonization. Juvenile and adult lake whitefish diet changed primarily to *Dreissena* mussels after *Diporeia* declined to negligible levels.

Hoyle, J.A. 2005. Status of lake whitefish (*Coregonus clupeaformis*) in Lake Ontario and the response to the disappearance of Diporeia spp. *In* Proceedings of a workshop on the dynamics of lake whitefish (*Coregonus clupeaformis*) and the amphipod Diporeia spp. in the Great Lakes. *Edited* by C. Mohr and T.F. Nalepa, Great Lakes Fish. Comm. Tech. Rep. 66 pp. 47-66.
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; delayed mean age at maturity; very poor reproductive success; changes in seasonal, geographic, and bathymetric distribution; and changes in feeding patterns.

Hoyle, J.A., Bowlby, J.N., and Morrison, B.J. 2008. Lake whitefish and walleye population responses to dreissenid mussel invasion in eastern Lake Ontario. Aquat. Ecosyst. Health Manage. 11: 403-411.
We reviewed responses associated with the invasion of dreissenid mussels by two eastern Lake Ontario fish populations and the fisheries they support. Resurging lake whitefish and walleye populations declined following dreissenid mussel invasion in the early 1990s. Impacts on whitefish were associated with the loss of a key diet item, Diporeia, and its replacement with diet items of lower energy value. Impacts featured a die-off, dispersal, declines in juvenile and adult condition and growth rates, delayed age-at-maturity, and several years of reproductive failure. Impacts on walleye were consistent with dreissenid driven ecosystem change, particularly, clearer water. The key response by the walleye population was a downward shift in recruitment levels. This shift appears to be due to a change in the stock-recruitment relationship caused by decreased survival during early life (i.e. egg to 4-months), and suggests that the carrying capacity for these early life stages has diminished. Currently, whitefish reproduction has resumed and walleye reproduction appears stabilized at a lower level. Recent (i.e. 2003 and 2005) whitefish year-classes were relatively large but the fish are growing slowly and annual survival rate is not yet known. The whitefish commercial harvest continues to decline in synchrony with the declining adult whitefish population. The walleye recreational fishery (i.e. effort and harvest) has stabilized at a smaller size consistent with lower walleye year-class strength.

Madenjian, C.P., Bunnell, D.B., Warner, D.M., Pothoven, S.A., Fahnenstiel, G.L., Nalpea, T.F., Vanderploeg, H.A., Tsehaye, I., Claramunt, R.M., Clark, R.D. Jr. 2015. Changes in the Lake Michigan food web following dreissenid mussel invasions: a synthesis. J. Great Lakes Res. 41(Supp. 3): 217-231.
Using various available time series for Lake Michigan, we examined changes in the Lake Michigan food web following the dreissenid mussel invasions and identified those changes most likely attributable to these invasions, thereby providing a synthesis. Expansion of the quagga mussel (*Dreissena rostriformis bugensis*) population into deeper waters, which began around 2004, appeared to have a substantial predatory effect on both phytoplankton abundance and primary production, with annual primary production in offshore (> 50 m deep) waters being reduced by about 35% by 2007. Primary production likely decreased in nearshore waters as well, primarily due to predatory effects exerted by the quagga mussel expansion. The drastic decline in *Diporeia* abundance in Lake Michigan during the 1990s and 2000s has been attributed to dreissenid mussel effects, but the exact mechanism by which the mussels were negatively affecting Diporeia abundance remains unknown. In turn, decreased *Diporeia* abundance was associated with reduced condition, growth, and/or energy density in alewife (*Alosa pseudoharengus*), lake whitefish (*Coregonus clupeaformis*), deepwater sculpin (*Myoxocephalus thompsonii*), and bloater (*Coregonus hoyi*). However, lake-wide biomass of salmonines, top predators in the food web, remained high during the 2000s, and consumption of alewives by salmonines actually increased between the 1980–1995 and 1996–2011 time periods. Moreover, abundance of the lake whitefish population, which supports Lake Michigan's most valuable commercial fishery, remained at historically high levels during the 2000s. Apparently, counterbalancing mechanisms operating within the complex Lake Michigan food web have enabled salmonines and lake whitefish to retain relatively high abundances despite reduced primary production.

McNickle, G.G., Rennie, M.D., and Sprules, W.G. 2006. Changes in bentic invertebrate communities of South Bay, Lake Huron, following invasion by zebra mussels (*Dreissena polymorpha*), and potential effects on lake whitefish (*Coregonus clupeaformis*) diet and growth. J. Great Lakes Res. 32: 180-193.
In this study we evaluated changes in benthic invertebrate communities of South Bay, Lake Huron following the invasion of zebra mussels (*Dreissena polymorpha*) and considered the implications for diets and growth of whitefish (*Coregonus clupeaformis*), a commercially important fish in the Great Lakes. Of the ten benthic invertebrate groups identified prior to invasion (1980–81), only densities of *Diporeia* and Oligochaeta have changed since the appearance of the zebra mussel, and only *Diporeia* and Chironomidae changed in relative abundance. These changes are similar to those observed in other areas of the Great Lakes, with the exception of an increase in Oligochaeta density. Post-invasion (2002–03) shallow-water communities appear to be more homogeneous, dominated by zebra mussels and Isopoda, whereas deep-water sites are more heterogeneous due to the loss of *Diporeia*. Additional data on *Diporeia* density for several years between 1959 and 2004 indicated that current low densities are not typical of South Bay. Based on changes in the benthic communities and published literature on whitefish diets, we predict that unless whitefish are able to switch to *Mysis* as an alternative to *Diporeia*, post-invasion whitefish diets will only contain a maximum of 57 to 84% of their former energy content. These predictions are likely underestimates, as they do not take into account increased energy costs associated with reductions in total invertebrate density at historical foraging depths.

Mosley, C., and Bootsma, H. 2015. Phosphorus recycling by profundal quagga mussels (*Dreissena rostriformis bugensis*) in Lake Michigan. J. Great Lakes Res. 41(Supp. 3): 38-48.
The effects of dreissenid mussels on plankton abundance and nutrient cycling in shallow, productive waters of the Great Lakes have been well-documented, but the effects of their more recent expansion into offshore regions have received much less attention. Understanding quagga mussel impact on Lake Michigan's phosphorus (P) fluxes is critical in assessing long-term implications for nutrient cycling and energy flow. In this study, P excretion and egestion rates were determined for mussels in the hypolimnion of Lake Michigan. Constant low temperatures and limited food supply contributed to a lower basal P excretion rate in profunda quagga mussels compared to the shallow phenotype. The P excretion:egestion ratio was approximately 3:2, highlighting the need to consider both of these pathways when assessing the effect of these filter feeders on nutrient dynamics. Total dissolved P (TDP) excretion rates ranged from 0.0002 to 0.0124 μmol $mgDW^{-1}$ d^{-1}, soluble reactive P (SRP) excretion rates ranged from 0.0002 to 0.0061 μmol $mgDW^{-1}$ d^{-1}, and particulate P (PP) egestion rates (feces + pseudofeces) ranged from 0.0007 to 0.0269 μmol $mgDW^{-1}$ d^{-1}. The ability of profunda mussels to alter P cycling dynamics is reflected in an increased hypolimnetic dissolved:particulate P ratio and the disappearance of the benthic nepheloid layer. On an areal basis, mussel P recycling rates are up to 11 times greater than P settling rates as determined by sediment traps, suggesting that mussel grazing has resulted in an increased delivery rate of P to the deep benthos and a shorter P residence time in the water column.

Nalepa, T.F., Fanslow, D.L., and Messick, G. 2005. Characteristics and potential causes of declining *Diporeia* spp. populations in southern Lake Michigan and Saginaw Bay, Lake Huron. ***In*** **Proceedings of a workshop on the dynamics of lake whitefish (*Coregonus clupeaformis*) and the amphipod *Diporeia* spp. in the Great Lakes. *Edited* by M.C. Mohr, and T. F. Nalepa. Great Lakes Fish. Comm. Tech. Rep. 66 pp. 157-188.**
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% 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.

Owens, R.W., and Dittman, D.E. 2010. Shifts in the diets of slimy sculpin (*Cottus cognatus*) and lake whitefish (*Coregonus clupeaformis*) in Lake Ontario following the collapse of the burrowing amphipod Diporeia. Aquat. Ecosyst. Health Manage. 6: 311-323.
In Lake Ontario, the diets of slimy sculpin *Cottus cognatus* and lake whitefish *Coregonus clupeaformis* shifted from a diet dominated by the burrowing amphipod, *Diporeia*, and to a lesser extent, *Mysis,* to a more diverse diet, after *Diporeia* collapsed, to one dominated by Mysis and prey that were formerly less important or uncommon such as Chironomidae, Oligochaeta, and Ostracoda. Additionally, lake whitefish still preyed on native mollusks like Sphaeriidae and Gastropoda, but also preyed on exotic mollusks, *Dreissena* spp., which are swallowed intact and subsequently crushed in its muscular stomach. Whether *Diporeia* was abundant (1992) or scarce (1999), selection indices for *Diporeia* by slimy sculpins was positive, suggesting that *Diporeia* was a preferred prey. Unlike lake whitefish, slimy sculpins avoided *Dreissena*; therefore, energy diverted to *Dreissena* production was a real loss for slimy sculpins. The shifts in the diet of these benthic fishes corresponded with drastic changes in the benthic community between 1992 and 1999. The collapse of *Diporeia*, formerly the most abundant macroinvertebrate in the benthic community, along with sharp declines in the abundance of Oligochaeta and Sphaeriidae, coincided with the establishment and rapid expansion of *Dreissena bugensis*, the quagga mussel, and to a lesser degree *Dreissena polymorpha*, the zebra mussel. It appears that the *Diporeia* population first collapsed at depths >70 m in southeastern Lake Ontario by autumn 1992, at shallower depths in the eastern Lake Ontario by 1995, and along the entire south shore line at depths <100 m, and perhaps in some areas >100 m by 1999. In response to the disappearance of *Diporeia*, populations of two native benthivores, slimy sculpin and lake whitefish, collapsed in eastern Lake Ontario, perhaps due in part to starvation, because *Diporeia* was their principal prey. Presently, alternative food resources do not appear sufficient to sustain these two benthivores at their former levels of abundance. We do not expect slimy sculpin and lake whitefish to recover unless *Diporeia* returns to earlier levels of abundance.

Owens, R.W., O'Gorman, R., Eckert, T.H., Lantry, B.F., and Dittman, D.E. 2005. Recovery and decline of lake whitefish in U.S. waters of eastern Lake Ontario, 1980-2001. *In* Proceedings of a workshop on the dynamics of lake whitefish (*Coregonus clupeaformis*) and the amphipod *Diporeia* spp. in the Great Lakes. *Edited* by L.C. Mohr and T.F. Nalepa. Great Lakes Fish. Comm. Tech. Rep. 66 pp. 141-155.
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.

Pothoven, S.A., Nalepa, T.F., Schneeberger, P.J., and Brandt, S.B. 2001. Changes in diet and body condition of lake whitefish in southern Lake Michigan associated with changes in benthos. N. Am. J. Fish. Manage. 21: 876-883.
We evaluated the long-term trends of the benthic macroinvertebrate community (1980–1999) and biological attributes of lake whitefish *Coregonus clupeaformis* (1985–1999) in southeastern Lake Michigan. We also determined what food types were important to lake whitefish in an area where the amphipod Diporeia had not yet declined in 1998 and how the diet of lake whitefish changed as Diporeia declined during 1999–2000. Zebra mussels *Dreissena polymorpha* invaded the study area in 1992; Diporeia began to decline in 1993 and was nearly absent by 1999. The body condition of lake whitefish decreased after 1993 and remained low thereafter. The length at age and weight at age of lake whitefish was lower in 1992–1999 than in 1985–1991. After declines of *Diporeia* off the city of Muskegon, Michigan, between 1998 and 1999–2000, the proportion of *Diporeia* in the diet by weight fell from 70% to 25% and the percent occurrence decreased from 81% to 45%. In contrast, the proportion of lake whitefish that ate other prey, such as *Mysis relicta* (an opossum shrimp), ostracods, oligochaetes, and zooplankton, increased in the same period. At sites south of Muskegon, where the density of Diporeia has been low since 1998, chironomids, zebra mussels, and fingernail clams (Shaeriidae family) were the most important diet items of lake whitefish. Decreases in body condition and growth are associated with the loss of the high-energy prey resource *Diporeia*, the consumption of prey with lower energy content, such as zebra mussels, and possible density-dependence. Commercial harvests of lake whitefish will probably decrease because of low body condition and growth. Future management may require changes in harvest quotas, size restrictions, and depth restrictions as zebra mussel-related impacts spread northward in Lake Michigan.

Peltonen, H., J. Ruuhijärvi, T. Malinen, J. Horppila, M. Olin, and J. Keto. 1999. The effects of food-web management on fish assemblage dynamics in a north temperate lake. Journal of Fish Biology 55: 54-67.
There was an intensive trawl fishery in the Enonselkä basin in Lake Vesijärvi (southern Finland) in 1989–1993 and thereafter the fishing intensity declined. The fish assemblage dynamics were studied both during the years of intensive trawling and for 3 years afterwards. Roach *Rutilus rutilus* dominated the fish assemblage before the mass removal. The intensive trawling effectively diminished the roach stock and the present fishing intensity has been sufficient to prevent its recovery. There were significant decreasing trends in the gillnet cpue (catch per unit effort) of bream *Abramis brama* (L.) and bleak *Alburnus alburnus* (L.) while increasing trend was observed in cpue of ruffe *Gymnocephalus cernuus* (L.) and vendace *Coregonus albula* (L.). Perch *Perca fluviatilis* L. and pikeperch *Stizostedion lucioperca* (L.) showed variations in cpue but no trends existed. The proportion of cyprinids decreased while that of percids and coregonids increased in the catches. The changes in the fish assemblage were induced by the intensive fishing and by the concomitant decline in the ecosystem productivity.

Rennie, M.D. 2014. Context-dependent changes in lake whitefish populations associated with dreissenid invasion. *In* T. F. Nalepa, and D. W. Schloesser. Quagga and Zebra Mussels Biology, Impacts, and Control. *Edited* by T.F. Nalepa and D.W. Schloesser. CRC Press pp. 661-680.
The manner in which an organism responds to a change in its environment can depend greatly on previous conditions. In this regard, lake whitefish (*Coregonus clupeaformis*) populations from a wide range of aquatic environments have demonstrated a variety of responses to the establishment of dreissenid mussels. A review of the literature indicated that individual growth rates and condition of lake whitefish have typically declined after dreissenid establishment where *Diporeia*-a key item of lake whitefish-have also declined in abundance. Temporal changes in lake whitefish growth and condition occurred following dreissenid establishment despite reported increases in lake whitefish consumption rates. A review of lake whitefish populations from noninvaded systems revealed declines in lake whitefish growth and condition as a common response to resource limitation, supporting the hypothesis that typical lake whitefish responses to dreissenid establishment are a function of resource limitation. In contrast, lake whitefish populations from shallow, nutrient-enriched lakes with dreissenid (Lake Erie where *Diporeia* has declined, and Lake Simcoe where *Diporeia* was absent prior to dreissenid establishment) show no evidence of declines in lake whitefish growth and/or condition after dreissenid establishment. Age at maturity was delayed in all but one population of 18 surveyed, regardless of whether dreissenid were established or *Diporeia* had declined in abundance. Body condition of lake whitefish appeared to closely track resource declines in most populations. However, growth declines sometimes appeared to be independent of trends in resource abundance, which suggests effects of other stressors besides dreissenids on lake whitefish growth rates. These stressors may include density dependence, climate warming, and changes in ecosystem community structure that may lead to increased interspecific competition.

Rennie, M.D., Ebener, M.P., and Wagner, T. 2008. Can migration mitigate the effects of ecosystem change? Patterns of dispersal, energy acquisition and allocation in Great Lakes whitefish (*Coregonus clupeaformis*). Biology and Management of Coregonid Fishes – 2008. Adv. Limnol. 63: 455-476.
Migration can be a behavioural response to poor or declining home range habitat quality and can occur when the costs of migration are overcome by the benefits of encountering higher quality resources elsewhere. Despite dramatic ecosystem-level changes in the benthic food web of the Laurentian Great Lakes since the colonization of dreissenid mussels, coincident changes in condition and growth rates among benthivorous lake whitefish populations have been variable. We hypothesized that this variation could be in part mitigated by differences in migratory habits among populations, where increased migration distance can result in an increased probability of encountering high-quality habitat (relative to the home range). Results from four Great Lakes populations support this hypothesis; relative growth rates increased regularly with migration distance. The population with the largest average migration distance also had the least reduction in size-at-age during a period of significant ecosystem change and among the highest estimated consumption and activity rates. In comparison, the population with the greatest declines in size-at-age was among the least mobile, demonstrating only moderate rates of consumption and activity. The least mobile population of lake whitefish was supported by a remnant Diporeia population and has experienced only moderate temporal growth declines. Our study provides evidence for the potential role of migration in mitigating the effects of ecosystem change on lake whitefish populations.

