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Documentation of a probable spawning run of cisco *Coregonus artedii* in the Spanish River, Ontario, Canada

Andrew E. Honsey^{a,*}, Ralph W. Tingley III^b, Katie V. Anweiler^b, Cory O. Brant^b, Marc Chalupnicki^c, Chris Davis^d, Steven A. Farha^b, Paul W. Fedorowicz^e, Todd Hayden^f, Philippa Kohn^g, Benjamin S. Leonhardt^b, Brian P. O'Malley^h

^a U.S. Geological Survey Great Lakes Science Center, Hammond Bay Biological Station, 11188 Ray Road, Millersburg, MI 49759, USA

^b U.S. Geological Survey Great Lakes Science Center, 1451 Green Road, Ann Arbor, MI 48105, USA

^c U.S. Geological Survey Great Lakes Science Center, Tunison Laboratory of Aquatic Science, 3075 Gracie Road, Cortland, NY 13045, USA

^d Ontario Ministry of Natural Resources, 1450 Seventh Avenue East, Owen Sound, ON N4K 2Z1, Canada

^e Ann Arbor, MI 48105, USA, Contractor to the U.S. Geological Survey Great Lakes Science Center

^f Department of Fisheries and Wildlife, Michigan State University, Hammond Bay Biological Station, 11188 Ray Dr., Millersburg, MI 49759, USA

^g The Nature Conservancy, 274 N Goodman St, Rochester, NY 14607, USA

^h U.S. Geological Survey Great Lakes Science Center, Lake Ontario Biological Station, 17 Lake St, Oswego, NY 13126, USA

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ABSTRACT

Coregonines were historically diverse and abundant in the Laurentian Great Lakes but declined throughout the 19th and 20th centuries due to multiple factors, including overfishing, habitat degradation, and interactions with invasive species. Great Lakes fishery managers are now working to restore coregonines across the basin. An important aspect of restoration efforts is the identification of key habitats, such as spawning habitats. Our understanding of the extent and diversity of coregonine spawning habitats in the Great Lakes is limited. Historical accounts suggest some cisco *Coregonus artedii* migrated to tributaries to spawn, but contemporary runs have not been reported. Moreover, cisco display considerable phenotypic variation, with different “forms” often occupying specific habitats or regions. We provide evidence for a previously undocumented spawning run of cisco in the Spanish River, a tributary to the North Channel of Lake Huron. We captured 31 mature and ripe fish (25 males, 6 females) approximately 52 km upstream of the river mouth on 15–16 November 2022. The fish ranged in age from 3–9 yr and total length from 287–394 mm. Of these 31 individuals, 27 were morphologically similar to *C. artedii manitoulinus*, a subspecies of cisco found in the North Channel; however, four individuals more closely resembled cisco captured in other areas of Lake Huron. These findings represent the best evidence of tributary spawning by cisco since the 1880s, and they have important implications for coregonine conservation and restoration efforts. Ongoing work aims to augment our understanding of the ecological and evolutionary importance of this population.

1. Introduction

Coregonines (ciscoes and whitefishes; Family Salmonidae, Subfamily Coregoninae) are among the most diverse and ecologically, economically, and culturally important groups of fishes in the Laurentian Great Lakes (hereafter Great Lakes; Duncan et al., 2023; Eshenroder et al., 2016; Koelz, 1929; Smith, 1968). Coregonine populations declined throughout the Great Lakes in the 19th and 20th centuries due to multiple factors, including habitat degradation, overexploitation, and

interactions with invasive species (Berst and Spangler, 1973; Bunnell et al., 2023; Christie, 1973; Eshenroder et al., 2016; Hartman, 1973; Lawrie and Rahrer, 1973; Wells and McLain, 1973), and many species are now considered extirpated from some lakes or extinct (Eshenroder et al., 2016). In response to these declines and to promote resilient fish communities and sustainable fisheries, managers have prioritized the conservation and restoration of Great Lakes coregonines (Bronte et al., 2017; Bunnell et al., 2023).

An important component of restoration and conservation efforts is

* Corresponding author.

E-mail address: ahonsey@usgs.gov (A.E. Honsey).

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the identification of key habitats, such as spawning habitats (Kondolf, 2000; Lewis et al., 1996), and the potentially distinct populations that use those habitats. Unfortunately, our contemporary and historic understanding of spawning habitats and behaviors for many Great Lakes coregonines is limited (see Paufler et al., 2021; Schaefer, 2019; Schaefer et al., 2022). Increasing our understanding of spawning habitats and behaviors will help to ensure that coregonine restoration efforts account for the “three R’s” of conservation biology: representation, resiliency, and redundancy (Shaffer and Stein, 2000). Populations that spawn on unique habitats may represent key aspects of diversity (e.g., genetic, phenotypic, behavioral, functional) that are worth conserving and may also contribute to species-wide resiliency to stochastic disturbance events. Conserving them or using them for restoration actions (e.g., stocking in other locations) can maintain or increase a species’ ability to withstand catastrophic events (i.e., redundancy). As such, advancing our understanding of coregonine spawning diversity is vital for informing restoration efforts.

Contemporary and historical evidence suggest that rivers can provide important spawning habitats for Great Lakes coregonines. Historical river spawning runs of lake whitefish *Coregonus clupeaformis* and cisco *C. artedii* were known to Indigenous peoples of the Great Lakes since time immemorial (Lytwyn, 1990) and utilized by early trading companies along tributaries to Lake Superior for decades leading up to the 1850s (Goodier, 1984). Lake whitefish (Roseman et al., 2007) and/or cisco (Fielder, 2000; Gatch et al., 2021) spawning has been recently documented in connecting waters of the Great Lakes (i.e., Detroit, Saint Marys, and Niagara rivers), indicating persistence or reestablishment of historic spawning populations (Goodyear et al., 1982; Milner, 1874). Further, the resurgence of lake whitefish spawning in Green Bay tributaries exemplifies the potential importance of these habitats for Great Lakes coregonine conservation and restoration; despite a legacy of habitat degradation and the eradication of spawning runs in the 1870s (Smiley, 1882), lake whitefish now spawn in all major tributaries in southern and central Green Bay, and recruitment from these systems likely contributes to high biomass in the region (Hansen, 2019; Ransom et al., 2022, 2021). While no additional lake whitefish spawning runs are currently documented in the literature in Great Lakes tributaries, historical accounts of fish in rivers during the spawning season exist throughout the basin prior to broad-scale habitat degradation and dam construction in the 19th and 20th centuries (Goodyear et al., 1982). Similarly, anecdotal evidence (Goodyear et al., 1982) and historical creel catch records (Michigan Department of Natural Resources, written communication, 3 May 2021) indicate that cisco spawned in Great Lakes tributaries, and expert-based assessments of historic spawning habitat suitability exist for some systems (Madison and Lockwood, 2004; O’Neal, 1997; Zorn and Sendek, 2001). However, there have been no published reports of cisco spawning in Great Lakes tributaries for approximately 140 years, with the last record occurring prior to 1885 in the Maumee River (tributary to Lake Erie; Goodyear et al., 1982). Given the challenges associated with sampling during the spawning period (late fall–winter), the resurgence of some populations (e.g., cisco in northeastern Lake Michigan; Claramunt et al., 2019), and the remediation and improvement of some habitats, it is possible that the extent of coregonine tributary spawning is greater than currently described.

Identifying tributary spawning populations may be particularly important for the conservation and restoration of Great Lakes coregonines, which are known to display considerable intraspecific phenotypic diversity (Eshenroder et al., 2016; Koelz, 1929) as well as high spawning site fidelity (e.g., Gatch et al., 2023). For example, four distinct ectomorphs or forms of cisco have been described in Lake Huron alone (Eshenroder et al., 2021a, 2021b), and the morphological differences among these forms have been hypothesized to arise as a result of rearing in distinct habitats (e.g., particular embayments or regions) and persist due to subsequent homing of adults to those natal habitats (Eshenroder et al., 2021b). It is plausible, if not likely, that these forms represent ecologically and/or evolutionarily significant groups, and

tributary spawning populations may represent additional undescribed diversity that is worth considering in conservation and restoration planning.

Our goal was to expand our knowledge of coregonine spawning in Great Lakes tributaries. Specifically, we sought to: (1) determine whether coregonines spawn in a large Great Lakes tributary, (2) gather demographic data on any coregonines captured during the spawning period in that tributary, and (3) compare the morphologies of any captured coregonines to those of other populations. To do this, we sampled a river located near a known coregonine spawning population of potential conservation and restoration interest, the Spanish River (tributary to Lake Huron) in Ontario, Canada. We document and provide baseline demographic information on a previously undescribed river spawning population of cisco, and we compare morphologies of Spanish River cisco to those of other individuals throughout Lake Huron. Our results provide vital information for ongoing coregonine conservation and restoration efforts in the Great Lakes.

