The Subtlety of Lake Superior Ciscoe Recruitment Dynamics

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Abstract

Objective: Lake Superior whitefish [Salmonidae: Coregoninae] have undergone high annual variability in survival to age-1 over the last 50-years, particularly within the dominant ciscoe flock of Bloater *Coregonus hoyi*, Cisco *C. artedi*, and Kiyi *C. Kiyi*. This work sought to determine if this variance was associated with hydrometeorological attributes that have also varied considerably over the same period.

Methods: Forty-seven years of age-1 Bloater and Cisco (1978-2024) and 12-years of age-1 Kiyi (2011-2024) density estimates and 42-years (1982-2024) of satellite derived lakewide ice cover, surface water temperature, air temperature, cloud cover, wind speed, and wind direction data were evaluated using Classification and Regression Tree models and correlation analyses. A decade of larval ciscoe data (2014-2024) were also incorporated into the evaluation to identify the critical period for their survival in Lake Superior.

Results: Lake Superior ciscoe year–class strength was highest when June water temperature was <4.8°C, January ice cover was >19%, and winds were calmer than average during the November to January spawning season. There was a threshold relationship where maximum survival to age-1 occurred when mean June surface water temperature was <4.8°C, and survival was often near zero when mean June water temperature was >4.8°C. This was true for Bloater, Cisco, and Kiyi. The critical period for survival appeared to be a few weeks post–hatching, which likely coincided with the initiation of exogenous feeding.

Conclusion: Calm winds during the spawning season may serve to reduce embryo disturbance and drift to unfavorable habitats and promote early ice formation. Development of early ice can foster more ice cover throughout the winter, leading to later ice breakup and reduced spring water temperature. Cold spring water temperature reduces the metabolic demands of larval deepwater ciscoes during a time of low zooplankton prey abundance.

Lay Summary

The extraordinary survival of the Lake Superior 2022 ciscoe [Salmonidae: Coregoninae *Coregonus hoyi, C. artedi*, and *C. Kiyi*) year-classes provided an incentive to re-assess causes underlying their dismal survival over the previous half-century. Year–class strength was highest when June water temperature was <5°C, January ice cover was >19%, and winds were calmer than average during the November to January spawning season. There was a threshold relationship where maximum survival to age-1 occurred when mean June surface water temperature was <4.8°C, and survival was often near zero when mean June water temperature was >4.8°C. The critical period for survival appeared to be a few weeks post–hatching, which likely coincided with the initiation of exogenous feeding. A lakewide mean June surface water temperature <4.9°C occurred 94% of the time between 1982 and 2024 when January maximum lakewide ice cover exceeded 19%. Understanding factors that limit ciscoe survival can improve stock management and help fishers better manage equipment investments.

Keywords

Coregonus, year-class strength, whitefish, Laurentian Great Lakes

Introduction

Whitefish [Salmonidae: Coregoninae] were the most important commercially harvested fish in the Laurentian Great Lakes (Bogue 2001) and ciscoes, subgenus *Leucichthys*, were the foremost family members (Eshenroder et al. 2016). Great Lakes ciscoe species included Blackfin Cisco *Coregonus nigripinnis*, Bloater *C. hoyi*, Cisco *C. artedi*, Deepwater Cisco *C. johannae*, Kiyi *C. Kiyi*, Longjaw Cisco *C. alpenae,* Shortjaw Cisco *C. zenithicus*, and Shortnose Cisco *C. reighardi* (Koelz 1929). Presently, few of these species persist at historic population levels and many have been extirpated from their native lakes (Eshenroder et al. 2016). Population declines during the 20th century were attributed to competition with invasive planktivorous fishes (Alewife, *Alosa pseudoharengus;* and Rainbow Smelt, *Osmerus mordax*), overfishing, parasitization by invasive Sea Lamprey, *Petromyzon marinus*, predation by introduced Pacific salmonids, *Oncorhynchus* spp., and interactions among these factors which collectively reduced survival of adult and juvenile fish (Smith 1964; Christie 1974; Lawrie 1978). In the 21st century, lower than historic population levels have been attributed to high interannual variability in survival to age-1 due to altered environmental conditions, and to a lesser extent negative interactions with invasive and introduced species (Hoff 2004; Stockwell et al. 2009; Rook et al. 2012; Rook et al. 2013; Bronte et al. 2017; Rook et al. 2021; Goldsworthy et al. 2024). This recent thinking led to an uptick in research on whitefish spawning and early life history to determine the underlying cause of poor survival of early life stages (Lucke et al. 2020; Lachance et al. 2021; Stewart et al. 2021a; Stewart et al. 2021b; Brown et al. 2022; Paufve et al. 2022; Ransom et al. 2022; Stewart et al. 2022b; Brown et al. 2024).

Understanding interannual variability in fish year–class strength, *sensu* Hjort (1914), has long been viewed as the “holy grail” of fishery science, as countless investigators have reported equivocal responses both within and among closely related species and across species' ranges (Myers 1998; Houde 2008; Szuwalski et al. 2015; Munch et al. 2018; Brosset et al. 2020). This portrayal reflects our knowledge of whitefish recruitment variability worldwide (Taylor et al. 1987; Jeppesen et al. 2012) and in Lake Superior, where Cisco year–class strength has been associated with a multitude of biotic (Selgeby et al. 1978; Selgeby 1985; Selgeby et al. 1994; Hoff 2004; Rook et al. 2013; Myers et al. 2014) and abiotic factors (Kinnunen 1997; Hoff 2004; Rook et al. 2013; Myers et al. 2015), as well as a half–century decline in nutrient inputs (Rook et al. 2021). Globally, contemporary changes in whitefish year–class strength have coincided with observed habitat warming over the past 30–years (Nyberg et al. 2001). However, many of these analyses were confounded by concurrent increases or decreases in nutrient loads and incursions of exotic species over the same time (Jeppesen et al. 2012; Eckmann 2013; Bunnell et al. 2014; Rook et al. 2021).

The notion that whitefish would respond negatively to a warming environment is judicious. Whitefish have a northern latitude distribution, spawning is coincident with fall–winter ice–cover formation, embryonic incubation occurs under ice–cover, and hatching is coincident with spring ice–breakup (Scott and Crossman 1973; Nyberg et al. 2001). However, documenting the relationship between warming thermal regimes and survival of whitefish early life stages has proven to be nuanced. For example, in a large study of twenty–four European lakes, mild winters that led to earlier ice–breakup were detrimental to Vendace *C. albula* year–class strength in some but not all lakes (Jeppesen et al. 2012). Further north in Lake Inari, Finland, warming appeared to favor Vendace recruitment (Puro-Tahvanainen and Salonen 2010). Likewise, survival of Vendace larvae in Lake Mälaren, Sweden was higher when water temperatures were slighter warmer than average but was lower when water temperatures rose too rapidly after ice breakup and hatching (Nyberg et al. 2001). In the Laurentian Great Lakes, relationships between whitefish year-class strength and winter severity were positive in Lake Erie from 1925 to 1949 (Van Oosten and Hile 1949; Lawler 1965) and mixed in Lake Michigan from 1958 to 1980 (Taylor et al. 1987). There is limited evidence linking thermal regimes to whitefish year–class strength in the Laurentian Great Lakes even though there are well documented contemporary decreases in lake ice formation, warming thermal regimes (Austin and Colman 2008; Wang et al. 2012; Van Cleave et al. 2014) and high interannual variability in whitefish year–class strength (Selgeby 1982; Bronte et al. 2003; Hoff 2004; Lepak et al. 2017; Goldsworthy et al. 2024) as compared to historical times (Dryer and Beil 1964; Dryer and Beil 1968; Selgeby 1982; Stockwell et al. 2009; Rook et al. 2021). However, recent experimental work found embryo survival, incubation period, and length–at–hatch of Laurentian Great Lakes Cisco populations to be inversely related to incubation temperatures and simulated ice cover, indicating that warmer winter conditions influence and likely reduce Cisco embryo and larval survival (Stewart et al. 2021a; Stewart et al. 2021b; Stewart et al. 2022a). The lack of a consistent measurable response by whitefish populations to changing thermal changes may be due to both the spatial and temporal complexity of lake thermal regimes (Zhong et al. 2019; Cannon et al. 2024) and the subtleties of fish recruitment dynamics (Houde 2008; Munch et al. 2018).

The Laurentian Great Lakes in general, and Lake Superior in particular, have been tracking or exceeding global hydrometeorological changes over the past century (Woolway et al. 2020; Sharma et al. 2021; Cannon et al. 2024), with the most prominent trends being a decrease in ice cover and an increase in water temperature (Austin and Colman 2008; Bai et al. 2012; Wang et al. 2012; White et al. 2018). In addition to these trends, an abrupt step–change in ice, thermal, evaporation, and wind regimes occurred in 1998. Compared to pre–1998 averages, average annual maximum ice cover on Lake Superior decreased from 75% to 46% and annual mean and maximum lakewide surface temperatures increased from 5.4 to 6.7°C and 15.5 to 17.9°C, respectively, with the greatest warming differences between the two periods occurring in summer–fall (Figure 1). Embedded within this post–1998 trend have been anomalous years with near record high ice formation (2003, 2009, 2014, 2015, 2019) and cold–water temperatures (2003, 2014) as well as a few exceptionally warm years (2010, 2012, 2016, 2024) that further deviated from the post–1998 warming trend. Higher than average ciscoe survival to age-1 also occurred in a few years since 1998 (Vinson et al. 2024; Vinson and Yule 2024).

