Quantifying a potential mechanism between ice cover and cisco recruitment success: what role does light play in cisco embryonic development?

Taylor R. Stewart1,3, Mark R. Vinson2, and Jason D. Stockwell3

1 Department of Biology, University of Vermont, Burlington, Vermont, USA

2 USGS Lake Superior Biological Station, Ashland, Wisconsin, USA

3 Rubenstein Ecosystem Science Laboratory, University of Vermont, Burlington, Vermont, USA

# ABSTRACT:

# INTRODUCTION:

Freshwater whitefishes, Salmonidae Coregoninae (hereafter coregonines) have played important economic and ecological roles throughout the northern hemisphere (Nyberg et al. 2001, Ebener et al. 2008b, 2008a, Vonlanthen et al. 2009, 2012, Lynch et al. 2015, 2016). Over the past 35 years, coregonine populations worldwide have experienced declines due to highly variable and weak year-class strengths (Nyberg et al. 2001, Myers et al. 2015). In the Laurentian Great Lakes, native coregonine conservation and restoration efforts are at the forefront of fisheries management efforts (Favé and Turgeon 2008, Zimmerman and Krueger 2009, Bronte et al. 2017). Historical coregonine declines have been attributed to overfishing, invasive species, habitat alterations, and competition (Stockwell et al. 2009, Lucke et al. 2020, Rosinski et al. 2020). However, reasons for failing to recover remain unknown. Climate-induced changes in early-life stage environments have been hypothesized as reasons for declining recruitment. Most coregonines are autumn spawners whose embryos incubate under ice throughout the winter (Karjalainen et al. 2000, Stockwell et al. 2009), and winter ice and water temperature regimes have changed over the past 20 years or more (Austin and Colman 2007, O’Reilly et al. 2015, Sharma et al. 2019). Future climate change predictions show that the timing and physical characteristics of winter and ice regimes are likely to drive some of the most important biological changes (Sharma et al. 2007, 2019, Woolway et al. 2020).

Year-class strength in most fish species, including coregonines, is thought to be established prior to the end of the first season of growth (Hjort 1914, Cushing 1990). Unlike larvae, embryos are static, leaving this early-life stage vulnerable to predation (Stockwell et al. 2014) and unable to evade inter-annual variation in winter conditions (Pepin 1991). Changes in winter severity and ice cover could alter developmental rates, embryo survival, and time of hatching (Karjalainen et al. 2015). Potential mechanisms by which ice cover might influence cisco development include the reduction of physical wave action (Walter et al. 2006, Austin and Colman 2007, Wang et al. 2010, Nguyen et al. 2017), more stable winter and spring water temperatures (Magnuson et al. 1997, Winslow et al. 2017), and less sunlight reaching the lake bottom (Bolsenga and Vanderploeg 1992, Hampton et al. 2015). Recent changes in ice cover coupled with poor coregoninerecruitment has led to hypotheses about the relationship between ice cover and embryo survival for decades without testing. Therefore, testing whether variable and declining ice regimes may impact coregonine early-life history is an important aspect of coregonine conservation and restoration efforts.

Lake ice cover can also play a critical role in physical and ecological processes (Sharma et al. 2020). Ice thickness and snow impact light penetration into the water column (Hampton et al. 2015), and can reduce light transmittance from 83% in open water to 62% under ice coverage, and to ≤ 10% under snow and ice coverage (Bolsenga and Vanderploeg 1992). Light is the most consistent abiotic factor in nature (Ruchin 2020). Light serves not only as a source of energy for aquatic ecosystems, but also can regulate fish phenology, behavior, and physiology (Ruchin 2007, Villamizar et al. 2011). The length of photoperiods characterize circadian rhythms and ensure that biological processes are synchronized with the environment (Marchesan et al. 2005, Gaston et al. 2013, Ruchin 2020). Additionally, the intensity of light exposure can alter the development, survival, and growth of fish (Villamizar et al. 2011, Ruchin 2020).

The impact of light exposure during fish embryogenesis varies across species (Ruchin 2020). Embryos from some salmonid species, including European whitefish *Coregonus lavaretus*, incubated under elevated light levels have higher mortality and deformity rates, slower formation of cartilaginous skeletal elements, decreased time to hatching, and smaller size-at-age; with development after organogenesis accelerated (Eisler 1958, 1961, MacCrimmon and Kwain 1969, Kwain 1975, Chernyaev 2007, Lyutikov 2012). However, other teleost species have had opposing responses, or no response, to high illumination (Iglesias et al. 1995, Mangor‐Jensen and Waiwood 1995, Seth et al. 2014). Consequently, increased light intensity during winter incubations, as a result of reduced ice and snow cover, may act as an additional stressor during coregonine embryo development for populations with seasonal ice cover. Understanding the impact ice and light have on coregonine embryogenesis, given the recent high variability observed in coregoninerecruitment, can help predict what the future of these species may look like under current climate trends to inform restoration efforts.

We experimentally measured how cisco embryos responded to different photoperiod intensities, as a proxy for different ice regimes. Our objective was to identify to what extent light influences cisco embryo survival, incubation duration, length and yolk-sac volume at hatching. We hypothesized that exposure to elevated light intensity (low ice cover) would accelerate embryogenesis, resulting in smaller yolk-sacs and lower embryo survival. We also hypothesized that populations adapted to lower light levels (high ice cover) are expected to experience more negative impacts from increasing light intensity.

# METHODS:

## Study Species and Locations

Cisco were collected from the Apostle Islands, Lake Superior (46.85, -90.55) and Chaumont Bay, Lake Ontario (44.05, -76.20) in December 2019. Lakes Superior and Ontario were chosen because the cisco populations sampled have different spawning habitats. Lake Superior cisco were aggregated and sampled at deeper depths, with little or no known expected preference in habitat (Dryer and Beil 1964, Paufve 2019). Lake Ontario cisco were aggregated in a shallow, protected bay and sampled on rocky shoal (Pritchard 1931, Paufve 2019). Ice conditions over the spawning locations sampled from each lake vary based on bathymetric depth, with shallower, more protected Lake Ontario having more consistent ice coverage than the deeper, open location in Lake Superior (Figure 1). However, light transmittance in deeper water is less than shallow water (Secchi 1864, Ramus et al. 1976, Preisendorfer 1986, Fleming-Lehtinen and Laamanen 2012). Consequently, the cisco populations we sampled from Lakes Superior and Ontario provide a contrast in ice cover and subsequent light exposure to coregonine embryos.