2. Methods

2.1. Study area

The Spanish River drains the seventh largest watershed in the Great Lakes basin and flows into the Whalesback Channel within the North Channel of Lake Huron (Forsyth et al., 2016; Fig. 1). Environmental degradation from historical logging activity, sewage treatment plants, a pulp and paper mill, and discharges from nearby mining activities led to the designation of the lower 52 km of the river (from an impassable dam in Espanola, Ontario to the river mouth) as an Area of Concern under the Canada-U.S. Great Lakes Water Quality Agreement (ECCC and EPA, 2022, ECCC and EPA, 2012). This section of river was reclassified as an Area in Recovery in 1999 following ecosystem restoration efforts (ECCC and EPA, 2022).

We chose to sample the Spanish River for spawning coregonines for three reasons. First, it is a large river with no natural or artificial barriers for 52 km, and as such, it provides a considerable area of accessible habitat that could be used by coregonines for spawning. Second, spawning populations of coregonines have been noted very close to (but not within) the Spanish River. Specifically, Koelz (1929) reported that a “well-differentiated” form of cisco, *C. artedii manitoulinus* (originally considered a distinct species by Jordan and Evermann, 1911), occurred in the North Channel and spawned in Aird Bay, just west of the Spanish River mouth (Fig. 1). This form was described as being darkly pigmented, particularly in the head, throughout the dorsal portion of the body, and in the fins. Koelz (1929) also noted that it was similar in body shape to blackfin cisco *C. nigripinnis*, as it had a longer head, larger eyes, longer maxillaries, longer paired fins, and a deeper body than most cisco from Lake Huron. Sampling conducted by the Ontario Ministry of Natural Resources (OMNR) found that individuals of this form continue to spawn in Aird Bay (see Eshenroder et al., 2021a, 2021b and below), and we sought to explore whether this population (or any other coregonine population) also spawns in the Spanish River. Finally, OMNR captured one cisco (135 mm total length) in the Spanish River near the Espanola Dam during an electrofishing survey on 10 April 2017, demonstrating that these fish can occupy the river well upstream of the mouth.

2.2. Sampling

We sampled a roughly 1.5 km stretch of the Spanish River immediately downstream of the Espanola Dam, approximately 52 km upstream of the river mouth in the North Channel (Fig. 1), via boat electrofishing from 14 to 16 November 2022. We chose this time period in an effort to maximize the probability of capturing coregonines that spawn or stage in relatively shallow waters in the late fall, such as lake whitefish and cisco (Ebener et al., 2021; Eshenroder et al., 2016; Koelz, 1929). Our electrofishing boat was equipped with a Smith-Root GPP-5.0

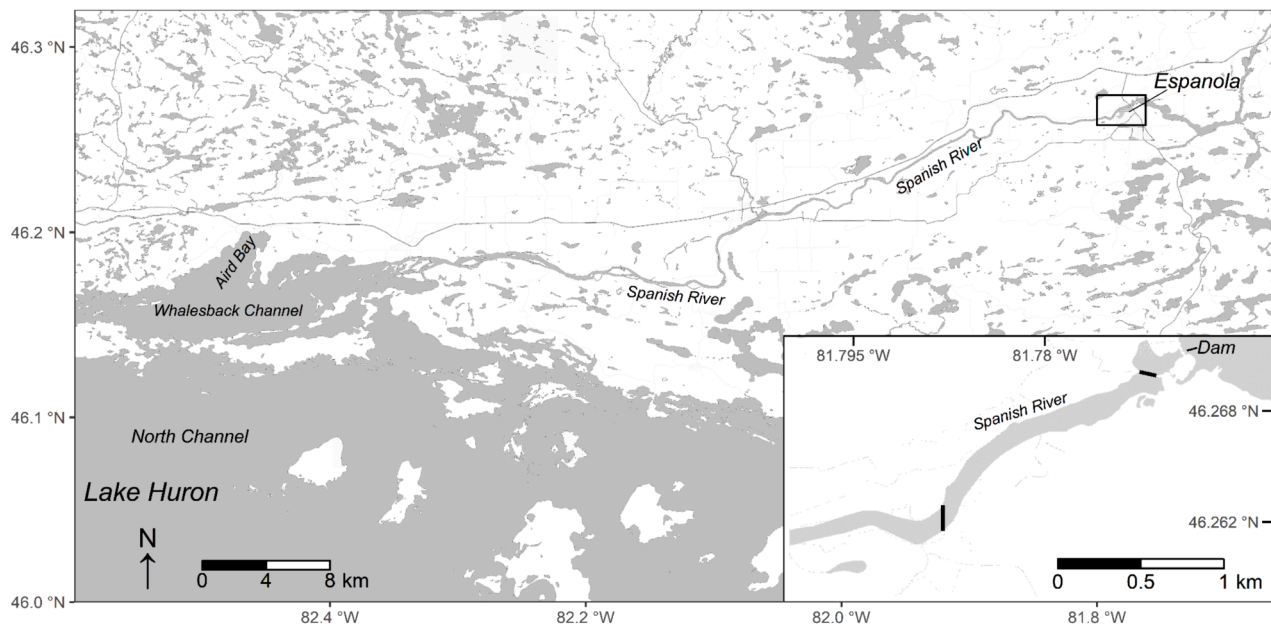


Fig. 1. Map of the Spanish River area, including Aird Bay, the Whalesback Channel, and the North Channel of Lake Huron, and Espanola, Ontario, Canada. Rectangle = study area. Inset: Detailed view of the study area on the Spanish River, including the dam in Espanola. Sampling occurred between the solid lines. Coordinates on the exterior map to the broader-scale map; coordinates on the interior of the inset map to the inset. Map tiles by Stamen Design under CC BY 3.0. Data by OpenStreetMap, under ODbL.

electrofisher (Smith-Root, Inc.), and we used the following settings: mode = 60 Hz direct current, range = “high”, percent of range = 30–60 % (adjusted as needed based on fish responses). We began sampling after dark (roughly 1900 h) each evening and continued for 2–3 h, with active shocking times ranging from 64 to 78 min across nights. We sampled by first traveling to the most upstream portion of the river that was suitable for electrofishing and safe to access (approximately 200 m from the dam; upstream solid line in Fig. 1 inset) and subsequently conducting controlled drifts while shocking until we reached a downstream bend in the river (approximately 1.75 km from the dam; downstream solid line in Fig. 1 inset). We repeated this process and altered drift lines to maximize coverage of the sampled area. When a suspected coregonine was sighted or captured, we conducted additional sampling in the vicinity to maximize catch. We visually inspected substrates where depth and water clarity allowed. For any captured coregonines, we (1) measured total length, (2) placed each individual in a plastic bag without water, and (3) placed all individuals in coolers with ice for transport to the Hammond Bay Biological Station in Millersburg, Michigan, USA, where we stored them at -20°C until further processing.

2.3. Processing

We measured standard lengths, wet weights, and gonad weights and identified the sex of all sampled coregonines. We also estimated individual ages using thin-sectioned sagittal otoliths. Specifically, we embedded at least one otolith from each fish in two-part epoxy resin (West System 105/207) and allowed it to dry for 48 h, after which we thin-sectioned each otolith on a transverse plane through the nucleus using a double-bladed saw (IsoMet, Buehler; 0.381 mm section thickness). Two readers enumerated annuli at 100x magnification, and age assignments were based on the agreement between the two readers. When the two readers disagreed (by 1 yr in all cases), a third independent reader provided an age estimate and age was assigned based on majority agreement among the three readers. We did not collect otoliths from three individuals which we reserved for preservation in the University of Michigan Museum of Zoology coregonine reference collection.

2.4. Morphology

We measured nine morphological characters on each specimen, including eight linear characters (body depth, dorsal fin height, head length, maxillary length, orbital length, pectoral fin length, pelvic fin length, and preorbital length) and one meristic character (total gill raker number) using the methods described in Eshenroder et al. (2016; see Electronic Supplementary Material (ESM) Fig. S1). These metrics have been shown to be useful for distinguishing among Great Lakes coregonines and have been used extensively in other studies (e.g., Eshenroder et al., 2021a, 2021b, 2016; Honsey et al., 2024a,b; Martin et al., 2023; O'Malley et al., 2021). To allow for comparisons of morphometric ratios for cisco and *C. artedii manitoulinus* described by Koelz (1929), we also measured the distance between the insertion of the pelvic and anal fins (pelvic-anal distance) per Eshenroder et al. (2016), but these data were not included in the morphological analyses described below in order to maximize comparability with previous studies and allow for the inclusion of additional data that did not contain measurements of this character (see below). These and other biological data for the Spanish River cisco collection are available via Honsey et al. (2024c).

To compare the morphologies of Spanish River cisco to those of other cisco collected near the river, we compiled data on the nine characters mentioned above from (1) 19 spawning cisco collected from Aird Bay (Fig. 1) by OMNR from 11 to 19 November 2016, and (2) non-spawning cisco collected by OMNR from multiple locations in the Whalesback Channel (including Aird Bay) from 26 to 30 September 2016 ($n = 7$) and 29 September – 10 October 2017 ($n = 16$; data published in Eshenroder et al., 2021a or available upon request). We note that these fish were measured by different individuals, and that the non-spawning samples may have included individuals from multiple spawning stocks.