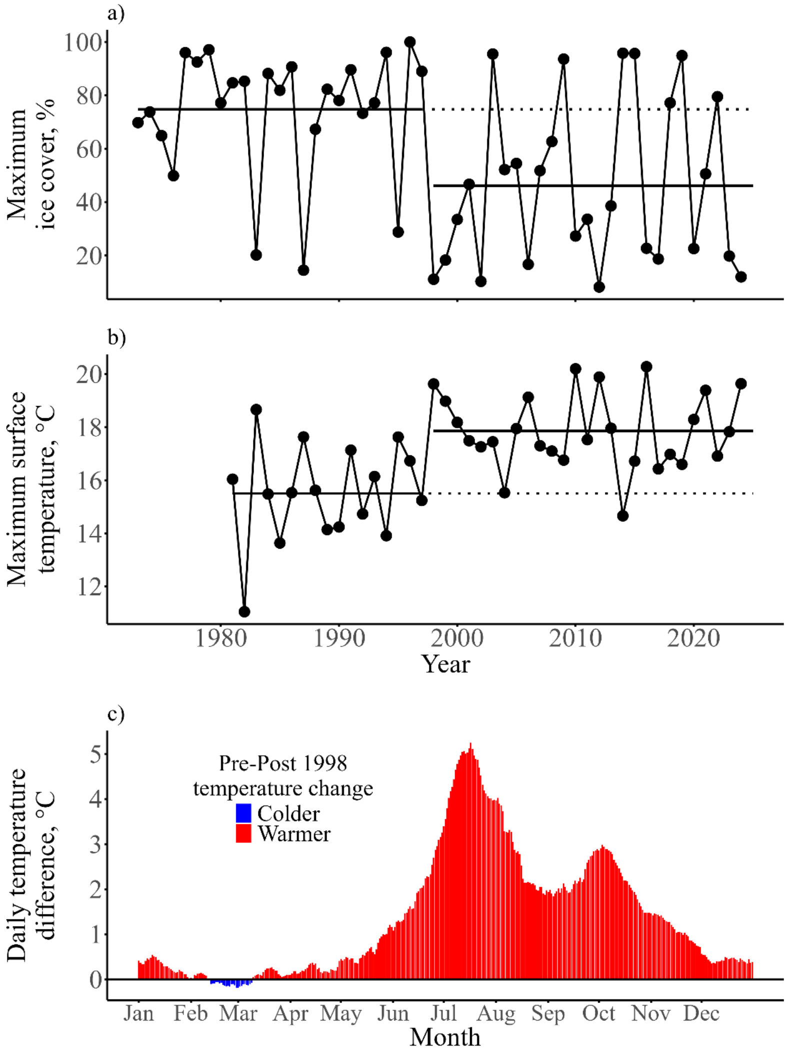


Figure 1. a) Lake Superior annual maximum fraction of the total lake surface area covered by ice and b) annual maximum lakewide average surface water temperature. Solid horizontal lines in a) and b) are averages for that period and dotted lines are averages for the pre–1998 period. c) Average daily difference in lakewide average surface water temperature before 1997, the pre–1998 step–change period, and between 1998 and 2024, the post–1998 step–change period. Ice cover data were scraped https://www.glerl.noaa.gov/data/ice/glicd/daily/sup.txt and water temperature data from https://coastwatch.glerl.noaa.gov/statistics/average–surface–water–

temperature–glsea/ for the years 1995-2024 and from https://podaac.jpl.nasa.gov/ for the years 1982–1994.

The post–1998 step–change was linked to a similar step–change in the Pacific Decadal Oscillation that occurred at the same time (Van Cleave et al. 2014) and to a strong El Niño Southern Oscillation event that occurred that year (Changnon 2000). The anomalous hydrometeorological years were also associated with teleconnection patterns and multidecadal climate oscillation indices (Bai et al. 2015; Wang et al. 2018; Lin et al. 2022; Cannon et al. 2024). Climate teleconnection patterns and multidecadal climate oscillations are measures designed to condense complex phenomena, typically spatially and temporally broad ocean thermal and atmospheric patterns, into simpler single variables that may explain variance in local observations (e.g., temperature, precipitation, species abundances) better than individual local climate variables. The relationship between climate indices and local climatic and ecological patterns is well established (Stenseth et al. 2002), including relationships with fish year–class strength, though primarily for marine species, e.g., Atlantic Cod *Gadus morhua* (Brander and Mohn 2004), European Anchovy *Engraulis encrasicolus* and Sardine *Sardina pilchardus* (Báez et al. 2022).

Bloater, Cisco, and Kiyi are the current dominant ciscoes in Lake Superior, and all have experienced contemporary population decreases and high interannual variability in survival to age-1 (Bronte et al. 2003; Stockwell et al. 2009; Lepak et al. 2017; Goldsworthy et al. 2024; Vinson et al. 2024). While closely related, subtle differences among the three species include body shape and size (Koelz 1931; Eshenroder et al. 2016), habitat and trophic niches (Rosinski et al. 2020), and reproductive phenology (Koelz 1931; Hile and Deason 1947; Dryer and Beil 1964; Dryer and Beil 1968; Vinson et al. 2023). Current thinking, based largely on historical accounts, is that the three species spawn in nearshore habitats (Koelz 1929; Hile and Deason 1947; Dryer and Beil 1964; Dryer and Beil 1968; Goodyear et al. 1982). However, contemporary spawning locations for Bloater and Kiyi in Lake Superior are not well documented (Vinson et al. 2023). Spawning timing appears sequential, Cisco in late November–December, Kiyi in December–January, and Bloater in February–March (Koelz 1929; Hile and Deason 1947; Dryer and Beil 1964; Dryer and Beil 1968; Vinson et al. 2023). Larvae hatch in spring in a similar sequence to their spawning (Lachance et al. 2021), though this is not well documented, as there was no reliable technique for identifying larval ciscoe species prior to 2020 (Ackiss et al. 2020). Earlier studies labeled all larval ciscoes as Cisco (Selgeby et al. 1978; Kinnunen 1997; Oyadomari and Auer 2004; Oyadomari and Auer 2008; Myers et al. 2015) when they were likely a mix of ciscoe species (Lachance et al. 2021).

Recent high interannual variability in Lake Superior's annual hydrometeorological conditions and ciscoe survival to age-1 provide an opportunity to reevaluate the interannual variability in Lake Superior age-1 ciscoe year–class strength. This analysis uses the same Cisco year–class strength data used in past evaluations (Kinnunen 1997; Hoff 2004; Rook et al. 2012; Rook et al. 2013; Rook et al. 2021), but with the benefit of more than a decade of recent year–class strength data. This includes data for the 2022 Lake Superior ciscoe year–classes, which were the largest estimated over the previous 47–years for Bloater and Cisco, and the previous 12–years for Kiyi (Vinson et al. 2024). A dozen years of larval ciscoe population data are also now available.

In contrast to previous analyses that evaluated Lake Superior region–specific Cisco year–class strength using stock–recruitment relationships and terrestrial station based environmental data within general linear models (Hoff 2004; Rook et al. 2012; Rook et al. 2013), this paper assessed interannual variability in Lake Superior ciscoe (Bloater, Cisco, and Kiyi) year–class strength by identifying environmental commonalities in ciscoe early life stage habitat conditions during years with high and low survival to age-1. Essentially, were years with higher survival colder or warmer, calmer or windier, cloudier or clearer, and did they have higher or lower potential predators compared to the long–term average of these conditions? Data were also evaluated to determine if threshold environmental conditions could be identified that appeared to underlie greater or lesser survival to age-1.

Methods

Age-1 ciscoe and all–age Rainbow Smelt population indices

Indices of Lake Superior age-1 ciscoe abundance (fish per ha) and total Rainbow Smelt biomass (kg per ha) were estimated annually from long–term fishery–independent surveys conducted by the U.S. Geological Survey. Rainbow Smelt have been identified as a potential predatory regulator of Cisco year–class strength (Selgeby et al. 1978; Myers et al. 2009). Bloater, Cisco, and Rainbow Smelt population estimates were derived from a spring nearshore (~<100 m deep) bottom trawl survey and Kiyi population estimates were derived from a summer offshore (~>100 m deep) bottom trawl survey (Figure 2). The nearshore survey was established in U.S. waters in 1978 and in Canadian waters in 1989. The offshore survey was established in both countries in 2011. Locations were sampled in roughly the same order each year and sampling dates at each location across years typically varied by less than a week. The nearshore survey began in mid–May and continued through the end of June and the offshore survey occurred during July. Age-1 Bloater and Cisco are estimated to be 11–13 months and age-1 Kiyi are 13–15 months of age when collected. Bottom trawl surveys in Lake Superior have been shown to accurately index age-1 ciscoes based on stock age structure from fishery independent assessments and commercial catches (Yule et al. 2008; Stockwell et al. 2009; Lepak et al. 2017; Goldsworthy et al. 2024).

The mean and median number of nearshore locations sampled annually were 69 and 76, respectively (range = 32–87) and the mean and median number of offshore locations sampled annually was 34 and 35, respectively (range = 30–36). Nearshore locations were trawled down the bank from shallow to deep. Nearshore mean and median start and end depths for the period–of–record (1978–2024) were 18 and 16 m (range 7–68 m) and 67 and 64 m (range 12–144 m), respectively. The mean and median nearshore distances trawled were 1.9 and 1.8 km (range 0.2–4.0 km). Offshore locations were trawled on-contour, with the mean and median difference between the trawl start and trawl end depths being 5 and 4 m, respectively. The mean and median start and end depths for the period–of–record (2011–2024) were 185 and 177 m (range 80–314 m), respectively. The mean and median offshore distance trawled was 1.4 km (range 1.2–1.7 km). For both surveys, a single bottom trawl tow was conducted with a 12–m Yankee bottom trawl with either a chain or rubber–disk foot rope at each location each year. The rubber disk foot rope trawl was fished at steeper rocker locations. Both nets had an 11.9 m head rope, 15.5 m foot rope, and 2.2 m wing height with stretch meshes of 89 mm at the mouth, 64 mm for the trammel, and 13 mm at the cod end. Both trawls were towed at approximately 4 km per ha. All trawling was done during daylight hours. Bottom trawl fishing area was calculated based on a fixed trawl wing spread of 7.8 m and the distance trawled based on the ship's global positioning system. Bottom depths were determined by the ship's fathometer prior to 2022 and a Marport trawl mensuration system (Marport.com) thereafter.

Bottom trawl catches were sorted by species, weighed in aggregate, counted, and total length was measured for a maximum of 50 individuals per species per trawl. Lengths of these individuals were extrapolated to the entire catch when more than 50 individuals were collected. Relative abundance of age-1 ciscoes (fish per ha) and Rainbow Smelt biomass (kg per ha) were estimated by dividing ciscoe sample counts or total Rainbow Smelt biomass by the area swept by each trawl tow (ha). Age-1 year–class strength was estimated as the mean lakewide abundance (fish per ha) of age-1 fish as determined by total length for nearshore collected Cisco <140 mm and Bloater <130 mm and for offshore collected Kiyi <110 mm. These age–size cutoffs were based on past age estimates, are approximate, and are known to vary among years (Dryer and Beil 1964; Dryer and Beil 1968; Lepak et al. 2017).

Larval ciscoe population indices

Beginning in 2014 larval ciscoes were collected concurrent with bottom trawling for age-1 ciscoes at each location (Figure 2) to identify the critical period (Hjort 1914; Hjort 1926) for Lake Superior ciscoe survival. Collections were made with a paired one–square–meter 500–micron mesh neuston net (model 9550, Sea–Gear Corporation, Melbourne, Florida). The bottom of the net frame was fished ~0.5 m below the lake surface for 10 minutes at ~4.0 km per h for ~0.7 km as determined from the Research Vessel Kiyi's global positioning system. No larval fish collections were made in 2020 and July 2021 due to COVID–related travel restrictions and in May 2023 due to a ship no-sail condition.

