

# **Spatial Units to Support Lake Erie Cisco *Coregonus artedi* Restoration**



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*Version 2026.1 March 11, 2026*

Citation: Egan, J. P., Ackiss, A. S., & Muir, A. M. (2026). Spatial units to support Lake Erie Cisco *Coregonus artedi* restoration. Available from: <https://www.greatlakesciscoes.org>

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# ABSTRACT

At the request of the Lake Erie Committee, spatial units for Lake Erie Cisco were delineated during spring 2024. Spatial units correspond to the reproductive habitat of extirpated (unoccupied spatial units) and extant (occupied spatial units) populations. Spatial units were delineated using a Council of Lake Committees-endorsed method that involves synthesizing data for evaluation by a panel with expertise on the focal organisms and ecosystems. By examining catch, survey, observational, and genetic data, an expert panel determined that no viable Cisco populations remain in Lake Erie. Experts delineated one eastern and one western unoccupied Cisco spatial unit in Lake Erie based on interpretation of historical movement and spawning locations and timing. The expert panel also identified eleven key questions that can be investigated to further inform Lake Erie Cisco restoration. The two unoccupied spatial units will form the basis of a follow-on threats and population viability assessments that together provide fishery managers science-based planning tools for Lake Erie Cisco restoration.

## 1. BACKGROUND

On May 3, 2023, the Lake Erie Committee requested application of the Great Lakes Coregonine Restoration Framework (Bunnell et al. 2023) planning steps to Lake Erie Cisco *Coregonus artedii* to inform the experimental reintroduction of Cisco into the New York waters of Lake Erie beginning in 2025 and Lake Erie Cisco restoration more generally. This report summarizes the results of the first planning step - spatial unit delineation. Spatial units are defined by reproductive habitat that was historically used by now extirpated organisms (unoccupied units) or is currently used by extant organisms (occupied units). Spatial units may be applied at population or subpopulation levels and provide a foundation for downstream planning, modeling, and restoration activities within the Coregonine Restoration Framework. Spatial units were delineated using a Council of Lake Committees-endorsed method that involves synthesis of relevant knowledge followed by an expert elicitation process to objectively evaluate Western scientific evidence for spatial unit criteria in a repeatable manner (Ackiss et al. 2023). Indigenous Knowledge can also be used to delineate spatial units, but was not available at the time of this assessment. Indigenous Knowledge could be used to delineate Lake Erie Cisco spatial units in the future. This report provides: (1) a synthesis of data used for the spatial unit assessment, (2) the results of the assessment, (3) maps depicting historical reproductive habitat and hypothesized and delineated spatial units, and (4) rationale for decisions made by the expert panel.

## 2. METHODS

### 2.1 Overview of spatial unit delineation approach

The Lake Erie Committee defined Lake Erie and its tributaries as the assessment area. Therefore, adjacent areas were not considered by this assessment. For example, testing for reproductive isolation between Lake Erie and Lake Huron, and other similar comparisons were outside the

scope of this work. To delineate spatial units within the defined assessment area, an expert panel formulated, then assessed spatial unit hypotheses using a structured scoring system and knowledge hierarchy consisting of criteria for unit delineation, lines of evidence, and data types (Ackiss et al. 2023). When experts assess spatial unit hypotheses, they consider whether there is sufficient evidence to support delineating at least the number of spatial units hypothesized. If a spatial unit hypothesis is accepted, experts can decide if they want to test a more complex hypothesis (i.e., with more spatial units). Delineating spatial units for Lake Erie Cisco involved seven major steps (see Appendix A), including pre-workshop steps, which crucially involved assembling an expert panel to conduct the assessment, and four steps (steps 4-7) based on the “Investigate, Discuss, Estimate, and Aggregate” (IDEA) Protocol for expert elicitation that occurred during spring 2024 via in-person and virtual workshops (Hemming et al. 2018).

## 2.2 Unoccupied spatial unit criteria

Prior to the spatial unit delineation workshop, the expert panel determined there was little evidence of contemporary occupancy of Lake Erie by Cisco. Therefore, unoccupied spatial unit hypotheses were formulated as the starting point for the formal assessment. Two criteria must be met to delineate an unoccupied spatial unit: (1) historical occupancy of the study area by focal organisms (Table 1) and (2) lack of contemporary occupancy of the study area by the focal organisms (Table 2). An additional criterion of reproductive isolation must be met to delineate multiple unoccupied spatial units within the assessment area (Table 3). The reproductive isolation criterion does not need to be tested to delineate a single unoccupied spatial unit and reproductive isolation between organisms within the study area relative to adjacent areas is not required (see Ackiss et al. 2023 for rationale). Criteria and lines of evidence are defined in Appendix A Table 1 and data types are defined in Appendix B Table 2.

## 2.3 Determining support for spatial unit criteria

Experts individually assigned scores to each data type that reflected the level of support they thought the data type provided for a line of evidence (data deficient = no score, no support = 0, low support = 1, moderate support = 2, and high support = 3). Then, individual scores from experts were averaged to determine the collective level of support each data type provided for a line of evidence (step 7 in section 2.1). Predetermined weights from Ackiss et al. (2023) were then applied to the average scores for each data type to generate final weighted average data type scores. Data type weights are based on their relevance, strength, and reliability in the context of the line of evidence in question. Data type weights are shown in Tables 1-3 and Ackiss et al. (2023) provide an in-depth explanation of data type weights selected for spatial unit delineation. For each line of evidence, a single categorical “rank” was assigned by averaging the weighted average data type scores, then rounding this number to the nearest rank. For example, a line of evidence score of 2.5 would be rounded to 3 (i.e., rank = high support). Data deficiencies are also tracked. A criterion is met if at least one line of evidence is assigned a moderate or high level of support.

## 3. RESULTS AND DISCUSSION

### 3.1 Expert panel and assessment facilitators

The expert panel was composed fourteen members representing State, Provincial, Federal, First Nations, and academic institutions and agencies: Ryan Lauzon (Chippewas of Nawash Unceded First Nation), Chris Vandergoot (Great Lakes Fishery Commission and Michigan State University), Dan Yule (US Geological Survey), Mark Dufour (US Geological Survey), Robin DeBruyne (US Geological Survey), Tom MacDougall (Ontario Ministry of Natural Resources and Forestry), Pascal Wilkins (New York State Department of Environmental Conservation), Andy Cook (Ontario Ministry of Natural Resources and Forestry), Justin Chiotti (US Fish and Wildlife Service), Joe Schmitt (US Geological Survey), James Roberts (US Geological Survey), John Buszkiewicz (Michigan Department of Natural Resources), Ann Marie Gorman (Ohio Department of Natural Resources), and Nick Mandrak (University of Toronto). The expert panel attended a workshop on February 5 and 6, 2024, to formulate and assess a one-unoccupied spatial unit hypothesis for Lake Erie Cisco. During this workshop, the panel determined that multi-spatial unit hypotheses should also be evaluated. Therefore, a virtual meeting was held March 7<sup>th</sup> 2024 to formulate two- and three-unoccupied spatial unit hypotheses of Lake Erie Cisco, which were refined and formally tested during a second workshop that was held virtually on April 2<sup>nd</sup> 2024.

The expert panel was supported by a facilitation team that included Josh Egan (Great Lakes Fishery Commission), Andrew Muir (Great Lakes Fishery Commission), Amanda Ackiss (US Geological Survey), Renee Renauer-Bova (Great Lakes Fishery Commission), Katie Anweiler (US Geological Survey), Katelyn King (University of Michigan), Cory Brant (US Geological Survey), and Karen Alofs (University of Michigan).

### 3.2 Data synthesis

Facilitators compiled a catalog of 53 references relevant to the spatial unit assessment with input from the expert panel (Tables 1-3). The CORHIST database (Brant et al. 2024) is an update of the review of historical accounts of Lake Erie Cisco spawning by Goodyear et al. (1982) containing additional information and georeferences. Georeferences for spawning occurrence data were obtained from CORHIST when available and both CORHIST and the original sources of spawning data were cited in these situations. Scientists with unpublished data also presented information to the expert panel. Summarized information from all sources informed the spatial unit delineations made by the expert panel.