## Crossing Design and Fertilization

Gametes were stripped from 12 females and 16 males and artificially fertilized under a blocked, nested full-sib, half-sib fertilization design to create 48 families from each lake. The crossing design maximized the amount of genetic variation and minimized the potential loss of multiple families if a female or male produced poor quality gametes, compared to a full-factorial design. Adults used in the experiment were divided into four fertilization blocks. A single block consisted of four males each paired with three unrelated females (Stewart et al. 2021).

Approximately 500 eggs per female were fertilized with an equal amount of milt (5-15 μl) from each male in the block and water used to activate the germ cells. The embryos were rinsed with water until the water ran clear. Reconstructed fresh water was used during fertilizations (OECD ISO 6341:2012) to standardize the chemical properties of the water used between lakes. Embryos were transported in coolers by shipping overnight for Lake Superior samples and driven same-day for Lake Ontario samples. A temperature logger recorded air temperature inside the cooler during transport (Lake Superior: mean (SD) = 2.80°C (0.21); Lake Ontario: mean (SD) = 3.28°C (0.37)). Demographic data (e.g., total length, mass, and egg diameter) were collected on adults. Fertilization success was determined by haphazardly assessing 10 embryos under microscopy within 72-hours post-fertilization (Oberlercher and Wanzenböck 2016). If fertilization was low (<30%), the family was removed from the experiment (Stewart et al. 2021).

## Rearing Conditions

Embryos from successfully fertilized families were individually distributed into 24-well cell culture microplates and incubated in 2 ml of reconstructed fresh water (Stewart et al. 2021). A total of 36 embryos per family were used for each of Lake Ontario and Lake Superior cisco. Families were randomly distributed across three microplates (*i.e.,* 12 eggs per family per microplate and two families per 24-well microplate).

Microplates from each population were incubated under three experimental light treatments to represent the light intensity under 90-100, 40-60, and 0-10% ice cover (Table 1), and followed mean weekly photoperiods with gradual sunrise and sunset transitions. Light treatments were chosen to mimic *in situ* winter, lakebed light measurements recorded from Lake Superior at 10 m of water in 2016-17. Remote-sensing ice data (U.S. National Ice Center) was used to quantify the daily percentage of ice cover above the light sensor (Figure 2). Embryos were incubated at a constant target water temperature of 4.0°C in a climate-controlled chamber (Conviron® E8; Table 2). Forced airflow was used in the climate-controlled chamber to ensure equal air circulation around the microplates and opaque, plastic sheeting was used to separate light treatments.

All microplates were covered to minimize evaporation and rotated (*i.e.,* orientation and position) weekly. Water temperature and light intensity were recorded hourly with loggers (HOBO® Water Temperature Pro v2 and JFE Advantech Co., Ltd. DEFI2-L) and daily mean values calculated. Microplates were checked weekly for dead eggs and the eye-up stage. During the hatch period, microplates were checked on a three-day cycle for newly hatched embryos. All hatched embryos were photographed and immediately preserved in 95% ethanol.

## Life-History and Morphological Traits

Embryo survival was estimated as the percent of embryos surviving between the eye-up and post-hatch stages. Incubation period was assessed by two variables: the number of days from fertilization to hatching (days post-fertilization; DPF) and the sum of the degree-days (accumulated degree-days; ADD). Total length-at-hatch (LAH; mm) and yolk-sac volume (YSV; mm3) were measured from five individuals per family at, or as close as possible to, 50% hatching for each family. Yolk-sac volume was calculated assuming the shape of an ellipse (Blaxter 1963):

where a = length of the yolk sac (mm) and b = height of the yolk sac (mm).

## Statistical Analyses and Estimation of Variance Components

To characterize the life-history and morphological traits, embryo survival was analyzed as a binomial response variable, and incubation period, length-at-hatch, and yolk-sac volume at hatching as continuous response variables. Because embryos were raised independently, the replication unit in the statistical models is the individual embryo and the design was unbalanced from different levels of embryo mortality. Therefore, binary data (i.e., embryo survival) were analyzed with binomial generalized linear mixed-effects models (LMM) and normally distributed data (i.e., incubation period, length-at-hatch, and yolk-sac volume) were analyzed with restricted maximum likelihood LMMs with the lme4 package (Bates et al. 2015). Population and incubation light treatment were included as fixed effects and female, male, family (female and male combination), and fertilization block as random effects. All traits and possible interactions were examined with backward, stepwise effect-selection using the buildmer package (Voeten 2020). The maximal model for each trait was selected by comparing a model including or lacking the term of interest to the reference model based on changes in log-likelihood, Akaike information criterion, Bayesian information criterion, and change in explained deviance. The significance for population, species, incubation temperature, interaction effects, and any random-effects selected were determined using a likelihood ratio test between the maximal model and reduced models with the model effect of interest removed.

To allow for population comparisons, the response to temperature for each trait was standardized to what we assumed was the optimal light treatment - the low light treatment (Table 1). For each trait, the within-family mean was calculated for each light treatment and the percent change from the optimal light intensity estimated. Standard error was calculated as the among-family variation in percent change.

All analyses were performed in R version 4.0.3 (R Core Team 2020).

# RESULTS:

## Spawning Adults

Lake Superior spawning adults used for gamete collection were larger in total length and fresh mass than Lake Ontario adults. However, Lake Ontario females had larger egg diameters than Lake Superior females (Table 3).

## Life-History and Morphological Traits and Variance Components

All traits, except embryo survival and LAH, had significant interaction effects between population and light treatments (maximum *P* = 0.005; Table 4). The interaction effects precluded any interpretation of main effects, but did suggest contrasting norms of reaction between populations. Below we describe the interaction effects and the light pairwise comparisons for embryo survival. All random effects (*i.e.,* female, male, and family) were significant (maximum *P* = 0.009) except female for embryo survival, male for embryo survival and YSV, and family for embryo survival, LAH and YSV (Table 4). All statistical model results can be found in Table 4.

### *Embryo Survival*

Embryo survival was highest for both populations at the medium light treatment, but lowest at the low light treatment for Lake Ontario and at the high light treatment for Lake Superior (Figure 3). Light and population main effects were significant, and all pairwise light treatment comparisons were significant (maximum *P* < 0.005). Embryo survival was higher for Lake Ontario at the high (98.4%) and medium (99.6%) light treatments than Lake Superior (85.3 and 89.3%, respectively) but not different between populations (0.9%) at the low light treatment (Figure 3).