Larval fish were immediately removed from the nets and identified as *Coregonus*; Deepwater Sculpin, *Myoxocephalus thompsonii*; Rainbow Smelt, or Pacific Salmon *Oncorhynchus* spp. based on morphological characters (Hinrichs 1979; Auer 1982). *Coregonus* larvae were counted and stored in 20 ml polyethylene scintillation vials filled with 90% ethanol. Larval *Coregonus* densities were calculated based on the number collected, the width of the sampling nets, and the net tow distance.

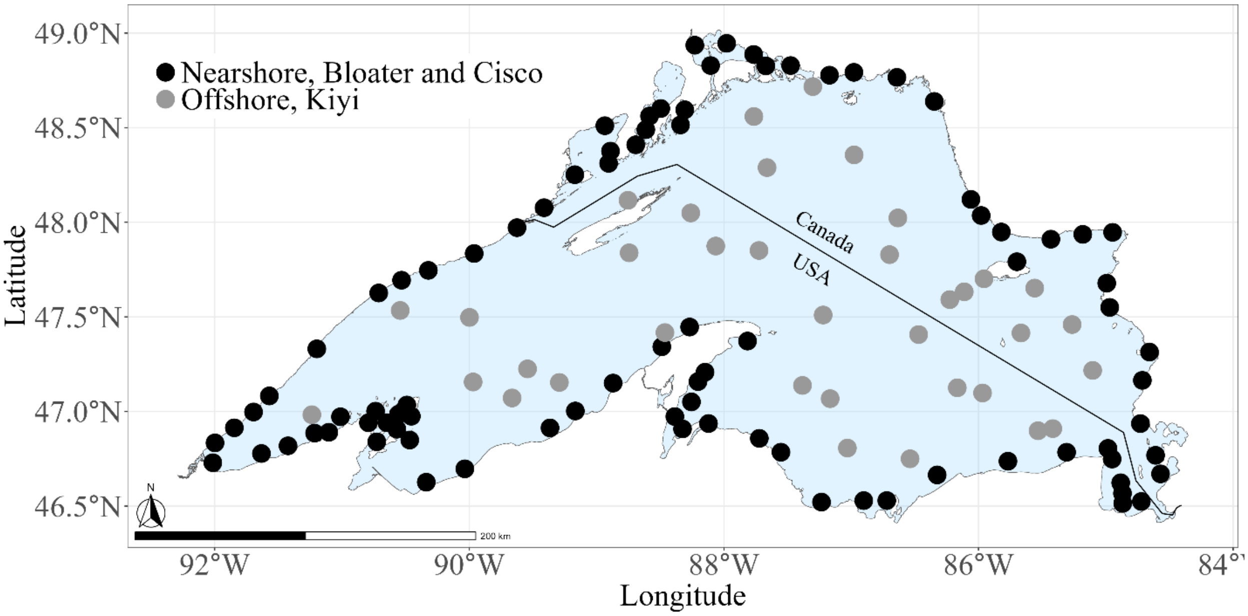


Figure 2. Lake Superior larval and age-1 ciscoe collection locations. Nearshore locations were bottom trawled for age-1 Bloater and Cisco in May and June from 1978–2024. Offshore locations were bottom trawled for age-1 Kiyi in July from 2011–2024. Larval ciscoes were collected with a surface trawl at all locations since 2014 concurrent with bottom trawling.

Environmental data

Environmental variables were selected based on *a priori* consideration of their effects on ciscoe survival to age-1. These variables included ice cover, surface water temperature, 2–m high air temperature, cloud cover, 10–m wind speed and direction, surface water chlorophyll concentration, and several regional climate indices. All environmental data were remotely sensed satellite derived data. Satellite–based weather measurements applied to a large landscape, like Lake Superior, have been found to capture the spatial structure of meteorological data than indices based on multiple ground stations (Mistry et al. 2022). These variables were used collectively in Classification and Regression Tree (CART) models (Therneau and Atkinson 2023) to predict years with high, moderate, and near zero ciscoe survival to age-1 and singularly to assess their relationship to annual ciscoe age-1 densities.

Ice cover data were daily fractional values of the percentage of the total lake surface area covered by ice for the years 1977–2024 that were scraped from https://www.glerl.noaa.gov/data/ice/glicd/daily/sup.txt. Surface water temperature data were daily lakewide values scraped from https://podaac.jpl.nasa.gov/ for the years 1982–1994 and from https://coastwatch.glerl.noaa.gov/statistics/average–surface–water–temperature–glsea/ for the years 1995–2024. Air temperature, cloud cover, and wind speed and direction were daily mean estimates made at 99 locations across the lake with a spatial resolution of approximately 32 km^2 (1.9 x 1.9 degrees) scraped from the National Oceanic and Atmospheric Administration's North American Regional Reanalysis project for the years 1979–2024, https://psl.noaa.gov/data/gridded/data.narr.html. Air temperatures were 2–m high estimates. Wind data were 10–m high u– and v–wind vector estimates. Cloud cover was an entire atmosphere estimate as a single layer. Chlorophyll estimates were used as a proxy for primary production phenology and were daily mass concentrations (mg per m^3) from 2003–2024 that were scraped from https://coastwatch.pfeg.noaa.gov/erddap/griddap/erdMH1chla1day_R2022SQ.html. Chlorophyll data had a spatial resolution of approximately 16 km^2. The number of daily chlorophyll observations across the lake varied widely from 1 to 5,446. The mean and median number of daily observations were 1,603 and 1,047, respectively. Values were summarized to daily lakewide values.

Climate indices were included in the analysis because interannual variation in ice cover and water temperatures in the Laurentian Great Lakes have been correlated with several climate indices (Bai et al. 2015; Wang et al. 2018; Lin et al. 2022; Cannon et al. 2024), but rarely with Laurentian Great Lakes' fish recruitment indices, cf. Bunnell et al. (2017). Synopses and data for major climate indices are available at: https://climatedataguide.ucar.edu/climate–data/overview–climate–indices. The indices selected were the Atlantic Multidecadal Oscillation, the El Niño/Southern Oscillation, the Eastern Pacific Oscillation, and the North Atlantic Oscillation. The Atlantic Multidecadal Oscillation is based on average anomalies of sea surface temperatures in the North Atlantic basin. Interannual variation in Laurentian Great Lakes ice cover and surface temperatures were correlated with the Atlantic Multidecadal Oscillation between 1979 and 2021 (Cannon et al. 2024). In general, years with warmer than average North Atlantic temperatures were associated with less than average ice cover and warmer water temperatures in the Laurentian Great Lakes. The Atlantic Multidecadal Oscillation index has not been associated, nor evaluated, with interannual variability in Laurentian Great Lakes fish year–class strength. The El Niño/Southern Oscillation Index is based on tropical Pacific Ocean sea level pressure, sea surface wind, sea surface temperature, and outgoing longwave radiation. The relationship between the El Niño/Southern Oscillation and Great Lakes thermal conditions depends on the strength of El Niño events. Strong El Niño events have been associated with less ice and warmer temperatures, while weak El Niño phases are associated with colder conditions (Rodionov and Assel 2003). Interannual variability in the El Niño/Southern Oscillation was not associated with variation in Bloater recruitment in Lake Michigan (Bunnell et al. 2017). The Eastern Pacific Oscillation index tracks atmospheric pressure and sea surface temperatures in the northeastern and subtropical Pacific Ocean. Negative Eastern Pacific Oscillation values indicate high pressure over the northeastern Pacific Ocean and Alaska and low pressure in the subtropical Pacific Ocean, which increases the flow of cold Arctic air into the continental United States. Positive Eastern Pacific Oscillation values produce the opposite effect. Annual maximum ice cover in the Laurentian Great Lakes has been associated with the Eastern Pacific Oscillation since the winter of 1997–98 (Lin et al. 2022). The North Atlantic Oscillation index tracks seasonal air pressure movements in the North Atlantic Ocean between Iceland and the Azores, Portugal. Negative North Atlantic Oscillation values have been associated with colder winter air temperatures and longer ice duration in the Laurentian Great Lakes (Bai et al. 2012) and to higher survival of Bloater to age-1 in Lake Michigan (Bunnell et al. 2017).

Monthly climate index values are from https://climatedataguide.ucar.edu/climate–data/overview–climate–indices and the mean for winter months (December, January, February) was calculated and used in analyses as previous work has identified these months as influencing Laurentian Great Lakes winter weather (Bai et al. 2012; Bunnell et al. 2017) except for the North Atlantic Oscillation index for which a winter based index was directly available (Hurrell et al. 2024). For example, the 2022 climate index value was based on the average of December 2021 and January and February 2022 values.

Data analysis and visualization

All data manipulations, statistical analyses, and visualizations were performed in R version 4.4.0 (R Development Core Team 2023). Data visualizations were produced using ggplot2 3.5.1

(Wickham 2016) unless otherwise noted. All statistical tests used an α value of 0.05 to determine statistical significance. Interannual variability in Bloater and Cisco age-1 densities were analyzed similarly. Interannual variability in Kiyi age-1 density was more generally assessed in comparison to the results described for Bloater and Cisco using correlation analyses as there were only 12–years of age-1 Kiyi data. Ice cover was summarized as the monthly maximum. Surface water temperature was summarized as the monthly mean, end–of–month cumulative degree days (sum of daily temperatures >0°) as a measure of warming rate, and the date of fall and spring stratification [surface temperature <3.98°C in fall or surface temperature >3.98°C in spring)] as a phenological indicator of the onset of isothermic and stratified thermal conditions. Fall turnover date was calculated during the fall spawning period for that year–class, which is the year before they hatch.

Summarizing wind vector data across a topographically diverse shoreline and a large spatial area like Lake Superior over a time frame that might influence survival of embryonic, larval, and young–of–year fish is challenging. For example, wind blowing from north to south would be an offshore wind on the north shore and an onshore wind on the south shore. Likewise, is the effect of a wind of 10 m per sec for one day similar to two days of 5 m per sec wind? To overcome some of these issues and to evaluate general patterns, wind speed was categorized as calmer or windier compared to the long–term average for each month and season. Wind direction was categorized as onshore or offshore. Wind data were distilled as follows, daily average 10–m high u– and v–wind vector estimates from 47 estimate locations located within 10 km of shore were converted to wind speed and direction (Grange 2014). For wind speed, monthly and seasonal wind speeds for each year were calculated and then compared to the period–of–record average for each location to determine whether that month and season was calmer or windier than the period–of–record average. An annual lakewide designation of calmer or windier was then assigned by tallying individual stations over monthly and seasonal timeframes. Daily average wind direction was summarized as onshore or offshore for each location based on that estimate's location around the lake and the predominant wind direction at that location for each day. Annual monthly and seasonal predominant directions were then summarized by tallying the two categories (onshore or offshore) across the estimate locations by month and season for each year. A lakewide monthly average wind speed from the 47 locations within 10 km of the shore was used in correlation analyses with annual age-1 ciscoe estimates. Chlorophyll concentration was summarized as monthly means and the day–of–the–year of maximum chlorophyll concentration, as a measure of primary productivity phenology.

