Final Project Report
Great Lakes Fish and Wildlife Restoration Act

Project Title: The importance of the larval stage to cisco recruitment variation in the Great Lakes

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Study Objectives: *We sampled multiple spawning/natal sites in Lake Superior and single sites in lakes Huron and Michigan to: (1) Examine inter-annual variability in larval densities within each site, across sites, and across lakes to determine consistency and synchronicity in recruitment patterns at the larval stage; (2) Correlate larval densities with spawning stock to identify if bottleneck occurs prior to or after the larval stage; (3) Examine the influence of growing conditions (as measured by prey resources and temperature) and rainbow smelt predation on larval cisco recruitment patterns to test the hypothesis that growth potential at the larval stage, and not predation, is the dominant factor governing recruitment variability.*

Completion of Objectives:

The research conducted to complete these objectives will form the basis of a doctoral dissertation in preparation by the senior author of this completion report. The dissertation is expected to be finished during 2013. Here we summarize the background, methods, results, and preliminary discussion of our research to address each of the objectives listed above.

Objective 1: *Examine inter-annual variability in larval densities within each site, across sites, and across lakes to determine consistency and synchronicity in recruitment patterns at the larval stage*

We divided this objective into two components. These components will be discussed separately.

Objective 1.1: Examine the inter-annual variability in larval densities within each site, across sites, and across lakes.

Most of the agencies that formulate the Lake Superior Technical Committee contributed to the sampling effort for this objective. We followed methods outlined by Myers et al. (2008) to sample larval cisco during the period of emergence (i.e., late April through early June) at multiple locations throughout the upper Great Lakes (Figure 1). Briefly, we used 0.5 m conical plankton nets equipped with 500 µm mesh. The nets were deployed off the stern of small vessels (i.e., <10 m) and towed for approximately 5 minutes through the surface stratum. We used a systematic sampling design with one sample site per 1,000 ha at a given location. Zoopankton samples were also collected at a subset of sites to assess the association between copepod nauplii density (the primary food of larval cisco) and cisco density. We used 0.5 m conical plankton nets equipped with 63 µm mesh. The nets were dropped to 5 m depth and lifted vertically to the surface. We calculated the average density of larvae and copepod nauplii for each synoptic survey at each location. We then examined the variability among years by plotting the distribution of estimates for each year at each location (Figure 2).

With the exception of 2009, densities of larval cisco at individual sites were fairly consistent across years. Thunder Bay and South Shore larval cisco densities in the year 2009 are clearly greater than the densities observed during other years. Black Bay was also sampled in 2009 yet the estimates of larval cisco abundance are modest compared to Thunder Bay and the South Shore (Figure 2). We assume that the low density in Black Bay is a product of limited numbers of spawners (see Objective 2).

We have evidence that the 2009 year-class was moderately successful across Lake Superior and that all other year classes were largely unsuccessful (see Objective 1.2). This suggests that larval surveys could serve as an index of cisco year-class strength; that is, indices of abundance from larval surveys appear to predict subsequent year-class strength reasonably well. This in turn implies that for cisco, year-class strength is determined prior to the end of the larval stage. If life stages after the larval phase were most critical for recruitment, we would have expected larval densities to be more consistent across years.

We originally hypothesized that high densities of zooplankton prey would lead to greater survival of age-0 cisco. Interestingly, there does not appear to be a positive relationship between larval cisco density and copepod nauplii density. Rather, nauplii densities appeared to be low while larval cisco densities were unusually high in 2009 at the Thunder Bay and South Shore sites (Figure 2). One explanation for this pattern might be that higher densities of larval cisco results in greater predation on zooplankton resources. Although this hypothesis is simple in concept, it is important to consider the densities of both larval cisco and copepod nauplii that were observed. During favorable conditions, our highest estimates of larval cisco density were approximately $1/m^3$. Contrary to this, our estimates of nauplii density were often > $5,000/m^3$. We doubt cisco larvae have the physical capabilities to capture and handle a significant portion of the nauplii population.

An alternative hypothesis would be that the spatial scale of our sampling was inappropriate. If zooplankton resources were aggregated into a more confined space, it would present a more favorable foraging arena for larval cisco. This scenario could also influence our density estimates given that we always integrate our sample across the entire path of the net. If given the opportunity to repeat the sampling effort, it would be difficult to make recommendations regarding the appropriate spatial scale for sampling. In fact, empirical sampling with nets may never be capable of obtaining accurate estimates of density at the scale that is critical for larval fish dynamics. However, we do believe that bio-physical models could help us gain a greater appreciation of the physical factors that could influence the distribution of both cisco larvae and zooplankton in the surface stratum. We believe it would be worthwhile to use physical models to explore how particles (i.e., larval fish and zooplankton) move within an aquatic environment at varying degrees of wind stress and temperature. This concept has been explored in the marine literature (Cury and Roy 1989), yet comparatively fewer studies have explored the fluid dynamics of water (e.g., Langmuir Cells) and how it may influence fish recruitment in freshwater.
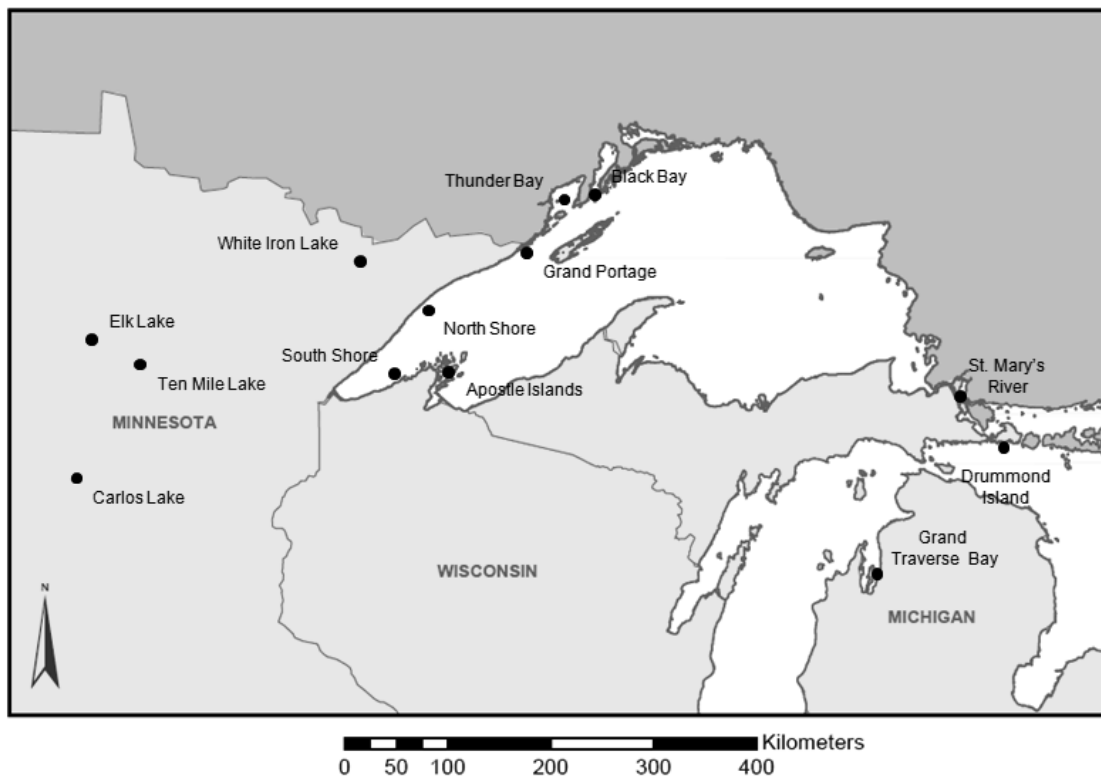

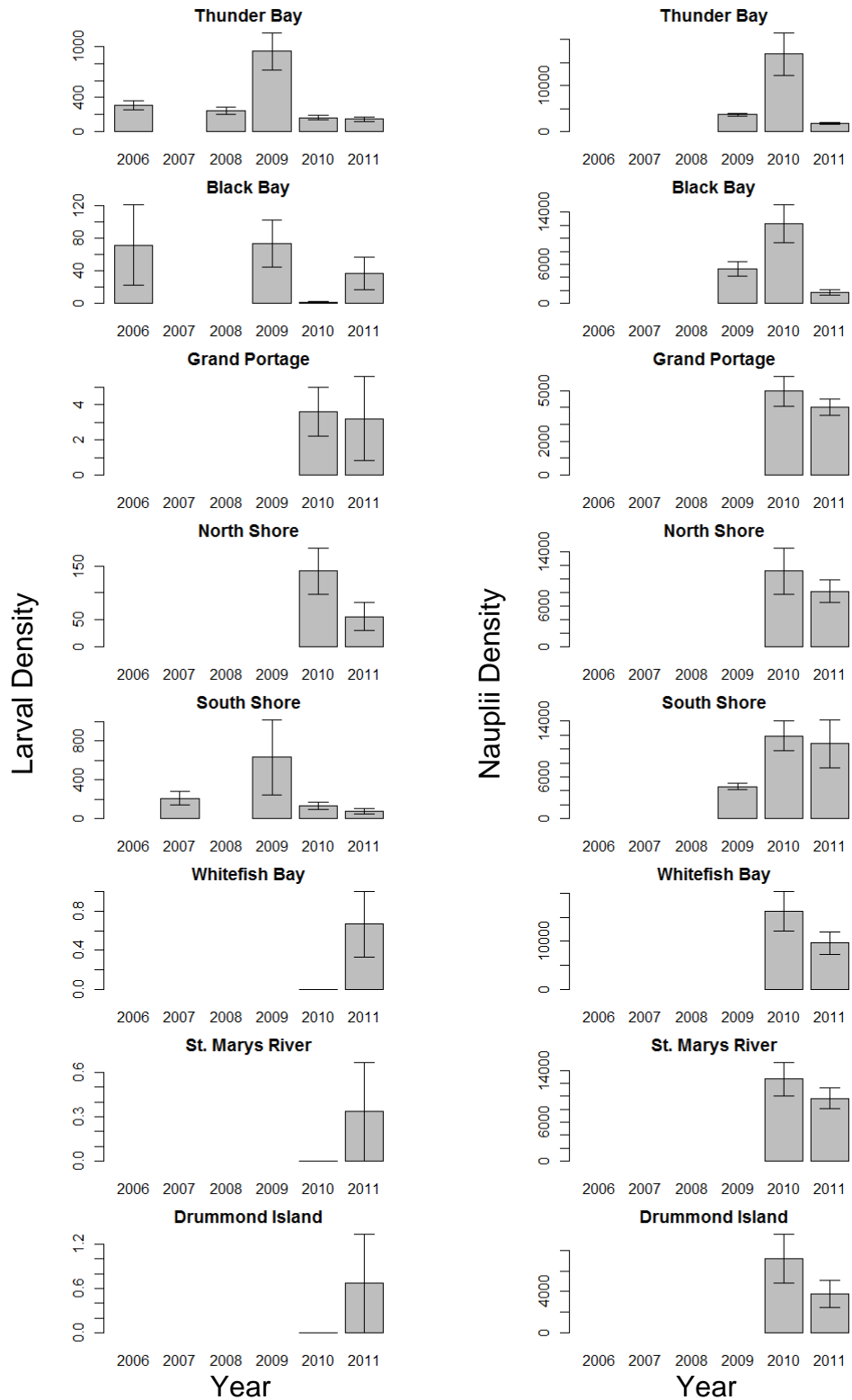Figure 1. Locations of cisco populations used in the analyses.

