THE IMPORTANCE OF THE LARVAL STAGE TO CISCO RECRUITMENT
VARIATION IN THE GREAT LAKES

By

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ABSTRACT

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Historically, cisco (*Coregonus artedi*) were the most prolific prey fish in the Great Lakes basin, serving as a vital energy link between native predators and plankton resources, as well as supporting the largest freshwater commercial fishery in North America. The collapse of cisco populations in the Great Lakes has been attributed to overfishing, habitat destruction, and invasive species. Cisco populations have recovered in Lake Superior and are increasing in abundance in Lake Huron, but remain severely restricted in the other Great Lakes. Despite nearly a century of research on cisco, our understanding of this species is still in its infancy. The body of research that constitutes this dissertation clearly shows that the larval stage is critically important for the survival of a given cisco year-class. Furthermore, this research demonstrates that the conditions cisco larvae are exposed to following hatching are typically not conducive to fast growth or increased survival. As a consequence, failure of year-classes across a broad geographic range is likely the norm while strong year-classes can only be expected to occur intermittently. My hope is that this information will help state, tribal, and federal authorities develop rehabilitation plans that acknowledge both the benefits and challenges associated with restoration of cisco throughout the Great Lakes basin.

ACKNOWLEDGMENTS

PREFACE

The first and second chapters of my dissertation have been published in the journals *Fisheries Research* and *Ecological Modelling*, respectively. I also plan to pursue publication of the third chapter at a later date. Given the large-scale, collaborative nature of this research, I believe it would be misleading to submit this dissertation using first-person singular grammar. Rather, I have chosen to submit the dissertation chapters using first-person plural grammar, as this more accurately reflects the contributions made by my coauthors during the entire research process.

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PERSPECTIVE

This dissertation represents the culmination of a large-scale research effort that aimed to better understand the early life history of cisco (Coregonus artedi) in the Great Lakes. Before presenting the details of the three studies that comprised the body of my research, this brief overview provides a context for the investigations, summarizes important findings, and offers a few key recommendations for Great Lakes fishery managers.

Historically, cisco (*Coregonus artedi*) were the most prolific prey fish in the Great Lakes basin and supported one of the largest freshwater commercial fisheries in North America (Stockwell et al., 2009). However, the sequential collapse of cisco populations in each of the Great Lakes (i.e., as a result of overfishing, habitat destruction, and invasive species) removed the species from their former ecological and socioeconomic position within the Great Lakes fishery (Stockwell, et al., 2009). Cisco populations have rebounded in Lake Superior and are increasing in Lake Huron, yet they remain severely restricted in the remaining Great Lakes. With few exceptions, fisheries scientists and decision-makers recognize the value of cisco restoration and sustainable management, as evidenced by the following text found within the Great Lakes Fishery Commission's "Fish-Community Objectives" for each of the Great Lakes:

Lake Ontario: "*The offshore benthic fish community will be composed of self-sustaining native fishes characterized by rehabilitated native prey fishes… Recent ecological changes indicate more-favorable conditions for the rehabilitation of the offshore benthic food web… the lake herring, primarily a pelagic species that also*

contributes to the benthic food web, produced several good year-classes in the 1990s." (Stewart et al., 1999)

Lake Erie: "*Prevent extinction by protecting rare, threatened, and endangered fish species [for example, lake sturgeon and lake herring] and their habitats."* (Ryan et al., 2003)

Lake Huron: "*Restore lake herring to a significant level and protect, where possible, rare deepwater ciscoes."* (DesJardine et al., 1995)

Lake Michigan: *"Maintain a diversity of planktivore (prey) species at population levels matched to primary production and to predator demands… Native planktivores should be encouraged now that alewife populations are reduced. Rehabilitation of native planktivores is a desirable objective that would increase the biological integrigty and diversity of the planktivore community. Two species of special concern are lake herring and emerald shiner."* (Eshenroder et al.,1995)

Lake Superior: *"A self-sustaining assemblage of prey dominated by indigenous species at population levels capable of supporting desired populations of predators and a managed commercial fishery… Historically, lake herring was the dominant prey fish in Lake Superior."* (Horns et al., 2003)

Despite nearly a century of research on cisco, our understanding of this species is still limited. Expert opinions consider the larval stage to be the most likely bottleneck for cisco recruitment, yet very little is known about this life-stage. A better understanding of the mechanisms that influence survival of larval cisco in Lake Superior could prove invaluable to fisheries managers on the Lower Great Lakes, as they consider the likelihood of cisco restoration given the current suite of impediments in each of the respective ecosystems. A number of hypotheses have been proposed to explain the

highly variable recruitment of cisco in Lake Superior and their slow recovery in the Lower Great Lakes. These include large-scale density independent factor(s), predation by rainbow smelt, and a combination of both biotic and abiotic factors. Within the first chapter of my dissertation, my coauthors and I used a quantitative approach to measure the spatial scale of cisco recruitment synchrony across the Upper Great Lakes region. We found that the measures of synchrony were consistent with the hypothesis that broad-scale environmental factors play an important role in synchronizing the recruitment patterns of disparate cisco populations. The second chapter of my dissertation concentrated on the relative importance of rainbow smelt predation and food availability as contributors to larval cisco mortality in Lake Superior. Our modeling results indicated that rainbow smelt predation may have limited survival at specific locations, yet the conditions for growth (i.e., temperature, prey availability) likely had a significant effect on survival across all locations. The final chapter of my dissertation focused on the role of water temperature in determining recruitment of cisco. Again, our modeling suggested that water temperature was most likely a proxy for conditions that enhanced foraging opportunities and limited metabolic costs.

I believe the body of research that constitutes this dissertation clearly shows that the larval stage is critically important for the survival of a given cisco year-class. Furthermore, I believe this research demonstrates that the conditions larval cisco are exposed to following hatching are typically not conducive to accelerated growth or increased survival. As a consequence, failed year-classes are the norm and strong year-classes can only be expected to occur intermittently. Because of the spasmodic recruitment patterns and relatively large size of adult cisco, it's not likely that the species

will ever support the predatory fish biomass (and the associated fisheries) that non-native forage species (i.e., alewife, rainbow smelt) once did. Thus, fisheries managers should carefully consider their expectations for restored cisco populations in the Lower Great Lakes. While the goal of restoring cisco for the sake of serving as forage for Pacific salmon may not be realistic, there does seem to be potential for cisco to assist with energy transfer from offshore areas to nearshore areas (*sensu* Stockwell et al., 2014). Thus, I believe the pursuit of cisco rehabilitation as a means of improving energy transfer and ecosystem function is a worthwhile endeavor and should be supported to the degree that other large-scale restoration projects have been supported in the Lower Great Lakes.

CHAPTER 1

SPATIAL SYNCHRONY IN CISCO RECRUITMENT

Abstract

We examined the spatial scale of recruitment variability for disparate cisco (*Coregonus artedi*) populations in the Great Lakes (n=8) and Minnesota inland lakes (n=4). We found that the scale of synchrony was approximately 400 km when all available data were utilized; much greater than the 50-km scale suggested for freshwater fish populations in an earlier global analysis. The presence of recruitment synchrony between Great Lakes and inland lake cisco populations supports the hypothesis that synchronicity is driven by climate and not dispersal. We also found synchrony in larval densities among three Lake Superior populations separated by 25-275 km, which further supports the hypothesis that broad-scale climatic factors are the cause of spatial synchrony. Among several candidate climate variables measured during the period of larval cisco emergence, maximum wind speeds exhibited the most similar spatial scale of synchrony to that observed for cisco. Other factors, such as average water temperatures, exhibited synchrony on broader spatial scales, which suggests they could also be contributing to recruitment synchrony. Our results provide evidence that abiotic factors can induce synchronous patterns of recruitment for populations of cisco inhabiting waters across a broad geographic range, and show that broad-scale synchrony of recruitment can occur in freshwater fish populations as well as those from marine systems.

Introduction

Separate populations of the same species are frequently observed to fluctuate synchronously (Post and Forchhammer, 2002), yet the mechanisms contributing to these patterns are often unclear. Understanding the spatial scale of synchrony can provide insight into the processes involved because different forcing mechanisms often operate at different spatial scales. For example, biotic factors (e.g., predation and competition) are generally believed to operate at local scales, while many abiotic factors (e.g., climate) operate at broader scales. The synchronizing effect of environmental factors is referred to as the "Moran effect" (Hudson and Cattadori, 1999). Moran's theorem states that the spatial correlation of population variation will equal the spatial correlation of environmental variation for those species whose dynamics are driven by similar environmental cues (Moran, 1953).

Sources of recruitment variation in fish populations have been the subject of much debate (Houde, 2008). Analyses by Myers et al. (1997) suggested the spatial scale of recruitment synchrony for marine fishes is approximately 500 km compared to only 50 km for freshwater fishes. Myers et al. (1997) concluded that biotic interactions regulated recruitment of freshwater species while abiotic factors were more important for marine species. While local biotic interactions certainly influence freshwater fish recruitment, the effects of abiotic factors like climate cannot be dismissed. For example, several studies have reported that indices of water temperature were correlated with patterns of walleye (*Sander vitreus*) year-class strength (Koonce et al., 1977; Busch et al., 1975; Schupp, 2002). In addition, Phelps et al. (2008) found that climatic variability

synchronized recruitment of common carp (*Cyprinus carpio*) across a 175-km^2 area in the Midwestern United States. Marjomäki et al. (2004) analyzed time-series of vendace (*Coregonus albula*) from 21 lakes in Finland (surface areas < 1,100 km^2) and found significant positive correlations among lakes in both recruitment and spawner indices for populations separated by 100-300 km. Bunnell et al. (2010) studied the Upper Great Lakes (>50,000 km^2) and found bloater (*Coregonus hoyi*) recruitment was synchronized at 600-800 km. These authors concluded that dispersal of bloater likely contributed to within-lake synchrony, but climate likely led to synchrony found across lakes because the dispersal mechanism seemed implausible. The inferences of Bunnell et al. (2010) were based on catches of 95-130 mm (age-0 and age-1) bloater, and thus dispersal of smaller bloater from natal areas to other sites in the same lake could not be ruled out. Collectively, these examples provide evidence that the spatial scale of synchrony in freshwater populations often exceeds 100 km, suggesting climate can influence fish recruitment in lacustrine environments.

Climate variables are strongly correlated over broad spatial scales (e.g., > 1000 km), especially in terms of mean annual values (Koenig, 2002). However, the magnitude of fish recruitment can be set in short time windows (Cushing, 1990). It follows that measuring spatial synchrony of abiotic factors using mean values that integrate too long a time period may mask the Moran effect. Marjomäki et al. (2004) found that vendace population indices and mean air temperature during the month following ice break-up were anisotropic, meaning patterns of synchrony were more evident along east-west axes than north-south axes. This observation highlights the influence of prevailing weather patterns and their movement across the landscape and

also underscores the need to consider both the spatial and temporal aspects of plausible bottlenecks when attempting to understand how climate may influence recruitment.

Another important consideration when trying to understand climate effects is the physical characteristics of the lakes under study. Myers et al. (1997) argued that regional weather systems should affect lakes and streams just as they would marine ecosystems. However, freshwater ecosystems vary extensively in size and shape and thus respond to climatic variables at different rates (Magnuson et al., 1997; Gerten and Adrian, 2001; George et al., 2004). Marjomäki et al. (2004) noted that the date of ice-break between Finnish lakes ranged from less than two to greater than four weeks across years, which highlights the variability that can occur in inland lakes, despite their geographic proximity. In contrast, the thermal inertia, internal currents, and hydrologic connectedness of larger systems, such as the Great Lakes, could lead to a more uniform response to climate through space. Thus, the difference in spatial synchrony for vendace and bloater could be interpreted as species-specific dependences on climatic variables or the heterogeneous response of different types of lakes exposed to similar climate regimes. Given the variability associated with freshwater lakes, broad-scale measures of spatial synchrony are an indication of the role of climate but finer-scale measures do not necessarily preclude the influence of climate.

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). In Lake Superior, cisco begin aggregating in October and spawn primarily during November and December (Stockwell

et al., 2009). After hatching, cisco larvae spend their early stages of development near the surface in May and June (Stockwell et al., 2009). There is strong evidence indicating that the year-class strength of cisco and other coregonines is established prior to the end of the larval stage (McCormick et al., 1971; Viljanen, 1988; Kinnunen, 1997), with the first few weeks after hatching being especially critical (Rice et al., 1987). Bronte et al. (2003) and Stockwell et al. (2009) showed that year-class strength was synchronized across Lake Superior cisco stocks, and concluded that climate drove these patterns. However, neither analysis provided quantitative estimates of spatial synchrony. Thus, our primary objective was to determine the spatial scale of synchrony for cisco within the Great Lakes, and to explore whether inclusion of populations outside the Great Lakes influenced our findings. To evaluate this objective we gathered data for cisco populations covering a broad spatial scale (>1000 km) occupying a range of lake sizes. We coupled this with an analysis of the spatial correlation of spring meteorological observations from offshore Great Lakes weather buoys, which led to the development of hypotheses regarding the potential influence of climatic variables on cisco recruitment. Although the role of climate in determining Lake Superior cisco recruitment has been speculated (Bronte et al., 2003; Stockwell et al., 2009), Bunnell et al. (2010) highlighted that it is wrong to assume population synchrony is driven solely by climatic events when dispersal of individuals could also explain the phenomenon. To better understand whether dispersal or climate drives cisco synchrony, we examined the inter-annual variability of larval cisco densities at three Lake Superior sites that were separated by 25–275 km. Finding spatial synchrony of larvae that were collected concurrently at

separate sites within weeks of emergence would provide evidence that climate, and not

dispersal, led to patterns observed by Bronte et al. (2003) and Stockwell et al. (2009).

Methods

Acoustic data collection and sample processing

We sampled 12 cisco populations across the Upper Great Lakes region (Figure 1) including 5 sites in Lake Superior, 2 sites in Lake Huron, 1 site in Lake Michigan, and 4 small lakes in northern Minnesota. Populations in the Great Lakes were assessed during November 2010 when cisco were aggregated for spawning (Yule et al., 2009), while populations in the Minnesota inland lakes were assessed during July and August 2010 (Ahrenstorff et al., 2013). The objective of both the autumn and summer surveys was to measure abundance of yearling and older pelagic fish so combining these datasets was deemed appropriate.
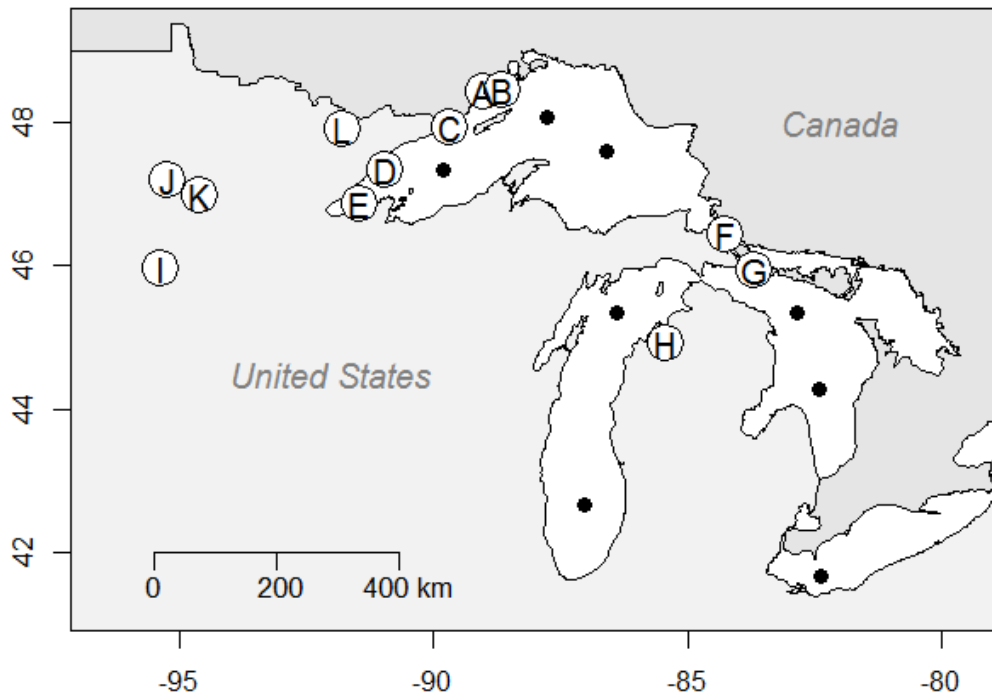
Figure 1. Locations of cisco populations (letters) and NOAA buoy stations (black dots) used to test the scale of spatial synchrony within the region. The letters in this map correspond to the letters used in other tables and figures.

Stockwell et al. (2009) showed that bottom trawl surveys do not adequately describe the age structure, density, or biomass of cisco in Lake Superior. Thus, night hydroacoustic surveys were coupled with netting to estimate abundance and characterize size and age structures of each population. Acoustic data collection and processing followed the Great Lakes standard operating procedure (Parker-Stetter et al., 2009; Rudstam et al., 2009). We collected between 6 and 131 km of acoustic data at each site, with indices of coverage (Aglen, 1983) ranging from 1.2 to 5.0 (Table 1). Using Echoview software version 4.90 (Myriax Pty Ltd., Tasmania, Australia), we defined cells on echograms measuring 10 m in height by 2 km in length and calculated total fish densities (#/ha) in each cell from 3 m below the surface to 0.5 m above the lakebed. Target strength (TS) distribution exports for each cell were used to estimate densities of two sizes of fish: small fish < 35.6 decibels (dB), and large fish $\geq$ -35.6 dB, coinciding to fish less than and greater than 250 mm, respectively (Yule et al., 2006; 2009). At Drummond Island the acoustic data from 2010 were compromised due to electrical interference, so we used acoustic data gathered during October 2009 for this site.

Midwater trawl catches were used to interpret acoustic data at Lake Superior sites, while gillnets were used at the much shallower Lake Huron, Lake Michigan, and Minnesota inland lake sites (Table 1). The gear deployed at each site (Table 1) was capable of catching yearling and older cisco. All captured fish were sorted to species and counted. We measured total length of all fish from most sites, but did sub-sample some large catches of non-target species. Fish that were not measured were assigned

Table 1. Sampling date(s), area sampled (km^2), kilometers (km) of acoustic data collected, degree of coverage, sampling gear, and number of samples collected to survey cisco populations across the Upper Great Lakes region. Sampling dates are for the year 2010, with the exception of Drummond Island, for which acoustic data were collected in 2009. The gear used to sample cisco included midwater trawls (MWT; 15.2 m headrope and footrope lines;13.7 m breast lines; 152 mm mesh at the mouth graduated to 13 mm at the cod end), bottom-set gillnets (BGN; graded-mesh, multifilament; 50.8 to 101.6 mm stretch measure in 12.7 mm increments), and vertical-set gillnets (VGN; graded-mesh monofilament gillnet; 9.5, 12.7, 19.0, 31.8 and 50.8 mm stretch measure).

Location	Area (km^2)	Date(s)	Acoustic Data (km)	Degree of Coverage	Gear (# Samples)
Lake Superior					
A) Thunder Bay	700	11/09-11	131	5.0	MWT (14)
B) Black Bay	300	11/12-13	82	4.7	MWT (7)
C) Grand Portage	100	11/14	24	2.4	MWT (4)
D) North Shore	100	11/08-09 & 11/15-17	12	1.2	MWT (7)
E) South Shore	300	11/16	65	3.8	MWT (7)
Lake Huron					
F) St. Mary's River	5	11/03	9	2.2	BGN (4)
G) Drummond Is.	10	10/15	14	3.1	BGN (3)
Lake Michigan					
H) Grand Traverse Bay	5	11/09	8	2.2	BGN (15)
Minnesota					
I) Carlos Lake	10.2	08/09	14	4.4	VGN (1)
J) Elk Lake	1.1	08/03	6	5.7	VGN (1)
K) Ten Mile Lake	20.4	07/19	14	3.1	VGN (1)
L) White Iron Lake	6.9	07/28	7	2.7	VGN (1)

a total length based on the measurement of ≥50 randomly-selected fish of the same species.

Yule et al. (2013a) used simulated fish communities to demonstrate that classification trees performed well as an acoustic apportionment method. For this reason we developed classification tree models (*sensu* Yule et al., 2013b) using the recursive partitioning package (Therneau and Atkinson, 2012) available in R (R Development Core Team 2011). Separate trees were developed for both large (≥ 250 mm) and small fish (< 250 mm) caught at each site in the Great Lakes. This size threshold and the associated TS cutoff (i.e., -35.6 dB) have been used to separate mature cisco from smaller pelagic fish (e.g., rainbow smelt (*Osmerus mordax*), juvenile cisco) during previous surveys of cisco populations in Lake Superior (Yule et al., 2006; 2009). Cisco caught in the Minnesota lakes were all smaller than 250 mm (Ahrestorff et al., 2013), leading us to develop a single classification tree for each inland lake. Species was the response variable while 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, locations where only a single sample was collected negated use of latitude and longitude while use of only bottom-set gillnets negated 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 (Zuur et al., 2007). In addition, terminal leaves with <10 fish were pruned (Yule et al. 2013). The

species proportions of the model terminal leaves were used to apportion the cell density estimates to species (*sensu* Yule et al. 2013a). If the model could not find a meaningful split of the data, we used the species proportions from all catches at a given site to apportion acoustic densities. We summed cisco density estimates across all cells in each 2-km segment and calculated an average density of small and large cisco (where applicable) using the 2-km segments as sample units.

Estimating year-class strength

Cisco were aged by one individual at North Shore Environmental Services (Thunder Bay, Ontario) using the crack and burn method of aging otoliths (Schreiner and Schram, 2001). Yule et al. (2008) showed that this ager using this method provided age estimates consistent with a Lake Superior recruitment index. We assigned ages to all cisco caught at each site using site-specific semi-random age-length keys (Ogle, 2012) constructed with 50 mm length bins. After assigning each captured cisco an age estimate, we assumed the catch at each site reflected the true population, and apportioned the average density of small and large cisco measured at each site to age classes.

Stockwell et al. (2009) used a von Bertalanffy growth curve to show that age-1 cisco caught in the Apostle Islands region of Lake Superior during November and December were approximately 150 mm. In addition, Yule et al. (2006) demonstrated that the majority of cisco collected using midwater trawls during a 2004 spawning assessment in the Apostle Islands were immature (i.e., 138-238 mm). The 2003 cisco year-class was deemed successful in Lake Superior (Stockwell et al., 2009), providing

evidence that age-1 and older cisco were vulnerable to our midwater trawl gear. Furthermore, graded-mesh gillnets have been used to characterize the size structure of cisco >100 mm (Ahrenstorff et al., 2013) so we assumed both gears provided an unbiased assessment of the populations.

A weighted catch-curve regression (Maceina and Bettoli, 1998) was fit to the age-specific, natural log (ln) transformed densities (i.e., age-1 to the maximum observed age) of each population and the relative strength or weakness of each year-class was defined by the studentized residual. A weighted regression was used for the analysis because cisco can live in excess of 20 years and exhibit spasmodic recruitment (Yule et al., 2008). Older and rarer cohorts are often underrepresented when sample size is low and thus, the influence of these cohorts is deflated by conducting an initial regression and using the predicted values of ln-transformed densities for each age as weights for a second regression procedure (Maceina and Pereira, 2007). Using Pearson product moment correlation coefficients, we compared the catch-curve residuals for each possible pairing of locations to determine whether population fluctuations were synchronous.

NOAA buoy observations

Climate and limnological data were obtained from eight offshore buoy stations in Lakes Superior, Michigan, Huron, and Erie (Figure 1) operated by the U.S. National Oceanic and Atmospheric Administration (NOAA). We used records between May 15 and June 15 for the years 1983 to 2010 because Lake Superior larval cisco emergence generally peaks during this period (Hatch and Underhill, 1988; Myers et al., 2009), and

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fish from the 1983-2010 year-classes were represented in our 2010 age estimates.
When there were multiple recordings for a single day, we used the average of the
measurements for that day. We calculated the Pearson product moment correlation
coefficient for each possible pair of buoy stations using the annual time series of
average air temperature, average surface water temperature, average wind speed, and
maximum wind speed.