### *Incubation Period (days post-fertilization)*

The number of days post-fertilization to hatching was highest for Lake Ontario at the low light treatment (115.47 days) and for Lake Superior at the high light treatment (101.22 days; Figure 3). Incubation period (DPF) was higher for Lake Ontario than Lake Superior across all light treatments (mean (SD) = 13.9 (0.8) days). Lake Ontario cisco had a decrease in DPF from the low light to the high light treatments (-0.7%), while Lake Superior had an increase from the low light to the high light treatments (1.9%; Figure 3).

### *Incubation Period (accumulated degree-days)*

The effect of population depended on light because the difference in ADD between populations was less pronounced at the high light treatment (60.8 ADD), while ADD was higher for Lake Ontario (497.7 and 485.9 ADD) than Lake Superior (427.5 and 420.8 ADD) at the low and medium light treatments, respectively (Figure 3). Lake Ontario ADD had a negative response from the low to high light treatments (-2.5%), while ADD for Lake Superior did not change from the low to high light treatments (0.05%; Figure 3).

### *Length-at-Hatch*

Light was not a component returned in the stepwise-selected model, but the population main effect between Lake Ontario and Lake Superior was significant (*P* < 0.001; Table 4). Lake Ontario had a higher LAH than Lake Superior across all light treatments (Figure 4). Lake Superior and Lake Ontario responded to increasing light intensity with a 3.2 and 0.2% respective decrease in LAH from the low to high light treatments (Figure 4).

### *Yolk-sac Volume*

Yolk-sac volume had a different response to light intensity between populations (Figure 4). The effect of population depended on light because the difference in YSV between populations was less pronounced at the low light treatment (0.22 mm3), while YSV was lower for Lake Ontario (0.35 and 0.37 mm3) than Lake Superior (0.67 and 0.63 mm3) at the high and medium light treatments, respectively (Figure 4). Lake Superior YSV had a positive response from the low to high light treatments (15.3%), while YSV for Lake Ontario had a negative response from the low to high light treatments (-5.5%; Figure 4).

# DISCUSSION:

Our incubation experiments demonstrated both similar and contrasting reaction norms to light intensity for life-history and morphological traits between cisco populations. First, we found contrasting responses to light intensity in embryo survival between populations. Second, increasing light intensity had minimal impact on incubation periods (both DPF and ADD) from both populations. Lastly, both populations had similar negative responses to light for LAH but contrasting responses in YSV. These results show that cisco from Lakes Superior and Ontario have differential responses to ice cover and subsequent light conditions.

Our prediction that both populations would have the highest survival at the low light treatment was not supported. Embryo survival had opposing responses to increasing light intensity because Lake Ontario cisco had a sharp decrease in survival at the low light treatment. This was surprising because ice conditions over the Lake Ontario spawning location are high, with assumed low light conditions, and this is the environment we expect cisco to be locally-adapted to. However, the Lake Ontario cisco spawning location is shallow (< 5 m) and would have low light attenuation when ice is not present. The high winter illuminance may allow the population of Lake Ontario cisco sampled to have higher resilience to light than deeper spawning cisco sampled from Lake Superior. Both populations had the highest embryo survival at the medium light levels suggesting that populations may be adapted to withstand some light exposure from high inter-annual variability in ice cover.

Despite finding an impact of light on embryo survival, different light intensities did not change, within the magnitude of biological significance, the length of incubation for either population. ﻿Light energy is known to have a similar effect as temperature on embryonic development of European whitefish; a negative correlation between the abiotic factor and development (Chernyaev 2007). This led us to expect cisco would respond similarly to European whitefish, but our results did not support our hypothesis that elevated levels of light intensity would accelerate embryogenesis. ﻿The greatest difference in incubation periods was between populations and likely caused by differences in embryo size, with larger embryos (*i.e.,* Lake Ontario cisco) requiring more time to develop (Hodson and Blunt 1986, Kamler 2008).

Even more striking, although no difference in incubation period was found across light treatments, a response to light in LAH and YSV was found. Lake Ontario cisco had a minimal change in LAH as light increased, but YSV responded negatively, suggesting that light intensified the metabolic demand of embryos and diverted energy away from somatic growth. However, Lake Superior cisco showed a strong trade-off between LAH and YSV and had a positive YSV response to increasing light. The negative relationship between LAH and YSV is a common response among temperature incubation studies (Blaxter 1991, Karjalainen et al. 2015, Stewart et al. 2021), but a change in incubation period is typically also found and explains the mechanistic basis behind morphological changes from temperature. In our experiment, light did not influence incubation period and therefore the length of development and metabolic demand over the length of the incubation cannot be the cause of this trade-off between LAH and YSV. Actual reasons remain unknown, however, the contrasting responses in YSV between populations suggests that each population has different levels of plasticity to light during embryogenesis.

﻿Environmental conditions experienced during embryo development can greatly influence life-history trajectories, performances, and reproductive success (Colby and Brooke 1970, Luczynski 1991, Karjalainen et al. 2015, Karjalainen et al. 2016). Our experiment did not quantify developmental stages, except eye pigmentation, so specific life-stage developmental rates are unknown. Organogenesis and ﻿having specialized organs of photoreception is known to be a critical developmental stage in relation to light (Chernyaev 2007) so the impact of light intensity could be further intensified during late-embryonic stages. Instead of consistent maximum light intensities for treatments, further studies examining the impact of changing light intensities throughout incubations (*e.g.,* decreased light during winter from ice cover and increased light during spring ice-out) will help determine the fine-scale impact light may have on specific development stages (*i.e.,* hatching) and organ, tissue, and skeletal formation.

﻿A certain contribution to light attenuation in water is made by turbidity, and should be considered along with the light intensity. Spring ice-out and river discharge can drastically increase the presence of suspended particulates and increase light absorption (REFS). The proximity of spawning grounds to shoreline and river outlets would likely impact the light exposure to embryos and the impact light may have on hatching and larval feeding. In this context, our study only examined one spawning location within each lake, however, various spawning locations and habitats do exist for both lakes (REFS). To further understand any adaption to local light conditions, expanding experimental studies to within-lake populations from various spawning locations, depths, and substrates would add to our understanding of the effect of light during embryogenesis. Additionally, comparing populations from higher latitude lakes which experience decreased winter sunlight would provide an additional contrast for local adaption and plasticity across populations.