2.5. Morphological analysis

We accounted for allometric effects of size on shape by calculating size-free morphometric ratios (Eshenroder et al., 2021a; Honsey et al., 2024a,b):

$$SFMR_i = \left(\frac{LM_i}{STL_r} \right) \times \left(\frac{STL_r}{STL_i} \right)^\beta,$$

where $SFMR_i$ is the size-free morphometric ratio for fish i , LM_i is a linear measurement for fish i (mm), STL_r is the reference standard length (mm), STL_i is the standard length of fish i (mm), and β is an estimated allometric exponent. Because individuals from the three groups overlapped in standard lengths (Spanish River: range = 222–306 mm; Aird Bay: range = 254–351 mm, Whalesback Channel: range = 186–319 mm), we used a single reference standard length for these size corrections calculated as the geometric mean standard length across individuals ($STL_r = 266.7$ mm). We did not size-correct total gill raker counts as they were not significantly correlated with standard lengths for these data.

We estimated β by conducting an analysis of covariance (ANCOVA; Zar, 1999) to determine which of the three models in Reist (1986) was most parsimonious for each measurement:

$\log(LM) \log(STL)$ (Model 1).

$\log(LM) \log(STL) + \text{Group}$ (Model 2).

$\log(LM) \log(STL) + \text{Group} + \log(STL) \times \text{Group}$, (Model 3).

where *Group* is a categorical variable describing the three groups (i.e., Spanish River, Aird Bay, Whalesback Channel). We used the regression coefficient(s) of $\log(STL)$ as estimate(s) of β . Selection of model 2 or model 3 would indicate differences in growth allometries (i.e., differences in morphological characters at a given size) among groups.

We used a multivariate analysis of variance (MANOVA) to test for differences in SFMRs and total gill raker numbers among groups. If MANOVA results indicated significant differences at $\alpha = 0.05$ based on the Wilks' λ test (Johnson and Wichern, 1998), we then used analyses of variance (ANOVA) and Tukey's honestly significant differences tests (Zar, 1999) to test for differences among groups for each character. We then visualized morphologies using principal components analysis (PCA; Jolliffe and Cadima, 2016), and we added 95 % confidence ellipses for each group on the plane created by the first two principal components. Finally, we calculated the percent overlap among pairs of ellipses as a percentage of the non-overlapping areas for each pair. We conducted all analyses in R version 4.3.2 (R Core Team, 2023) using the packages "FactoMineR" (Le et al., 2008) for principal component analysis, "Factoextra" (Kassambara and Mundt, 2020) and "ggplot2" (Wickham, 2016) for visualization, and "SIBER" (Jackson and Parnell, 2023) for calculating ellipse overlap.

2.6. Morphological analysis – additional data

In order to contextualize the observed variation in morphologies among the groups mentioned above, we also compiled data describing the same morphometric and meristic characters for cisco from three additional areas of Lake Huron that are known to show varying morphology compared to North Channel samples: (1) spawning individuals collected from Government Bay (Les Cheneaux Islands) in northern Lake Huron by the U.S. Fish and Wildlife Service in November 2016 ($n = 52$) and 2017 ($n = 13$); (2) individuals from the western Bruce Peninsula (termed "Nawash shorthead cisco" in Eshenroder et al., 2021a) collected off of Howdenville, Ontario by (a) the Saugeen Ojibway Nation via the commercial fishery in October–November 2019 ($n = 56$; likely staging and/or spawning) and (b) OMNR in June 2019 ($n = 6$; non-spawning); and (3) non-spawning individuals from Parry Sound within Georgian Bay collected by OMNR in July 2017 ($n = 21$), July–August 2018 ($n = 22$), and July 2019 ($n = 3$; ESM Fig. S2; data published in Eshenroder et al., 2021a or available upon request). Because size distributions differed among these fish and the Spanish River, Whalesback Channel, and Aird Bay individuals, we calculated size-free morphometric ratios for these fish using group-specific reference standard lengths ($STL_r = 325.8$ mm, 250.25 mm, and 338.0 mm for Government Bay, Parry Sound, and Nawash, respectively; see Eshenroder et al., 2021a; Martin et al., 2023) and by estimating β using model 1 for

each group. We then conducted a second PCA to compare overall morphologies among groups, again adding 95 % confidence ellipses on the plane of the first two principal components for each group and calculating overlap among ellipse pairs.

3. Results

3.1. Sampling and demographics

We collected 31 cisco across the three sampling events (see Fig. 2 for example specimens). We did not capture any other coregonines. Individuals appeared to occupy habitats with rock and gravel substrates based on visual inspection. Catch rates increased across sampling events from 0 to 0.37 cisco per shocking minute as surface water temperatures decreased from 9.3–8.2 °C. Individuals ranged in total length from 287–394 mm (mean = 338.6 mm, SD=26.5 mm; Fig. 3), standard length from 222–306 mm (mean = 265.5 mm, SD=20.8 mm), and wet weight from 201–634 g (mean = 386.2 g, SD=103.3 g). All females ($n = 6$; 19 %) were gravid, and female gonadosomatic indices (GSI) ranged from 12–15 % (mean = 14 %, SD=1%). All males ($n = 25$; 81 %) were mature, with GSI ranging from 1–3 % (mean = 2 %, SD=0.05 %). Estimated ages ($n = 26$) ranged from 3–9 yr (mean = 6.3 yr, SD=1.2 yr), with the most common ages being 6 (50 %), 7 (23 %), and 5 (12 %; Fig. 3). In addition to the three individuals preserved as museum specimens, we were unable to estimate ages for two individuals due to damaged otoliths.

3.2. Morphology

Spanish River cisco were more similar in some morphometric ratios (e.g., standard length/head length, head length/orbital length) and total gill raker numbers to averages across all Lake Huron *C. artedii* measured by Koelz (1929) than to the representative samples of *C. artedii manitoulinus* that he identified (Table 1). However, Spanish River cisco were more similar to Koelz's (1929) *C. artedii manitoulinus* than to the pelagic, historically abundant "typical" *C. artedii* (see Eshenroder et al., 2016) in ratios of body depth and dorsal height to standard length, and Spanish River cisco had shorter preorbitals and longer maxillaries relative to head length than both "typical" *C. artedii* and *C. artedii manitoulinus* (Table 2).

Our ANCOVA results indicated that model 2 or model 3 were most parsimonious for all size-corrected morphometric characters except for pectoral fin length and body depth (ESM Table S1), indicating that growth allometries (i.e., morphologies) generally differed among cisco from the Spanish River, Aird Bay, and Whalesback Channel. Moreover, the MANOVA suggested significant differences among characters ($\lambda = 0.12$, $F_{18,124} = 13.25$, $p < 0.001$), and subsequent ANOVA and Tukey's tests indicated that Spanish River cisco significantly differed from Aird Bay and Whalesback Channel cisco in multiple characters (Fig. 4). Specifically, Spanish River cisco had slightly shallower bodies than Whalesback Channel fish ($F_{2,70} = 4.03$, $p = 0.022$; Fig. 4a), middling dorsal fin lengths ($F_{2,70} = 20.07$, $p < 0.001$; Fig. 4b), shorter heads ($F_{2,70} = 25.57$, $p < 0.001$) and maxillaries ($F_{2,70} = 7.39$, $p = 0.001$) and smaller eyes ($F_{2,70} = 7.11$, $p = 0.002$) than Aird Bay fish (Fig. 4c–e), and shorter pelvic fins ($F_{2,70} = 26.88$, $p < 0.001$) and preorbitals ($F_{2,70} = 21.43$, $p < 0.001$) than both Aird Bay and Whalesback Channel fish (Fig. 4g,h). Pectoral fin lengths ($F_{2,70} = 0.16$, $p = 0.86$; Fig. 4f) and total gill raker numbers ($F_{2,70} = 0.98$, $p = 0.38$; Fig. 4i) did not significantly differ among individuals from the three groups.

Despite these differences in size-corrected characters, our PCA results indicated substantial overlap in overall morphologies among cisco from the Spanish River, Aird Bay, and Whalesback Channel (Fig. 5a). In particular, Whalesback Channel fish overlapped considerably with both Spanish River and Aird Bay individuals on the first two principal components (55 % and 40 % overlap, respectively), with the latter two groups displaying slightly less overlap (35 %). Notably, the Spanish River collection included four individuals that differed considerably in



Fig. 2. Example images of cisco *Coregonus artedii* collected from the Spanish River, Ontario, Canada from 15 to 16 November 2022. (a) A large, gravid female (standard length = 296 mm), (b) a large male with heavily pigmented fins (standard length = 306 mm), (c) an average-sized male (standard length = 263 mm), (d) a relatively small, gravid female (standard length = 256 mm). (c) and (d) were two of the four individuals that were morphometrically similar to cisco from Government Bay, Les Cheneaux Islands (see Fig. 5).