Figure 2. Observed densities of larval cisco (number/1,000 m^3) and copepod nauplii (number/m^3) at sampling locations throughout the upper Great Lakes. Error bars are one standard error.

Objective 1.2: Examine synchronicity in recruitment patterns.

Cisco (*Coregonus artedi*) are a widely distributed freshwater species in the northern regions of North America and can be found in both the Laurentian Great Lakes and deep inland lakes (Scott and Crossman 1998). Bronte et al. (2003) and Stockwell et al. (2009) provided evidence that year-class strength was synchronized across Lake Superior cisco stocks and concluded that large-scale abiotic processes were responsible for the observed patterns. However, as was highlighted by Bunnell et al. (2010), it is difficult to assume population synchrony is the result of synchronized climatic events when dispersal of individuals cannot be ignored. To better understand whether dispersal or climate drives synchrony of Lake Superior cisco recruitment, we examined the inter-annual variability in larval cisco densities across the Upper Great Lakes (Objective 1.1). Due to the limited mobility of larval fish, we hypothesized that spatial synchrony at the larval phase would strengthen the view that large-scale environmental factors are important for determining cisco recruitment. Given that Objective 1.1 provided evidence that larval cisco densities were synchronized, we used Objective 1.2 to better understand the large-scale climatic factors that might be influencing cisco recruitment.

Climatic stochasticity and the resulting synchronization of animal populations are often referred to as the Moran effect (Phelps et al. 2008). Moran's theorem states that the spatial correlation of population variation will equal the environmental correlation in populations with identical linear dynamics (Moran 1953). To look for evidence of the Moran Effect on cisco we considered cisco populations covering a broad spatial scale (>1000 km) and from a range of lake sizes. We coupled this with an analysis of the site-to-site correlation of spring meteorological observations from offshore Great Lakes weather buoys.

We sampled 12 discrete cisco populations in the year 2010 (Figure 1). Sampling was carried out by several agencies and institutions across the upper Great Lakes region. Cisco populations in Minnesota inland lakes were assessed during July and August while populations in the Great Lakes were assessed during November. Hydroacoustics were coupled with a netting effort to survey each cisco population. Acoustic data collection and processing followed the Great Lakes standard operating procedure (Parker-Stetter et al. 2009).

The researchers that participated in this study used different sampling gears to collect fish. We operated under the assumption that each researcher used the best gear available for the given location, and that the sample was appropriate for apportioning acoustic targets and estimating abundance of cisco. All catches were sorted to species and we measured total length of all fish from most catches, but did sub-sample some large catches. Fish that were not measured were assigned a total length based on the measurement of ≥100 randomly selected fish of the same species.

We used classification tree models to apportion acoustic targets to species. Trees were developed using the recursive partitioning package (Therneau and Atkinson 2012) available in R (R Development Core Team 2011). Separate trees were developed for both large and small fish caught at each site. Species was the response variable for each tree while year, latitude, longitude, bathymetric depth, and depth of capture were potential explanatory variables. The number of samples collected and the characteristics of certain sampling approaches negated the use of some explanatory variables. For example, use of a single vertical gill net negated the use of "latitude" and "longitude" while use of bottom set gill nets negated the use of "capture depth." Trees were first constructed using a liberal complexity parameter (0.0001) and then pruned back based on the cross-validation error associated with each of the splits. We chose the smallest tree in which the point estimate of cross validation error fell within one standard error of the minimum cross validation error. Only terminal leaves with ≥10 fish were considered. The species proportions of the terminal leaves were used to apportion acoustic targets to species. If the model could not find a meaningful split of the data, we simply used the species proportions from the catches to apportion acoustic targets.

All intervals were integrated across depths and then averaged to generate a single estimate of density. In an effort to limit rounding errors in subsequent calculations we standardized all density estimates to number of fish per 1,000 ha. We assigned ages to cisco of given lengths using semi-random age length keys (Ogle 2012) constructed with 50 mm length bins. All cisco were aged using the crack and burn method of aging otoliths. The maximum length category in the age-length key was used to assign ages to the few fish that were greater than the maximum length category. We also had a limited number of cisco that were smaller than the minimum length category of the age-length key for a given assessment. Under this circumstance we assigned the age using the mean-length-at-age analysis reported by Stockwell et al. (2009). We multiplied the proportions-at-age by the average acoustic density to determine the density of each year-class.

A weighted catch-curve regression (Maceina and Bettoli 1998) was fit to the age frequency distribution (i.e., age-1 to the maximum observed age) of each population and the relative strength or weakness of each year-class was defined as the internally studentized residual. A weighted regression was used for the analysis because cisco are known live in excess of 20 years (Yule et al. 2008) and exhibit sporadic recruitment (Stockwell et al. 2009). Older and rarer cohorts are often represented less accurately (i.e., due to small samples of fish collected) and thus, a weighted regression deflates the importance of these cohorts. Pearson product moment correlation coefficients were used to determine whether population fluctuations were synchronous among locations. All analyses were conducted using R (R Development Core Team 2011). Results of the catch curve analysis can be found in Figure 1.

Meteorological and limnological data were obtained from eight offshore NOAA buoy stations in Lakes Superior, Michigan, Huron, and Erie. We used records between May 15 and June 15 for the years 1983 to 2011 because this is the period of larval cisco emergence in Lake Superior (Myers et al. 2006). When there were multiple records for a single day, we used the average. We examined the spatial correlation of average air temperature, average water temperature, average wind speed, and maximum wind speed for each year using Pearson product moment correlation coefficients.

We followed the methods used by Myers et al. (1997) in their global, multi-species meta-analysis in order to ensure comparability of results. As was highlighted by Myers et al. (1997), a simple estimate of the spatial scale of synchrony is the distance over which the pairwise correlation between recruitment time series is reduced by a factor e^{-1}, (i.e., the exponential decay rate or the *e*-folding scale; Myers et al. 1997). Using iterative least squares, we fit the following model

$$\rho(d) = \rho_0 e^{-\frac{d}{v}}$$

where ρ_0 is the correlation between two stocks at zero separation, v is the e-folding scale, and d is the distance between populations in kilometers. In this model, we constrain ρ_0 to have an absolute value of 1 or less. To take into account that some correlation-distance relationships might have a "shoulder" at d=0, we also fit the following model developed by Myers et al. (1997)

$$\rho(d) = \rho_1 e^{-0.5\left(\frac{d}{\sigma}\right)^2}$$

where σ is a fitted parameter, analogous to v, above. Pairwise correlations were only included if the recruitment time-series for the two populations had an overlap of at least 5 years.
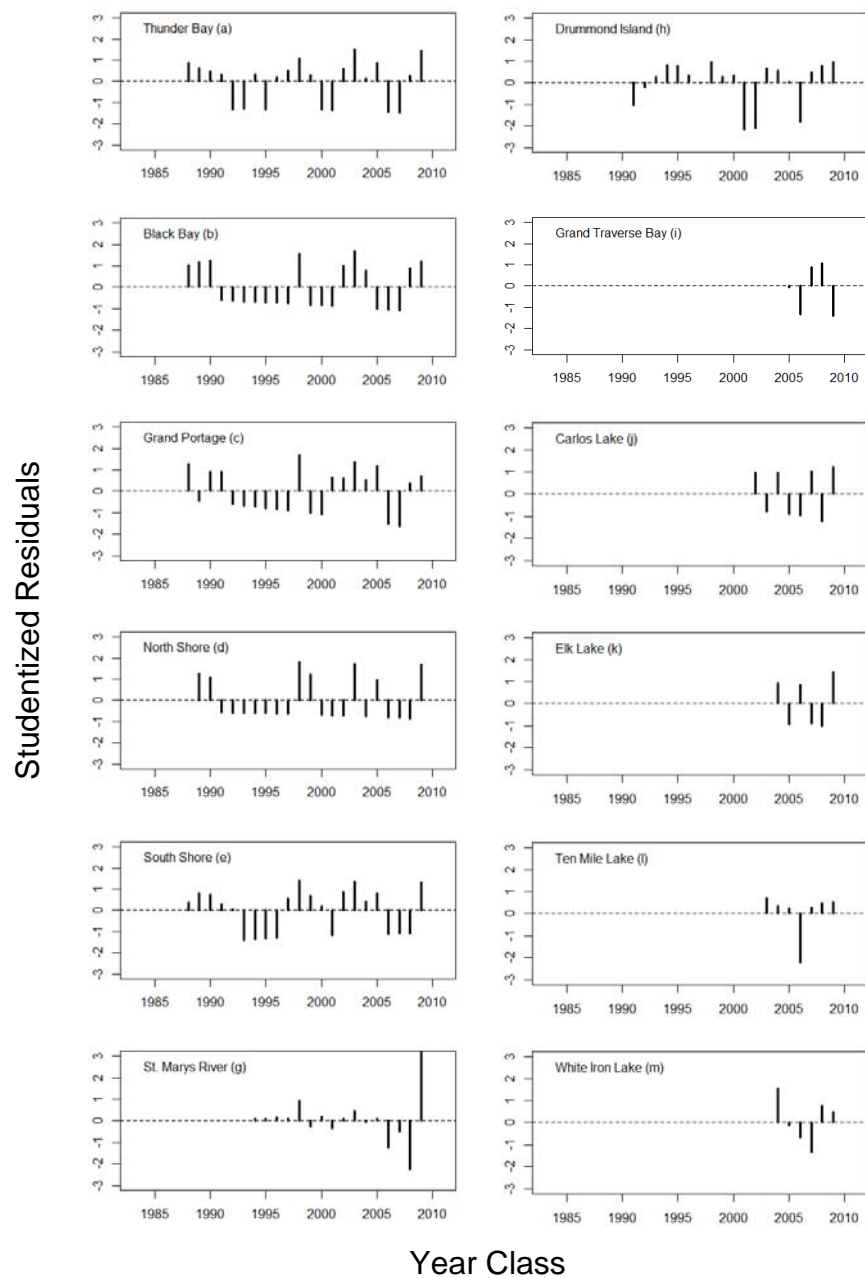
Figure 3. Time-series of residuals from catch-curve regressions. These residuals serve as indexes of year-class strength for cisco populations in the Great Lakes (a-i) and Minnesota inland lakes (j-m).

