

Declining Recruitment of Lake Whitefish to Fisheries in the Laurentian Great Lakes: Management Considerations and Research Priorities



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Cover photograph of post-larval YOY Lake Whitefish (the least understood life stage of the species) courtesy Andrew Muir, June 2, 2005, Fayette State Park, Big Bay de Noc, Lake Michigan.

Declining Recruitment of Lake Whitefish to Fisheries in the Laurentian Great Lakes: Management Considerations and Research Priorities

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Frontispiece. The Laurentian Great Lakes showing locations referenced in the text (top), and Lake Whitefish management units (bottom).

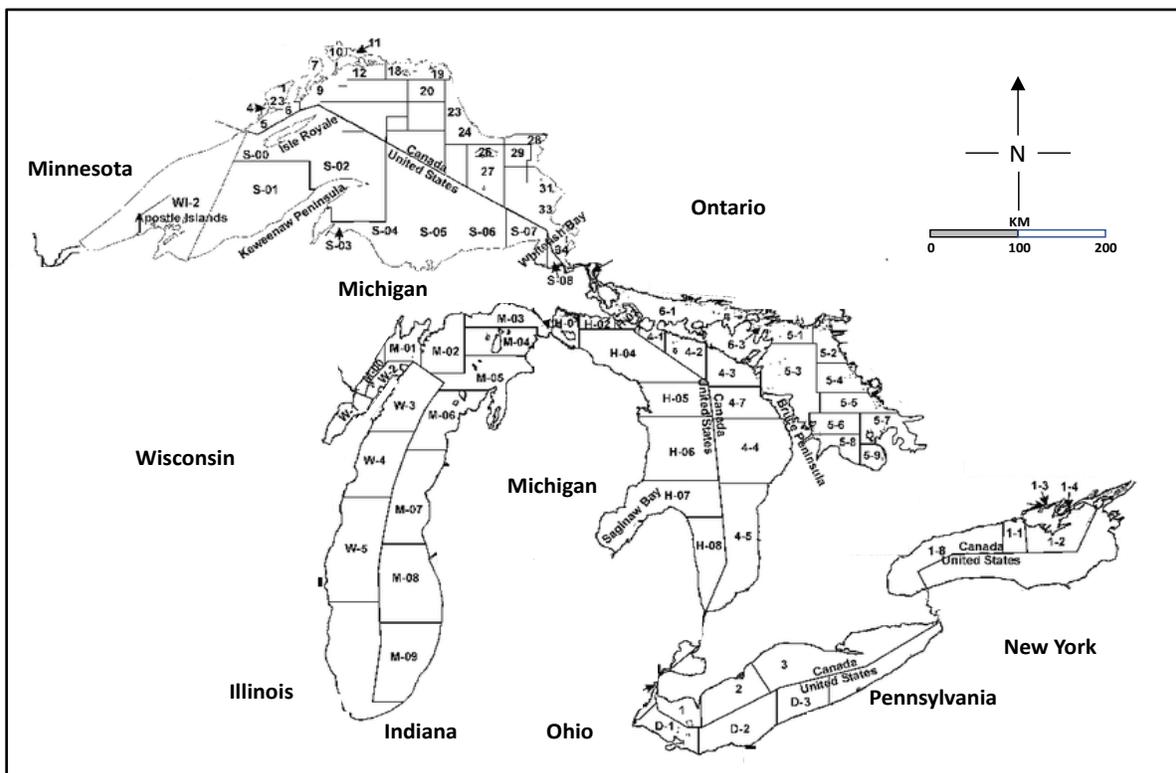


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ABSTRACT

We conducted a review of the physical and biological processes that affect recruitment of Lake Whitefish (*Coregonus clupeaformis*) to commercial fisheries in the Laurentian Great Lakes because numerous stocks have declined precipitously since contemporary abundance and yield peaked in the late 1990s. Lake Whitefish recruitment dynamics are largely defined in nearshore high-energy zones <7 m deep where gametes are deposited in fall and fertilized embryos incubate over winter. Reproductive habitat constitutes about 2% of the total surface area of the Great Lakes, with most of it in Lake Huron, and over 75% of it in embayments. Lake Whitefish also spawns in tributaries, particularly those to Green Bay, Lake Michigan, and these stocks have expanded over the last decade in comparison to stocks in the lake's main basin, which have declined. Water temperatures of the Great Lakes have been increasing through time, reducing the density and duration of ice cover, which is important for protecting embryos from currents generated by strong winds. The amount and extent of ice cover has been declining since the late 1990s, and this trend will continue, negatively affecting recruitment. The role of water levels in recruitment remains unknown, but shallow nursery areas in embayments will be most affected by changing water levels. At least 93 reproductive habitats occur in the Great Lakes, and adult Lake Whitefish live mainly within a 110-km radius of their spawning shoals. Consequently, fishery yields comprise multiple spawning stocks that differ in their reproductive productivity. We identified 24 potential management areas where commercial-fishery and biological data can be pooled from adjacent spawning stocks into a single larger mixed-stock fishery assessment, which should produce less-biased estimates of spawning-stock biomass than if individual stocks were treated as though mixing did not occur. The 2003 to 2012 year-classes, produced at high levels of adult abundance, experienced the greatest declines in recruitment. The number of recruits per kilogram of spawners declined 76-80% in Lakes Michigan and Huron but doubled in Lake Superior. Correspondence between larval density and subsequent year-class production appears to be uncorrelated, but the relationship is likely driven by the ratio of zooplankton density to larval density. Abundant calanoid and cyclopoid copepods in waters <7 m deep during late March through early May are critical for growth and survival of larvae. Based on distribution in fall and winter, Round Goby (*Neogobius melanostomus*) may not negatively affect Lake Whitefish reproduction. We conclude that predation of Lake Whitefish by Lake Trout (*Salvelinus namaycush*) has not been a cause of the declines in recruitment. Although Sea Lamprey (*Petromyzon marinus*) kills adult Lake Whitefish, it also is not a cause of the recent declines in recruitment. Pathogens and parasites may have played a role in the decline in Lake Whitefish stocks in the Great Lakes. Changes in the food web of the four lower Great Lakes due to expansion of dreissenids (*Dreissena polymorpha* and *D. bugensis*) have probably affected the physical and biological productivity of Lake Whitefish reproductive habitat, but the specific mechanism(s) remains unknown. Spawning biomass appears sufficient to support both recruitment and fisheries, but survival of early life stages is insufficient, suggesting that carrying capacity of reproductive habitats has been degraded during 2000-2019. We do not view stocking as an effective tool for managing Lake Whitefish in the Great Lakes, but if stocking is to be undertaken, agencies must ensure that stocked fish can be distinguished from naturally produced fish at all life stages. We recommend that managers on Lakes Michigan, Huron, and Ontario establish a Lake Whitefish working group; give high priority to research targeted at estimating the unfished biomass of stocks; create areas that provide additional protection from exploitation for a portion of the year; provide the least-productive stocks additional protections from exploitation; reduce current levels of exploitation on the most highly fished stocks; expand the length of spawning-

season closures or implement a spawning-season closure, if one does not exist; and reduce the maximum-total-mortality-control rule to less than 65% where it is used to set harvest limits. Lastly, we recommend the creation of a small-scale dreissenid control program with the goal of increasing primary production and Lake Whitefish recruitment in reproductive habitats of Lakes Michigan, Huron, and Ontario.

INTRODUCTION

This report, structured as a white paper, is a critical review of biotic and abiotic processes that affect Lake Whitefish (*Coregonus clupeaformis*) recruitment in the Laurentian Great Lakes. A mechanistic understanding of factors important to Lake Whitefish recruitment has been elusive, likely owing to the dynamic interactions of biological and physical processes and the modifying effects of climate change and invasive species. Despite a century of research on Lake Whitefish life history and recruitment, many fruitful research questions remain unanswered or even identified. Our audience comprises researchers and managers, who necessarily are contending with the diminishment of Lake Whitefish, historically one of the most important and iconic species synonymous with the Great Lakes.

“Recruitment” in the traditional sense is the entry of new individuals to that portion of the population being harvested by a fishery. The harvest of new recruits is a function of their abundance and the rate at which they grow into the harvestable portion of the population or move on to fishing grounds (Beverton and Holt 1957; Ricker 1975). More recently, Ludsin et al. (2014) defined recruitment as “the addition of new members of a population to the first life stage at which natural mortality stabilizes to near adult levels.” They pointed out increased recognition that recruitment is largely controlled by biological and physical processes that affect natural mortality of early life stages and that the rate of early natural mortality is highly variable. Most fishery biologists and managers in the Great Lakes basin consider recruitment to be the addition of new individuals to the population, regardless of the life stage at which it occurs. Indirect regulation of recruitment by physical processes that alter feeding, growth, condition, and survival is generally viewed to be more important than direct mortality during the early life stage (Ludsin et al. 2014).

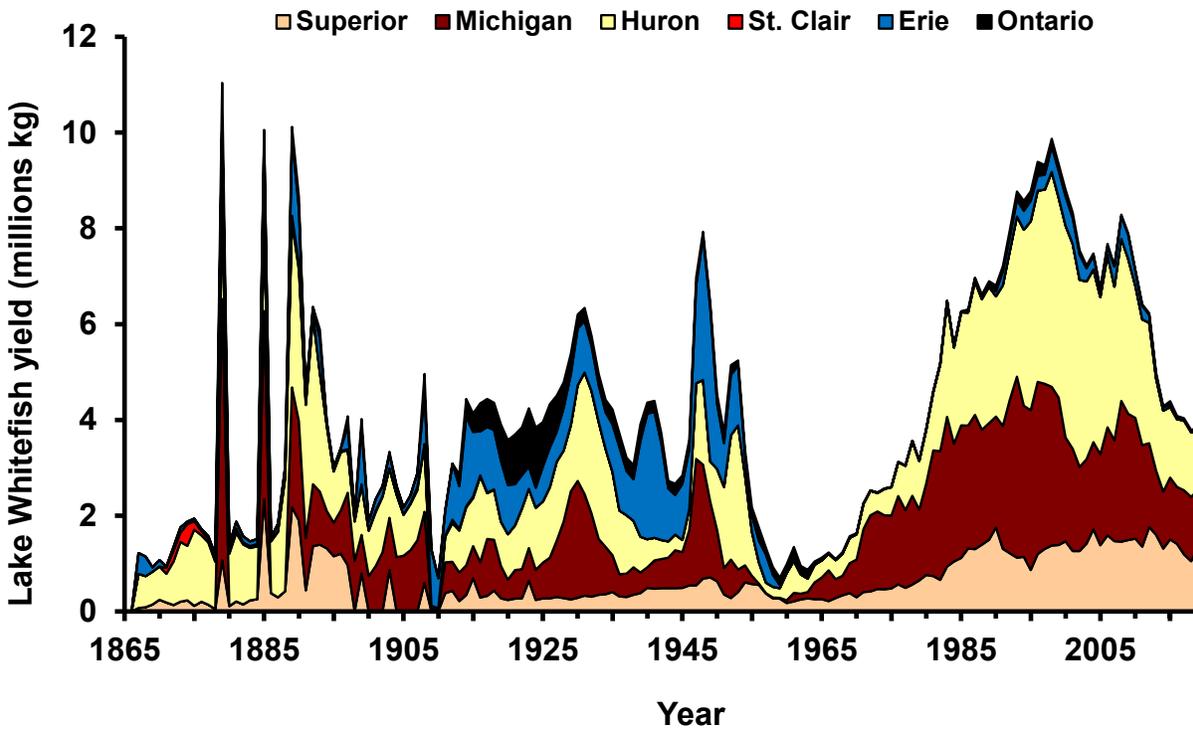
Throughout we are referring to recruitment as a two-stage process. First, embryo and larval stages suffer extremely high rates of natural mortality (>99%) that affect subsequent recruitment. Second, once year-class abundance is established in the first year or two of life, juveniles suffer lower natural mortality rates (<15-30%) similar to that of adults, and their recruitment is a function of growth rate and migration to fishing grounds.

Variations in abundance of year-classes and changes to the rates at which year-classes enter the fishery have direct effects on yield (Gerdeaux 2004; Anneville et al. 2009). Typically, recruitment from large year-classes with fast-growing individuals substantially increases fishery yield, which may be maintained for decades as these year-classes persist in the fishery (Christie 1963). Conversely, recruitment from small year-classes with slow-growing individuals can also occur, sometimes for decades, sharply reducing yield and spawning biomass, as has occurred after the year 2000 for Cisco (*C. artedii*) in Lake Superior, for Bloater (*C. hoyi*) in Lakes Michigan and Huron (Oldenburg et al. 2007; Bunnell et al. 2009a; Stockwell et al. 2009; Rook et al. 2012), and for Lake Whitefish, in particular throughout Lakes Michigan, Huron, and Ontario (Hoyle et al. 1999, 2011; Ebener et al. 2008; Modeling Subcommittee, Technical Fisheries Committee 2017).

After decades of experiencing consistently high levels of recruitment that expanded population biomass and abundance (Casselman et al. 1996; Ebener 1997; Cook et al. 2005; Mohr and Ebener 2005; Schneeberger et al. 2005), both early-life-stage and juvenile recruitment of Lake Whitefish began to decline during the early 2000s, precipitating a slow decline of commercial-fishery yield in all four lower Great Lakes (Mohr and Nalepa 2005;

Ebener et al. 2008; Brenden et al. 2010a; Lenart and Caroffino 2017; Lake Erie CWTG 2017). Recruitment of Lake Whitefish in Lake Superior has been more consistent than in the four lower lakes, consequently commercial-fishery yield from there has remained high, keeping the basinwide yield from collapsing (Fig. 1).

Fig. 1. Commercial-fishery yield of Lake Whitefish from the Great Lakes, 1867-2019. Records prior to 1911 are incomplete.



Declines in recruitment of Lake Whitefish to the fishery were preceded by sizable declines in growth and condition of harvestable-sized fish in Lakes Michigan, Huron, and Ontario. Declines in Lake Whitefish growth began in the late 1990s after non-native dreissenids (*Dreissena polymorpha* and *D. bugensis*) became established in the early 1990s (Hoyle 2005; Schneeberger et al. 2005; Mohr and Ebener 2005). Since then, invasive mussels have played a huge role in restructuring Great Lakes food webs (Madenjian et al. 2002, 2015a; Dobiesz et al. 2005; Bunnell et al. 2009a, 2018; Rennie 2013). The establishment of massive populations of dreissenids has affected every life stage of Lake Whitefish and altered its dynamics to the detriment of the populations and fisheries in all Great Lakes, except Superior where dreissenids are rare (Hoyle et al. 2011; Rennie 2013; Fera et al. 2015; Gobin et al. 2015, 2016; Fera et al. 2017). Since the late 1990s, growth rates of Lake Whitefish in Lakes Superior and Erie have been more stable than in Lakes Michigan, Huron, and Ontario (Rennie 2013; Fera et al. 2015).

Lake Whitefish is not the lone Great Lakes fish that has experienced large non-stationary variations in recruitment. Bloater in Lakes Michigan and Huron (Madenjian et al. 2002; Dobiesz et al. 2005), Burbot (*Lota lota*) and Yellow Perch (*Perca flavescens*) in Lake Michigan (Madenjian et al. 2002), and Cisco in Lake Superior (Bronte et al. 2003; Stockwell et al. 2009) have all gone through substantial increases in recruitment, which in turn were followed by just as substantial declines. Recruitment-driven changes in abundance bolstered population abundance for 10-20 years before the effects of reduced recruitment lowered abundance for another 10-20 years. Rainbow Smelt (*Osmerus mordax*) in Lake Michigan has also undergone non-stationary recruitment, but its stock-recruit productivity has increased through time (Feiner et al. 2015).

Physical and biological processes have been identified as important to recruitment dynamics of Great Lakes fish. Declines in Sea Lamprey (*Petromyzon marinus*) abundance and its predation on Great Lakes fish in combination with implementation of harvest management strategies have been responsible for recovery of Lake Whitefish populations in the Great Lakes (Jensen 1976; Spangler and Collins 1980; Reckahn 1995; Ebener 1997; Madenjian et al. 2002; Mohr and Ebener 2007; Ebener et al. 2008). Declines in Alewife (*Alosa pseudoharengus*) abundance through top-down effects of predators and bottom-up effects caused by dreissenids have been implicated in the recovery of Walleye (*Sander vitreous*) (Fielder et al. 2007), Emerald Shiner (*Notropis atherinoides*) (Madenjian et al. 2002, 2008), Deepwater Sculpin (*Myoxocephalus thompsonii*), Yellow Perch, and Burbot (Madenjian et al. 2002, 2008; Stapanian et al. 2008). Water temperature, wind intensity, and Rainbow Smelt predation were linked to changes in Cisco recruitment dynamics (Stockwell et al. 2009; Rook et al. 2012; Myers et al. 2015).

Ludsin et al. (2014) believed that variation in growth and survival during early life stages was critical to understanding recruitment variability in ecosystems such as the Great Lakes. They felt that even minor fluctuations in early-life-stage growth and survival can exert a strong influence on future recruitment because they may extend the time young fish are vulnerable to physical processes, which indirectly reduce survival of early life stages. Further, because climate warming holds great potential to alter the physical conditions and processes of large lake ecosystems (Straile et al. 2007; Anneville et al. 2009; Lynch et al. 2015), continued research into how warming will act independently and interactively with other large-scale ecosystem processes (like altered nutrient regimes and invasive species) will be critical for understanding and predicting future recruitment patterns.

Our review follows three other reviews focused on the well-being of Lake Whitefish in the Great Lakes. Declines in abundance and growth of Lake Whitefish and declines in abundance of a major diet item, the benthic amphipod *Diporeia* spp. (hereafter, *Diporeia*), to near absence in the four lower lakes resulted in the Lake Whitefish-*Diporeia* Workshop held in 2002 (Mohr and Nalepa 2005). Next, Brenden et al. (2010b) oversaw the publication of a special supplement of the Journal of Great Lakes Research: “Assessing the Health of Lake Whitefish Populations in the Laurentian Great Lakes: Lessons Learned and Research Recommendations” (Brenden et al. 2010b). The publication’s purpose was to disseminate the results from two large-scale projects funded by the Great Lakes Fishery Trust. These reviews evaluated the effects of changes in growth and condition on natural mortality and recruitment of Lake Whitefish in Lakes Michigan, Huron, and Superior. Shortly thereafter, Rennie (2013) conducted a literature assessment of factors affecting Lake Whitefish growth and condition, and the Ontario Ministry of Natural Resources and Forestry (OMNRF) embarked on a study of variations in larval Lake Whitefish survival and abundance in three areas of Lake Huron. Ongoing now, experts led by the U.S. Fish and Wildlife Service are exploring means to quantify Sea Lamprey marking/mortality on Lake Whitefish and other species. We benefited greatly from these efforts and draw extensively on their findings. Our approach is wide ranging and, accordingly, is organized around three broad topics: physical processes, stock structure, and biological processes. These topics are followed by sections on management considerations and research priorities. Our objective is to be thorough and topical while providing a needed compendium of information on Lake Whitefish of the Great Lakes.

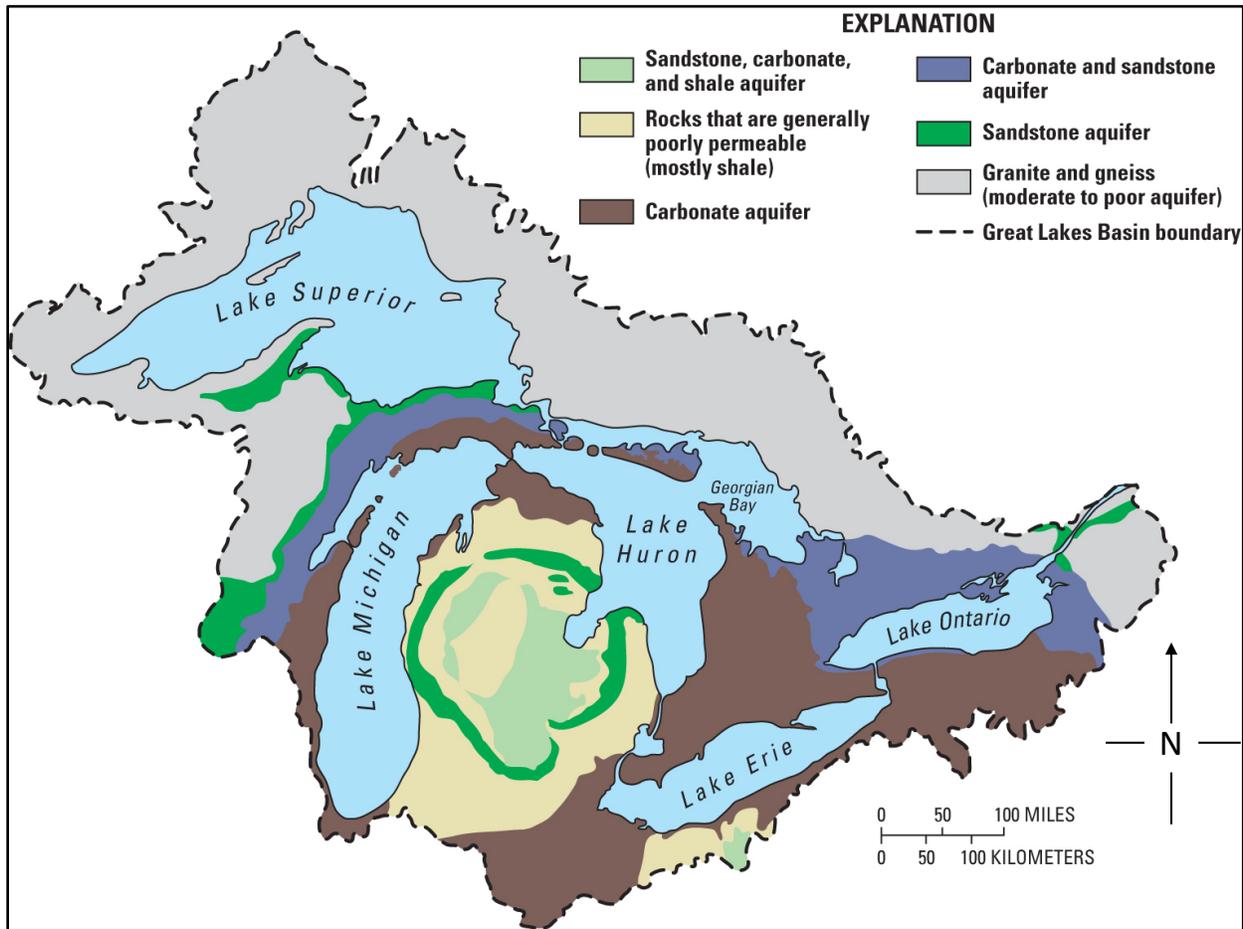
PHYSICAL PROCESSES

Geology of the Basin

Sedimentary limestone and sandstone and Canadian Shield granite form the geological foundation of Lake Whitefish spawning habitat in the Great Lakes basin (see Goodyear et al. 1982; Roseman et al. 2007). Many of the Lake Whitefish spawning shoals in the four lower Great Lakes are in carbonate (limestone) formations from old coral reefs, which encircle Lakes Michigan, Huron, Erie, and southern Lake Ontario, and in sandstone formations, which encompass eastern and northern Lake Ontario, a small part of Lake Huron, northwestern Lake Michigan, and the southern shore of Lake Superior (Fig. 2). Canadian Shield granite is the dominate geological formation of Lake Superior, northern Georgian Bay, and the North Channel in Lake Huron. Limestone and sandstone rocks are relatively soft and easily eroded, but they form differently on spawning shoals. Limestone breaks into highly irregular shapes called grab rock or honeycomb limestone by commercial fishermen because limestone is so easily entangled in nets that it appears to grab fishing gear. Sandstone, on the other hand, tends to break into more regularly shaped rounded or square pieces that are much smoother. Canadian Shield rock is rounded and smooth like sandstone but much harder, and it does not erode as easily. The limestone and sandstone geological features, unfortunately, also provide a good source of minerals for shell development of dreissenids, which have played such a huge role in restructuring the food webs of the four lower Great Lakes (Mohr and Nalepa 2005; Barbiero et al. 2006; Bunnell et al. 2009b; Higgins and Vander Zanden 2010; Barbiero et al. 2011; Ives et al. 2018). Thus, geology has a sizable effect on Lake Whitefish recruitment dynamics.

Post-glacial deposits of clay, sand, gravel, and boulders overlay limestone, sandstone, and granite formations in many areas of the Great Lakes. These glacial-drift features include moraines, mounds of poorly sorted rocks called till, drumlins, and eskers of well-sorted sand and gravel. Drumlins appear to be a unique feature used extensively for spawning by Lake Trout (*Salvelinus namaycush*) in Lake Huron (Riley et al. 2014) and probably by Lake Whitefish as well. Many Lake Whitefish spawning shoals comprise all of these glacial deposits. Large boulders and smaller till are common features of the shoreline and shallow nearshore spawning shoals where wind, wave action, and ice scour transport finer particles away from shore. As water depth increases on spawning shoals, substrates change to till, then gravel, then sand, and finally clay (see Hindley et al. 1977; Freeberg et al. 1990).

Fig. 2. Geologic formations underlying the Great Lakes basin and Lake Whitefish spawning shoals (<https://water.usgs.gov/ogw/pubs/WRI004008/figure02.htm> U.S. Geological Survey Water Resources Investigations Report 00-4008).



Spawning and Nursery Habitat

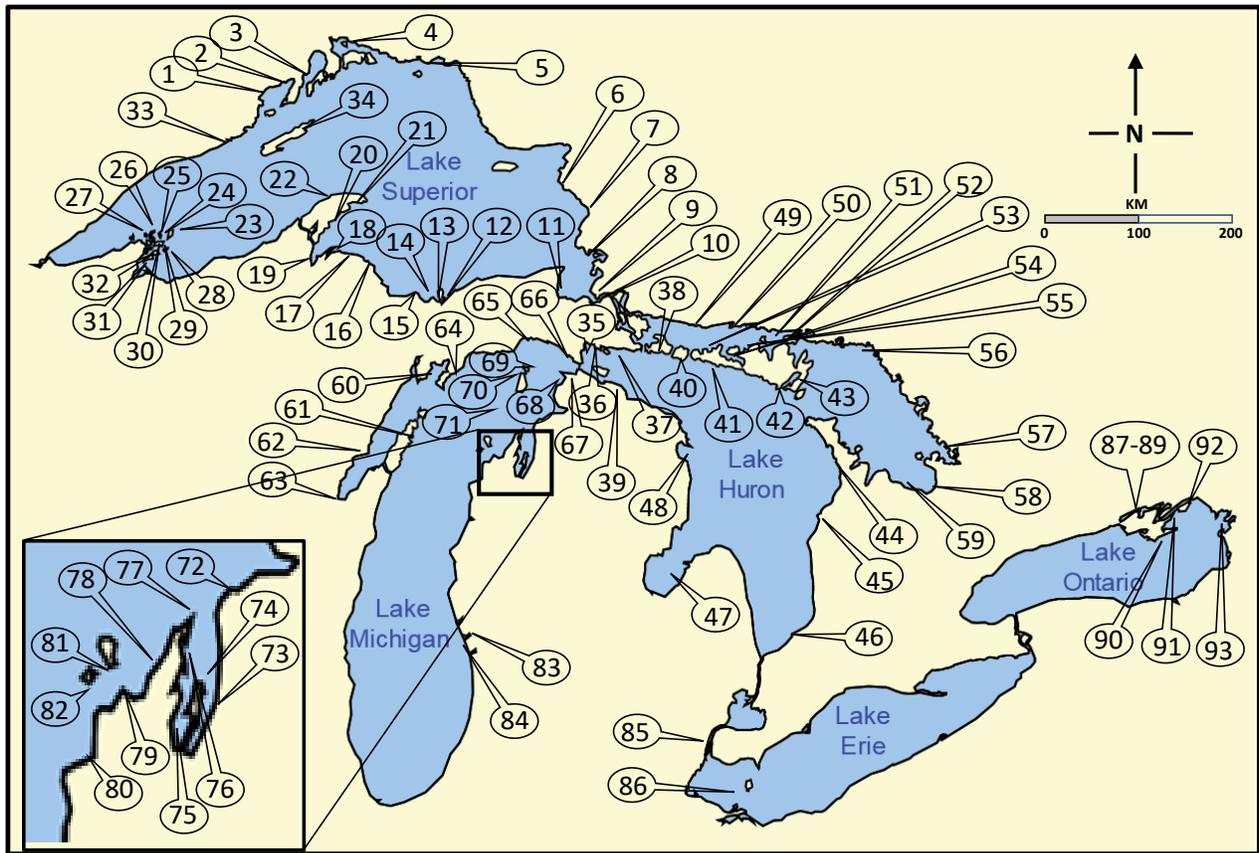
Recruitment dynamics of Lake Whitefish in the Great Lakes are largely defined in nearshore high-energy zones mostly in water <7 m deep where adults deposit gametes in fall, and the fertilized embryos incubate over winter. Adult Lake Whitefish are broadcast spawners and typically deposit gametes from late October through mid-December in 1-9 m of water over rock and gravel areas adjacent to shorelines and on the outside of embayments (Hart 1930; Reckahn 1970; Hoagman 1973; Hindley et al. 1977; Freeberg et al. 1990; Roseman et al. 2007; McKenna and Johnson 2009). Embryos were found at depths <9 m in the east arm of Grand Traverse Bay, Lake Michigan, during 1982-1984, but 74% to 87% were found at depths <3 m (Freeberg et al. 1990). In the Detroit River, embryos were found in high-flow areas that contained rock cobble and broken limestone substrates in 5-7 m of water (Roseman et al. 2007; Fischer et al. 2018). Maximum densities of European Whitefish (*Coregonus lavaretus*) embryos occurred at 10 m in Lake Sempach, Switzerland, and, although embryos were found as deep as 50 m, the more-advanced developmental stages were found only at 10 m (Ventling-Schwank and Müller

1991). Lake Whitefish embryos on spawning shoals in Lake Simcoe, Ontario, were found only in water <4 m deep (Hindley et al. 1977).

Adjacent to spawning areas are shallow, soft-bottomed embayments that provide protection to larvae transported from the spawning shoals by winds and currents or by their own locomotion. Larvae are found in shallow water over hard-bottom substrates immediately after hatch, but, shortly thereafter, they move into nursery areas that are typically <3 m deep, warm quickly, and offer reasonable protection from strong wind-generated currents, which could otherwise transport them offshore after hatching (Hart 1930; Faber 1970; Reckahn 1970; Hoagman 1973). In South Bay, Lake Huron, young Lake Whitefish were collected in the shallowest areas that were <1 m deep during late June and early July trawl surveys (Reckahn 1970). Young were captured near the surface in shallow bays immediately adjacent to areas with emergent *Scripus* spp. beds in South Bay, the Bay of Quinte in Lake Ontario, and North Bay in Lake Michigan (Hart 1930; Faber 1970; Reckahn 1970; Hoagman 1973). In southwestern Whitefish Bay, Lake Superior, Lake Whitefish <30-mm total length (TL) in late May and early June were usually captured in beach seines over sand substrates that contained scattered boulders (M.P.E., unpublished data). In the Baltic Sea's Gulf of Bothnia, the most-important factors describing areas where larvae of the European Whitefish were found were shore profile; distance to sandy, shallow shore; distance to the 20-m depth contour; and week of ice breakup (Veneranta et al. 2013). The earliest larval stages of European Whitefish were found in various habitats close to the shoreline, but the highest densities were along gently sloping and shallow sandy shores (Veneranta et al. 2013), as were larvae of Lake Whitefish in Whitefish Bay, Lake Superior. The importance of these very nearshore and shallow soft-bottomed areas to Lake Whitefish recruitment cannot be overstated. Variation in the availability and amount of shallow nearshore areas with soft-bottomed substrates likely contributes to spatial differences in Lake Whitefish recruitment across the Great Lakes.

Lake Whitefish reproductive habitat constitutes about 484,000 ha or roughly 2% of the total surface area of the Great Lakes. At least 93 Lake Whitefish spawning shoals with adjacent shallow larval nursery areas (Fig. 3) occur in the Great Lakes, with the majority of these in Lake Superior (34) followed in order by Lake Huron (26), Michigan (25), Ontario (6), and Erie (2). By contrast, on an area basis, most of the Lake Whitefish reproductive habitat occurs in Lake Huron (61%), followed in order by Lakes Michigan and Erie (both 14%), Lake Superior (8%), and Lake Ontario (3%). The size of individual spawning and nursery shoals ranges from 6 ha at a shoal along Isle Royale, Lake Superior, to 151,800 ha in Saginaw Bay, Lake Huron. The average size of individual reproductive habitats is 4,800 ha, but the median reproductive habitat is 863 ha. The smallest spawning shoals were at Isle Royale where five of the six shoals around the island were less than 100 ha each and the largest shoal was only 205 ha. On the other hand, the top-ten reproductive habitats by size were all >10,000 ha and six of them were in Lake Huron. These estimates of reproductive habitat should be viewed as minimum values because we did not account for all possible spawning aggregations and larval habitat, which includes areas that have been poorly studied or not documented.

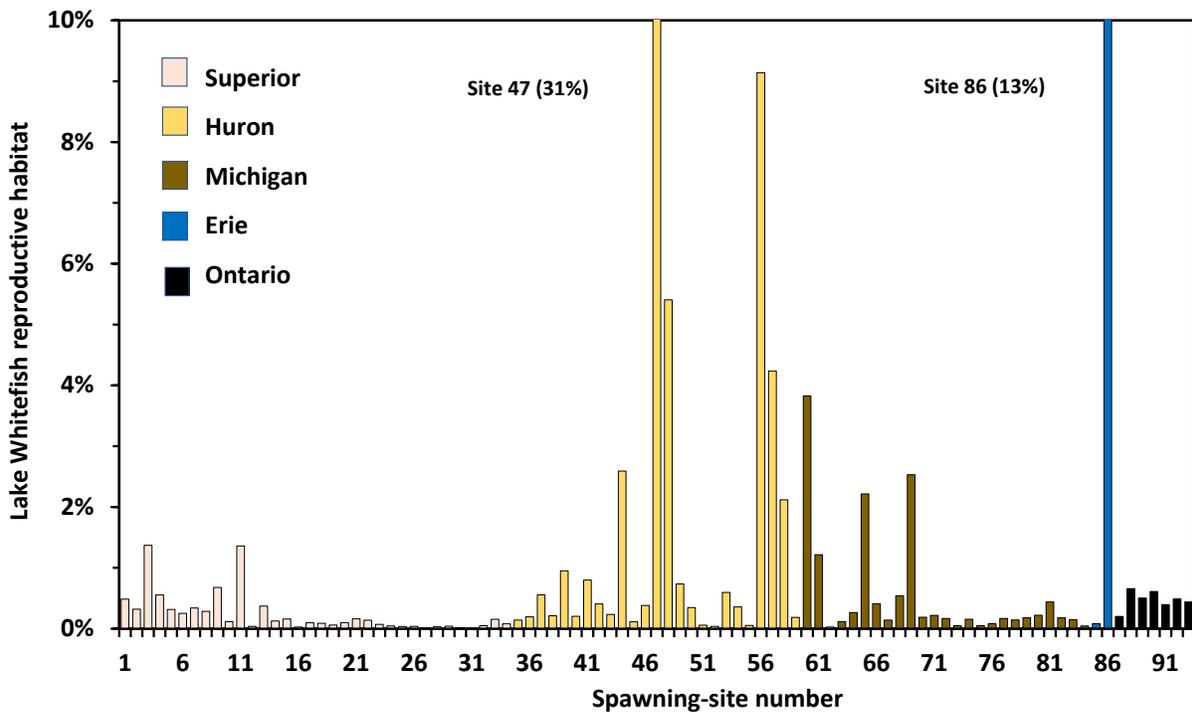
Fig. 3. Documented Lake Whitefish spawning sites and larval nursery areas in the Great Lakes basin. Numbers correspond to spawning sites listed in Appendix A. Sites were identified and their areas determined based on Coberly and Horrall (1980), Loftus (1980), Goodyear et al. (1982), and from personal observation (M.P.E).



Lake Whitefish does spawn in some tributaries to the Great Lakes and in connecting channels. The Menominee (site 62) and Fox (site 63) Rivers in Lake Michigan and the Detroit River (site 85) (Fig. 3) all have spawning aggregations of Lake Whitefish (Roseman et al. 2007; Fischer et al. 2018; Ransom et al. 2021). Total reproductive habitat in these rivers is small in comparison to many in-lake habitats. Reproductive habitat ranges from 130 to 700 ha in these three rivers as measured from the first upstream barrier to the river mouth. Nearly all of these tributary spawning stocks have been recovering slowly for over a century as they were common spawning areas before land clearance, lumbering, and shipping improvements destroyed them (Wells and McClain 1973; Goodyear et al. 1982; Roseman et al. 2007). The St. Marys River, the connecting channel between Lakes Superior and Huron, historically contained a large aggregation of Lake Whitefish in the rapids, but it is unknown if the fish spawned there. However, although current stocks in the rapids are small in comparison, reproduction does occur annually in the St. Marys River (Jude et al. 1998). Other historically important Lake Whitefish spawning tributaries in the Great Lakes include the St. Louis, Montreal, and Nipigon Rivers in Lake Superior, tributaries to Green Bay in Lake Michigan (Wells and McClain 1973), and the Detroit River (Todd 1986).