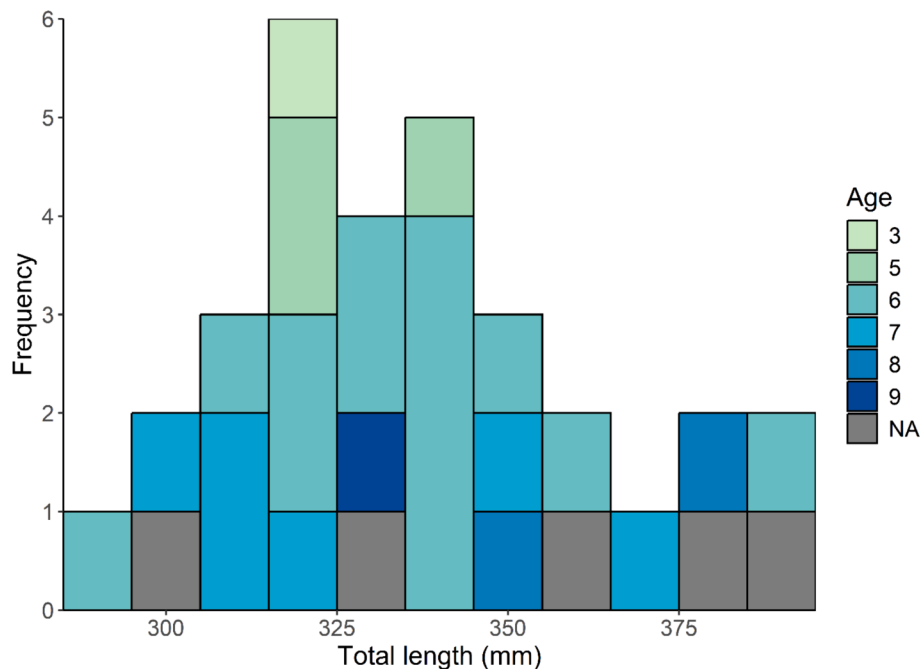


Fig. 3. Total lengths and ages (estimated from otoliths) of 31 cisco *Coregonus artedii* collected from the Spanish River, Ontario, Canada from 15 to 16 November 2022. Individuals that were not aged (“NA”) include three specimens reserved for the University of Michigan Museum of Zoology (otoliths not taken) and two individuals with damaged otoliths.

Table 1

Mean, standard deviation (SD), and range of three morphometric ratios and total number of gill rakers for (1) two groups of cisco *Coregonus artedii* based on representative specimens (manitoulinus) or frequency distributions (all artedii) from Koelz (1929) collected from Lake Huron from 1917 to 1924 and (2) a sample of cisco collected from the Spanish River, Ontario, Canada just downstream of the Espanola Dam from November 14–16, 2022. STL=standard length, HLL=head length, OOL=orbital length, PAD=pelvic-anal distance, PVL=pelvic fin length, TGR=total number of gill rakers. n = sample size for TGR for “artedii (all)” (sample sizes vary slightly for other characters) and for all characters for the other two groups.

Form/Sample	n	STL/HLL		HLL/OOL		PAD/PVL		TGR	
		Mean ± SD	Range	Mean ± SD	Range	Mean ± SD	Range	Mean ± SD	Range
artedii (all)	302	4.4 ± 0.2	3.9–5.0	4.0 ± 0.2	3.4–5.1	1.7 ± 0.1	1.1–2.1	47.1 ± 2.2	40–53
manitoulinus	10	4.1 ± 0.1	4.0–4.3	3.7 ± 0.1	3.4–3.8	1.4 ± 0.2	1.1–1.6	45.7 ± 1.3	43–47
Spanish River	31	4.4 ± 0.2	4.0–4.8	3.9 ± 0.3	3.4–4.6	1.6 ± 0.1	1.3–1.9	48.3 ± 2.1	44–52

morphology from other individuals in the three groups, with particularly shallow body depths and short pectoral fins (along with lower values in some other characters; four points on the negative extreme of

PC1 in Fig. 5a). These individuals included three males and one female, and two of these four are shown in Fig. 2c-d for reference.

Our PCA including additional data showed that, in general, Spanish

Table 2

Mean, standard deviation (SD), and range of four morphometric ratios for (1) two forms of cisco *Coregonus artedii* (“typical” *artedii* and *manitoulinus*; see [Eshenroder et al. 2016](#)) based on representative specimens selected by [Koelz \(1929\)](#) collected from Lake Huron from 1917 to 1924 and (2) a sample of cisco collected from the Spanish River, Ontario, Canada just downstream of the Espanola Dam from November 14–16, 2022. n = sample size, STL=standard length, BDD=body depth, HLL=head length, POL=preorbital length, MXL=maxillary length, DOH=dorsal fin height.

Form/Sample	n	STL/BDD		HLL/POL		HLL/MXL		STL/DOH	
		Mean \pm SD	Range	Mean \pm SD	Range	Mean \pm SD	Range	Mean \pm SD	Range
<i>artedii</i> (typical)	40	4.4 \pm 0.4	3.7–5.4	3.9 \pm 0.2	3.5–4.3	2.9 \pm 0.2	2.6–3.2	7.5 \pm 0.7	6.3–8.9
<i>manitoulinus</i>	10	3.6 \pm 0.2	3.4–4.0	3.9 \pm 0.2	3.7–4.2	2.7 \pm 0.1	2.5–2.8	5.7 \pm 0.8	4.9–7.7
Spanish River	31	3.6 \pm 0.3	3.1–4.3	4.4 \pm 0.3	4.0–5.3	3.1 \pm 0.2	2.7–3.4	5.2 \pm 0.5	4.5–6.1

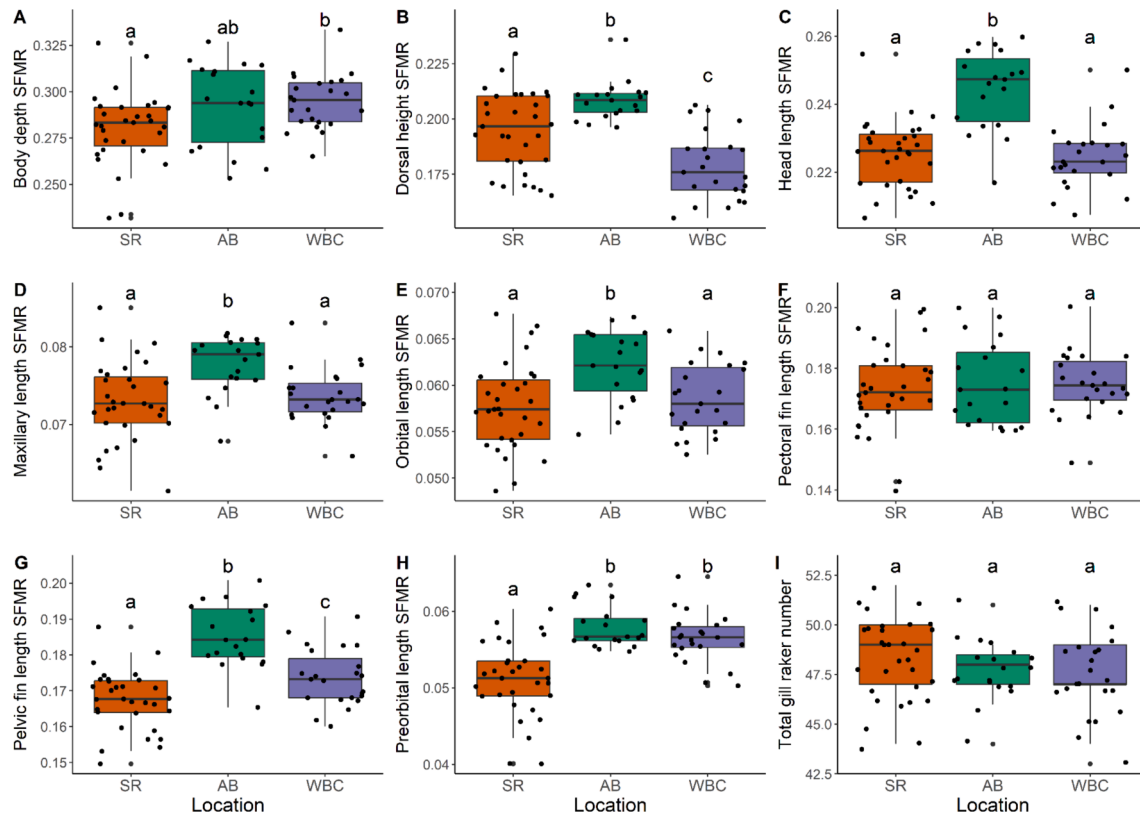


Fig. 4. Size-free morphometric ratios for eight morphometric characters and total gill raker numbers for cisco *Coregonus artedii* from three locations (SR=Spanish River, AB=Aird Bay, WBC=Whalesback Channel; see [Fig. 1](#)). Letters above boxplots denote statistically significant differences based on ANOVA and post-hoc Tukey's tests. See ESM [Fig. S1](#) for descriptions of each measurement.