Estimating the spatial scale of synchrony

We followed the methods of Myers et al. (1997) in their global, multi-species
meta-analysis in order to ensure comparability of results. According to Myers et al.
(1997), a simple estimate of the spatial scale of synchrony is the distance over which
the pairwise correlation coefficients between recruitment (defined as the catch-curve
residuals) or climate 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 straight-line distance (km) between populations or buoys. The
parameter *d* was measured by first converting coordinates from decimal degrees to
UTM, which allowed us to calculate the distance between the two points using the
Pythagorean theorem. In this model, we constrained 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 for cisco recruitment were only included when two populations had at least five year classes in common. Comparing the spatial scale of synchrony for cisco populations to that of environmental variables guided our evaluation of potential factors driving cisco recruitment in the region.

Evaluating the role of dispersal in Lake Superior

Inclusion of data from four Minnesota inland lakes allowed us to evaluate the hypothesis that dispersal might be the mechanism responsible for synchrony of recruitment. To further consider this possibility we examined larval cisco densities collected over five years (2006-2011) at three Lake Superior sites (Thunder Bay, Black Bay, and South Shore; Figure 1), separated by 25-275 km. These data were collected as larvae emerged at each site, so dispersal between sites could not explain any observed co-variation. An individual sample consisted of measuring larval densities (No. per 1000 m³) at individual stations (~ 1 station per 1000 ha, see Myers et al. 2009 for example survey designs) using the capture methods of Myers et al. (2008). Only samples collected between May 15 and June 15 were used in the analysis because it is the period when the majority of cisco had hatched. Due to logistical constraints, all sites were not sampled in all years. An ANOVA model was used to determine whether the ln-

transformed larval cisco densities varied with respect to year, site, or the interaction between year and site. Tukey's multiple comparison procedure was used to interpret significant differences identified by the ANOVAs. Prior to transformation, we added the minimum density observation greater than zero to all density estimates from the given location. Evidence of a significant main effect of year, and the absence of a significant year-by-site interaction would suggest that a common factor was influencing larval density among these sites.

RESULTS

The apparent synchrony in cisco recruitment across the region seems to be largely due to high recruitment during some years (e.g., 2009) and low recruitment during others (e.g., 2006) (Figures 2 & 3). In Lake Superior and Lake Huron, synchrony appears to be the result of predominately poor recruitment in conjunction with occasional strong year-classes (e.g. 1998, 2003). Although populations in Lake Superior and Lake Huron were characterized by infrequent recruitment, they appear to have greater longevity (≥ 15 years) than cisco in Lake Michigan and the Minnesota inland lakes (≤ 8 years) investigated (Figure 2).

The exponential fit between distance and the decay of the pairwise correlation of the residuals from the catch curves showed that the e-folding scale for populations in the Great Lakes was 245 km (SE=135) to 236 km (SE=83), depending on the model (Figure 4, Table 2). Meanwhile, when cisco populations from both the Great Lakes and Minnesota inland lakes were combined the e-folding scale was 468 km (SE=234) to 359 km (SE=99), which suggests that inclusion of inland lake cisco populations did not lower estimates of spatial synchrony. The variation in correlation coefficients was large and contained a considerable number of negative values, yet these results are consistent with those presented by Myers et al. (1997) for marine species. Many of the negative values were the result of comparisons between Grand Traverse Bay and other populations (Figure 4), which suggests recruitment dynamics at Grand Traverse Bay were unique. When comparisons with Grand Traverse Bay and Minnesota inland lakes
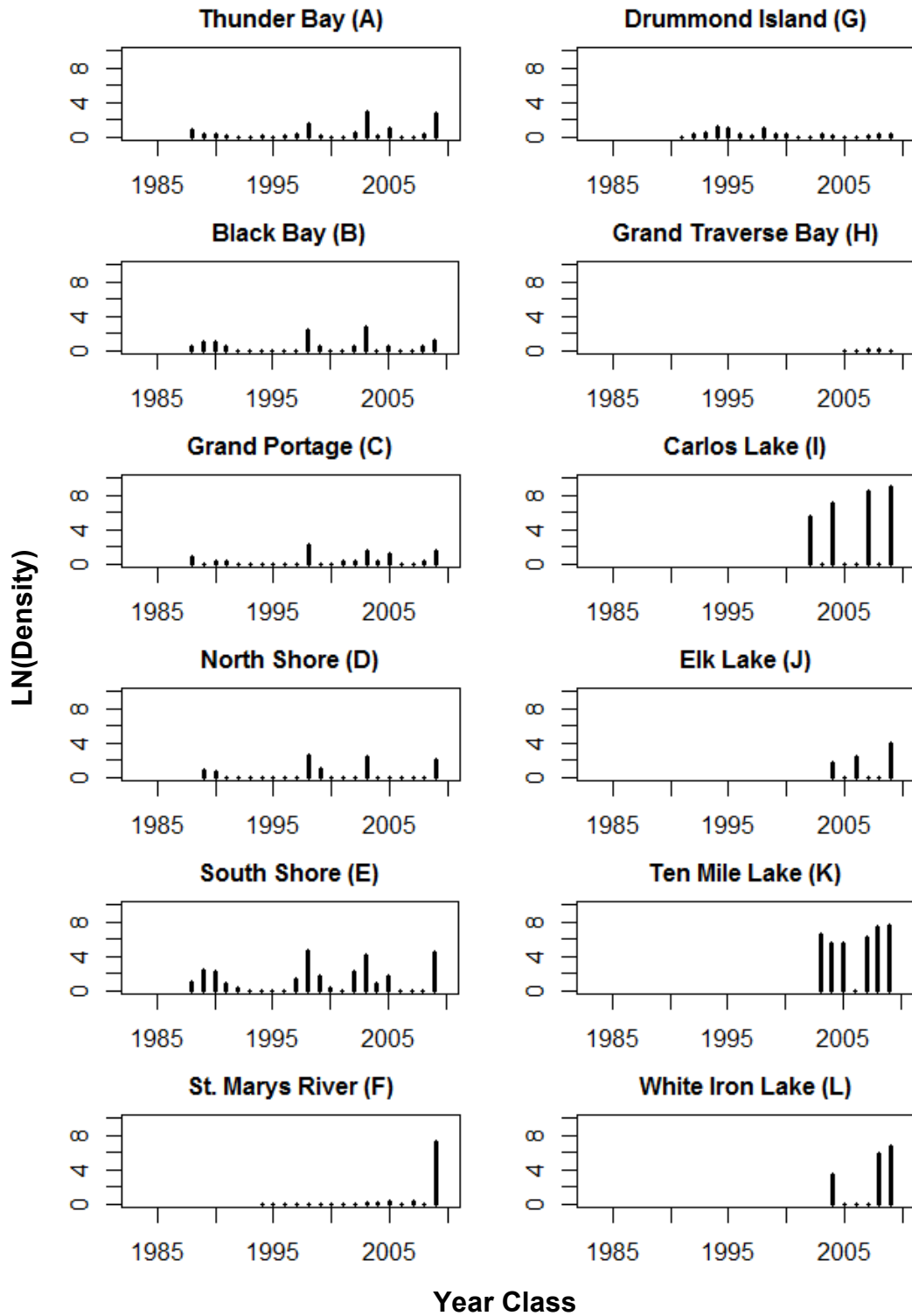
Figure 2. Ln-transformed density (#/ha) of individual cisco year-classes at sites in the Great Lakes (A-H) and Minnesota inland lakes (I-L).

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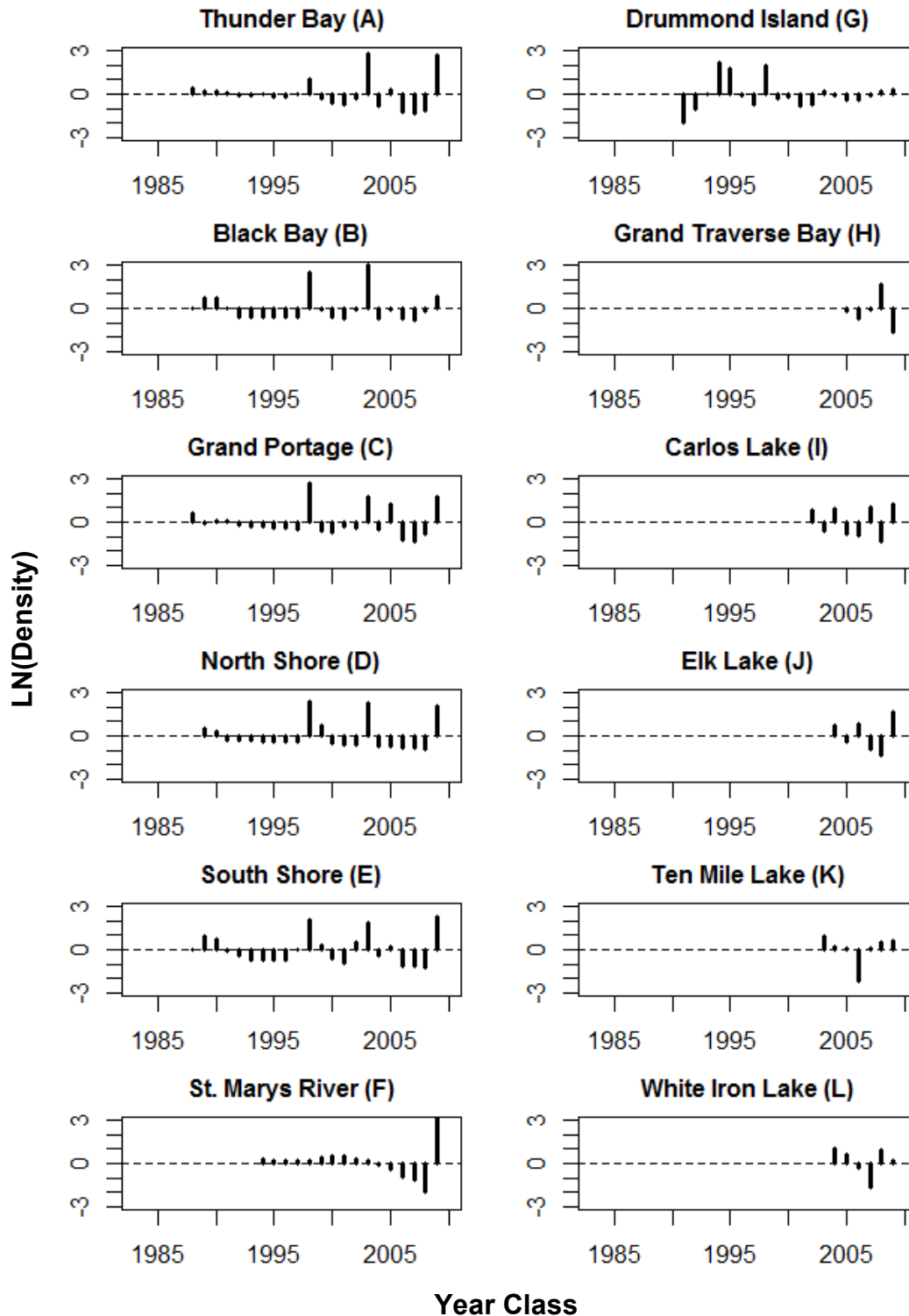
Figure 3. Residuals from catch-curve regressions, which serve as indexes of year-class strength for cisco populations in the Great Lakes (A-H) and Minnesota inland lakes (I-L).healthy.
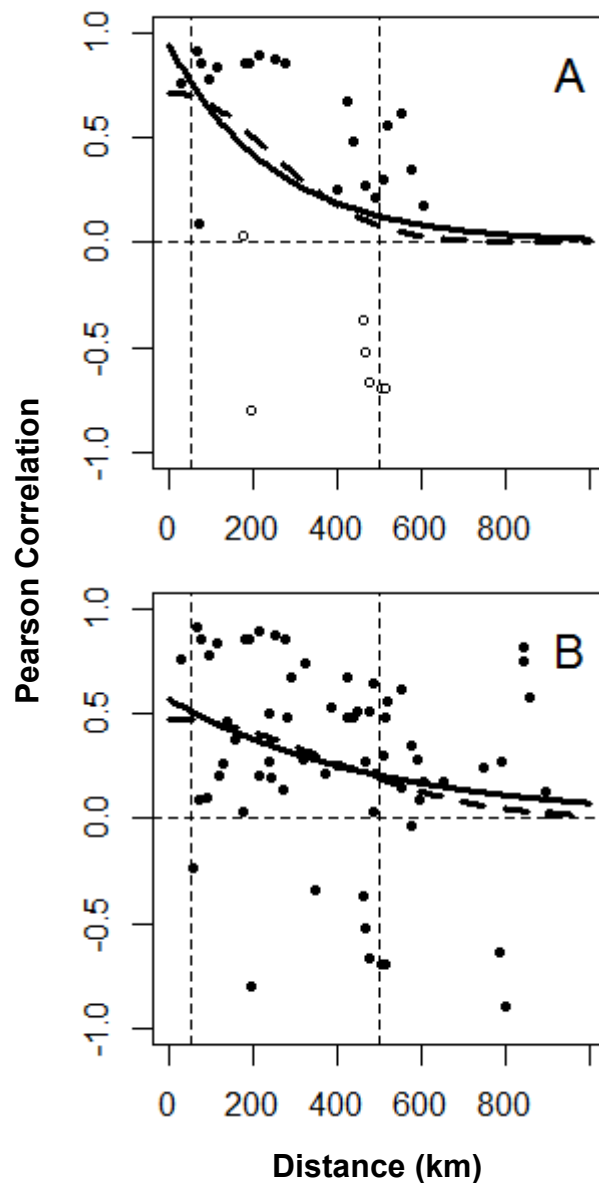
Figure 4. Spatial scale of synchrony between pairs of cisco populations in the Great Lakes (A) and also for pairs of cisco populationms in the Great Lakes and Minnesota inland lakes (B). Fits of the models $\rho_0 e^{-\frac{d}{v}}$ (solid curve) and $\rho_1 e^{-0.5\left(\frac{d}{\sigma}\right)^2}$ (broken curve) suggest the scale of spatial syncrony extends to approximately 240 km for Great Lakes populations and to 400 km when all available populations were included in the analysis. According to Myers et al. (1997), the expected scale of spatial synchrony for freshwater and marine species is 50 km and 500 km (vertical dashed lines), respectively. Horizontal dashed line represents zero correlation. Open circles in "A" show comparisons between the Grand Traverse Bay cisco population and other Great Lakes cisco populations.

were excluded, the spatial scale of synchrony for the remaining cisco populations in the Upper Great Lakes was 724 km (SE=259) to 431 km (SE=69).

Correlations between average spring (May 15 to June 15) air temperature, surface water temperature, or wind speed and buoy separation distance generally declined in a linear fashion, while maximum wind speed declined exponentially (Figure 5). The correlation scale (i.e., σ) is greater than 800 km for average spring air temperature, water temperature, and wind speed (Table 2). However, the correlation scale of maximum wind speed was only 388 km, quite similar to the estimate of σ for cisco recruitment (Table 2).

Larval densities varied significantly (p<0.001) according to year and site (Figure 6), but the interaction of year and site was not significant. Thunder Bay had significantly greater average larval densities than both the South Shore and Black Bay sites (p<0.001), and mean densities at South Shore exceeded that of Black Bay (p<0.003). Compared to the other five years when sampling occurred, larval densities were highest in 2009 (p<0.001). This result is consistent with our age estimates of yearling and older cisco at these three Lake Superior sites (Figures 2 & 3) which, together with the observed covariation in larval densities among these sites, raises doubt that dispersal drives patterns of spatial synchronicity.

Table 2. Parameter estimates and their standard errors (SE) for the two models used to describe the spatial scale of correlation of cisco recruitment and meteorological data. The meteorological variables that were investigated include average air temperature, average water temperature, average wind speed, and maximum wind speed. Observations are from May 15 to June 15 for the years 1983-2011.

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)
Cisco Recruitment								
Great Lakes	26	0.52	0.95 (0.36)	245 (135)	26	0.52	0.73 (0.21)	236 (83)
All Lakes	64	0.44	0.58 (0.18)	468 (234)	64	0.44	0.48 (0.11)	359 (99)
Meteorlogical Variables								
Average air temperature	26	0.16	0.85 (0.09)	2499 (1397)	26	0.16	0.80 (0.05)	983 (231)
Average water temperature	26	0.12	0.94 (0.07)	1938 (617)	26	0.12	0.86 (0.04)	911 (136)
Average wind speed	26	0.13	0.67 (0.07)	1553 (644)	26	0.13	0.59 (0.05)	853 (192)
Maximum wind speed	26	0.25	0.68 (0.25)	396 (181)	26	0.26	0.45 (0.13)	388 (114)
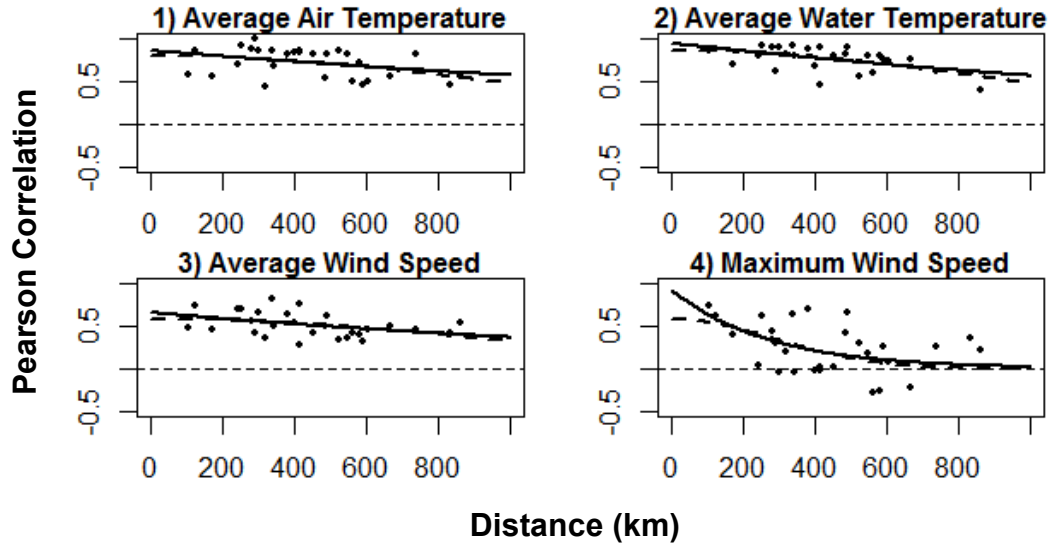
Figure 5. Correlation of 1) average air temperature 2) average water temperature 3) average wind speed and 4) maximum wind speed between pairs of NOAA's Great Lakes buoys versus distance. Observations are from May 15 to June 15 for the years 1983-2011. Models used to estimate spatial scale of synchrony include $\rho_0 e^{-\frac{d}{v}}$ (solid curve) and $\rho_1 e^{-0.5\left(\frac{d}{\sigma}\right)^2}$ (broken curve). Horizontal dashed line represents zero correlation.
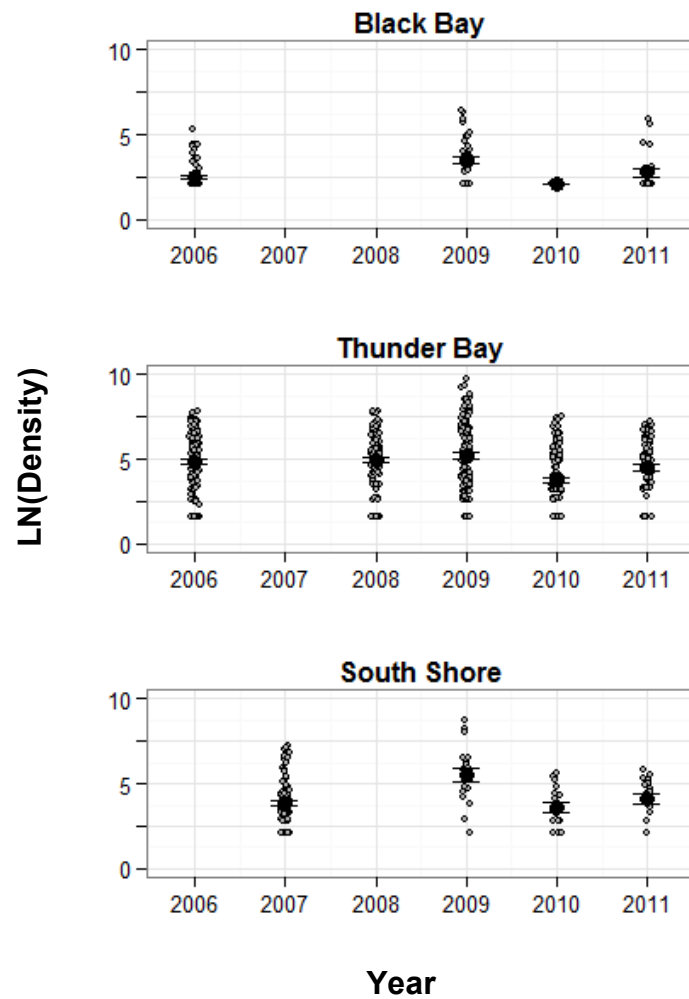
Figure 6. Ln-transformed larval cisco density during spring emergence (15 May – 15 June) at three locations in Lake Superior. Bold points indicate the mean and error bars are 1 SE. Raw data points are offset horizontally for visual purposes. Years with no sampling effort are blank.

Discussion

Ecologists have largely accepted that populations of many species fluctuate in synchrony over broad spatial scales (Ranta et al., 1998; Liebhold et al., 2004). Despite general acceptance, there is less agreement about the mechanisms driving the phenomenon. The two major factors hypothesized to be involved in synchronization of the dynamics of disparate populations are climate and dispersal (Koenig, 1999). Our study attempted to separate the effects of dispersal from those of the Moran effect by examining the synchrony of cisco recruitment for populations both within and outside the Great Lakes. We identified substantial synchrony in the recruitment dynamics of cisco across a broad spatial range and believe our argument for the Moran effect is strengthened by the inclusion of populations for which dispersal is not possible. In addition, the positive relationship between larval cisco density and subsequent year-class strength at Lake Superior sites separated by approximately 250 km is further evidence against dispersal being the cause of synchronous recruitment patterns. However, it needs to be mentioned that pelagic fish larvae in the Great Lakes can be transported distances >120 km (Dettmers et al., 2005). Furthermore, cisco larvae in Lake Superior may be transported great distances from major spawning sites by longshore currents (Oyadomari and Auer, 2008). While the role of dispersal cannot be ruled out completely, we believe our results suggest that factors that have a similar influence on geographically-disjunct populations are the more probable cause of spatial synchrony in cisco recruitment.

Our estimates of the model parameters provide evidence that the e-folding scale for cisco recruitment (Table 2) likely exceeds what Myers et al. (1997) would have predicted for a freshwater species. Myers et al. (1997) argued that variability in freshwater fish recruitment depends predominately on biotic influences operating at fine scales, while recruitment of marine species is largely determined by environmental factors operating at much broader scales. However, only five freshwater species were considered by Myers et al. (1997) and it is unclear whether the populations were from the Great Lakes or inland lakes. We hypothesize that the size of the system in which a population resides plays a more important role in the recruitment process than salinity. Lakes in the Laurentian Great Lakes and Precambrian Shield Region respond strongly to climate (Magnuson et al., 1997), yet differences in morphometry, hydrology, and other physical factors all contribute to systems responding uniquely. For example, smaller lakes will have a shorter fetch, less consistent mixing currents and less thermal inertia, while larger systems will be characterized by longer fetch, stronger currents and more thermal inertia. For this reason the Great Lakes behave much like inland seas and exhibit physical processes characteristic of the coastal regions of oceans (Rao and Schwab, 2007). Thus, we believe the conclusions of Myers et al. (1997) could be misleading and that lower measures of spatial synchrony associated with freshwater species could simply be an artifact of the heterogeneity of individual ecosystems and their differential response to abiotic factors.

