

MONOGRAPH

CISCOES

(*Coregonus*, Subgenus *Leucichthys*)
OF THE LAURENTIAN GREAT LAKES AND LAKE NIPIGON



Great Lakes Fishery Commission

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CISCOES

(*Coregonus*, Subgenus *Leucichthys*)

OF THE LAURENTIAN GREAT LAKES AND LAKE NIPIGON

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Picking Bait Nets

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MAP OF PLACE NAMES



DEDICATIONS

WALTER N. KOELZ

Walter N. Koelz was born in 1895 in Waterloo, Michigan, in a home located just west of Ann Arbor where he spent a good deal of his life, including his final years. His undergraduate work was at Olivet College and his graduate work at the University of Michigan under the mentorship of Jacob Reighard. He was awarded a PhD in 1920. His graduate work and continuing research as curator of fishes at the University of Michigan Museum of Zoology and as an employee of the U.S. Bureau of Fisheries focused in particular on the ciscoes (subgenus *Leucichthys*) of the Great Lakes and Lake Nipigon, the systematics of which were poorly described. His seminal work, *Coregonid Fishes of the Great Lakes*, was published in 1929. This monograph captured well the diversity of what had been a bewildering hodge-podge of conflicting and incomplete descriptions and remains today a remarkable account of Great Lakes natural history. Here, he described nine species of cisco, naming four along with 12 subspecies. These taxa were later reduced to seven, but herein were increased to eight, which are now referred to as forms. What he classified as subspecies are viewed currently as distinct populations that represented important elements of an endemic fish fauna.

This monograph was his last publication on fishes. His interests diverged to birds, plants, and cultural artifacts. Early in his career, in 1925, he joined the MacMillan-Byrd Expedition to the American Arctic, representing the bureau as the ship's naturalist. His forays outside North America began in 1930 and continued off and on until 1953. During this period, he collected prodigiously, tramping through India, Iran, Nepal, and Tibet. He is said to have collected over 50,000 birds and tens of thousands of plants. His collected materials reside in the Kew Botanical Gardens (London); the New York Botanical Gardens; the American Museum of Natural History; and at the University of Michigan Museum of Zoology, Museum of Anthropology, and Herbarium. He was said to be reclusive and eccentric, refusing to wear shoes even during winter, living in an unheated house, and forgoing owning a car. After his death in 1989, his personal artifacts, museum-quality collectibles, were auctioned off by Christie's of New York, and the proceeds were bequeathed to the Nature Conservancy, an organization that he deeply respected. He unquestionably led an unusual, even romantic, life and was said to have been perhaps the last Victorian explorer.

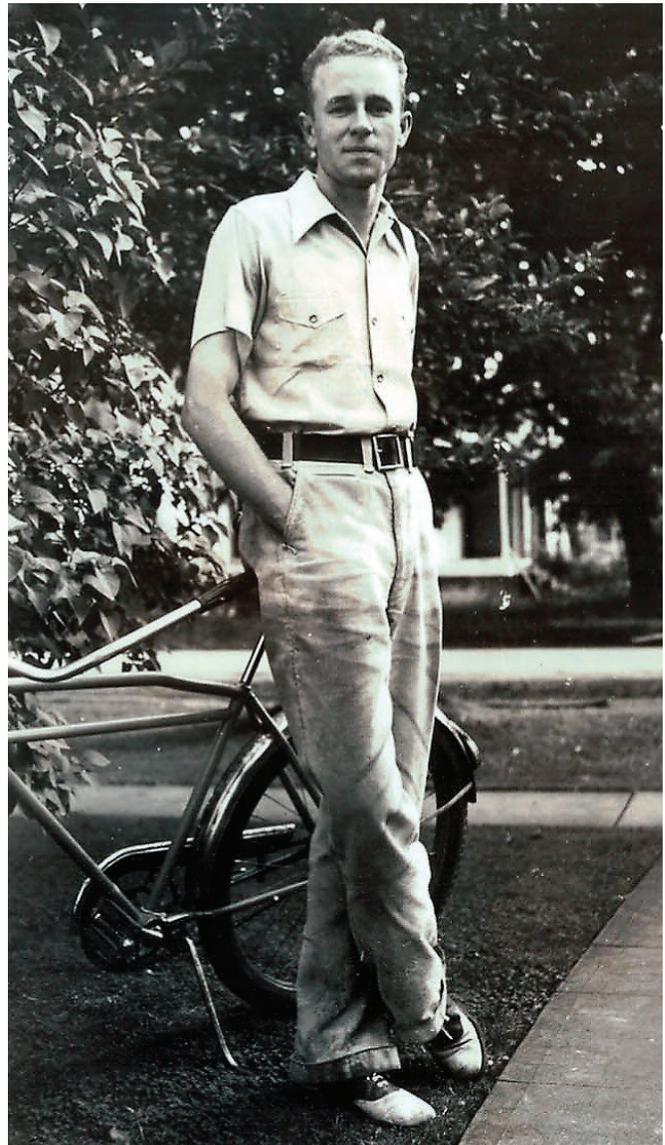


Adapted from the Bentley Historical Library website (photograph courtesy of the Bentley Historical Library).

STANFORD H. SMITH

Stanford H. Smith was born in Twin Falls, Idaho, in 1920. His mother was a school teacher and his father a professor of entomology at Stanford University, for which he was named. Following completion of undergraduate studies at Oregon State University in 1943, he conducted studies for the U.S. Fish and Wildlife Service in California on trout and salmon populations impacted by dams. Leaving California in 1949 but not the service, he worked on advanced degrees at the University of Michigan, receiving a PhD in zoology in 1954 under Jacob Reighard, who earlier had mentored Walter Koelz. Smith's dissertation on the lake herring (now Cisco) of Green Bay, Lake Michigan, remains a formative work on the natural history of this species in the Great Lakes. Just when he matriculated from the university, the service launched the R/V *Cisco*—a fortuitous event—he was put in charge of its fishery and limnological investigations. Now he was in a position to direct research, and one outcome of special relevance to the current study was the Great Lakes Cisco Project. During 1955-1972, he continued the work of Koelz, compiling morphological data on Great Lakes ciscoes. These populations were then suffering diminishment and threatened even with extirpation.

He continued work supervising field research up to 1966 with what became the Bureau of Commercial Fisheries, after which he undertook a senior scientist role, producing among others his seminal paper in 1968 on fishery exploitation and species succession. Then misfortune! Changes in leadership at the Ann Arbor laboratory resulted in his departure in 1972 for a more administrative position with the regional office of the same agency. He was at the height of his scientific prowess when he departed and presumably had much more to contribute, but he never wrote another paper (the Great Lakes Fishery Commission published in 1995 a manuscript that he had written much earlier). Before leaving, however, Stanford archived his extensive collections of ciscoes at the University of Michigan Museum of Zoology where they remain. From 1977 until his death in 2013, the Smiths traveled in small motor homes throughout Australia, Europe, and Alaska. Smith was a great naturalist, extraordinarily inquisitive, and a lover of nature. We are grateful to have this opportunity to honor him in a study that uses so much of the data he generated. One can only wonder what he would have contributed had he been able to continue his work on the ciscoes of the Great Lakes.



Photograph courtesy of Stanford H. Smith's daughter, Karen Risch.

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Special thanks to Howard Sivertson of the Sivertson Gallery—Art of the North (www.sivertson.com) for his remarkable paintings depicting the historical cisco fishery of Isle Royale, Lake Superior. We are grateful to the following for providing specimens from the noted locations: Joanne and Kendall Dewey from their fishery on the Bay of Quinte, Lake Ontario; Chris Olds and Steve Lenart of the U.S. Fish and Wildlife Service from Lake Huron; Randy Claramunt of the Michigan Department of Natural Resources from Lake Michigan; the skippers and crews of the R/Vs *Everett H* from Lake Superior, *Grayling* from Lake Huron, and *Nipigon Osprey* from Lake Nipigon. Whitney Woelmer of the U.S. Geological Survey digitized data from Koelz (1929) and from the Great Lakes Cisco Project and thereby made a particularly important contribution. Kim Caldwell, Janice McKee, and Cheryl Widdifield of Fisheries and Oceans Canada and Scott Reid of the Ontario Ministry of Natural Resources and Forestry contributed morphometric data from thousands of ciscoes for which we are deeply indebted. Doug Nelson, Ichthyology Collection Manager at the University of Michigan Museum of Zoology was very helpful in providing access to archival specimens. Dave Benion of the Great Lakes Science Center generated the historical and contemporary distribution maps, which greatly enhanced this publication. Jesse Howell of Kolossos Printing, Ann Arbor, Michigan, scanned and spent countless hours doing subtle color adjustments for all of the color illustrations.

