Rationale, Prospects and Recommended Actions for Rehabilitation of Native Forage Fishes in Lake Michigan

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Native Planktivore Task Group Report

to the

Lake Michigan Committee

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Contents

Executive summary

The non-native forage base in Lake Michigan is declining to all-time low levels of abundance along with the productivity of the lake ecosystem, making the sustainability of the valuable salmonine fishery uncertain. Interest in restoring native planktivores, cisco, deepwater cisco (aka “chubs”) and emerald shiners, has increased among managers and stakeholders. These fishes were the energy conduits that converted offshore/benthic primary and secondary production into fish flesh for consumption by top predators, and man.

Currently reintroduction efforts are underway at various stages and scales in lakes Michigan, Huron, and Ontario. The obvious historical factors credited with the declines of these fishes - overfishing, potentially competing non-native planktivores, and poor water quality for over wintering eggs – are now reduced, and the niche formerly occupied by these natives fishes appears to be available. Residual populations of the original bentho-pelagic coregonine complex - Cisco *Coregonus artedi*, Bloater *C. hoyi*, Deepwater Cisco *C. johannae*, Kiyi *C. Kiyi*, Blackfin Cisco *C. nigripinnis*, Shortnose Cisco *C. reighardi*, Long-jaw Cisco *C. alpenae* and Shortjaw Cisco *C. zenithicus* - has been reduced to much smaller populations of bloater in deep water, and cisco along the Michigan shoreline.

Restoration options are limited to one or more of the following: 1) reintroductions of lost or depleted forms from existing Great Lakes populations, 2) protection of residual populations to foster expansion, and 3) restoration of habitat, if that is perceived to be the problem. For reintroductions, cisco would be the easiest to implement and have the most positive ecological impact. Uncertainty exists around which source-populations to use and the genetic risks associated with using extant populations outside Lake Michigan for gamete sources.

Even though productivity of the system has been reduced since the invasion of dressinid mussels, the zooplankton community in Lake Michigan is similar to that in Lake Superior, where that lakes’ full complement of coregonines has persisted. The collapse of *Diporeia* poses additional uncertainty, however *Mysis* continue to remain abundant.

There are risks associated with all strategies, including doing nothing at all, hence more work is needed to come to some universal understanding among agencies of the probable risks compared to those risks currently perceived.

Introduction and rationale

Charge from Lake Michigan Committee

For the last 50 years, populations of the non-native Alewife *Alosa pseudoharengus* and rainbow smelt *Osmerus mordax* have served as the primary forage fish in Lake Michigan (Jude et al. 1987; Madenjian et al. 1998). Since the 1990s these species have declined drastically from predation and low levels of recruitment (Madenjian et al. 2002, 2005). Additionally, declines in primary and secondary production have also occurred in Lake Michigan (and elsewhere; Fahnenstiel et al. 2010; Barbiero et al. 2012; Vanderploeg et al. 2012). Both of these changes have raised concern about the sustainability of the salmonine predator populations and the valuable fisheries they support.

To partially address this concern, the Lake Michigan Committee formed a Native Planktivore Task Group in the spring of 2012 to scope out the issues related to the restoration of native planktivores in Lake Michigan. The charge was to develop a “white paper” that articulates the candidate species for consideration, the impediments as well as opportunities for reintroduction or recovery, specific management actions that can foster both, and a summary of research/information needs.

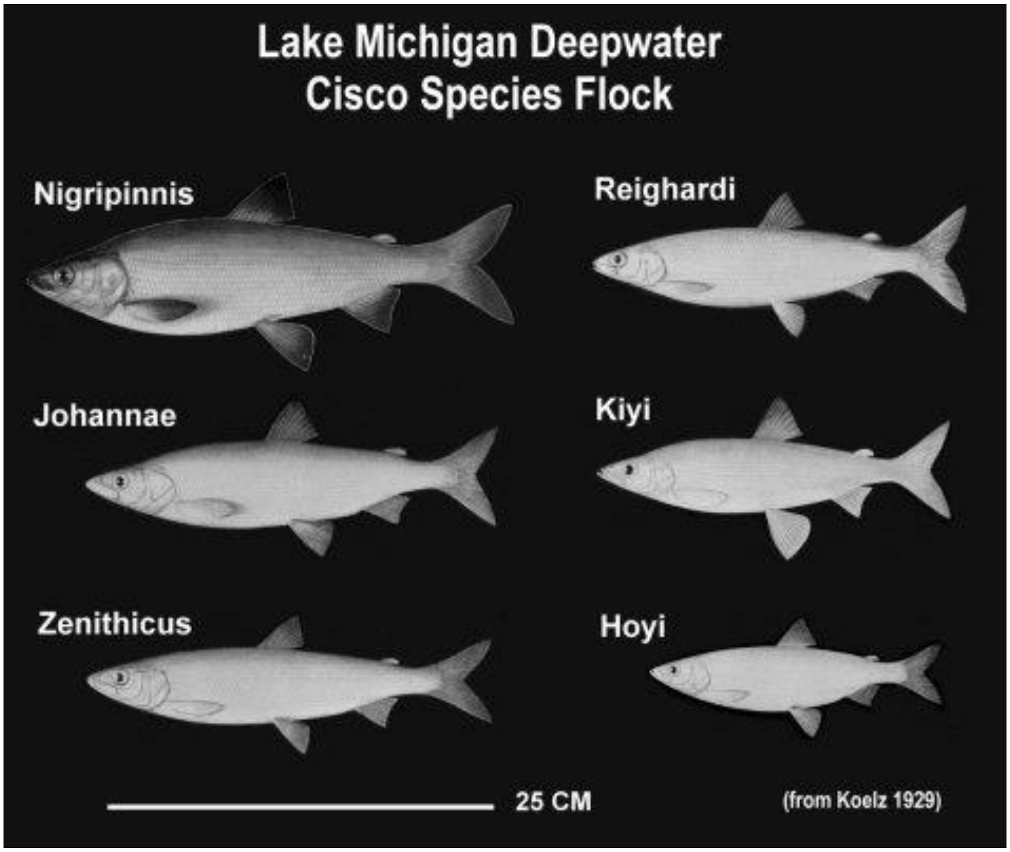

Figure 1. The deepwater Ciscoes from Lake Michigan (individual figures from Koelz 1929).

Rationale for the charge

Historically, the Great Lakes had one of the most diverse assemblage of coregonines in North America (Koelz 1929). Eight deepwater species were originally recognized. Lakes Michigan and Huron contained the most diverse group of deepwater coregonines: Bloater *Coregonus hoyi*, Deepwater Cisco *C. johannae*, Kiyi *C. Kiyi*, Blackfin Cisco *C. nigripinnis*, Shortnose Cisco *C. reighardi*, Long-jaw Cisco *C. alpenae* and Shortjaw Cisco *C. zenithicus* (Figure 1; Table 1). It is now thought that the latter two species were actually synonymous hence *C. alpenae* was for some time no longer recognized, although Eshenroder et al. (2016) recently suggested this change may be inaccurate based on historical descriptions of spawning aggregations (Koelz 1929) and isotope-driven diet information (Schmidt et al. 2011). In addition to the deepwater assemblage which was mostly bentho-pelagic, the more pelagic-oriented Cisco *C. artedi* (formerly known as lake herring) was also present in all lakes. The Deepwater, Longjaw, Shortnose Ciscoes are considered extinct while the others underwent extirpation due to overfishing and predation by the invasive sea lamprey *Petromyzon marinus* during the last century (Smith 1968).

Table 1. Previous distribution and status of Cisco and deepwater Ciscoes in the Laurentian Great Lakes (From Eshenroder et al. 2016).

Major Form (species)	**Lake**					
	Superior	**Michigan**	**Huron**	**Erie**	**Ontario**	**Nipigon**
Longjaw *alpenae*	–	Extinct	Introgressed	Extinct	–	–
Cisco *artedi*	**Extant** **Ubiquitous/ abundant**	**Extant** **restricted**	**Extant** **restricted**	Extirpated	**Extant** **very restricted**	**Extant** **?**
Bloater *hoyi*	**Extant**	**Extant** **restricted**	Introgressed	–	Reintroduced	**Extant**
Deepwater *johannae*	–	Extinct	Extinct	–	–	–
Kiyi *kiyi*	**Extant** **very abundant**	Extirpated	Introgressed	–	Extirpated	–
Blackfin *nigripinnis*	Uncertain	Extirpated	Extirpated	–	–	**Extant**
Shortnose *reighardi*	Uncertain	Extinct	Introgressed	–	Extinct	–
Shortjaw *zenithicus*	**Extant**	Extirpated	Introgressed	–	–	**Extant**

Of the native deepwater bentho-pelagic coregonines (Van Oosten and Deason 1938; Smith 1964; 1968) that served as prey for Lake Trout *Salvelinus namaycush* and Burbot *Lota lota* in Lake Michigan, only the Bloater and isolated populations (mostly in the northeast) of Cisco remain. Lake Whitefish *C. clupeaformis* and Round Whitefish *Prosopium cylindraceum* persisted in self-sustaining populations but were never common forage for predators. Bloater populations have remained low since the mid-1990s (Madenjian et al. 2002) due to poor recruitment, although the 2016 year-class resulted in the highest density in the USGS bottom trawl survey since 1990. With the rapid loss of Alewives observed in Lake Huron (Riley et al. 2008), which resulted in the demise of the Chinook salmon fishery (Brenden et al. 2012), and with no alternative pelagic forage fish available, concern is growing among management agencies and some users as to the future of the forage base in Lake Michigan and predators it supports.

Status and trends in forage fish and plankton communities

Alewives, Bloater, and Rainbow Smelt have dominated the diet of salmon and trout in Lake Michigan since the 1960s, with Rainbow Smelt contributing to the diet of Lake Trout likely since 1940s, as they were rare in stomachs previously (Van Oosten and Deason 1938). Since the early 1970s, both the biomass and numerical density of Alewives have been declining in part from predation by Chinook Salmon that limit parental stock size and recruitment, and from productivity changes due to pollution abatement and redirection of energy by dressinid mussels. The last 10 years has experienced the lowest Alewife densities on record (Figure 2), and have prompted state agencies to reduce stocking of Chinook Salmon to reduce predatory demand for the remaining Alewives while accommodating increasing levels of Chinook Salmon natural reproduction. Over 60% of Chinook Salmon captured in the open water sport fishery in 2016 were wild (Kornis et al. 2017).

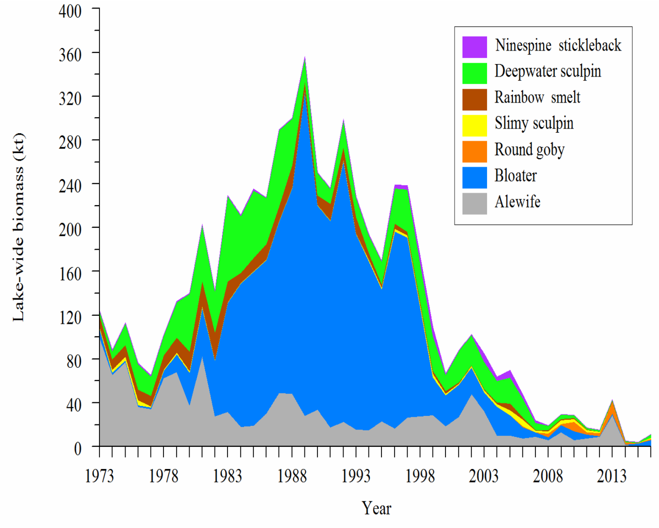

Figure 2. Estimated forage biomass by species in Lake Michigan from bottom trawls during 1973-2016. (Bunnell et al. 2017).

Bloater biomass has also been depressed since the mid-1990s from very low levels of recruitment since the early 1990s, and although several mechanisms (sculpin egg and fry predation, climate, fecundity/ condition reductions) have been suggested, no one factor fully explains the declines in recruitment (Bunnell et al. 2014). Biomass of Rainbow Smelt has also been low for the past 15 years. The consumption by predators of both Bloater and Rainbow Smelt is now only a fraction of that when prey populations where larger.

Changes in primary and secondary production have also occurred in Lake Michigan where trophic conditions now resemble that of Lake Superior (Barbiero et al. 2012; Figure 3). Increasing oligotrophication in the open waters of Lake Michigan is evidenced by:

- declines in spring total phosphorus and particulate phosphorus,
- increases in spring soluble silica concentrations consistent with decreases in primary productivity,
- increasing water transparencies,
- lack of a characteristic spring diatom bloom,
- loss of cladocerans and the increased importance of calanoid

copepods, in particular *Limnocalanus,*

- decreases in *Diporeia* in offshore waters (indirectly related)

See Bunnell et al. (2017) for a detailed description of changes in Lake Michigan. All these changes have resulted in algal productivity and crustacean zooplankton communities similar to that of Lake Superior in recent history (Barbiero et al. 2012). While lower primary and secondary productivity may be responsible for the decline in recruitment of forage fishes observed during recent years, sustained lower productivity and the current prey base will certainly limit the future apical predator biomass in Lake Michigan.

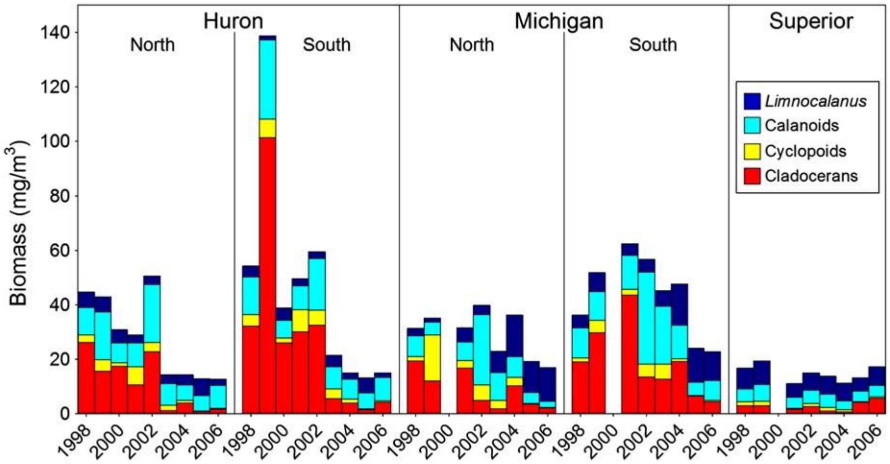

Figure 3. Average basin-wide biomass for crustacean zooplankton by lake. (Figure 8 from Barbiero et al. 2012).

The Cisco and extant deepwater ciscoes

Cisco

The Cisco is a schooling pelagic planktivore found in cold lakes in Canada and northern United States (Scott and Crossman 1973). They can also survive in mesotrophic lakes if sufficient oxygen exists (MacKay 1963). Cisco were found in all the Great Lakes and contributed to most of the recorded landings of the historical commercial fishery. Predation on Cisco and deepwater Ciscoes moved offshore energy from primary and secondary sources to support the largest Lake Trout populations in the world. Thus ciscoes provided the key mechanism to transfer energy from phytoplankton and zooplankton up the food chain, and from deepwater to shallow water and the hypolimnion to support predatory fish.

Egg deposition by Cisco spawning aggregations in near and offshore areas in the fall provided a 6-month resource subsidy from the offshore pelagia to the nearshore benthic community in the form of energy-rich eggs (Stockwell et al. 2014). In contrast to Cisco, Alewife and Rainbow Smelt also deposit eggs in nearshore areas and tributaries but in spring where the duration of availability as food to benthivores is only days or weeks as opposed to months for cisco. Alewife and Rainbow Smelt are also rich in thiaminase (Fitzsimons et al. 1998), the cause of thiamine deficiency that is thought to reduce egg viability and fry survival in salmonines that consume them (McDonald et al. 1998).