﻿This study brings a new finding on the influence light intensity has on cisco embryo development and the impact changing ice regimes may have on cisco survival and recruitment.

We were unable to distinguish ﻿cisco populations with only a negative or only a positive reaction to light, and ﻿light is likely to have a differential effect on a number of physiological and biochemical processes. Optimal light preferences are adaptations of cisco to their specific ecological niche and spawning habitat, which we found to be different between the populations examined. Our results provide a significant step towards understanding the recent high variability observed in coregonine recruitment and help predict what the future of these species may look like under current climate trends to inform restoration efforts.

# ACKNOWLEDGMENTS:

We thank the staff at the Wisconsin Department of Natural Resources Bayfield Fisheries Field Station, United States Geological Survey (USGS) Tunison Laboratory of Aquatic Science, and New York State Department of Environmental Conservation Cape Vincent Fisheries Station for conducting field collections of spawning adults. We also thank Rachel Taylor, Dan Yule, and Caroline Rosinski for help with fertilizations and experiment maintenance. XXXX provided the USGS solicited review that strengthened the manuscript, as did anonymous peer reviewers. This work was funded by the USGS grant number XXXX. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

# LITERATURE CITED:

Austin, J. A., and S. M. Colman. 2007. Lake Superior summer water temperatures are increasing more rapidly than regional temperatures: A positive ice-albedo feedback. Geophysical Research Letters 34:1–5.

Bates, D., M. Mächler, B. Bolker, and S. Walker. 2015. Fitting Linear Mixed-Effects Models Using lme4. Journal of Statistical Software; Vol 1, Issue 1 (2015).

Blaxter, J. H. S. 1963. The influence of egg size on herring larvae (Clupea harengus L). J. Cons. Int. Explor. Mer 28:211–240.

Bolsenga, S. J., and H. A. Vanderploeg. 1992. Estimating photosynthetically available radiation into open and ice-covered freshwater lakes from surface characteristics; a high transmittance case study. Hydrobiologia 243–244:95–104.

Bronte, C. R., D. B. Bunnell, S. R. David, R. Gordon, D. Gorsky, M. J. Millard, J. Read, R. A. Stein, and L. Vaccaro. 2017. Report from the workshop on coregonine restoration science. US Geological Survey.

Chernyaev, Z. A. 2007. Factors and possible mechanisms causing changes in the rate of embryonic development of bony fish (with reference to Coregonidae). Journal of Ichthyology 47:494–503.

Cushing, D. H. 1990. Plankton production and year-class strength in fish populations: An update of the match/mismatch hypothesis. Advances in Marine Biology 26:249–293.

Dryer, W. R., and J. Beil. 1964. Life history of lake herring in Lake Superior. Fish. Bull 63:493–530.

Ebener, M. P., R. E. Kinnunen, P. J. Schneeberger, L. C. Mohr, J. A. Hoyle, and P. Peeters. 2008a. Management of commercial fisheries for lake whitefish in the Laurentian Great Lakes of North America. International governance of fisheries ecosystems: learning from the past, finding solutions for the future. American Fisheries Society, Bethesda, Maryland:99–143.

Ebener, M. P., J. D. Stockwell, D. L. Yule, O. T. Gorman, T. R. Hrabik, R. E. Kinnunen, W. P. Mattes, J. K. Oyadomari, D. R. Schreiner, S. Geving, K. Scribner, S. T. Schram, M. J. Seider, and S. P. Sitar. 2008b. Status of cisco (Coregonus artedi) in Lake Superior during 1970-2006 and management and research considerations.

Eisler, R. 1958. Some effects of artificial light on salmon eggs and larvae. Transactions of the American Fisheries Society 87:151–162.

Eisler, R. 1961. Effects of visible radiation on salmonoid embryos and larvae. Growth 25:281–346.

Favé, M.-J., and J. Turgeon. 2008. Patterns of genetic diversity in Great Lakes bloaters (Coregonus hoyi) with a view to future reintroduction in Lake Ontario. Conservation Genetics 9:281–293.

Fleming-Lehtinen, V., and M. Laamanen. 2012. Long-term changes in Secchi depth and the role of phytoplankton in explaining light attenuation in the Baltic Sea. Estuarine, Coastal and Shelf Science 102:1–10.

Gaston, K. J., J. Bennie, T. W. Davies, and J. Hopkins. 2013. The ecological impacts of nighttime light pollution: a mechanistic appraisal. Biological reviews 88:912–927.

Hampton, S. E., M. V Moore, T. Ozersky, E. H. Stanley, C. M. Polashenski, and A. W. E. Galloway. 2015. Heating up a cold subject: prospects for under-ice plankton research in lakes. Journal of plankton research 37:277–284.

Hjort, J. 1914. Fluctuations in the great fisheries of Norther Europe. Pages 1–228 Rapports et Procés-Verbaux. ICES.

Iglesias, J., G. Rodríguez-Ojea, and J. B. Peleteiro. 1995. Effect of light and temperature on the development of turbot eggs (Scophthalmus maximus L.). Pages 40–44 ICES Marine Science Symposia. Copenhagen, Denmark: International Council for the Exploration of the Sea, 1991-.

Karjalainen, J., H. Auvinen, H. Helminen, T. J. Marjomäki, T. Niva, J. Sarvala, and M. Viljanen. 2000. Unpredictability of ﬁsh recruitment - interannual variation in YOY abundance.

Karjalainen, J., T. Keskinen, M. Pulkkanen, and T. J. Marjomäki. 2015. Climate change alters the egg development dynamics in cold-water adapted coregonids. Environmental Biology of Fishes 98:979–991.

Kwain, W.-H. 1975. Embryonic development, early growth and meristic variation in rainbow trout (Salmo gairdneri) exposed to combinations of light intensity and temperature. Journal of the Fisheries Research Board of Canada 32:397–402.

Lucke, V. S., T. R. Stewart, M. R. Vinson, J. D. Glase, and J. D. Stockwell. 2020. Larval Coregonus spp. diets and zooplankton community patterns in the Apostle Islands, Lake Superior. Journal of Great Lakes Research.

