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ENVIRONMENTAL INFLUENCES ON THE GROWTH OF INLAND CISCO POPULATIONS IN THREE MINNESOTA SENTINEL LAKES

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ENVIRONMENTAL INFLUENCES ON THE GROWTH OF INLAND CISCO POPULATIONS IN THREE MINNESOTA SENTINEL LAKES

Edward Carlson

Cisco *Coregonus artedi* are a pelagic cold-water fish that are widely distributed throughout many inland lakes across the northern Midwest and play an important role as forage for large piscivores. Inland Cisco populations have been observed to vary in their overall size and recruitment potential based on the system in which they are found. Cisco are sensitive to oxythermal stress and with climate change, land use, and invasive species effects becoming more prevalent in Minnesota, aspects of lake ecosystems are changing, ultimately making Cisco more susceptible to these stressors. To investigate how different factors were affecting the population dynamics of inland Cisco, three lakes with a range of size structure and densities were selected within Minnesota's northern lakes and forests and north central hardwoods ecoregions. Targeted, standardized, annual pelagic fish sampling was conducted from 2013-2019 using a combination of hydroacoustic sonar and vertical gillnets. Fish sampled in vertical gillnets were measured, weighed, and used to aid hydroacoustic estimates for Cisco abundance and biomass. In addition, metrics that describe the pelagic oxythermal habitat, food availability, and fish density were collected to understand how different environmental factors were influencing inland Cisco populations. A total of 16 linear regression and mixed effect models were developed for two selected response variables: upper 95th % total length (mm) and standardized age-0 density (no $\cdot$ ha-m^{-3}). Cyclopoid copeopod densities explained the most variability in the observed size differences found in Cisco ($t = 4.05$, var = 2796) while Cisco biomass best explained the variability amongst the age-0 density response variable ($p < 0.01$. $R^2 = 0.41$). Additionally, the number of growing degree days at dissolved oxygen of 3.0 mg/L explained variability in both selected response variables ($t = 2.36$, var = 3632; $p = 0.022$, $R^2 = 0.29$). The results from this study document the importance of zooplankton prey and oxythermal habitat on Cisco and therefore provide fisheries managers with further knowledge to help closely monitor these populations.

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Environmental influences on the growth of inland cisco populations in three Minnesota Sentinel Lakes

Edward Carlson, Casey Schoenebeck, Beth Holbrook, Andrew Hafs

Abstract

Cisco *Coregonus artedi* are a pelagic cold-water fish that are widely distributed throughout many inland lakes across the northern Midwest and play an important role as forage for large piscivores. Inland Cisco populations have been observed to vary in their overall size and recruitment potential based on the system in which they are found. Since Cisco are sensitive to oxythermal stress, they are at risk from stressors such as climate change, land use, and invasive species which are ultimately changing aspects of lake ecosystems. To investigate how different factors were affecting the population dynamics of inland Cisco, three lakes with a range of size structure and densities were selected within Minnesota's northern lakes and forests and north central hardwoods ecoregions. Targeted, standardized, annual pelagic fish sampling was conducted from 2013-2019 using hydroacoustic sonar and vertical gillnets. Fish sampled in vertical gillnets were measured, weighed, and used to aid hydroacoustic estimates of Cisco abundance and biomass. In addition, metrics that describe the pelagic oxythermal habitat, food availability, and fish density were collected to understand the relationship between inland Cisco populations and different environmental factors. A total of 16 linear regression and mixed effect models were developed for two selected response variables: upper 95th percentile of total length (mm) and standardized age-0 density (no. · ha-m^{-3}). Cyclopoid copepod densities explained the most variability in the observed size differences found in Cisco ($t = 4.05$, $var = 2796$) while Cisco biomass best explained the variability amongst the age-0 density response variable ($p < 0.01$. $R^2 = 0.41$). Additionally, the number of growing degree days at dissolved oxygen of 3.0 mg/L explained variability in both selected response variables ($t = 2.36$, $var = 3632$; $p = 0.022$, $R^2 = 0.29$). The results from this study document the importance of prey and oxythermal habitat on Cisco and therefore provide fisheries managers with further knowledge to help closely monitor these populations.

Introduction

Throughout temperate North America, inland aquatic systems differ in their biological, chemical, and physical characteristics. The differences in these characteristics have the potential to affect different fish species that inhabit these aquatic systems. Cisco *Coregonus artedi* are an important link to pelagic energy flow, transferring energy from primary producers found throughout benthic and littoral zones to tertiary consumers and ultimately supporting large piscivores (McInerny 2014; Bronte et al. 2018: Herwig et al. 2021). Cisco are classified as cold-water fish species that require cold water temperatures and high dissolved oxygen levels to survive. Since Cisco are sensitive to oxythermal stress, they are also at risk from stressors like climate change. Mean annual air temperatures and growing seasons have increased significantly since 1980 in Minnesota, likely contributing to extended stratification periods and resulting in fewer lakes being suitable for Cisco (Jacobson et al. 2012). Due to the importance of Cisco to aquatic ecosystems, it is crucial to understand how different environmental stressors have the potential to influence the population dynamics of inland Cisco.

The differences in the population dynamics of Cisco between aquatic systems could be attributed to multiple environmental factors such as: habitat, food availability, fish density, evolutionary adaptations, and recruitment. Studies have shown the habitat in which Cisco occupy is often limited due to two primary factors: low dissolved oxygen levels within the hypolimnion and warmer water temperatures within the epilimnion (Rudstam & Magnuson 1985). For example, the lethal oxythermal boundary for Cisco is dependent on the combination of both temperature and oxygen concentrations (e.g., 23 ˚C at 5.0 mg/L, 22.0 ˚C at 3.0 mg/L, 19.5 ˚C at 1.0 mg/L) for Cisco (Jacobson et al. 2008). Interestingly, these limitations create a “squeeze” effect which can push Cisco higher into a narrow part of the water column where temperatures are often warmer and more optimal for growth (14.5 ˚C; Edsall & DeSourcie 2002). However, it may be evolutionary advantageous for Cisco found within cold, well oxygenated systems to stay deep in the water column and away from predators, resulting in slower growth but potentially increasing longevity and fecundity of individual fish. In systems where oxygenated, cold-water refuge is limited, Cisco may grow faster, and mortality may occur at earlier ages because of pelagic habitat parameters that metabolically constrain Cisco. Concurrently, increases in light attenuation within water bodies can influence predation on certain forage species, suggesting the more light that penetrates the water column, the deeper Cisco will reside in the water column to avoid predation (Sandström 1999). Although there has been little research on the conditions that produce the fastest growth rates of Cisco, Hile (1936) documented that Cisco growth depends on local conditions within an individual lake and therefore lake specific pelagic habitat could explain size differences in Cisco populations across inland systems.

Food availability could influence the growth of inland Cisco populations based on the density and biomass of available zooplankton taxa present within a system. Cisco are generalist feeders that consume a range of zooplankton taxa such as *Copepods* and small cladocerans to macro-invertebrates such as *Chaoborus spp.* and *Hexagenia spp.* (Aku & Tonn 1999; Ahrenstorff et al. 2013). Zooplankton densities have been positively correlated with the average size of Cisco (mm), supporting the hypothesis that populations of Cisco could be competing for a common, limiting resource in some lakes (Ahrenstorff et al. 2013). Available food resources and the density of Cisco may interact to influence the growth of inland Cisco populations. Evidence of density dependence among Cisco populations were found in five northern Wisconsin lakes where the mean total length of age-2+ fish (mm) decreased as Cisco catch per unit effort increased (Rudstam 1983). Differences in food availability in combination with the number of Cisco present within a system could explain differences in Cisco maximum lengths across inland systems.

An additional factor that may play a role in influencing inland Cisco populations is the recruitment of young fish into a population. Although never fully investigated within inland lakes, factors that drive Cisco recruitment have been more commonly documented throughout the Great Lakes. Lake dynamics related to water temperature and maximum wind speed have been observed to induce synchronous patterns of recruitment in populations of Cisco (Myers et al. 2015). Additionally, age-1 Cisco recruitment was negatively correlated with adult spawning stock size and positively correlated with the interaction between average wind speed and air temperature during the time of hatch in a study conducted on Lake Superior (Rook et al. 2013). Lastly, larger female total length was positively correlated with egg size diameter in a study of Cisco in Lakes Huron and Michigan (Koenigbauer et al. 2022). Cisco hatched from larger eggs may have a higher nutritional content which could contribute to faster growth rates and ultimately increasing their chances in being recruited to the population.

Certain environmental changes may occur at a faster pace than Cisco can adapt within their environment (Jacobson et al. 2017). Climate change may cause environments of lake ecosystems to change by increasing air temperatures and extending the duration of autumn seasons, resulting in increased lake stratification periods and loss of environmental conditions that support populations of Cisco (Stefan et al. 1992; Jacobson et al. 2012; Bigalke 2020). Additionally, Zebra mussel *Dreisenna polymorpha* introductions have been documented to shift energy pathways towards benthic and littoral zones, potentially forcing Cisco to depend on energy sources that are found outside their normal pelagic habitat (Jaeger Miehls et al. 2009). Other invasive species introductions, such as spiny waterflea *Bythotrephes longimanus*, caused a reverse trophic cascade in which ultimately replaced Cisco as the dominant zooplanktivore within a northern Wisconsin lake (Walsh et al. 2017). The introduction of invasive species may cause alterations in the food web, creating increased competition with Cisco and resulting in an environment that benefits the newly introduced species. Lastly, urbanization of forests was identified as a primary threat to Cisco populations across Minnesota when observing catchments of Cisco refuge lakes (Jacobson et al. 2011). Increases in urbanization surrounding lakes that contain Cisco populations could result in poor water quality that rapidly changes the environment in which Cisco reside. The inability to adapt to certain environmental changes caused by climate change, invasive species, and changes in land use may be contributing factors to why Cisco size and recruitment varies among different systems.

Although multiple environmental factors related to habitat, food availability, fish densities, and rapidly changing environments have been hypothesized to influence Cisco population dynamics, the reason for the variation in recruitment and size among Cisco populations in inland lakes is still largely under studied. Therefore, the objective of this study was to determine if specific environmental factors were correlated with 1) the recruitment of age-0 Cisco and 2) the upper 95% total length of age-1+ Cisco within inland populations. Data related to oxythermal habitat, available food resources, and abundances of Cisco were collected and analyzed to better describe their influences on these two key population dynamic metrics related to inland Cisco populations.

Methods

The three lakes used in this study were Carlos, Elk, and Ten Mile, and are found within the northern lakes and northcentral hardwoods ecoregions of Minnesota (Table 1; Figure 1). All three lakes have populations of Cisco and range in their size, depth, and productivity, which provided an opportunity to further conduct research on environmental factors that may affect these populations. Carlos is a 1,054 ha lake located in Douglas County, Minnesota, and has a maximum depth of 49.7 m. As of 2009, Carlos has been infested with Zebra Mussels and has undergone a shift towards a decrease in lake productivity, resulting in lower zooplankton densities and deeper Secchi depth measurements (MNDNR 2019). The pelagic piscivorous predators found within Carlos include Northern Pike *Esox lucius* and Walleye *Sander vitreus*. Elk Lake is located within Itasca State Park in Clearwater County, Minnesota and has a surface area of 123 ha with a maximum depth of 28.3 m. Elk Lake is the only Sentinel Lake in this study with a population of Muskellunge and includes the two other pelagic piscivorous predators (Northern Pike and Walleye). Ten Mile Lake is located in Cass County, Minnesota and has a surface area of 2,023 ha with a maximum depth of 63.4 m. Throughout the years of sampling Cisco in Ten Mile, the size of Cisco has been very small an often classified as a dwarf subspecies (Shields et al. 1990). In 2019, small populations of Zebra Mussel veligers were documented in Ten Mile and have not impacted the lake ecosystem since their original discovery (MNDNR 2019). Northern Pike and Walleye are the dominant pelagic piscivorous predators found within Ten Mile Lake.

Habitat- Discrete temperature and dissolved oxygen profiles were conducted at the maximum depth within each lake using a multiparameter sonde meter during the months of June, July, and August (Carlos: 2013-2019; Elk: 2013-2016, 2018-2019; Ten Mile: 2013-2019). Measurements were taken at set intervals (½ meter or 1 meter) until the thermocline and then switched to 2-meter intervals until the maximum depth of the lake was reached. To evaluate oxythermal habitat, temperature and dissolved oxygen data were used to calculate the temperature where dissolved oxygen was 3.0 mg/L (TDO3 °C; Jacobson et al. 2010). This metric was calculated by compiling all temperature and dissolved oxygen profiles for a given year and lake and then interpolating between depths within each profile to estimate the temperature where dissolved oxygen was 3.0 mg/L. If the dissolved oxygen concentration throughout the entire water column was above 3.0 mg/L, then the temperature at the bottom of the lake was used as the metric. After all temperatures were compiled, an annual point estimate of TDO3 was selected using the highest value from August profiles. Due to limitations in data collection, there was no data available to calculate TDO3 during peak stratification in Carlos (2014) and Elk (2017).