Cisco are greatly depleted throughout the Great Lakes (Fitzsimons and O’Gorman 2006) although some recovery has occurred in Lake Superior (Bronte et al. 2003; Stockwell et al. 2009). As with most coregonines, these fish historically had distinct morphological types (Koelz 1929) that still persist today (Yule et al. 2013). Koelz (1929) originally described three cisco morphotypes as a ‘slim terete’ morphotype (*Leucichthys artedi artedi*), a‘deep compressed’ morphotype (*L. artedi albus*), and a deep-bodied form (*L. artedi manitoulinus*) resembling tullibee in western Canadian lakes. The most common Great Lakes Cisco was a pelagic form (*L. artedi artedi*) that tended to spawn in embayments, shallow waters, but also pelagically in deep water (Smith 1956; Dryer and Beil 1964). In Saginaw Bay, Lake Huron commercial fishermen reported fall spawning runs up the Saginaw River prior to industrial pollution (Van Oosten 1929). Given the diversity of reported spawning habitat historically, it is not clear whether Cisco are just non-specific with respect to spawning habitat preference or whether habitat preference varies with Cisco morphotypes. Multiple spawning strategies are adaptive in that it can maximize habitat use and resource partitioning and insure some recruitment occurs. Spawning aggregations of the pelagic form (*artedi artedi*) in Green Bay, Lake Michigan and Saginaw Bay, Lake Huron were immense (Koelz 1929), and represented most of the harvestable biomass from Lakes Michigan, Huron and Superior but a considerable biomass of the *albus* form was taken from western Lake Erie and the Detroit River, that was once the largest freshwater fishery in the world prior to their decline in 1920s (Van Oosten 1930). *Albus* populations are found in northern Lake Huron and an *albus*–like form found in Grand Traverse Bay (Eshenroder et al. 2016). Across the Great Lakes today, the largest populations are in Lake Superior (*artedi artedi*), but densities there may be less than those historically (Stockwell et al. 2009).

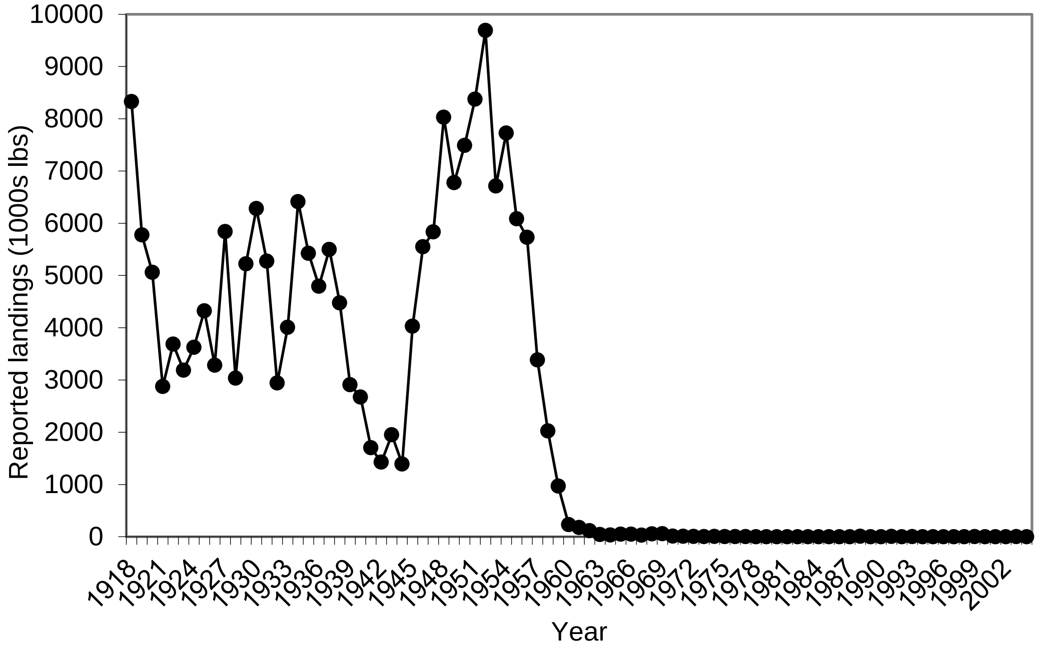

Figure 4. Commercial landings of Cisco in Lake Michigan, 1918-2007(Baldwin et al. 2009).

During the first half of the 1900s, Cisco frequently constituted from 25% to > 50% of the commercial production in the upper four lakes (Smith 1972). Most Cisco harvested from Lake Michigan in the late 1800s to mid-1900s came from the Michigan and Wisconsin waters of Green Bay (Smith 1956; Baldwin et al. 2009) but smaller fisheries existed throughout the lake. An annual average of 4.85 million pounds was harvested from Lake Michigan from 1918 to 1958 before its major decline (Figure 4). In 1952, Green Bay produced 39% of Cisco from all United States waters of the Great Lakes with most fish landed in Michigan waters of the bay during 1948-1952 (Smith 1956).

Overfishing, habitat degradation, and invasive species are credited with the collapse of Ciscoes and deepwater Ciscoes throughout the Great Lakes during 1900-1965 (VanOosten 1929; Anderson and Smith 1971; Smith 1972; Wells and McLain 1973; Bailey and Smith 1981; Selgeby 1982; Fleischer 1992), although the relative contribution of these effects is still debated.

Lightly-regulated fisheries on fall spawning aggregations reduced parental stocks and led to recruitment overfishing likely beyond levels that were sustainable (Selgeby 1982). Habitat degradation via pollution in Saginaw Bay appeared to be correlated with reduced growth rate of Cisco (VanOosten 1929). Sediments containing high levels of silt and organic matter was thought to lower Cisco egg viability in western Lake Superior (Anderson and Smith 1971). Madenjian et al. (2008a), in a retrospective analysis of the impacts of Alewives, indicated that collapses of the Cisco populations in Lakes Michigan, Huron, Erie, and Ontario were likely related to environmental degradation of key spawning areas in conjunction with overfishing, rather than due to the effects of Alewives. Dissolved oxygen concentrations below 1 mg/L were measured in lower Green Bay under the ice, on the lake bottom, as early as 1938, and substantially worsened by 1955 (Epstein et al. 1974), and should have resulted in > 90% egg mortality (Brooke and Colby 1980). Overwinter dissolved oxygen conditions are now suitable for egg incubation in Green Bay and likely elsewhere (Madenjian et al. 2011). In contrast, Wells and McLain (1972, 1973) concluded that invasive sea lamprey and Alewife populations affected fish communities in Lake Michigan more than either accelerated eutrophication or fishery exploitation.

Sea lamprey predation on Cisco were suggested (Pritchard 1931; Smith 1972) and Rainbow Smelt were also implicated in the declines in Cisco, especially in Lake Superior, because larval and young-of-the-year Cisco are consumed by Rainbow Smelt (Anderson and Smith 1971; Selgeby et al. 1978; Swenson and Heist 1981; Loftus and Hulsman 1986; Evans and Waring 1987). Bronte et al. (2003) suggested that if Rainbow Smelt were depressing Cisco abundance in Lake Superior, the 90% reduction in Rainbow Smelt biomass that occurred during 1978–1981 should have led to increased recruitment of Ciscoes that did not occur until 1984. Myers et al. (2009) suggested that added pressure of Rainbow Smelt predation may be sufficient to dampen the magnitude of year-classes that otherwise may have been successful in the absence of Rainbow Smelt. Definitive proof regarding all hypotheses is lacking.

Madenjian et al. (2008a) concluded that Alewives likely had minimal impact on Ciscoes, because the latter have an early life history similar to that of Lake Whitefish that were and continue to be unaffected by Alewives. They concluded that evidence for adverse effects of Alewives on Cisco abundance was weak, given the mismatch in the timing of the Alewife invasions, longevity of Ciscoes, and timing of Cisco population collapses. Yellow perch *Perca flavescens* (Pritchard 1931), ruffe *Gymnocephalus cernuus* (Selgeby 1998), and lake whitefish (Stockwell et al. 2014) consume Cisco eggs over the winter, and possibly this could restrict recruitment at low Cisco population sizes. Shallow water predation is only important if Cisco egg deposition to limited there, which is not the case with the varied life history of this fish.

Lake-wide bottom-trawl and mid-water-trawl/hydroacoustic surveys, long used to measure Cisco recruitment and standing stock abundances in Lake Superior (Bronte et al. 2003), encounter very few if any Cisco in Lake Michigan (see Figure 7), which further reinforces the limited residual distribution and extremely low densities of Cisco. Captures of a few juvenile fish in Wisconsin's waters of Green Bay in 2013, adults in the Beaver Islands, and farther south at the Ludington pump storage site, suggest some expansion or that other small populations exist. A form of Cisco referred to as *albus-like* in Eshenroder et al. (2016) is common in northern Lake Huron, and populations are much larger than those in Lake Michigan. Population expansion outside the northern main basin of Lake Huron and the North Channel has not occurred to date and suggests that some ecological factor, is impeding range expansion. Attempts to collect gametes during 2015-2017 have yet to detect large aggregations of adults and may hamper adequate collections (Roger Gordon; personal communication).

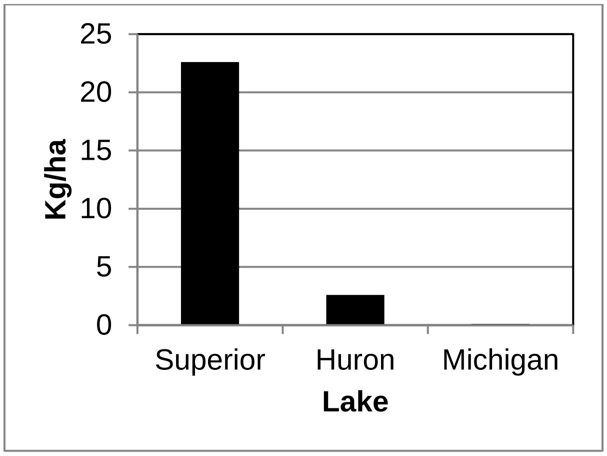

Figure 5. *By lake comparison of densities of adult Cisco in fall as measured by hydroacoustics. Source: Yule et al. 2013; D. Warner, USGS-GLSC; R. Claramunt, MIDNR*.

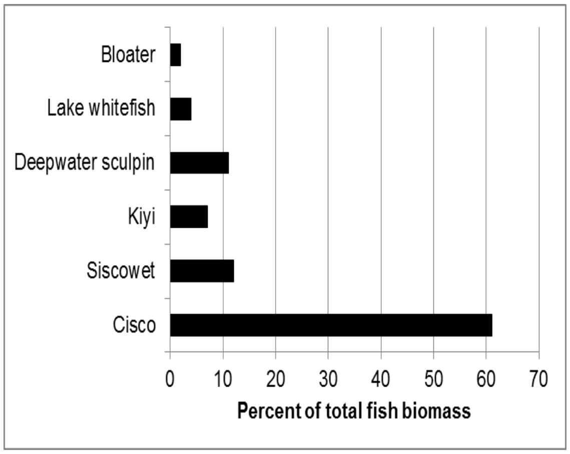

Figure 6. *Percent of total fish biomass for top 6 species in Lake Superior, 2001-2008 (from Gorman et al. 2012).*

Currently Lake Superior contains the largest Cisco populations in the Great Lakes, and during 2001-2008, Cisco made up 61% of the total fish biomass (Gorman et al. 2012; Figure 5, 6) but has declined due to poor recruitment. These populations support a commercial harvest in excess of annually 1.5 million pounds in Minnesota (fresh market) and Wisconsin waters (roe market) (Figure 7). Fisheries take about

900,000 lbs in Thunder Bay and Black Bay, Ontario. However, Lake Superior Cisco have only had one large year class (2003) since 1990, so fishing levels are being reduced and concerns exist about the potential implications of continued recruitment failure (USGS 2016).

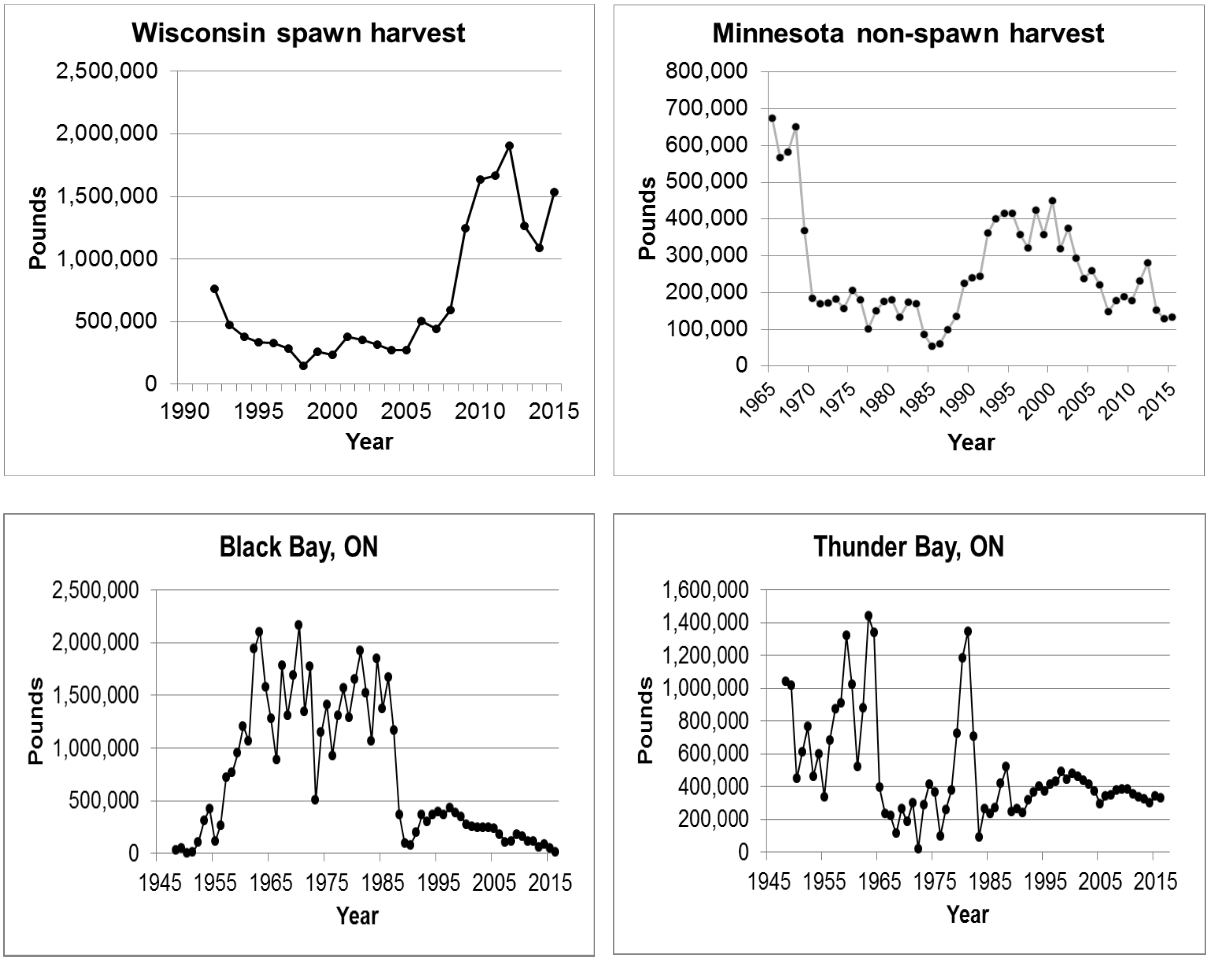

Figure 7. Recent commercial harvest of cisco in Wisconsin, Minnesota, and Ontario waters of Lake Superior (Data provided by WIDNR, Bayfield, MNDNR, Duluth, and OMNRF, Thunder Bay).

Blackfin Cisco

Within the Great Lakes, Blackfin Cisco formerly occupied Lake Michigan, Lake Huron proper, excluding the North Channel, and Georgian Bay at suitable depths (Koelz 1929), and the species remains extant in Lake Nipigon (Todd and Smith 1992; Turgeon et al. 1999), and lakes in Algonquin Provincial Park, Ontario (Mark Ridgeway, ONMR, personal communication). Accounts were also reported from Lake Superior (USGS 2016). This fish was distinguished by its large size (> 250 mm SL), deep ovate body, relatively long paired fins, usually having more than 43 gill-rakers and heavily pigmented body and fins (Koelz 1929); it was the largest of the deepwater Ciscoes inhabiting Lake Michigan (Smith 1964). This species was important in the commercial fishery in Grand Traverse Bay, Lake Michigan (Milner 1874). The last specimen from Lake Michigan was seen in 1955 (Smith 1964) and none were taken in Lake Huron during investigations conducted in 1956 (Eshenroder and Burnham-Curtis 1999), making 1923 the last record for Lake Huron (Koelz 1929). In Lake Nipigon, the Blackfin Cisco remains widespread at suitable depths (Koelz 1929; Turgeon et al. 1999).