In addition, we thank the following for their contributions: Mark Ebener of the Chippewa-Ottawa Resource Authority; Jason Link of Woods Hole; Chris Davis, Tom MacDougall, and Rick Salmon of the Ontario Ministry of Natural Resources and Forestry; Tara Bell, Sofia Dabrowski, Allison DeRose, Scott Nelson, Tim O'Brien, Carson Pritchard, Wendy Stott, and Thomas Todd (retired) of the Great Lakes Science Center; and Julie Turgeon of Laval University. Charles Bronte (U.S. Fish and Wildlife Service) and Lynda Corkum (University of Windsor, retired) provided reviews for which we are grateful. Funding for this project was provided by the Great Lakes Fishery Commission, Great Lakes Fishery Trust, U.S. Geological Survey, Fisheries and Oceans Canada, and the Sea Grants of Michigan, New York, Minnesota, and Wisconsin. The layout of this publication owes to Todd Marsee of Michigan Sea Grant, who brought together artwork, graphics, and text in a visually appealing and reader-friendly design that captures well the grandness of the Great Lakes and its foremost endemic fishes—the ciscoes.

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ABSTRACT

This study of the ciscoes (*Coregonus*, subgenus *Leucichthys*) of the Great Lakes and Lake Nipigon represents a furtherance through 2015 of field research initiated by Walter Koelz in 1917 and continued by Stanford Smith in the mid-1900s—a period spanning nearly a century. Like Koelz’s study, this work contains information on taxonomy, geographical distribution, ecology, and status of species (here considered forms). Of the seven currently recognized forms (*C. artedi*, *C. hoyi*, *C. johanna*, *C. kiyi*, *C. nigripinnis*, *C. reighardi*, and *C. zenithicus*) described by Koelz as major in his 1929 monograph, two (*C. johanna* and *C. reighardi*) are extinct. In addition, *C. alpenae*, described by Koelz but subsequently synonymized with *C. zenithicus*, although extinct, is recognized as valid making a total of eight major forms. Six of these forms, all but *C. artedi* and *C. hoyi*, have been lost from Lake Michigan, and seven have been lost from Lake Huron, leaving in Lake Huron only *C. artedi* and an introgressed deepwater form that we term a hybrid swarm. *C. artedi* appears, like its sister form *C. alpenae*, to have been lost from Lake Erie. Only *C. artedi* remains extant in Lake Ontario, its three sister forms (*C. hoyi*, *C. kiyi*, and *C. reighardi*) having disappeared long ago.

Lakes Superior and Nipigon have retained their original species flocks consisting of four forms each: *C. artedi*, *C. hoyi*, and *C. zenithicus* in both lakes; *C. kiyi* in Lake Superior; and *C. nigripinnis* in Lake Nipigon. Morphological deviations from the morphotypes described by Koelz have been modest in contemporary samples. Overall, *C. kiyi* and *C. artedi* were the most morphologically stable forms while *C. hoyi*, *C. nigripinnis*, and *C. zenithicus* were the least stable. Although contemporary populations of *C. artedi* from Lakes Michigan and Huron are highly diverged from the morphotypes described by Koelz, the contemporary samples were of undescribed deep-bodied forms unlikely to have been sampled by Koelz because of their association with bays. Of the two intact species flocks, Lake Nipigon’s was much less stable morphologically than Lake Superior’s even though Lake Nipigon is far less disturbed. Two priorities for research are determining the role of developmental plasticity in morphological divergence, especially within *C. zenithicus* of Lake Superior, and the basis for morphological divergence in *C. artedi*.



Cisco from the Bay of Quinte, Lake Ontario

Image by AMM.

THE COREGONINE PROBLEM

The coregonines are taxonomically problematic owing to a bewildering array of phenotypic diversity often resulting in greater within than among lakes variation. Svårdson (1949) introduced the concept, referred to then as the “coregonid problem,” in connection with morphological anomalies observed in transplanted and hybridized whitefishes inhabiting Swedish lakes. Use of the term “coregonid” suggests that *Coregonus* species are in their own family Coregonidae. As *Coregonus* species are currently considered to be in the subfamily Coregoninae within the family Salmonidae, the term “coregonine problem” is preferred here. The coregonine problem has continued to be of considerable interest in the Great Lakes region, particularly for ciscoes (LeSueur 1818; Bailey and Smith 1981; Smith and Todd 1984; Todd and Smith 1992; Phillips and Ehlinger 1995;

Turgeon et al. 1999; Turgeon and Bernatchez 2003). The central questions have been accounting for expression of alternative phenotypes within a form (Lindsey 1981), defining across lakes the taxonomy of forms similar in morphology and genetic signature (e.g., Todd and Smith 1992), and determining phylogeny (e.g., Smith and Todd 1984). Genetic separation of ciscoes living allopatrically or sympatrically has proven elusive (Reed et al. 1998; Turgeon et al. 1999), resulting in a recommendation to taxonomically treat North American ciscoes of the *C. artedi* complex as a single taxon, *C. artedi (sensu lato)* (Turgeon and Bernatchez 2003; Turgeon et al. 2016). This recommendation was intended to refocus research from defining species to defining ecologically significant units (ESUs), that is, those populations having exceptional gill raker counts, unique depth distributions, distinctive



Arrangement of Fish Shipping Boxes Documenting Commercial Operators in Minnesota Waters
Lake Superior north shore, ca. 1916 (photograph by William F. Roleff, courtesy of the Minnesota Historical Society).

reproductive behaviors, or critical functional roles (see also Phillips and Ehlinger 1995). The ESU approach is more suited to resolving the functional relationships among populations in terms of nutrient and energy cycling as begun in the Great Lakes by Schmidt et al. (2009, 2011), Stockwell et al. (2010a), Ahrenstorff et al. (2011), and Gorman et al. (2012a, 2012b). The lack of a suitable field guide to the ciscoes of the Great Lakes and Lake Nipigon has impeded the detection of ESUs, especially now that extirpations and hybridizations within the species complex (Todd and Stedman 1989; Todd and Smith 1992) described by Koelz (1929) have diminished the utility of his key. Further, delineation of a form is typically based on an appraisal of several traits, none of which are definitive alone, a problem that favors a weighting process based on probability rather than the fixed outcomes typical of a dichotomous key.

In one sense, this publication is an attempt to redress the coregonine problem for the ciscoes of the Great Lakes and Lake Nipigon and, in doing so, faces two immediate issues: how to treat the forms taxonomically and how to organize the keys. Koelz (1929) recognized nine species and seven subspecies within the *C. artedi* complex, of which all but two species and two subspecies were deepwater forms. Scott and Crossman (1998) synonymized *C. nipigon* with *C. artedi* and thereby reduced the species count to eight. Bailey and Smith (1981) reduced the species count to seven, eliminating *C. alpenae* (synonymized with *C. zenithicus*). They noted further that the six remaining species of deepwater ciscoes could be considered stocks (now forms) within a complex of closely related forms, leaving *C. artedi* as the sole valid taxon. Similarly, all of the forms addressed in this publication are presumed to have evolved from *C. artedi* following the Wisconsin Glacial Episode as per Eshenroder et al. (1999) and Turgeon and Bernatchez (2003). Here, the eight species of *Coregonus* described by Koelz (*artedi*, *alpenae*, *hoyi*, *kiyi*, *johannae*, *nigripinnis*, *reighardi*, and *zenithicus*) are considered morphs or forms as are his subspecies. Of these eight, five (*artedi*, *hoyi*, *kiyi*, *nigripinnis*, and *zenithicus*) are extant (Fig. 1). For simplicity and where clear-cut, the generic name, *Coregonus*, is dropped in favor of specific and/or subspecific names (Table 1). This approach harkens back to a practice of calling them “named species,” i.e., species only in name (Bailey and Smith 1981).