**Table 1.** Information synthesis for the “Historically viable population” criterion to assess spatial units for Cisco *Coregonus artedi* in Lake Erie. References (n = 33) organized by line of evidence and data type. The expert panel reviewed all sources in detail and the data type narratives presented here only briefly summarize key information. Data type weights are shown before references in parentheses: + = weight of one applied to data type and ++ = weight of two applied to data type. Weights are not applied when data types are scored as data deficient. Gray shaded cells indicate the data type was not applicable to assess the line of evidence. Data deficient means that no data of a particular type were available at the time of assessment.

Data type	Line of evidence		
	Non-ephemeral presence	Reproduction	Genetic / omic
<b>Harvest</b>	(+): Milner (1874); Hardin (1894); Koelz (1926); U.S. Bureau of Fisheries (1928); Van Oosten (1930); Scott (1951); Hartman (1973); Regier and Hartman (1973); Cox (2016); GLFC (2022)		
<b>Survey</b>	(++): Kendall & Marsh (1898)		
<b>Modeled probability of occurrence</b>	(+): K. King (Michigan Department of Natural Resources, oral personal communications, 5-6 February, 7 March, and 2 April 2024)		
<b>Demography</b>		(+): Clemens (1922); Scott (1951)	
<b>Reproductive status</b>		(++): Scott (1951); Brant et al. (2024)	
<b>Observation</b>	(+): Milner (1874); Kumlien and True (1887); Goode (1887); Post Express (1893); Hardin (1894); Wilmot and Harris (1894); Pittsburgh Press (1909); Jordan and Everman (1911); Ryall (1913); Dymond (1922); Clemens (1922); Clemens and Bigelow (1922); Van Oosten (1928); Koelz (1929); Scott (1951); Biologist’s Log (1957); Lake Erie Cisco Collections Cleveland (1960); Goodyear et al. (1982); Cox (2016)	(+): Kerr and Kerr (1860-1898); Milner (1874); Kumlien and True (1887); Snell and Collins (1890); Post Express (1893); Wilmot and Harris 1894; Rathbun and Wakeham (1897); Pittsburgh Press (1909); Ryall (1913); Clemens (1922); U.S. Bureau of Fisheries (1928); Koelz (1929); Scott (1951); Langlois (1954); R. Hile (personal communication, 1979, cited by Goodyear et al. 1982); A. Larsen (personal communication, 1979, cited by Goodyear et al. 1982); M. Trautman (personal communication, 1979, cited by Goodyear et al. 1982); Goodyear et al. (1982); Cox (2016); Brant et al. (2024)	
<b>Genetic / omic</b>			(++): A. Ackiss (U.S. Geological Survey, oral personal communications, 5-6 February, 7 March, and 2 April 2024)
<b>Telemetry</b>	(++): Data deficient		
<b>Conventional marking</b>	(+): Data deficient		
<b>Microchemistry</b>	(+): Data deficient		

**Table 2.** Information synthesis for the “Lack of contemporary occupancy” criterion to assess spatial units for Cisco Coregonus artedi in Lake Erie. References (n = 22) organized by line of evidence and data type. The expert panel reviewed all sources in detail and the data type narratives presented here only briefly summarize key information. Data type weights are shown before references in parentheses: + = weight of one applied to data type and ++ = weight of two applied to data type. Weights are not applied when data types are scored as data deficient. Gray shaded cells indicate the data type was not applicable to assess the line of evidence. Data deficient means that no data of a particular type were available at the time of assessment.

Data type	Line of evidence	
	Absence of target organisms	Genetic / omic
<b>Harvest</b>	(+): Van Oosten (1930); Hartman (1973); Regier and Hartman (1973); Cox (2016); GLFC (2022)	
<b>Survey</b>	(++): Eshenroder et al. (2023); Prichard et al. (2017); Amidon et al. (2019); Keretz (2019); Amidon et al. (2021a,b); Roseman et al. (2020); DeBruyne et al. (2022); Deller et al. (2022); Chiotti et al. (2023); Cochran and Castiglione (2023); Roberts and Schmitt (2024); Wilkins (2025)	
<b>Modeled probability of occurrence</b>	(+): Data deficient	
<b>Observation</b>	(+): Goodyear et al. (1982); Cox (2016); Coldwater Task Group (2019)	
<b>Genetic / omic</b>		(++): A. Ackiss (U.S. Geological Survey, oral personal communications, 5-6 February, 7 March, and 2 April 2024)
<b>Telemetry</b>	(++): Data deficient	
<b>Conventional marking</b>	(+): Data deficient	
<b>Microchemistry</b>	(+): Data deficient	

**Table 3.** Information synthesis for the “Reproductive isolation” criterion invoked to assess multiple spatial units for Cisco *Coregonus artedi* in Lake Erie. References (n = 10) organized by line of evidence and data type. The expert panel reviewed all sources in detail and the data type narratives presented here only briefly summarize key information. Data type weights are shown before references in parentheses: + = weight of one applied to data type and ++ = weight of two applied to data type. Weights are not applied when data types are scored as data deficient. Gray shaded cells indicate the data type was not applicable to assess the line of evidence. Data deficient means that no data of a particular type were available at the time of assessment.

Data type	Line of evidence		
	Limited movement or migration	Reproductive differences	Genetic / omic divergence
Harvest		(+): GLFC (2022)	
Survey		(++): Data deficient	
Demography		(+): Koelz (1929), Clemens (1922), Van Oosten (1930), Scott (1951)	
Reproductive status		(++): Scott (1951), Brant et al. (2024)	
Observation	(++): Post Express (1893); Pittsburgh Press (1909); Koelz (1929); Scott (1951); Goodyear et al. (1982)	(++): Post Express (1893); Pittsburgh Press (1909); Koelz (1929); Scott (1951); Goodyear et al. (1982); Brant et al. (2024)	
Genetic / omic			(++): A. Ackiss (U.S. Geological Survey, oral personal communications, 5-6 February, 7 March, and 2 April 2024)
Telemetry	(++): Data deficient	(++): Data deficient	
Conventional marking	(+): Data deficient		
Microchemistry	(+): Data deficient		

### 3.3 Focal taxon

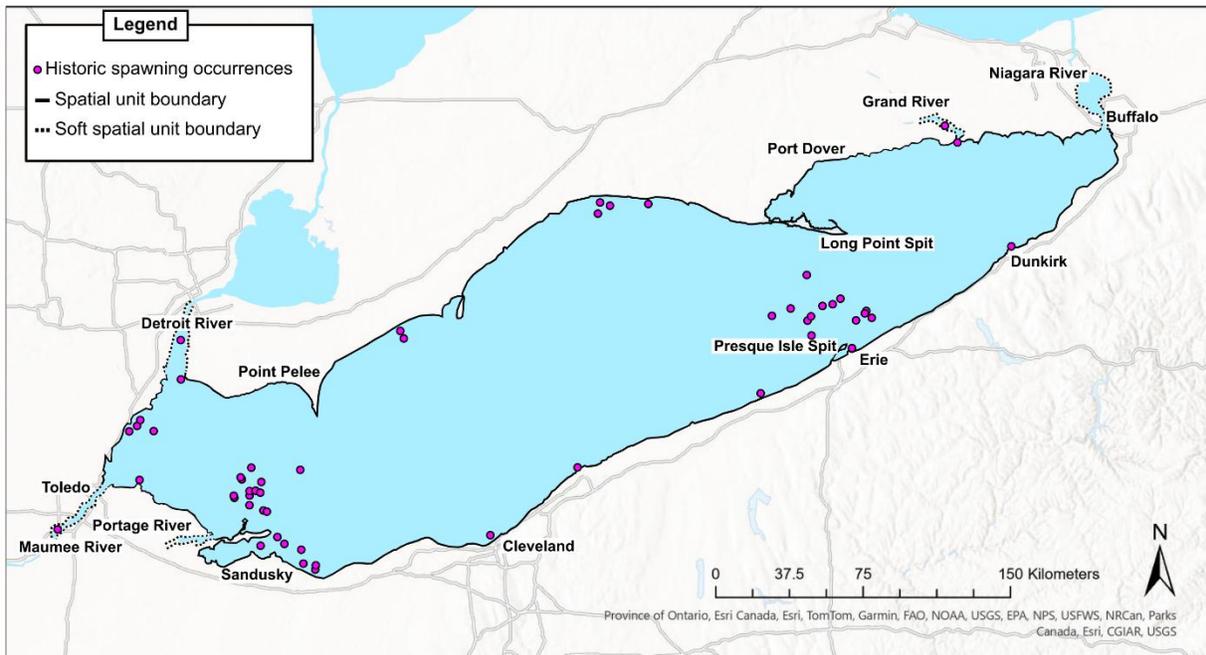
Two Cisco subspecies historically occurred in Lake Erie: *C. artedi artedi* and *C. artedi albus* (Jordan and Evermann 1911; Koelz 1929; Oldenburg et al. 2007; Eshenroder et al. 2023). *C. artedi albus* was much more abundant and dominated harvest, while *C. artedi artedi* was relatively rare and primarily occurred in the western portion of the Lake (Koelz 1929). However, the two Cisco subspecies were harvested together and could only be distinguished by subtle differences in body depth, paired fin length, adipose fin size, scale counts, and dorsal coloration (Koelz 1929). Consequently, historical fisheries and scientific data for Lake Erie Cisco were almost exclusively reported at the species level and did not distinguish between the two subspecies. Additionally, there is evidence that both forms spawned together (Koelz 1929) and to date, genetic analysis of historical samples have only identified a single Cisco genotype that appears unique to Lake Erie (A. Ackiss, U.S. Geological Survey, oral personal communications, 5-6 February, 7 March, and 2 April 2024). Therefore, workshop facilitators and the expert panel determined that it was most appropriate to conduct the spatial unit assessment at the species level (i.e., focal taxon = *C. artedi*), rather than the subspecies level.

