CISCO SPAWNING IN CHAUMONT BAY, LAKE ONTARIO

A Thesis

Presented to the Faculty of the Graduate School

of Cornell University

in Partial Fulfillment of the Requirements for the Degree of

Master of Science

by

Ellen Maureen George

May 2016

ABSTRACT

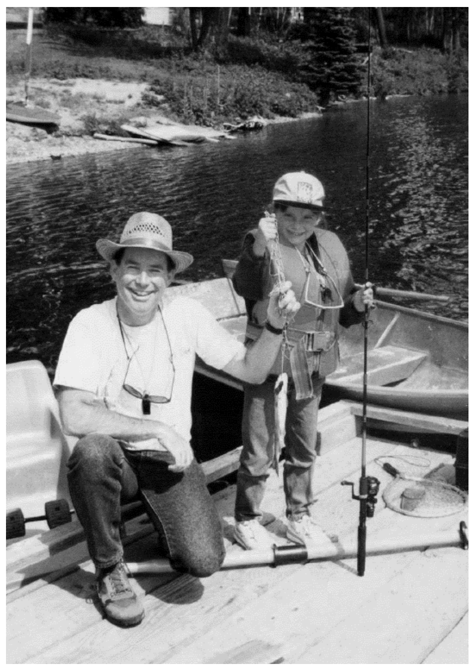
Cisco *Coregonus artedi* are an important prey fish for many Great Lakes predators, including lake trout *Salvelinus namaycush*. Their numbers have declined drastically in the last century due to the impacts of invasive species, overfishing, and habitat degradation. Chaumont Bay, New York contains one of the last remaining spawning populations of cisco in Lake Ontario. This thesis synthesizes over 100 years of cisco research, and documents the first confirmation of cisco spawning in Chaumont Bay in decades. Sampling was accomplished using a custom egg pumping device designed to collect eggs through lake ice, and eggs were identified to species using genetic barcoding. Cisco exhibited a strong spawning habitat preference for shallow, rocky shoals in Chaumont Bay. Establishing self-sustaining spawning stocks of cisco is a key objective to their restoration in Lake Ontario, and the results from this study will be used to inform managers and guide restoration initiatives.

BIOGRAPHICAL SKETCH

Ellen George grew up near the ocean in the beautiful beach town of Ventura, California. She fell in love with fish while hiking, backpacking and fly fishing on treasured wilderness excursions with her father, Randy, and her adventurous mother and sister. She attended the University of Puget Sound in Tacoma, Washington, and graduated in 2010 with a Bachelor of Science degree in Biology and a minor in Environmental Studies. After graduation, she worked as a fisheries technician in Shenandoah National Park and for the USGS Great Lakes Science Center in Ann Arbor, Michigan. Her other life adventures include working as a zookeeper, dog trainer, kayaking and sailing instructor, dive shop lackey, and backpacking trip leader. She arrived at Cornell University in August 2013 to study fisheries biology with Dr. Lars Rudstam of the Department of Natural Resources. She is an active member of the Cornell Student Subunit of the American Fisheries Society, and a volunteer for the International Association of Great Lakes Research Communications Committee. When she is not working she enjoys fishing, hunting, SCUBA diving, cross-country skiing, camping and hiking with her dog, handspinning and knitting, and is a performing dancer.

For my Dad,

who taught me how to fish.



ACKNOWLEDGEMENTS

I would like to thank my committee for their support and guidance, including my advisor, Dr. Lars Rudstam, and committee members Dr. Patrick Sullivan (Cornell University) and Dr. Darran Crabtree (The Nature Conservancy of New York). I would also like to thank my coauthors for the journal article representing the second chapter of this thesis: Wendylee Stott, Curtis Karboski, Edward Roseman (USGS-GLSC), and Brian Young (Cornell University). This research was funded by The Nature Conservancy of Central and Western New York through a generous grant from the Margaret L. Wendt Foundation, with additional in-kind support from the USGS Great Lakes Science Center and Lake Ontario Biological Station and the New York State Department of Environmental Conservation. Special thanks to Michael Connerton (NYSDEC); Patrick Schulze, Matthew Paufve, Cody Deiterle, Brian Lantry, and Brian Weidel (USGS-GLSC); Sarah Burnet, Thomas Brooking, and Peter Kite (Cornell University) for field and laboratory assistance. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

LIST OF ILLUSTRATIONS

INTRODUCTION

Cisco *Coregonus artedi* are a schooling, cold-water, zooplanktivorous fish native to the north-central United States and Canada. They were once one of the most abundant fish species in the region, and supported large commercial fisheries in all five of the Great Lakes in the early 1900's. Overfishing, habitat degradation, and impacts from invasive species such as rainbow smelt *Osmerus mordax*, alewife *Alosa pseudoharengus*, and sea lamprey *Petromyzon marinus* lead to the collapse of these fisheries, beginning with Lake Erie in the 1940's and ending with the decline in Lake Superior in the 1970's. Today, only Lake Superior retains a stock substantial enough to support a commercial fishery. Cisco have been extirpated from Lake Erie, and abundances in Lakes Huron, Michigan and Ontario remain low.

Recently, there has been an increased momentum for restoring cisco populations in the Great Lakes. Cisco, along with other coregonines such as bloater *Coregonus hoyi* and lake whitefish *C. clupeaformis*, were historically important native prey fish species for predators such as lake trout *Salvelinus namaycush* and Atlantic salmon *Salmo salar*. However, the aquatic food web of the Great Lakes has changed substantially in the last few decades. Invasive species such as alewife and rainbow smelt now dominate the prey fish biomass, and make up the majority of the diet of lake trout and Atlantic salmon. Alewife and rainbow smelt are high in thiaminase, an enzyme that breaks down vitamin B1, or thiamin, in the bodies of adult salmonid predators. This thiamin deficiency can lead to early mortality syndrome in salmonid larvae, and in some cases has been linked to complete recruitment failure. In contrast to invasive prey fish species, native coregonines such as cisco are low in thiaminase and rich in thiamin. By restoring native prey fish species such as cisco, we can in turn promote the restoration of salmonid predators such as lake trout and Atlantic salmon.

Lake Ontario is the easternmost and final lake in the Great Lakes chain. Along with the rest of the Great Lakes system, Lake Ontario has undergone many dramatic changes in the last 200 years due to human activity. Prior to European settlement, the Lake Ontario food web was characterized by a diverse prey base of coregonines, shiners, and sculpins, with Atlantic salmon, lake trout and burbot *Lota lota* as its top predators. By the 1960's overfishing, the invasion of exotic species, and poor water quality had led to the reduction of large predators and the complete extirpation of Atlantic salmon. Today Lake Ontario supports a popular and lucrative sport fishery supported mostly by introduced Chinook salmon *Oncorhynchus tshawytscha* and coho salmon *O. kisutch*, with a prey fish base overwhelmingly dominated by alewife and rainbow smelt. This food web anchored by exotic species is problematic for two reasons. First, Lake Ontario is also impacted by thiamin deficiency problems stemming from a diet rich in alewives. Sport fishermen regularly report dying or disabled steelhead and salmon along the banks of the Salmon River, New York, a popular eastern shore fishing destination. Second, the introduced prey fish/Pacific salmonid ecosystem paradigm is inherently unstable, as alewife and rainbow smelt are prone to wide fluctuations in abundance and die-offs in the Great Lakes. Additionally, there is evidence that increased predation pressure from Pacific salmonids contributed to the collapse of the prey fish community in Lake Huron, whose Chinook salmon sport fishery has yet to recover.

These cautionary tales have lead managers to emphasize the importance of restoring native food webs in Lake Ontario. Lake trout and Atlantic salmon recovery is currently a key objective for Lake Ontario, and this goal includes the restoration of native coregonine populations such as cisco. Unfortunately, not much is known about the cisco population in Lake Ontario, including population size, diversity, and spawning habits. About a decade ago, perch fishermen alerted researchers from the USGS Great Lakes Science Center and New York State Department of Environmental Conservation that cisco were returning to Chaumont Bay, New York during the fall spawning season. USGS has routinely collected ripe cisco in the bay for use as hatchery stock since then; however, whether spawning was actually occurring in the bay and on what substrate remained unknown.

The objective of this thesis is to synthesize what we already know about cisco in the Great Lakes, and use that knowledge to evaluate the status of the spawning stock in Chaumont Bay, Lake Ontario. Chapter one presents a review of over 100 years of cisco research, including adult and early life history stages, spawning behavior, their commercial history and collapse in the Great Lakes, and potential avenues for restoration. In the second chapter, we apply these findings to the specific context of the Chaumont Bay, Lake Ontario cisco population. By using a custom designed egg pumping device and genetic barcoding, we were able to confirm the existence of the only known spawning stock of cisco in the U.S. waters of Lake Ontario, and identify their preferred spawning substrate. Establishing self-sustaining spawning stocks of cisco is a key objective to their restoration in Lake Ontario. The results from this study will be used to inform managers and guide future restoration efforts, including searching for other suitable spawning areas, identify potential sites for restoration, and identify other factors that may be limiting cisco recovery in Lake Ontario.

CHAPTER 1

THE HISTORY AND ECOLOGY OF CISCO *COREGONUS ARTEDI*

IN THE GREAT LAKES

Distribution and General Biology

Cisco *Coregonus artedi* were once an abundant and commercially important species in the Great Lakes. Evermann and Smith (1896) reported that "in all the Great Lakes the lake herring, or cisco, is more abundant than any other whitefish. It is taken at enormous quantities each year, and in most lakes is the object of a special fishery." By the middle of the 20th century the cisco fishery fell victim to intense exploitation and dwindling stocks, declining to a mere fraction of their historical abundance (Scott and Crossman 1973). Habitat destruction and the impacts of invasive species such as sea lamprey *Petromyzon marinus,* alewife *Alosa pseudoharengus,* and rainbow smelt *Osmerus mordax* also contributed to their collapse (Scott and Crossman 1973, Crowder 1980, Davis and Todd 1998).

Cisco were described by LeSueur in 1818, based on two type specimens from Lake Erie (Buffalo, NY) and Lake Ontario (Lewiston, Ontario; Scott and Crossman 1973). Their genus name *Coregonus* means "angle eye," and their species name *artedi* is in honor of the Swedish naturalist Peter Artedi. Cisco belong to the family Salmonidae and subfamily Coregoninae, and possess an adipose fin (Nelson et al. 2004).

Cisco are known throughout their range by many common names, which has led to no shortage of confusion among fishermen, scientists, and managers. They are also known as lake herring, blueback herring, grayback herring, greenback herring, shore herring (Evermann and Smith 1896), shoal water herring, Quinte herring (Pritchard 1931), tullibee (Stewart and Watkinson

2004), and many other localized names too numerous to mention. In Lake Erie, large cisco were often marketed as "ciscoette" or "siscowet" (Evermann and Smith 1896). Many of the common names include the term "herring," most likely due to the cisco's resemblance to the well-known Atlantic herring, *Clupea harengus* (Dryer and Beil 1964). Although origins of the name cisco is disputed, Evermann and Smith (1896) offer an amusing story of a fishmonger named "Cisco," who peddled his catch to local farmers as "Cisco's herring." The name "tullibee" is said to originate from the Cree word "ottonneebees," the transliterated version of which Sir John Richardson attributed to fur traders (Scott and Crossman 1973). Today "cisco" and "lake herring" are the most widely used, with the name "tullibee" reserved for the cisco inhabiting inland lakes of northern Minnesota and Wisconsin.

Cisco display wide variation in morphometry, pigmentation, meristics, and behavior across their extensive range that lead to this large number of synonyms (Scott and Crossman 1973). The wide range in physical characteristics has also resulted in many scientists describing the different morphs as separate species, which is a topic of constant debate amongst fisheries biologists (Dryer and Beil 1964, Scott and Crossman 1973). Koelz (1927) described no less than 26 separate species of cisco, many of which were only found in a single lake. Scott and Crossman (1973) expressed dismay at this practice, stating that "such an approach to taxonomy of this wide ranging and variable species is totally unrealistic. If the same approach were followed throughout the extensive Canadian range the result would be taxonomic chaos." When determining the species present in a certain lake, their advice is to compare them within the lake, as physical characteristics of a single species can vary significantly between systems. Although many researchers have attempted to identify separate forms within lakes (Turgeon et al. 1999, Muir et al. 2014), few have been successful at identifying genetic differences between expected subspecies (Todd 1981, Reed et al. 1998).

Cisco are found throughout an extensive range, from the north-central to eastern United States and across most of Canada (Scott and Crossman 1973). Their range extends north to Hudson Bay, where they enter coastal salt waters. However, the majority of cisco populations occur in lakes, including both small inland lakes and the five Great Lakes. Cisco are a schooling, cold water fish and are most commonly found in deep water during the summer (Dryer and Beil 1964). They may become distributed throughout the water column in the spring and late fall, when surface waters are cooler. Younger fish less than 2 years of age may be more demersal, as they are often caught in bottom trawls in Lake Superior (Stockwell et al. 2006). Adult cisco may be more pelagic, as they are more common in midwater trawls. Many populations exhibit a diel migration, although the direction and magnitude of this migration depends on food availability (Ahrenstorff et al. 2013). In lakes with low zooplankton densities, cisco may move out of their preferred thermal and dissolved oxygen range to enhance foraging opportunities. In lakes with higher zooplankton densities, cisco movements corresponded with predator avoidance and thermal regulation. Cisco have an upper thermal limit of 20°C for adults and 26°C for juveniles and a lower thermal limit of 0°C, and only exist in lakes that provide adequate thermal refuges for their survival (Edsall and Colby 1970, Ebener et al. 2008). Cisco generally avoid temperatures above 17°C: Rudstam et al. (1993) reported that no cisco were caught where the water temperature exceeded 15°C. Cisco have a low tolerance for high temperatures and low dissolved oxygen levels; the presence of cisco in a lake is often an indicator of good water quality, while their extirpation is often an indicator of environmental changes (Honsey et al. 2016). Cisco were found to school during the day and disperse at night in Lake Opeongo, Ontario (Milne et al. 2005). The light threshold at which they schooled corresponded with the level at which lake trout can detect prey, suggesting that schooling is a predator defense strategy. Schooling may also enhance foraging opportunities in the lake.