Cumulative oxythermal habitat was calculated using the number of growing degree days at the temperature where dissolved oxygen was 3.0 mg/L (GDD at TDO3). To keep the number of days consistent between lakes, a 62-day period from July 1st to August 31st was selected and values were interpolated between dates when discrete profiles were taken. This metric was calculated by using the estimated TDO3 value from a given date and subtracting the temperature where larval Cisco growth increased significantly in Minnesota inland lakes (3.0 °C; McCormick et al. 1971). All temperature values were then summed across July and August if the individual daily GDD value was above the predetermined instantaneous growth temperature value (> 3.0°C). The following equation was used to calculate GDD at TDO3 ($°C \cdot days^{-1}$):

$$GDD\ TDO3 = \sum (TDO3 - T_0) \tag{1}$$

where *TDO3* was the temperature at dissolved oxygen of 3.0 mg/L and T_0 was the base temperature of 3.0 °C. Due to limitations in data collection, GDD at TDO3 could not be calculated during some years in two lakes (Carlos: 2014, 2019; Elk: 2017).

Water temperature loggers (Onset HOBO V2) were deployed in each study lake to collect hourly temperature data at 1-meter intervals in the epi- and metalimnion, and were placed at geometrically increasing intervals (1, 2, 3, 4, then 5 m until bottom) in the hypolimnion for a subset of years (Carlos: 2013-2019; Elk: 2014-2019; Ten Mile: 2017-2019; MNDNR 2020). The median temperature at the lower limit of the metalimnion was calculated for each year and lake using the rLakeAnalyzer package in R to better describe temperatures at the upper ranges of Cisco habitat from June, July, and August (Winslow et al. 2019). Similarly to the growing degree day method used for TDO3, a 90-day period from June 1st to August 31st was selected and an additional growing degree day metric for the metalimnion was calculated (GDD at Metalimnion). This metric was calculated by using the temperature at the median lower limit of the metalimnion from a given date and subtracting the temperature where larval Cisco growth increased significantly in Minnesota inland lakes (3.0 °C; McCormick et al. 1971). The following equation was used to calculate GDD at the metalimnion:

$$GDD\ Metalimnion = \sum (LLML - T_0) \tag{2}$$

Where $LLML$ was the median temperature at the lower limit of the metalimnion and T_0 was the base temperature. Due to limitations in data collection, the median lower limit metalimnion temperature and GDD at the metalimnion metrics were not calculated in two lakes during some years (Elk: 2013; Ten Mile:2013-2016.

Data on light attenuation was collected using a Secchi disk. Multiple Secchi depth measurements were taken during the months of June, July, and August on each lake from 2013-2019 and then averaged for each year to observe trends in light attenuation amongst the three study lakes.

Zooplankton Densities & Biomass- Zooplankton were collected by the Minnesota Pollution Control Agency following methods outlined by Heiskary et al. (2016). Vertical zooplankton tows (30-cm mouth, 80-um mesh) were conducted monthly from May to October at the maximum depth of each study lake from 2013-2019. Zooplankton samples were rinsed into plastic Nalgene bottles and preserved in 100% reagent alcohol for further identification in the lab. Samples were processed by the Minnesota Department of Natural Resources, Ecological and Water Resources Division. Zooplankton were counted, measured, and divided into four taxonomic categories: calanoid copepods, cyclopoid copepods, large daphnids, and small cladocerans. The sum of taxa densities (no. $\cdot$ L^{-1}) for each month were averaged over the six-month sampling period to estimate the average zooplankton density for each year and lake combination. Biomass estimates ($\mu g \cdot L^{-1}$) were calculated using length-weight regression coefficients for individual dry weight of taxa collected (Dumont et al. 1975; Culver et al. 1985). Average biomass estimates for each lake and year combination were calculated similarly to zooplankton densities.

Cisco Abundance & Biomass- Vertical gillnets were deployed and retrieved by the Minnesota Department of Natural Resources- Fisheries Research Unit and Sentinel Lakes Program following standardized lake survey protocols (MNDNR 2017). The vertical gillnets consisted of seven panels of monofilament webbing (bar-measure mesh x panel width): 9.5 mm x 0.9 m, 12.7 mm x 0.9 m, 19.0 mm x 1.2 m, 25.4 mm x 1.8 m, 31.8 mm x 3.0 m, 38.1 mm x 3.0 m, 44.5 x 3.0 m and were set overnight in the deepest location(s) of each study lake, once a year between late June and early September. The number of nets set for sampling each year consisted of one full complement of nets except the following years where multiple complements of nets were used: Carlos, 2014-2018 and Ten Mile, 2013-2014. A subset of Cisco (5 fish/10 mm length group) caught in vertical gillnets from 2016-2019 in Carlos and 2018-2019 in Elk and Ten Mile were sacrificed for age analysis. Additionally, vertical gillnet data were used to aid in interpreting data collected by hydroacoustic surveys.

Abundance and biomass of Cisco were estimated using hydroacoustic sonar methods outlined by Holbrook and Staples (2013). Hydroacoustic data were collected by the Minnesota Department of Natural Resources, Fisheries Research Unit and Sentinel Lakes Program using a Simrad 38-kHz 9.6° split beam transducer and a EK60 transceiver with a pulse duration of 0.26 ms. The transducer was mounted to a vertical pole and submerged in the water, where the beam was directed perpendicular to the water’s surface (downward). Prior to each survey, the hydroacoustic unit was calibrated with a tungsten-carbide reference sphere (Parker-Stetter et al. 2009; ICES 2015). Hydroacoustic surveys were conducted at least one hour after sunset during peak stratification periods from early July to early September from 2013-2019 to ensure that Cisco shoals were dispersed and there was thermal separation between cold- and warm-water species. Hydroacoustic surveys were conducted annually using standardized transects. Nearfield depths less than 4 m were excluded from the analysis. Epilimnetic depths were also eliminated from the analysis when temperature profiles indicated temperatures > 20 °C and vertical gill net data indicated Cisco were not captured at these depths.

Once the surveys were completed, hydroacoustic data were analyzed using Echoview Software (Versions: 5.3-12.0; Myriax Software Pty., Hobart, Tasmania). Fish density (ρ_v, individuals · m^{-3}) of each 1-m deep by 20-m horizontal analysis cell was calculated using the standard hydroacoustic equation:

(3) $$\rho_{vs} = \frac{p_s}{\bar{\sigma}_{bs}} \times s_v$$

where p_s was the expected proportion of the total number of fish belonging to species *S*, $\bar{\sigma}_{bs}$ was the weighted mean backscattering cross-section of all species, and s_v was the linear form of the volume backscatter (S_v) from each analysis cell, calculated with the equation:

(4) $$s_v = 10^{\frac{s_v}{10}}$$

Due to targeted sampling methods that eliminated thermal overlap between cold- and warm-water species, all forage-fish sized hydroacoustic targets below the epilimnion were assumed to be Cisco, so the weighed mean backscatter, $\bar{\sigma}_{bs}$, was simplified to:

(5) $$\bar{\sigma}_{bs} = 10\,\frac{TS}{10}$$

where *TS* is the expected target strength expected from an individual Cisco. TS was estimated from single target data, with single targets grouped into fish tracks that likely came from the same fish. Fish tracks were exported and summarized by 1-m depth intervals and applied to depth-discrete backscatter to calculate density and biomass.

Since the three study lakes had various lengths of Cisco present, a minimum decibel threshold was applied based on fish track data for each lake. The thresholds were determined by combining fish track data from all years, using Jenks optimization method to identify break points between clusters, and identifying the break point that best corresponded with the minimum length of age-1 Cisco for each lake using vertical gill net data to help guide the decision (Table 2). A threshold 6.0 dB lower than the identified fish track threshold was applied to $\mathrm{S_v}$ backscatter data.

Biomass estimates were also calculated for each analysis cell. A published regression from Rudstam et al. (1987) was used to convert *TS* to a mean length (mm) and then to a mean weight using lake-specific length-weight regressions that were developed based on vertical gill net catches. This mean weight was then multiplied by the density estimate to calculate cell-specific biomass estimates.

Cell-specific density and biomass estimates were summarized into 20-m horizontal cells and the relationship with depth was modeled using a best-fit autoregressive-moving average model to account for temporal correlations in the data. These models were then applied to volumetric bathymetric data to estimate whole-lake population (individuals) and biomass (kg) estimates, and confidence intervals were bootstrapped to estimate variability. Whole lake population and biomass estimates were then divided by the pelagic volumes (km^3) of each lake to standardize the density and biomass estimates used as predictor variables for the analysis.

Data Analysis- To assess the objective of this study, linear regression and linear mixed effect model approaches, similar to the methods of Peirce et al. (2013), were used to determine which predictor variables best explained the designated response variable. The first response variable used in this analysis was the upper 95% total length of age-1+ Cisco (mm). The upper 95% total length was calculated by applying lake-specific minimum thresholds (Table 2) to fish track hydroacoustic data and then extracting the upper 95% lengths using Program R (R Core Team 2020). To account for autocorrelations and repeated measures within individual lakes, lake was nested as a random effect for all models with the upper 95% total length response variable using the lme4 R package (Douglas et al. 2015). A total of 16 models were developed for this selected response variable and t-values were used to determine significance ($t > |2|$).

The second response variable used in this study was standardized age-0 density of Cisco (no. · ha-m^{-3}). Age-0 densities were calculated by applying lake-specific maximum thresholds to fish track hydroacoustic data to estimate the number of age-0 Cisco during each sampling event (Table 2). Since the resolution of individual fish tracks in Ten Mile was low due to the high densities of Cisco found below the thermocline, age-0 density was standardized by lake to make densities more comparable using the following equation:

(6) $$Z = \frac{(x-\mu)}{\sigma}$$

where age-0 density, x, was subtracted from the mean age-0 density, μ, and divided by the standard deviation, σ. The number of age-0 Cisco captured was then divided by the total volume of water sampled by the beam during the hydroacoustic event. Lake nested as a random effect was initially used for the age-0 density response variable, however, lake as a random effect was determined to be insignificant and therefore, a linear regression model approach was used for all models for this selected response variable. The same 16 models were used for the age-0 density response variable and p-values were used to determine significance ($p < 0.05$).

A total of 16 predictor variables were used in this analysis and were a combination of environmental factors that had the potential to influence the size and recruitment of Cisco found within the three study lakes (Table 3). Each predictor variable was tested individually against each selected response variable. Correlation matrices were analyzed between zooplankton taxa-specific densities and biomasses, and it was determined that calanoid, cyclopoid, and large daphnid densities were highly correlated with biomasses ($R^2 > 0.90$) and therefore, densities were only used for those taxa in this analysis.

Principal component analyses were used to further understand the correlations among all variables using methods outlined by Pech & Laloë (1997). Uncorrelated values were identified as principal components 1 and 2 and created to maximize the variance for each selected response variable. The newly created values were then plotted on a 2-dimnesional graph to better visualize how each variable related with one another. Variables with arrows pointing in the most similar direction for a designated principal component were deemed the most correlated with one another. Additional lake-year combinations were plotted to better understand how each variable related to each individual lake for a given year.

Results

Four key components related to the population dynamics of inland Cisco were observed throughout the course of the study (2013-2019) to better understand the differences in the three systems over time. The average total length of Cisco age-1+ from hydroacoustic surveys varied by year in Elk, but were rather consistent across all years in the other two lakes (Figure 2). Cisco biomass was highest in Elk, while Cisco density was highest in Ten Mile across all years (Figure 2). Patterns in standardized age-0 Cisco density peaked from 2015-2017 in Elk and showed similar trends between Carlos and Ten Mile across all years (Figure 2).

The suite of predictor variables used to investigate Cisco population dynamics in this study were dissimilar among lakes. The values for TDO3 varied by 10 °C among the three lakes, ranging from 4.47 °C in Carlos (2014) to 14.89 °C in Elk (2014; Table 3). The median temperatures at the lower limit of the metalimnion across all years were similar in Elk and Ten Mile (Elk: 8.56 °C, SD = 0.70; Ten Mile: 9.44 °C, SD = 0.41) while Carlos had a slightly higher temperature at 12.20 °C (SD = 1.17). Secchi depth values were similar on average in Ten Mile (5.97 m, SD = 0.29) and Carlos (6.04 m, SD = 0.70) and lower in Elk (3.14 m, SD = 0.69). Zooplankton densities varied by taxa with the highest observed value found from the cyclopoid taxa group (Elk: 19.65 no. · L^{-1}) and the lowest observed from the large daphnid taxa group (Ten Mile: 0.10 no. · L^{-1}; Table 3). The same trend in total zooplankton biomass was observed between lakes with Elk having the highest observed biomass (2015: 86.10 μg · L^{-1}) and Ten Mile having the lowest (2013: 20.80 μg · L^{-1}; Table 3). On average, Cisco densities observed in Ten Mile (14.21 no. · km^{-3}, SD = 5.27) were at a three-fold magnitude difference than in the other two lakes (Elk: 5.36 no. · km^{-3}, SD = 1.55; Carlos: 3.98 no. · km^{-3}, SD = 0.82). Cisco biomass, on average, ranged from 0.25 kg · km^{-3} (SD = 0.03) in Carlos to 0.88 kg · km^{-3} (SD = 0.19) in Elk with Ten Mile fish having biomasses most similar to Carlos at 0.26 kg · km^{-3} (SD = 0.07).