### 3.4 Support for spatial unit hypotheses

The expert panel formulated unoccupied spatial unit hypotheses for one, two, and three spatial units within the assessment area of Lake Erie and its tributaries. Inside the boundaries of spatial units, historical Lake Erie Cisco reproductive habitat suitability models predict the distribution of spawning habitat (K. King, Michigan Department of Natural Resources, oral personal communications, 5-6 February, 7 March, and 2 April 2024). Modeled reproductive habitat suitability data were not available for Lake Erie tributaries; therefore, the expert panel included tributaries in spatial units for which there was sufficient evidence of historical spawning, but did not place hard upper boundaries on lotic portions of spatial units due to insufficient data.

#### 3.4.1 One-unoccupied spatial unit hypothesis

**Lake Erie Cisco comprised a single historical population that is no longer present (i.e., was extirpated).** The boundaries of the corresponding single-spatial unit hypothesis are defined by the shores of Lake Erie apart from locations where tributary rivers, in which Cisco historically spawned, flow into Lake Erie (Figure 1). These rivers, which are included in this spatial unit but do not have hard upstream boundaries due to insufficient data, are: (1) the Niagara River (Kerr and Kerr 1860-1898), (2) Grand River (Clemens 1922; Koelz 1929; Goodyear et al. 1982), (3) Maumee River (M. Trautman, personal communication, 1979, cited by Goodyear et al. 1982), (4) Portage River (Snell and Collins 1890), and (5) Detroit River (Milner 1874; Goode 1887; Wilmot and Harris 1894; M. Trautman, personal communication, 1979, cited by Goodyear et al. 1982).



**Figure 1.** Map of Lake Erie with historical spawning observations from CORHIST (Brant et al. 2024) and black lines demarcating the boundaries of the spatial unit proposed by the one-unoccupied spatial unit hypothesis.

### 3.4.1.1 Assessment results and discussion

**Both criteria (historically viable population and lack of contemporary occupancy) for delineating the one-unoccupied spatial unit hypothesis were met. The reproductive isolation criterion is not tested for single-unit hypotheses.**

#### Historically viable population criterion

The historically viable population criterion received high support from the genetic / omic line of evidence, moderate support from the non-ephemeral presence line of evidence, and moderate support from the reproduction line of evidence (Table 4). Given that only one line of evidence was required to achieve at least a moderate level of support, this criterion was met.

#### LINES OF EVIDENCE

##### *Non-ephemeral presence*

Harvest, modeled probability of occurrence, and observation data types provided **high support** for the non-ephemeral presence line of evidence and the survey data type provided **moderate support**.

*Harvest data (high support)* - A substantial quantity of harvest data spanning the period of 1867-2020 indicated the historical presence of Cisco throughout Lake Erie (Milner 1874; Hardin 1894; Koelz 1926; U.S. Bureau of Fisheries 1928; Van Oosten 1930; Scott 1951; Hartman 1973; Regier and Hartman 1973; Cox 2016; GLFC 2022). Lake Erie Cisco once supported the biggest commercial fishery in the Great Lakes with the largest recorded annual harvest of ~ 49 million pounds occurring in 1918 (Hartman 1973). Cisco were primarily harvested with gill, pound, and trap nets (Koelz 1926, 1929). Important historical commercial fishing ports for Cisco were widely distributed throughout Lake Erie and included Cleveland, Ashtabula, Erie, and Dunkirk in the USA and Port Maitland, Port Dover, Port Burwell, Port Stanley, and Rondeau in Canada (Koelz 1926). The distribution of fishing effort in space and time was indicative of large numbers of Cisco widely distributed throughout Lake Erie, and thus the harvest data type was assigned a score of **high support** for the non-ephemeral presence line of evidence.

*Survey data (moderate support)* - Kendall and Marsh (1898) surveyed fish during August and September 1898 in Put-In-Bay, Ohio and near Ashtabula, Ohio during October 1898. Kendall and Marsh (1898) collected ciscoes at both locations, but due to the limited temporal and spatial scope of this survey, the expert panel assigned the survey data type a score of **moderate support** for the non-ephemeral presence line of evidence.

*Modeled probability of occurrence data (high support)* – K. King (Michigan Department of Natural Resources, oral personal communications, 5-6 February, 7 March, and 2 April 2024) generated a maximum entropy (Elith et al. 2011) historical reproductive habitat suitability model using georeferenced historical Cisco spawning records from CORHIST (spawning occurrence data range: 1877-1957). Ten environmental variables were considered for maximum entropy modeling (bathymetry [meters], historical substrate [categorical variable with 14 substrate categories], predicted reefs [predicted reef suitability from 0-1], fetch [meters], tributary influence [categorical variable based on

stream order, weighted by watershed and interfluvial area, and decayed by distance and water depth], coefficient of variation of ice duration [days] during the historical time period, mean ice duration during the historical time period [days], distance to delta wetlands [kilometers], distance to protected wetlands [kilometers], and distance to open wetlands [kilometers]). Five variables with the most predictive power (coefficient of variation of ice duration during the historical time period, distance to protected wetlands, historical substrate, predicted reefs, and fetch) were selected for the final model. King et al.'s model predicted that suitable reproductive habitat for Cisco was historically distributed in the Western, Central, and Eastern basins of Lake Erie with particularly large expanses of suitable habitat in the westernmost portion of the lake near Sandusky (OH, USA) and Detroit (MI, USA), along the Long-Point-Erie Ridge (Ontario, CAN and PA, USA) Clear Creek Ridge (Ontario, CAN and PA, USA), and Pennsylvania Ridge (PA, USA), around the Presque Isle Spit (PA, USA) and north of the Long Point Spit (ON, CAN; Figure 1). The expert panel determined that the reproductive habitat suitability model strongly indicated that historically, Lake Erie had ample suitable spawning habitat to support a viable Cisco population. Therefore, the modeled probability of occurrence data type was assigned a score of high support for the non-ephemeral presence line of evidence.

*Observational data (high support)* - Many observations from the late 1800s through the mid-1900s provided evidence of the historical occurrence of Cisco throughout Lake Erie (Milner 1874; Kumlien and True 1887; Goode 1887; Pittsburgh Press (1909); Jordan and Evermann 1911; Ryall 1913; Dymond 1922; Clemens 1922; Clemens and Bigelow 1922; Van Oosten 1928; Koelz 1929; Scott 1951; Biologist's Log 1957; Lake Erie Cisco Collections Cleveland 1960; Goodyear et al. 1982; Cox 2016). Several observational reports indicated that Cisco were abundant and widely distributed in Lake Erie, which led the expert panel to assign the observational data type a score of high support for the non-ephemeral presence line of evidence.

### *Reproduction*

The observational data type provided high support to the reproduction line of evidence and demography and reproductive status data types provided moderate support.

