Journal of Great Lakes Research

Shining a light on Laurentian Great Lakes cisco (Coregonus artedi): how ice coverage may impact embryonic development
--Manuscript Draft--

Abstract:	Changes in winter conditions, such as decreased ice coverage and duration, have been observed in the Laurentian Great Lakes over the past 20+ years and hypothetically linked to low Coregonus spp. survival to age-1. Most cisco (Coregonus artedi) populations are autumn spawners whose embryos incubate under ice throughout the winter. The quantity and quality of light during winter is regulated by ice and snow coverage, and light has been shown to affect embryo survival and development in some teleosts. We experimentally evaluated how cisco embryos from lakes Superior and Ontario responded to three light treatments that represented day-light intensity under 0-10, 40-60, and 90-100% ice coverage. Embryonic response measures included two developmental factors (embryo survival and incubation period) and two morphological traits (length-at-hatch and yolk-sac volume). Embryo survival was highest at the medium light treatment and decreased at high and low treatments for both populations suggesting cisco may be adapted to withstand some light exposure from inter-annual variability in ice coverage. Light intensity had no overall effect on length of incubation. Length-at-hatch decreased with increasing light in Lake Superior, but had no effect in Lake Ontario. Yolk-sac volume was positively correlated with increasing light in Lake Superior and negatively correlated in Lake Ontario. Contrasting responses in embryo development between lakes suggests differences in populations' flexibility to light. These results provide a step towards better understanding the recent high variability observed in coregonine recruitment and may help predict what the future of this species may look like under current climate trends.

1   Shining a light on Laurentian Great Lakes cisco (*Coregonus artedi*): how ice coverage may

2   impact embryonic development

3

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17

18   **Abstract:**

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20   in the Laurentian Great Lakes over the past 20+ years and hypothetically linked to low

21   *Coregonus* spp. survival to age-1. Most cisco (*Coregonus artedi*) populations are autumn

22   spawners whose embryos incubate under ice throughout the winter. The quantity and quality of

23   light during winter is regulated by ice and snow coverage, and light has been shown to affect

24   embryo survival and development in some teleosts. We experimentally evaluated how cisco

25   embryos from lakes Superior and Ontario responded to three light treatments that represented

26   day-light intensity under 0-10, 40-60, and 90-100% ice coverage. Embryonic response measures

27   included two developmental factors (embryo survival and incubation period) and two

28   morphological traits (length-at-hatch and yolk-sac volume). Embryo survival was highest at the

29   medium light treatment and decreased at high and low treatments for both populations

30   suggesting cisco may be adapted to withstand some light exposure from inter-annual variability

31   in ice coverage. Light intensity had no overall effect on length of incubation. Length-at-hatch

32   decreased with increasing light in Lake Superior, but had no effect in Lake Ontario. Yolk-sac

33   volume was positively correlated with increasing light in Lake Superior and negatively

34   correlated in Lake Ontario. Contrasting responses in embryo development between lakes

35   suggests differences in populations' flexibility to light. These results provide a step towards

36   better understanding the recent high variability observed in coregonine recruitment and may help

37   predict what the future of this species may look like under current climate trends.

38

39   **Keywords**: Coregonus; cisco; climate change; embryo incubation; ice coverage; light intensity

40

Introduction:

Freshwater whitefishes, Salmonidae Coregoninae (hereafter coregonines) play important economic (Ebener et al., 2008) and ecological (Lynch et al., 2010; Nyberg et al., 2001; Stockwell et al., 2014) roles throughout the northern hemisphere, but populations have declined over the past century (Eshenroder et al., 2016). Historical coregonine declines were attributed to overfishing, invasive species, habitat alterations, and competition (Anneville et al., 2009; Rosinski et al., 2020; Stockwell et al., 2009). More recently, coregonine populations worldwide have experienced declines due to highly variable and low survival to age-1 (Lepak et al., 2017; Nyberg et al., 2001; Parks and Rypel, 2018) which have been associated with climate-induced changes in early-life stage environments (Nyberg et al., 2001). However, an underlying mechanism between changing lake environments and coregonine year-class strength has yet to be established.

Year-class strength in most fish species, including coregonines, is thought to be established prior to the end of the first season of growth (Cushing, 1990; Hjort, 1914; Karjalainen et al., 2015). Most coregonines are autumn spawners whose embryos incubate under ice throughout the winter (Karjalainen et al., 2000; Stockwell et al., 2009). Embryos are static, which leaves them vulnerable to predation (Stockwell et al., 2014) and unable to evade detrimental changes in winter environmental conditions (Pepin, 1991). Changes in winter conditions, such as decreased ice coverage and duration, that have been observed over the past 20+ years (Austin and Colman, 2007; O'Reilly et al., 2015; Sharma et al., 2019), could alter developmental rates, embryo survival, and time of hatching (Karjalainen et al., 2015). Potential mechanisms by which ice coverage influences coregonine embryonic development include reduction of physical wave action (Austin and Colman, 2007; Nguyen et al., 2017; Walter et al., 2006; Wang et al., 2010), more stable winter and spring water temperatures (Magnuson et al., 1997; Winslow et al., 2017), and the amount of sunlight reaching the lake bottom (Bolsenga and Vanderploeg, 1992; Hampton et al., 2015).