Cisco are primarily plankton feeders throughout their life. There is little consensus on the preferred prey type of cisco, and diet appears to be inconsistent across systems. Cisco are reported to feed on cladocerans and copepods (Stone 1938), *Daphnia* and *Leptodera* (Luecke et al. 1992), *Hexagenia* and *Chaoborus* (Ahrenstorff et al. 2013), *Mysis, Pontoporeia*, and immature stages of aquatic insects such as mayflies and caddisflies (Dryer and Beil 1964). Langford (1938) found that *Daphnia* and mayfly nymphs were the primary food of adult cisco in shallow water, while in deeper water *Diaptomus oregonensis* was more often consumed. Link et al. (1995) found that cisco positively selected for *Limnocalanus* and *Diaptomus.* In Lake Mendota, Wisconsin, cisco selected for larger zooplankton (Luecke et al. 1992). However, a study on cisco diets in Pallette Lake, Wisconsin found little selectivity for zooplankton species or size, consuming instead whatever zooplankton was seasonally abundant (Engel 1976). On occasion cisco will also ingest small fish (Hrabik et al. 1998), and salted or fresh minnows are often used as bait for cisco by recreational ice fishermen (Scott and Crossman 1973).

Adult cisco from inland lakes often weigh between 0.5-1.5 pounds, and in the Great Lakes can reach weights of 3-4 pounds (Scott and Crossman 1973). The largest recorded cisco was an 8 pound, 7 year old female caught in Lake Erie in 1949. Females are often reported to be deeper bodied and larger than males (Dryer and Beil 1964). Cisco of up to twelve years of age are often reported in growth studies (Hile 1936), but may live even longer. Although cisco eggs are deposited in the fall, age and growth is considered to begin the following spring when the larvae hatch out. Dryer and Beil (1964) found that the annulus was beginning to form in all fish by

August, but some cisco began displaying new annuli in early summer. Younger fish appeared to begin growth earlier in the year. The authors cautioned that extreme care should be taken in aging fish caught in the spring and early summer, due to the differences in annuli formation. Aging by scales was first demonstrated by Van Oosten (1929), although using scales likely underestimates the age of fish older than age 4 (Ebener et al. 2008). The scales below the dorsal fin and above the lateral line vary the least in size and shape, and should be used for aging (Stone 1938). False annuli due to thermal stress are observed in both scales and otoliths (Hile 1936, Smith 1985), and were referred to as "summer checks" by Stone (1938).

It is often difficult to estimate cisco population sizes, as cisco disperse into deeper waters after spawning. Cisco are likely underestimated in Lake Superior, where abundances are quantified using bottom trawling (Stockwell et al. 2006). More accurate population estimates can be calculated using night midwater trawls and acoustic gear. Few surveys in the Great Lakes target cisco, and they are usually caught as bycatch in studies concerning other species (Ebener et al. 2008). Because of this, stock estimates across the Great Lakes where cisco are not the targeted species are rough estimates at best. Exploited cisco populations often display wild swings in sex ratio, stock size, and other population metrics (Dryer and Beil 1964). Exploited populations often display a higher proportion of females and an increase in the mean age of spawners (Bowen et al. 1991). Variation in sex ratios may limit recruitment and regulate population size, and could perhaps drive population cycles (Bowen et al. 1991, Madenjian et al. 2002). Recruitment is highly erratic, even in relatively stable populations such as Lake Superior (Ebener et al. 2008). Spawning populations are often highly dependent on a few successful year classes. However, there does appear to be large-scale synchrony between successful year classes (Dryer and Beil 1964, O'Gorman et al. 2007). This suggests that recruitment may be heavily influenced by weather patterns and climate (Myers et al. 2015). Hoff (2004) found that cisco recruitment was significantly correlated with April water temperatures and wind speed. Recruitment in lake whitefish *Coregonus clupeaformis*, a closely related coregonine, was found to be positively related to cold winters and stable ice cover (Taylor et al. 1987).

There appears to be little mixing between cisco spawning stocks. Hoff (2004) concluded that stocks did not mix in Wisconsin, due to differing numbers of parasites on separate spawning populations. Bronte (1996) was able to discriminate between different spawning stocks of cisco by examining trace elements in otoliths. Additionally, analysis of microsatellite loci in Lake Superior cisco indicated the presence of distinct stocks, rather than a panmictic population (Ebener et al. 2008).

Spawning Behavior

Cisco spawning takes place in the fall, usually during November and December throughout the Great Lakes (Dryer and Beil 1964, Auer 1982). The timing of spawning is highly dependent on temperature. Cisco move into spawning areas when the water reaches 6°C (Auer 1982), and spawning occurs between 3° and 5°C. Dryer and Beil (1964) reported cisco spawning at 3.6°C in Lake Superior. This timing based on temperature appears to be consistent across the Great Lakes, including lakes at lower latitudes. For example, Stone (1938) caught spawning cisco in trap nets in Irondequoit Bay, Lake Ontario, when the water temperature was 3.6°C. In many locations, ice is already starting to form along the shoreline, or spawning may even occur under the ice in colder areas (Brown and Moffett 1942, Smith 1985, Stewart and Watkinson 2004). Stewart and Watkinson commented on the unique challenges associated with studying cisco during the spawning season, noting that “the ice cover during the late fall [and] early winter period is often too thin to support vehicles, people, or equipment.”

Males are often reported to arrive on the spawning grounds first, with females following (Cahn 1927, Colby and Brooke 1973, Scott and Crossman 1973). In some cases there is evidence of a size difference as well, with larger males arriving earlier than smaller males. The males develop pearl organs, or tubercules, on their sides along each row of scales prior to spawning (Pritchard 1931). This causes them to feel rough to the touch. Females sometimes (Koelz 1927) or never (Pritchard 1931) develop spawning tubercules, with reports varying based on lake and author. Females have a fecundity of 8 to 36 thousand eggs per fish, with larger females producing more eggs than smaller females (Stone 1938).

Although much attention has been given to the water temperature and month of spawning, there is only anecdotal evidence concerning the time of day that spawning occurs. Many reports suggest that spawning happens at night, or just after sunset (Brown and Moffett 1942, Colby and Brooke 1973, Hinrichs and Brooke 1975). Brown and Moffett reported seeing dozens of fish break the surface at night while spawning in Pickerel Lake, Michigan.

Cisco are broadcast spawners; however, there is little agreement on the preferred spawning substrate of cisco (Auer 1982). Reported substrates vary widely across lakes and authors, with some even stating that they are habitat generalists and show no preference (Dryer and Beil 1964). Among spawning stocks that appear to exhibit a preference, the reported substrates range from “finger rock” and sand (Goodyear et al. 1982), vegetation (Colby and Brooke 1973, Zollweg and Leathe 2000), rock and gravel shoals (Scott and Crossman 1973), gravel and rubble (Hinrichs and Brooke 1975), mud (Stone 1938), and honeycomb bedrock and reefs (Organ et al. 1979).

In most locations cisco move in to shallow nearshore areas to spawn. Many embayments famously hosted large spawning runs of cisco, such as Chaumont Bay and the Bay of Quinte in Lake Ontario (Evermann and Smith 1896, Pritchard 1931, Goodyear et al. 1982). Spawning usually occurs in shallow water between 3 and 7.6m (Auer 1982). In Lake Ontario, cisco were found to spawn in as little as 4 feet in Irondequoit Bay (Stone 1938) and 10 feet in the Bay of Quinte (Pritchard 1931). Hinrichs and Brooke (1975) collected fish in zero to 1.3 m of water in Pallette Lake, Wisconsin, and reported hearing fish breaking the surface. Fish return to deeper water after spawning (Goodyear et al. 1982). However, in some locations pelagic spawning populations may occur. In Lake Superior, Dryer and Beil (1964) described how fishermen followed a pelagic aggregation of cisco as they moved into deeper waters during spawning. The fish first congregated on shallow (3-6 fathom; 5-11 m) reefs near the Apostle Islands before moving offshore. Scanning with the fish magnifier of the ship's depth recorder showed cisco aggregating at midwater depths of 5-15 fathoms (9-27 m) over 35 fathoms (64 m) of water, which suggests that they were spawning pelagically. The fish then moved deeper to 20 fathoms (36 m), where the bulk of spawning occurred. The last large catches were made at 60-70 fathoms (110-128 m). This unusual behavior was also reported by Koelz (1926) who described fish moving from 8 to 20 fathoms (15-37 m) during spawning. Finally, there is evidence that some populations may spawn on the bottom in deep water. Dryer and Beil (1964) noted that commercial fishermen on the south shore of Lake Superior often catch large numbers of spawning cisco in bottom set gill nets. In Lake Ontario a form of cisco called the "blueback herring" was said to spawn in the western end of the lake in 90-180 ft (27-55 m) of water (Goodyear et al. 1982).

Cisco spawning often occurs about one to two weeks after lake whitefish *Coregonus clupeaformis* spawning (Pritchard 1931, Scott and Crossman 1973). In many areas, cisco and lake whitefish are reported to spawn on the same substrate (Pritchard 1931, Organ et al. 1979). This may pose some risk to cisco, as lake whitefish and cisco are known to successfully hybridize in a hatchery setting (Garside and Christie 1962). There is also anecdotal evidence of lake whitefish/cisco hybrids occurring naturally in the wild. Stewart and Watkinson (2004) described these hybrids as showing characteristics of both parents, with a cisco-like terminal mouth and the longer snout and jaws of a lake whitefish. Hybrids also have longer, more slender, and more numerous gill rakers than a lake whitefish. Evermann and Smith (1896) reported catching an unusual looking lake whitefish in Dunkirk, NY. The specimen had a longer projecting jaw than a normal lake whitefish, a sharper snout, and a higher number of gill rakers. Although the authors were "not at all inclined to admit the occurrence in nature of hybrids among fishes, [they were] disposed to regard this specimen as a hybrid between the true whitefish *C. clupeaformis* and the lake herring." Their colleague at the United States Fish Commission, a certain Dr. Bean, informed them that "it had been common practice among fish culturists at the stations about the Great Lakes to fertilize the eggs of the true whitefish with the milt from the lake herring." Planting these hybrids was apparently most common in Lake Erie, where the fishermen called them "mongrel whitefish." Although fishermen report that these hybrids have underdeveloped gonads in comparison to spawning cisco and may be sterile (J. Hoyle, Ontario Ministry of Natural Resources, personal comm.), the F1 hybrid offspring of other coregonine pairs can be fertile (Kahilainen et al. 2011). Hybridization may pose a risk to the recovery of cisco in the Great Lakes (Todd and Stedman 1989). When hybridization occurs, the less abundant species is often at risk of extirpation via introgression (Rhymer and Simberloff 1996). In areas where cisco and lake whitefish share spawning substrate and cisco numbers are low, shifts in the timing of spawning due to climate change may lead to overlap of cisco and lake whitefish spawning and an increase in hybridization.

Egg Development

After deposition in the fall, cisco eggs overwinter and hatch out the following spring. Eggs are demersal, semi-adhesive, and 2-3mm in diameter (Colby and Brooke 1973, Auer 1982). The chorion is clear and colorless, and the yolk is pale yellow to light amber. The eggs contain between 100 and 200 small, spherical oil globules 0.2mm in diameter. Hinrichs and Brooke (1975) contains a detailed, day by day account of cisco egg development. An embryo was distinguishable by 8 days at 10°C, the eyes were pigmented by 15 days, and melanophores appeared by 28 days. Due to the high incubation temperature, this schedule of development is markedly more rapid than development in the wild.

Egg development and the quality of the larvae hatched depend strongly on water temperature. Colby and Brooke (1970, 1973) conducted two major studies on the development of cisco eggs, both in the laboratory and in the wild at Pickerel Lake, Michigan. They found that development rates are closely temperature dependent, with eggs developing slower at colder temperatures. The slowest development took place at 0.5°C, with 236 days from deposition to hatching, and the shortest development occurred at 10°C, with only 37 days to hatching (Colby and Brooke 1970). There appears to be an upper and lower thermal threshold to egg survival; eggs did not survive to hatching at 0 or 12.1°C. The authors used the results from their laboratory incubation experiments to construct a hatching model, which was compared to actual temperature readings and hatch dates in the field (Colby and Brooke 1973). Their model was accurate in predicting hatch date based on water temperature within one to two days.

Although Colby and Brooke (1973) showed that cisco can be successfully hatched at an accelerated rate at high temperatures, many studies suggest that cisco develop best at colder temperatures and with longer incubation times. Coregonine eggs held at lower temperatures produce larvae that are larger, have fewer physical deformities, and experience higher survivorship than those held at higher temperatures (Colby and Brooke 1970, Hinrichs and Brooke 1975, Brooke 1975). The optimum temperature for cisco development is between 2 and 8°C (Colby and Brooke 1970).

Cisco egg development is also sensitive to dissolved oxygen (DO) levels. DO concentrations of 1 mg/L could result in up to 90% egg mortality (Brooke and Colby 1980). In this same study, Brooke and Colby found that cisco eggs incubated at 4% DO had the highest survivorship and lowest proportion of physical deformities, and levels below 4% at various temperatures were hostile to embryo development. They also found discrepancies in how low DO levels affected development at different stages: eggs held at colder incubation temperatures experienced lower survivorship when low DO occurred at early development stages, while eggs held at higher incubation temperatures experienced adverse effects when low DO occurred at later stages. Embryos displayed a decreasing DO demand at lower incubation temperatures, suggesting that cisco eggs can tolerate lower DO levels when water temperatures remain cold. It has been suggested that insufficient DO has played a part in the collapse of several Great Lakes cisco stocks (Brooke and Colby 1980, Madenjian et al. 2011). DO concentrations of less than 1 mg/L were frequently measured in Green Bay, Lake Michigan between 1938 and 1955, due to high phosphorus, sediment, and biological oxygen demand loading from the Fox River (Epstein et al. 1974). The collapse of the cisco spawning population appeared to be synchronized with the destruction of their spawning habitat in Green Bay (Madenjian et al. 2011). Additionally, substrate type may impact egg survivorship due to differences in DO levels. Fine particle mud substrate can easily suffocate salmonid eggs by discouraging oxygen circulation (Greig et al.

2005). Anderson and Smith (1971) found that cisco egg survival was higher on sand substrate than on silt.

Finally, cisco eggs are consumed by a variety of predators. Stone (1938) found cisco eggs in the stomachs of brown bullhead *Ameiurus nebulosus*, yellow perch *Perca flavescens*, and mudpuppy *Necturus maculosus*. Of the yellow perch, Pritchard (1931) wrote that it “was by far the worst destroyer of eggs among the fish that live over the cisco spawning grounds.” Cisco are also known to cannibalize their own eggs (Stone 1938). Cisco eggs likely provide a rich source of energy during the winter months, especially in shallow spawning areas that likely do not experience high rates of production under ice cover (Stockwell et al. 2014). In this way, spawning cisco are probably an important transporter of energy from the pelagic to nearshore zone.