Lake Michigan gill-net surveys during 1930-1932, indicated Blackfin Cisco reached peak abundance at depths of 122-138 m in northern waters and 150 m in southern waters, and along with Kiyi, inhabited the deepest waters of all six species of deepwater Ciscoes (Bunnell et al. 2012a). This fish was rarely taken by commercial fishermen in less than 75 m (Koelz 1929). Spawning is thought to have occurred in early winter in Lake Michigan (Koelz 1929; Becker 1983; Bunnell et al. 2012a).

No diet data exists from historical Lake Michigan samples. Limited samples from Lake Huron suggested Blackfin Cisco fed on *Mysis* (Koelz 1929), and more recently those collected in Lake Nipigon fed on *M. diluviana* and copepods (Turgeon et al. 1999). The $\delta^{15}N$ signatures of fish collected by Koelz indicated a trophic level similar to Cisco (Schmidt et al. 2011), but its $\delta^{13}C$ signature was similar to Bloater, Shortnose, and Shortjaw Cisco that inhabited deep waters of Lake Nipigon. The isotopic signatures of the Blackfin Cisco from Lake Nipigon appear anomalous, which may be because adults occupy the widest range of depths of any coregonine in this lake.

Bloater

The Bloater was the smallest of the original flock of six deepwater Ciscoes in Lake Michigan and today it remains the only extant deepwater form. Hybridization between Bloater and other remnant Cisco populations during 1950s and 1960s was possible (see Todd and Stedman 1989; Eshenroder et al. 2016), and has over the past century undergone ontogenetic shifts in resource use. For example, Bloater now rely more on benthic prey relative to the pre-Alewife food web (Crowder and Crawford 1984) and live deeper (> 90 m) now than in the 1930s (50-70) (Bunnell et al. 2012a).

Adult Bloater occur in offshore (> 60 m depth), hypolimnetic waters and undergo diel vertical migrations (TeWinkel and Fleischer 1999) to feed on *Mysis*, *Diporeia*, and zooplankton (Hondorp et al. 2005; Davis et al. 2007). Within this relatively cold and stable environment, bloater spawn between January and March, and eggs incubate for up to four months (Rice et al. 1987a, b; USFWS unpublished data). The larvae remain benthic for up to the first four weeks of life (Rice et al. 1987a,b) and then shift to warm pelagic waters for one or two years (Crowder and Crawford 1984; Rice et al. 1987a,b). Despite dominating the prey fish biomass during the 1980s and 1990s (Madenjian et al. 2002), Bloater never became as prevalent as Alewives in the diets of the three top piscivores, Chinook salmon (Jude et al 1987; Warner et al. 2008), Lake Trout (Madenjian et al. 1998), and Burbot (Fratt et al. 1997; Jacobs et al. 2010). Bloater are still found throughout Lake Michigan, although their abundance is at its lowest level since the early 1970s (Bunnell et al. 2013) owing to consistently low recruitment since 1991. Commercial harvest now is only a fraction of what it was in the 1980s.

The mechanisms that determine Bloater recruitment (i.e., survival in their first year of life) are not understood, and multiple factors are likely at work. For example, fecundity has declined with Bloater energetic condition (Bunnell et al. 2009) and predation on incubating eggs (by native sculpins) could be having population-level consequences under some conditions (Bunnell et al. 2014). Madenjian et al. (2002)

proposed that Bloater undergo a 30-year cycle of abundance, but exactly how this cycle could be regulated remains unknown. A skewed sex ratio, where females greatly outnumber males, correlates with poor Bloater recruitment (i.e., higher recruitment when ratio is more balanced, Bunnell et al. 2006) and could be responsible if females do not spawn all of their eggs when few males compose the adult population. Finally, the broad synchrony of Bloater recruitment between the late 1970s and mid-2000s across lakes Superior, Michigan, and Huron suggested that some unknown basin-wide climate driver (Bunnell et al. 2010) could be critical. Since 2005, however, Bloater recruitment has greatly increased in Lake Huron after Alewives collapsed and led to higher recent levels of adult Bloater abundance (Roseman et al. 2013). While little resurgence has been detected in Lake Michigan, the 2016 year class was the largest on record since 1990.

Kiyi

The Kiyi is the second smallest of the original flock of six deepwater Ciscos in Lake Michigan. Today, it is extirpated from lakes Michigan, Huron, and Ontario, but remains abundant only in Lake Superior. It is also present in inland Canadian lakes from Lake Nipigon to the northwest to Great Slave Lake (Lee et al. 1980).

In Lake Michigan, this form segregated themselves from other deepwater cisco based on bottom depth, gill raker characteristics, and spawning (timing and depth, see Koelz 1929; Smith 1964; Bunnell et al. 2012a). Kiyi historically occupied the deepest depths of Lake Michigan (i.e., 120 – 150 m bottom depth) as they do in Lake Superior, along with the Blackfin Cisco. Kiyi grew slower, had fewer gill rakers that other forms, and spawned in fall (rather than winter) compared to Blackfin cisco. Other life history characteristics associated with the historic Lake Michigan Kiyi population circa 1930 included a skewed sex ratio (female predominance) and a relatively small size at maturity (~175 mm total length, Deason and Hile 1947). The latest observations from 1940s suggest that Kiyi from Lake Michigan fed heavily on *Diporeia* and *Mysis* (Bersamin 1958). The proportion of Kiyi within the deepwater Cisco assemblage declined between 1930 and 1961 (Smith 1964). During 1962-1969, the U.S. Fish and Wildlife (now U.S. Geological Survey) collected no more than five Kiyi annually from Lake Michigan, and the last one was observed in 1975. The exact mechanism underlying the extirpation of Kiyi from Lake Michigan is not clear, but as with the demise of other deepwater Ciscoes, the combined negative effects of overfishing coupled with sea lamprey parasitism were likely the primary causes (Wells and McLain 1973).

In Lake Superior, the ecological role of Kiyi is not markedly different from historic descriptions of those in Lake Michigan. Kiyi are the most abundant deepwater Cisco in Lake Superior today (USGS 2016) and in the Great Lakes in general. They undergo large diel vertical migrations (Gorman et al. 2012b) and rely almost exclusively on *Mysis relicta* as their prey (Ahrenstorff et al. 2011; Isaac et al. 2012). Their sex ratio also is skewed towards females given their greater longevity (Pratt and Chong 2012). Their maximum size has been estimated at 301 mm fork length but most are much smaller (Pratt and Chong 2012). They are consumed by siscowet Lake Trout that occur at these deeper depths. Recently Kiyi densities have been declining in Lake Superior.

Shortjaw Cisco

The historic distribution of Shortjaw Cisco included laked Michigan, Huron, Erie, and Superior, and 22 inland Canadian lakes ranging from southern Ontario to Great Slave Lake in the Northwest Territories (Todd 2003; Murray and Reist 2003). In Lake Michigan, Shortjaw Cisco were historically found “along the shores” throughout Lake Michigan, except Green Bay (Koelz 1929).

Shortjaw Cisco is distinguished by its relatively large size, elongate body, long snout, shallow head and relatively short length and low count of gill rakers (36-43, usually <40) (Koelz, 1929; Becker, 1983). They generally occur at intermediate depths between 51-128 m during much of the year—though only in deeper waters when shallow water is nearby, and move into shallower waters (18-55 m) to spawn (Koelz 1929). Their association with transitional areas, deep water near shallow water, may relate to an affinity for sloping habitats (Naumann and Crawford 2009). Spawning occurred in Lake Michigan in November over sand or clay substrates (Koelz 1929). They reach reproductive maturity at age three or four (Moffett 1957). Shortjaw Cisco feed largely on *Mysis*, but sometimes also consume a high proportion of *Diporeia* (Koelz 1929).

Historic records of Longjaw Cisco are now considered synonymous with *C. zenithicus* due to high morphometric and ecological overlap (Bunnell et al. 2012a), though they have been referenced as separate species or forms by recent sources (Williams and Miller 1990; Scott and Crossman 1973, Turgeon and Bernatchez 2003; Eshenroder et al. 2016). In general, historic records of Longjaw Cisco, particularly during spawning, tended to be in northern Lake Michigan and Shortjaw Cisco tended to be in southern Lake Michigan (Koelz 1929). The slightly larger Longjaw Cisco (Smith, 1964) may have represented a Shortjaw Cisco form or may simply have occurred in areas where better growth was attainable.

Shortjaw Cisco was extirpated from Lake Michigan (last verified in 1975) and Lake Erie (last verified in 1957; Todd, 2003). They were also once thought to be extirpated from Lake Huron, after a 21-year period without an encounter, but more recent collections in Georgian Bay—starting in 2003—indicated that a small remnant population persists (Naumann and Crawford 2009). Eshenroder et al. (2016), however, hypothesize that Shortjaw Cisco is indeed extirpated from Lake Huron, having introgressed with Bloater several decades ago. In Lake Superior they were once ranked the most abundant deepwater cisco, and second to Cisco (Van Oosten, 1937), but now are rare (Hoff and Todd 2004; Bronte et al. 2010). Shortjaw Cisco populations were abundant in Lake Nipigon (Todd 2003) but are now declining due to unknown reasons. Factors that have contributed to their population declines elsewhere include overfishing, habitat degradation, and changes in competition and predation as a result of invasive species introductions and declines in keystone predator populations (Smith 1964, 1968; Todd 2003; Bronte et al. 2010).

Shortjaw Cisco was important in the historic Lake Michigan fishery, and made up 21% of the catch in the 1930s (Todd 2003). When present and abundant they are an important food item for deepwater forms of Lake Trout. Shortjaw Cisco and the Cisco are the ancestral Coregonine forms that colonized the Great Lakes following glaciation (Todd 2003). The radiation that resulted from this lineage is significant and substantial, and indicates that this form may be important in the future diversification of fishes in the deepwaters of the Great Lakes (Todd 2003). Unfortunately, all remnant Great Lakes populations are currently too small to support gamete collections for re-introduction, with the possible exception of Lake Nipigon.

The Emerald shiner

The Emerald Shiner *Notropis atherinoides* is another native planktivore that may be considered for restoration. This schooling pelagic fish found in large lakes from the Mackenzie River, Canada to the Gulf of Mexico (Scott and Crossman 1973; Pflieger 1997). It is short lived with a maximum age of 4 years and maximum size of 110 mm (Pflieger 1997). First spawning can occur at age 1, but more typically at age 2+ and is in spring using a variety of substrates that include rounded boulders, course rubble, gravel and sand (Campbell and MacCrimmon 1970). After spawning, adults are widely distributed in the epilimnion at temperatures between 18-23 C (Campbell and MacCrimmon 1970; Schaeffer et al 2008), where they form schools during day and disperse at night (Trautman 1981). Once water temperatures decline, these fish move in mass to inshore waters in the fall (Campbell and MacCrimmon 1970; Wells and McLain 1973).

Emerald Shiners feed on plankton ranging from algae to protozoa to microcrustaceans to midge larvae (Scott and Crossman 1973). Young-of-year eat algae, rotifers, protozoa and small zooplankton (Fuchs 1967). Adults consume Daphnidae, *Leptodora, Diaptomus*, Bosminidae, *Bythotrephes,* and cyclopoid copepods (Flittner 1964, Fuchs 1967, Campbell and MacCrimmon 1970, Muth and Busch 1989, and Hartman et al 1992). Little diet overlap occurs with other planktivores sampled at the same time (Hartman et al 1992, Pothoven et al 2009). In the Great Lakes, this species is a trophic bridge between small plankton and larger piscivores. In Lake Simco, Emerald Shiners are eaten by mostly inshore piscivores including Yellow Perch, Rainbow Smelt, Burbot, Lake Trout, rock bass *Ambloplites rupestris*, smallmouth bass *Micropterus dolomieu*, and pumpkinseed *Lepomis gibbosus* (Campbell and MacCrimmon 1970), a similar nearshore predator assemblage to that in most of the Great Lakes.

Emerald Shiner populations declined greatly in Lake Michigan between 1956 and 1962 (Wells and McLain 1973). While data prior to 1960 are not available, populations were dense enough in fall to clog cooling water intake screens of power plants (Flittner 1964) and vessel engines (Wells and McLain 1973). The collapse started in northern Lake Michigan and then moved south, corresponding to the Alewife invasion front (Wells 1977). Thereafter and into the 1970s, only localized populations upstream of drowned river mouths existed (i.e., Edsall 1964). Bottom trawl surveys collected no Emerald Shiners from 1973–2013 (Bunnell et al. 2006; David Warner, USGS Great Lakes Science Center, Personal Communication). Madenjian et al. (2002) showed very low catches of Emerald Shiners during 1984-2000 despite a 90% reduction in Alewife biomass, which still remains the case today as this species is not documented in bottom-trawl survey reports (see Bunnell et al. 2013).

While Lake Michigan populations are presently very low, Emerald Shiner biomass in Lake Huron drastically increased from 0 fish/ha in 2004 to 523 fish/ha by 2006 following the nearly complete collapse of Alewive populations (Schaeffer et al

2008). Similarly, large increases in Emerald Shiner catches by commercial bait operations in Lake Huron began in 2005 (Schaeffer et al 2008) and these catches continue today (MIDNR, unpublished data).

The collapse of Emerald Shiner populations has been attributed to increases in Alewives (Smith 1970). The likely mechanism was a combination of Alewife competition with Emerald Shiners for zooplankton or direct consumption of their eggs and larvae (Stewart et al. 1981; Schaeffer et al. 2008). Overfishing and habitat degradation are considered unlikely factors (Wells and McLain 1973). A retrospective analysis of the effects of Alewives on native fishes (Madenjian et al. 2008b) and the dramatic increase in Emerald Shiners in Lake Huron after the Alewive collapse there, support this hypothesis (Schaeffer et al 2008) .

Interactions with Rainbow Smelt, which were introduced into the upper Great Lakes Basin in 1912 (Creaser 1925), has also been suggested as cause for the decline. This is unlikely for two reasons: first, Emerald Shiner populations were large prior to 1960 when Rainbow Smelt populations were also large throughout Lake Michigan. Large Rainbow Smelt population declines in the 2000s in Lake Michigan (Bunnell et al. 2006) have not led to direct increases in Emerald Shiners; second, a relatively low amount of direct predation occurs by Rainbow Smelt on Emerald Shiners. Young-of-year Rainbow Smelt feed mostly on small-sized zooplankton (Evans and Loftus 1987), and have very different temperature requirements than Emerald Shiners. Rainbow Smelt larger than 170 mm in fork length prey on other fish including Emerald Shiners (MacCrimmon and Pugsley 1979). However the overall differences in food and habitat use indicated that Rainbow Smelt were unable to extirpate native planktivores in large lakes (Rooney and Paterson 2009).

Emerald Shiners are tolerant of habitat degradation and are commonly found in areas with high sedimentation and dissolved solids, and poor water quality (Scott and Crossman 1973; Pflieger 1997). Although some habitat changes have occurred at the landscape scale, substantial areas of Lake Michigan were left un-altered, so substantial residual habitat should have been available to complete their life cycle. Emerald Shiner populations declined first in northern Lake Michigan where habitat alteration was minimal, which supports the hypothesis that habitat alteration was not a factor in population declines (Wells 1977). Reduced populations of key predators, such as Lake Trout, Walleye *Sander vitreus* and Yellow Perch, should have reduced predation pressure and led to larger populations of Emerald Shiners, not small ones. Thus, all of the evidence appears to point to Alewife interactions as the principal cause of the large declines in Emerald Shiner populations, and likely continues to be responsible for their depressed state (Madenjian et al. 2008b).

Impediments to and opportunities for reintroduction/recovery

Extinction and extirpation of forms

Extinction of at least two coregonine forms and extirpation of three other forms in Lake Michigan complicate or prevent reintroduction and restoration. Deepwater Cisco was last reported in Lake Michigan in 1951 (Moffet 1957, Wells 1968) and is now presumed to be globally extinct (IUCN 2013). Shortnose Cisco was last documented in

Lake Michigan in 1982 (Webb and Todd 1995) and is considered globally critically endangered (IUCN 2013). Kiyi and Shortjaw Cisco were last reported in Lake Michigan in 1974, and 1975, respectively (Parker 1989, COSEWIC 2003) and are now considered extirpated from the lake. Both Kiyi and Shortjaw Cisco persist in Lake Superior, but Shortjaw Cisco is now very rare (Hoff and Todd 2004). Blackfin Cisco was last reported in Lake Michigan in 1955 (COSEWIC 2007) and is now found only in Lake Nipigon and a few other Canadian lakes (Nelson et al. 2004; Eshenroder et al. 2016).