Lynch, A. J., S. J. Cooke, A. M. Deines, S. D. Bower, D. B. Bunnell, I. G. Cowx, V. M. Nguyen, J. Nohner, K. Phouthavong, B. Riley, M. W. Rogers, W. W. Taylor, W. Woelmer, S.-J. Youn, and T. D. Beard. 2016. The social, economic, and environmental importance of inland fish and fisheries. Environmental Reviews 24:115–121.

Lynch, A. J., W. W. Taylor, T. D. Beard, and B. M. Lofgren. 2015. Climate change projections for lake whitefish (Coregonus clupeaformis) recruitment in the 1836 Treaty Waters of the Upper Great Lakes. Journal of Great Lakes Research 41:415–422.

Lyutikov, A. A. 2012. Influence of illumination on the survival and development of larvae of inconnu Stenodus leucichthys nelma (Salmoniformes: Coregonidae). Journal of Ichthyology 52:575–578.

MacCrimmon, H. R., and W.-H. Kwain. 1969. Influence of light on early development and meristic characters in the rainbow trout, Salmo gairdneri Richardson. Canadian Journal of Zoology 47:631–637.

Magnuson, J. J., K. E. Webster, R. A. Assel, C. J. Bowser, P. J. Dillon, J. G. Eaton, H. E. Evans, E. J. Fee, R. I. Hall, and L. R. Mortsch. 1997. Potential effects of climate changes on aquatic systems: Laurentian Great Lakes and Precambrian Shield Region. Hydrological processes 11:825–871.

Mangor‐Jensen, A., and K. G. Waiwood. 1995. The effect of light exposure on buoyancy of halibut eggs. Journal of Fish Biology 47:18–25.

Marchesan, M., M. Spoto, L. Verginella, and E. A. Ferrero. 2005. Behavioural effects of artificial light on fish species of commercial interest. Fisheries research 73:171–185.

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

Nguyen, T. D., N. Hawley, and M. S. Phanikumar. 2017. Ice cover, winter circulation, and exchange in Saginaw Bay and Lake Huron. Limnology and Oceanography 62:376–393.

Nyberg, P., E. Bergstrand, E. Degerman, and O. Enderlein. 2001. Recruitment of pelagic fish in an unstable climate: studies in Sweden’s four largest lakes. Ambio 30:559–564.

O’Reilly, C. M., R. J. Rowley, P. Schneider, J. D. Lenters, P. B. Mcintyre, and B. M. Kraemer. 2015. Rapid and highly variable warming of lake surface waters around the globe. Geophysical Research Letters 42:1–9.

Oberlercher, T. M., and J. Wanzenböck. 2016. Impact of electric fishing on egg survival of whitefish, Coregonus lavaretus. Fisheries Management and Ecology 23:540–547.

Paufve, M. 2019. Diversity in spawning habitat across Great Lakes Cisco populations.

Pepin, P. 1991. Effect of temperature and size on development, mortality, and survival rates of the pelagic early life history stages of marine fish. Canadian Journal of Fisheries and Aquatic Sciences 48:503–518.

Preisendorfer, R. W. 1986. Secchi disk science: Visual optics of natural waters 1. Limnology and oceanography 31:909–926.

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

R Core Team. 2020. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Ramus, J., S. I. Beale, D. Mauzerall, and K. L. Howard. 1976. Changes in photosynthetic pigment concentration in seaweeds as a function of water depth. Marine Biology 37:223–229.

Rosinski, C. L., M. R. Vinson, and D. L. Yule. 2020. Niche Partitioning among Native Ciscoes and Nonnative Rainbow Smelt in Lake Superior. Transactions of the American Fisheries Society 149:184–203.

Ruchin, A. B. 2007. Effect of photoperiod on growth, physiologica and hematological indices of juvenile Siberian sturgeon Acipenser baerii. Biology Bulletin 34:583–589.

Ruchin, A. B. 2020. Effect of illumination on fish and amphibian: development, growth, physiological and biochemical processes. Reviews in Aquaculture.

Secchi, P. A. 1864. Relazione delle esperienze fatte a bordo della pontificia pirocorvetta Imacolata Concezione per determinare la trasparenza del mare. Memoria del PA Secchi. Il Nuovo Cimento Giornale de Fisica, Chimica e Storia Naturale, Ottobre 1864, Published 1865 20:205–237.

Seth, S. N. M., H. T. Nai, M. K. Rosli, S. Saad, N. M. Noor, and M. Yukinori. 2014. Egg hatching rates of brown-marbled grouper, Epinephelus fuscoguttatus under different light wavelengths and intensities. MJS 33:150–154.

Sharma, S., K. Blagrave, J. J. Magnuson, C. M. O’Reilly, S. Oliver, R. D. Batt, M. R. Magee, D. Straile, G. A. Weyhenmeyer, and L. A. Winslow. 2019. Widespread loss of lake ice around the Northern Hemisphere in a warming world. Nature Climate Change 9:227.

Sharma, S., D. A. Jackson, C. K. Minns, and B. J. Shuter. 2007. Will northern fish populations be in hot water because of climate change? Global Change Biology 13:2052–2064.

Sharma, S., M. F. Meyer, J. Culpepper, X. Yang, S. E. Hampton, S. A. Berger, M. R. Brousil, S. C. Fradkin, S. N. Higgins, and K. J. Jankowski. 2020. Integrating perspectives to understand lake ice dynamics in a changing world. Journal of Geophysical Research: Biogeosciences 125:e2020JG005799.

Stockwell, J. D., M. P. Ebener, J. A. Black, O. T. Gorman, T. R. Hrabik, R. E. Kinnunen, W. P. Mattes, J. K. Oyadomari, S. T. Schram, D. R. Schreiner, M. J. Seider, S. P. Sitar, and D. L. Yule. 2009. A Synthesis of Cisco Recovery in Lake Superior: Implications for Native Fish Rehabilitation in the Laurentian Great Lakes. North American Journal of Fisheries Management 29:626–652.

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

Villamizar, N., B. Blanco-Vives, H. Migaud, A. Davie, S. Carboni, F. J. Sanchez-Vazquez, and F. J. Sánchez-Vázquez. 2011. Effects of light during early larval development of some aquacultured teleosts: a review. Aquaculture 315:86–94.

Voeten, C. C. 2020. buildmer: Stepwise Elimination and Term Reordering for Mixed-Effects Regression.