*Observational data (high support)* - The expert panel found that observational data provided compelling evidence of the historical reproduction of Cisco in Lake Erie (Kerr and Kerr 1860-1898; Milner 1874; Kumlien and True 1887; Snell and Collins 1890; Post Express (1893); Rathbun and Wakeham 1897; Pittsburgh Press (1909); Ryall 1913; Clemens 1922; U.S. Bureau of Fisheries 1928; Koelz 1929; Scott 1951; Langlois 1954; R. Hile, personal communication, 1979, cited by Goodyear et al. 1982; A. Larsen, personal communication, 1979, cited by Goodyear et al. 1982; M. Trautman, personal communication, 1979, cited by Goodyear et al. 1982; Goodyear et al. 1982; Cox 2016). The review of historical accounts of Lake Erie Cisco spawning by Goodyear et al. (1982) and the CORHIST database (Brant et al. 2024) were foundational to this portion of the data synthesis/assessment. Plotting CORHIST spawning observations revealed several core regions that historically, were likely key areas used by Cisco for spawning (Figure 1). Additionally, observational data indicated that when Lake Erie Cisco were abundant,

they spawned in many locations throughout the lake, including outside of these core areas (Koelz 1929; Goodyear et al. 1982). Based on the large quantity of observational data indicating historical Cisco reproduction, the expert panel assigned the observational data type a score of high support for the reproduction line of evidence.

*Demographic data (moderate support)* - The expert panel found that demographic data provided evidence of multiple year classes of Cisco in Lake Erie in multiple locations, indicative of consistent reproduction. Clemens (1922) sampled Cisco during 1920 from the Central and East Basins of Lake Erie and estimated that their ages ranged from 1 to 11 years, but did not report sample sizes. Scott (1951) estimated the ages of 1200 Cisco from the eastern and western regions of Lake Erie (exact sampling locations not reported) and identified 1941, 1942, 1943, 1944, and 1945 year-classes. Age estimates by Clemens (1922) and Scott (1951) were based on scales, which are now known to underestimate Cisco ages (Aass 1972; Mills and Beamish 1980; Oyadomari and Auer 2007); therefore, more age classes were likely present. The demographic data type was assigned a score of moderate support due to the small quantity of available data in terms of numbers of fish, locations, and time points sampled as well as some uncertainty about precisely when, where, and how many fish were aged by Clemens (1922) and Scott (1951).

*Reproductive status data (moderate support)* - Scott (1951) was the only source of reproductive status data, which reported the fecundity of 16 female Cisco from the 1943 year-class and two from the 1944 year-class based on egg counts (additional methodological details were not reported). Scott (1951) did not report where specimens were collected. The expert panel found that reproductive status data indicated historical reproduction of Cisco in Lake Erie, but assigned the reproductive status data type a moderate support score for the reproduction line of evidence due to the limited quantity of data.

#### *Genetic / omic*

The genetic/omic data type provided high support to the genetic / omic line of evidence.

*Genetic / omic data (high support)* - The expert panel reviewed single nucleotide polymorphism genetic data (A. Ackiss, U.S. Geological Survey, oral personal communications, 5-6 February, 7 March, and 2 April 2024) generated using “genotyping-in-thousands by sequencing” (GT-seq) methods (Campbell et al. 2015). This dataset contained data from 176 ciscos obtained via archived scale samples (collected between 1927-1943) from fish captured throughout Lake Erie, including in the vicinities of Cedar Point, OH (n = 4), Sandusky, OH (n = 26), Vermilion, OH (n = 6), Lorain, OH (n = 10), Erie, PA (n = 74), and Dunkirk, NY (n = 19) in the USA and Port Dover, ON (n = 37) in Canada. Samples from Lake Huron were also included in this dataset for comparison. The expert panel determined that the genetic data strongly supported the historic presence of Cisco in Lake Erie and showed that Lake Erie Cisco were distinct from Lake Huron Cisco. The expert panel assigned the genetic / omic data type a score of high support for the genetic / omic line of evidence.

**Table 4. Results describing how the criterion of “historically viable population” for unoccupied spatial unit criterion for one-, two-, and three-unit hypotheses was met.** This criterion was assessed once at the lakewide scale, rather than separately for each spatial-unit hypothesis. Unweighted “data type scores” show the average scores for each data type prior to weighting and SD is the standard deviation of data type scores among individual expert panelists. “Line of evidence ranks” show the overall support a line of evidence provides for the spatial unit criterion (no support = gray shading, low support = yellow shading, moderate support = orange shading, and high support = red shading). Ranks were calculated by weighting, then averaging associated data type scores.

Line of evidence	Data type	Data type score	SD	Line of evidence rank
Non-ephemeral presence	Harvest	3.00	0.00	Moderate (2.44)
	Survey	1.79	0.63	
	Modeled prob of occurrence	2.71	0.48	
	Observational	2.93	0.28	
Reproduction	Observational	2.93	0.27	Moderate (2.41)
	Demography	2.00	0.55	
	Reproductive status	2.36	0.50	
Genetic / omic	Genetic / omic	3.00	0.00	High (3.00)

#### Lack of contemporary occupancy criterion

The lack of contemporary occupancy criterion received high support from both the contemporary absence and genetic / omic lines of evidence (Table 5). Given that one line of evidence was required to achieve at least a moderate level of support to meet this criterion, the lack of contemporary occupancy criterion was met.

#### LINES OF EVIDENCE

##### *Contemporary absence*

The harvest, survey, and observation data types provided **high support** for the contemporary absence line of evidence. The modeled probability of occurrence, telemetry, conventional marking, and microchemistry data types were **data deficient**.

*Harvest data (high support)* - The Cisco fishery crashed by the mid-1900s and 1965 is the final year any Cisco harvests were reported, including as bycatch (Hartman 1973; Regier and Hartman 1973; GLFC 2022). The collapse of the Cisco fishery was documented by many harvest data from several sources and the harvest data painted a clear picture indicative of the extirpation of Cisco from Lake Erie. Thus, experts gave the harvest data type a score of **high support** for the contemporary absence line of evidence.

*Survey data (high support)* - Decades of contemporary surveys dating back to 1978 (earlier survey work was not considered relevant for this criterion) captured only 8 Cisco (collected in 2010 [n=1], 2019 [n = 2], 2020 [n=1], 2021 [n=2], 2022 [n=1], and 2023 [n=1]) all in the Western Basin of Lake Erie (Eshenroder et al. 2023; Prichard et al. 2017; Amidon et al. 2019; Roseman et al. 2020; Amidon et al. 2021a,b; DeBruyne et al. 2022; Deller et al. 2022; Chiotti et al. 2023; Cochran and Castiglione 2023; Roberts and

Schmitt, 2024; Wilkins 2025). For this line of evidence, we considered all surveys that could have captured Cisco, even if Cisco were not targeted. Not all Lake Erie survey data has been published; however, several members of the expert panel participated in unpublished survey work and were able to confirm that these surveys captured no additional Cisco. Therefore, experts determined that these data indicated that no viable populations of Cisco currently exist in Lake Erie and consequently, assigned a score of high support to the survey data type for the contemporary absence line of evidence.

*Observational data (high support)* - The expert panel reviewed multiple sources that suggested Cisco are not currently present in Lake Erie (Goodyear et al. 1982; Cox 2016; Coldwater Task Group 2019). Furthermore, expert panel members’ own observations made while conducting Lake Erie research and management activities indicated that Cisco are rarely encountered in Lake Erie. Thus, the expert panel assigned a score of high support to the observational data type for the contemporary absence line of evidence.

*Genetic / omic*

The genetic / omic data type provided high support for the genetic / omic line of evidence.