Rennie, M.D., Sprules, W.G., and Johnson, T.B. 2009. Resource switching in fish following a major food web disruption. Oecologia 159: 789-802.
Dreissenid mussels (*Dreissena polymorpha* and D. *bugensis*) have re-engineered Great Lakes ecosystems since their introduction in the late 1980s. Dreissenids can have major indirect impacts on profundal

habitats by redirecting nutrients and energy away from pelagic production (which supplies profundal production) and depositing nutrients and energy in the nearshore zones that they occupy. However, strong empirical evidence for the effects of this redirection of resources on fish populations is currently lacking. Here, we report significant shifts in isotopic signatures, depth distribution and diets of a coldwater profundal fish population that are all consistent with a greater reliance on nearshore resources after the establishment of dreissenid mussels in South Bay, Lake Huron. Isotopic signatures of scales collected from 5-year-old lake whitefish (*Coregonus clupeaformis*) demonstrated remarkable stability over the 50-year period prior to the establishment of dreissenids (1947–1997) and a sudden and significant change in isotopic signatures (3‰ enrichment in δ13C and 1‰ depletion in δ15N) after their establishment (2001–2005). These dramatic shifts in isotopic signatures were accompanied by a coincident shift in the mean depth of capture of lake whitefish towards the nearshore. A comparison of previously unpublished pre-invasion diets of lake whitefish from South Bay with contemporary diets collected between 2002 and 2005 also indicate a greater reliance on nearshore prey after the invasion of dreissenid mussels. This study is the first to report changes in the carbon source available to lake whitefish associated with restructured benthic communities after the appearance of dreissenid mussels. Further, this study contributes to a growing body of work that demonstrates the ecological insights that can be gained through isotopic analysis of archived fish bony tissues in ecosystems that have experienced significant levels of disturbance.

Rennie, M.D., Johnson, T.B., and Sprules, W.G. 2012. Energy acquisition and allocation pattern of lake whitefish (*Coregonus clupeaformis*) are modified when dreissenids are present. Can. J. Fish. Aquat. Sci. 69: 41-59.

We evaluated the effects of dreissenid-induced food web changes on rates of lake whitefish (*Coregonus clupeaformis*) energy acquisition and allocation in North American populations. We used mass-balance models of lake whitefish growth and methylmercury accumulation in 17 populations with and without dreissenids present to estimate and contrast rates of activity (ACT), consumption (C) and conversion efficiency (V). Historical estimates were also generated for a single lake whitefish population during dreissenid establishment. Bioenergetic estimates from both scenarios were compared with densities of Diporeia, a historically important diet component of lake whitefish. Mean lake whitefish ACT and C estimates in populations with dreissenids were significantly greater: 1.3–2 times those of populations without dreissenids. Conversion efficiencies scaled positively and significantly, while C and ACT varied negatively and significantly with Diporeia abundance. Our results suggest that changes in lake whitefish activity may affect density estimates — and ultimately sustainable management quotas — for this species. Our results also show that reported declines in lake whitefish individual growth rates in South Bay, Lake Huron, can be explained by increased activity rates due to increased foraging activity in an energetically depleted prey community.

Rennie, M.D., Weidel, B.C., Claramunt, R.M., and Dunlop, E.S. 2015. Changes in depth occupied by Great Lakes lake whitefish populations and the influence of survey design. J. Great Lakes Res. 41: 1150-1161.

Understanding fish habitat use is important in determining conditions that ultimately affect fish energetics, growth and reproduction. Great Lakes lake whitefish (*Coregonus clupeaformis*) have demonstrated dramatic changes in growth and life history traits since the appearance of dreissenid mussels in the Great Lakes, but the role of habitat occupancy in driving these changes is poorly understood. To better understand temporal changes in lake whitefish depth of capture (Dw), we compiled a database of fishery-independent surveys representing multiple populations across all five Laurentian Great Lakes. By demonstrating the importance of survey design in estimating Dw, we describe a novel method for detecting survey-based bias in Dw and removing potentially biased data.

Using unbiased Dw estimates, we show clear differences in the pattern and timing of changes in lake whitefish Dw between our reference sites (Lake Superior) and those that have experienced significant benthic food web changes (lakes Michigan, Huron, Erie and Ontario). Lake whitefish Dw in Lake Superior tended to gradually shift to shallower waters, but changed rapidly in other locations coincident with dreissenid establishment and declines in *Diporeia* densities. Almost all lake whitefish populations that were exposed to dreissenids demonstrated deeper Dw following benthic food web change, though a subset of these populations subsequently shifted to more shallow depths. In some cases in lakes Huron and Ontario, shifts towards more shallow Dw are occurring well after documented *Diporeia* collapse, suggesting the role of other drivers such as habitat availability or reliance on alternative prey sources.

Sierszen, M.E., Hrabik, T.R., Stockwell, J.D., Cotter, A.M., Hoffman, J.C., Yule, D.L. 2014. Depth gradients in food-web processes linking habitat in large lakes: Lake Superior as an exemplar ecosystem. Freshwater Biol. 59: 2122-2136.
In large lakes around the world, depth-based changes in the abundance and distribution of invertebrate and fish species suggest that there may be concomitant changes in patterns of resource allocation. Using Lake Superior of the Laurentian Great Lakes as an example, we explored this idea through stable isotope analyses of 13 major fish taxa. Patterns in carbon and nitrogen isotope ratios revealed use of both littoral and profundal benthos among populations of most taxa analyzed regardless of the depth of their habitat, providing evidence of nearshore–offshore trophic linkages in the largest freshwater lake by area in the world. Isotope-mixing model results indicated that the overall importance of benthic food-web pathways to fish was highest in nearshore species, whereas the importance of planktonic pathways increased in offshore species. These characteristics, shared with the Great Lakes of Africa, Russia and Japan, appear to be governed by two key processes: high benthic production in nearshore waters and the prevalence of diel vertical migration (DVM) among offshore invertebrate and fish taxa. DVM facilitates use of pelagic food resources by deep-water biota and represents an important process of trophic linkage among habitats in large lakes. Support of whole-lake food webs through trophic linkages among pelagic, profundal and littoral habitats appears to be integral to the functioning of large lakes. These linkages can be disrupted though ecosystem disturbance such as eutrophication or the effects of invasive species and should be considered in native species restoration efforts.

Turschak, B.A., Bunnell, D., Czesny, S., Höök, T.O., Janssen, J. Warner, D., and Bootsma, H.A. 2014. Nearshore energy subsidies support Lake Michigan fishes and invertebrates following major changes in food web structure. Ecology 95: 1243-1252.
Aquatic food webs that incorporate multiple energy channels (e.g., nearshore benthic and pelagic) with varying productivity and turnover rates convey stability to biological communities by providing independent energy sources. Within the Lake Michigan food web, invasive dreissenid mussels have caused rapid changes to food web structure and potentially altered the channels through which consumers acquire energy. We used stable C and N isotopes to determine how Lake Michigan food web structure has changed in the past decade, coincident with the expansion of dreissenid mussels, decreased pelagic phytoplankton production, and increased nearshore benthic algal production. Fish and invertebrate samples collected from sites around Lake Michigan were analyzed to determine taxa-specific 13C:12C (δ13C) and 15N:14N (δ15N) ratios. Sampling took place during two distinct periods, 2002–2003 and 2010–2012, that spanned the period of dreissenid expansion, and included nearshore, pelagic and profundal fish and invertebrate taxa. The magnitude and direction of the δ13C shift indicated significantly greater reliance upon nearshore benthic energy sources among nearly all fish taxa as well as profundal invertebrates following dreissenid expansion. Although the mechanisms underlying this δ13C shift likely varied among species, possible causes include the transport of benthic algal production to offshore waters and increased feeding on nearshore prey items by pelagic and profundal

species. δ15N shifts were more variable and of smaller magnitude across taxa, although declines in δ15N among some pelagic fishes suggest a shift to alternative prey resources. Lake Michigan fishes and invertebrates appear to have responded to dreissenid-induced changes in nutrient and energy pathways by switching from pelagic to alternative nearshore energy subsidies. Although large shifts in energy allocation (i.e., pelagic to nearshore benthic) resulting from invasive species appear to affect total production at upper trophic levels, changes in trophic structure and utilization of novel energy pathways may help to stabilize food webs following species invasions.

Vanderploeg, H.A., Nalepa, T.F., Jude, D.J., Mills, E.L., Holeck, K.T., Liebig, J.R., Grigorovich, I.A., and Ojaveer, H. 2002. Disperal and emerging ecological impacts of Ponto-Caspian species in the Laurentian Great Lakes. Can. J. Fish. Aquat. Sci. 59:1209-1228.

We describe, explain, and "predict" dispersal and ecosystem impacts of six Ponto-Caspian endemic species that recently invaded the Great Lakes via ballast water. The zebra mussel, *Dreissena polymorpha*, and quagga mussel, *Dreissena bugensis*, continue to colonize hard and soft substrates of the Great Lakes and are changing ecosystem function through mechanisms of ecosystem engineering (increased water clarity and reef building), fouling native mussels, high particle filtration rate with selective rejection of colonial cyanobacteria in pseudofeces, alteration of nutrient ratios, and facilitation of the rapid spread of their Ponto-Caspian associates, the benthic amphipod *Echinogammarus ischnus* and the round goby, *Neogobius melanostomus*, which feeds on zebra mussels. The tubenose goby, *Proterorhinus marmoratus*, which does not feed on zebra mussels, has not spread rapidly. Impacts of these benthic invaders vary with site: in some shallow areas, habitat changes and the *Dreissena* round goby piscivore food chain have improved conditions for certain native game fishes and waterfowl; in offshore waters, *Dreissena* is competing for settling algae with the native amphipod *Diporeia* spp., which are disappearing to the detriment of the native deep-water fish community. The predatory cladoceran *Cercopagis pengoi* may compete with small fishes for zooplankton and increase food-chain length.

Fish Community Effects

Bence, J.R, Bergstedt, R.A., Christie, G.C., Cochran, P.A., Ebener, M.P., Koonce, J.F., Rutter, M.A., Swink, W.D. 2003. Sea lamprey (*Petromyzon marinus*) parasite-host interactions in the Great Lakes. J. Great Lakes Res. 29: 253–282.

Prediction of how host mortality responds to efforts to control sea lampreys (*Petromyzon marinus*) is central to the integrated management strategy for sea lamprey (IMSL) in the Great Lakes. A parasite-host submodel is used as part of this strategy, and this includes a type-2 multi-species functional response, a developmental response, but no numerical response. General patterns of host species and size selection are consistent with the model assumptions, but some observations appear to diverge. For example, some patterns in sea lamprey marking on hosts suggest increases in selectivity for less preferred hosts and lower host survival when preferred hosts are scarce. Nevertheless, many of the IMSL assumptions may be adequate under conditions targeted by fish community objectives. Of great concern is the possibility that the survival of young parasites (parasitic-phase sea lampreys) varies substantially among lakes or over time. Joint analysis of abundance estimates for parasites being produced in streams and returning spawners could address this. Data on sea lamprey marks is a critical source of information on sea lamprey activity and potential effects. Theory connecting observed marks to sea lamprey feeding activity and host mortality is reviewed. Uncertainties regarding healing and attachment times, the probability of hosts surviving attacks, and problems in consistent classification of marks have led to widely divergent estimates of damages caused by sea lamprey. Laboratory and field studies are recommended to provide a firmer linkage between host blood loss, host mortality, and observed marks on surviving hosts, so as to improve estimates of damage.

Bronte, C.R., Ebener, M.P., Schreiner, D.R., DeVault, D.S., Petzold, M.M., Jensen, D.A., Richards, C., and Lozano, S.J. 2003. Fish community change in Lake Superior, 1970-2000. Can. J. Fish. Aquat. Sci. 60: 1552-1574.
Changes in Lake Superior's fish community are reviewed from 1970 to 2000. Lake trout (*Salvelinus namaycush*) and lake whitefish (*Coregonus clupeaformis*) stocks have increased substantially and may be approaching ancestral states. Lake herring (*Coregonus artedi*) have also recovered, but under sporadic recruitment. Contaminant levels have declined and are in equilibrium with inputs, but toxaphene levels are higher than in all other Great Lakes. Sea lamprey (*Petromyzon marinus*) control, harvest limits, and stocking fostered recoveries of lake trout and allowed establishment of small nonnative salmonine populations. Natural reproduction supports most salmonine populations, therefore further stocking is not required. Nonnative salmonines will likely remain minor components of the fish community. Forage biomass has shifted from exotic rainbow smelt (*Osmerus mordax*) to native species, and high predation may prevent their recovery. Introductions of exotics have increased and threaten the recovering fish community. Agencies have little influence on the abundance of forage fish or the major predator, siscowet lake trout, and must now focus on habitat protection and enhancement in nearshore areas and prevent additional species introductions to further restoration. Persistence of Lake Superior's native deepwater species is in contrast to other Great Lakes where restoration will be difficult in the absence of these ecologically important fishes.

Casselman, J.M., Brown, D.M., and Hoyle, J.A. 1996. Resurgence of lake whitefish, *Coregonus clupeaformis*, in Lake Ontario in the 1980s. Great Lakes Res. Review 2(2):20-28.
Lake whitefish (*Coregonus clupeaformis*) is Lake Ontario's most important commercial species. The population was low in 1900, increased substantially in the early 1920s, then declined steadily up to the 1930s. Only a remnant population existed from the 1960s to the 1970s. A major resurgence commenced in the late 1970s and early 1980s, producing a population at least twice as great as at any time since 1900. Eastern Lake Ontario has two major spawning stocks; "lake" (south shore, Prince Edward County) and "bay" (Bay of Quinte). Quantitative scale characteristics have been developed that discriminate these stocks 90% of the time. The present resurgence began in 1977 and progressed more quickly in the lake (approx. 2 years). The lake stock contributed to the resurgence of the bay stock and in the late 1980s expanded to the west end of Lake Ontario, re-establishing another spawning stock. This resurgence resulted from increased recruitment because of favourable severe winter conditions (1976-77 and 1977-78) and from increased fry survival associated with winterkill of predators (i.e. alewife and white perch) and with increased lake trout predation on predators (i.e., rainbow smelt). This resurgence signals the re-establishment of a more diverse, self-sustaining cold-water fish community in Lake Ontario.

Evans, D.O. and Waring, P. 1987. Changes in the multispecies, winter angling fishery of Lake Simcoe, Ontario, 1961-83: invasion by rainbow smelt, *Osmerus mordax*, and the roles of intra-specific interactions. Can. J. Fish. Aquat. Sci. 44(Supp. 2): 182-197.
Winter creel surveys revealed major changes in the abundance of five fish species (lake trout, *Salvelinus namaycush*, lake whitefish, *Coregonus clupeaformis*, lake herring, *Coregonus artedii*, yellow perch, *Perca flavescens*, and rainbow smelt, *Osmerus mordax*) in Lake Simcoe (1961–83). Variations in abundance were in part caused by intra- and interspecific factors. Catches in alternate years for both lake herring and rainbow smelt were inversely correlated, suggesting negative interactions between their young-of-the-year and yearlings. Similarly, an inverse relation between parental stock size and recruitment

explained a significant component of the catch variation of lake herring and yellow perch. Natural recruitment of lake trout declined during the 1950s (associated with eutrophication effects), and in the early 1960s, rainbow smelt invaded the fake. Lake whitefish abundance declined in the early 1970s as smelt abundance increased; the decline in whitefish recruitment was probably caused by interaction between smelt and whitefish young-of-the-year. Catches of yellow perch were positively correlated with rainbow smelt and negatively correlated with lake whitefish. Lake herring also increased when lake whitefish density was low. Increased abundance of lake trout after 1975 (due to stocking) appears to have resulted in lower densities of lake herring, rainbow smelt, and yellow perch and the reestablishment of lake whitefish recruitment at a low level. These results suggest that a large predator (lake trout) can have a major influence on the structure of a fish community, by direct and indirect effects.

Harvey, C. J., Ebener, M.P., White, C.K. 2008. Spatial and ontogenetic variability of sea lamprey diets in Lake Superior. J. Great Lakes Res. 34: 434–449.
Invasive sea lamprey (*Petromyzon marinus*) remain an important source of fish mortality in the Laurentian Great Lakes, yet assessing their impact is hindered by lack of quantitative diet information. We examined nitrogen and carbon stable isotope ratios (δ15N and δ13C) of sea lamprey and host species in six ecoregions of Lake Superior, mainly in 2002–2004. Data implied that most sea lamprey fed primarily on upper trophic level species, including forms of lake trout (*Salvelinus namaycush*). However, in Ontario waters, particularly semi-enclosed Black Bay, sea lamprey relied heavily on lower trophic levels, such as coregonines (*Coregonus* spp.) and suckers (*Catostomus* spp.). Sea lamprey δ15N and δ13C generally increased with sea lamprey size, implying dependence on higher trophic levels later in life. Most parasitic sea lamprey that we captured were attached to either lean lake trout (35% of observed attachments), lake whitefish (*Coregonus clupeaformis*; 25%), or cisco (C. *artedii*; 25%); the latter sea lamprey were typically < 15 g. Survey- and fishery-dependent wounding rate data compiled from 1986–2005 suggest that lean and siscowet lake trout were selectively parasitized by sea lamprey, which is consistent with our stable isotope data. Our results largely support the notion that lake trout are the principal host species in Lake Superior. However, stable isotope evidence that sea lamprey feed at lower trophic levels in some regions argues for comprehensive monitoring of sea lamprey impacts throughout the fish community in systems that sea lamprey have invaded.