Sunlight (i.e., photoperiod) is the most consistent abiotic factor in nature (Ruchin, 2020) and can regulate fish development phenology, behavior, and physiology (Ruchin, 2007; Villamizar et al., 2011). The length of photoperiods characterize circadian rhythms and ensure that biological

3

72 processes are synchronized with the environment (Gaston et al., 2013; Marchesan et al., 2005;

73 Ruchin, 2020). In seasonally ice-covered lakes, winter lake light levels are regulated by ice

74 coverage and snow depth (Bolsenga and Vanderploeg, 1992; Hampton et al., 2015). Ice can

75 reduce light transmittance to 62% under clear ice, and to $\leq 10\%$ under snow covered ice

76 (Bolsenga and Vanderploeg, 1992).

77

78 Salmonid embryos incubated under elevated light levels had higher mortality and deformity

79 rates, slower formation of cartilaginous skeletal elements, decreased time to hatching, and

80 smaller size-at-age; with accelerated development after organogenesis (Chernyaev, 2007; Eisler,

81 1961, 1958; Kwain, 1975; MacCrimmon and Kwain, 1969). However, other teleosts (e.g., turbot

82 *Scophthalmus maximus*, Atlantic halibut *Hippoglossus hippoglossus*, brown-marbled grouper

83 *Epinephelus fuscoguttatus*) exhibit opposite responses, or no response, to light illumination

84 (Iglesias et al., 1995; Mangor- Jensen and Waiwood, 1995; Ruchin, 2020; Seth et al., 2014). To

85 our knowledge, no previous work has examined the effects of light on coregonine embryos from

86 North America.

87

88 We experimentally evaluated how cisco (*Coregonus artedi*) embryos responded to different

89 photoperiod intensities, as a proxy for different ice coverages. We hypothesized that exposure to

90 elevated light intensity (a proxy for low ice coverage) decreases embryo survival and accelerates

91 embryogenesis, resulting in earlier hatching, larger yolk-sacs, and shorter lengths-at-hatch. Our

92 objective was to identify the extent to which light influences cisco embryo survival, incubation

93 duration, and length and yolk-sac volume at hatching. If our hypothesis is supported, we would

94 expect populations adapted to lower light levels (high ice coverage) to experience a greater

95 magnitude of change as light intensity increases.

96

97 **Methods:**

98 *Ethics*

99 All work described here was approved for ethical animal care under University of Vermont's

100 Institutional Animal Care and Use Committee (Protocol # PROTO202000021).

101

102   *Study Species and Locations*

103   Mature cisco were collected from the Apostle Islands, Lake Superior (46.85°, -90.55°) and

104   Chaumont Bay, Lake Ontario (44.05°, -76.20°) in December 2019. Lake Superior cisco were

105   collected at an open lake location at depths between 15 and 50 m. Lake Ontario cisco were

106   collected in a shallow, protected bay on rocky shoals at depths between 2 to 5 m. Historical

107   (1973-2020) ice conditions over the sampled spawning locations varied between lakes with the

108   shallower, more protected Lake Ontario spawning site having more consistent ice coverage

109   between January and March than the deeper, open location in Lake Superior (Figure 1). The

110   different spawning habitats provide a contrast in light levels that coregonine embryos from each

111   population would naturally experience because maximum light availability decreases with depth

112   (Fleming-Lehtinen and Laamanen, 2012; Preisendorfer, 1986; Ramus et al., 1976; Secchi, 1864)

113   and winter light availability is further restricted by ice and snow conditions.

114

115   *Crossing Design and Fertilization*

116   The design is fully described in Stewart et al., (2021). Briefly, gametes were stripped from 12

117   females and 16 males from each lake and artificially fertilized to create 48 families from each

118   lake. Reconstructed fresh water was used during fertilizations and rearing (OECD ISO

119   6341:2012) to standardize the chemical properties of the water used between lakes. Embryos

120   were transported to the University of Vermont in coolers by shipping overnight for Lake

121   Superior samples and driven the same-day for Lake Ontario samples. A temperature logger

122   recorded air temperature inside the cooler during transport (Lake Superior: mean (SD) = 2.80°C

123   (0.21); Lake Ontario: mean (SD) = 3.28°C (0.37)). Total length, mass, and egg diameter were

124   collected from the spawned adults. Fertilization success was determined by assessing 10

125   haphazardly selected embryos under microscopy (Oberlercher and Wanzenböck, 2016). If

126   fertilization was low (<30%), the family was removed from the experiment.