Cisco documented in Lake Michigan where mostly the 'slim terete or “subterete”' form (artedi artedi) (Koelz 1929). Albus and manitoulinus forms, were not described by Koelz (1929) from Lake Michigan but may have been missed based on sampling locations. Some remnant populations of both these types appear restricted to northern Lake Huron (Yule et al. 2013). The most common extant form in Lake Michigan is thought to be an *albus-like* form having a body depth similar to Bloater, a small head, and pectoral fins and is found in small populations in selected areas of northern Lake Michigan (“false-albus” in Eshenroder et al. 2016). This population is expanding in size, which is promising, but may be a principally nearshore form that spawns in shallow water. Small (compared to Lake Superior) spawning populations have been documented in Grand Traverse and Little Traverse Bays (Kevin Donner, Little Traverse Bay Bands of Odawa Indians, unpublished data) and appear to be increasing in both number and distribution along the eastern shoreline. Juvenile Cisco have been recently captured in Green Bay in Wisconsin (Tammie Paoli, WIDNR, Peshtigo, WI, personal communication) but catches are rare and intermittent there as well as isolated locations along the Wisconsin shoreline.

Exploitation of remnant populations

Excessive commercial harvest was responsible, in part, for the decline of coregonines in Lake Michigan (Moffet 1957; Smith 1970). Since then, management of Lake Michigan fisheries has changed with fewer licensed fishermen, stronger regulations, improved stock assessments and quota limitations. Currently, Illinois and Indiana do not allow commercial harvest of Cisco, and Illinois, Wisconsin and Michigan allow only the harvest of Bloater, and the Chippewa Ottawa Resource Authority (CORA) allows harvest of both forms. Commercial harvest of Cisco by CORA-licensed fishermen in Lake Michigan generally occurs as by-catch and ranged from 0 to 27,000 lbs annually during 1990-2016 (Figure 8).

During this same period, annual commercial harvest of Bloater declined from 1.4 million kg to 10,000 kg in Lake Michigan (Figure 9). Bloater harvest is subject to few effort restrictions for Michigan- and CORA- licensed fishermen (e.g., 2000 Consent Decree) and harvest limits have not been established. Wisconsin-licensed fishermen are limited by a quota of 7.9 million kg (3.6 million pounds; Stepp 2012), but these limits are not biologically based or logistically attainable. Lake-wide biomass of Bloater estimated by bottom trawl surveys was approximately 2 million kg (0.9 million pounds) in 2012 (Bunnell et al. 2012b), but exploitation (harvest/biomass) has been less than 0.2% since 1990 (Figure 10).

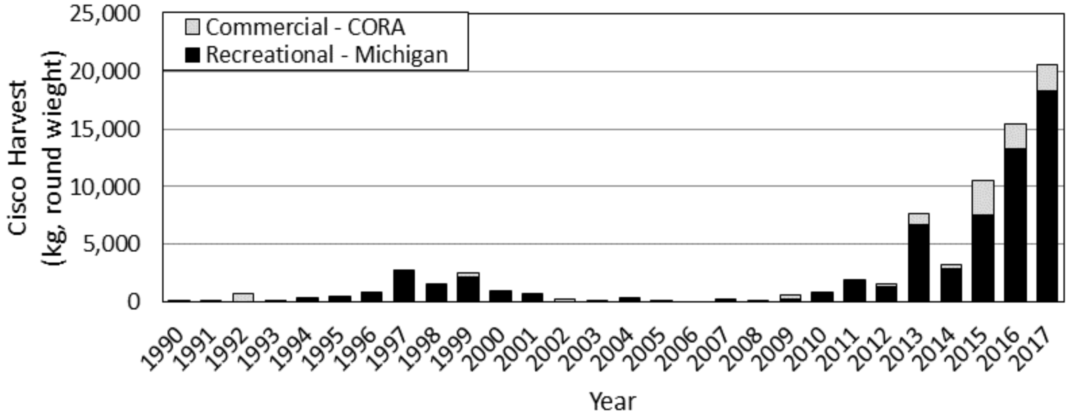

Figure 8. Recent commercial and recreational landings of Cisco in Michigan waters of Lake Michigan 1990-2016. WI, IN, and IL do not allow harvest of Cisco.

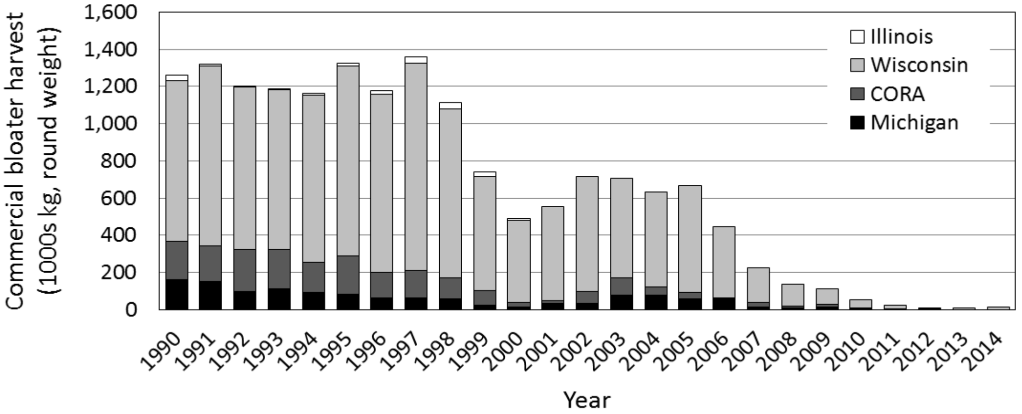

Figure 9. Recent commercial landings of Bloater by jurisdiction in Lake Michigan 1990-2014.

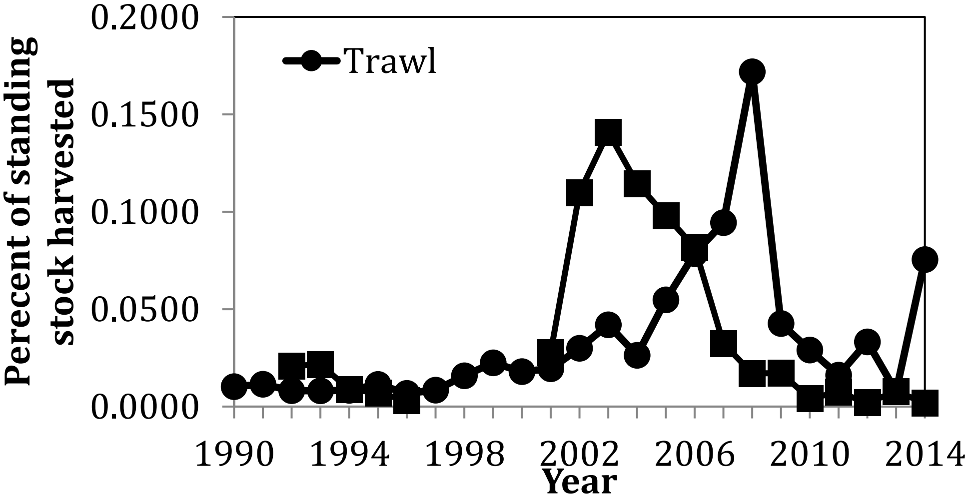

Figure 10. Simple exploitation (harvest/biomass) of bloater in Lake Michigan, 1990-2014). Based on total harvest and biomass estimates from the USGS fall bottom trawl survey, and the coordinated USGS/MIDNR/USFWS acoustic survey.

Commercial harvest of Emerald Shiner in Lake Michigan is poorly documented but is thought not likely to impede rehabilitation. CORA and the states of Indiana, Illinois, and Wisconsin do not currently commercially harvest Emerald Shiner. Michigan-licensed baitfish harvesters take the species occasionally in small numbers (about 8,000 fish per year) in tributaries. Given the high biomass of Emerald Shiners available to fisheries in nearby Lake Huron, it is highly unlikely that Lake Michigan catches will increase to a level of concern.

Recreational fisheries do not target Bloater or Emerald Shiners, but targeted fisheries may affect recovery of Cisco if harvest exceeds population capacity to increase. A growing recreational fishery in in northeastern Lake Michigan targets Cisco with an estimated harvest of about 20,000 kg in 2017. Large Cisco have recently increased in abundance throughout northeastern and eastern Lake Michigan and that has led to additional targeted fishing beyond Grand Traverse Bay (Randy Claramunt, Michigan Department of Natural Resources – Charlevoix Research Station, personal communication). This activity will need to be carefully managed to prevent over harvest of recovering populations.

Influence of predators

The importance of Pacific salmon predation in reducing Alewife biomass cannot be overstated. Assuming that non-native Alewife and Rainbow Smelt are impediments to the restoration of native planktivores (this is not conclusive), predation by salmonines may have increased the probability of their recovery. Although naturalized Pacific salmon can forage on coregonines (Conner et al. 1993, Rybicki and Clapp 1996, Kitchell et al. 2000, Warner et al. 2008; Roseman et al. 2014), their predation is generally not believed to limit their recovery. The densities of initial reintroductions will be low and, once dispersed, a salmon’s encounter probability with ciscoes will be much lower than even the residual alewife and rainbow smelt population, as documented in Lake Huron (Roseman et al. 2014). Chinook salmon consume all available sizes of alewives in Lake Michigan (40-190 mm total length) (B. Leonhardt, Purdue University; personal communication) hence alewives are always in the available predation window. The apical size of most Cisco exceed that of alewives hence they can escape Chinook salmon predation once they exceed 200 mm total length. It is unknown whether Emerald Shiners would be a significant forage for Pacific salmon (Schaeffer et al. 2008) but this predation has been observed recently in Lake Huron (Roseman et al. 2014).

Many native nearshore predators (i.e., esocids, centracids, percids) are known to consume Emerald Shiners (Becker 1983) but no evidence exists that any one species acting as a keystone predator to Emerald Shiners—possibly because of this predator diversity. Native nearshore predators are generally within or below historic population densities in Lake Michigan, and it is unlikely any will be a significant impediment in the restoration of Emerald Shiner.

Sea Lamprey proliferation in the late 1950s completely changed the community structure of Lake Michigan (Madenjian et al. 2002). Sea lamprey reduced populations of large bodied fishes, including Cisco, blackfin Cisco, Shortjaw Cisco, and Shortnose Cisco (Smith 1964, 1968). In addition, sea lamprey predation (along with fishing) was a major factor in the Lake Trout collapse (Wells and McLain 1972, 1973), which contributed to shifts in planktivore populations (discussed above). Out-migrating newly transformed sea lamprey are known to prey upon deepwater ciscoes and Cisco in the fall (Young et al. 1996). Sea lamprey control continues to suppress numbers in recent years, particularly with increased efforts in the Manistique River (http://www.glfc.org/pubs/pdfs/4.1.3%20SL%20Status_Michigan%20(Mar%202017).pdf).

Alewife predation on eggs and larval stages on native fish clearly played a significant role in the decline of Emerald Shiners (Crowder 1980; Schaeffer et al. 2008; Madenjian et al. 2008a) and, as previously mentioned, is speculated to have negatively affected deepwater ciscoes (Smith 1968; Eshenroder and Burnham-Curtis 1999). The pelagic waters used by Alewife are key habitat for either the eggs, larvae or juveniles of Cisco and deepwater cisco (Smith 1972; Crowder 1980; Eshenroder and Burnham-Curtis 1999), which may be consumed by Alewife. However, Madenjian et al. (2008a) found that Cisco and Bloater population trends in the Great Lakes did not correspond with Alewife abundance, indicating that spatial overlap between coregonine larvae and Alewife is likely minimal. In addition to these direct effects on native planktivores, Alewives also alter zooplankton community structure (Wells 1970) and affect Lake Trout populations through predation on fry (Krueger et al. 1995) and to some extent via EMS (Riley et al. 2011).

Rainbow Smelt predation may have been a more significant issue for Cisco, because Rainbow Smelt habitat commonly includes Cisco spawning and nursery areas (Smith 1972; Crowder 1980; Loftus and Hulsman 1986; Krueger and Hrabik 2005). Smith (1972) pointed out that Cisco populations declined in the presence of Rainbow Smelt, but did not become rare until Alewife proliferated, indicating that there may be a combined effect of Rainbow Smelt and Alewife on Cisco. But Madenjian et al. (2008a) found no evidence to support direct Alewife affects in Cisco populations. Rainbow smelt predation may also contribute to suppression of Emerald Shiner populations due to high habitat overlap (Smith 1972), but Alewife predation on eggs and larvae likely plays a more significant role (Crowder 1980; Schaeffer et al. 2008; Madenjian et al. 2008a).

Given the real or perceived effects that Alewife and Rainbow Smelt have on native fishes, their abundances are important considerations in the restoration of native planktivores. Alewife and Sea Lamprey populations declined enough by the 1980s to allow for Burbot recovery (Eshenroder and Burnham-Curtis 1999, Madenjian et al. 2002), but alewives have declined to their lowest levels (USGS 2016). Rainbow Smelt populations have also declined considerably in recent years (Madenjian et al. 2010). It is not clear whether current Alewife densities in Lake Michigan are low enough to allow for recovery of Cisco or Emerald Shiner. The collapse of Alewife in Lake Huron has facilitated increases in densities of Emerald Shiners (Schaeffer et al. 2008), possible Cisco (Warner et al. 2009), and in Bloater recruitment (Roseman et al. 2013). The density of Alewife that will allow for native planktivore recovery along with maintaining key recreational salmon fisheries continues to be a dilemma that Great Lakes managers are struggling to understand (Dettmers et al. 2012). Evidence of recent increases in Lake Michigan Cisco populations in the face of lower Alewife populations is encouraging (Randy Claramunt, Michigan Department of Natural Resources – Fisheries Division, unpublished data).

Habitat alteration

Lake Michigan planktivore populations have been affected by a wide variety of physical, chemical, and biological stressors. Major stressors include changes in habitat, degraded water quality, and changes in predation pressure and food resources due to invasive species. The relative influence of these stressors is unknown because many of these ecosystem changes occurred simultaneously and were interrelated making individual effects difficult to determine (Smith 1972; Eshenroder and Burnham-Curtis 1999). However, evidence of effects for some influences is stronger than others.

Physical habitat—Human development (marinas, jetties, dredging, filling, and dock construction) alter inshore physical habitat in the Great Lakes, rather than offshore (Rutherford et al. 2004). These activities can directly degrade or destroy spawning or nursery habitat, such that which occurred in the building of the shipping channels in the Detroit River (Smith 1915), or they can affect them indirectly through disruption of flow patterns (Meadows et al. 2005; Herdendorf 1973), and changes in sediment transport (O'Brien et al. 1999; Shabica et al. 2004; Garza and Whitman 2004; Morang et al. 2011). While these effects are mostly nearshore (Rutherford et al. 2004), sediments are diverted by large man-made structures or by direct dredge spoil deposition into offshore areas that disrupt trophic dynamics through changes in upwelling/downwelling cycles (Meadows et al. 2005). Excessive sedimentation from rivers degrades nearshore spawning and nursery habitats (Rutherford et al. 2004, Madenjian et al. 2011), and had some localized offshore impacts (Murray and Reist 2003). Other habitat stressors include: the construction of pipelines, electric transmission lines, and communication lines; oil and gas development; or windmill construction (Rutherford et al. 2004). In addition, river and drowned river mouths have been highly modified by development and only 18% of tributary habitat is now available to Lake Michigan fishes due to dams (Rutherford et al. 2004). These formerly connected river habitats may have been important to some Cisco and Emerald Shiner populations.