Slightly over 75% of all Lake Whitefish reproductive habitat occurs in embayments. Besides containing substantial amounts of spawning shoals and protection from ice cover for developing embryos, the embayments also contain substantial shallow areas preferred by larval Lake Whitefish and have higher productivity, which enhances food availability for young Lake Whitefish. The sheer volume of larval and spawning habitat in embayments indicates that most Lake Whitefish recruitment originates there. The largest reproductive habitats (see Fig. 3) are in Saginaw Bay (site 47), western Lake Erie (site 86), northern Georgian Bay (site 56), Alpena (site 48), southern Georgian Bay (site 57), and Big Bay de Noc (site 60) (Fig. 4). The eastern Door Peninsula in Lake Michigan (site 61) and the Fishing Islands in Lake Huron (site 44) have exceptionally large aggregations of spawning shoals in the main basin of each lake, but they have far less larval habitat than the embayments (Hoagman 1973; Coberly and Horrall 1980; Claramunt et al. 2010b; Overdyk 2011; Ryan and Crawford 2014).

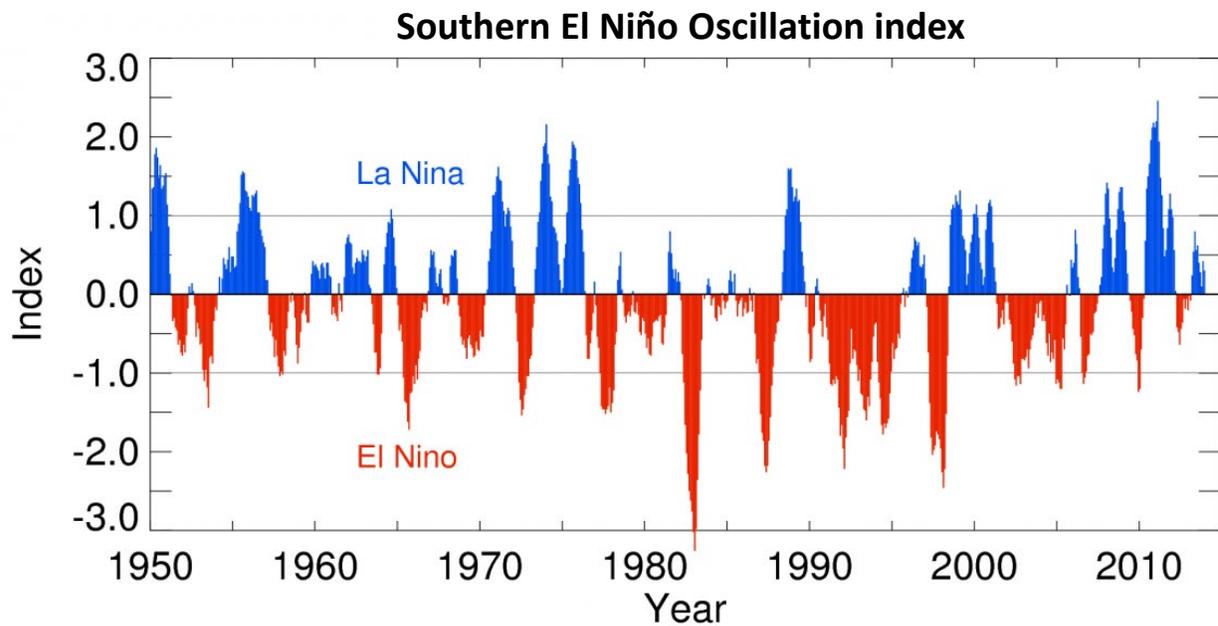
Fig. 4. Percentage of the total Great Lakes Lake Whitefish reproductive habitat <7 m deep in each of 93 reproductive habitats (Lake Superior sites: 1-34; Lake Huron sites: 35-59; Lake Michigan sites: 60-84; Lake Erie sites: 85-86; Lake Ontario sites: 87-93; see Fig. 3 for the location of each numbered spawning site).



Large-Scale Climate Effects

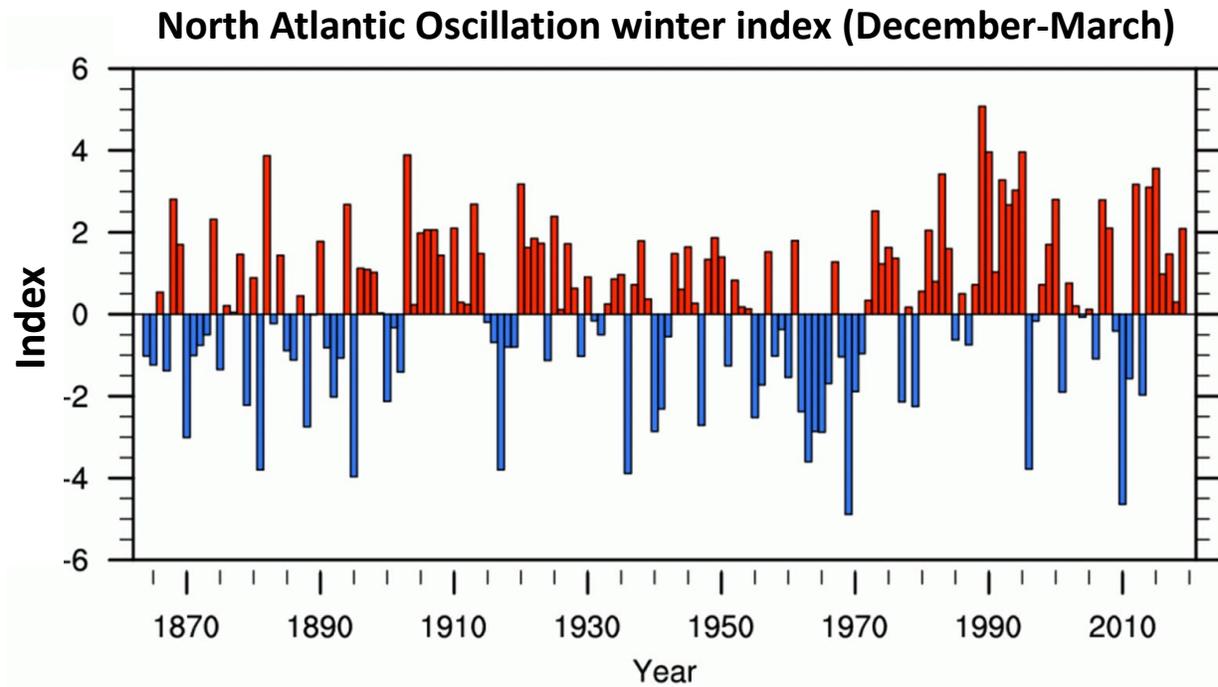
Much of the variation in precipitation and temperature in the Great Lakes basin is driven by climatic forcing functions that occur in the Pacific and Atlantic Oceans. The El Niño-Southern Oscillation (ENSO) and the North Atlantic Oscillation (NAO) are the dominant forcing functions influencing weather in the Great Lakes basin. The ENSO is caused by atmospheric-ocean interactions in equatorial waters of the Pacific Ocean from the international date line to the western coast of South America. El Niño is the warm phase of the ENSO whereas La Niña is the cold phase. A time-series index of ENSO has been created from normalized sea-level pressure fluctuations at Tahiti minus those at Darwin, Australia (Fig. 5). During an El Niño event, pressure is higher than normal at Darwin and lower at Tahiti, making the index negative (Stenseth et al. 2003).

Fig. 5. The Southern El Niño Oscillation ² index from 1950-2019 (top panel) and the North Atlantic Oscillation winter index ³ (December-March) from 1864-2019 (bottom panel).



²<http://faculty.washington.edu/kessler/ENSO/soi-shade-ncep-b.gif>.

³<https://climatedataguide.ucar.edu/climate-data/hurrell-north-atlantic-oscillation-nao-index-station-based>.



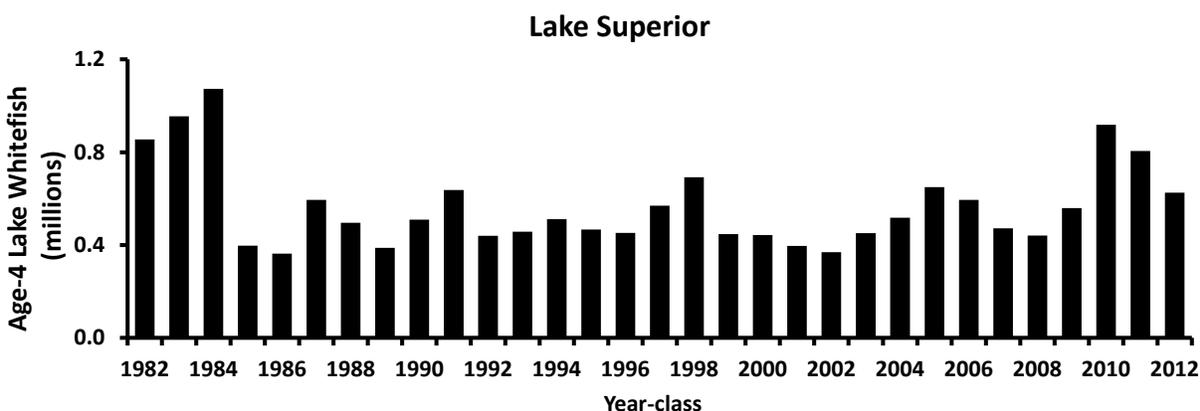
The NAO is the primary source of winter climate variability in the North Atlantic region from central North America to Europe. It alternates between a subtropical high near the Azores in the mid-Atlantic Ocean and an Arctic low-pressure system that sits permanently over Iceland. The NAO index (Fig. 5) varies from year to year, but, since 1980, it has tended to remain in one phase or the other (Hurrell and Loon 1997; Hurrell et al. 2001). The changes in pressure gradient for both the ENSO and NAO produce large changes in wind speed; moisture; heat; and intensity, frequency, and paths of winter storms (Hurrell et al. 2001). When the NAO index is positive, there is a stronger than normal subtropical high pressure and a much-deeper Icelandic low pressure, which causes warm wet winters in Europe, cold dry winters in eastern Canada, and mild, wet winters in the eastern and central U.S. A negative NAO index is a sign that the subtropical high and Icelandic low are both weak, which allows Arctic air to move southward into the central and eastern U.S., causing very cold and snowy winters (see <http://www.ldeo.columbia.edu/res/pi/NAO/>). Both the ENSO and NAO dictate climate variability and strongly affect agricultural yield, water management, fish populations, zooplankton production, and terrestrial ecology (Hurrell et al. 2001). These two large-scale climate processes will continue to influence recruitment of Lake Whitefish in the Great Lakes. As climate warming continues to unfold, its effect on Lake Whitefish recruitment could be profound as both the ENSO and NAO will affect air and water temperature, ice cover, and currents that will either directly or indirectly affect survival, dispersal, and growth of early life stages (Christie 1963; Henderson et al. 1983; Reckahn 1986; Brown et al. 1993; Straile et al. 2007; Anneville et al. 2009; Lynch et al. 2010, 2015).

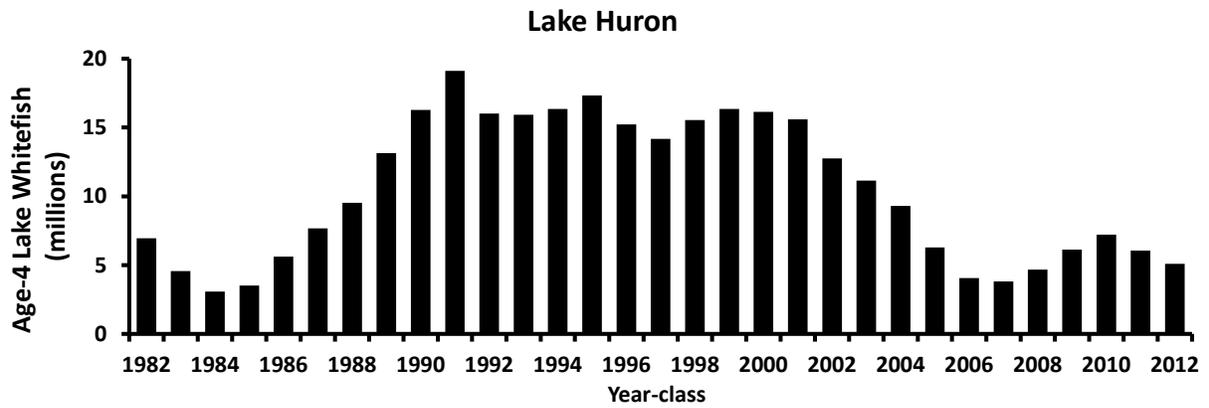
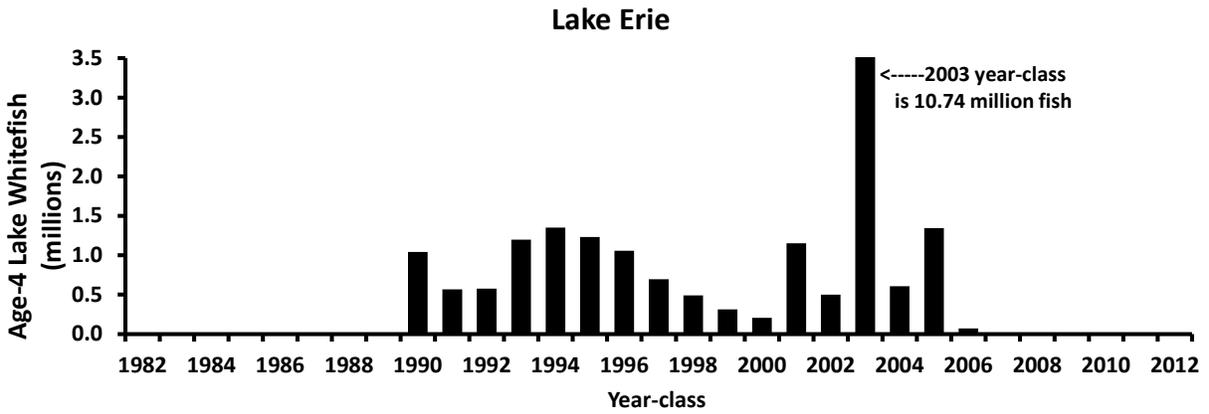
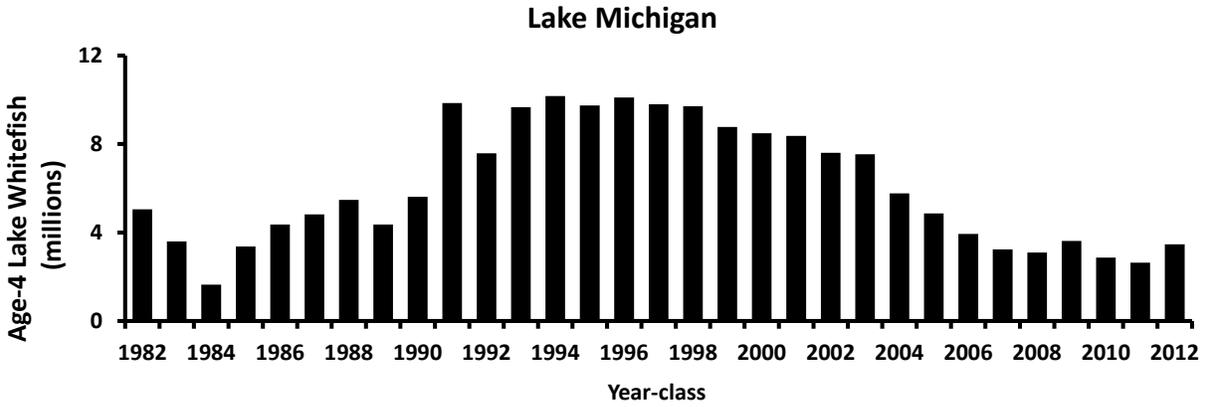
Temperature

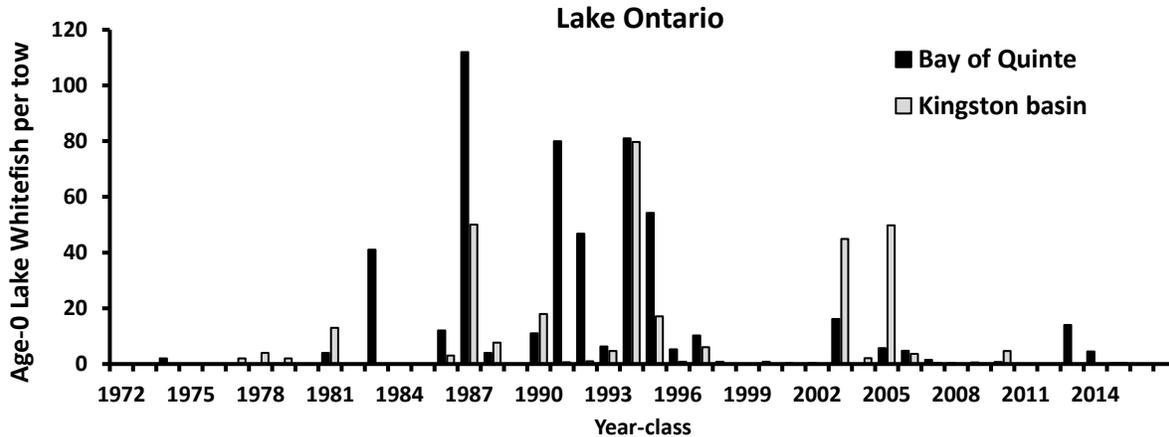
Cold temperatures are an important component of Lake Whitefish reproductive ecology. The species dispersed into North America and south into the Great Lakes from northern Europe and Asia through the Arctic Ocean, and their populations survived in the Mississippian refugium at the edge of the glacial ice sheets for thousands of years (Lindsey et al. 1970; Franzin and Clayton 1977; Bernatchez and Dobson 1991). Thus, a prerequisite for Lake Whitefish existence is to be highly tolerant of cold temperatures. The Great Lakes represent the most-southern extent of Lake Whitefish distribution in North America (Lindsey et al. 1970), and the lakes' large surface area, great depths, and slow rates of warming and cooling allow Lake Whitefish to exist at latitudes where it otherwise could not exist because water temperatures would be too warm for its survival.

Recruitment variability typically increases for highly fecund species and species at the edge of their range (Myers 2001). Reproductive success and recruitment of Lake Whitefish in Lake Superior are more stable than recruitment in the other lakes, which are further south and warmer. Although commercial yields of Lake Whitefish have been declining in all four lakes below Superior due to reduced recruitment, yield (Fig. 1) and recruitment in Lake Superior have been amazingly stable (Lake Erie CWTG 2017; Modeling Subcommittee, Technical Fisheries Committee 2016, 2017). For example, statistical catch-at-age (SCAA) models have shown recruitment of age-4 fish to commercial fisheries in Lake Superior to be very consistent during 1986-2016 while recruitment to fisheries in Lakes Huron and Michigan declined by nearly two-thirds and recruitment in Lake Erie nearly collapsed (Fig. 6). In Lake Ontario, stock-assessment estimates of recruitment are not available, but estimates of young-of-the-year (YOY) recruitment have followed the same trends as in Lakes Huron, Michigan, and Erie (Fig. 6). Variability between the highest and lowest levels of mean recruitment at age 4 was 2.9-fold for stocks in central and eastern Lake Superior, 3.9-fold for seven stocks in Lake Michigan, 5.6-fold in all basins of Lake Huron, and 17,000-fold for western Lake Erie. Increased variability at lower latitudes supports the notion that variability in Lake Whitefish recruitment increases with increased temperature and proximity to the southern edge of its geographic distribution. The similarity in recruitment variability and trends among the four lower Great Lakes may not be due solely to temperature but rather is likely a coupling of physical (habitat, temperature) and biological (food web, invasive species) processes.

Fig. 6. Abundance at age 4 of the 1982-2012 year-classes of Lake Whitefish in selected areas (Appendix B) of Lakes Superior, Michigan, Huron, and Erie estimated from statistical catch-at-age stock assessments and the number of age-0 Lake Whitefish of the 1972-2017 year-classes captured in bottom trawls in two areas of Lake Ontario. Note that the y-axis scale differs among panels.







Water temperatures of the Great Lakes have been increasing through time (Trumpickas et al. 2009; Mason et al. 2016), reducing the density and duration of ice cover, which is important for protecting Lake Whitefish embryos from strong wind-generated currents (Taylor et al. 1987; Ventling-Schwank and Müller 1991; Brown et al. 1993; McKenna and Johnson 2009; Lynch et al. 2015; Mason et al. 2016). Increased water temperature and rate of warming may also increase natural mortality and advance hatching dates of Lake Whitefish, which could potentially create a mismatch with zooplankton production (Berlin et al. 1977; Patrick et al. 2013; Veneranta et al. 2013). As early as the 1920s and 1930s, researchers had determined that Lake Whitefish embryos reared at colder temperatures attained larger sizes at hatch (13.4 to 15.0 mm TL) than embryos reared at warmer temperatures for shorter periods of time (8 to 11 mm TL) (Hall 1925; Price 1940). In addition, Price (1940) reared Lake Whitefish embryos at temperatures ranging from 0 to 10° C and found that no embryos hatched at the two temperature extremes, and that, at water temperatures of 0.5 to 6° C, embryo hatch rates were uniform at about 58%.

Recruitment of Cisco and Yellow Perch is positively associated with warm spring water temperatures in the Great Lakes (Myers et al. 2015; Honsey et al. 2016), and warm spring temperatures may also increase growth and survival of Lake Whitefish larvae. Ryan and Crawford (2014), however, found no association of larval Lake Whitefish abundance or distribution with temperature in Stokes Bay of the Fishing Islands (site 44) reproductive habitat (see Fig. 3). Growth of age-1 Lake Whitefish was positively correlated with spring water temperature, and temporal declines in spring water temperatures reduced growth rates of Lake Whitefish in South Bay, Lake Huron, dampening the growth increases related to higher water levels (Henderson et al. 1983; Reckahn 1986). An increase in Great Lakes water temperature is likely to increase juvenile and adult Lake Whitefish growth rate as well as biomass and yield, partially counteracting declines in survival and abundance of early life stages that may occur because of increased temperatures.

Ice Cover

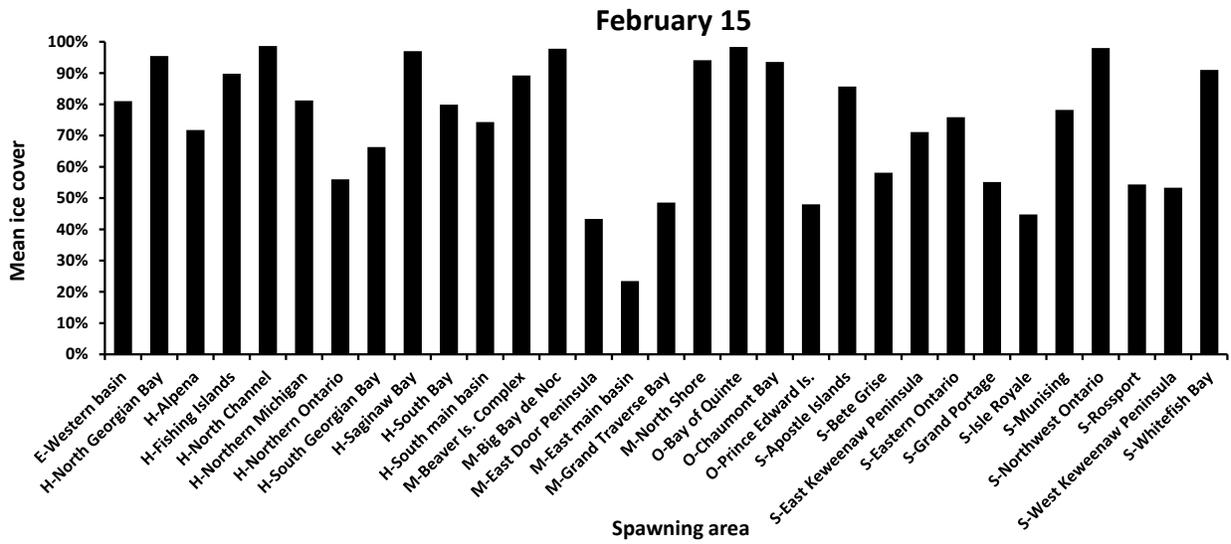
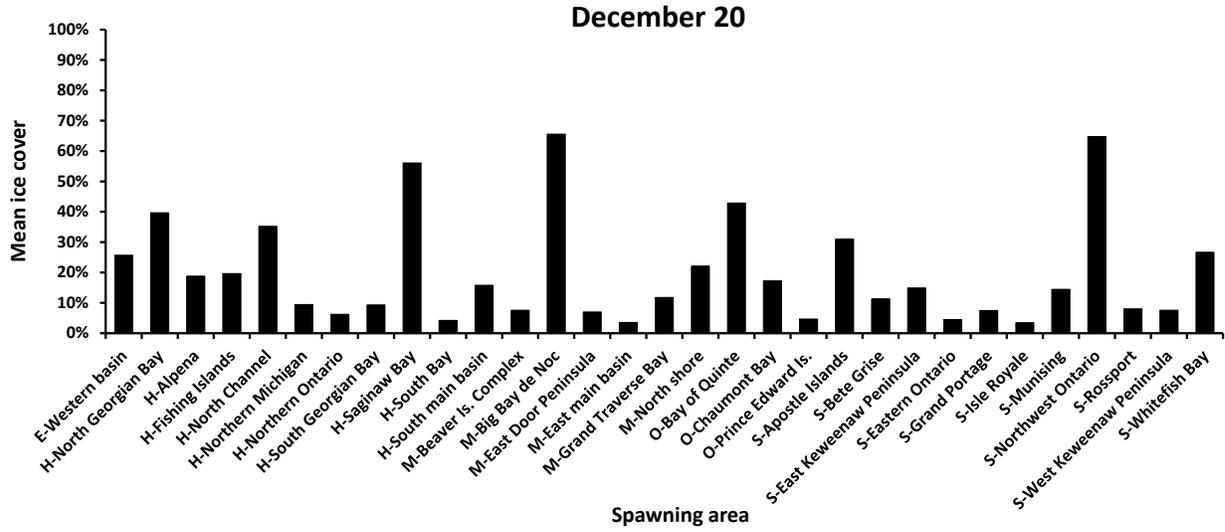
Reproducing in cold-water environments requires Lake Whitefish to adapt to ice. Ice cover is known to both enhance and degrade Lake Whitefish recruitment in the Great Lakes (Taylor et al. 1987; Brown et al. 1993), and many Lake Whitefish spawning shoals occur in embayments or along shorelines where ice formation is persistent each winter, typically beginning in December (Assel et al. 1983). Throughout the range of Lake Whitefish outside of the Great Lakes, ice cover is an annual event and is thought to protect embryos from waves and currents generated by strong winds that may dislodge them or infill interstitial spaces with fine sediments and suffocate them (Taylor et al. 1987; Freeberg et al. 1990; Brown et al. 1993). Nearly all Lake Whitefish spawning

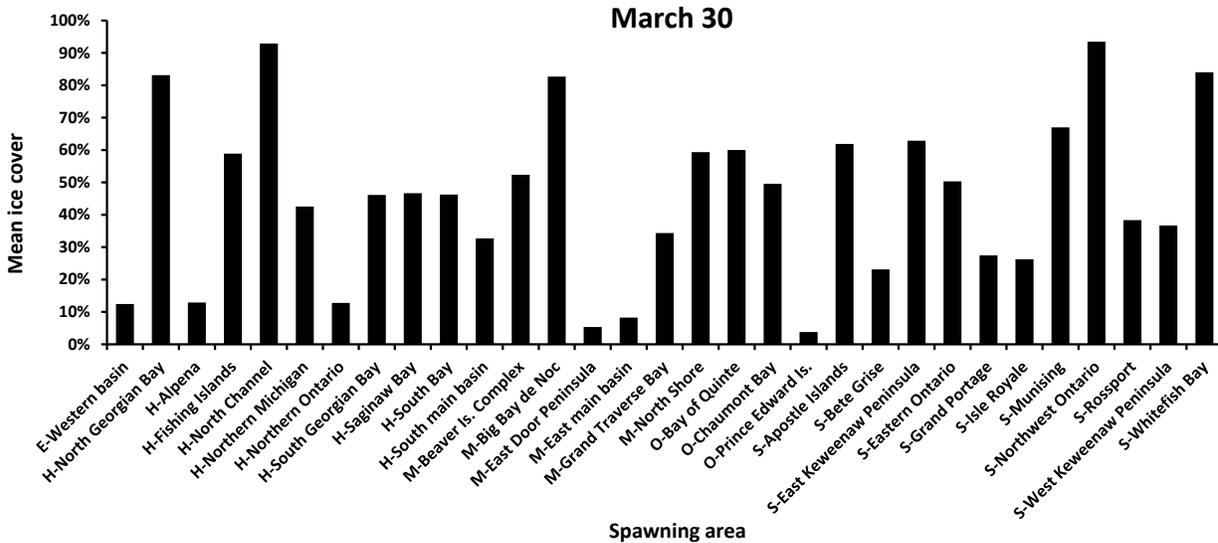
is complete by mid-December in the Great Lakes (Freeberg et al. 1990; Patrick et al. 2013), and both November and December are notoriously windy months with storms producing winds of $80 \text{ km}\cdot\text{h}^{-1}$.

Early ice cover can protect embryos from storms (Taylor et al. 1987). Reproductive habitats that experience at least 50% ice cover by December 20 are in large embayments (Assel et al. 1983; Wang et al. 2017) where much of the reproductive habitat is located. Areas (see Fig. 3) with early ice cover include Big Bay de Noc of northern Lake Michigan (site 60); Thunder, Black, and Nipigon Bays of northwestern Lake Superior (sites 1-4); and Saginaw Bay of Lake Huron (site 47) (Fig. 7). Other areas, such as the Apostle Islands (sites 23-32), Whitefish Bay (sites 8-11), the north shore of Lake Michigan (sites 65-67), the North Channel (sites 49-55), northern Georgian Bay (site 56), and the Bay of Quinte (sites 87-89) experience at least 20% ice cover by December 20. Survival of Lake Whitefish embryos in Grand Traverse Bay, Lake Michigan, was only 0.6%, and none survived in sand and clay regions when ice did not form during the winter (Freeberg et al. 1990). In a Swiss lake, strong currents were thought to account for the 80% decline in the number of embryos of *Coregonus* spp. (Ventling-Schwank and Müller 1991), presumably because there was little ice cover. We suspect that embryos incubating on marginal bottom substrates (slabs of rock, sand, clay) benefit the most from early ice cover.

On the other hand, many Lake Whitefish spawning areas have little to no ice cover by December 20, and either they do not get consistent ice cover until mid-February or they seldom get consistent ice cover. Thus, Lake Whitefish embryos incubating in many reproductive habitats have no protection from wind-generated waves and currents for much of the winter, yet these sites do support substantial commercial fisheries. In Lake Michigan, the eastern Door Peninsula spawning shoals (site 61; see Fig. 3) averaged only 7%, 23%, and 8% ice cover on December 20, February 15, and March 30, respectively, 1973-2016 (Fig. 7, Appendix B), yet these spawning shoals support a large spawning aggregation of Lake Whitefish, which has produced yields of over 1.0 million kg in some years. The same is true of northern Michigan (sites 35-39) and northern Ontario (sites 40-43) spawning shoals in Lake Huron (see Fig. 3) where ice cover was only 6-9%, 56-81%, and 13-43% on December 20, February 15, and March 30, respectively, 1973-2016, yet these two areas combined have produced yields of more than 1.5 million kg and recruitment of up to 5.8 million age-4 fish in some years (Appendix B). Ice cover of more than 40% was a good predictor of Lake Whitefish recruitment in Big Bay de Noc (site 60), and ice cover of 70% was a good predictor of Lake Whitefish recruitment at spawning shoals on the north shore of Lake Michigan (sites 65-72; see Fig. 3) (Brown et al. 1993). Spawning-stock size and spring temperature were also important parameters in the predictive stock-recruitment models of Brown et al. (1993). Thus, although ice cover is important to good recruitment, other physical-biological parameters must also be important.

Fig. 7. Mean percentage of ice cover at Lake Whitefish spawning sites in the Great Lakes as estimated from NOAA ice-cover maps (Assel et al. 1983; Wang et al. 2017) on December 20, February 15, and March 30, 1973-2016. If ice-cover maps were not available for those days, the next closest day was used in the analysis. Letters before the spawning-area names indicate the Great Lake in which the area is located (E = Erie; H = Huron; M = Michigan; O = Ontario; S = Superior).

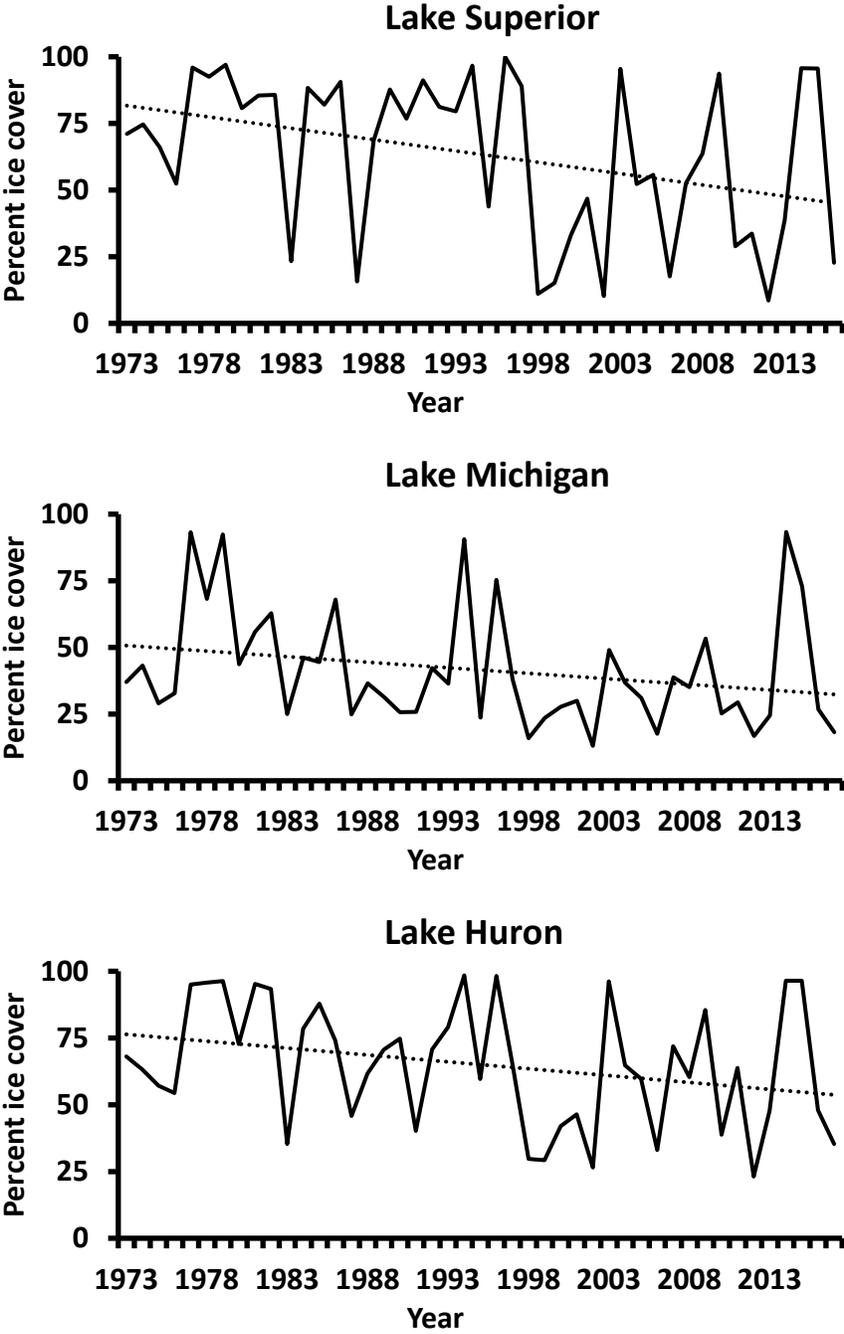


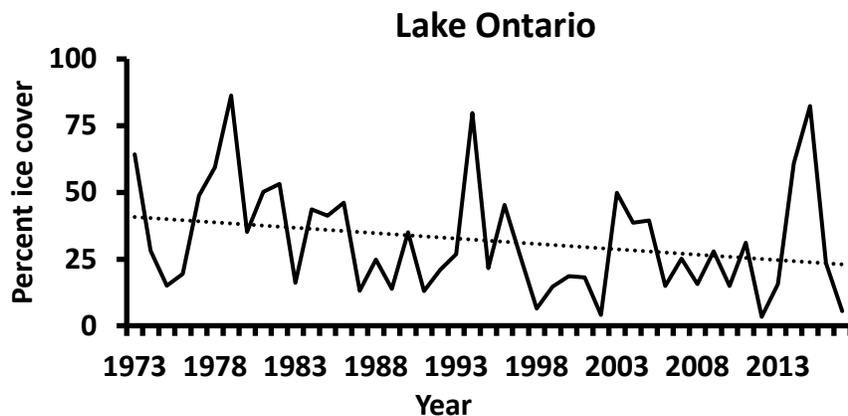
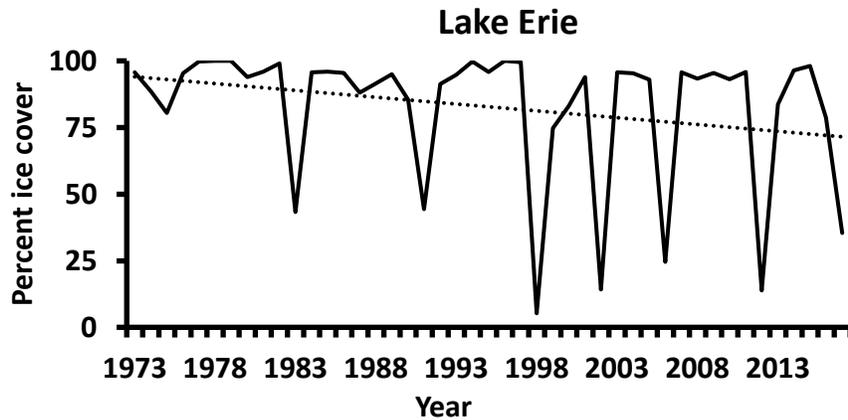


Although early ice cover may protect embryos from waves and currents, extended ice cover may also enhance embryo incubation and growth of larval Lake Whitefish (Bidgood 1974; Naesje and Jonsson 1988; Eckmann and Pusch 1991). The longer Lake Whitefish embryos incubate under ice cover, the larger the larvae tend to be at hatch, which should enhance their survival (Eckmann and Pusch 1991). European Whitefish embryos exposed to flowing water hatched in fewer heating degree days and more uniformly through time than embryos protected from flowing water (Naesje and Jonsson 1988). Also, ice cover may help increase production of zooplankton during the winter in embayments, which will influence ration and first feeding of larval Lake Whitefish (Vanderploeg et al. 1992). In areas such as Big Bay de Noc in northern Lake Michigan, the North Channel and Saginaw Bay in Lake Huron, and Whitefish Bay and northwestern Ontario in Lake Superior, ice cover exceeded 70% on March 30, 1973-2016. Thus, extended ice cover into March and April may be equally as important as early ice cover.