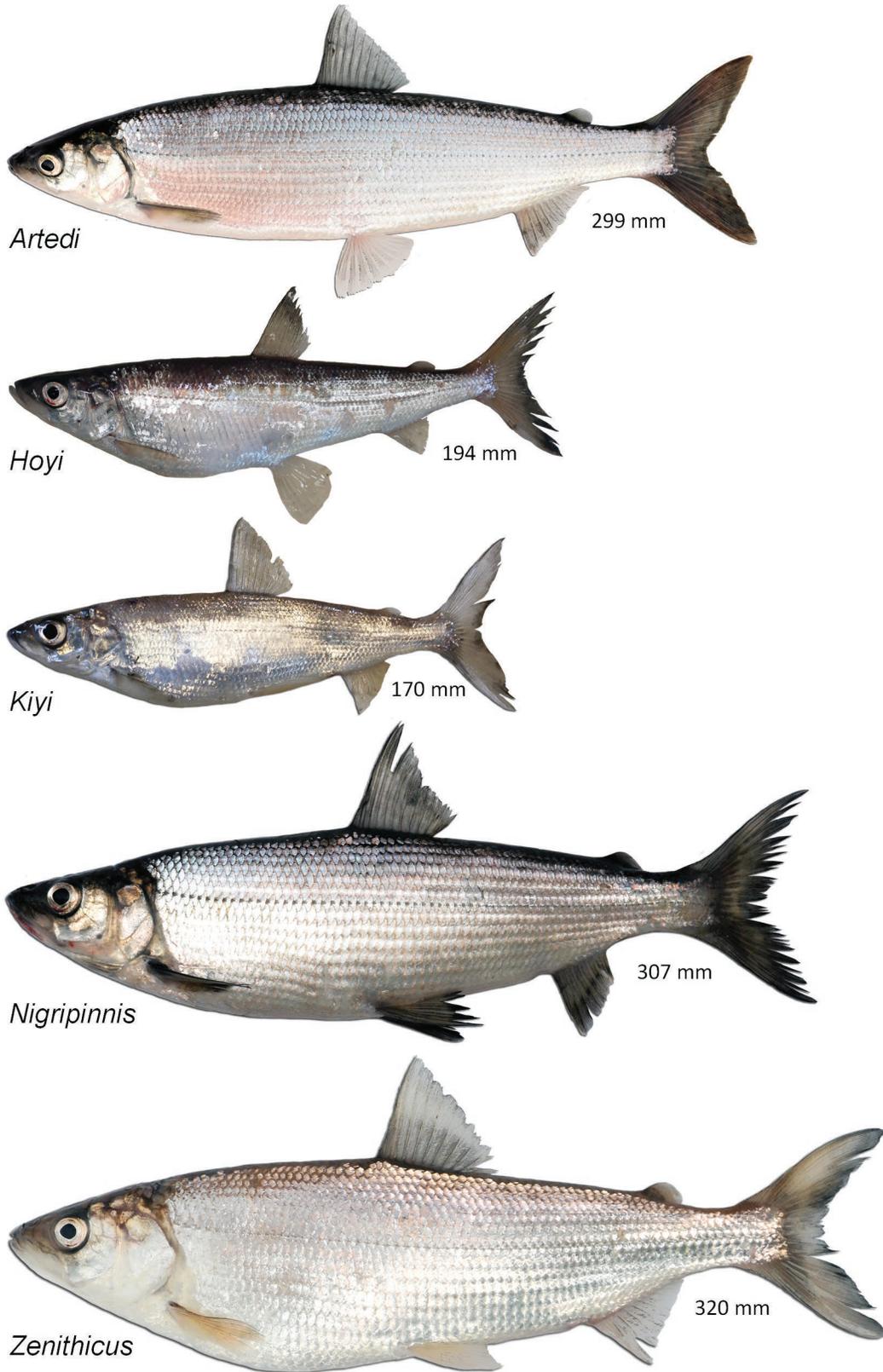
Limiting this publication to the accepted seven “species” (excluding *alpenae*) arguably would have resulted in diminished prospects for identifying ESUs within the *C. artedi* complex. Notable examples were provided recently by Schmidt et al. (2011), who reported significant

isotopic distances on the $\delta^{15}\text{N}$ axis between Koelz’s museum-preserved samples of *zenithicus* and *reighardi* from Lake Superior and between *zenithicus* and *alpenae* from Lakes Michigan and Huron. These findings indicate that, although *reighardi* of Lake Superior and *alpenae* of Lakes Michigan and Huron appear, based on morphology, to be synonymous in these lakes with *zenithicus* (Todd and Smith 1980; Bailey and Smith 1981), they differed ecologically. Emerging and new technologies will likely provide more precise methods for distinguishing forms now considered invalid or simply overlooked, perhaps resulting in additional surprises. Accordingly, this publication provides accounts similar to those of Scott and Crossman (1998) for each of the seven accepted species (Page et al. 2013). Within the Taxonomy subsection of each *Main Forms* account, synonymies among named species are identified as are the subspecies described by Koelz (1929). Within the *Lake Accounts* section, the objective is to describe the diversity at the time of Koelz (1929) while documenting new characteristics resulting from selection, genetic drift, hybridization, and introgression (Bailey and Smith 1981; Todd and Stedman 1989), now important for identification. Further, in the *Lake Accounts* section, the important differences between the named species and the synonymized forms within that lake are discussed, but a synonymized form that differs only marginally from its sister form may not be included in the quick key for that lake.

Table 1. Scientific, common, convenient, and general names of ciscoes discussed in this publication.

Scientific	Common	Convenient (Herein)
<i>C. alpenae</i>	Longjaw Cisco	<i>alpenae</i>
<i>C. artedi</i>	Cisco	<i>artedi/typical artedi</i>
<i>albus</i>	Albus	<i>albus</i>
<i>manitoulinus</i>	Manitoulinus	<i>manitoulinus</i>
<i>C. hoyi</i>	Bloater	<i>hoyi</i>
<i>C. kiyi</i>	Kiyi	<i>kiyi</i>
<i>C. johannae</i>	Deepwater Cisco	<i>johannae</i>
<i>C. nigripinnis</i>	Blackfin Cisco	<i>nigripinnis</i>
<i>C. reighardi</i>	Shortnose Cisco	<i>reighardi</i>
<i>C. zenithicus</i>	Shortjaw Cisco	<i>zenithicus</i>
General		
cisco	Individual cisco of any type	
ciscoes	Plural of cisco	
deepwater cisco	Individual of any of the above forms, except <i>C. artedi</i>	
deepwater ciscoes	Plural of deepwater cisco	

Fig. 1. Extant ciscoes of the Laurentian Great Lakes (images by AMM).



ORGANIZATION

Although the diversity of ciscoes within the Great Lakes has been reduced markedly since Koelz (1929) published his monograph (Todd and Smith 1992), the need for an updated guide to identification remains for several reasons. First, a number of the “species” recognized by Koelz have been synonymized (see *Main Forms* section). Second, although three species recognized by Koelz are considered extinct (*alpenae*, *johannae*, and *reighardi*), individuals with similar characteristics may reappear. Third, hybridization has lessened the differences among forms (Todd and Stedman 1989), resulting in fish that appear to be intermediate between the species recognized by Koelz (Pratt and Chong 2012). Fourth, the diversity of ciscoes in Lakes Superior and Nipigon remains intact creating widespread interest in these fishes as potential sources for re-establishing ciscoes extirpated from the lower Great Lakes. Fifth, the metrics in Koelz (1929), such as standard-length-to-head-length ratio, were not treated statistically, making quantitative comparisons among forms difficult (see *Appendix: Morphometric and Meristic Data*, Navigating Koelz subsection). Sixth, extensive statistically formatted data from the mid-1900s and from contemporary collections are available digitally and will be helpful in making identifications and assessing changes in characters of taxonomic interest. This publication addresses all of these needs and, in so doing, will make field and laboratory identification of ciscoes less onerous and thereby contribute to improved understanding and conservation. This publication, however, is not intended as a replacement of Koelz’s monograph, which remains a rich repository of cisco biology nearly one hundred years after he began his field work.

Two organizing principles underlie this publication. First, for simplicity, each “species” is treated in the *Main Forms* section of this publication as if it were a distinct lineage with more or less similar traits in each lake of occurrence. These accounts are intended to provide a brief, synthetic overview of the taxonomy, morphology, distribution, and ecology among what had been recognized as species without having to piece the information together from individual accounts. This approach is feasible in that what had been recognized as species were morphologically and ecologically similar, apparently owing to canalization not phylogeny (discussed further below and in *Status of Ciscoes* section). The *Main Forms* accounts are not intended to be used for identification.

The second organizing principle relates to our emerging understanding of the coregonine problem. Recent studies indicate that genetic and morphometric variation among forms (i.e., “species”) within a lake is less than the variation within a form across its range (Turgeon and Bernatchez 2001a, 2003; Turgeon et al. 2016), indicating the forms most likely evolved sympatrically within each lake post-glacially. Acceptance of this model of divergence implies that lake-based keys are likely to be more precise than a universal key for separating forms. With fewer forms to contend with under a lake approach, the keys can focus on phenotypic differences within forms, e.g., differences described by Koelz (1929) that may endure (Yule et al. 2013). Moreover, differences among the keys for the same form can provide a measure of the phenotypic diversity within forms. Such phenotypic diversity is of great interest as it may provide insights on the relationship between environment and phenotype and is, fittingly, part of what piqued Svärdsön’s interest in the coregonine problem. For these reasons, the *Lake Accounts* section presents for each lake a quick key, color illustrations, and temporal deviations within forms. For reasons mentioned above, dichotomous keys are not helpful in discriminating among ciscoes; therefore, the quick keys use a weighted system of nine quantitative character states to help identify forms. These character states are emphasized and discussed in the *Lake Accounts* section. Further, an appendix provides quantitative diagnostics by form and lake that span three time periods: 1920s and early 1930s, 1950s-early 1970s, and contemporary (2000s). Contemporary data are expected to be the most relevant for identification of recent collections, whereas the historical data will be important for documenting changes in character states, such as in gill raker counts, owing to selection, drift, hybridization, or changes in environmental cues that regulate plasticity. Inclusion of the extirpated and extinct forms in this publication allows a glimpse at the diversity of each lake’s species flock at the time of settlement. The inclusion of extirpated and extinct forms also acknowledges that individuals resembling any of these forms could appear, as was recently documented for two forms of *artedi* (Yule et al. 2013).