Our estimates of the correlation scale for recruitment of cisco were similar to the results of Rook et al. (2012), which projected that the spatial scale for modeling stock-recruitment dynamics of cisco in Lake Superior was approximately 260 km. However,

the analysis by Rook et al. (2012) did not explicitly measure how the correlation

between stocks weakened with distance, making comparisons to the global analysis by

Myers et al. (1997) difficult. Instead, their inferences were based on the stock-

recruitment relationships developed for regions across Lake Superior using density

estimates derived from spring bottom trawl samples. There are at least five recent

papers in the fisheries literature documenting that day bottom trawl sampling provides

estimates of adult cisco abundance that are biased low (Johnson et al., 2004; Mason et

al., 2005; Stockwell et al., 2006; Yule et al., 2007; Stockwell et al., 2009). Stockwell et

al. (2006) went on to conclude that earlier attempts to develop stock-recruitment

relationships using spring bottom trawl estimates (e.g., Hoff, 2004) were wrong because

the sampling approach lacked the precision necessary to develop meaningful

relationships (*sensu* Walters and Ludwig, 1981). Stockwell et al. (2006) also argued that

Hoff's (2004) search for factors other than adult stock biomass (e.g., lake trout

(*Salvelinus namaycush*) abundance, slimy sculpin (*Cottus cognatus*) biomass, April

wind speeds) to explain cisco recruitment was undermined by the use of an

inappropriate sampling gear, leading to results that were "tenuous at best". Recently,

Rook et al. (2013) used an approach similar to Hoff (2004) and found an effect of April

wind speed (i.e., during the spring when cisco begin hatching) and April air

temperatures (i.e., when cisco are 11-12 months of age) on measures of cisco

recruitment from bottom trawls. Having conducted extensive larval sampling in Lake

Superior over several years, it has been our experience that cisco are not captured in

surface waters until the month of May (Figure 7), which calls into question how

unhatched cisco could be influenced by April winds. Furthermore, the magnitude of

cisco recruitment is believed to be established before cisco reach age-1 (Stockwell et al., 2009), meaning the effect of April air temperatures on cisco that are already age-1 is likely trivial. Yule (1926) demonstrated that we sometimes get "nonsense-correlations" between time-series, for which we cannot provide a reasonable defense for how the relationship arose. To advance our understanding of cisco population dynamics in the Great Lakes, we suggest that analyses be based on regular acoustic surveys rather than demersal trawling.
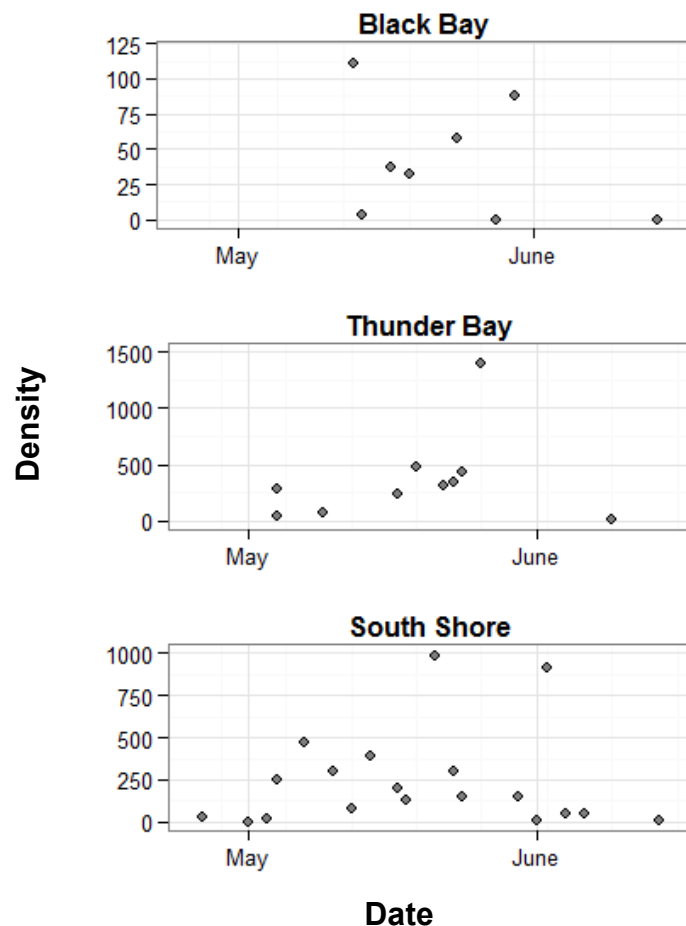
Figure 7. Average densities (#/1000 m^3) of larval cisco versus the average date of sampling for surveys conducted at three locations in Lake Superior. Surveys were conducted between 2006 and 2011.

We found that 2009 larval cisco densities were an indicator of subsequent year-class strength, which suggests that processes operating prior to the end of the larval-stage may be important. Houde (1994) argued that differences between the averaged vital rates (e.g., growth rates, mortality rates) and energetics of fish larvae (Houde and Zastrow, 1993) suggests that juvenile-stage dynamics are more important in determining recruitment levels and variability of freshwater species, while larval-stage dynamics are more important in marine species. Contrary to the results of Houde (1994), evidence suggests year-class strength of coregonines is largely determined during the first few weeks after larval hatching in both European (Viljanen, 1988; Huusko and Sutela, 1998; Auvinen et al., 2000) and North American (Taylor and Freeburg, 1984; Rice et al., 1987; Oyadomari and Auer, 2007) freshwater lakes. Compared to older stages of development, cisco larvae are disproportionately vulnerable to subtle changes in temperature (McCormick et al., 1971) and wind driven currents (Oyadomari and Auer, 2008), which is consistent with the observations of this study. Sensitivity to these factors is compounded by the fact that spring (i.e., period of larval cisco emergence) is usually characterized by higher wind speeds and variable temperatures (Rao and Schwab, 2007).

Our findings suggest that the generalizations of Houde (1994) and Myers et al. (1997) might not apply to all freshwater species and systems. Classification of species and their recruitment dynamics based on whether they inhabit marine or freshwater ecosystems is just one approach. An ecological classification (e.g., Balon, 1975) that considers the early life history of species and the environments they inhabit may provide greater insight about factors that regulate recruitment, particularly across space.

Although studies that examine the effects of physical processes on fish recruitment have been more common in the marine literature, the Great Lakes and other freshwater systems provide ample opportunities for similar research. A greater appreciation of physical-biological coupling and recruitment variability will be invaluable for attempts to develop integrated, ecosystem based fisheries management strategies (Ludsin et al., 2014).

It is plausible that a calm spring could lead to more stable environmental conditions (Rao and Schwab, 2007) and therefore reduce the likelihood of larvae being advected to colder and less productive offshore waters (Zhao et al., 2009). A warmer environment would encourage greater production of zooplankton (Shuter and Ing, 1997; Stockwell and Johannsson, 1997) and ultimately increase rates of age-0 cisco development. In general, larvae that obtain larger sizes have greater swimming capabilities, are more successful at feeding, are more resistant to starvation, and are less susceptible to predation (Miller et al., 1988). Based on the time-series of spring maximum wind speeds in western and central Lake Superior, two years with the least severe spring wind events were 1984 and 2003 (Figure 8). Interestingly, two of the largest cisco year-classes in Lake Superior recruited during these same years (Stockwell et al., 2009). The 1998 cisco year-class was also large, yet the maximum wind event that spring was moderate compared to other years (Figure 8). However, temperatures during the spring of 1998 were also high (Figure 8), which could have ameliorated the effect of moderate wind. The 2009 cisco year-class was also successful (Figures 2 & 3) and the maximum wind event occurred on May 16 during the spring of that year. After that date, the maximum average daily wind speed was 7.0 km/hr. Based
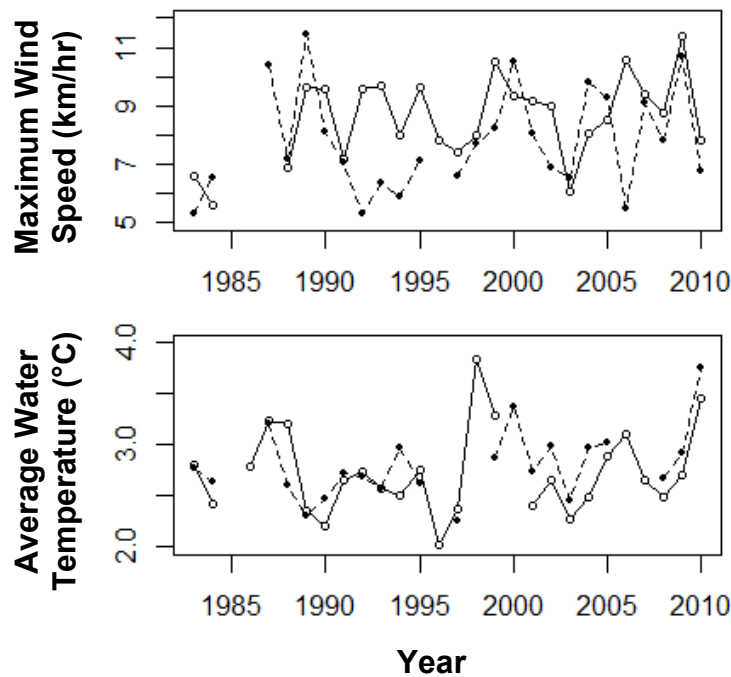
Figure 8. Time-series of the maximum wind speed (top) and average water temperature (bottom) during spring at the western (dashed line, solid circles) and central (solid line, open circles) offshore NOAA buoys in Lake Superior. Years with no data are missing.

on our 2009 sampling in Thunder Bay, we found that larval cisco densities were

486/1000 m^3 (SE=113) and 1399/1000 m^3 (SE=321) on May 19 and May 26,

respectively. Similarly, larval cisco densities along the South Shore in 2009 were 3/1000

m^3 (SE=2) on May 1 and 981/1000 m^3 (SE=468) on May 21. Based on this information,

we speculate that the strong wind events of 2009 may have occurred prior to the bulk of

hatching and thus few age-0 cisco were vulnerable to surface currents at that time. 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 6). This information leads us to conclude

that any environmental factor (or combination of factors) that exhibits measures of synchrony greater than or equal to the scale of cisco recruitment synchrony (i.e., wind, water temperature) could play a dynamic role in the determination of cisco year-class strength and thus contribute to the broad scale of cisco population synchrony within the Upper Great Lakes region.

Freshwater ecosystems appear to be especially sensitive to changes in climate as these systems are often characterized by distinct seasonal patterns in physical and biological processes. Anthropogenic climate change has caused Lake Superior summer surface water temperatures to increase approximately 2.5°C during the period of 1979-2006 (Austin and Colman, 2007), which is significantly greater than the rate of regional atmospheric warming. In addition, Desai et al. (2009) argued that increasing air and surface water temperatures could be causing the observed increase in average wind speeds due to the destabilization of boundary layers, which allows energy from winds aloft to be transferred to the lake surface more efficiently. As a result, surface wind speeds are increasing by nearly 5% per decade, which is again greater than the trends in wind speeds over land (Desai et al., 2009). These alterations to the physical environment could have a profound influence on trophic interactions, as even subtle changes in temperature can decouple species from favorable growing conditions (Cushing, 1990). Höök et al. (2006) provided evidence that current velocities in the Great Lakes can far exceed larval fish swimming capabilities, leading to the displacement of larvae from favorable nursery habitat. Similarly, Zhao et al. (2009) used a three-dimensional hydrodynamic-ecological model to demonstrate that wind-driven currents can have a negative impact on walleye recruitment in the western basin of

Lake Erie. Our findings suggest that a windier environment could also have a negative influence on age-0 cisco, so we suggest that fisheries managers and scientists 1) pay close attention to cisco recruitment patterns in coming years and 2) consider the use of physical-biological models as a means of investigating the mechanisms that drive recruitment.

CHAPTER 2

FORAGING AND PREDATION RISK FOR LARVAL CISCO (COREGONUS ARTEDI) IN LAKE SUPERIOR: A MODELING SYNTHESIS OF EMPIRICAL SURVEY DATA

Abstract

The relative importance of predation and food availability as contributors to larval cisco (*Coregonus artedi*) mortality in Lake Superior were investigated using a visual foraging model to evaluate potential predation pressure by rainbow smelt (*Osmerus mordax*) and a bioenergetic model to evaluate potential starvation risk. The models were informed by observations of rainbow smelt, larval cisco, and zooplankton abundance at three Lake Superior locations during the period of spring larval cisco emergence and surface-oriented foraging. Predation risk was highest at Black Bay, Ontario, where average rainbow smelt densities were >1000·ha^{-1}. Turbid conditions at the Twin Ports, Wisconsin-Minnesota, affected larval cisco predation risk because rainbow smelt remained suspended in the upper water column (0-10 m depths) during daylight, placing them alongside larval cisco during both day and night hours. Predation risk was low at Cornucopia, Wisconsin, owing to low smelt densities (< 400·ha^{-1}) and deep light penetration, which kept rainbow smelt near the lakebed and far from larvae during daylight. *In situ* zooplankton density estimates were low compared to values used to develop the larval coregonid bioenergetics model, leading to predictions of negative growth rates for 10 mm larvae at all three locations. The model predicted that 15 mm larvae were capable of attaining positive growth at Cornucopia and the Twin Ports where low water temperatures (2-6 °C) decreased their metabolic costs. Larval

prey resources were highest at Black Bay, but warmer water temperatures there offset the benefit of increased prey availability. A sensitivity analysis performed on the rainbow smelt visual foraging model showed it was relatively insensitive, while the coregonid bioenergetics model showed absolute growth rate predictions were highly sensitive to input parameters (i.e., 20% parameter perturbation led to order of magnitudes difference in model estimates). Our modeling indicated that rainbow smelt predation may limit larval cisco survival at Black Bay and to a lesser extent at Twin Ports and that starvation may be a major source of mortality at all three locations. The framework we describe has potential to further our understanding of the relative importance of starvation and predation on larval fish survivorship, provided information on prey resources available to larvae are measured at sufficiently fine spatial scales and the models provide a realistic depiction of the dynamic processes that larvae experience.

Introduction

Variability in inter-annual recruitment is a critical source of uncertainty in fisheries science. It is generally agreed that factors acting on early stages of development, especially the larval stage, can have a large influence on fish population dynamics (Miller et al., 1988; Houde, 1989a). Faster growth through the larval stage is believed to contribute to increased survival (Ware, 1975; Blaxter, 1986; Houde, 1989a) because larger, more developed larvae are better able to capture prey and evade predators than smaller members of a cohort (Blaxter, 1986; Miller et al., 1988). Lake-dwelling coregonines (*Coregonus* spp.) are noted for large fluctuations in recruitment (Marjomäki et al., 2004; Stockwell et al., 2009), yet mechanisms affecting growth and survival of these fish during early life stages have not been widely studied.

Cisco (*Coregonus artedi*) were once the most prolific fish species in each of the Laurentian Great Lakes (Koelz, 1929; Smith, 1968). Multiple stressors, including overexploitation, exotic species interactions, and habitat degradation led to precipitous declines by the middle of the 20th century (Smith, 1968). Subsequently, only populations in the Upper Great Lakes have shown signs of recovery, but abundance remains well below historic levels due to infrequent recruitment (Stockwell et al., 2009). Bronte et al. (2003) suggested that highly variable recruitment is a symptom of the current ecosystem structure, while Yule et al. (2008) argued that sporadic recruitment events were likely a natural characteristic of Lake Superior cisco. While there have been attempts to describe cisco recruitment dynamics using stock-recruitment relationships (Hoff, 2004; Rook et al., 2012; Rook et al., 2013), simple descriptive models have not

provided adequate predictions of year-class strength (Letcher et al., 1996; Rothschild, 2000). An alternative and potentially more fruitful approach for understanding larval cisco survival is to examine the mechanisms underlying dynamic processes (Letcher et al., 1996; Beauchamp et al., 1999). Understanding the processes affecting larval cisco growth and predation risk in Lake Superior could benefit their management, and inform restoration efforts in the lower Great Lakes (Zimmerman and Krueger, 2009).

Rainbow smelt (*Osmerus mordax*) have been repeatedly linked to poor recruitment of coregonids (Crowder, 1980; Loftus and Hulsman, 1986). Strong evidence exists for negative interactions between adult rainbow smelt and age-0 cisco in both the Great Lakes (Selgeby et al., 1978) and smaller inland lakes (Evans and Loftus, 1987; Hrabik et al., 1998). 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 in Sparkling Lake, Wisconsin, during an 8-year period. This overlap placed young cisco in close proximity to predatory rainbow smelt and ultimately led to their extirpation.

Spatial overlap between predator and prey is an obvious prerequisite for predation (Ahrens et al., 2012), yet few studies have accounted for the degree of overlap when evaluating interactions between rainbow smelt and larval cisco in the larger Great Lakes. Myers et al. (2009) demonstrated that estimates of larval mortality caused by rainbow smelt predation were sensitive to how data were analyzed. They showed that when predator and prey densities were averaged over large geographic areas (> 10,000 ha) the impact of predation was high, but when analyzed at a finer

scale (1000 ha), the impact of predation was lower. However, Myers et al. (2009) did not measure the degree of overlap between rainbow smelt and larval cisco in the vertical dimension, nor with respect to time. Within a 24 h period, risk of predation could fluctuate dramatically, as cisco larvae are known to be aggregated near the surface (Myers et al., 2009) while rainbow smelt normally exhibit a strong negative phototaxis resulting in diel vertical migrations (Heist and Swenson, 1983). However, turbid conditions are known to affect rainbow smelt vertical distributions (Heist and Swenson, 1983) due to the shadowing the water column, which results in rainbow smelt being found near the lake surface during daylight (Heist and Swenson, 1983; Myers et al., 2009). This phenomenon led us to predict that the risk of larval cisco mortality as a result of rainbow smelt predation would be greatest under turbid conditions due to the prolonged spatiotemporal overlap of both predator and prey in surface waters (Figure 9).

Larval fish are vulnerable to predation, but are also predators themselves. Dabrowski (1989) argued that starvation can be a factor in larval coregonid mortality and should be emphasized in studies of recruitment. The ratio of active and standard metabolism is inversely related to size of age-0 coregonids (Dabrowski et al., 1989), leading to high metabolic costs for small larvae and therefore a greater need to encounter sufficient numbers of prey early in larval life. The 'match/mismatch' hypothesis has been proposed as an explanation for variability in recruitment observed in many fish stocks (Cushing, 1990) and suggests recruitment variation can be explained by the extent to which energetic demands of young fish and availability of suitable prey are synchronized in space and time. Thus, understanding how
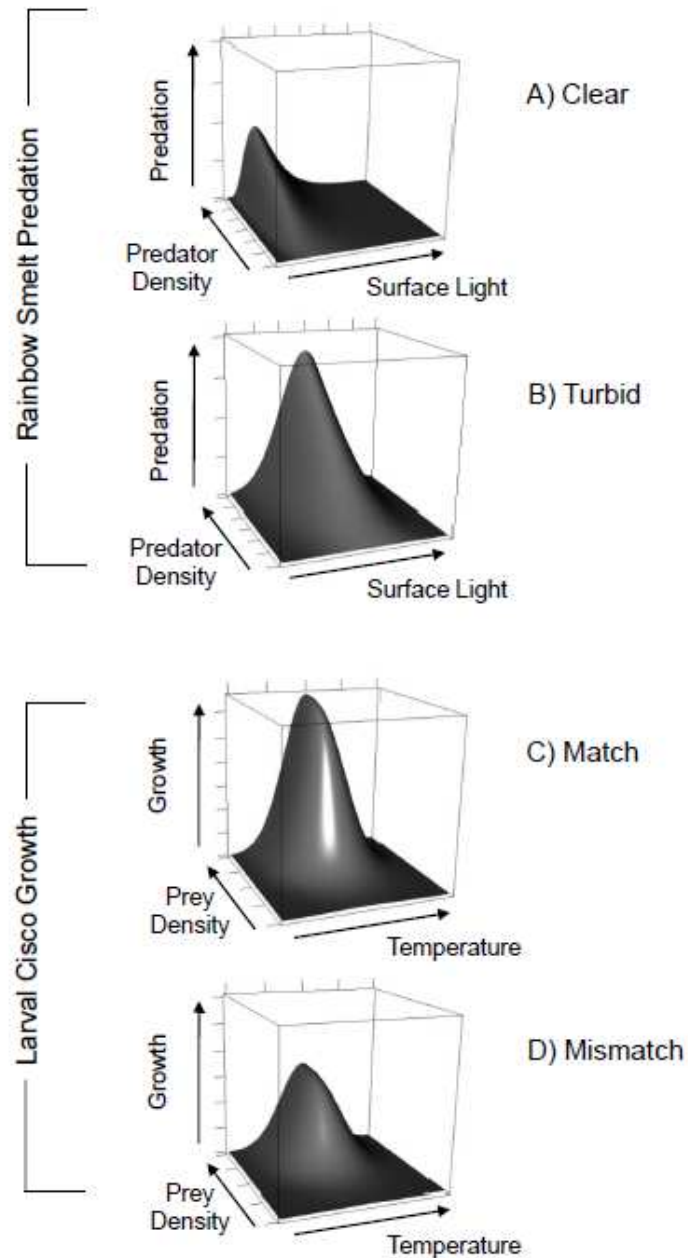
Figure 9. Conceptual model that depicts factors believed to influence predation risk and growth for larval cisco in Lake Superior. Under clear water conditions rainbow normally undergo diel vertical migrations, which could limit the impact of predation on larval cisco (A). The consequence of turbid conditions could be increased overlap between rainbow smelt and larval cisco, resulting in greater risk of predation (B). The "match/mismatch" hypothesis suggests that increased overlap between larval cisco and their prey should result in increased larval growth, leading to higher levels of recruitment (C). However, larvae that are incapable of encountering sufficient prey during periods of greatest metabolic demand will suffer from reduced growth rates and recruitment will be low (D).

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distributions of larval cisco and zooplankton effect encounter rates is important for evaluating hypotheses related to cisco growth and subsequent recruitment in Lake Superior (Figure 9).

The primary goal of this research was to evaluate the relative importance of predation and starvation as causes of mortality for cisco larvae. Our first objective was to document the extent of overlap in spatial and temporal distributions of rainbow smelt, larval cisco, and zooplankton during spring at three locations in Lake Superior that support cisco populations. Our second objective was to incorporate this empirical data into a modeling framework that accounted for observed differences in overlap between predators and prey. We also sought to better understand which factors had the greatest effect on model results by conducting a sensitivity analysis. Our last objective was to use modeling results to evaluate factors that may influence larval cisco predation risk and growth potential within Lake Superior.