CART analyses were conducted to determine which hydrometeorological variables and climate indices best predicted years with high (top 15% of all years), moderate (top 25% of all years), and near–zero Bloater and Cisco survival to age-1 using the rpart R package version 4.1.23 (Therneau and Atkinson 2023). For Bloater, year–class strength class cutoffs were >27 (high) and >9 (moderate) age-1 Bloater per ha, which occurred in 6 and 11 years, respectively (Figure 3). For Cisco, the cutoffs were 175 (high) and 18 (moderate) age-1 Cisco per ha, which occurred in 6 and 11 years, respectively (Figure 3). The near zero recruitment group cutoff was <1 age-1 fish per ha for Bloater and Cisco, which occurred in 22 and 17 years, respectively (Figure 3). Years with abundances >1 and <9 fish per ha for Bloater and <18 for Cisco were labeled as marginal in a few data plots. Data were modeled for the years 1982–2024 as 1982 was the first year that lakewide remotely sensed surface water temperature data were available. Chlorophyll data were not included in CART analyses as the data were not available prior to 2003, but these data were assessed in correlation analyses. Rpart model parameters were adjusted following guidance in Therneau and Atkinson (2023) to limit under– and over–fitting of models. Splits that did not increase the overall R^2 of the classification model by 1% were pruned (cp = 0.01). Cross–validation was set to 100 to identify additional nodes that should be pruned. The minimum number of observations in a terminal node was set to four which was roughly 10% of the total years of data.

Spearman's rank correlation analyses were used to assess the relationship among Bloater, Cisco, and Kiyi age-1 density estimates and between species specific age-1 density estimates and hydrometeorological variables, climate indices, and Rainbow Smelt biomass using the corrplot R package version 0.95 (Wei and Simko 2017).

Results

Age-1 ciscoe and Rainbow Smelt population indices

Annual Lake Superior age-1 ciscoe abundance estimates varied up to a 100,000–fold difference among years. Bloater ranged from 0–140 age-1 fish per ha and Cisco ranged from 0.01–1,019 age-1 fish per ha from 1978–2024. Kiyi ranged from 0–54 age-1 fish per ha from 2011–2023 (Figure 3). For all three ciscoe species, age-1 densities were near or less than one fish per ha for more than half of the period–of–record. The highest estimated age-1 density for all three ciscoes was the 2022 year–class. There was no significant temporal trend in age-1 densities for Bloater ($p = 0.569$), Cisco ($p = 0.829$), or Kiyi ($p = 0.182$), nor was there a step–change in ciscoe recruitment for the years evaluated as has occurred with Lake Superior ice and water regimes (Figure 1). Annual age-1 densities were highly correlated among the three species (Bloater–Cisco, $r = 0.91$, df = 45, $p < 0.001$, Bloater–Kiyi, $r = 0.94$, df = 11, $p < 0.001$, Cisco–Kiyi, r=0.92, df = 11, $p < 0.001$). A year with high age-1 survival for Cisco was also a year of high survival for Bloater and Kiyi and vice–versa indicating drivers of year–class strength among these Lake Superior ciscoe species were similar. Annual Rainbow Smelt biomass estimates ranged from 0.2–3.7 kg per ha and declined ($p = 0.002$) over the survey period (Figure 4a). The relationship between Rainbow Smelt biomass and age-1 ciscoe densities was positive ($p = 0.01$), implying no negative impact of Rainbow Smelt population biomass on survival of ciscoes to age-1 on a lakewide basis (Figure 4b–d).

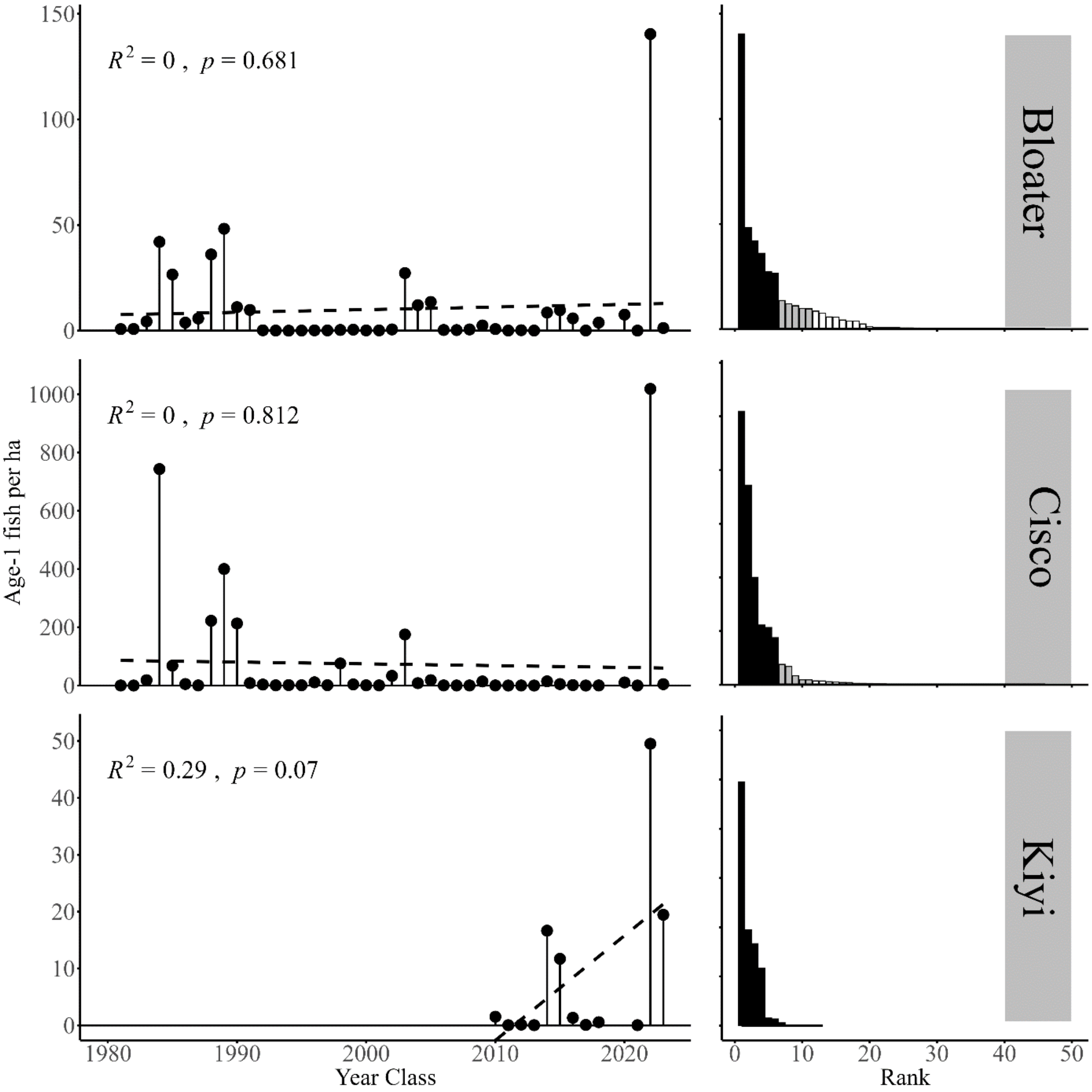
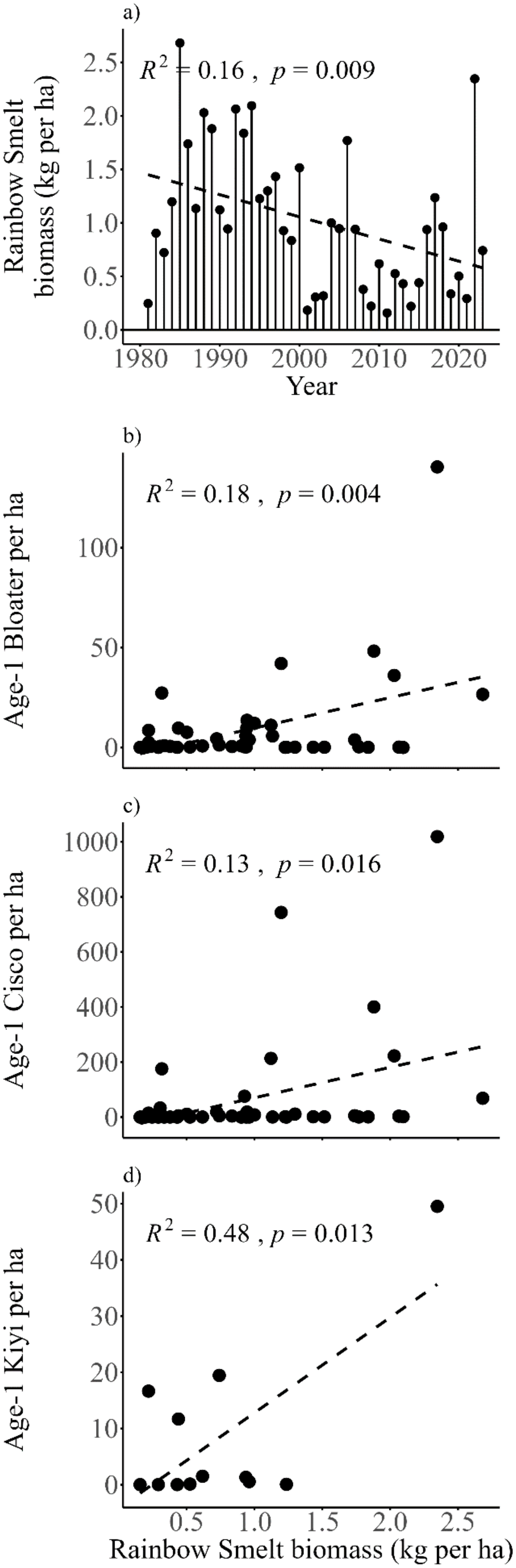


Figure 3. Annual estimated age-1 abundance of Lake Superior Bloater, Cisco, and Kiyi. Plots on the left show the high annual variability in year–class strength. Plots on the right show the skewed distributions for all species. For Bloater and Cisco, histogram bars are shaded to show the upper 15% (black) and 25% (black and gray) of years used in the CART models. Data were available for 47 years for Bloater and Cisco (1978–2024, sans 2020) and 12 years for Kiyi (2011–2024, sans 2020 and 2021 due to COVID). Note different y–axis scales.