Hatching and Larval Stage

After developing over the winter, cisco larvae hatch out early in the spring, often between April and May (John and Hasler 1956, Auer 1982, Loftus and Hulsman 1986). In many locations that experience winter ice cover, cisco are observed hatching just before or after the ice breaks up (Colby and Brooke 1973, Clady 1976, Loftus and Hulsman 1986). Loftus (1986) experienced the highest catches of cisco larvae just after ice break up in Twelve Mile Lake, Ontario. Colby and Brooke (1973) observed the first cisco fry on the day the lake became ice free in Pickerel Lake, Michigan. The break up of lake ice corresponded with a rapid increase in water temperature to 6°C, which appears to have instigated hatching. Not much is known about the timing of hatching in relation to lake whitefish larvae. There is anecdotal evidence that they may hatch after lake whitefish; Pritchard (1931) found that cisco hatch from three to four weeks later than lake whitefish in the Bay of Quinte, presumably due to the difference in spawning times between the two species. However, this relationship may not be consistent across systems. Roseman and O’Brien (2013) found that catches of larval lake whitefish peaked later than cisco in northern Lake Huron.

Cisco larvae range between 8.5 and 12.8 mm in total length at hatching (Auer 1982). Length is dependent on water temperature during incubation, with colder incubation temperatures producing larger larvae (Colby and Brooke 1970). Larvae then move away from the spawning location, either up to shallow depths in deep-spawning populations (Selgeby et al. 1978) or more often into shallow nearshore areas (Pritchard 1931, Faber 1970, Clady 1976, Roseman and O’Brien 2013). Clady (1976) found the highest numbers of cisco larvae in shallow, protected embayments less than 3.7 m deep in Oneida Lake. Greeley and Greene (1931) collected cisco larvae with a seine in 1.2 m of water, and even dipped them up with a pail in water just a few centimeters deep. In some systems, cisco larvae appear to utilize protective habitat. Pritchard (1931) found larvae swimming amongst cattails and reeds in Prinyer Cove, Lake Ontario. Adams and Hankinson (1928) suggested that this aggregation inshore was active, not passive, as larvae were found far from spawning areas. However, in systems with large currents such as the Keewenaw current in Lake Superior, larval dispersion may depend on the movement of the water (Oyadomari and Auer 2008).

Cisco larvae are caught in the highest densities at the surface, regardless of water depth (Faber 1970). Pritchard (1931) found larvae in the surface waters of the Bay of Quinte, but caught none at depth. Larvae were concentrated in the upper 1.8 m of water in Oneida Lake, New York (Clady 1976). At night, their distribution is less clear. Cisco larvae were caught frequently during daytime surface tows in northern Lake Huron, but only one individual was caught during nighttime surface sampling (Roseman and O’Brien 2013). Lake whitefish larvae appear to feed on the bottom at night, due to the presence of benthic harpacticoid copepods in their guts (Johnson et al. 2009); perhaps larval cisco display a similar diel migration. Larvae are positively phototactic during the first few days after hatching, which some researchers have capitalized on to sample them at night (Colby and Brooke 1973, Johnson et al. 2009).

Cisco larvae are visual predators, and require light to feed (Scott and Crossman 1973). There is little consensus on when feeding begins and what their preferred prey are. Larvae may begin to feed immediately (Scott and Crossman 1973), although Pritchard (1931) observed that feeding did not begin until ten days after hatching. Cisco larvae have been found to prey on *Daphnia* spp. and other cladocerans (Brown and Moffett 1942, Davis and Todd 1992, 1998), copepods and copepodites (Pritchard 1931, John and Hasler 1956, Davis and Todd 1998), and perhaps algae when they first start feeding (Pritchard 1931). Selectivity and prey preference does not appear to be consistent across systems or studies.

Cisco larval distribution often overlaps with lake whitefish larvae (Davis and Todd 1998). Cisco and lake whitefish often consume similar prey items, and their diet overlap could be as high as 70 – 90%. Cisco larvae eat less and grow slower when lake whitefish larvae are present. Lake whitefish hatch out larger (Auer 1982), grow faster and have a larger gape size than cisco, and were able to overcome gape limitation and begin feeding on large *Daphnia* and adult copepods before larval cisco did (Davis and Todd 1998). Lake whitefish are also more aggressive feeders than cisco, and attack and capture more prey (Savino and Hudson 1995). These factors suggest that larval cisco could be outcompeted by larval lake whitefish, causing them to remain at a smaller size for longer (Davis and Todd 1998). This may not only decrease individual fitness, but also leave larval cisco vulnerable to predators for a longer time.

Table 1. Physical and morphometric characteristics used to identify larval lake whitefish *Coregonus clupeaformis* and larval cisco *C. artedi*. Parameters are from [1]Auer (1982) and [2]Fudge et al. (1986). TL = total length, SL = standard length.

Characteristic	Cisco	Lake Whitefish
Mouth position	Terminal	Becomes subterminal at 20-26 mm TL[1,2]
Preanal myomere count	35 - 38[1] or 35 - 41[2]	39[1] or 39 – 43[2]
Pairing of dorsal melanophores	Unpaired[1]	Paired[1,2], may appear unpaired depending on degree of contraction[2]
Size of dorsal melanophores	Small to medium (less than or equal to one myomere)[1]	Large (greater than width of one myomere)[1]
Distribution of dorsal melanophores	Concentrated near posterior in fish <18 mm SL[2]	Evenly distributed along length of fish[2]
TL at hatching	8.5 – 12.8 mm[1]	12 – 13 mm[1]
TL at complete absorption of yolk sac	13 mm[1]	14 – 16 mm[1]

A second difficulty arises when larval cisco and lake whitefish share the same location. The two species are challenging to distinguish between at the larval stage, before the lake whitefish mouth has differentiated and become subterminal (Fudge et al. 1986). Considerable overlap in phenotypic characteristics exists at most stages of larval development (Auer 1982). There are three major characteristics that are most frequently utilized when identifying cisco and lake whitefish larvae; dorsal pigmentation, preanal myomere count, and total length (Table 1). Although Fudge et al. (1986) found that many of these metrics were statistically significant between species, the overlap in ranges for each metric was substantial enough that use for identification was impractical. Pigmentation in particular is an untrustworthy tool, as melanophores can expand and contract in response to environmental variables such as light (Hinrichs 1979). Coregonines are often highly plastic, and physical characteristics used during larval identification may not be consistent across systems. Fudge et al (1986) suggested that location-specific type specimens and keys should be developed for any study utilizing visual identification of coregonine larvae. Luckily, biochemical methods such as isoelectric focusing of proteins (Fudge et al. 1986) and DNA barcoding of the mitochondrial cytochrome C oxidase *I* gene (Ivanova et al. 2007, Schlei et al. 2008) have been successful in consistently distinguishing between similar coregonines, including cisco and lake whitefish.

The larval life stage is vitally important to fish species, and factors affecting early life history stages are likely to determine ultimate population abundance and stability (Taylor et al. 1987, Miller et al. 1988). Low recruitment in Lake Superior is likely due in part to mortality during the larval stage (Hatch et al. 1988). A suite of both biotic and abiotic factors may influence cisco larval survival in the Great Lakes. Competition with larvae of other species such as lake whitefish and bloater *Coregonus hoyi* has been suggested as a contributing factor to the continued low abundance of cisco in Lakes Huron and Michigan (Davis and Todd 1992, Todd and Davis 1995). Also, due to the timing of hatching, cisco larvae may not have access to large energy-rich prey such as daphnids (Davis and Todd 1998). Cisco larvae often hatch out in April, and most cladocerans do not appear in the Great Lakes until later months (Balcer et al. 1984). Abiotic factors such as water temperature and wind speed may play a role in larval survival: the optimum temperature for cisco growth is 13 - 18°C (McCormick et al. 1971), and April water temperatures are significantly correlated with cisco recruitment (Hoff 2004).

Finally, predation on cisco larvae by alewife and rainbow smelt may have a large impact on the cisco population (Ebener et al. 2008). Both of these invasive species are able to consume coregonine larvae: alewife will eat small lake whitefish larvae up to 18mm TL (Hoagman 1974) , and rainbow smelt will consume lake whitefish up to 34mm TL (Gorsky and Zydlewski 2013). Rainbow smelt consumed 3-11% of the cisco larvae in the Bay of Quinte, Lake Ontario (Selgeby et al. 1978), 15-52% of larvae in Black Bay, Lake Superior, and 37-100% of larvae in Thunder Bay, Lake Superior (Myers et al. 2009). Loftus (1986) reported that smelt predation on coregonine larvae was intense in Twelve Mile Lake, Ontario: smelt ate an average of 8.4 larvae per smelt per day, which when combined with natural mortality was predicted to result in 100% mortality for lake whitefish and greatly reduced survivorship for cisco as well. Smelt predation on larval cisco may have contributed to their collapse in Lake Superior (Swenson 1978), and a combination of alewife and rainbow smelt predation on larvae likely contributed to other Great Lakes recruitment failures as well (Crowder 1980). Assessing the impact of predation on larval survival can be difficult, since larvae can be digested in predator stomachs in as little as one hour.

Commercial History and Collapse

Cisco have historically been one of the most important commercial species in the Great Lakes. Prior to 1899, fishing for cisco was primarily a cottage industry and fish were mostly taken for local consumption (Koelz 1926). Commercial fishing for coregonines grew as an industry in the late 1800's; by 1908 cisco had assumed the top position in total Great Lakes catches and harvest averaged 19 million pounds/year in American waters (Koelz 1926, Dryer and Beil 1964). In the early decades the regional harvest was dominated by Lake Erie, but by the middle of the 20th century Lake Superior brought in the majority of the cisco catch. From 1925-1961, Lake Superior netted 12 million pounds of cisco, which comprised 64% of the total catch in U.S. waters of the Great Lakes (Dryer and Beil 1964). In 1941 cisco represented 56.9% of the total Lake Superior fishery value, at $854,000 per year ($13.9 million in 2015, adjusted for inflation).

Walter Koelz provided an exceptionally detailed and thorough review of Great Lakes fisheries in his report to the U.S. Commissioner of Fisheries in 1926. This remains one of the best sources for early cisco fishery information, including catch statistics, fishing practices, gear types, regulations or lack thereof, and even musings on the conservation of species that he was beginning to suspect were under threat from poor management practices (Koelz 1926). In 1925, cisco was the most common fish caught across the Great Lakes. Adult fish were taken mostly during the fall spawning run, when congregation inshore made them easier to catch. Gill nets were used in all of the Great Lakes: common mesh sizes ranged from 2 ⅛ to 3 inches, and nets were set both on the bottom and floating at the surface depending on location and behavior of local cisco populations (Illustration 1). Pound nets were also used, and were the primary method of catching fish in Saginaw Bay, Lake Huron (Illustration 2). Early fishermen used rowboats and sailboats to set nets; however, by the early 1900's steam power had eclipsed the use of small boats in the lakes, and large steam tugs were used to bring in even larger quantities of fish. The one exception was Lake Ontario, where rowboats and shore fishing remained in use even after fisheries in other lakes had switched to steam power. Fish were either salted and packed in barrels, smoked, or sold fresh. In the early years of the fishery salting was preferred, as cisco have soft flesh that spoils quickly with poor handling (Dryer and Beil 1964). When sold fresh, fish were layered with ice and shipped in boxes through regional distributors (Koelz 1926). After the advent of refrigeration, fish could be frozen and stored for longer periods of time. The roe of cisco and lake whitefish was also increasingly made into caviar, after the decline of sturgeon populations led to shortages of this delicacy. In the 1940's mink farming for the fur industry became popular, and a large portion of the cisco catch was sold as mink food (Dryer and Beil 1964). In 1961, about half of the cisco caught in Bayfield, Wisconsin were salted for human consumption, and the remaining half was sold for mink feed.

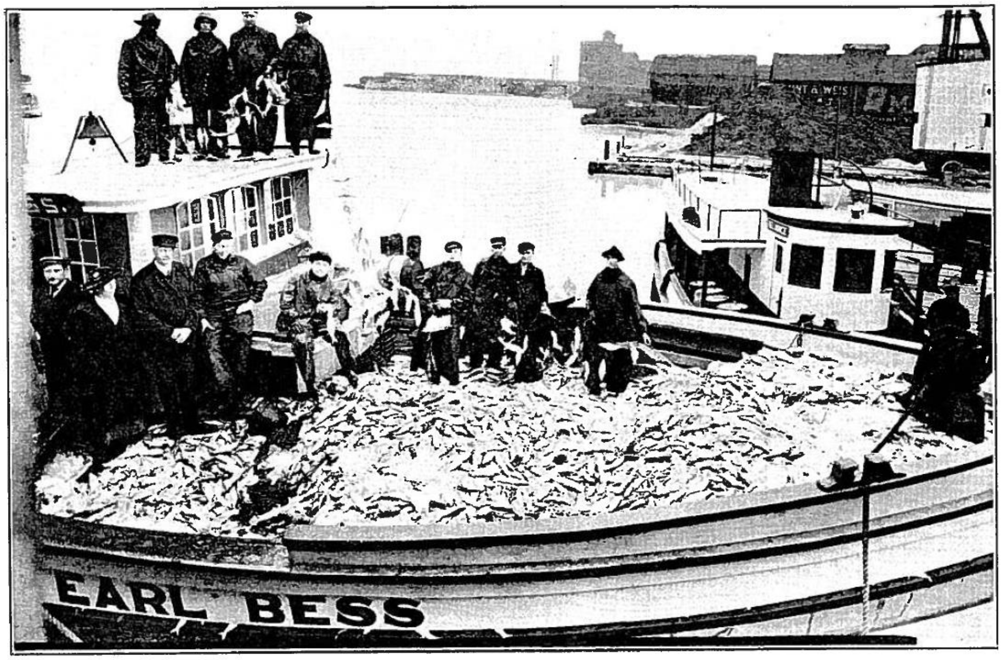


Illustration 1. A 30-ton catch of Lake Erie cisco on the commercial fishing ship "Earl Bess," November 1918. The lift was so heavy that the nets were not cleared of fish as they were lifted, which was usually done (Koelz 1926).

Illustration 2. A pound net filled with cisco is lifted. Pound nets were the primary means of harvesting cisco in Saginaw Bay, Lake Huron (Koelz 1926).