127

128   *Rearing Conditions*

129   Embryos were individually distributed into 24-well cell culture microplates and incubated in 2

130   ml of reconstructed fresh water (Stewart et al., 2021). A total of 36 embryos were used for each

131   Lake Ontario and Lake Superior cisco family. Families were randomly distributed across three

132   microplates (i.e., 12 eggs per family per microplate resulting in two families per 24-well

133   microplate).

134

135   Microplates from each population were incubated under three light treatments (0.6-6.2 μmol m^{-2}

136   s^{-1}) that represented day-light intensity under 0-10 (low), 40-60 (medium), and 90-100 % (high)

137   ice coverage (Table 1), and followed mean weekly photoperiods with gradual sunrise and sunset

138   transitions. Light intensities for each treatment were chosen to mimic *in situ* winter, lakebed light

139   measurements that were previously recorded with a photometer (JFE Advantech Co., Ltd.

140   DEFI2-L) from Lake Superior (46.97°, -90.99°) at 10 m of water in 2016-17. Remote-sensing ice

141   data (U.S. National Ice Center; usicecenter.gov) were used to quantify the daily percentage of ice

142   coverage above the light sensor (Figure 2). Embryos were incubated at a constant target water

143   temperature of 4.0°C in a climate-controlled chamber (Conviron® E8; Table 2). Forced airflow

144   was used in the climate-controlled chamber to ensure equal air circulation around the microplates

145   and opaque, plastic sheeting was used to separate light treatments. Microplates were covered

146   with transparent lids to minimize evaporation and rotated (i.e., orientation and position within the

147   incubator) weekly. Water temperature and light intensity were recorded hourly with loggers

148   (HOBO® Water Temperature Pro v2 and JFE Advantech Co., Ltd. DEFI2-L) and daily mean

149   values calculated (Table 1). During the hatch period, microplates were checked on a three-day

150   cycle for newly hatched embryos. All hatched embryos were photographed ventrally (Nikon®

151   D5600 and Nikon® AF-S DX 18-55mm lens) and then immediately preserved in 95% ethanol.

152   Egg size at fertilization, total length-at-hatch, and post-hatching yolk-sac axes were measured

153   from photographed images using Olympus® LCmicro.

154

155   *Developmental and Morphological Traits*

156   Embryo survival was estimated as the percent of embryos surviving between eye-up and post-

157   hatch stages. Incubation period was assessed with two variables: the number of days from

158   fertilization to hatching (days post-fertilization; DPF) and the sum of the degree-days

159   (accumulated degree-days; ADD). Total length-at-hatch (LAH; mm) and yolk-sac volume (YSV;

160   mm^3) were measured from five individuals per family at, or as close as possible to, 50% hatching

161   for each family. Yolk-sac volume was calculated assuming the shape of an ellipse (Blaxter,

162   1963):

$$YSV = \frac{\pi}{6}ab^2$$

163

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

165

166   *Statistical Analyses*

167   Embryo survival was analyzed as a binomial response variable, with incubation period, length-

168   at-hatch, and yolk-sac volume at hatching as continuous response variables. Because embryos

169   were raised independently, the replication unit in the statistical models is the individual embryo

170   and the design was unbalanced due to different levels of embryo mortality. All non-proportional

171   data were visually checked for approximate normality using histograms and Q-Q plots. A cubic

172   transformation was applied to LAH and a cubic root transformation was applied to DPF, ADD,

173   and YSV to normalize the distributions. Embryo survival was analyzed with binomial

174   generalized linear mixed-effects models, and variables with distributions not strongly deviating

175   from normal (i.e., incubation period, LAH, and YSV) were analyzed with restricted maximum

176   likelihood linear mixed-effects models with the *lme4* package v.1.1-26 (Bates et al., 2015).

177   Population and incubation light treatment were included as fixed effects and female, male,

178   female x male, and fertilization block as random effects. All traits and possible interactions were

179   examined with backward, stepwise effect-selection and the maximal model for each trait selected

180   using the *buildmer* package v.1.7.1 (Voeten, 2020). The significance for population, species,

181   incubation temperature, interaction effects, and any random-effects selected were determined

182   using a likelihood ratio test between the maximal model and reduced models with the model

183   effect of interest removed.

184

185   To enable population comparisons, the response to temperature for each trait was standardized to

186   what we assumed was the optimal light treatment - the low light treatment (Table 1). For each

187   trait, the within-family mean was calculated for each light treatment and the percent change from

188   the optimal light intensity estimated. Standard error was calculated as the among-family

189   variation in percent change.