The upper 95% total length of Cisco observed from single target hydroacoustic data ranged from 103.00 to 275.80 mm, a difference of 172.80 mm (Figure 3). Six predictor variables were determined to have a significant correlation with the upper 95% total length, including cyclopoid densities (t = 4.05, var = 2796), total zooplankton density (t = 3.72, var = 3204), total zooplankton biomass (t = 2.92, var = 3410), small cladoceran density (t = 2.76, var = 3326), growing degree days at TDO3 (t = 2.36, var = 3632) and small cladoceran biomass (t = 2.24, var = 3639; Table 4; Figure 4). Secchi depth explained the most variation in the upper 95% total length, indicated by the lowest variance value amongst all predictor variables, but was determined to be insignificant ($t = -1.96$, var = 2426; Table 4; Figure A5). All other variables tested were not significant including year (Table 4; Figure A4; Figure A5).

Age-0 densities of Cisco observed from singlet target hydroacoustic were most variable in Elk across all systems, indicated by minimum and maximum age-0 density values of 0.44 no. · ha-m^{-3} and 16.33 no. · ha-m^{-3}, respectively (standardized: min = -0.83 no. · ha-m^{-3}, max = 1.63 no. · ha-m^{-3}). The predictor variables that were determined to have a significant influence on standardized age-0 density were Cisco biomass ($p < 0.01$, $R^2 = 0.41$), large daphnid density ($p < 0.01$, $R^2 = 0.34$) and GDD at TDO3 ($p = 0.02$, $R^2 = 0.29$; Table 5; Figure 5). All other variables tested against standardized age-0 density were determined to be insignificant (Table 5; Figure A6, Figure A7).

Principal component analysis was used to further elucidate correlations amongst all variables. Principal component 1 (PC1) accounted for 57% of the overall variation in the data, while principal component 2 (PC2) accounted for 17%. Both components were considered bipolar, indicated by variables found on both positive and negative axes for each component within the analysis. TDO3, GDD at TDO3, Small cladoceran density and biomass, and zooplankton density were all found on the positive axis for both PC1 and PC2 along with the upper 95% total length response variable (Figure 6). Other variables that were found on the positive axis for PC1 included cyclopoid density, and Cisco biomass (Figure 6). Secchi depth, GDD at metalimnion, and median lower limit metalimnion temperature variables were found on the positive axis for PC2, but not PC1 (Figure 6). Cisco density was the only variable negatively correlated for both principal components. Standardized age-0 density was positively correlated with most taxa specific zooplankton densities (excluding calanoids), total zooplankton density, and total zooplankton biomass located on both the PC1 and PC2 axes (Figure 7). Additionally, TDO3, GDD at TDO3, and Cisco Biomass were located on the positive axis for PC1, while Secchi depth, Cisco density, and calanoid density were located on the positive axis for PC2 (Figure 7). Median metalimnion temperature was the only variable that was negatively correlated for both principal components when compared to age-0 density of Cisco.

Discussion

This study demonstrated that thermal dynamics within lakes play an important role in influencing size structure and recruitment of inland Cisco. Although the TDO3 metric alone did not significantly explain Cisco size structure, the GDD at TDO3 metric did, and that relationship varied among the three lakes indicated by a positive relationship in Elk and negligible relationships in the other two lakes. The number of growing degree days where dissolved oxygen was 3.0 mg/L provided an estimate of the cumulative thermal conditions for Cisco at depths where there was adequate oxygen. Increased hypoxic conditions throughout the summer, particularly in more productive lakes, may cause Cisco to move into warmer water temperatures where there is sufficient oxygen. If food resources are adequate, these warmer temperatures may cause increased growth rates particularly around 14.5 °C which has been documented to be the optimal temperature for Cisco growth (Edsall & DeSorcie 2002). Other studies have documented that preferred Cisco temperatures coincided with the highest temperature at which Cisco could maintain respiratory independence (Rudstam & Magnuson 1985). Additionally, Cisco found in lakes with lower TDO3 values throughout the stratified season, such as Ten Mile, have a greater volume of oxythermal habitat to move throughout the water column than lakes with higher TDO3 values such as Elk. Contributing factors to the observed differences in thermal dynamics of the three study lakes likely include lake size and max depth. Maximum depth was strongly associated with high dissolved oxygen concentrations at depth of capture for Cisco (Grow et al. 2022). Ten Mile has a maximum depth of 63.4 m and on average, the depth at which TDO3 occurs is 54.8 m (SD = 10.6), leaving Cisco with 45.0 m of water before reaching warmer waters found above the metalimnion (Figure 8). Similar maximum depths can be found in Carlos, but not Elk. Elk has a shallower maximum depth and the corresponding TDO3 depth occurred higher in the water column during the stratified season (Figure 8). This leaves Cisco with a narrow oxythermal layer due to their need for high dissolved oxygen concentrations and avoidance of warm epilimnetic waters. Similar results have been observed where Cisco were found higher in the water column due to increased TDO3 values and therefore were larger in size (Jacobson et al. 2020; Grow et al. 2022). The present study documents the importance of thermal dynamics in explaining the variation amongst Cisco size found from different systems.

Although the reason for the influences of GDD at TDO3 on growth of adult Cisco is better understood, the reasons for its relationship with the age-0 density of Cisco is still unclear. Upon hatching from eggs in late spring, larval Cisco occupy nearshore habitats and are more tolerant of warmer water temperatures than adult Cisco (Colby & Brooke 1969; McCormick et al. 1971). As water temperatures increase throughout late spring and early summer, the metabolic demand for larval Cisco increases causing increased consumption (Oyadomari & Auer 2008). With the combination of increasing food intake and water currents, larval Cisco begin to grow larger and move to offshore habitats (Clady 1976). Although age-0 Cisco do not occupy the same depths as adults, there is evidence to support that age-0 Cisco still occupy depths below the epilimnion and are susceptible to oxygen restrictions that may occur (Holbrook & Carlson 2018). Results from this study indicate the effect of oxygen limiting parameters may have a lesser effect on age-0 Cisco since they are already found higher in the water column and are more tolerant of warmer water temperatures. Age-0 Cisco found within Carlos and Ten Mile may experience colder temperatures where oxygen is liming, having a lower effect on their densities compared to Elk where temperatures are warmer. Concurrently, the age-0 densities of Cisco may be more positively influenced by warmer water temperature due to the increased anoxic conditions below the metalimnion found in Elk. To further understand the thermal dynamic influences on the age-0 densities of Cisco, further research should be conducted on the temperature and dissolved oxygen parameters in which they reside.

Various zooplankton taxa may be positively correlated with Cisco size structure and densities at different stages of life. Small cladoceran biomass, small cladoceran density, and cyclopoid density were all significantly correlated with the size of age 1+ Cisco in Elk, but not in Carlos or Ten Mile. Although there was more food available on average in Elk across all years, the growth of a fish is a function of both the food available to consume and temperature (Brandt 1993). Across the three lakes, the limiting factor that most likely contributed to the smaller sizes observed in Carlos and Ten Mile was lower water temperature, which resulted in Cisco not having to feed as much to maintain their metabolism. It is hypothesized that the water temperature in Elk, in combination with the more food available within the system, provided more favorable conditions to produce larger fish. Additionally, zooplankton taxa present in the three lakes of this study have been observed to inhabit specific depths within the water column and therefore may influence the food available for Cisco. Depending on the time of day when zooplankton densities are most abundant, Cisco may follow the peaks of these densities throughout water column to meet their metabolic demands. Engel (1976) documented that Cisco ate the most readily available zooplankton species within their depth range; primarily feeding on small cladocerans, cyclopoid copepods and large daphnids. Diets of Cisco found in Carlos and Ten Mile were primarily composed of copepods (50-80%) while diets of Cisco from Elk were primarily composed of *Chaoborus spp.* (60%) and *Daphnia* spp. (30%), which contradicts the positive correlation between cyclopoid copepods densities and Cisco size in Elk observed from this study (Ahrenstorff et al. 2013). Lastly, Cisco may be limited to specific parts of the water column due to oxygen restrictions experienced during peak stratification periods. When oxygen was injected into a treatment basin within Amisk Lake, Alberta, Cisco primarily fed on *D. longiremis* and *Chironomus* spp. while Cisco found within the reference basin primarily fed on *Daphnia pulex*, *Chaborus* spp., and *D. g. mendotae* species where oxygen had been depleted (Aku & Tonn 1999). This is likely due to the greater tolerance of low dissolved oxygen concentrations exhibited by *D. longiremis* and *Chironomous spp.*, creating a refuge for these two species from predation by Cisco (Engel 1976; Taggart 1984; Aku & Tonn 1999). The variation in Cisco size can best be explained by a combination of specific zooplankton densities and oxythermal conditions which may cause Cisco to move throughout the water column and occupy depths where food and temperatures are most optimal for growth.

The results from this study also provide relevant information between the correlations of specific zooplankton species and age-0 Cisco density. Large daphnid density was positively correlated with the age-0 density of Cisco in Elk, but negativity correlated in Carlos and Ten Mile. Possible contributions to the correlations observed between the three lakes could be attributed to the timing of sampling. In particular, the large daphnid densities observed in 2015 and 2016 in Elk were significantly higher compared to all other years sampled for each lake and could be driving the positive correlation observed within the present study. The timing of sampling within Elk during 2015 and 2016 could have coincided with diel vertical migration events of large daphnids. Large daphnids often exhibit diel vertical migration behavior as a predator avoidance strategy during certain photoperiods (Dini & Carpenter 1992; Dodson et al. 1997; Ebert 2005). Additionally, as large daphnids migrate from the hypolimnion during vertical migration events, larval Cisco could be feeding on the large daphnids that rise into the upper reaches of the hypolimnion and metalimnion. However, adult Cisco and other zooplanktivorous fish may feed on most of the zooplankton prey that rise during these vertical migration events and leave larval Cisco that reside higher in the water column with a limited food supply. In order to test this hypothesis, diets from both age-0 Cisco and adult Cisco would need to be analyzed and compared to further determine if certain age classes of Cisco can outcompete others for food resources. Studies have documented a significantly higher proportion of age-2 and younger Cisco with empty stomachs compared to age-3 and older Cisco, supporting the idea that adult Cisco may be more successful at foraging (Aku & Tonn 1999). Additionally, adult Cisco have the ability to gulp/pump filter feed by opening and closing their mouths 2-3 times per second to capture multiple zooplankton prey at once (Janssen 1978; Lentz 1986). The ability to catch multiple small cladocerans at once compared to individually seeking out singular large daphnids may be the reason why different zooplankton species influence different life stages of Cisco.

Cisco biomass was a significant predictor when explaining the variation in age-0 Cisco density. Total Cisco biomass estimates observed in Elk were approximately three times the estimated biomasses observed in Carlos and Ten Mile. The correlations in Cisco biomass among the three lakes followed similar trends to what was observed through the age-0 densities throughout the study years. Elk was positively correlated with Cisco biomass while Carlos and Ten Mile were both negatively correlated with Cisco biomass. It is hypothesized that Elk age-0 densities are driven more by internal processes where there is likely an opening in the adult population for the age-0 Cisco to recruit into.

During the years preceding the spike in age-0 densities in Elk, the population is most likely composed of sexually mature female fish in which have ample resources to use and put towards reproduction, resulting in observed larger Cisco biomasses. Subsequent years in Elk are likely composed of age-0 fish, indicated by strong recruiting classes of age-0 Cisco from 2015-2017 and resulting in smaller Cisco biomasses. Carlos and Ten Mile age-0 densities are likely more driven by external processes such as wind and water temperature and therefore, only see peaks in age-0 densities when lake conditions are favorable for recruitment. Cisco populations in Lake Superior have been documented to be compromised of young age classes dominated by males and increased female dominance with age classes 2+ when population densities are low (Bowen et al. 1991). Other studies have documented female sex ratio having the greatest effect in explaining the variation in recruitment of Bloater *Coregonus hoyi* in Lake Michigan, supporting the idea that recruitment of coregonids is related to the number of female fish present within the population (Bunnel et al. 2006). Body condition and fecundity of female Cisco was also greatest in Lake Michigan and Huron, indicating that female Cisco may put more effort towards reproduction in systems where recruitment is more sporadic (Yule et al. 2020). After further analysis of the correlations between Cisco biomass and age-0 density, variation in Cisco recruitment can best be explained by different internal and external processes occurring within systems that best support their populations of Cisco.