Rationale for sampling locations

We chose three Lake Superior study locations (Figure 10) that provided contrast in cisco spawner abundance, as determined by recent surveys of pre-spawning aggregations. Cornucopia, Wisconsin, supports a large adult standing stock with densities exceeding $250 \cdot ha^{-1}$ (Yule et al., 2009; 2012). Abundance near the port cities of Duluth, Minnesota, and Superior, Wisconsin, (hereafter, Twin Ports) is intermediate ($84 \cdot ha^{-1}$; Yule et al., 2012), while abundance inside Black Bay is comparatively low ($19 \cdot ha^{-1}$; Yule et al., 2006).
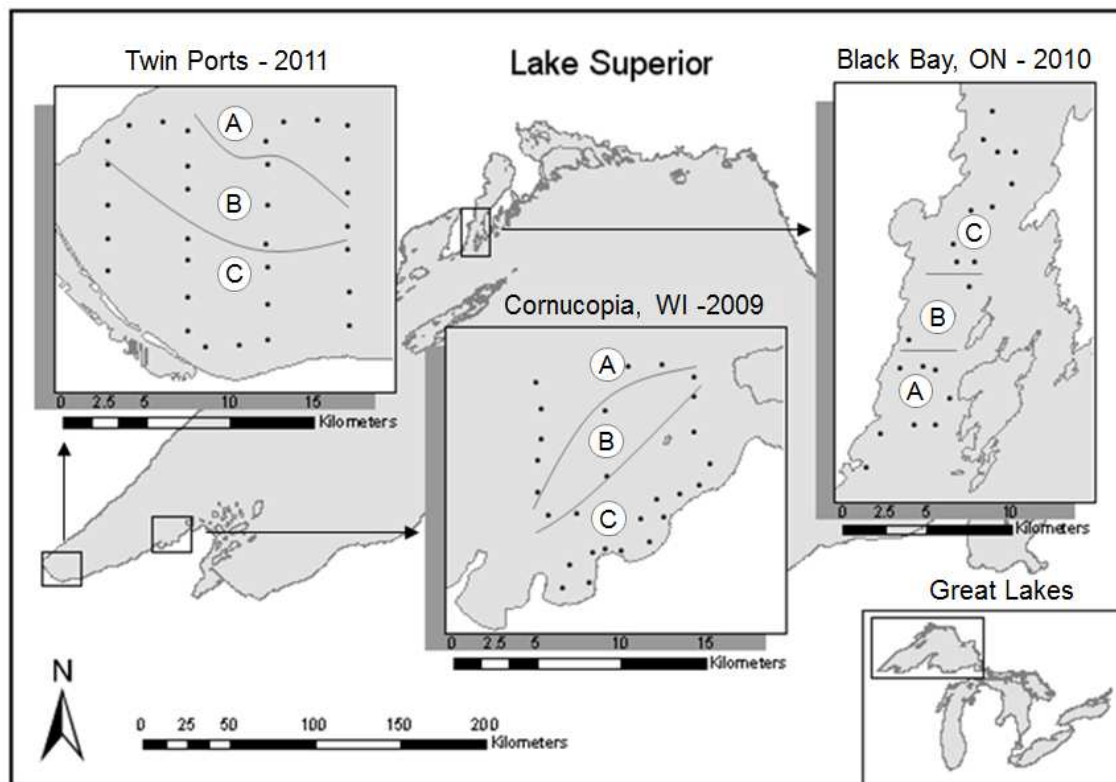
Figure 10. Sampling locations in Lake Superior. Letters indicate stations while dots (•) indicate 2-km acoustic intervals. Grey contours indicate the division of acoustic intervals into depth strata, which were then coupled with the respective stations.

Spatial patterns in Lake Superior limnological conditions are driven and maintained by land use in adjacent watersheds (Yurista et al., 2011), resulting in fairly predictable patterns at specific locations. Compared to other nearshore waters, turbidity and zooplankton biomass is typically high at the Twin Ports (Yurista and Kelly, 2009; Yurista et al., 2011). Like the Twin Ports, Black Bay is highly productive and is subject to reduced water transparency in the spring of some years depending on the magnitude of spring runoff (LaMP, 2000). Conversely, both turbidity and zooplankton biomass near Cornucopia are comparatively low (Yurista and Kelly, 2009). It follows that these locations afforded us an opportunity to explore factors that may be driving variation in stock status by testing predictions of how turbidity influences interactions between larval cisco and rainbow smelt and prey availability influences growth of larval cisco (Figure 9).

Methods

Field sampling

We developed a sampling approach that was repeated at each location (Figure 10) over three springs; Cornucopia during 2009, Black Bay during 2010, and the Twin Ports during 2011. Each sample was classified as belonging to one of three areas (i.e., stations), corresponding to a gradient from offshore (A) to nearshore (C) habitat (Figure 10). Sampling targeted ichthyoplankton, zooplankton, and pelagic fish. We completed three synoptic surveys at each location with temporal intervals of approximately two weeks (Table 3). Departures from this rule were the result of adverse weather and logistical constraints. 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, while night samples were collected between 0.5 h after nautical twilight and 0.5 h before nautical sunrise. During night collections, ship deck lights were turned off.

Ichthyoplankton, zooplankton, and limnological samples

Vertical distribution of larval cisco 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 location we selected three fixed stations (Figure 10) where the tucker trawl was deployed at 25, 15, and 5 m below the surface. A sample was also collected at the surface using a 0.5 m diameter conical zooplankton net with 500 μm mesh towed horizontally at 2-3 $m \cdot s^{-1}$ for 5 minutes (Myers et al., 2008). The tucker trawl was

Table 3. Dates of sampling events at three locations in Lake Superior.

Location (Year)	Sampling Event	Ichthyoplankton		Zooplankton		Pelagic Fish	
		Day	Night	Day	Night	Day	Night
Cornucopia, WI (2009)	1(K,C)	4/28– 5/5	5/7–8	4/30	5/2	4/24–30	5/1–5
	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 (2010)	1(K)	5/14– 17	5/17–18	5/14–16	5/19	5/16	5/18 –19
	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
Twin Ports (2011)	1(K)	4/25–28	4/28	5/5	5/2–3	5/5	5/3– 4
	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 "Sampling Event" column indicate which vessel was used for the given survey (K = R/V *Kiyi*, C = R/V *Coaster II*).

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 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^{-1}. Prior to retrieval, a second messenger closed the net so that the sample was not compromised during ascent. Once closed, the coordinates were recorded and the volume sampled was calculated as the product of distance traveled and area of the trawl mouth. Methods for preservation, identification, enumeration, and measurement of icthyoplankton were described previously (Myers et al., 2009).

Selgeby et al. (1994) showed that the diet of larval cisco collected from Lake Superior was dominated by immature copepods, with larvae ≤ 13 mm consuming more nauplii than copepodites. To capture these small-bodied zooplankton we sampled with a 0.5 m diameter collapsible plankton net equipped with 63 μm mesh. Samples were collected at each station 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 from the outside to wash all organisms into the collection bucket. Organisms were preserved with 95% ethyl alcohol and stained with rose bengal. Zooplankton samples were divided into equal parts using a wheel splitter. The sample was fractioned until a manageable number of organisms were in a given subsample. The fractioned sample was condensed and copepod nauplii were enumerated by counting two 1-mL aliquots. Aliquots were placed on a gridded slide and nauplii were counted using a compound microscope. The average number of nauplii·mL^{-1} (mean of the 2 aliquots) was multiplied

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by the volume of the fractioned sample to estimate the total number of nauplii in the fractioned sample. In addition, a dissecting microscope was used to coarsely identify (to genus) and enumerate copepodites within the fractioned sample. We estimated the total number of nauplii and copepodites in the entire sample and then standardized estimates to the number of organisms·m^{-3}. Density estimates were converted to energy (J·m^{-3}) by assuming individual nauplii and copepodites were 0.04875 J and 0.08062 J, respectively (Dabrowski et al., 1988).

Secchi depth was recorded on the shaded side of the vessel, and a thermal profile was collected using a SEACAT Model 19 Profiler (Sea-Bird Electronics, Inc., Bellevue, Washington) at each station during each survey. Water samples were collected at depths of 25, 15, 5 m, and the surface at each station during each survey to measure total suspended solids. These samples were processed at US EPA, Mid-Continent Ecology Division, Large Lakes Research Station (Duluth, MN) using established protocols (Ref. No. CHG-005; Rev. No. 2).

Pelagic fish

Acoustic methods and trawl gear were used to estimate abundance and the horizontal and vertical distributions 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 6.8°. Acoustic data were collected using two vessels (Table 3). When sampling with the R/V *Kiyi*, the transducer was mounted through a well in the hull to a depth of 2.3 m below the surface of lake. When sampling aboard the R/V *Coaster II*, the transducer was mounted on a tow body and deployed at

1 m depth. Acoustic data 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 33 mm calibration sphere with an expected target strength (TS) of -40.5 dB. If the measured sphere TS deviated by more than 1 dB from expected TS, offsets were applied. Acoustic data were processed using standard procedures (Parker-Stetter et al., 2009) with Echoview software (version 3.45.54.2627, Sonar Data Pty Ltd., Tasmania, Australia). Briefly, regions of echograms containing non-fish echoes (e.g., noise from electrical interference) were excluded from analysis. A line was added to each echogram at 0.5 m above the lake bed to exclude bottom echoes. Surface lines were added at 4.1 m and 2.8 m depth for the R/V *Kiyi* and R/V *Coaster II* acoustic data, respectively, because acoustic information above these depths was unreliable due to the deployment depths and transducer near-fields. The water column was analyzed in 10 m depth layers with transects divided into 2-km-long intervals. The minimum TS and volume backscattering strength thresholds were set at -60 dB and -66 dB, respectively. Fish density (number·ha^{-1}) in each cell was calculated by echo integration (Parker-Stetter et al., 2009). We assumed estimated density from the surface line to 10 m depth of each interval reflected density above the surface line.

Bottom trawls were collected to assess rainbow smelt densities near the lakebed during daylight, and midwater trawl samples were collected to interpret the nighttime acoustic collections. All trawl samples were collected with the R/V *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 total of 34 midwater trawl samples and 26 bottom trawl samples were collected (Table 4). 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.

Prior studies have shown that pelagic fish species occupy predictable water column depths at night in coastal areas of Lake Superior when the lake is isothermic. Most rainbow smelt and adult cisco occupy the uppermost 40 m of the water column, while deepwater ciscoes (mostly bloater, *Coregonus hoyi*) are predominant at depths > 40 m (Myers et al., 2009; Gorman et al., 2012; Kocovsky et al., 2013). When estimating species densities we followed the methods of Myers et al. (2009) and assumed all targets < -44.59 dB in the upper 40 m of the water column were rainbow smelt. Bathymetric depth was used to group acoustic intervals with stations at the Cornucopia and Superior locations (Figure 10). Because of the trough-shaped bathymetry of Black Bay, acoustic intervals were grouped to stations based on latitude (Figure 10). Average

Table 4. 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)	Sampling Event	Midwater Trawls			Bottom Trawls		
		No. Trawls	Average Catch (SE)	Average Length (SE)	No. Trawls	Average Catch (SE)	Average Length (SE)
Cornucopia, 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)	-	-	-
Twin Ports	1	5	42 (33)	119 (10)	4	433 (230)	93 (14)
(2011)	2	6	201 (115)	101 (9)	4	171 (31)	122(1)
	3	-	-	-	-	-	-

rainbow smelt densities at each station were estimated using the acoustic intervals as replicates.

Investigating spatial and temporal distributions

We used ANOVA models to determine whether the ln-transformed densities of rainbow smelt (#/10,000 m^3), larval cisco (#/1000 m^3), and zooplankton (J·m^{-3}) varied with respect to photoperiod (day or night), sampling event (1, 2, or 3; see Table 3), station (A, B, or C; see Figure 10), or depth below the surface (0, 5, 15, or 25 m) at each location. Each model was fully balanced and all factors were treated as fixed effects. We tested the significance of all main effects and all two-way interactions but ignored higher-level interactions. Using a Bonferroni correction, we evaluated individual tests at a significance level of 0.005.

Predation and foraging models

We combined data from our field study with literature-supported parameter values to develop two models of cisco trophic interactions. First, we modeled predation by rainbow smelt on larval cisco using an encounter rate model (Gerritsen and Strickler, 1977) to estimate the effective overall search volume for the estimated rainbow smelt population at each location. Second, we modeled larval cisco feeding and growth using a foraging/bioenergetics model developed specifically for larval coregonids (Dabrowski et al.,1989). The models were used to compare estimates of rainbow smelt predation pressure and larval cisco growth amongst locations and to interpret these differences in terms of prevalent ecological conditions.

Rainbow smelt foraging model

The encounter rate model of Gerritsen and Strickler (1977) estimates the effective volume searched by a predator as a function of the predator's reaction distance to prey, and the effective swimming speeds of both predator and prey (Table 5, Equation 5.1). We used this quantity, together with the observed density of rainbow smelt at each location, station, sampling event, and depth stratum to calculate an overall search volume for each rainbow smelt population. The individual search volumes ($m^3 \cdot s^{-1}$) were scaled by density ($\# \cdot m^{-3}$) to estimate the proportion of the total water volume searched by the population per day (% of total volume$\cdot$day^{-1}).

Reaction distance of rainbow smelt was modeled using the approach of Jensen et al. (2006). These authors used observations of cisco feeding on *Limnocalanus* (Link and Edsall, 1996) to modify the parameters of the reaction distance model developed by Wright and O'Brien (1984) for planktivorous white crappie (*Pomoxis annularis*). We modeled the reaction distance of rainbow smelt to larval cisco as a function of larval cisco length, turbidity, and depth- and time-specific light intensity (Table 5, Equations 5.2-5.5). Light intensity at the surface was estimated using the program SUNSET (Janiczek and DeYoung, 1987) which required latitude, longitude, date, time and deviation from Greenwich mean time. We used the Lambert-Beer equation (Hutchinson, 1957, Table 5, Equation 5.4) to estimate light levels at depth. The light extinction coefficient established by Koschel (1985) was a function of secchi depth (Table 5, Equation 5.5). We used observed values of secchi depth and turbidity (total suspended solids) to apply these equations.

Rainbow smelt are believed to swim slowly and spend much of their time motionless in the water column (Lantry and Stewart, 1993). Rather than model rainbow smelt as completely motionless, we assumed individuals swam at 0.5 body lengths per second (Table 5, Equation 5.6), which is slower than typically assumed for actively foraging fishes. Observed average rainbow smelt lengths (Table 4) were used to calculate swimming speeds. Cisco larvae were assumed to be 10 mm and their swimming velocity was estimated using the relationship provided by Dabrowski et al. (1989) for coregonid larvae (Table 5, Equation 5.7).

Table 5. Equations and parameters used in the rainbow smelt foraging model. Sources: (1) Gerritsen and Strickler, 1977; (2) Link and Edsall, 1996; (3) Jensen et al., 2006; (4) Hutchinson, 1957; (5) Koschel, 1985; (6) Dabrowski, 1989; (7) Karjalainen, 1992; (8) Janiczek and DeYoung, 1987.

	Description	Equation	Source
E.5.1	Search Volume	$SV = \begin{cases} \left(\dfrac{\pi RD^2}{3}\right)\left(\dfrac{3v^2 + u^2}{v}\right) & for\ v \geq u \\ \left(\dfrac{\pi RD^2}{3}\right)\left(\dfrac{3u^2 + v^2}{u}\right) & for\ u \geq v \end{cases}$	1
E.5.2	Reaction distance (m)	$RD = 1.44\beta(CL\text{-}0.2)$	2, 3
E.5.3	Reaction distance coefficient	$\beta = 1.65[1.49 + 7.86 \arctan(I_z)](1+(\tau/30)+4.6)$	3
E.5.4	Light level at depth (lx)	$I_Z = I_0\, e^{-zk}$	4
E.5.5	Extinction coefficient (m^{-1})	$k = 0.88 SD^{0.416}$	5
E.5.6	Rainbow smelt swimming speed (cm/s)	$v = 0.5\,TL$	
E.5.7	Larval cisco swimming speed (cm/s)	$u = 0.1926 e^{1.282 CL}$	6, 7

Model Parameters

	Description	Equation	Source
P.5.1	Light level at surface (lux)	I_0; See text	8
P.5.2	Secchi depth (m)	SD; mean = 5.4, range = 1.7-11.0	
P.5.3	Total Suspended Solids (mg/L)	TSS; mean = 0.92, range = 0.37-3.38	
P.5.4	Turbidity (NTU)	$\tau = TSS$	Assumption
P.5.5	Rainbow smelt total length	TL; See Table 2	
P.5.6	Larval cisco total length	CL; Fixed at 1 cm	

Larval cisco bioenergetic model

We used the bioenergetic model developed for coregonid larvae (Dabrowski et al., 1988; Dabrowski, 1989; Dabrowski et al., 1989) to simulate growth of larvae at each location. Growth was calculated for 10 mm larvae because it is the size at which the eleuthero-embryo switches from endogenous to exogenous feeding (Dabrowski et al. 2008). We also calculated the growth of 15 mm larvae, as this is the size that cisco larvae begin metamorphosis to the juvenile stage.

Growth was calculated by expanding a general bioenergetics model for larval growth (Table 6, Equation 6.1), using the modifications by Ware (1975) and Dabrowski et al. (1988) to the Holling functional response equation (Holling, 1965; Table 6, Equation 6.2). As was highlighted by Dabrowski et al. (1988), this model assumes that the relationship between food ingestion rate and food concentration is asymptotic and can be solved by specifying the search capacity of the predator and the density of the prey. An asymptotic increase in food consumption rate is offset by an exponential increase in the metabolic rate (Dabrowski, 1989). Active metabolism (Table 6, Equations 6.3-6.5) was assumed during feeding while standard metabolism (Table 6, Equation 6.3) was assumed for the remainder of the day. Standard metabolism as a function of larval TL was estimated using the equation provided by Karjalainen (1992), which is based on interpretations of the results reported by Dabrowski (1986a; 1986b) and Kaushik et al. (1986). We assumed a feeding duration (i.e., active metabolism) of 15 h because: 1) coregonid larvae are believed to be relatively inactive during darkness (Dabrowski, 1982) and 2) surface illuminance was > 10 lux (i.e., the approximate light level at nautical twilight) for approximately 15 h during the month of May. Dabrowski et

al. (1988) reported using a Q_{10} of 2.41 to scale both active and standard metabolism estimates from the larval coregonid bioenergetics model. The measurements of Q_{10} were developed using temperatures ≥ 14 °C, so we scaled our estimates of metabolism against this standard.

Given that copepod nauplii and early stage copepodites are usually the first food of larval coregonids (Dabrowski, 1989; Karjalainen, 1991), we only considered empirical estimates of these prey items. In addition, the probability of successful prey capture by larval coregonids varies with prey type and can be as low as 3% for larvae feeding on copepodites (Braum, 1967). Based on the simulations of Dabrowski et al. (1988) we assumed 10 mm larvae captured nauplii and copepodites at a rate of 60% and 3%, respectively, while 15 mm larvae captured them at 85% and 30%. Handling time is defined as the time required to capture and consume one prey item (Werner, 1974) and is known to vary according to the body size of both the predator and the prey (Ware, 1978). The relationships between handling time and fish body length provided by Dabrowski et al. (1988) were used to calculate the handling times of nauplii and copepodites (Table 6, Equations 6.9-6.10).

We followed the approach of Karjalainen (1992) and converted energy ingested to dry and wet mass (*DM* and *WM*, respectively) using the coefficients of 46 J·mgC^{-1}, 0.5025 mgC·mgDM^{-1}, and 0.11 mgDM·mgWM^{-1}. We assumed energy density of cisco larvae was 4134 J·g^{-1} *WM* (Dabrowski et al., 1988) and calculated *WM* of larvae using the relationship provided by Karjalainen (1992; Table 6, Equation 6.12). Growth was reported as the % change in wet mass after a 24 h period.

Table 6. Equations and parameters used in the larval cisco bioenergetics model. Sources: (1) Holling, 1965; (2) Ware, 1975, (3) Dabrowski et al., 1988; (4) Dabrowski, 1986a, b, c; Kaushik et al., 1986; (5) Karjalainen, 1992; (6) Dabrowski, 1989.

Description		Equation	Source
E.6.1	General growth model	$G = qI - R$	
E.6.2	Expanded growth model	$G = q\dfrac{yVp_{1,2}}{1 + yVp_{1,2}h_{1,2}} - a e^{bV}$	1, 2, 3
Respiration (R ; J·fish^{-1}·h^{-1})			
E.6.3	Standard metabolism of larvae	$a = 0.1272 e^{0.7344\,TL}$	4, 5
E.6.4	Swimming speed (cm·s^{-1})	$V = 0.1926 e^{1.282\,TL}$	6, 5
E.6.5	Slope of activity equation	$b = 6.76 e^{-1.094}$	3
Ingestion (I ; J·fish^{-1}·h^{-1})			
E.6.6	Net energy absorption coefficient	$q = r \cdot (1\text{-}SDA)$	
E.6.7	Area successfully searched (m^3·h^{-1})	$y = s \cdot c$	
E.6.8	Area of the visual field (m^2)	$s = 0.0001217\,TL\text{-}5.0306\times10^{-6}$	3
E.6.9	Handling time (nauplii; h·J^{-1})	$h_1 = 0.08464 e^{-1.0848\,TL}$	3
E.6.10	Handling time (copepodites; h·J^{-1})	$h_2 = 3.0124 e^{-1.55107\,TL}$	3
E.6.11	Swimming speed (m·h^{-1})	$V = 6.932 e^{1.282\,TL}$	6
E.6.12	Wet Mass (mg)	$WM = 3.184\,TL^{3.663}$	5
Model Parameters			
P.6.1	Dependence of R on temperature	$Q_{10} = 2.41$	3
P.6.2	Prey density (nauplii; J·m^{-3})	$p1$; Measured	
P.6.3	Prey density (copepodites; J·m^{-3})	$p2$; Measured	
P.6.4	Probability of prey capture	c ; See text	3
P.6.5	Duration of active swimming/feeding (h)	15	
P.6.6	Absorption coefficient	$r = 0.75$	3
P.6.7	Specific dynamic action coefficient	$SDA = 0.28$	3
P.6.8	Total Length (cm)	$TL = 1.0$ or 1.5	

Sensitivity analysis

      We performed an individual parameter perturbation analysis (*sensu* Letcher et al., 1996), to test the proportional sensitivity of model outputs (i.e., search volume of rainbow smelt and growth of larval cisco) to individual model parameters. Each parameter was varied by ±20% and the models were rerun. Sensitivities were calculated as y_+ or y_- divided by y_0, where y_+ and y_- were the output values with an individual parameter adjusted ±20%, respectively, and y_0 was the mean output using the unadjusted parameter. Sensitivities were reported as a percentage of the unadjusted output. This analysis indicated which parameters had the greatest influence on model predictions and provided insight as to which variables or processes could cause the level of variability associated with inter-annual cisco recruitment in Lake Superior.

Results

Spatial and temporal distributions

Rainbow smelt densities at Cornucopia varied significantly by photoperiod, station, and depth (Table 7, Figure 11). Night densities generally exceeded day densities at all depths. Although the station by depth interaction was not significant at this location (P = 0.37), night densities were largely homogenous with depth at stations B and C, but increased with depth at station A. Moreover, densities were generally higher at the two shallowest stations (B and C) during both photoperiods. Distributions of rainbow smelt in Black Bay during spring were dynamic, varying significantly by photoperiod, sampling event, station and depth (Table 7, Figure 11). The three two-way interactions that included photoperiod were all significant. Nighttime densities were generally higher than daytime densities at all depths, but differences were less pronounced at increasing depths. Daytime densities at 0-10 m and 10-20 m depths were relatively high at the two shallowest stations (B and C). At the Twin Ports, rainbow smelt densities varied significantly by photoperiod, station, and depth. Like with the other two locations, differences in day and night densities at the Twin Ports decreased with depth. Daytime densities in the 0-10 m and 10-20 m layers at the shallowest station (C) exceeded nighttime densities at these layers at the two deeper stations. The higher daytime densities in surface waters closest to shore at the Twin Ports coincided with high turbidity, creating low light conditions near the surface.