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According to Myers et al. (1997), we would have expected the correlation-distance relationship for cisco recruitment to deteriorate at a relatively short distance (i.e., <50km). However, it is clear that the spatial scale of synchrony for cisco recruitment is more similar to marine species than it is to other freshwater species (Figure 4; Table 1). Our estimates of the model parameters provide evidence that the e-folding scale for cisco recruitment is approximately 500 km (Table 1), which is strikingly similar to the estimates Myers et al. (1997) generated for a host of marine species.
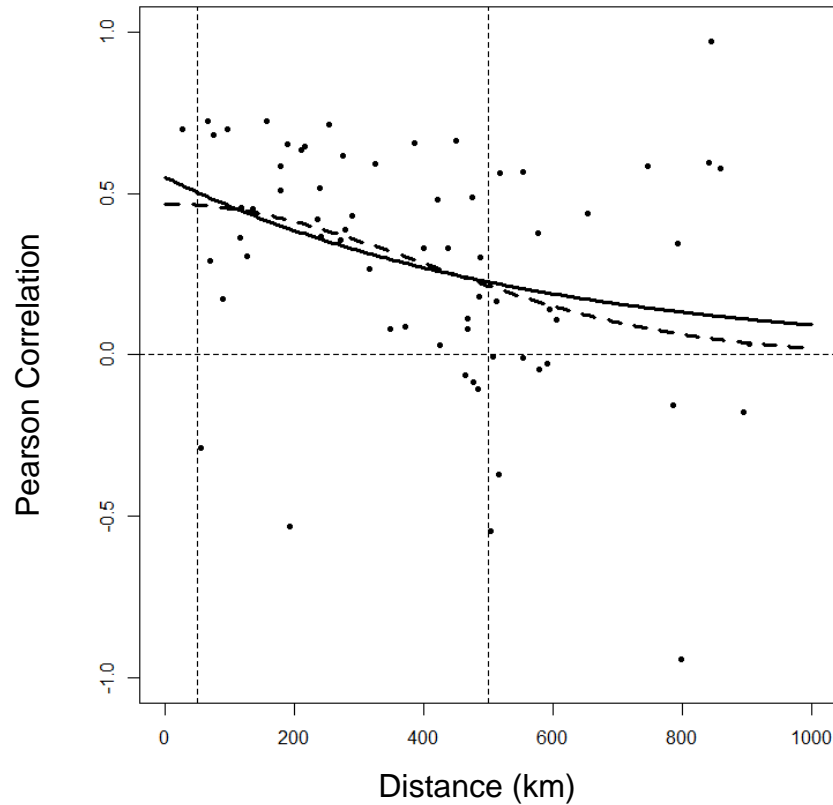

Figure 4. Correlation of recruitment between pairs of cisco stocks versus distance. All populations were sampled in 2010. Fits of the models $\rho_0 e^{-\frac{d}{v}}$ (solid curve) and $\rho_1 e^{-0.5\left(\frac{d}{\sigma}\right)^2}$ (broken curve).

Table 1. The parameter estimates and their standard errors (SE) for the two models used to describe the spatial scale of correlation of cisco recruitment meteorlogical data. The meteorlogical variables that were investigated include a) average spring air temperature, b) average spring water temperature, c) average spring wind speed and, d) maximum average daily spring wind speed. See text for further detail.

Data	$\rho_0 e^{-\frac{d}{v}}$				$\rho_1 e^{-0.5\left(\frac{d}{\sigma}\right)^2}$			
	df	RSE	ρ_0 (SE)	v (SE)	df	RSE	ρ_1 (SE)	σ (SE)
Recruitment	64	0.346	0.55 (0.13)	561 (238)	64	0.346	0.47 (0.08)	400 (91)
Meteorlogical Variables								
a	26	0.159	0.85 (0.09)	2499 (1397)	26	0.155	0.80 (0.05)	983 (231)
b	26	0.122	0.94 (0.07)	1938 (617)	26	0.118	0.86 (0.04)	911 (136)
c	26	0.132	0.67 (0.07)	1553 (644)	26	0.134	0.59 (0.05)	853 (192)
d	26	0.252	0.68 (0.25)	396 (181)	26	0.260	0.45 (0.13)	388 (114)

The site-to-site correlation of measures related to wind and thermal forcing versus separation of Great Lakes weather stations are shown in Figure 4. The correlation scale (i.e., σ) is greater than 800 km for average spring air temperature, water temperature, and wind speed (Table 1). However, the correlation scale of maximum average daily wind speed was only 388 km, which is similar to the estimate of 400 km for cisco recruitment (Table 1). We felt that the similarity between estimates of σ warranted further investigation of the relationship between cisco recruitment and strong wind events during the spring period.

We first plotted the time-series of maximum average daily wind speed and water temperature using the buoy data from the western arm of Lake Superior. Interestingly, the two years with the least severe wind event were 1984 and 2003, which were also two of the largest cisco year-classes since the collapse of cisco in Lake Superior (Stockwell et al. 2009). We speculate that strong wind

events could advect larvae from warmer, more productive, nearshore areas into the colder, less productive offshore waters. The 1998 cisco year-class was also very large (Stockwell et al. 2009), yet the maximum wind event was moderately severe (Figure 5). What is intriguing about the 1998 year-class is that temperatures were extremely high during the spring of that year (Figure 5). It is plausible that a calm spring would encourage warmer nearshore surface water temperatures by limiting the probability of upwelling events. It is then also plausible that a warmer environment would encourage production of zooplankton prey and ultimately increase rates of age-0 cisco development. Faster rates of growth are believed to increase survival by helping larval fish escape predation bottlenecks sooner (Miller et al. 1988). This suggests that both wind and temperature play a dynamic role in cisco recruitment.
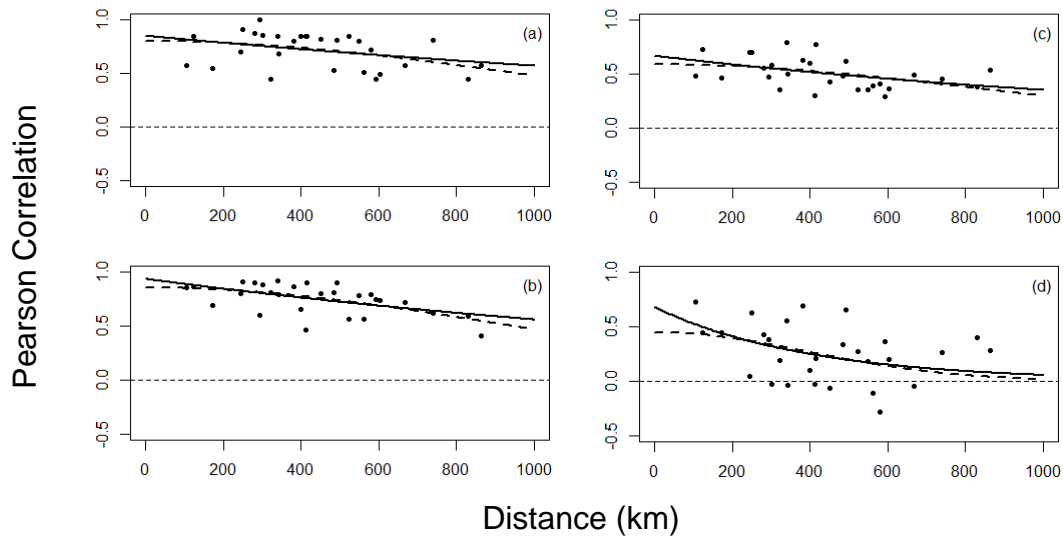

Figure 4. Correlation of a) average spring air temperature b) average spring water temperature c) average spring wind speed and d) maximum average daily spring wind speed between pairs of NOAA's Great Lakes buoys versus distance. Observations are from May 15 to June 15 for the years 1983-2011. Fits of the models $\rho_0 e^{-\frac{d}{v}}$ (solid curve) and $\rho_1 e^{-0.5\left(\frac{d}{\sigma}\right)^2}$ (broken curve).
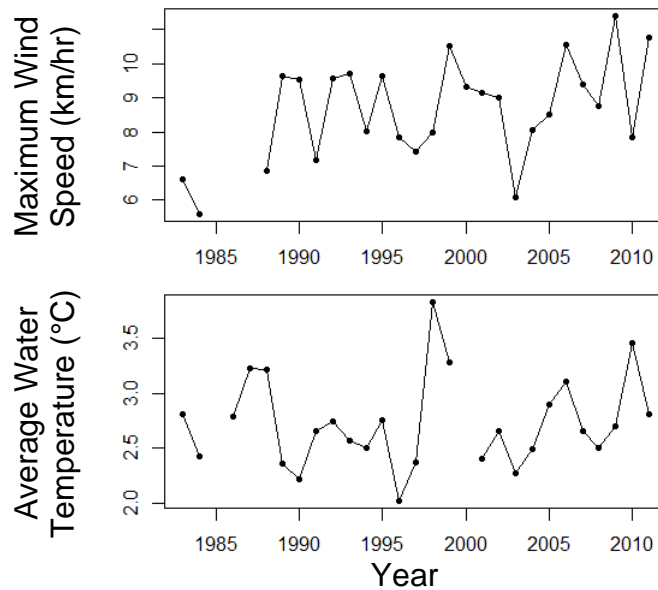
Figure 5. Time-series of the average water temperature (top) and maximum average daily wind speed (bottom) during spring at the offshore NOAA buoy in the western arm of Lake Superior. Years with inadequate data are missing.