SUCCESSION IN THE CISCO FISHERIES

Each of the Great Lakes and Lake Nipigon before settlement supported a complex of ciscoes (species flocks) that varied among lakes and proved to be particularly vulnerable to overfishing and introduced species. To varying degrees within each lake, the fishery induced a successional process, first by removing the larger forms, which facilitated their replacement by smaller forms, and, second, by disturbing the reproductive barriers that presumably had allowed what were recently evolved forms to differentiate (Smith 1964, 1968; Anneville et al. 2015). At the same time, over-exploitation of the Lake Trout (*Salvelinus namaycush*) relieved predation pressure on the smallest ciscoes, further promoting their proliferation and possible competition with larger-bodied ciscoes (Smith 1968). Succession varied among lakes owing to differences in cisco diversity, predation pressure, fishing effort, physiochemical modification, and the abundance of non-native species.

Early fisheries for *artedi* operated with beach seines on spring feeding migrations and on autumn spawning migrations. Pound nets, gillnets, and trapnets were also important in the expansion of the early fisheries, particularly as advanced locomotion allowed operators to move farther offshore. As nearshore *artedi* were depleted

and demand for smoked *artedi* increased, fisheries moved farther offshore and began pursuing deepwater ciscoes (marketed as chubs). During the lumbering heyday, sawdust, bark, and logs were discarded into waterways blocking streams and altering the physical and chemical properties of nearshore spawning and nursery habitats (Koelz 1926). Extensive cobble mining impacted nearshore spawning areas on the eastern shore of Lake Ontario and southern Georgian Bay, among other places.

The first lake to be settled by Europeans and fished intensively was Lake Ontario, although aboriginal fishing had been conducted on all of the lakes for millennia. Fishing for *artedi* inshore began in Lake Ontario by about 1800 before a record of landings was established (Smith 1995). Fishing for deepwater ciscoes began after 1875 and focused on the largest of three forms, *reighardi* (referred to as Bloater by Koelz 1926), whose populations were depleted by the late 1920s, by which time the fishery had shifted to *hoyi* (Pritchard 1931). Succession among the deepwater ciscoes was essentially complete by 1983 (Owens et al. 2003). Thereafter, only a much-reduced *artedi* fishery continued, harvest having peaked much earlier, during the 1930s (Christie 1973). Lake Erie supported the least diverse cisco complex, having only two



Unloading a Gillnet Saturated with Cisco

Autumn 1899, Booth Fish Company Dock (old North Dock), Bayfield, Wisconsin, Lake Superior (photograph courtesy of Robert Nelson, Bill Gover, and Marti Peterson of the Bayfield Heritage Association; Hadland Collection).

forms, but, nonetheless, one of these, a deep-bodied form of *artedi* (*albus*) once supported the largest commercial fishery in the Great Lakes (Scott 1951), while the other, *zenithicus*, was so rare that it was not identified until 1957 (Scott and Smith 1962). The *albus* fishery began as early as 1815 (Koelz 1926), peaked in 1918 when 22,000 tonnes were landed (Van Oosten 1930), and ended by the 1960s. If *zenithicus* was fished out, it was likely only as bycatch or in response to the proliferation of Rainbow Smelt (*Osmerus mordax*), whose rise, interrupted by a massive die-off, paralleled the decline of *albus* (Van Oosten 1947; Baldwin et al. 2009).

Succession within the ciscoes of Lakes Michigan and Huron was similar owing mainly to identical species complexes in each lake, although the timing of successional events differed. Both lakes supported a dominant *artedi* population and six forms of deepwater ciscoes (seven if *alpenae* is included). In both lakes, until the early 1900s, fishing for *artedi* was constrained by a market preference for deep-bodied Lake Erie *artedi albus*, although massive spawning runs in Green and Saginaw Bays allowed for high landings of low-valued fish. Commercial fisheries for *artedi* remain in Lake Huron's Georgian Bay and North Channel, but the spawning runs in Green and Saginaw Bays vanished during the mid-1900s. The deepwater cisco fishery was more important economically than the *artedi* fishery in both lakes and started in Lake Michigan around the 1890s and in Lake Huron at the beginning of the 20th century (Koelz 1926). Lake Michigan's deepwater ciscoes were preferred in markets such that successional events occurred there earlier. In particular, the two largest-bodied forms were depleted already by the time Koelz (1926) completed his field work in 1924. By the late 1950s, the medium-sized ciscoes were undergoing hybridization (Smith 1964), resulting in succession to a single, small form, phenotypically most similar to *hoyi* (see *Lake Accounts* section, Ciscoes of Lake Michigan subsection). In Lake Huron, two pulses of intensive fishing for deepwater ciscoes in the mid-1900s resulted in a single, small-bodied, hybridized form (Todd and Stedman 1989; Dobiesz et al. 2005; this publication).

Succession among Lake Superior ciscoes was not as severe as in the other lakes owing to the later start of fishing and to lesser market demand (Koelz 1926). *Artedi* is currently undergoing recovery (Stockwell et al. 2009) as is *zenithicus*, the largest of the three forms of deepwater cisco (Gorman and Todd 2007; Pratt and Chong 2012). The recent recovery of Lake Trout in Lake Superior was likely a factor in improvements in cisco populations, which is consistent with the idea that the abundance of a top predator played a role in succession

(Cox and Kitchell 2004; Bronte et al. 2010; Gorman 2012; Pratt et al. 2016). Lake Nipigon's cisco complex, comprising *artedi* and four deepwater ciscoes, was essentially unfished and remains intact although reduced in biomass, especially for *artedi* and *zenithicus* (see *Lake Accounts* section, Ciscoes of Lake Nipigon subsection).

The completion and subsequent modifications of the Erie and Welland Canals allowed the Sea Lamprey (*Petromyzon marinus*) and Alewife (*Alosa pseudoharengus*) to invade the upper lakes and were, along with the intentionally introduced Rainbow Smelt, among the earliest and most destructive invaders (Eshenroder and Lantry 2012; Eshenroder 2014). The exact role that each played in altering the cisco species complexes remains debatable (Madenjian et al. 2008; Madenjian et al. 2011; Eshenroder 2014). Recent studies implicate the rainbow smelt as a major predator on *artedi* larvae (Myers et al. 2009; Rook et al. 2013). The Alewife is suspect owing to the complete elimination of deepwater ciscoes from Lake Ontario (see *Lake Accounts* section, Ciscoes of Lake Ontario subsection), and the Sea Lamprey is unquestionably a major predator on deepwater ciscoes (Smith 1968; Lawrie and Rahrer 1973; Johnson and Anderson 1980; Mills et al. 1993; Madenjian et al. 2008; Madenjian et al. 2011; Eshenroder 2014). This overview of cisco succession is intended to provide only a sketch of the events that occurred in each lake. Although additional material is presented in the *Lake Accounts* section of this publication, readers are referred to Koelz (1926) and Smith (1964, 1968) for more-thorough descriptions.



Gus Cadotte Dressing Deepwater Ciscoes

Off Sand Island, Lake Superior, ca. 1950 (photograph courtesy of Robert J. Nelson, Bayfield, Wisconsin).

STATUS OF CISCOES

Koelz’s (1929) monograph was the first comprehensive accounting of the status of ciscoes in each of the Great Lakes and Lake Nipigon and was last updated by Todd and Smith (1992). Their classification presumed that major forms were species and minor forms were reproductively isolated “ecological and seasonal species.” The classification adopted here differs somewhat. It recognizes *C. artedi* as the only basal species and the remaining taxa, including *C. artedi* phenotypes, as forms, either major or minor. Major forms (Table 2) are those inferred to be genetically diverged from a founder (*C. artedi*) into distinct types within each lake (discussed below). Minor forms are assumed to be alternative (plastic) phenotypes of a major form. The classification proposed here is meant to distinguish forms that differ in

morphology, behavior, and (or) ecology. It does not imply phylogeny, is not phylogenetic, and a formal systematic revision of *Leucichthys* is required. All of these ciscoes were considered by Turgeon and Bernatchez (2003) to be *C. artedi* (*sensu lato*). Retention of Koelz’s nomenclature, however, is necessary for discussing these forms across six lakes and three time periods. Otherwise, for example, a systematically correct alternative to *nigripinnis* of Lake Michigan would be “*C. artedi* (phenotype *C. nigripinnis nigripinnis* of Koelz) of Lake Michigan,” an awkward arrangement for a group of fishes already complicated by common names (Cisco, Deepwater Cisco; Page et al. 2013) that mimic general names (cisco, ciscoes, and deepwater ciscoes).

Table 2. Status of the major forms of ciscoes in the Great Lakes and Lake Nipigon (updated from Todd and Smith 1992). Forms in Lake Huron that have introgressed into a hybrid swarm are considered to be extirpated/extinct, although elements of their morphology may persist (see below). Extant forms are in bold.