190

191   All analyses were performed in R version 4.0.4 (R Core Team, 2021).

192

193 **Results:**

194 *Spawning Adult and Egg Measurements*

195 Lake Superior spawning adults ranged from 326-503 mm (total length mean (SD) = 412.5 (40.8)

196 mm) and 298.9-970.0 g (fresh mass mean (SD) = 589.1 (171.4) g), and were larger in total length

197 and fresh mass than Lake Ontario adults which ranged from 321-425 mm (mean (SD) = 372.5

198 (25.3) mm) and 280.5-795.8 g (mean (SD) = 496.6 (126.4) g). Egg diameter was larger in Lake

199 Ontario (mean (SD) = 2.30 (0.08) mm) than Lake Superior (mean (SD) = 2.14 (0.12) mm).

200

201 *Developmental and Morphological Traits*

202 Incubation period (both DPF and ADD) and YSV had significant interaction effects between

203 population and light treatments (maximum $P = 0.008$; Table 3). The interaction effects precluded

204 any interpretation of main effects for incubation period and YSV, but did suggest contrasting

205 norms of reaction between populations. Below we describe the interaction effects for incubation

206 period and YSV, and the population main effects and light treatment pairwise comparisons for

207 embryo survival and LAH. All random effects (i.e., female, male, and female x male) were

208 significant (maximum $P = 0.009$) except female for embryo survival, male for embryo survival

209 and YSV, and female x male for embryo survival and LAH (Table 3). All statistical model

210 results can be found in Table 3.

211

212 *Embryo Survival*

213 Embryo survival was highest for both populations at the medium light treatment, but lowest at

214 the low light treatment for Lake Ontario and at the high light treatment for Lake Superior (Figure

215 3). Light and population main effects were significant. Only Lake Ontario pairwise light

216 treatment comparisons with the low light treatment were significant (Low - Medium $P < 0.001$;

217 Low - High $P < 0.001$). All pairwise light treatment comparisons for Lake Superior were not

218 significant (minimum $P = 0.089$). Embryo survival was higher for Lake Ontario at the high

219 (98.4%) and medium (99.6%) light treatments than for Lake Superior (85.3 and 89.3%,

220 respectively) but there was no difference between populations at the low light treatment (0.9%;

221 Figure 3).

222

223 *Incubation Period*

224 The number of days between fertilization and hatching was highest for Lake Ontario at the low

225 light treatment (115.47 days) and for Lake Superior at the high light treatment (101.22 days;

226 Figure 3). Lake Ontario cisco had a decrease in DPF from the low light to the high light

227 treatments (-0.7%), while Lake Superior had an increase from the low light to the high light

228 treatments (1.9%; Figure 3). Incubation period (DPF) was longer for Lake Ontario than Lake

229 Superior across all light treatments (mean (SD) difference = 13.9 (0.8) days).

230

231 The effect of light depended on population because the difference in ADD between populations

232 was less pronounced at the high light treatment (difference = 60.8 ADD), while ADD was higher

233 for Lake Ontario at the low and medium light treatments (497.7 and 485.9 ADD, respectively)

234 than Lake Superior (427.5 and 420.8 ADD, respectively; Figure 3). Lake Ontario ADD had a

235 negative response from the low to high light treatments (-2.5%), while ADD for Lake Superior

236 did not change from the low to high light treatments (0.05%; Figure 3).

237

238 *Length-at-Hatch*

239 Light was not a component returned in the stepwise-selected model, but the population main

240 effect between Lake Ontario and Lake Superior was significant ($P < 0.001$; Table 3). Lake

241 Ontario had a higher LAH than Lake Superior across all light treatments (Figure 4). Length-at-

242 hatch decreased with increasing light by 3.2 and 0.2% in Lake Superior and Lake Ontario

243 populations, respectively (Figure 4).

244

245 *Yolk-sac Volume*

246 Yolk-sac volume had a different response to light intensity between populations (Figure 4). The

247 effect of light depended on population because the difference in YSV between populations was

248 less pronounced at the low light treatment (0.22 mm^3), while YSV was lower for Lake Ontario at

249 the high and medium light treatments (0.35 and 0.37 mm^3, respectively) than Lake Superior

250 (0.67 and 0.63 mm^3, respectively; Figure 4). YSV increased from the low to high light treatments

251 (15.3%) in Lake Superior and decreased from the low to high light treatments (-5.5%) in Lake

252 Ontario (Figure 4).

253

Discussion:

254 **Discussion:**

255 Developmental and morphological traits for Lake Superior and Lake Ontario cisco populations

256 demonstrated similar and contrasting reaction norms to incubation light intensity. First, we found

257 different responses to light intensity in embryo survival. Second, increasing light intensity had

258 minimal impact on incubation periods (DPF and ADD) for both populations. Lastly, each

259 population responded differently to light for LAH and YSV. Consequently, cisco from lakes

260 Superior and Ontario are likely to have different responses to changes in ice coverage and

261 subsequent light conditions.