Ecological conditions within lakes influence Cisco independently and therefore may be the reason that size and recruitment varies amongst different systems. After further analysis of each response variable used in this study, it was clear that each lake stood apart from one another in explaining Cisco size structure and recruitment and the responses were influenced by each predictor variable independently. Cisco in Ten Mile were characterized by small upper 95% total lengths, relatively consistent age-0 densities, and negligible effects with individual predictor variables. A combination of lake morphometry, high dissolved oxygen concentrations, and low temperatures created ample amounts of pelagic cold-water habitat for Cisco within Ten Mile. Cisco found in Elk were characterized by large upper 95% total lengths, more sporadic age-0 densities, and stronger effects with each predictor variable. A combination of low dissolved oxygen, warm water, and greater lake productivity caused more variable lake conditions between years. Cisco that reside within Elk Lake are prime candidates for the “squeeze” effect where hypoxic hypolimnetic oxygen concentrations cause Cisco to move up in the water column and occupy warmer water temperatures that may cause faster growth rates. Lastly, Cisco found in Carlos were characterized by intermediate upper 95% total lengths, consistent age-0 densities, and low effect sizes among predictor variables. Cisco within Carlos only experienced hypoxic hypolimnetic concentrations towards the end of stratification periods, experienced warmer water temperatures found at the metalimnion, and exhibited similar effects from lake size and productivity to that of Ten Mile. The likely contributions to the increased temperatures found at the metalimnion in Carlos could be related to the lower position latitudinally compared to the other two lakes. Furthermore, Cisco biomass was documented as an important predictor for incoming recruiting classes of age-0 Cisco in systems with sporadic recruitment. This study also supplied supporting information on the importance of species-specific zooplankton taxa to different life stages of Cisco. Finally, this study provided supporting information of the significance of oxythermal habitat in determining the size structure and recruitment of Cisco across different systems. As climate change, invasion of non-native species, and changes in land use continue to increase throughout Minnesota lakes, the importance of monitoring their effects on the oxythermal habitat and food resources available to Cisco is crucial. The results yielded from this study will allow fisheries biologist to better assess the potential effects these stressors have on the environments in which inland Cisco populations reside.

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Tables

Table 1- Physical characteristics of Carlos, Elk, and Ten Mile lakes.

Lake	**Lake Type**	**Lake Area** (ha)	**Maximum Depth** (m)	**Pelagic Zone** (% > 6 m)
Carlos	Mesotrophic	1,054	49.7	64.6
Elk	Mesotrophic	123	28.3	76.0
Ten Mile	Mesotrophic	2,023	63.4	73.7

Table 2- Single target thresholds for each study lake from hydroacoustic surveys conducted between 2013-2019 with minimum Cisco length calculated using the equation published by Rudstam et al. (1987).

Lake	**Horizontal Cell Size** (m)	**Single Target Threshold** (-dB)	**Single Target Max Size** (-dB)	**Min Length** (mm)
Carlos	20.0	-44.0	-31	114.6
Elk	20.0	-45.0	-31	103.7
Ten Mile	20.0	-52.0	-36	49.4

Table 3- Variable codes and descriptions used in the linear regression and mixed effect model development with additional descriptive statistics such as: minimum, maximum, mean, and standard error values to predict the selected response variable.

Code	Description	Min-Max	Mean	SE
Upper 95% Total Length	Upper 95% total length of age 1+ Cisco (mm)	103.0-275.8	174.7	12.0
Age-0 Density	Age-0 Cisco density standardized by lake (no · ha-m^{-3})	0.44-16.33	-0.214	0.149
Lake	Lake ID	-	-	-
Year	Year ID	2013-2019	-	-
TDO3	Temperature at dissolved oxygen of 3.0 mg · L^{-1} (°C)	4.47-14.9	8.08	0.662
GDD at TDO3	Cumulative growing degree days at TDO3 (°C · day^{-1})	93.2-497.1	272.1	28.5
GDD at Metalimnion	Cumulative growing degree days at metalimnion (°C · day^{-1})	340.3-922.7	640.7	44.2
LLML	Median lower limit metalimnion temperature (°C)	7.26-13.5	10.3	0.487
Secchi Depth	Average Secchi depth (m)	2.00-7.00	5.05	0.327
Calanoid Density	Average calanoid density (no. · L^{-1})	0.698-4.96	1.78	0.289
Cyclopoid Density	Average cyclopoid density (no. · L^{-1})	2.82-19.7	4.87	0.881
Large Daphnid Density	Average large daphnid density (no. · L^{-1})	0.104-1.97	0.552	0.105
Small Cladoceran Density	Average small cladoceran density (no. · L^{-1})	1.18-8.86	2.62	0.351
Zooplankton Density	Average zooplankton density of taxa combined (no. · L^{-1})	8.00-37.2	14.9	1.46
Small Cladoceran Biomass	Average small cladoceran biomass (no. · L^{-1})	3.14-12.0	5.70	0.432
Zooplankton Biomass	Average zooplankton biomass of taxa combined (no. ·L^{-1})	20.8-86.1	41.6	3.36
Cisco Density	Cisco Density (no. · pelagic km^{-3})	2.88-21.92	1570	286
Cisco Biomass	Cisco Biomass (kg · pelagic km^{-3})	0.161-1.15	0.46	0.07

Table 4- Candidate models used for the response variable analysis of the upper 95% total length of Cisco age-1+. Predictor variable variance, t-value significance, and effect size were included for comparison amongst variables. For code name definitions, see Table 3.

Model	**Variance**	**t-value**	**Slope**
~ 1 + (1|Lake)	3911	4.81	-
~ Cyclopoid Density + (1|Lake)	2796	4.05	3.90
~ Zooplankton Density + (1|Lake)	3204	3.72	1.95
~ Zooplankton Biomass + (1|Lake)	3410	2.92	0.71
~ Small Cladoceran Density + (1|Lake)	3326	2.76	6.45
~ GDD at TDO3 + (1|Lake)	3632	2.36	0.08
~ Small Cladoceran Biomass + (1|Lake)	3639	2.24	4.17
~ Secchi Depth + (1|Lake)	2426	-1.96	-12.45
~ Large Daphnid Density + (1|Lake)	3256	1.90	17.43
~ TDO3 + (1|Lake)	3724	1.85	2.69
~ Cisco Biomass + (1|Lake)	2556	1.61	52.47
~ Cisco Density + (1|Lake)	3017	-1.36	-1.70
~ Year + (1|Lake)	3991	1.12	2.12
~ LLML + (1|Lake)	4339	0.33	1.70
~ GDD at Metalimnion + (1|Lake)	4220	0.20	0.01
~ Calanoid Density + (1|Lake)	3798	0.19	-1.00

Table 5- Candidate models used for the response variable analysis of the standardized age-0 density. Predictor variable variance, t-value significance, and effect size were included for comparison amongst variables.

Model	**R^2**	**p-value**	**Slope**
~ Cisco Biomass	0.41	< 0.01	1.37
~ Large Daphnid Density	0.34	< 0.01	0.82
~ GDD at TDO3	0.29	0.02	< 0.01
~ Small Cladoceran Density	0.14	0.07	0.17
~ Cyclopoid Density	0.16	0.07	0.07
~ Secchi Depth	0.15	0.08	-0.18
~ Zooplankton Density	0.13	0.11	0.04
~ TDO3	0.13	0.12	0.07
~ 1	-	0.17	-0.21
~ Calanoid Density	0.06	0.27	-0.13
~ LLML	0.08	0.30	-0.11
~ Zooplankton Biomass	0.06	0.30	0.01
~ GDD at Metalimnion	0.05	0.40	< 0.01
~ Year	0.02	0.56	0.05
~ Cisco Density	0.01	0.60	-0.01
~ Small Cladoceran Biomass	< 0.01	0.78	0.02

Figures

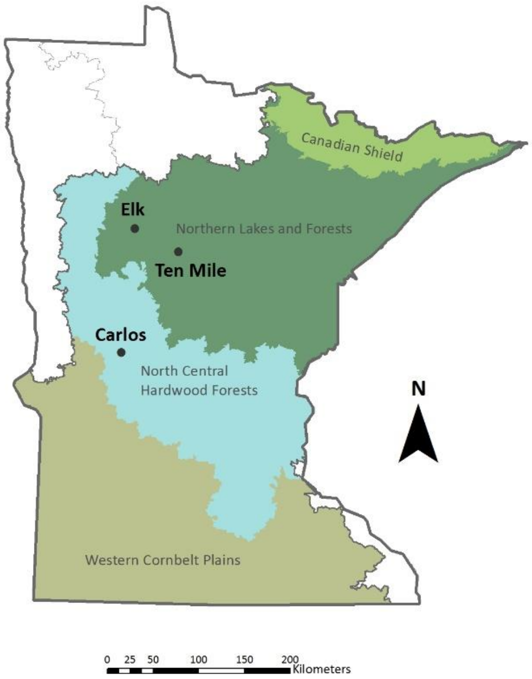

Figure 1- Locations of Carlos, Elk, and Ten Mile throughout Minnesota’s north central hardwood and northern lakes ecoregions.

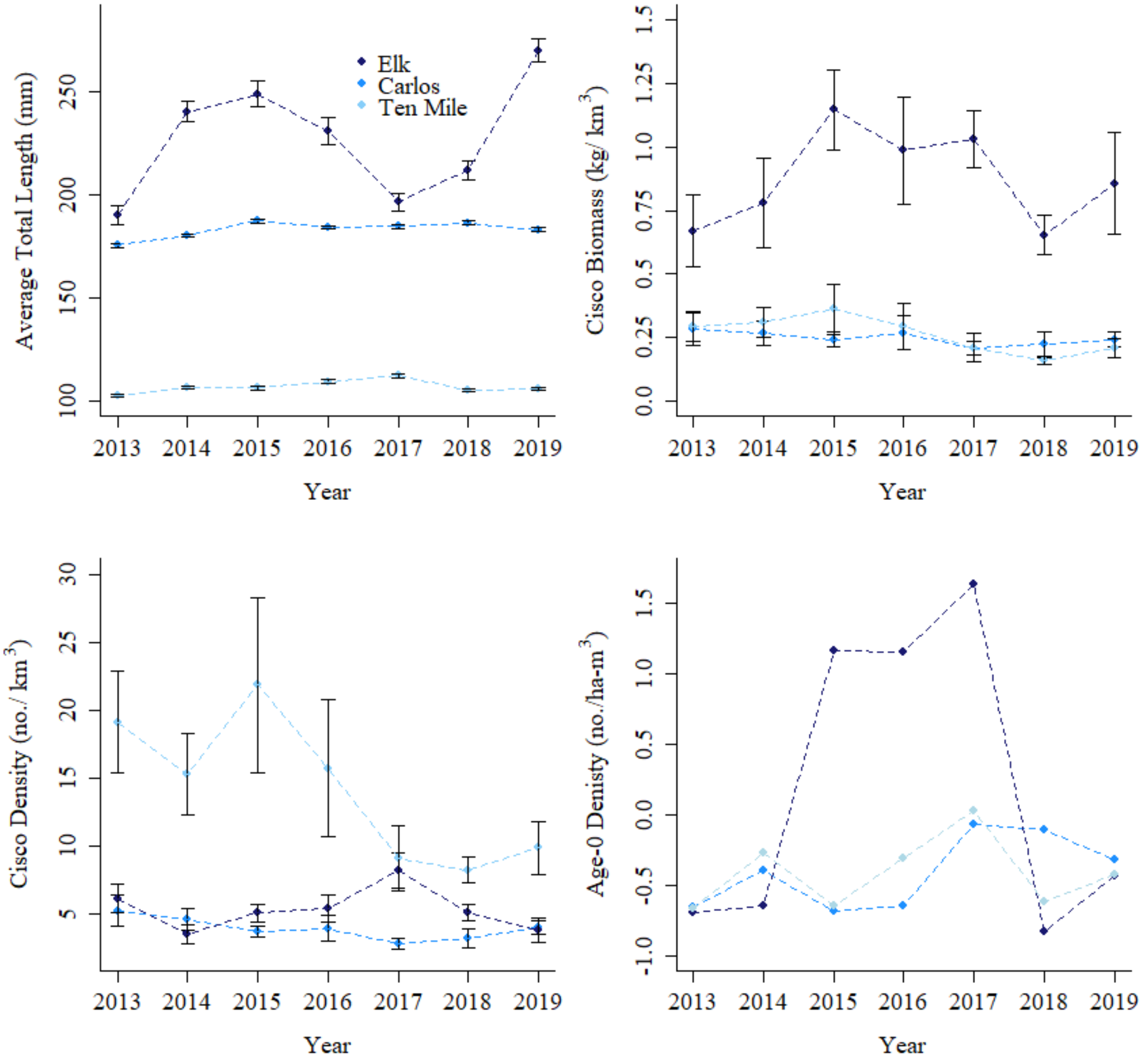

Figure 2- Time series plots of Cisco average total length, biomass, whole lake density, and standardized age-0 density calculated from single target and total backscatter hydroacoustic data in Carlos, Elk, and Ten Mile from 2013-2019. Bars represent 95% confidence intervals.