In Lake Ontario the majority of the U.S. catch of cisco was taken at the east end of the lake, from Sodus Bay to the St. Lawrence River (Koelz 1926). The heyday of cisco fishing in Lake Ontario was during the late 1800's, before the expansion of the Great Lakes commercial fishery in the early 1900's. Fishing for cisco was a defining characteristic of many of the communities along the eastern shore of Lake Ontario, and there exists an entertaining oral history about the early days of the cisco fishery ("Chaumont cisco is returning" 1915, Palmer 2002). Early fishing for cisco was done with "scaffs," or scoop nets, which consisted of a large square net suspended on a pole. The scaff was lowered into the water with the pole and then suddenly lifted, hauling the fish up into the air and back to the bank (Palmer 2002). In 1820 the first seine was introduced to Jefferson County, and soon became the dominant method of capturing cisco ("Chaumont cisco is returning" 1915). The seines were 200 to 2,000 feet long, coated with coal tar, and stabilized with large stone weights and cedar floats. The nets were attached to shore with large windlasses and deployed at night. To deploy the net, a small boat or "yawl" would draw the net in a wide circle and back to shore. The net was then hauled in by men or horses. In the 1840's gill nets were introduced, followed by pound nets in the 1870's. Gill netted fish were considered inferior, as the fish usually expired in the net and quickly spoiled. Unsold fish were often used as cheap fertilizer on local farms.

Many families in Chaumont Bay and other fishing towns relied on salted cisco as a source of protein during the long winters, as cisco were "as cheap as they were toothsome ("Chaumont cisco is returning" 1915)." Many men, women and children were employed in the cisco fishery. The primary way of transporting the fish to the cleaning shed was to shovel them into baskets, which were carried on the shoulders or back. The phrase "ciscoe-back" became a local term of derision for the fishermen, and when used in contempt by members of a neighboring town "was sufficient to start a full-sized brawl (Palmer 2002).” A more agreeable term was “cisco chaser,” which is charmingly featured in a song that was performed by a quartet in Chaumont, NY:

“We hail from old Che-mo,
habitat of the ciscoe,
down where the lake winds blow,
from Ontario.
We’re sailor men, fishermen,
happy and gay.
Ciscoe chasers are we,
We sing at our work,
and make our work play.
Ciscoe chasers are we.”

Unfortunately, the American Lake Ontario cisco fishery declined significantly by the late 1800’s. By 1885, many theories existed about the disappearance of cisco from Chaumont Bay, but “oldtimers simply said the lake was fished out (“Lake Ontario fisheries” 1885).”

Once described as having an unbelievable abundance of “unprecedented numbers of millions” in the Great Lakes (Scott and Crossman 1973), the commercial cisco fisheries collapsed in all five of the lakes between the 1920’s and 1970’s (Berst and Spangler 1973). Lake Erie was the first to experience commercial collapse in the 1920’s (Koelz 1926, Van Oosten 1930), followed by Lake Ontario with the collapse of the Bay of Quinte fishery in 1945 (Christie et al. 1987). The last lake to experience a decline was Lake Superior in the 1970’s (Bowen et al. 1991), although development of Lake Superior Herring Subcommittee of the Lake Superior Committee in 1973 helped contribute to their modest recovery (Ebener et al. 2008). Although cisco numbers in Lake Superior are greatly reduced it still maintains a viable commercial fishery, which is more than can be said for the other Great Lakes. Lake Superior was responsible for 94% of the total cisco harvest in 2000; only small amounts of cisco are harvested in the other Great Lakes. Populations remain low in Lake Ontario and Lake Erie (Scott and Crossman 1973), Lake Huron (Berst and Spangler 1973), and Lake Michigan (Bunnell et al. 2006). Currently, fishing restrictions are managed in Lake Superior by individual states and provinces, and vary across jurisdictions. For example, Minnesota employs a total allowable catch system, while Wisconsin imposes no restrictions on fishing effort (Ebener et al. 2008). Subsistence fishing by Native American and First Nations groups is now included in management statistics, and is closely regulated. Most cisco are caught by gill nets, although some trawling is practiced. Although historically most fish were sold for meat, the roe trade has now become more lucrative. Additionally, some localized recreational fisheries have developed, most notably the recreational ice fishery.

The decline of cisco across the Great Lakes was due to many factors, including overfishing, habitat destruction, and adverse effects of invasive species. Scott and Crossman (1973) summarized the story of cisco in the Great Lakes as "one of increasing exploitation and dwindling stocks…It was naïve to expect that any population of organisms could withstand such continuous and intense exploitations at the same time that the habitat was being destroyed by such activities as gravel removal, gas well drilling, and sewage discharge." Overexploitation was certainly the primary factor in the decimation of cisco stocks across the Great Lakes, leaving the remaining population vulnerable to other stresses such as habitat destruction and invasive species (Smith 1968, Selgeby 1982).

Habitat destruction was a major contributor to cisco decline across the Great Lakes. Low dissolved oxygen levels (DO) have been implicated in the collapse of several cisco stocks across the Great Lakes (Epstein et al. 1974, Brooke and Colby 1980, Madenjian et al. 2011). Nutrient loading from the Fox River led to low DO concentrations on spawning grounds in Green Bay, Lake Michigan, which likely contributed to cisco recruitment failure. Adults are vulnerable to low DO levels as well; McCrimmon (1952) suggested that low oxygen levels in the hypolimnion led to large die offs of cisco in Lake Simcoe, Ontario. In some areas spawning substrate was physically damaged due to gravel mining or waste dumping (Scott and Crossman 1973). Koelz (1926) remarked that wheat screening dumped on cisco spawning grounds may have affected their reproduction in Thunder Bay, Lake Superior. Cisco habitat is also at risk from climate change as water temperatures warm. The lethal upper thermal limit for adult cisco is 20°C, and they avoid temperatures above 17°C (Edsall and Colby 1970, Ebener et al. 2008). Thermal stress due to rising water temperatures and shrinking thermal refuges is thought to have contributed to the extirpation of cisco in Oneida Lake, New York (Mills et al. 1978, Smith 1985).

Interspecific interactions with invasive species such as rainbow smelt, alewife, and sea lamprey *Petromyzon marinus* may also have contributed to the decline of cisco. In Oneida Lake 80% of dead adult cisco had lamprey scars, and sea lamprey predation may have compromised their ability to withstand thermal stress (Smith 1985). In Lake Superior, 19% of sea lamprey collected were attached to cisco, and the largest lamprey were capable of killing their host (Ebener et al. 2008). However, many cisco stocks appear to have collapsed independently of the presence of sea lamprey, which suggests that they were not the only culprit in the decline of cisco as is often thought (Scott and Crossman 1973). Although the presence of invasive alewife is sometimes linked to stock declines (Crowder 1980), the presence of rainbow smelt appears to show a more robust relationship with cisco collapses (Anderson and Smith 1971, Berst and Spangler 1973, Crowder 1980, Hrabik et al. 1998). In Lake Michigan, shifts in abundance of cisco are complementary to shifts in the abundance of rainbow smelt (Van Oosten 1947, Smith 1968). The 1945 collapse of the Bay of Quinte stock coincided with the proliferation of rainbow smelt in the area (Christie et al. 1987). Smelt affect cisco in two ways; first, by competing with cisco for zooplankton prey (Anderson and Smith 1971, Hoff 2004), and second by consuming large numbers of cisco larvae (Selgeby et al. 1978, Loftus and Hulsman 1986, Myers et al. 2009).

Cisco Restoration

The collapse of cisco across the Great Lakes had severe ramifications for both the economic livelihood of the fishery and the health of the aquatic food web. Historically, cisco were possibly a keystone species, as their massive population must have had far reaching influence on every other part of the food web (Hoff 2004).

Today, much of the impetus for restoration of native coregonines stems from the desire to restore native lake trout *Salvelinus namaycush* and Atlantic salmon *Salmo salar*. Cisco are an important component of the lake trout diet, and prior to their collapse cisco were lake trout's primary prey species (Scott and Crossman 1973, Hoff 2004). Across the Great Lakes, lake trout and Atlantic salmon prey primarily on invasive alewife and rainbow smelt. Alewife make up the majority of the prey fish biomass in Lake Ontario, followed by rainbow smelt (Mills et al. 2003, Walsh et al. 2015). Reflecting this, alewives are the primary diet item of lake trout in Lake Ontario, with rainbow smelt claiming second place (Brandt 1986). This poses a serious problem for salmonine predators in the Great Lakes, as invasive alewife and rainbow smelt are high in the enzyme thiaminase (Tillitt et al. 2005, Riley and Evans 2008). High levels of thiaminase leads to a vitamin B1 (thiamin) deficiency, which is associated with early mortality syndrome (EMS) in salmonines (Fisher et al. 1996, Ketola et al. 2000, Jaroszewska et al. 2009). Yolk-sac larvae are affected by EMS during the swim-up stage and die before first feeding (Jaroszewska et al. 2009), and there is evidence that adult fish are also affected negatively by thiamin deficiencies (Brown et al. 2005). Thiamin deficiency was responsible for the complete recruitment failure of Atlantic salmon in Cayuga Lake (Fisher et al. 1996), and is suspected to be the cause of continued recruitment failure in Great Lakes salmonines (Fisher et al. 1996, Ketola et al. 2000, Brown et al. 2005). In contrast to invasive alewife and rainbow smelt, cisco are very low in thiaminase and are a valuable source of thiamin (Klocke et al. 1947, Riley and Evans 2008). An abundant population of cisco is required to sustain lake trout recovery, as they cannot subsist on a diet of invasive smelt and alewife (Mason et al. 1998). Building a prey base of thiamin-rich native species such as cisco is a major objective in the restoration of Great Lakes salmonines (Stewart et al. 2013).

Several goals need to be met in order to promote the restoration of cisco in the Great Lakes, including spawning habitat restoration, water quality management, and reduction of invasive species. Many restoration initiatives in the past have failed, often due to questionable management techniques. In 20th century, restoration efforts focused heavily on stocking cisco from wild harvested eggs and milt. Stone (1938) was highly critical of this process, and doubted that the stripping of fish helped to conserve the species. First, stripping kills the fish, and fish to be stripped were not selected based on age. This meant that many young fish were only able to spawn once or twice before expiring, instead of returning year after year to spawn naturally in the bay. Since older females produce more eggs, Stone recommended that only older fish should be stripped. Second, the progeny were often stocked while still very young, as eyed eggs or fry. This left them vulnerable to predators and environmental dangers that could be lessened if the fish were stocked at a later stage. Several contemporary management plans have learned from these mistakes, and recognize the importance of managing invasive species, habitat quality, and fishing effort in addition to hatchery supplementation (Krueger and Hrabik 2005, Oldenburg et al. 2007, Stockwell et al. 2009).

Lack of healthy, self-sustaining spawning stocks is the single greatest impediment to cisco restoration in the Great Lakes (Fitzsimons and O'Gorman 2006). In order to maintain spawning stocks, commercial and recreational harvest must be limited where applicable. Lake Superior already has management plans in place, which are implemented individually by states and provinces (Ebener et al. 2008). Limits on the recreational fishery are rare; Michigan imposes a 12 fish per day recreational limit, but other states such as New York have no recreational fishing regulations regarding cisco (Ebener et al. 2008, New York State Department of Environmental Conservation 2016).

Restoration of spawning habitat is also a key step towards cisco recovery (Stewart et al. 2013). Although low dissolved oxygen (DO) levels were once significant threats to cisco recruitment, there is evidence that some of the spawning areas that previously experienced low DO due to pollution runoff have recovered, and could now support cisco egg development (Madenjian et al. 2011). Even in Lake Erie, where environmental conditions were particularly degraded, current environmental conditions may not hamper restoration (Oldenburg et al. 2007). Reduction of runoff from agricultural and urban environments would also help cisco populations. In Indiana, remnant cisco populations persist in lakes with low catchment areas, probably because those lakes experience less nutrient loading from land use (Honsey et al. 2016). When choosing potential areas for restoration, consider DO levels, surrounding land use, and the effect that storms and other weather events may have on the survival of eggs and fry (Oldenburg et al. 2007, Madenjian et al. 2011, Honsey et al. 2016).

Finally, reduction in the abundance of rainbow smelt and alewife through the management of predators can help restore cisco populations (Krueger and Hrabik 2005). Reduction in fishing mortality of walleye in Wisconsin lakes resulted in a decline in the rainbow smelt population and corresponding increase in the cisco population. In Lake Erie, the restoration of walleye and lake trout have been proposed to aid in cisco recovery by suppressing alewife and smelt populations (Oldenburg et al. 2007).

Fisheries managers have only recently realized the value of restored cisco populations to the stability of Great Lakes food webs (Fitzsimons and O'Gorman 2006, Ebener et al. 2008). By promoting the restoration of native prey fish such as cisco, we can in turn promote the recovery of valuable Great Lakes predators such as lake trout and Atlantic salmon. Furthermore, their restoration will help to foster the health and sustainability of recreational and commercial fisheries, and those who enjoy and depend on them.

CHAPTER 2

CONFIRMATION OF CISCO SPAWNING IN CHAUMONT BAY, LAKE ONTARIO USING AN EGG PUMPING DEVICE

Abstract

Cisco *Coregonus artedi* are an important prey fish for many Great Lakes predators, including lake trout *Salvelinus namaycush*. Their numbers have declined drastically in the last century due to the impacts of invasive species, overfishing, and habitat degradation. Chaumont Bay, New York contains one of the last remaining spawning populations of cisco in Lake Ontario. This study documents the first confirmation of cisco spawning in Chaumont Bay in decades, through use of an egg pumping device specifically developed to sample eggs through lake ice. Eggs were identified to species using genetic barcoding of the mitochondrial cytochrome *c* oxidase I (COI) gene. Cisco exhibited a strong spawning habitat preference for shallow, rocky shoals in Chaumont Bay. Contemporary knowledge of spawning behavior is instrumental to the successful restoration of cisco in Lake Ontario and across the Great Lakes.

Introduction

Cisco *Coregonus artedi* was once an abundant and commercially important species in the Great Lakes. Evermann and Smith (1896) reported that “in all the Great Lakes the lake herring, or cisco, is more abundant than any other whitefish. It is taken at enormous quantities each year, and in most of the lakes is the object of a special fishery.” By the middle of the 20th century the cisco fishery fell victim to intense exploitation and dwindling stocks, declining to a mere fraction of their historical abundance (Scott and Crossman 1973). Habitat destruction through practices such as gravel mining, gas well drilling, and sewage discharge may have contributed to the collapse (Scott and Crossman 1973, Davis and Todd 1998).