Major Form	Lake					
	Superior	Michigan	Huron	Erie	Ontario	Nipigon
<i>alpenae</i>	–	Extinct	Introgressed	Extinct	–	–
<i>artedi</i>	Extant	Extant	Extant	Extirpated	Extant	Extant
<i>hoi</i>	Extant	Extant	Introgressed	–	Reintroduced	Extant
<i>johanna</i>	–	Extinct	Extinct	–	–	–
<i>kiyi</i>	Extant	Extirpated	Introgressed	–	Extirpated	–
<i>nigripinnis</i>	Uncertain	Extinct	Extinct	–	–	Extant
<i>reighardi</i>	Uncertain	Extinct	Introgressed	–	Extinct	–
<i>zenithicus</i>	Extant	Extirpated	Introgressed	–	–	Extant



Packing Smoked Bluefin Whitefish (*C. nigripinnis cyanopterus*)

Duluth, Minnesota, ca. 1940 (photograph courtesy of the Minnesota Historical Society).

Indirect evidence supports the hypothesis that the main forms within a lake are genetically differentiated. If individual forms within a lake resulted entirely from plastic responses by the colonizing form (*C. artedii*) to differing environments, one would not expect to find long-term persistence of only a single form of deepwater cisco where formerly a species flock existed, as with *hoyi* of Lake Michigan. None of the six extirpated/ extinct phenotypes from Lake Michigan (Table 2) have reappeared even after almost 50 years. Instead, contemporary *hoyi* closely resembles historical *hoyi* (see *Lake Accounts* section, Ciscoes of Lake Michigan subsection). Also, one might expect that the recent shift in *hoyi* depth distribution to deeper waters (Bunnell et al. 2012a) would have been accompanied by a reappearance of a deep-dwelling sister form, such as *johannae*, *kiyi*, or *nigripinnis*, but these historical forms remain absent. The apparent collapse of the deepwater cisco community of Lake Huron into what appears to be a hybrid swarm (see *Lake Accounts* section, Ciscoes of Lake Huron subsection) also supports the view that these forms were genetically differentiated historically. None of the previously recognized forms reemerged as might be expected had these forms resulted from plasticity alone.

Direct evidence of a genetic basis for phenotypic differences among forms is limited. In rearing experiments involving morphological comparisons between wild parents and their domesticated progeny, Todd et al. (1981) found a genetic basis for morphological differences between *hoyi* and *kiyi* but not between *zenithicus* and *alpenae*. Detection of genetic divergence between forms within the lakes considered here has been unsuccessful, except that in Lake Nipigon *zenithicus* was slightly differentiated from all other forms (Turgeon et al. 1999; Turgeon and Bernatchez 2003; Turgeon et al. 2016). The lack of differentiation between *hoyi* of Lake Michigan and what was thought to be *hoyi* of Lake Huron (Fave and Turgeon 2008), which turned out to be a hybridized cisco, is of interest. These hybrids are the only living source of markers from two forms (*reighardi* and *alpenae*) now considered extinct (Table 2).

Although phenotypic plasticity does not explain what is known about the main forms, it offers an intriguing explanation for their origin. As reviewed in Pfennig et al. (2010), when directional selection favors divergent phenotypes, “the developmental genetic pathways underlying plasticity provide...the genetic variation on which selection can act, promoting the evolution

of diverse phenotypes.” These phenotypes then may assimilate into fixed types, and in environments with similar selection pressures result in replicate radiations, as appears to have occurred repeatedly to varying degrees, in each of the Great Lakes and Lake Nipigon (Turgeon et al. 2016). The most remarkable examples of morphological similarity are those populations of *kiyi*, *nigripinnis*, and *reighardi* separated by an entire Great Lake (Table 2).

Alternatively, selection for phenotypic plasticity may occur, resulting in phenotypes not genetically different (West-Eberhard 2005). Plasticity may account for the *albus* and *manitoulinus* forms of *artedi*, which were not recognized by Koelz (1929) as main forms, either because they appeared together during spawning (*albus* and typical *artedi*) or intergraded morphologically (*manitoulinus*). Todd and Smith (1980) found that morphologically based distance coefficients between populations of *reighardi* *dymondi* and *zenithicus* within Lakes Superior and Nipigon were similar (0.9-1.1) to distance coefficients within populations of *zenithicus* in these same lakes (0.9), implying to them that sympatric *r. dymondi* and *zenithicus* were conspecific. In contrast, distance coefficients between *reighardi* of Lake Michigan and these same populations were larger (1.3-1.7), indicating to them a higher taxonomic rank for *reighardi* of Lake Michigan than for *r. dymondi* of Lake Superior. Their findings are consistent with the concept advanced here of major forms genetically fixed to some extent and of minor forms resulting mostly from plasticity.

Regarding major forms, *alpenae* had been synonymized with *zenithicus* (Bailey and Smith 1981). Here, *alpenae* is designated a major form owing to four lines of evidence. First, *alpenae* was isolated from *zenithicus* when spawning in Lakes Michigan and Huron (Koelz 1929); second, the two differ substantially in that the mouth of *alpenae* is superior whereas the mouth of *zenithicus* is inferior (see *Epilogue* section); third, the two forms had distinctive isotopic niches (Schmidt et al. 2011); and fourth, their histories of change in gill raker number in Lake Michigan were dissimilar (see *Lake Accounts* section, Ciscoes of Lake Michigan subsection, *Zenithicus* subsection). This reversal in taxonomy is tempered by Todd et al. (1981) who found that, although adult *alpenae* and *zenithicus* collected from southeastern Lake Michigan were distinct morphologically, their progeny reared under controlled conditions were not. It is also tempered by the expectation that different isotopic signatures could occur in phenotypes resulting from plasticity.

The five (major) forms of deepwater ciscoes extant in Lake Huron as of 1956 (*alpenae*, *hoyi*, *kiyi*, *reighardi*, and *zenithicus*) are viewed as comprising a single hybrid swarm as opposed to residual, atypical populations of *artedi*, *hoyi*, and *zenithicus*, and, thus, are designated introgressed (see *Lake Accounts* section, Ciscoes of Lake Huron subsection). Under this concept, *hoyi* and *zenithicus* of Lake Huron are no longer valid names for captures made after the early 1950s in Georgian Bay and after the late 1960s elsewhere, whereas *artedi* of Lake Huron remains valid for shallow-water collections.

Regarding minor forms, *r. dymondi*, described by Koelz (1929) from Lakes Superior and Nipigon, is designated minor as is *nigripinnis cyanopterus* of Lake Superior. Both may be plastic forms of *zenithicus* (see *Lake Accounts* section). Unlike *dymondi*, which had a distinct isotopic niche in both lakes, *cyanopterus* did not have an isotopic niche distinct from *zenithicus* in Lake Superior (Schmidt et al. 2011). *Coregonus nigripinnis regalis* of Lake Nipigon is considered to be *C. nigripinnis*. In keeping with previous taxonomy (Scott and Crossman 1998), *C. nipigon* is not accepted as a major or minor form in Lake Nipigon. In recognition of its distinctive morphology, the *orientalis* subspecies name given by Koelz is retained for *kiyi* of Lake Ontario. It appears to be a major form whose development did not quite parallel that of *kiyi* of the upper Great Lakes.

This arrangement of major and minor forms is provisional in that morphological data alone cannot be considered definitive in assessing whether phenotypically similar forms result from plasticity or genetic divergence (e.g., Turgeon et al. 2016). This shortcoming is evident in the uncertain treatment of *r. dymondi* and *n. cyanopterus* of Lake Superior and some hesitancy in making *albus*, despite its sharp divergence from typical *artedi* in Lakes Michigan and Huron, a minor form. Revision of these findings is anticipated, even in the near future, as information from breeding experiments, transplanting, and transcriptomics materializes. Nonetheless, and in the interim, a provisional framework is sorely needed to focus research and management, especially now that reintroduction has begun. This publication, based on digitized data for nearly 15,000 specimens, establishes a context upon which the implications of new findings can be interpreted more readily and synthetically.