He, J.X., Bence, J.R., Madenjian, C.P., Pothoven, S.A., Dobiesz, N.E., Fielder, D.G., Johnson, J.E., Ebener, M.P., Cottrillm, R.A., Mohr, L.C., and Koproski, S.R. 2015. Coupling age-structured stock assessment and fish bioenergetics models: a system of time-varying models for quantifying piscivory patterns during the rapid trophic shift in the main basin of Lake Huron. Can. J. Fish. Aquat. Sci. 72: 7-23.
The authors quantified piscivory patterns in the main basin of Lake Huron during 1984–2010 and found that the biomass transfer from prey fish to piscivores remained consistently high despite the rapid major trophic shift in the food webs. We coupled age-structured stock assessment models and fish bioenergetics models for lake trout (*Salvelinus namaycush*), Chinook salmon (*Oncorhynchus tshawytscha*), walleye (*Sander vitreus*), and lake whitefish (*Coregonus clupeaformis*). The model system also included time-varying parameters or variables of growth, length–mass relations, maturity schedules, energy density, and diets. These time-varying models reflected the dynamic connections that a fish cohort responded to year-to-year ecosystem changes at different ages and body sizes. We found that the ratio of annual predation by lake trout, Chinook salmon, and walleye combined with the biomass indices of age-1 and older alewives (*Alosa pseudoharengus*) and rainbow smelt (*Osmerus mordax*) increased more than tenfold during 1987–2010, and such increases in predation pressure were structured by relatively stable biomass of the three piscivores and stepwise declines in the biomass of alewives and rainbow smelt. The piscivore stability was supported by the use of alternative energy

pathways and changes in relative composition of the three piscivores. In addition, lake whitefish became a new piscivore by feeding on round goby (*Neogobius melanostomus*). Their total fish consumption rivaled that of the other piscivores combined, although fish were still a modest proportion of their diet. Overall, the use of alternative energy pathways by piscivores allowed the increases in predation pressure on dominant diet species.

Hrabik, T.R., Magnuson, J.J., and McLain, A.S. 1998. Predicting the effects of rainbow smelt on native fishes in small lakes: evidence from long-term research on two lakes. Can. J. Fish. Aquat. Sci. 55: 1364-1371.
We assessed predictability of negative interactions between native fishes and exotic rainbow smelt (*Osmerus mordax*) through field experiments and long-term data analysis for two lakes in Wisconsin. Predictions were made based on thermal preferences, diet characteristics, and published accounts of interactions between smelt and yellow perch (*Perca flavescens*) and smelt and cisco (*Coregonus artedii*). Our results indicate predation is the most likely cause for the extirpation of cisco from Sparkling Lake in 1990. In Crystal Lake, native yellow perch experienced significant overlap in distribution and diet with smelt. The condition of adult perch was negatively correlated with smelt abundance indicating competition was occurring. Smelt feed on a wide size range of prey items making this species a threat to native fishes, especially when spatial overlap is high. Information on spatial and temporal overlap and diet enable useful predictions about the effect of smelt invasions on native fishes.

Krueger, D.M., and Hrabik, T.R. 2005. Food web alterations that promote native species: the recovery of cisco (*Coregonus artedi*) populations through management of native piscivores. Can. J. Fish. Aquat. Sci. 62: 2177-2188.
We evaluated the effects of fisheries management on food webs in three northern Wisconsin lakes with exotic rainbow smelt (*Osmerus mordax*). In two of the lakes, restrictions on fishing reduced mortality rates on adult walleye (*Sander vitreus*) during the study period. In these lakes, walleye populations increased concurrently with a decline in rainbow smelt populations. As rainbow smelt populations declined in both lakes, native cisco (*Coregonus artedi*) populations increased. Our analysis of walleye diets illustrated that walleye fed selectively on rainbow smelt but did not feed on cisco during the summer months. When entered into bioenergetics simulations, this information demonstrates that walleye predation alone was enough to cause the observed rainbow smelt declines in our study lakes. Our results indicate that increased walleye density allows for a parallel increase in cisco density. Based on our results, fishery regulations to restore walleye to high densities in lakes invaded by rainbow smelt may restore native planktivores that have co-evolved traits.

Loftus, D.H., and Hulsman, P.F. 1986. Predation on larval lake whitefish (*Coregonus clupeaformis*) and lake herring (C. *artedi*) by adult rainbow smelt (*Osmerus mordax*). Can. J. Fish. Aquat. Sci. 43: 812-818.
Rainbow smelt (*Osmerus mordax*) predation on larval lake whitefish (*Coregonus clupeaformis*) and lake herring (C. *artedii*) in Twelve Mile Lake, Ontario, was intense in 1984. Coregonid larvae hatched in early April as smelt spawning was ending. Predation was continuous for a 7-wk period, beginning at the onset of hatching. Numbers of coregonid larvae observed in smelt stomachs were directly proportional ($p \leq 0.005$) to their abundance in the lake. During the week when the larvae were most abundant, they occurred in 93% of the smelt stomachs containing food. The corresponding average daily consumption was 8.4 larvae per smelt. Simulation of the combined effects of smelt predation and "natural" mortality indicated that mortality of lake whitefish may be 100%. Survival of herring larvae must be greatly reduced as well. Rainbow smelt became established in Twelve Mile Lake in the 1950's; their effect on larval whitefish survival may have been aggravated by intensified dipnetting of spawning lake whitefish

during the 1960's. There has been little or no recruitment of young whitefish to the population since 1975, although dipnetting for adults ceased in about 1970. Our results support the hypothesis that the primary cause of recruitment failure of this whitefish population is predation by smelt.

Madenjian, C.P., Fahnenstiel, G.L., Johengen, T.H., Nalepa, T.F., Vanderploeg, H.A., Fleischer, G.W., Schneeberger, P.J., Benjamin, D.M., Smith, E.B., Bence, J.R., Rutherford, E.S., Lavis, D.S., Robertson, D.M., Jude, D.J., and Ebener, M.P. 2002. Dynamics of the Lake Michigan food web, 1970-2000. Can. J. Fish. Aquat. Sci. 59: 736-753.
The authors document changes in the Lake Michigan food web between 1970 and 2000 and identify the factors responsible for these changes. Control of sea lamprey (*Petromyzon marinus*) and alewife (*Alosa pseudoharengus)* populations in Lake Michigan, beginning in the 1950s and 1960s, had profound effects on the food web. Recoveries of lake whitefish (*Coregonus clupeaformis*) and burbot (*Lota lota*) populations, as well as the buildup of salmonine populations, were attributable, at least in part, to sea lamprey control. Based on our analyses, predation by salmonines was primarily responsible for the reduction in alewife abundance during the 1970s and early 1980s. In turn, the decrease in alewife abundance likely contributed to recoveries of deepwater sculpin (*Myoxocephalus thompsoni*), yellow perch (*Perca flavescens*), and burbot populations during the 1970s and 1980s. Decrease in the abundance of all three dominant benthic macroinvertebrate groups, including *Diporeia*, oligochaetes, and sphaeriids, during the 1980s in nearshore waters (50 m deep) of Lake Michigan, was attributable to a decrease in primary production linked to a decline in phosphorus loadings. Continued decrease in Diporeia abundance during the 1990s was associated with the zebra mussel (*Dreissena polymorpha*) invasion, but specific mechanisms for zebra mussels affecting Diporeia abundance remain unidentified.

Madenjian, C., O'Gorman, R., Bunnell, D.B., Argyle, R.L., Roseman, E.F., Warner, D.M., Stockwell, J.D., and Stapanian, M.A. 2008. Adverse effects of alewives on Laurentian Great Lakes fish communities. N. Am. J. Fish. Manage. 28: 263-282.
The alewife *Alosa pseudoharengus*, an invader to the Laurentian Great Lakes from the Atlantic Ocean, has been blamed for causing major disruptions of Great Lakes fish communities during the past 50 years. We reviewed the literature and examined long-term data on fish abundances in the Great Lakes to develop a new synthesis on the negative effects of alewives on Great Lakes fish communities. The results indicated that certain fish populations are substantially more vulnerable to the effects of alewives than others. More specifically, the effects of alewives on other fish populations appeared to follow a continuum—from such fishes as slimy sculpin *Cottus cognatus*, lake whitefish *Coregonus clupeaformis*, and bloater *Coregonus hoyi*, which were relatively unsusceptible—to Atlantic salmon *Salmo salar*, lake trout *Salvelinus namaycush*, and emerald shiner *Notropis atherinoides*, which were highly susceptible. Intermediate species in this continuum included yellow perch *Perca flavescens*, deepwater sculpin *Myoxocephalus thompsonii*, and burbot *Lota lota*. The predominant mechanism by which alewives exerted their negative effect appeared to be predation on the larvae of other fishes. The key factor in the extirpation of Atlantic salmon from Lake Ontario, however, was probably early mortality syndrome induced by a diet rich in alewives. We conclude that the degree of restoration of the native Great Lakes fish community depends in part on the degree of control of the alewife population.

Myers, J.T., Jones, M.L., Stockwell, J.D., and Yule, D.L. 2009. Reassessment of the predatory effects of rainbow smelt on ciscoes in Lake Superior. T. Am. Fish. Soc. 138: 1352-1368.
Evidence from small lakes suggests that predation on larval ciscoes *Coregonus artedi* by nonnative rainbow smelt *Osmerus mordax* can lead to cisco suppression or extirpation. However, evidence from larger lakes has led to equivocal conclusions. In this study, we examine the potential predation effects of rainbow smelt in two adjacent but contrasting embayments in Lake Superior (Thunder and Black bays,

Ontario). During May 2006, we sampled the ichthyoplankton, pelagic fish communities, and diet composition of rainbow smelt in both bays. Using acoustics and midwater trawling, we estimated rainbow smelt densities to be 476 ± 34/ha (mean ± SE) in Thunder Bay and 3,435 ± 460/ha in Black Bay. We used a bioenergetics model to estimate the proportion of cisco larvae consumed by rainbow smelt. Our results suggest that predation by rainbow smelt accounts for 15–52% and 37–100% of the mortality of larval ciscoes in Thunder and Black bays, respectively, depending on the predator feeding rate and the scale of predator–prey overlap. We also examined the sensitivity of past conclusions (based on 1974 field collections) to assumptions of temporal overlap between rainbow smelt and larval ciscoes and estimates of rainbow smelt abundance derived from bottom trawl samples. After adjusting these parameters to reflect current understanding, we found that the previous predation estimates may have been conservative. We conclude that rainbow smelt may have been a more important contributor to the demise and slow recovery of ciscoes in Lake Superior than previously thought.

Nester, R.T., and Poe, T.P. 1984. Predation on lake whitefish eggs by longnose suckers. J. Great Lakes Res. 10: 327-328.
In November 1981, we observed intense predation on lake whitefish (*Coregonus clupeaformis*) eggs by longnose suckers (*Catostomus catostomus*) on lake whitefish spawning grounds in northwestern Lake Huron. Since longnose suckers commonly frequent the same habitat used by spawning lake whitefish, there exists the potential for high losses of eggs due to sucker predation.

Stockwell, J.D., Ebener, M.P., Black, J.A., Gorman, O.T., Hrabik, T.R., Kinnunen, R.E., Mattes, W.P., Oyadomari, J.K., Schram, S.T., Schreiner, D.R., Seider, M.J., Sitar, S.P., and Yule, D.L. 2009. A synthesis of cisco recovery in Lake Superior: implications for native fish rehabilitation in the Laurentian Great Lakes. N. Am. J. Fish. Manage. 29: 626-652.
Populations of cisco *Coregonus artedi* in the Laurentian Great Lakes supported large-scale commercial fisheries and were the primary forage of piscivores during the first half of the 20th century. However, by 1970 populations had collapsed in all of the lakes. Since then, ciscoes have staged a recovery in Lake Superior. In this synthesis, we describe the status of ciscoes in Lake Superior during 1970–2006 and provide a comprehensive review of their ecology. Better understanding of age estimation techniques, application of hydroacoustic and midwater trawl sampling, and compilation of long-term data sets have advanced our understanding of the species. Management agencies contemplating rehabilitation of cisco populations should recognize that (1) knowledge of cisco ecology and population dynamics is increasing; (2) ciscoes are long-lived; (3) Great Lakes populations are probably composed of both shallow-water and deepwater spawning forms; (4) large year-classes can be produced from small adult stocks; (5) large variation in year-class strength is probably intrinsic to Great Lakes populations; (6) despite the longevity and early maturity of ciscoes, stocks can be overfished because large year-classes are produced infrequently; (7) regional environmental factors appear to play a large role in reproductive success; and (8) rainbow smelt *Osmerus mordax* are likely to have a negative effect on cisco recruitment under certain conditions. A top-down approach for rehabilitating lake trout *Salvelinus namaycush* in Lake Superior probably benefited cisco recovery through lake trout predation on invasive rainbow smelt populations. We argue that managing for populations of exotic alewives *Alosa pseudoharengus* to support popular recreational fisheries of exotic Pacific salmonids in the other Great Lakes conflicts with stocking efforts to rehabilitate native lake trout in those lakes. If native fish rehabilitation is a serious and primary goal for management agencies in the Great Lakes basin, we propose that an ecosystem-based approach to modifying the environment for the benefit of native fish species (i.e., decimation or eradication of invasive species) is required.

Reckahn, J.A. 1995. A graphical paradigm for the sequential reduction and spectacular rehabilitation of the lake whitefish of Lake Huron. *In* The Lake Huron Ecosystem: Ecology, Fisheries, and Management. *Edited* by M. Munawar, T. Edsall, and J. Leach. Michigan State University Press pp. 171-190.
One of the most spectacularly successful programs of fish rehabilitation has been steadily building in the Laurentian Great Lakes since 1960 and 1961. In those years the first round of chemical treatments for control of the sea lamprey *Petromyzon marinus* was applied to tributaries of Georgian Bay (Cucin & Regier 1965; Berst & Waini 1967). The search for the effective lampricide known as TFM (3-trifluoromethyl-4-nitrophenol) was a major accomplishment in itself and was carried out on the shore of Lake Huron at the Hammond Bay Laboratory of the US Fish & Wildlife Service (Applegate et al. 1961). At present (1993), the explosive up surge in commercial yields of lake whitefish *Coregonus clupeaformis* (Fig. I) can properly be called an "irruption", "a sudden upsurge in numbers esp. when natural ecological checks and balances are disturbed", Merriam Webster (1986). But the irruption has been primarily an event in the main lake basin of Lake Huron and, to a lesser extent, in the North Channel (Fig I). In Georgian Bay there has been a 45-year gap in production of strong year-classes. Clearly more than just a lamprey problem has existed in this basin. Rehabilitation of Great Lakes coregonines (whitefishes) has recently been summarized in the 1990 "Coregonid Symposium" held in Quebec City (Fleischer 1992; Reckahn 1992). There were multiple causes exerted over many years for the several collapses and subsequent resurgence of the lake whitefish in the Great Lakes. Earlier, a symposium on Georgian Bay and the North Channel had been published (Munawar,1988). In this present symposium, Spangler & Peters (1995) summarize some of the important factors for Lake Huron, particularly the intensive fisheries in the 1800's, that impacted whitefish and other species. Some other, more recent factors, which they have not discussed, I have included in this paper. In particular, I want to stress the detrimental role of the smelt.

Riley, S.C., Roseman, E.F., Nichols, S.J., O'Brien, T.P., Kiley, S.C., and Schaeffer, J.S. 2008. Deepwater demersal fish community collapse in Lake Huron. T. Am. Fish. Soc. 137: 1879-1890.
Long-term fish community surveys were carried out in the Michigan waters of Lake Huron using bottom trawls from 1976 to 2006. Trends in abundance indices for common species (those caught in 10% or more of trawl tows) were estimated for two periods: Early (1976-1991) and late (1994-2006). All common species significantly decreased in abundance during the late period with the exception of the johnny darter *Etheostoma nigrum* and spottail shiner *Notropis hudsonius*, which showed no significant trends, and the round goby *Neogobius melanostomus*, which increased in abundance. Percentage decreases in abundance indices between 1994-1995 and 2005-2006 ranged from 66.4% to 99.9%, and seven species decreased in abundance by more than 90%. The mean biomass of all common species in 2006 was the lowest observed in the time series and was less than 5% of that observed in the mid-1990s. The mean number of common species captured per trawl has also decreased since the mid-1990s. Several factors, including recent invasion of the lake by multiple exotic species, may have contributed to these declines, but insufficient published data are currently available to determine which factors are most important. Our observations suggest that significant changes have occurred in the ecology of Lake Huron since the mid-1990s. The extent of these changes indicates that the deepwater demersal fish community in Lake Huron is undergoing collapse.

Riley, S.C., Rinchard, J., Ebener, M.P., Tillitt, D.E., Munkittrick, K.R., Parrott, J.L., and Allen, J.D. 2011. Thiamine concentrations in lake whitefish eggs from the upper Great Lakes are related to maternal diet. J. Great Lakes Res. 37: 732-737.
Thiamine deficiency is responsible for reproductive impairment in several species of salmonines in the Great lakes, and is thought to be caused by the consumption of prey containing thiaminase, a thiamine-

degrading enzyme. Because thiaminase levels are extremely high in dreissenid mussels, fish that prey on them may be susceptible to thiamine deficiency. We determined thiamine concentrations in lake whitefish *Coregonus clupeaformis* eggs from the upper Laurentian Great Lakes to assess the potential for thiamine deficiency and to determine if thiamine concentrations in lake whitefish eggs were related to maternal diet. Mean thiamine concentrations in lake whitefish eggs were highest in Lake Huron, intermediate in Lake Superior, and lowest in Lake Michigan. Some fish had thiamine concentrations below putative thresholds for lethal and sublethal effects in salmonines, suggesting that some larval lake whitefish may currently be at risk of at least sublethal effects of low thiamine concentrations, although thiamine thresholds are unknown for lake whitefish. Egg thiamine concentrations in lake whitefish eggs were statistically significantly related to isotopic carbon signatures, suggesting that egg thiamine levels were related to maternal diet, but low egg thiamine concentrations did not appear to be associated with a diet of dreissenids. Egg thiamine concentrations were not statistically significantly related to multifunction oxidase induction, suggesting that lower egg thiamine concentrations in lake whitefish were not related to contaminant exposure.