There is no direct evidence linking physical habitat alteration to the decline in or suppression of native planktivore populations in Lake Michigan. Emerald Shiner could be most vulnerable to physical habitat modifications because of their exclusive reliance on nearshore habitats. At the same time, Emerald Shiner habitat is relatively general and tolerant of spawning habitat modification. Hence, their declines are not believed to be related to spawning habitat degradation (Koonce et al. 1996). Cisco has been described to spawn in a variety of habitats (pelagic waters, nearshore waters and embayments, tributaries), and future research will be required to determine whether specialized spawning habitat preference is related to Cisco morphotype. Nonetheless, given that many of the historic Cisco spawning areas are adjacent to current areas of shoreline development and major river outlets, it is likely that some spawning or nursery habitats have been directly or indirectly affected. Furthermore, given that Lake Michigan Cisco were reported to historically run up Lake Michigan tributaries (e.g., Manistique, Manistee, Muskegon, Grand Rivers based on Michigan DNR River Assessment reports) and tributary flow in most of those systems have been altered, Cisco diversity may have been lost owing to loss of habitat. At the lakewide level, however, habitat degradation, alone, cannot explain the dramatic Cisco decline because of the propensity for Cisco to spawn in a variety of habitats (reefs, pelagic open-water). For example, among the contemporary Cisco populations in Grand Traverse Bay, an existing reef has dock pilings embedded into about half of it and the remaining portion of the reef is a remnant Cisco spawning site (Barton et al. 2011). It is possible that Shortjaw Cisco, Bloater, and Shortnose Cisco (Bunnell et al. 2012a) that use relatively shallower offshore spawning or nursery habitat have been affected (Murray and Reist 2003), but habitat loss is considered a less significant factor in their overall decline.

Physical habitat has also been altered by the proliferation of Dressinid mussels and *Cladophora* on spawning reefs and other habitats that can fundamentally change physical habitat structure, change currents, sediment deposition, and erosion rates (Marsden et al. 2005). These changes can also lead to chemical habitat changes. These effects were not responsible for the historical declines of native planktivores because Dressinids colonization occurred well afterward, and it is unknown whether they would complicate recovery efforts. High densities of mussels can prevent eggs from entering interstitial spaces hence reducing survival (Marsden and Chotkowski 2001) but their physical habitat effects may be less important in deepwater where wave action is absent and interstitial predators are less abundant (Janssen et al. 2007). Similarly, *Cladophora* would not affect deepwater habitats since the maximum expected depth for *Cladophora* is about 30 m (Higgins et al. 2008). Therefore, the potential physical habitat impacts caused by Dressinids and *Cladophora* are likely to be limited to Cisco and Emerald Shiner, especially given the recent Cisco population expansion seen in eastern Lake Michigan.

Chemical habitat—Native planktivores are most susceptible to chemical habitat alterations during egg and larval stages (Madenjian et al. 2011), and nearshore habitats are more susceptible to chemical pollution than offshore habitats (Rutherford et al. 2004). Potential chemical habitat stressors include eutrophication, low dissolved oxygen, toxins, or turbidity. There is little research in this area, but eutrophication and excessive sedimentation are significant sources of nearshore spawning and nursery habitat degradation, particularly in shallow bays (Fielder 2002; Madenjian et al. 2008a; Madenjian et al. 2011). It is also likely that historic land use (i.e., clear-cutting the landscape) and degraded water quality from untreated discharge of industrial, domestic sewage and milling wastes in tributaries effectively created barriers to planktivore use and eliminated adfluvial populations.

Madenjian et al. (2008a) concluded that degraded water quality in key spawning areas was the primary driver for historic Great Lakes Cisco collapses. In particular, eutrophication had driven benthic dissolved oxygen to such low levels in important Cisco nursery areas, such as Green Bay, that eggs were unable to survive through the winter (Madenjian et al. 2011). Fortunately as a result of the implementation of the Clean Water Act, these conditions have improved in most Great Lakes waters and oxygen levels are now sufficient to support overwintering of Cisco eggs (Madenjian et al. 2011). Deepwater Ciscoes were likely not directly affected by eutrophication in Lake Michigan, though it has been mentioned as a possible factor in their decline (e.g., Smith 1972). It is difficult to rule this factor out entirely since their population declines were concurrent with eutrophication and populations persisted in Lake Superior that did not experience productivity increases. Though the decline of Emerald Shiners is not attributed to poor water quality, they are somewhat sensitive to water quality degradation (Arend et al. 2011). Some eutrophication issues persist in the Lake Michigan nearshore (Bootsma et al. 2012), but the offshore is now highly oligotrophic (Vanderploeg et al. 2012).

Colonization by Dressinids or *Cladophora* sp. can also result in changes in chemical habitat. For example, high Dressinid densities can change interstitial flow that results in build-up of feces and pseudofeces that can reduce benthic oxygen concentrations (Marsden and Chotkowski 2001, Nalepa et al. 2005, Janssen et al. 2007). Excessive *Cladophora* sp. growth can result in reduced benthic oxygen and higher ammonia concentrations (Sly 1988). Chemical habitat effects from Dressinids would be concentrated in deepwater reefs unaffected by wave action (Janssen et al. 2007), and more sheltered nearshore reefs that are not regularly flushed by wave action. Chemical habitat effects from *Cladophora* could degrade a variety of nearshore habitats but only for cisco that spawn nearshore.

Biological habitat—Biological habitat alteration has occurred in the open waters of Lake Michigan through the proliferation of invasive species, intentional species introductions, and through changes in food web dynamics. Major changes that affected native planktivores include changes in predation (and parasitism) rates, loss of prey due to competition, and disruption of lower trophic dynamics.

More recently, high densities of round goby *Neogobius melanostomus* and rusty crayfish *Orconectes rusticus* on Cisco nearshore spawning habitat has been suggested to potentially impair Cisco recovery (Fitzsimons and O'Gorman 2006; Jonas et al. 2005; Barton et al. 2011). Actual effects cannot be measured under current conditions of low Cisco egg deposition, and highlight the need for higher densities of Lake Trout to act as the keystone predator on potential egg consumers. Recent increases in Cisco abundances under high densities of Round Goby likely rule out the hypothesis as a primary limiting factor. Round Goby also occur in deeper offshore waters during late fall through early spring (Schaeffer et al. 2005; Walsh et al. 2007) so it is possible that predation on deepwater Cisco eggs or larvae could be significant if densities are high, but currently there is no direct evidence of such predation on eggs (Mychek-Londer et al. 2013) and recent increases of deepwater cisco (i.e., hybrid swarm) in Lake Huron also suggest Round Goby egg predation is not regulating coregonines.

Invasive species have also affected food resources for native planktivores, as previously discussed. The recent reductions in open-water nutrients and lower primary and secondary productivity in offshore Lake Michigan waters is likely from a concentration of nutrients in nearshore (Hecky et al. 2004) and benthic zones (Cuhel and Aguilar 2013) made unavailable from Dressenid proliferation. In addition to the loss of the spring phytoplankton bloom and reduced plankton productivity (Evans et al. 2011), production of cladocerans (Vanderploeg et al. 2012), and *Diporeia* sp. has declined significantly (Nalepa et al 2009). Concurrently, densities of the invasive zooplankton predator *Bythotrephes longiramus* have increased in some years (Vanderploeg et al. 2012), which has contributed to additional reductions in cladoceran zooplankton productivity. To avoid predation by *Bythotrephes*, Cladocerans move deeper in the water column, below the thermocline where the water is colder and growth is reduced (Pangle and Peacor 2006). These food web changes have reduced the available food resources to Lake Michigan planktivores and contributed to their declines

(Madenjian et al. 2008b; Claramunt et al. 2012).

These food web changes have had negative effects on Alewife, Rainbow Smelt and other fishes (Madenjian et al. 2008b; Claramunt et al. 2012). While cladocerans are an important prey for Cisco, and *Diporei*a sp. are important prey for Shortnose Cisco, Shortjaw Cisco and Bloater (Koelz 1929, Bersamin 1958; Becker 1983), the current food web changes are not likely to be as disruptive to coregonines (Dettmers et al. 2012) given their ability to also consume native mysids and hypolimnetic calanoid copepods such as *Limnocalanus macrurus*. Despite reductions in zooplankton biomass, *L. macrurus* has increased in Lake Michigan (Vanderploeg et al. 2012) and this large, hypolimnetic zooplankton is an important coregonine prey item, especially for Cisco (Link et al. 1995, Link and Hoff 1998). The invasive *Bythotrephes* is also consumed by Cisco (Coulas et al. 1998). More importantly, many of coregonines have persisted in Lake Superior under oligotrophic conditions (Eshenroder and Burnham-Curtis 1999; Dettmers et al. 2012), similar to the reduced offshore pelagic states of Lake Michigan and Huron. In addition, Lake Michigan was certainly more oligotrophic historically than what we have known over the last century (Schelske et al. 2006). In fact, Lake Michigan was at its most productive during 1950-1970 (Schelske et al. 2006) when many of these native planktivore populations collapsed or were extirpated. Therefore, these native planktivores are likely to thrive under the more oligotrophic conditions Lake Michigan is currently experiencing than those that existed in the mid to late 1900s. As a result, restoration of native planktivore populations may be able to thrive and support top predators (Eshenroder and Burnham-Curtis 1999), particularly under the current food web structure (Dettmers et al. 2012).

The “open” niche

It has generally been assumed that after the decline of Cisco and deepwater ciscoes, their spatial and trophic niche was occupied by Alewives and Rainbow Smelt. Stable isotope analyses (SIA) of carbon and nitrogen has been extensively used to map trophic relationships, describe food web changes, and assess ecosystem health. The ratio of carbon stable isotopes (13C:12C, hereafter ‘δ13C’) indicates an organism’s primary source of carbon because δ13C values typically differ for primary producers from different energy pathways. In aquatic systems δ13C values are depleted from offshore pelagic energy sources and enriched from nearshore benthic energy sources (France 1995). By contrast, the ratio of nitrogen stable isotopes (15N:14N, hereafter ‘δ15N’) is typically enriched by 3-4% per trophic level and thus can be used to map trophic positions within a food web (Vander Zanden & Rasmussen 1999). Therefore, analyzing both δ13C and δ15N from fish tissues can provide information regarding life history, feeding, and movement. Recent stable isotope analysis on historic and contemporary specimens from Lake Michigan suggest that the niche formerly occupied by deepwater Ciscoes and Cisco remains unoccupied (Schmidt 2008), and that since the early part of the last century, the niches of Rainbow Smelt and Alewife are distinct relative to that of deepwater Ciscoes and Cisco (Figure 11). Historically, deepwater Ciscoes fed principally on both *Mysis* and *Diporeia* (Bersamin 1958), and Cisco on crustacean zooplankton. While *Diporeia* densities have declined significantly over the past 20 years (Nalepa et al. 2005), *Mysis* densities have not changed much (Madenjian

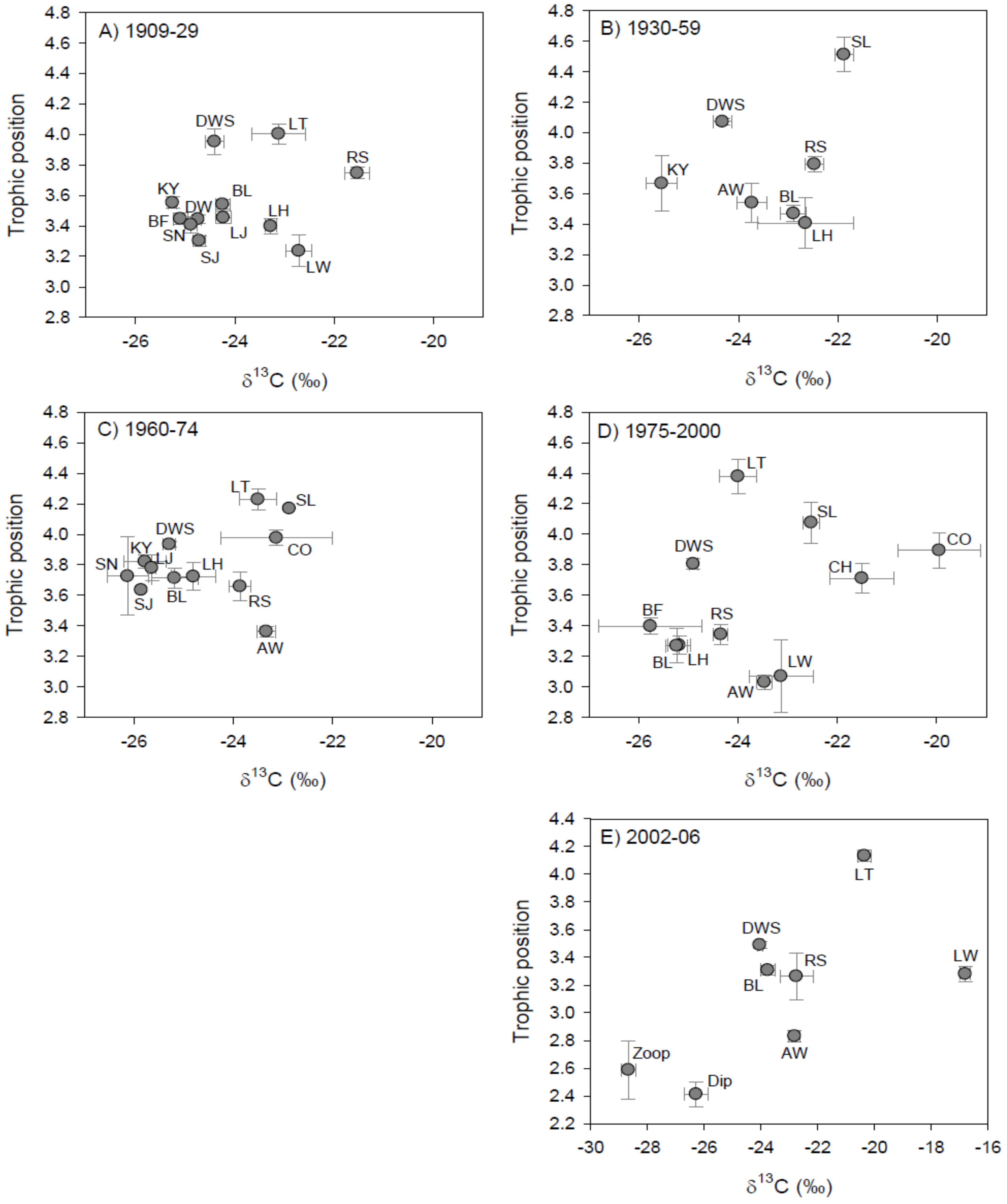

Figure 11. Stable isotope food web diagrams of the Lake Michigan offshore fish community for all time periods. Each point represents the mean δ13C and trophic position for a given species. Error bars show ± 1 standard error from the mean. Data labels are as follows: DWS = deepwater sculpin, LW = lake whitefish, LH = lake herring, SN = Shortnose Cisco, SJ = Shortjaw Cisco, BL = Bloater, KY = Kiyi, BF = blackfin Cisco, DW = deepwater Cisco, LJ = longjaw Cisco, LT = lake trout, SL = sea lamprey, RS = Rainbow Smelt, AW = Alewife, CH = Chinook salmon, CO = coho salmon, Zoop = zooplankton, Dip = Diporeia. (Schmidt 2008).

et al. 2015; Figure 12). Mysis have shown to be an important food item for Kiyi in Lake Superior and their diel vertical interactions are important to energy flow between habitats and trophic levels (Ahrenstorff et al. 2011).

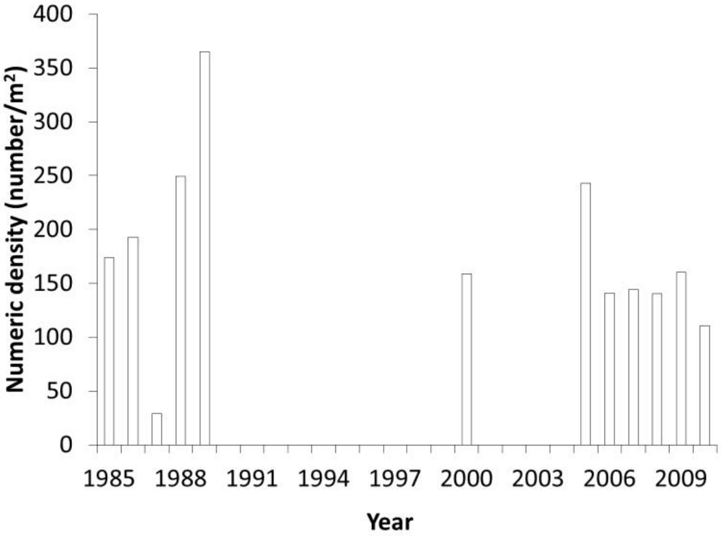

Figure 12. Numerical density of Mysis in Lake Michigan, 1985-2010. (Madenjian et al. 2015)

Probability for culture and existing efforts

Coregonine culture on the Great Lakes dates back to the 1870s when many state, Canadian federal and provincial agencies, and the U.S Federal government were engaged in stocking Lake Whitefish and Cisco fry to augment declining fisheries (Todd 1986). Between 1870 and 1960 more than 6 billion Cisco fry (along with 32 billion Lake Whitefish) were stocked into the Great Lakes to augment existing populations in order to sustain high commercial harvest levels (Todd 1986). These efforts generally failed because too few fish were stocked, life stages stocked were too small, and conditions for fry stocking were likely not correct for good survival, and evaluations were inadequate or lacking.