We plotted the environmental variables against our index of cisco recruitment (see Figure 3) for two populations in Lake Superior (Figure 6). These data show that almost all of the poor recruitment events are associated with a maximum wind event > 8 km/hr. On the other hand, the highest index of recruitment is associated with the highest recorded wind event. This data point represents the 2009 year-class and the maximum wind event in 2009 occurred on May 16. After this date, the maximum average daily wind speed was 7.0 km/hr. Based on our 2009 sampling in Thunder Bay, we found that larval cisco densities were 486/1,000m^3 (SE=113) and 1,399/1000m^3 (SE=321) on May 19 and May 26, respectively. Similarly, larval cisco densities along the South Shore were 3/1000m^3 (SE=2) on May 1 and 981/1000m^3 (SE=468) on May 21. Based on this information, we speculate that the strong wind event may have occurred prior to the bulk of hatching and thus age-0 cisco were not vulnerable to the wind at the surface in this year. In contrast, strong wind events occurred on May 5 (9.2 km/hr) and then again on May 25 (9.4 km/hr) during the spring of 2007. Eight synoptic surveys were conducted along the South Shore in 2007 between April 26 and June 14, yet larval cisco densities never reached the levels observed in 2009 (Figure 2).
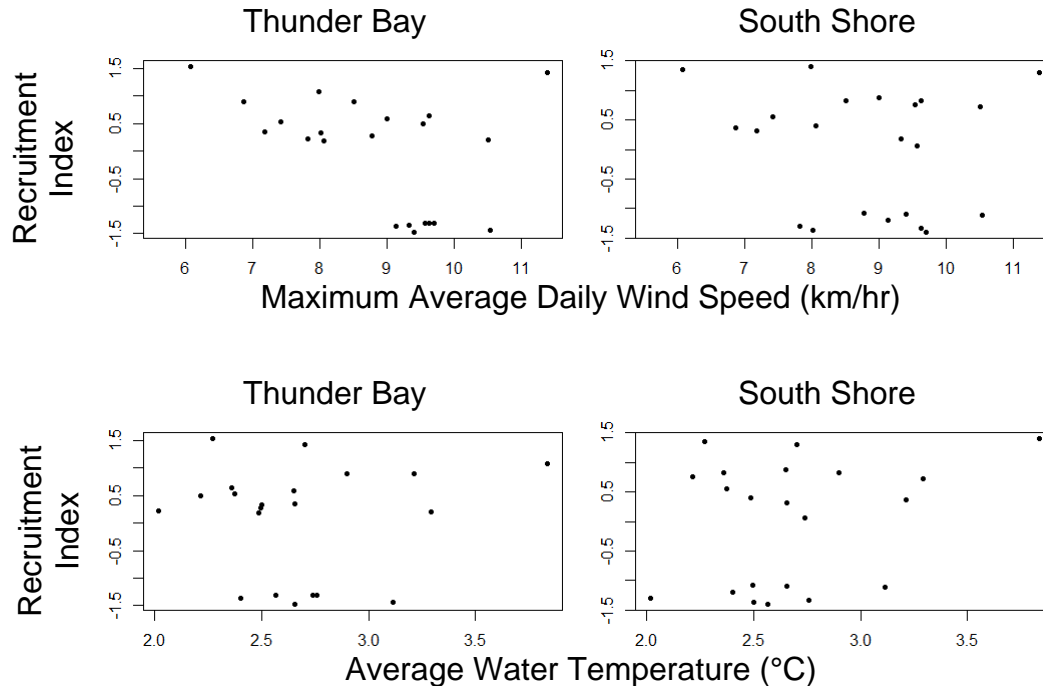
Figure 6. Scatterplots of environmental variables versus an index of cisco recruitment for two cisco populations in Lake Superior.

These findings suggest that climatic variables (e.g., wind and temperature) drive the variability and large-scale synchrony associated with cisco recruitment. Our estimate of the correlation scale for cisco recruitment variation (i.e., approximately 500 km) stands in contrast to the findings of Myers et al. (1997), where they argued that variability in freshwater fish recruitment depends predominately on biotic influences operating at small scales, particularly predation, while recruitment of marine species is largely determined by environmental factors operating at much larger scales (Myers et al. 1997). We hypothesize that the size of the system in which the population resides plays a more important role in the recruitment process than salinity. Smaller lakes will have a shorter fetch and less thermal inertia, while a larger system will be characterized by a longer fetch and more thermal inertia. For this reason the Great Lakes behave more like a small ocean system than like small inland lakes. Despite the evidence presented by Myers et al. (1997), we encourage fisheries scientists to always consider the role of climate in freshwater fish population dynamics.

Objective 2: *Correlate larval densities with spawning stock to identify if bottleneck occurs prior to or after the larval stage*

In our initial proposal we hypothesized that favorable growing conditions would lead to greater recruitment (Figure 7). We also assumed we could better understand when the bottleneck to cisco recruitment occurs by comparing larval densities and spawning stock. We postulated that greater larval cisco densities during successful recruitment events would suggest that the bottleneck to recruitment occurs before or during the larval phase. No relationship between spawning stock and larval abundance would suggest that events after the larval phase are most critical for recruitment.
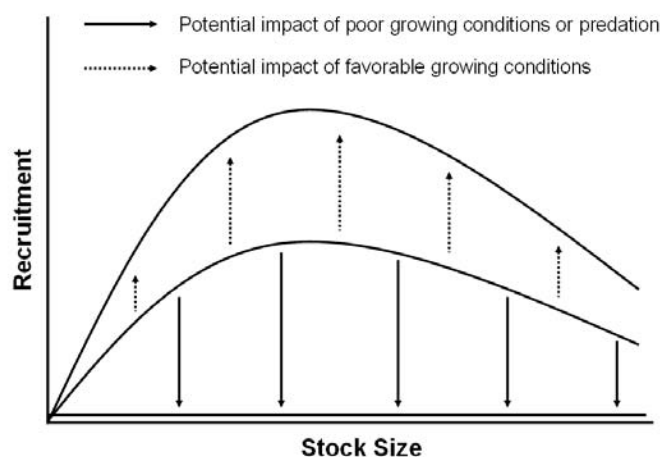

Figure 7. The hypothesized effect of growing conditions and predation by exotic rainbow smelt on cisco recruitment. Cisco recruitment will be nil under poor growing conditions and/or high rainbow smelt predation on larvae. Recruitment will increase under favorable growing conditions and no rainbow smelt predation.

We used methods similar to those described in Objective 1. Unfortunately, logistical constraints prevented us from sampling more sites in the spring of 2009, which appeared to be a moderately successful cisco year-class in Lake Superior and Lake Huron (Figure 3). Despite sampling only a few populations, it is clear that densities of cisco larvae were higher in 2009 than the densities observed in other years (Figures 2 and 8).

Patterns of cisco recruitment have been described as "boom" and "bust" yet a better description might be "mostly bust" and "sometimes boom". It is clear that large, intermittent year-classes (e.g., 1984, 1998, 2003) support the population for a significant period of time. We put forth considerable effort and resources to sample cisco larvae over the span of six years and were lucky enough to observe a single, moderately successful year class. Larval densities in 2009 were nearly three times those observed in other years. The high densities at the larval phase

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appear to have translated into greater numbers of recruits, as measured by the abundance of age-1 cisco during subsequent hydroacoustic and midwater trawl surveys (Figure 3). We believe this suggests that the mechanisms that determine cisco recruitment in the Upper Great Lakes operate either prior to or during the larval phase. We advocate that future research concerning cisco recruitment focus on this period.
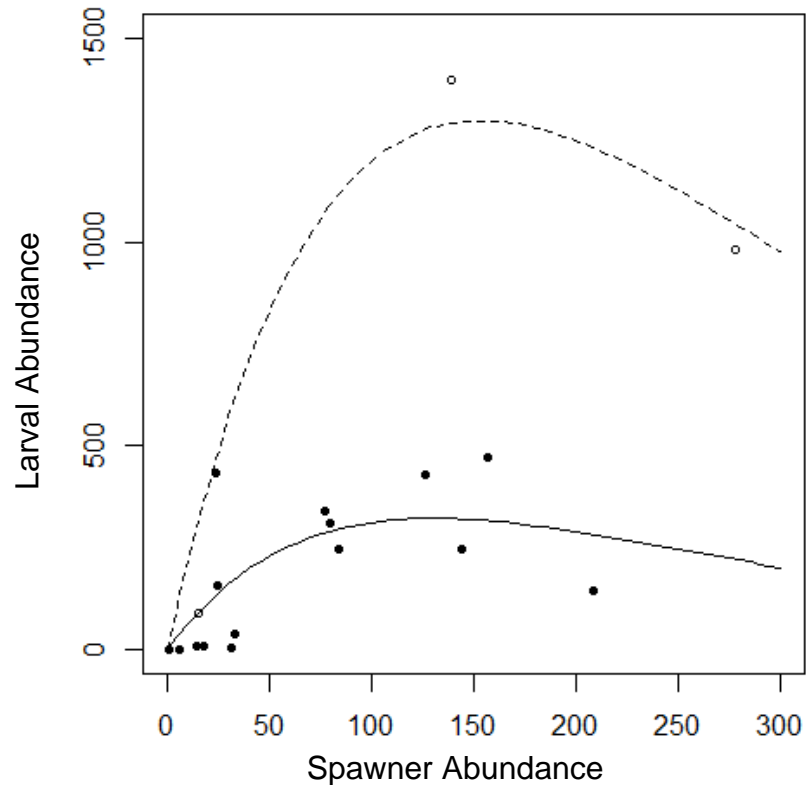

Figure 8. Relationship between cisco spawner abundance (number/ha) and the resulting larval abundance (number/1,000m^3). Separate Ricker models were fit to the 2009 year-class (open circles with the dashed line) and the 2006, 2007, 2008, and 2010 year-classes (closed circles with the solid line). The Ricker models were fit for the purpose of discussion and visual aid.

Objective 3: *Examine the influence of growing conditions (as measured by prey resources and temperature) and rainbow smelt predation on larval cisco recruitment patterns to test the hypothesis that growth potential at the larval stage, and not predation, is the dominant factor governing recruitment variability*

We conducted two studies to achieve this objective. These studies will be discussed separately.

Objective 3.1: *Temperature and cisco (Coregonus artedi) recruitment in Lake Superior: evaluating the match/mismatch hypothesis using a modeling approach*

There is wide recognition that density-independent environmental factors often determine survival of fish species during early stages of development (Cushing 1990). However, the mechanisms by which environmental factors influence recruitment are rarely understood (Myers et al. 1997). The match/mismatch hypothesis seeks to explain recruitment variation by emphasizing that the energetic demands of age-0 fish must be met. More specifically, when the most crucial periods of age-0 fish growth coincide with the production of their main prey (i.e., early stages of zooplankton), recruitment will be high. Conversely, when there is a mismatch between food requirements and food availability, recruitment will be low. Species have evolved such that their phenology (i.e., timing of seasonal activities and ecological processes) is related to prevailing climate conditions (Stenseth et al. 2002). Thus, inter-annual variation in environmental factors (e.g., surface water temperature) can affect ecological patterns and processes by altering the spatiotemporal overlap between trophic levels.

Cisco larvae emerge in the spring (Anderson and Smith 1971, Selgeby et al. 1978, Hatch and Underhill 1988) and are 9-10 mm TL at hatch (John and Hasler 1956; Hinrichs and Booke 1975). The relatively large size of cisco at hatch would lead some to believe they have a reduced risk of starvation and greater probability of surviving to the juvenile stage (Miller et al. 1988; Houde 1991). However, temporal overlap between the production of age-0 cisco and production of their prey (i.e., copepod nauplii and copepodites; Anderson and Smith 1971; Savino et al. 1994; Selgeby et al. 1994), has not been investigated. The availability of food to individual cisco larvae would cause the larval stage to be either brief or protracted, which would have important implications for the magnitude of recruitment that is ultimately realized (Houde 1987; Cushing 1990).