Figure 4. a) Lake Superior annual estimated Rainbow Smelt biomass and the relationship between annual Rainbow Smelt biomass (kg per ha) estimates and age-1 Bloater (b), Cisco (c), and Kiyi (d) density estimates (fish per ha). Data were available for 47 years for Rainbow Smelt, Bloater, and Cisco (1978–2024, sans 2020) and 12 years for Kiyi (2011–2024), sans 2020 and 2021 due to COVID. Note different y–axis scales.



Year–class strength associations with environmental variables

The most consistent pattern between environmental attributes and ciscoe survival to age-1 was the relationship with June water temperature which was promoted by early winter ice cover and fall wind speed. CART analyses indicated that for years with high (upper 15%) Bloater (>26 per ha) and Cisco (>175 per ha) age-1 densities the primary predictor was a mean June surface water temperature ≤4.8°C and the secondary predictor was lower than average wind speeds during fall. This temperature threshold was met in all six years and the wind threshold was met in five of the six years with high survival to age-1 for Bloater and Cisco. The primary predictor of moderate Bloater survival to age-1 (upper 25%, ≥9 per ha) was >20% ice cover in January which occurred in ten of eleven years and the secondary predictor was mean February water temperatures between 0.5 and 1.3°C which occurred in eight of eleven years. The primary predictor of moderate Cisco survival (18 per ha) was calm December wind which occurred in ten of eleven years and the secondary predictor was a mean June surface water temperature ≤4.9 □□C, which occurred in seven of ten years. The primary predictor of near–zero survival to age-1 for Bloater and Cisco was January maximum ice cover <19% which occurred in 16 of 22 years for Bloater and in 14 of 17 years for Cisco. The secondary predictor of near zero survival to age-1 for Bloater was calm spring wind which occurred in five of six years and for Cisco it was a mean December surface water temperature <4.4°C which occurred in 12 of 14 years.

Prior to 1998, mean June surface water temperature was <5°C in 14 of the previous 16 years and Bloater and Cisco survival to age-1 was in the top 25% in six of those fourteen years. Beginning in 1998, mean June surface water temperature was >5°C in 24 of the next 26 years and survival to age-1 was near zero for Bloater and Cisco in 15 and 14 of those 24 years, respectively, with age-1 density estimates never in the top 25% up until 2022. The only two–

years when mean June surface water temperatures were <5°C after 1998 were in 2003 and 2022 and Bloater and Cisco survival to age-1 was high in both years (upper 15%, Figures 3 and 5). Prior to 1998, age-1 Bloater and Cisco densities were near zero in six of 14 years for Bloater and two of 14 years for Cisco when mean June surface water temperature was <5 □□C. Thus, a mean June surface water temperature <5°C did not guarantee high survival of Bloater or Cisco before the thermal regime change in 1998, but it did in the two years this happened after 1998.

Spearman rank correlations between ice cover and age-1 ciscoe densities were positive and significant for Bloater in January and February, Cisco in January and March, and for Kiyi in April (Figure 6). Mean monthly surface temperature and age-1 ciscoe densities were negative and significantly correlated for four of 12 months for Bloater (June–July, October–November), eight months for Cisco (January, May–November), and seven months for Kiyi (January, March–August, Figure 6). Significant correlations with monthly degree day sums, a proxy for warming rates, were all negative for the same months as was observed for mean monthly surface water temperature as well as February for Kiyi (Figure 6). Age-1 densities for all three ciscoes were positively related to spring turnover date; the later the turnover date – the higher the age-1 ciscoe densities were (Figure 6). These results indicate that warm spring temperatures and rapid spring warming were detrimental to age–0 ciscoe survival, the opposite of many previous findings (Svärdson 1951; Christie 1963; Eckmann et al. 1988; Rey and Eckmann 1989; Eckmann and Pusch 1991; Helminen and Sarvala 1994; Helminen et al. 1997; Kinnunen 1997; Hoff 2004; Anneville et al. 2009; Eckmann 2013; Rook et al. 2013; Kangur et al. 2020). Age-1 ciscoe densities were not correlated with fall turnover date for any of the three ciscoe species.

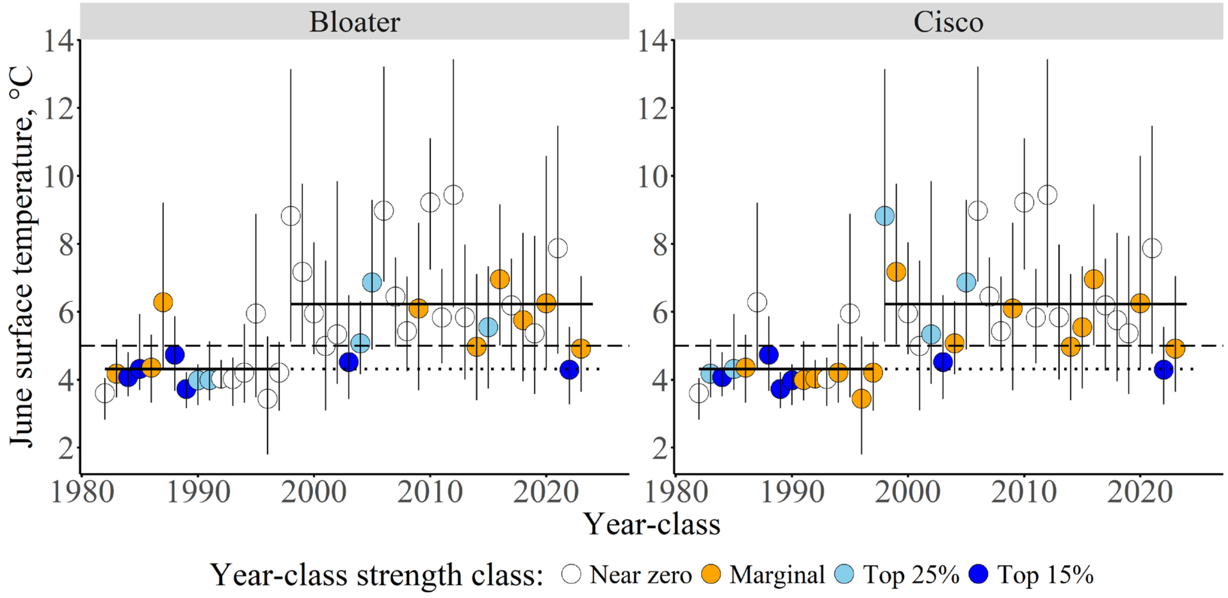


Figure 5. Lake Superior annual lakewide average June surface water temperature and Bloater and Cisco year–class strength classification group. Mean June surface water temperatures were near or <5°C for 9 of the 11 years with Bloater and Cisco year–class strength in the top 25% of all years. Year–class strength group cutoffs were <1 age-1 fish per ha for near zero years, ≥9 age-1 Bloater per ha and >18 age-1 Cisco per ha for years in the top 25%, ≥26 age-1 Bloater per ha and >175 age-1 Cisco per ha for years in the top 15%, and marginal for other years. Points are mean June surface water temperatures and vertical lines are the range. Solid horizontal lines are temperature averages before 1997 (4.3°C), the pre–1998 step–change period, and between 1998 and 2024 (6.3°C), the post–1998 step–change period. Dotted lines are temperature averages for the pre–1998 period. The dashed line at 5°C is the temperature threshold in June that explains some of the variance in Bloater and Cisco survival to age-1.

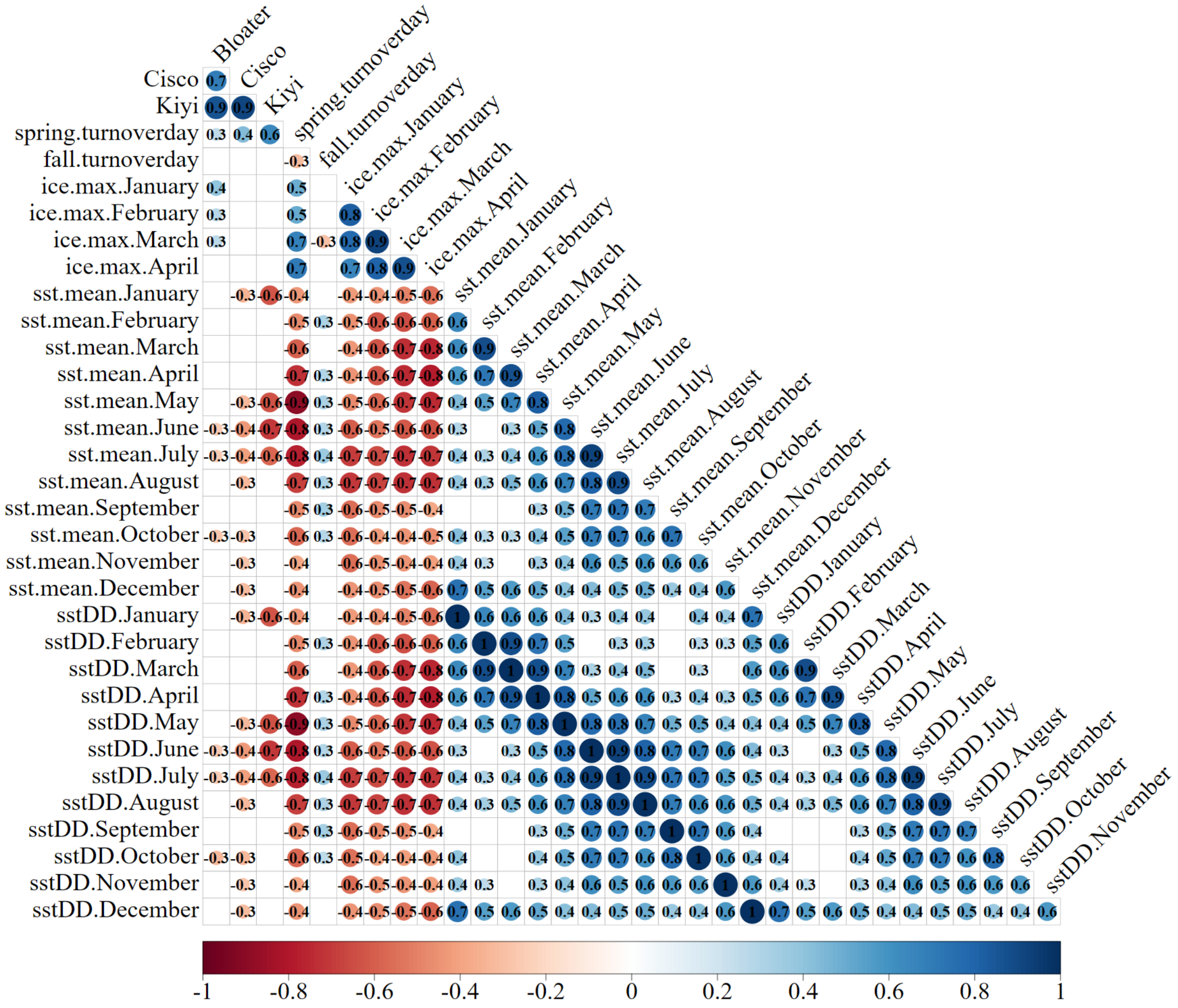


Figure 6. Spearman correlation matrix for annual Lake Superior Bloater, Cisco, and Kiyi age-1 densities and annual spring and fall turnover dates (surface temperature > or <3.98°C), maximum monthly fractional ice cover, monthly mean surface water temperature (sst), and end–of–month cumulative degree days (sstDD, sum of daily temperatures >0°) as a measure of warming rate. Matrix shading and point size express the strength of positive (blue) and negative (red) spearman correlation r values that were statistically significant at p < 0.05. Blank squares were not statistically significant. Correlations and the matrix were created using the R–stats corrplot package (Wei and Simko 2017).