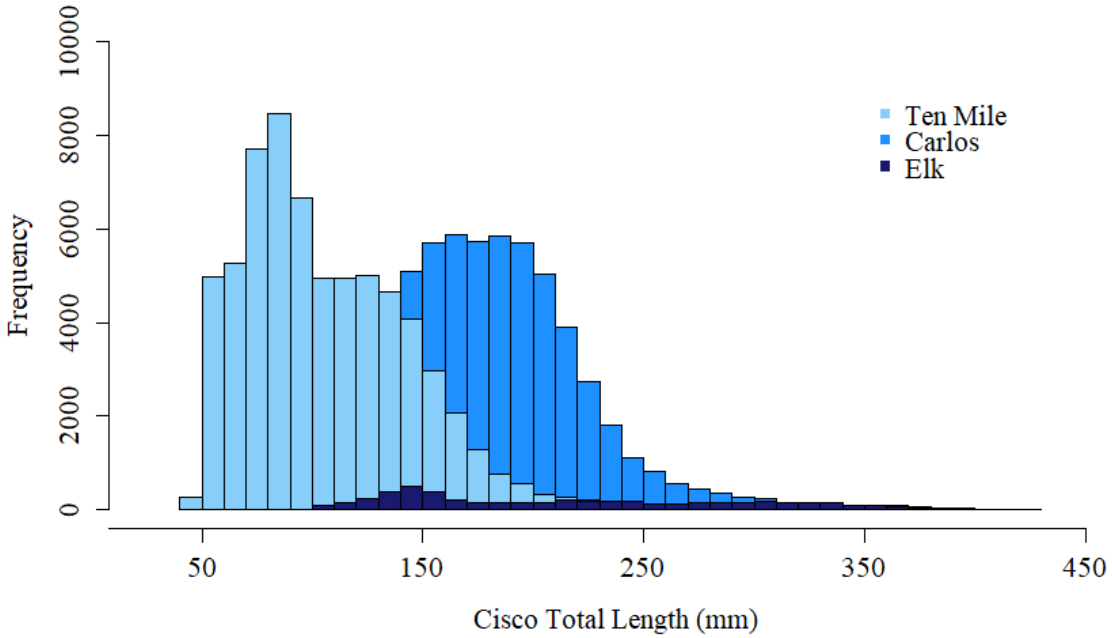

Figure 3- Length frequency distributions of Cisco total length from single target hydroacoustic data for Carlos, Elk, and Ten Mile from 2013-2019.

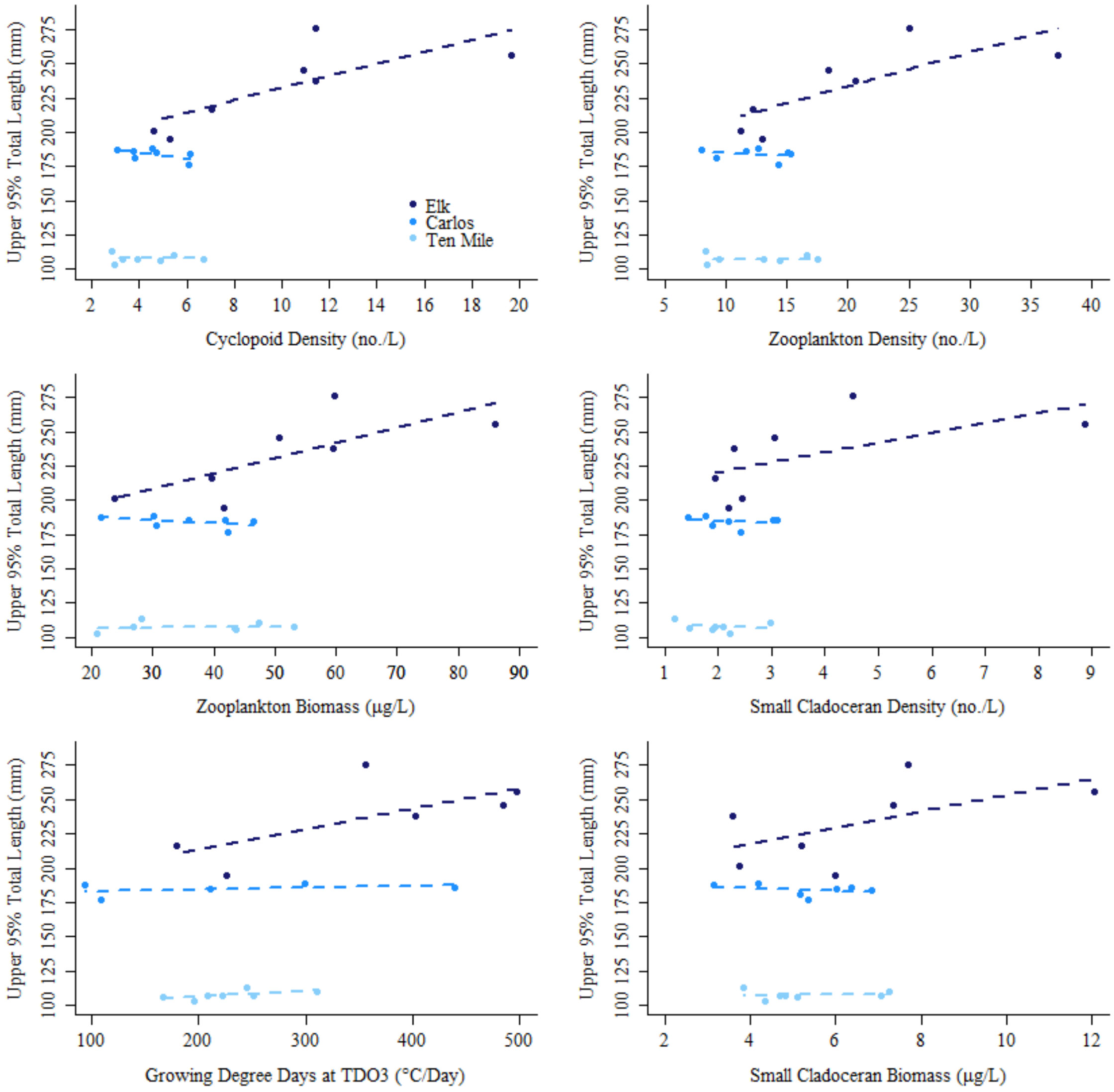

Figure 4- Significant relationships between the response variable of the upper 95% total length of Cisco age-1+ and associated predictor variables: average cyclopoid density (t = 4.05, var = 2795), zooplankton density (t = 3.72, var = 3204), zooplankton biomass (t = 2.91, var = 3410), average small cladoceran density (t = 2.76, var = 3326), growing degree days at dissolved oxygen of 3.0 mg/L (t = 2.36, var = 3632, and average small cladoceran biomass (t = 2.24, var = 3639), respectively.

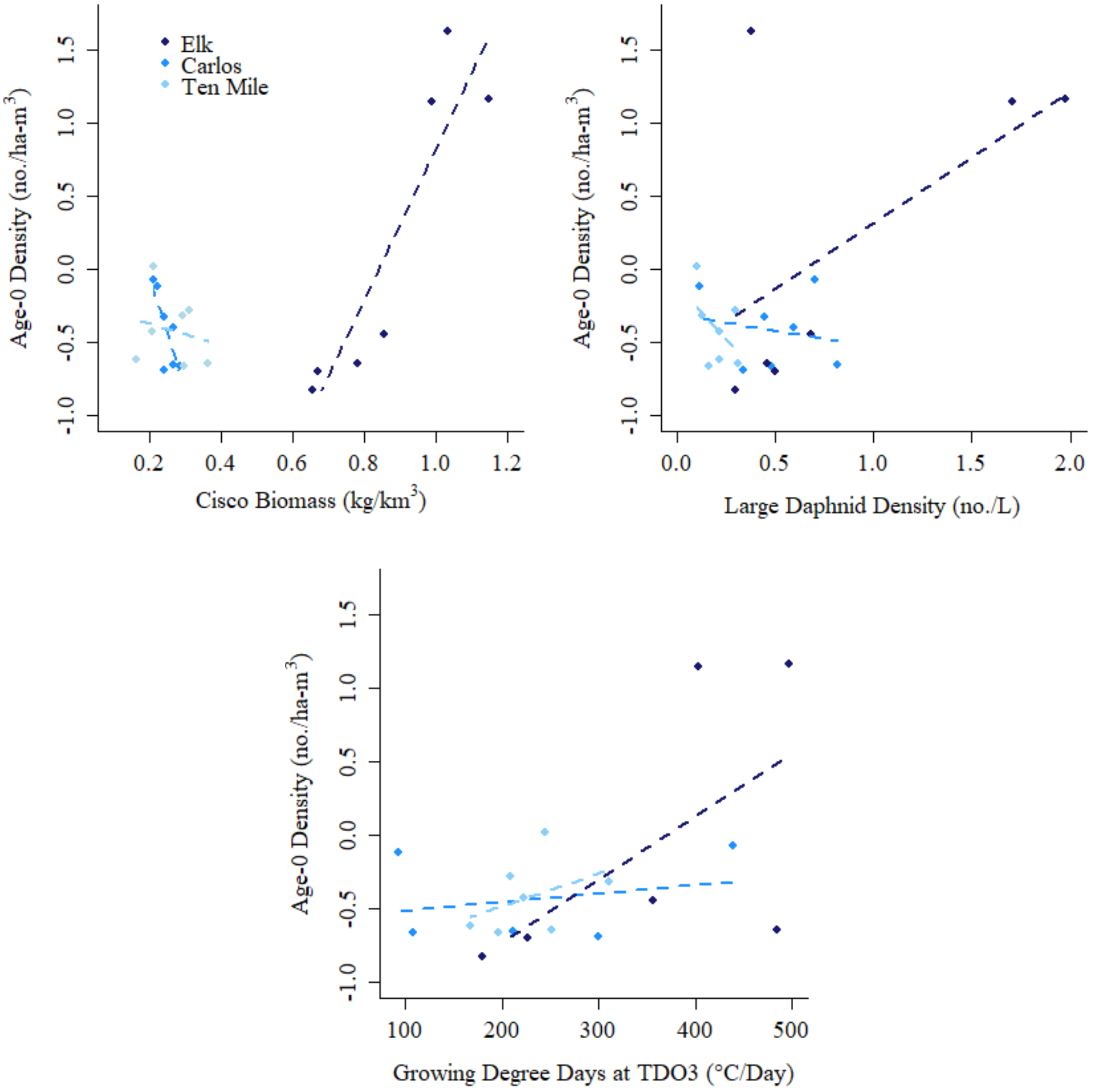

Figure 5- Significant relationships between the selected response variable of standardized age-0 density and associated predictor variables: Cisco biomass ($p < 0.01$, $R^2 = 0.41$), average large daphnid density ($p < 0.01$, $R^2 = 0.34$), and growing degree days where dissolved oxygen was 3.0 mg/L ($p = 0.02$ $R^2 = 0.29$), respectively.

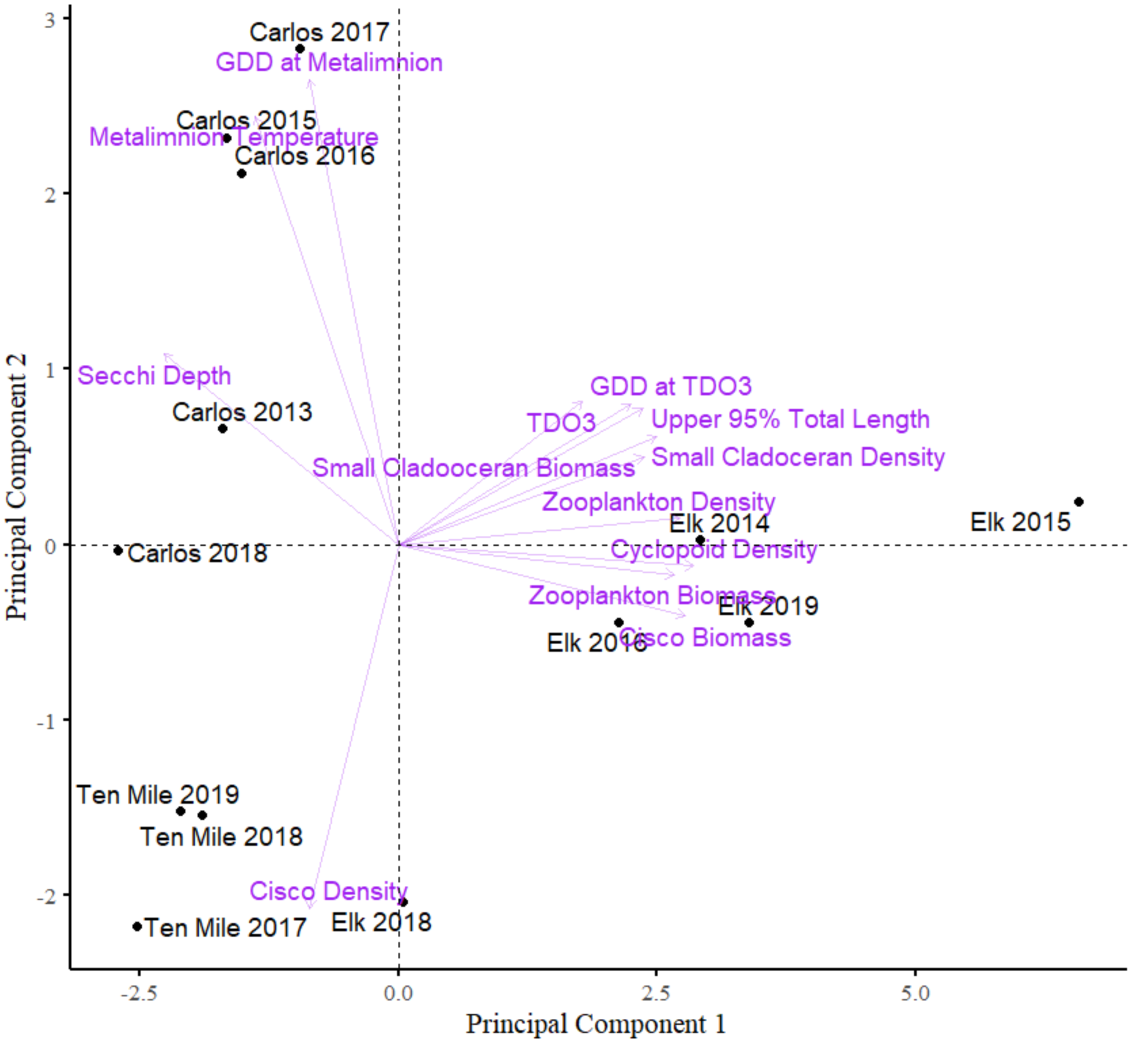

Figure 6- Principal components one and two used in principal component analysis to further understand correlations among all variables and the upper 95% total length of Cisco (PC1= 0.57, PC2 = 0.17). Purple text indicates individual variables and black text indicates lake year combinations used in the analysis. Individual variables and lake-year combinations that lie within close parameters with one another share similar principal components and therefore account for similarities in variation among the data.