Cisco spawning habits in the Great Lakes vary widely and have been associated with several types of substrates and a range of depths. Cisco move inshore to spawn in the late fall when the water temperature reaches approximately 6 °C (Auer 1982). It is often reported that males enter the area first, with females arriving soon after (Stone 1938, Colby and Brooke 1973, Scott and Crossman 1973). Spawning usually occurs in shallow waters between 0.5 and 8 m of depth when the water temperature is between 3 and 5 °C (Colby and Brooke 1973, Scott and Crossman 1973, Auer 1982). Stone (1938) recovered cisco eggs in 1 - 2 m of water in Irondequoit Bay, Lake Ontario. Cisco have been reported to spawn on a variety of substrates (Auer 1982), including rock, gravel (Scott and Crossman 1973), mud (Stone 1938), and vegetation (Colby and Brooke 1973).

Chaumont Bay, New York (Figure 1) was a historically important spawning ground for Lake Ontario cisco, as reported in documents dating back to the 1800's (Evermann and Smith 1896, Goodyear et al. 1982). Today, Chaumont Bay holds the last known naturally reproducing stock of cisco in the United States waters of Lake Ontario, as the other historical stocks of Irondequoit Bay, Sodus Bay, and Fox and Grenadier Islands have disappeared. In Canadian waters, cisco are frequently caught in commercial gillnets during spawning season in the Bay of Quinte: however, spawning has not been documented in recent decades (J. Hoyle, Ontario Ministry of Natural Resources and Forestry, personal communication).

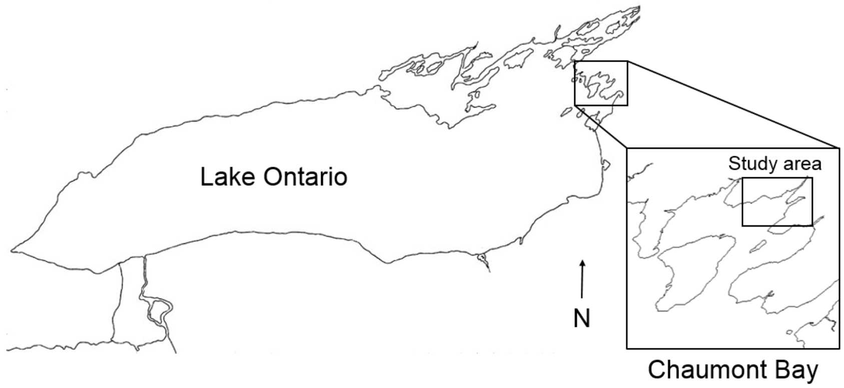


Figure 1. Map of the study area in Chaumont Bay, Lake Ontario.

Although Lake Ontario cisco abundance is likely heavily dependent on the spawning success of the Chaumont Bay and Bay of Quinte populations, little is known of their spawning behavior or the degree of their reproductive success. Successful spawning in Chaumont Bay has not been confirmed in several decades, and the details of their reproduction and spawning habitat preferences in the bay remain unknown. While ripe females are regularly caught in trap nets in November and December, only lake whitefish *Coregonus clupeaformis* larvae have been collected in the spring (McKenna and Johnson 2009, Johnson et al. 2009) and cisco eggs have not been found. Using an egg pumping device specifically designed for this project, our study documents the first confirmation of cisco spawning in Chaumont Bay in decades, and describes the abiotic factors associated with spawning locations.

Methods

Egg pump design.— Cisco are often difficult to study during spawning and egg incubation periods due to harsh winter weather conditions and ice cover in spawning areas (Stewart and Watkinson 2004). During November and December 2013 when cisco were returning to

Chaumont Bay, an early ice set made accessing the spawning area difficult and dangerous. From January through April, while the eggs were developing, Chaumont Bay was covered in ice up to 0.9 m thick. These conditions necessitated a novel sampling technique developed specifically for collecting eggs through thick ice cover. Sampling with diaphragm or centrifugal pumps has been used for decades to collect fish eggs and larvae (Gibbons and Fraser 1937, Manz 1964, Taggart and Leggett 1984, Petering and Van Den Avyle 1988, Powlik et al. 1991, Roseman et al. 2007); however, pump setups of these types are usually deployed from a boat and require ice-free lake conditions. We based our design on the methods described in Roseman et al. (2007) to collect lake whitefish eggs on the Detroit River and adapted them for use in a stationary position to collect eggs through the ice. Although some past studies have used centrifugal pumps with success (Manz 1964), a diaphragm pump was chosen in order to minimize damage to eggs.

The egg pumping device consisted of three main components: a welded metal sampling box, a 3-in (7.6-cm) gasoline powered diaphragm pump, and a plastic egg collection basket. The sampling box was constructed using ⅛-in (3.2-mm) galvanized sheet metal (Illustration 3). Dimensions measured 12 cm H x 50 cm W x 46 cm L in a rectangular prism shape. All corners were welded, and the bottom of the box was left open. A conduit hub was attached to a 2-in (5.1-cm) hole in the center top, and a 2-in (5.1-cm) x 1¼-in (3.2-cm) reducing male hose barb fitting was threaded into the conduit hub. A 1¼-in (3.2-cm) sump pump discharge hose kit connected the sampling box to the diaphragm pump intake. Four ⅓-in (7.9-mm) eye bolts were installed in the top four corners, and connected to a single 9.5 cm welded steel O-ring by a 60 cm piece of ¼-in (6.4-mm) solid braid poly line. This allowed us to raise and lower the box through the ice, as well as manipulate its position underwater. A 3-in (7.6-cm) collapsible output hose led from the diaphragm pump outflow to a plastic collection basket lined with three layers of 0.5 mm x 1.5 mm fiberglass window screen mesh.

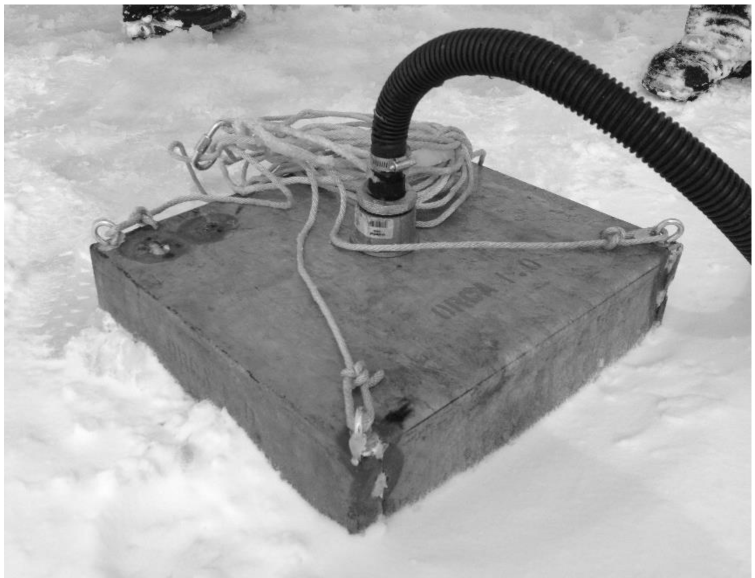


Illustration 3. Egg sampling box constructed of welded galvanized sheet metal, dimensions 12 cm H x 50 cm W x 46 cm L. The box was successful in collecting samples on a variety of substrates, including fractured bedrock, vegetation, and mud, and at depths up to 7.6 m.

Egg collection.— Sampling for coregonine eggs was conducted at 29 sites in Chaumont Bay, Lake Ontario by egg pumping in March of 2014 (Figures 1, 2). Sites were selected to represent a variety of habitat types and depths, to achieve even spatial coverage, and to correspond with locations where radio tagged fish were located in the fall of 2013 (E. George, unpublished data). Each site was sampled once during the study period. Sampling dates were March 14 (6 sites), March 19 (7 sites), March 26 (10 sites), and April 1, 2014 (6 sites). An average of 0.75 m of ice covered the bay for the entire sampling period, and water temperatures remained between 0.8 and 1.9 °C.

An opening of approximately 0.6 m^2 was cut in the ice using a gasoline powered ice auger and a chainsaw for deployment of equipment. Bottom temperature was measured using a handheld YSI probe, and substrate type was visually identified with a SeaViewer underwater camera. Pumping was accomplished by lowering the sampling box portion of the egg pumping device to the lake bottom. At each site the diaphragm pump was first allowed to run for 30 seconds to flush the line. The pump then ran for five minutes, during which time the outflow was filtered through the basket in order to collect eggs and detritus. The sampling box was periodically lifted and moved in order to stir up the sediment, as well as to sample a larger area of substrate. Eggs collected in the basket were transported in chilled lake water to the laboratory, where they were measured and photographed under a microscope and fixed in 95% ethanol.

Genetics.— Eggs were identified to species using genetic barcoding of the mitochondrial cytochrome *c* oxidase I (COI) gene. Confirmed cisco and lake whitefish fin clip tissue samples from various locations in the Great Lakes were used as DNA reference samples. DNA was extracted from the eggs using the DNEasy Kit (Qiagen, Valencia CA). Extracted DNA was examined for quality on 2% agarose gels and was quantified using spectrophotometry (Cary UV-Vis by Agilent). The DNA (200-250ng) was amplified via PCR using primers VR1_t1 and VF2_t1 according to the procedures described in Ivanova et al. (2007). Species were identified by analyzing the restriction fragment length polymorphisms (RFLP) of the COI region. Sequences for cisco and lake whitefish were selected from GenBank (www.ncbi.nlm.nih.gov/sites/gquery; cisco accession numbers: EU523944, EU523943, and EU523945, lake whitefish accession numbers: EU523957, EU523958, and EU523959), and a restriction enzyme (RE) that would cut the COI region in cisco and lake whitefish differently was determined using RestrictionMapper v.3.0 (www.restrictionmapper.org). The enzyme

*Eco109*I was chosen to create a unique banding pattern for each species. Restriction enzyme digests were performed in a 15 µL reaction that included 10 Units of the RE and the manufacturer's recommended buffer (New England BioLabs). DNA fragments were separated on 2% agarose gels, stained with ethidium bromide, and photographed under ultraviolet light. Banding patterns of the known species samples were compared with those of the eggs to identify each egg to species.

Statistical analysis and figure construction was accomplished using R version 3.0.1 (2013). Maps were constructed using open source bathymetric data from the NOAA National Geophysical Data Center (1999) and the maptools (Bivand et al. 2014) and sp (Pebesma et al. 2014) packages for R.

Results

The egg pumping device was successful at sampling over a variety of substrates and depths in Chaumont Bay. Samples were collected at depths from 1.2 to 7.6 m and on bedrock, vegetation, sand, and mud substrates (Table 3). In addition to coregonine eggs, the pump also collected silt, small rocks, vegetation, dreissenid mussel shells, live amphipods and other invertebrates. Eggs were undamaged, and many of the embryos inside were still alive and were often observed moving under the microscope.

A total of 59 coregonine eggs were collected from Chaumont Bay. Of these, 41 produced sufficient DNA for genetic analysis. Dead eggs, which showed no larval development and often displayed signs of decay at the time of collection, did not produce sufficient DNA and could not be identified. All of the identifiable eggs fit the cisco/bloater profile. Bloater *Coregonus hoyi*, however, were not caught in Chaumont Bay in 2013 fall trap net surveys, and have not been caught in Lake Ontario since 1983 (Baldwin 1999). In addition, bloater spawn only in waters deeper than 36 m (Scott and Crossman 1973). Therefore, we considered all identifiable eggs to be cisco. No lake whitefish eggs were found during this study.

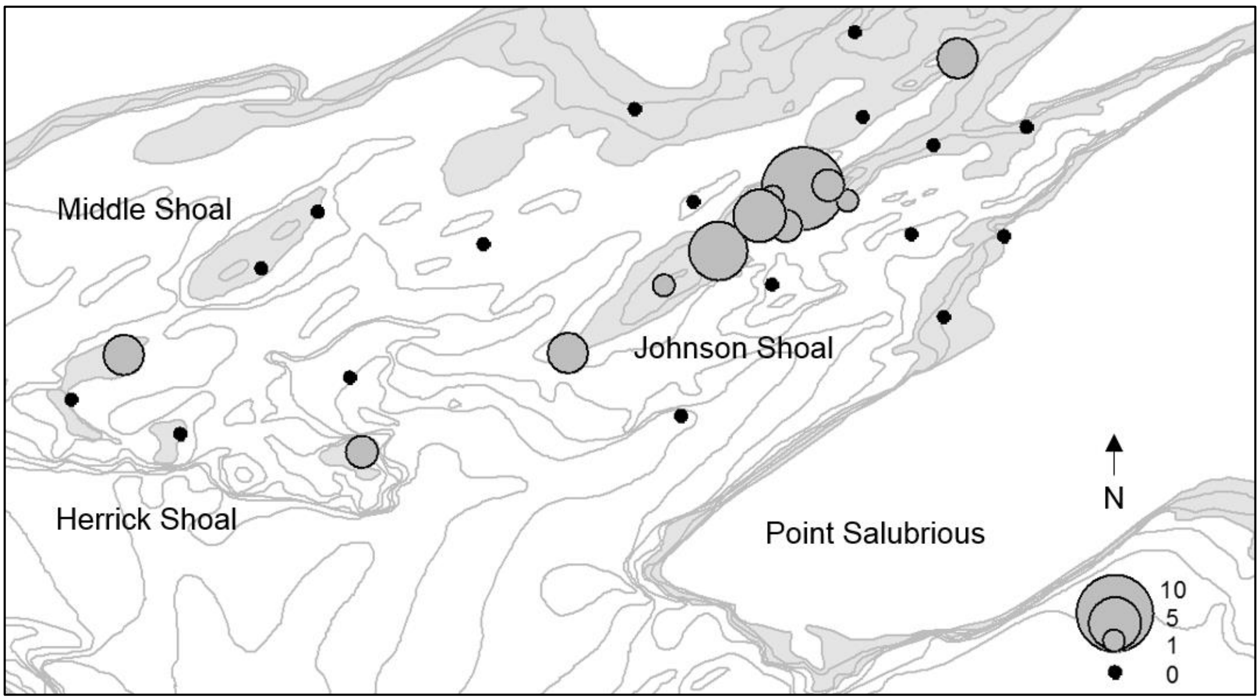


Figure 2. Count of genetically confirmed cisco eggs collected at 29 sites in Chaumont Bay, Lake Ontario. Bubble diameter indicates total number of cisco eggs at each site. The maximum number of eggs collected at a single site was 12 eggs. Black points indicate zero eggs collected at that site. Gray lines represent 1 m bathymetric contours; areas shallower than 3 m in depth are indicated by light gray shading. The three shoal areas in Chaumont Bay are Johnson, Herrick and Middle Shoals. Cisco eggs are closely associated with shoal areas in Chaumont Bay, with 38 of the total 41 cisco eggs found on Johnson and Herrick Shoals.