The relationships between ciscoe age-1 densities and other environmental attributes were mostly non–significant. Significant correlations with wind speed were positive in May for Bloater (r = 0.3), negative in February and October for Cisco (r = -0.3), negative in February for Kiyi (r = -0.8). Significant correlations between ciscoe age-1 densities and mean monthly cloud cover were weak and limited to Bloater in July (r = –0.2) and November (r = –0.3), Cisco in February (r = –0.3), and Kiyi in July (r = 0.5), and August (r = 0.7). Significant correlations with mean monthly chlorophyll concentration were few, all negative, and limited to Bloater in February (r = –0.4), Cisco in February and March (both months, r = –0.4), and Kiyi in December (r = –0.7). There was no relationship between the day–of–the–year of maximum chlorophyll concentration and ciscoe age-1 densities. Significant correlations with climate indices were inconsistent except for with the North Atlantic Oscillation index. There was one significant association with the El Niño/Southern Oscillation (Bloater, r = 0.2) and Eastern Pacific Oscillation indexes (Kiyi, r = – 0.4), and three associations with the North Atlantic Oscillation index: Bloater (r = 0.3), Cisco (r = 0.3), and Kiyi (r = 0.5).

Larval ciscoe survival

Lake Superior larval ciscoe abundance estimates were highest in May, followed by lower population estimates in June and July, in all years except in 2014 when June abundances were higher than May, possibly due to ice not vacating the lake until June. June abundances were on average 73% (range 24–94%) less than that observed in May, and July estimates were on average 68% (range 23–96%) less than that observed in June (Figure 7). In 2022, the year with the highest ciscoe survival to age-1, these month–to–month declines were 24 and 25%, and mean

July 2022 lakewide larval ciscoe abundances (441 fish per ha) were 51–95% higher than any other year’s July abundance estimate (7–218 fish per ha). This indicates the critical period for Lake Superior ciscoe recruitment is June–July. Similar to the age-1 ciscoe analysis, larval survival in July, the latest sampling month, was highest in 2022, which had the lowest mean June and second lowest mean July surface water temperature, 4.3 and 7.8°, respectively (Figure 5).

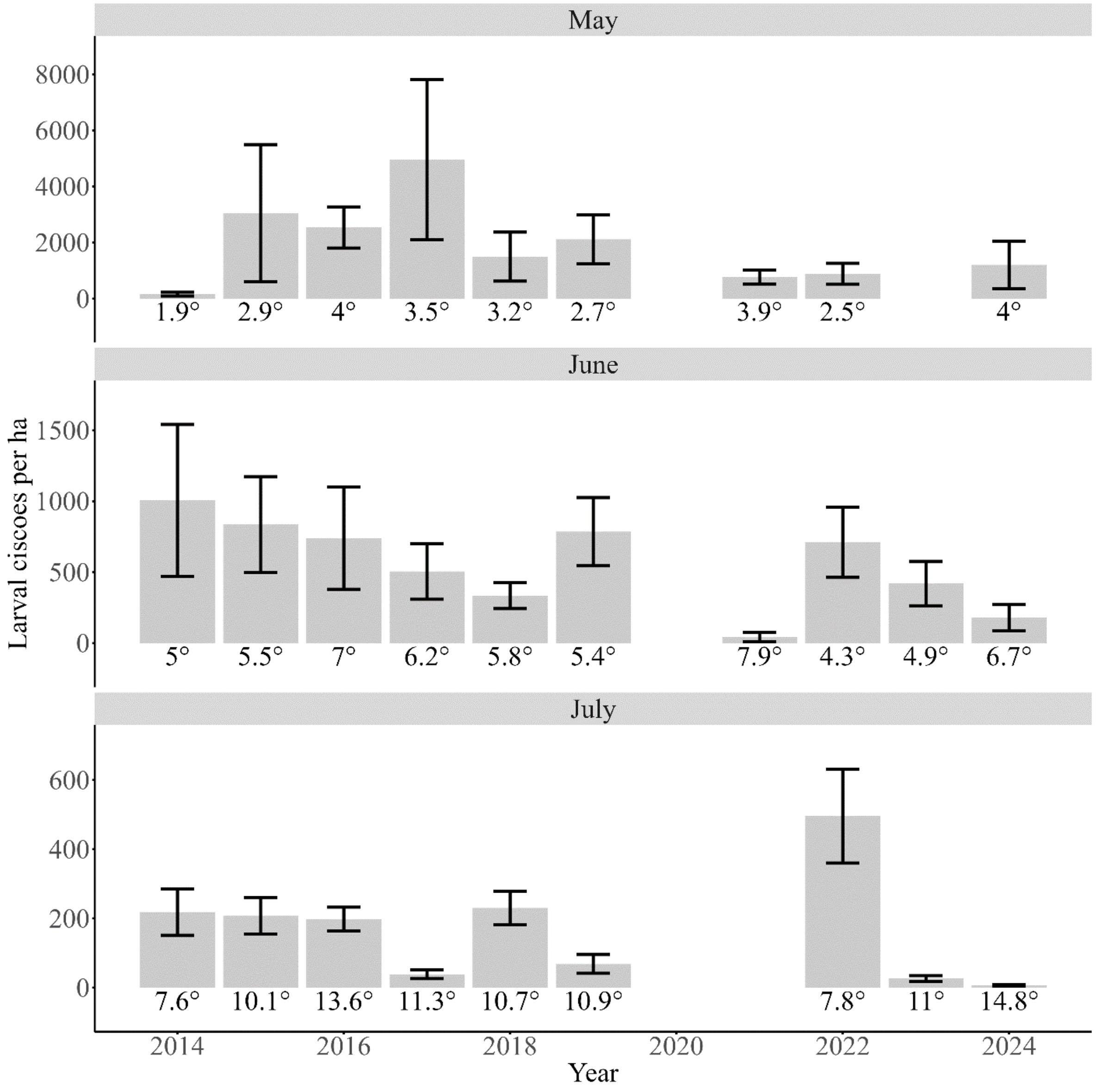


Figure 7. Lake Superior lakewide average larval ciscoe abundances (fish per ha ± standard error) for May, June, and July from 2014–2024. Numbers beneath bars are the lakewide mean monthly surface water temperature, °C. Sampling locations were from nearshore habitats (~<100 m) in May–June and from offshore habitats (~>100 m) in July. No sampling occurred in 2020 and in 2021 sampling only occurred in USA waters and no sampling was done in July 2021 due to COVID travel restrictions and in May 2023 no sampling occurred due to a ship no-sail condition. Sampling locations are shown in Figure 2. Note different y–axis scales.

June water temperature

Data for this project were also used to address the question of what environmental factors best predict June water temperatures <5°, the primary predictor of high ciscoe survival to age-1. Mean June water temperatures were <5° in 16 of the 42 years evaluated (1982–2024). CART analysis showed that in 15 of those 16 years, maximum January ice cover was ≥19%, and in 11 of those 15 years January cloud cover was less than the long–term average of 77% cloud cover. Spearman correlation coefficients between mean monthly surface water temperature for all 12 months were negatively and significantly related to maximum ice cover in January, February, March, and April (Figure 6). Relationships between climate indices and June surface water temperature were non-significant.

Discussion

Lake Superior ciscoe year–class strength was highest when June water temperature was <5°C, total lakewide January ice cover was >19%, and winds were calmer than average during November to January. Potential mechanisms underlying these factors might be calm fall–early winter wind lessens embryo disturbance and drift to unfavorable habitats and promotes early ice formation (Miller 1952). Greater January ice cover leads to more ice cover throughout the winter (Figure 6) which leads to later ice breakup which reduces spring water temperature (Figure 6). Cold spring water temperature reduces ciscoe larval metabolic demand (Myers et al. 2014) during a time of low zooplankton prey abundance (Watson and Wilson 1978; Gorman et al. 2009; Myers et al. 2014; Pawlowski et al. 2018; Dobosenski et al. 2024).

There was a threshold relationship where maximum survival to age-1 occurred when mean June surface water temperature was <4.8°, and survival was often near zero when mean June water temperature was >4.8°. This was true for Bloater, Cisco, and Kiyi. The significance of June water temperature in regulating ciscoe survival to age-1 was supported by a decade of larval ciscoe sampling which indicated that the critical period for survival was in June–July, a few weeks post–hatching when larval ciscoe began exogenous feeding (Oyadomari and Auer 2004; Oyadomari and Auer 2008; Myers et al. 2015; Lucke et al. 2020). While multiple mechanisms affect year–class survival at different points during their life, the consistency and strength of the relationships reported here provide an improved understanding of the Lake Superior ciscoe recruitment bottleneck and the relationships among winter ice formation, water temperature, and ciscoe year–class strength.