MORPHOLOGY OF CISCOES

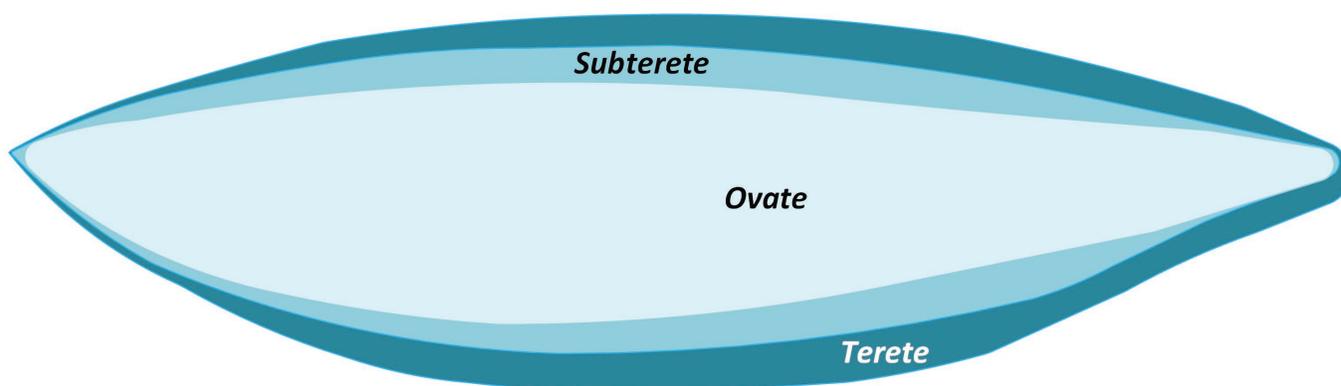
BODY SHAPE

Body shape (Fig. 2) is typically the first morphological attribute considered when making an identification. None of the ciscoes considered here have a unique shape that of itself is definitive for a particular form, but shape is helpful in making an identification. Two attributes of body shape, profile and cross section, are important features of cisco morphology. Koelz (1929) recognized two profile groups. One group, containing *alpenae*, *artedi* (includes *albus* and *manitoulinus*), *hoyi*, *reighardi*, and *zenithicus*, was categorized as having a more or less elliptical profile and a second group, containing *johannaes*, *kiyi*, and *nigripinnis*, was categorized as having an asymmetrical profile. The dorsal profile of the elliptical group was described as tapering convexly from the snout up to a point or section of the trunk where maximum depth is reached and then tapering downward and rearward to the caudal peduncle. The ventral profile of this group complements the dorsal profile such that the two profiles when merged mimic, roughly, an ellipse. The elliptical model is less appropriate for the second group because its dorsal and ventral profiles are not symmetrical. Owing to an ovate (egg-like) shape, the anterior half of the ventral profile in this group (less so in *johannaes*) falls more rapidly from the snout such that the curvature of the anterior and posterior halves do not match. The anterior half of the profile is more rounded while the

posterior ventral profile rises from the ventral fins in nearly a straight line. Koelz broke the elliptical group into two subgroups, one described as terete and the other as subterete. The taper of the ellipse in terete forms (*albus*, *hoyi*, *manitoulinus*, and *reighardi*) was said to rise and fall more prominently than in subterete forms (*alpenae*, typical *artedi*, and *zenithicus*). Further, the subterete forms, having less body depth, were said to appear more elongate than terete forms.

The idealized body shapes described above are typically distorted by overinflation of the swim bladder (bloating) when ciscoes are hauled to surface waters. For example, when *hoyi* is retrieved from deep water, its thin body wall may be stretched substantially, resulting in an ovate-appearing body profile. A distorted body wall in any cisco is evidenced by loss of scales, particularly those behind the operculum and above the pectoral fin (the area adjacent to the anterior swim bladder), and by loss of imbrication (overlap) in scales retained in the same area, i.e., the retained scales become separated. Stretching of the body wall, resulting in loss of scale imbrication can be detected by comparing scales from along the back with those adjacent to the swim bladder. With experience, an undistorted ventral body profile may be recreated by eye.

Fig. 2. Idealized cisco body profiles.



Cross-sectional shape relates to the amount of lateral compression and is not consistent within the two groups categorized by profile or even within the terete and subterete subgroups. Typical *artedi* and *reighardi* are the least compressed forms (nearly round in cross section) and the remaining forms are compressed to varying degrees. Koelz (1929) described *kiyi* and *manitoulinus* as most compressed and *albus*, *alpenae*, *hoyi*, *johanna*, *nigripinnis*, and *zenithicus* as least compressed. The degree of compression can vary during ontogeny and with growth rate, making the amount of compression a coarse diagnostic. Compression, as measured by the ratio of body depth to width, is not quantified in this publication, but Koelz (1929) gives these ratios in his tabular data for representative fish.

Koelz (1929) also used the term fusiform to describe body shape, referring to *alpenae*, typical *artedi*, *johanna*, and *kiyi* as fusiform. Although the term is commonly defined as torpedo-like, why he categorized these particular forms, which vary greatly in profile and cross section, as being fusiform is unclear. Due to this problem, the term fusiform is not used further.

HEAD SHAPE

When making an identification, the shape of the head in profile is the second most-important morphological characteristic, after body shape. Like body shape, head shape of itself is usually not definitive for a particular form, but several forms have distinctive head profiles (Fig. 3). The most-distinctive profiles are those of *hoyi*, which is flat dorsally, and of *reighardi* and *zenithicus*, which have blunted (truncated) snouts. Ciscoes typically have a triangular-shaped head, but the apex of this triangle is blunted in *reighardi* and *zenithicus* owing to the sharp downward angle of the premaxillaries. In other ciscoes, the premaxillaries tend to follow the curvature of the head. The terms Koelz (1929) used to describe variations in triangularity among ciscoes with non-blunted snouts are qualitative (acutely, broadly, elongated) and in of themselves difficult to apply. The illustrations in Fig. 3, however, will be helpful in training the eye to discern among head shapes and in providing a ready reference for comparisons with actual specimens.

MORPHOMETRICS AND MERISTICS

Morphometrics, the use of body dimensions, such as head length expressed typically as a ratio with another body part as a crude standardization for size, and meristics, counts of body parts (here gill rakers; Fig 3.), are used as quantitative metrics to discriminate among cisco forms (Table 3; Figs. 4, 5). To facilitate discrimination, this publication provides an appendix with extensive morphometric and meristic data for each of the Great Lakes and Lake Nipigon and, where available, for each of three time periods: an early period (1917-1924) encompassing Koelz (1929), a middle period (1950-1975) encompassing collections made under the direction of Stanford Smith of the U.S. Geological Survey's (USGS) Great Lakes Science Center, and a contemporary period (2003-2013) encompassing collections made by the authors and their collaborators.

A secondary objective of providing a time series of quantitative data was to allow detection of temporal changes in phenotype associated with environmental changes, shifts in species composition, and introgression (Smith 1968; Todd and Stedman 1989). The material in the appendix is used extensively throughout this publication to document those metrics of special diagnostic value. How these particular metrics were selected, how they are to be taken, and how they can be used are discussed in the following.

Fig. 3. Line drawings depicting lateral head profile, jaw orientation, snout configuration, and organization of the major craniofacial bones.