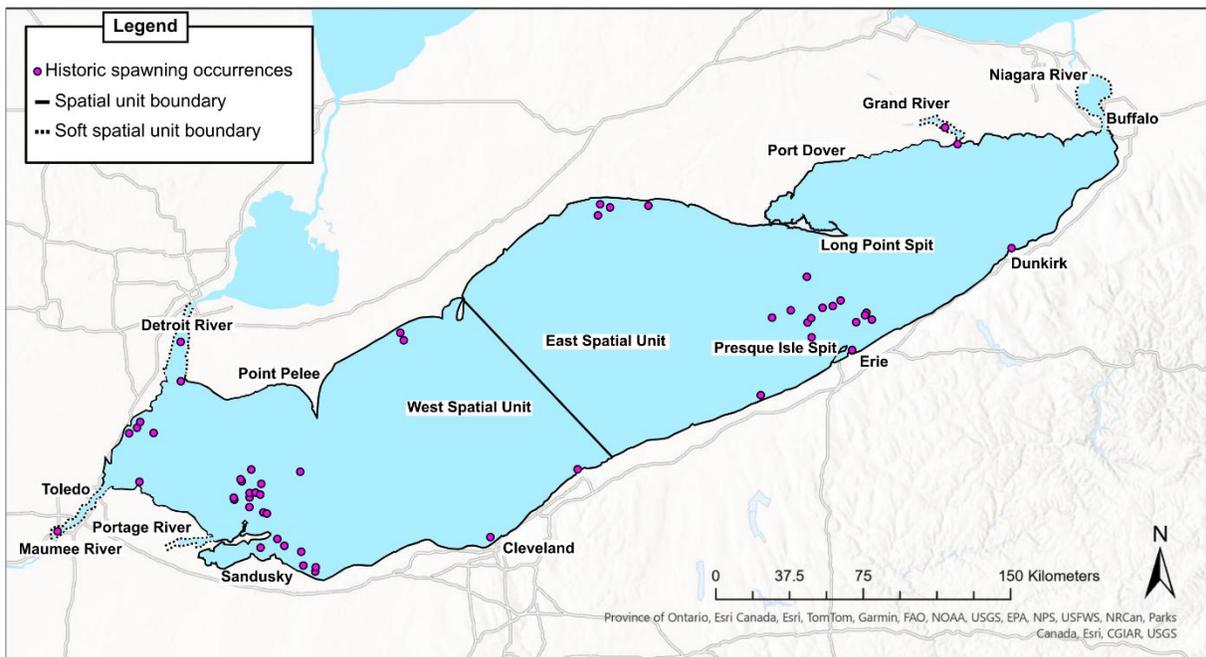
*Genetic / omic data (high support)* – A. Ackiss (U.S. Geological Survey, oral personal communications, 5-6 February, 7 March, and 2 April 2024) genotyped eight Cisco captured during contemporary survey work using GT-seq approaches (Campbell et al. 2015). All Cisco had genotypes corresponding to upstream Lake Huron Cisco, rather than historical Lake Erie Cisco, suggesting these individuals were transients to Lake Erie from Lake Huron. Therefore, experts determined that there is strong genetic / omic evidence that no viable populations of Cisco currently exist in Lake Erie and assigned the genetic / omic data type a score of high support for the genetic / omic line of evidence.

**Table 5. Results describing how the criterion of “contemporary absence” for unoccupied spatial unit criterion was met.** This criterion was assessed once at the lakewide scale, rather than separately for each spatial-unit hypothesis. Unweighted “data type scores” show the average scores for each data type prior to weighting and SD is the standard deviation of data type scores among individual expert panelists. “Line of evidence ranks” show the overall support a line of evidence provides for the spatial unit criterion (shading: no support = gray, low support = yellow, moderate support = orange, and high support = red). Ranks were calculated by weighting, then averaging associated data type scores. “-” indicates data deficiency.

Line of evidence	Data type	Data type score	SD	Line of evidence rank
Absence	Harvest	2.71	0.45	High (2.69)
	Survey	2.71	0.45	
	Modeled prob of occurrence	-	-	
	Observational	2.64	0.50	
	Telemetry	-	-	
	Conventional marking	-	-	
	Microchemistry	-	-	
Genetic / omic	Genetic / omic	2.57	0.51	High (2.57)

### 3.3.2 Two-unoccupied spatial unit hypothesis

Lake Erie Cisco comprised two historical populations that are no longer present (i.e., were extirpated). Corresponding to these populations is a West Spatial Unit comprising the Western Basin of Lake Erie and a portion of the Central Basin of Lake Erie and an East Spatial Unit comprising a portion of the Central Basin of Lake Erie and the Eastern Basin of Lake Erie (Figure 2). Each unit is comprised of areas within Lake Erie and its tributaries that historically supported Cisco reproduction. The western, northern, and southern boundaries of the West Spatial Unit and the eastern, northern, and southern boundaries of the East Spatial Unit are defined by the shores of Lake Erie, apart from where tributary rivers, in which Cisco historically spawned, flow into Lake Erie. The Maumee, Portage, and Detroit Rivers are included in the West Unit and the Grand and Niagara rivers are included in the East Unit. The boundary separating the West Spatial Unit from the East Spatial Unit (i.e., eastern boundary of the western unit and the western boundary of the eastern unit) runs diagonally southeast across the lake. The northern edge of the spatial unit boundary meets the shore northeast of Pointe aux Pins, Ontario, Canada (42.381655, -81.816360). The southern edge of the boundary meets the shore Southwest of Ashtabula, Ohio, USA (41.830376, -81.072629). The placement of the boundary between the spatial units was informed by the distribution of modeled historical reproductive habitat (spatial unit boundaries correspond with breaks in otherwise relatively continuous reproductive habitat adjacent to the shorelines of Lake Erie; K. King, Michigan Department of Natural Resources, oral personal communications, 5-6 February, 7 March, and 2 April 2024), the locations of historical spawning records (Brant et al. 2024), bathymetry, and hydrodynamic patterns (Saylor and Miller 1987).



**Figure 2.** Map of Lake Erie with historical spawning observations from CORHIST (Brant et al. 2024) and black lines demarcating the boundaries of the East and West Spatial Units proposed by the two-unoccupied spatial unit hypothesis.

### 3.3.2.2 Assessment results and discussion

**All three criteria required for delineating two unoccupied spatial units were met. Results from assessment of the historically viable population and lack of contemporary occupancy criteria were assessed once and are reported above. Results from assessment of the additional reproductive isolation criterion for delineating multiple spatial units are reported here for the two-unoccupied spatial unit hypothesis.**

#### Reproductive isolation criterion

The reproductive isolation criterion received moderate support from the limited movement or migration and reproductive differences lines of evidence and no support from the genetic / omic line of evidence (Table 6). Given that only one line of evidence was required to achieve at least a moderate level of support, the criterion for reproductive isolation between two unoccupied spatial units was met.

#### LINES OF EVIDENCE

##### *Limited movement or migration*

Observational data provided **moderate support** for the limited movement or migration line of evidence. The telemetry, conventional marking, and microchemistry data types were **data deficient**.

*Observational data (moderate support)* - Several observations indicated that some Lake Erie Cisco individuals stayed in the eastern portion of the lake year-round (non-migratory behavior), including to spawn, while others undertook a seasonal migration (migratory behavior), occupying the western portion of the lake during cooler months, including during the spawning period (November and December), and moving east during the warmest summer months, particularly August (Post Express 1893); Pittsburgh Press, 1909; Koelz 1929; Scott 1951; Goodyear et al. 1982). Experts assigned the observational data type a score of **moderate support** for the limited movement or migration line of evidence because Lake Erie Cisco exhibited both migratory and non-migratory movement patterns that may have resulted in reproductive isolation between the eastern and western portions of the lake. However, experts also identified many unresolved questions about Lake Erie Cisco movement, such as whether or not individuals consistently exhibited the same movement patterns during each reproductive cycle, or whether individuals undertook spawning migrations every year.

##### *Reproductive differences*

The harvest and observation data types provided **moderate support** for the reproductive differences line of evidence and the demography and reproductive status data types provided **low support**. The telemetry and survey data types were **data deficient**.

*Harvest data (moderate support)* - Synthesis of harvest data (GLFC 2022) suggested that there were historical differences in spawn timing between the western and eastern portions of Lake Erie. Commercial fishers often targeted Cisco when they aggregated at shallower depths for spawning (Koelz 1929). Cisco catches peaked earlier in the western

end of Lake Erie than in the eastern end, suggesting earlier spawn timing in the western end of Lake Erie than in the eastern end. The expert panel assigned a score of moderate support because differences in the timing of peak harvests between the eastern and western regions of the lake were distinct and occurred almost every year. However, the link between the timing of harvest and spawning was only sufficient to generate a score of moderate support (i.e., not all harvests were associated with spawning). For example, in some locations, peak harvests may have corresponded with fish aggregating to spawn, while in others, they may have been associated with schools of fish moving through an area en route to spawning grounds.

*Observational data (moderate support)* - Several reports ranging from the late 1800s to the mid-1900s indicated that fish spawned between mid-November to early December, spawning earlier in the western end of Lake Erie than the eastern end (Post Express 1893; Pittsburgh Press, 1909; Koelz 1929; Scott 1951; Goodyear et al. 1982). Experts assigned observational data a score of moderate support for the reproductive differences line of evidence because there were several reports of east-west differences in spawn timing, but also indications that the east-west difference in spawn-timing may have represented a gradient, rather than discrete differences in spawn timing between the two hypothesized spatial units.