Cisco eggs were closely associated with shoal areas in Chaumont Bay. Shoal-type substrate was defined as shallow (≤ 4.5 m depth) areas located away from shore with a substrate primarily composed of fractured bedrock, gravel, and dreissenid mussel shells. This shoal-type substrate was located on three shoal areas in Chaumont Bay: Johnson, Middle, and Herrick Shoals (Figure 2). Other substrate types included weedy, muddy, and nearshore rocky (shallow ≤ 4.5 m depth sites with fractured bedrock or gravel located adjacent to the shoreline). Thirty-eight of the 41 genetically identified cisco eggs were found in shoal areas (Figure 3, Table 3), specifically Johnson and Herrick Shoals. A single coregonine egg was found on Middle Shoal, but did not produce sufficient DNA to be identified. The three confirmed cisco eggs that were not located on the shoals were found on a nearshore rocky substrate. However, of the seven total eggs collected at this nearshore site, four of them were dead. No live cisco eggs were found in weedy or muddy substrates.

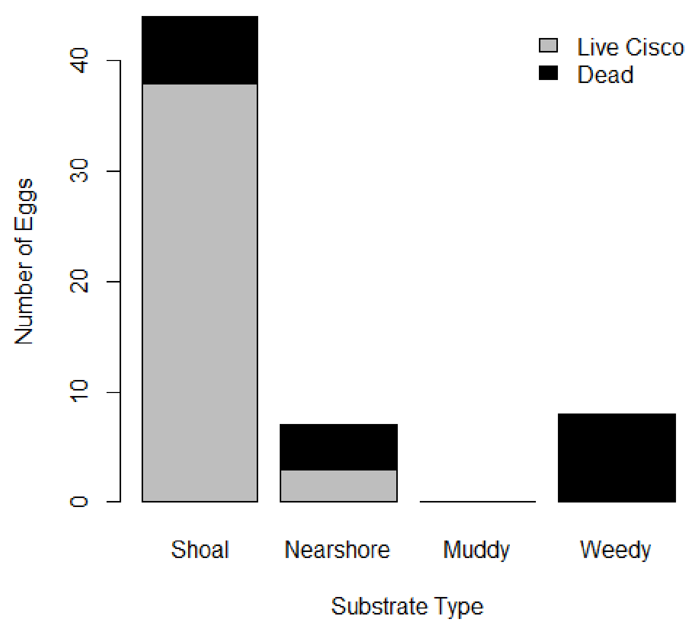


Figure 3. Number of live genetically confirmed cisco eggs (gray) and dead eggs (black) on different substrates in Chaumont Bay. Substrate types included shoal (*N* = 17), nearshore rocky (*N* = 4), muddy (*N* = 2), and weedy (*N* = 4). The majority of live cisco eggs (38) were found on shoals. No live cisco eggs were found in muddy or weedy locations.

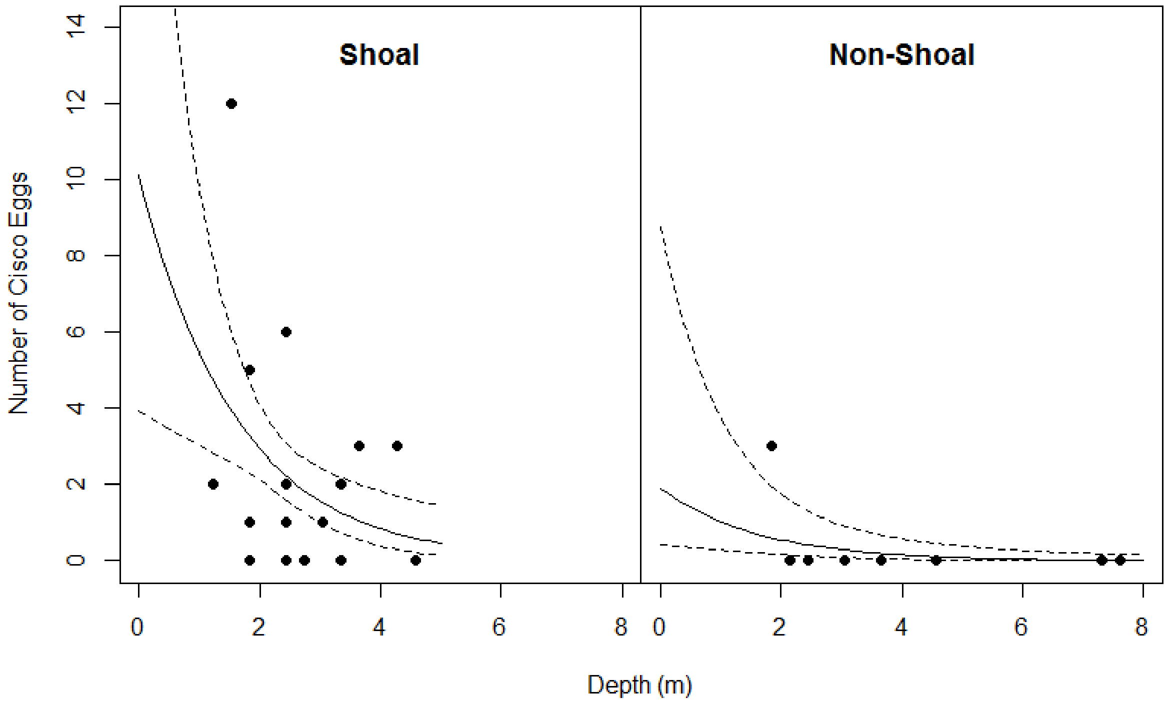


Figure 4. Number of cisco eggs across depth in shoal and non-shoal habitat types. Black points indicate number of live cisco eggs collected at egg pumping sites in Chaumont Bay. Lines represent fit (solid) and 95% confidence intervals (dashed) for a generalized linear model using depth and shoal-type habitat parameters. Both habitat and depth were significant predictors of number of cisco eggs, with higher numbers of eggs found on shoal type habitats and at shallower depths.

Table 2. Regression output for a generalized linear model using a variance structure based on the Poisson distribution. Habitat types were categorized as either shoal or non-shoal (including weedy, muddy, and nearshore rocky substrates). Both depth and shoal-type habitat were significant predictors of number of cisco eggs, with more eggs found on shoals and at shallow depths.

	Estimate	**Std. Error**	**z value**	**Pr(>|z|)**
Intercept	0.65	0.78	0.84	0.402
Depth	-0.19	0.06	-3.05	0.002
Shoal	1.66	0.60	2.76	0.006

The relationship between cisco egg abundance and abiotic variables such as depth and habitat type were examined with a generalized linear model using a variance structure based on the Poisson distribution. Habitat type was defined as either shoal or non-shoal type habitat, which included weedy, muddy, and nearshore rocky substrates. This categorization strengthened the model due to low sample sizes on non-shoal type substrates. Both depth and habitat type were significant predictors of number of cisco eggs (GLM, $P < 0.01$, Table 2). Cisco egg numbers were much higher on shoals than on non-shoal type habitats. On both habitat types, higher numbers of cisco eggs were found at shallower depths.

Table 3. Number of sites (N), sum of live, genetically confirmed cisco eggs (Cisco Eggs), mean count of live, genetically confirmed cisco eggs per site (Mean ±SE), sum of dead eggs that did not produce sufficient DNA to be identified (Dead Eggs), depth range (m), and temperature range (°C) across different substrates in Chaumont Bay. Shoals were defined as shallow areas located away from shore with a substrate primarily composed of fractured bedrock, gravel, and shells. Nearshore areas were defined as fractured bedrock, gravel, and shell areas located adjacent to shore. Two sites had unknown substrate types due to inadequate video footage.

Substrate type	**N**	**Cisco eggs**	**Mean (±SE)**	**Dead eggs**	**Depth (m)**	**Temp (°C)**
Shoal	17	38	2.23 ± 0.75	6	1.2 - 4.5	0.5 - 1.9
Nearshore rocky	4	3	0.75 ± 0.75	4	1.8 - 3.0	0.8 - 1.2
Muddy	2	0	0	8	7.3 - 7.6	1.2 - 1.5
Weedy	4	0	0	0	2.4 - 4.5	0.9 - 1.3
Unknown	2	0	0	0	4.5 - 5.4	1.2 - 1.9

Water temperatures ranged from 0.5 to 1.9 °C across Chaumont Bay sampling sites (Table 3). Water temperature was highly correlated with depth, with higher temperatures at deeper sites (Pearson's $R = 0.54$). Sites sampled on April 1, 2014, were excluded from the analysis of temperature across depth, as temperatures collected on that date were significantly higher than those at the start of the survey (T-test: $T = -2.4$, df = 6.9, $P < 0.05$). Conditions on April 1, 2014, were noticeably different from the rest of the survey, as the air temperature had warmed considerably and the ice was beginning to thaw in the spring weather. Depth sampled was not significantly different between sampling days (ANOVA: $F = 2.37$; df = 3, 25; $P = 0.09$), which suggests that the differences in temperature across sampling days was not related to depth.

Discussion

Cisco in Chaumont Bay appear to have a strong preference for shallow, cold, rocky shoal-type spawning habitat (Figures 2, 3, 4; Table 3). Live cisco eggs were found exclusively on rocky substrates, which in Chaumont Bay consists mostly of fractured bedrock overlain with dreissenid mussels and a limited amount of cobble. Cisco also prefer spawning on offshore shoals instead of nearshore areas: although rocky habitat similar to the type found on the shoals occurs along much of the shoreline in the bay, only 7% of Cisco eggs were found in the nearshore. Johnson and Herrick Shoals produced the largest number of cisco eggs, with 93% of eggs occurring at these locations.

Although historical accounts describe cisco spawning on a wide variety of substrates (Stone 1938, Colby and Brooke 1973, Scott and Crossman 1973, Auer 1982), contemporary Chaumont Bay cisco appear to be habitat specialists. There are several possible explanations for this discrepancy. In the past cisco were much more widely distributed, and occurred in locations where available spawning habitat types were limited. For example, Colby and Brooke (1973) studied a population of cisco in Pickerel Lake, MI, a smaller inland lake where vegetation and mud were the only available substrate types. Consequently, vegetation and mud were reported as known cisco spawning habitat. Secondly, cisco used to be one of the most abundant fish in the Great Lakes (Evermann and Smith 1896), and their spawning aggregations were truly enormous. Therefore, it is possible that the limited amount of preferred rocky shoal habitat was easily overwhelmed, and inevitable spillover into the surrounding substrates created an assumption that cisco were spawning habitat generalists. Density dependent habitat use is seen across many species (Rosenzweig 1981, McAughey and Gunn 1995), and high egg densities often have a negative effect on egg survival (Peck 1986, Lehtonen and Kvarnemo 2015). As spawning aggregation size increases in density-dependent populations, the quality of habitat utilized decreases as individuals move to lower quality habitat (Whitham 1980, McAughey and Gunn 1995). Dispersal may be advantageous in large populations, as individuals may experience higher reproductive success if they move away from crowded traditional spawning sites (Morris 1987). In small populations, however, dispersing to lower quality habitats may be detrimental. The current small population size of Chaumont Bay cisco may enable them to select for areas of preferred high-quality substrate.

The shallow rocky shoals found in Chaumont Bay likely provide high quality cisco egg habitat, because water temperature is lower near the ice during winter inverse stratification (Wetzel 2001). Water temperature not only affects the timing of spawning behavior, but also the health and development of incubating eggs. Cisco larvae benefit from a long and cold incubation. Eggs held at lower temperatures produce larvae that are larger, have fewer physical deformities, and experience higher survivorship than those held at higher temperatures (Colby and Brooke 1970, Hinrichs and Brooke 1975, Brooke 1975). Larger larvae are better able to avoid predators, capture prey, and swim to nursery habitat than smaller larvae (Lindström 1962). A temperature difference of only a few degrees can have a marked impact on incubation duration: an increase of just 1°C during incubation could result in cisco larvae hatching two weeks earlier in a natural setting (Colby and Brooke 1973, Auer 1982). Larvae that hatch weeks earlier may encounter drastically different prey availability, especially in the early spring when zooplankton abundance is low (Watson 1976). This may result in either increased mortality as larvae switch from endogenous to exogenous feeding (Taylor and Freeberg 1984), or a slowed growth rate that exposes smaller larvae to predation for a longer period of time (Lindström 1962). Therefore, the colder water was found in shoal areas increases the potential quality of these spawning sites.

Mud habitats were found exclusively at deep sites (>7.3 m), with shallow sites displaying only shoal-type or weedy substrate. No eggs were found at the deep, muddy sites. These sites are most likely poor habitats for three reasons: first, deeper sites are the warmest and coregonines appear to prefer colder spawning locations. Second, coregonines appear to spawn only in shallow habitats. Third, fine-particle mud substrate can easily suffocate salmonid eggs by discouraging oxygen circulation (Greig et al. 2005). Anderson and Smith (1971) found that cisco egg survival was lower in areas with silt substrate. Therefore, we were not surprised to see an absence of spawning at deep and muddy sites.

Our results highlight the importance of understanding cisco spawning behavior in the Great Lakes in order to inform future restoration and management. Historically, cisco were reported to prefer a wide variety of spawning habitats. We found that cisco in Chaumont Bay are highly selective in their habitat preferences, spawning exclusively on shallow rocky shoal areas and avoiding the vegetation and mud habitats that were previously reported. Restoration of native coregonines has been identified as one of the key objectives for Lake Ontario ecosystem management: specifically, an increase in the cisco spawning populations of Chaumont Bay and the Bay of Quinte will be considered an indicator of recovery success (Stewart et al. 2013, Ontario Ministry of Natural Resources 2014). Current, updated knowledge of cisco spawning behavior and habitat preferences will be essential for successful cisco restoration efforts in Lake Ontario and across the Great Lakes.

REFERENCES

Adams, C. C., and T. L. Hankinson. 1928. The ecology and economics of Oneida Lake fish. Roosevelt Wildlife Annual 1:235–548.