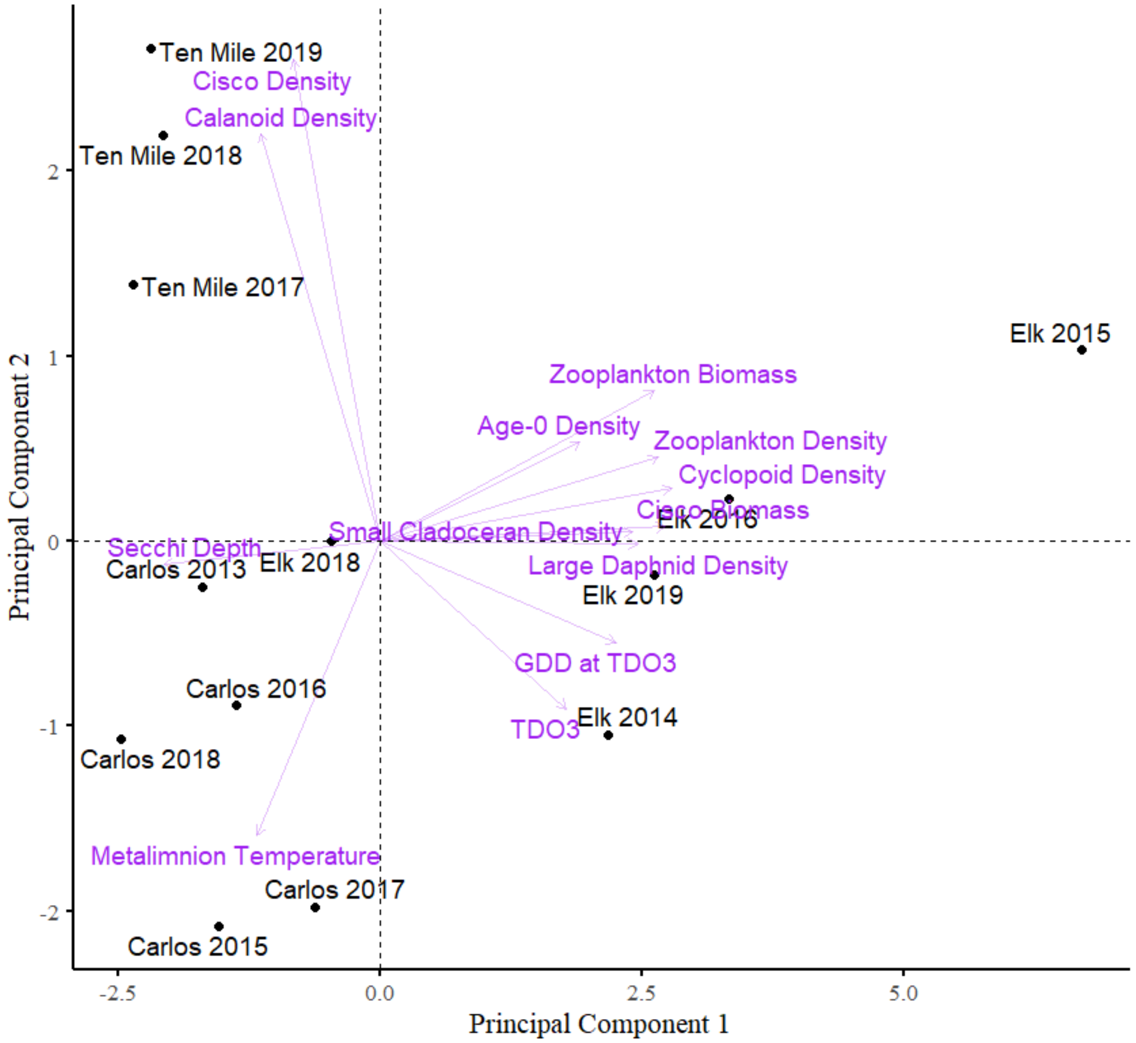

Figure 7- Principal components one and two used in principal components analysis to further understand correlations among all variables and the standardized age-0 Cisco density metric (PC1= 0.56, PC2 = 0.17). Purple text indicates individual variables and black text indicates lake year combinations used in the analysis. Individual variables and lake-year combinations that lie within close parameters with one another share similar principal components and therefore account for similarities in variation among the data.

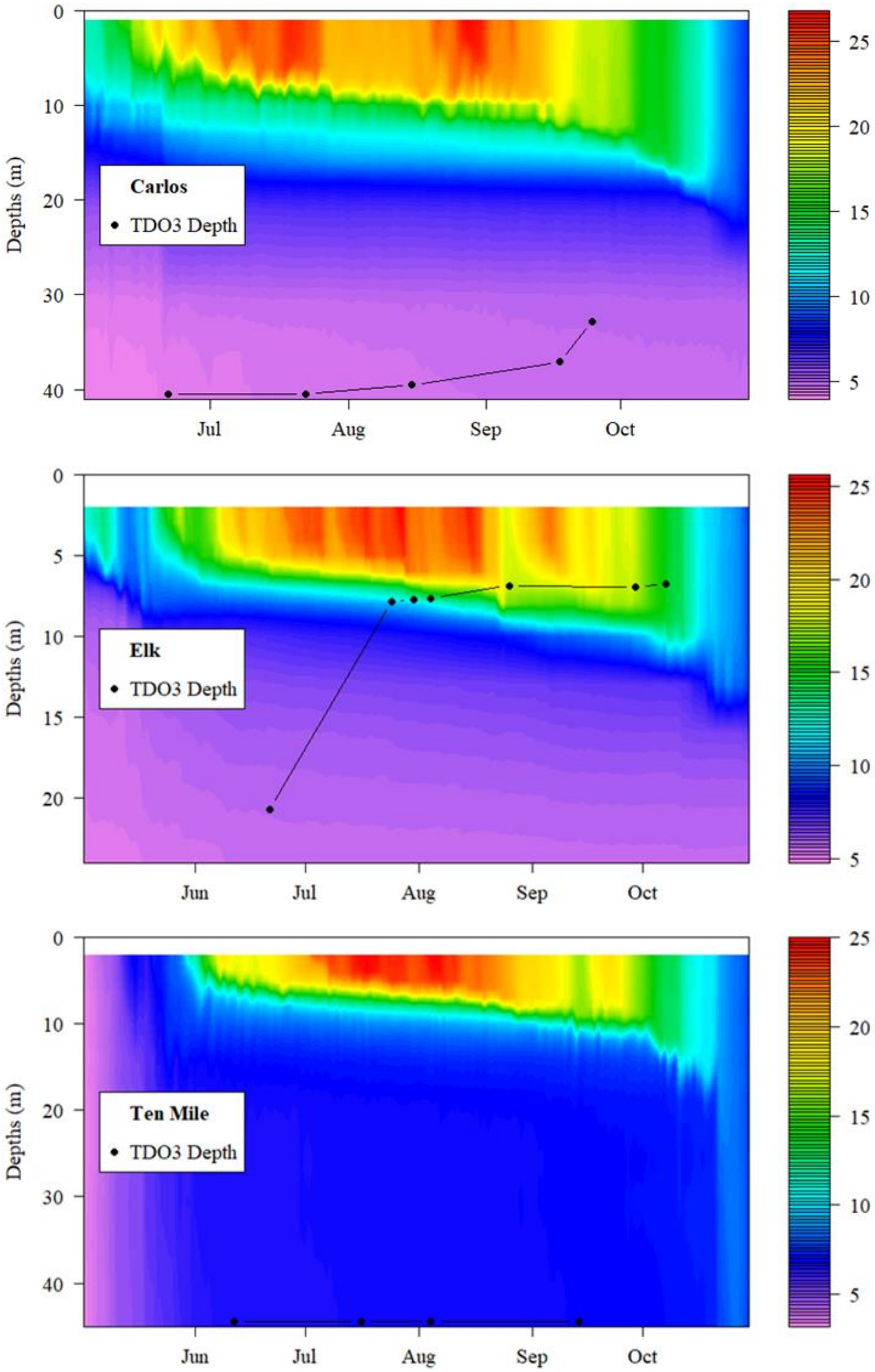

Figure 8- Heat plots of temperatures reached throughout the water column during a stratified season with depths where dissolved oxygen was 3.0 mg/L additionally plotted to better visualize the different oxythermal habitats Cisco experience within Carlos (2013), Elk (2015), and Ten Mile (2019).

Appendix

Tables

Table A1- Data used for Carlos.

Lake	**Year**	**Age 0 Density** (no. · ha^{-3})	**Upper 95% Total Length** (mm)	**TDO3** (°C)	**GDD at TDO3** (°C · day^{-1})	**Lower Limit Metalimnion Temperature** (°C)	**GDD at Metalimnion** (°C · day^{-1})	**Secchi Depth** (m)	**Calanoid Density** (no. · L^{-1})
Carlos	2013	-0.663	176.5	4.70	108.3	12.3	764.7	5.9	1.81
Carlos	2014	-0.399	181.3	-	-	11.3	756.1	5.2	1.14
Carlos	2015	-0.691	188.5	12.7	299.3	13.5	828.0	6.9	1.45
Carlos	2016	-0.647	185.0	6.33	210.6	13.1	911.4	7.0	2.13
Carlos	2017	-0.068	185.9	9.90	439.3	13.2	922.7	6.2	1.55
Carlos	2018	-0.114	187.4	4.47	93.2	10.2	652.2	5.4	0.97
Carlos	2019	-0.322	184.0	5.84	-	12.1	831.6	5.7	2.63

Table A1 (Continued)- Data used for Carlos.

Lake	**Year**	**Cyclopoid Density** (no. · L^{-1})	**Large Daphnid Density** (no. · L^{-1})	**Small Cladoceran Density** (no. · L^{-1})	**Small Cladoceran Biomass** (µg · L^{-1})	**Zooplankton Density** (no. · L^{-1})	**Zooplankton Biomass** (µg · L^{-1})	**Cisco Density** (no. · km^{-3})	**Cisco Biomass** (kg · km^{-3})
Carlos	2013	6.06	0.482	2.43	5.34	14.3	42.3	5.3	39.4
Carlos	2014	3.80	0.595	1.90	5.16	9.2	30.6	4.7	37.0
Carlos	2015	4.53	0.341	1.76	4.18	12.7	30.1	3.8	33.4
Carlos	2016	4.71	0.820	3.03	6.03	15.1	41.8	4.0	37.1
Carlos	2017	3.74	0.705	3.11	6.38	11.7	35.8	2.9	28.9
Carlos	2018	3.06	0.120	1.43	3.14	8.0	21.6	3.2	30.9
Carlos	2019	6.13	0.445	2.20	6.85	15.3	46.4	4.1	33.6

Table A2- Data used for Elk.

Lake	**Year**	**Age 0 Density** (no. · ha^{-3})	**Upper 95% Total Length** (mm)	**TDO3** (°C)	**GDD at TDO3** (°C · day^{-1})	**Lower Limit Metalimnion Temperature** (°C)	**GDD at Metalimnion** (°C · day^{-1})	**Secchi Depth** (m)	**Calanoid Density** (no. · L^{-1})
Elk	2013	-0.669	194.7	7.13	226.6	-	-	3.8	1.95
Elk	2014	-0.644	245.6	14.9	485.0	8.62	525.4	2.5	1.25
Elk	2015	1.16	255.6	11.0	497.1	8.69	528.2	3.8	1.57
Elk	2016	1.15	237.6	12.3	403.4	9.31	586.5	3.2	1.48
Elk	2017	1.63	201.1	-	-	8.94	547.8	3.1	0.853
Elk	2018	-0.827	216.4	6.26	179.1	7.26	391.5	3.6	0.698
Elk	2019	-0.438	275.8	9.37	355.6	8.56	512.9	2.0	1.17

Table A2 (Continued)- Data used for Elk.