Water temperature is a well-demonstrated environmental driver of large-lake zooplankton abundance and ontogeny (Watson and Wilson 1978; Brown and Branstrator 2004). Lake Superior has been historically classified as ultraoligitrophic (Matheson and Munawar 1978; Munawar and Munawar 1978) and vertically averaged mean zooplankton abundance has been predominately low throughout most of the lake (Watson and Wilson 1978). However,

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zooplankton distributions in Lake Superior are known to be very patchy (Olson 1969) and densities within patches can rival the densities observed in productive marine environments (Megard et al. 1997; Zhoa et al. 2001). Given the positive relationship between water temperature and zooplankton densities (Watson and Wilson 1978; Brown and Branstrator 2004), it's not surprising that mature cisco cast their eggs in nearshore areas (Dryer and Beil 1964) and that larvae reside at the surface (Oyadomari and Auer 2004; Myers et al. 2008), as these waters are the first to warm in the spring and support the highest densities of zooplankton in Lake Superior (Zhao et al. 2001). The patchiness of spatial distributions and the strong linkage between zooplankton dynamics and water temperature suggests that match/mismatch between age-0 cisco and their zooplankton prey is a plausible mechanism regulating cisco recruitment in Lake Superior.

Despite evidence of a positive relationship between spring and summer temperatures and coregonid growth and recruitment (Christie 1863; McCormick et al. 1971; Rey and Eckmann 1989; Karjalainen 1991; English 1991), little is known about the mechanism(s) by which temperature influences cisco recruitment in Lake Superior. For some species of coregonids, researchers have concluded that temperature is the sole driver of recruitment dynamics (Eckmann et al.1988, Eckmann and Pusch 1989, 1991, Rey and Eckmann 1989). Other researchers argue that the energy balance of age-0 coregonids is delicate and that the role of starvation as a critical factor in age-0 coregonid mortality must be emphasized (Dabrowski 1981; Viljanen 1988; Dabrowski 1989). This is an important distinction between hypotheses concerning the role of temperature and recruitment; the first hypothesis suggests age-0 coregonids are temperature-limited while the second hypothesis suggests age-0 coregonids are food-limited.

We used two different models to simulate the growth of age-0 cisco through the larval stage in Thunder Bay (Lake Superior). Archived temperature recordings from Thunder Bay were used to drive the dynamics of both models. The "temperature-limited model" strictly used water temperature to simulate growth while the "food-limited model" used temperature to simulate zooplankton densities and the rates of encounter between cisco larvae and their prey. Within the simulations, we assumed recruitment occurred at 15 mm TL as this size has been associated with shifts in habitat and catchability (Stockwell et al. 2009). The magnitude of simulated recruitment was compared to empirically derived estimates of Thunder Bay cisco year-class-strength. Components of the models are described in detail below.

Virtual population analysis (VPA) was used to estimate age-specific abundance of female cisco for the years 1996-2006 in Thunder Bay. Age-specific abundance for a given year (N_t) was estimated using the age-specific abundance in the subsequent year (N_{t+1}) and the age-specific, instantaneous, total mortality (Z_t):

$N_t = N_{t+1} e^{Z_t}$.

Based on the results of Yule et al. (2008), we assumed Z_t for cohorts ≥ 9 years was 0.22. The cisco population in Thunder Bay was surveyed in 2005, 2007, 2008, 2009, and 2010 (Figure 9) using similar hydroacoustics and midwater trawling methodologies (Yule et al. 2007, Yule et al. 2008a, Yule et al. 2008b, Yule et al. 2009). Given the 2003 year-class was not included in the Yule et al. (2008) analysis, we used a catch curve of at-large females from the 2003 year-class to estimate Z_t for cohorts < 9 years (Figure 10). Interestingly, the estimate of Z_t for cohorts < 9 years was the same as the Z_t for cohorts ≥ 9 years (Z_t = 0.22). The previously mentioned surveys (i.e., 2005, 2007, 2008, 2009, 2010) were used as starting points to back-calculate abundance-at-age for Thunder Bay cisco. We used the average of the estimates of age-2 abundance to generate a single estimate of cohort year-class-strength.
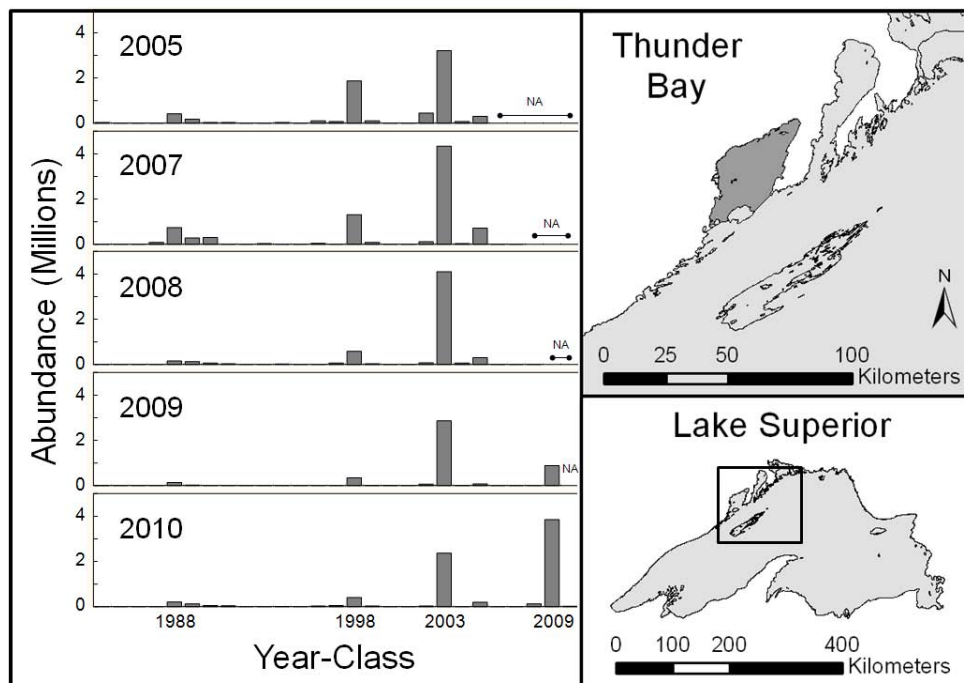
Figure 9. Results of hydroacoustic and midwater trawl surveys (Left) targeting spawning cisco in Thunder Bay (Right). The year of the survey is in the upper left corner of graphs and the source of the data can be found in the text. Each graph shows the abundance of at-large, female cisco apportioned to year-class. The x-axis is the same for each graph and "NA" indicates information is not available (i.e., due to the year of the survey).
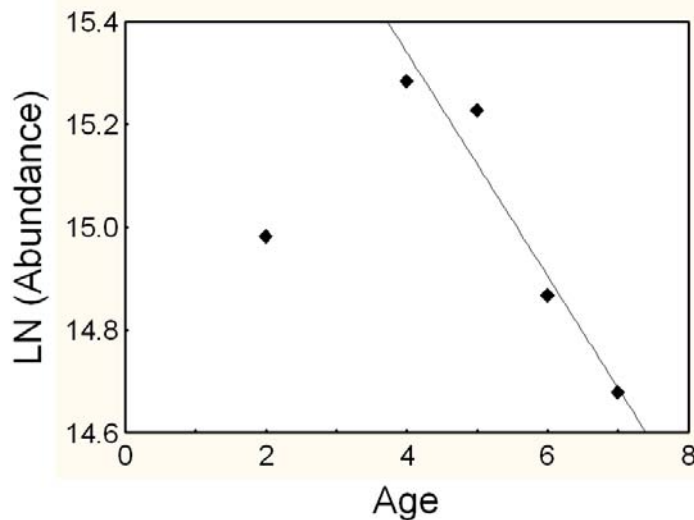
Figure 10. Catch curve analysis of female cisco from the 2003 year-class in Thunder Bay. Only ages 4-7 (i.e. descending limb) were used to estimate mortality. The slope of the regression equation (i.e. estimate of Z_t) was 0.22.

Using the results of the VPA, we also estimated the number of eggs cast for a given year-class. We estimated length-at-age (L_a) using the relationship provided by Yule et al. (2007), calculated mass (M) using the L:M relationship provided by Yule et al. (2008), and finally determined fecundity (F) using the M:F relationship provided by Yule et al. (2006). The total number of eggs cast (EC) for a given year-class was the sum of the eggs cast by year-classes ≥ 2 years:

$$\sum_{a=2}^{21} EC = A_a P_a F$$

where A is abundance, P is the proportion mature, and the subscript "*a*" designates age (Table 2). Our comparison of the estimate of eggs cast for the 2006 year class (6.8×10^{10}) to an observed estimate of 2006 larval cisco abundance (4.6×10^{8}) in Thunder Bay (Myers et al. 2009) led us to assume that survival of eggs to the larval stage was 1% for all year classes.

The thermal environment of Thunder Bay was characterized using estimates of surface and sub-surface temperature from 1996-2006. Sub-surface temperature was recorded at the face of the Bare Point Water Treatment Facility intake pipe (Thunder Bay, Ontario). The intake extends approximately 733 m into Lake Superior and is located 10.1 m above the lakebed. The bathymetric depth at this location is 18.3 m. Daily estimates of sub-surface temperature were the average of three samples collected every 24 hours. A 5-day running average was used to smooth fine-scale variability.

Surface temperature was recorded by the Great Lakes Surface Environmental Analysis (GLSEA); a digital map of Great Lakes surface water temperature and ice cover produced daily at the NOAA Great Lakes Environmental Research Laboratory (GLERL) in Ann Arbor, Michigan through the NOAA CoastWatch program. Surface water temperatures for the GLSEA were derived from polar-orbiting satellite imagery and were updated daily with information from the previous day's satellite imagery. If no imagery was available, a smoothing algorithm was applied to interpolate missing data. Estimates of temperature for 1996 to mid-2003 were recorded with an aerial resolution of 2.6 km while estimates from mid-2003 to 2006 were recorded with an aerial resolution of 1.3 km. We generated a single estimate of surface water temperature by calculating the arithmetic mean of all pixels within Thunder Bay for each day.

John and Hasler (1956) argued that the dates of hatching of cisco eggs in Lake Mendota (Wisconsin) were probably not affected by any factor except temperature after the departure of ice. We identified ice departure in Thunder Bay as the day when surface water temperature rose above 1°C. After the ice departed we assumed cisco eggs accrued an additional 50 degree-days on the bottom of the lake before peak hatching (PH). We distributed larvae according to a normal distribution N(PH, 100) for each of the years simulated. Larvae were assumed to be 9 mm at hatch and take 1 d to reach the surface (John and Hasler 1956, Hinrichs and Booke 1975).

Temperature-Limited Model

McCormick et al. (1971) used a lab experiment, in which age-0 cisco were fed ad libitum, to demonstrate that growth of age-0 cisco was positively related to temperature. To simulate growth of age-0 cisco, we used the temperature-dependent, instantaneous rates (expressed as percent per day) reported by McCormick et al. (Table 1 in McCormick et al. 1971) to calculate the daily increase in wet mass (WM). We assumed a linear relationship between the estimates of temperature-dependent growth. Age-0 cisco growth in WM was converted to an estimate of TL using the relationship provided by Karjalainen (1992; Table 2). Houde and Zastrow (1993) used a metanalysis to examine the ecosystem-specific, dynamic properties of larval fish. Based on their analysis of freshwater fish larvae, we assumed age-0 cisco experienced an instantaneous mortality rate (Z, d^{-1}) of 0.16 (Houde and Zastrow 1993) until they reached 15 mm. All individuals that reached 15 mm were integrated for an index of simulated recruitment. Individuals that did not reach 15 mm by 31 July were assumed to die.