Rösch, R., and Schmid, W. 1996. Ruffe (*Gymnocephalus cernuus* L.), newly introduced into Lake Constance: preliminary data on population biology and possible effects on whitefish (*Coregonus lavaretus* L.). Ann. Zool. Fennici 33: 467-471.
In 1987, ruffe (*Gymnocephalus cernuus* L.) was recorded for the first time in Lake Constance, Germany. Since then its population has increased dramatically. This species is now (1995) found in high numbers throughout the lake from inshore areas to depths up to 100 m. In autumn 1994, the ruffe population consisted of fish of an age of 0+ to 3+. Maximum body length was 16 cm. At the end of the first year ruffe attained an average body length of 7.6 ± 0.9 cm (mean ± S.D.), at the end of the second year 10.4 ± 1.1 cm. During the growing season ruffe were bottom feeders, preying mainly on chironomids and detritus. However, during the spawning season of whitefish (*Coregonus lavaretus* L.) in December ruffe switched to whitefish eggs as a main prey. In December 1993, high numbers of eggs were found in the stomachs of all ruffe investigated with a maximum of 322 eggs in a ruffe of 16 cm body length and 60.1 g body wet weight. In December 1994, ruffe started predation on whitefish eggs at the end of the spawning period, but the percentage of ruffe preying on whitefish eggs did not exceed 60%. Due to this egg predation, negative impacts on the natural reproduction of nearshore spawning whitefish are to be expected. There is also a possibility of interactions during the growing season with the commercially important perch (*Perca fluviatilis* L.) population.

Spangler, G.R., and Collins, J.J. 1980. Response of lake whitefish (*Coregonus clupeaformis*) to the control of sea lamprey (*Petromyzon marinus*) in Lake Huron. Can. J. Fish. Aquat. Sci. 37:2039-2046.
Changes in population parameters of three stocks of whitefish (*Coregonus clupeaformis*) in Lake Huron following control of sea lamprey (*Petromyzon marinus*) have varied between the major basins of the lake. In the North Channel and main basin, whitefish survival rates increased significantly, from values of 23 to 37% and 16 to 24%, respectively. In both areas the abundance of lamprey declined while whitefish increased. In Georgian Bay, whitefish populations did not reflect changes attributable to lamprey control, possibly because of low lamprey abundance. During the control period, whitefish survival rates declined from 57 to 39%, abundance declined and growth rates increased.

Spangler, G.R., Robson, D.S., and Regier, H.A. 1980. Estimates of lamprey-induced mortality in whitefish, *Coregonus clupeaformis*. Can. J. Fish. Aquat. Sci 37:2146-2150.
The seasonal rate of lamprey attack upon lake whitefish in Lake Huron is estimable as the proportion of recently wounded fish in the catch. The nonfatal lamprey attack rate is estimable from the accumulation of healed scars observed on a cohort of marked (tagged) fish sampled throughout the fishing season.

The difference between these estimates is an estimate of the fatal lamprey attack coefficient. In northern Lake Huron, lamprey attacks on whitefish are most frequent during August to November. The fatal lamprey attack rate is greatest during late summer when a large proportion of attacks results in the death of the host. Approximately 75% of the lamprey attacks on whitefish are fatal during mid-June to mid-November

Vainikka, A., Jakubavičūitė, E., and Hyvärinen, P. 2017. Synchronous decline of three morphologically distinct whitefish (*Coregonus lavaretus*) stocks in Lake Oulujarvi with concurrent changes in the fish community. Fish. Res. 196: 34-46.
Identification of ecologically mediated mechanisms that drive population dynamical changes in fish communities and polymorphic fish stocks such as those of whitefish, *Coregonus lavaretus*, requires data that are seldom available in freshwater systems. We assessed the stock of each morphologically distinguishable whitefish form (native lesser sparsely-rakered whitefish, native blue whitefish and stocked northern densely-rakered whitefish) in the Lake Oulujärvi during 1973–2014, and related temporal variations in population dynamics to environmental data and catch per unit of effort (CPUE) data on other species having fisheries significance. The results demonstrated a synchronous major decline in the abundance of the native whitefish forms and a decline in the length-at-age of all forms. During the study period, summer time water temperature increased and surface water phosphorous concentration decreased. Recruitment in all whitefish forms showed Ricker-type dependence on spawning stock biomass but little residual correlation with the environmental parameters. Cross-correlation analyses suggested that the re-establishment of pikeperch *Sander lucioperca* population affected negatively both the recruitment and biomass of whitefish but the exact effect mechanisms require further assessment. Our results exemplify that ecosystem-based fisheries management in inland waters must take into account both natural and human-induced environmental changes as well as stockings, and that knowledge-based inland fisheries management is inherently data-intensive.

Fish Health

Brenden, T.O., Ebener, M.P., Sutton, T.M. 2010a. Assessing the health of lake whitefish populations in the Laurentian Great Lakes. J. Great Lakes Res. 36(Supp. 1): 1-5.
The papers assembled in this special issue significantly advance the present understanding of the health and status of lake whitefish *Coregonus clupeaformis* populations in the Laurentian Great Lakes. Although lake whitefish have recovered remarkably from the low abundances of the late 1950s and early 1960s, recent reductions in growth rates and body condition have raised concerns as to the future sustainability of Great Lakes populations. Declines in growth rates and condition were first observed in the late 1970s and early 1980s, which was when abundance levels of many Great Lakes lake whitefish populations began returning to historically high levels (Fig. 1). Researchers have postulated a number of explanations for why lake whitefish growth rates and condition have declined and, as of yet, shown little signs of recovering. These include density-dependent regulation as a result of the species' burgeoning abundance, food-web changes that have at least partly resulted from the invasion and expansion of dreissenid mussels *Dreissena polymorpha* and D. *bugensis*, and environmental change stemming from global warming.

Brenden, T.O., Ebener, M.P., Sutton, T.M., Jones, M.L., Arts, M.T., Johnson, T.B., Koops, M.A., Wright, G.M., and Faisal, M. 2010b. Assessing the health of lake whitefish populations in the Laurentian Great Lakes: lessons learned and research. J. Great Lakes Res. 36(Supp. 1): 135-139.

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.

Corwell, E.R., Anderson, G.B., Coleman, D., Getchell, R.G., Groocok, G.H., Warg, J.V., Cruz, A.M., Casey, J.W., Bain, M.B., and Bower, P.R. 2015. Applying multi-scale occupancy models to infer host and site occupancy of an emerging viral fish pathogen in the Great Lakes. J. Great Lakes Res. 41: 520-529.
Emerging pathogens in wildlife are being described at an increasing rate, but the methods used to describe their dynamics in wildlife populations have been slow to develop. Understanding pathogen prevalence and risk factors for infection are critical first components of developing wildlife disease management. However, the estimation of these attributes can be biased by imperfect detection of the pathogen. In this study, we adopt a multi-scale site occupancy model to estimate the probability of pathogen detection when the diagnostic test is imperfect, host detection is imperfect, and detection can be measured at multiple scales. In addition, this model allowed the comparison of different diagnostic tests for pathogen presence. We then applied this model to the detection of viral hemorrhagic septicemia virus (VHSV) in wild fish populations in the Great Lakes. We show that VHSV is still widely distributed in the Great Lakes, and that a multi-scale model can identify additional risk factors to those identified by previous logistic regression approaches. We also estimate detection probabilities using molecular and traditional virological methods. Although our approach has several limitations, it has important implications in the management and modeling of VHSV and other emerging pathogens in aquatic wildlife.

Enzmann, P.J., and Konrad, M. 1990. Antibodies against VHS in whitefish of the Lake of Constance, West Germany. B. Eur. Assoc. Fish Pat. 10: 24-25.
Antibodies against viral haemorrhagic septicaemia virus (VHS-virus) strain Fl, were found in whitefish (*Coregonus* sp.) in Lake Constance in up to 4% of fish caught.

Faisal, M., Fayed, W., Brenden, T.O., Noor, A., Ebener, M.P., Wright, G.M., and Jones, M.L. 2010a. Widespread infection of lake whitefish *Coregonus clupeaformis* with the swimbladder nematode *Cystidicola farionis* in northern lakes Michigan and Huron. J. Great Lakes Res. 36(Supp.1): 18-28.
We estimated the prevalence, intensity, and abundance of swimbladder nematode infection in 1281 lake whitefish (*Coregonus clupeaformis*) collected from four sites in northern lakes Huron (Cheboygan and DeTour Village) and Michigan (Big Bay de Noc and Naubinway) from fall 2003 through summer 2006. Morphological examination of nematode egg, larval, and mature stages through light and

scanning electron microscopy revealed characteristics consistent with that of *Cystidicola farionis* Fischer 1798. Total C. *farionis* prevalence was 26.94%, while the mean intensity and abundance of infection was 26.72 and 7.21 nematodes/fish, respectively. Although we detected C. farionis in all four stocks that were examined, Lake Huron stocks generally had higher prevalence, intensity, and abundance of infection than Lake Michigan stocks. A distinct seasonal fluctuation in prevalence, abundance, and intensity of C. *farionis* was observed, which does not coincide with reported C. *farionis* development in other fish species. Lake whitefish that were heavily infected with C. *farionis* were found to have thickened swimbladder walls with deteriorated mucosa lining, which could affect swimbladder function. Whether C. *farionis* infection may be negatively impacting lake whitefish stocks in the Great Lakes is unclear; continued monitoring of C. *farionis* infection should be conducted to measure responses of lake whitefish stocks to infection levels.

Faisal, M., Loch, T.P., Brenden, T.O., Eissa, A.E., Ebener, M.P., Wright, G.M., and Jones, M.L. 2010b. Assessment of *Renibacterium salmoninarum* infection in four lake whitefish (*Coregonus clupeaformis*) stocks from northern lakes Huron and Michigan. J. Great Lakes Res. 36(Supp. 1): 29-37.
Lake whitefish (*Coregonus clupeaformis*) from four stocks in northern Lakes Michigan and Huron were collected seasonally from fall 2003 through summer 2006 and examined for the presence of *Renibacterium salmoninarum*, the causative agent of bacterial kidney disease (BKD), using culture techniques on modified kidney disease medium (MKDM) and the quantitative enzyme-linked immunosorbent assay (Q-ELISA). R. *salmoninarum* was detected in 62.31% (according to Q-ELISA) of the 1284 examined lake whitefish, with some fish displaying the typical signs of BKD, such as renal congestion, swelling, and whitish nodules. Kidney cultures on MKDM yielded bacteria with morphological and biochemical characteristics identical to those of R. *salmoninarum* recovered from other Great Lakes fish species, as well as those from other parts of the world. Isolate identification was confirmed via nested polymerase chain reaction. Antibiograms demonstrated high sensitivity to enrofloxacin and ciprofloxacin, sensitivity to oxytetracycline, erythromycin, azithromycin, chloramphenicol, novobiocin, and carbenicillin, and resistance to polymyxin B, clindamycin, and kanamycin. Statistical analysis of R. *salmoninarum* prevalence and intensities revealed significant interactions among stocks, years and sampling seasons, with highest prevalence generally in fall and frequent wide variation in prevalence and intensity from one season to the next for a particular stock. It was surprising to find that the prevalence of R. *salmoninarum* exceeded 50% in the four stocks, much higher than originally thought. Moreover, a positive association between R. *salmoninarum* intensity and the abundance of the swimbladder nematode, *Cystidicola farionis*, was identified. Our findings suggest that Great Lakes lake whitefish are vulnerable to serious fish pathogens.

Faisal, M., Eissa, A.E., and Starliper, C.E. 2010c. Recovery of *Renibacterium salmoninarum* from naturally infected salmonine stocks in Michigan using a modified culture protocol. J. Adv. Res. 1: 95-102.
Renibacterium salmoninarum, the causative agent of bacterial kidney disease (BKD), is a fastidious and slow-growing bacterium that is extremely difficult to grow in vitro. Herein, we describe a modified primary culture protocol that encompasses a modified bacteriological culture medium and a tissue processing procedure. In order to facilitate the release of R. *salmoninarum* from granulomatous tissues, kidneys of infected fish were homogenized in a high-speed stomacher. The kidney disease medium (KDM2), routinely used for primary culture of R. *salmoninarum* was modified by the addition of antibiotics and metabolites. When a relatively large inoculum of diluted kidney homogenate was streak-plate inoculated onto the modified KDM2, colonial growth of R. *salmoninarum* was achieved within 5–7 days, compared to the standard of two weeks or more. The modified procedure was then used to determine the prevalence of R. *salmoninarum* among representative captive and feral salmonid stocks

in Michigan. Prevalence and clinical manifestations varied among species, strains of fish, and locations; however, R. *salmoninarum* isolates were biochemically homogenous. The improved primary culture procedure described in this study enabled selective and quick isolation of R. *salmoninarum*. Also, the isolates retrieved in this study constitute a unique biological resource for future studies of R. *salmoninarum* in the Laurentian Great Lakes.

Faisal, M., Fayed, W., Nour, A., and Brenden, T. 2011. Spatio-temporal dynamics of gastrointestinal helminths infecting four lake whitefish (*Coregonus clupeaformis*) stocks in northern lakes Michigan and Huron, U.S.A. J. Parasitol. 97: 760-774.
This study was undertaken to identify the community composition, structure, and dynamics of helminths infecting the gastrointestinal tract (GIT) of lake whitefish (*Coregonus clupeaformis*) collected from 4 sites in northern lakes Huron (Cheboygan and De Tour Village) and Michigan (Big Bay de Noc and Naubinway) from fall 2003 through summer 2006. A total of 21,203 helminths was retrieved from the GITs of 1,284 lake whitefish. Approximately 42% (SE = 1.4%) of the examined lake whitefish were infected with at least 1 helminth species in their GIT, with a mean intensity of 39.4 worms/fish (SE = 0.3) and a mean abundance of 16.4 worms/fish (SE = 0.1). Collected helminths appeared to be generalists and consisted of 2 phyla (Acanthocephala and Cestoda) and 5 species (*Acanthocephalus dirus*, *Neoechinorhynchus tumidus*, *Echinorhynchus salmonis*, *Cyathocephalus truncatus*, and *Bothriocephalus* sp.). Lake whitefish from Lake Huron on average had greater infection prevalence, abundance, and intensity than did fish from Lake Michigan. Infection parameters for each of the helminth species generally followed the same pattern observed for the combined data. *Acanthocephalus dirus* was the most prevalent and abundant helminth in lake whitefish GITs, although intensity of infection was the greatest for C. *truncatus*. Helminth infection parameters often peaked in the spring while diversity was greatest in the winter samples. There was substantial temporal variability in helminth infections with prevalence, abundance, and intensity often fluctuating widely on consecutive sampling occasions. Analysis of the GIT helminth community composition suggested that 3 (Big Bay de Noc, De Tour Village, and Cheboygan) of the 4 primary spawning sites, overall, had similar community compositions. The reason for the observed spatial and temporal variability in the lake whitefish GIT helminth infections remains to be elucidated. The findings of this study represent the most comprehensive parasitological study ever conducted on lake whitefish in the Great Lakes and will provide valuable information for future comparisons.

Faisal, M., Shavalier, M., Kim, R.K., Millard, E.V., Gunn, M.R., Winters, A.D., Schulz, C.A., Eissa, A., Thomas, M.V., Wolgamood, M., Whelan, G. E., and Winton, J. 2012. Spread of the emerging viral hemorrhagic septicemia virus stain, genotype IVb, in Michigan, USA. Viruses 4: 734-760.
In 2003, viral hemorrhagic septicemia virus (VHSV) emerged in the Laurentian Great Lakes causing serious losses in a number of ecologically and recreationally important fish species. Within six years, despite concerted managerial preventive measures, the virus spread into the five Great Lakes and to a number of inland waterbodies. In response to this emerging threat, cooperative efforts between the Michigan Department of Natural Resources (MI DNR), the Michigan State University Aquatic Animal Health Laboratory (MSU-AAHL), and the United States Department of Agriculture-Animal and Plant Health Inspection Services (USDA-APHIS) were focused on performing a series of general and VHSV-targeted surveillances to determine the extent of virus trafficking in the State of Michigan. Herein we describe six years (2005–2010) of testing, covering hundreds of sites throughout Michigan’s Upper and Lower Peninsulas. A total of 96,228 fish representing 73 species were checked for lesions suggestive of VHSV and their internal organs tested for the presence of VHSV using susceptible cell lines. Of the 1,823 cases tested, 30 cases from 19 fish species tested positive for VHSV by tissue culture and were confirmed by reverse transcriptase polymerase chain reaction (RT-PCR). Gene sequence analyses of all

VHSV isolates retrieved in Michigan demonstrated that they belong to the emerging sublineage “b” of the North American VHSV genotype IV. These findings underscore the complexity of VHSV ecology in the Great Lakes basin and the critical need for rigorous legislation and regulatory guidelines in order to reduce the virus spread within and outside of the Laurentian Great Lakes watershed.

Loch, T.P., and Faisal, M. 2010a. Infection of lake whitefish (*Coregonus clupeaformis*) with motile *Aeromonas* spp. in the Laurentian Great Lakes. J. Great Lakes Res. 36(Supp. 1): 6-12.
Infections with motile *Aeromonas* species were detected in lake whitefish collected over a one-year period from four stocks within lakes Michigan and Huron, USA. Sixty-nine isolates were recovered from the kidneys and swim-bladders of sixty-four infected fish. Representative isolates were Gram-negative bacilli that produced cytochrome oxidase, grew in the absence of salt, were facultative anaerobes, and were resistant to the vibriostatic agent 2,4-diamino,6,7-di-isopropylpteridine. Phenotypic characterization placed twenty-two isolates into the A. *hydrophila* complex, twelve into the A. *sobria* complex, and one into the A. *caviae* complex, while six isolates were characterized as A. *allosaccharophila,* two as A. *veronii* bv. *veronii*, and one as A. *popoffi*. The prevalence of infection by motile aeromonads varied by site and season, with lake whitefish sampled in the summer having a significantly higher prevalence. Clinical signs in lake whitefish infected only with *Aeromonas* spp. included congestion and hemorrhaging in the fins and musculature; generalized pallor; congestion, hemorrhaging, and multifocal necrotic foci within the liver; moderate to severe splenomegaly; congestion and swelling of the kidneys; ascites within the peritoneal cavity; and hemorrhagic enteritis. This study provides evidence on the wide spread prevalence of motile aeromonad infections in lake whitefish stocks inhabiting northern lakes Michigan and Huron.