Densities of cisco larvae varied significantly by sampling event and depth at Cornucopia and by depth at the Twin Ports, but densities at Black Bay were

Table 7. Significance of factors affecting density estimates of rainbow smelt, larval cisco, and zooplankton during spring at three locations in Lake Superior. We report the analysis of variance (ANOVA) probabilities for the ln-transformed densities of each group, with respect to four factors (P = photoperiod, E = sampling event, S = station, and D = depth below surface) and their two-way interactions. An asterisk next to a probability indicates significance at the 0.005 level.

| Actor | Location | n | ANOVA Probability | | | | | | | | | |
			P	E	S	D	$P \times E$	$P \times S$	$P \times D$	$E \times S$	$E \times D$	$S \times D$
Rainbow Smelt	Cornucopia, WI	54	0.00*	0.12	0.00*	0.00*	0.19	0.14	0.63	0.88	0.05	0.37
	Black Bay, ON	54	0.00*	0.08	0.00*	0.64	0.00*	0.00*	0.00*	0.80	0.27	0.11
	Twin Ports	54	0.00*	0.02	0.00*	0.01	0.56	0.11	0.00*	0.45	0.01	0.00*
Larval Cisco	Cornucopia, WI	72	0.95	0.00*	0.28	0.00*	0.55	0.05	0.01	0.38	0.09	0.82
	Black Bay, ON	72	0.02	0.05	0.02	0.37	0.09	0.05	0.04	0.02	0.45	0.81
	Twin Ports	72	0.22	0.04	0.15	0.00*	0.08	0.81	0.30	0.48	0.19	0.13
Zooplankton	Cornucopia, WI	54	0.72	0.00*	0.25	0.00*	0.08	0.66	0.55	0.72	0.06	0.36
	Black Bay, ON	54	0.14	0.00*	0.32	0.00*	0.11	0.30	0.45	0.15	0.08	0.95
	Twin Ports	54	0.93	0.00*	0.04	0.00*	0.87	0.49	0.62	0.09	0.98	0.02
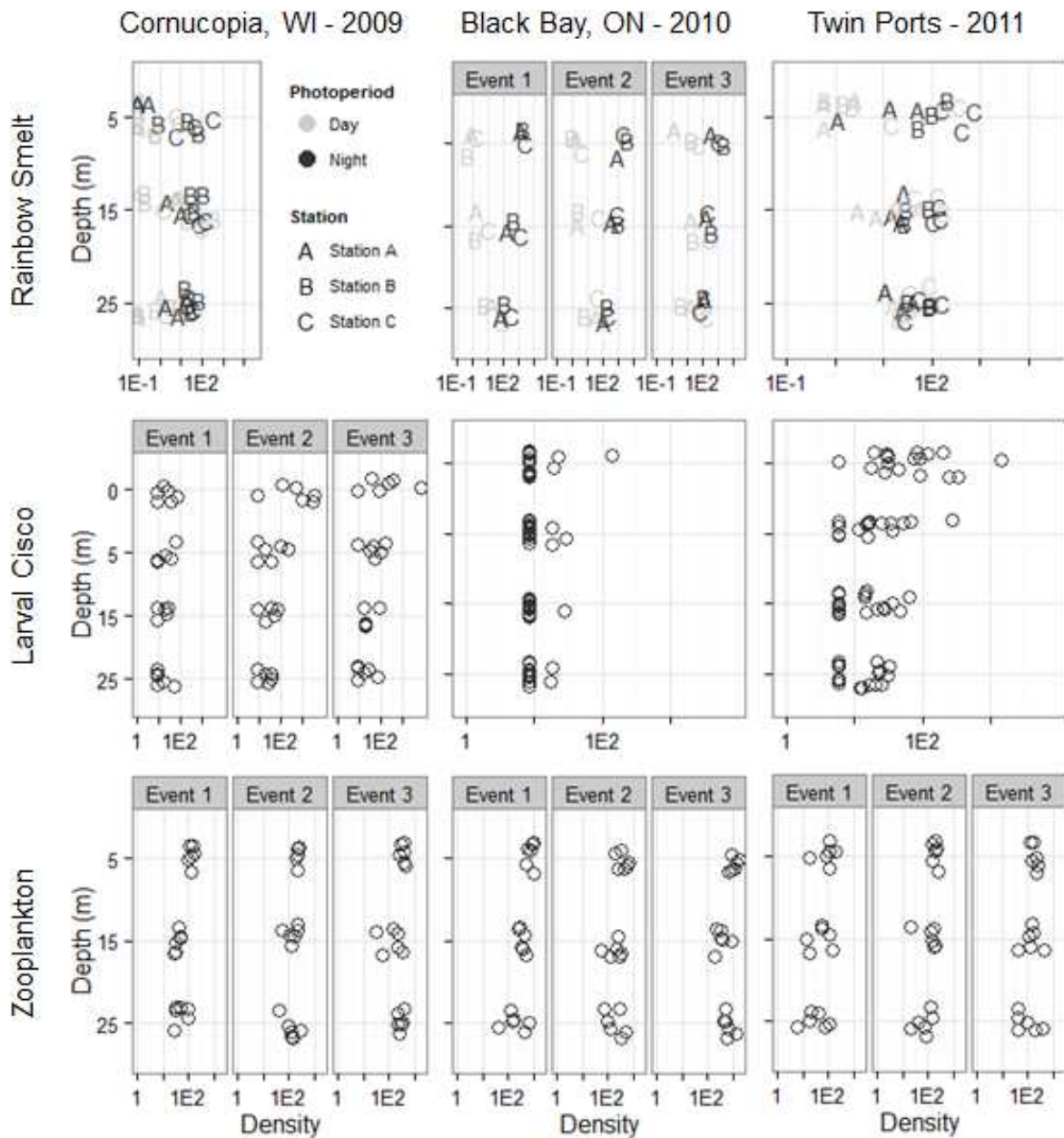
Figure 11. Summary of the factors affecting density estimates of rainbow smelt (#/100,000 m^3), larval cisco (#/1,000 m^3), and zooplankton (J·m^{-3}) during spring at three locations in Lake Superior. Data points are offset vertically for visual purposes.

comparatively low and did not vary significantly over the factors examined (Table 7, Figure 11). Densities of cisco larvae at Cornucopia declined with depth, and were greatest during the last two sampling events. Larval densities at the Twin Ports also declined with depth, but did not vary significantly by sampling event.

At each location the availability of zooplankton varied according to sampling event and depth (Table 7) with the highest energy densities generally observed during latter sampling events in the uppermost 0-10 m of the water column.

Predation and foraging models

    Rainbow smelt foraging model

Percent of total volume searched per day by rainbow smelt varied across space and through time at each location (Figure 12). Densities of rainbow smelt at Cornucopia were generally < 100·ha^{-1}. During the final sampling event at station C (closest to shore), diel vertical migration (DVM) by rainbow smelt led to estimated day and night densities in the 0-10 m layer of 9 and 393 individuals ha^{-1}, respectively. This behavior appears to have limited the potential for interaction between rainbow smelt and larval cisco at Cornucopia because 1) cisco larvae were concentrated near the surface (Figure 11), and 2) while rainbow smelt and cisco larvae overlapped at night, the search volume of rainbow smelt was reduced due to the effect of low light levels on reaction distance.

The highest densities of rainbow smelt were found at Black Bay (Figure 11), with nighttime densities in the 0-10 m stratum generally > 1000·ha^{-1}. This high abundance resulted in high rainbow smelt search volumes through space and time, especially at stations B and C (Figure 12). Cisco larvae were only collected in 12.5% of the Black Bay larval samples (Figure 11), with the highest observed density just 128 larvae / 1000 m^3.

Rainbow smelt densities at the Twin Ports were generally < 500·ha^{-1} (Figure 11), but rainbow smelt search volumes varied considerably through space and time (Figure 12). Search volume was highest at station C (closest to the south shore) during the last two sampling events (Figure 12). While rainbow smelt normally undergo DVM, daytime densities near the surface at this station were estimated at 370 fish ha^{-1}. Estimates of

suspended solids at this station were the highest observed during this study. Given

cisco larvae were also concentrated near the surface (Figures 11 and 12), high turbidity

likely increased the risk of predation by rainbow smelt.
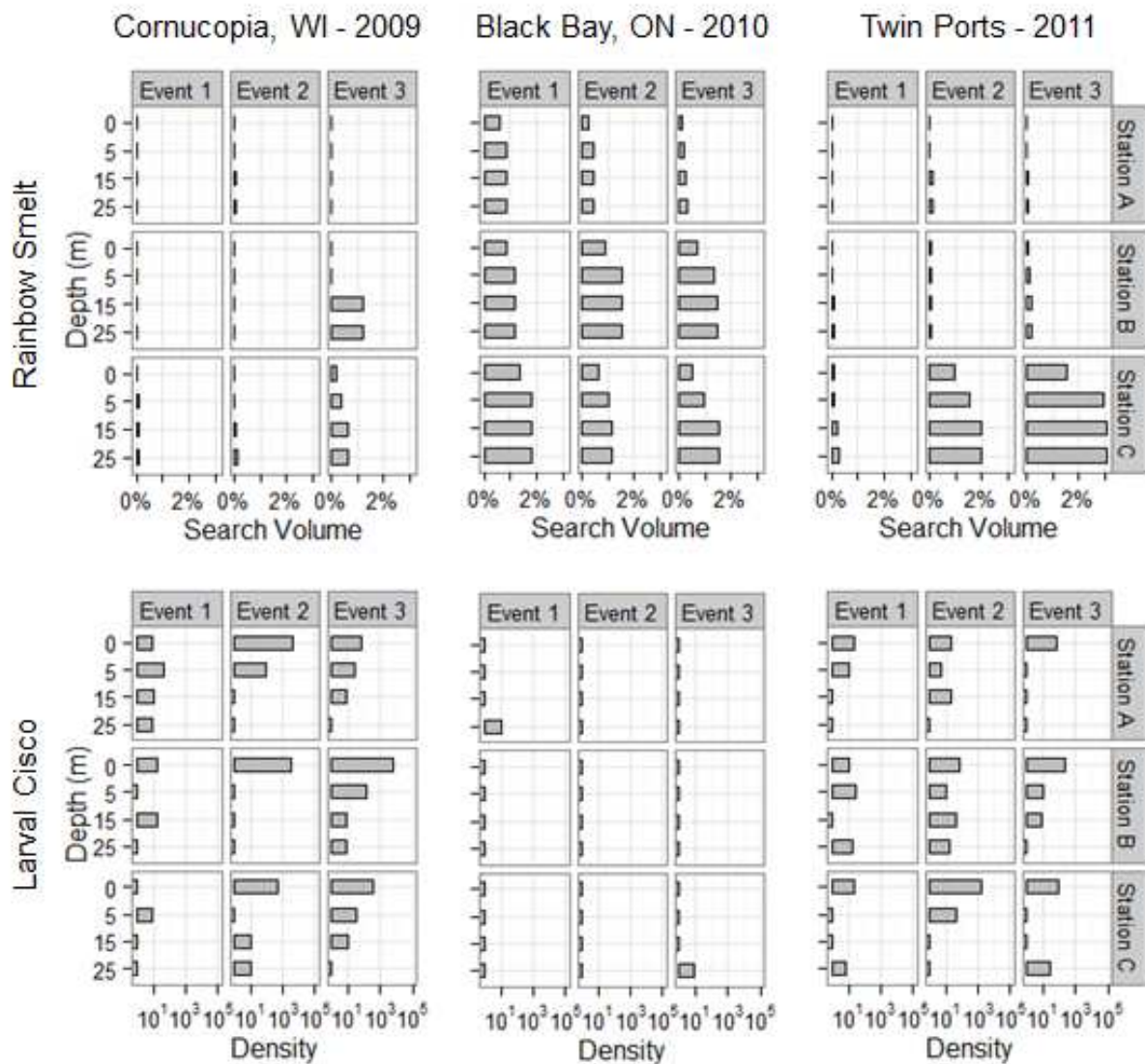
Figure 12. Search volume of rainbow smelt (% of total volume·day^{-1}) and density of cisco larvae (#/1000 m^3) over space and through time at three locations in Lake Superior.

There were large differences in the simulated growth rates of 10 and 15 mm cisco larvae (Figure 13). *In situ* zooplankton density estimates in the present study were low (range = 6 – 1,770 J·m^{-3}) compared to the values used to develop the larval coregonid bioenergetics model (range = 431–17,248 J·m^{-3}; Dabrowski et al., 1988), leading to negative growth rates for 10 mm larvae at all locations. Growth of 15 mm larvae was mostly positive at the Cornucopia and Twin Ports locations (Figure 13), especially near the surface where zooplankton densities were highest (Figure 11). In contrast, estimated growth of 15 mm larvae was predominately negative at Black Bay (Figure 13), despite zooplankton densities there being roughly twice that of the other locations (Figure 11). Given larvae were not satiated within our simulations, the effect of water temperature was more pronounced than the effect of prey availability. The increase in metabolic activity caused by higher water temperatures resulted in a negative relationship between temperature and 15 mm larval growth (Figure 14). In addition, because of the disproportionate influence of temperature, growth of 15 mm cisco larvae was predicted to be negative at some of the highest zooplankton densities (> 1500 J·m^{3}) observed, and highest at temperatures ranging from 2-6 °C (Figure 14).
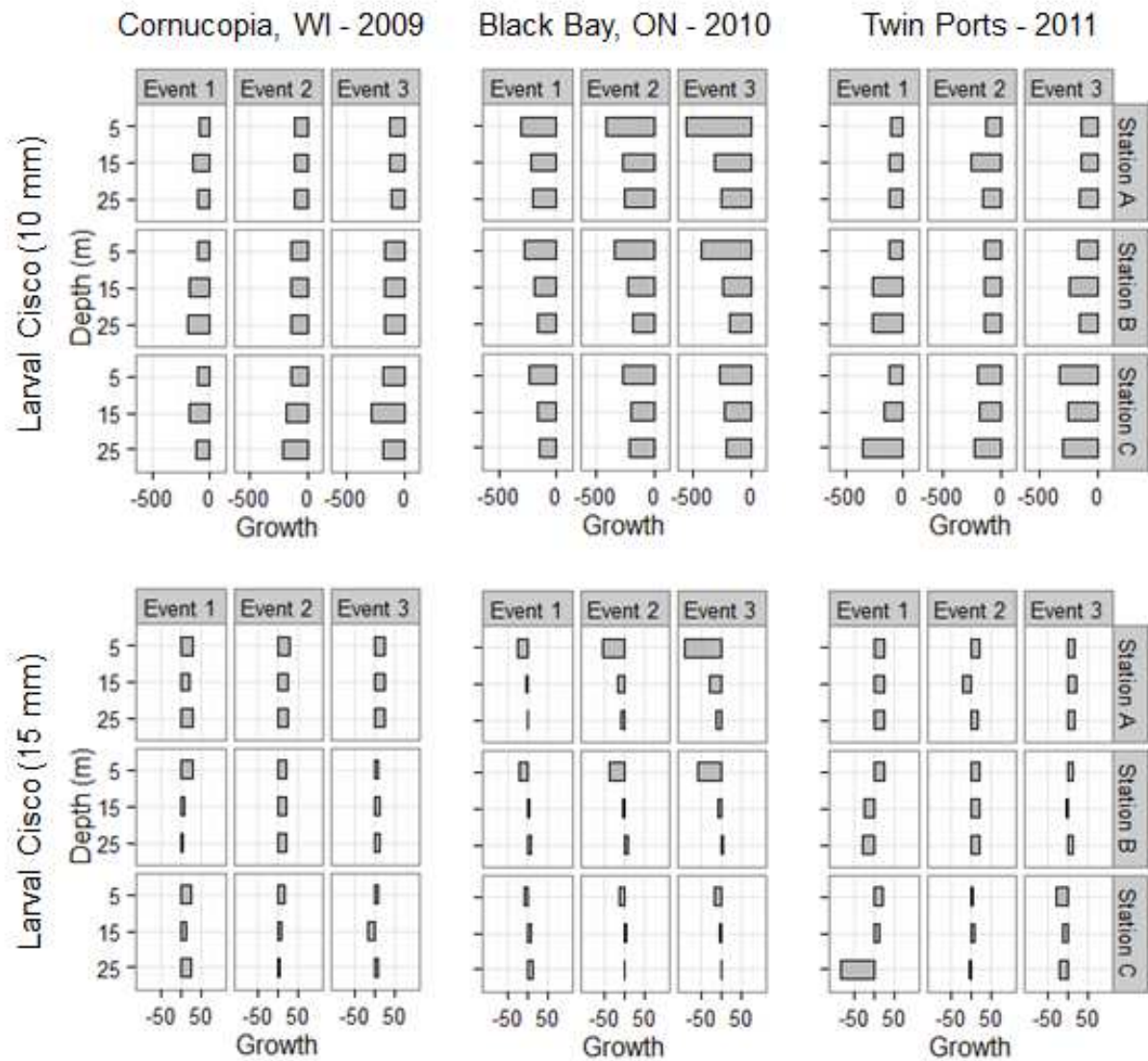
Figure 13. Simulated growth (% change in wet mass) of 10 and 15 mm cisco larvae over space and through time at three locations in Lake Superior.
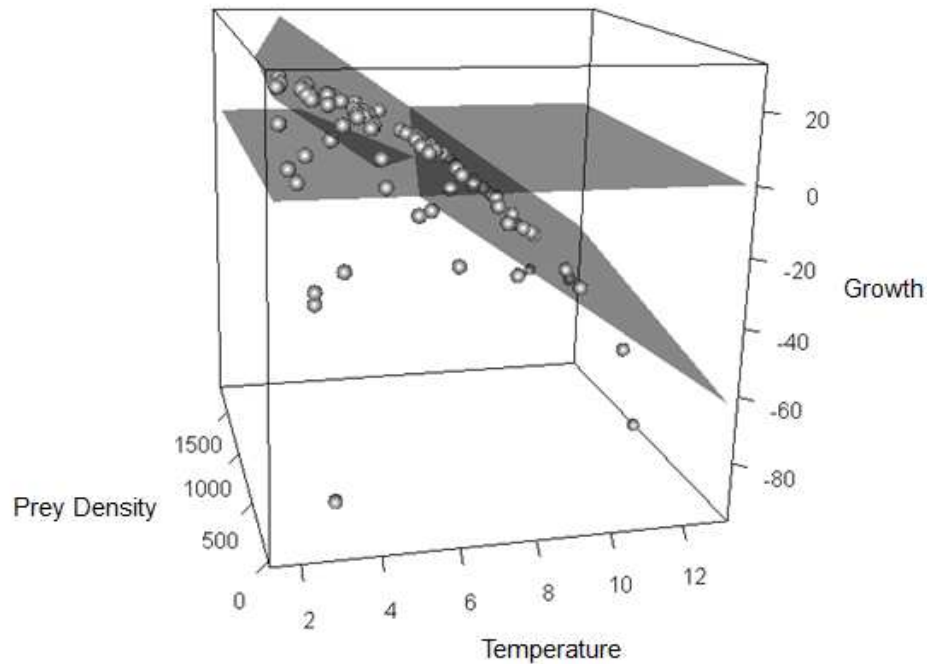
Figure 14. Results of the larval coregonid bioenergetics model and the simulated effect of temperature (°C) and prey density (J·m^{-3}) on the expected growth (% change in wet mass) of 15 mm cisco larvae in Lake Superior. The horizontal plane depicts conditions that produce zero growth while the angled plane is a linear model (i.e., Growth ~ Prey Density + Temperature).

Sensitivity analysis

The rainbow smelt foraging model was relatively insensitive to individual parameter perturbations. For example, a 20% change in rainbow smelt and larval cisco swimming speeds resulted in < 20% change in rainbow smelt search volume. In addition, a 20% change to the light parameters (I_0, k, I_z, $τ$) led to < 10% change in search volume. However, a 20% perturbation in the reaction distance coefficient (β) resulted in ~40% change in search volume, which is consistent with the results of Jensen et al. (2006).

Compared to the rainbow smelt foraging model, most parameters within the larval coregonid bioenergetics model were sensitive to perturbations. Dabrowski et al.

(1988) noted that growth is likely to be affected markedly by swimming activity. Our results were consistent with those of Dabrowski et al. (1988), as a 20% change in parameters related to active metabolism (b, V, Q_{10}) led to estimates of growth that differed by two orders of magnitude. The sensitivity of model predictions decreased as fish increased in length, as a 20% increase and 20% decrease in total length led to a 2000% and 5000% change in growth, respectively. This difference is caused by the dramatic change in the metabolic rate-swimming speed relationship, for which smaller fish are metabolically less efficient (Dabrowski et al., 1988). Compared to swimming activity, the effect of temperature and prey density had a less pronounced effect on growth, as a 20% perturbation led to approximately 600% change in growth for both variables. The sensitivity analysis shows that small changes to the foraging arena of larval fish can have a significant influence on growth (Houde, 1987; Houde, 1989a). Standard metabolism is characterized by inactivity, so a 20% perturbation resulted in only a 60% change in growth.

Parameters related to larval coregonid ingestion were generally less sensitive compared to parameters related to metabolism. For example, a 20% change to the visual acuity of larvae (s) caused a 50-70% change in growth. In addition, changes to capture probabilities for nauplii and copepodites generally had a proportional or slightly greater effect on growth. While the handling time associated with nauplii was relatively insensitive (i.e., 20% change to $h1$ yielded a 51% change in growth), the handling time of copepodites was very sensitive (i.e., 20% change to $h2$ yielded a >1000% change in growth).

Discussion

The goal of this study was to incorporate empirical observations within a modeling framework to explore hypotheses related to cisco recruitment in Lake Superior. Our use of the rainbow smelt foraging model and the larval coregonid bioenergetic model provided a unique perspective on age-0 cisco dynamics that could not have been determined from measures of predator and prey abundance alone. Assuming our modeling portrays a reasonable depiction of the foraging arenas experienced by larval cisco, our results suggest that mechanisms influencing survival can vary across Lake Superior. For example, the ability of larval cisco to encounter sufficient prey appears to influence each of the cisco populations we examined while the effect of rainbow smelt predation appears to be more localized in space and time. In addition, our modeling shows that abiotic factors (e.g., turbidity, temperature) can profoundly affect dynamic processes and biological interactions, which complicates attempts to use simple hypotheses that focus on single processes to explain larval cisco survival.

Our modeling shows that favorable conditions for larval survival can be found at Cornucopia, and at Twin Port sites when turbidity is low, which is consistent with our understanding of current stock status (Yule et al., 2012). Although rainbow smelt abundance in Lake Superior has declined in recent years (Gorman, 2007), we concur with the findings of Rook et al. (2013) showing high concentrations of rainbow smelt in areas utilized by larval cisco still presents a major challenge to certain cisco populations. Our modeling corroborates the previous findings of Myers et al. (2009)

showing rainbow smelt predation could be responsible for the poor status of cisco in Black Bay. It needs to be mentioned that more than 1300 rainbow smelt stomachs from Black Bay were examined in 2010 and no cisco larvae were found (U.S. Geological Survey, Great Lakes Science Center, Lake Superior Biological Station, Unpublished Data). However, given their depressed status, the absence of cisco larvae from rainbow smelt stomachs is not unexpected, as there were simply very few larvae for rainbow smelt to consume. With rainbow smelt densities > $1000 \cdot ha^{-1}$ and larval cisco densities < $100 \cdot ha^{-1}$, only one in ten rainbow smelt would need to consume a single larvae (i.e., during the period in which larvae are vulnerable to predation) to account for a complete loss of a year-class.

Contrast degradation theory predicts that moderately turbid environments should be advantageous for small fish like rainbow smelt because their search capacity is impaired to a lesser extent than the search capacity of large piscivores (De Robertis et al., 2003). Swenson (1978) demonstrated that light penetration in western Lake Superior is reduced significantly by red clay turbidity and that rainbow smelt respond to low light conditions by moving into the upper 12 m of the water column, where they can presumably hunt with a reduced risk of being the hunted. The results of our study are consistent with Swenson (1978) and suggest that under turbid conditions, lower densities of rainbow smelt can impose a risk of predation to larvae that is similar to clear-water areas supporting high rainbow smelt densities. While evidence suggests large-scale physical processes are responsible for the variability and synchrony associated with cisco recruitment in Lake Superior (Myers et al., 2015), predation by rainbow smelt may act to dampen the magnitude of successful year classes (Myers et

al., 2009). The combination of infrequent and dampened recruitment could limit the potential for cisco to reach historical levels in Lake Superior (Bronte et al., 2003).