Food-Limited Model

We used the bioenergetic and foraging model (Table 2) developed for coregonid larvae to simulate the growth of age-0 cisco through the larval stage. The general model for larval growth (G) is:

$$G = R - qI$$

where R is respiration, I is food ingestion, and q is a coefficient of net energy absorption (Table 2). Food ingestion was calculated using the foraging model developed by Dabrowski and company (Dabrowski et al. 1988, Dabrowski 1989) and implemented by Karjalainen (1992). Parameter values used for the model can be found in Table 2.

Cisco larvae feed predominately on copepod nauplii and copepodites (Anderson and Smith 1971, Savino et al. 1994, Selgeby et al. 1994). Watson and Wilson (1978) argued that surface water temperature in Lake Superior was the most important determinant of zooplankton standing stock. They also suggested that both the magnitude and timing of zooplankton biomass maxima was influenced by the differential heating of surface waters at various locations across the lake (Watson and Wilson 1978). We simulated zooplankton biomass (B_{ZP}; mg/m^3) in Thunder Bay using the following relationship provided by Watson and Wilson (1978):

$$\log_e B_{ZP} = \frac{0.79\ (T_{surface} \cdot D)}{10^3} + 1.37,$$

where $T_{surface}$ is surface water temperature (°C) and D is time (expressed as Julian days -100). Munawar and Wilson (1978) showed that the naupliar portion of B_{ZP} declined after spring. Based on the information reported in Figure 1 of Munawar and Wilson (1978), we assumed the naupliar portion of B_{ZP} was 20% for all dates prior to 15 May and then declined from 20% on May 15 to 10% on July 31. We converted our estimate of nauplii biomass (B_{ZP-N}) to volumetric energy density (J/m^3) using the mass energy density reported for copepod zooplankton (3,016 J/g) by Cummins and Wuycheck (1971). Abundance of nauplii was determined by dividing B_{ZP-N} by the average weight of individual nauplii (Table 3).

We used the results of Brown and Branstrator (2004) to estimate that copepodites of *Cyclops sp.* and *Diaptomus sp.* were 6.5 and 2.8 times more abundant, respectively, than nauplii in the western arm of Lake Superior during May 2001 (Table 3). We used these ratios to simulate the abundance of copepodites in Thunder Bay relative to the abundance of nauplii. The average lengths of copepodites, as reported by Link and Hoff (1998), were combined with the regression equations established by Culver et al. (1985) to calculate dry mass (DM). DM was converted to WM assuming a constant ratio of 15% (Flint 1986). Biomass of copepodites (B_{ZP-C}) was converted to volumetric energy density using the previously described relationship for copepod zooplankton

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(Cummins and Wuycheck 1971). *Cyclops sp.* copepodites and *Diaptomus sp.* copepodites were assumed to be equally susceptible to predation by age-0 cisco. We assumed the probability of capturing and ingesting copepodites was zero for 9 mm cisco and increased linearly to one for 15 mm cisco.

Table 2. Biological and physical parameters used in the models.

Symbol	Parameter Description	Value or Equation
Eggs Cast		
L_a	Length-at-age (mm)	$L_a = 381.1171\left(1-e^{-0.386894 \cdot a}\right)$
M	Mass (g)	$LN(M) = -12.7 + 3.16 \cdot LN(L_a)$
A_a	Abundance-at-age	See text
P_a	Proportion mature	Age-2, -3, -4 = 0.22, 0.64, 0.90; ≥ Age-5 = 1
F	Fecundity	$F = 44.5 \cdot M - 440.4$
Temperature-Limited Model		
$T_{surface}$	Surface temperature (°C)	See text
G	Growth (%/d)	See text
Z	Mortality of age-0 cisco	0.16
Food-Limited Model		
TL	Total Length (mm)	Simulated
WM	Wet mass (g)	$WM = 3.184\,TL^{3.663}$
STM	Standard metabolism of larvae	$STM = 0.1272 e^{0.7344\,TL}$
V	Swimming speed (cm/s)	$V = 0.1926 e^{1.282\,TL}$
b	Slope of activity equation	$b = 6.76 e^{-1.094}$
ACT	Active metabolism	$ACT = STM\, e^{bV}$
Q_{10}	Dependence of R on temperature	2.41
s	Area of the visual field (m^{-3})	$s = 0.0001217\,TL - 5.0306 \times 10^{-6}$
c	Probability of successful prey capture	$c = (0.8703\,TL - 0.81603)/(TL + 0.32115)$
$D_{ZP-N,C}$	Prey density (J/m3)	See text
h	Handling time (h/J)	$h = 3.0124 e^{-1.55107\,TL}$
$F(T)$	Temperature-dependent function of h	$F(T) = 3.81599 e^{-0.116\,TL}$
V	Swimming speed (m/h)	$V = 6.932 e^{1.282\,TL}$
FT	Feeding time (h)	16
r	Absorption coefficient	0.75
SDA	Specific dynamic action coefficient	0.28
q	Net energy absorption coefficient	$q = r \cdot (1-SDA)$

Table 3. Characteristics of immature crustacean zooplankton in Lake Superior.

| Variable | Nauplii | Copepodites | | Source |
		Cyclops sp.	Diaptomus sp.	
Density (#/m^3)	91	589	251	Brown and Branstrator 2004
Length (mm)	0.36	0.53	0.71	Link and Hoff 1998
Wet Mass (µg)	3.40*	11.07	17.07	Culver et al. 1985

*Average expected WM of calanoid nauplii and cyclopoid nauplii.

Standard metabolism (STM) with respect to the total length of age-0 cisco (TL) was estimated using the equation provided by Karjalainen (1992), which is based on interpretations of the results reported by Dabrowski (1986a, b) and Kaushik et al. (1986). Handling time (h) with respect to TL$_{LC}$ and temperature (Table X) was estimated using the equation provided by Karjalainen et al. (1992), which is based on interpretations of the results reported by Rösh (1986) and Dabrowski (1989). Coregonid larvae are believed to be visual feeders and thus need light to identify and capture prey (Dabrowski 1982). For this reason, we assumed feeding and active metabolism (ACT) occurred for 16 hours while standard metabolism occurred for the remainder of the day.

Energy ingested was converted to dry and wet mass (DM and WM, respectively) using the relationships provided in Table 2. We assumed energy density of cisco larvae was 4134 J/g WM. We converted larval cisco growth in WM to an estimate of TL using the relationship provided by Karjalainen (1992; Table 2). Similar to the "temperature-limited model," we assumed age-0 cisco experienced a daily mortality rate of 0.16 (Houde and Zastrow 1993) until they reached 15 mm. Individuals that did not reach 15 mm by 31 July were assumed to die. All individuals that reached 15 mm were integrated for an index of simulated recruitment.

Our simulations provided evidence that water temperature can play a key role in recruitment of cisco. The 1998 year-class was successful in Lake Superior (Figures 3 and 9) and was also large for both the "temperature-limited" and "food-limited" models (Figure 11). The variation associated with the abundance of recruits is less for the "temperature-limited" model than for the "food-limited" model. We believe this is an important distinction between the models given that cisco recruitment is usually characterized as "boom" or "bust" (Stockwell et al. 2009).

We recognize the "temperature-limited" and "food-limited" models are both ultimately driven by temperature, so it is not surprising that the results look fairly similar. However, we argue that simulation models are not always intended to be used as tools for prediction. The fact that the simulations from the "food-limited"

model are similar to the "temperature-limited" model is actually encouraging. The "food- limited" model highlights that the nutritional requirements of larval cisco must be met and that temperature could be an important mediator of the overlap between larvae and their prey (Figure 12). In essence, the "food-limited" model suggests a plausible mechanism (e.g., match/mismatch) by which temperature could influence recruitment.

The simulated number of recruits for the 2003 year-class was also relatively large (Figure 11), which corresponds with the observation that the 2003 cisco year-class was also successful in Lake Superior. Water temperature at an offshore buoy in the western arm of Lake Superior was low during the spring of 2003 yet winds were relatively calm. We speculate that the calm winds allowed the nearshore surface waters to warm without being mixed due to an upwelling event. Again, this suggests that both wind and water temperature are important factors for cisco recruitment.
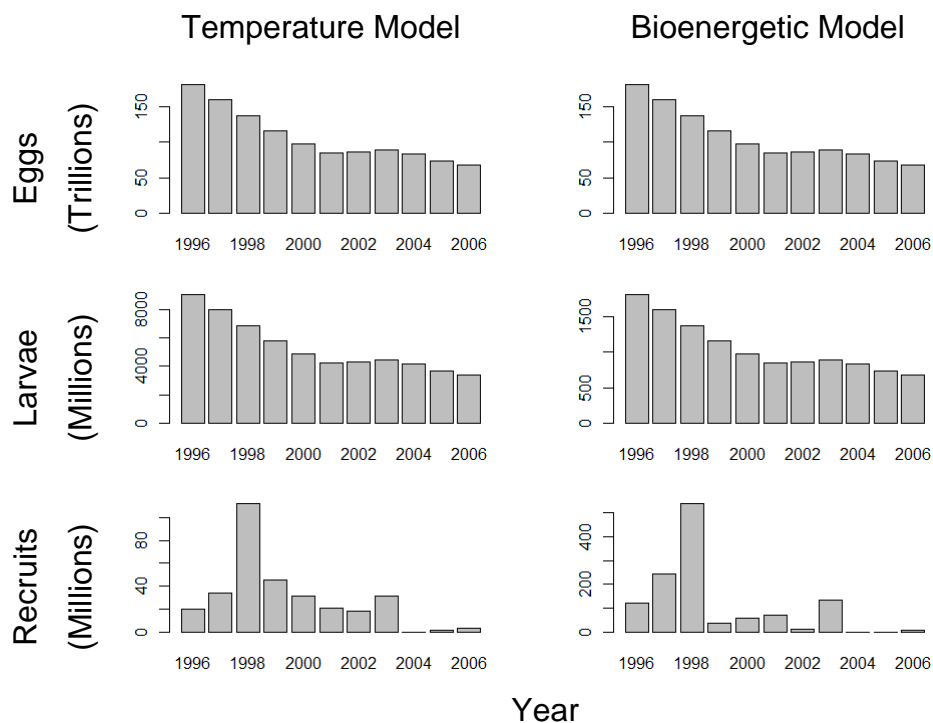