Loch, T.P., and Faisal, M. 2010b. Isolation of *Aeromonas salmonicida* subspecies *salmonicida* from lake whitefish (*Coregonus clupeaformis*) inhabiting lakes Michigan and Huron. J. Great Lakes Res. 36(Supp. 1): 13-17.
Herein we describe the first report of Aeromonas salmonicida subspecies *salmonicida* infections in lake whitefish (*Coregonus clupeaformis*) collected from four sites in lakes Michigan and Huron, Michigan, USA. The bacterium was isolated from the kidneys of four out of 1286 lake whitefish that were tested over a three-year period. The four isolates were phenotypically similar to one another and exhibited the morphological, colonial, and biochemical traits typical of A. *salmonicida* subspecies *salmonicida*. Amplification of 16S rRNA genes specific to A. *salmonicida* subspecies *salmonicida* via polymerase chain reaction and subsequent gel electrophoresis analyses confirmed the identity of the four lake whitefish isolates. Clinical signs associated with infection included extensive external hemorrhaging, exophthalmia, splenomegaly, splenic and renal congestion, fibrinous adhesions of the spleen and liver, and hemorrhagic enteritis. Histopathological examination of infected fish revealed multi-focal hemorrhage and infiltration of lymphocytes and histiocytes in subdermal adipose tissues and musculature. A low infection incidence of A. *salmonicida salmonicida* in Great Lakes lake whitefish does not preclude the fact that overt signs of disease were observed in infected individuals and that lake whitefish may act as a reservoir for this bacterium that is highly pathogenic to numerous fish species.

Loch, T.P., and Faisal, M. 2011. Infectious diseases of lake whitefish (*Coregonus clupformis*) in the Laurentian Great Lakes. *In* Aquatic Animal Health: a continuing dialogue between Russia and the United States. Proceedings of the Third Bilateral Conference Between the United States and Russia: Aquatic Animal Health 2009. 12-20 July 2009. *Edited* by R.C. Cipriano, A. Bruckner, and I.S. Shchelkunov. Michigan State University, East Lansing, Michigan., Shepherdstown, West Virginia. pp. 195-215.

Lake whitefish (*Coregonus clupeaformis*) are indigenous within the Great Lakes basin and comprise its most economically important fishery. However, recent reductions in growth, condition, and size of harvested Great Lakes lake whitefish have created an impetus to determine those factors that contributed to this decline. Information on the diseases and pathogens of Great Lakes lake whitefish is limited. Herein, we review literature on fish pathogens of Great Lakes lake whitefish and also present clinical cases recently submitted to the Aquatic Animal Health Laboratory at Michigan State University. Reports that describe metazoan infections of Great Lakes lake whitefish are more abundant than those that involve microbial pathogens. Infestations by swimbladder nematodes (e.g. *Cystidicola farionis*) are most important in terms of prevalence, intensity, and pathological impacts. Two gram positive bacteria, Renibacterium salmoninarum and Carnobacterium sp., are widespread among lake whitefish stocks and have been associated with clinical disease. Bacteria of the genus Aeromanas (e.g., A. *salmonicida*, A. *sobria*) are also prevalent. Viral Hemorrhagic Septicemia Virus has also been isolated from a single lake whitefish within Lake Huron. This review highlights the urgent need to further investigate microbial threats to lake whitefish residing within the Laurentian Great Lakes.

Meier, W., Ahne, W., and Jørgensen, P.E.V. 1986. Fish viruses: viral haemorrhagic septicaemia in whitefish (*Coregonus* spp.). J. Applied Ichthol. 2: 181-186.
In two independent investigations, performed simultaneously during 1984 in Munich-FRG and Bern-CH, resp., Viral Haemorrhagic Septicaemia-Virus (VHS) has been detected in white fish (Coregonus sp.), generally showing typical septicaemic haemorrhages. The serological identification of the agent with VHS-F1 rabbit antiserum snowed a relationship to VHS2 (Swiss-isolate) and VHS3 (Germanisolate). The susceptibility of white fish and rainbow trout to the agents has been compared. The mortality rates varied from 28 to 54% for the white fish and from 40 to 80% for the rainbow trout depending on the infection dose. Pathoanatomical findings were: anemia, ascites, scattered intermuscular and subcutaneous haemorrhages. By light microscopy, the most prominent findings were focal necrosis in liver, spleen, pancreas, intestinal mucosa and the haematopoietic part of the kidney. In the urinary forming part of the kidney severe tubulonephrosis was observed.

Meier, W., M. Schmitt, and T. Wahli. 1994. Viral hemorrhagic septicemia (VHS) of nonsalmonids. Annu. Rev. Fish Dis. 4: 359-373.
Viral hemorrhagic septicemia (VHS) is a viscerotropic disease of fish that can cause enormous losses in European rainbow trout populations. Although previously thought to be species specific, recent reports have indicated that other non-salmonid fish species, such as pike, whitefish, grayling, turbot, and herring, can become mortally infected with VHS. This paper reviews several cases of natural VHS-outbreaks in nonsalmonids. Pike, whitefish, grayling, turbot and Pacific herring infected with VHS displayed symptoms typical of hemorrhagic septicemia. The isolation and serological identification of the viruses from all of the infected fish species revealed a close relation to the Egtved-virus strain F1. The virus isolates from diseased pike and rainbow trout were capable of infecting their respective host fish. Experimental infections of pike, whitefish, and grayling fry with Egtved virus strain F1 resulted in high mortalities, with symptoms typical of VHS. Although experiments with older fish suggested an age-dependent decrease in susceptibility, the virus could be isolated from most of the infected fish after several months of experimental infection (carrier status). Histological and electron microscopical findings were comparable to those seen in VHS-infected rainbow trout. The susceptibility of non-salmonid species to VHS infection is disconcerting with respect to the potential losses of the economically important turbot, Pacific herring, and whitefish, as well as the ecologically valuable grayling which is threatened by extinction. If the VHS susceptible non-salmonid species can also support the propagation of the Egtved-virus, it could acquire carrier-status and, as a result, represent a “natural” reservoir for the virus.

Skall, H.F., Kjær, T.E., and Olesen, N.J. 2004. Investigation of wild caught whitefish*, Coregonus lavaretus* (L.) for infection with viral hemorrhagic septicemia virus (VHSV) and experimental challenge of whitefish with VHSV. J. Fish Dis. 27: 401-408.

One hundred and forty-eight wild whitefish, *Coregonus lavaretus* (L.), were caught by electrofishing and sampled for virological examination in December 1999 and 2000, during migration from the brackish water feeding grounds to the freshwater spawning grounds, where the whitefish may come into contact with farmed rainbow trout. All samples were examined on cell cultures. No viruses were isolated. Three viral hemorrhagic septicemia virus (VHSV) isolates of different origin were tested in infection trials by immersion and intraperitoneal (IP) injection, using 1.5 g farmed whitefish: an isolate from wild caught marine fish, a farmed rainbow trout isolate with a suspected marine origin and a classical freshwater isolate. The isolates were highly pathogenic by IP injection where 99–100% of the whitefish died. Using an immersion challenge the rainbow trout isolates were moderately pathogenic with approximately 20% mortality, whereas the marine isolate was virtually non-pathogenic. At the end of the experiment it was possible to isolate VHSV from survivors infected with the marine and suspected marine isolates. Because of the low infection rate in wild whitefish in Denmark, the role of whitefish in the spread of VHSV in Denmark is probably not significant. The experimental studies, however, showed that whitefish are potential carriers of VHSV as they suffer only low mortality after infection but continue to carry virus.

Stepien, C.A., Pierce, L.R., Leaman, D.W., Niner, M.D., and Shepherd, B.S. 2015. Mutation in a novel fish viral hemorrhagic septicemia (VHS) substrain since its first appearance in the Laurentian Great Lakes. PLoS One 10(8): e0135146. Available online at: doi:10.1371/journal.pone.0135146.

Viral Hemorrhagic Septicemia virus (VHSv) is an RNA rhabdovirus, which causes one of the world's most serious fish diseases, infecting >80 freshwater and marine species across the Northern Hemisphere. A new, novel, and especially virulent substrain—VHSv-IVb—first appeared in the Laurentian Great Lakes about a decade ago, resulting in massive fish kills. It rapidly spread and has genetically diversified. This study analyzes temporal and spatial mutational patterns of VHSv-IVb across the Great Lakes for the novel non-virion (Nv) gene that is unique to this group of novirhabdoviruses, in relation to its glycoprotein (G), phosphoprotein (P), and matrix (M) genes. Results show that the Nv-gene has been evolving the fastest (k = 2.0x10-3 substitutions/site/year), with the G-gene at ~1/7 that rate (k = 2.8x10-4). Most (all but one) of the 12 unique Nv- haplotypes identified encode different amino acids, totaling 26 changes. Among the 12 corresponding G-gene haplotypes, seven vary in amino acids with eight total changes. The P- and M- genes are more evolutionarily conserved, evolving at just ~1/15 (k = 1.2x10-4) of the Nv-gene's rate. The 12 isolates contained four Pgene haplotypes with two amino acid changes, and six M-gene haplotypes with three aminoacid differences. Patterns of evolutionary changes coincided among the genes for some of the isolates, but appeared independent in others. New viral variants were discovered following the large 2006 outbreak; such differentiation may have been in response to fish populations developing resistance, meriting further investigation. Two 2012 variants were isolated by us from central Lake Erie fish that lacked classic VHSv symptoms, having genetically distinctive Nv-, G-, and M-gene sequences (with one of them also differing in its P-gene); they differ from each other by a G-gene amino acid change and also differ from all other isolates by a shared Nv-gene amino acid change. Such rapid evolutionary differentiation may allow new viral variants to evade fish host recognition and immune responses, facilitating longtime persistence along with expansion to new geographic areas.

Thompson, T.M., Batts, W.N., Faisal, M., Bowser, P., Casey, J.W., Phillips, K., Garver, K.A., Winton, J., Kurath, G. 2011. Emergence of viral hemorrhagic septicemia virus in the North American Great Lakes region is associated with low viral genetic diversity. Dis. Aquat. Organ. 96: 29-43.

Viral hemorrhagic septicemia virus (VHSV) is a fish rhabdovirus that causes disease in a broad range of marine and freshwater hosts. The known geographic range includes the Northern Atlantic and Pacific Oceans, and recently it has invaded the Great Lakes region of North America. The goal of this work was to characterize genetic diversity of Great Lakes VHSV isolates at the early stage of this viral emergence by comparing a partial glycoprotein (G) gene sequence (669 nt) of 108 isolates collected from 2003 to 2009 from 31 species and at 37 sites. Phylogenetic analysis showed that all isolates fell into sub-lineage IVb within the major VHSV genetic group IV. Among these 108 isolates, genetic diversity was low, with a maximum of 1.05% within the 669 nt region. There were 11 unique sequences, designated vcG001 to vcG011. Two dominant sequence types, vcG001 and vcG002, accounted for 90% (97 of 108) of the isolates. The vcG001 isolates were most widespread. We saw no apparent association of sequence type with host or year of isolation, but we did note a spatial pattern, in which vcG002 isolates were more prevalent in the easternmost sub-regions, including inland New York state and the St. Lawrence Seaway. Different sequence types were found among isolates from single disease outbreaks, and mixtures of types were evident within 2 isolates from individual fish. Overall, the genetic diversity of VHSV in the Great Lakes region was found to be extremely low, consistent with an introduction of a new virus into a geographic region with previously naïve host populations.

Wagner, T., Jones, M.L., Ebener, M.P., Arts, M.T., Brenden, T.O., Honeyfield, D.C., Wright, G.M., and Faisal, M. 2010. Spatial and temporal dynamics of lake whitefish (*Coregonus clupeaformis*) health indicators: linking individual-based indicators to a management-relevant endpoint. J. Great Lakes Res. 36(Supp. 1): 121-134.

We examined the spatial and temporal dynamics of health indicators in four lake whitefish (*Coregonus clupeaformis*) stocks located in northern lakes Michigan and Huron from 2003 to 2006. The specific objectives were to (1) quantify spatial and temporal variability in health indicators; (2) examine relationships among nutritional indicators and stock-specific spatial and temporal dynamics of pathogen prevalence and intensity of infection; and (3) examine relationships between indicators measured on individual fish and stock-specific estimates of natural mortality. The percent of the total variation attributed to spatial and temporal sources varied greatly depending on the health indicator examined. The most notable pattern was a downward trend in the concentration of highly unsaturated fatty acids (HUFAs), observed in all stocks, in the polar lipid fraction of lake whitefish dorsal muscle tissue over the three study years. Variation among stocks and years for some indicators were correlated with the prevalence and intensity of the swimbladder nematode *Cystidicola farionis*, suggesting that our measures of fish health were related, at some level, with disease dynamics. We did not find relationships between spatial patterns in fish health indicators and estimates of natural mortality rates for the stocks. Our research highlights the complexity of the interactions between fish nutritional status, disease dynamics, and natural mortality in wild fish populations. Additional research that identifies thresholds of health indicators, below (or above) which survival may be reduced, will greatly help in understanding the relationship between indicators measured on individual fish and potential population-level effects.

Stocking

Amtstaetter, F., and Willox, C.C. 2004. Survival and growth of lake whitefish from two stocking strategies in Lake Simcoe, Ontario. N. Am. J. Fish. Manage. 24: 1214-1220.

To determine the more efficient stocking strategy for lake whitefish *Coregonus clupeaformis* in Lake Simcoe, Ontario, we compared growth and survival of fish stocked as fall fingerlings and as spring yearlings. Paired lots were stocked in April and October from the 1986 to 1991 year-classes. Survival and growth of fish from the two rearing practices were indexed as the relative abundance and length of 6-year-old lake whitefish captured with trap nets during fall spawning runs from 1992 to 1997. No difference in relative abundance or length between lake whitefish stocked at 6 months of age and those stocked at 12 months of age was detected. This contradicts results reported for many other fish species, which have exhibited greater survival rates when stocked as yearlings rather than fingerlings. As a result of these findings, all lake whitefish stocked into Lake Simcoe are stocked in the fall when the fish are 6 months of age, thus freeing up limited hatchery space for other purposes.

Berg, S., Jeppesen, E., Søndergaard, M., and Mortensen, E. 1994. Environmental effects of introducing whitefish, *Coregonus lavaretus* (L.), in Lake Ring. Hydrobiologia 275/276:71-79.
The impact of whitefish (*Coregonus lavaretus* (L.)) on the trophic structure of eutrophic lakes was studied in Lake Ring, a small eutrophic Danish lake (22.5 ha, mean depth 2.9 m) in which the natural fish fauna is dominated by pike (Esox lucius L.), perch (*Perea fluviatilis* L.), and eel (Anguilla anguilla (L.)), roach (*Rutilus ruti*/us (L.)) and burbot (*Lota Iota* (L.)) being the only other fish species present. A total of 10,993 0+ whitefish were stocked in the lake from October 1989 to July 1990 and the structure of the fish, zooplankton and benthic invertebrate communities studied during the period 1989-91. Stomach contents analysis revealed that the whitefish mainly ate *Daphnia* and copepods in 1990-91, the proportion of copepods decreasing with increasing size of the fish and Daphnia being the overall most important food source. The density of *Daphnia* in the lake decreased from 72 individuals L^{-1} in 1989 to 9 individuals L^{-1} in 1991; concomitantly the large species *Daphnia magna* and D. pulex almost disappeared and the density of cyclopoid copepods increased from 72 to 101 individuals L^{-1}, presumably because of improved food conditions, while that of calanoid copepods remained virtually unchanged. As a result, chlorphyll-a increased from 19 to 47 ug L^{-1} and Secchi depth decreased from 2.4 m to 1. 7 m, despite there being no change in total P and total N (0.6 mg P L^{-1} and 1.3 mg N L^{-1} respectively). Changes were also observed in the benthic invertebrates; Chaoborus, oligochaetes, and chironomids all decreased, whereas *Pisidium* increased. It is concluded that the stocking of whitefish in eutrophic lakes for commercial purposes may delay their recovery, or even lead to enhanced eutrophication.

Brooke, L.T. 1975. Effect of different constant incubation temperatures on egg survival and embryonic development in lake whitefish (*Coregonus clupeaformis*). T. Am. Fish. Soc. 104: 555-559.
Eggs of lake whitefish (*Coregonus clupeaformis*) were incubated in a constant-flow incubator at constant temperatures of 0.5, 2.0, 4.0, 5.9, 7.8, and 10.0 C. The time from fertilization to median hatch was inversely related to temperature, and ranged from 41.7 days at 10.0 C to 182 days at 0.5 C. The percentage hatch was highest (70.9-73.3%) at 4.0, 5.9, and 7.8 C, and was greatly reduced (6.0-28.4%) at 0.5, 2.0, and 10.0 C. The mortality of embryos was greatest during the early stages of development. Abnormally developed fry were most frequent (85.9% of the hatch) at 10.0 C, and least frequent (2.8%) at 4.0 C. Mean lengths of fry at hatching were shorter at 7.8 and 10.0 C (12.4 and 8.8 mm, respectively) than at lower temperatures (13.1 to 13.5 mm). The optimum temperature range for incubation of lake whitefish eggs was 3.2 to 8.1 C. Equations were derived for predicting development time to 20 successive stages, and to hatching, at constant incubation temperatures and at fluctuating daily mean water temperatures.