262

263 Our hypothesis that embryo survival would be highest at the lowest light treatment was not

264 supported. Embryo survival was highest for both populations at the medium light levels,

265 suggesting that populations may be adapted to withstand some light exposure from high inter-

266 annual variability in ice coverage. This result was contradictory to that observed in two Pacific

267 salmonid species (chinook salmon *Oncorhynchus tshawytscha* and rainbow trout *Oncorhynchus*

268 *mykiss*) for which embryo survival was highest at the lowest light exposures evaluated (0.04

269 μmol m^{-2} s^{-1}; Eisler, 1961, 1958; Kwain, 1975). Lake Ontario cisco had a sharper decrease in

270 survival than Lake Superior cisco at the low light treatment. The difference was surprising

271 because average historical ice coverage over the Lake Ontario spawning location is higher than

272 the Lake Superior spawning location, and thus low light conditions are more likely to occur for

273 Lake Ontario cisco embryos. However, the Lake Ontario cisco spawning location is shallow (< 5

274 m) and would have high light intensity with little or no ice coverage. Higher variability in winter

275 illuminance may allow the population of Lake Ontario cisco sampled to have greater flexibility

276 to higher light conditions than deeper spawning cisco sampled from Lake Superior.

277

278 Our hypothesis that elevated light intensity would accelerate embryogenesis was not

279 supported. The greatest difference in incubation periods was between populations, and was likely

280 due to differences in embryo size, as larger embryos (i.e., Lake Ontario cisco) require more time

281 to develop (Hodson and Blunt, 1986; Kamler, 2008). Previous studies of other salmonid species

282 (European whitefish *Coregonus lavaretus*, chinook salmon, rainbow trout) found increasing light

283 intensity decreased the length of incubation (Chernyaev, 2007; Eisler, 1958; Kwain, 1975).

284

285 In contrast to incubation period, LAH and YSV responded to the light treatment and matched our
286 hypotheses, but responses differed between populations. Lake Ontario cisco exhibited minimal
287 change in LAH as light increased, but YSV decreased, suggesting that light intensity increased
288 the metabolic demand of embryos and diverted energy away from somatic growth. In
289 comparison, Lake Superior cisco showed a trade-off between LAH and YSV. A negative
290 relationship between LAH and YSV is a common finding in fish temperature incubation studies
291 (Blaxter, 1991; Karjalainen et al., 2015; Stewart et al., 2021), but the relationship is usually
292 found alongside a change in incubation period as basal metabolic demand consumes yolk as a
293 function of the length of incubation. We found that light influenced incubation periods similarly
294 among light treatments; therefore, the trade-off between LAH and YSV in Lake Superior cisco
295 suggests decreased rates of yolk conversion into somatic tissue occurred as light intensity
296 increased. This suggests future decreases in ice coverage and subsequent increases in embryonic
297 light exposure may result in smaller, less-robust larvae, which may explain the lack of observed
298 survival of Lake Superior cisco and other coregonines to age-1 over the past 20 years (Lepak et
299 al., 2017; Stockwell et al., 2009). The reasons underlying differences between Lakes Ontario and
300 Superior remain unknown. However, the contrasting responses in LAH and YSV between
301 populations suggests that embryogenesis for each population has different levels of plasticity to
302 light.
303
304 Embryo development is sensitive to environmental conditions, which can greatly influence life-
305 history trajectories, performances, and reproductive success (Colby and Brooke, 1970;
306 Karjalainen et al., 2016; Luczynski, 1991). We did not quantify developmental stages, except eye
307 pigmentation, so specific life-stage developmental rates are unknown. Changes in the frequency
308 of light (i.e., periodicity) can have adverse effects on fish embryos after yolk plug closure and
309 first vertebrate trunk segment formation (Abdel-Rahim et al., 2019; Chernyaev, 2007, 1993;
310 Ruchin, 2020). Fluctuating light cycles (e.g., 6:6h light:dark) and constant light (e.g., 24h light)
311 accelerated the rate of embryonic development compared to 'normal' photoperiods (e.g., 12:12h
312 light:dark; Chernyaev, 2007, 1993; John and Hasler, 1956; Ruchin, 2020). Photoperiod
313 disruptions can inhibit the pineal organ and melatonin synthesis, which is critical to regulate and
314 synchronize diurnal and seasonal biological rhythms (Delgado et al., 1987; Ekstrzöm and Meissl,
315 1997; Falcón et al., 2010; Roberts, 1978). The role photoperiod and the endocrine system plays

316   in embryo development and phenology remains unknown for coregonines. Further studies that

317   examine the impact of changing light intensities and photoperiods throughout incubations (e.g.,

318   decreased or no light during winter from ice coverage and increased light intensity and

319   periodicity during spring ice-out) will help determine the fine-scale influence light and

320   photoperiod may have on specific development stages (i.e., hatching), hormone regulation, and

321   organ, tissue, and skeletal formation.