Figure 11. Results of the "temperature-limited" and "food-limited" models used to explore the dynamics of cisco early life history.
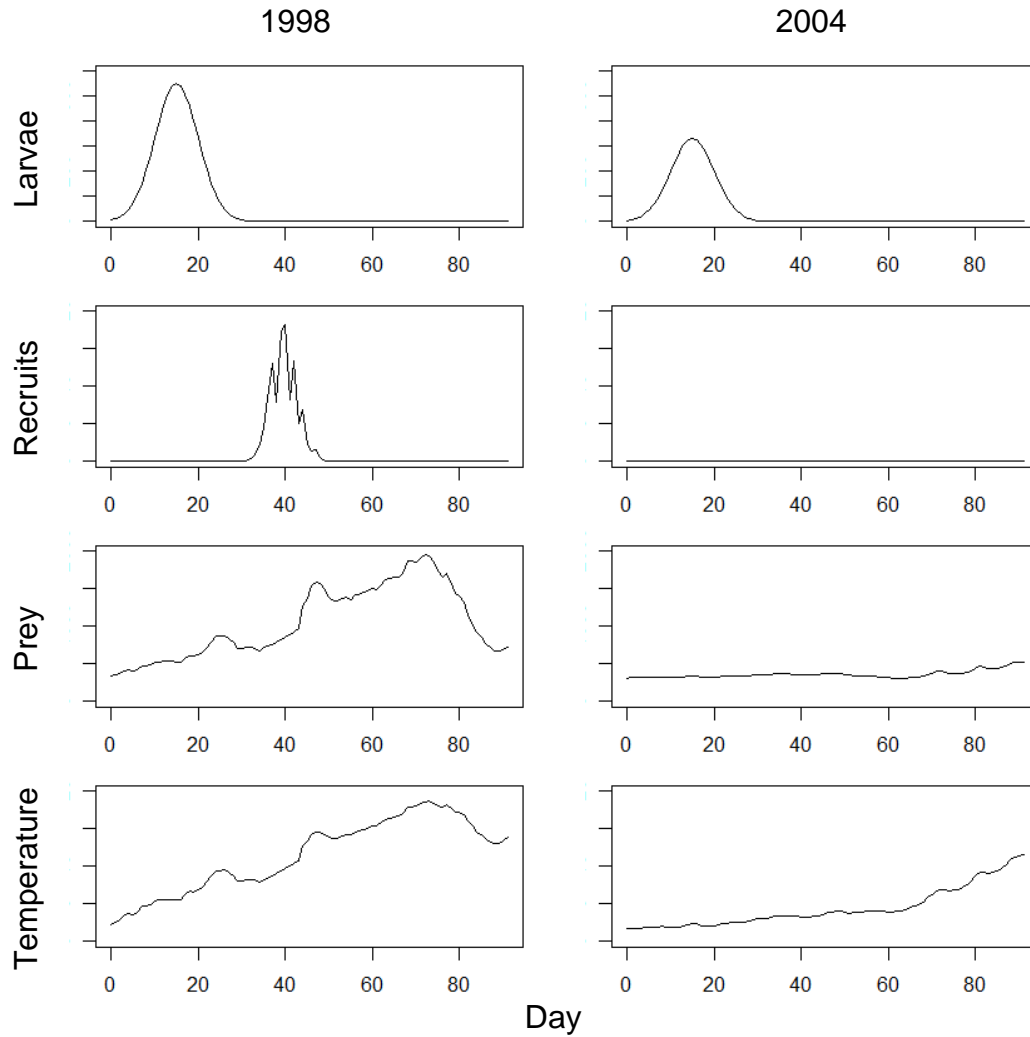
Figure 12. An example of 1998 and 2004 simulation results for the "food-limited" model. In an attempt to emphasize just the trends, we have not included the values associated with each of the variables. The y-axis scales are the same for both simulations of each respective variable. On the x-axes, day zero equals May 1.

Objective 3.2: *Spatial and temporal overlap between larval cisco (Coregonus artedi) and their associated predators and prey*

Variability in inter-annual recruitment is a critical source of uncertainty for fisheries managers. It is generally agreed that factors acting on early stages of development, especially the larval stage, have an overriding influence on recruitment of fishes. Faster growth through the larval stage is believed to contribute to increased survival (Ware 1975, Blaxter 1986, Houde 1989) because larger, more developed larvae are more capable of capturing prey and evading predators than smaller members of the cohort (Blaxter 1986). Coregonid fish populations are noted for large fluctuations in recruitment (Stockwell et al. 2009), yet little is known about the mechanisms controlling growth and survival of these fish during early life stages.

Rainbow smelt have been repeatedly linked to the decline of coregonids within the Great Lakes Basin (Crowder 1980, Loftus and Hulsman 1986, Hrabik et al. 1998, Myers et al. 2009). Strong evidence exists for negative interactions between adult rainbow smelt and age-0 cisco in inland lakes (Evans and Loftus 1987, Hrabik et al. 1998) and predation is often cited as the likely mechanism. Loftus and Hulsman (1986) found that predation by rainbow smelt on larval coregonids in Twelve Mile Lake (Ontario) was continuous through the hatching period and accounted for 100% mortality. Hrabik et al (1998) found that adult smelt and age-0 cisco occupied similar thermal habitat nearly 55% of the time during an 8-year period. This overlap placed young cisco in close proximity to predatory rainbow smelt and ultimately led to the extirpation of cisco in Sparkling Lake (Wisconsin).

Spatial overlap between predator and prey is an obvious prerequisite for predation, yet few studies have accounted for the degree of overlap when evaluating interactions between rainbow smelt and larval cisco in the Great Lakes. Consequently, the effect of rainbow smelt predation on cisco recruitment in these larger systems is still unclear. Myers et al. (2009) demonstrated that assumptions relating to heterogeneous horizontal distributions of rainbow smelt and larval cisco can influence the perceived impact of predation. However, the degree of interaction between rainbow smelt and larval cisco in both the vertical and horizontal dimension with respect to time has not been investigated. Rainbow smelt perform distinct diel vertical migrations (Heist and Swenson 1983) while cisco larvae are aggregated near the surface (Myers et al. 2009). Fluctuating degrees of overlap could have important consequences for the vulnerability of larval cisco to predation by rainbow smelt.

Larval fish are vulnerable to predation but are also predators themselves. Dabrowski (1989a,1989b) argues that starvation is a factor in larval mortality and must be emphasized in studies of coregonid recruitment. The delicate energy balance of larval fish requires that they encounter sufficient numbers of prey at appropriate times. The 'match/mismatch' hypothesis has been proposed as an

explanation for the variability in recruitment observed in many fish stocks (Cushing 1990). The hypothesis suggests recruitment variation can be explained by the relative overlap between energetic demands of young fish and availability of suitable prey. Understanding the rate of encounters between larval cisco and zooplankton is important for evaluating hypotheses related to cisco growth and subsequent recruitment in Lake Superior.

We developed a sampling approach that was repeated at three locations in Lake Superior (Figure 13) during the spring of 2009, 2010, and 2011. Sampling targeted ichthyoplankton, zooplankton, and adult pelagic fish. We completed three synoptic surveys at each location with intervals of approximately two weeks. Departures from this general rule were the result of adverse weather conditions or logistical constraints. Sampling dates are given in Table 4. Each survey consisted of day and night sampling to account for changes in distributions as a result of photoperiod. Day samples were collected between sunrise and sunset. Night samples were collected between 0.5 h after nautical twilight and 0.5 h before nautical sunrise. During the night collections, all back deck lights were turned off.
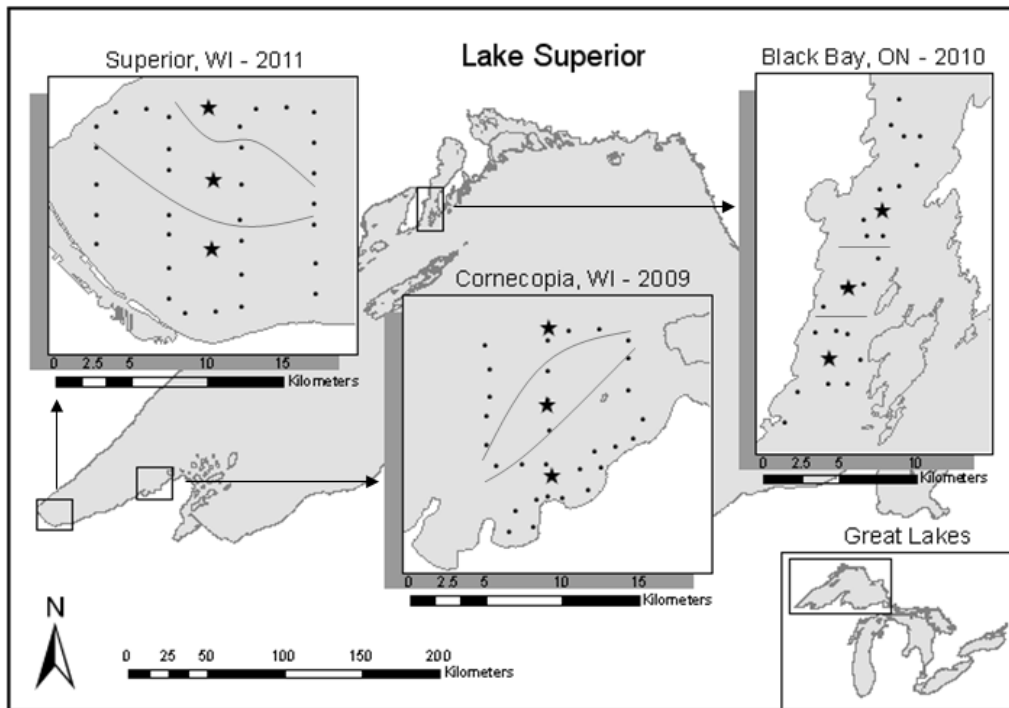

Figure 13. Sampling locations in Lake Superior. Stars (★) indicate intensive sites while dots (●) indicate 2-km acoustic intervals. Grey contours indicate the division of acoustic intervals into depth strata.

Table 4. Dates of sampling events at three locations in Lake Superior.

Location (Year)	Survey	Ichthyoplankton		Zooplankton		Pelagic Fish	
		Day	Night	Day	Night	Day	Night
Cornecopia, WI	1(K,C)	4/28– 5/5	5/7–8	4/30	5/2	4/24–30	5/1–5
(2009)	2(K,C)	5/21	5/21–22	5/12	5/19	5/11–12	5/11–19
	3(K,C)	6/2	5/27–28	5/27	5/29	5/26–28	5/26–29
Black Bay, ON	1(K)	5/14– 17	5/17–18	5/14–16	5/19	5/16	5/18 –19
(2010)	2(C)	5/28 – 6/2	6/3	5/28–29	6/1–2	6/4–6	6/3–5
	3(K)	6/14	6/13–14	6/14–19	6/20–21	6/19	6/20–21
Superior, WI	1(K)	4/25–28	4/28	5/5	5/2–3	5/5	5/3– 4
(2011)	2(C)	5/7–11	5/11–12	5/18	5/16	5/18	5/16–17
	3(K)	5/20–23	5/23	6/6	6/11–12	6/6–8	6/12–14

Note: Acoustic samples were collected aboard the R/V *Kiyi* (length = 32.6 m, power = 1200 hp) and the R/V *Coaster II* (length = 7.9 m, power = 350 hp). Letters in parentheses in the Survey column indicate which vessel was used for the given survey (K = R/V *Kiyi*, C = R/V *Coaster II*).