*Demographic data* - Demographic data (Clemens 1922; Scott 1951) did not suggest reproductive differences between the hypothesized spatial units. Demographic data were limited in number and sampling did not allow for robust comparisons between different regions of Lake Erie. Clemens (1922) sampled Cisco during 1920 from the Central and East Basins of Lake Erie and estimated that their ages ranged from 1 to 11 years, but did not report data in a way that allowed for comparisons of age structure between the two hypothesized spatial units. Scott (1951) published a fish age dataset that allowed for comparisons between the hypothesized West and East spatial units, but data were limited to the 1941, 1942, 1943, 1944, and 1945 year-classes and found that both sides of the lake had very similar age structures. Hence, the panel scored the demographic data type as low support for the reproductive differences line of evidence.

*Reproductive status data (low support)* - Reproductive status data did not provide evidence of reproductive differences between the hypothesized spatial units. Reproductive status data were only reported by a single study: Scott (1951) only estimated the fecundity of 18 cisco (12 age 2 and 6 age 3 Cisco based on egg counts) and did not report specific collection locality information. Therefore, the panel scored the demographic data type and reproductive status data type as low support for the reproductive differences line of evidence.

#### *Genetic / omic divergence*

Genetic/omic data provided **no support** for the genetic / omic divergence line of evidence.

*Genetic / omic data (no support)* - There were no distinct groupings detected in the unique Lake Erie Cisco genetic cluster in historical single nucleotide polymorphism data

(A. Ackiss, U.S. Geological Survey, oral personal communications, 5-6 February, 7 March, and 2 April 2024). Therefore, the expert panel assigned the genetic / omic data type a score of no support for the genetic / omic divergence line of evidence.

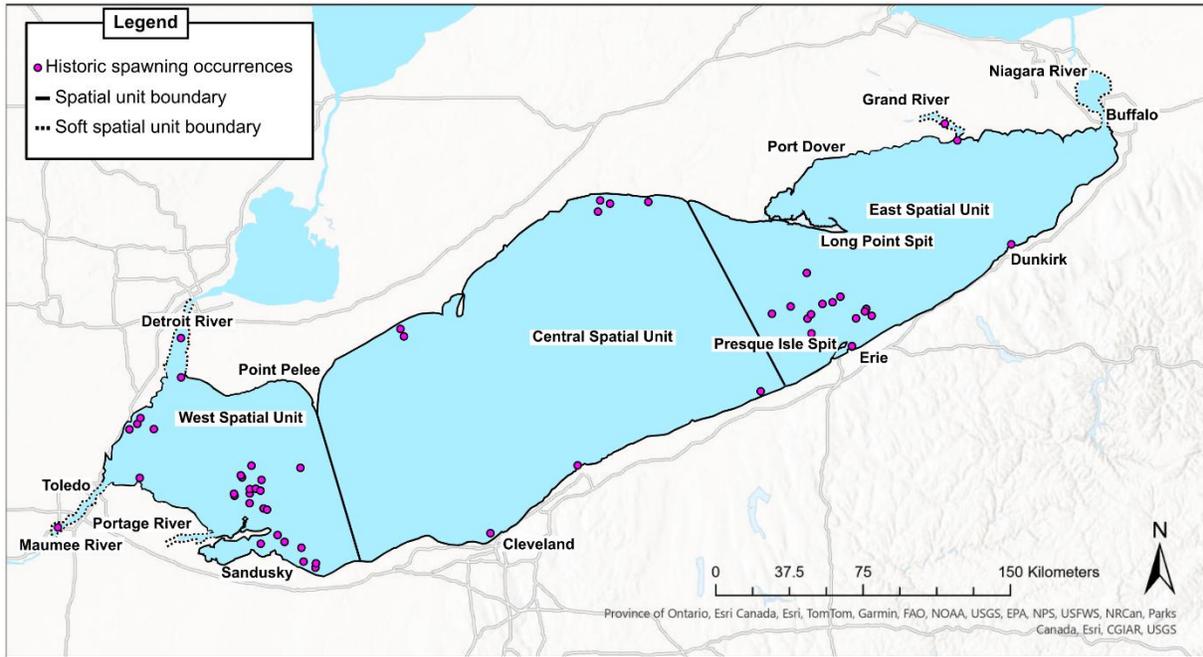
**Table 6. Results showing how the “reproductive isolation” criterion for the two-spatial unit hypothesis was met.** Unweighted “data type scores” show the average scores for each data type prior to weighting and SD is the standard deviation of data type scores among individual expert panelists. “Line of evidence ranks” show the overall support a line of evidence provides for the spatial unit criterion (shading: no support = gray, low support = yellow, moderate support = orange, and high support = red). Ranks were calculated by weighting, then averaging associated data type scores. “-” indicates data deficiency.

Line of evidence	Data type	Data type score	SD	Line of evidence rank
Limited movement or migration	Observational	1.70	0.64	Moderate support (1.70)
	Telemetry	-	-	
	Conventional marking	-	-	
	Microchemistry	-	-	
Reproductive differences	Harvest	2.00	0.75	Moderate support (1.56)
	Observational	1.90	0.70	
	Survey	-	-	
	Demography	0.70	0.78	
	Reproductive status	1.44	0.68	
	Telemetry	-	-	
Genetic / omic divergence	Genetic / omic	0.10	0.30	No support (0.10)

### 3.3.3 Three-unoccupied spatial unit hypothesis

**Lake Erie Cisco comprised three historical populations that are no longer present (i.e., were extirpated). West, Central, and East Spatial Units correspond to these hypothesized populations.** The western, northern, and southern boundaries of the West Spatial Unit, northern and southern boundaries of the Central Spatial Unit, and the eastern, northern, and southern boundaries of the East Spatial Unit are defined by the shores of Lake Erie, apart from locations where tributary rivers, in which Cisco historically spawned, flow into Lake Erie (Figure 3). The Maumee, Portage, and Detroit Rivers are included in the West Unit, the Grand River is included in the Central Unit, and the Niagara River is included in the East Unit. The boundary separating the West Unit from the Central Unit (i.e., eastern boundary of the West Unit and the western boundary of the Central Unit) runs diagonally southeast across the lake. The northern edge of this boundary meets the shore at Point Pelee, Ontario, Canada (41.908746, -82.509150). The southern edge of this boundary meets the shore in Vermilion, Ohio, USA (41.430067, -82.313757). The boundary separating the Central Unit from the East Unit meets the shore in the north southeast of Port Burwell, Ontario, Canada (42.636578, -80.807785) and meets the shore in the south near Lake City, Pennsylvania, USA (42.029703, -80.352294). Placement of the spatial unit boundaries was informed by bathymetry, the distribution of modeled historical reproductive habitat (K. King, Michigan Department of Natural Resources, oral personal communications, 5-6 February, 7 March, and 2 April 2024), the locations of historical spawning records (Brant et al. 2024), and hydrodynamic patterns (Saylor and Miller 1987). The boundaries

correspond with breaks in otherwise relatively continuous reproductive habitat adjacent to the shorelines and reefs as well as the boundaries between the west, east, and central basins of Lake Erie.



**Figure 3.** Map of Lake Erie with historical spawning observations from CORHIST (Brant et al. 2024) and black lines demarcating the boundaries of the East, Central, and West Spatial Units proposed by the three-unoccupied spatial unit hypothesis.

### 3.3.3.2 Assessment results and discussion

**The reproductive isolation criterion for delineating three unoccupied spatial was not met. Results from assessment of the historically viable population and lack of contemporary occupancy criteria were assessed once and are reported above. Results from assessment of the additional reproductive isolation criterion for delineating multiple spatial units are reported here for the three-unoccupied spatial unit hypothesis.**

#### Reproductive isolation criterion

The reproductive isolation criterion received low support from the limited movement or migration and reproductive differences lines of evidence and the genetic / omic divergence criterion received no support from the genetic / omic line of evidence (Table 7).

#### LINES OF EVIDENCE

##### *Limited movement or migration*

Observational data provided **low support** for the limited movement or migration line of evidence. The telemetry, conventional marking, and microchemistry data types were **data deficient**.