Vonlanthen, P., D. Bittner, A. G. Hudson, K. A. Young, R. Müller, B. Lundsgaard-Hansen, D. Roy, S. Di Piazza, C. R. Largiader, O. Seehausen, C. R. Largiadèr, and O. Seehausen. 2012. Eutrophication causes speciation reversal in whitefish adaptive radiations. Nature 482:357–362.

Vonlanthen, P., D. Roy, A. G. Hudson, C. R. Largiadèr, D. Bittner, and O. Seehausen. 2009. Divergence along a steep ecological gradient in lake whitefish (Coregonus sp.). Journal of Evolutionary Biology 22:498–514.

Walter, B., D. J. Cavalieri, K. L. Thornhill, and A. J. Gasiewski. 2006. Aircraft measurements of heat fluxes over wind-driven coastal polynyas in the Bering Sea. IEEE transactions on geoscience and remote sensing 44:3118–3134.

Wang, J., H. Hu, D. Schwab, G. Leshkevich, D. Beletsky, N. Hawley, and A. Clites. 2010. Development of the Great Lakes ice-circulation model (GLIM): application to Lake Erie in 2003–2004. Journal of Great Lakes Research 36:425–436.

Winslow, L. A., J. S. Read, G. J. A. Hansen, K. C. Rose, and D. M. Robertson. 2017. Seasonality of change: Summer warming rates do not fully represent effects of climate change on lake temperatures. Limnology and Oceanography 62:2168–2178.

Woolway, R. I., B. M. Kraemer, J. D. Lenters, C. J. Merchant, C. M. O’Reilly, and S. Sharma. 2020. Global lake responses to climate change. Nature Reviews Earth & Environment:1–16.

Zimmerman, M. S., and C. C. Krueger. 2009. An Ecosystem Perspective on Re-establishing Native Deepwater Fishes in the Laurentian Great Lakes. North American Journal of Fisheries Management 29:1352–1371.

# TABLES:

Table 1. Mean ± SD photon flux (μmol m-2 s-1) for three ice regimes from Lake Superior and corresponding laboratory experimental light conditions.

|  |  |  |  |
| --- | --- | --- | --- |
|  | Ice Cover (Light Treatment) | | |
| Location | > 90% (Low) | 40-60% (Medium) | < 10% (High) |
| Lake Superior | 1.96 ± 1.07 | 3.35 ± 2.54 | 5.45 ± 5.88 |
| Laboratory | 0.62 ± 0.06 | 3.85 ± 1.88 | 6.15 ± 0.99 |

Table 2. Mean ± SD water temperatures (°C) during embryo incubations from each light treatment for Lakes Superior and Ontario.

|  |  |  |  |
| --- | --- | --- | --- |
|  | Light Treatment | | |
| Lake | High | Medium | Low |
| Superior | 4.25 ± 0.24 | 4.28 ± 0.28 | 4.34 ± 0.34 |
| Ontario | 4.24 ± 0.25 | 4.28 ± 0.28 | 4.36 ± 0.36 |

Table 3. Mean ± SD total length (TL) and fresh mass (FM) of the female and males and egg diameters (ED) of the females from Lakes Superior and Ontario cisco (*Coregonus artedi*) used in the experiment.

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
|  | Lake Superior | | |  | Lake Ontario | | |
| Sex | TL (mm) | FM (g) | ED (mm) |  | TL (mm) | FM (g) | ED (mm) |
| Female | 428.92  ± 44.40 | 676.02  ± 181.51 | 2.14  ± 0.12 |  | 380.33  ± 24.18 | 567.59  ± 122.89 | 2.30  ± 0.08 |
| Male | 400.25  ± 34.35 | 523.82  ± 134.65 | -- |  | 366.56  ± 25.30 | 443.29  ± 103.16 | -- |

Table 4. Likelihood ratio test output for each model selected for embryo survival (%), incubation period (number of days post-fertilization; DPF), incubation period (accumulated degree-days; ADD), length-at-hatch (mm), and yolk-sac volume (mm3) from Lakes Superior and Ontario cisco (*Coregonus artedi*). pop indicates population. The full model that was selected is bolded for each trait.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| Trait | Model | Effect Tested | df | χ2 | p-value |
| Embryo Survival | **light + pop** |  |  |  |  |
| pop | light | 2 | 181.92 | < 0.001 |
|  | light | pop | 1 | 95.00 | < 0.001 |
| Incubation Period (DPF) | **light + pop + light:pop + female:male + female + male** |  |  |  |  |
| pop + female:male + female + male | light | 2 | 11.12 | 0.004 |
| light + female:male + female + male | pop | 1 | 2974.54 | < 0.001 |
|  | light + pop + female:male + female + male | light:pop | 2 | 10.75 | 0.005 |
|  | light + pop + light:pop + female + male | female:male | 1 | 84.36 | < 0.001 |
|  | light + pop + light:pop + female:male + male | female | 1 | 25.07 | < 0.001 |
|  | light + pop + light:pop + female:male + female | male | 1 | 10.78 | 0.001 |
| Incubation Period (ADD) | **light + pop + light:pop + female:male + female + male** |  |  |  |  |
| pop + female:male + female + male | light | 2 | 56.01 | < 0.001 |
| light + female:male + female + male | pop | 1 | 3,041.75 | < 0.001 |
|  | light + pop + female:male + female + male | light:pop | 2 | 17.39 | < 0.001 |
|  | light + pop + light:pop + female + male | female:male | 1 | 84.44 | < 0.001 |
|  | light + pop + light:pop + female:male + male | female | 1 | 10.76 | 0.001 |
|  | light + pop + light:pop + female:male + female | male | 1 | 25.03 | < 0.001 |
| Length-at-Hatch | **pop + female + male** |  |  |  |  |
| female + male | pop | 1 | 334.33 | < 0.001 |
| pop + male | female | 1 | 74.32 | < 0.001 |
|  | pop + female | male | 1 | 6.80 | 0.009 |
| Yolk-sac Volume | **light + pop + light:pop + female + male** |  |  |  |  |
| pop + female + male | light | 2 | 7.18 | 0.028 |
| light + female + male | pop | 1 | 712.29 | < 0.001 |
| light + pop + female + male | light:pop | 2 | 26.84 | < 0.001 |
|  | light + pop + light:pop + male | female | 1 | 130.50 | < 0.001 |
|  | light + pop + light:pop + female | male | 1 | 2.87 | 0.090 |