Ongoing coregonine culture in the Great Lakes by the Ontario Ministry of Natural Resources and Forestry has concentrated on Lake Whitefish for stocking into Lake Simcoe. Europeans have been culturing large numbers of coregonines for decades from both wild and captive broodstocks mostly for fishery augmentation and mitigation but also to support a large aquaculture industry. Reconnaissance visits to Finland in 2012 and 2014 by state, federal and provincial staff indicated that large scale methods used there are appropriate and can be implemented for Great Lakes applications (http://www.glfc.org/research/reports/2013_BRO_77002.htm). There is a lot known about coregonine culture and stocking success already but mostly focused on European whitefish *Coregonus lavaretus* and other shallow waters forms.

In general, the key issues that need to be resolved before hatcheries can achieve production scales of coregonines are: 1) identifying donor stocks for gametes that are not genetically bottlenecked, with little disease risk, can provide sufficient mating pairs (minimum of 100 over the entire spawning period) and where collections will not impair the sustainability of the donor stock; 2) logistics associated with collection of viable gametes in the fall and winter (ongoing); 3) whether wild gametes will be sufficient to meet production needs or be logistically feasible to collect, as opposed to captive broodstocks; 4) optimal incubation and rearing temperatures; and 5) optimal rearing densities. It is known that standard salmonine hatchery feeds will work for Cisco (Johnson et al. 2012; Fischer et al. 2016), but many other commercial formulations work well in Northern Europe (P. Heinimaa, Finnish Game and Fisheries Research Institute, personal communication), without the need for enhancement with live feed.

The ultimate goal of any fish restoration program involving the use of propagated individuals is the efficient transfer of intact genetic characteristics and allelic frequencies from wild donor populations to those being created or enhanced. Restoration or enhancement programs should be cognizant of the inherent risks involved with the use of hatchery-produced fish even when wild conspecific populations are used as gamete sources. This can be especially evident when introduced populations have the ability to interbreed with their founding stock, with possible genetic consequences inversely proportional with the size of donor population (Araki et al. 2007, Hindar et al 1991). Complicating factors such as high fecundity, reluctance to equalize familial contributions, and low survival in hatchery conditions can exacerbate loss of effective population size of hatchery stocks, and decrease allelic richness of stocked populations (Allendorf 1993). Every practicable effort should be made to maximize selected founding stock contributions to culture programs to offset these challenges. Guidance for effective population sizes necessary to minimize inbreeding and inherent genetic drift within managed fishery populations varies among experts with a general consensus that a minimum of 50 -200 effective founding individuals may retain 99% of heterozygosity present in founding populations (Kincaid 1983; Kapuscinski and Jacobsen 1987;Tringali et al. 1998). Given the aforementioned challenges associated with the culture of coregonines, agencies should make every effort to maximize contributing founding stocks with a target of at least 100 representative pairs contributing to a given year class of wild sourced production fish. In the event that donor stocks or logistical concerns cannot support such efforts, plans should be established to maximize the effective population size through mating schemes and familial equalization techniques.

Many of the culture issues above are currently being dealt with in recent initiatives as both Cisco and Bloaters have been recently cultured in the Great Lakes. Cisco have been cultured experimentally at the University of Wisconsin – Stevens Point Northern Aquaculture Demonstration Facility using gametes from Apostle Islands in Lake Superior (Greg Fischer, University of Wisconsin – Stevens Point, personal communication). From 2006-2010, the Michigan Department of Natural Resources experimentally cultured Cisco to develop recommendations for potential future cisco stocking programs in Lake Huron (Johnson et al. 2012). In the final year of the project 773,000 eggs were taken from 60 pairings of live ripe Cisco across two different collection dates from the Upper St. Mary’s River population. Egg fertilization rate averaged 44%. Egg and fry mortalities were very high and likely due to high incubation temperatures following chiller breakdowns, and only 9,495 spring fingerlings survived to stocking (Johnson et al. 2012). Spring fingerlings were OTC marked and stocked into Thunder Bay in 2008-2010, where Cisco have not been collected in recent decades (LHTC 2007). Monitoring efforts were already established in Thunder Bay that could be used to evaluate stocking success. A variety of lessons learned were outlined in

Johnson et al. (2012). It was determined that the Upper St. Mary's River population could provide up to one million eggs, so an additional source of eggs should be located to increase egg numbers. Broodstock that are not already ripe could be staged in nets until ripe. Walleye egg incubation methods were effective for Cisco, as are Chinook Salmon rearing and feeding methods. Production was discontinued as this was a proof of concept study and not a production effort.

A pilot project to rear and stock Cisco was launched in Lake Ontario by the US Geological Survey, Tunison Laboratory of Aquatic Sciences and the New York State Department of Environmental Conservation. The project was initiated in 2011 when approximately 70 adult Cisco were collected for gametes in Chaumont Bay in eastern Lake Ontario, the only known Cisco spawning site in New York waters. Since 2012, 280,000 fall fingerling Ciscoes (about 135 mm total length) have been stocked in historic spawning sites of Irondequoit Bay and Sodus Bay. All Ciscoes released since 2013 have been marked with calcein. Three adult Cisco were trap netted by USGS crews in Irondequoit Bay in the fall of 2016 for the first time since 1939. Region 5 of the USFWS has now joined this effort and about 125,000 spring fingerling Cisco (about 50 mm total length) reared at Lamar, PA will be stocked into Sodus Bay, along with another 125,000 reared by USGS in June, 2017. An additional 100,000+ fall fingerlings reared by USGS will be stocked into Sodus Bay in the fall of 2017.

A trial effort to rear and stock cisco is being carried out by the Little Traverse Bay Band of Odawa Indians in Lake Michigan. Since 2013, gametes have been collected annually from adult Cisco from Grand Traverse Bay in late November and early December and reared at a new LTBBOI hatchery. Crews target collection of eggs from 30 adult pairs, which has yielded between 244,500 and 893,195 eggs annually. Fecundity ranged between 20,000 and 55,000 eggs per female. Hatching success ranged from 26 to 53%, and was strongly influenced by the availability of female fish at peak ripeness. Since 2015, pens have been used to hold captured adult Cisco to harvest eggs at optimum ripeness. Fingerlings are raised in circular tanks, fed commercially available pelleted feeds, and can attain total lengths of 60 mm 160-180 days post hatch under appropriate lighting regimes (minimum 18hrs light per day) and tank densities (typically less than 18g/L). Mortality rates are minimal under these conditions. Fingerlings from each year class are marked with OTC and stocked in summer and fall and yearlings are stocked the following year (Table 2). An evaluation of marking strategies determined that coded wire tags placed in the nape of the neck in combination with fin clips yields both high tag retention rates (>95%) and low mortality (<5%). Cisco tagged in the snout exhibited far lower tag retention (<40%). Since 2014, approximately 150,000 juvenile Cisco have been stocked in Little Traverse Bay. Efforts are underway to recapture stocked Cisco and evaluate their performance in the wild.

A cooperative effort by USFWS, OMNRF, USGS, NYDEC, and GLFC to re-establish Bloater in Lake Ontario was initiated in 2010, with an objective to produce at least 500,000 juvenile Bloater annually but these efforts are still considered experimental. Collection of gametes of wild-caught Lake Michigan Bloater off Two Rivers, WI, deemed to be genetically appropriate as a source population (Fave and Turgeon 2008), has occurred annually in January and February since 2011, first with gill nets and then with bottom trawls. Collections have ranged from 306,000 eggs to 2.0 million eggs annually. Egg fertilization proportions have been highly variable across locations and among years and low fertilization rates are due to low fecundity, likely due to some eggs being in a pre-ovulation stage. The percentage of eggs to eye up has ranged 1.5 to 74%, but both are below what is needed to reach production goals. Egg survival was very poor in 2011, but generally increased thereafter largely due to improvements in adult fish condition and egg-take methods. About 500,000 juvenile bloater have been released into Lake Ontario during 2012-2016. The work has resulted in many lessons learned and the project team has prepared standard operating procedures for Bloater egg collection. Brood stocks of the 2011-2016 year classes were established from these collections. It is expected that production levels could be reached in 3-5 years with additional investment and continued refinement of gamete collection and rearing practices anticipated with the completion of research projects that address feeds, temperatures and rearing densities. Results from these activities and recent visits to facilities in Finland indicate that most methods are available to culture these species. Success with Bloater may suggest that other deepwater species could be cultured if gametes are logistically available from suitable donor populations.

Table 2. A summary of experimental cisco stocking operations in Little Traverse Bay, Lake Michigan conducted by the Little Traverse Bay Bands of Odawa Indians.

Year	Month	Stocking Target	Number Stocked	Avg. Length (mm)	Avg. weight (g)	Fin Clip	Coded Wire Tag	OTC application
2014	July	50,000	49,966	66	1.9	N	N	Immersion
2014	November	5,000	7,939	100	7.5	N	Y	Immersion
2015	April	-	2,040	187	58.9	RP	Y	Immersion
2015	July	50,000	-	-	-	-	-	-
2015	October	25,000	9,603	115	12.7	RP	Y	Immersion
2016	April	15,000	2,730	186	61.0	RP	Y	Feed
2016	August	50,000	50,447	72	2.6	N	N	Feed
2016	October	25,000	18,324	99	7.3	LP	Y	Feed
2017	May	15,000	11,764	159	36	RP	Y	Feed

Short et al. (1998) examined potential options to rear Emerald Shiners, and while feasible, it is likely to be more difficult and expensive at production scales compared to other minnows because of the extra care required managing stress throughout rearing and transportation. At this time, there are no commercial operations rearing Emerald Shiners in spite of the high market prices for this species, which reinforces the technical and logistical constraints with their culture.

Considerations for gamete sources

The following criteria should be considered when selecting source populations for gamete collection for brood stock development or production fish to be stocked into Lake Michigan:

- Population viability - Populations for gamete harvest should be stable or increasing in abundance, not those restricted in size, gamete availability or that have a potential to be harmed by the gamete collections. A suitable donor population should not exhibit an attenuated age-structure, with the appropriate number of age classes past age of first maturity as expected for stable populations, and be of sufficient density to achieve the requisite number of mating pairs over the entire spanning run. A conservative approach to gamete collection to ensure continued viability of the donor population would be to take gametes on a periodic basis as opposed to annually.
- Disease status – Propagation sources should pose no significant disease risk to the hatchery and stocking location. Disease monitoring of fish propagated from captive and wild populations in hatcheries is standard practice in fish management and diseases such as (BKD, VHS, etc) should be given special consideration. Strict gamete disinfection protocols should be in place to address pathogens regardless of their presences or prevalence in the source population. Appropriate alternative gamete collection locations should be identified in the event that source populations become diseased.

  From a long-term perspective, the least risk from disease introduction comes from taking gametes from waters hydrologically connected. The lowest risk waters are those upstream from the waters to be stocked because pathogens already are being transported passively downstream, however pathogen survival rates outside of hosts reduced chance of persistence, and long water retention times likely preclude active transport of live pathogens from lake to lake. In the unique case of Lake Michigan, Lake Huron has a significant connection to Lake Michigan via the Straits of Mackinac and contains viable populations of Bloater (less important for supplementation in Lake Michigan due to their ubiquitous distribution in the lake; Table 1). Fortunately, the Lake Superior drainage is upstream of Lake Michigan connected via the St. Mary's River with an outflow near the Straits of Mackinac.
- Environmental matching – Source populations should come from waters similar to where they will be stocked in terms of the physical (e.g., climate, depth, temperature) and biotic variables (e.g., predators, prey) as these populations may have accumulated genetic adaptations for life in large lakes due to exposure to common selection pressures. Typically, these source populations should be geographically proximate but not limited to Lake Michigan. For example, taking gametes from small inland lakes or from river systems should not be used for stocking the large bay or the lake proper.
- Genetic diversity- Source populations should be the genetically diverse and free from inbreeding depression and bottlenecks. Genetic considerations for propagation and stocking for supplementation and re-introduction have been extensively considered in many publications (e.g., Kincaid et al. 1993, Lichatowich et al. 2006; Meffe 1995). These concerns include: maintenance of population structure and diversity; preventing introgression and hybridization; and loss of diversity due to propagation practices. However, these risks need to be more fully evaluated and placed into context given of the short evolutionary history of ciscoes, their recent separation into the principal Great Lakes basins,

the genetic similarity among populations and forms, and the fact that ecomorphotypes remained distinct and identifiable in Koelz's day when stock sizes where much higher. Concerns over disrupting highly adapted genetically isolated populations is less of concern for the coregonines than, for example, Lake Sturgeon. What is important is to choose gamete sources geographically proximate to the waters to be stocked and with life histories that approximate those intended to be restored. Nearest neighbor gamete sources, Lake Huron and Lake Superior, and possibly Lake Nipigon, are likely to share a common evolutionary history with Lake Michigan, and have forms and life histories that have accumulated adaptations useful for survival and reproduction in the waters stocked. Because the form diversity is richest upstream from Lake Michigan, using coregonine populations from either Lake Superior or Lake Nipigon meets the most considerations of population viability, disease risk, life history and geographical proximity, and should also be considered as a gamete source for propagation and stocking into Lake Michigan.

- Life History – Historically, Cisco exhibited multiple life histories and eco-morphotypic forms. Restoration efforts, which will be logistically challenging, should center on forms that provide most of the historical biomass, spatial occupation, and diverse ecosystem services that are intended to be restored. The coregonine taxonomic complex offers a diversity of forms that contain variable phenotypic traits related to depth habitation and gill raker morphology (among others) that permit distinct spatial and trophic niches, that diversify the food web (Schmidt et al. 2011). Thus, restoring this native diversity to Lake Michigan's community of forage fishes will enable effective and efficient use of the energy resources of the lake.

Considerations regarding genetic diversity and the origin of cisco forms

Genetic diversity can be packaged in species and in populations within species; however, among coregonines, the distinction of species is highly blurred and has been the long-term focus of research to unravel the complex inter-relationships among the various forms (e.g., Koelz 1929, 1931; Bailey and Smith 1981; Todd et al. 1981; Turgeon and Bernatchez 2001). In the "The Coregonus Problem" in Bailey and Smith (1981: page 1555), they state "the species-level classification of ciscoes and chubs has never been wholly satisfactory … the acknowledged [by Koelz 1929] lack of characters that completely separate these forms suggests that they may be locally distinct stocks or groups of stocks rather than species" (page 1556). More recently, Turgeon and Bernatchez (2003) in a survey of North American ciscoes similarly concluded based on mitochondrial and microsatellite genetic data that the genetic variation observed reflected geography rather than taxonomy and therefore recommended that a single taxon be recognized, *Coregonus artedi sensu lato* (see also Turgeon et al.1999 for similar results regarding Lake Nipigon ciscoes). Strong evidence exists that the coregonine froms arose independently within each lake or geographic area due to common selection pressures as opposed to post glacial colonization of distinct species. The implications for management of the "Coregonus Problem" are that if the appropriate level of genetic diversity exists in the lake, or is introduced, eventually with time (such as 10,000 years) the morphs may arise again, but only if the same selection pressures exist as did historically. Given the uncertainty of the latter, the introduction of the extant forms from other sources to Lake Michigan may speed this process but the probability of success is unknown.