Vertical distribution of cisco larvae was assessed using a 0.5 x 0.5 m tucker trawl (Aquatic Research Instruments, Hope, Idaho) equipped with a 500 µm mesh net. At each sampling location we selected three intensive sites where the tucker trawl was deployed (Figure 13). Samples were collected at 25, 15, and 5 m below the surface. A sample was also collected at the surface using a 0.5 m (diameter) conical net with 500 µm mesh following methods of Myers et al. (2008). The tucker trawl was deployed and retrieved with the assistance of a hydraulic winch on the research vessel (R/V *Coaster II*. Once the trawl reached the desired depth a brass messenger was used to trigger the opening of the trawl. After the trawl opened the coordinates were recorded and the net was towed for 5 min at 6-7 km/hr. Prior to retrieval, a second messenger closed the net so that the sample was not compromised during its ascent. Coordinates were recorded once the net closed and the volume filtered was calculated as the product of distance traveled and area of the trawl mouth. Methods for preservation, identification, enumeration, and measurement of icthyoplankton were similar to those of Myers et al. (2009).

Zooplankton samples were collected using a 0.5 m (diameter) collapsible plankton net equipped with 63 µm mesh. Zooplankton samples were collected at the same intensive sites described previously at discrete depths; 30-20, 20-10, and 10-0 m. The net was initially deployed to the deeper depth, retrieved vertically to the shallower depth, and then closed using a messenger. Once onboard, the net was sprayed thoroughly from the outside to wash all organisms into the collection bucket. Organisms in the collection bucket were washed into a

250 mL sample jar and preserved in 95% ethyl alcohol. Rose bengal was used to stain the organisms in the sample.

Zooplankton samples were divided into equal parts using a wheel splitter. The sample continued to be fractioned until a manageable number of organisms were in a given subsample (i.e. approximately 100-200 adult and juvenile organisms). The fractioned sample was condensed and placed in a wheel counter. All juvenile and adult zooplankton were identified to genus using a dissecting microscope. Copepod nauplii were enumerated by collecting a 1 mL sample from a fractioned sample. The 1 mL sample was placed on a gridded slide and all nauplii were counted using a compound microscope. This was done twice for the fractioned sample. The average number of nauplii·mL^{-1} was multiplied by the volume of the fractioned sample to estimate the total number of nauplii within the fractioned sample. We estimated the total number of adult, juvenile, and naupliar stages of zooplankton within the entire sample and then standardized estimates to the number of organisms·m^{-3}.

Hydroacoustics and midwater trawling were used to estimate abundance and distribution of pelagic fish. We used a DT-X digital echosounder (Biosonics, Inc., Seattle, Washington) equipped with a 120 kHz split-beam circular transducer with a half power beam width of 6.78. Acoustic data were collected aboard two vessels. When sampling aboard the *Kiyi*, the transducer was mounted through a well in the hull, approximately 2.3 m below the surface of lake. When sampling aboard the *Coaster II*, the transducer was mounted on a 1.2 m tow body and deployed approximately 1 m below the surface on the port side of the vessel. Acoustic signals were collected with BioSonics Visual Acquisition Software (version 4.1) and output files were stored to a laptop computer hard drive. Vessel position was recorded with an Ashtech BRG2 (Ashtech Corp., Santa Clara, California) differentially corrected global positioning system unit and embedded within acoustic data files. A transmit pulse duration of 0.4 ms and sampling rate of 5 pings·s^{-1} were used at all times. The acoustic systems were calibrated during each survey using a 33mm calibration sphere with expected target strength (TS) of -40.5 dB. If measured sphere TS deviated by more than 1 db from expected TS then offsets were used when acoustic data were processed.

Acoustic data were processed using Echoview software (version 3.45.54.2627, SonarData Pty Ltd., Tasmania, Australia). Regions of echograms containing non-fish echoes (e.g. noise from electrical interference) were excluded from analysis. A line was drawn in each echogram at approximately 0.5 m above the lake bed to exclude bottom echoes. The water column was analyzed in 10 m depth layers and the transects were divided into 2 km intervals. We applied a minimum threshold of -65 dB before measuring the average volume backscattering of fish echoes in each 10 m x 2 km cell.

All midwater and bottom trawls were collected with the *Kiyi*. The midwater trawl had 15.2 m headrope and footrope lines and 13.7 m breast lines. The nylon

mesh graduated from 300 mm stretch measure at the mouth to 12 mm at the cod end. The bottom trawl (3/4 Yankee trawl number 35) had an 11.9 m headrope, 15.5 m footrope, and 2.2 m high wing lines with 89 mm stretch mesh at the mouth, 64 mm stretch mesh at the trammel, and 12 mm mesh at the cod end. A summary of the midwater and bottom trawl effort can be found in Table 5.

Trawl catches were sorted by species and weighed in aggregate to the nearest gram. For small catches (<50 individuals per species), all fish were measured to the nearest millimeter total length (TL). For larger catches, at least 50 individuals per species were selected randomly and measured for TL and the remaining fish were counted.

Table 5. Average catch (#/trawl) and average length (mm) of rainbow smelt caught in midwater trawls and bottom trawls collected at three locations in Lake Superior. Dashes indicate no trawls were collected during the respective survey.

Location (Year)	Survey	Midwater Trawls			Bottom Trawls		
		No. Trawls	Average Catch (SE)	Average Length (SE)	No. Trawls	Average Catch (SE)	Average Length (SE)
Cornecopia, WI	1	4	18 (7)	67 (8)	4	319 (185)	72 (7)
(2009)	2	4	29 (13)	79 (6)	3	188 (63)	80 (9)
	3	2	9 (2)	63 (2)	3	5 (4)	59 (13)
Black Bay, ON	1	6	966 (283)	98 (3)	6	110 (66)	92 (7)
(2010)	2	-	-	-	-	-	-
	3	7	378 (124)	109 (4)	-	-	-
Superior, WI	1	5	42 (33)	119 (10)	4	433 (230)	93 (14)
(2011)	2	6	201 (115)	101 (9)	4	171 (31)	122(1)
	3	-	-	-	-	-	-

The results for this objective confirmed that larval cisco are largely confined to the surface stratum. In 2009, outside Cornucopia, WI, the average density of larval cisco in the surface stratum during day light hours was $1,579/1,000m^3$ (SE=771). Meanwhile, average density at the depths sampled below the surface was $16/1,000m^3$ (SE=11). Very few cisco larvae were captured in Black Bay and thus we were not able to observe any patterns in vertical distribution. The vertical distribution of larval cisco in Superior, WI was similar to the pattern observed in Cornucopia, with a large portion of the larvae caught at the surface. However, as was highlighted in objective 1.1, larval densities in 2011 (i.e., $223/1,000 m^3$, SE=156). were lower compared to the observations in 2009.

Nauplii densities were consistently highest in the surface waters at all three sites, during both day and night. The densities of nauplii at Cornucopia and Superior, WI were similar, with average densities of approximately 5,000/m^3 at both sites. The densities of nauplii in Black Bay were nearly 2.5 times greater than the other sites. This leads us to believe that lack of food for larval cisco is not likely to be the cause of the poor recruitment that has been typical of the Black Bay cisco population.

Total rainbow smelt densities were modest at Cornucopia, WI and Superior, WI, yet extremely high in Black Bay (Figure 14). Complicating the issue of high rainbow smelt densities in Black Bay is the fact that >50% of the population migrates to the surface stratum at night, which puts the exotic predators in close proximity to larval cisco. These results are consistent with the findings of Myers et al. (2009). The spatiotemporal overlap between high densities of rainbow smelt and the apparently preferred habitat of larval cisco is likely to limit the potential for successful cisco recruitment in Black Bay.
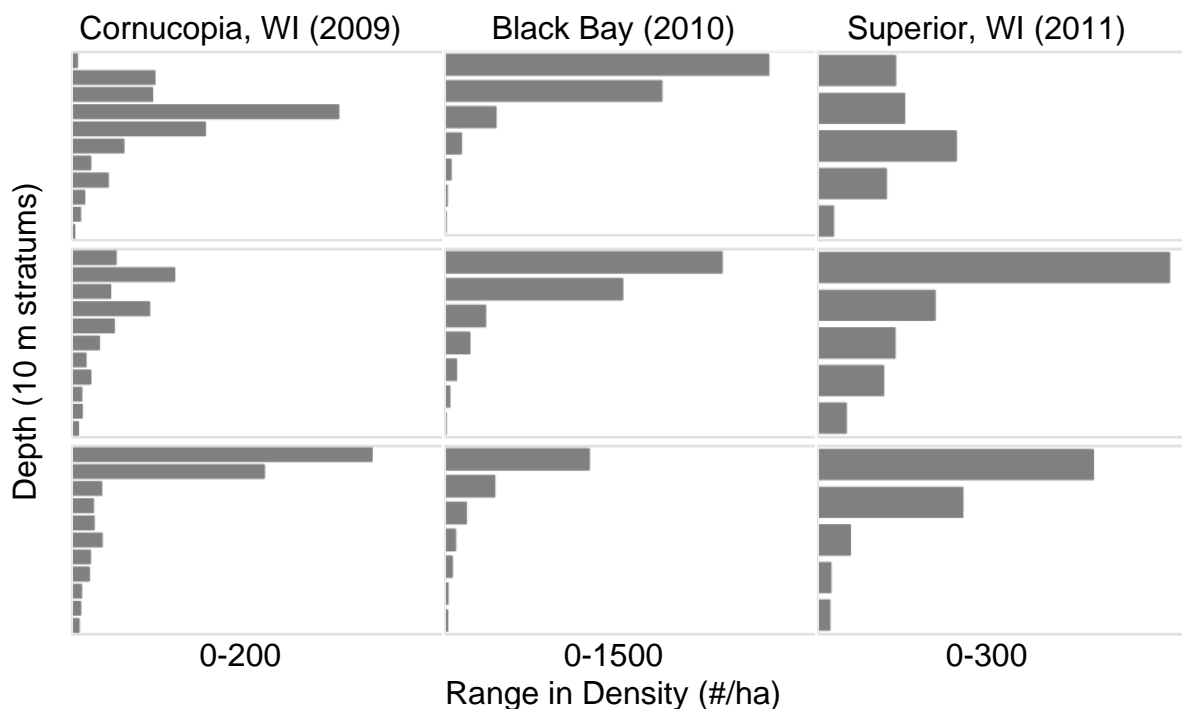

Figure 14. Vertical distribution of rainbow smelt during the night at three locations in Lake Superior.

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