The continuing decline in the amount of ice cover on the Great Lakes due to a warming climate will affect Lake Whitefish recruitment, but the effects will depend upon location of the spawning shoals because the changes in ice cover are patchy (Mason et al. 2016). Ice cover has undergone a consistent long-term decline (Fig. 8) and summer surface water temperatures have continued to increase in the Great Lakes, but these patterns vary by region in each lake in relation to bathymetry, predominant wind direction, and circulation patterns. Loss of ice cover and increased summer surface water temperatures have been greater on Lake Superior than in the other lakes and greater in northern and eastern areas of Lakes Superior, Huron, and Michigan (Mason et al. 2016). Spawning shoals along the eastern Door Peninsula in Lake Michigan will likely be less affected by declining ice cover than areas such as Whitefish Bay in Lake Superior and the North Channel and Saginaw Bay in Lake Huron. Declining ice cover will change water circulation and warming patterns that will in turn influence dispersal of Lake Whitefish larvae and the ratios of zooplankton to larval Lake Whitefish (Taylor et al. 1987; Freeberg et al. 1990).

Fig. 8. Percent ice cover on each Great Lake (solid line) and trendline (dashed line) of percent ice cover during the winters of 1973-2017 (A. Clites, NOAA/GLERL, unpublished data).





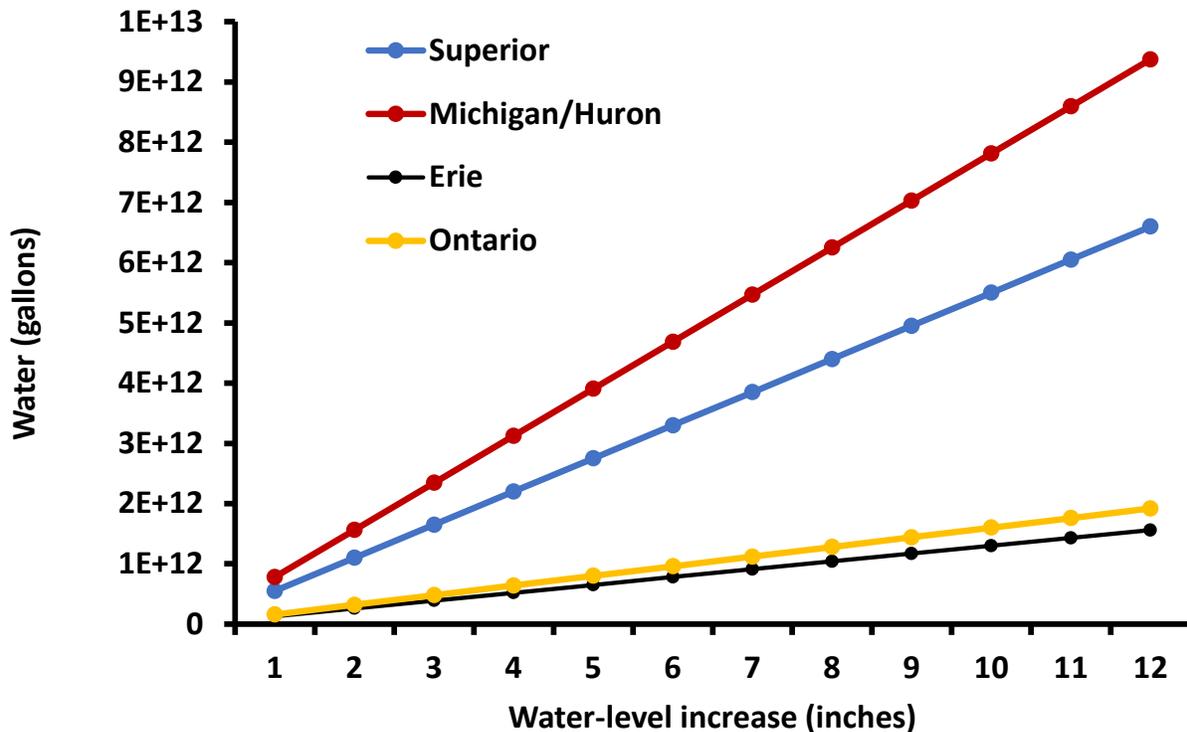
Water Levels

High and stable water levels, which are believed to increase nutrient concentrations and primary and secondary production, provide larval fish additional prey and cover for protection from predators (see Casselman and Lewis 1996). Low water levels should then have the opposite effect, which is to reduce nutrients and cover in very-nearshore areas. Trends in mean weight of age-4 and older Lake Whitefish in South Bay, Lake Huron, were directly correlated to trends in water levels (see Fig. 7 in Reckahn 1986). Increases in growth associated with higher water levels were detected in the first growing season in South Bay, and the trends followed through to older age-classes. There appeared to be a 32-year cycle to the trends in water levels and Lake Whitefish growth that ultimately would be reflected in commercial-fishery yield (Reckahn 1986). Annual water levels in Lakes Michigan and Huron appear to be driven by the NAO, which affects precipitation and runoff, and appears to produce 8- and 12-year oscillations in water levels (Hanrahan et al. 2009).

Small changes in water levels are accentuated in shallow nursery areas and, as water levels change, so does the amount of space available for interactions between larval Lake Whitefish and its prey. In the Great Lakes, small changes in water levels add or remove trillions of gallons of water (Fig. 9). Any changes to available habitat will affect larval Lake Whitefish survival, growth, and recruitment (Hayes et al. 1996). Lower water levels may

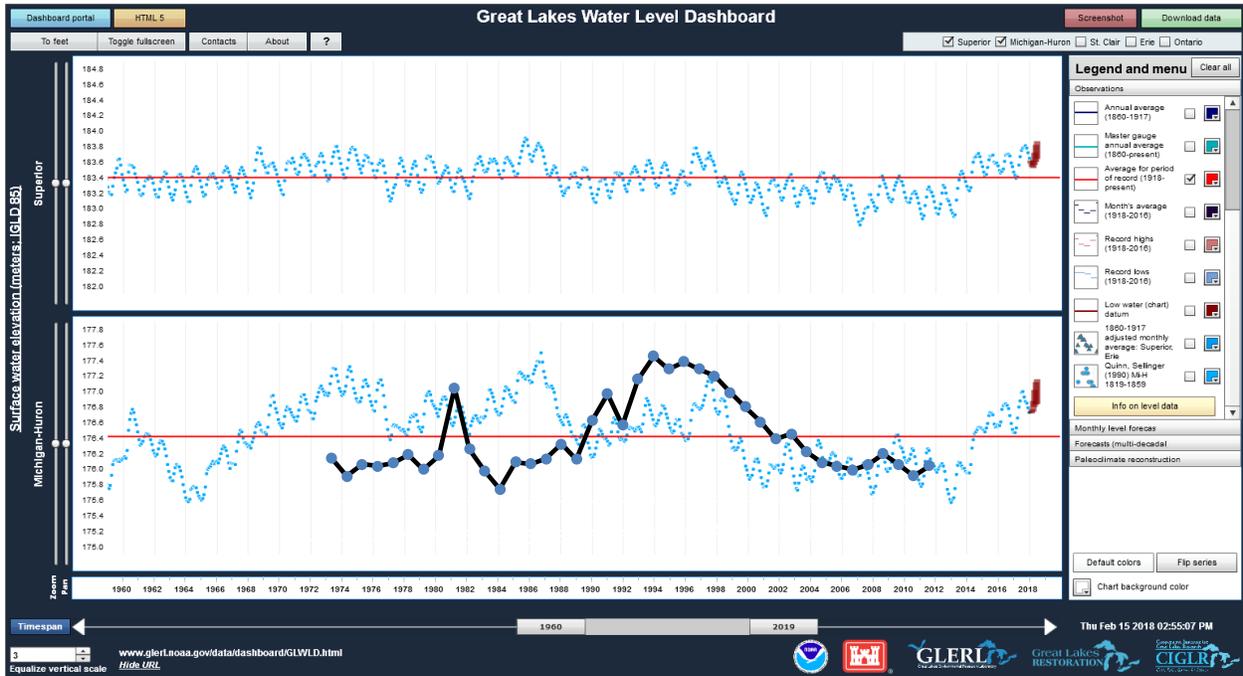
expose spawning shoals and nursery areas, reduce biomass of available zooplankton, and increase overlap between larval fish and their prey, potentially increasing larval consumption and growth but also increasing prospects for density-dependent suppression of growth and starvation mortality. Reductions in available space for larval Lake Whitefish will reduce the slope of the stock-recruitment relationship while changes in density-dependent growth will change the height of the asymptote (see Hayes et al. 1996). Higher water levels will increase available larval habitat and increase zooplankton biomass because of increased nutrient loading.

Fig. 9. Gallons of water added to each Great Lake by 1-inch increases in water levels.



After being at or above long-term averages during the 1970s, 1980s, and 1990s, water levels in Lakes Superior and Michigan/Huron (hydraulically one lake) remained below average during 1999-2014 (Fig. 10). Water levels in Lakes Michigan/Huron were on average about 0.4 m below the long-term average for 16 years before they began to rise again in 2015 and approached record levels in 2020. Because many larval and post-larval YOY fish inhabit waters <0.4 m deep during their first few months of life, much of their usual habitat would have been lost during the exceptionally low water years. Lake Whitefish recruitment in many areas of northern Lakes Michigan and Huron began to decline about the same time as water levels began to decline (Fig. 10) with recruitment of the 2003-2012 year-classes being the lowest since the mid- to late-1980s.

Fig. 10. Monthly water levels in Lake Superior (top panel) and Lakes Michigan/Huron (bottom panel) for 1959-2018 and abundance at age 4 (solid blue line) of Lake Whitefish from the Big Bay de Noc spawning stock in northern Green Bay, Lake Michigan, 1973-2012 year-classes. The red horizontal lines show the long-term average annual water level during 1959-2018 for each lake, and the red smudged line at the end of the time series shows projected water levels for 2018 by the U.S. Army Corps of Engineers (water-level data taken from <https://www.glerl.noaa.gov/data/dashboard/GLWLD.html>).



Declines in water levels after 1998 occurred simultaneously with the arrival and expansion of dreissenids; consequently, reduced productivity in nearshore areas due to mussels and reduced water volumes appear to be coupled. As dreissenids reduced nearshore productivity during 1999-2014, lower water levels further reduced both nutrient loading from nearshore areas and the space available for larval Lake Whitefish to feed and shelter from predators. In boreal Lake Osensjøen, Norway, Linlökken and Sandlund (2016) reported that both Vendace (*Coregonus albula*) and the European Whitefish year-class strength showed a strong positive relationship with July/August mean air temperature. Whitefish recruitment was negatively affected by a new water-regulation regime that lowered lake levels because recruitment was positively correlated with water level after hatching. Whitefish recruitment was also enhanced by late ice-out. Linlökken and Sandlund concluded that increasing summer temperatures benefit recruitment of both Vendace and European Whitefish whereas low water level caused by water regulation and early ice-out caused by climate warming would harm Whitefish recruitment.

Reckahn (1970) and Linlökken and Sandlund (2016) illustrate how multiple environmental stressors interact concurrently to affect recruitment in *Coregonus* and how changing water levels and timing of ice-off could affect Lake Whitefish recruitment in the Great Lakes. Fishery biologists and managers in the Great Lakes need a more-detailed understanding of how physical factors influence recruitment at each spawning shoal, starting with some of the more-important ones, such as those off of the Door Peninsula in Lake Michigan and off of Alpena and the Fishing Islands in Lake Huron. Specifically, we need to know how changing

temperatures and water levels, coupled with changing ice cover and wind intensity, interact to affect spawning shoals and nursery habitats at specific locations.

Research Priority: Disentangling biotic and abiotic effects on Lake Whitefish recruitment will be difficult but should be a focus of future research.

Currents

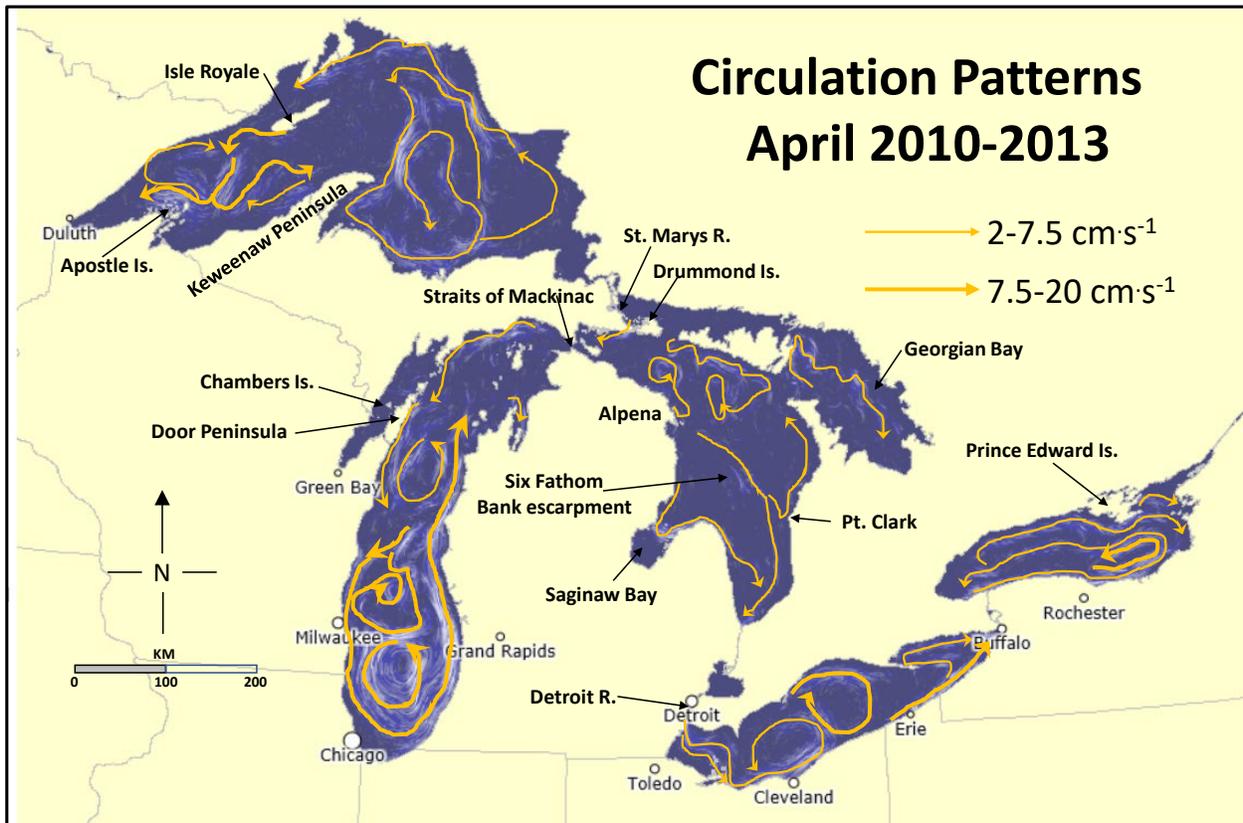
Dispersal of larval fish in the Great Lakes is driven by currents and short-term storm events that occur during the 1-2 weeks when larvae have limited locomotion. Cisco and Bloater recruitment in the Great Lakes has been shown to be highly synchronous and driven by large-scale physical events (Bunnell et al. 2010; Meyers et al. 2015). Dispersal by currents is likely a cause of within-lake synchrony in Bloater populations of Lakes Superior, Huron, and Michigan. Large-scale physical factors caused a 16-fold difference in stock-recruitment relationships of Cisco among different areas in Lake Superior, and large-scale physical factors had a greater effect on recruitment than did small-scale biotic factors (Rook et al. 2012). In the Great Lakes, wind intensity in spring was the primary driver of Cisco recruitment synchrony, followed by temperature (Myers et al. 2015). Spring wind intensity along with spawning-stock density was an important predictor of larval Lake Whitefish density at six spawning shoals in Lake Michigan and one spawning shoal in Lake Superior during 2005 and 2006 (Claramunt et al. 2010b). Thus, spatial patterns of both Cisco and Lake Whitefish density and their food can be largely influenced by storm-driven currents. However, in comparison to Cisco and Bloater larvae, Lake Whitefish larvae are relatively strong swimmers and may not necessarily be as vulnerable to strong current velocities. Hart (1930) reported larval Lake Whitefish were able to swim about $2.5 \text{ cm}\cdot\text{s}^{-1}$ and able to avoid predation by Yellow Perch.

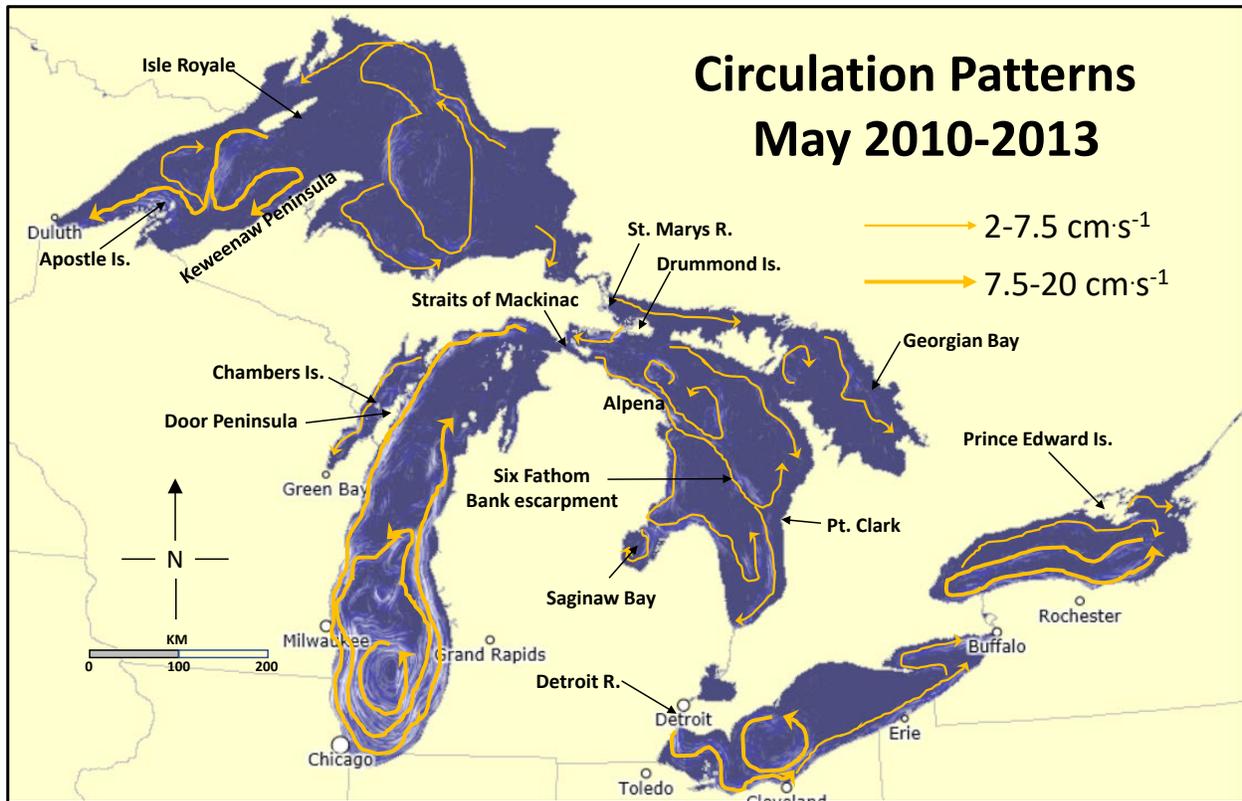
Currents are generally stronger during winter and spring than during summer and fall, and the direction of currents in spring when larvae emerge is generally opposite during the summer (Reckahn 1970; Beletsky et al. 1999; <https://www.glerl.noaa.gov/res/glcfs/currents/glcfs-currents-month.php>). Because winter currents are stronger than summer currents, annual circulation patterns reflect winter conditions more than conditions in other seasons (Beletsky et al. 1999). In terms of current effects on dispersal and survival of Lake Whitefish larvae, we define strong currents as being more than the $2.5 \text{ cm}\cdot\text{s}^{-1}$ swimming speed of larvae observed by Hart (1930). We suspect that many currents in the spring are much greater than $2.5 \text{ cm}\cdot\text{s}^{-1}$ because Hoagman (1973) reported current velocities of $5.3\text{-}9.3 \text{ cm}\cdot\text{s}^{-1}$ in the eastern Door Peninsula area of Lake Michigan.

Circulation patterns tend to be counterclockwise in Lakes Huron, Michigan, and Superior whereas, in Lakes Erie and Ontario, circulation is characterized by two-gyre patterns (Beletsky et al. 1999). In Lake Ontario, two major circulation patterns occur, but only the clockwise current along the north shore that moves directly along the spawning shoals of Prince Edward Island (site 90; see Fig. 3) will likely affect dispersal of Lake Whitefish larvae into the Kingston basin if they do not occupy shallow nursery areas immediately after hatching (Fig. 11). In Lake Erie, two current patterns occur but probably only the strong flow from the Detroit River into the western basin will disperse Lake Whitefish larvae. In Lake Huron, the primary circulation pattern is from northern Michigan into central and southern waters. Particularly during May, Lake Huron currents move water south along the western shore into Saginaw Bay before leaving the bay and traveling south into the southern main basin. A second current splits from the main current at Alpena and travels southeast along the Six Fathom Bank escarpment towards Point Clark before heading south (Fig. 11). Water coming out of the St. Marys River at Drummond Island moves westward toward the Straits of Mackinac in Lake Huron, and, in Georgian Bay, currents move from the northern spawning shoals (site 56) to the southern spawning shoals (sites 57-59) (see Fig. 3). In Lake Michigan, a large and strong circulation pattern sets up in April and May, moving from the north-shore spawning shoals (sites 65-67) to the western shore of the lake past the eastern Door Peninsula and continuing into the very southern portion of the lake before moving back north toward the Leland spawning

shoals (sites 78-82) (see Fig. 3). Lake Michigan currents in May move water from Big Bay de Noc spawning shoals (site 60) south along the western shore of Green Bay into lower Green Bay. This pattern in Green Bay is likely the reason that Hoagman (1973) noted that larval Lake Whitefish showed up at the same time each year at the shallow spit along the east side of Chambers Island (Fig. 11) in central Green Bay. In Lake Superior, two circulation patterns occur, one east of the Keweenaw Peninsula and one west of it. The western Lake Superior current flows from Isle Royale to the south and splits near the Apostle Islands where it then moves west through the island spawning shoals (sites 23-32) or east along the northwest shore of the Keweenaw Peninsula (Fig. 11).

Fig. 11. Mean depth-averaged water circulation patterns in the Great Lakes during April (top panel) and May (bottom panel), 2010-2013 (<https://www.glerl.noaa.gov/res/glcfs/currents/glcfs-currents-month.php>).





Water currents associated with strong winds during mid-April to mid-May could potentially move larval Lake Whitefish long distances from warm shallow water near shore to colder water offshore, suppressing growth and increasing natural mortality. A lack of ice cover during winter would further exacerbate early-life-stage mortality by exposing embryos to strong currents that may disrupt incubation. The role of currents and circulation patterns in dispersing young Lake Whitefish remains unknown throughout the Great Lakes. Most past researchers that tried to understand Lake Whitefish recruitment focused on the role of adults, ice cover, and air and water temperature and ignored storm intensity and frequency and their potential role of either directly influencing mortality of early life stages or indirectly influencing mortality by dispersing larvae to inhospitable areas (Henderson et al. 1983; Taylor et al. 1987; Brown et al. 1993; Anneville et al. 2009; Lynch et al. 2015).

Research Priority: The coupling of ice cover, storm events, and current patterns and their effects on early life stages can only be understood through expanded field sampling and modeling efforts, such as those being implemented by the NOAA/Great Lakes Environmental Research Laboratory's Great Lakes Coastal Forecasting System, integrated with demographic data such as spawning biomass, recruitment, and growth generated from SCAA stock assessments (https://www.glerl.noaa.gov/res/Programs/ipemf/GLCFS_nextgen.html).

STOCK STRUCTURE

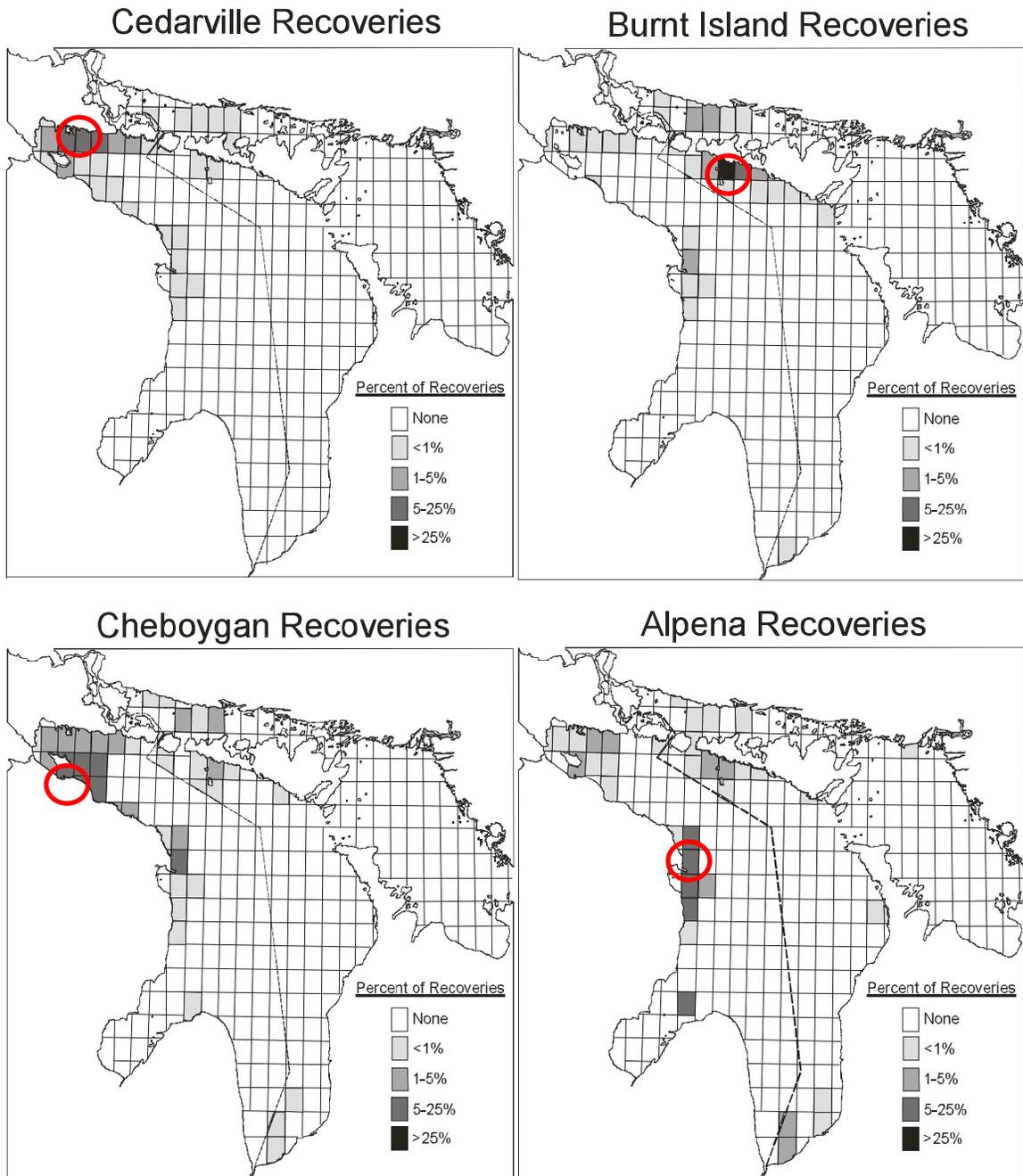
Movements and Intermixing

We identified 93 potentially different spawning aggregations in the Great Lakes (see Fig. 3), but the number of discrete overlapping stocks that could be effectively managed is less than 93. A key recommendation from the Lake Whitefish-*Diporeia* Workshop in 2002 was to identify the geographic distribution of Lake Whitefish stocks and their genetic and phenotypic variability (Bernatchez 2005), and some progress has been made. For example, a coordinated mark-recapture study of eight geographically distinct Lake Whitefish spawning stocks was conducted in the main basin of Lake Huron during 2003-2008, but the results of the study were not published. Tag returns from commercial and recreational fisheries are a measure of stock movement as well as the spatial distribution of commercial-fishing effort. Tagged adult fish from each stock were widely distributed throughout Lake Huron and contributed to the commercial harvest in multiple management units and every basin (Fig. 12). Fish from five of the eight stocks contributed to the commercial harvest in the North Channel, but only the Fishing Islands stock was consistently captured in Georgian Bay. Mark-recapture studies in Lake Superior have taken place in Whitefish Bay and around the Keweenaw Peninsula but for the most part, these studies, too, are not published (Fig. 13).

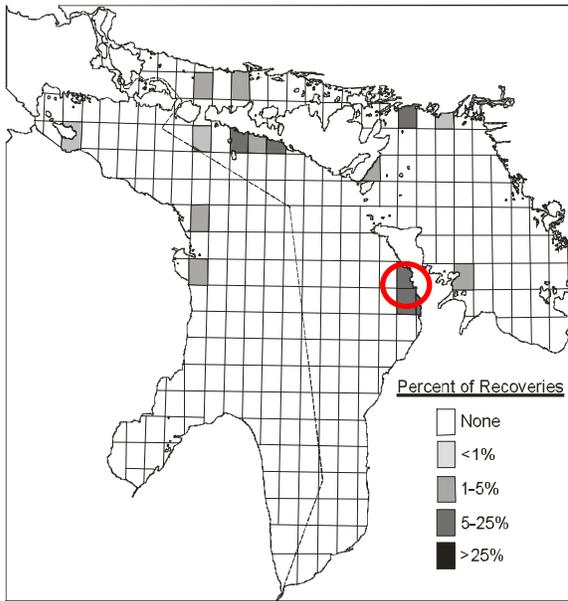
Research Priority: Compile basinwide tagging data along with recent acoustic-telemetry and genomic data to better elucidate Lake Whitefish stock structure.

Mark-recapture studies, genetic mixed-stock analysis of commercial-fishery harvests, and stable-isotope analysis have documented distinct stock structures and spatial distributions of Lake Whitefish in the Great Lakes (Casselman et al. 1981; Ihssen et al. 1981; Ebener and Copes 1985; Scheerer and Taylor 1985; Ebener 1990; Walker et al. 1993; VanDeHey et al. 2009, 2010; Ebener et al. 2010a; Andvik et al. 2016; Nathan et al. 2016; Eberts et al. 2017). Commercial harvests of Lake Whitefish within nearly every Lake Whitefish management unit of the Great Lakes comprise fish from multiple spawning shoals so basically the entire fishery is a genetically mixed-stock fishery (Imhof et al. 1980; VanDeHey et al. 2009, 2010; Stott et al. 2010; Andvik et al. 2016). Gene flow apparently is moderately high among genetic stocks in each Great Lake. In Lake Michigan, for example, the Big Bay de Noc and eastern Door Peninsula stocks (see Fig. 3) show a high degree of genetic overlap (Andvik et al. 2016; Nathan et al. 2016) even though the two spawning shoals are spatially segregated by roughly 75 km. We suspect the same is true of many stocks in other lakes as there is low among-stock genetic diversity and substantial mixing of stocks during the non-spawning season (Ebener et al. 2010a; Stott et al. 2010).

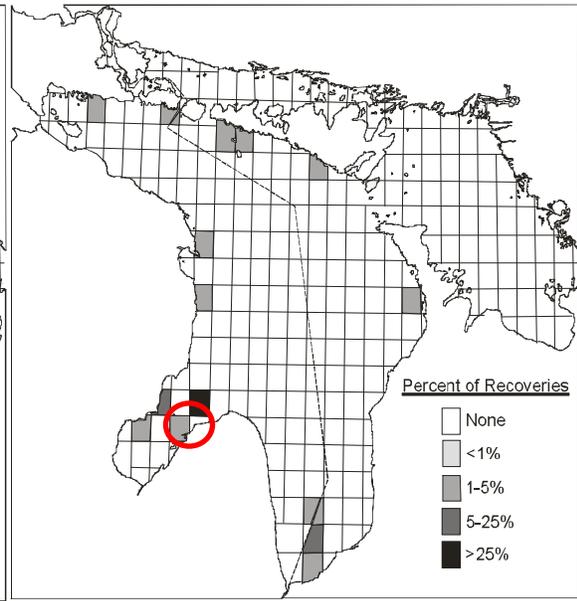
Fig. 12. Percentage of tagged Lake Whitefish recovered by commercial and recreational fisheries in 10-min statistical grids of Lake Huron from December 2003 through December 2012 for fish from eight spawning aggregations in the main basin of Lake Huron tagged in November-December, 2003-2006. Red circles indicate tagging sites.