322

323   Sunlight intensity, albedo, and attenuation are strongly influenced by the angle of the sunlight,

324   which is determined by season and latitude (Forsythe et al., 1995; Goldberg and Klein, 1977).

325   Latitude and sun angle are negatively correlated and this negative relationship is strongest at the

326   winter solstice in the northern hemisphere (Goldberg and Klein, 1977; Wielgolaski and Inouye,

327   2003). Lake Ontario is at a lower latitude and thus experiences a higher sun angle than Lake

328   Superior, which results in a more intense and longer period of daylight. Our light treatments

329   were calculated from light sensors deployed only in Lake Superior; thus, the experimental light

330   intensity treatments for Lake Ontario cisco may not have captured an accurate light environment

331   representation. Under-ice light data from more lakes, depths, and habitats would add to our

332   understanding of cisco embryo light environments and improve the authenticity of experimental

333   treatments. Additionally, comparing populations from high latitude lakes which experience

334   decreased winter sunlight would provide an additional contrast for local adaptation and plasticity

335   across geographic regions.

336

337   Turbidity also contributes to light attenuation, and spring ice-out and river discharge can

338   drastically increase the presence of suspended particulates and light absorption (Shao et al.,

339   2019). Hydrological responses to climate change indicate earlier and protracted winter/spring

340   runoff and higher runoff volume (Blahušiaková et al., 2020; Cutforth et al., 1999; Shen et al.,

341   2018). Seasonal runoff, including snowmelt pulses, often drive high nutrient loads and primary

342   productivity in temperate lakes (Isles et al., 2017; Rosenberg and Schroth, 2017). Runoff

343   entering ice-covered lakes is expected to suspend near the ice surface, rather than mixing into the

344   water column (Cortés et al., 2017; Yang et al., 2020), and therefore, have implications on when

345   nutrients are used by primary producers and the onset of spring plankton blooms (Sommer et al.,

346   2012). If the timing of spring plankton blooms changes as a result of earlier and protracted

347   winter/spring nutrient loads, the potential mis-match between interacting species may produce

348   bottom-up consequences (Rogers et al., 2020). Our results showed changing light intensities did

349   not affect cisco hatch dates; thus, the ability of cisco to match optimal spring nursery conditions

350   may be weakened if coregonines do not respond to changing ice conditions similarly to the

351   plankton community (Cushing, 1990; Myers et al., 2015). The proximity of spawning and

352   nursery grounds to shoreline and river outlets would likely impact the synchrony between

353   coregonine larvae and planktonic prey.

354

355   Many fish species are iteroparous and in some species individuals repeatedly use the same

356   spawning location (Marsden et al., 1995; Skjæraasen et al., 2011; Thorrold et al., 2001). The

357   question of what constrains the choice of a spawning location cannot be separated from the

358   question of what constrains early-life development and survival (Ciannelli et al., 2015; Iles and

359   Sinclair, 1982; Petitgas et al., 2012; Sinclair and Iles, 1989). Embryo survival is largely

360   determined by incubation habitat (e.g., water temperature, light exposure, oxygen availability,

361   protection from predators), thus, selective pressure is focused on 'correct' and adaptive choices of

362   spawning sites by the parents. The amount of spawning plasticity (e.g., spawning site selection,

363   fidelity to spawning sites, spawning time) among populations could serve as an indicator for the

364   level of evolutionary constraints for offspring (Ciannelli et al., 2015). For example, Atlantic

365   herring (*Clupea harengus*) exhibit a wide range of reproductive strategies across diverse

366   geographical locations, but have limited spawning site plasticity because embryo survival is

367   dependent on substrate and vegetation (Petitgas et al., 2012). Coregonines are considered to be

368   behaviorally and developmentally plastic and do not appear to be constrained by a spawning

369   habitat type (Karjalainen et al., 2015; Muir et al., 2013; Paufve, 2019); however, our

370   understanding of coregonine reproductive behavior and spawning-site selection is limited. The

371   selection of deeper or shallower spawning locations would provide a gradient in environment

372   conditions (e.g., light, temperature) depending on population-specific habitat requirements, and

373   both suitable nearshore and offshore spawning habitats are likely to be present in each sampled

374   lake (Goodyear, 1982; Paufve, 2019).

375

376   The existence of varying trait responses between populations raises questions concerning causal

377   mechanisms. Genomic studies can aid our understanding by determining what functional

378   pathways could be up or down-regulated due to light energy. Any potential changes in metabolic

379   or catabolic genes from light will enhance trait analyses and allow further partitioning of the

380   effects of light from other energy demanding environmental variables (e.g., temperature).