Lake	**Year**	**Cyclopoid Density** (no. · L^{-1})	**Large Daphnid Density** (no. · L^{-1})	**Small Cladoceran Density** (no. · L^{-1})	**Small Cladoceran Biomass** (µg · L^{-1})	**Zooplankton Density** (no. · L^{-1})	**Zooplankton Biomass** (µg · L^{-1})	**Cisco Density** (no. · km^{-3})	**Cisco Biomass** (kg · km^{-3})
Elk	2013	5.29	0.501	2.20	5.99	13.0	41.7	6.1	7.87
Elk	2014	10.9	0.461	3.06	7.34	18.4	50.6	3.6	9.18
Elk	2015	19.7	1.97	8.86	12.0	37.2	86.1	5.1	13.5
Elk	2016	11.4	1.71	2.29	3.59	20.6	59.5	5.4	11.6
Elk	2017	4.58	0.381	2.45	3.74	11.2	23.7	8.2	12.1
Elk	2018	7.04	0.299	1.94	5.18	12.2	39.7	5.2	7.68
Elk	2019	11.4	0.679	4.52	7.68	25.0	59.8	3.9	10.1

Table A3- Data used for Ten Mile.

Lake	**Year**	**Age 0 Density** (no. · ha^{-3})	**Upper 95% Total Length** (mm)	**TDO3** (°C)	**GDD at TDO3** (°C · day^{-1})	**Lower Limit Metalimnion Temperature** (°C)	**GDD at Metalimnion** (°C · day^{-1})	**Secchi Depth** (m)	**Calanoid Density** (no. · L^{-1})
Ten Mile	2013	-0.664	103.0	6.02	196.0	-	-	5.6	1.78
Ten Mile	2014	-0.276	107.2	6.40	208.9	-	-	6.1	3.04
Ten Mile	2015	-0.644	107.2	6.91	251.1	-	-	6.5	4.96
Ten Mile	2016	-0.313	110.2	8.70	310.2	-	-	5.8	4.41
Ten Mile	2017	0.022	113.2	7.50	244.9	9.67	340.3	5.8	2.97
Ten Mile	2018	-0.618	106.0	6.50	166.7	8.97	548.5	6.1	4.26
Ten Mile	2019	-0.426	106.9	6.51	222.5	9.68	603.1	5.9	4.64

Table A3 (Continued)- Data used for Ten Mile.

Lake	**Year**	**Cyclopoid Density** (no. · L^{-1})	**Large Daphnid Density** (no. · L^{-1})	**Small Cladoceran Density** (no. · L^{-1})	**Small Cladoceran Biomass** (µg · L^{-1})	**Zooplankton Density** (no. · L^{-1})	**Zooplankton Biomass** (µg · L^{-1})	**Cisco Density** (no. · km^{-3})	**Cisco Biomass** (kg · km^{-3})
Ten Mile	2013	2.93	0.167	2.23	4.36	8.50	20.8	19.1	87.3
Ten Mile	2014	3.32	0.302	2.09	4.69	9.50	26.8	15.3	92.5
Ten Mile	2015	6.69	0.312	1.95	7.06	17.5	53.1	21.9	107.4
Ten Mile	2016	5.48	0.129	2.97	7.26	16.6	47.3	15.7	86.9
Ten Mile	2017	2.81	0.104	1.18	3.84	8.30	28.2	9.1	62.4
Ten Mile	2018	4.87	0.218	1.88	5.11	14.4	43.6	8.3	47.3
Ten Mile	2019	3.92	0.221	1.46	4.81	13.1	43.4	9.9	61.8

Figures

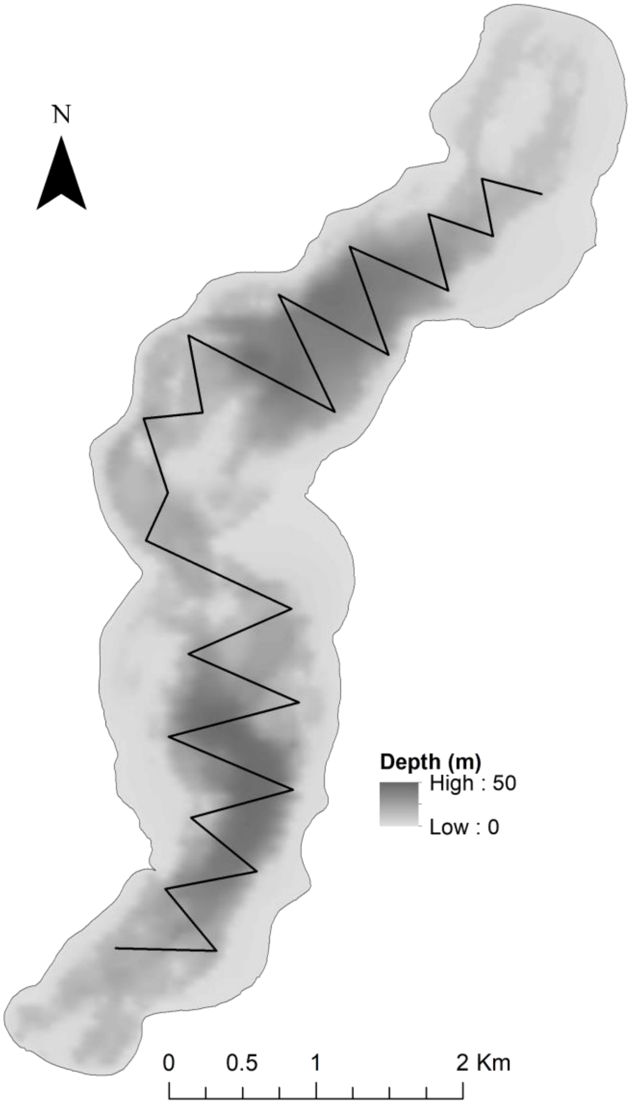

Figure A1- Map of Carlos Lake with hydroacoustic transects located in Douglass County, Minnesota.

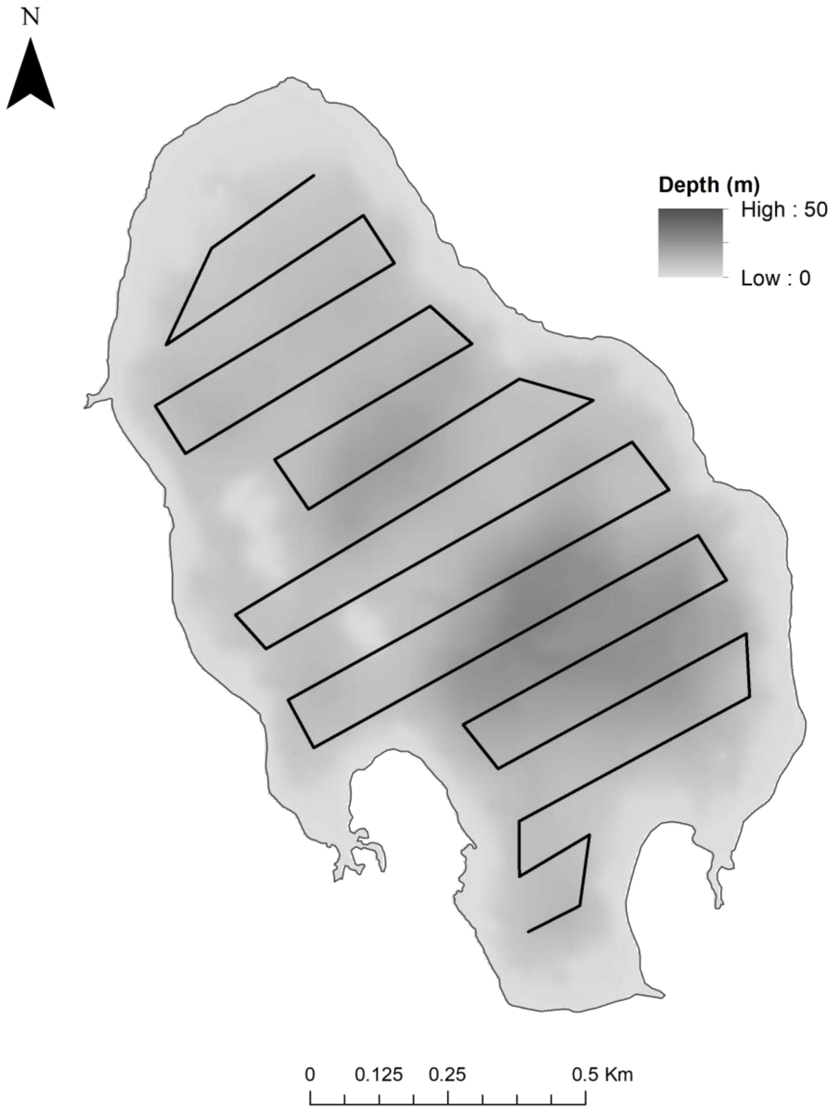

Figure A2- Map of Elk Lake with hydroacoustic transects located in Clearwater County, Minnesota.

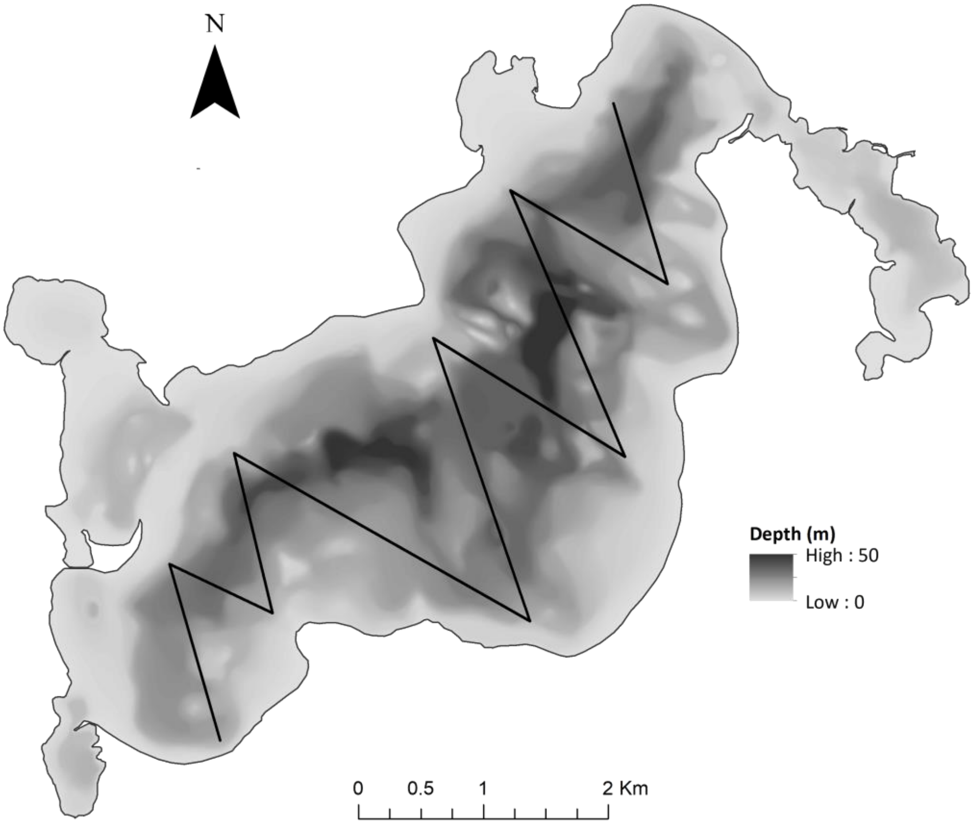

Figure A3- Map of Ten Mile Lake with hydroacoustic transects located in Cass County, Minnesota.