Potential source populations

The creation of hatchery broodstocks for reintroduction or augmentation of wild populations should be done with careful consideration. The difficulty involved in the collection of adequate representative founding stocks can be significant, especially with small populations. Ignoring the negative effects of a small founding population will decrease the probability of maintaining diversity by introducing inbreeding depression and genetic drift (Allendorf et al. 1987; Kapuscinski and Jacobson 1987). Conservatively, new broodstocks or gamate sources should be founded on a minimum of 100 paired matings (Kapuscinski and Lanan 1986) spread across the spawning season and over three year classes (Erdahl 1993). This strategy, with careful mating schemes and periodic source population integration, will slow the loss of founding genetic diversity in hatchery stocks.

Cisco – Goodyear et al. (1982) provided the locations of many historic spawning sites, and some have been visited recently in fall by agencies survey crews but with few or no Cisco captured. Continued sampling is planned to survey other locations. Given the lack of ubiquitous widespread recruitment and observations of adults, it is likely that many of these aforementioned populations are very small or have been extirpated. Small Cisco populations are present northeastern Lake Michigan in Grand Traverse Bay (Barton et al. 2011), Lake Charlevoix (Randy Claramunt, Michigan Department of Natural Resources – Charlevoix Research Station, personal communication), East Bay Grand Traverse Bay – Elk Rapids and Little Traverse Bay (Kevin Donner, Little Traverse Band of Odawa Indians, unpublished data). Some populations, such as at Elk Rapids, may be larger than expected (Kevin Donner, Little Traverse Bands of Odawa Indians, personal communication). These fish have been captured in spawning condition are known to spawn in shallow water on rocks nearshore but also have been capture pelagically over 100 ft of water in spawning condition.

There is disagreement on the ecomorphoytype designation of this Cisco; Eshenroder et al (in review) suggest it is a diverged form of Lake Huron shorthead cisco, whereas others suggest that it is similar to typical artedi of Lake Superior. Analysis of geometric morphology by Kyle Broadway indicates that contemporary Lake Michigan cisco are more similar to contemporary Lake Superior cisco than preserved samples of Lake Michigan artedi and Lake Erie albus forms collected by Koelz in the 1910’s, and that differences among all groups are driven by body depth and head shape. Differing morphometric methodologies may account for these disagreements. The dominant historic form in Lake Michigan was more pelagic and offshore and looked similar to all other Great Lakes Cisco with this life history (Koelz 1929), and may be a more likely candidate for restoration than historically lesser abundance forms.

Similar to the Lake Trout restoration program (Krueger et al. 1983), gamete sources outside Lake Michigan may have to be considered, if remnant gamete sources are inadequate, from the wrong habitat, or are genetically compromised. Lake Superior has many large and easily accessible spawning aggregations in the Apostle Island, Keweenaw Bay and other locations. They could serve as gamete sources, and are logistically feasible for gamete collection, and can result in hundreds of matings. Lake Huron contains some populations as well but in lower densities compared to Lake Superior (Figure 5). Collections in northern Lake Huron by the U.S. Fish and Wildlife Service in 2015 (4-27 fish/hr/1000ft) and 2016 resulted in low catch rates relative to spawning populations in Lake Ontario (Mike Connerton, New York Department of Environmental Conservation, unpublished data) or Lake Superior (Yule et al. 2008), but additional work is require to better document these stocks. In 2017, it took 8 nights of netting to capture 125 mating pairs at the Les Cheneaux Islands, and catches were highly variable among sites and nights.

Deepwater Ciscoes – As stated before, Shortnose Cisco (COSEWIC 2003) and Deepwater Cisco are globally extinct (IUCN 2013). Remnant populations of Blackfin Cisco exist only in Lake Nipigon and a few other inland lakes in Canada northwest of Lake Superior, and in Algonquin Provincial Park, Ontario (Mark Ridgeway, OMNR, personal communication). Shortjaw Cisco is found in Lake Superior but at low densities; they may be unable to support adequate gamete collections. They are also found in Lake Nipigon and a few other inland lakes in Canada northwest of Lake Superior (COSEWIC 2003). Kiyi are only now found in Lake Superior and are abundant in waters greater than 100 m (Pratt 2012), but appear to be in decline in recent years (Mark Vinson, USGS-GLSC, personal communication). Bloater are still present and ubiquitous in water greater than 60 m in Lake Michigan (Bunnell et al. 2017) and would not be considered for culture.

We suggest a continuum of the probability of success based on the number, size, and location of genetically appropriate donor populations, and the season of gamete availability (Figure 13). These factors more strongly influence success probability compared to culture logistics.

Cisco is the most likely candidate to begin reintroductions through culture. Although there is a large reserve of Kiyi in Lake Superior that could serve as donors, there is some uncertainty regarding the spawning season as it may be prolonged over months or seasons. Capture and egg collection procedures would be similar for Kiyi as those used for bloater now on Lake Michigan for Lake Ontario effort, and the aim would be to develop a brood stock for production fish.

Figure 13. Continuum of probability of success for reestablishing ciscoes in Lake Michigan.

Special consideration for cisco source populations

We consider Cisco (*C. artedi*) reintroductions to be most important ecologically, the easiest to execute, and the most likely to succeed. Because there are resident populations in Lake Michigan there is considerable disagreement among Lake Michigan biologists on:

1. The need for stocking given that current populations are expanding, and a belief that they may be able to populate the whole lake,
2. That existing Lake Michigan populations may represent the typical artedi form/ecotype that made up most of the historical populations in Lake Michigan,
3. If expanded stocking were to occur, whether to use only Lake Michigan populations as gametes sources or to go to other Great Lakes with larger populations, and
4. The perceived and real genetic risks to existing populations of going to outside gamete sources for stocking production fish.

To address this last issue we consulted a panel of geneticists (Table 3) from both inside and outside the basin to provide input on specific questions below that we hoped would resolve uncertainties of risks and provide guidance on appropriate donor populations. The questions asked and summarized responses provided are presented below. In not all instances did the panel provide complete responses.

1) **Genetic Diversity** – Is the genetic diversity within potential source populations of *C. artedi* in Lake Michigan similar to other Great Lakes populations (e.g., lakes Huron or Superior) in terms of such measures as heterozygosity, allelic diversity, allelic richness (*Ar*), and private allelic richness (P *Ar*)? Are genetic diversity measures related to relative measures of population abundance?

H_o: All populations have similar measures of genetic variation and no relationship exists between the level of genetic variation expressed and population abundance.

2) **Effective Population Size** – Do substantial differences occur in estimates of effective population size N_e among the *C. artedi* population sampled from lakes Michigan, Huron, and Superior? Does evidence exist that any of these populations have undergone a bottleneck in population size and as a result have reduced genetic diversity? If reduced genetic diversity is evident, can we infer fitness given different selective processes in each lake (e.g., life history traits, competition with invasive species, prey availability, etc)?

H_o: All populations have high levels of estimated Ne and no evidence exists for a loss of genetic diversity.

3) **Genetic Differentiation** – What is the level of genetic differentiation among populations of *C. artedi* in lakes Michigan, Huron, and Superior using measures and tests such as G tests, F_{ST}, individual-based principal coordinates analysis (PCoA), coordinated analysis of allelic frequencies using multiple coinertia analysis (MCOA), and

analyses of molecular variance (AMOVA)?

H_o: No genetic differentiation is detectable among the populations when neutral genetic variation is compared.

4) **Best Donor Populations** – For those populations where genetic data are available, which population(s) would serve as the best genetic source(s) for a reintroduction program into Lake Michigan? What are the risks to Lake Michigan or to the donor populations if it was used? What is the level of uncertainty in your recommendation?

5) **Secondary Sources** – Which populations would serve as an acceptable choice as a gamete source, if the best genetic source population would be at risk and could not provide enough gametes or was logistically difficult to sample? What are the risks to Lake Michigan or to the donor populations if it was used? What is the level of uncertainty in your recommendation?

Table 3. Summarized responses from geneticists regarding potential source populations for Lake Michigan

Question	L. Bernachez Univ. of Laval	T. Dowling Wayne State Univ.	J. Turgeon Univ. of Laval	K. Scribner MI State Univ.	W. Stott USGS/MSU	B. Sloss Univ. of WI Stevens Pt.
1) Genetic Diversity – Is the genetic diversity within potential source populations of C. artedi in Lake Michigan similar to Lake Superior and Lake Huron populations in terms of such measures as heterozygosity, allelic diversity, allelic richness (Ar), and private allelic richness (P Ar)? Are genetic diversity measures related to relative measures of population abundance? Does evidence exist that any of these populations have undergone a bottleneck in population size and as a result have reduced genetic diversity? This information could be useful in selecting sources. Likely, if some sources showed very low diversity values or indications of having sustained a recent bottleneck, then these sources might be deemed to be less desirable.	GTB diversity lower but comparable to other populations. Few private alleles in any population. No obvious sign of bottleneck in Lake Michigan, but lower diversity could be due to smaller population size or fewer subpopulations. GTB could be used for source pop. but higher diversity exists elsewhere in lake Superior.	Sample sizes good but sampling unbalanced. Have to make assumption that samples are representative of distribution from each lake (esp. important for broodstock collection). Allelic Richness Ar: Higher in Lake Superior, lower in Lake Michigan similar to lakes Huron and Ontario. Gene diversity-Lake Michigan reduced relative to others.	Can't reject Ho "All pops have similar genetic diversity, no relationship between diversity and population size, no loss of diversity.	Sample sites don't differ greatly, however statistical tests are not provided on differences, therefore can't reject hypothesis, doesn't appear to be differences.	Genetic diversity similar among sites, slightly higher in Lake Superior than the others. No info on population abundance.	Lake Michigan-Grand Traverse Bay-lower genetic diversity than others. Need data on population abundance. No bottleneck test results provided, but evidence of bottleneck in Grand Traverse Bay stock can be inferred due to low allelic diversity. Reject Ho, significant differences among sampled populations apparent.

Question	L. Bernachez Univ. of Laval	T. Dowling Wayne State Univ.	J. Turgeon Univ. of Laval	K. Scribner MI State Univ.	W. Stott USGS/MSU	B. Sloss Univ. of WI Stevens Pt.
2) Effective Population Size – Do substantial differences occur in estimates of effective population size Ne among the C. artedi population sampled from lakes Michigan, Huron, and Superior? Do some populations have very low Ne such that sampling gametes from them could raise conservation concerns about population viability?	Used LD method. Substantial variation among samples. GTB lowest, at lower limit for Lake Michigan, caution using Lake Michigan as source. Western Lake Superior low Ne values despite high diversity-likely part of metapopulation. Northern Lake Superior and Lake Huron have high Ne values. To be consistent with diversity recommendation- use northern Lake Superior as source.	Used LD method. Lake Michigan and one Lake Ontario have lower Ne than all the others.	Can't reject Ho	Data on Ne ambiguous. Samples are likely admixtures of age classes and populations, which can bias Ne estimates (esp. LD-based). Need age structure to interpret results.	Lake Superior pops have larger estimates. None indicate that collection sites are associated with pops that are at critically low sizes.	LD estimates of Ne "iffy" because estimate was infinity for 8 of the samples. Based on low point estimates for GTB, Bay of Quinte, and Brule River, should not use those due to low Ne and risk to source pop.

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3) Genetic Differentiation – What is the level of genetic differentiation among populations of C. artedi in lakes Michigan, Huron, and Superior using measures and tests such as G tests, FST, individual-based principal coordinates analysis (PCoA), coordinated analysis of allelic frequencies using multiple coinertia analysis (MCOA), and analyses of molecular variance (AMOVA)? High levels of differentiation might suggest that some sources would be better suited for introduction than others.	Differentiation among Lake Superior samples weak, suggesting substantial gene flow, and supporting meta-population concept. Lake Superior divergent from lakes Ontario and Huron. GTB in Lake Michigan most different (likely due to low diversity). Levels in Lake Michigan are low such that genetic rescue could be used, without issue of outbreeding depression. Thunder Bay recommended as source since it has second lowest differentiation.	Some differentiation-based on many significant pair-wise comparisons of Fst. However, Structure detected K=2. Likely considerable admixture, with possible exception of Lake Superior vs. other lakes. Overall very limited stock structure.	Ho can be rejected, lakes are different. L.Michigan seems slightly more differentiated by not significantly so ("gut feeling")	Sampling not expansive, esp. Lake Superior. More msat and mtDNA data is available (Scribner and Stott) that could provide greater resolution. Other data shows two primary groups-Superior and Huron/Michigan, consistent with results here. Data suggest that Lake Superior may not be the best.	Lake Superior pops in one group and others in another group. GTB site was the most divergent.	Lake Michigan different from all other potential sources. Significant structuring among pops within basins, e.g. Lake Superior, but more similar within basin than between basin. Overall degree of differences "shallow", but high Fst for Lake Michigan remant population is unique and of interest to conserve.

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4) Best Donor Populations – For those populations where genetic data are available, which population(s) would serve as the best genetic source(s) for a reintroduction program into Lake Michigan? What are the risks to Lake Michigan remnants or to the donor populations if it was used? What is the level of uncertainty in your recommendation? By combining the information from 1, 2, and 3, are there indications that some sources are more genetically suited for Lake Michigan and that can be safely sampled.	Thunder Bay, Grand Portage Black Bay. Translocation opposed to GTB given low Ne and diversity. A genetic rescue from populations with higher diversity, Ne and not very genetically distinct.	Depends on goal: Lake Superior to be used if you want increase genetic diversity. Use lower lakes or all lakes if you want to reflect population structure and genetic diversity. He'd favor sources from multiple lakes.	Any population, even Lake Michigan-as it's diversity, lower than the rest, is still high.	More data available-should also evaluate to aid in donor determination. But based on data provided, Lake Michigan/Huron best.	Main Lake Michigan basin populations isn't included, so should add them (available?) to determine if they would be the best fit first.	Based on information from 1, 2,and 3 some sources are more genetically suited for Lake Michigan and can be safely sampled.
5) Secondary Sources – Which populations would serve as acceptable choices as gamete sources, if the best genetic source population would be at risk and could not provide enough gametes or was logistically difficult to sample? What are the risks to Lake Michigan or to the donor populations if the secondary sources were used? What is the uncertainty in your recommendations?	Thunder Bay, Grand Portage Black Bay	Set up replicates of experimental crosses.	True risk is not having pelagic cisco in the lake-taking fish from secondary source (nearby inland lake connected to great lakes), is a low risk. Genetic rescue may be needed.	other Lake Michigan/Lake Huron sources	Can't really say without inclusion of main Lake Michigan sites.	GTB, St. Mary's River and Drummond Island, primarily due to geographic proximity. Strictly based on genetic data-Chaumont Bay and Bay of Quinte.

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6a) What aspects of cisco genetic diversity are most important to consider when making choices about **broodstock development**?	A rigorous breeding plan with semi- or full-factorial design, balance Nb and expected prop. Or captive progeny relative to the wild	Levels of genetic variation and geographic structure, including potentially adaptive and neutral genetic variation	Avoid inbreeding, have as many different parental pairs as possible.	variation in coding genes associated with adaptation	broodstock size should be large to capture the diversity of that stock, and for safe collection.	Genomics approach
6b) Based on your knowledge of the existing available data, what do you see as the most **important information gaps?**	Lack of information about adaptive divergence	Need more samples, esp. Lake Huron, impact of mattings between lake source, adaptive differences between lakes	Assess the role of plasticity in determining morphology and niche utilization	variation in coding genes associated with adaptation	Additional data from main basin of Lake Michigan and north channel of Lake Huron were not available at time of this analysis, but should be included.. Need to assess if additional remnant pops in Lake Michigan exist. Also evaluate relationship between genetics and phenotype.	Genomics data

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6c) What sort of **genetics-related monitoring** will be necessary if a broodstock is developed?	Temporally monitor success of stocked progeny, parentage-based tagging	Track genetic parameters to see if stocking has impacts on genetic variation		Mark all hatchery individuals, maintain pedigrees of crosses. Genetic monitoring of existing wild and hatchery fish, test crosses of sources should be made to evaluate outbreeding depression.	Ensure that diversity of wild has been captured in brood, central database with genetic profile for all strains to assess origin of future captures of hatchery and wild ciscoes.	Genomics based parentage, parental success, allele diversity and frequency monitoring (which could be done with microsats)

The results of this exercise yielded widely differing opinions on which source population to use and the acceptability of others but some general patterns emerged:

- All populations had similar genetic diversity with Lake Michigan populations slightly lower than all others and the highest diversity in Lake Superior.
- Effective population sizes may be higher in Lake Superior and lower in Lakes Ontario and Michigan; some could not make determinations based the data and analysis.
- Lake Superior populations have low differentiation suggesting a metapopulation structure - 2 overall groups: Lake Superior and all other Lakes. Grand Traverse Bay, the only population sampled in Lake Michigan, was the most different. Differences among populations are small.
- Best donor populations recommendations were inconclusive, and ranged from Lake Superior, to all sources, to any source, to just Lake Michigan/Huron.
- Brood stocks should be developed using a rigorous breeding plan, with high numbers of parents, to include a high variation of adaptive genes.
- Implement genetic monitoring to track performance of stocked fish (as opposed to tagging) and measure effects on residual wild populations.