*Observational data (low support)* - Observational data indicated that historically, a subset of Lake Erie ciscos undertook seasonal spawning migrations (Post Express 1893; Pittsburgh Press 1909; Koelz 1929; Scott 1951; Goodyear et al. 1982). However, the expert panel did not find evidence for three distinct migratory patterns or other movements indicative of three spatial units, and therefore assigned a score of low support to the observational data type for the limited movement or migration line of evidence.

#### *Reproductive differences*

Harvest, observation, demography, and reproductive status data types provided **low support** for the reproductive differences line of evidence. The telemetry and survey data types were **data deficient**.

*Harvest data (low support)* - Harvest data indicated that spawn timing was different in the eastern and western portions of the lake, but the expert panel found very limited evidence of three distinct spawning windows corresponding to the three hypothesized spatial units (i.e., differences between east and west were apparent, but not east versus central or west versus central; GLFC 2022). Therefore, the panel scored the harvest data type as low support for the reproductive differences line of evidence.

*Observational data (low support)* - Observational data suggested differences in spawn timing between the eastern and western portions of Lake Erie. However, there was little evidence of three distinct spawning periods associated with each of the three hypothesized spatial units (Post Express 1893; Pittsburgh Press 1909; Koelz 1929; Scott 1951; Goodyear et al. 1982). This led the panel to score the observational data type as low support for the reproductive differences line of evidence.

*Demographic data (low support)* - Demographic data did not reveal discrete demographic differences between the three hypothesized spatial units (Clemens 1922; Scott 1951). Clemens (1922) sampled Cisco during 1920 from the Central and East Basins of Lake Erie and estimated that their ages ranged from 1 to 11 years, but did not report data in a way that allowed for comparisons of age structure between the two hypothesized spatial units. Scott (1951) published fish age data, but this dataset did not allow for comparisons between all three hypothesized spatial units. Hence, the expert panel scored the demographic data type as low support for the reproductive differences line of evidence.

*Reproductive status data (low support)* - Reproductive status data did not allow for comparisons between the three hypothesized spatial units. A single study (Scott 1951) reported reproductive status data (fecundity data from 18 female Cisco), but did not provide specific collection locality information. Thus, the panel scored the reproductive status data type as low support for the reproductive differences line of evidence.

#### *Genetic / omic divergence*

Genetic / omic data provided **no support** for the genetic / omic divergence line of evidence.

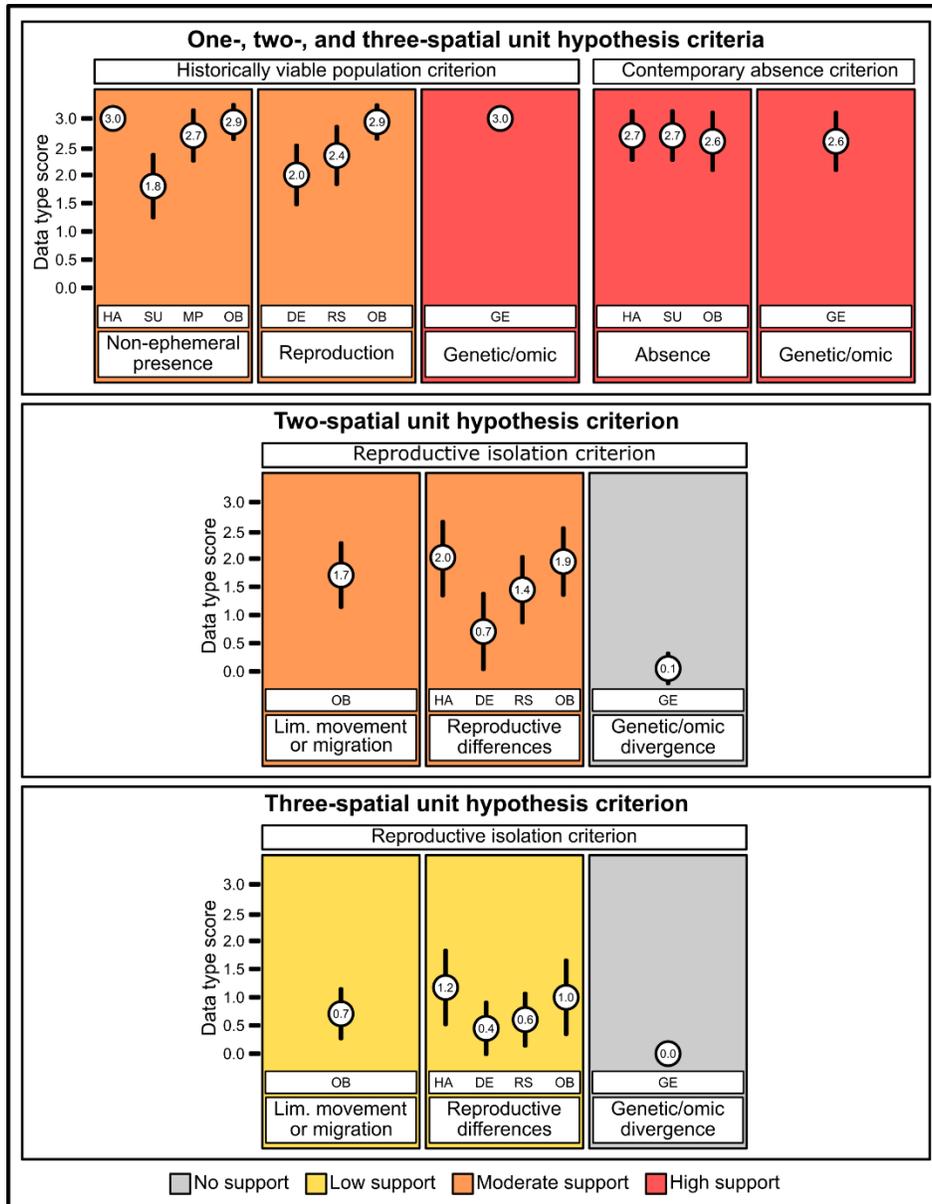
*Genetic / omic data (no support)* - Additional genetic groups corresponding to the three hypothesized spatial units were not detected within the unique Lake Erie Cisco genetic cluster in historical single nucleotide polymorphism data (A. Ackiss, U.S. Geological Survey, oral personal communications, 5-6 February, 7 March, and 2 April 2024). Consequently, the expert panel scored the genetic / omic data type as no support for the genetic / omic divergence line of evidence.

**Table 7. Results showing that the “reproductive isolation” criterion for the three-spatial unit hypothesis was not met.** Unweighted “data type scores” show the average scores for each data type prior to weighting and SD is the standard deviation of data type scores among individual expert panelists. “Line of evidence ranks” show the overall support a line of evidence provides for the spatial unit criterion (shading: no support = gray, low support = yellow, moderate support = orange, and high support = red). Ranks were calculated by weighting, then averaging associated data type scores. “-” indicates data deficiency.

Line of evidence	Data type	Data type score	SD	Line of evidence rank
Limited movement or migration	Observational	0.70	0.46	Low support (0.70)
	Telemetry	-	-	
	Conventional marking	-	-	
	Microchemistry	-	-	
Reproductive differences	Harvest	1.20	0.75	Low support (0.79)
	Observational	1.00	0.77	
	Survey	-	-	
	Demographic	0.40	0.49	
	Reproductive status	0.56	0.50	
	Telemetry	-	-	
Genetic / omic divergence	Genetic / omic	0.00	0.00	No support (0.00)

### 3.4 Delineated unoccupied Lake Erie Cisco spatial units

The most complex spatial unit hypothesis for which the criteria are met determines the spatial units that are delineated (Ackiss et al. 2023). This assessment determined that the criteria were met for the one- and two-unoccupied spatial unit hypotheses, but not the three-unoccupied spatial unit hypothesis (Tables 4-7; Figure 4). Therefore, **two spatial units are delineated for Lake Erie Cisco** as described in section 3.3.2 above. These spatial units should be viewed as the most complex hypothesis for historical Lake Erie Cisco population structure that was supported by the data that were synthesized for this assessment. If new data become available, future assessments can revise Lake Erie Cisco spatial units. Furthermore, Indigenous Knowledge may also delineate spatial units for Lake Erie Cisco in the future, which may or may not be congruent with the spatial units delineated using Western Science.