Warmer surface water temperatures are believed to encourage growth of coregonid larvae, yet the mechanism by which water temperature mediates growth and subsequent recruitment has not been well defined. The argument that cisco larvae are temperature-limited as opposed to food-limited is largely dependent on the research of McCormick et al. (1971). These authors showed a positive relationship between temperature and instantaneous growth rates. However, cisco larvae in the McCormick et al. (1971) experiment were fed *ad libitum*, a condition that cannot be assumed to occur in the environment. McCormick et al. (1971) recognized that optimum temperatures in a hatchery setting are likely to differ from those in the environment and highlighted that as food becomes limiting, the temperature for optimum growth will be progressively lowered. This inference is consistent with our results, as the highest rates of growth were predicted to occur at the locations with low (2-6 °C) spring water temperatures (Figure 14). From a bioenergetic perspective, temperature can have strong influence on growth, yet it is unlikely to be the sole driver of growth in an oligotrophic system (Houde, 1989b). Rather, temperature also affects prey density, which can influence larval growth. We found that prey availability increased through the spring sampling period, which is consistent with previous studies in Lake Superior that showed zooplankton biomass was directly proportional to water temperature and exposure time (Watson and Wilson, 1978; Zhou et al., 2001). We believe increased prey density in response to increased water temperature is a more plausible explanation for the apparent relationship between temperature and cisco recruitment because it is

more consistent with factors known to govern growth of fish (Brandt and Hartman, 1993).

Our sensitivity analysis of the larval cisco bioenergetic model demonstrated greater sensitivity to copepodite handling time than nauplii handling time. Dabrowski et al. (1988) found that coregonid larvae fed the same amounts of energy of the two different prey types displayed strikingly different growth rates, with larvae fed strictly nauplii growing at rates nearly ten times faster compared to a diet of strictly copepodites. While an individual copepodite provides just 1.65 times more energy compared to an individual nauplii, the handling time associated with copepodites is approximately 22 times greater than the handling time associated with nauplii for a 10 mm larvae. Greater densities of nauplii, which increases the probability of encounters with larval fish, and the apparent metabolic benefit of focusing on nauplii, suggests larvae should preferentially consume nauplii during early stages of development. The availability of appropriately sized zooplankton could conceivably create "match/mismatch" scenarios for larval cisco in Lake Superior.

The bioenergetic model for coregonid larvae suggests that the levels of prey available to newly hatched larval cisco at the three Lake Superior study locations were inadequate. Dabrowski (1989) simulated positive growth of larvae at 5°C with a food density of 212 copepodites/L, which translates to approximately 17,000 $J \cdot m^{-3}$. In comparison, the highest density of zooplankton observed in this study was approximately 1,770 $J \cdot m^{-3}$, nearly 10 times lower than the prey density used by Dabrowski (1989). Evidence suggests zooplankton abundance estimates from integrative sampling gear may not adequately reflect the true availability of prey for

larval fish (Owen, 1989) and that the patchiness of zooplankton can have an important influence on the rate of encounters that larval fish actually experience (Letcher and Rice, 1997). Density of organisms within patches can be orders of magnitude higher than the estimate generated by an integrated sample (Owen, 1989), which has obvious implications for larvae that are able to exploit these regions of higher prey density (Letcher and Rice, 1997). Zhou et al (2001) used a high-resolution optical plankton counter to determine that Lake Superior zooplankton densities were greatest in the upper 10 m of the nearshore water column, which is consistent with the results of this study. However, even within the 10 m surface stratum there was considerable variation in densities, with the highest concentration of zooplankton being found at the warmest surface waters (Zhou et al., 2001). Megard et al. (1997) used acoustic methods to identify complex zooplankton distributions and water movements in western Lake Superior that would have otherwise escaped detection by conventional plankton nets. In fact, maximum concentrations of Lake Superior zooplankton detected by acoustic sampling were approximately 27 times larger than the arithmetic mean concentration. In contrast, McNaught (1979) reported that conventional net sampling on Lake Huron yielded maximum zooplankton concentrations that were only 2-6 times larger than the arithmetic mean. Despite our attempts to measure densities of zooplankton with respect to space and time, our net sampling approach was likely too coarse to effectively determine the true density of prey encountered by larval cisco, especially at the surface. Future studies of larval fish dynamics would benefit from the use of more advanced technologies (e.g., optical plankton counters, acoustic methods) that are better suited for understanding fine-scale spatial distributions of organisms.

Integrated samples from conical zooplankton nets also fail to incorporate the positive effects of small-scale turbulence on contact rates between predators and prey (Rothschild and Osborn, 1988). The larval coregonid bioenergetic model (Dabrowski, 1989; Dabrowski et al., 1989) assumes that contact between larval fish and zooplankton is a function of predator activity and prey density. This approach may underestimate the true velocity of organisms in a pelagic environment, as it disregards the influence of kinetic energy. Increased movement of both predators and prey as a result of turbulence has been shown to have a positive influence on contact rates without the additional metabolic expenditures associated with swimming (MacKenzie and Leggett, 1991; MacKenzie et al., 1994). The sensitivity of the larval coregonid bioenergetics model to swimming activity suggests growth rates can be dramatically improved via relatively minor reductions in swimming. Increased motion of both larvae and zooplankton by means of turbulence could explain how coregonid larvae, which appear to have a delicate energy balance (Dabrowski et al., 1988; Dabrowski, 1989), are able to limit swimming activity and resist starvation within an oligotropic system (Rice et al., 1987).

To date, multidisciplinary approaches for investigating variability in recruitment have been more common in studies of marine species compared to freshwater species (Miller, 2007). However, more attention is now being given to physical-biological models as a means of understanding recruitment of fish in the Great Lakes (Ludsin et al., 2014). These integrated approaches have given fisheries scientists and managers a greater appreciation of the processes that contribute to the development of individual year-classes (e.g., Zhao et al., 2009) and future developments are likely to have important

implications for Great Lakes fisheries management. Bennington et al. (2010) developed

a three-dimensional, hydrodynamic model capable of simulating Lake Superior

circulation and thermal structure between 1979 and 2006. Results of their model

suggested that increased surface temperatures over the same time period (Austin and

Colman, 2007) have also triggered increased wind speeds (Desai et al., 2009),

increased current speeds, and declining ice coverage (Assel et al., 2003). Coupling a

physical model of Lake Superior with information related to the spatiotemporal

distributions of larval cisco, as well as their associated predators and prey, could be a

promising avenue of research that furthers our understanding of fish recruitment in the

Great Lakes.

CHAPTER 3

TEMPERATURE AND CISCO (COREGONUS ARTEDI) RECRUITMENT IN LAKE SUPERIOR: EVALUATING THE MATCH/MISMATCH HYPOTHESIS USING A MODELING APPROACH

Abstract

Water temperature is a critical factor affecting the growth and survival of larval coregonids (*Coregonus spp.*), yet the mechanism by which temperature influences the recruitment dynamics of cisco (*C. artedi*) in Lake Superior is not well understood. We used a modeling approach to explore whether survival of larval cisco was more likely to be limited by the direct effect of temperature on growth or by the indirect effect of temperature on the availability of food. Archived temperature data from Thunder Bay (Lake Superior, 1996-2006) were used as input to drive the dynamics of two different models. The "direct temperature" model assumed water temperature was the sole driver of larval cisco growth, while the "indirect temperature" model assumed water temperature drove the degree of temporal overlap between cisco larvae and the abundance of planktonic prey. Both the direct and indirect temperature models suggested that larval cisco survival was above average in 1998 and 2003, which corresponded well with an observed index of cisco recruitment. However, the indirect temperature model generated estimates of recruitment that more closely resembled the overall "boom or bust" pattern of cisco recruitment that was observed in Lake Superior over the period of the study. While water temperature does appear to play a role in

recruitment of cisco, our modeling suggests that it is most likely a proxy for conditions

that enhance foraging opportunities and limit metabolic costs.

Introduction

Understanding the drivers of fish recruitment continues to be a central question in fishery ecology (Houde 2008). Since the seminal work of Hjort (1914), the larval phase has been considered to be extremely important in the formation of year-class strength. Fish larvae that are capable of attaining larger sizes will generally experience reduced mortality rates (Miller et al., 1988) and thus, any factor that augments larval growth may ultimately increase the magnitude of recruitment. One environmental factor that universally affects growth of larval fish is water temperature (Eckmann, 2013), which can operate directly via its influence on enzymatic reactions or indirectly by modifying the foraging arenas experienced by fish larvae (Ahrens et al., 2011). While numerous studies have identified positive correlations between water temperature and recruitment (Pepin, 1991), the causal mechanisms by which recruitment is determined are not well understood (Rose, 2000; Ludsin et al., 2014). Simple descriptive relationships rarely provide adequate explanations of year-class strength drivers (Letcher et al., 1996). Consequently, mechanistic simulation models have emerged as valuable tools for identifying factors that might contribute to year-class strength.

One hypothesis that has sought to explain recruitment variation is the match/mismatch hypothesis (Cushing, 1990), which emphasizes the importance of energetic demands of larval fish relative to the phenology of food availability. More specifically, when critical periods for larval fish development coincide with the production of planktonic prey, recruitment is expected to be high. Conversely, when there is a mismatch between energetic requirements and prey availability, recruitment is

expected to be low, either due to starvation or increased vulnerability to predation because larvae are in a weakened state. While the Great Lakes exhibit ecological and physical processes similar to the coastal oceans, the match/mismatch hypothesis has received far less attention in freshwater compared to marine systems (e.g., Fortier et al., 1995; Platt et al., 2003; Edwards and Richardson, 2004). However, Winder and Schindler (2004) demonstrated that subtle changes in the temperature of lentic environments can lead to substantial changes to the phenology of ecological processes, which suggests the match/mismatch hypothesis could also apply to the Great Lakes and other freshwater systems.

Nyberg et al. (2001) hypothesized that autumn spawning coregonines have evolved in cold temperate regions so that the timing of egg hatching is generally synchronized with ice break-up and warming spring conditions, which also triggers sharp increases in the abundance of crustacean zooplankton (Watson, 1974). Cisco (*Coregonus artedi*) larvae are 9-10 mm at hatch (John and Hasler, 1956; Hinrichs and Booke, 1975) and emerge in Lake Superior after ice break-up (Anderson and Smith, 1971; Selgeby et al., 1978; Hatch and Underhill, 1988). Compared to other species, the relatively large size of cisco larvae suggests a reduced risk of starvation and greater probability of surviving to the juvenile stage (Miller et al., 1988). However, the interannual variation in the degree of overlap between cisco larvae and high abundances of suitable prey is poorly understood and could have important implications for the magnitude of recruitment that is ultimately realized (Houde, 1987; Cushing, 1990). Houde (1989) demonstrated that subtle differences in growth or mortality rates could exert a greater effect on recruitment than substantial episodic events, such as

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failed egg production or large-scale advective loss of eggs or larvae. Thus, year-to-year differences in the availability of prey for larval cisco could cause the larval stage to be either brief or protracted, leading to the large differences in year-class-strength that have characterized cisco in Lake Superior (Yule et al., 2008a; Stockwell et al., 2009).

Water temperature is a well-demonstrated environmental driver of zooplankton abundance and ontogeny (McLaren, 1963; Watson and Wilson, 1978; Brown and Branstrator, 2004). Lake Superior has been classified as ultraoligitrophic (Matheson and Munawar, 1978; Munawar and Munawar, 1978) with abundance of zooplankton generally low compared to the lower Great Lakes (Watson and Wilson, 1978; Yurista et al., 2009). However, zooplankton distributions in Lake Superior are known to be very patchy (Zhou et al., 2001) and densities within patches can rival the densities observed in productive marine environments (Megard et al., 1997). Despite evidence of a positive relationship between spring and summer temperatures and coregonid growth and recruitment in both European and North American lakes (Christie, 1963; McCormick et al., 1971; Rey and Eckmann, 1989; Karjalainen, 1991), little is known about the mechanism(s) by which temperature influences cisco recruitment in Lake Superior. Some researchers have concluded that temperature directly drives growth and thus recruitment of some species of coregonids (Eckmann et al., 1988, Eckmann and Pusch, 1989; Rey and Eckmann, 1989), implying that food availability is not a limiting factor. Others have argued that variation in food availability, and thus starvation, can have an overriding influence on recruitment (Dabrowski 1981, 1989; Viljanen 1988). Food availability may depend on temperature dynamics, but the effect of temperature on recruitment is more indirect for this alternative hypothesis.

The objective of this study was to use modeling to examine these two alternative hypotheses about the role of water temperature in mediating cisco recruitment, and to compare model predictions to observed recruitment variation in Lake Superior over an 11-year period. We used back-calculated estimates of adult cisco abundance and archived temperature records as input to two different models that simulated growth of cisco larvae. Our first hypotheses was that larval cisco growth was governed by spring water temperatures, independent of the availability of food; our second hypothesis was that water temperatures determined the timing of cisco hatch and the phenology of zooplankton prey availability, thereby influencing the degree of annual overlap between cisco larvae and their prey. The relative level of support for the competing hypotheses was assessed by comparing model results to observed estimates of year-class strength.

Methods

Model overview

     We used two different models to simulate the early life history of 11 cisco cohorts (1996-2006) in a large (66,579 ha) Lake Superior embayment (Thunder Bay, Ontario; Figure 15). For both models we simulated the dynamics of daily cohorts from the period of egg deposition through larval metamorphosis. Each cohort experienced daily growth and mortality until they either reached 15 mm or expired. Recruitment was calculated as the sum of all larvae surviving to 15 mm, as this size has been linked to ontogenetic shifts to deeper water and reduced susceptibility to the sampling gear used to capture smaller conspecifics (Stockwell et al., 2009).
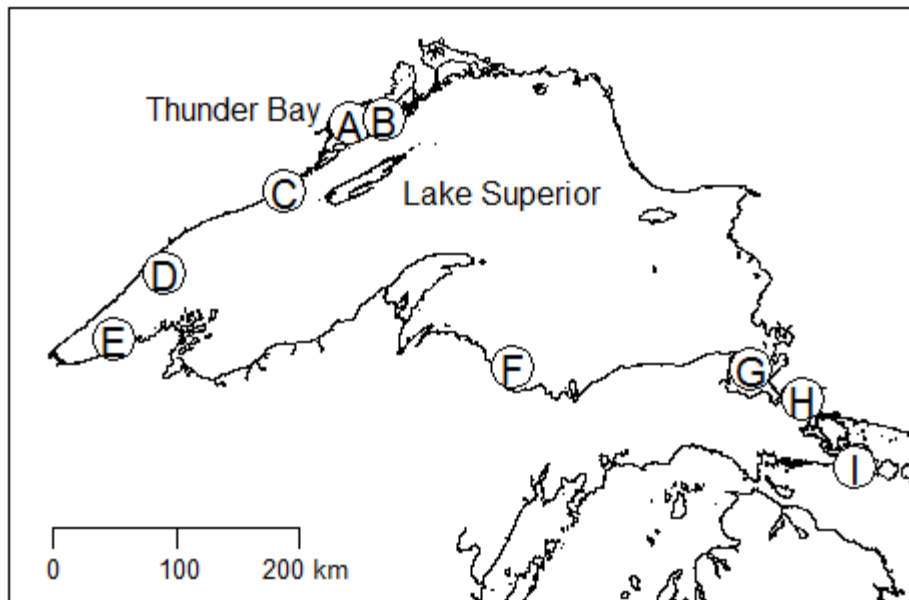
Figure 15. Map of Lake Superior showing the location of Thunder Bay. Letters indicate the sampling locations associated with Figures 23 and 24.

Egg deposition and hatching

Virtual population analysis (VPA) was used to reconstruct the age-specific abundance of mature female cisco in Thunder Bay for 1996-2006. We used cohort estimates of abundance from the 2007 survey of spawning cisco (Yule et al., 2008b) as starting values for the VPA because this survey had the potential to sample all cohorts that would have been at-large in Thunder Bay from 1996-2006. Age-specific (i) abundance (N) for a given year (t) was estimated using the following equation:

(Eq. 1) $\quad N_{i,t} = N_{i+1,t+1} e^{Z_i}$

where Z_i is age-specific total instantaneous mortality. Based on the results of Yule et al. (2008a), we set Z_i at 0.22 for cohorts ≥ 9 years of age. The cisco population in Thunder Bay was surveyed in 2005, 2007, 2008, 2009, and 2010 using similar hydroacoustic and midwater trawling methodologies (Yule et al., 2006; 2008b; 2009; 2010). Because the 2003 year-class was not included in the Yule et al. (2008a) analysis, we fit a catch curve to 2005-2010 abundance estimates of at-large females from the 2003 year-class. Based on this analysis, Z_i for cohorts ≥ 4 and < 9 years was estimated at 0.22.

The total number of eggs from which a given year-class was derived was the product of age-specific abundance (Figure 16) and fecundity (i.e., eggs female^{-1}). Yule et al. (2008a) showed that 95% of females ≥ 250 mm were mature, leading us to assume that cisco first spawned at age-3. To predict fecundity (F) of individual females, we used the relationship provided by Yule et al. (2006):

(Eq. 2) $\quad F = -86.5 + 46.5 \times \mathrm{mass(g)},$

where mass of individual females was predicted using the total length (TL) in mm to

mass in grams relationship provided by Yule et al. (2008a):

(Eq. 3) $log_e(\text{mass}) = -11.58 + (2.99 \times log_e\text{TL})$.

TL was estimated using the Von Bertalanffy growth equation for female cisco provided

by Yule et al. (2008b):

(Eq. 4) $\text{TL} = 381.1171 * (1 - e^{(-0.387*\text{Age})})$.

Einsele (1965) stated that one to ten adults will result from 10,000 naturally spawned

coregonid eggs. Given the lack of information related to the survival of cisco eggs, we

simply assumed 1% of the eggs that were cast survived to the larval stage. Because we

were interested in comparing the relative abundance of cohorts across years, our

conclusions were not sensitive to this assumption.

Archived (1996-2006) temperature data from Thunder Bay were used as input to

drive the dynamics of both models. 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. The depth at the site is 18.3 m,

but the pipe is suspended 10.1 m above the lakebed. Daily estimates of sub-surface
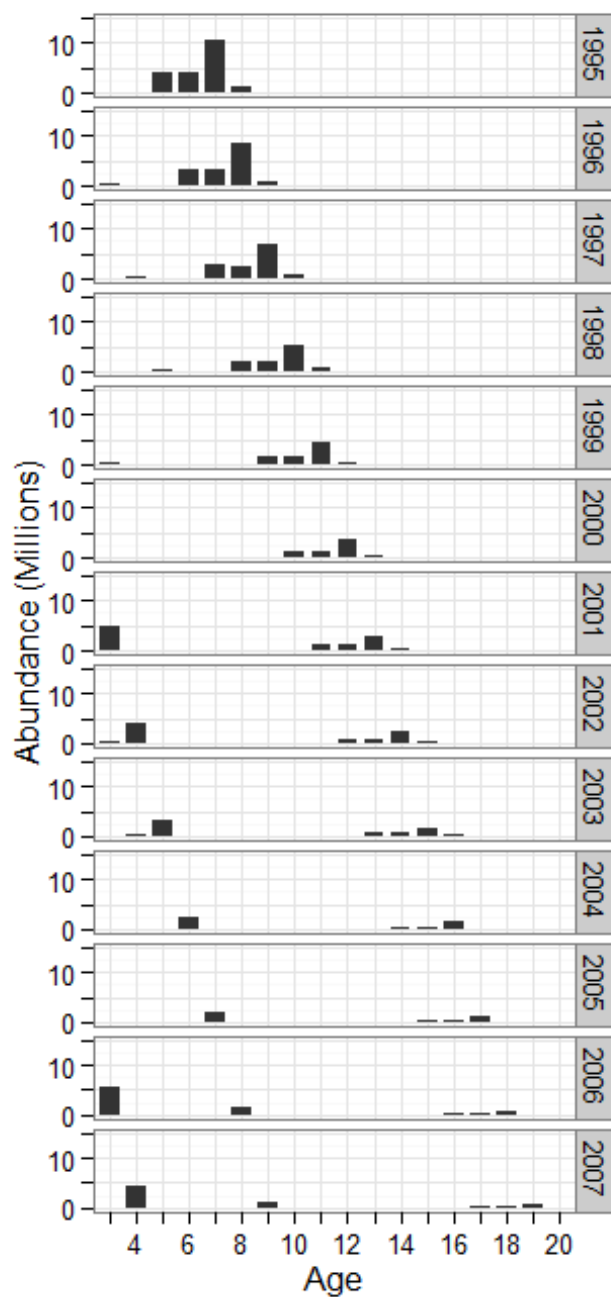
Figure 16. Results of the virtual population analysis (VPA) used to reconstruct the abundance-at-age of spawning female cisco in Thunder Bay. Abundance estimates from a hydroacoustic and midwater trawl survey conducted in Thunder Bay during the fall of 2007 (Yule et al., 2008b) served as the starting values for the VPA.

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); digital maps of Great Lakes surface water temperature and ice cover produced daily by the National Oceanic and Atmospheric Administration, Great Lakes Environmental Research Laboratory (NOAA/GLERL) in Ann Arbor, Michigan, through the NOAA CoastWatch program. Surface water temperatures from 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 2600 m (i.e., dimension of square raster) while estimates from mid-2003 to 2006 were recorded with an aerial resolution of 1300 m. We generated a single estimate of surface water temperature by calculating the arithmetic mean of all estimates within Thunder Bay for each day.

John and Hasler (1956) argued that the timing of cisco egg hatching in Lake Mendota, Wisconsin, was not likely affected by any other factor except water temperatures during the late stages of the incubation period. In addition, these authors suggested that cisco eggs required at least an additional 50 degree days after ice departure to hatch, which at temperatures of 4-5°C would mean hatching occurred approximately 10-12 days after ice departure. For our simulations we assumed egg deposition was normally distributed, with a standard deviation of 10 days, and that this temporal distribution persisted throughout the incubation period. We also assumed ice departed Thunder Bay when surface water temperatures rose above 1°C and that the

first daily cohort of eggs began their accumulation of degree-days on the day following ice departure, so long as that day was after 15-April. If ice departure occurred after 01-May then we assumed that the first daily cohort of eggs began their accumulation of degree days on 01-May. Subsequent daily cohorts began their accumulation of degree days in a consecutive fashion according to the original temporal distribution of egg deposition. Once a daily cohort accrued 50 degree-days (i.e., based on sub-surface water temperatures) they were assumed to hatch. Larvae were assumed to be 10 mm at hatch with surface migration taking 1 d (John and Hasler 1956, Hinrichs and Booke 1975).

Direct temperature model

McCormick et al. (1971) demonstrated that when reared cisco larvae were satiated, growth was positively related to temperature. We used observed surface water temperatures, along with the temperature-dependent, instantaneous growth rates reported by McCormick et al. (1971; Figure 17A), to calculate the daily increase in larval cisco wet mass (WM). We interpolated linearly between the observations of McCormick et al. (1971). Larval cisco growth in WM was converted to an estimate of TL by rearranging the relationship provided by Karjalainen (1992; Figure 17B):

(Eq. 5) $WM = 3.184\,TL^{3.663}$.