Options for reintroduction/recovery

There are many efforts underway to study existing populations in Lake Michigan and elsewhere that will add to our understanding. The recent and rapid proliferation of new information, including genetics on the forms of *C. artedi*, has prevented sufficient time to discuss the implications for reintroduction. In fact, all of the relevant material has not been aggregated and distributed yet, although this accomplishment is not far off. The task group anticipates that an informal workshop aimed at resolving as many of the areas of contention as possible will be necessary. As such, a decision on these options at this time would be subject to aspects of uncertainty, which will likely be addressed over the following timelines:

- Over the coming months, a comprehensive morphometric analysis of Cisco from Lake Michigan will be complete and will provide more certainty regarding extant forms.
- Within the next six months to a year, analyses of neutral genetic markers and otolith microchemistry of extant Lake Michigan ciscoes will be complete, and will hopefully inform further discussions (with a neutral moderator) to produce recommendations on a common understanding.
- Within the next two years, analysis of adaptive genetic markers in Great Lakes cisco should be complete. It will further inform our understanding of forms and their suitability for transplantation, if desired. A reconvened task group should be able to determine whether waiting for results on adaptive genetic structure is advisable before moving forward with any management option.

All members of the current task group agree that the endeavor to reintroduce or not reintroduce *C. artedi* will have ramifications far into the future and should be based on a thorough examination of all of the available data.

The options listed below represent potential management actions that could be implemented pursuant to restoration of coregonines in Lake Michigan. Each option includes a summary of the benefits, risks, feasibility and information needs that are specific to that approach.

Cisco (formerly known as "lake herring")

Option A: No stocking. Do not propagate and stock Cisco into Lake Michigan.

Benefits: Not stocking Cisco from outside Lake Michigan would protect existing populations from the risk of genetic introgression (outbreeding depression) with introduced Cisco. Genetic introgression is defined as the movement of genes from one population into another by the repeated backcrossing of an interspecific hybrid with one of its parent sources that reduces survival of offspring. Cisco are increasing in abundance in certain areas of eastern Lake Michigan, and a "wait and see approach" would allow for a better understanding of this expansion.

Risks: The risk of taking no action is that existing populations may undergo no additional or only marginal increases in number and distribution. This appears to be the case in Lake Huron, where populations in northern part (i.e., North Channel and Georgian Bay) of the lake have not colonized Saginaw Bay. Hence, most of Lake Michigan could remain lightly populated by planktivorous fish. Lake Michigan pelagic prey is at all-time lows, and a need for management actions that can lead to a broader prey size distribution, greater prey densities and energy flow to predators. Moreover, the dearth of planktivores in the pelagia makes it easier for another unknown exotic planktivore to colonize these waters.

Feasibility: Feasible. No resources or actions required.

Information Needs: The seasonal distribution and abundance of Cisco in Lake Michigan must be measured in an unbiased manner to document new populations, changes in distribution, and done lake-wide. Benchmarks, with metrics comparable to other populations outside Lake Michigan, should be developed to clearly determine and evaluate progress. Observations should be reconciled with historic information on (e.g., ecomorpotype, habitat) Lake Michigan populations.

Option B: Stock Cisco using gametes only from Lake Michigan populations.

Under this option, gametes would be collected only from suitable Lake Michigan stocks for production and/or captive brood stock development. Gametes may be collected from newly discovered populations from Lake Michigan as they are identified and characterized but, only if they are large enough to support large-scale gamete collection and have the requisite genetic diversity.

Benefits: Contemporary Lake Michigan stocks of Cisco that have persisted may have experienced selective pressures that provide an adaptive advantage over those elsewhere. This reduces genetic risks from stocks outside Lake Michigan stocks. Grand Traverse Bay and Little Traverse Bay may provide a reliable consistent source of gametes that may be increased. There may be undocumented spawning stocks that may be available to diversify the available fish to stock. Disease monitoring during gamete collections initiated in 2013 has not detected any key pathogens in these potential donor stocks used for egg takes or in hatchery-reared progeny.

Risks: Cisco from Grand Traverse Bay exhibit slightly less genetic diversity than in lakes Huron and Superior though the importance of this difference is unclear. Using only Lake Michigan fish eliminates the possibility of providing genetic diversity from elsewhere on which natural selection could act (Krueger et al. 1981). Genetic drift can cause losses of genetic variation in small populations. Drift results in populations less adaptable to new selection pressures, such as changes in climate or productivity, because some of the genetic variation that selection could have acted on is missing. Expanding the range of the GTB population via stocking other sites should be informed by a more expansive genetic inventory of nearby populations, so as to prevent introgression between adjacent genetically distinct populations. If nearby genetically distinct spawning populations are detected, the question will be whether they could benefit from supplementation, e.g., they exhibit less genetic variation or used as another gamete source to diversify the production fish. Otherwise, stocking on top of existing wild populations presents risks of reducing the effective population size of the combined population even when stocked fish result from parental numbers theorized to be adequate (Christie et al. 2012). These risks can be minimized with good hatchery practices.

There is also risk that Lake Michigan Cisco populations cannot provide sufficient gametes to rear and stock Cisco at high enough densities to support direct stocking from wild eggs sources.

Feasibility: Annual collection of gametes from 30 adult pairs from Grand Traverse Bay to stock into Little Traverse Bay is ongoing. Annual collection of gametes from a minimum of 100 adult pairs over the entirety of the spawning run is recommended to minimize loss of genetic diversity. This amount is logistically feasible, would yield 2-3 million eggs, and could begin immediately.

Information needs: Additional information on the status, distribution and genetic diversity of other Cisco spawning aggregations is needed. Verification of adequate gamete volume to satisfy production needs and to maintain genetic diversity is required.

Option C: Use gametes from larger Cisco populations from outside Lake Michigan. This option would entail gamete collection from Cisco in Lake Superior for production and/or captive brood stock development. Introducing the Lake Huron cisco can also be considered but not until more is known about the genetics, distribution and abundance of existing populations.

Benefits: Larger populations would provide reliable, consistent, and more logistically feasible sources for the large number of one-on-one fertilizations that need to be sampled across the spawning period. This would allow for consistent and reliable gamete collections and potentially stocking of much larger numbers of fish annually, which could greatly increase the potential for increasing the role of Cisco as a major pelagic prey fish at lakewide scales in a shorter time-frame compared to using smaller source populations. In addition, if it is determined that Lake Michigan lacks a pelagic, broadcast spawner, the re-introduction of this form may facilitate more rapid lake wide expansion as it spends a large portion of the year in offshore waters. Lake Superior populations that are commercially harvested could be accessed via commercial fishers, although fishery independent sampling is possible. Repeated sampling poses no impact to source populations as they are large. Source populations in Lake Superior are well-known and accessible and are the principal form that may have dominated historical populations in all lakes except Lake Erie (Koelz 1929), and appear presently to be slightly more diverse that cisco in lakes Michigan and Huron.

Risks: Introduced stocks could introgress with existing Lake Michigan stocks. Stocking should be informed by more expansive genetic inventory of extant populations, so as to assess the risk of introgression between populations. The risk of introgression may be reduced by introducing fish in areas distant from existing populations however introgression risk may become greater as lake-wide restoration goals are achieved but may be minimal since these forms coexisted historically at much higher population levels. Disease transfer risks from one lake to another exist but could be minimized with consistent and standardized fish health surveillance of donor stocks, proper isolation protocols, and appropriate fish health inspections of production fish practiced universally in hatcheries.

Feasibility: Feasible logistically possible and could begin immediately. Numerous large stocks identified as potential candidates.

Information needs: Verification of adequate gamete volume to address production needs and genetic issues is required.

Option D: Stock Cisco using gametes from a broad range of donor populations

Under this option, gametes would be collected across lakes from multiple stocks that may vary in life history strategy and habitat uses (e.g., river spawners if located). These donor stocks could be reared separately for captive brood stock development.

Benefits: Reestablishment of an extirpated species or life history strategy may be best achieved by maximizing genetic diversity (Krueger et al. 1981) for natural selection to operate on and ensuring the best adapted stock is developed. Furthermore, establishing a diversity of cisco stocks could that exploit different habitats could increase resilience (Hilborn et al. 2003)

Risks: This approach would risk potential for introduced stocks to introgress with current Lake Michigan stocks reducing the survival potential. There is also a risk that resulting intermediates may not be adaptable to local environments (e.g. outbreeding depression).

Feasibility: Feasible but logistically difficult and expensive to maintain separate brood. Annual collection of gametes is ongoing in Lakes Huron and Michigan so progeny from two donors soon could be stocked at a selected location. At this time, there are no known donor sources for river-spawning cisco, although there are historical accounts that they existed. Other source populations exist in Lake Ontario. Protocols do not currently exist that specify what proportions should be derived from each source and how to match donor sources with target stocking location. These protocols can be determined leading to an appropriate genetic management program for implementation.

Information needs: Additional genetic and fish health information is needed on all potential donor stocks before large scale gamete collections begin. Verification of adequate gamete volume to address production needs and genetic issues is required.

<u>Option E: Habitat Rehabilitation or Conservation in Selected Areas</u>. Restoration of habitat in areas where improvements may increase recruitment.

Benefits: Where spawning or nursery habitat are limiting, habitat rehabilitation may help to improve recruitment. This option could benefit either existing populations or newly stocked populations. Benefits could be maximized if restoration areas were designated as “refuges” (akin to the Lake Michigan lake trout refuges) to reduce effects of exploitation, if deemed excessive.

Risks: No real risk, particularly if research is conducted to inform restoration efforts. While there is no evidence at this time that habitat is limiting in Lake Michigan, costs associated with perceived habitat improvements could be wasted. If other factors are impairing population growth, this option may not be successful.

Feasibility: The feasibility of rehabilitation is situationally dependent. Depending on the location there are three options: 1) no intervention may be needed, 2) improvement may be feasible through habitat manipulations, or 3) it may not be feasible because of other factors not related to physical habitat manipulation.

Information needs: Mapping of historical spawning habitats would inform potential new sites for restoration, for refuge creation, or for sampling for undiscovered populations. For current Cisco populations, potential habitat limitations and restoration potential needs to be assessed in key Cisco spawning and nursery habitats in a range of populations to inform what constitutes critical habitat and to inform restoration projects.

Implementation of a restoration plan is not limited to one option but could be a combination of options.

Kiyi: This would entail gamete collections from Lake Superior or Lake Nipigon for captive broodstock development and stocking of production fish.

Benefits: Kiyi would co-occupy deepwater portions of Lake Michigan that are currently occupied by Bloater and provide additional deepwater forage for Lake Trout. Kiyi are ubiquitous in Lake Superior beyond 80 m, are the most numerous deepwater cisco in the Great Lakes, and are not threatened by anthropomorphic sources. Re-establishment in Lake Michigan may provide greater long-term conservation security for the form. Kiyi are bentho-pelagic feeders and consumes *Mysis*. *Mysis* play important roles in benthic-pelagic coupling; because Kiyi would likely occupy deeper depths than Hoyi, there is potential for Kiyi to provide this functional contribution through excretion and through their pelagic larval stage in even more of the lake.

Risks: No genetic risk as this form is extirpated from Lake Michigan. At the same time potential introgression with existing Bloater populations may be of concern. Disease transfer risks from one lake to another are minimized with a full fish health history, surveillance fish pathogen testing, standard isolation protocols, and fish health certification of any production fish.

Feasibility: Potentially highly feasible if sufficient gametes can be collected to establish brood stock. Experience in winter gamete collection, rearing, and stocking Bloater from Lake Michigan to Lake Ontario is ongoing on since 2010, and can be applied to Kiyi. Culture is feasible given the successes in rearing Cisco and Bloater. Ice conditions on Lake Superior could impede access to gamete sources.

Information needs: Information on location and seasonality of spawning aggregations and maturity schedules, and fish health are needed. Lake Superior populations are large, but spawning season and locations are not well known. Spawning is thought to take place in late fall and early winter and ice conditions on Lake Superior could impede access. Gamete maturation schedules are unknown as it appears that females can have eggs at other times (C Bronte; personal observation and reported by Koelz (1929) in Lake Ontario). If Kiyi have a protracted spawning season, it could complicate gamete collections.

Shortjaw Cisco: This would entail gamete collection from Lake Nipigon for captive broodstock development and stocking of production fish. Lake Huron and Lake Superior populations are too small to support gamete collections (see Mandrak et al. 2014; Hoff and Todd 2004; Bronte et al. 2010).

Benefits: Shortjaw Cisco would provide additional prey at intermediate depths and shallower depths during the spawning season. Their re-establishment in Lake Michigan would also provide a buffer against the potential for extirpation from Lake Superior.

Risks: Genetic evidence suggest that Shortjaw Cisco in Lake Nipigon are from the western ancestral line associated with the James Bay drainage as compared to other Great Lakes Shortjaw Cisco that belong to the eastern race associated with the Atlantic drainage (Turgeon et al. 2016). Potential introgression with existing Bloater populations may be of concern. Disease transfer risks could be minimized with a full fish health history, surveillance fish pathogen testing, standard isolation protocols, and fish health certification of production fish.

Feasibility: The feasibility for this form is low because of their rarity. Shortjaw Cisco, which was historically the most numerous deepwater cisco in Lake Superior in the 1920s (Koelz 1929; Hoff and Todd 2004), are now the rarest deepwater cisco; are a threatened species in Canada and in Ontario; and are considered vulnerable to extinction (i.e. global G3 ranking) by Natureserve. The population in Georgian Bay is thought to be extirpated, though the Lake Nipigon population has been reported as relatively common (Todd 2003) but now in decline (Rick Salmon, OMNRF, personal commination).

Information needs: Information on genetic diversity, abundance, stock location and seasonality of spawning aggregations, maturity schedules, and fish health information are needed from Lake Nipigon. Feasibility of using these fish should be conducted after sufficient information is available.

Blackfin Cisco: This would entail gamete collection from Lake Nipigon for captive broodstock development and stocking of production fish. Another source could be potentially from inlands lakes in the Algonquin Park region but little is known yet about these populations.

Benefits: Blackfin Cisco would occupy deepwater portions of Lake Michigan that are currently occupied by Bloater. Historically these fish were deeper than Bloater (Bunnell et al. 2012a). This form could provide deepwater forage potential for Lake Trout. This was the largest deepwater cisco in body sze and their young can provide prey to predators as well as support fisheries should populations reach a sufficient population size.

Risks: Risk is low since they are extirpated from Lake Michigan. Potential introgression with existing Bloater populations may be of concern. Disease transfer risks from one lake to another could be minimized with a full fish health history, surveillance fish pathogen testing, standard isolation protocols, and fish health certification of any production fish.

Feasibility: The feasibility is unknown and likely dependent on the size, availability, and logistics of populations in Lake Nipigon and the newly discovered populations in the Algonquin Park region, of which little is known. Experience in winter gamete collections are ongoing since 2010 for Bloater in Lake Michigan to support rearing and stocking in Lake Ontario and can be applied to this form.

Information needs: Information on genetic diversity, abundance, stock location and seasonality of spawning aggregations, maturity schedules, and fish health information are from source populations in Lake Nipigon and the newly discovered lakes in the Algonquin Park lakes. An analysis of the overall feasibility of using these fish should be conducted after sufficient information is available.

Bloater reintroductions/harvest restrictions. No stocking advised because viable populations are still present in Lake Michigan, and may even be increasing. The only other management option would be harvest restrictions but exploitation is already thought to be very low. Populations are low due to unexplained poor recruitment of the last 15 years and additional investigations should be done to examine why Bloater have not recovered. Contemporary harvest rates need to be re-evaluated relative to the standing stock to understand the effect of harvest and to inform future harvest restrictions. Harvest restrictions would have no ecological risks but some constituents would be affected.

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