381

382   **Conclusion:**

383   Given the extensive degree of developmental plasticity in coregonines, propagation has been

384   proposed as a practical way to reintroduce native species from lakes with extirpated or reduced

385   population levels (Bronte et al., 2017; Zimmerman and Krueger, 2009). A key uncertainty to

386   maximizing restoration efforts is whether managers should prioritize survival in propagation

387   methods by mimicking natural environmental conditions (Bronte et al., 2017). Our study

388   highlights the potential role of winter light conditions, the influence of light intensity on cisco

389   embryo development, and the impact changing ice regimes may have on cisco survival and

390   recruitment in the wild. We did not identify a consistent directional reaction between and within

391   the two cisco populations to increasing light, and light is likely to have a differential effect on a

392   number of physiological and biochemical processes. Large-scale, cross-lake propagation and

393   reintroduction efforts are likely to be limited by the ability to match cisco phenotypes and

394   optimal incubation conditions. Our results provide a step towards better understanding the recent

395   high variability observed in coregonine recruitment and may help predict what the future of this

396   species may look like under current climate trends.

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664

665 **Tables:**

666

667 Table 1. Mean daily $\pm$ SD light intensity (μmol m^{-2} s^{-1}) for three ice coverage classes from Lake

668 Superior and corresponding laboratory experimental light conditions.

669

Location	Ice Coverage (Light Treatment)		
	> 90% (Low)	40-60% (Medium)	< 10% (High)
Lake Superior	2.0 $\pm$ 1.1	3.4 $\pm$ 2.5	5.5 $\pm$ 5.9
Laboratory	0.6 $\pm$ 0.1	3.9 $\pm$ 1.9	6.2 $\pm$ 1.0

670

671 Table 2. Mean daily ± SD water temperatures (°C) during embryo incubations from each light

672 treatment for Lakes Superior and Ontario.

673

	Light Treatment		
Lake	High	Medium	Low
Superior	4.3 ± 0.2	4.3 ± 0.3	4.3 ± 0.3
Ontario	4.2 ± 0.3	4.3 ± 0.3	4.4 ± 0.4

674

675 Table 3. Likelihood ratio test output for each model selected for embryo survival (%), incubation

676 period (number of days post-fertilization (DPF) and accumulated degree days (°C; ADD)),

677 length-at-hatch (mm), and yolk-sac volume (mm^3) from Lakes Superior and Ontario cisco

678 (*Coregonus artedi*). pop indicates population. The full model that was selected is bolded for each

679 trait.

680

Trait	Model	Effect Tested	df	χ^2	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	10.80	0.005
	light + female:male + female + male	pop	1	3,023.89	< 0.001
	light + pop + female:male + female + male	light:pop	2	9.66	0.008
	light + pop + light:pop + female + male	female:male	1	79.91	< 0.001
	light + pop + light:pop + female:male + male	female	1	25.29	< 0.001
	light + pop + light:pop + female:male + female	male	1	10.80	0.001
Incubation Period (ADD)	**light + pop + light:pop + female:male + female + male**				
	pop + female:male + female + male	light	2	51.72	< 0.001
	light + female:male + female + male	pop	1	3,092.41	< 0.001
	light + pop + female:male + female + male	light:pop	2	13.23	0.001
	light + pop + light:pop + female + male	female:male	1	79.99	< 0.001
	light + pop + light:pop + female:male + male	female	1	25.25	< 0.001
	light + pop + light:pop + female:male + female	male	1	10.75	< 0.001
Length-at-Hatch	**pop + female + male**				
	female + male	pop	1	373.34	< 0.001
	pop + male	female	1	100.97	< 0.001
	pop + female	male	1	11.37	< 0.001
Yolk-sac Volume	**light + pop + light:pop + female:male + female**				
	pop + female:male + female	light	2	1.96	0.376
	light + female:male + female	pop	1	712.18	< 0.001
	light + pop + female:male + female	light:pop	2	19.04	< 0.001
	light + pop + light:pop + female	female:male	1	6.52	< 0.001
	light + pop + light:pop + female:male	female	1	38.94	< 0.001

681

Figure captions:

683

684   Figure 1. Histogram of annual mean ice coverage between 1-Jan and 15-Mar from 1973-2020 for

685   the sampling location in Lake Superior (top) and Lake Ontario (bottom). Error bars represent the

686   interquartile range and point indicates median. Ice coverage data was obtained from the U.S.

687   National Ice Center (usicecenter.gov/).

688

689   Figure 2. Daily ice coverage (%; blue line) and light intensity (μmol m^{-2} s^{-1}; gray line) based on

690   light sensors set at 10 m depth off Sand Island, Lake Superior. Ice coverage data above the

691   sensor was obtained from the U.S. National Ice Center (usicecenter.gov/).