River cisco were more morphologically similar to cisco collected near the Spanish River than to cisco from other areas of Lake Huron ([Fig. 5c](#)). In this analysis, Spanish River cisco overlapped most with cisco from the Whalesback Channel (55 %), followed by those from Aird Bay (40 %), Government Bay (20 %), Parry Sound (12 %), and Nawash (7 %). Moreover, Spanish River cisco generally aligned in morphology with *C. artedii manitoulinus* based on a similar analysis by [Eshenroder et al. \(2021a\)](#); see [Fig. 4](#) therein), and the four outliers from the Spanish River were more morphologically similar to Government Bay (Les Cheneaux Islands) and Nawash (western Bruce Peninsula) individuals than to other Spanish River and Whalesback Channel fish. That said, these comparisons reflect morphology for each group at their respective reference sizes and are thus influenced by the differing sizes of individuals among groups.

4. Discussion

Our findings provide strong evidence for a cisco spawning run in the Spanish River. Our study site was roughly 52 km upstream of the river mouth, and we argue it is unlikely that cisco would travel that far

upstream during the spawning season only to return to the lake to spawn. In addition, all captured individuals had ripe gonads, and we found that catch rates increased across sampling days as water temperatures decreased, which is consistent with expectations for the early portion of a spawning run ([Dryer and Beil, 1964](#); [George, 2019](#)). Collected cisco occupied habitats with rock and gravel substrates, which aligns with observations of cisco spawning habitat in some other systems (though we note that additional work is needed to better describe the habitats used by Spanish River spawners; [George et al., 2017](#); [Goodyear et al., 1982](#); [Pauve et al., 2021](#); [Scott and Crossman, 1998](#); [Weidel et al., 2023](#)), and the timing of the spawning run aligned closely with observed spawning peaks for other cisco populations in northern Lake Huron (e. g., Government Bay, Les Cheneaux Islands; J. Bonilla-Gomez, U.S. Fish and Wildlife Service, written communication, 16 Feb 2024). Our catches were dominated by males, which is typical for coregonines during the early portion of the spawning period ([Cahn, 1927](#); [Colby and Brooke, 1973](#); [George, 2019](#)). Finally, additional sampling as part of ongoing acoustic telemetry work on 22 Nov 2023 found ripe and running male and female cisco at the same location, confirming that individuals were spawning there (results forthcoming). As such, our findings represent

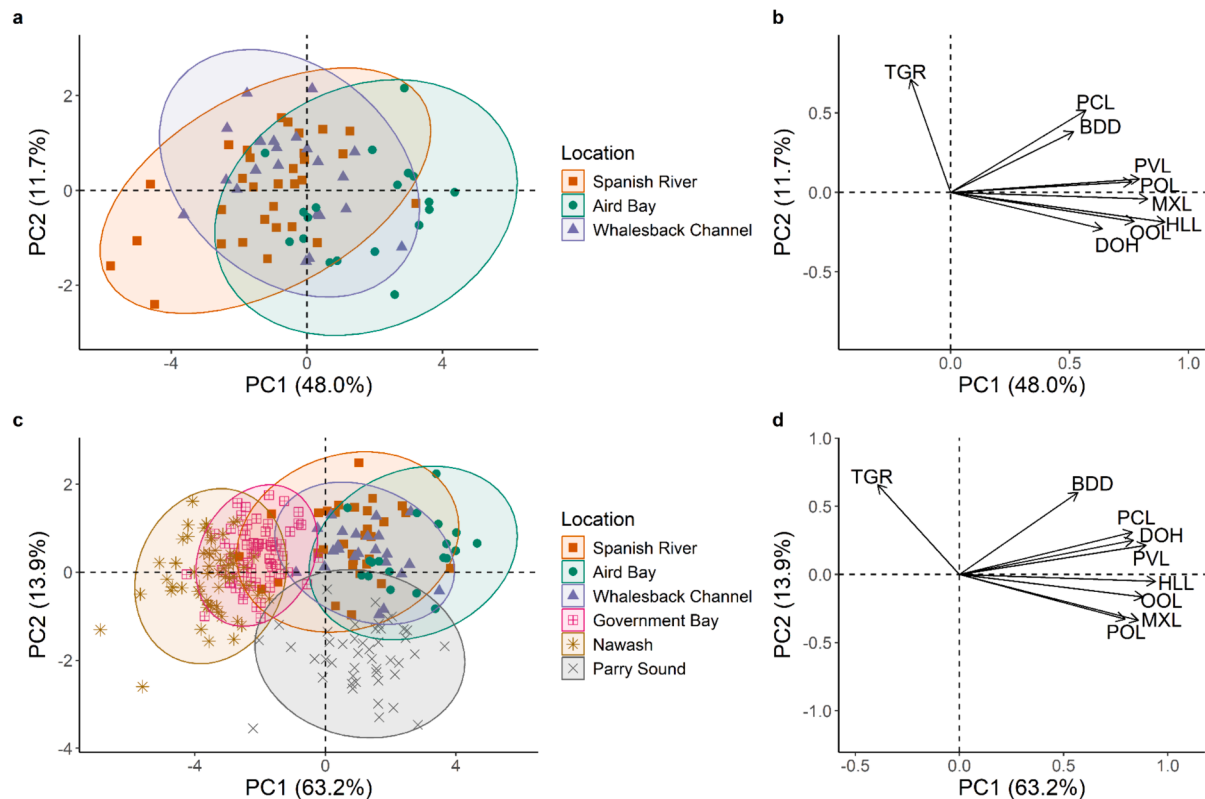


Fig. 5. Principal component analyses of size-corrected morphometric and meristic characters for cisco *Coregonus artedii* captured from multiple locations in Lake Huron. (a) Individuals collected immediately downstream of the Espanola Dam as part of this study (Spanish River) and near the river mouth in the Whalesback Channel (Aird Bay, Whalesback Channel). (b) Variable loadings for (a). (c) Samples in (a) plotted alongside additional samples from other areas of Lake Huron, including from Government Bay in the Les Cheneaux Islands (Government Bay), near Howdenvale (Nawash), and in Parry Sound (Parry Sound; see ESM Fig. S2). (d) Variable loadings for (c). BDD=body depth, DOH=dorsal fin height, HLL=head length, MXL=maxillary length, OOL=orbital length, PCL=pectoral fin length, PVL=pelvic fin length, POL=preorbital length, TGR=total number of gill rakers.

the first evidence of cisco spawning in a Great Lakes tributary in at least 140 years. Ongoing work is investigating the potential ecological and evolutionary significance of this population, the results of which will be critical for coregonine conservation and restoration planning in the Great Lakes (Bunnell et al., 2023).

In general, our results support the notion that Spanish River cisco are *C. artedii manitoulinus* per Koelz (1929). Our specimens were generally darkly pigmented, especially in the head and fins, aligning with Koelz's (1929) description. They were also similar in body size to many historical (Koelz, 1929) and contemporary (Eshenroder et al., 2021a, 2016) populations described as *manitoulinus*, and they were slightly smaller than some other contemporary cisco populations (e.g., Les Cheneaux Islands, Lake Huron; "Nawash" cisco, Lake Huron; Grand Traverse Bay, Lake Michigan; Breaker et al., 2020; Eshenroder et al., 2021a). Moreover, our specimens were similar in many morphometric ratios to Koelz's (1929) *manitoulinus*, with deeper bodies and shorter dorsal fins than the historically dominant, pelagic "typical" *C. artedii*. However, we note that Koelz's (1929) *manitoulinus* were chosen as "representative" specimens and therefore likely constitute an extreme subset of the 10 individuals that most closely resembled this "local race"; relatedly, Koelz (1929) noted that these individuals were "known to intergrade" with the common *C. artedii*, and our collection appears to include individuals on a gradient of morphological similarity between Koelz's (1929) historical *manitoulinus* and other contemporary cisco populations (see below). In addition, Spanish River cisco displayed longer maxillaries and shorter preorbitals relative to head length than historical specimens, which could represent shifts in these characters through time, unique morphology in this population, and/or differences in measurement techniques through time (see Eshenroder et al., 2016).