Ahrenstorff, T. D., T. R. Hrabik, P. C. Jacobson, and D. L. Pereira. 2013. Food resource effects on diel movements and body size of cisco in north-temperate lakes. Oecologia 173(4):1309–1320.

Anderson, E. D., and L. L. Smith. 1971. Factors affecting abundance of lake herring (*Coregonus artedii* LeSueur) in western Lake Superior. Transactions of the American Fisheries Society 100(4):691–707.

Auer, N. A., editor. 1982. Identification of larval fishes of the Great Lakes basin with emphasis on the Lake Michigan drainage. Special Publication 82-3 of the Great Lakes Fishery Commission, Ann Arbor, MI.

Balcer, M. D., N. L. Korda, and S. I. Dodson. 1984. Zooplankton of the Great Lakes: a guide to the identification and ecology of the common crustacean species. University of Wisconsin Press.

Baldwin, B. 1999. Native prey fish re-introduction into Lake Ontario: Bloater (*Coregonus hoyi*). Page 40. Discussion paper, Great Lakes Fishery Commission.

Berst, A. H., and G. R. Spangler. 1973. Lake Huron: the ecology of the fish community and man’s effects on it. Great Lakes Fishery Commission.

Bowen, S. H., D. J. D’Angelo, S. H. Arnold, M. J. Keniry, and R. J. Albrecht. 1991. Density-dependent maturation, growth, and female dominance in Lake Superior lake herring (*Coregonus artedii*). Canadian Journal of Fisheries and Aquatic Sciences 48(4):569–576.

Brandt, S. B. 1986. Food of trout and salmon in Lake Ontario. Journal of Great Lakes Research 12(3):200–205.

Bronte, C. R., R. J. Hesselberg, J. A. Shoesmith, and M. H. Hoff. 1996. Discrimination among spawning concentrations of Lake Superior lake herring based on trace element profiles in sagittae. Transactions of the American Fisheries Society 125(6):852–859.

Brooke, L. T. 1975. Effect of different constant incubation temperatures on egg survival and embryonic development in lake whitefish (*Coregonus clupeaformis*). Transactions of the American Fisheries Society 104(3):555–559.

Brooke, L. T., and P. J. Colby. 1980. Development and survival of embryos of lake herring at different constant oxygen concentrations and temperatures. The Progressive Fish-Culturist 42(1):3–9.

Brown, C. J. D., and J. W. Moffett. 1942. Observations on the number of eggs and feeding habits of the cisco (*Leucichthys artedi*) in Swains Lake, Jackson County, Michigan. Copeia 1942(3):149.

Brown, S. B., J. D. Fitzsimons, D. C. Honeyfield, and D. E. Tillitt. 2005. Implications of thiamine deficiency in Great Lakes salmonines. Journal of Aquatic Animal Health 17(1):113–124.

Bunnell, D. B., C. P. Madenjian, and R. M. Claramunt. 2006. Long-term changes of the Lake Michigan fish community following the reduction of exotic alewife (*Alosa pseudoharengus*). Canadian Journal of Fisheries and Aquatic Sciences 63:2434–2446.

Cahn, A. R. 1927. An ecological study of southern Wisconsin fishes: the brook silverside (*Labidesthes sicculus*) and the cisco (*Leucichthys artedi*) in their relations to the region. Illinois Biological Monographs 11(1).

Chaumont cisco is returning. 1915. Syracuse Herald (November 28).

Christie, W. J., K. A. Scott, P. G. Sly, and R. H. Strus. 1987. Recent changes in the aquatic food web of eastern Lake Ontario. Canadian Journal of Fisheries and Aquatic Sciences 44(2):37–52.

Clady, M. D. 1976. Distribution and abundance of larval ciscoes, *Coregonus artedii*, and Burbot, *Lota lota*, in Oneida Lake. Journal of Great Lakes Research 2(2):234–247.

Colby, P. J., and L. T. Brooke. 1970. Survival and development of lake herring (*Coregonus artedii*) eggs at various incubation temperatures. Pages 417–428 *in* C. C. Lindsay and C. S. Woods, editors. Biology of coregonid fishes. University of Manitoba Press, Winnipeg.

Colby, P. J., and L. T. Brooke. 1973. Effects of temperature on embryonic development of lake herring (*Coregonus artedii*). Journal of the Fisheries Research Board of Canada 30:799–810.

Crowder, L. B. 1980. Alewife, rainbow smelt and native fishes in Lake Michigan: competition or predation? Environmental Biology of Fishes 5(3):225–233.

Davis, B. M., and T. N. Todd. 1992. Diet overlap in larval lake herring (*Coregonus artedi*) and bloaters (*Coregonus hoyi*). Polskie Archiwum Hydrobiologii 39(3–4):279–287.

Davis, B. M., and T. N. Todd. 1998. Competition between larval lake herring (*Coregonus artedi*) and lake whitefish (*Coregonus clupeaformis*) for zooplankon. Canadian Journal of Fisheries and Aquatic Sciences 55:1140–1148.

Dryer, W. R., and J. Beil. 1964. Life history of lake herring in Lake Superior. Fishery Bulletin 63(3):493–530.

Ebener, M. P., J. D. Stockwell, D. L. Yule, O. T. Gorman, T. R. Hrabik, R. E. Kinnunen, W. P. Mattes, J. K. Oyadomari, D. R. Schreiner, and S. Geving. 2008. Status of cisco (*Coregonus artedi*) in Lake Superior during 1970-2006 and management and research considerations. Great Lakes Fishery Commission Special Publication.

Edsall, T. A., and P. J. Colby. 1970. Temperature tolerance of young-of-the-year cisco, *Coregonus artedii*. Transactions of the American Fisheries Society 99(3):526–531.

Engel, S. 1976. Food habits and prey selection of coho salmon (*Oncorhynchus kisutch*) and cisco (*Coregonus artedii*) in relation to zooplankton dynamics in Pallette Lake, Wisconsin. Transactions of the American Fisheries Society 105(5):607–614.

Epstein, E., M. Bryans, D. Mezei, and D. Patterson. 1974. Lower Green Bay: an evaluation of existing and historical conditions. Report EPA-905/9-74-006, U.S. Environmental Protection Agency, Chicago, Illinois.

Evermann, B. W., and H. M. Smith. 1896. The whitefishes of North America. Pages 283–324. Report of the U.S. Commissioner of Fish and Fisheries.

Faber, D. J. 1970. Ecological observations on newly hatched lake whitefish in South Bay, Lake Huron. Pages 481–500 *in* C. C. Lindsay and C. S. Woods, editors. Biology of coregonid fishes. University of Manitoba Press, Winnipeg.

Fisher, J. P., J. D. Fitzsimons, G. F. Combs, and J. M. Spitsbergen. 1996. Naturally occurring thiamine deficiency causing reproductive failure in Finger Lakes Atlantic salmon and Great Lakes lake trout. Transactions of the American Fisheries Society 125(2):167–178.

Fitzsimons, J. D., and R. O'Gorman. 2006. Status and assessment, research, and restoration needs for lake herring in the Great Lakes. Canadian Technical Report of Fisheries and Aquatic Science 2638.

Fudge, R. J. P., R. A. Bodaly, and M. Viljanen. 1986. Identification of larval lake whitefish (*Coregonus clupeaformis)* and cisco (*Coregonus artedi)* from southern Indian Lake, Manitoba by pigmentation characteristics and by isoelectric focusing of whole body protein extracts. Fishes and Oceans, Canada.

Garside, E. T., and W. J. Christie. 1962. Experimental hybridization among three coregonine fishes. Transactions of the American Fisheries Society 91(2):196–200.

Gibbons, S. G., and J. H. Fraser. 1937. The centrifugal pump and suction hose as a method of collecting plankton samples. Journal du Conseil 12(2):155–170.

Goodyear, C. S., T. A. Edsall, D. M. Ormsby Dempsey, G. D. Moss, and P. E. Polansky. 1982. Atlas of spawning and nursery areas of Great Lakes fishes. U.S. Fish and Wildlife Service, Washington D.C.

Gorsky, D., and J. Zydlewski. 2013. Experimental evaluation of size-dependent predation by adult post-spawned rainbow smelt on larval lake whitefish. North American Journal of Fisheries Management 33(1):163–169.

Greeley, J. R., and C. W. Greene. 1931. A biological survey of the St. Lawrence watershed. Pages 44–94. New York Conservation Department.

Greig, S. M., D. A. Sear, and P. A. Carling. 2005. The impact of fine sediment accumulation on the survival of incubating salmon progeny: implications for sediment management. Science of the Total Environment 344(1–3):241–258.

Hatch, J. T., J. C. Underhill, and R. D. Hoyt. 1988. Abundance, distribution, growth, and mortality of larval lake herring in western Lake Superior. Pages 96–103. American Fisheries Society Symposium (5).

Hile, R. 1936. Age and growth of the cisco, *Leucichthys artedi* (LeSueur), in the lakes of the northeastern highlands, Wisconsin. Bulletin of the Bureau of Fisheries Vol. 48, Bulletin No. 19.

Hinrichs, M. A. 1979. A description and key of the eggs and larvae of five species of fish in the subfamily Coregoninae. M.Sc. Thesis, University of Wisconsin, Stevens Point, Wisconsin.

Hinrichs, M. A., and H. E. Brooke. 1975. Egg development and larval feeding of lake herring, *Coregonus artedii* (LeSueur). The Museum of Natural History, University of Wisconsin, Stevens Point. Reports on flora and fauna of Wisconsin. 10(4):75–86.

Hoagman, W. J. 1974. Feeding by alewives (*Alosa pseudoharengus*) on larval lake whitefish (*Coregonus clupeaformis*) in the laboratory. Journal of the Fisheries Research Board of Canada 31(2):229–230.

Hoff, M. H. 2004. Biotic and abiotic factors related to lake herring recruitment in the Wisconsin waters of Lake Superior, 1984–1998. Journal of Great Lakes Research 30:423–433.

Honsey, A. E., S. B. Donabauer, and T. O. Höök. 2016. An analysis of lake morphometric and land-use characteristics that promote persistence of cisco in Indiana. Transactions of the American Fisheries Society 145(2):363–373.

Hrabik, T. R., J. J. Magnuson, and A. S. McLain. 1998. Predicting the effects of rainbow smelt on native fishes in small lakes: evidence from long-term research on two lakes. Canadian Journal of Fisheries and Aquatic Sciences 55(6):1364–1371.

Ivanova, N. V., T. S. Zemlak, R. H. Hanner, and P. D. N. Hebert. 2007. Universal primer cocktails for fish DNA barcoding. Molecular Ecology Notes 7(4):544–548.

Jaroszewska, M., B. J. Lee, K. Dabrowski, S. Czesny, J. Rinchard, P. Trzeciak, and B. Wilczyńska. 2009. Effects of vitamin B1 (thiamine) deficiency in lake trout (*Salvelinus namaycush*) alevins at hatching stage. Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology 154(2):255–262.

John, K. R., and A. D. Hasler. 1956. Observations on some factors affecting the hatching of eggs and the survival of young shallow-water cisco, *Leucichthys artedi* LeSueur, in Lake Mendota, Wisconsin. Limnology and Oceanography 1(3):176–194.

Johnson, J. H., J. E. McKenna, M. A. Chalupnicki, T. Wallbridge, and R. Chiavelli. 2009. Feeding ecology of lake whitefish larvae in eastern Lake Ontario. Journal of Great Lakes Research 35(4):603–607.

Kahilainen, K. K., K. Østbye, C. Harrod, T. Shikano, T. Malinen, and J. Merilä. 2011. Species introduction promotes hybridization and introgression in Coregonus: is there sign of selection against hybrids? Molecular Ecology 20(18):3838–3855.

Ketola, H. G., P. R. Bowser, G. A. Wooster, L. R. Wedge, and S. S. Hurst. 2000. Effects of thiamine on reproduction of Atlantic salmon and a new hypothesis for their extirpation in Lake Ontario. Transactions of the American Fisheries Society 129(2):607–612.

Klocke, J. F., P. I. Tack, M. A. Ohlson, R. Nitchals, E. Leffler, and N. S. Henry. 1947. Nutritive value of fish from Michigan waters. Journal of Food Science 12(1):36–43.

Koelz, W. 1926. Fishing industry of the Great Lakes. Appendix XI to the Report of the U.S. Commissioner of Fisheries, 1925. Washington, DC.

Koelz, W. 1927. Coregonid fishes of the Great Lakes. Bulletin of the Bureau of Fisheries 43(2).

Krueger, D. M., and T. R. Hrabik. 2005. Food web alterations that promote native species: the recovery of cisco (*Coregonus artedi*) populations through management of native piscivores. Canadian Journal of Fisheries and Aquatic Sciences 62(10):2177–2188.

Lake Ontario fisheries. 1885. The Oswego Palladium (July 9).

Langford, R. R. 1938. The food of the Lake Nipissing cisco, *Leucichthys artedi* (LeSueur), with special reference to the utilization of the limnetic crustacean. University of Toronto Studies Biological Series 45. Publications of the Ontario Fisheries Research Laboratory 57:143–190.

Lehtonen, T., and C. Kvarnemo. 2015. Density effects on fish egg survival and infections depend on salinity. Marine Ecology Progress Series 540:183–191.

Lindström, T. H. 1962. Life history of whitefish young (*Coregonus*) in two lake reservoirs. Institute of Freshwater Research Drottningholm 44:113–144.

Link, J., J. H. Selgeby, M. H. Hoff, and C. Haskell. 1995. Winter diet of lake herring (*Coregonus artedi*) in western Lake Superior. Journal of Great Lakes Research 21(3):395–399.

Loftus, D. H., and P. F. Hulsman. 1986. Predation on larval lake whitefish (*Coregonus clupeaformis*) and lake herring (*C. artedii*) by adult rainbow smelt (*Osmerus mordax*). Canadian Journal of Fisheries and Aquatic Sciences 43(4):812–818.

Luecke, C., L. G. Rudstam, and Y. Allen. 1992. Interannual patterns of planktivory 1987–89: an analysis of vertebrate and invertebrate planktivores. Pages 275–302 *in* J. F. Kitchell, editor. Food web management. Springer-Verlag New York Inc.

Madenjian, C. P., G. L. Fahnenstiel, T. H. Johengen, T. F. Nalepa, H. A. Vanderploeg, G. W. Fleischer, P. J. Schneeberger, D. M. Benjamin, E. B. Smith, J. R. Bence, E. S. Rutherford, D. S. Lavis, D. M. Robertson, D. J. Jude, and M. P. Ebener. 2002. Dynamics of the Lake Michigan food web, 1970-2000. Canadian Journal of Fisheries and Aquatic Sciences 59(4):736–753.