Pronounced variability in year–class strength is typical in fishes (Hjort 1914; Myers 1998; Guildford et al. 2008; Houde 2008). As the relative volume of information on Laurentian Great Lakes ciscoe year–class strength variability is paltry compared to North American Lake Whitefish and European whitefish species, comparisons herein are made with all freshwater whitefish species as appropriate. For freshwater whitefish, year–class strength variability has been observed to be cyclic due to intra–specific population regulation (Helminen and Sarvala 1994; Marjomäki et al. 2021), irregular in response to annual variations in environmental attributes, spawning stock biomass, and prey and predator populations (Fechhelm and Fissel 1988; Hoff 2004; Rook et al. 2013; Zimmerman et al. 2013; Myers et al. 2015), and trending with contemporary lake warming (Nyberg et al. 2001; Jeppesen et al. 2012; Kangur et al. 2020) and nutrient loadings (Rook et al. 2021). This analysis found Lake Superior ciscoe year–class strength to be irregular between 1978 and 2024, with generally weaker year–classes predominating since 1998. Prior to 1998, Bloater and Cisco survival to age-1 was near zero in seven of 21 years. Since 1998, Bloater and Cisco survival to age-1 was near zero in 13 of 26 years. This change in year–class survival frequency coincides with observed changes in Lake Superior hydrometeorological attributes (Austin and Colman 2008; Bai et al. 2012; Wang et al. 2012; Van Cleave et al. 2014; White et al. 2018).

Ice, Temperature, and Year–class Strength

Ice duration and water temperature have a history of being associated with annual variability in freshwater whitefish year–class strength. For ice, previous associations were similar to this study; colder years with higher ice concentrations or longer ice duration were associated with stronger year–classes (Van Oosten and Hile 1949; Taylor et al. 1987; Freeberg et al. 1990; Brown et al. 1993; Nyberg et al. 2001). Ice cover is thought to promote embryonic and early larval survival by protecting embryos from the physical damage of wind and wave action (Taylor et al. 1987; Brown et al. 1993) and reducing light (John and Hasler 1956; Stewart et al. 2021b). This study could not evaluate those potential mechanisms, but it does provide evidence that in Lake Superior early ice–cover leads to greater overall ice cover and lower temperatures throughout the year which appeared to promote larval ciscoe survival here and in recent laboratory experiments (Stewart et al. 2021b; Stewart et al. 2022b).

The relationship between annual water temperature regimes and whitefish year–class strength is well–studied but remains uncertain despite the positive influence ice appears to have on year–class strength survival (Taylor et al. 1987; Brown et al. 1993; Nyberg et al. 2001). Strong whitefish year–classes have more commonly been associated with warm spring–summer temperatures (Svärdson 1951; Christie 1963; Eckmann et al. 1988; Rey and Eckmann 1989;

Eckmann and Pusch 1991; Helminen and Sarvala 1994; Helminen et al. 1997; Kinnunen 1997; Hoff 2004; Anneville et al. 2009; Eckmann 2013; Rook et al. 2013; Kangur et al. 2020) than with cold spring–summer temperatures (Lawler 1965; Taylor et al. 1987; Brown et al. 1993; Bourinet et al. 2023). The postulated mechanism behind warmer spring water temperatures and stronger year–classes is that warmer temperatures increase larval growth which enhances survival (Eckmann et al. 1988; Myers et al. 2014). More rapid growth can increase swimming efficiency, foraging effectiveness, and predator avoidance (Blaxter 1986). Warmer temperatures also increase metabolic activity, so prey abundance and consumption must outweigh the increased metabolic costs for growth, and ultimately survival, to occur (Myers et al. 2014).

Explanations for colder years producing stronger whitefish year–classes have been framed in terms of adaptation to historical conditions (Stewart et al. 2022b) and bioenergetics (Myers et al. 2014). Strong Lake Superior ciscoe year–classes seem to support both theories. Prior to 2022, 2003 was the only year after the 1998 hydrometeorological regime change with a mean June water temperature similar to the pre–1998 (historical) mean (Figure 5) and this was the last year with high ciscoe survival to age-1 (Figure 5). Adult ciscoe populations had been in decline due to lack of recruitment since 2003 (Goldsworthy et al. 2024; Vinson and Yule 2024), so this recruitment event was likely not a stock–recruitment response. Several recent reviews have found stock–recruitment relationships explained much less variation in fish recruitment than environmental factors when survival to age-1 appears less dependent on total egg production, as estimated by spawner stock biomass, and more dependent on survival of larvae with respect to environmental factors such as prey availability, temperature, and predation pressure (Olsen et al. 2011; Szuwalski et al. 2015; Sellinger et al. 2024). This seems to be the case for whitefish worldwide (Eckmann and Pusch 1991; Helminen and Sarvala 1994) including

Lake Superior (Bronte et al. 2003; Hoff 2004; Goldsworthy et al. 2024). Similarly, strong Lake Erie Lake Whitefish year–classes from 1925–1949, were only observed when fall, winter, and spring water temperatures were at or below the long–term average, with the single exception of 1934 (Lawler 1965). However, similar thermal conditions in neighboring Lakes Huron and Ontario during the same years did not produce strong Lake Whitefish year–classes, for unexplained and likely subtle reasons (Lawler 1965). Stronger Lake Whitefish year–classes in Lake Ontario appeared to require both cold Novembers and warm Aprils (Christie 1963).

Equally convincing evidence of the importance of near–historical temperature regimes come from bioenergetics modeling (Myers et al. 2014). This work indicated that growth for 10–15 mm Lake Superior Cisco larvae in May–June was only positive at water temperatures <6°C, with the optimal temperature mediated by prey abundance, the lower the prey availability the lower the optimal temperature. Based on this modeling and typical low spring nearshore Lake Superior zooplankton densities (Watson and Wilson 1978; Gorman et al. 2009; Myers et al. 2014; Pawlowski et al. 2018; Dobosenski et al. 2024), recently hatched Cisco larvae likely find consuming enough prey to grow at water temperatures >6°C challenging. As spring progresses into summer and water temperature warms, zooplankton populations increase (Watson and Wilson 1978; Zhou et al. 2001; Pawlowski et al. 2018), which lessens the spring temperature–prey bottleneck (Myers et al. 2014). At this point in the phenological cycle, the popular theory of warmer water increasing larval whitefish survival may hold true in Lake Superior (Kinnunen 1997; Hoff 2004; Rook et al. 2013) and elsewhere. In 1984 and 2022, the two strongest Lake Superior ciscoe year–classes (Figure 3), mean surface water temperatures increased rapidly from two of the lowest temperatures in June, 4.1 and 4.3°C, in 1984 and 2022 respectively, to 13.9 and

14.2°C in August 1984 and 2022 respectively, slightly above the pre–1998 average August temperature of 13.5°C (Figure 8).

Cold spring temperature, while a strong predictor of year–class strength, was not a guarantee of a strong year–class. In six and two of 14 years prior to 1998, Bloater and Cisco respectively, had near zero survival to age-1 when mean June surface water temperature was <4.8°C. In these years, the critical factor was likely something other than temperature, possibly intraspecific competition, prey availability, or predation. The greater failure of Bloater to achieve stronger year–classes during these years, despite presumably ideal June water temperature as compared to Cisco, may be related to their later hatch date (Lachance et al. 2021) or some other unmet and unmeasured niche requirement. The most recent Lake Superior ciscoe year–class that underperformed when environmental conditions appeared optimal was the polar vortex year of 2014, when ice formation was early and ice breakup was late (Clites et al. 2014). In 2014, maximum January ice cover was 78% and the lake was not ice free until June 6. Comparable January ice cover in 1984 and 2022 was 41 and 25%, respectively. Mean nearshore fall–winter wind speeds were similar; 4.7, 5.3, and 5.3 m per sec in 1984, 2014, and 2022, respectively. Mean June surface water temperature was 4.1, 5.0, and 4.3°C in 1984, 2014, and 2022, respectively. The mean June surface water temperature in 2014 was above the CART model threshold for Cisco and Bloater year–classes in the upper 15%, but only by 0.2°C, which seems insignificant at a lakewide monthly scale. The prominent difference in thermal conditions in 2014 was colder temperatures in January, February, and May as compared to 1984 and 2022 (Figure 9). June lakewide average larval ciscoe densities were slightly higher in 2014 than other years, likely due to later hatching, but there was little survival of these fish through July (Figure 7).

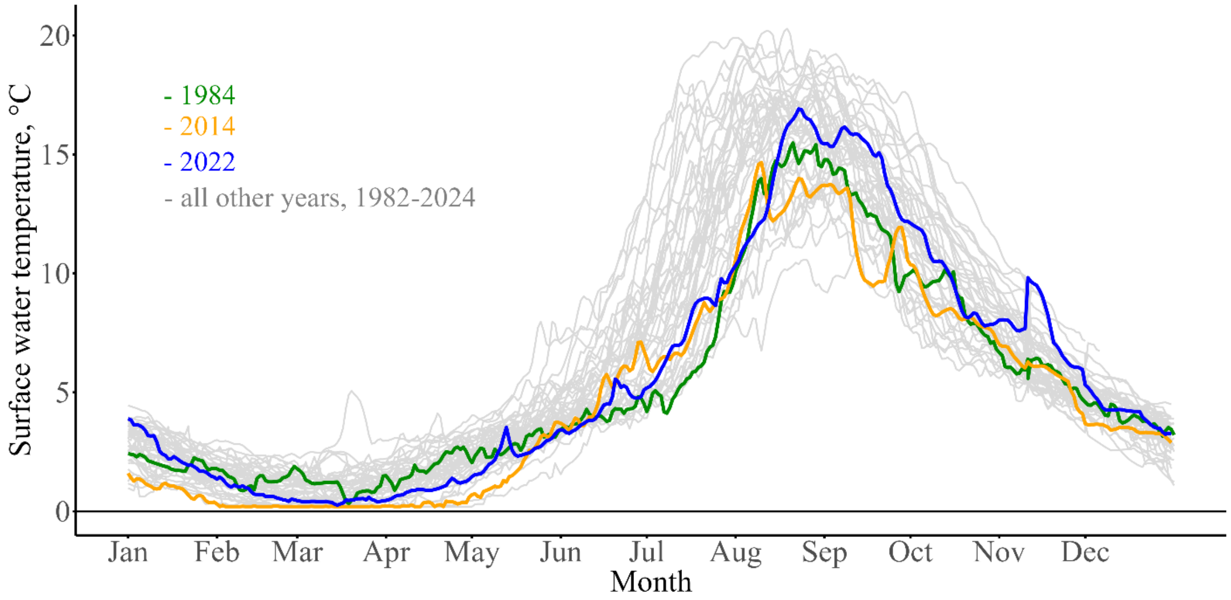


Figure 8. Lake Superior remotely sensed annual daily lakewide average surface water temperature from 1982–2024. Each line is an individual year. The two years with the highest ciscoe year–class strengths, 2022 and 1984, and the exceptionally cold winter, 2014, are highlighted. Cisco year–class strength in 2014 was ranked 13th for Bloater and 12th for Cisco out of 47 years and 3rd out of 12 years for Kiyi. All three years had similar low June and rapidly warming summer temperatures.