The results of our analysis of size-corrected morphometric and

meristic characters provide further evidence that the Spanish River cisco is *C. artedii manitoulinus*, and they highlight some potentially important differences among populations that warrant further study. We found that Spanish River cisco were more similar in overall morphology to cisco collected during the spawning period in Aird Bay and at other times throughout the Whalesback Channel (both of which were considered *manitoulinus* in Eshenroder et al., 2021a, 2021b) than they were to cisco collected in three other regions of Lake Huron (Fig. 5c), though we highlight that some of these samples were also collected outside of the spawning period. Interestingly, four cisco collected in the Spanish River had shallower bodies and shorter pectoral fins relative to their size than all other individuals from this region, and they were more morphologically similar to cisco from Government Bay (Les Cheneaux Islands) and "Nawash" cisco from the western Bruce Peninsula (see ESM Fig. S2), though we note that these comparisons are nuanced due to differing size distributions (and therefore differing reference lengths used in size corrections) among groups. It is possible that these individuals represent intergradation with other cisco populations (Koelz, 1929), migration of individuals from other areas to spawn in the Spanish River, or simply natural variation, as coregonines display substantial phenotypic plasticity (Eshenroder et al., 2021b; Lindsey, 1981). In addition, we found that Spanish River cisco significantly differed from both Aird Bay and Whalesback Channel cisco in some morphometric characters. Specifically, dorsal fin heights for Spanish River cisco fell intermediate to those of Aird Bay and Whalesback Channel fish, and Spanish River cisco had shorter pelvic fins and preorbitals than fish from the other two groups. It is possible that these differences represent adaptations to the river environment, which these individuals likely experienced during early life (assuming high spawning site fidelity, which has been shown in cisco; Gatch et al., 2023) if not longer (e.g.,

these individuals may be river residents or may use river habitats regularly), although pectoral fins are generally longer in salmonids reared in higher versus lower flows (Pakkasmaa and Piironen, 2000; Pelis and McCormick, 2003). Ongoing work (described below) will help to determine whether the Spanish River spawning population displays any genetic differentiation, indicating the presence of multiple spawning groups using this habitat, and future work investigating whether the observed morphological differences between Spanish River cisco and other nearby populations are ecologically significant is merited.

We found that Spanish River cisco displayed relatively broad age diversity that was not tightly linked to size (i.e., high variation in size-at-age). Age 6 individuals comprised half of our sample and included both the smallest and largest individuals we captured (287 and 394 mm total length, respectively), as well as many individuals between these extremes. Our sample also included substantial proportions of fish of other ages, including ages 5 and 7. The fact that our sample included high proportions of successive ages suggests that this population may have more consistent recruitment than some other cisco populations. For instance, cisco in Lake Superior display “boom-and-bust” recruitment dynamics, with strong year-classes often separated by many years (Cox and Kitchell, 2004; Myers et al., 2015; Rook et al., 2012). It is plausible that the relative insensitivity of the Spanish River to large-scale abiotic factors that are hypothesized to drive cisco recruitment in large systems such as Lake Superior (e.g., wind; Myers et al., 2015) may lead to more consistent recruitment in this population. Similarly, the relatively high productivity and (presumably) high abundance of prey for cisco in early life stages in the Spanish River compared to more oligotrophic, offshore waters (e.g., total phosphorus $\approx 14\text{--}20\ \mu\text{g} \cdot \text{L}^{-1}$ near the Spanish River mouth in the 1990s; total phosphorus in Lake Superior $\approx 2\text{--}4\ \mu\text{g} \cdot \text{L}^{-1}$; Barbiero et al., 2012; Rosa et al., 1995) may lead to more consistent early life survival and recruitment across years. Ransom et al. (2021) estimated that lake whitefish larvae inhabited Green Bay tributaries for 2–18 days (depending on flows and distances to river mouths), which could encompass critical periods of early life mortality. Notably, all of Ransom et al.’s (2021) sampling locations were closer to river mouths than our study site (maximum = 11 km versus 52 km in our study); as such, Spanish River cisco larvae may have considerably longer drift times. Additional work on the drift times and demographics of this population would provide further insight into cisco recruitment dynamics and drivers across systems and habitats. Moreover, additional research may provide valuable information regarding the contribution (s) of this and potential other river spawning populations to the dynamics of the broader metapopulation in the North Channel and/or throughout Lake Huron via portfolio effects (Hilborn and Quinn, 2003; Schindler et al., 2010), which in turn may influence conservation and restoration priorities for river spawning populations (Bunnell et al., 2023).

Given the history of environmental degradation in the Spanish River and its current status as an Area in Recovery (ECCC and EPA, 2022), our findings echo those of others (Ransom et al., 2021) demonstrating the capacity for coregonines to spawn in formerly degraded river habitats. The fact that coregonines can utilize these habitats speaks to the potential for restoration actions, including habitat restoration and fish reintroductions, to succeed in rivers in the Great Lakes region and elsewhere. As such, coregonine restoration planning (e.g., Bunnell et al., 2023) may benefit from consideration of such actions, particularly given the potential for river runs to contribute substantially to metapopulations (Hansen, 2019; Hilborn and Quinn, 2003; Ransom et al., 2022, 2021).

This work is part of a broader suite of ongoing work on Great Lakes coregonine river spawning. We, along with other colleagues, have sampled multiple Great Lakes tributaries and connecting channels using various methods, including electrofishing, gill netting, larval sampling via neuston net tows, and environmental DNA sampling. Results from this work are forthcoming, although we note that the results presented herein represent the best evidence for a robust Great Lakes tributary

spawning coregonine population that we have found to date. Alongside these efforts, we are also engaged in ongoing work to better understand the evolutionary and ecological significance of the Spanish River cisco population. For instance, we are using low-coverage whole genome sequencing to assess the evolutionary uniqueness and significance of this population, as well as the potential for multiple genetic groups to be spawning on the same habitats. We are also using acoustic telemetry to better understand the movement ecology, spawning run timing, and habitat use of this population. Results from these efforts will help to further inform both our evolutionary and ecological understanding of Spanish River cisco and coregonine conservation and restoration efforts more broadly.

5. Conclusions

We present strong evidence for a cisco spawning run in the Spanish River, the best evidence of Great Lakes tributary spawning by cisco since the 1880s. This population represents previously undescribed ecological (and potentially genetic) diversity, and conserving it may help to promote species-wide *resiliency* and *redundancy* (Shaffer and Stein, 2000). In addition, these findings further show that Great Lakes coregonines can utilize previously degraded habitats, highlighting the potential for restoration actions in rivers to succeed. Future surveys of additional tributaries for coregonine spawning runs could help to inform conservation and restoration efforts for these fishes in the Great Lakes and beyond.

CRedit authorship contribution statement

Andrew E. Honsey: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing. **Ralph W. Tingley:** Conceptualization, Funding acquisition, Investigation, Methodology, Writing – original draft, Writing – review & editing. **Katie V. Anweiler:** Data curation, Investigation, Writing – original draft, Writing – review & editing. **Cory O. Brant:** Investigation, Methodology, Writing – review & editing. **Marc Chalupnicki:** Conceptualization, Funding acquisition, Writing – review & editing. **Chris Davis:** Conceptualization, Funding acquisition, Writing – review & editing. **Steven A. Farha:** Investigation, Methodology, Writing – review & editing, Writing – original draft. **Paul W. Fedorowicz:** Investigation, Methodology, Writing – review & editing. **Todd Hayden:** Conceptualization, Funding acquisition, Writing – review & editing. **Philippa Kohn:** Conceptualization, Funding acquisition, Writing – review & editing. **Benjamin S. Leonhardt:** Investigation, Methodology, Writing – original draft, Writing – review & editing. **Brian P. O’Malley:** Conceptualization, Funding acquisition, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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not imply endorsement by the U.S. Government.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jglr.2024.102421>.