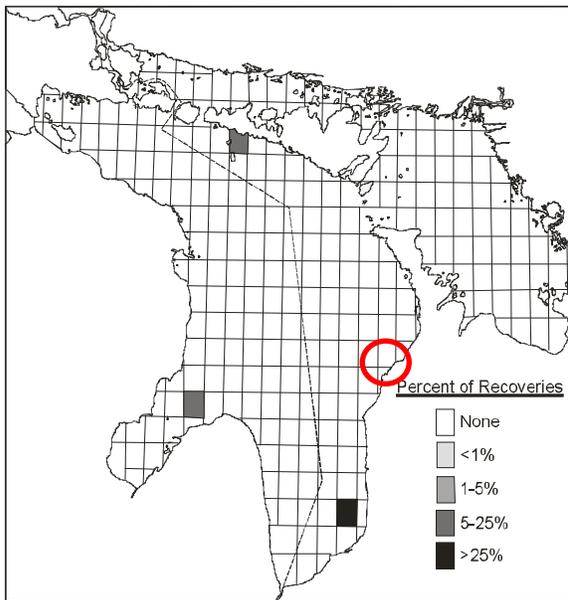
Fishing Islands Recoveries



Saginaw Bay Recoveries



Douglas Point Recoveries



Sarnia Recoveries

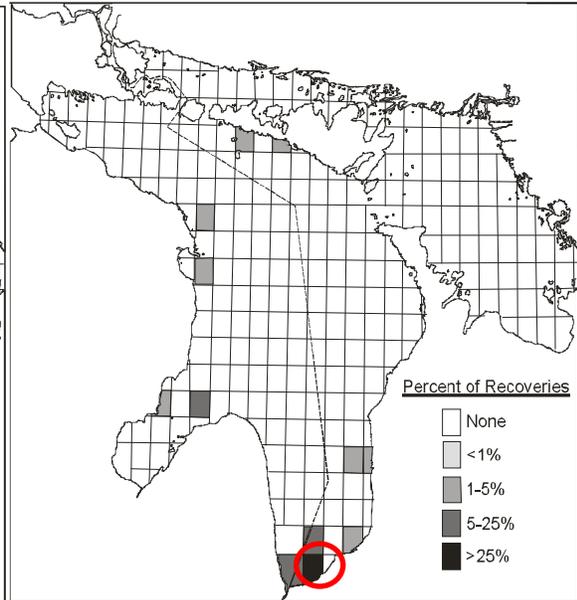
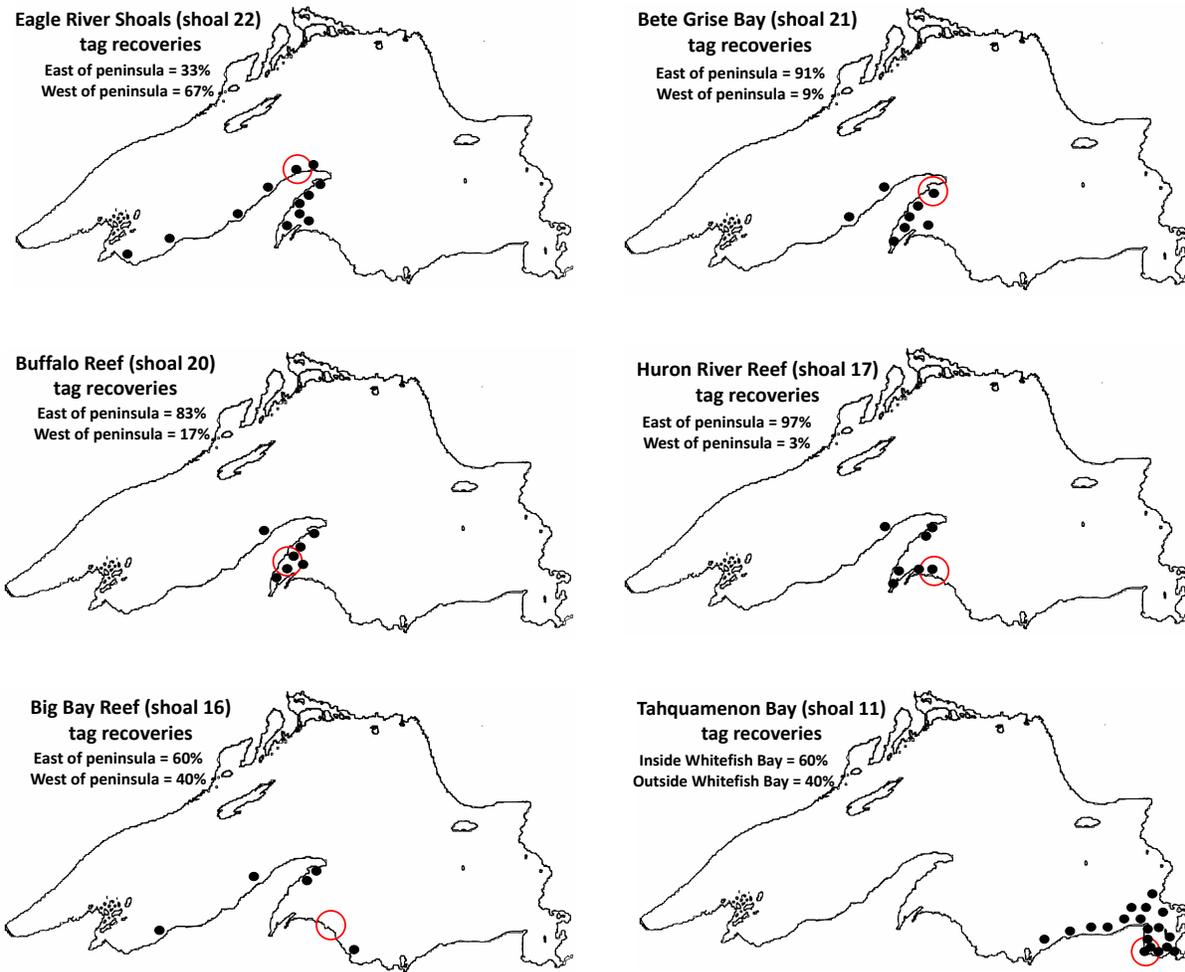


Fig. 13. Spatial distribution of tagged Lake Whitefish recovered (closed dark circles) by commercial fisheries in Lake Superior during 1987-1997 for Lake Whitefish tagged at six spawning shoals (open red circles) in southern Lake Superior by the Great Lakes Indian Fish and Wildlife Commission during 1987-1996 and the Chippewa Ottawa Resource Authority (CORA) during 1981-1986.



Based on unpublished and published mark-recapture studies conducted during 1975-2008 in Lakes Superior, Huron, and Michigan, it appears that an adult Lake Whitefish typically lives within a 110-km radius of its spawning shoal. The average maximum shoreline distance from the tagging site to the most-distant capture location was 345 km and ranged from 45 to 770 km (Table 1). The average radius of tag recaptures from individual spawning shoals to the most-distant recovery was 112 km and ranged from 45-170 km. Of all tag recoveries, 68% were made in the management unit of tagging, and 87% were made in the management unit where tagged or in 1-2 adjacent units (i.e., east and west or north and south). Average Euclidean movement distance based on regression-tree analysis of stock, year, tagging site, sex, and length of tagged fish in the 50th, 75th, and 95th quantiles was 14 km (range, 9-81 km), 21 km (range, 9-191 km), and 101 km (range, 29-292 km), respectively, for Lake Whitefish combined from (see Fig. 3) the Big Bay de Noc (site 60) and north shore stocks (sites 65-67) of Lake Michigan and the Cheboygan (site 39) and Cedarville (site 37) stocks of Lake Huron during 2003-2008 (Ebener et al. 2010a). Fish from the Big Bay Reef (site 16), Alpena (site 48), and Fishing Islands

(site 44) reproductive sites appear to have broader geographic distributions than other stocks, as only 62-67% of recaptures from these sites were in the unit of tagging or in adjacent units (see Fig. 3). Stable-isotope analysis also suggested broad spatial distributions of adult fish from Lake Huron (Eberts et al. 2017).

Lake Whitefish in Lake Superior appears to move shorter distances than Lake Whitefish in Lakes Huron or Michigan. For the six spawning shoals in Lake Superior where mark-recapture studies have been conducted, the maximum distance traveled averaged 198 km, the average radius was 86 km, the percent of tag recoveries in the unit of tagging averaged 63%, and the percent of recoveries in the unit of tagging and adjacent units was 88%. Corresponding values were 408 km, 109 km, 84%, and 94% in Lake Michigan, and 425 km, 137 km, 61%, and 81% in Lake Huron.

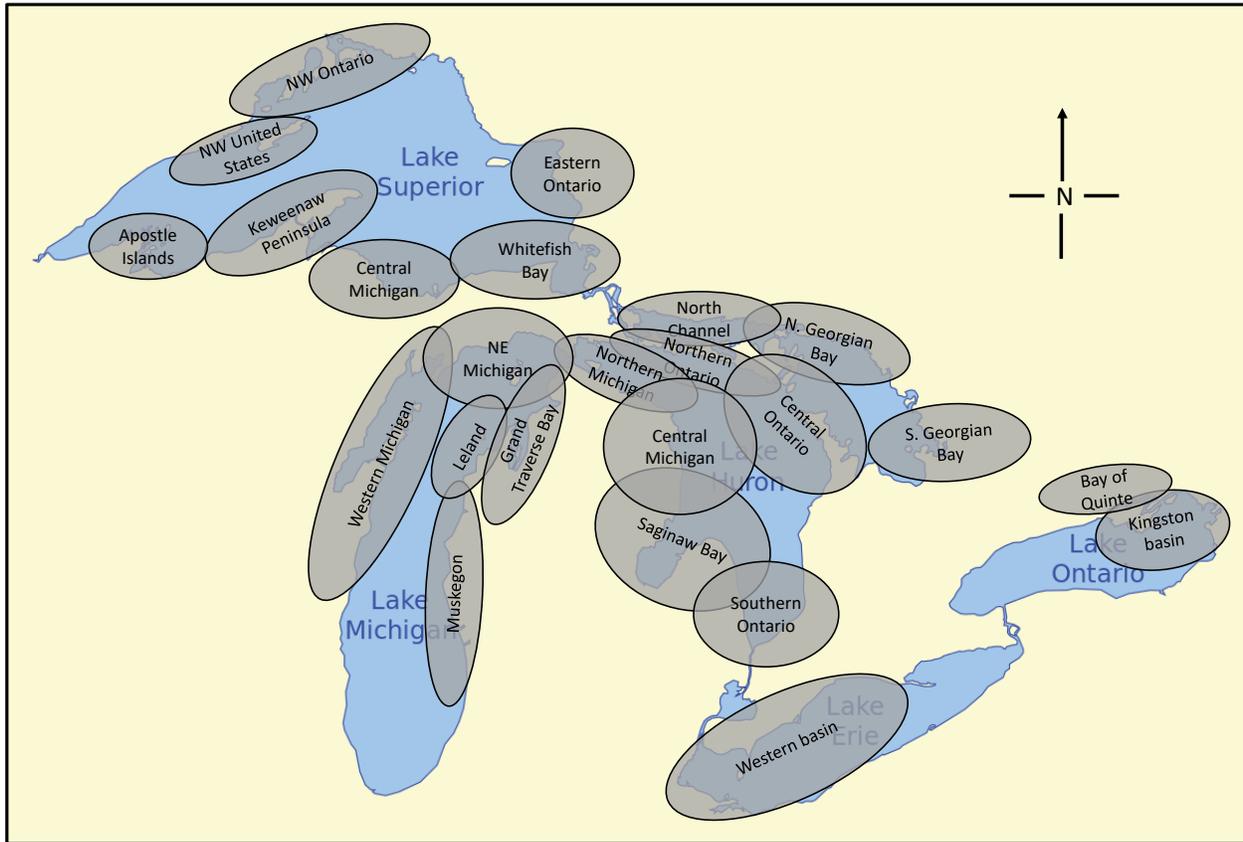
Adult Lake Whitefish appear to home back to natal spawning shoals. Tag recoveries in Lake Michigan in Grand Traverse Bay, Big Bay de Noc, and at Naubinway and in Lake Huron at Cheboygan and Cedarville (Fig. 12) all demonstrated strong homing by adult Lake Whitefish to their respective spawning shoals. In some instances, previously tagged and released ripe and spawning Lake Whitefish were captured at the exact same site on the same date one to four years after being released (Ebener and Copes 1985; Walker et al. 1993; Ebener et al. 2010a). Although natal homing of Lake Whitefish is well documented in the Great Lakes, straying also appears to be common. Lake Whitefish spawning aggregations in tributaries to lower Green Bay, Lake Michigan (Ransom et al. 2021), have been increasing over the last two decades, and genetic analyses indicates they are a mixture of spawning stocks most likely originating from Big Bay de Noc and the eastern Door Peninsula (Imhof et al. 1980; Andvik et al. 2016; Nathan et al. 2016). However, straying from natal reproductive habitats has not been sufficient to alter the genetic makeup of Lake Whitefish stocks in the Great Lakes as there is considerable evidence of temporal stability in their genetic structure (Stott et al. 2013; Nathan et al. 2016).

We propose aggregated management areas within each Great Lake (Fig. 14) to reflect (1) spatial distributions from mark-recapture studies, (2) genetic mixed-stock analysis, (3) stable-isotope analysis, and (4) expert judgement. Pooling the commercial-fishery and biological data from adjacent management units into a single larger management area for a mixed-stock fishery is intended to allow for estimates of spawning-stock biomass that are less biased than if individual management units were treated as if mixing did not occur (Li et al. 2014; Andvik et al. 2016). Further, accounting for mixing rates in a management area will also provide unbiased estimates of spawning-stock biomass, but not when mixing rate is very low or very high (Li et al. 2014). The management areas we propose are not mutually exclusive and are expected to account for roughly 95% of the fish from each reproductive habitat within the management area. Ongoing genetic and acoustic-telemetry studies will refine our proposed management areas.

Table 1. Four measures of the geographic distribution of Lake Whitefish from various spawning stocks in Lakes Superior, Huron, and Michigan as synthesized from mark-recapture studies of adult fish during 1976-2008. Maximum distance traveled is a rough approximation measured along the shoreline in a straight line from the spawning shoals where fish were tagged and released to the most-distant tag recovery. The maximum radius is the linear distance from the tagging site to the most-distant tag recovery. The percentages of tagged fish recovered are for the Lake Whitefish management unit in which they were tagged and for that management unit and the next two adjacent management units combined. Data are from published papers (Ebener and Copes 1985; Scheerer and Taylor 1985; Walker et al. 1993; Ebener et al. 2010a), agency reports (Ebener 1990), and unpublished information from the Great Lakes Indian Fish and Wildlife Commission (W. Mattes, Great Lakes Indian Fish and Wildlife Commission, personal communication, 2018) and the Chippewa Ottawa Resource Authority (M.P.E., unpublished data).

Lake	Spawning Stock		Maximum Distance Traveled (km)	Maximum Radius from Site (km)	Percent of Recaptures	
	Shoal Name	Number			In Unit	In Unit and Adjacent Units
Superior	Eagle River Shoals	22	190	65	40	75
	Bete Grise	21	115	50	85	98
	Buffalo Reef	20	160	62	64	100
	Huron River Reef	17	245	67	83	97
	Big Bay Reef	16	340	170	33	67
	Tahquamenon Bay	11	140	100	75	90
Huron	Cedarville	37	200	150	53	95
	Cheboygan	39	400	130	42	79
	Alpena	48	630	130	29	62
	Saginaw Bay	47	640	140	79	94
	Sarnia	46	390	160	82	82
	Fishing Islands	44	325	150	57	63
Michigan	Burnt Island	41	390	100	83	89
	Big Bay de Noc	60	770	140	88	94
	Eastern Door Peninsula	61	625	170	45	78
	Naubinway	65	360	90	93	99
	Grand Traverse Bay	73-77	45	45	100	100
	Leland	78-80	240	100	93	99
Mean			345	112	68	87

Fig. 14. Proposed Lake Whitefish management areas in the Great Lakes that encompass the great majority of adult Lake Whitefish originating from reproductive habitats within the management area.



Genetic mixed-stock analysis should be expanded to each of the Great Lakes and integrated into annual monitoring programs to estimate the contribution of each reproductive habitat to fishery harvests because mixing will vary through time (Ebener et al. 2005; VanDeHey et al. 2009; Andvik et al. 2016; Nathan et al. 2016). Collecting a fin sample for genetic analysis during biological monitoring of fishery harvests or during fishery-independent surveys should be as routine as measuring lengths and determining weights or taking scales and otoliths for age estimation. Regularly scheduled sampling of spawning aggregations of adult Lake Whitefish from each of the major reproductive habitats will also be required to monitor the genetic structure of each stock (Stott et al. 2010; Stott et al. 2013; Nathan et al. 2016) because the allele frequencies of less than one-third of Lake Whitefish spawning stocks have been described in the Great Lakes. The percent contribution of each reproductive habitat or spawning stock to commercial-fishery yield can then be integrated as a movement matrix in SCAA stock assessments to account for varying annual contributions of each spawning stock to the harvest.

Genetic analysis of Lake Whitefish stocks has been ongoing since the 1970s (Franzin and Clayton 1977; Imhof et al. 1980; Ihssen et al. 1981), and, although geneticists and researchers have urged for over 40 years that agencies need to manage on a genetic-stock basis (Spangler et al. 1981), management based on genetic stocks does not occur. The time has come to integrate genetic structure into management of Lake Whitefish in the Great Lakes, particularly because recruitment is declining across the four lower Great Lakes and the less-abundant stocks may be more vulnerable to overexploitation. The frequency and geographic scale of mixed-stock analysis

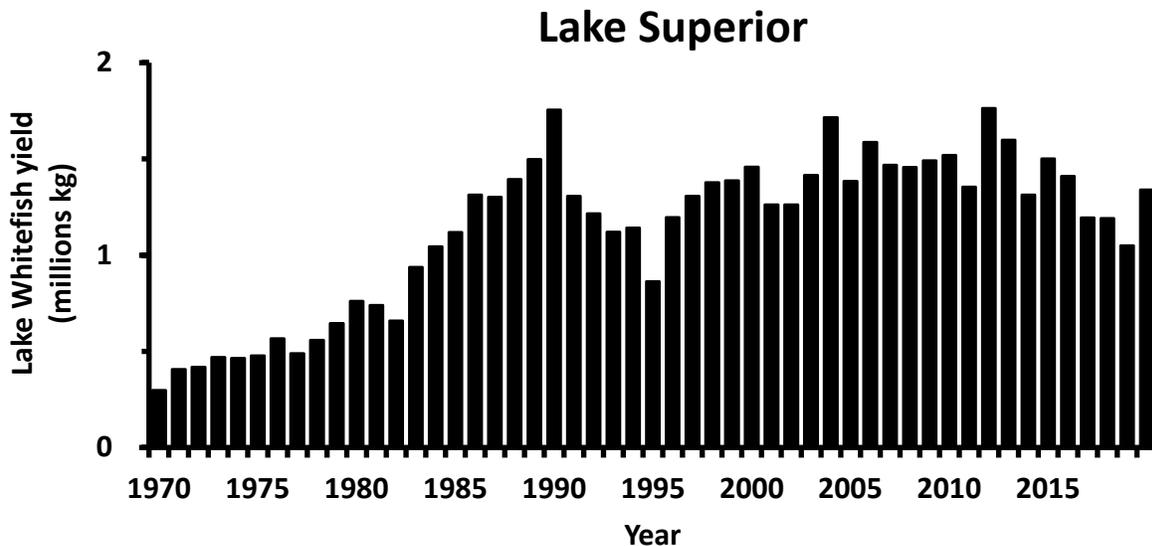
will be more difficult in Lakes Superior and Huron because of more stocks in Lake Superior and because mixing of stocks in Lake Huron is probably greater than in the other lakes (Stott et al. 2013; Eberts et al. 2017) (Fig 12).

Yield

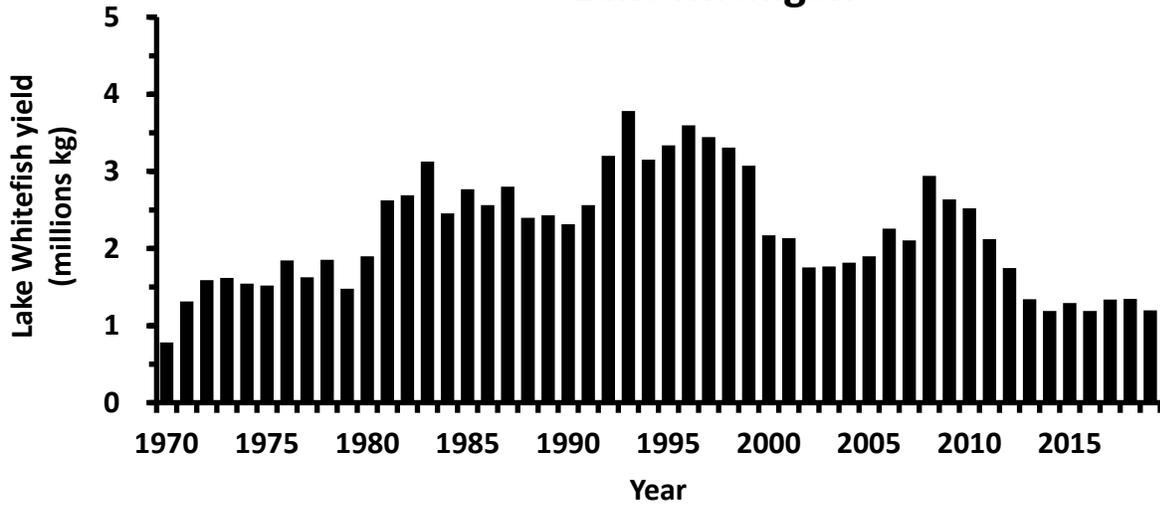
The annual yield of Lake Whitefish from the Great Lakes declined by 54% from its contemporary peak in 1998 to 2019, the most-recent year of reporting. Yield averaged 6.9 million kg (SD, 1.6 million kg) during 1981-2019, the period of most-consistent reporting by all agencies. Peak yield was 9.9 million kg in 1998 and the lowest yield was 4.1 million kg in 2016. From the peak year on each lake to 2019, yield declined 24% in Lake Superior, 68% in Lake Michigan, 57% in Lake Huron, 92% in Lake Erie, and 84% in Lake Ontario (Fig. 15). Annual yield from the peak year through 2019 declined 60,500 kg•yr⁻¹ in Lake Superior (2012-2019), 99,500 kg•yr⁻¹ in Lake Michigan (1993-2019), 121,700 kg•yr⁻¹ in Lake Huron (1998-2019), 29,500 kg•yr⁻¹ in Lake Erie (2000-2019), and 10,800 kg•yr⁻¹ in Lake Ontario (1996-2019). In Lake Superior, annual yield increased by 16,200 kg•yr⁻¹ from 1981 to 2019 and, compared to the other lakes, remained remarkably stable since the late 1980s.

Changes in yield illustrate how less-diverse stock structure bolsters declines in recruitment and subsequent adult abundance. The largest declines in yield occurred on Lakes Erie and Ontario, which have the least-diverse stock structure while the more-diverse stock structures on the upper three lakes likely prevented more-severe declines in yield. The number and type of fisheries and management policy certainly affect yield, but the abiotic and biotic processes that drive recruitment appear to have had a larger effect on declining yield of Lake Whitefish than did the fisheries or management.

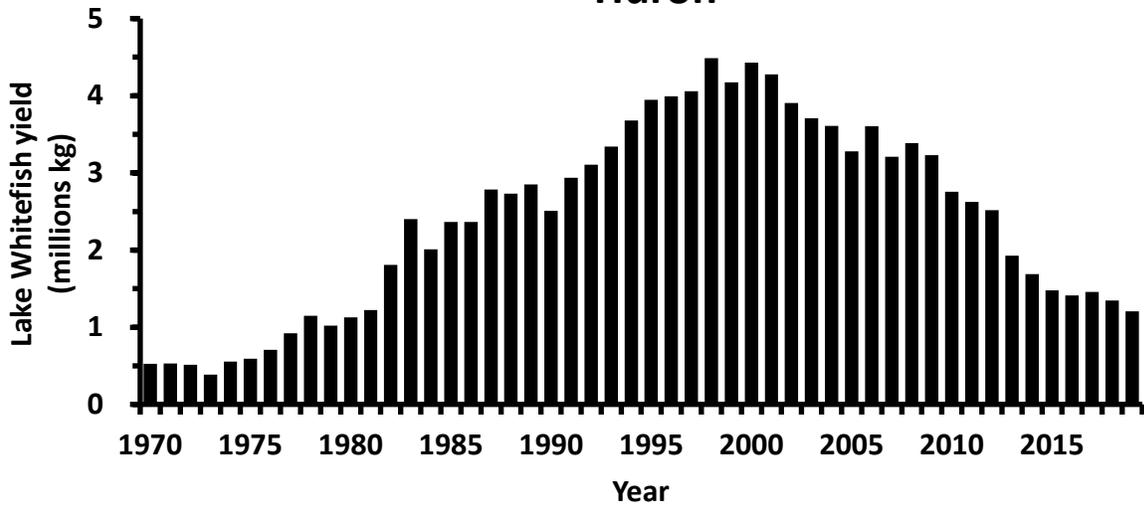
Fig. 15. Yield (millions of kg) of Lake Whitefish from each Great Lake and from all Great Lakes combined, 1970-2019. Note differences in scale of y-axis.



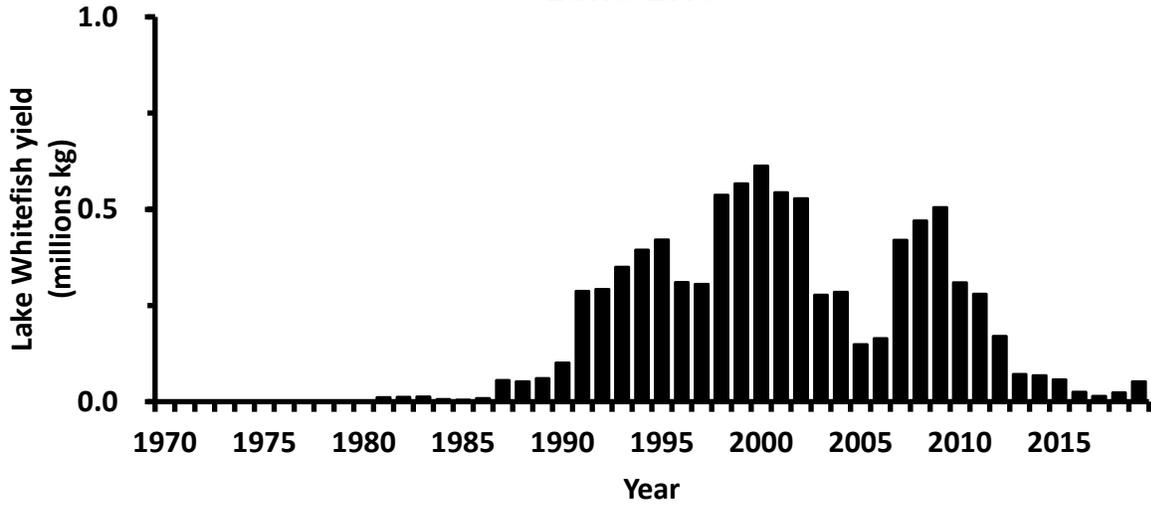
Lake Michigan



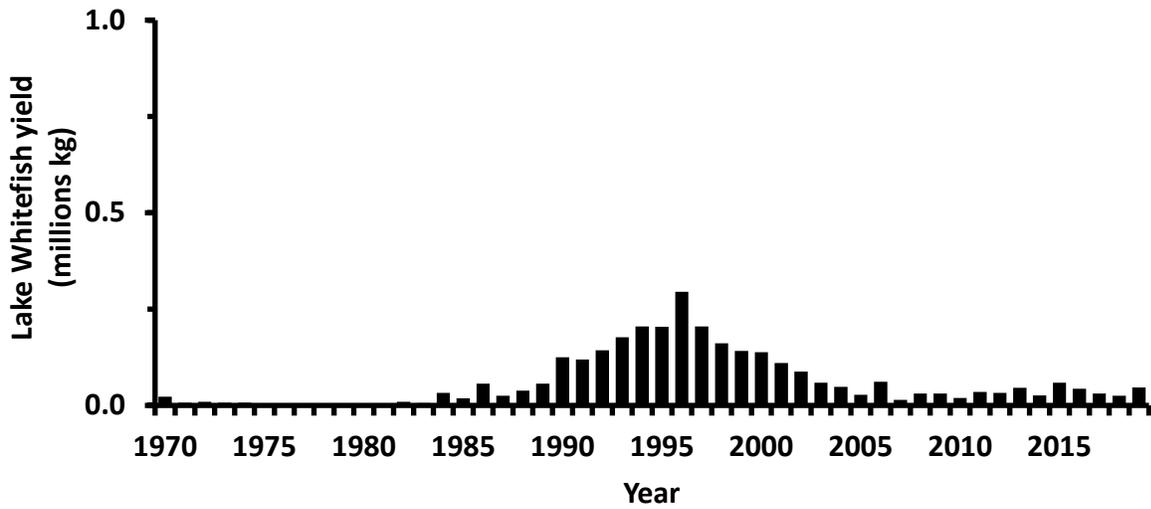
Huron

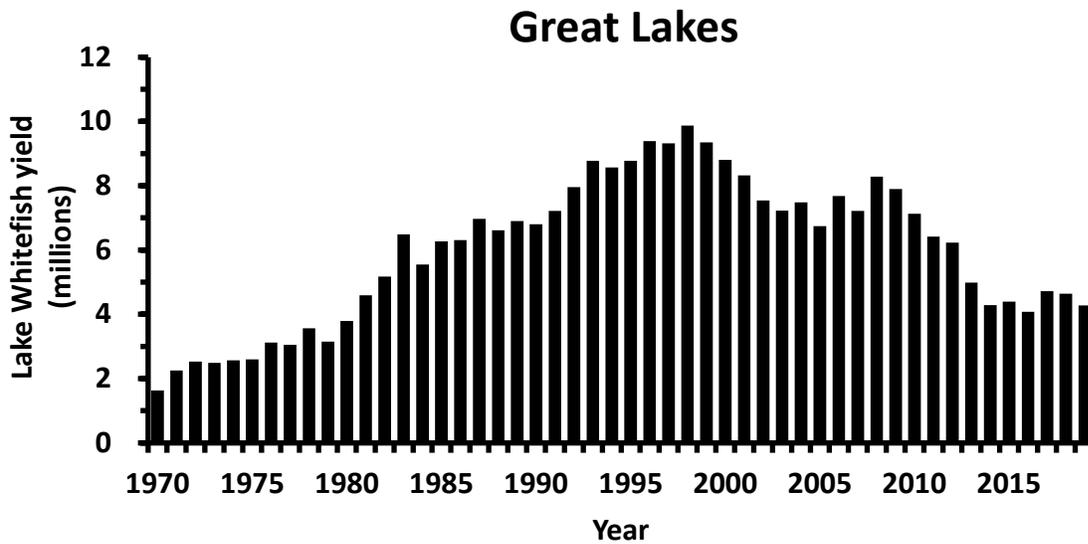


Lake Erie



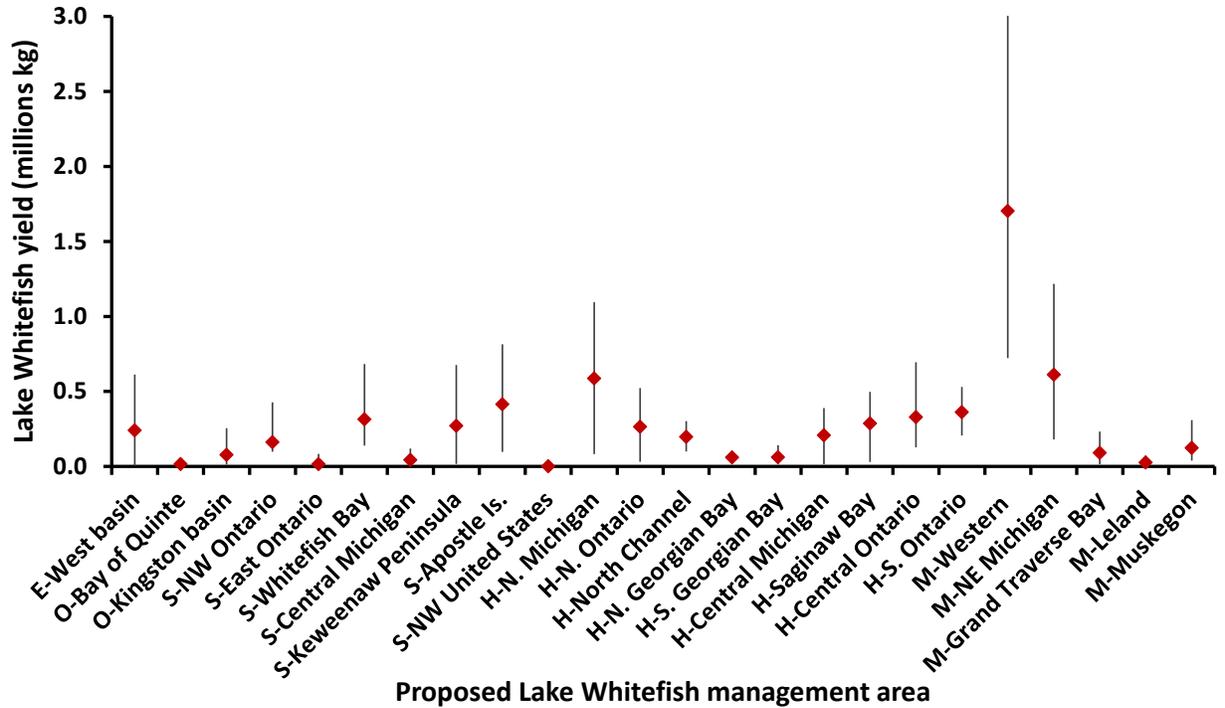
Lake Ontario





The most-diverse stock structure (see Fig. 14) and largest yields occur in Lake Huron, but the most-productive individual stocks occur in Lake Michigan. During 1981-2016, the annual yield averaged 2.9 million kg from Lake Huron, 2.4 million kg from Lake Michigan, 1.3 million kg from Lake Superior, 0.2 million kg from Lake Erie, and 0.08 million kg from Lake Ontario (Fig. 16). Among our proposed Lake Whitefish management areas, the largest yield came from the western Lake Michigan management area where it averaged 1.7 million kg during 1981-2016. Spawning aggregations in the northeastern Lake Michigan area produced the second-largest average annual yield (0.61 million kg), followed (in order) by the northern Michigan area of Lake Huron (0.59 million kg), the Apostle Islands area of western Lake Superior (0.42 million kg), the southern Ontario area of Lake Ontario (0.36 million kg), the central Ontario area of Lake Huron (0.33 million kg), and the Whitefish Bay (0.31 million kg) and Keweenaw Bay areas of Lake Superior (0.27 million kg). The lowest average yield of less than 26,000 kg was produced in the Bay of Quinte area of Lake Ontario, northwest U.S. waters area of Lake Superior, and the Leland area of Lake Michigan.

Fig. 16. Average annual yield (millions kg) of Lake Whitefish (red diamonds) and the range of annual yield (vertical black lines) from proposed Lake Whitefish management areas (see Fig. 14) in the Great Lakes, 1981-2016. Letters before the management-areas names indicate the Great Lake in which the area is located (E = Erie; H = Huron; M = Michigan; O = Ontario; S = Superior).



The proposed western Lake Michigan management area has at least four reproductive habitats contributing to yield—Big Bay de Noc in northern Green Bay, the eastern Door Peninsula, the Menominee River in lower Green Bay, and various spawning aggregations in northern Lake Michigan (Andvik et al. 2016). The Fox River, Oconto River, and possibly other rivers in Green Bay also have spawning aggregations of Lake Whitefish, further expanding stock structure in the western Lake Michigan management area (Ransom et al. 2021). We have proposed the adoption of 24 Lake Whitefish management areas in the Great Lakes based on mark-recapture studies, genetic and isotope analyses, and expert judgement.

Research Priority: Estimate the contribution of each reproductive habitat (stock) to fishery yield, particularly in Lakes Michigan and Huron, using, for example, genetic mixed-stock analysis (Anvik et al. 2016).

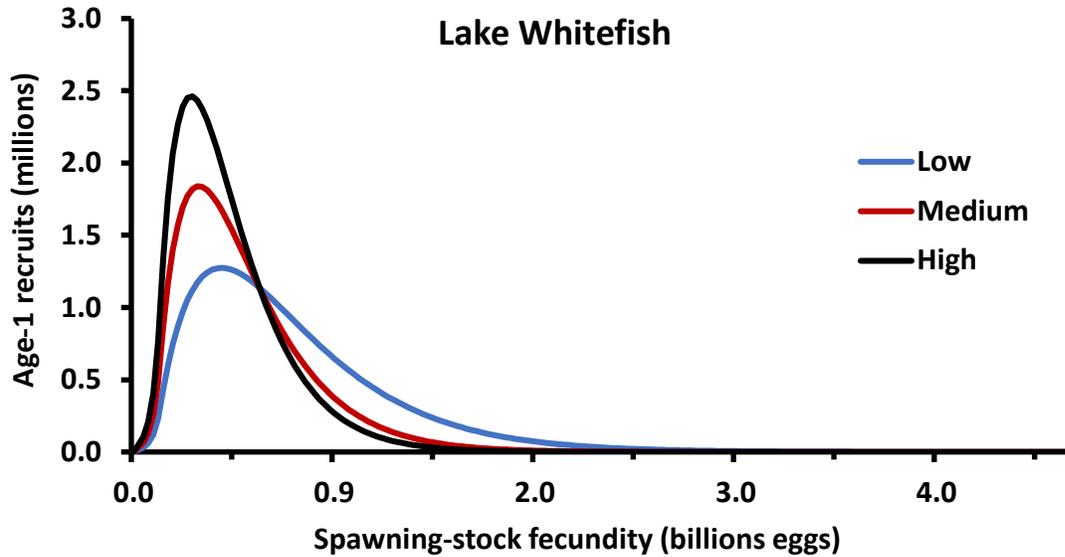
BIOLOGICAL PROCESSES

Stock and Recruitment

Spawning-stock biomass is critical to recruitment because it is both a driver and a constraint in the Great Lakes. Adult abundance has always been shown to be an important driver of recruitment in analyses designed to understand Lake Whitefish stock-recruitment relationships, to predict harvest levels, or to evaluate harvest-control rules (Henderson et al. 1983; Jacobsen and Taylor 1985; Taylor et al. 1987; Brown et al. 1993; Deroba and Bence 2012; Molton et al. 2013; Lynch et al. 2015; Li et al. 2016). At low adult stock sizes, egg deposition is the most-important factor driving recruitment because, even if larval survival is high, their density will not be limited by zooplankton abundance (Taylor et al. 1987). At moderate and high adult stock sizes, egg deposition is not that important because larval survival and subsequent recruitment to the stock is limited by zooplankton availability and winter weather conditions, which combine to increase the variability in recruitment at any given level of adult abundance. The highest adult stock sizes of Lake Whitefish in South Bay, Lake Huron, produced some of the smallest levels of recruitment, and, in northern Lake Michigan, there was a 12-fold difference in annual recruitment at similar adult stock sizes (Henderson et al. 1983; Taylor et al. 1987). Thus, Lake Whitefish recruitment is largely determined by interactions between adult stock size, which determines subsequent egg deposition, and physical-biological processes that affect embryo and larval survival (Brown et al. 1993; Lynch et al. 2015).