Drouin, M.A., Kidd, R.B., Hyne, J.D. 1986. Intensive culture of lake whitefish (*Coregonus clupeaformis* Mitchell) using *Artemia* and artificial feed. Aquaculture 59: 107-118.
Whitefish larvae were reared using combinations of live *Artemia* nauplii and trout starter. In all cases survival was greater than 93% at 9 weeks of age. Growth did not differ significantly (P>0.1) between high and low feeding rates of live nauplii; however, an opercular cover malformation was detected at the

lower rate. A conversion program was developed for the practical use of *Artemia* nauplii. Whitefish were successfully converted to trout starter at 7 weeks of age and 140 mg. Trout starter alone was inadequate for early rearing. Decapsulated, lyophylized cysts of *Artemia* were almost a replacement for live *Artemia* nauplii except for a low incidence of opercular cover malformation. Advanced rearing to yearling size was easily performed with trout feed. Additional mortalities were less than 3% to 14 months of age at stocking.

Eckmann, R., Czerkies, P., Helms, and Kleibs, K. 1998. Evaluating the effectiveness of stocking vendace (*Coregonus albula* (L.)) eleutheroembryos by alizarin marking of otoliths. Adv. Limnol. 50: 457-463.
Lake Werbellin (804 ha, 18 m mean depth), a mesotrophic lake in north-eastern Germany yielded between <1 and 14 tons (1.2 and 17.4 kg/ha) of vendace during the 1970's and 1980's. For the last 20 years, the lake has been stocked annually with 0.5 -3.3 million eleutheroembryos (620-4100 per ha) in early spring, but the population is presumably self-sustaining. The contribution of stocking to commercial yields has never been assessed. In spring 1994, 1.5 million embryos were marked by immersion In Alizarin Red S (150 mg/l for 3 hr) prior to stocking. Survival rate was better than 90% after 48 hr (76% in one tank where the concentration had been higher initially) and ranged from 74 to 83% after 24 d (21 % in one tank). Mark quality was excellent, as was mark retention after almost two years. In autumn 1995, more than one thousand specimens of the 1994 year-class were sampled from the lake. Lapilli and sagittae were removed. embedded in epoxy resin, ground and polished, and examined under ultraviolet light. Only 1.3 % of fish (14 specimens) were marked. We conclude that natural reproduction in Lake Werbellin was successful in 1994. The cost/benefit ratio of stocking was above unity. Evaluation of stocking programs in which eleutheroembryos are added to self-sustaining coregonid populations is strongly recommended.

Eckmann, R. 2003. Allizarin marking of whitefish, *Coregonus lavaretus* otoliths. Fisheries Manag. Ecol. 10: 233-239.
Alizarin red S from 200 to 5000 mg L^{-1} was used to mark the otoliths of whitefish embryos *Coregonus lavaretus* (L.) from 5 days after fertilization until shortly before hatching, to develop a method for evaluating the effect of stocking whitefish. Mark quality depended on developmental stage at the time of immersion. The best results were obtained when the otolith primordia had formed and had started aggregating to form the innermost part of the nucleus. This was verified by in vitro staining of otoliths where the primordia were more intensely stained than the remaining part of the nucleus. The volume ratio eggs to ARS solution, which was 1:10 in all but two treatments, must be observed when comparing fluorochrome concentrations, as mark quality decreased at higher ratios of 1:5 and 1:2. An average mortality rate of 35% in the most successful treatments was considered tolerable for a mass-marking programme being used under commercial hatchery conditions. This method for marking otoliths of whitefish embryos with ARS during egg incubation is recommended for all cases where marking of larvae is not possible.

Eckmann, R., Kugler, M., and Ruhlé, C. 2007. Evaluating the success of large-scale whitefish stocking at Lake Constance. Adv. Limnol. 60: 361-368.
Artificial incubation of whitefish eggs at Lake Constance (L.C.) started in 1887/88. Today there are six hatcheries at Upper L.C. which all use refrigerated water to delay hatching. They stock around 350 million recently hatched and 3-5 million prefed whitefish larvae annually. Despite this long history of artificial incubation at L.C., it remains unknown whether stocking indeed fulfils its aims, to dampen yearly yield fluctuations and/or to increase yields. We used a newly developed method to label the otoliths of whitefish embryos during incubation with Alizarin Red S (ARS) to evaluate the contribution of

unfed hatchery larvae to cohort size. In winter 2003, 600 L of whitefish eggs were treated with ARS and by early April around 40 million larvae were released. In autumn 2003, the otoliths of age-0 whitefish sampled from the lake were examined. We found that 18 out of a total of 290 fish originated from the marking experiment. Since only 10% of stocked larvae had been marked, the contribution of hatchery-reared fish to the cohort 2003 was estimated as 62% with binomial confidence intervals of 42 and 79%. It should, however, not be concluded that stocking is necessary to maintain the current level of commercial yields, since it still remains unknown whether hatchery fish are added to the naturally recruited stock leading to stronger cohorts, or whether stocking only increases intraspecific competition without enhancing cohort size.

Gerdeaux, D. 2004. The recent restoration of the whitefish fisheries in Lake Geneva: the roles of stocking, reoligotrophication, and climate change. Ann. Zool. Fennici. 41: 181-189.
The recent history of the whitefish fishery in Lake Geneva has been very positive. Yields over the last seven years have not been attained for 50 years. Stocking has been increased for 10 years. Stocking was first done with larvae, but now with larvae and also juveniles and fingerlings. Stocking could explain the beginning of the increases in whitefish stocks but cannot completely explain the present level of the stock. Other causes are necessary to explain the situation. Lake Geneva sustained a stage of eutrophication (total phosphorus increasing from 20 µg l-1 to 90 µg l-1) from 1960 to the mid-1970s. Phosphorus levels have been decreasing since then. Improved water quality has contributed to the restoration of the whitefish population. Climate change has also contributed to better recruitment of whitefish. Stocking seems now to be superfluous and will be restricted in the future to fingerlings.

Jokikokko, E., Leskelä, A., and Huhmarniemi, A. 2002. The effect of stocking size on the winter survival of whitefish, *Coregonus lavaretus* (L.), in the Gulf of Bothnia, Baltic Sea. Fisheries Manag. Ecol. 9: 79-85.
The anadromous whitefish, *Coregonus lavaretus* (L.), is the most numerous fish species stocked in the Gulf of Bothnia, Baltic Sea. One-summer-old-whitefish fingerlings are mostly 8–10 cm long when released annually in September–October, whereas the wild whitefish are 10–12 cm at that time. About 6 million, one-summer-old, spray-marked, whitefish were released in the northern and central parts of the Gulf in 1995–1998. To study the effect of the stocking length on the survival of the marked fish, the length of the recaptured whitefish as 1-year-olds was back-calculated. Altogether 1106 whitefish recaptured in the Gulf of Bothnia were analyzed. The back-calculated length was slightly greater than the stocking length but not as large as the length of the wild fish. In the central part of the Gulf of Bothnia, where the mean stocking length was more than 10 cm, the back-calculated length was 10.5–11.1 cm. In the northern part of the Gulf the mean stocking length varied between 8.8 and 10.0 cm annually, and the corresponding back-calculated mean lengths were 9.3–9.7 cm. It also seemed that bigger fingerlings started their feeding migration earlier or they migrated faster than the smaller ones to the southern parts of the Gulf of Bothnia.

Jokikokko, E., Huhmarniemi, A. 2014. The large-scale stocking of young anadromous whitefish (*Coregonus lavaretus*) and corresponding catches of returning spawners in the River Tornionjoki, northern Baltic Sea. Fisheries Manag. Ecol. 21: 250-258.
Stocking and fishing effort are two important potentially conflicting factors in fish stock management that require appropriate assessment to ensure a sustainable fishery. In the River Tornionjoki, which discharges into the northern Baltic Sea, a summer-ascending whitefish, *Coregonus lavaretus* L., stock has long been a target by traditional dipnet fishing. Enhancement stocking of young whitefish started in the River Tornionjoki in the 1970s after a collapse in catches, with millions of age-0 whitefish stocked annually in the river, but after about three decades, the stocking rates were considerably reduced. As a

result, dipnet catches of whitefish in the Kukkolankoski Rapids rose simultaneously, peaking in the 1980s and 1990s, and then subsequently decreased. There was a significant positive correlation between stocking intensity and catch, both in weight and in numbers, revealing a strong relationship between whitefish releases and dipnet catch. Changes in gillnet fishing effort in the sea affected dipnet catches in weight as well as in mean size of captured whitefish. When the combined effect of stocking and gillnet effort was evaluated, only stocking significantly affected dipnet catches.

Leskelä: A., Jokikokko, E., Huhmarniemi, A., Siira A., and Savolaine, H. 2002. Stocking results of spray-marked one-summer old anadromous European whitefish in the Gulf of Bothnia. Ann. Zool. Fennici. 41: 171-179.
About 6 million one-summer-old, fluorescent pigment marked whitefish were released in the northern and central parts of the Gulf of Bothnia in 1995—1998. Growth and dispersal of the stocked fish were followed by detecting and recording marked whitefish in samples from the professional fisheries catch during 1999—2002. The yield produced by stocked fish was estimated by assuming that the proportion of the marked fish in the total catch was the same as in the samples. The total yield from the stockings in 1995 was estimated to be 55—90 kg/1000 released fingerlings. A better result from the stockings could be achieved by increasing the recruitment size in the fishery. Even for the 1995 stockings, a few of the released fish were probably still migrating in the sea at the end of the study period, although the main part had already been caught. For fish released in 1996 or later, no exact estimates of total yield can be given, as a considerable part of the catch was still to come. The estimates from the preliminary re-catches, however, suggest that the stockings in northern parts produce lower catches than stockings in central parts of the Gulf of Bothnia.

Oldenburg, K., Stapanian, M.A., Ryan, P.A., and Holm, E. 2007. Potential strategies for recovery of lake whitefish and lake herring stocks in eastern Lake Erie. J. Great Lakes Res. 33(Supp. 1): 46-58.
Lake Erie sustained large populations of ciscoes (Salmonidae: Coregoninae) 120 years ago. By the end of the 19th century, abundance of lake whitefish (*Coregonus clupeaformis*) had declined drastically. By 1925, the lake herring (a cisco) population (*Coregonus artedii*) had collapsed, although a limited lake herring fishery persisted in the eastern basin until the 1950s. In the latter part of the 20th century, the composition of the fish community changed as oligotrophication proceeded. Since 1984, a limited recovery of lake whitefish has occurred, however no recovery was evident for lake herring. Current ecological conditions in Lake Erie probably will not inhibit recovery of the coregonine species. Recovery of walleye (Sander vitreus) and efforts to rehabilitate the native lake trout (*Salvelinus namaycush*) in Lake Erie will probably assist recovery because these piscivores reduce populations of alewife (*Alosa pseudoharengus*) and rainbow smelt (*Osmerus mordax*), which inhibit reproductive success of coregonines. Although there are considerable spawning substrates available to coregonine species in eastern Lake Erie, eggs and fry would probably be displaced by storm surge from most shoals. Site selection for stocking or seeding of eggs should consider the reproductive life cycle of the stocked fish and suitable protection from storm events. Two potential sites in the eastern basin have been identified. Recommended management procedures, including commercial fisheries, are suggested to assist in recovery. Stocking in the eastern basin of Lake Erie is recommended for both species, as conditions are adequate and the native spawning population in the eastern basin is low. For lake herring, consideration should be given to match ecophenotypes as much as possible. Egg seeding is recommended. Egg seeding of lake whitefish should be considered initially, with fingerling or yearling stocking suggested if unsuccessful. Spawning stocks of whitefish in the western basin of Lake Erie could be utilized.

Perga, M.-E., Mesmet, M., Enters, and Reyss, J.-L. 2010. A century of bottom-up and top-down driven changes on lake planktonic food web: a paleoecological and paleoisotopic study of Lake Annecy, France. Limnol. Oceanogr. 55: 803-816.
We reconstructed the changes in the planktonic food web of an oligotrophic subalpine lake over the past century, combining paleoecological methods and historical monitoring data. Analyses of organic matter δ15N from sediment cores show that nutrient enrichment started in the 1910s and intensified from the 1930s. Subsequent changes in sediment organic carbon content and accumulation rates, carotenoid pigment concentrations, organic matter δ13C, and cladoceran subfossil remains show that excess nutrient inputs triggered bottom-up-driven increases in lake primary production, as well as in Daphnia abundance. Daphnia size, however, started to decrease in the late 1930s, indicating an increasing size-selective predation from zooplanktivorous whitefish populations (*Coregonus lavaretus*) that had been fostered by stocking and increased food availability. Whitefish predation is likely to have indirectly facilitated the establishment of *Bosmina longirostris*. With decreasing nutrient concentrations, Daphnia abundance decreased, but their size declined, presumably due to an ongoing size-selective predation. At this same time, Bosmina abundance doubled as a likely result of released interspecific competition from smaller Daphnia. δ15N analyses on subfossil cladoceran remains revealed that these changes in cladoceran community structure were accompanied by major changes in the food web. In spite of successful measures to reduce nutrient inputs from the late 1960s and reduced primary production, anoxia still occurs every summer at the lake bottom. These patterns are the consequence of a still relatively high export of phytoplankton-derived organic matter to the sediment as a result of strong top-down effects on the planktonic food chain.

Raitaniemi, J., Malinen, T., Nyberg, K., and Rask, M. 1999. The growth of whitefish in relation to water quality and fish species composition. J. Fish Biol. 54: 741-756.
Water quality in 16 Finnish lakes did not affect directly densely gill-rakered whitefish growth, except possibly in an acid (pH 4·9) lake, Iso Lehmaälampi, where acidity may have retarded the growth of whitefish. The density of roach affected whitefish growth in the second year of life: highest growth rates were in lakes without a roach population and lowest growth rates in lakes having strong roach populations. Competition by vendace also retarded the growth of young whitefish. The efficient mass removal of roach from a eutrophic lake was considered to have increased the growth rate of young whitefish. It is suggested that an examination of the fish species composition and relative abundance, as well as the growth of whitefish, can be used as an aid in predicting the success of stocking with whitefish.

Rasmussen, K. 1990. Some positive and negative effects of stocking whitefish on the ecosystem redevelopment of Hjarbæk Fjord, Denmark. *Hydrobiologia* 200/201: 593-602.
In 1984 the County of Viborg introduced a large-scale programme to improve the water quality in Hjarbæk Fjord, a freshwater fjord cut off from the sea in 1964. Measures were taken to reduce the discharges of nutrients from various sources. To reduce the nuisance of chironomids a large release of whitefish (*Coregonus lavaretus* L.) was incorporated in the programme. The effects of these efforts on the fish, benthos and plankton communities were studied during a period of five years. The whitefish established a self-reproducing population with a very good growth rate, and may have created quantitative and qualitative changes in the plankton community. Observed changes in the benthos community may also be related to predation by whitefish. The study did not confirm that whitefish could actually control the population of chironomids and diminish, thus, the nuisance caused by them. The stocking of whitefish created an exploitable fish stock of a valuable fish species in the hypertrophic Hjarbæk Fjord.

Salojärvi, K., and Huusko, A. 2008. Results of whitefish, *Coregonus lavaretus* L., fingerling stocking in the lower part of the Sotkamo water course, northern Finland. Aquat. Res. 21: 229-244.
The efficiency of stocking with whitefish, *Coregonus lavaretus* L., fingerlings was assessed in a large lake system with a naturally reproducing local whitefish stock. After the start of the stocking programme, the whitefish catch increased. The proportion of stocked whitefish in the catch was ca. 50%. The calculated yield per thousand released fingerlings was 57 ± 18kg. Further, the efficiency of stocking may be indicated by the following facts. Prior to stocking, the whitefish catch decreased, evidently due to recruitment overfishing. It was suggested that this situation was corrected by stocking with fingerlings and the whitefish catch then increased. The catch per unit of effort (CPUE) generally decreases with increasing fishing effort, but in this case the CPUE remained at the same level in spite of a considerable increase in fishing effort. The growth rate depends on the density of the fish stock. In this case the growth rate declined, possibly due to the fact that fingerling stocking increased the population density.

Thomas, G., Quoß, H., Hartman,J., and Eckmann, R. 2009. Human-induced changes in the reproductive traits of Lake Constance common whitefish (*Coregonus lavaretus*). J. Evolution. Biol. 22: 88-96.
Size-selective fishery harvest leads to phenotypic changes in fish reproductive traits. When these changes represent an evolutionary response of a stock, they may have severe consequences for future stock dynamics and yields. In freshwater ecosystems, reproductive traits may also be affected by other human impacts such as changes in system productivity. The present study uses regression analysis to evaluate the impacts of changes in lake trophy and of an intensive size-selective harvest over several decades on the reproductive traits of common whitefish in Lake Constance between 1963 and 1999. Fecundity was strongly linked to lake trophy but was also related to the calendar year, suggesting an evolutionary response to size-selective harvest and to massive stocking of the lake with hatchery-reared larvae. The present study is an example of how fish reproductive traits are influenced by the combined action of various human impacts: changes in system productivity, size-selective harvest and massive stocking.

Todd, T.N. 1986. Artificial propagation of coregonines in the management of the Laurentian Great Lakes. Biology, exploitation, rearing and propagation of coregonid fishes. Arch. Hydrobiol., Adv. Limnol. 22: 31-50.
Numerous stresses caused wide fluctuations in the abundance of Great Lakes coregonine fishes during the last century. State, Provincial, and Federal agencies attempted to bolster these fisheries by stocking more than 32 billion fry of lake whitefish (*Coregonus clupeaformis*) and 6 billion fry of lake herring (C. *artedii*) over a period of about 90 years (1870-1960). Propagation efforts were unsuccessful in arresting the decline of these fishes, perhaps because the stocking densities were too low. It appears that stocking densities must exceed 41% of the natural hatch to produce measurable success in a planting program that augments natural reproduction. Stocking of any of the Great Lakes with lake whitefish at these levels would require several billion fry per lake annually. Such a program is too large to be practical and intensified protection of the remaining stocks would be more cost effective. A species such as the shortnose cisco (C. *reighardi*) which has only a small number of extant individuals and can therefore be significantly augmented with fewer stocked fish, may be a much better candidate for propagation than is the lake whitefish. Propagation of coregonines in the Great Lakes should be considered only in localities that have little or no natural recruitment and then only for rehabilitation, and only if accompanied by adequate assessment of the performance of the stocked fish.