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 larval cisco experienced an instantaneous mortality rate (Z, d^{-1}) of

0.16 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 summed across daily hatch

cohorts to obtain an annual index of recruitment.
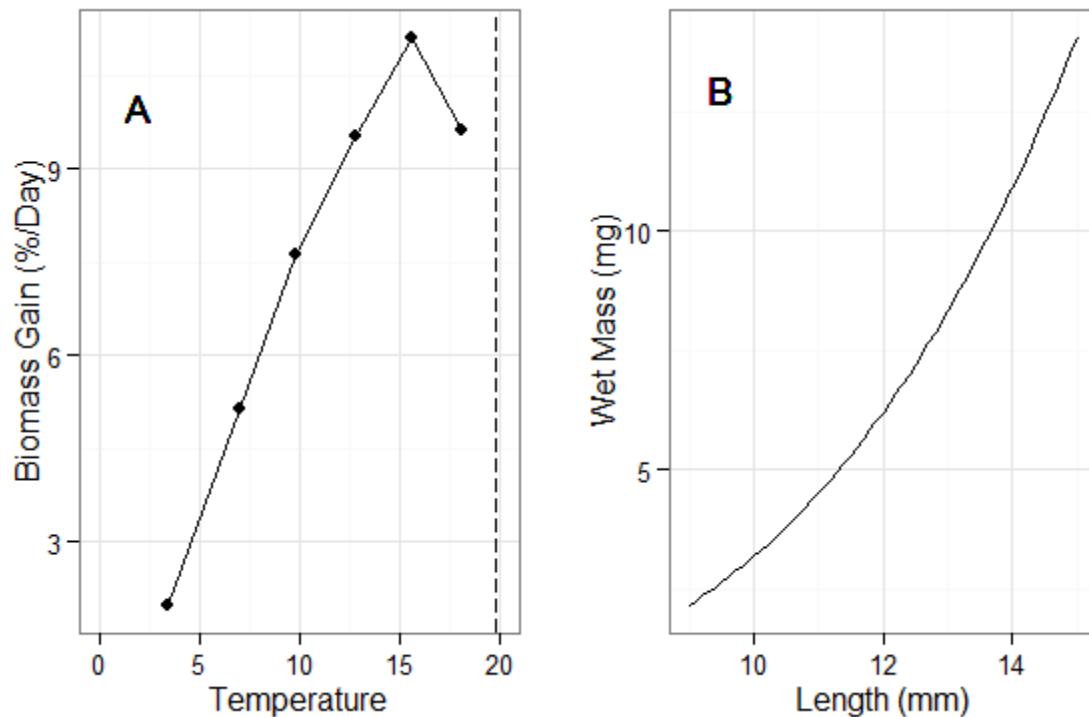
Figure 17. Reproduction of the results reported by A) McCormick et al. (1971) and B) Karjalainen (1992). The relationship between temperature and biomass gain for laboratory-reared larval cisco (McCormick et al., 1971) was used to calculate the growth in our "direct temperature model". The relationship provided by Karjalainen (1992) was used to convert growth in mass to growth in length for both the "direct temperature model" and the "indirect temperature model". Vertical dashed line in A) shows the upper lethal temperature for larval cisco.

We used the bioenergetic model (Table 8, Eq. 7) developed for coregonid larvae (Dabrowski et al., 1988, 1989; Dabrowski, 1989) to simulate growth from hatching through the larval stage. Growth was calculated by expanding the terms for both ingestion and respiration (Table 8, Eq. 8). Energy gains as a result of increased swimming speeds are counterbalanced by the increased metabolic rates associated with maintaining greater swimming speeds (Table 8, Eq. 10). Standard metabolism (Table 8, Eq. 11) with respect to the TL of larval cisco 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). Coregonid larvae are believed to be visual feeders, needing light to identify and capture prey (John and Hasler, 1956; Dabrowski, 1982). For this reason, we assumed feeding and active metabolism occurred between sunrise and sunset, while standard metabolism occurred over the remainder of the day. The period between sunrise and sunset was determined using a web-based application developed by the United States Naval Observatory (available at: http://aa.usno.navy.mil/data/docs/Dur_OneYear.php). Dabrowski et al. (1988) reported using a Q_{10} (i.e., the rate of change as a consequence a 10 °C temperature change) of 2.41 to scale both active and standard metabolism estimates from the larval coregonid bioenergetics model. The measurements of Q_{10} were developed using temperatures ≥14 °C, so we scaled our estimates of metabolism against this standard.

Food ingestion was calculated using the foraging model (Table 8, Eq. 14) advanced by Dabrowski et al. (1988), which is effectively a modification of the Holling type 2 functional response equation (Holling, 1965). This model assumes that the rate

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Table 8. Equations and parameters used in the larval cisco bioenergetics model. Sources: (1) Holling, 1965; (2) Ware, 1975, (3) Dabrowski et al., 1988; (4) Dabrowski, 1986a, b; Kaushik et al., 1986; (5) Karjalainen, 1992; (6) Dabrowski, 1989.

Description		Equation	Source
Eq. 7	General growth model	$G = qI - R$	
Eq. 8	Expanded growth model	$G = q\dfrac{yVp}{1 + yVph} - a\,e^{bV}$	1, 2, 3
Eq. 9	Net energy absorption coefficient	$q = r \cdot (1\text{-}SDA)$	
Respiration (R; J·fish^{-1}·h^{-1})			
Eq. 10	Metabolism of larvae	$R = a\,e^{bV}$	
Eq. 11	Standard metabolism of larvae	$a = 0.1272\,e^{0.7344\,TL}$	4, 5
Eq. 12	Swimming speed (cm·s^{-1})	$V = 0.1926\,e^{1.282\,TL}$	6, 5
Eq. 13	Slope of activity equation	$b = 6.76\,e^{-1.094}$	3
Ingestion (I; J·fish^{-1}·h^{-1})			
Eq. 14	Ingestion of food	$I = \dfrac{yVp}{1 + yVph}$	1, 2, 3
Eq. 15	Swimming speed (m·h^{-1})	$V = 6.932\,e^{1.282\,TL}$	6
Eq. 16	Handling time (h·J^{-1})	$h = 0.08464\,e^{-1.0848\,TL}$	3
Eq. 17	Area successfully searched (m^3·h^{-1})	$y = s \cdot c$	
Eq. 18	Area of the visual field (m^2)	$s = 0.0001217\,TL\text{-}5.0306 \times 10^{-6}$	3
Model Parameters			
Par. 1	Absorption coefficient	$r = 0.75$	3
Par. 2	Specific dynamic action coefficient	$SDA = 0.28$	3
Par. 3	Dependence of R on temperature	$Q_{10} = 2.41$	3
Par. 4	Probability of prey capture	$c = 0.85$	3
Par. 5	Prey density (J·m^{-3})	$p =$ Simulated	See text
Par. 6	Duration of active swimming/feeding (h)	Sunrise to sunset	See text
Par. 7	Total Length (cm)	$TL =$ Simulated	

of food ingestion is dependent on optimum swimming speeds (Table 8, Eq. 15), prey

densities encountered by larvae, handling time per unit energy return (Table 8, Eq. 16),

and the area successfully searched (Table 8, Eq. 17), which is the probability of

successful prey capture multiplied by the perception distance and area (Table 8, Eq.

18). Cisco larvae are known to feed predominately on copepod nauplii (Anderson and

Smith 1971, Savino et al. 1994, Selgeby et al. 1994), leading us to assume the

probability of successful capture was 0.85 (Table 8; Par. 2). Watson and Wilson (1978)

reported that surface water temperature in Lake Superior was the most important

determinant of zooplankton standing stock and 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. We simulated zooplankton biomass

density in Thunder Bay for a given day using the relationship provided by Watson and

Wilson (1978):

(Eq. 6) $\quad \log_e \text{Zooplankton Biomass} = \frac{0.79\,(\text{T·D})}{10^3} + 1.37,$

where zooplankton biomass is expressed as mg m^{-3} (i.e., dry weight), T is surface water

temperature (°C), and D is a time variable (i.e., ordinal date -100) used to fix the

temporal baseline to the period of minimum surface water temperature. Based on

Munawar and Wilson (1978), we assumed the naupliar portion of the zooplankton

biomass was 20% for all dates prior to 15 May and then declined linearly from 20% on

May 15 to 10% on July 31. Density of nauplii (No. m^{-3}) was determined by dividing

biomass by 0.4 µg, which is the average dry weight of individual nauplii according to the

United States Environmental Protection Agencies (EPA) standard operating procedure for zooplankton analysis (EPA, 2010). Density estimates were converted to energy (J m^{-3}) by assuming individual nauplii were 0.04875 J (Dabrowski et al., 1988). Preliminary modeling showed that simulated prey densities were insufficient for positive growth and recruitment. To promote the possibility of positive growth of 10 mm larvae in our simulations, we opted to adjust estimates predicted by the Watson and Wilson (1971) model by a factor of 4, which allowed for positive growth scenarios and created simulated prey densities that were more consistent with recent empirical observations (Myers et al., 2014).

We followed the approach of Karjalainen (1992) and converted energy ingested to dry and wet mass (DM and WM, respectively) using the coefficients of 46 J mgC^{-1}, 0.5025 mgC mgDM^{-1} (Salonen et al., 1976), and 0.11 mgDM mgWM^{-1} (Dumont et al., 1975). Larval cisco growth in WM was converted to an estimate of TL by rearranging the relationship provided by Karjalainen (1992; Eq. 5). Similar to the direct temperature model, we assumed age-0 cisco experienced a daily mortality rate of 0.16 (Houde and Zastrow, 1993) until they reached 15 mm, and individuals not reaching 15 mm by 31 July were assumed to die. All individuals that reached 15 mm were summed to index the abundance of recruits.

Model comparison

To estimate survival of larvae during a given year we divided the number of individuals that reached 15 mm by the number of larvae that hatched, which effectively accounted for the differences in the initial number of eggs cast. Survival estimates from

the direct and indirect temperature models were standardized by dividing individual estimates by the sum of estimates across years. Standardization facilitated comparisons between models and with the results of a spring bottom trawl survey conducted by the U.S. Geological Survey (USGS), Great Lakes Science Center. This bottom trawl survey, which includes roughly 80 stations around the periphery of Lake Superior, sampled annually since 1978, has been shown to provide a useful empirical index of recruitment, based on catches of age-1 cisco (Bronte et al., 2003; Yule et al. 2008a). Point estimates from the observed recruitment index were standardized using the same procedure described for the models. We used measures of rank correlation and standard deviation (σ) to compare the results of the simulation models to the observed recruitment index.

Results

Inter-annual variability in estimates of water temperature (Figure 18) led to differences in the simulated timing of peak hatching between years (Figure 19). For example, early ice departure during the springs of 1998-2000 (Figure 18) led to simulations where larval cisco hatched predominately in early May (Figure 19). However, late ice conditions and cold temperatures in the springs of 1996 and 1997 delayed the onset of simulated hatching and thus the peak in hatching did not occur until after the middle of May. Our modeling demonstrated that early hatching could be advantageous to larvae (e.g., 1998 cohort) when it provided access to potential growth opportunities (Figures 20 and 21). However, it did not guarantee enhanced survival, as poor growing conditions post-hatch precluded the benefit associated with early hatching for some cohorts (e.g. 2000 and 2004-2006 cohorts; Figures 20 and 21). Delayed hatching for the 2003 cohort may have increased survival by insulating larvae from poor growing conditions during late April and early May (Figure 19). Our modeling indicated that conditions for the 2003 cohort likely improved shortly after hatching commenced, leading to enhanced growth and increased survival predictions (Figures 20 and 21).

As a consequence of model assumptions, the direct temperature model predicted cisco larvae reached 15 mm at approximately the same time each year while the indirect temperature model showed a wider range in dates (Figure 20). Also, the direct temperature model suggested that several daily cohorts survived to 15 mm in most years and that successful recruitment occurred over the span of weeks. In contrast, the indirect temperature model suggested successful recruitment was a rare occurrence
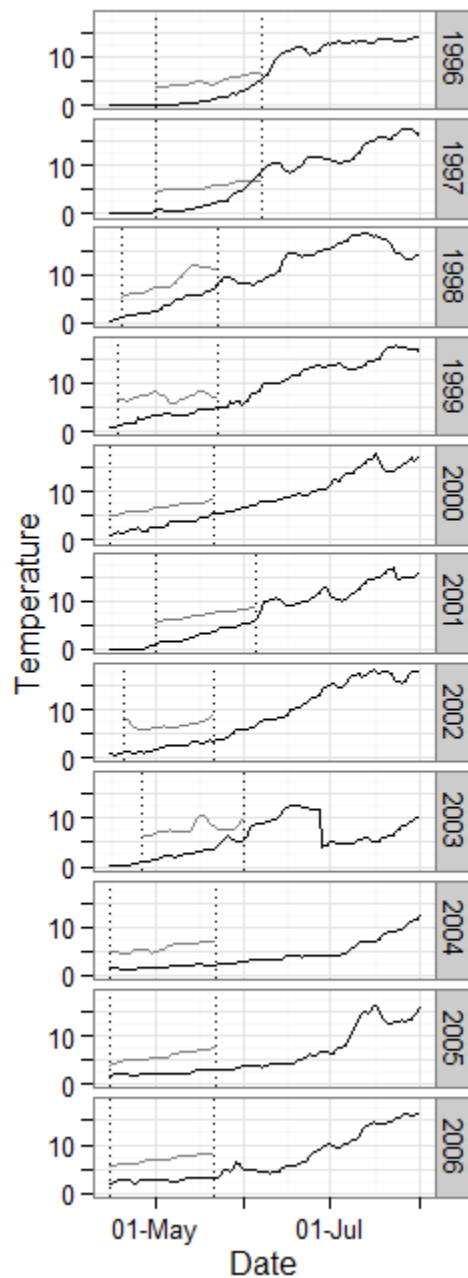
Figure 18. Temperature (°C) at the surface (black line) and 8.2 m below the surface (grey line) in Thunder Bay, Lake Superior during the period of larval cisco hatching and development, 1996-2006. Only sub-surface temperatures during the period when eggs were accumulating degree-days are shown (i.e., between dotted lines). Surface and sub-surface temperatures were estimated using different methodologies (see text).
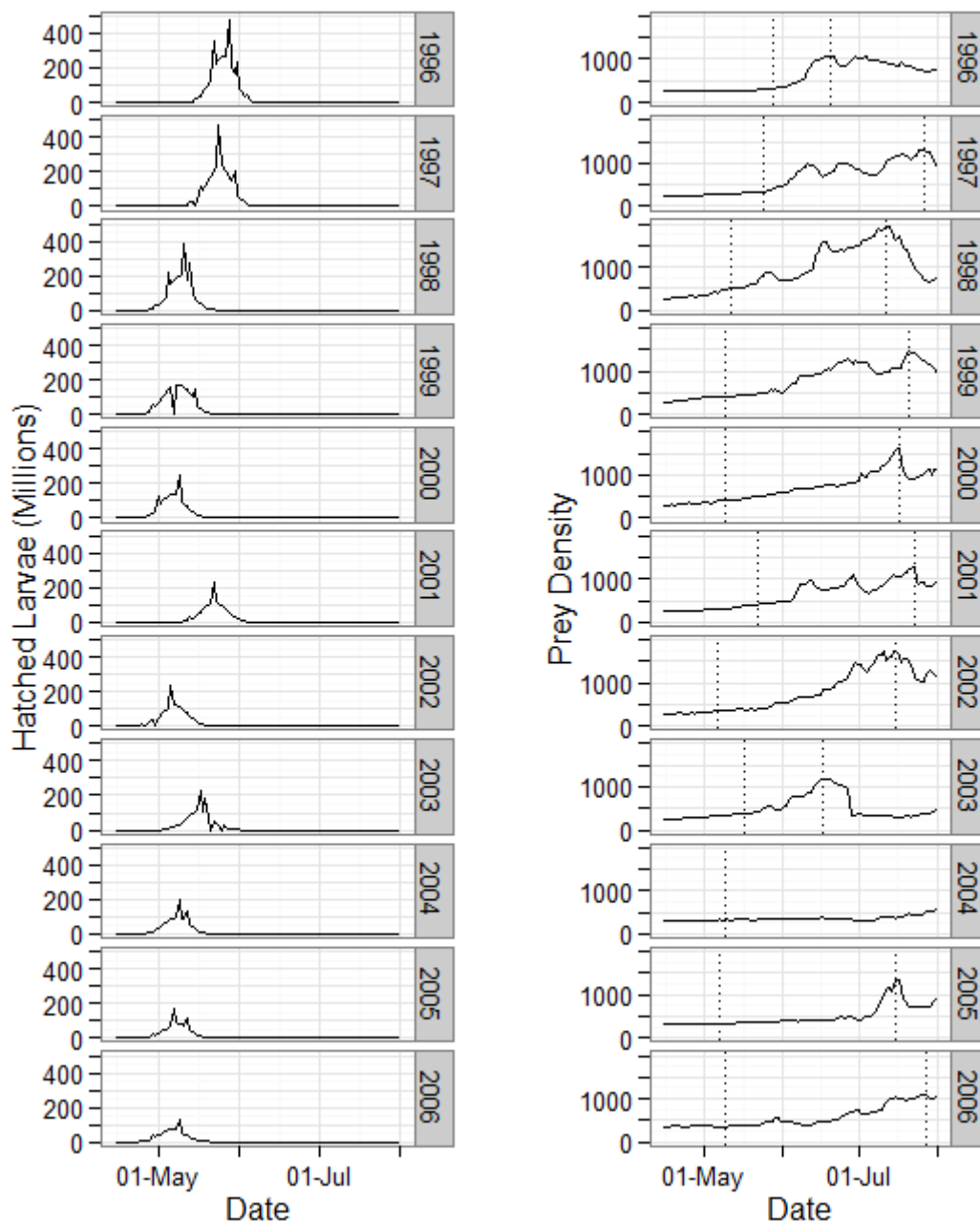
Figure 19. Simulated distribution of hatched cisco larvae and the simulated prey densities (J m^{-3}) available to cisco during the period of larval development, 1996-2006. Vertical dotted lines prior to 01-June represent the date of peak larval cisco hatching while the vertical dotted lines after 01-June represent the date of maximum prey density.
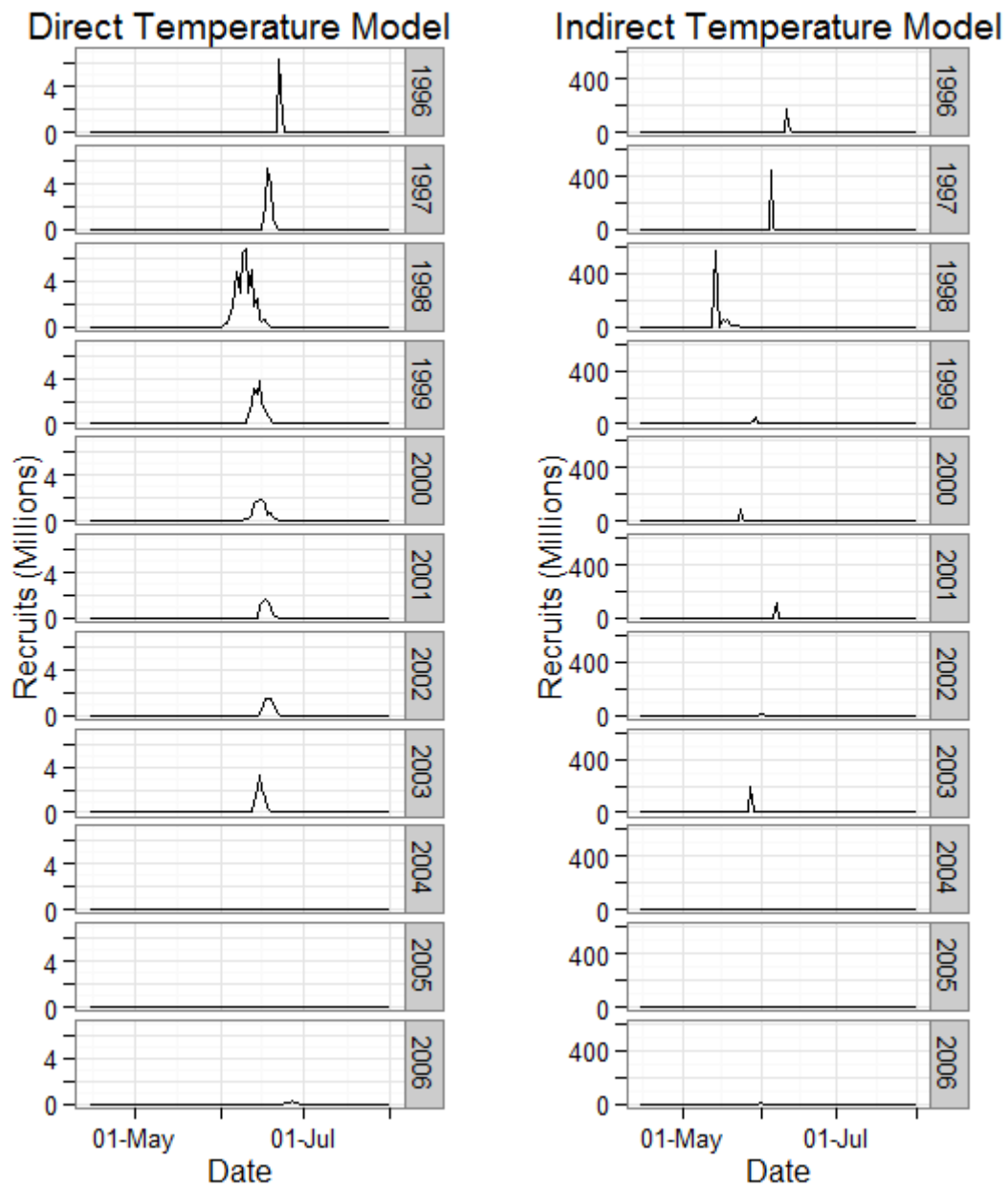
Figure 20. Abundance of larval cisco surviving to 15 mm, as predicted by the direct and indirect temperature models.
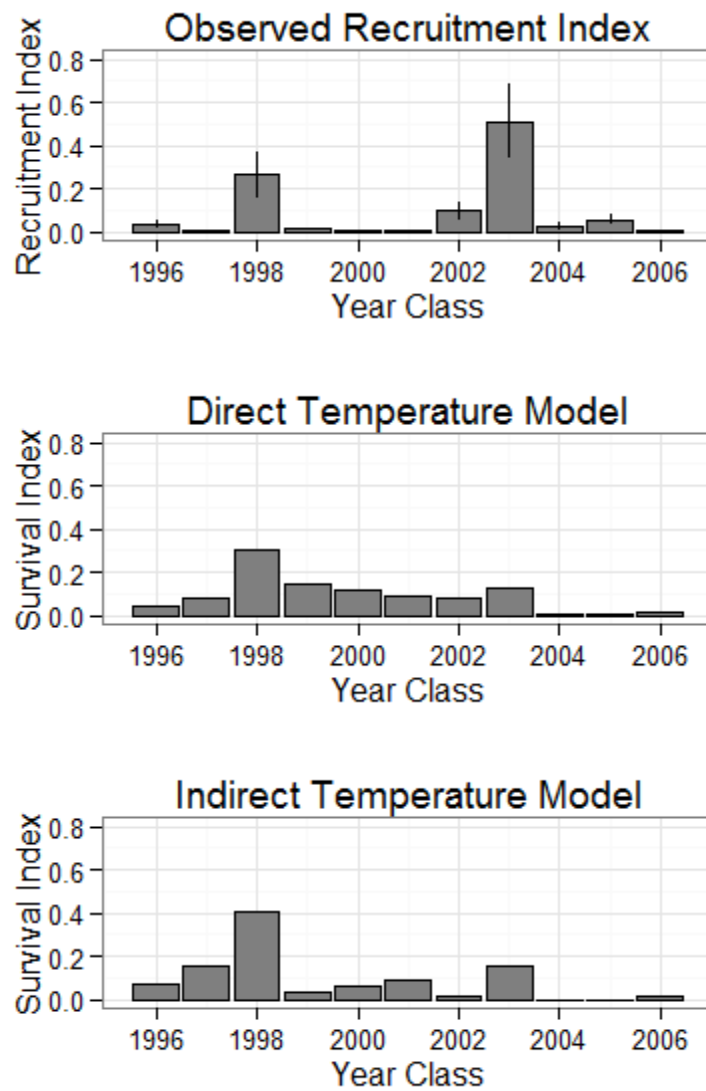
Figure 21. Relative index of cisco year-class strength in Lake Superior (based on the catches of age-1 cisco during the USGS-Great Lakes Science Center spring bottom trawl survey, 1996-2006) along with the results of the direct and indirect temperature models used to explore the larval survival. Error bars associated with the observed recruitment index are 1 SE.

and only happened for a few daily cohorts in most years (Figure 20). While there appears to be a relationship between the maximum density of prey and the magnitude of recruitment that was simulated (Figures 19 and 20), in actuality the date of maximum prey density had little effect on simulated recruitment. For example, hatching for the 1998 cohort was predicted to occur between April 27 and May 23 (Figure 19). Meanwhile, the indirect temperature model predicted that maximum recruitment occurred on May 14 (Figure 20), which was 58 days prior to the date of peak prey density (Figure 19). Similarly, in the spring of 2003 the peak in recruitment occurred on May 28 (Figure 20), which was 21 days prior to the peak in prey abundance (Figure 19). Thus, inter-annual differences in maximum prey densities had little impact on survival estimates. Rather, access to prey densities that promoted positive growth within 1-2 weeks after hatching was more likely to enhance simulated survival.