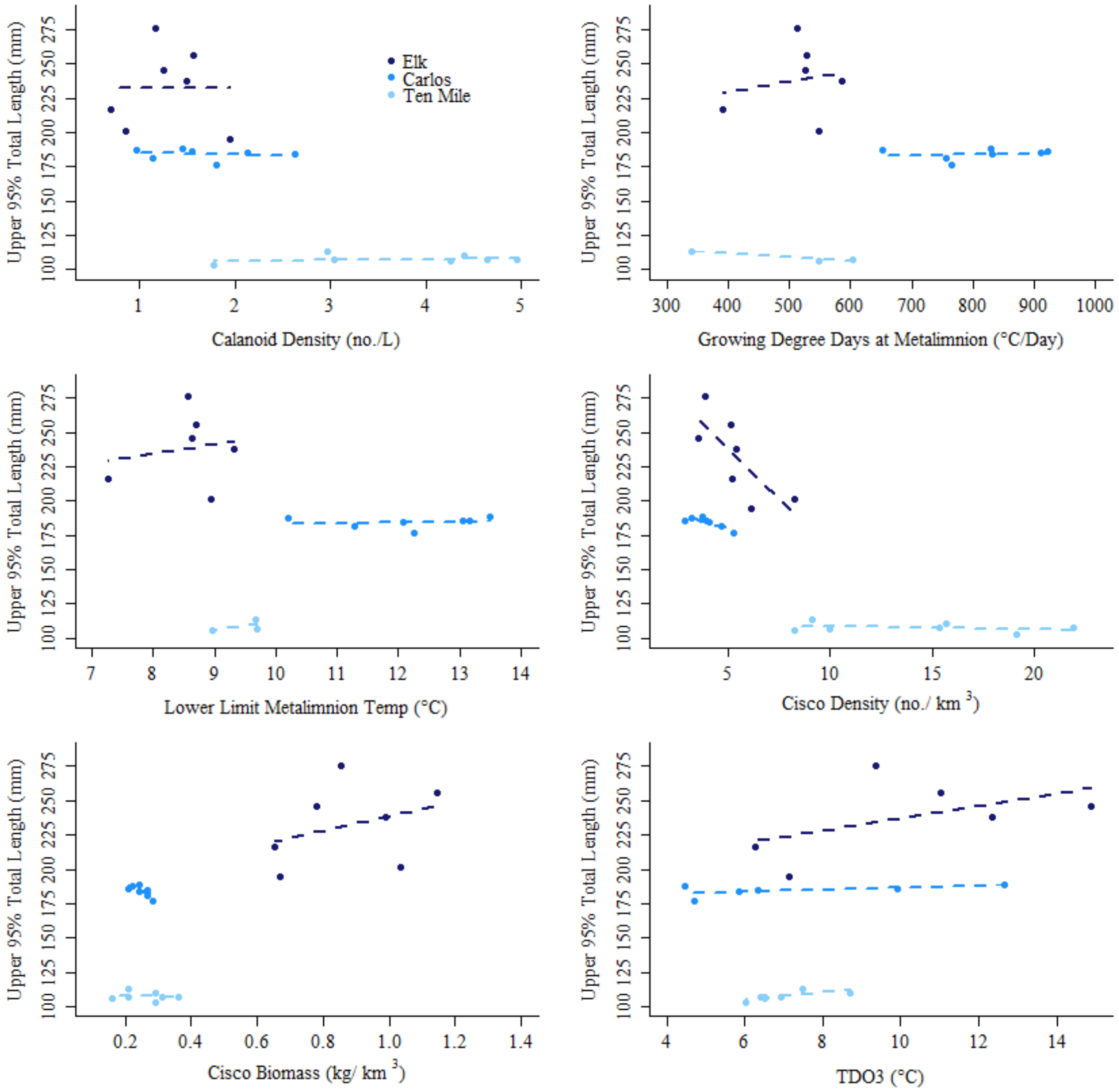

Figure A4- The upper 95% total length of Cisco age-1+ as a function of average calanoid density (t = -0.19, var = 3798), growing degree days at the metalimnion (t = 0.20, var = 4220), median lower limit metalimnion temperature (t = 0.33, var = 4339), Cisco biomass (t = -0.40, var = 3497), Cisco density (t = -1.08, var = 3029), and the temperature at dissolved oxygen of 3.0 mg/L (t = 1.12, var = 3911), respectively.

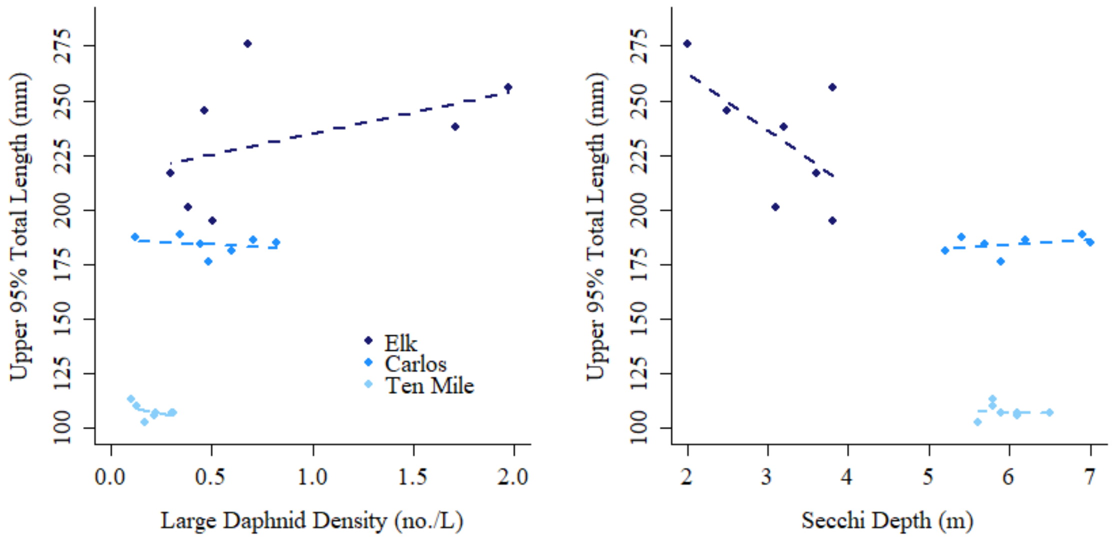

Figure A5- The upper 95% total length of Cisco age-1+ as a function of average large daphnid density (t = 1.90, var = 3256), and Secchi depth (t = -1.96, var = 2426).

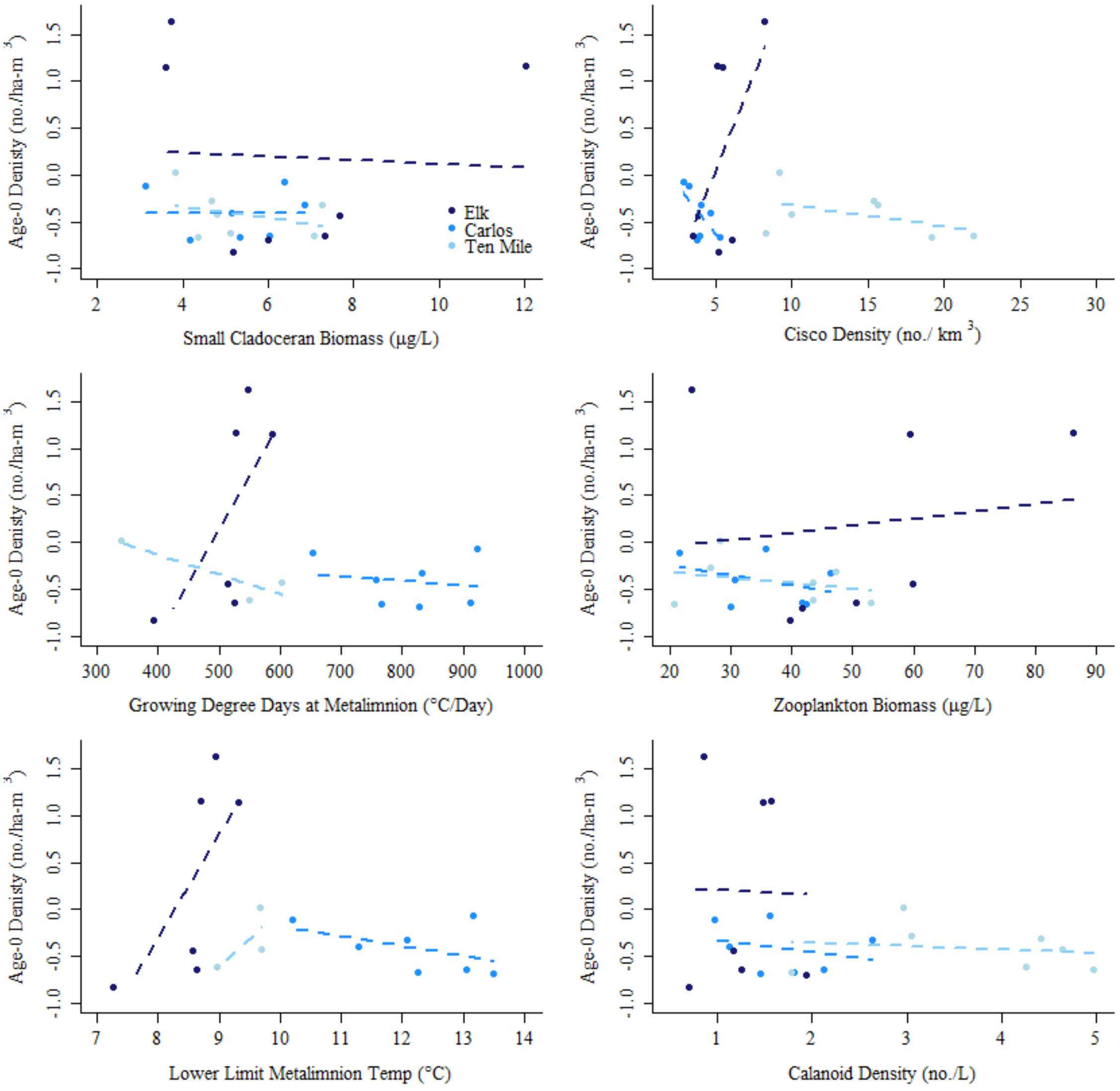

Figure A6- Standardized age-0 density as a function of average small cladoceran biomass ($p = 0.78$, $R^2 < 0.01$), Cisco density ($p = 0.35$, $R^2 = 0.04$), growing degree days at the metalimnion ($p = 0.56$, $R^2 = 0.05$), average zooplankton biomass ($p = 0.30$, $R^2 = 0.06$), median lower limit metalimnion temperature ($p = 0.30$, $R^2 = 0.08$), and average calanoid density ($p = 0.27$, $R^2 = 0.06$), respectively.

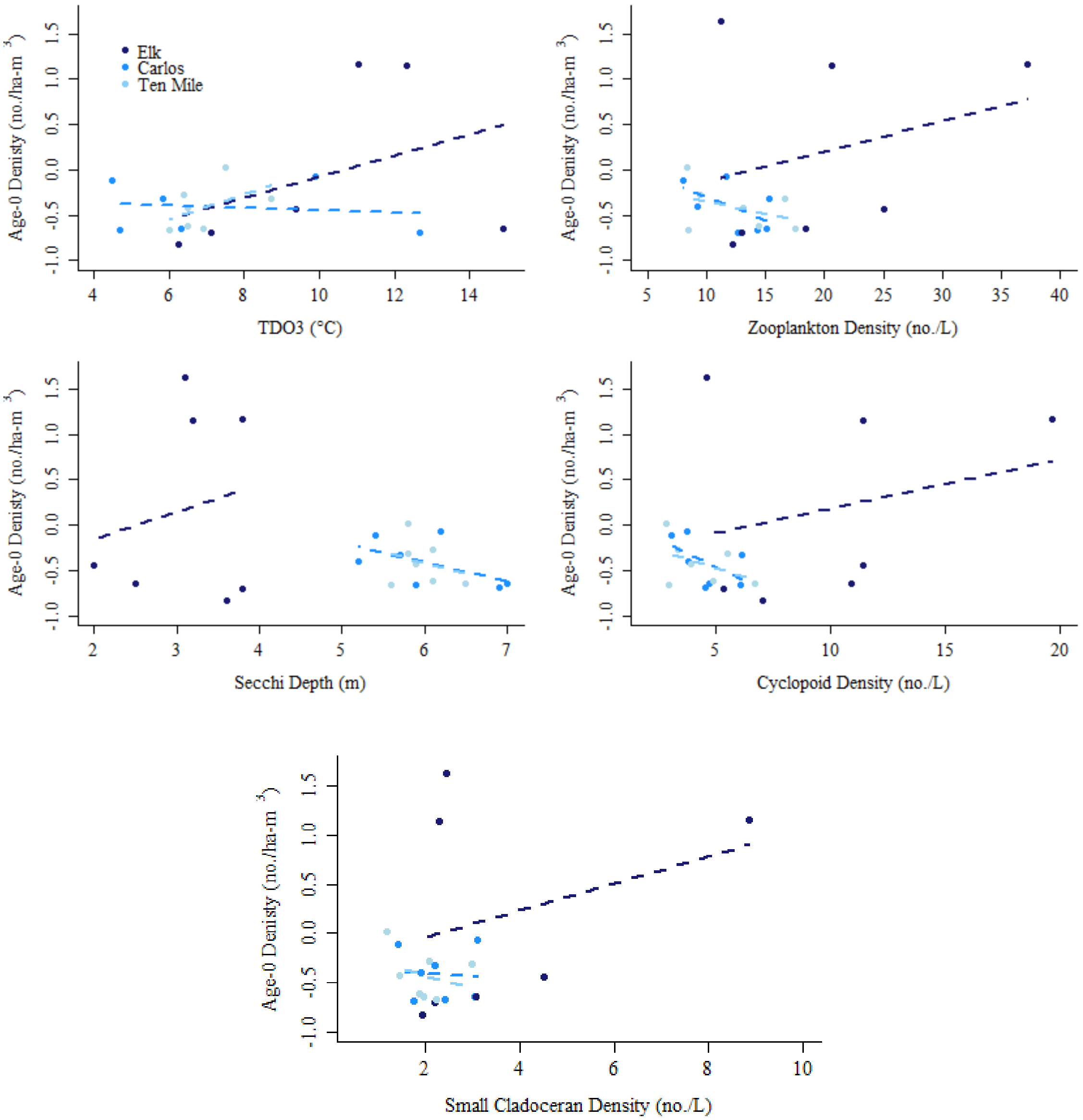

Figure A7- Standardized age-0 density as a function of the temperature at dissolved oxygen of 3.0 mg/L (p = 0.12, $R^2 = 0.13$), average zooplankton density (p = 0.11, $R^2 = 0.13$), average Secchi depth (p = 0.08, $R^2 = 0.15$), average cyclopoid density (p = 0.07, $R^2 = 0.16$), and average small cladoceran density (p = 0.07, $R^2 = 0.14$), respectively.