Management Implications

Curtis, G.L., Bronte, C.R., and Selgeby, J.H. 1993. Forecasting contributions of lake whitefish year-classes to a Lake Superior commercial fishery from estimates of yearling abundance. N. Am. J. Fish. Manage. 13: 349-352.

We developed a simple linear regression model to forecast year-class contributions to lake whitefish *Coregonus clupeaformis* to the commercial harvest in the Apostle Islands region of Lake Superior. We indexed year-class strength from catches of yearling fish in bottom trawl samples. Recruitment of each year-class was measured by it relative abundance in the fishery at age 6. The relation between recruitment to the commercial fishery and year-class strength indices was positive and significant ($r2 = 0.67$, $P < 0.01$). The model produced reliable estimates of recruitment to the fishery within the range of the regression. Projected recruitment of the 1983-1987 year-classes to the fishery in 1989-1993 should be sufficient to sustain current levels of harvest through 1993.

Deroba, J.J., and Bence, J.R. 2009. Developing model-based indices of lake whitefish abundance using commercial fishery catch and effort data in lakes Huron, Michigan, and Superior. N. Am. J. Fish. Manage. 29: 50-63.

Fishery catch per effort (CPE) is often used to assess relative fish abundance, and in many Great Lakes and other freshwater applications the CPE index is based on either an average or the ratio of summed aggregate catch to summed aggregate effort. In particular, assessments used to estimate the abundance of lake whitefish *Coregonus clupeaformis* and recommend harvest quotas in 1836 Treaty-ceded waters of Lakes Huron, Michigan, and Superior assume that commercial CPE from gill-net and trap-net fisheries is proportional to abundance; however, CPE may change due to factors other than abundance, leading to violations of this assumption. To account for sources of CPE variation that are not attributable to abundance, general linear mixed models (GLMMs) were developed for each management unit and least-squares means (LSMs) for each year were used as the index of abundance. The effect of using the GLMM method for standardization was evaluated by examining the temporal trends in the proportional difference between LSMs and CPE (i.e., aggregate catch divided by aggregate effort for each year). Of the random effects included in the final GLMM for the gill-net fishery, license holder accounted for the most variation. The fixed effect of boat size category on CPE depended on lake; on average, there was little difference between boat sizes in Lake Superior, whereas large boats had a lower CPE than medium and small boats in Lakes Michigan and Huron. On average, CPE was higher from October to December than during other months. The proportional difference between LSMs and CPE trended through time in some management units, suggesting the importance of adjusting fishery CPE for effects like boat size, season, and license holder. Factors that influence lake whitefish commercial fishery CPE are similar to factors important for marine commercial fisheries.

Deroba, J.J., and Bence, J.R. 2012. Evaluating harvest controls rules for lake whitefish in the Great Lakes: accounting for variable life-history traits. Fish. Res. 121-122: 88-103.

Few studies have evaluated the performance of harvest control rules while considering uncertainties in life history traits and the management process. We conducted such a study using an age-structured simulation based on lake whitefish in the Great Lakes. The control rules compared were a constant fishing mortality (constantF), conditional constant catch (CCC), biomass-based (BB), and constantF and BB with a 15% limit on the interannual change in the target catch (constantF-lim, BB-lim, respectively). Our application of the CCC and BB rules was conditioned on having reliable estimates of some reference point (e.g., unfished biomass). With appropriate policy parameters, the BB and constantF rules attained higher average yield and spawning stock biomass than other control rules. At yields that could be achieved by all rules, the CCC, constantF-lim, and BB-lim rules had the lowest yearly variability in yield,

but at the cost of more frequent low biomass. The relative performance of the control rules was generally consistent with previous research that did not include the variation in life history traits unique to our simulations, which suggested that these variable traits did not affect relative control rule performance. The BB rule achieved more yield and less risk of low biomass than the constantF rule currently used for lake whitefish, with only a modest increase in yield variability. Given that the BB rule requires a stock-specific estimate of unfished biomass, and the constantF rule does not, this result suggests that reliable estimates of unfished biomass could provide substantial value.

DesJardine, R.L., Gorenflo, T.K., Payne, R.N., and Schrouder, J.D. 1995. Fish-community objectives for Lake Huron. Great Lakes Fish. Comm. Spec. Pub. 95-1.
This document sets out whole-lake fish-community objectives (FCOs) for Lake Huron and further commits management agencies, through the process of concensus, to the protection and restoration of the lake's fish community. FCOs describe the "desirable" fish community bound by certain ecological concepts and guiding principles and provide an umbrella under which management agencies are expected to develop more-specific plans and strategies. The objectives are not always quantitative, but there they are quantitative and expressed as fish yields, the yields are viewed-not as targets-but as an indication of community response. The FCO for coregonines is to "maintain the present diversity of coregonines; manage lake whitefish and ciscoes at levels capable of sustaining annual harvests of 3.8 million kg; and to restore lake herring to a significant level and protect, where possible, rare deepwater ciscoes. At the time FCOs where written in the early 1990s commercial landings of whitefish were among some of the highest on record for the main basin, the North Channel, and outer Saginaw Bay, but lake whitefish in Georgian Bay had yet to recover to the same extent.

Ebener, M.P., Bence, J.R., Newman, K.R., Schneeberger, P.J. 2005. Application of statistical catch-at-age models to assess lake whitefish stocks in the 1836 treaty ceded waters of the upper Great Lakes. *In* Proceedings of a workshop on the dynamics of lake whitefish (*Coregonus clupeaformis*) and the amphipod *Diporeia* spp. in the Great Lakes. *Edited* by L.C. Mohr, and T.F. Nalepa. Great Lakes Fish. Comm. Tech. Rep. 66 pp. 271-309.
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 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.

Ebener, M.P., Kinnunen, R.E., Mohr, L.C., Schneeberger, P.J., Hoyle, J.A., Peeters, P. 2008. Management of commercial fisheries for lake whitefish in the Laurentian Great Lakes of North America. *In* International Governance of Fisheries Ecosystems: Learning from the Past, Finding

Solutions for the Future. ***Edited*** **by M.G. Schechter, W.W. Taylor, N.J. Leonard. Amer. Fish. Soc. Symposium 62 pp. 99–143.**
The authors describe the status of the commercial fishery for lake whitefish in the Great lakes in relation to the fish's population dynamics, ecological change, market demands, and the global economy, and document evolution of management policies for regulating the fishery.

Ebener, M.P., Brenden, T.O., and Jones, M.L. 2010b. Estimates of fishing and natural mortality rates for four lake whitefish stocks in northern lakes Huron and Michigan. J. Great Lakes Res. 36(Supp. 1): 110-120.
We analyzed tag-recovery data to estimate instantaneous fishing (F) and natural mortality (M) rates of four lake whitefish stocks in lakes Michigan and Huron during 2004–2007. We tagged and released 22,452 adult lake whitefish of which 8.7% were subsequently recovered. Annual tag-reporting rates ranged from 17.8% to 56.2%. Tag retention was high for the first 5–6 months after tagging, but tag loss increased substantially thereafter. Nine tag-recovery models were evaluated with respect to whether F and/or M varied among stocks, lakes, or years. There was support for three models based on Akaike information criteria. The best model had yearly and stock-specific estimates of F of 0.03 to 0.79 and lake-specific estimates of M of 0.35 for Lake Michigan and 0.60 for Lake Huron. The second best model had yearly and stock-specific estimates of F of 0.04 to 0.71 and a constant estimate for M of 0.52. The third model had yearly and stock-specific estimates of F of 0.04 to 0.85 and stock-specific estimates of M of 0.32 to 0.67. Model-averaged estimates of F ranged from 0.04 to 0.78 and were substantially different than statistical catch-at-age estimates of F. Model-averaged estimates of M ranged from 0.40 to 0.59 and were greater than estimates obtained from prediction equations, possibly due to sea lamprey-induced mortality. We recommend that tag-recovery estimates of F and M be used as Bayesian priors in future lake whitefish stock assessments to help refine mortality estimates for the stocks.

Eshenroder, R.A., Holey, M.E., Gorenflo, T.K., and Clark, R.D., Jr. 1995. Fish-community objectives for Lake Michigan. Great Lakes Fish. Comm. Spec. Pub. 95-3.
The Lake Michigan Committee created fish-community Objectives (FCOs) to provide a framework for future decision making. Although seemingly straightforward, consensus management of complex systems like Lake Michigan is challenging partly because scientific understanding of the ecology of the lake will always be incomplete. Managers and their clients and others concerned about Lake Michigan will continually face uncertainty about the best management policies. Establishment of fish-community objectives will help define a unified direction and purpose for the multitude of management activities occurring around the lake. Also, this document will focus attention on important issues and help communicate priorities to fishery and environmental managers, researchers, and public-policy makers. Major reports on progress toward achieving the objectives are scheduled at 3-yr intervals. Interim reports are given each year at the annual meeting of the Lake Michigan Committee. The FCO for lake whitefish is embedded in the "Benthivore Objective" to "Maintain self-sustaining stocks of lake whitefish, round whitefish, sturgeon, suckers, and burbot. The expected annual yield of lake whitefish should be 1.8-2.7 million kg (4 to 6 million lb)." The demand for lake whitefish will continue to foster a desire to sustain the current (1990s) 1.8-2.7 million kg yield for Lake Michigan, but the amount of variability around that yield is not well understood. To the extent possible, river-running lake whitefish populations should be restored where they were historically important.

Fussell-DeVanna, K.M., Smith, R.E.H., Fraker, M.E., Boegman, L., Frank, K.T., Miller, T.J., Tyson, J.T., Arend, K.K., Boisclair, D., Guildford, S.J., Hecky, R.E., Höök, T.O., Jensen, O.P., Llopiz, J.K., May, C.J., Najjar, R.G., Rudstam, L.G., Taggart, C.T., and Ludsin, S.A. 2016. A perspective on needed research,

modeling, and management approaches that can enhance Great Lakes fisheries management under changing ecosystem conditions. J. Great Lakes Res. 42: 743-752.
The Great Lakes Fishery Commission sponsored a 2-day workshop that sought to enhance the ability of Great Lakes agencies to understand, predict, and ideally manage fisheries production in the face of changes in natural and anthropogenic forcings (e.g., climate, invasive species, and nutrients). The workshop brought together 18 marine and freshwater researchers with collective expertise in aquatic ecology, physical oceanography, limnology, climate modeling, and ecosystem modeling, and two individuals with fisheries management expertise. We report on the outcome of a writing exercise undertaken as part of this workshop that challenged each participant to identify three needs, which if addressed, could most improve the ability of Great Lakes agencies to manage their fisheries in the face of ecosystem change. Participant responses fell into two categories. The first identified gaps in ecological understanding, including how physical and biological processes can regulate early life growth and survival, how life-history strategies vary across species and within populations, and how anthropogenic stressors (e.g., nutrient runoff, climate change) can interact to influence fish populations. The second category pointed to the need for improved approaches to research (e.g., meta-analytic, comparative, spatial translation) and management (e.g., mechanistic management models, consideration of multi-stock management), and also identified the need for improved predictive models of the physical environment and associated ecosystem monitoring programs. While some progress has been made toward addressing these needs, we believe that a continued focus will be necessary to enable optimal fisheries management responses to forthcoming ecosystem change.

Horns, W.H., Bronte, C.R., Busiahn, T.R., Ebener, M.P., Eshenroder, R.L., Gorenflo,T., Kmiecik, N., Mattes, W., Peck, J.W., Petzold, M., and Schreiner, D.R. 2003. Fish-community objectives for Lake Superior. Great Lakes Fish. Comm. Spec. Pub. 03-01.
The development of fish-community objectives for each lake is mandated by A Joint Strategic Plan for Management of Great Lakes Fisheries (Great Lakes Fishery Commission 1997). That multiagency agreement also reflects a commitment to habitat protection and restoration through the following statement: The Parties must exercise their full authority and influence in every available arena to meet the ecological, chemical, and physical needs of desired fish communities. Accordingly, these fish-community objectives highlight habitat issues. The first objective summarizes the agencies' habitat concerns: Achieve no net loss of the productive capacity of habitat supporting Lake Superior fishes. Where feasible, restore habitats that have been degraded and have lost their capacity for fish production. Reduce contaminants so that all fish are safe to eat. Develop comprehensive and detailed inventories of habitats. The fish-community objectives were developed in conformity with twelve guiding principles that summarize the values and practical realities that constrain or guide fisheries management on Lake Superior. Additional objectives pertain to prey species, lake trout (*Salvelinus namaycush*), lake whitefish (*Coregonus clupeaformis*), walleye (*Stizostedion vitreum vitreum*), lake sturgeon (Acipenser fulvescens), brook trout (*Salvelinus fontinalis*), pacific salmon (*Oncorhynchus* spp.), and trout (Salmonidae spp.), sea lamprey (*Petromyzon marinus*), nuisance species, and species diversity. Habitat issues impeding achievement of any objective are described. The most-pressing habitat concerns are in streams and embayments, and accordingly affect: tributary-spawning species, including brook trout, walleye, and lake sturgeon; warm- or cool-water species, including yellow perch (*Perca flavescens*), northern pike (*Esox lucius*), and smallmouth bass (*Micropterus dolomieu*). Although numerous non-native species have invaded Lake Superior, with the effective control of sea lamprey, the offshore fish community has returned to a condition broadly similar to that which existed prior to the modern era. The agencies envision an offshore fish community dominated by lake trout as the top predator and requiring the continued control or eradication of sea lamprey. The FCO for lake whitefish is to "maintain self-sustaining populations within the range of abundance observed during 1990-99."

Huhmarniemi, A., Salmi, J. 1999. Attitude and opinions of commercial fishermen on whitefish management in the Gulf of Bothnia, Finland. Fisheries Manag. Ecol. 6: 221-232.
Catches of anadromous whitefish in the Gulf of Bothnia have declined since the early 1990s. It is generally assumed that the cause is overfishing. The professional fishermen interviewed in the present study were united in the opinion that it is necessary to set limits on the fishing of whitefish, but had differing views about the means of achieving this. These different arguments involved separate whitefish stocks, various types of gear and different motives for fishing. Most of the professional fishermen accepted a minimum mesh size for gill nets. Other means proposed included setting limits on non-professional fishing and sales of catches. There were conflicting attitudes about seasonal restrictions because their experiences with fishing restrictions for salmon had been negative. On the whole, decision-making requires more regional information on whitefish stocks and fishing, but also on the social and economic flexibility of fishermen.

Irwin, B.J., Wagner, T., Bence, J.R., Kepler, M.V., Liu, W., and Hayes, D.R. 2013. Estimating spatial and temporal components of variation for fisheries count data using negative binomial mixed models. Trans. Am. Fish. Soc. 142: 171-183.
Partitioning total variability into its component temporal and spatial sources is a powerful way to better understand time series and elucidate trends. The data available for such analyses of fish and other populations are usually nonnegative integer counts of the number of organisms, often dominated by many low values with few observations of relatively high abundance. These characteristics are not well approximated by the Gaussian distribution. We present a detailed description of a negative binomial mixed-model framework that can be used to model count data and quantify temporal and spatial variability. We applied these models to data from four fishery-independent surveys of Walleyes *Sander vitreus* across the Great Lakes basin. Specifically, we fitted models to gill-net catches from Wisconsin waters of Lake Superior; Oneida Lake, New York; Saginaw Bay in Lake Huron, Michigan; and Ohio waters of Lake Erie. These long-term monitoring surveys varied in overall sampling intensity, the total catch of Walleyes, and the proportion of zero catches. Parameter estimation included the negative binomial scaling parameter, and we quantified the random effects as the variations among gill-net sampling sites, the variations among sampled years, and site × year interactions. This framework (i.e., the application of a mixed model appropriate for count data in a variance-partitioning context) represents a flexible approach that has implications for monitoring programs (e.g., trend detection) and for examining the potential of individual variance components to serve as response metrics to large-scale anthropogenic perturbations or ecological changes.

Jensen, A.L. 1976. Assessment of the Unites States lake whitefish (*Coregonus clupeaformis*) fisheries of Lake Superior, Lake Michigan, and Lake Huron. J. Fish. Res. Board Can. 33: 747-759.
The logistic surplus production model is applied to lake whitefish (*Coregonus clupeaformis*) yield and effort data from Lake Superior, Lake Michigan, and Lake Huron. The fitted models indicate that the whitefish populations in most areas of the lakes have been overexploited, and that in these areas yield was below the maximum sustainable yield before sea lamprey (*Petromyzon marinus*) predation took its toll. In some areas of Lake Superior the whitefish populations are not overexploited. The sea lamprey is the apparent cause of the decrease in the whitefish population that occurred in northern Lake Michigan during the 1950s.

Jacobson, P.C., Taylor, W.W. 1985. Simulation of harvest strategies for a fluctuating population of lake whitefish. N. Am. J. Fish. Manage. 5: 537-546.
A simulation model was developed to evaluate the performances of two harvest management strategies, constant effort and constant quota, in relation to the magnitude and variability of annual yield for a population of lake whitefish (*Coregonus clupeaformis*) in northern Lake Michigan. The model consisted of an age-structured, dynamic pool model incorporating a stock-recruitment function subject to environmental variability. Trap-net and gill-net selectivity functions specified the fishing mortality rates operating on each cohort. A constant effort policy produced relatively larger sustainable yields than a constant quota policy. However, the constant quota policy out-performed the effort policy in terms of reducing the variability in annual yield. The model incorporates the effects of different potential fishing efforts that might be expended in pursuit of the quota. A high risk of population collapse was associated with quota management if a large quota was combined with a high potential fishing effort.