Reproductive productivity of Lake Whitefish stocks varies substantially in the Great Lakes and has a marked effect on sustainability of exploited stocks. Reproductive productivity influences the stability of yield, stock viability, and the appropriateness of harvest-control rules (Deroba and Bence 2012; Molton et al. 2013; Li et al. 2016). In evaluating harvest-control rules or stability of spawning-stock biomass, reproductive productivity was categorized as either low, medium, or high based on parameters of the Ricker stock-recruitment relationship (see Deroba and Bence 2012; Li et al. 2016). Peak recruitment, the rate of increase in recruitment with spawning biomass, and the density-dependent effect of adult biomass on recruitment increased from low- to high-productivity stocks (Fig. 17). Although peak recruitment is much less in low-productivity stocks, low-productivity stocks can sustain higher levels of recruitment at larger stock sizes than high- and medium-productivity stocks.

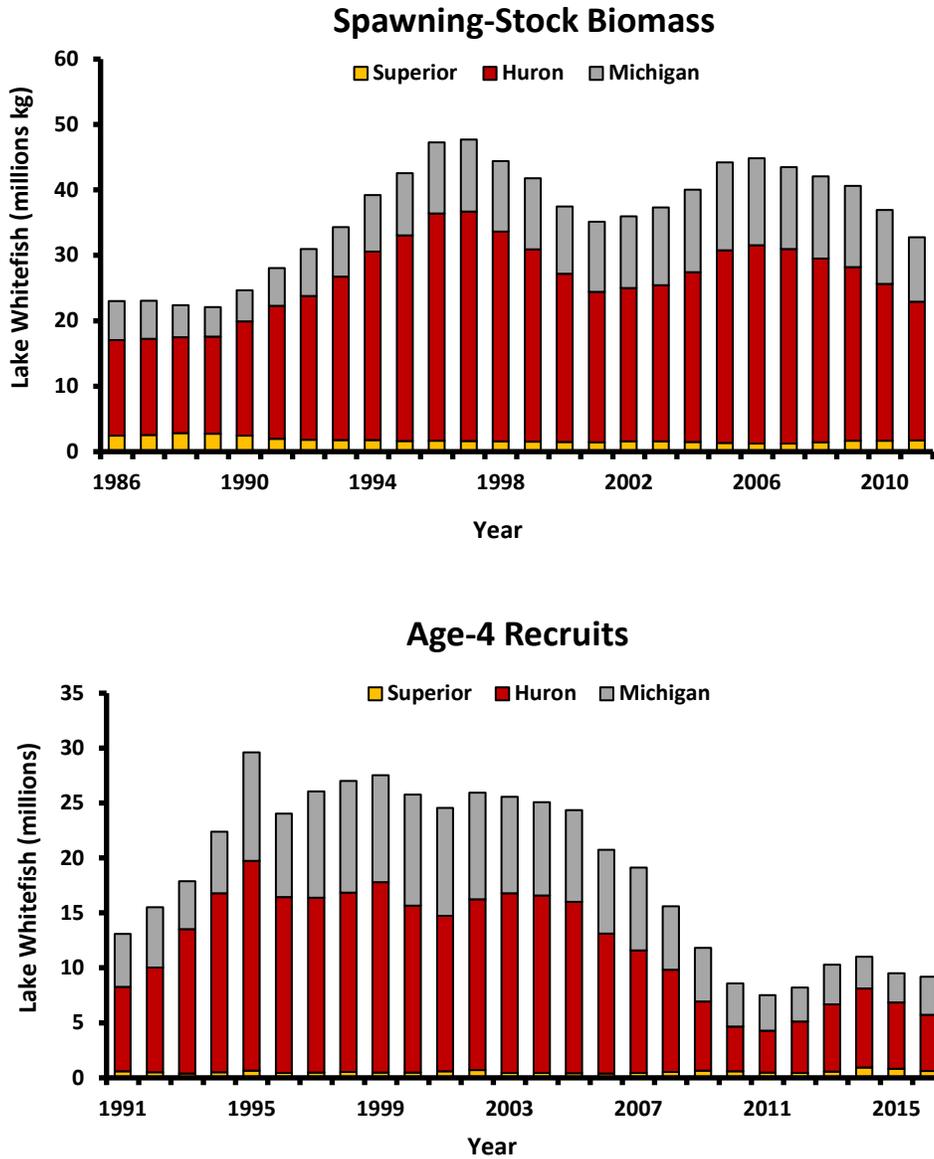
Fig. 17. Stock-recruitment curves for stocks of Lake Whitefish of low, medium, and high reproductive productivity in the Great Lakes. Curves were developed using a Ricker stock-recruitment relationship of the form reported by Molton et al. (2013) and values of alpha (α) and beta (β) reported by Li et al. (2016) for low ($\alpha = 5.23\text{E-}04$, $\beta = 1.51\text{E-}10$), medium ($\alpha = 1.13\text{E-}03$, $\beta = 2.26\text{E-}10$), and high ($\alpha = 1.82\text{E-}03$, $\beta = 2.72\text{E-}10$) productivity stocks. Spawning-stock fecundity was estimated as number adults * proportion females (50%) * mean weight (kg) of a female spawner * an average fecundity of 19,000 eggs•kg⁻¹ spawner. Recruitment is the number of age-1 fish resulting from egg deposition.



Fortunately, spawning-stock biomass and estimates of recruitment (Appendix B) to the fishable stock are stock demographics for which there are consistent and reliable estimates for the upper Great Lakes. Agencies conducting SCAA stock assessments in Michigan and Ontario waters of Lake Huron regularly produce estimates of spawning-stock biomass and recruitment (Modeling Subcommittee, Technical Fisheries Committee 2017; A. Cottrill, Ontario MNRF, personal communication, 2018). Annual spawning-stock biomass in modeled areas of Lakes Superior, Huron, and Michigan varied only two-fold during 1991-2016 from 22.1 to 44.8 million kg. Subsequent recruitment of age-4 Lake Whitefish five years later varied four-fold from 7.5 million to 30.2 million fish per year and was at its lowest levels during 2010-2016 (Fig. 18).

Spawning biomass of Lake Whitefish appears to be sufficient to support both recruitment and fisheries, but survival of early life stages is insufficient, suggesting that carrying capacity of spawning and nursery habitat has been degraded over the last two decades. Gobin et al. (2015) showed that, after dreissenids became established in Lake Huron, density-dependent growth and stock-recruitment relationships were altered. For example, although spawning biomass in southern Lake Huron was relatively constant during 2000-2009, the number of recruits (R) produced per biomass of spawners (S) was declining (Gobin et al. 2015). Because carrying capacity has changed over time, fitting a simple Ricker stock-recruit relationship is not appropriate. Instead, models must account for large-scale variability in recruitment due to extrinsic factors as per Lynch et al. (2015). They found that models including one or more climate variables, such as temperature, wind, and ice cover, explained significantly ($\Delta AIC_c > 3$) more variation in recruitment than did models with only stock and recruitment parameters.

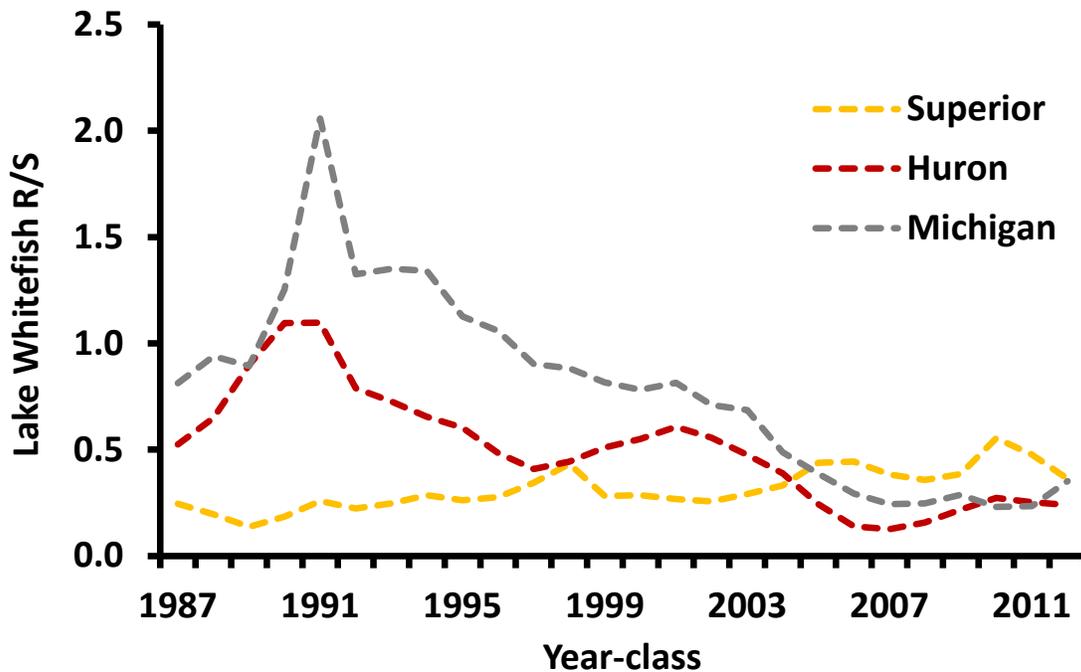
Fig. 18. Statistical catch-at-age estimates of Lake Whitefish spawning-stock biomass (kg) during 1986-2016 and subsequent numbers of age-4 fish recruited to the fishable stocks during 1991-2016 in modeled whitefish management units of Lakes Superior, Huron, and Michigan.



The R/S ratio has shown a long-term decline in Lakes Huron and Michigan but, based upon output from SCAA stock assessments, has increased through time in Lake Superior (Fig. 19). The R/S for Lake Huron was highest for the 1989-1992 year-classes, averaging about one age-4 recruit•kg⁻¹ of spawners, but, for subsequent year-classes, the ratio declined nearly annually and averaged only 0.2 age-4 recruits•kg⁻¹ of spawners for the 2006-2012 year-classes. Similarly, the R/S for Lake Michigan declined from an average of 1.3 age-4 recruits•kg⁻¹ of spawners for the 1990-1996 year-classes to 0.3 age-4 recruits•kg⁻¹ of spawners for the 2006-2012 year-classes. The magnitude of these declines and their effects on stock productivity cannot be overstated—the declines mean

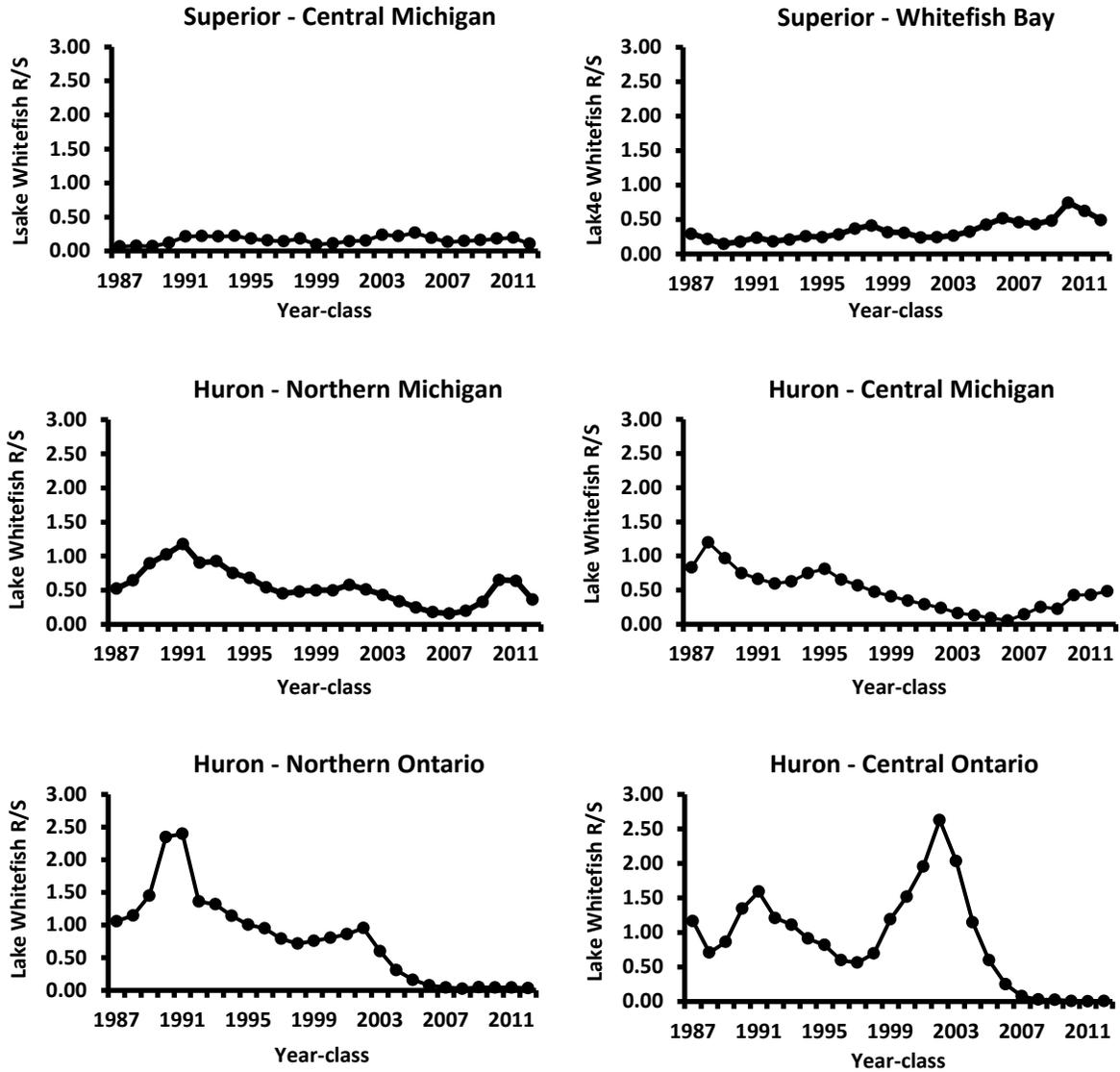
that one kg of spawning females (roughly 1 female) now typically produces only 0.2 recruits in Lakes Huron and Michigan. Some recovery of R/S has occurred in Lakes Huron and Michigan for the 2008 to 2012 year-classes, which may owe more to increased growth rates of fish instead of increased rates of reproduction. In Lake Superior, the R/S increased two-fold from an average of 0.2 age-4 recruits•kg⁻¹ of spawners for the 1987-1992 year-classes to 0.4 age-4 recruits•kg⁻¹ of spawners for the 2005-2012 year-classes. Conditions in Lake Superior are becoming more suitable for Lake Whitefish possibly due to warming lake temperatures (Austin and Coleman 2008), although the potential effects of dreissenid establishment in embayments is a concern. Although the extent of ice cover has declined as Lake Superior has warmed over the last three decades, ice cover may not play as large a role in Lake Whitefish recruitment in Lake Superior as it does in the other Great Lakes (Taylor et al. 1987; Brown et al. 1993).

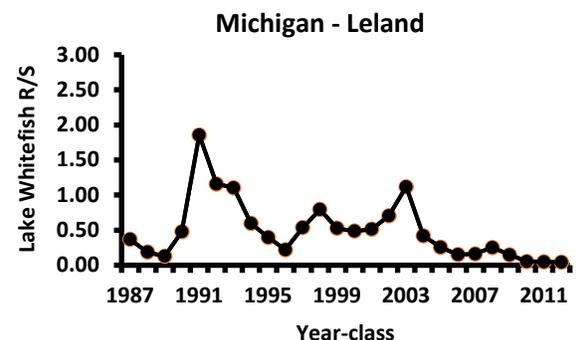
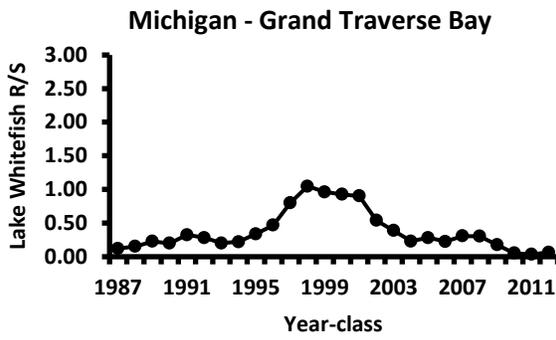
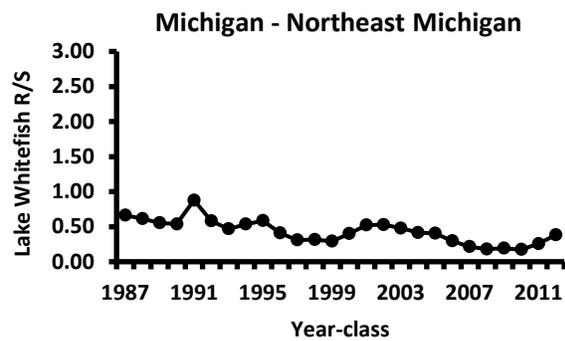
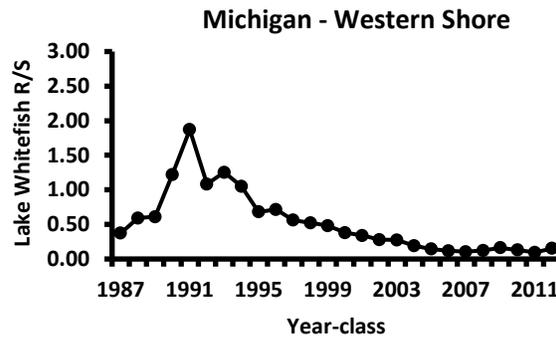
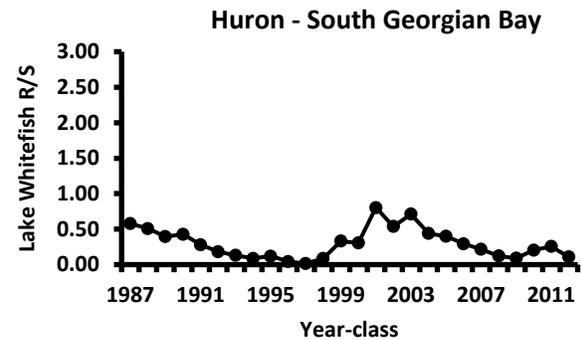
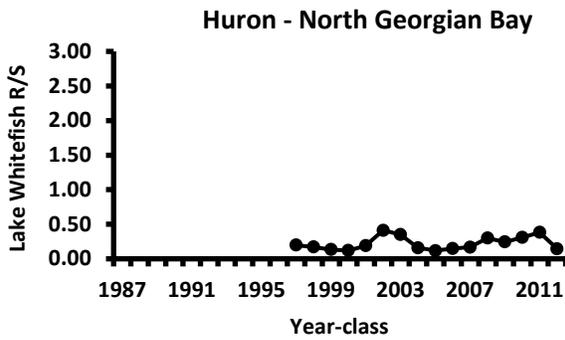
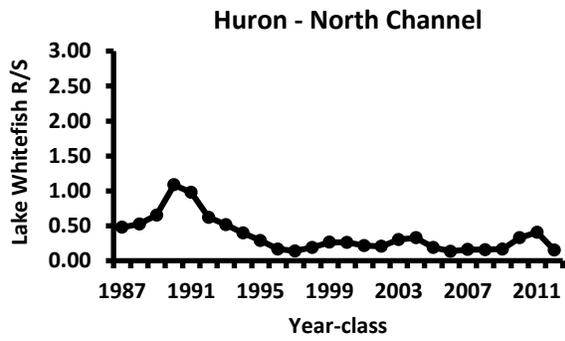
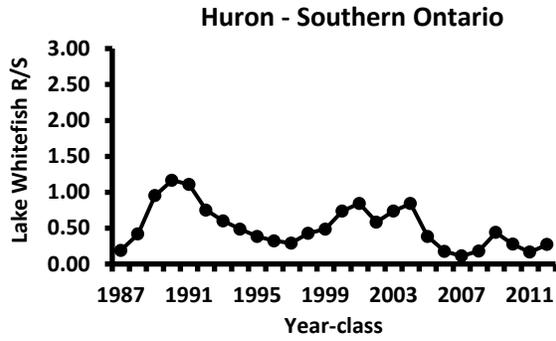
Fig. 19. The number of age-4 Lake Whitefish recruits (R) produced per kg of spawners (S) for the 1987 to 2012 year-classes in Lakes Superior, Huron, and Michigan based upon statistical catch-at-age stock assessments (see Lenart and Caroffino 2017).

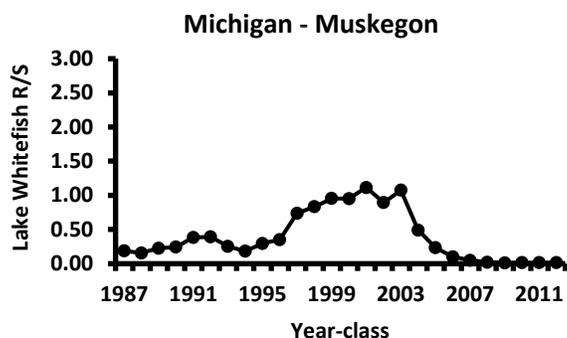


The temporal change in the R/S ratio for the 1987 to 2012 year-classes was not consistent across our proposed management areas within a lake (Fig. 14). In Lake Superior, the R/S ratio increased through time in the two management areas where SCAA output was available, but more so in the Whitefish Bay area than in the central Michigan area (Fig. 20). The largest declines in the R/S ratio in Lake Huron occurred in northern and central Ontario waters of the main basin and southern Georgian Bay while the R/S ratio was stable but lower than during the 1980s and 1990s in other areas. In Lake Michigan, the R/S ratio declined to low levels in all management areas, except northeastern Lake Michigan.

Fig. 20. The number of age-4 Lake Whitefish recruits (R) per kilogram of spawners (S) in various proposed management areas (Fig. 14) of Lakes Superior, Huron, and Michigan for the 1987 to 2012 year-classes. Estimates of recruitment and spawner biomass were based upon output from statistical catch-at-age stock assessments (see Lenart and Caroffino 2017).







Shifts in the R/S relationships of European Whitefish also have been observed. Analysis of long-term catches from the deep, peri-alpine Lake Geneva in central Europe, showed a shift in the stock-recruitment relationship that was mainly related to large-scale meteorological factors (Anneville et al. 2009). In Lake Geneva, higher water temperatures in spring may have improved larval survival and hence recruitment of European Whitefish by better matching the hatching date of larvae with the development of their zooplankton prey and by the positive effect of temperature on larval growth (Anneville et al. 2009).

The areal production from Lake Whitefish reproductive habitats in the Great Lakes varies considerably among our proposed management areas. The number of age-4 recruits ranged from 6 to 1,302 fish•ha⁻¹ of reproductive habitat among the 15 management areas where the number of recruits could be determined (Table 2). We do not believe that the southern Ontario area of the main basin of Lake Huron has sufficient reproductive habitat to produce the unusually high number of recruits (mean = 2.5 million) that were estimated from the SCAA stock assessments. Rather, based on our knowledge of reproductive habitat and movements of adult Lake Whitefish (see Fig. 12), we believe most of the fish harvested in southern Ontario waters of Lake Huron recruit to the fishery from locations in Michigan waters such as Cheboygan, Alpena, and Saginaw Bay (Fig. 12). Excluding the southern Ontario management area in the main basin of Lake Huron, recruitment averaged 82 recruits•ha⁻¹ of reproductive habitat across the upper Great Lakes. The most-productive habitats were consistently in Lake Huron, except for the Muskegon area in Lake Michigan. In the Muskegon area, Lake Whitefish spawn in the connecting channel between Lake Michigan and Muskegon Lake and not in the lake proper (S. Pothoven, NOAA/GLERL, personal communication, 2020). The average R/S ratio for all management areas, excluding southern Ontario, was 0.4 age-4 fish•kg⁻¹ of spawners.

Although our knowledge of Lake Whitefish stock-recruitment relationships is advancing, we still cannot describe the relationship for most of the 93 spawning aggregations. More pointedly, our analysis describes only the relationship for aggregations of spawning stocks, not the relationships for individual reproductive habitats. For example, we know of at least four spatially separated spawning stocks in Whitefish Bay, Lake Superior, that intermix during the non-spawning season and contribute to commercial fisheries, yet we know nothing about the productivity of each of the spawning aggregations. All four of these stocks are subject to the harvest-control rule of 65% maximum total annual mortality established for management of Lake Whitefish in 1836 Treaty waters (Ebener et al. 2005; Molton et al. 2013; Modeling Subcommittee, Technical Fisheries Committee 2017), yet Molton et al. (2013) showed that lower-productivity stocks could easily be overexploited under the control rule.

Table 2. The average areal production of age-4 recruits (R) of Lake Whitefish from whitefish reproductive habitats in proposed management areas of Lakes Superior, Huron, Michigan, and Erie during 1986-2016. Also shown for each management area are the amount (ha) of reproductive habitat, the average biomass (kg) of spawners (S), and the R/S ratio. The average recruits and spawners were calculated based on the most-recent statistical catch-at-age model for each management area and do not incorporate a mixed-stock approach to stock assessment. Letter preceding the name of each management area designates the Great Lake in which the area is located (S = Superior; H = Huron M = Michigan; E = Erie) (NC = not calculated).

Lake and Management Area	Reproductive Habitat (ha)	Average Recruits (number)	Average Spawners (kg)	Recruits per ha	R/S
S-Whitefish Bay	11,800	427,400	1,260,529	36.2	0.339
S-Central Michigan	4,000	138,600	497,449	34.7	0.279
H-Northern Michigan	10,000	1,810,900	3,147,236	181.1	0.575
H-Northern Ontario	7,900	972,100	1,344,249	123.1	0.723
H-North Channel	10,600	563,600	1,750,197	160.7	0.322
H-Central Ontario	13,100	1,703,300	2,944,285	188.8	0.579
H-Southern Ontario	1,900	2,473,300	5,464,284	1,301.7	0.453
H-Central Michigan	26,200	2,418,100	6,668,233	92.3	0.363
H-Saginaw Bay	151,700	2,590,100	NC	17.1	NC
H-North Georgian Bay	44,200	255,500	933,083	5.8	0.274
H-South Georgian Bay	31,700	358,000	1,523,583	11.3	0.235
M-Northeast Michigan	20,600	1,173,500	2,683,092	57.0	0.437
M-Grand Traverse Bay	2,600	163,400	552,847	62.8	0.296
M-Leland	5,600	59,000	190,007	10.5	0.311
M-Muskegon	900	229,200	887,311	254.7	0.258
M-Western Michigan	26,400	1,652,800	4,895,088	62.6	0.338
E-Western basin	65,500	1,008,200	NC	15.4	NC
	434,700	17,997,000	34,741,471	153.9	0.4

We believe that the reproductive productivity of nearly all Lake Whitefish stocks in the four lower Great Lakes has declined to low levels due almost certainly to proliferation of dreissenids. This conclusion is obvious from analysis of stock-recruitment relationships that show increasing productivity of Lake Whitefish stocks in Lake Superior where dreissenids are rare and declining productivity of whitefish stocks in the four lower lakes, all of which have an abundance of dreissenids. What we do not know is how dreissenids interact with abiotic drivers to affect reproduction and recruitment.

Research Priority: Estimate the productive capacity of each exploited stock, however difficult that may be.

Early Life Stages

We are aware of only one study of the Great Lakes basin that estimated the density of Lake Whitefish embryos on spawning shoals. Densities in Lake Simcoe, Ontario, ranged from 12-332•m⁻² and averaged 165•m⁻² (Hindley et al. 1977). Although Freeberg et al. (1990) did not report the density of embryos in Grand Traverse Bay, Lake Michigan, 41-59% of embryos were deposited in less than 1.5 m of water. In Lake Sempach, Switzerland, maximum densities of 70 embryos•m⁻² of *Coregonus* spp. occurred in water <10-m deep (Ventling-Schwank and Müller 1991).

Survival of Lake Whitefish embryos is generally poor, even on high-quality substrates, so small changes in their survival can produce large changes in recruitment. Hart (1930) reported that only 13% of the 15 Lake Whitefish embryos sampled through the ice were still alive on spawning shoals in the Bay of Quinte on February 29 and March 1, 1928. Overwinter survival of embryos did not exceed 7% in any depth strata in Grand Traverse Bay, Lake Michigan, during the winters of 1982-1984 (Freeberg et al. 1990). Survival of embryos in Grand Traverse Bay was almost four-fold greater during the year when ice covered the spawning shoals than in the ice-free year when survival was only 0.6% and only embryos at <1.5 m survived the winter (Taylor et al. 1987; Freeberg et al. 1990). Survival of Lake Whitefish embryos placed in baskets on spawning shoals in Lake Simcoe was only 0.5% after 90 days, and predation of embryos by Mottled Sculpin (*Cottus bairdi*) appeared to be a major source of mortality because oxygen levels, pH, and water temperatures seemed acceptable for embryonic development (Hindley et al. 1977). No other *in situ* work, to our knowledge, has been conducted in the Great Lakes basin to determine the ecology of Lake Whitefish at the embryo stage as it relates to physical-biological coupling and subsequent recruitment. Overwinter survival of embryos in Lake Sempach, Switzerland, was <1% during 1987-1989; at some sites, oxygen deficiency in the sediments was likely the cause of the low survival whereas, at other sites, wind-induced water currents may have provided sufficient oxygen to increase embryo survival (Ventling-Schwank and Müller 1991). Several laboratory studies have linked embryo hatching and survival to incubation temperatures and substrates. These studies have shown that lower water temperatures during incubation (2-5° C) result in higher survival of embryos (Lim et al. 2017; Eme et al. 2018) and that temperature regimes in hatchery systems need to mimic thermal regimes in the wild to keep embryos' survival high (Mitz et al. 2016, 2019; Lim et al. 2017).

Although sampling the embryo stage of Lake Whitefish over winter is difficult, large spawning shoals in protected areas like Big Bay de Noc, Saginaw Bay, the three bays in northwestern Ontario waters of Lake Superior, and the North Channel and northwestern Georgian Bay offer researchers relatively protected areas where the ecology of Lake Whitefish embryos could be studied with a reasonable level of intensity. After studies in these more-protected areas are completed and sampling strategies are developed, studies could be expanded to more-exposed spawning shoals like those in Michigan and Ontario waters of central Lake Huron and the eastern Door Peninsula in Lake Michigan, where open water will present researchers with difficulties in sampling (see Fredricks 1982; Freeberg et al. 1990) not encountered on more-protected ice-covered spawning shoals.

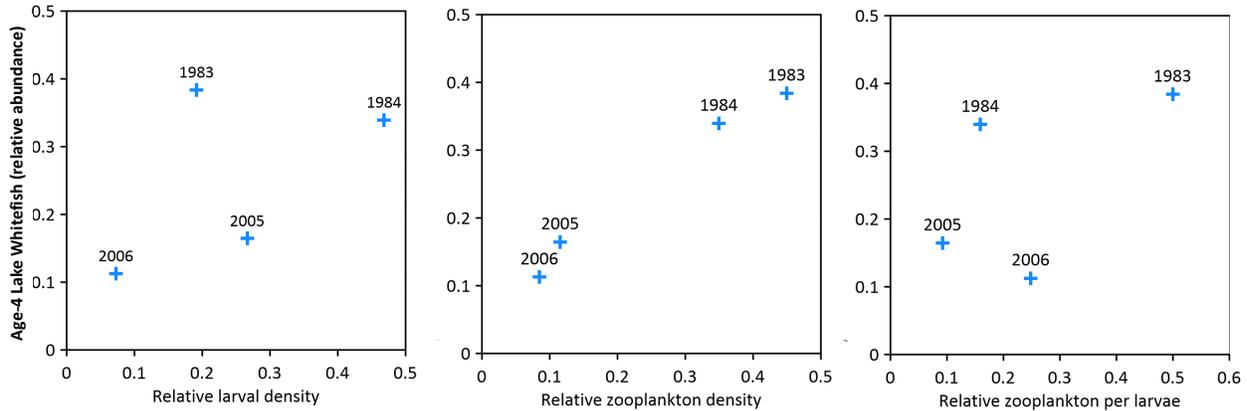
The Lake Whitefish larval stage has been more extensively studied than the embryo stage, although many important knowledge gaps remain. Larval Lake Whitefish hatch in the spring immediately following ice-out as water temperatures rise from 4 to 10° C. Larvae begin exogenous feeding on zooplankton closely following hatch, with research indicating a diet preference for copepods, including both adults and nauplii (Hoagman 1973; Freeberg et al. 1990; Claramunt et al. 2010a; Pothoven et al. 2014). The post-hatch period presents a good opportunity to study early life history because larvae can be found near the lake surface close to spawning shoals, and they are easily captured using larval fish nets towed from small vessels (Hoagman 1973; Faber 1970; Reckahn 1970) or pulled by hand. Currents and basin morphology will dictate how far larvae will be transported from spawning shoals as larvae can be found across each Great Lake over all depths, including in the middle of the lakes.

One of the more-important studies of biotic and abiotic factors that contributes to variation in Lake Whitefish larval density, survival, and growth was Freeberg et al. (1990), who found that overwinter embryo survival and zooplankton density at the time of hatch were drivers of larval density and survival in Grand Traverse Bay, Lake Michigan. Embryo survival was a function of the amount of ice cover, with an early cold winter leading to increased survival. Catches of larvae in 1984 were initially 3.7 times greater than in 1983, but, by week 6 after hatch, catches in 1984 were only 2.1 times greater than in 1983 (Freeberg et al. 1990). The ratio of zooplankton to larvae was much greater in 1983 than 1984, and the ratio declined through the spring in 1984 but not in 1983. In 1983, when zooplankton density was high relative to larval density, larval growth rates and survival were higher. The relevance of the Freeberg et al. (1990) findings to the current recruitment decline is important given that they support the leading hypothesis for the decline, i.e., that lower food availability has caused poor survival of larval fish (Bunnell et al. 2018). Specifically, it shows the potential for larval growth and survival to be influenced by zooplankton and copepod availability. The study by Freeberg et al. (1990) shows the value of (1) following a year-class from the embryo through to post-hatch larvae, which allows explicit consideration of how embryo survival translates into larval density; and (2) sampling larvae repeatedly over the course of a season, which allows metrics like growth rate and survival to be calculated for fixed periods. Extending this type of sampling regime over many years would be extremely powerful for understanding the key drivers of larval dynamics.

Claramunt et al. (2010b) examined spatial patterns in Lake Whitefish larval density near spawning shoals in Lake Michigan and found a substantial increase in average larval density (number•1,000 m⁻³ ±SE) from 2005 (16.6 ± 24.8) to 2006 (373.7 ± 28.3) at six spawning shoals. Variation in larval density was best explained by larval length, spring wind intensity, and adult density. Temperature, winter ice cover, and spring zooplankton density were not important drivers of larval density in the Claramunt et al. (2010b) study. Spatial variation in larval density among spawning shoals in Lake Michigan was substantial, indicating that certain key spawning shoals seem to provide more suitable locations for larval survival than did others. For example, large catches of larvae have been made at the eastern Door Peninsula spawning shoal (site 61; Fig. 3) in 2006 (>1900 larvae•m⁻³), and Hoagman (1973) reported catching between 2,900 and 5,100 larvae per day from April 25 to May 8, 1970, in the same area, indicating a very-productive habitat at times.

Larval density and magnitude of the subsequent year-class does not correspond well. Fredrick (1982) reported that, based on larval catches, the 1975 year-class was substantially less abundant than either the 1974 or 1976 year-classes at the eastern Door Peninsula spawning shoal (see Fig. 3; Appendix A) in Lake Michigan, but Ebener and Copes (1985) reported that the 1975 year-class during 1975-1980 was a larger component of the commercial harvest from the same stock than either the 1974 or 1976 year-classes. In Lake Constance of central Europe, year-class abundance was not established at the larval stage but rather at a post-larval stage weeks after hatching (Eckmann and Pusch 1991). In Grand Traverse Bay, Lake Michigan, abundances of the 1983-1984 year-class at age 4 were higher than abundances of 2005-2006 year-class fish at age 4, yet larval densities from Freeberg et al. (1990) and Claramunt et al. (2010b) did not show this same pattern (Fig. 21). There was, however, a positive linear relationship between zooplankton density and corresponding age-4 recruitment (Fig. 21), highlighting the potential importance of food availability during the larval stage for determining year-class strength. Zooplankton densities and age-4 recruitment in the 1980s, prior to establishment of dreissenids, were much higher than in the mid-2000s. The highest zooplankton (z) density and highest ratio of zooplankton per larvae (f) occurred in 1983, which also produced the highest abundance of age-4 Lake Whitefish. The results from Freeberg et al. (1990) and Claramunt et al. (2010b) show the relative degree that larval Lake Whitefish and zooplankton density determine subsequent recruitment to the adult stock and the fishery harvest.