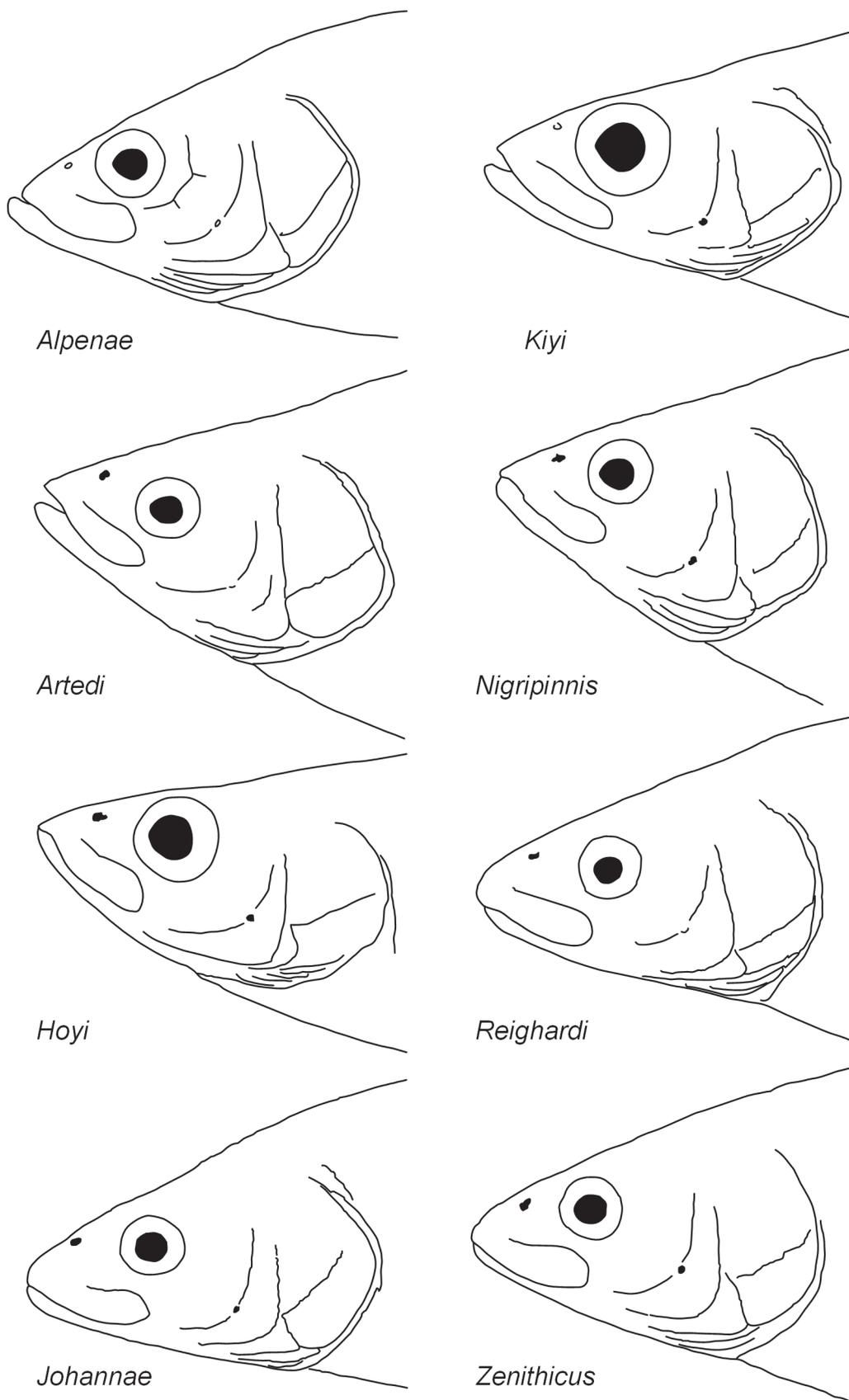
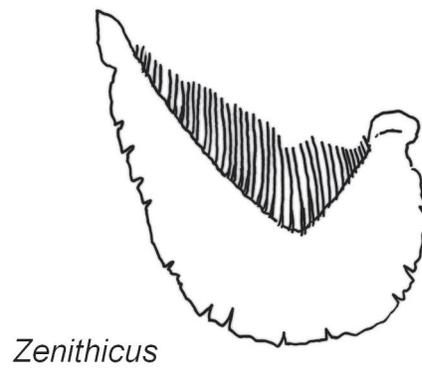
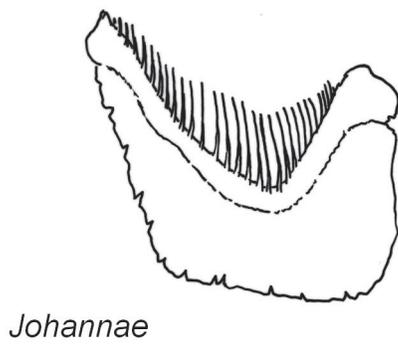
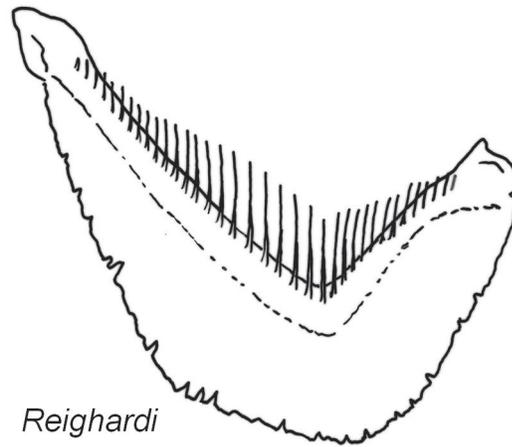
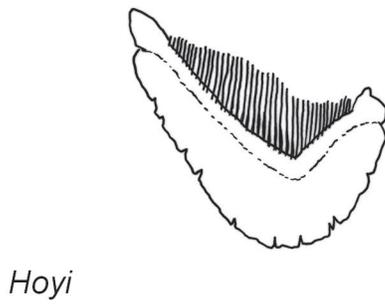
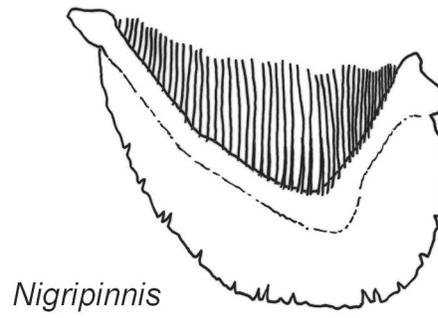
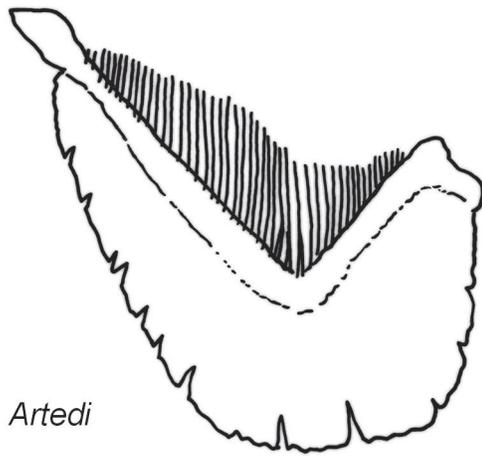
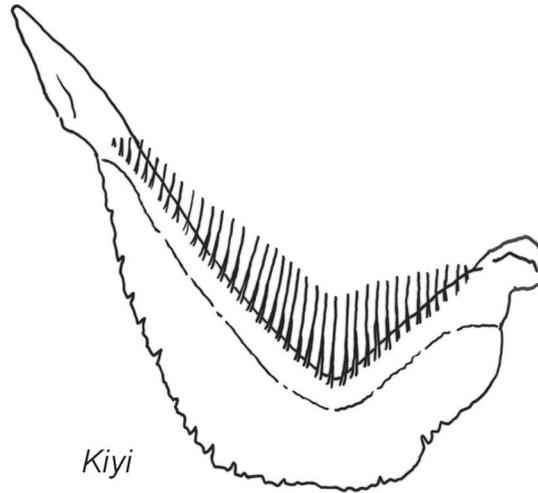
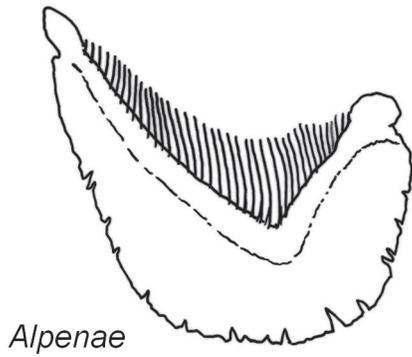


Fig. 4. Examples of gill rakers of the main forms.



Of the 32 metrics enumerated by Koelz (1929), only nine (head length, body depth, snout length, orbital length, maxillary length, dorsal fin height, pectoral fin length, pelvic fin length, and total gill rakers) are included in the appendix. Of these nine, body depth was infrequently measured in the middle period (Smith thought it difficult to determine accurately in bloated fish). Koelz and Smith measured body depth at the point where it was maximum, whereas contemporary fish were measured at the origin of the dorsal fin. The difference in these methods is thought to be slight. Dorsal fin height was measured in the contemporary period only for Lake Ontario in 2013 and Lake Superior in 2009-2010. Therefore, eight, rather than nine, metrics are typically provided for the middle and contemporary periods. Of the nine metrics, five (head length, orbital length, total gill rakers, and pectoral and pelvic fin lengths) were selected because they were among the six body metrics given special attention (frequency distributions) in Koelz (1929). He also provided a frequency distribution for lateral-line scales (his Table 7), but its diagnostic value was determined to be marginal. The differences in lateral line scales between the major forms were all less than two standard deviations (SDs) and the differences between populations of the same form would be even less. The remaining four metrics (body depth, snout length, maxillary length, and dorsal fin height) were selected because they were shown to have discriminatory power in principal component analyses (Todd et al. 1981; Smith and Todd 1984).

How measurements were taken and the ratios calculated differed in two important ways among the three time periods. First, in the early and middle periods, distances were measured point to point in three-dimensional space irrespective of the horizontal plane of the fish. In the contemporary period, distances reflect a two-dimensional flat surface, as if taken from an image, and do not account for landmarks being in different planes, although images were not used to make contemporary measurements. Therefore, for contemporary data, lengths of small body parts that are strongly curved across planes, such as preorbital length (snout, POL) and maxillary (MXL) (see Table 3 for abbreviations), are underestimated enough to make it appear that these body parts have shortened considerably as compared to the early and middle periods (neither method attempted to capture the true length of curved surfaces). Second, the tools used to measure morphology and the condition of samples differed among periods. Contemporary measurements were taken with a digital caliper on specimens that were fresh or recently frozen and thawed. By contrast, Koelz used a fine dividers (for short measurements) and a Vernier caliper (for long measurements) on fresh or recently preserved (presumably in formalin) specimens and read the fine-dividers measurements off a rule. The digital caliper, which unlike a dividers, has blunt jaws in lieu of sharp points, resulted in consistently shorter measurements of the snout and maxillary across all forms. This bias compounds the previously mentioned bias owing to measuring in two vs. three planes.

Fig. 5. Morphometric and meristic characters; definitions are given in Table 3.