Given that surface water temperature was used to simulate larval growth (i.e., both models) and the availability of prey (i.e., indirect temperature model), it is not surprising that broad patterns of recruitment for the two models were similar (Figure 21). Simulated larval cisco survival was above average in 1998 and 2003 and below average in 2004, 2005, and 2006 for both the direct and indirect temperature models, which corresponded well with empirical indices of cisco recruitment (Figure 21). Although there were similarities between results of the two models, there were also important differences. For example, the direct temperature model suggested the 1997 cohort was weak and the 1999 year class was moderate, but the indirect temperature model predicted the opposite. In addition, simulations from the direct temperature model led to annual survival estimates that were less variable ($\sigma = 0.0046$) than the survival

estimates generated by the indirect temperature model (σ = 0.1145). In comparison, the observed recruitment index had a σ of 0.1589. Estimates of correlation between models results and the observed recruitment index did not shed light on whether either model compared favorably over the other. Using the Spearman method, the direct temperature model had a slightly greater correlation coefficient (r_s = 0.209) compared to the indirect temperature model (r_s = 0.118). In contrast, Pearson correlations were slightly greater for the indirect temperature model (r_p = 0.537) than the direct temperature model (r_p = 0.486). The apparent relationship between model results and empirical indices (Figure 22), albeit weak, suggests water temperature does indeed play an important role in larval cisco survival in Thunder Bay.
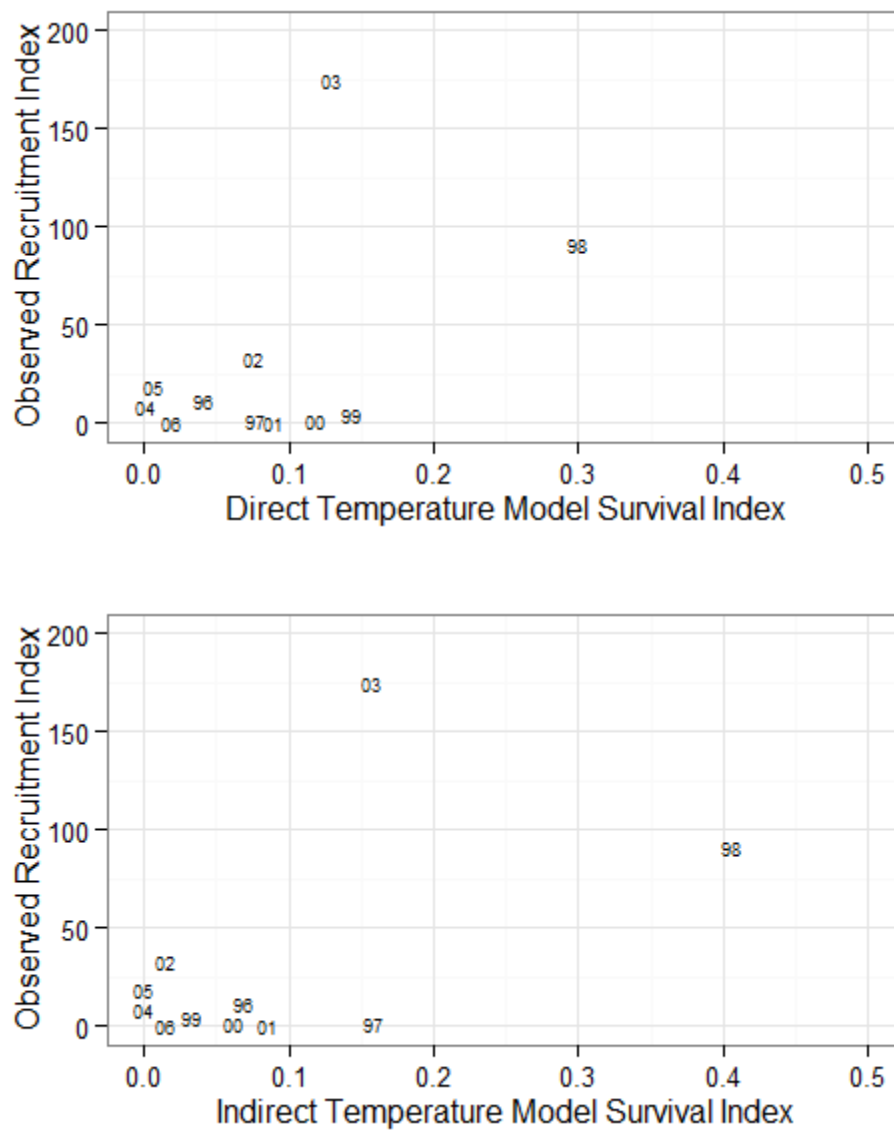
Figure 22. Plot of model estimates of relative survival versus the index of cisco year-class strength generated by the USGS spring bottom trawl survey. Data points are symbolized by year-class.

Discussion

Both the direct and indirect temperature models compared reasonably well with the observed recruitment index, which lends support to the hypothesis that inter-annual variability associated with water temperature in Thunder Bay could play a key role in recruitment levels of cisco. However, the indirect temperature model provided survival estimates that more closely resembled the "boom or bust" pattern of observed recruitment, suggesting the indirect effects of temperature on survival may be more important than direct effects. The prey densities that were simulated within this study were often < 500 J m^{-3} when cisco larvae hatched (Figure 19). While these simulated estimates of prey density were low compared to the prey densities used to develop the larval coregonid bioenergetic model (range = 431 – 17,248 J m^{-3}; Dabrowski et al., 1988), they do compare reasonably well with the results of recent sampling efforts across Lake Superior and northern Lake Huron (Figure 23). During the period of larval cisco hatching (Figure 24), prey densities were often < 500 J m^{-3} and rarely exceeded 1500 J m^{-3}. Thus, the effect of temperature on larval cisco hatching and prey availability may create scenarios where cisco larvae are either satiated or prey-limited, a likely possibility for the Great Lakes where physical processes are known to profoundly influence the distribution of planktonic organisms (Megard et al. 1997; Beletsky et al., 2007; Zhao et al., 2009). The match/mismatch hypothesis (Cushing, 1990) provides a reasonable explanation for the high degree of inter-annual variability associated with Lake Superior cisco recruitment.
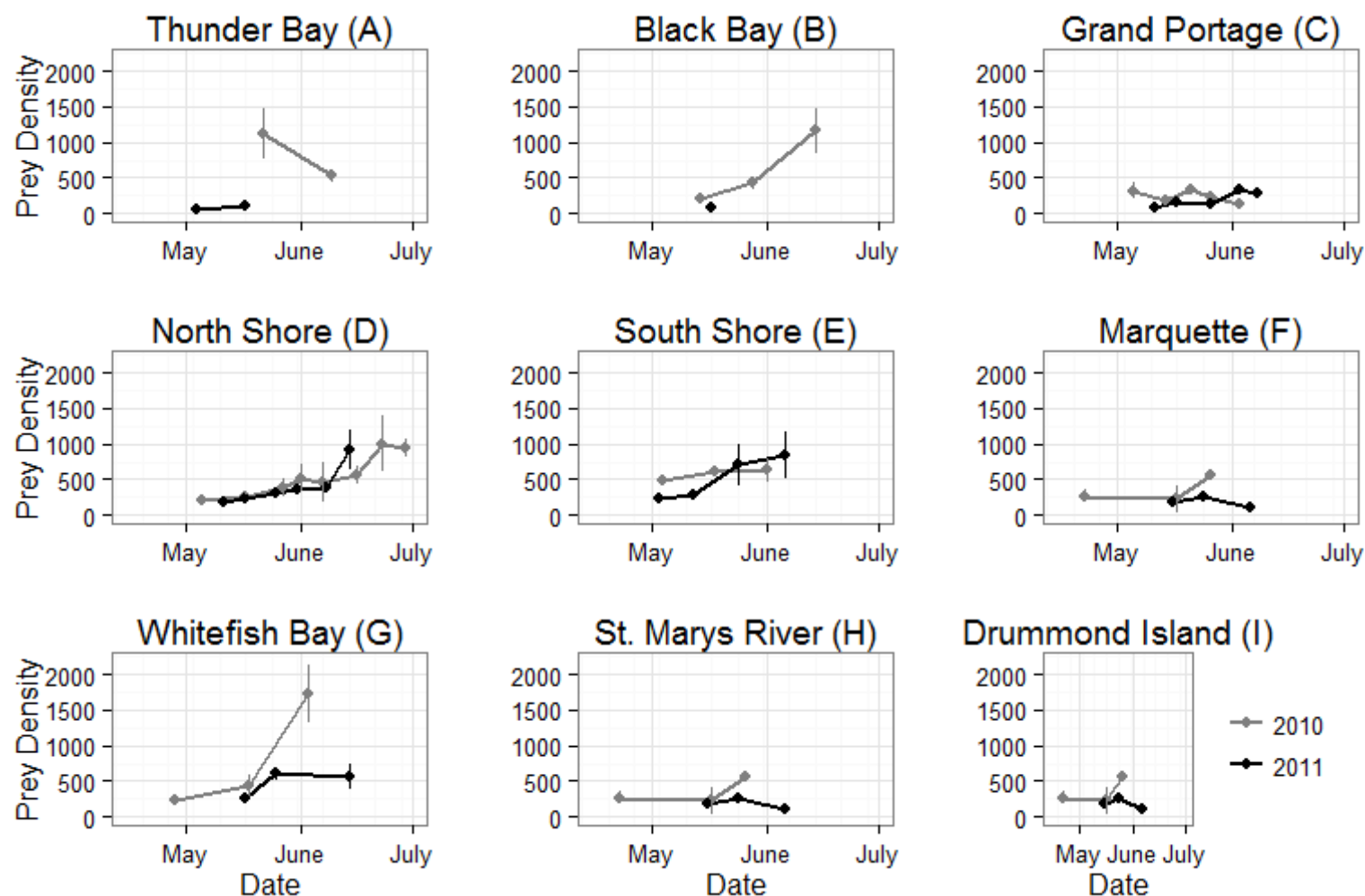
Figure 23. Empirical estimates of nauplii energy density (J m^{-3}) at locations across Lake Superior (A-G) and in northern Lake Huron (H-I) during the spring of 2010 and 2011. Samples were collected between zero and 5 m below the surface using the methods outlined in Myers et al. (2014). Error bars are 1 SE.
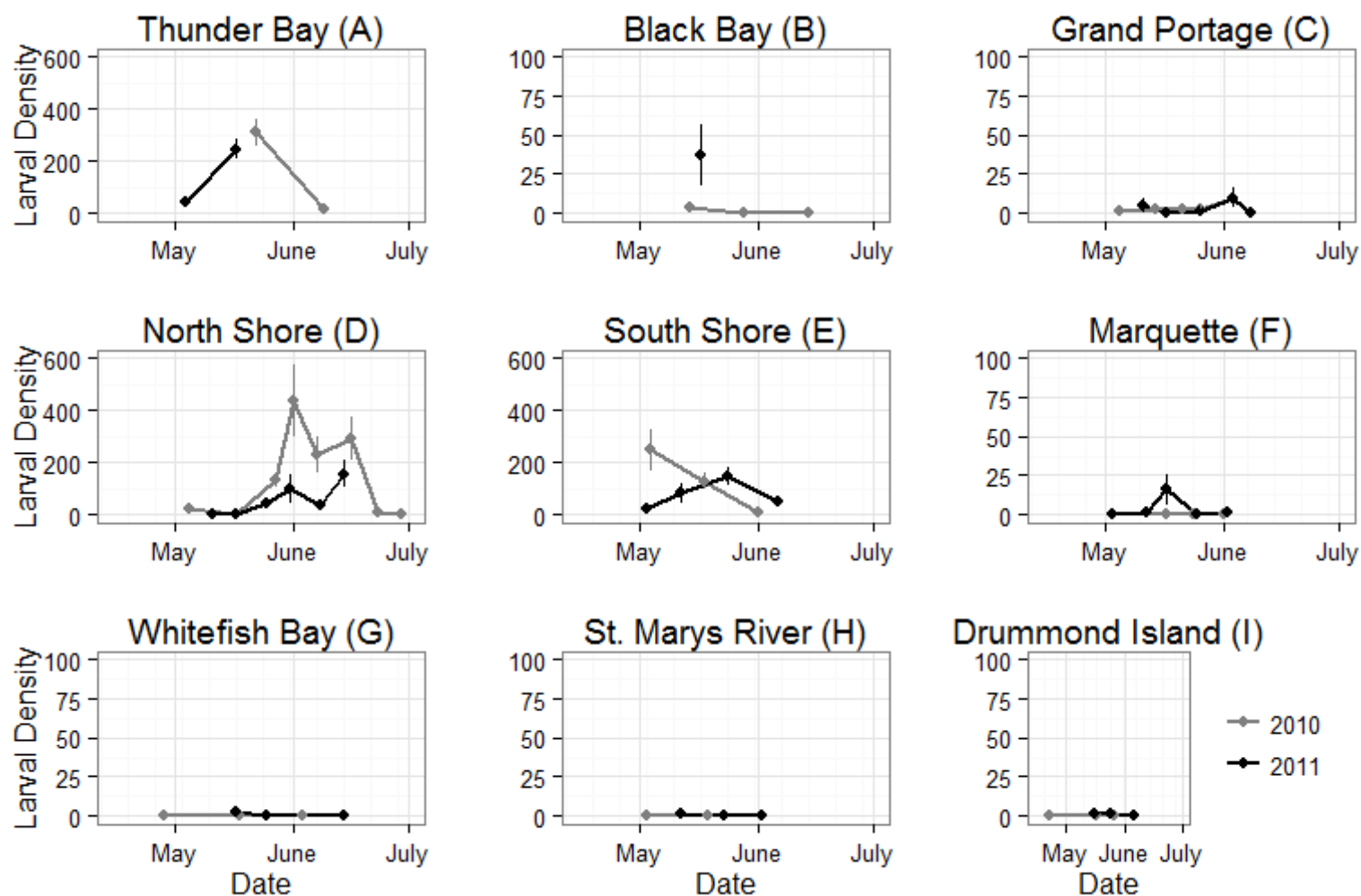
Figure 24. Empirical estimates of larval cisco density (#/1000 m^3) at locations across Lake Superior (A-G) and in northern Lake Huron (H-I) during the spring of 2010 and 2011. Samples were collected from surface stratum using the methods outlined in Myers et al. (2014). Note that y-axis limits are not the same for all panels. Error bars are 1 SE.

Within our simulations, the fate of a daily cohort was often determined prior to the peak in spring temperatures or prey densities. We believe this observation suggests that the foraging arenas experienced by larvae during their first 1-2 weeks in surface waters could have a disproportionate effect on survival compared to the conditions at later dates. Many researchers have dismissed the hypothesis that coregonid larvae are susceptible to increased mortality due to insufficient prey densities (Kinnunen, 1997) because laboratory-reared larvae are often capable of surviving prolonged periods of starvation (e.g., John and Hasler, 1956; Rey and Eckman, 1989; Rice et al., 1987). Taylor and Freeburg (1984) studied the effect of food ration on larval lake whitefish (*Coregonus clupeaformis*) in a laboratory setting and showed that regardless of the food ration, there was no mortality until day 15 of the experiment. However, larvae that were fed reduced rations were said to "lie motionless at the bottom of tanks" while larvae fed higher rations were said to be "robust and active." Once larvae had absorbed their yolk-sacs and were completely reliant on exogenous food sources, mortality rates rose dramatically. All larvae died within 1 week except those that were fed the highest food rations, which experienced little or no reductions in survival. Similarly, Rellstab et al. (2004) used an analysis of zooplankton time-series and larval lake whitefish (*Coregonus zugensis*) feeding experiments to demonstrate that the re-oligotrophication of Lake Lucerne (Switzerland) ultimately led to reductions in lake whitefish year-class strength. They also showed that food concentrations ≤ 20 zooplankton per liter (i.e., approximately 1000 J m^{-3}) led to elevated rates of larval mortality, but not until after the first 15 days of the experiment. Bloater (*Coregonus hoyi*) larvae in Lake Michigan were thought to be extremely resistant to starvation because laboratory experiments showed

that starved larvae took 25 days to reach 50% mortality (Rice et al., 1987). The absence

of slow growing larvae in field samples led to the conclusion that starvation was not

likely a bottleneck, yet the years in which sampling occurred (i.e., 1982 and 1983) were

relatively strong recruitment years for bloater (Rice et al., 1987). Rice et al. (1987)

postulated that the rapid growth rates of larvae collected in the field may have resulted

from the increased abundance of zooplankton, which likely stemmed from a decline in

alewife (*Alosa pseudoharengus*). Thus, it is possible that bloater larvae may have only

been sampled during favorable conditions (i.e., high zooplankton abundance), making it

difficult to assess the effect of low rations on bloater recruitement. Taylor and Freeburg

(1984) noted that the ability of coregonid larvae to survive poor food conditions for

upwards of three weeks may be an adaptation for living in highly variable environments.

One view is that this evolved adaptation insulates larval coregonids from the effects of

starvation, yet another view is that the adaptation highlights the significance of prey

availability as an important factor in setting recruitment.

Populations of coregonids are known to exhibit synchrony in recruitment patterns

across broad geographic ranges (Marjomäki et al., 2004; Bunnell et al., 2010 ; Myers et

al., 2015), which underscores the probability that large-scale abiotic factors (e.g.,

temperature, wind, etc.) influence recruitment. However, while water temperatures at

different locations may be correlated, they are not necessarily the same. If we were to

accept the premise that water temperature were the sole driver of cisco recruitment in

the Great Lakes then we would 1) expect recruitment to be greater at lower latitudes

compared to higher latitudes and 2) expect that the incidence of successful recruitment

events in Lake Superior would be increasing as a result of increasing surface water

temperatures (Austin et al., 2007). However, the existence of remnant cisco stocks in the lower Great Lakes (Yule et al., 2013c) that have not recovered (Zimmerman and Krueger, 2009) casts doubt on the first of these expectations, and the fact that sporadic and dampened recruitment continues to limit cisco in Lake Superior (Stockwell et al., 2009) does not support the latter expectation. Nyberg et al. (2001) reported that rapid increases in the water temperature shortly after the ice-break of Swedish lakes benefited the year-class strength of vendace (*Coregonus albula*) by ensuring the overlap between larvae and ample food. Thus, their observations were consistent with the match/mismatch hypothesis, as heavy ice coverage could have reduced the risk of premature hatching and increased the probability of aligning larval fish with an "optimum spring window". Interestingly, Taylor et al. (1987) showed that densities of larval lake whitefish after a cold winter with prevalent ice on Lake Michigan were nearly fourfold greater than the preceding year, which was characterized by a mild winter and no ice. Furthermore, heavy ice coverage appears to be a prerequisite for successful cisco recruitment in Lake Superior, as most of the strong year-classes over a 35 year period have been produced when large portions of the lake were frozen (Figure 25). One exception was the 1998 year-class, which was successful despite little ice coverage. Our modeling may provide an explanation for this, as the unusually warm temperatures associated with 1998 led to simulated larvae encountering high prey densities despite an early hatch date (Figure 19). We hypothesize that the broad spatial scale of synchrony associated with cisco recruitment in the Upper Great Lakes (Myers et al., 2015) is likely caused by environmental factors, which may include the effects of ice
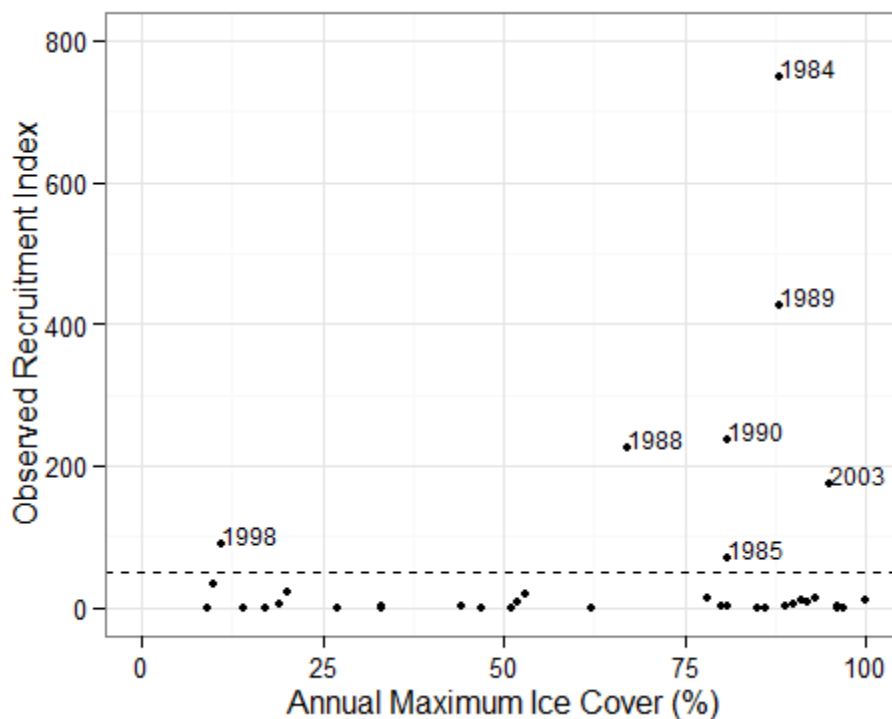
Figure 25. Maximum ice coverage on Lake Superior versus the relative year class strength of cisco in Lake Superior, 1977-2012. Ice coverage data was reported by NOAA/GLERL (available at: http://www.glerl.noaa.gov/data/ice/ice.html) and the observed recruitment index was generated by the USGS spring bottom trawl survey. Only those years for which the recruitment index was greater than 50 fish ha^{-1} (horizontal dashed line) were labeled with the appropriate year-class.

coverage and the timing and magnitude of spring warming on the temporal overlap between larvae and their preferred prey.

Fish larvae are hatched into an extremely variable and unforgiving environment, leading to high mortality rates and stochastic recruitment patterns (Burrow et al., 2011). Determining the factors that influence recruitment has been "the Holy Grail" of fishery science since the seminal work of Hjort, which identified the larval stage as a likely bottleneck (Houde, 2008). The scientific community has pursued the "recruitment problem" as if it has been a puzzle waiting to be solved. However, Houde (2008)

recently explained that "solving the problem" may be an unrealistic goal and that we should rather strive to appreciate recruitment variability, explain its causes, and consider its implications for management. The results of our modeling efforts are consistent with other studies that have shown a positive relationship between spring water temperature and recruitment (Eckmann et al., 1988; Rey and Eckmann, 1989; Kinnunen, 1997). However, we believe our results suggest that the indirect temperature model provides a more likely explanation for the relationship between water temperature and recruitment, with water temperature simultaneously driving the phenology of larval cisco emergence and exogenous feeding, and the dynamics of their planktonic prey. We encourage further examination of the relationship between larval fish survival and temperature and recommend that future studies give careful consideration to the potential mechanisms by which temperature can influence growth.

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