Fig. 21. Relative abundance of four year-classes of Lake Whitefish at age 4 in relation to relative larval density, zooplankton density, and zooplankton per larvae. Lake Whitefish numbers at age 4 were estimated from statistical catch-at-age stock assessments (Lenart and Caroffino 2017), and relative rankings are the value/sum of all values. All data are for the 1983, 1984, 2005, and 2006 year-classes produced at the Elk Rapids spawning shoal in Grand Traverse Bay, Lake Michigan, as reported by Freeberg et al. (1990) and Claramunt et al. (2010b).



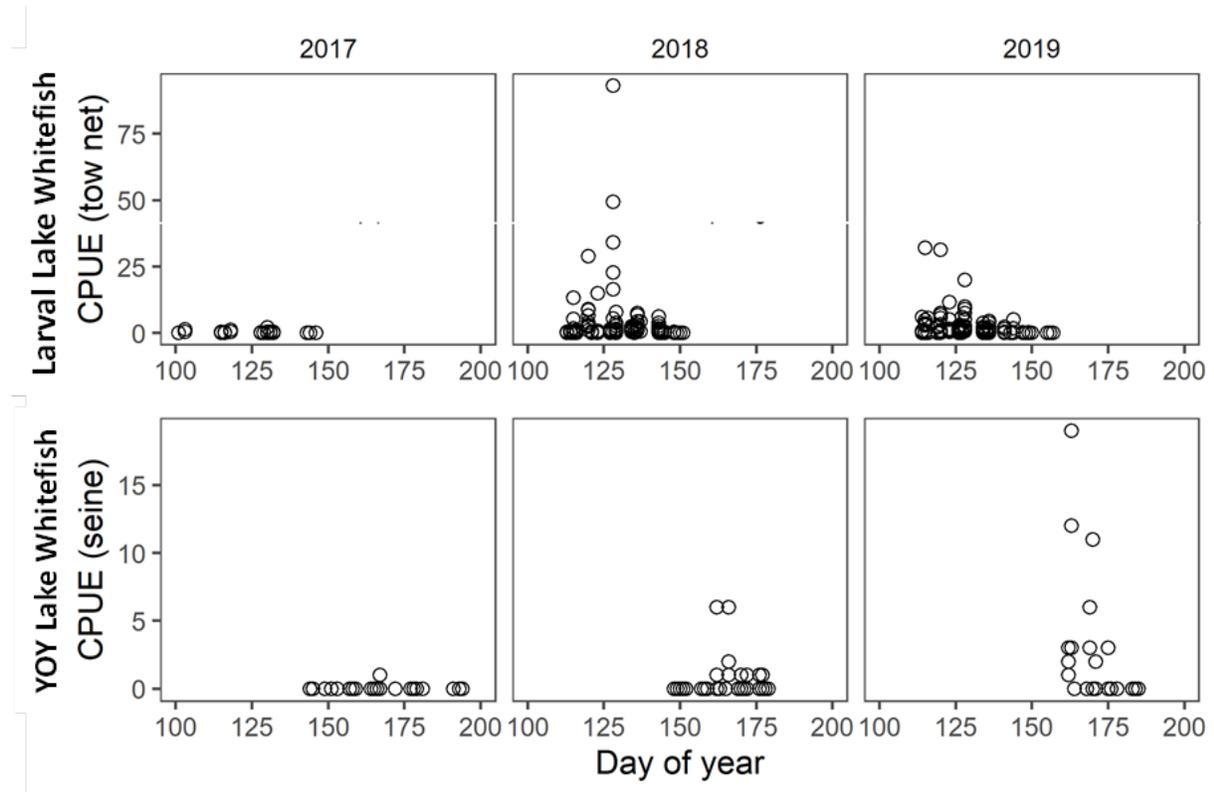
The findings reviewed above are consistent with the notion that Lake Whitefish, prior to the recent period of recruitment declines, showed relatively high year-to-year stability in abundance near the age of recruitment to the fishery as compared to the higher degree of variation in larval density. This finding implies that, in the mid-2000s and possibly earlier, year-class strength was set or established at some point in the life cycle after early post-hatch. In other words, in some years, large numbers of larvae are produced, but this does not translate into high abundance of age-4 and older fish. The question is where does the constraint presently lie given the ecosystem changes since the arrival of dreissenids.

Although earlier studies provide clues about potential drivers of larval density (e.g., Freeberg et al. 1990; Claramunt et al. 2010b), the studies cannot pinpoint the causes of the more-precipitous recent declines in recruitment of Lake Whitefish. One of the current leading hypotheses for these declines is that the filter feeding of dreissenids has reduced the amount of food available to larvae, leading to poor survival (Bunnell et al. 2018). Hoyle et al. (2011) reported that, in the Bay of Quinte, Lake Ontario, recruitment of post-larval YOY in August was correlated with availability of zooplankton prey in spring and larval growth, and that prey abundance was 89% lower during 2003-2005 than during 1991-1996 before the establishment of dreissenids. Claramunt et al. (2010b) found no link between zooplankton density and larval density at the time of emergence; however, it was not known if larval survival at or beyond this initial post-hatch window was impacted by zooplankton availability at the time of hatch or thereafter. Furthermore, two years of larval sampling would be insufficient for identifying statistical relationships between larval density and the abiotic variables described previously. Longer-term studies of larval dynamics are needed to identify the role of biological and environmental factors in recruitment variation of Lake Whitefish.

More recently, research by the OMNRF at the Fishing Islands spawning shoal in the east-central main basin of Lake Huron found a high degree of year-to-year variability in larval and post-larval density during 2017-2019, leading to two insights (Fig. 22; E.S.D., unpublished data). First, substantial variability in larval density occurred despite little presumed variation in spawning-stock biomass of the parents, much like that observed by Claramunt et al. (2010b). Second, post-larval YOY production was not strongly correlated with production of larvae. These

insights suggest that the recent decline in recruitment owes, in part, to events occurring after, not only during, the larval stage. In summary, abiotic variables appear to be driving year-to-year variability in larval density whereas some other factor (e.g., food availability) may be limiting post-larval survival and thereby contributing to the recent declines in juvenile recruitment.

Fig. 22. Catch-per-unit effort (CPUE) of Lake Whitefish larvae in towed nets (top panels) and Lake Whitefish young-of-the-year (YOY) in seines (bottom panels) during surveys conducted by the Ontario Ministry of Natural Resources and Forestry at reproductive habitat in the Fishing Islands (site 44; see Fig. 3) of Lake Huron during April through June, 2017-2019. Larval catch is per minute of tow-net effort whereas post-larval YOY catch is per seine haul (E.S.D., unpublished data).



In view of the above findings from east-central Lake Huron, more effort is needed on sampling post-larval YOY. To date, the most (and perhaps only) comprehensive study of YOY Lake Whitefish in the Great Lakes was conducted by Reckahn (1970) in South Bay, Lake Huron, between 1965 and 1969. Reckahn's study involved stratified sampling over depths ranging from 4-58 m using small bottom trawls between late June and early October. During June-July, post-larval YOY were caught close to shore in <1 m of water adjacent to sites thought to provide suitable larval habitat. Fish left these shallow areas by about mid-July and dispersed into 15-16 m depths where they remained tightly coupled to the 17° C isotherm and where there were few potential predators (Reckahn 1970). A notable shift in Lake Whitefish ecology occurred after mid-August that involved a reduction in growth rate and a migration from the metalimnion into the hypolimnion. Depths occupied by post-larval YOY increased from 15-16 m in mid-August to 20-25 m in mid-September and to 30 m by early October (Reckahn

1970, Fig. 2). A telling quote in the introduction that is not resolved by the end of Reckahn's paper and that still holds true today reads "the time at which year class strength of whitefish is established is still not known with precision." Reckahn's (1970) sampling design and results should serve as a basis for developing a sampling program in other parts of the Great Lakes that targets post-larval YOY so as to identify the factors affecting their survival.

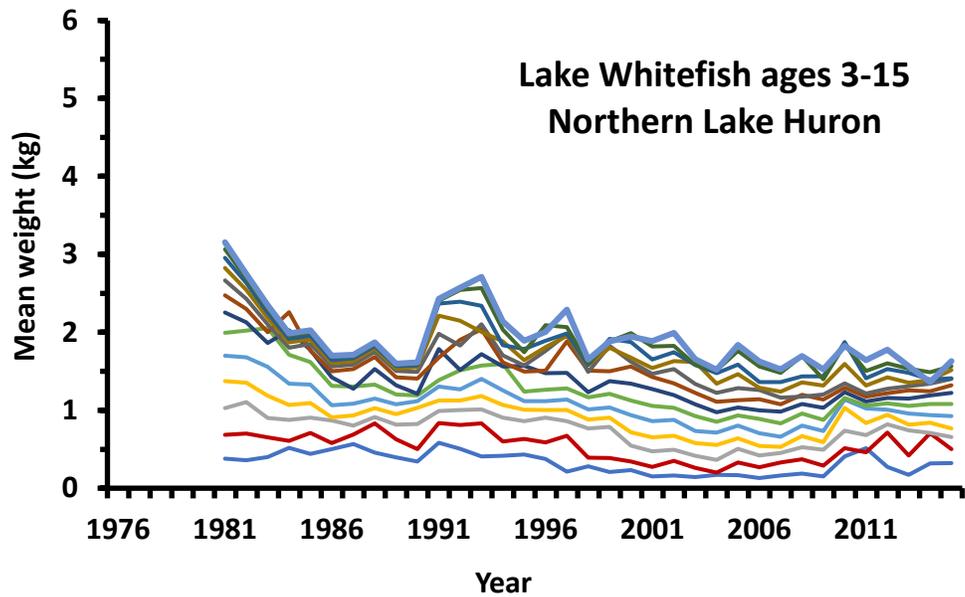
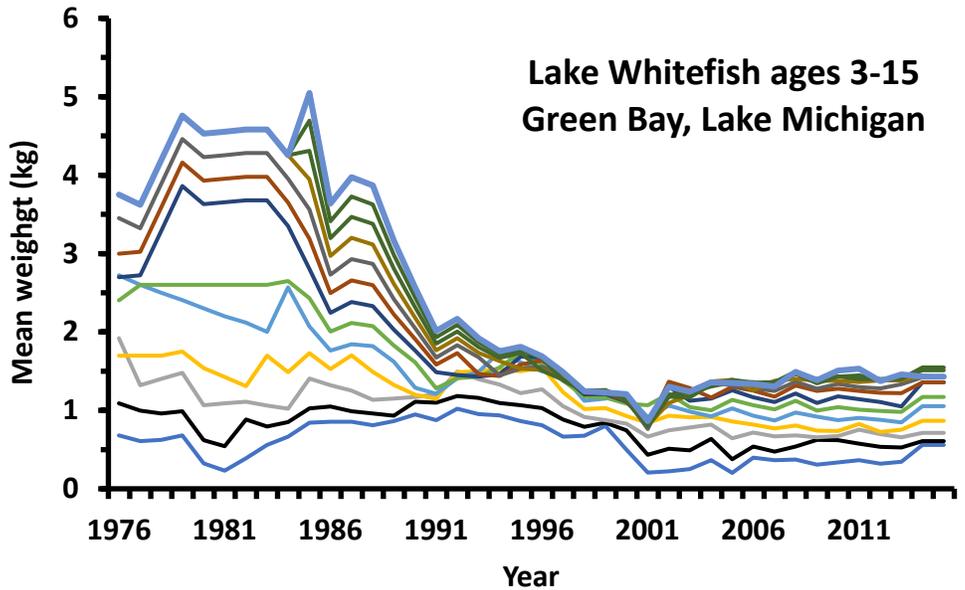
Research Priority: Establish early-life-stage monitoring sites across the Great Lakes to better understand how embryo survival is affected by physical and biological processes.

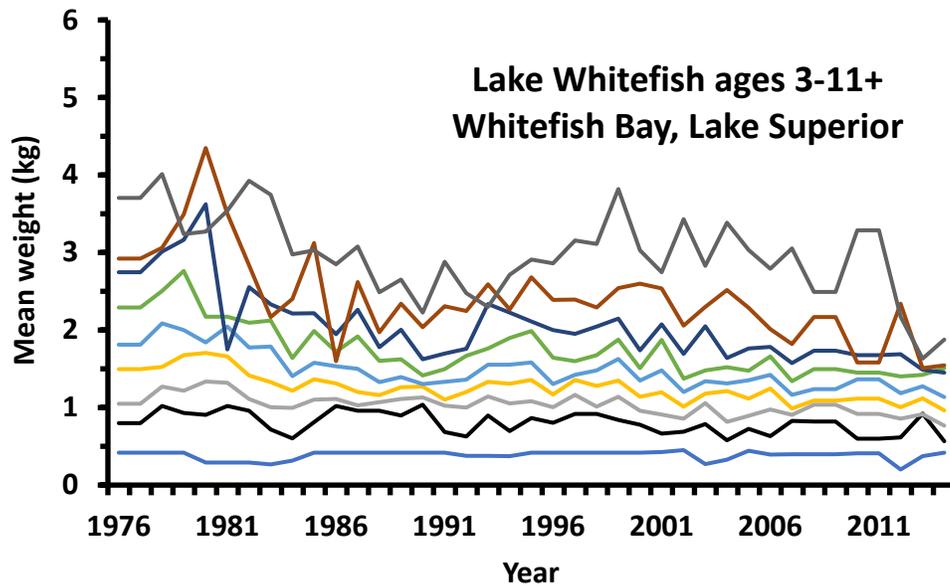
Growth, Condition, and Energetics

In response to severe declines in Lake Whitefish growth and condition during the 2000s, a coordinated basinwide effort was targeted at identifying links among growth, condition, energetics, and recruitment. Fifteen manuscripts from this effort were published on topics ranging from pathogens, movement and stock mixing, feeding, recruitment potential, and natural mortality and its relationship to fish-health indicators (Brenden et al. 2010a). Although these efforts generated considerable new knowledge, a good mechanistic understanding of the links among growth, condition, and energetics and how they influence recruitment remains elusive. Below we explore what was learned from the most-recent efforts and make recommendations for further research.

Development of SCAA stock assessments of Lake Whitefish has advanced our understanding of recruitment because large volumes of data collected over many years were consolidated, along with mortality and abundance data (Ebener et al. 2005; Truesdell and Bence 2016; Lenart and Caroffino 2017). Age, length, and weight information consolidated for these stock assessments illustrate how severe the declines in growth and condition have been in all of the Great Lakes, except Lake Superior (Fig. 23). Mean weight-at-age for Lake Michigan's Big Bay de Noc stock (site 60; see Fig. 3) declined precipitously beginning in the late 1980s whereas similar declines in northern Michigan waters of Lake Huron began several years later. By 2015, mean weight of age-3 and older fish had declined by 50% and mean weight of all ages was compressed between 0.3 and 1.6 kg in Lakes Huron and Michigan. By comparison, mean weight-at-age in Whitefish Bay, Lake Superior, exhibited annual variability but only a slight temporal decline, which was related more to density dependence than changes in the food web (Pratt et al. 2016). Weight-at-age did increase slightly after 2001 in Lake Michigan and after 2009 in northern Lake Huron. Declines in mean weight-at-age and condition also occurred in Ontario waters of Lake Huron (Mohr and Ebener 2005; Fera et al. 2015), in other areas of Lake Michigan (Pothoven et al. 2001; Schneeberger et al. 2005), and in Lake Ontario (Hoyle 2005). The declines in growth and condition in these three lakes were attributed to the loss of an important food for Lake Whitefish, *Diporeia* (Nalepa et al. 2005, 2014; Fera et al. 2015). Growth and condition did not decline in Lake Erie even though *Diporeia* populations there were also nearly eliminated (Cook et al. 2005; Fera et al. 2015) because, it was postulated, there were sufficient other benthic invertebrate prey to compensate for the loss of *Diporeia* (Cook et al. 2005). Although Lake Whitefish diet did change in Lakes Michigan, Huron, and Ontario after the loss of *Diporeia* (Pothoven and Madenjian 2008), alternative prey obviously was not sufficient (see Pothoven et al. 2006) to offset the loss of *Diporeia*.

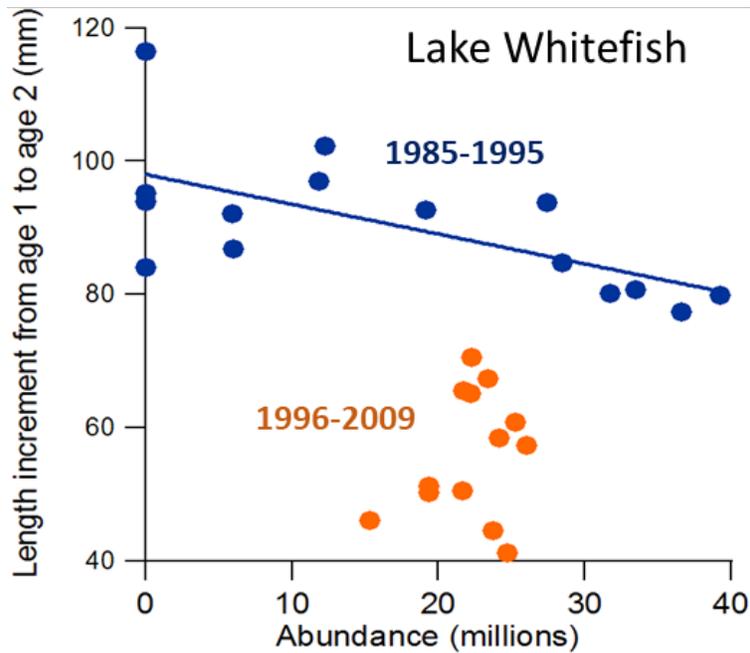
Fig. 23. Predicted mean weights of age-3 and older Lake Whitefish during 1976-2015 in three areas of the Great Lakes—northern Green Bay, Lake Michigan (top panel); northern Michigan waters of Lake Huron (middle panel); and western Whitefish Bay, Lake Superior (bottom panel). Mean weights were predicted by fitting time-varying von Bertalanffy growth and length-weight functions to length- and weight-at-age data (see He et al. 2015).





The loss of *Diporeia* was not the only cause of declines in Lake Whitefish growth and condition in the Great Lakes. Density-dependent and density-independent factors, other than the decline of *Diporeia* associated with the colonization of dreissenids, were also partially responsible. Lake Whitefish year-class production in the Great Lakes was exceptional beginning in the late 1980s and extending through the early 2000s (see Fig. 6) as dreissenids were becoming abundant, and *Diporeia* populations began to decline. Kratzer et al. (2007) evaluated Lake Whitefish fecundity, egg lipid content, and total ovary lipid content in selected areas of Lakes Huron, Michigan, and Superior in two time periods with different Lake Whitefish and *Diporeia* densities. They reported that (1) egg lipid content was higher in 2003-2005 than in 1986-1987 regardless of changes in Lake Whitefish abundance or *Diporeia* densities, (2) total ovary lipid content and Lake Whitefish abundance were inversely related while there was no significant ($P > 0.05$) relationship between total ovary lipid content and *Diporeia* density, and (3) the amount of energy Lake Whitefish invested in egg production was more closely associated with its abundance than with *Diporeia* density. Wright and Ebener (2007) reported, too, that the lowest lipid levels in Lake Whitefish filets from Lake Michigan occurred after 1994; growth rate was negatively related to abundance, albeit only weakly; and the lowest growth rates occurred when lipid levels were low and abundance and biomass were high. Further, DeBruyne et al. (2008) reported that declines in growth and condition coupled with increases in relative abundance were contributing to the observed stock changes in southern Lake Michigan while, in northern Lake Michigan, density-independent mechanisms (such as food-web changes) were influencing stocks. In southern Lake Huron, declines in growth from the 1980s and 1990s could be explained, in part, by increases in stock abundance and biomass, but, following the establishment of dreissenids, growth declined independent of stock size (Fig. 24) (Fera et al. 2015). Going outside the Great Lakes, Herbst et al. (2013) concluded that diet and condition of Lake Whitefish in Lake Champlain were not negatively affected by the dreissenid invasion.

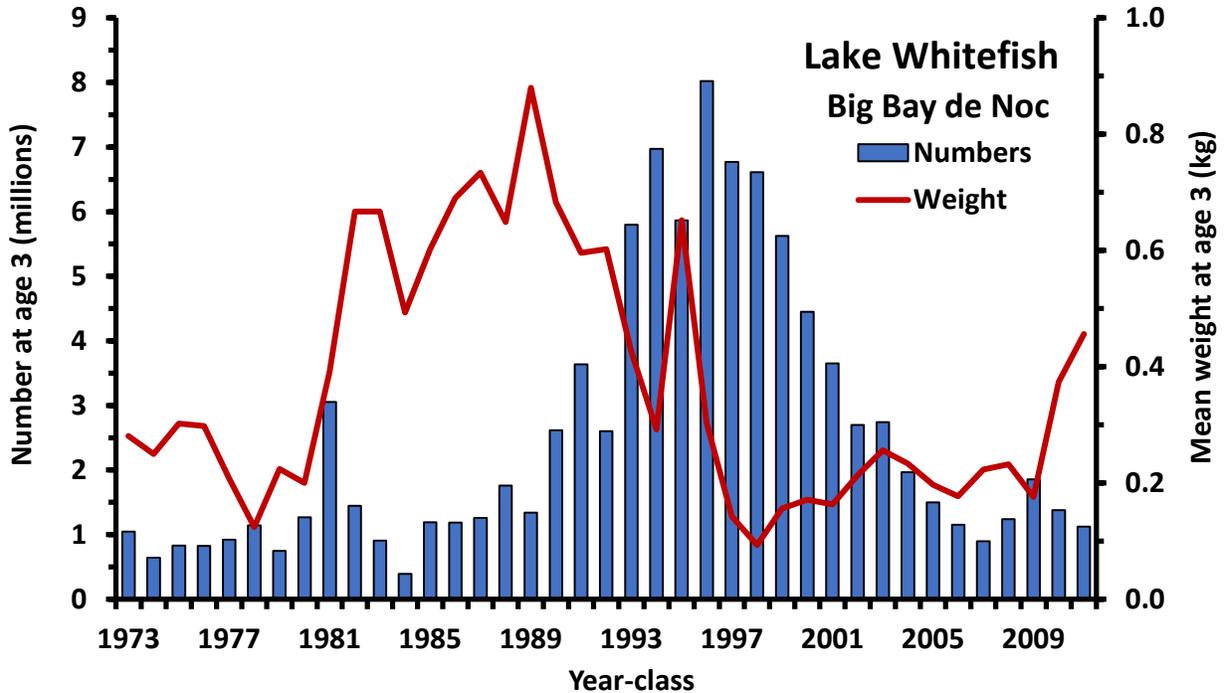
Fig. 24. Growth in length (mm) of age-1 Lake Whitefish in the Ontario waters of Lake Huron's southern main basin in relation to stock abundance prior to (1985-1995) and after (1996-2009) establishment of dreissenids. Data from Gobin et al. (2015).



Lake Whitefish from Big Bay de Noc provide another example of how growth was no longer density dependent post dreissenids (Fig. 25). Based on SCAA modeling, abundance increased slowly from the 1973 to the 1989 year-class but mean weight at age 3 increased two-fold from the 1973 to the 1989 year-class. Abundance increased over five-fold from the 1989 to the 1996 year-class. However, as these exceptionally large year-classes recruited to the fishery, weight at age 3 quickly declined and reached its lowest level in 1998. Thereafter, mean weight did increase but it did not return to the levels observed in the 1980s even though year-class abundance was the same as in the 1980s. Density dependence appeared to be important in regulating growth through the 1990s but thereafter density-independent factors controlled growth.

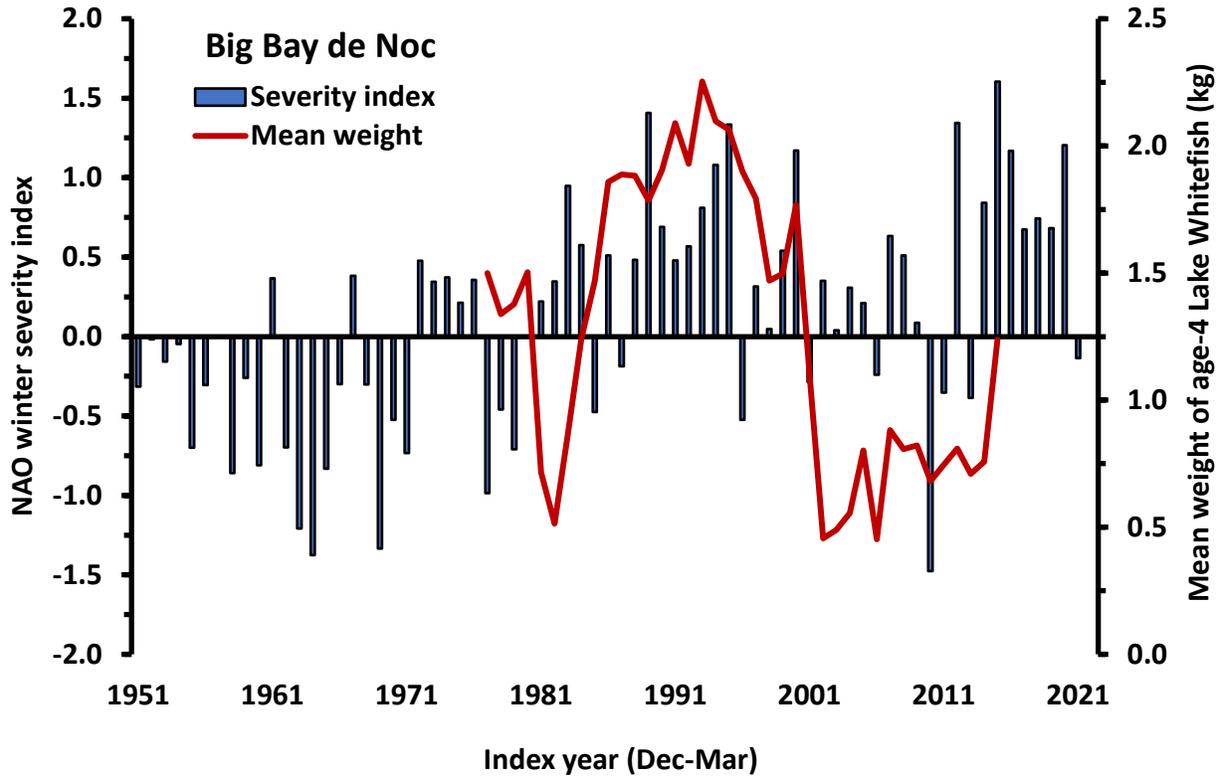
Large-scale weather patterns driven by the NAO appear to be the primary density-independent driver affecting changes in mean weight of Lake Whitefish in Big Bay de Noc (Fig. 26). The change in mean weight at age 4 tended to fluctuate with changes in the NAO winter severity index from 1976 to 2014. Positive index values (warm winters) were associated with favorable conditions for growth whereas negative index values (cold winters) were associated with unfavorable conditions for growth. Mean weight of age-4 fish was heaviest during 1985-1995, which corresponds to the period of consistently high NAO index values (Fig. 26). Some of the best recruitment for Lake Whitefish in the Great Lakes occurred during 1985-1995 when the NAO created warmer and wetter winters that should have suppressed embryo survival, suggesting that good larval growth can compensate for reduced embryo survival.

Fig. 25. Numbers (millions) and mean weight (kg) of age-3 Lake Whitefish for the 1973 to 2011 year-classes from Big Bay de Noc (Fig. 3; Appendix A) in northern Green Bay, Lake Michigan. Number of fish was estimated from statistical catch-at-age analysis whereas mean weight was predicted using time-varying von Bertalanffy growth and length-weight functions (He et al. 2015).



Hidden in the relationship between winter temperature and growth is the invasion of dreissenids, the loss of *Diporeia*, and density-dependent responses in growth and reproduction. More importantly, if temperature change driven by the NAO can influence growth of juvenile and adult Lake Whitefish, the NAO influence on growth of larval fish and natural mortality must be substantial. Clearly, development of long-term monitoring programs will be essential for disentangling NAO effects on Lake Whitefish stock dynamics (Pothoven 2019).

Fig. 26. The North Atlantic Oscillation (NAO) winter severity index from 1951 to 2021 and mean weight of age-4 Lake Whitefish from Big Bay de Noc in northern Green Bay, Lake Michigan, during 1976-2016. Winter severity index values are the mean values for December through March. Mean weight at age 4 was predicted using time-varying von Bertalanffy growth and length-weight functions (He et al. 2015). Monthly values for the severity index were obtained from <https://climatedataguide.ucar.edu/climate-data/hurrell-north-atlantic-oscillation-nao-index-station-based>.

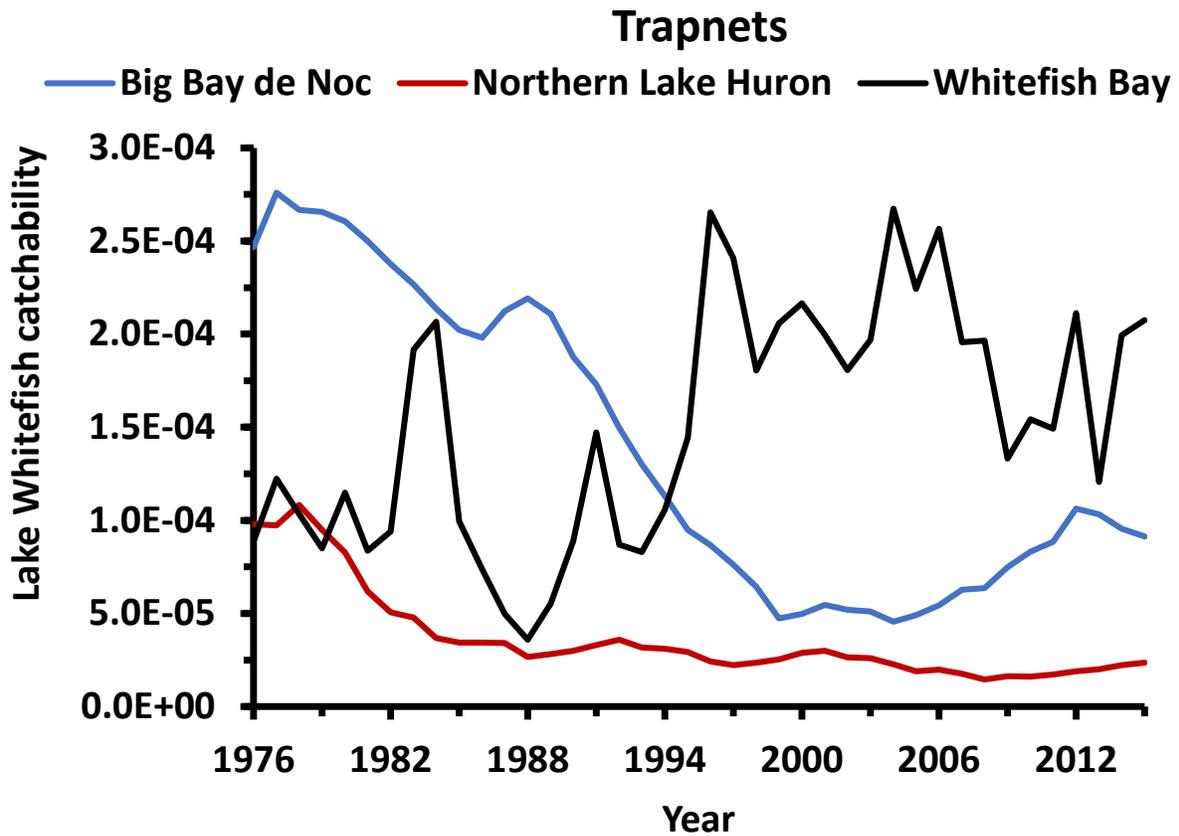


Catchability

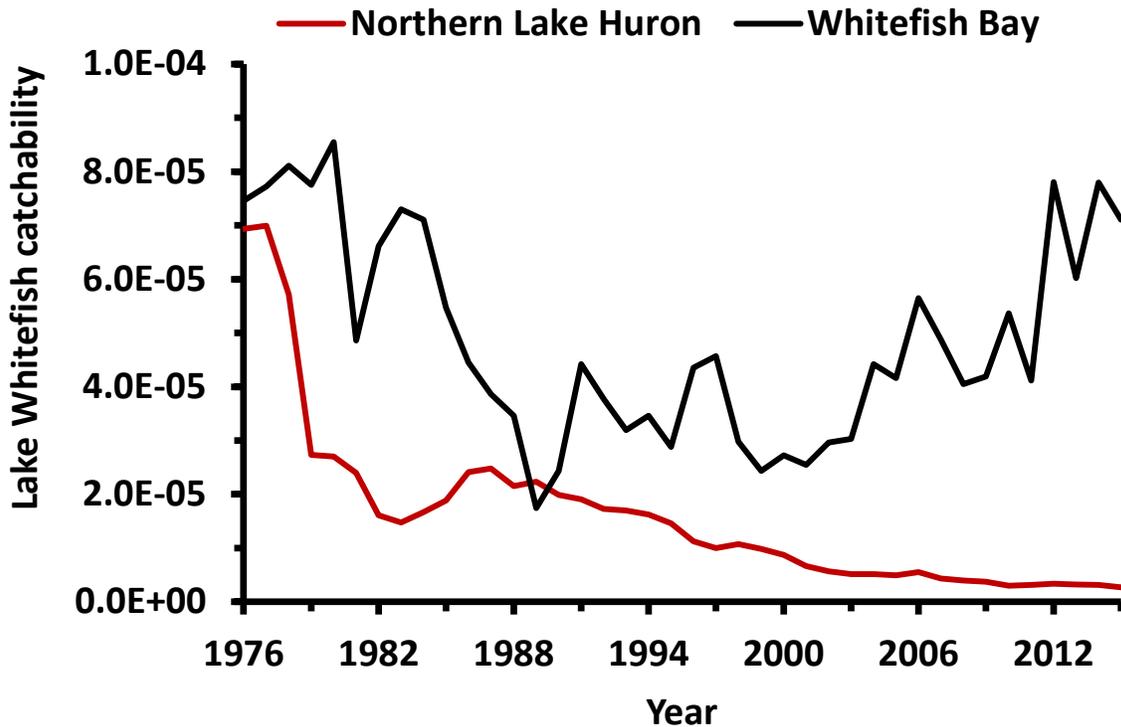
Catchability of Lake Whitefish to commercial-fishing gear has declined substantially in portions of the Great Lakes since the 1970s, leading some commercial fishermen to believe that the declines in yield are more about reduced catchability than declining recruitment and abundance. Catchability has changed because of declines in growth and condition, increased water clarity, and fouling of commercial gear by the filamentous algae *Cladophora* spp. (Ebener et al. 2008). Lake Whitefish from some spawning stocks now appear to range over larger geographic areas than prior to the large decreases in recruitment and arrival of dreissenids whereas the distribution of other stocks has not changed (see Ebener et al. 2010a). Catchability to commercial-fishing gear has declined substantially in Lakes Michigan and Huron but not in Lake Superior (Fig. 27). Certainly, the initial declines in catchability were a consequence of declining growth and condition that reduced fish girth and thus lowered vulnerability to the mesh sizes used in gillnets and trapnets. Reduced condition also affected the marketability of small but still legal-sized fish (Ebener et al. 2008). However, the continual annual decline in catchability of fish from northern Lake Huron (Fig. 27) was attributed to reduced encounter rates with fishing

gear because movement of fish has increased; fish now forage over a larger geographic area some of which experiences little to no commercial-fishing activity (Ebener et al. 2010a). If Lake Whitefish nowadays are allocating more energy to foraging than to somatic or gametic growth, then recruitment could be affected due to reduced production of gametes. Despite changes in growth rate, foraging behavior, and *Cladophora* spp. abundance, the observed declines in recruitment and abundance are real and should not be written-off as simply a consequence of reduced catchability.

Fig. 27. Catchability of Lake Whitefish to commercial trapnets and gillnets in Big Bay de Noc, Lake Michigan, northern Lake Huron, and Whitefish Bay, Lake Superior, during 1975-2015 as predicted from statistical catch-at-age stock assessments. Note that the scales of the two panels differ. Catchability is the proportion of the fishable stock captured in a unit of fishing effort.



Gillnets



Parental Condition

The influence of adult condition on subsequent recruitment of Lake Whitefish has been investigated but no clear linkage has been found, pointing to the importance of exogenous factors in determining survival during early life. Length at hatch and feeding and growth of larvae were positively related to lipid content (Brown and Taylor 1992), suggesting that condition of females may be an important driver of larval survival and subsequent recruitment. However, Muir et al. (2010) reported that female condition and egg quality explained only 39% of the variation in physiological condition of juvenile Lake Whitefish in Lake Michigan whereas spawning location explained most of the variation. Of interest, Blukacz et al. (2010) found that body size and condition of male Lake Whitefish from northern Lake Michigan and the Bay of Quinte, Lake Ontario, were important predictors of sperm size and sperm swimming speed, but how sperm quality affects survival of early life stages remains unknown.