Li, Y., Bence, J.R., and Brenden, T.O. 2016. The influence of stock assessment frequency on the achievement of fishery management objectives. N. Am. J. Fish. Manage. 36: 793-812.
Because of resource limitations with respect to both funding and staff expertise, there is growing interest among fishery management agencies in moving from annual to less-frequent assessments of fish stocks. We conducted simulations based on Lake Whitefish Coregonus clupeaformis populations in the Laurentian Great Lakes to evaluate (1) how statistical catch-at-age assessment frequency, the time lag between data collection and assessment, and approaches to setting target harvests in the years between assessments affected the achievement of management objectives; and (2) how the outcomes were influenced by the quality of assessment data, features of the populations, and characteristics of the fisheries exploiting the populations. We found that as assessments became less frequent, relative yields were reduced and the risk of stock depletion and interannual variation in yield increased. The effects of less-frequent assessments were ameliorated in populations with greater levels of productivity and when target mortality was lower. Conversely, the effects of assessment frequency were largely insensitive to changes in recruitment variation or the quality of assessment data. A 1-year lag between data collection and assessment when assessments were conducted annually primarily affected the risk of stock depletion and the interannual variation in yield. As recruitment variation increased, relative yield also became sensitive to the 1-year lag. Approaches to setting harvest targets in years between full assessments were less important than assessment frequency, and no single approach consistently outperformed other rules. Although populations with low productivity were the most sensitive to changes in assessment frequency and the lag between data collection and assessment, the management of those populations benefited to a greater extent from implementation of an appropriate target mortality rate than from more-frequent assessments or removal of the 1-year lag.

Ludsin, S.A., DeVanna, K.M., and Smith, R.E.H. 2014. Physical-biological coupling and the challenge of understanding fish recruitment in freshwater lakes. Can. J. Fish. Aquat. Sci. 71: 775-794.
Marine fisheries recruitment research has emphasized approaches that explore physical–biological interactions during early life stages (ELS). Herein, we review evidence that such approaches would benefit our understanding of fish recruitment in large freshwater lakes, which exhibit similar physical processes and contain fishes with comparable life-history characteristics as marine ecosystems. A review of the primary literature (1965–2008) for freshwater and marine ecosystems revealed that coupled biophysical research on fish ELS (*i*) has benefited our ability to understand and predict fish recruitment in marine ecosystems; (*ii*) has been virtually absent from small lake ecosystems but has been growing in the Laurentian Great Lakes; and (*iii*) has shown that similar to marine ecosystems, physical processes can control fish recruitment in large lakes through direct and indirect pathways, often involving

interactions between biological processes and physicochemical conditions. In addition to identifying specific research gaps and opportunities, this perspective points to the need for increased research on physical–biological coupling in large lake ecosystems, as well as the continued erosion of barriers between marine and freshwater fisheries recruitment science.

McMurtry, M.J., Willox, C.C., and Smith, T.C. 1997. An overview of fisheries management for Lake Simcoe. Lake Reserv. Manage. 13: 199-213.
Eutrophication, increased fishing pressure, habitat destruction and invasion of non-native plants and animals have transformed Lake Simcoe and its assemblage of fishes over the past 150 years. Notable changes include extirpation of lake sturgeon (*Acipenser fulvescens*), decline of muskellunge (*Esox masquinongy*), and failure of recruitment of lake trout (*Salvelinus namaycush*) and lake whitefish (*Coregonus clupeaformis*). Many species, including lake trout, lake whitefish, lake herring (*Coregonus artedi*), and yellow perch (*Perca flacescens*), have undergone major fluctuations in abundance. Fisheries management actions have evolved with changes in the lake ecosystem and changes in scientific knowledge. Early regulations substantially restricted the commercial fishery and imposed many of the existing controls on the sport fishery. Along period of adjustment and addition to these regulations along with reliance on supplemental stocking (i.e., stocking of a species where a self-reproducing population of that species exists) of native fish as well as introduction of non-native fish followed. In the last 3 decades, a scientific approach and ample monitoring have been established as basic requirements for making sound management decisions. Supplemental stocking of native species and stocking of non-native species have been largely replaced by stocking of native species for rehabilitation. Successful fisheries management in the future will need to address the uncertainty about the state of complex aquatic ecosystems and identify the possible states of the system and the probable consequences of specific management actions.

Modeling Subcommittee, Technical Fisheries Committee. 2016. Technical Fisheries Committee Administrative Report 2016: Status of Lake Trout and Lake Whitefish Populations in the 1836 Treaty-Ceded Waters of Lakes Superior, Huron and Michigan, with Recommended Yield and Effort Levels for 2016. Available at: http://www.michigan.gov/greatlakesconsentdecree.
This document outlines the status of Lake Trout and Lake Whitefish stocks in the 1836 Treaty waters of the Great Lakes as assessed by the 2000 Consent Decree's Modeling Subcommittee. We retain here the revised report format first instituted in 2013. The objective of the revised format is to provide a more succinct, consistent summary while maintaining focus on the primary purposes of the report, which are to describe the status of each stock in the context of establishing harvest limits according to the terms of the Decree, and to document important technical changes in the stock assessment process. Model-generated yield limits and actual yield and effort limits for 2016 are provided. In instances where actual yield limits for shared-allocation whitefish units differ from model-generated yield limits, a brief explanation is provided. For non-shared whitefish units, where the tribes have exclusive commercial fishing opportunities, harvest regulation guideline, as established by the Chippewa-Ottawa Resource Authority, serve as final yield limits - these may differ from the model-generated limits. Population models for lake whitefish are on a one-year lag, so estimates reported here are derived from data through 2014. Model-generated yield limits and actual yield and effort limits for 2016 are provided.

Modeling Subcommittee, Technical Fisheries Committee. 2017. Technical Fisheries Committee Administrative Report 2017: Status of Lake Trout and Lake Whitefish Populations in the 1836 Treaty-Ceded Waters of Lakes Superior, Huron and Michigan, with Recommended Yield and Effort Levels for 2017. Available at: http://www.michigan.gov/greatlakesconsentdecree.

This document outlines the status of lake trout and lake whitefish stocks in the 1836 Treaty waters of the Great Lakes as assessed by the 2000 Consent Decree's Modeling Subcommittee. The primary purposes of the report are to describe the status of each managed stock in the context of establishing harvest limits according to the terms of the Decree, and to document important technical changes in the stock assessment process. Except in a few cases, statistical catch-at-age models have been developed for each management unit where the provisions of the Decree apply. Estimates from the SCAA models are utilized in projection models that incorporate the mortality target and allocation rules of the Decree to calculate model-recommended yield limits for these units. Annual mortality rate targets are 65% for lake whitefish, though a complementary rule for Lake Whitefish reduces mortality below the target rate if spawning potential ratio falls below 0.2. Model-derived yield limits, along with the actual yield and effort limits for 2017, are provided. For more in-depth technical detail on stock-assessment structure, see the 2011 version of this report available at https://www.michigan.gov/documents/dnr/2011-status-report_371584_7.pdf.

Molton, K.J., Brenden, T.O., and Bence, J.R. 2013. Harvest levels that conserve spawning biomass can provide larger and more stable and sustainable yields in intermixed fisheries. Fish. Res. 147: 264-283.
We conducted a simulation-based evaluation of constant fishing mortality control rule performance for four intermixing fish populations patterned after lake whitefish (*Coregonus clupeaformis*) fisheries in the Great Lakes. Various scenarios consisting of different assumed productivity and mixing levels for the spawning populations were examined to explore how harvest level performance changed under conditions that lake whitefish, as well as other fish populations, may encounter. The simulation framework included an operating model that represented the true dynamics of the populations, the harvests from fisheries exploiting the intermixed populations, and a full age-structured assessment of each exploited stock. Four harvest levels were evaluated: a 65% total annual mortality harvest level that presently is used to manage lake whitefish fisheries in northern lakes Michigan and Huron and three more conservative levels (35, 45, and 55% total annual mortality harvest levels). Under many investigated scenarios, the current 65% harvest level was found to have a high risk of overexploiting lower productivity spawning populations, which reduced aggregate yield for the modeled system. The 55 and 45% harvest levels resulted in the largest aggregate yields for many of the examined scenarios, although the 45% harvest level was better at reducing risks to sustainability of individual spawning populations. Inter-annual variation in yield generally declined as harvest levels became more conservative. Our analysis suggests that harvest levels that conserve spawning biomass can provide multiple benefits for intermixed fisheries including greater yields, reduced inter-annual variability in yields, and lower risk of depleting low productivity spawning populations. We encourage the implementation of precautionary harvest rates for intermixed fisheries to help protect less productive populations.

Patriarche, M.H. 1977. Biological basis for management of lake whitefish in the Michigan waters of northern Lake Michigan. T. Am. Fish. Soc. 106: 295-308.
Stocks of lake whitefish (*Coregonus clupeaformis*) have supported an intensive commercial fishery in the Michigan waters of Lake Michigan for over a century. However, certain biological indicators suggested that recent upsurges in the catch reflect overfishing, and fish managers should institute measures to assure a stabilized population and fishery. A biological basis for establishing quotas is described in this paper, using information from the 1968–73 commercial fisheries in statistical districts MM-1 and MM-3 and a modification of Rickerˈs dynamic pool model. Natural mortality rates computed for an unfished population of whitefish in the lower end of nearby Grand Traverse Bay were important components of the model. Quota possibilities were based on the premise that the annual harvest should be confined to weight gained each year by the harvestable portion of the population. Six computations of equilibrium

yields were made. A comparison of actual harvests and adjusted yields revealed an average annual over-harvest of 28% during the period 1968–72 in the two statistical districts. Total biomass for six age groups (I-VI) in three Michigan statistical districts of northern Lake Michigan was computed to be 6,660 tonnes in 1972. Approximately 2,695 tonnes (60%) of the total biomass in MM-1 and MM-3 were susceptible to exploitation. Adjusted 1972 yields based on both biomass calculations and the modified dynamic pool model differed by only 0.3%. A change in the minimum total length limit (from 432 to 482 mm) to build up a depleted stock also was discussed. Increased spawning stock, more spawning opportunities, and greater egg deposition should result from this regulation change.

Stewart, T.J., Bence, J.R., Bergstedt, R.A., Ebener, M.P., Lupi, F., and Rutter, M.A. 2003. Recommendations for assessing sea lamprey damages: toward optimizing the control program in the Great Lakes. J. Great Lakes Res. 29(Suppl 1): 783-793.
The Great Lakes sea lamprey (*Petromyzon marinus*) control program currently allocates stream treatments to optimize the number of juvenile sea lampreys killed for a given level of control. Although the economic benefits derived from control appear to outweigh the dollars spent on control efforts, optimizing the number of sea lampreys killed will not necessarily optimize the economic benefits provided by the fish communities. These benefits include both non-consumptive and fishery values. We emphasize that the biological damages caused by each juvenile sea lamprey will vary, as will the economic value associated with each host that is killed. We consider issues related to assessing damages due to sea lampreys, taking into account effects on the fish community and fisheries, so as to improve the sea lamprey control program. We recommend a consolidation of information regarding the valuation of benefits, better understanding of variation in host-parasite interactions among the Great Lakes, and integration of the control program with other fisheries management objectives and activities. Adoption of these recommendations should promote lake trout rehabilitation in the Great Lakes, healthy fish communities and prudent use of limited fishery management resources.

Tiffany, V.E., Irwin, B.J., Wagner, T., Rudstam, R.G., Jackson, J.R., and Bence, J.R. 2017. Using variance structure to quantify responses to perturbations in fish catches. Trans. Am. Fish. Soc. 146: 584-593.
We present a case study evaluation of gill-net catches of Walleye *Sander vitreus* to assess potential effects of large-scale changes in Oneida Lake, New York, including the disruption of trophic interactions by double-crested cormorants *Phalacrocorax auritus* and invasive dreissenid mussels. We used the empirical long-term gill-net time series and a negative binomial linear mixed model to partition the variability in catches into spatial and coherent temporal variance components, hypothesizing that variance partitioning can help quantify spatiotemporal variability and determine whether variance structure differs before and after large-scale perturbations. We found that the mean catch and the total variability of catches decreased following perturbation but that not all sampling locations responded in a consistent manner. There was also evidence of some spatial homogenization concurrent with a restructuring of the relative productivity of individual sites. Specifically, offshore sites generally became more productive following the estimated break point in the gill-net time series. These results provide support for the idea that variance structure is responsive to large-scale perturbations; therefore, variance components have potential utility as statistical indicators of response to a changing environment more broadly. The modeling approach described herein is flexible and would be transferable to other systems and metrics. For example, variance partitioning could be used to examine responses to alternative management regimes, to compare variability across physiographic regions, and to describe differences among climate zones. Understanding how individual variance components respond to perturbation may yield finer-scale insights into ecological shifts than focusing on patterns in the mean responses or total variability alone.

Wagner, T., Vandergoot, C.S., and Tyson, J. 2009. Evaluating the power to detect temporal trends in fishery-independent surveys: a case study based on gill nets set in the Ohio waters of Lake Erie for walleyes. N. Amer. J. Fish. Mgt. 29: 805-816.
Fishery-independent (FI) surveys provide critical information used for the sustainable management and conservation of fish populations. Because fisheries management often requires the effects of management actions to be evaluated and detected within a relatively short time frame, it is important that research be directed toward FI survey evaluation, especially with respect to the ability to detect temporal trends. Using annual FI gill-net survey data for Lake Erie walleyes *Sander vitreus* collected from 1978 to 2006 as a case study, our goals were to (1) highlight the usefulness of hierarchical models for estimating spatial and temporal sources of variation in catch per effort (CPE); (2) demonstrate how the resulting variance estimates can be used to examine the statistical power to detect temporal trends in CPE in relation to sample size, duration of sampling, and decisions regarding what data are most appropriate for analysis; and (3) discuss recommendations for evaluating FI surveys and analyzing the resulting data to support fisheries management. This case study illustrated that the statistical power to detect temporal trends was low over relatively short sampling periods (e.g., 5–10 years) unless the annual decline in CPE reached 10–20%. For example, if 50 sites were sampled each year, a 10% annual decline in CPE would not be detected with more than 0.80 power until 15 years of sampling, and a 5% annual decline would not be detected with more than 0.8 power for approximately 22 years. Because the evaluation of FI surveys is essential for ensuring that trends in fish populations can be detected over management-relevant time periods, we suggest using a meta-analysis–type approach across systems to quantify sources of spatial and temporal variation. This approach can be used to evaluate and identify sampling designs that increase the ability of managers to make inferences about trends in fish stocks.

Wagner, T., Midway, S.R., Vidal, T., Irwin, B.J., and Jackson, J.R. 2016. Detecting unusual temporal patterns in fisheries time series data. Trans. Am. Fish. Soc. 145: 786-794.
Long-term sampling of fisheries data is an important source of information for making inferences about the temporal dynamics of populations that support ecologically and economically important fisheries. For example, time series of catch-per-effort data are often examined for the presence of long-term trends. However, it is also of interest to know whether certain sampled locations are exhibiting temporal patterns that deviate from the overall pattern exhibited across all sampled locations. Patterns at these “unusual” sites may be the result of site-specific abiotic (e.g., habitat) or biotic (e.g., the presence of an invasive species) factors that cause these sites to respond differently to natural or anthropogenic drivers of population dynamics or to management actions. We present a Bayesian model selection approach that allows for detection of unique sites—locations that display temporal patterns with documentable inconsistencies relative to the overall global average temporal pattern. We applied this modeling approach to long-term gill-net data collected from a fixed-site, standardized sampling program for Yellow Perch *Perca flavescens* in Oneida Lake, New York, but the approach is also relevant to shorter time series data. We used this approach to identify six sites with distinct temporal patterns that differed from the lakewide trend, and we describe the magnitude of the difference between these patterns and the lakewide average trend. Detection of unique sites may be informative for management decisions related to prioritizing rehabilitation or restoration efforts, stocking, or determining fishable areas and for further understanding changes in ecosystem dynamics.

Zuccarino-Crowe, C.M., Taylor, W.W., Hansen, M.J., and Seider, M.J. 2016. Effects of lake trout refuges on lake whitefish and cisco in the Apostle Islands of Lake Superior. J. Great Lakes Res. 42: 1092-1101.
Lake trout refuges in the Apostle Islands region of Lake Superior are analogous to the concept of marine protected areas. These refuges, established specifically for lake trout (*Salvelinus namaycush*) and closed

to most forms of recreational and commercial fishing, were implicated as one of several management actions leading to successful rehabilitation of Lake Superior lake trout. To investigate the potential significance of Gull Island Shoal and Devils Island Shoal refuges for populations of not only lake trout but also other fish species, relative abundances of lake trout, lake whitefish (*Coregonus clupeaformis*), and cisco (*Coregonus artedi*) were compared between areas sampled inside versus outside of refuge boundaries. During 1982–2010, lake trout relative abundance was higher and increased faster inside the refuges, where lake trout fishing was prohibited, than outside the refuges. Over the same period, lake whitefish relative abundance increased faster inside than outside the refuges. Both evaluations provided clear evidence that refuges protected these species. In contrast, trends in relative abundance of cisco, a prey item of lake trout, did not differ significantly between areas inside and outside the refuges. This result did not suggest indirect or cascading refuge effects due to changes in predator levels. Overall, this study highlights the potential of species-specific refuges to benefit other fish species beyond those that were the refuges' original target. Improved understanding of refuge effects on multiple species of Great Lakes fishes can be valuable for developing rationales for refuge establishment and predicting associated fish community-level effects.