# FIGURES:

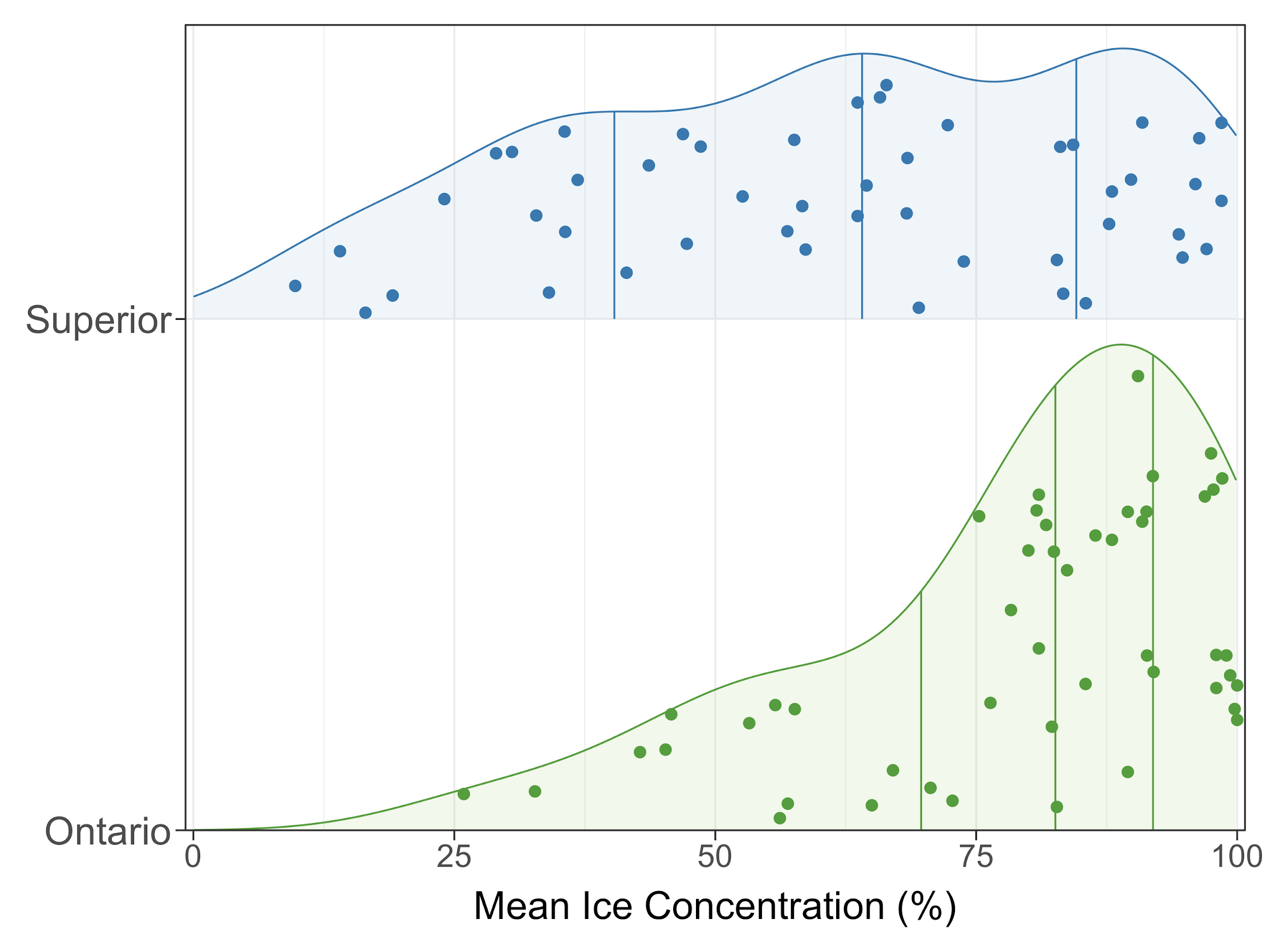
****

Figure 1. Kernel density estimates of annual mean ice concentration between 1-Jan and 15-Mar from 1973-2020 for each sampling location in Lake Superior (top; blue) and Lake Ontario (bottom; green). The height of the density curve is proportional between lakes and the vertical lines represent quartiles. Points represent each year (n = 48) and were jittered vertically to show distributions. Ice coverage data was collected from the U.S. National Ice Center.

Chart, histogram

Description automatically generated

Figure 2. Daily ice coverage (%; blue line) and light intensity (μmol m-2 s-1; gray line) relationship based on light sensors set at 10 m depth off Sand Island, Lake Superior. Ice coverage data above the sensor was collected from the U.S. National Ice Center.