Reduced growth, condition, and energetics experienced by Lake Whitefish in the Great Lakes may have a disproportionate effect on survival of males and sperm activity, both of which could affect recruitment. Madenjian et al. (2015b) evaluated polychlorinated biphenyl (PCB) concentration in somatic tissues of Lake Whitefish from northern Lake Huron and concluded that males had greater energy expenditure than females stemming from greater activity and a higher resting metabolic rate. The PCB concentrations were on average 34% higher in males than females indicating that males must have eaten more food than females (Madenjian et al. 2015b). Further, whole-fish PCB concentrations were between 17 and 43% greater in males than in females for Lake Whitefish, Burbot, Sea Lamprey, Cisco, Walleye, Summer Flounder (*Paralichthys dentatus*), and Coho Salmon (*Oncorhynchus kisutch*) (Madenjian et al. 2016). Sex-related differences in PCB concentration were not

a consequence of the shedding of eggs by spawning females nor were they due to size differences between sexes (Madenjian 2020). Further, Blukacz et al. (2010) found that male Lake Whitefish from multiple stocks in Lakes Michigan and Superior had positive relationships between relative testes mass and residual soma mass. Parental 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 males (Blukacz et al. 2010).

To our knowledge, only one field study in the Great Lakes has evaluated the influence of physiological condition of female Lake Whitefish on recruitment. Muir (2008) and Muir et al. (2010) attempted to relate size, age, condition, and body composition of female Lake Whitefish to subsequent condition of juveniles in Lake Michigan, but, during 2004-2006, no maternal effect in terms of egg provisioning was detected. Apparently, in periods when food resources are limited, individual females divert most of their energy to egg development at the expense of physiological condition. Density-dependent intraspecific competition or environmental conditions were postulated to be much more consequential drivers of Lake Whitefish recruitment than physiological condition of females (Muir et al. 2010). If condition of a female drops below some unknown threshold, as might have occurred in Lake Michigan after the study was conducted, egg development and recruitment could have been affected.

Research Priority: Conduct laboratory studies to determine if there is a threshold level of adult condition beyond which larval or juvenile condition is reduced.

Prey Selection

Our understanding of prey selection by Lake Whitefish has expanded greatly since the sharp declines in Lake Whitefish growth and condition that followed the arrival of dreissenids in the late 1980s. Unfortunately, linking prey selection to changes in Lake Whitefish recruitment has not occurred. Lake Whitefish is an opportunistic feeder whose prey preferences change with size, age, and location (Hart 1930; Reckahn 1970; Fredricks 1982; Claramunt et al. 2010a; Hoyle et al. 2011; Pothoven et al. 2014; Pothoven 2019). Larvae begin feeding exogenously on small-sized cyclopoid copepods until they reach about 17 mm TL (Freeberg et al. 1990; Johnson et al. 2009; Claramunt et al. 2010a; Hoyle et al. 2011; Pothoven et al. 2014; Pothoven 2019), when they begin switching to cladocerans (*Daphnia* and *Bosminidae*). In July and at sizes >45 mm TL, post-larval YOY develop a subterminal mouth and their prey selection changes to benthic invertebrates such as chironomids and mollusks (Claramunt et al. 2010a; Pothoven et al. 2014). During summer, Lake Whitefish post-larval YOY ate mainly large-bodied cladoceran zooplankton in Lakes Huron and Michigan (Pothoven and Nalepa 2006; Pothoven et al. 2014; Pothoven 2019). Age-1 and older fish ≤ 350 mm TL ate macroinvertebrates, especially Chironomidae in the spring, and zooplankton, if eaten, were generally most important in the summer; molluscs were a minor part of their diet (Pothoven and Nalepa 2006). After the loss of *Diporeia* in Lake Huron, Lake Whitefish >350 mm TL ate mainly native molluscs and dreissenids (Pothoven and Nalepa 2006). Lake Whitefish ate over 900 kt of dreissenids in Lakes Huron (800 kt) and Michigan (109 kt) from 1998 to 2004 (Madenjian et al. 2010), but dreissenids currently make up very little of the Lake Whitefish diet as a consequence of the decline by 2010 of *D. polymorpha* in shallow water and the subsequent increase in *D. bugensis* in deep water (Hoyle 2005; Nalepa et al. 2014). Large-sized Lake Whitefish commonly eat small fish such as YOY Alewife and Rainbow Smelt, Ninespine Stickleback (*Pungitius pungitius*), Round Goby (*Neogobius melanostomus*), and sculpins (Cottidae) (Pothoven and Madenjian 2013). The proportion of fish in the diet of Lake Whitefish in Lake Huron doubled from 2002-2006 to 2007-2011.

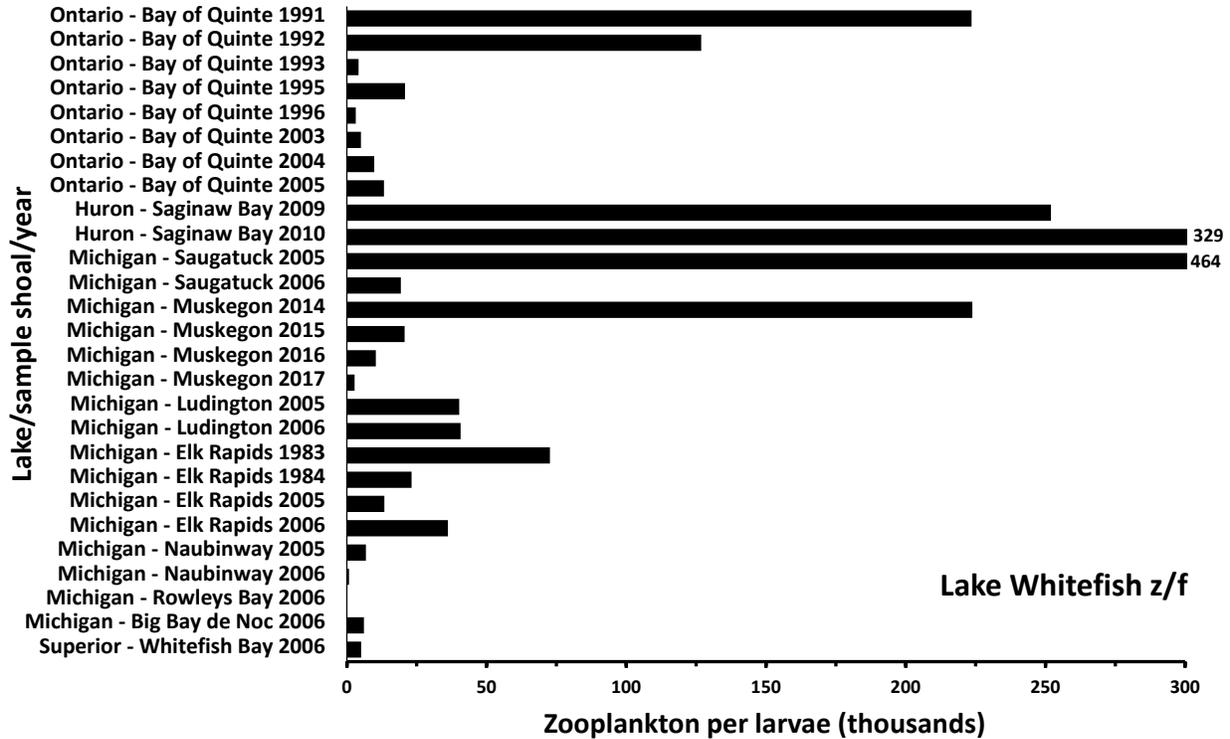
Energy content of prey and energy density of individual Lake Whitefish change substantially throughout life. Energy content of food eaten by post-larval YOY was greater than for large-sized Lake Whitefish in Lake Huron, particularly those adults that ate shelled organisms during 2002-2004 (Pothoven and Nalepa 2006). McNickle et al. (2006) predicted that, unless Lake Whitefish in South Bay, Lake Huron, switched to *Mysis diluviana* from *Diporeia* after establishment of dreissenids, the energy content of its food would decline 57-84%. Pothoven et

al. (2014) reported that energy density of YOY Lake Whitefish in Saginaw Bay, Lake Huron, increased 55% from June to July, when they shifted from eating pelagic zooplankton to eating macroinvertebrates (mainly Chironomidae). Energy density, however, subsequently declined when post-larval YOY switched to feeding on Chydoridae and Sphaeriidae in August and September. Energy density and lipid content of Lake Whitefish were lower in Lake Michigan during 2002-2004 than in 1969-1971, which was attributed to variations in diet and prey energy content, as well as to factors that affect feeding rates such as stock density and prey abundance (Pothoven et al. 2006). Increased consumption of fish by adult Lake Whitefish in Lake Huron from 2002-2006 to 2007-2011 did not improve their condition (Pothoven and Madenjian 2013).

Abundance of cyclopoid and calanoid copepods is an important determinant of Lake Whitefish recruitment in the Great Lakes. These zooplankters are eaten almost solely by young Lake Whitefish from immediately after hatching to the initiation of benthic feeding. Declines in abundance of cyclopoid and calanoid copepods in Lakes Huron, Michigan, and Ontario since 2003 (Barbiero et al. 2009; Hoyle et al. 2011; Vanderploeg et al. 2012; Rudstram et al. 2020), although occurring in offshore waters, may be limiting larval survival and growth in nearshore waters of the main basins of the three lakes. However, zooplankton is still abundant in embayments such as Saginaw Bay (Pothoven et al. 2014) and Green Bay. The ontogenetic shift of YOY fish from eating primarily pelagic zooplankton to eating benthic macroinvertebrates may also be a critical phase in determining Lake Whitefish recruitment, as their energy density increases during this time (Pothoven et al. 2014).

We reviewed studies that reported both zooplankton and YOY (larval and post-larval) Lake Whitefish densities in reproductive habitats in Lakes Superior (Claramunt et al. 2010b), Huron (Pothoven et al. 2014), Michigan (Freeberg et al. 1990; Claramunt et al. 2010b; Pothoven 2019), and Ontario (Hoyle et al. 2011) and found that the ratio of zooplankton density to the density of larval and post-larval YOY Lake Whitefish in nearshore areas is highly variable across the Great Lakes (Fig. 28; Appendix C). The z/f ranged from 96 in Rowleys Bay of the eastern Door Peninsula reproductive habitat in Lake Michigan in 2006 to 464,000 at Saugatuck in the Muskegon reproductive habitat in southeastern Lake Michigan in 2005. The z/f average declined from 47,900 in 1983-1984 to 24,800 in 2005-2006 at Elk Rapids in the Grand Traverse Bay reproductive habitat in Lake Michigan and from 175,200 in 1991-1992 to 9,400 in 1993-1996 and 2003-2005 in the Bay of Quinte reproductive habitat in Lake Ontario. The average z/f across reproductive habitats was 73,000 but it was less than 25,000 in 17 of the 27 observations (Fig. 28). More recently, z/f was generally higher in Saginaw Bay than in other reproductive habitats, and recruitment has been more stable there than in other areas of Lake Huron. Unfortunately, we lack the data to quantify changes in z/f at sites between the peak of Lake Whitefish recruitment in the 1980s-1990s and the current low levels.

Fig. 28. Ratios of the number of zooplankton (z) to the number of larval Lake Whitefish (f) per cubic meter at various locations in Lakes Superior, Michigan, Huron, and Ontario, as reported in studies conducted during 1983-2017 (Appendix C).



Food Web

Food webs across the Great Lakes, but to a lesser extent in Lake Superior, have changed markedly during the past two decades (Ives et al. 2018). Top-down control (i.e., lower trophic levels structured by predation from top piscivores) and bottom-up control (i.e., higher trophic levels structured by restrictions at lower trophic levels) have likely contributed to changing ecosystem dynamics in the Great Lakes (Bunnell et al. 2014; Kao et al. 2016). Evidence (reviewed below) suggests that the primary drivers of food-web dynamics during the past two decades have been bottom-up forces largely associated with (1) reduced nutrient input (all lakes except Erie) coupled with a reduced ability to translate nutrients into fish biomass, and (2) ecosystem engineering by invasive dreissenids, particularly as they relate to changes in Lake Whitefish habitat and food resources. Note that changing nutrient dynamics (1 above) is caused, in part, by dreissenids (2 above), and our knowledge of these two potential drivers of Lake Whitefish dynamics is largely limited to effects at the juvenile and adult life stages—little directed research has been done on effects at early life stages. Adult fish in Lakes Huron and Michigan have undergone a shift from a diet dominated by energy-rich and nutrient-dense native benthic invertebrates (*Diporeia* and *Mysis diluviana*) to energy-poor dreissenids and Round Goby (Pothoven and Madenjian 2013; He et al. 2015; Madenjian et al. 2015a).

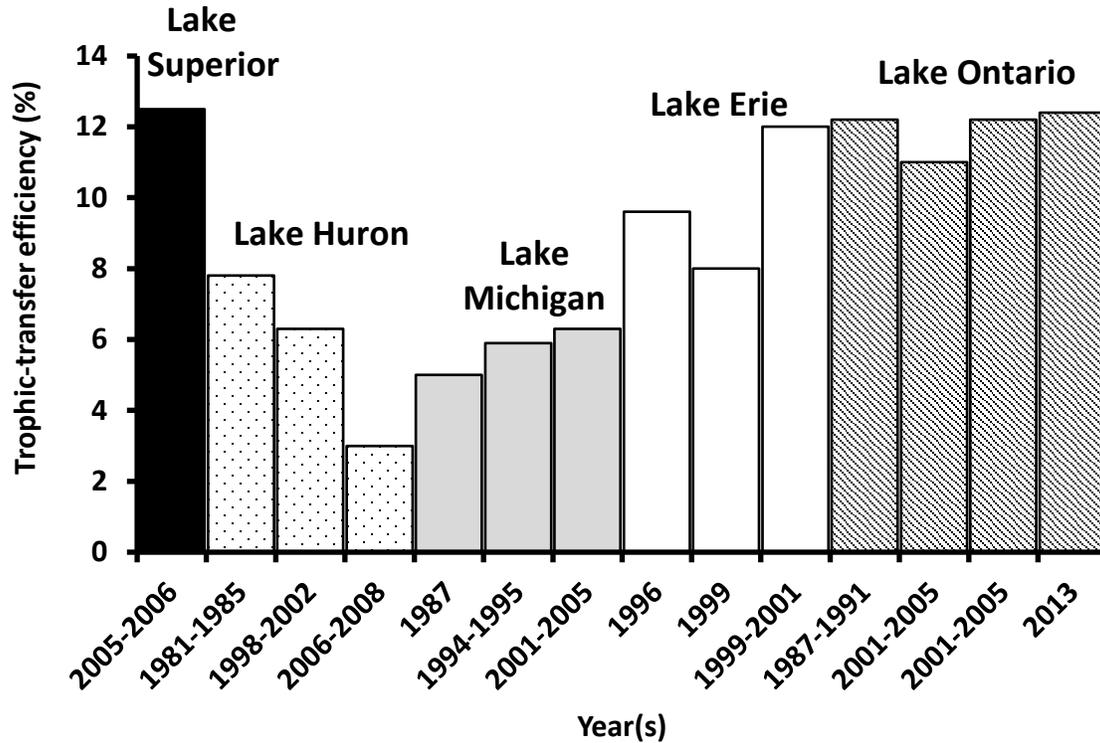
Analysis of stable isotopes has shown how establishment of dreissenids has resulted in Lake Whitefish feeding more benthically inshore. Fera et al. (2017) examined long-term trends in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ stable isotopes from all five Great Lakes. The $\delta^{13}\text{C}$ isotope ratios became more enriched following establishment of dreissenids whereas $\delta^{15}\text{N}$ ratios declined. Lake Whitefish from Lake Superior, which lacks established dreissenid populations, did not show these trends. The changes in stable-isotope ratios, in all lakes except Superior, are consistent with an increased reliance on benthic nearshore energy sources in the diet following a shift in ecosystem energy pathways engineered by dreissenids (Rennie et al. 2009), a finding supported by shifts in Lake Whitefish depth distribution to shallow water and by reduced growth rate of Lake Whitefish (Riley and Adams 2010; Fera et al. 2015; Rennie et al. 2015).

Fagan et al. (2017) conducted various analyses of Lake Whitefish from Lakes Superior, Michigan, and Erie to evaluate links between its decline in growth and condition and the loss of *Diporeia* populations. They reported that Lake Whitefish stocks with higher growth rates and reproductive potential had higher total lipids and that stocks with low concentrations of muscle lipid had smaller eggs, but muscle total lipid and the essential fatty acid DHA (docosahexaenoic acid) were not correlated to *Diporeia* consumption. Lake Michigan fish had lower growth, reproduction, and lipid stores than did fish from stocks in Lakes Erie and Superior. Fagan et al. (2017) concluded that Lake Whitefish in Lake Michigan may still feed on *Diporeia* but that Lake Whitefish appeared to be unable to eat the quantities necessary to maintain historical growth and reproduction. Fish from Lakes Erie and Superior had higher growth rates and lipid values with no indication of reliance on *Diporeia*. These authors concluded that, although differences in prey resources may affect Lake Whitefish stocks, *Diporeia* abundance alone cannot explain differences in condition among the stocks they studied.

Nutrients

Total fish biomass in a lake is limited by nutrients, particularly total phosphorus (TP) concentrations (Stewart et al. 2018), but this relationship can be modified by several interacting biotic and abiotic factors. Modifiers include management activities such as stocking, altering predator-prey balance, changes in fishery regulations, and changes in water clarity owing to changes in nutrient inputs. These factors modify how efficiently and among which fish species energy and material are transferred from lower trophic levels to top predators, which, in turn, influence the production potential of fisheries (Stewart et al. 2018). A measure of food-web efficiency, trophic-transfer efficiency (TTE), accounts for the energy that is transferred between trophic levels in food webs (Stewart et al. 2018). Across the Great Lakes, TTE ranged from 3.4 to 12.7% (mean = 8.9%) meaning that, on average, only 8.9% of the energy from prey fish, larger zooplankton, and benthic organisms (Trophic level III) reaches predatory fish (Trophic levels IV and V). Stewart et al. (2018) found that, during the 1980s, Lake Huron TTE was about 8%, close to the Great Lakes basinwide average, but TTE declined to 6.5% in the early 2000s and to 3.5% in the late 2000s. For comparison, the relatively intact food web of Lake Superior had a TTE of 12.7% during 2005-2006 (Fig. 29). Of interest here, the number of Lake Whitefish recruits-per-spawner-biomass in Lake Superior is slowly increasing while biomass has remained stable, coincident with warming waters (Cline et al. 2013).

Fig. 29. Trophic-transfer efficiency in each of the five Great Lakes during various time periods. Note that two separate assessments of TTE were conducted in Lake Ontario during 2001-2005. Data taken from Stewart et al. (2018).



Dreissenids

A meta-analysis of the effects of dreissenids on freshwater food webs revealed a shift in energy flow from a pelagic-profundal to a benthic-littoral pathway (Higgins and Vander Zanden 2010). That conclusion was supported by large reductions in mean biomass of phytoplankton (-35 to -78%) and zooplankton (-40 to -77%) across 68 lakes and 11 rivers. In contrast, components of the benthic energy pathway all increased post-dreissenids: benthic algal and macrophyte biomass (+170 to +180%), sediment-associated bacteria (about +2,000%), non-dreissenid zoobenthic biomass (+160 to +210%), and total zoobenthic biomass, which includes dreissenid soft tissues (+2,000%). Consistent with the generalized effects of dreissenids on productivity summarized above, the dreissenid-wrought changes in the lower food web shifted energy pathways from pelagic-profundal to benthic-littoral, changing Lake Whitefish distributions and food habits (Higgins and Vander Zanden 2010). In Lake Michigan, annual primary production in offshore waters (>50 m deep) was reduced by about 35% by 2007 when dreissenids were well established (Madenjian et al. 2015a).

Fish Community Effects

Lake Whitefish lives in association with a limited number of other Great Lakes fish depending upon its life stage. Larval Lake Whitefish overlap in time and space with larvae and juveniles of White Sucker (*Catostomus commersoni*), Burbot, Cisco, Round Whitefish (*Prosopium cylindraceum*), Rainbow Smelt, Emerald Shiner, Spottail Shiner (*Notropis hudsonius*), Alewife, Deepwater Sculpin, Trout-Perch (*Percopsis omiscomaycus*), and Round Goby (Faber 1970; Reckahn 1970; Fredricks 1982). Juvenile and adult Lake Whitefish are commonly captured during spring and early summer in deep water (25-50 m) in association with Lake Trout (see Bergstedt et al. 2016), Burbot, Longnose Sucker (*Catostomus catostomus*), and Sea Lamprey whereas, during autumn, adults are commonly captured in shallow water in association with Lake Trout, Cisco, and Walleye.

No studies have established a causal relationship between competition or predation and Lake Whitefish survival or recruitment in the Great Lakes. Madenjian et al. (2008) concluded that Lake Whitefish was likely not affected by Alewife predation in the Great Lakes as their stocks had collapsed before Alewife became abundant and yield increased during years of peak Alewife abundance. Rainbow Smelt has been linked to recruitment failure of Lake Whitefish in small inland lakes of Ontario (Loftus and Hulsman 1986; Evans and Loftus 1987), but those same causal linkages have only been hypothesized in the Great Lakes. Casselman et al. (1996) postulated that resurgence of Lake Whitefish in the Kingston basin of Lake Ontario began with the 1977 year-class due to early and prolonged ice cover, which increased survival of embryos and caused winterkills of the putative larval Lake Whitefish predators, Alewife, and White Perch (*Morone americanus*). Casselman et al. (1996) also speculated that a much-larger resurgence, which began in the mid-1980s (Fig. 6), was facilitated by a relaxation of Rainbow Smelt predation on early life stages of Lake Whitefish—smelt numbers in the Kingston basin having been greatly reduced by a flourishing population of reestablished Lake Trout. Certainly, pre- and post-spawn adult Rainbow Smelt overlap spatially with larval Lake Whitefish as both species are common in shallow nearshore areas during April and May, and larval Lake Whitefish can be eaten by adult smelt (Loftus and Hulsman 1986; Gorsky and Zydlewski 2013). As stated by Gorsky and Zydlewski (2013) “the overall impact that Rainbow Smelt predation will have on Lake Whitefish stocks is dependent on the growth rate of Lake Whitefish, environmental conditions that cause the Lake Whitefish hatching period to coincide with the Rainbow Smelt spawning period, and the degree of overlap in habitat use between spawning Rainbow Smelt, non-spawning subadult Rainbow Smelt, and hatching Lake Whitefish.” Annual monitoring of adult Rainbow Smelt abundance and smelt diet at important Lake Whitefish reproductive habitats would identify the extent of interactions between the two species.

Sea Lamprey predation suppressed abundance of adult Lake Whitefish and their recruitment in the Great Lakes during the middle of the twentieth century (Jensen 1976; Spangler and Collins 1980; Reckahn 1995; Madenjian et al. 2008). Recruitment was likely suppressed by reduced egg deposition caused by Sea Lamprey killing mature Lake Whitefish, but we doubt that present-day Sea Lamprey populations are suppressing Lake Whitefish recruitment. The resurgence in recruitment of Lake Whitefish in the Great Lakes, particularly in Lake Huron, during 1991-2003 occurred despite substantial Sea Lamprey predation on adult fish (Ebener et al. 2010b).

Based on field studies of Round Goby bathymetric distributions, gobies may not affect Lake Whitefish recruitment. Field studies show that most gobies inhabit waters >10 m deep and that a large portion of the goby population inhabits waters >30 m deep during the fall and winter when Lake Whitefish embryos are developing in <7 m of water. Bottom-trawl surveys in 2-100 m of water in Lake Huron during August-November of 1999-2003 found gobies abundant at depths >20 m and basically absent in 10 m of water (Schaeffer et al. 2005). Further, Walsh et al. (2007) during late April 2002-2005 captured large numbers of Round Goby with bottom trawls in 45-130 m of water in Lake Ontario but captured no gobies at 35 m. Both Schaeffer et al. (2005) and Walsh et al. (2007) reported that Round Goby ate mainly dreissenids, *Mysis diluviana*, and other macroinvertebrates. Fish remains were present in the diet of 8% of gobies captured in Lake Ontario (Walsh et

al. 2007) and 13% from Lake Huron (Schaeffer et al. 2005), but the remains could not be identified to genus or species. No fish embryos were found in Round Goby from either of these studies. In summary, there is no empirical evidence that Round Goby inhibits survival of Lake Whitefish embryos, but, nonetheless, Round Goby predation could be included in the embryo survival study we are advocating on selected Lake Whitefish spawning shoals (see Early Life Stages section).

Resource managers are under considerable pressure from commercial fishermen, who claim that predation by Lake Trout is affecting Lake Whitefish recruitment. We do not find evidence for this assertion. We have rarely observed Lake Whitefish in the stomachs of Lake Trout. We offer the following arguments for the lack of a negative influence by Lake Trout on Lake Whitefish recruitment

1. Both species co-evolved in North America and have partitioned their environments by specializing on different food items, indicating that there is little resource competition. Certainly, in Lake Superior, Lake Whitefish recruitment has been stable and is increasing even though Lake Trout density is likely greater than in any other Great Lake. In the Kingston basin of Lake Ontario, a resurgence of Lake Whitefish reproduction took place in the mid-1980s following the reestablishment of a Lake Trout stock (Casselman et al. 1996).
2. Lake Trout does not appear to eat enough Lake Whitefish to affect the stocks (Dryer et al. 1965; Conner et al. 1993; Ray et al. 2007; Gamble et al. 2011; Roseman et al. 2014). Roseman et al. (2014) found less than 1% frequency-of-occurrence of Lake Whitefish in the diet of sport-caught Lake Trout from Lake Huron. Conner et al. (1993), Ray et al. (2007), and Gamble et al. (2011) did not even mention the occurrence of Lake Whitefish in the diet of Lake Trout from Lake Superior.
3. Lake Whitefish and Lake Trout habitats overlap little. Stable-isotope data show little to no niche overlap in diet or habitat between the adults of both species in Lake Superior (Harvey et al. 2008). Bergstedt et al. (2016) reported substantial habitat separation of Lake Whitefish and Lake Trout in Lake Huron with the greatest separation occurring in July. Finally, Jones and Langseth (2012) reported that their “ecosystem model explored tradeoffs between Lake Trout rehabilitation and a yield objective for Lake Whitefish and found little evidence for indirect interactions between the two species.”
4. We infer that the decline of Alewife populations and changes in nutrient cycling due to food-web engineering by dreissenids, coupled with large-scale environment alterations due to climate change, created a situation where Lakes Huron and Michigan are now more conducive to reproduction by Lake Trout than by Lake Whitefish, making it appear that rising numbers of Lake Trout were responsible for declining numbers of Lake Whitefish.

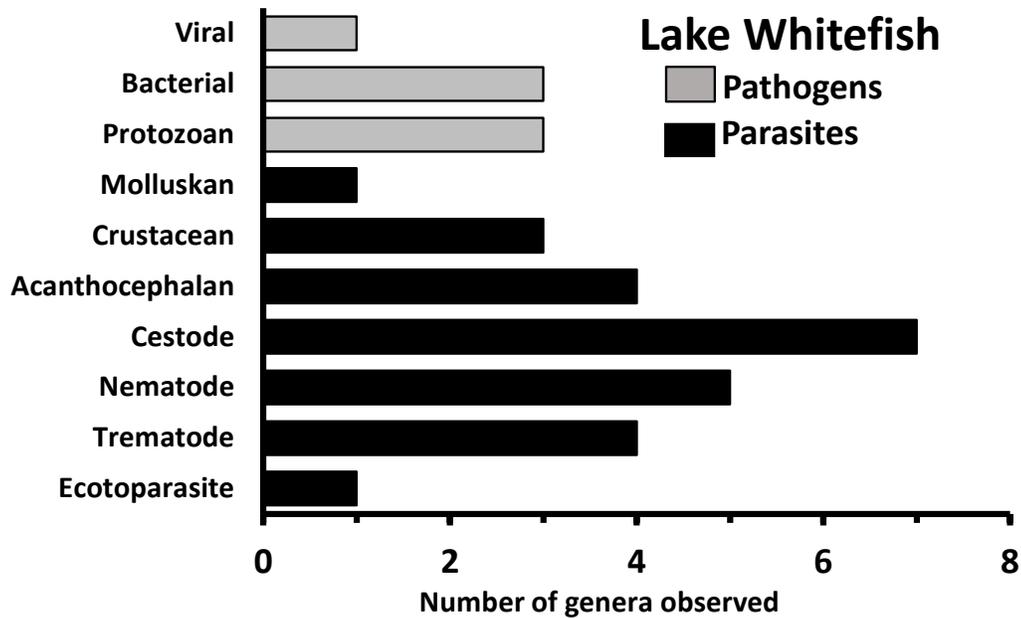
Despite the lack of empirical evidence to date for the role of Lake Trout in the declines of Lake Whitefish, the effects of Lake Trout on Lake Whitefish remain an issue that needs further attention given the perspectives shared by commercial fishermen and indigenous communities (Gobin and Lauzon 2019). These stakeholders have a local perspective and knowledge, which are not included in the empirical studies reported above. Local fishermen have reported seeing higher incidences of Lake Whitefish in the stomachs of Lake Trout, and there are concerns that stocking of Lake Trout coupled with changes in the ecosystem might be influencing Lake Whitefish (Gobin and Lauzon 2019). More targeted research done in collaboration with commercial and indigenous fishermen would help address concerns about the potential impact of Lake Trout on Lake Whitefish.

Fish Health

Pathogens and parasites may have played a role in the decline in Lake Whitefish stocks in the Great Lakes. Since the 1960s, numerous species of microbial pathogens and parasites have been identified in Lake Whitefish from the Great Lakes, with parasites such as cestodes, nematodes, trematodes, and acanthocephalans being much more prevalent than bacterial, viral, or protozoan pathogens (Fig. 30) (Faisal et al. 2011; Loch and Faisal 2011;

Muzzall and Whelan 2011). Whether or not parasites are influencing Lake Whitefish stocks is uncertain and hard to detect, barring mass mortalities. The nematode *Cystidicola* spp. is the most-common nematode found in Lake Whitefish in the Great Lakes (Loch and Faisal 2011), probably because benthic macroinvertebrates, a major food item of Lake Whitefish, are intermediate hosts for *Cystidicola* spp.

Fig. 30. Number of genera of various types of pathogens and parasites found in Lake Whitefish from the Great Lakes. Information taken from tables and text in Loch and Faisal (2011).



The swimbladder nematode *Cystidicola farionis* found in Lake Whitefish from northern Lakes Michigan and Huron has the potential to negatively impact stocks. During 2003-2006, *C. farionis* was found in over 25% of Lake Whitefish from four stocks in northern Lakes Michigan and Huron (Faisal et al. 2010a). Lake Whitefish from northern Lake Huron had much-higher infection rates than those from Lake Michigan. Based on these high infection rates and seasonal fluctuations of infection rates, Faisal et al. (2010a) suggested that *C. farionis* may be a new migrant to Lake Whitefish stocks in Lake Michigan, and it may be responsible for an unknown level of mortality in adults because it alters swimbladder structure and function.

Microbial pathogens are known to be a cause of mortality of adult Lake Whitefish and may also be a leading cause of mortality in larval and pre-recruit Lake Whitefish. Loch and Faisal (2011) reported that the bacteria *Renibacterium salmoninarum*, the causative agent of bacterial kidney disease (BKD), and *Carnobacterium* spp. were widespread among Lake Whitefish stocks and that both have been associated with clinical disease. Moreover, *R. salmoninarum* and *Carnobacterium* spp. can be transmitted vertically from parents to progeny. Other bacteria, such as *Aeromonas salmonicida* and *A. sobria*, are also prevalent in Lake Whitefish. Viral hemorrhagic septicemia virus (HSVv) has been found in Lake Whitefish from the Great Lakes (Thompson et al. 2011). A die-off of Lake Whitefish was first observed in Lake Ontario in 1997 and again in later years, but the cause of the mortalities was not identified (Hoyle 2005).

We suspect HSVv and BKD played a role in the decline in recruitment of Lake Whitefish. A Lake Whitefish (30 examined) collected in northern Michigan waters of Lake Huron in 2005 tested positive for HSVv (Loch and Faisal 2011), and HSVv is now widely distributed throughout the Great Lakes (Cornwell et al. 2015). Adult Lake Whitefish with internal hemorrhaging, the clinical signs of HSVv, are common in Lakes Superior, Huron, and Michigan during May and June as waters begin to warm. Fish with internal hemorrhaging have been observed in Whitefish Bay, Lake Superior; Big Bay de Noc, Lake Michigan; and the Straits of Mackinac (M.P.E., personal observation). Over 60% of adult Lake Whitefish collected from northern Lakes Michigan and Huron during 2003-2006 tested positive for the presence of *R. salmoninarum*, which likely affected their survival (Faisal et al. 2010b; Loch and Faisal 2011). Lake Whitefish collected from northern Michigan waters of Lake Huron in 2004 showed clinical signs of BKD (Fig. 31). Preliminary results from a 2018-2019 study found a higher prevalence of BKD and *Carnobacterium* spp. in adults from stocks exhibiting poor recruitment (eastern Door Peninsula and Alpena) than in adults from stocks experiencing average or good recruitment (Menominee River and Saginaw Bay) (T. Loch, Michigan State University, personal communication, 2020).

Fig. 31. Dorsal view of the body cavity of a Lake Whitefish collected from northern Lake Huron near Detour, Michigan, in 2004 showing active clinical signs (white nodules) of *Renibacterium salmoninarum*, the causative agent of bacterial kidney disease (BKD).



MANAGEMENT CONSIDERATIONS

In February 2018, a workshop was held by the Great Lakes Fishery Commission (GLFC) for managers from Lakes Superior, Huron, and Michigan to discuss the consequences of reduced Lake Whitefish recruitment and to develop priorities for research on recruitment and management actions (GLFC 2018). Managers identified four high-priority activities—management of dreissenids, management of other community factors, managing Lake Whitefish harvest, and stocking Lake Whitefish. In the sections that follow, we make specific recommendations to fishery agencies regarding these priorities.

Management of Dreissenids

We propose implementation of an experimental dreissenid control program on selected Lake Whitefish spawning shoals and in adjacent larval habitats. We are not promoting control of dreissenid populations in offshore areas. We hypothesize that dreissenids have changed the productivity of Lake Whitefish spawning shoals by degrading bottom substrates (Fig. 32) and reducing the abundance of copepods important in the diet of larval whitefish. Habitat degradation by dreissenids has likely altered spawning-substrate selection by adult Lake Whitefish, increased embryo mortality, and increased intraspecific competition for zooplankton by larvae, which, in turn, reduces larval growth and increase mortality.

The goal of dreissenid control is to increase both primary production and recruitment of Lake Whitefish in reproductive habitats of Lakes Michigan, Huron, and Ontario. The objectives would be to determine the effects of dreissenids on Lake Whitefish embryo survival and on zooplankton densities with the penultimate goal of designing a control program to improve recruitment. Because there are billions of eggs deposited annually by adult fish in the Great Lakes, a small decline in natural mortality of, for example, 0.04%, from 99.95% to 99.91%, from embryo to age 1 should result in a nearly two-fold increase in abundance at age 1. Thus, changes in natural mortality do not have to be large to change recruitment. We envision that natural mortality of embryos and larvae could be decreased enough through dreissenid control to increase recruitment of Lake Whitefish.

Dreissenid control should be initiated on small degraded reproductive habitats such as in Grand Traverse Bay in Lake Michigan, Bay of Quinte in Lake Ontario, South Bay in Lake Huron, and other areas where both control and subsequent biological sampling would be logistically doable. Bottom substrates, zooplankton densities, embryo and larval survival, and community interactions at dreissenid control sites should be compared to small spawning shoals not degraded by dreissenids in the same lake. In addition, these same studies should be conducted in Lake Superior and in inland lakes without dreissenids to assess whether differences are due to control actions or other random effects. Michigan is already conducting an experimental dreissenid control program on an historically used spawning reef in northern Lake Michigan near Leland. If control is found to be cost effective, control should be expanded to larger reproductive habitats along the eastern Door Peninsula in Lake Michigan and to Alpena and the Fishing Islands in central Lake Huron. These three reproductive habitats accounted for roughly 75% of the commercial Lake Whitefish yield from the Great Lakes before the declines in recruitment.

Fig. 32. Historically used Lake Whitefish spawning shoal (Horseshoe Reef) in Grand Traverse Bay, Lake Michigan, covered with *Cladophora* spp. and dreissenids in August 2006 (photograph provided by E. Olsen, Grand Traverse Band of Ottawa and Chippewa Indians).