In the review of the literature, major differences in the reported associations between spring water temperature and year–class strength among whitefish species or between European and North American populations were not detected. Differences within and among studies were often complex. For instance, survival of Vendace larvae in Lake Mälaren, Sweden was substantially higher when ice breakup occurred after April 5, indicating that a cold spring was beneficial and when water temperatures were slightly warmer than average the week of hatching, indicating a post-hatch warming trend was also beneficial. Additionally, survival was appreciably lower if water temperatures rose too rapidly which increased predation on the larvae by warmwater Perch, *Perca fluviatilis* (Nyberg et al. 2001). This indicates that strong Vendace year–classes in Lake Mälaren, required multiple conditions to be just right. In two adjacent lakes, substantial ice was beneficial, but a faster warmup in spring did not reduce Vendace larvae survival due to fewer predators (Nyberg et al. 2001). Lake productivity was suggested as a factor influencing differences in the associations between spring temperature and stronger whitefish year–classes in European alpine lakes, where more eutrophic waters responded more favorably to warmer temperature than did oligotrophic lakes (Eckmann 2013). This theory fits with Myers et al. (2014) bioenergetics modeling.

Wind and Year–class Strength

Wind can influence whitefish year–class strength during the fall during spawning season, through the winter during embryonic development, and in spring post–hatching. In this study, calmer fall winds were a predictor of strong Bloater and Cisco year–class strength. Reduced wind during fall spawning may decrease egg drift to unfavorable deposition habitats and promotes ice formation that could protect embryos from physical damage (Miller 1952; Taylor et al. 1987; Freeberg et al. 1990). None of the studies reviewed found the opposite effect. Winter wind speed was not associated with ciscoe year–class strength, nor were any studies found that evaluated the influence of winter wind speed on whitefish year–class strength. The effect of post–hatch spring wind speed on Lake Superior Cisco year–class strength has been evaluated in four previous studies: two studies observed positive associations (Hoff 2004; Rook et al. 2013) and two observed negative associations (Myers et al. 2015; McKinney et al. 2018). This study found no strong correlations and little predictive power of spring wind speed on ciscoe year–

class strengths. Across species and systems, the effect of wind speed on larval fish survival has varied and has often not held up under re-analyses (Myers 1998), despite the many hypotheses that indicate calm winds increase larval survival by providing a more stable thermal environment and higher prey densities (Lasker 1981; Houde 2008).

An approach to evaluating wind direction in marine systems has been to compare the influence of onshore to offshore winds. Onshore winds may increase the likelihood of larval fish being carried into warmer, more eutrophic nearshore habitat, while offshore winds may promote dispersal of larvae away from nearshore spawning areas, potentially reducing interspecific competition. Both wind–driven transport directions have been associated with stronger year–classes. Onshore winds were linked to stronger year–classes of Atlantic Cod in the Gulf of Maine (Churchill et al. 2011) and Sardines, *Sardinops sagax* in Northern Benguela (Stenevik et al. 2003), whereas offshore winds were linked to strong year–classes of Anchovies in the Bay of Biscay (Allain et al. 2001) and Baltic Sprat *Sprattus sprattus* in the Baltic Sea (Baumann et al. 2006). Along–shore winds were associated with Arctic Cisco *C. autumnalis* year–class strength in the Beaufort Sea, Alaska (Fechhelm and Fissel 1988; Fechhelm and Griffiths 1990). In this study, offshore winds predominated on a lakewide basis at monthly and seasonal time steps for all 42–years evaluated, so this effect could not be evaluated.

Rainbow Smelt and Cisco Year–class Strength

The impact of Rainbow Smelt predation on larval Cisco in Lake Superior was evaluated in 1974 in the Apostle Islands and Black Bay (Selgeby et al. 1978; Selgeby et al. 1994) and in 2006 in Black and Thunder Bays (Myers et al. 2009) through population estimates and stomach content analyses. Black Bay is shallow, eutrophic, and supports a Rainbow Smelt population much higher than other nearshore areas in Lake Superior (U.S. Geological Survey 2022). The 1974 study concluded that Rainbow Smelt predation on Cisco larvae was not a major factor suppressing Cisco stocks. The 2006 study concluded that Rainbow Smelt predation on Cisco larvae may dampen the magnitude of Cisco year–classes. Similar to this study, Hoff (2004) observed a positive association between Rainbow Smelt population size and Cisco year–class strength. Hoff (2004) interpreted this finding as Rainbow Smelt provide a readily available prey for Lake Trout *Salvelinus namaycush*, thereby reducing Lake Trout predation on young–of–year Cisco. The lakewide predatory impact of Rainbow Smelt on larval ciscoe is likely low given their near exclusive occupation of shallow nearshore areas and bays (Rosinski et al. 2020) and the more widespread lakewide distribution of ciscoe larvae (Vinson et al. 2023). The positive associations observed here between Rainbow Smelt population size and ciscoe year–class strengths support this conclusion.

Critical Period For Larval Cisco Survival

For more than a century it has been widely accepted that the population size of a year–class is determined between the embryonic and fry stage (Hjort 1914; Hart 1931; Van Oosten and Hile 1949; Houde 2016). There is little information on embryonic survival of Lake Superior ciscoe, though it is known a substantial number of Cisco embryos are consumed by Lake Whitefish (Stockwell et al. 2014). Lake Superior larval ciscoe hatch between late–March and June with hatch dates varying by species and in response to winter–spring temperatures (Anderson and Smith 1971; Oyadomari and Auer 2008; Lucke et al. 2020; Lachance et al. 2021; Vinson et al. 2023). The larval ciscoe data presented here indicates the post–emergence critical period occurred between June and July in the years 2014–2024, based on the low survival rates observed during this time. This timeline of 4–6 weeks post hatching and after yolk absorption (Lucke et al. 2020; Lachance et al. 2021) aligns with the bioenergetics framework described by Myers et al. (2014). A similar critical period timeline was estimated for European Whitefish *C. lavaretus* in Lake Constance, Germany, Switzerland, and Austria (Eckmann and Pusch 1991) and Vendace in Finland (Viljanen 1988).

The synchrony between fish hatching and zooplankton prey availability, known as the 'match–mismatch' hypothesis, has long underlaid the critical–period concept and for an equally long time has been hard to demonstrate (Cushing 1990). The hypothesis may be most relevant to northern fishes that hatch in spring, when temperatures can vary widely depending on winter severity and duration, which in turn effects the timing of zooplankton production and fish hatching (Houde 2016; Régnier et al. 2019; Stewart et al. 2021a; Stewart et al. 2022b). This appears to be the case for Lake Superior ciscoe, as spring thermal conditions measured to date are well within the species' thermal tolerances (McCormick et al. 1971). Thus, temperature variability itself is not lethal, it is temperature's role in the complex interaction among ciscoe hatching, the transition from endogenous to exogenous feeding, and zooplankton prey availability that determines if conditions are just right for larval survival.

Future Lake Superior ciscoe year–classes

Present temperature trends indicate strong Lake Superior ciscoe year–classes could be rare in the future. The three environmental factors most strongly associated with Lake Superior ciscoe year–class strength are trending in unfavorable directions. Ice cover is decreasing (Van Cleave et al. 2014). Spring–summer water temperatures are warming (Austin and Colman 2008). Wind speed is increasing (Desai et al. 2009). However, the cold June and the subsequent high ciscoe year–

class strength in 2022 was not due to a record amount of ice but rather to moderately high ice cover and a cool spring. This indicates that the ~5°C June surface water temperature threshold can be achieved without record breaking ice cover. At the end of January 2022, ice cover was 25% and the maximum ice cover reached 80% on March 15, levels similar to the long–term pre–1998 average and far from record breaking. Another possibility is that episodes of extremely cold winter weather, like the polar vortex in 2014 (Clites et al. 2014), may become increasingly more frequent (Hanna et al. 2024) which might intermittently buffer the impact of the current warming trend.

The age composition of adult Lake Superior Cisco from commercial fisheries and agency assessments tracks the age-1 index data presented here (Yule et al. 2008; Stockwell et al. 2009; Lepak et al. 2017; Goldsworthy et al. 2024). Cisco harvest since 2010 has been supported by a one–in–twenty–year sized year-class (2003) which is dying off and a few moderate one–in–four-to-five-year sized year–classes (2009, 2014–2015) (Goldsworthy et al. 2024). Cisco year–class strength in these years was 175, 14, 14, and 5 age-1 Cisco per ha, respectively. Further evaluation of the relationship between Cisco year–class strength and Cisco harvest would provide valuable information on the size and frequency of different year-class strengths required to sustain the fishery.

Year–class strength can depend upon many factors, all of which are necessary, and all of which are variable. There were three earlier studies that evaluated annual variability in Lake Superior Cisco year-strength using the same fish collection dataset evaluated here; 11-years from 1982-1992 (Kinnunen 1997), 14-years from 1984 to 1998 (Hoff 2004), and 26-years from 1979 to 2006 (Rook et al. 2013), as well as this study of 46-years. All four studies came to different conclusions as to the factors regulating Lake Superior Cisco year-class strength. This analysis was a work–in–progress for more than a decade and it wasn't until the large 2022 ciscoe year–classes and the inclusion of a decade of larval ciscoe population data that the conclusions presented here became apparent. Johan Hjort wrote more than a century ago (Hjort 1914:203), *"only experience extending over a long period of time can enable us to ascertain with certainty the variation of the different determining factors, and to discover how far one and the same factor is in all cases of decisive importance, or whether, in the course of the development of the fish, there may be several, each varying so greatly as to possibly determine the character of the year's production"*. Re–analyses of year–class strength data sets with additional data have generally not held up (Myers 1998), so time will tell if the factors identified here as strongly influencing Lake Superior ciscoe year–class strength will hold up to re–analyses.

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Ethics statement - All sampling and handling of fish were carried out in accordance with guidelines for the care and use of fishes by the American Fisheries Society (http://fisheries.org/docs/wp/Guidelines-for-Use-of-Fishes.pdf). All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

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Data Availability - Internet data links were checked on March 13, 2025.

Fish data: https://doi.org/10.5066/F75M63X0 (U.S. Geological Survey 2022)

Ice cover data: https://www.glerl.noaa.gov/data/ice/glicd/daily/sup.txt

Water temperature data: https://coastwatch.glerl.noaa.gov/statistics/average-surface-water-temperature-glsea/ for the years 1995-2024 and from https://podaac.jpl.nasa.gov/ for the years 1982–1994.

Air temperature, cloud cover, and wind data: https://psl.noaa.gov/data/gridded/data.narr.html

Chlorophyll data:
https://coastwatch.pfeg.noaa.gov/erddap/griddap/erdMH1chla1day_R2022SQ.html

Climate indices: https://climatedataguide.ucar.edu/climate-data/indices

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