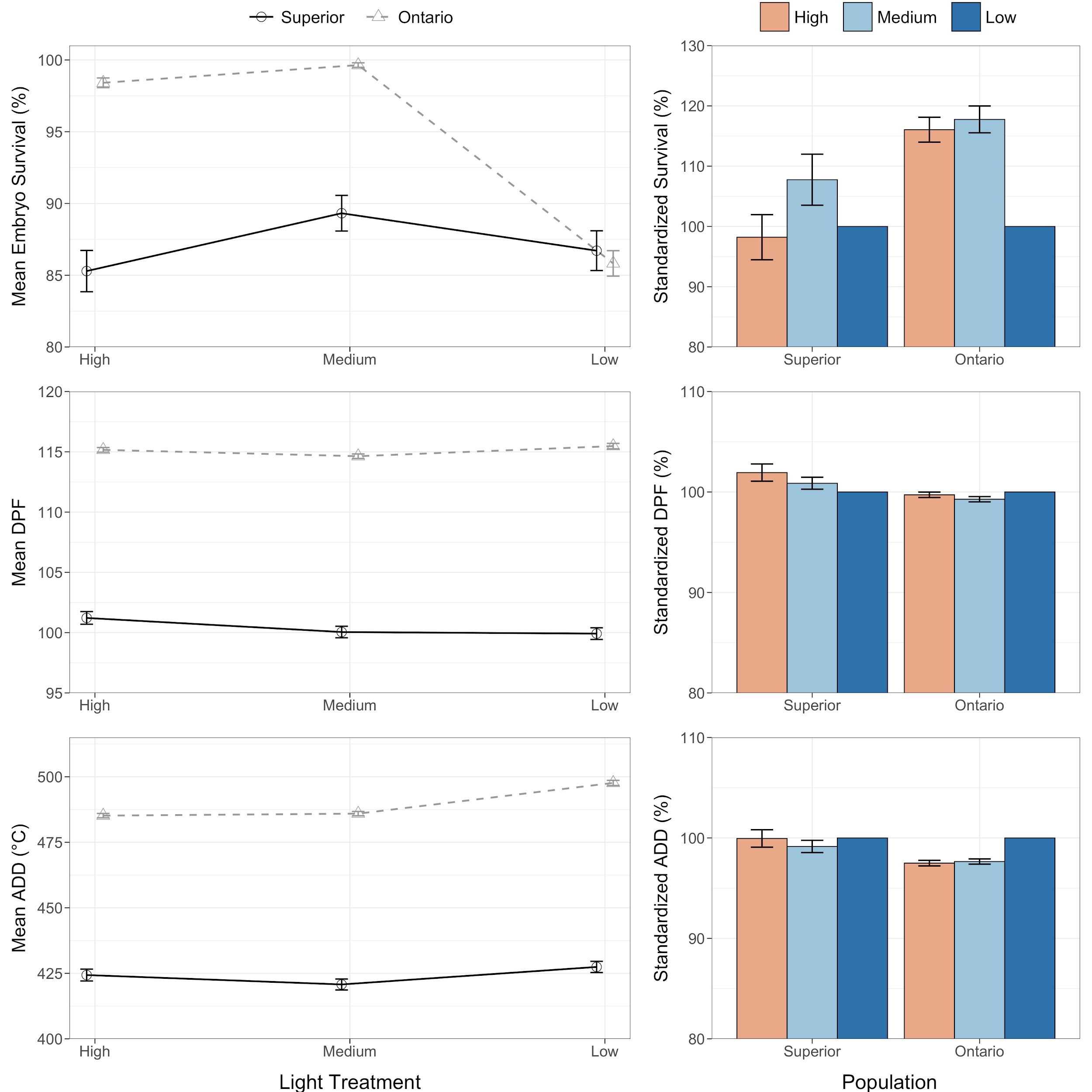
****

Figure 3. Mean embryo survival (%), incubation period (number of days post-fertilization; DPF), and incubation period (accumulated degree days (°C); ADD) at each incubation light treatment (left) and standardized responses to light within each population (right) from Lake Superior and Lake Ontario cisco (*Coregonus artedi*). Error bars indicate standard error.

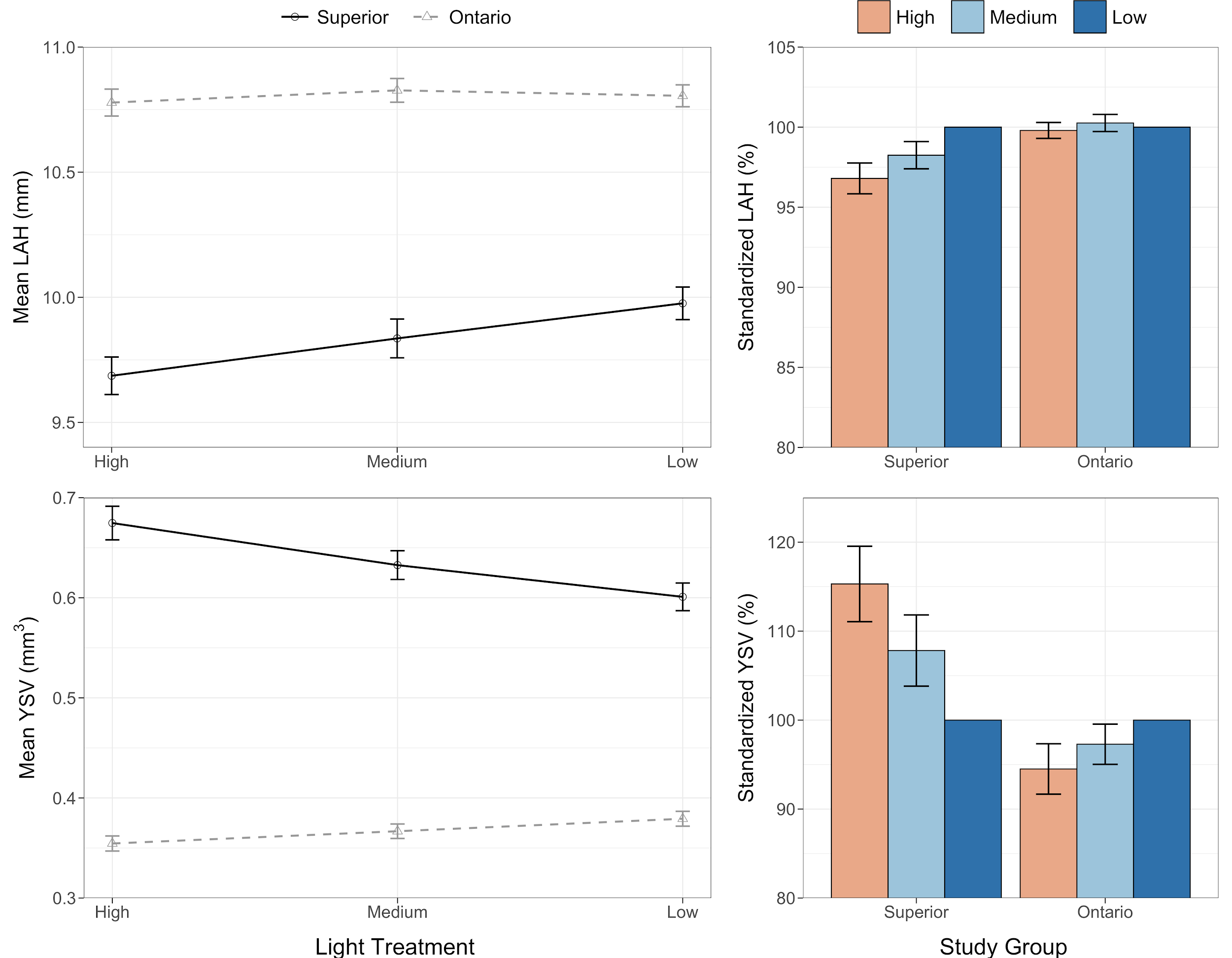
****

Figure 4. Mean length-at-hatch (mm; LAH) and yolk-sac volume (mm3; YSV) at each incubation light treatment (left) and standardized responses to light within each population (right) from Lake Superior and Lake Ontario cisco (*Coregonus artedi*). Error bars indicate standard error.