**Figure 4.** Summary of spatial unit assessment results. The “historically viable population” and “contemporary absence” criteria were assessed once for the entirety of the unoccupied space and applied to the one-, two-, and three-unoccupied spatial unit hypotheses. The “reproductive isolation” criterion was assessed separately for the two- and three-unoccupied spatial unit hypotheses. Circles show the average “data type scores” for each data type prior to weighting and vertical black bars show the standard deviation (SD) of data type scores among individual expert panelists. Data type codes: HA = harvest, SU = survey, MP = modeled probability of occurrence, OB = observation, DE = demography, RS = reproductive status, and GE = genetic / omic. Data deficient data types are not shown (See Tables 4-7). Shading within each line of evidence box corresponds to the “line of evidence rank,” which shows the overall support a line of evidence provides for the spatial unit criterion (shading: no support = gray, low support = yellow, moderate support = orange, and high support = red). Ranks are calculated by weighting, then averaging associated data type scores.

### 3.5 Key knowledge gaps

Many knowledge gaps inhibited spatial unit delineation (see data poor and data deficient data types in tables 1-3). Knowledge gaps included the use of rivers by Cisco and connections between Lakes Erie and Huron, as well as uncertainties with respect to historical associations between phenotypic and genotypic variation in Lake Erie Cisco (see eleven key questions related to these topics below). Resolving these, and other knowledge gaps can facilitate future refinements to Lake Erie Cisco spatial units and further facilitate restoration planning.

#### Movement of Cisco between Lake Erie and Lake Huron

1. Did Cisco regularly move between Lakes Huron and Erie?
2. If Cisco did regularly move between Lakes Huron and Erie, were these movements associated with foraging, spawning, or both?
3. If Cisco did regularly move between Lakes Huron and Erie, were these movements associated with hybridization between fish of Lake Huron origin and fish of Lake Erie origin?
4. Are the fish collected in Lake Erie during the contemporary period, preliminarily identified as Cisco, migrants from Lake Huron (an idea mentioned by Koelz 1929) or Lake Erie residents?

#### Use of rivers by Lake Erie Cisco

5. Did Cisco that used rivers represent distinct (sub)populations?
6. Which rivers did Cisco use for spawning?
7. How far did Cisco travel up rivers and where were the key spawning areas within rivers?
8. Did river-spawning Cisco individuals reproduce during the same time periods as nearby lake-spawning individuals?

#### Genotypic and phenotypic diversity

9. Were *C. artedi artedi* and *C. artedi albus* genetically distinct?
10. Were there distinct genetic clusters in Lake Erie Cisco in addition to the potential genetic distinctiveness of the two subspecies?
11. How distinct were the ecologies *C. artedi artedi* and *C. artedi albus*? Historical data were almost exclusively reported at the species level (i.e., did not distinguish between the two subspecies). Therefore, ecological differences between the subspecies are largely unknown.

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# Appendices

## Appendix A: Spatial unit delineation steps

### Pre-workshop steps

- (1) *Initial preparations*: Facilitators synthesized data for Lake Erie Cisco from peer-reviewed articles, gray literature (e.g., agency reports), online databases (e.g., GLFC 2022 and Brant et al. 2024), and museum records. Data pertaining to Cisco outside of Lake Erie and data from other Lake Erie fishes (i.e., proxy data) were not used for this assessment following the recommendation of the team responsible for spatial unit delineation method development. Facilitators generated a data synthesis that concisely summarized key information. Then, facilitators assembled an expert panel with a wide range of expertise related to Lake Erie Cisco and the data types evaluated during this assessment (see section 3.1). The experts reviewed the data synthesis and added relevant references, unpublished data, and personal observations that were missing.
- (2) *Formulate a priori spatial unit hypotheses*: Meetings were held during which the expert panel formulated three *a priori* unoccupied spatial unit hypotheses for Lake Erie Cisco to formally test during the spatial unit delineation workshop based on the data synthesis and their expert knowledge. This step, and the following steps, may be repeated in an iterative manner, if necessary, which was the case for this assessment; After assessing a one-spatial unit hypothesis, these steps were repeated to facilitate subsequent testing of two- and three-spatial unit hypotheses.
- (3) *Revise data synthesis*: Facilitators restructured the data synthesis to conform to the knowledge hierarchy for unoccupied spatial units (see section 2.2 and Tables 2-4) and aid interpretation of data in the context of the *a priori* hypotheses.

### Spatial unit delineation workshop (IDEA Protocol)

- (4) *Investigate*: Experts reviewed the revised data synthesis, then made any necessary adjustments to the *a priori* spatial unit hypotheses. Then, for each hypothesis, experts independently and anonymously assigned scores to data types based on the amount of support they thought data provided for the line of evidence under consideration (data deficient = no score, no support = 0, low support = 1, moderate support = 2, and high support = 3).
- (5) *Discuss*: After the initial round of scoring, experts discussed their scores, including points of consensus and conflict.
- (6) *Estimate*: A final round of independent scoring was conducted in which experts could retain their original scores, or change them based on the discussion. For all three spatial unit hypotheses assessed, steps 5-7 were repeated for every data type associated with each line of evidence for all criteria (Tables 1-4).
- (7) *Aggregate*: Facilitators aggregated individual scores using the methods described in section 2.3 to determine the level of support the expert panel collectively thought data types provided for lines of evidence (i.e., weighted average data type scores) and lines of evidence provided for criteria (i.e., line of evidence ranks).

## Appendix B: Definitions

**Appendix B Table 1.** Definitions of unoccupied spatial unit criteria and lines of evidence.

<b>Historical occupancy criterion:</b> historical (i.e., prior to European colonization) presence of a naturally reproducing (sub)population over an extended period of time.	
<b>Line of evidence</b>	<b>Definition</b>
Non-ephemeral historical presence	Persistent historical presence of the focal organism.
Reproduction	Historical occurrence of natural reproduction indicative of a reproductively viable population or population segment of the focal organism.
Genetic / omic	Genetic or other “omic” data derived from the underlying genetic architecture that support the historical occurrence of the focal organism.
<b>Lack of contemporary occupancy criterion:</b> Focal organism is entirely absent from the focal area or only ephemerally present.	
<b>Line of evidence</b>	<b>Definition</b>
Absence of target organism	Lack of persistent contemporary presence of focal organism.
Genetic / omic	Genetic or other “omic” data derived from the underlying genetic architecture that support the contemporary absence of the focal organism.
<b>Historical reproductive isolation criterion:</b> historical (i.e., prior to European colonization) reproductive isolation between hypothesized spatial units. Reproductive isolation need not to have been absolute.	
<b>Line of evidence</b>	<b>Definition</b>
Limited movement and/or migration	Limited movement of focal organism between hypothesized spatial units during the reproductive period and/or migrations to disparate localities for reproduction.
Reproductive differences	Differences between hypothesized spatial units in reproductive time, habitat, behavior, or morphology of reproductive organs that lead to assortative or non-random mating.
Genetic / omic divergence	Genetic or other “omic” data derived from the underlying genetic architecture indicative of historical reproductive isolation among hypothesized spatial units.

**Appendix B Table 2.** Definitions of data types associated with unoccupied spatial unit criteria and lines of evidence.

Term	Definition
Conventional marking	Information about the movement/occurrence of focal organism gained by marking individuals (e.g., fin clip, elastomer tag), typically via mark-recapture approaches.
Demography	Demographic data, including births, deaths, age structure at specific locations, etc.
Genetic/omic	Genetic or ‘omic’ data, which encompasses a broad subset of data types including genomic, transcriptomic, proteomic, lipidomic, and metabolomic, that describe or derive from the underlying genomic architecture of a species.
Harvest	Data derived from recreational or commercial fisheries, such as catch quantity data.
Microchemistry	Data characterizing the chemical signatures in tissues that can provide information about occurrence, movement and barriers to movement, and resource use.
Modeled probability of occurrence	Models of the probability of the historical non-ephemeral occurrence of focal organism.
Observation	Local knowledge (e.g., interviews of fishers) or other qualitative or quantitative data that are not harvest-associated and do not meet requirements of a formal survey.
Reproductive status	Data describing the reproductive status of individuals, such as fecundity data, gonadosomatic indices, state of maturity, and maturity schedules.
Resource partitioning	Information about organismal resource use that describes variation in fundamental niches (i.e., heritable phenotypic variation), rather than in realized niches, and may represent local adaptation. Data could include trophic ecology, diet, feeding; stable isotopes; fatty acids, contaminants.
Survey	Fisheries independent data collected using approaches that attempt to address biases that may result from methodology, temporal, or spatial factors.
Telemetry	Information about the movement/occurrence of focal organism gained via telecommunication.