692

693   Figure 3. Mean embryo survival (%) and incubation period (number of days post-fertilization

694   (DPF) and accumulated degree days (°C; ADD)) at each incubation light treatment (left) and

695   standardized responses to assumed optimal light conditions (i.e., low) within each population (%;

696   right) from Lake Superior and Lake Ontario cisco (*Coregonus artedi*). Error bars indicate

697   standard error.
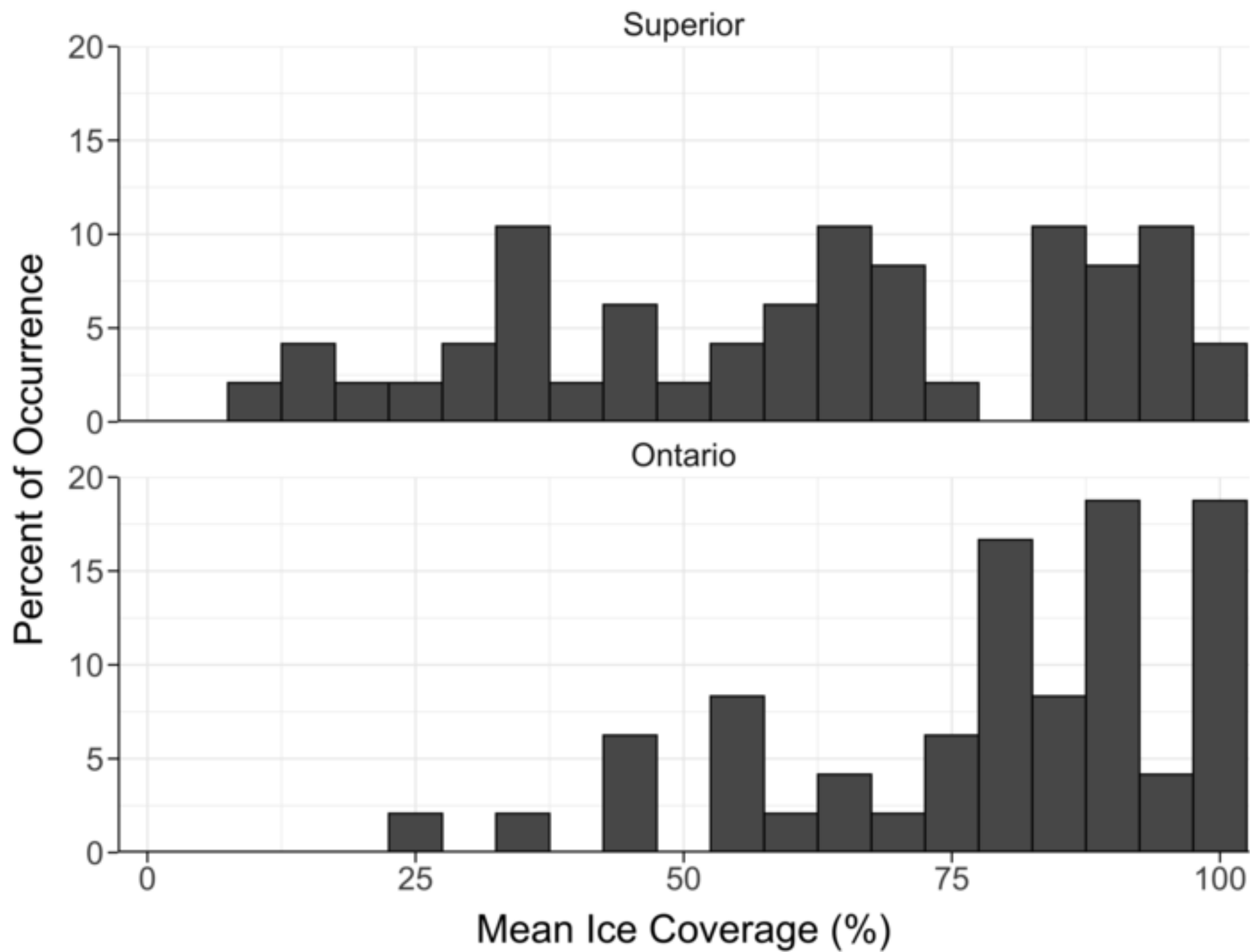
698

699   Figure 4. Mean length-at-hatch (mm; LAH) and yolk-sac volume (mm^3; YSV) at each incubation

700   light treatment (left) and standardized responses to assumed optimal light conditions (i.e., low)

701   within each population (%; right) from Lake Superior and Lake Ontario cisco (*Coregonus*

702   *artedi*). Error bars indicate standard error.

Figure 1

Figure 2

Figure 3

Figure 4

Figure 4