Management of Other Community Factors

Managers at the February 2018 workshop wanted to know the effect of Lake Trout predation on Lake Whitefish; the potential effects of Lake Whitefish and Lake Trout competition for spawning habitat; the effects, if any, on behavior of Lake Whitefish when it overlaps spatially with Lake Trout other than at spawning; and, the effects of any changed behavior on Lake Whitefish productivity (GLFC 2018). Although scientific evidence indicates little predation or competition for food resources between the two species, information on interactions between the two species on spawning shoals or during early life stages is scant. Reefs along the southern shore of Drummond Island in northern Lake Huron where Lake Trout (see Riley et al. 2014) and Lake Whitefish spawn are recommended as a study site.

Harvest Management

Managers at the workshop also questioned if Lake Whitefish fisheries were sustainable and, more specifically, if harvest levels are inhibiting stock recovery and if the current economic and cultural value system can be adjusted to be compatible with current stock levels (GLFC 2018). We are not prepared to discuss adjustment of perceptions or values of commercial fishermen, but this topic certainly has been addressed for numerous fisheries around the world (Huhmarniemi and Salmi 1999). On the other hand, we can discuss sustainability of Lake Whitefish stocks and the fishery.

Numerous studies have pointed out that contemporary Lake Whitefish stocks are not capable of supporting the late 1990s and early 2000s yields because of changes to the food web brought about by dreissenids (McNickle et al. 2006; Bunnell et al. 2009b; Rennie et al. 2012; Gobin et al. 2015; Fera et al. 2017).

Deroba and Bence (2012) evaluated several harvest-control rules for Lake Whitefish in the Great Lakes and pointed out that a biomass-based harvest-control rule achieved more yield, less risk of low biomass, and only a modest increase in yield variability than did the constant-fishing-mortality-control rule currently used to manage harvests in 1836 Treaty waters. They also pointed out that reliable estimates of unfished biomass could provide substantial value to managing the fishery. Spawning-stock-biomass per recruit (SSBR) in an unfished stock is a biological reference point used to set Lake Whitefish harvest limits in 1836 Treaty waters (Ebener et al. 2005; Deroba and Bence 2012). Because determining SSBR in an unfished stock involves knowing its natural mortality rate, reliability of harvest limits in fished stocks can be improved by knowing more about natural mortality rate of Lake Whitefish and, subsequently, SSBR in unfished stocks. Areas where unfished biomass can be estimated include Grand Traverse Bay, Lake Michigan; the Alpena area, Lake Huron; and along the western side of the Keweenaw Peninsula because these areas were unexploited prior to the mid-1970s and early 1980s (Peck 1994; M.P.E., personal observation).

Relevant here, Molton et al. (2013) reported that a total-annual-mortality-harvest-control rule of 65% had a high risk of overexploiting low-productivity spawning stocks, which could reduce aggregate yield more than total mortality rates of 35-55%. In addition, 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 stocks. Accordingly, Molton et al. (2013) encouraged the implementation of precautionary harvest rates for mixed-stock fisheries to protect less-productive stocks. As we have shown, nearly all Lake Whitefish fisheries on the Great Lakes exploit mixed stocks. In fact, low-productivity stocks benefit more from implementation of an appropriate target mortality rate than from more-frequent stock assessments (Li et al. 2016). A hint of the impact of fishing on Lake Whitefish stocks is evidenced in the ability of stocks inside refuges to increase faster than those outside of refuges in the Apostle Islands area of Lake Superior (Zuccarino-Crowe et al. 2016).

Management Priority: Current harvest-control rules, particularly in the 1836 Treaty waters of Lakes Michigan and Huron (see Ebener et al. 2005), should be modified to reflect the new productivity regime.

Our review supports revising the current management regime for Lake Whitefish and provides the basis for doing so. Managers can decide on the best options given competing priorities. We recommend

- Stock-specific management of harvest instead of the current mixed-fishery approach
- Statistical analyses to estimate the unfished biomass of the most-important populations to aid in estimating harvest limits
- Creation of refuges or protected areas that provide Lake Whitefish with added protection from exploitation for at least a portion of the year to stabilize adult abundance caused by declining recruitment
- Additional protection from exploitation for the least-productive stocks
- Expansion of the length of spawning-season closures in the states of Wisconsin and Michigan and implement a spawning-season closure in the Province of Ontario
- Reduction of the maximum annual mortality of the harvest-control rule to <65%

Stocking

Fishery managers have again asked whether stocking of Lake Whitefish should be considered as a response to stakeholder concerns over declining stocks. Here we review past stocking efforts undertaken in the Great Lakes and briefly review relevant stocking programs outside of the Great Lakes. Historical Lake Whitefish stocking efforts in the Great Lakes were evaluated by Koelz (1926) and Todd (1986), and the logistics of augmenting modern-day stocks in Lakes Michigan and Huron were evaluated by Bence et al. (2019).

Historical Stocking in the Great Lakes

In response to severe declines in Lake Whitefish harvests across the Great Lakes during the late 1800s, substantial stocking programs were implemented by the Dominion of Canada and the U.S. (Clark 1910; Downing 1910; Reighard 1910). Between 1870 and 1960, fishery agencies stocked over 32 billion Lake Whitefish larvae in the Great Lakes (Todd 1986). Based upon the historical plantings, Reighard (1910) recommended stocking levels of 100 larvae•pound⁻¹ of fish harvested. Bringing harvest back up to a peak of about 10 million kg would require increasing the harvestable stock by 3 million kg, which, at 100 larvae per acre, would require planting 600 million larvae annually.

Koelz (1926) noted that taking and hatching eggs of commercial species for larval planting was increasing in the Great Lakes but that, despite the practice having enthusiastic supporters, judging its efficacy was difficult, given the natural fluctuations in fish populations. He urged that “studies to evaluate the effectiveness of propagation should be begun without delay.” Despite claims of commercial fishermen that stocking bolstered their yield, Van Oosten (1942) was unable to establish a causal relationship between larval plantings and commercial harvest during 1920-1940 and concluded that yield in Lake Erie was not dependent on, or noticeably affected by, larval plantings. Similarly, in the Bay of Quinte, Lake Ontario, as many as 208 million larvae were planted per year between 1927 and 1945. No correlation existed between the number planted during 1924-1946 and the harvest of Lake Whitefish during 1929-1951 (Lapworth 1956). The largest number of larvae planted (208 million in 1927) was followed by the lowest harvest of the entire time period (43,100 kg in 1932), and, although no larvae were planted in 1945, the commercial harvest in 1950 was approximately normal at 73,500 kg (Lapworth 1956). Finally, Lasenby et al. (2001) wrote that early Lake Whitefish plantings involved the release of embryos or larvae for a 50-year period before studies demonstrated that larval plantings made no significant contribution to established Lake Whitefish stocks in the Great Lakes (Van Oosten 1942; Lapworth 1956; Christie 1963).

Following the work of Lapworth (1956), a decade-long, alternate-year larval planting experiment was undertaken in the Canadian waters of the Kingston basin of Lake Ontario. Between 13 and 55 million larvae (mean 27.7 million) were planted in the Bay of Quinte in even-numbered years during 1944-1954, yet these plantings failed to produce a zig-zag pattern of yield (Christie 1963). Estimates of recruits per spawner in the Bay of Quinte were not affected by the fry plantings (Christie 1963).

Life Stage for Stocking

Lake Whitefish stocking likely would have to use advanced life stages, such as fall fingerlings or age-1 fish, to have prospects of success. Fall fingerlings and yearlings have been stocked successfully in Lake Simcoe, Ontario, but fall fingerlings have been the primary life stage used since the late 1980s because they are cheaper to raise than yearlings (Lasenby et al. 2001; Amtstaetter and Willox 2004). Stocking continues to the present day in Lake Simcoe at about 100,000 fingerlings per year. Despite these stocking levels, catch rates of wild and stocked Lake Whitefish in index nets and the recreational fishery have declined since about 2009 after dreissenids and Round Goby established. *Diporeia* is not native in Lake Simcoe (Finigan et al. 2018) so dreissenids could not have affected *Diporeia* in the same way as in the Great Lakes. Summer fingerlings were found to be less desirable for augmenting stocks in the Great Lakes because of their poor survival whereas fall fingerlings or yearlings displayed better survival (Bence et al. 2019).

Stocking in Europe

European countries have established successful large-scale stocking programs for European Whitefish and Vendace. Stocking programs were undertaken to either supplement fishery yield and dampen fluctuations in yield (Leskelä et al. 2002; Gerdeaux 2004; Eckmann et al. 2007; Salojärvi and Huusko 2008; Jokikokko and Huhmarniemi 2014) or to establish stocks (Rasmussen 1990; Berg et al. 1994). Stocking of six million European Whitefish in the Gulf of Bothnia during 1995-1998 produced commercial-fishery yields of 55 to 90 kg•1,000⁻¹ fingerlings stocked during 1999-2002, but yields of stocked fish were not uniformly beneficial on a regional basis (Leskelä et al. 2002). Stocked European Whitefish made up 50% of the fishery yield from the Sotkama waterway in northern Finland and produced yields that averaged 57 kg•1,000⁻¹ fingerlings stocked (Salojärvi and Huusko 2008). Yield from a dipnet fishery in the River Tornionjoki, a tributary to the northern Baltic Sea, increased during the 1980s and 1990s in response to the stocking of millions of YOY anadromous European Whitefish, and, when stocking was reduced, yields declined (Jokikokko and Huhmarniemi 2014). Stocked fish made up 62% of the 2003 year-class of YOY European Whitefish captured in Lake Constance in south-central Europe (Eckmann et al. 2007), but the authors could not determine if hatchery fish actually increased abundance of the extant population or if stocking only increased intraspecific competition without enhancing cohort abundance. Abundance and fishery yield of European Whitefish in Lake Geneva, Switzerland, increased within the first 10 years after stocking began (Gerdeaux 2004), but subsequent increases in abundance and fishery yields were driven by increased recruitment that resulted more from improved water quality and climate change than from stocking.

Extrinsic Recruitment Drivers

If Lake Whitefish recruitment dynamics are largely driven or modified by density-independent processes, stocking is not a wise management tool unless the life stage stocked is older than the life stage that is subject to the mortality constraint. The NAO, ice cover, wind-driven currents, and zooplankton abundance (factors that are responsible for much of the variation in the stock-recruitment relationship) are density-independent and cannot be overcome by stocking. Straille et al. (2007) reviewed a 52-year-long record of European Whitefish year-class strength and reported that it was influenced by the NAO even though the lake was experiencing strong anthropogenic influences on Lake Whitefish stock dynamics due to oligotrophication, intensive fishing, and large-scale stocking.

Food Web Limitation

Currently, fishery managers are facing the same pressure that they did during the late 1800s to resort to stocking as a management tool, but a major difference is that contemporary Great Lakes food webs differ markedly from those of the late 1800s; in particular, the near absence of *Diporeia* outside of Lake Superior has greatly diminished the prey base (Fig. 29). The reduced prey base has slowed Lake Whitefish growth, and growth rate plays an important role in Lake Whitefish recruitment. Also, if Great Lakes food-web productivity has changed as discussed herein, then stocking could be counterproductive and generate competition or other density-dependent dynamics, which negatively affect existing stocks. Stocking of only 11,000 YOY European Whitefish in a 22-ha eutrophic lake in Denmark caused *Daphnia* spp. populations to decline by 88% over the course of one year and caused the near depletion of large *D. pulex* and *D. magna* populations, which led to increased chlorophyll *a* concentrations and decreased Secchi-disk readings, despite no changes in TP or total nitrogen in the lake (Berg et al. 1994). Benthic invertebrates also declined after introduction of YOY whitefish (Rasmussen 1990; Berg et al. 1994). Predation by European Whitefish also restructured zooplankton populations in a pre-alpine lake in France (Perga et al. 2010) by reducing abundance of *Daphnia* spp. and increasing abundance of *Bosmina longirostris*.

We offer five arguments for not stocking Lake Whitefish to supplement extant Lake Whitefish stocks in the Great Lakes.

1. Results from over 50 years of stocking Lake Whitefish larvae demonstrate clearly that this life stage is not effective at augmenting stocks in the Great Lakes. The number of larvae that would have to be stocked to bolster abundance and yield far exceeds the capacity of the present hatchery systems. In addition, given that the mortality rate of early life stages is currently high in the Great Lakes, stocking larvae would not overcome the bottleneck.
2. The life stage at which year-class strength is established is uncertain but could occur after the first year of life. Therefore, an effective stocking program might require rearing fish to age 1 or older, sharply increasing hatchery costs (see Bence et al. 2019) and domestication effects.
3. Lake Whitefish growth and its subsequent survival and reproduction are strongly influenced by density-independent variables, such as climate, which cannot be mitigated by stocking.
4. Lower-food-web changes over the last two decades have reduced the productivity of the Great Lakes for Lake Whitefish such that stocking could further exacerbate the recruitment problem by suppressing naturally produced fish.
5. The widescale movement of Lake Whitefish documented in the mark-recapture studies reviewed earlier suggests that stocked fish might also move widely, thus potentially influencing reproductive success of smaller, vulnerable stocks. Furthermore, given widescale movement, stocking in one jurisdiction would undoubtedly influence stocks in other jurisdictions.

Our arguments against stocking Lake Whitefish to augment stocks and yields do not consider the extensive analysis of survival and economic costs addressed by Bence et al. (2019) who concluded “under pessimistic assumptions regarding survival, a major enhancement of Lake Whitefish fishery yields through hatchery operations is probably not feasible.” Further, as natural reproduction by Lake Trout and Chinook Salmon (*Oncorhynchus tshawytscha*) has increased in the Great Lakes, salmonine stocking programs have been severely reduced or eliminated (Pratt et al. 2016; Claramunt et al. 2019; Borgeson et al. 2020; Lenart et al. 2020), and, since Lake Whitefish stocks are self-sustaining, we suspect stocking them would also need to be eliminated after a short period. We suspect that a few isolated successes can be achieved by stocking Lake Whitefish, but we also believe, given the food-web changes in the Great Lakes and our collective experience with stocking salmonines, that stocking Lake Whitefish on top of naturally reproducing stocks will ultimately fail to consistently supplement its abundance or stabilize yields. There are far-cheaper and more-feasible management options and assessment approaches worth considering before venturing into stocking.

If stocking is used as a tool to augment Lake Whitefish stocks, hatchery fish should be marked to distinguish them from those naturally produced. Marking techniques have improved and now include coded-wire tags (Bronte et al. 2012), thermal marks (Negus 1997), dyes (Eckmann et al. 1998, 2007), genetic markers (Eldridge et al. 2002; Brenden et al. 2018), and oxytetracycline (Fielder 2002). Regardless of the method used to mark fish, agencies will have to expand their capacity to collect, store, and analyze marks, all of which will increase costs. Before stocking Lake Whitefish is considered as a method to increase yield in the Great Lakes, it would be prudent to obtain more-definitive answers about the causes of the declines in recruitment. Although we do not support supplemental stocking of Lake Whitefish, we do support management efforts to reestablish stocks by stocking in historically important habitats where Lake Whitefish has been extirpated.

Agency Approaches

We foresee that the institutional framework by which Lake Whitefish is managed under the aegis of the GLFC can be improved and offer the following

- Lake committees should task their technical committees with establishing working groups with the responsibility to develop surveys that will lead to effective long-term monitoring of Lake Whitefish recruitment.
- Agencies such as CORA, states of Wisconsin and Michigan, OMNRF, and Canadian First Nations, all of which manage large-scale commercial fisheries and burgeoning recreational fisheries for Lake Whitefish, should make Lake Whitefish research a high priority. Towards that end, we recommend that agencies either commit to maintaining existing long-term ecological studies that include Lake Whitefish or commit to funding long-term studies related to Lake Whitefish. We acknowledge that fishery management agencies must prioritize research and assessment activities and that internal priorities for allocating research and assessment exist within every agency. Agencies should consider eliminating or modifying short-term and targeted studies to allow for more long-term ecological studies. A re-assessment and, if warranted, a re-allocation of assessment efforts is needed regularly to maintain cost effectiveness.
- Current recruitment indices for Lake Whitefish should be evaluated to determine if they could be integrated to produce a lakewide index for each year-class. Although there does not appear to be synchrony in recruitment among stocks in a lake (Zischke et al. 2017), it is obvious that large spawning aggregations influence lakewide estimates of recruitment (Fig. 6) and yield (Figs. 15, 16). Therefore, a lakewide estimate of recruitment would prove useful for monitoring Lake Whitefish stocks. For example, sampling programs could be integrated into a single index of recruitment that includes the post-larval YOY sampling being conducted for the Modeling Subcommittee of the Technical Fisheries Committee, which oversees management of fisheries in 1836 Treaty waters of Michigan; onboard monitoring of commercial trapnet fisheries by CORA; and fishery-independent surveys targeting Lake Whitefish and Lake Trout.
- Bottom-trawl surveys conducted by the U.S. Geological Survey's Great Lakes Science Center (USGS-GLSC) on Lakes Michigan and Huron appear to track Lake Whitefish recruitment and abundance and can be modified to provide additional information. Lake Whitefish captured during these surveys should be aged, and the spatial scale of the sampling should be modified to better monitor recruitment of the most-productive stocks (Fig. 14). We recommend that the Council of Lake Committees consider modifying its Memorandum of Agreement with the USGS-GLSC to include assessment of Lake Whitefish in Lakes Michigan and Huron and collection of the demographic data needed for estimation of recruitment indices.
- The genetic mixed-stock analysis of Lake Whitefish stocks in Lakes Superior, Huron, Erie, and Ontario should be expanded (see Isermann et al. 2020). Collection of tissue samples for genetic analysis should become an integral component of all biological sampling by fishery agencies.

RESEARCH PRIORITIES

In this document, we identified seven research priorities related to understanding Lake Whitefish recruitment dynamics

1. Disentangling biotic and abiotic effects on recruitment
2. Expanding field sampling and modelling efforts of ice cover, storm events, and current patterns to understand their effects on early life stages and integrating these efforts with stock demographics from SCAA stock assessments
3. Compiling basinwide tagging data with recent acoustic-telemetry and genomic data to better elucidate stock structure
4. Estimating the contribution of each reproductive habitat (stock) to fishery yield
5. Estimating stock-recruitment relationships of each exploited stock
6. Establishing early-life-stage monitoring sites across the Great Lakes to understand how embryo survival is affected by physical and biological processes
7. Conducting laboratory studies to determine if there is a threshold level of condition beyond which larval or juvenile condition is reduced

Some of these research priorities were established a century ago, which shows how hard implementation can be. Foremost, we need to know what factor or combination of factors is causing the current low levels of recruitment and, if there is a recruitment constraint currently limiting reproduction, at what life stage the constraint is expressed. Our list of proposed research priorities encompasses unanswered research priorities from old studies and unanswered priorities from more-recent studies that have emerged since 2014. Based on our consolidation of processes that influence Lake Whitefish recruitment in the Great Lakes, we present the following research questions in order of importance. Although the feasibility of going from a research-finding to a management action was considered, it was not the primary driver of our ordering.

YOY and Juvenile Life Stages

1. At what densities and composition of zooplankton are larval growth and survival negatively affected?
2. How do survival and growth of larvae, post-larval YOY, and juvenile life stages vary with changes in ecosystem productivity?

Reproductive Habitat

3. Is control of dreissenids on selected spawning shoals economically feasible as a method to improve recruitment?
4. Can productivity of reproductive habitat in the main basins of Lakes Michigan, Huron, and Ontario be sufficiently improved to increase recruitment?
5. What physical and biological processes are drivers and constraints to Lake Whitefish recruitment in the Great Lakes, and do they produce synchrony across regions in recruitment (Zischke et al. 2017)?
 - a. Do variations in wind-driven-water circulation patterns disperse larval Lake Whitefish in ways that affect homing back to natal spawning shoals?
 - b. Can physical-biological models of recruitment be created like that for Lake Erie Walleye (Zhao et al. 2009)?

6. How does the early onset of ice cover over spawning shoals influence survival and growth of Lake Whitefish embryos?
 - a. Can the effects of ice cover be disentangled from other factors (such as predation, zooplankton production, and food-web effects) that affect survival and growth of embryos?
7. Which tributaries historically supported spawning aggregations of Lake Whitefish?
 - a. What are the prospects for rehabilitating or restoring tributary spawning stocks outside of Green Bay, Lake Michigan?
8. Can existing river spawning stocks in Green Bay, Lake Michigan, be used to enhance depleted river-run stocks or to reestablish extirpated river-run stocks?
 - a. Is rehabilitation of tributary spawning stocks enhanced by having spawning migrations in nearby tributaries?

Stock Structure

9. What is the contribution of each spawning shoal and nursery area to fishery yields?
10. What are the genetic and phenotypic variations among Lake Whitefish from different spawning shoals, and, if there is substantial phenotypic variation among spawning shoals, can these be related to spawning behavior and habitat selection—timing of spawning, site location (river vs. lake), substrate characteristics, embayment vs. main-basin shoals?
11. Do genetic and phenotypic structuring occur within a spawning-shoal complex, and, if so, does that affect early-life-stage survival, growth, and subsequent spatial distribution?
 - a. Is variability in the timing of larval hatch related to life-history structuring among spawners, i.e., large females spawn first and first-time spawners last.

Fish Community Interactions

12. Are diseases reducing recruitment?
13. What are the density and diet of Round Goby on Lake Whitefish spawning shoals from mid-November through mid-May, and can gobies suppress recruitment?
14. Are there competitive interactions between Lake Trout and Lake Whitefish for spawning habitat?
15. Do early life stages of Lake Trout suppress Lake Whitefish recruitment?

Addressing the questions above will involve a combination of laboratory and field studies and modeling exercises. First, models that elucidate how physical and biological factors couple to influence recruitment dynamics will need to be developed (Ludsin et al. 2014; Fussell-DeVanna et al. 2016; Bunnell et al. 2018). Laboratory studies will be required to investigate how changes in zooplankton density and quality could potentially affect larval Lake Whitefish growth and survival (Rennie 2013) in the wild. After these zooplankton and larval relationships are established in the laboratory, agencies should consider measuring them in various reproductive habitats in the Great Lakes to confirm or refute the laboratory findings. We are emphatic that the studies of Reckahn (1970), Hoagman (1973), Freeberg et al. (1990), Claramunt et al. (2010a, b) and Hoyle et al. (2011) should be replicated broadly across the Great Lakes in habitats that are highly productive (Lake Erie, Saginaw Bay, and Green Bay), moderately productive (North Channel and northern Lake Michigan), and marginally productive (main basins of Lakes Huron and Michigan and Georgian Bay). These same studies should

be conducted at multiple sites in Lake Superior and outside the Great Lakes basin to act as controls for the findings in the four lower lakes.

Tributary, embayment, and connecting-channel habitats have borne the brunt of anthropogenic degradation. Many of the tributaries to Green Bay on Lake Michigan once harbored spawning aggregations of Lake Whitefish, but habitat degradation eliminated these stocks by the 1860s (see Wells and McClain 1973). Over the last few decades, sizable spawning runs have reestablished in tributaries to Green Bay, such as the Menominee, Fox, and Oconto Rivers (Ransom et al. 2021), and their combined recruitment is sufficient to support both recreational and commercial fisheries, which combined harvest hundreds of thousands of fish annually from lower Green Bay (S. Hansen, Wisconsin DNR, personal communication, 2019). There are other tributaries to Green Bay that could potentially support spawning aggregations, but these tributaries have not been surveyed to assess if Lake Whitefish are spawning in them.

The St. Marys and Detroit Rivers historically supported large aggregations of Lake Whitefish but overfishing and channelization to support interlake shipping essentially eliminated these stocks (Todd 1986; Roseman et al. 2007). The Detroit River stock supported a fall seine fishery that captured adult fish, and the stock spawning in the river quite likely supported commercial-fishery yields in Lake Erie because larvae would drift downstream. The St. Marys River rapids contained a large aggregation of Lake Whitefish that supported an Indigenous dipnet fishery and possibly yields throughout the river and the North Channel of Lake Huron. Restoring reproductive habitat and rehabilitation of spawning aggregations in both of these connecting channels would likely increase recruitment to fisheries in Lakes Huron and Erie. Innovative genetic or amino-acid isotope techniques should be developed to estimate the historical and present-day contributions of river spawning stocks to extant stocks and fishery yields.

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APPENDICES

Appendix A

Summary of physical attributes for spawning shoals in our proposed Lake Whitefish management areas in each Great Lake: the amount of reproductive habitat (ha); the mean percent of ice cover on December 20, February 15, and March 30 during 1973-2017; the maximum wind fetch (km); and the direction of maximum fetch. The amount of reproductive habitat was estimated by measuring the distance along the shoreline of spawning shoals and adjacent shallow embayments out to a depth of 7 m using Google Earth. Maximum fetch is the longest distance between the center of a reproductive habitat and the opposite side of the water body.

Lake	Proposed Management Area	Spawning Shoal (Number/Name)	Reproductive Habitat <7 m (ha)	Percent Ice Cover		Maximum Fetch Direction/Length (km)	
				Dec/Feb/	Mar		
Superior	NW Ontario	1 Thunder Bay west	2,681	65/98/93		NE 35	
		2 Thunder Bay north	1,550	65/98/93		SW 45	
		3 Black Bay	6,630	65/98/93		SW 45	
		4 Nipigon Bay	2,681	65/98/93		SE 33	
		5 Terrace Bay	1,533	8/54/38		SW 353	
	Eastern Ontario	6 Gargantua	1,233	5/76/50		W 425	
		7 Agawa Bay	1,644	5/76/50		NW 300	
		Whitefish Bay	8 Sandy Islands	1,384	27/91/94		NW 340
	9 Gros Cap		3,282	27/91/94		NW 45	
	Central Michigan		10 Birch Point	553	27/91/94		NW 50
			11 Tahquamenon Bay	6,581	27/91/94		NE 50
			12 Grand Island	183	15/78/67		NNW 265
			13 Autrain Point	1,798	15/78/67		NNW 265
			14 Autrain Island	615	15/78/67		NNW 260
		Keweenaw Peninsula	15 Laughing Fish Point	767	15/78/67		NNW 250
			16 Big Bay Reef	132	15/71/63		NNE 220
			17 Huron River Reef	476	15/71/63		NNE 225
			18 Point Abbaye Reef	432	15/71/63		NE 220
			19 Pequaming	286	15/71/63		NE 70
	20 Buffalo Reef		487	15/71/63		E 270	
	21 Bete Grise		786	11/58/23		E 245	
	22 Eagle River Shoals		679	8/53/37		SW 265	
	Apostle Islands	23 Outer Island	345	31/86/62		NE 345	
		24 North Twin Island	213	31/86/62		NE 360	
		25 South Twin Island	177	31/86/62		NE 365	
		26 Rock Island Shoal	179	31/86/62		NE 365	
		27 York Island Shoal	47	31/86/62		NE 370	
		28 Michigan Island	148	31/86/62		NE 350	
		29 Cat Island	195	31/86/62		NE 360	
		30 Otter Island	72	31/86/62		NE 370	
		31 Oak Island Shoal	9	31/86/62		NE 365	
		32 Madeline Island Reef	234	31/86/62		NE 360	
	NW United States	33 Grand Portage	747	8/55/27		SSW 168	
		34 Isle Royale	386	3/45/26		SSE 352	
Huron	Northern Michigan	35 Rabbits Back	690	10/81/43		SE 310	
		36 St. Martin Bay	943	10/81/43		SE 305	
		37 Cedarville	2,694	10/81/43		SE 282	
		38 Drummond Island	1,023	10/81/43		SSE 325	

Lake	Proposed Management Area	Spawning Shoal (Number/Name)	Reproductive Habitat <7 m (ha)	Percent Ice Cover Dec/Feb/Mar	Maximum Fetch Direction/Length (km)		
Michigan	Northern Ontario	39	Cheboygan	4,607	10/81/43	ESE 255	
		40	Cockburn Island	983	6/56/13	SSE 325	
		41	Burnt Island	3,866	6/56/13	SSE 310	
		42	South Bay mouth	1,962	6/56/13	S 285	
		43	South Bay	1,135	4/80/46	S 285	
	Central Ontario	44	Fishing Islands	12,539	20/90/59	NW 290	
		45	Douglas Point	544	20/90/59	NW 285	
	Southern Ontario	46	Sarnia	1,852	16/74/33	NNW 330	
	Saginaw Bay	47	Tawas Point to Oak Point	151,753	56/97/47	NE 255	
	Central Michigan	48	Alpena	26,164	19/72/13	SSE 230	
		49	Thessalon River to Blind River	3,553	36/99/93	SE 75	
	North Channel	50	Blind River	1,678	36/99/93	WSW 70	
		51	Clapperton Island	285	36/99/93	SSE 20	
		52	Bedford Island	188	36/99/93	N 30	
		53	Vidal Bay Shoal	2,888	36/99/93	NW 80	
		54	Henry Island	1,727	36/99/93	NNW 30	
		55	Horace Point	256	36/99/93	NW 85	
		North Georgian Bay	56	Mink Island to Bad River	44,230	38/95/83	SSE 180
		South Georgian Bay	57	Bennets Bank to McQuade Bay	20,501	9/66/46	NW 170
		58	Nottawasaga Bay	10,257	9/66/46	NW 200	
		59	Meaford	898	9/66/46	NNW 170	
	Michigan	Western Michigan	60	Big Bay de Noc	18,512	66/98/83	SW 175
			61	Eastern Door Peninsula	5,888	7/43/5	S 395
			62	Menominee River	133		0
			63	Fox River	566		0
		Northeast Michigan	64	Portage Bay	1,288	7/43/5	SSW 460
			65	Naubinway	10,718	22/94/59	SW 390
			66	Straits of Mackinac North	1,986	22/94/59	SW 30
			67	Straits of Mackinac South	687	22/89/52	NW 65
68			Sturgeon Bay	2,613	8/89/52	SW 225	
69			Garden Island to Hog Island shoals	12,249	8/89/52	WNW 65	
70			Beaver Island North	905	8/89/52	NW 55	
71			Fox Island	1,061	8/89/52	SW 190	
72			Fisherman's Island	818	8/89/52	NW 100	
Grand Traverse Bay			73	Elk Rapids	234	12/49/34	N 75
		74	Mission Point	746	12/49/34	N 120	
		75	Lee Point	233	12/49/34	S 15	
		76	Northport Bay	395	12/49/34	SE 20	
Leland		77	Lighthouse Point	814	12/49/34	NW 95	
		78	Leland	700	4/23/8	NNW 115	
		79	Pyramid Point	863	4/23/8	WSW 105	
		80	Platte Bay Shoal	1,065	4/23/8	NW 85	
Muskegon		81	North Manitou Island Shoal	2,123	4/23/8	SW 225	
		82	South Manitou Island Shoal	863	4/23/8	SW 260	
		83	Muskegon River	717		0	
	84	Muskegon Lake	221	4/23/8	SSW 190		
Erie	Western basin	85	Detroit River	400		0	
		86	Western basin	65,113	26/81/12	ENE 340	
Ontario	Bay of Quinte	87	Glenora	975	43/98/60	SW 5	
		88	Big Island	3,186	43/98/60	NW 10	

Lake	Proposed Management Area	Spawning Shoal (Number/Name)	Reproductive Habitat <7 m (ha)	Percent Ice Cover Dec/Feb/Mar	Maximum Fetch Direction/Length (km)
		89 Belleville Airport	2,441	43/98/60	NE 22
	Kingston basin	90 Prince Edward Island	2,965	5/48/4	SSW 85
		91 NE Prince Edward Island	1,912	5/48/4	SE 75
		92 Amherst Island	2,218	5/48/4	SSW 90
		93 Chaumont Bay	2,374	17/94/59	SW 5

Appendix B

For Lake Whitefish in each proposed management area of the Great Lakes, the amount of reproductive habitat (ha); the mean, minimum, and maximum annual reported commercial-fishery yield (kg) during 1981-2016; and the estimated number of age-4 recruits during 1986-2016. The number of age-4 recruits was estimated through statistical catch-at-age analysis. In some management areas, the number of recruits was obtained by summing estimates of age-4 recruits in adjacent management units (see Modeling Subcommittee, Technical Fisheries Committee 2016, 2017).

Lake	Proposed Management Area	Reproductive Habitat (ha)	Yield (kg), 1981-2016 ⁴			Number of Age-4 Recruits, 1986-2016 ⁵		
			Mean	Min.	Max.	Mean	Min.	Max.
Superior	NW Ontario	15,100	162,100	98,100	426,800	No data	No data	No data
	Eastern Ontario	2,900	15,700	0	83,700	No data	No data	No data
	Whitefish Bay	11,800	314,200	139,100	682,800	427,400	258,400	789,600
	Central Michigan	3,400	43,800	14,700	118,900	138,600	74,800	350,500
	Keweenaw Peninsula	3,300	224,200	15,300	485,100	No data	No data	No data
	Apostle Islands	1,600	414,800	97,600	815,100	No data	No data	No data
	NW United States	1,100	1,500	10	10,200	No data	No data	No data
Huron	Northern Michigan	10,000	587,000	82,100	1,095,500	1,810,900	508,800	3,148,800
	Northern Ontario	7,900	264,400	31,000	521,900	972,100	26,400	2,717,800
	North Channel	10,600	197,400	99,700	302,800	563,600	107,000	1,587,400
	Central Ontario	13,100	328,900	127,100	694,800	1,703,300	13,600	4,337,200
	Southern Ontario	1,900	362,000	206,400	530,200	2,473,300	594,100	5,394,600
	Central Michigan	26,200	207,500	15,200	389,100	2,418,100	554,700	5,860,100
	Saginaw Bay	151,800	286,900	29,800	496,600	2,590,100	1,294,100	3,533,000
	North Georgian Bay	44,200	60,800	33,400	91,200	255,500	91,400	508,100
	South Georgian Bay	31,700	61,400	18,700	141,700	358,000	30,300	1,189,600
Michigan	Northeast Michigan	31,000	611,500	180,600	1,217,800	1,173,500	470,900	2,069,400
	Grand Traverse Bay	2,400	91,100	15,900	232,300	163,400	22,100	334,000
	Leland	5,600	26,000	0	72,100	59,000	4,800	187,500
	Muskegon	900	123,300	39,600	309,300	229,200	16,400	754,700
	Western Michigan	26,400	1,703,000	1,126,200	2,619,100	1,652,800	272,500	3,459,900
Erie	Western basin	65,500	241,100	4,500	613,300	1,008,200	600	10,754,100
Ontario	Bay of Quinte	6,600	15,000	1,300	46,200	No data	No data	No data
	Eastern basin	9,500	78,000	12,200	254,400	No data	No data	No data

⁴Yield for years 1993-2016 in Lake Ontario, 1985-2016 in S. Georgian Bay and Southern Ontario, and 1996-2016 in N. Georgian Bay.

⁵Recruits for years 1996-2016 in N. Georgian Bay and 2005-2016 in Saginaw Bay.

Appendix C

The ratio of zooplankton (z) to larval Lake Whitefish (f) and catch-per-unit effort (CPUE) of larval and post-larval young-of-the-year (YOY) Lake Whitefish reported in studies conducted at various reproductive habitats throughout the Great Lakes during 1983-2017. Zooplankton and larvae were generally captured with neuston nets of 333, 700, or 1,000 microns mesh whereas post-larval YOY fish were captured with seines during the day. Zooplankton densities and larval CPUE are expressed as the number per cubic meter of water. Post-larval YOY CPUE is expressed as the number per seine haul, except in Lake Ontario where CPUE is expressed as the number per bottom-trawl tow.

Lake	Location	Year	z/f	CPUE	
				Larvae	YOY
Ontario	Bay of Quinte	1991 ⁶	223,560	0.0169	80.0
		1992 ⁶	126,825	0.0633	46.8
		1993 ⁶	4,182	0.3418	6.3
		1995 ⁶	20,782	0.1325	54.3
		1996 ⁶	3,162	1.0688	5.3
		2003 ⁶	5,061	0.0903	16.2
		2004 ⁶	9,811	0.0446	0.0
		2005 ⁶	13,287	0.0287	5.7
Huron	Saginaw Bay	2009 ⁷	251,957	0.0320	1.8
		2010 ⁹	328,857	0.0040	1.5
Michigan	Elk Rapids	1983 ⁸	72,671	0.0161	No sampling
		1984 ⁸	23,155	0.0393	No sampling
		2005 ⁹	13,452	0.0224	20.0
		2006 ⁹	36,164	0.0061	5.7
	Big Bay de Noc	2006 ⁹	6,084	0.1027	13.3
		Naubinway	2005 ⁹	6,782	0.0148
	2006 ⁹		768	0.1785	5.7
	Rowleys Bay	2006 ⁹	96	1.9223	7.4
	Ludington	2005 ⁹	4,0205	0.0113	40.0
		2006 ⁹	4,0679	0.0086	7.8
	Muskegon	2014 ¹⁰	223,819	0.37	21.0
		2015 ¹⁰	20,686	0.94	86.0
		2016 ¹⁰	10,403	0.04	84.0
		2017 ¹⁰	2,746	0.15	200.0
	Saugatuck	2005 ⁹	464,261	0.0045	2.2
		2006 ⁹	19,310	0.0242	3.6
Superior	Whitefish Bay	2006 ⁹	5,110	0.0714	12.0

⁶Hoyle et al. (2011).

⁷Pothoven et al. (2014).

⁸Freeberg et al. (1990).

⁹Claramunt et al. (2010b).

¹⁰Pothoven (2019).

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