References

- Barbiero, R.P., Lesht, B.M., Warren, G.J., 2012. Convergence of trophic state and the lower food web in Lakes Huron, Michigan and Superior. *J. Great Lakes Res.* 38, 368–380. <https://doi.org/10.1016/j.jglr.2012.03.009>.
- Berst, A.H., Spangler, G.R., 1973. Lake Huron: the ecology of the fish community and man's effects on it. Great Lakes Fishery Commission Technical Report 21.
- Breaker, B.S., Pangle, K.L., Donner, K.C., Smith, J.B., Turschak, B.A., Claramunt, R.M., Bunnell, D.B., Jonas, J.L., 2020. Piscivory in recovering Lake Michigan cisco (*Coregonus artedii*): The role of invasive species. *J. Great Lakes Res.* 46, 1402–1411. <https://doi.org/10.1016/j.jglr.2020.06.013>.
- Bronte, C.R., Bunnell, D.B., David, S.R., Gordon, R., Gorsky, D., Millard, M.J., Read, J., Stein, R.A., Vaccaro, L., 2017. Report from the workshop on coregonine restoration science. US Geological Survey Open-File Report 2017-1081, Reston, VA, USA.
- Bunnell, D.B., Ackiss, A.S., Alofs, K.M., Brant, C.O., Bronte, C.R., Claramunt, R.M., Dettmers, J.M., Honsey, A.E., Mandrak, N.E., Muir, A.M., Jr, V.J.S., Smith, D.R., Strach, R.M., Sweka, J.A., Weidel, B.C., Mattes, W.P., Newman, K.R., 2023. A science and management partnership to restore coregonine diversity to the Laurentian Great Lakes. *Environ. Rev.* 31, 716–738. <https://doi.org/10.1139/er-2022-0109>.
- Cahn, A.R., 1927. An ecological study of southern Wisconsin fishes: the brook silverside (*Labidesthes sicculus*) and the cisco (*Leucichthys artedii*) in their relations to the region. Ill. Biol. Monogr. 11.
- Christie, W.J., 1973. A review of the changes in the fish species composition of Lake Ontario. Great Lakes Fishery Commission Technical Report 23.
- Claramunt, R.M., Smith, J., Donner, K., Povolito, A., Herbert, M.E., Galarowicz, T., Claramunt, T.L., DeBoe, S., Stott, W., Jonas, J.L., 2019. Resurgence of cisco (*Coregonus artedii*) in Lake Michigan. *J. Great Lakes Res.* 45, 821–829. <https://doi.org/10.1016/j.jglr.2019.04.004>.
- Colby, P.J., Brooke, L.T., 1973. Effects of temperature on embryonic development of lake herring (*Coregonus artedii*). *J. Fish. Res. Bd. Can.* 30, 799–810. <https://doi.org/10.1139/f73-135>.
- Cox, S.P., Kitchell, J.F., 2004. Lake superior ecosystem, 1929–1998: simulating alternative hypotheses for recruitment failure of lake herring (*Coregonus artedii*). *Bull. Mar. Sci.* 74, 671–683.
- Dryer, W.R., Beil, J., 1964. Life history of lake herring in Lake Superior. *Fish. Bull.* 63, 493–530.
- Duncan, A.T., Lauzon, R., Harpur, C., 2023. An investigation into Saugeen Ojibway Nation-based ecological knowledge on the ciscoes (*Coregonus* spp.) of Lake Huron. *J. Great Lakes Res.* 49, S138–S147. <https://doi.org/10.1016/j.jglr.2023.02.004>.
- Ebener, M.P., Dunlop, E.S., Muir, A.M., 2021. Declining recruitment of lake whitefish to fisheries in the Laurentian Great Lakes: management considerations and research priorities. In: Great Lakes Fishery Commission Miscellaneous Publication 2021-01, p. 95. Available from www.glfrc.org/pubs/misc/2021-01.pdf.
- Environment and Climate Change Canada (ECCC), U.S. Environmental Protection Agency (EPA), 2012. The 2012 Great Lakes Water Quality Agreement. Available at <https://binational.net/agreement/>.
- Environment and Climate Change Canada (ECCC), U.S. Environmental Protection Agency (EPA), 2022. 2022 Progress Report of the Parties. Available at <https://binational.net/wp-content/uploads/2022/07/2022-Progress-Report-of-the-Parties.pdf>.
- Eshenroder, R.L., Vecsei, P., Gorman, O.T., Yule, D.L., Pratt, T.C., Mandrak, N.E., Bunnell, D.B., Muir, A.M., 2016. Ciscoes (*Coregonus*, subgenus *Leucichthys*) of the Laurentian Great Lakes and Lake Nipigon. Great Lakes Fishery Commission, Ann Arbor, MI, USA.
- Eshenroder, R.L., Kao, Y., O'Brien, T.P., Olds, C.M., Davis, C.L., Duncan, A.T., 2021a. Replacement of the typical artedii form of *Coregonus artedii* in Lake Huron by endemic shallow-water Ciscoes, including putative hybrids. *Trans. Am. Fish. Soc.* 150, 792–806. <https://doi.org/10.1002/tafs.10328>.
- Eshenroder, R.L., Olds, C.M., Kao, Y.-C., Davis, C.L., Kinney, D.N., Muir, A.M., 2021b. Status of cisco (*Coregonus artedii*) ecomorphs in Lake Huron, 1917–2016, with speculations about phenotypic plasticity in shorthead cisco. *Adv. Limnol. Biol. Manage. Coregonid Fishes* 2017 (66), 383–402. https://doi.org/10.1127/adv_limnol/2021/0066.
- Felder, D.G., 2000. Lake Herring Spawning Grounds of the St. Marys river with some potential implications for early spring navigation. *N. Am. J. Fish. Manag.* 20, 552–561.
- Forsyth, D.K., Riseng, C.M., Wehrly, K.E., Mason, L.A., Gaiot, J., Hollenhorst, T., Johnston, C.M., Wyrzykowski, C., Annis, G., Castiglione, C., Todd, K., Robertson, M., Infante, D.M., Wang, L., McKenna, J.E., Whelan, G., 2016. The Great Lakes Hydrography Dataset: consistent, binational watersheds for the Laurentian Great Lakes basin. *J. Am. Water Resour. Assoc.* 52, 1068–1088. <https://doi.org/10.1111/1752-1688.12435>.
- Gatch, A., Gorsky, D., Biesinger, Z., Bruestle, E., Lee, K., Karboski, C., Bartron, M.L., Wagner, T., 2021. Evidence of successful river spawning by lake trout (*Salvelinus namaycush*) in the Lower Niagara River, Lake Ontario. *J. Great Lakes Res.* 47, 486–493. <https://doi.org/10.1016/j.jglr.2020.12.007>.
- Gatch, A.J., Gorsky, D., Weidel, B.C., Biesinger, Z.F., Connerton, M.J., Davis, C., Lachance, H., O'Malley, B.P., 2023. Seasonal habitat utilization provides evidence for site fidelity during both spawn and non-spawning seasons in Lake Ontario cisco *Coregonus artedii*. *J. Great Lakes Res.* 49, 1045–1058. <https://doi.org/10.1016/j.jglr.2023.06.008>.
- George, E., 2019. The history and ecology of Cisco *Coregonus artedii* in the Laurentian Great Lakes. *Aquat. Ecosyst. Health Manag.* 22, 280–293. <https://doi.org/10.1080/14634988.2019.1670461>.
- George, E.M., Stott, W., Young, B.P., Karboski, C.T., Crabtree, D.L., Roseman, E.F., Rudstam, L.G., 2017. Confirmation of cisco spawning in Chaumont Bay, Lake Ontario using an egg pumping device. *J. Great Lakes Res.* 43, 204–208. <https://doi.org/10.1016/j.jglr.2017.03.024>.
- Goodier, J.L., 1984. The nineteenth-century fisheries of the Hudson's bay company trading posts on lake superior: a biogeographical study. *Canad. Geograph. Géographies Canadiennes* 28, 341–357. <https://doi.org/10.1111/j.1541-0064.1984.tb01608.x>.
- Goodyear, C.S., Edsall, T.A., Ormsby Dempsey, D.M., Moss, G.D., Polanski, P.E., 1982. Atlas of the spawning and nursery areas of Great Lakes fishes, FWS/OBS-82. ed. U.S. Fish and Wildlife Service, Washington, DC.
- Hansen, S., 2019. Lake Whitefish. In: Lake Michigan Management Reports to the Great Lakes Fishery Commission. Wisconsin Department of Natural Resources, Madison, Wisconsin, pp. 37–43.
- Hartman, W.L., 1973. Effects of exploitation, environmental changes, and new species on the fish habitats and resources of Lake Erie. Great Lakes Fishery Commission Technical Report 22.
- Hilborn, R., Quinn, T.P., Schindler, D.E., Rogers, D.E., 2003. Biocomplexity and fisheries sustainability. *Proc. Natl. Acad. Sci. USA* 100, 6564–6568. <https://doi.org/10.1073/pnas.1037274100>.
- Honsey, A.E., Anweiler, K.V., Bunnell, D.B., Brant, C.O., Hoffman, G., O'Malley, B.P., Keeler, K.M., Olds, C., Kraus, J., Kao, Y.-C., Stott, W., 2024a. Impacts of artificial rearing on cisco *Coregonus artedii* morphology, including pugheadedness. *Can. J. Zool.* 102, 586–599. <https://doi.org/10.1139/cjz-2023-0195>.
- Honsey, A.E., Kao, Y.-C., Olds, C., Bunnell, D.B., 2024b. Morphological differences between wild and hatchery-reared Bloater (*Coregonus hoyi*) from Lake Michigan, USA. *Fish. Manag. Ecol.* 31, e12653.
- Honsey, A.E., Tingley III, R.W., Anweiler, K.V., Brant, C.O., Farha, S.A., Fedorowicz, P. W., Leonhardt, B.S., Eshenroder, R.L., 2024c. Demographic, morphometric, and meristic data describing cisco (*Coregonus artedii*) captured in the Spanish River, Ontario, Canada, 15–16 November 2022. U.S. Geological Survey Data Release. <https://doi.org/10.5066/P1N2WFEJ>.
- Jackson, A., Parnell, A., 2023. SIBER: Stable isotope Bayesian ellipses in R. R package version 2.1.7. <<https://CRAN.R-project.org/package=SIBER>>.
- Johnson, R.A., Wichern, D.W., 1998. Applied multivariate statistical analysis, 4th ed. Prentice Hall, Englewood Cliffs, NJ, USA.
- Jolliffe, I.T., Cadima, J., 2016. Principal component analysis: a review and recent developments. *Phil. Trans. R. Soc. A* 374, 20150202. <https://doi.org/10.1098/rsta.2015.0202>.
- Jordan, D.S., Evermann, B.W., 1911. A review of the salmonid fishes of the Great Lakes, with notes on the whitefishes of other regions. *Bull. Bureau Fish.* 29, 1–41.
- Kassambara, A., Mundt, F., 2020. factextra: extract and visualize the results of multivariate data analyses. R package version 1.0.7. <https://CRAN.R-project.org/package=factextra>.
- Koelz, W., 1929. Coregonid fishes of the Great Lakes. *Bulletin of the U.S. Bur. Fish.* 43, 297–643.
- Kondolf, G.M., 2000. Some suggested guidelines for geomorphic aspects of anadromous salmonid habitat restoration proposals. *Restor. Ecol.* 8, 48–56. <https://doi.org/10.1046/j.1526-100x.2000.80007.x>.
- Lawrie, A.H., Rahrer, J.F., 1973. Lake superior: a case history of the lake and its fisheries. Great Lakes Fish. Comm. Tech. Rep. 19.
- Le, S., Josse, J., Huisson, F., 2008. FactoMineR: an R package for multivariate analysis. *J. Stat. Softw.* 25, 1–18.
- Lewis, C.A., Lester, N.P., Bradshaw, A.D., Fitzgibbon, J.E., Fuller, K., Hakanson, L., Richards, C., 1996. Considerations of scale in habitat conservation and restoration. *Can. J. Fish. Aquat. Sci.* 53, 440–445.
- Lindsey, C.C., 1981. Stocks are chameleons: plasticity in gill rakers of coregonid fishes. *Can. J. Fish. Aquat. Sci.* 38, 1497–1506. <https://doi.org/10.1139/f81-202>.
- Lytwin, V.P., 1990. Ojibwa and Ottawa Fisheries around Manitoulin Island: Historical and Geographical Perspectives on Aboriginal and Treaty Fishing Rights. *Nativ. Stud. Rev.* 6, 1–30.
- Madison, G., Lockwood, R.N., 2004. Manistique river assessment, Michigan Department of Natural Resources. Fisheries Special Report 31. Ann Arbor, MI, USA.
- Martin, B.E., O'Malley, B., Eshenroder, R.L., Kao, Y.-C., Olds, C.M., O'Brien, T.P., Davis, C.L., 2023. Comparison of traditional and geometric morphometrics using Lake Huron ciscoes of the *Coregonus artedii* complex. *Trans. Am. Fish. Soc.* 152, 296–309. <https://doi.org/10.1002/tafs.10403>.
- Milner, J.W., 1874. Report on the fisheries of the Great Lakes: the result of inquiries prosecuted in 1871 and 1872. In: Report of the US Commissioner of Fish and Fisheries for 1872 and 1873, pp. 1–78.
- Myers, J.T., Yule, D.L., Jones, M.L., Ahrenstorff, T.D., Hrabik, T.R., Claramunt, R.M., Ebener, M.P., Berglund, E.K., 2015. Spatial synchrony in cisco recruitment. *Fish. Res.* 165, 11–21. <https://doi.org/10.1016/j.fishres.2014.12.014>.
- O'Malley, B.P., Schmitt, J.D., Holden, J.P., Weidel, B.C., 2021. Comparison of specimen- and image-based morphometrics for cisco. *J. Fish Wildl. Manag.* 12, 208–215. <https://doi.org/10.3996/jfwm-20-029>.
- O'Neal, R.P., 1997. Muskegon River Watershed Assessment (No. Michigan Department of Natural Resources, Fisheries Division Special Report 19). Lansing, MI, USA.