Madenjian, C. P., E. S. Rutherford, M. A. Blouin, B. J. Sederberg, and J. R. Elliott. 2011. Spawning habitat unsuitability: an impediment to cisco rehabilitation in Lake Michigan? North American Journal of Fisheries Management 31(5):905–913.

Manz, J. V. 1964. A pumping device used to collect walleye eggs from offshore spawning areas in western Lake Erie. Transactions of the American Fisheries Society 93(2):204–206.

Mason, D. M., T. B. Johnson, and J. F. Kitchell. 1998. Consequences of prey fish community dynamics on lake trout (*Salvelinus namaycush*) foraging efficiency in Lake Superior. Canadian Journal of Fisheries and Aquatic Sciences 55(5):1273–1284.

McAughey, S. C., and J. M. Gunn. 1995. The behavioral response of lake trout to a loss of traditional spawning sites. Journal of Great Lakes Research 21 (Supplement 1):375–383.

McCormick, J. H., B. R. Jones, and R. F. Syrett. 1971. Temperature requirements for growth and survival of larval ciscos (*Coregonus artedii*). Journal of the Fisheries Board of Canada 28(6):924–927.

McCrimmon, H. R. 1952. Morality of coregonid fishes in Lake Simcoe during spring temperature warm-up. The Canadian Field Naturalist 66(4).

McKenna, J. E., and J. H. Johnson. 2009. Spatial and temporal variation in distribution of larval lake whitefish in eastern Lake Ontario: Signs of recovery? Journal of Great Lakes Research 35(1):94–100.

Miller, T. J., L. B. Crowder, J. A. Rice, and E. A. Marschall. 1988. Larval size and recruitment mechanisms in fishes: toward a conceptual framework. Canadian Journal of Fisheries and Aquatic Sciences 45(9):1657–1670.

Mills, E. L., J. M. Casselman, R. Dermott, J. D. Fitzsimons, G. Gal, K. T. Holeck, J. A. Hoyle, O. E. Johannsson, B. F. Lantry, J. C. Makarewicz, E. S. Millard, I. F. Munawar, R. O'Gorman, R. W. Owens, L. G. Rudstam, T. Schaner, and T. J. Stewart. 2003. Lake Ontario: food web dynamics in a changing ecosystem (1970-2000). Canadian Journal of Fisheries and Aquatic Sciences 60:471–490.

Mills, E. L., J. L. Forney, M. D. Clady, W. R. Schaffner, and J. A. Bloomfield. 1978. Oneida Lake. Lakes of New York State: ecology of the lakes of western New York 2:367–451.

Milne, S. W., B. J. Shuter, and W. G. Sprules. 2005. The schooling and foraging ecology of lake herring (*Coregonus artedi*) in Lake Opeongo, Ontario, Canada. Canadian Journal of Fisheries and Aquatic Sciences 62(6):1210–1218.

Morris, D. W. 1987. Tests of density-dependent habitat selection in a patchy environment. Ecological Monographs 57(4):269.

Muir, A. M., P. Vecsei, M. Power, C. C. Krueger, and J. D. Reist. 2014. Morphology and life history of the Great Slave Lake ciscoes (Salmoniformes: Coregonidae). Ecology of Freshwater Fish 23(3):453–469.

Myers, J. T., M. L. Jones, J. D. Stockwell, and D. L. Yule. 2009. Reassessment of the predatory effects of rainbow smelt on ciscoes in Lake Superior. Transactions of the American Fisheries Society 138(6):1352–1368.

Myers, J. T., D. L. Yule, M. L. Jones, T. D. Ahrenstorff, T. R. Hrabik, R. M. Claramunt, M. P. Ebener, and E. K. Berglund. 2015. Spatial synchrony in cisco recruitment. Fisheries Research 165:11–21.

Nelson, J. S., E. J. Crossman, H. Espinosa-Pérez, L. T. Findley, C. R. Gilbert, R. N. Lea, and J. D. Williams. 2004. Common and scientific names of fishes from the United States, Canada and Mexico. American Fisheries Society.

New York State Department of Environmental Conservation. 2016. New York Freshwater Fishing 2016/2017 Official Regulations Guide. 1st edition.

O'Gorman, R., O. Gorman, and D. Bunnell. 2007. Great Lakes prey fish populations: a cross-basin view of status and trends in 2007. Great Lakes Fishery Committee Upper and Lower Lakes Committee Meetings, March 19-23. Ypsilanti, Michigan.

Oldenburg, K., M. A. Stapanian, P. A. Ryan, and E. Holm. 2007. Potential strategies for recovery of lake whitefish and lake herring stocks in eastern Lake Erie. Journal of Great Lakes Research 33(sp1):46–58.

Ontario Ministry of Natural Resources. 2014. Lake Ontario fish communities and fisheries: 2013 annual report of the Lake Ontario Management Unit. Ontario Ministry of Natural Resources, Picton, Ontario.

Organ, W. L., G. L. Towns, M. O. Walter, R. B. Pelletier, and D. A. Riege. 1979. Past and presently known spawning grounds of fishes in the Michigan coastal waters of the Great Lakes. Michigan Department of Natural Resources, Ann Arbor, MI.

Oyadomari, J. K., and N. A. Auer. 2008. Transport and growth of larval cisco (*Coregonus artedi*) in the Keweenaw Current region of Lake Superior. Canadian Journal of Fisheries and Aquatic Sciences 65(7):1447–1458.

Palmer, R. 2002. The "Ciscoe Chasers" of Chaumont Bay. http://freepages.genealogy.rootsweb.ancestry.com/~twigs2000/ciscoe.html.

Peck, J. W. 1986. Dynamics of reproduction by hatchery lake trout on a man-made spawning reef. Journal of Great Lakes Research 12(4):293–303.

Petering, R. W., and M. J. Van Den Avyle. 1988. Relative efficiency of a pump for sampling larval gizzard and threadfin shad. Transactions of the American Fisheries Society 117(1):78–83.

Powlik, J. J., M. A. St John, and R. W. Blake. 1991. A retrospective of plankton pumping systems, with notes on the comparative efficiency of towed nets. Journal of Plankton Research 13(5):901–912.

Pritchard, A. L. 1931. Spawning habits and fry of the cisco (*Leucichthys artedi*) in Lake Ontario. Contributions to Canadian Biology and Fisheries 6(1):225–240.

Reed, K. M., M. O. Dorschner, T. N. Todd, and R. B. Phillips. 1998. Sequence analysis of the mitochondrial DNA control region of ciscoes (genus *Coregonus*): taxonomic implications for the Great Lakes species flock. Molecular Ecology 7(9):1091–1096.

Rhymer, J. M., and D. Simberloff. 1996. Extinction by hybridization and introgression. Annual Review of Ecology and Systematics 27:83–109.

Riley, S. C., and A. N. Evans. 2008. Phylogenetic and ecological characteristics associated with thiaminase activity in Laurentian Great Lakes fishes. Transactions of the American Fisheries Society 137(1):147–157.

Roseman, E. F., G. W. Kennedy, J. Boase, B. A. Manny, T. N. Todd, and W. Stott. 2007. Evidence of lake whitefish spawning in the Detroit River: implications for habitat and population recovery. Journal of Great Lakes Research 33(2):397–406.

Roseman, E. F., and T. P. O'Brien. 2013. Spatial distribution of pelagic fish larvae in the northern main basin of Lake Huron. Aquatic Ecosystem Health and Management 16(3):311–321.

Rosenzweig, M. L. 1981. A theory of habitat selection. Ecology 62(2):327.

Rudstam, L. G. 1993. The rise and fall of a dominant planktivore: direct and indirect effects on zooplankton. Ecology 74(2):303–319.

Savino, J. F., and P. L. Hudson. 1995. Feeding competition between larval lake whitefish and lake herring. Pages 153–162 *in* Biology and management of coregonid fishes, 1993. E. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart, Germany.

Schlei, O. L., A. Crête-Lafrenière, A. R. Whiteley, R. J. Brown, J. B. Olsen, L. Bernatchez, and J. K. Wenburg. 2008. DNA barcoding of eight North American coregonine species. Molecular Ecology Resources 8(6):1212–1218.

Scott, W. B., and E. J. Crossman. 1973. Freshwater fishes of Canada. Bulletin of the Fisheries Research Board of Canada (184).

Selgeby, J. H. 1982. Decline of lake herring (*Coregonus artedii*) in Lake Superior: an analysis of the Wisconsin herring fishery, 1936-78. Canadian Journal of Fisheries and Aquatic Sciences 39(4):554–563.

Selgeby, J. H., W. R. MacCallum, and D. V. Swedberg. 1978. Predation by rainbow smelt (*Osmerus mordax*) on lake herring (*Coregonus artedii*) in western Lake Superior. Journal of the Fisheries Research Board of Canada 35:1457–1463.

Smith, C. L. 1985. The inland fishes of New York State. New York State Department of Environmental Conservation, Albany, NY.

Smith, S. H. 1968. Species succession and fishery exploitation in the Great Lakes. Journal of the Fisheries Board of Canada 25(4):667–693.

Stewart, K., and D. Watkinson. 2004. Freshwater fishes of Manitoba. University of Manitoba Press, Winnipeg.

Stewart, T. J., A. Todd, and S. LaPan. 2013. Fish community objectives for Lake Ontario. Great Lakes Fishery Commission, Lake Ontario Committee.

Stockwell, J. D., M. P. Ebener, J. A. Black, O. T. Gorman, T. R. Hrabik, R. E. Kinnunen, W. P. Mattes, J. K. Oyadomari, S. T. Schram, D. R. Schreiner, M. J. Seider, S. P. Sitar, and D. L. Yule. 2009. A synthesis of cisco recovery in Lake Superior: implications for native fish rehabilitation in the Laurentian Great Lakes. North American Journal of Fisheries Management 29(3):626–652.

Stockwell, J. D., D. L. Yule, O. T. Gorman, E. J. Isaac, and S. A. Moore. 2006. Evaluation of bottom trawls as compared to acoustics to assess adult lake herring (*Coregonus artedi*) abundance in Lake Superior. Journal of Great Lakes Research 32(2):280–292.

Stockwell, J. D., D. L. Yule, T. R. Hrabik, M. E. Sierszen, and E. J. Isaac. 2014. Habitat coupling in a large lake system: delivery of an energy subsidy by an offshore planktivore to the nearshore zone of Lake Superior. Freshwater Biology 59(6):1197–1212.

Stone, U. B. 1938. Growth, habits, and fecundity of the ciscoes of Irondequoit Bay, New York. Transactions of the American Fisheries Society 67(1):234–245.

Swenson, W. A. 1978. Influence of turbidity on fish abundance in western Lake Superior. Report of the Environmental Protection Agency, Environmental Research Laboratory. EPA 600/3-78-067.

Taggart, C. T., and W. C. Leggett. 1984. Efficiency of large-volume plankton pumps, and evaluation of a design suitable for deployment from small boats. Canadian Journal of Fisheries and Aquatic Sciences 41(10):1428–1435.

Taylor, W. W., and M. H. Freeberg. 1984. Effect of food abundance on larval lake whitefish, *Coregonus clupeaformis* Mitchill, growth and survival. Journal of Fish Biology 25(6):733–741.

Taylor, W. W., M. A. Smale, and M. H. Freeberg. 1987. Biotic and abiotic determinants of lake whitefish (*Coregonus clupeaformis*) recruitment in northeastern Lake Michigan. Canadian Journal of Fisheries and Aquatic Sciences 44(2):313–323.

Tillitt, D. E., J. L. Zajicek, S. B. Brown, L. R. Brown, J. D. Fitzsimons, D. C. Honeyfield, M. E. Holey, and G. M. Wright. 2005. Thiamine and thiaminase status in forage fish of salmonines from Lake Michigan. Journal of Aquatic Animal Health 17(1):13–25.

Todd, T. N. 1981. Allelic variability in species and stocks of Lake Superior ciscoes (Coregoninae). Canadian Journal of Fisheries and Aquatic Sciences 38(12):1808–1813.

Todd, T. N., and B. M. Davis. 1995. Effects of fish density and relative abundance on competition between larval lake herring and lake whitefish for zooplankton. Pages 163–171 *in* Biology and management of coregonid fishes, 1993. E. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart, Germany.

Todd, T. N., and R. M. Stedman. 1989. Hybridization of ciscoes (*Coregonus* spp.) in Lake Huron. Canadian Journal of Zoology 67(7):1679–1685.

Turgeon, J., A. Estoup, and L. Bernatchez. 1999. Species flock in the North American Great Lakes: molecular ecology of Lake Nipigon ciscoes (Teleostei: Coregonidae: *Coregonus*). Evolution 53(6):1857.

Van Oosten, J. 1929. Life history of the cisco (*Leucichthys artedi* LeSueur) of Lake Huron as revealed by its scales, with a critique of the scale method. Bulletin of the U.S. Bureau of Fisheries 44:265–268.

Van Oosten, J. 1930. The disappearance of the Lake Erie cisco – a preliminary report. Transactions of the American Fisheries Society 60(1):204–214.

Van Oosten, J. 1947. Mortality of smelt, *Osmerus mordax* (Mitchill), in Lakes Huron and Michigan during the fall and winter of 1942–1943. Transactions of the American Fisheries Society 74(1):310–337.

Walsh, M. G., B. C. Weidel, M. J. Connerton, and J. Holden. 2015. Status of important prey fishes in the U.S. waters of Lake Ontario, 2014: alewife, rainbow smelt, sculpins, and round goby. Section 12 *in* NYSDEC 2015 Annual Report, Bureau of Fisheries Lake Ontario Unit and St. Lawrence River Unit to the Great Lakes Fisheries Comissions' Lake Ontario Committee.

Watson, N. H. F. 1976. Seasonal distribution and abundance of crustacean zooplankton in Lake Erie, 1970. Journal of the Fisheries Board of Canada 33(3):612–621.

Wetzel, R. G. 2001. Limnology: lake and river ecosystems, 3rd edition. Academic Press, San Diego, CA.

Whitham, T. G. 1980. The theory of habitat selection: examined and extended using pemphigus aphids. The American Naturalist 115(4):449–466.

Zollweg, E. C., and S. Leathe. 2000. Tiber cisco spawning study. U.S. Department of the Interior, Bureau of Reclamation Montana Area Office, Billings, Montana.