- Pakkasmaa, S., Piironen, J., 2000. Water velocity shapes juvenile salmonids. *Evol. Ecol.* 14, 721–730. <https://doi.org/10.1023/A:1011691810801>.
- Paufve, M.R., Sethi, S.A., Weidel, B.C., Lantry, B.F., Yule, D.L., Rudstam, L.G., Jonas, J.L., Berglund, E., Connerton, M.J., Gorsky, D., Herbert, M.E., Smith, J., 2021. Diversity in spawning habitat use among Great Lakes Cisco populations. *Ecol. Freshw. Fish* 1–10. <https://doi.org/10.1111/eff.12637>.
- Pelis, R.M., McCormick, S.D., 2003. Fin development in stream- and hatchery-reared Atlantic salmon. *Aquaculture* 220, 525–536. [https://doi.org/10.1016/S0044-8486\(02\)00625-7](https://doi.org/10.1016/S0044-8486(02)00625-7).
- R Core Team, 2023. R: a language and environment for statistical computing.
- Ransom, A.L., Houghton, C.J., Hanson, S.D., Hansen, S.P., Doerr, L.R., Forsythe, P.S., 2021. Recolonization of lake whitefish river spawning ecotypes and estimates of riverine larval production in Green Bay, Lake Michigan. *J. Great Lakes Res.* 47, 213–225. <https://doi.org/10.1016/j.jglr.2020.11.011>.
- Ransom, A.L., Houghton, C.J., Hanson, S.D., Hansen, S.P., Shaffer, M., Forsythe, P.S., 2022. Larval lake whitefish distribution in the open waters of Green Bay, Lake Michigan. *J. Great Lakes Res.* 48, 229–237. <https://doi.org/10.1016/j.jglr.2021.11.003>.
- Reist, J.D., 1986. An empirical evaluation of coefficients used in residual and allometric adjustment of size covariation. *Can. J. Zool.* 64, 1363–1368.
- Rook, B.J., Hansen, M.J., Gorman, O.T., 2012. The spatial scale for cisco recruitment dynamics in Lake Superior during 1978–2007. *N. Am. J. Fish Manag.* 32, 499–514. <https://doi.org/10.1080/02755947.2012.680005>.
- Rosa, F., Reynoldson, T.B., Mudroch, A., 1995. Investigations of the Spanish River area of the North Channel of Lake Huron III. Suspended sediment transport, sediment porewater and water chemistry characterization (No. NWRI Contribution 95-179). Environ. Canada.
- Roseman, E.F., Kennedy, G.W., Boase, J., Manny, B.A., Todd, T.N., Stott, W., 2007. Evidence of Lake Whitefish Spawning in the Detroit River: Implications for Habitat and Population Recovery. *J. Great Lakes Res.* 33, 397–406.
- Schaefer, H., 2019. Predicting spawning habitat for lake whitefish *Coregonus clupeaformis* and cisco *Coregonus artedii* in the Lake Erie and Lake Ontario regions using classification and regression tree (CART) and random forest models. University of Michigan, Ann Arbor, MI. PhD Thesis.
- Schaefer, H.M., Honsey, A.E., Bunnell, D.B., Weidel, B.C., DeBruyne, R., Diana, J.S., Gorsky, D., Roseman, E.F., 2022. Predicting physical and geomorphic habitat associated with historical lake whitefish and cisco spawning locations in Lakes Erie and Ontario. *J. Great Lakes Res.* 48, 1636–1646. <https://doi.org/10.1016/j.jglr.2022.08.014>.
- Schindler, D.E., Hilborn, R., Chasco, B., Boatright, C.P., Quinn, T.P., Rogers, L.A., Webster, M.S., 2010. Population diversity and the portfolio effect in an exploited species. *Nature* 465, 609–612. <https://doi.org/10.1038/nature09060>.
- Scott, W.B., Crossman, E.J., 1998. *Freshwater Fishes of Canada*. Galt House Publications Ltd., Oakville, ON, CA.
- Shaffer, M.L., Stein, M.A., 2000. Safeguarding our precious heritage. In: Stein, B.A., Kutner, L.S., Adams, J.S. (Eds.), *Precious Heritage: the Status of Biodiversity in the United States*. Oxford University Press, New York, pp. 301–321.
- Smiley, C.W., 1882. Changes in the fisheries of the Great Lakes during the decade, 1870–1880. *Trans. Am. Fisheries Soc.* 28–37.
- Smith, S.H., 1968. Species succession and fishery exploitation in the Great Lakes. *J. Fish. Res. Board Can.* 25, 667–693. <https://doi.org/10.1139/f68-063>.
- Weidel, B.C., Davis, C., O'Malley, B.P., Lachance, H., Osborne, C.A., Gatch, A.J., Furgal, S.L., Mackey, G.E., Chalupnicki, M.A., Sard, N.M., Heisey, A., Connerton, M. J., Lantry, B.F., 2023. Field and laboratory validation of new sampling gear to quantify coregonine egg deposition and larval emergence across spawning habitat gradients. *J. Great Lakes Res.* 49, 1059–1068. <https://doi.org/10.1016/j.jglr.2023.06.010>.
- Wells, L., McLain, A.L., 1973. Lake Michigan: man's effects on native fish stocks and other biota. Great Lakes Fishery Commission. Tech. Rep. 20.
- Wickham, H., 2016. *ggplot2: Elegant graphics for data analysis*. Springer-Verlag, New York.
- Zar, J.H., 1999. *Biostatistical analysis*, 4th ed. Prentice Hall, Upper Saddle River, New Jersey, USA.
- Zorn, T.G., Sendek, S.P., 2001. Au sable river assessment, michigan department of natural resources. Fisheries Division, Special Report 26. Ann Arbor, MI, USA.