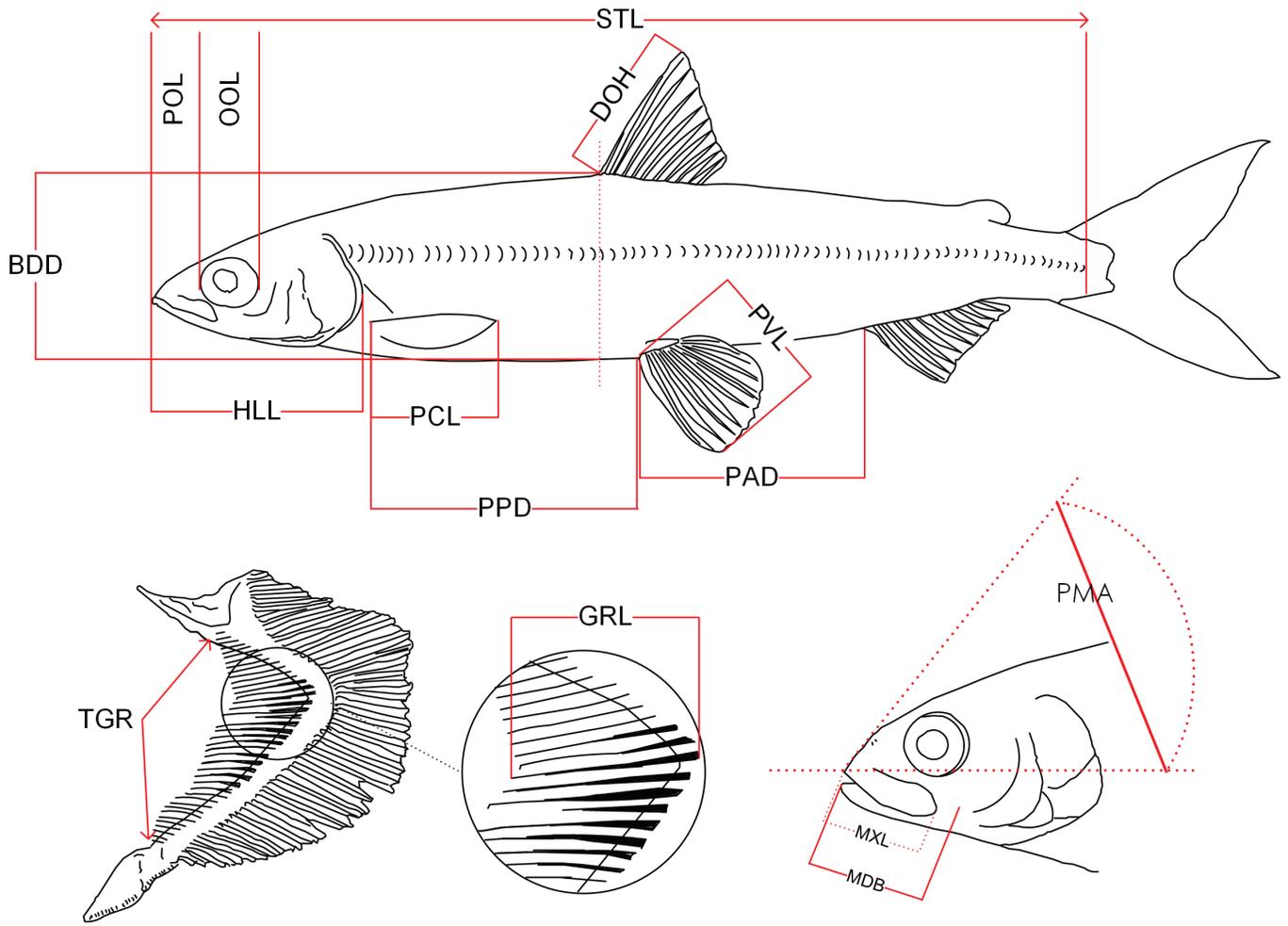


Table 3. Abbreviations and definitions of body-measurement characters.

Abbreviation	Character (mm Unless Indicated Otherwise)	Definition
BDD	Body depth	Vertical distance from the origin of the dorsal fin to the ventral surface of the body ¹ .
DOH	Dorsal fin height	Distance from the origin of the dorsal fin to the tip of the longest ray ² .
GRL	Gill raker length	Distance from the tip of the longest raker to its base.
HLL	Head length	Distance from the tip of the snout to the most extreme posterior margin of the operculum, not counting the opercular membrane, as measured parallel to the longitudinal axis of the fish.
MDB	Mandible length	Distance from the most-anterior point of the lower jaw to the posterior edge of the mandibular joint bone ³ .
MXL	Maxillary length	Distance from the most-anterior point of the premaxillary to the posterior end of the maxillary bone.
OOL	Orbital length (eye)	Distance between the anterior and posterior fleshy margins of the orbit with calipers anchored against margins of orbital rim ¹ .
PAD	Pelvic-anal distance	Distance between the anterior insertions of the pelvic and anal fins ² .
PCL	Pectoral fin length	Distance from the origin of the fin to the tip of the longest ray ² .
PMA	Premaxillary angle (degrees)	Angle between the horizontal axis of the head and the symphysis of the premaxillaries ² .
POL	Preorbital length (snout)	Tip of the snout to the anterior fleshy margin of the orbital rim with calipers anchored against the rim ¹ .
PVL	Pelvic fin length	Distance from the origin of the fin to the tip of the longest ray ² .
PPD	Pectoral-pelvic distance	Distance between the anterior insertions of the pectoral and pelvic fins ² .
STL	Standard length	Distance from the tip of the premaxillary to the caudal flexure, i.e., the crease created when the tail is flexed ¹ .
TGR	Total gill rakers (number)	The total number of rakers, including the bony rudiments, on the first gill arch ² .

¹Vuorinen et al. (1993); ²Koelz (1929); ³Trautman (1981).

MEASUREMENT CORRECTIONS FOR SNOUT AND MAXILLARY

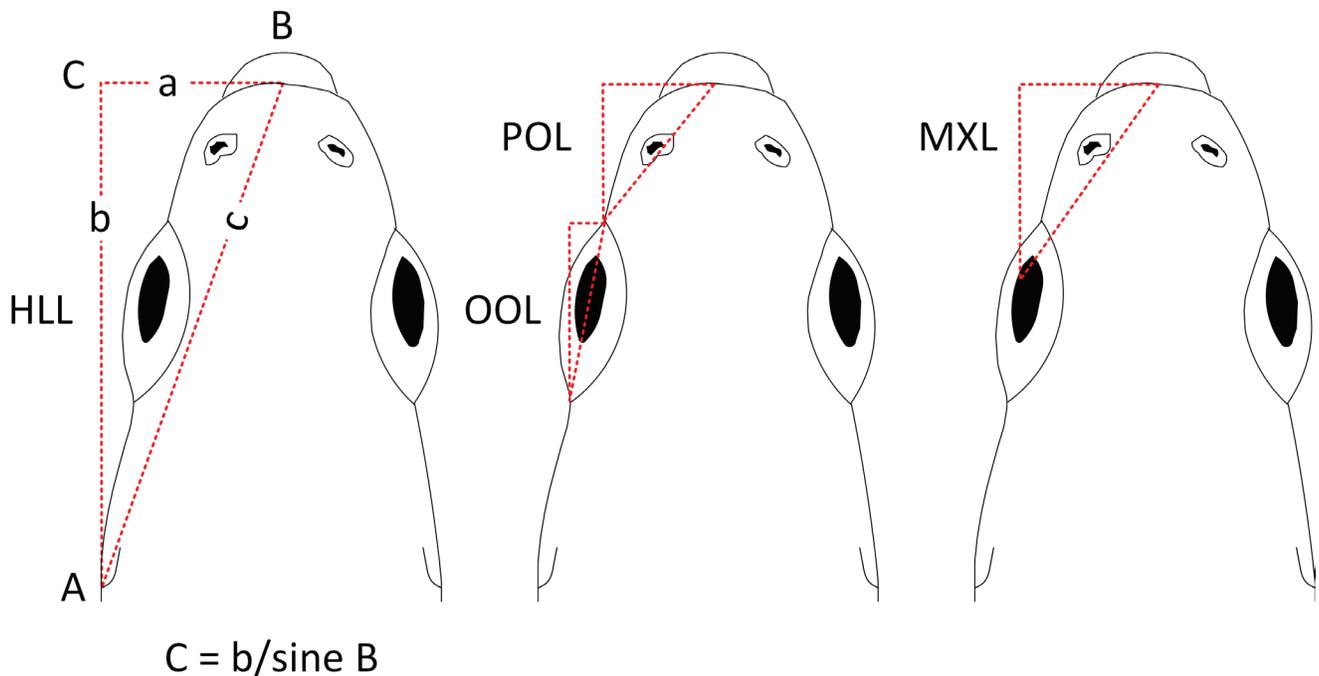
To provide corrections for measurement biases, POL and MXL were measured in the manner of Koelz (fine-point dividers across planes) and in the contemporary manner (digital caliper within one plane) on *zenithicus* and *artedi* (size range, 174-387 mm). This analysis was restricted to two forms because HLL/POL and HLL/MXL varied little among all four forms from both Lakes Superior and Nipigon (Appendix Tables 2B and 7B). The differences in length between the two methods, however, proved inconsistent as corrections. Therefore, a second method of estimating correction factors, based on geometry, was undertaken. This method employed digital images of side and dorsal views of the head. Caliper-like (simulated) measurements of HLL, POL, and MXL were represented by leg b of a right triangle superimposed on a dorsal view of the head (Fig. 6). This triangle is constructed as if in a horizontal plane going through the symphysis of the premaxillaries (Fig. 6). Once the length of leg b is determined and located transversely by leg a, the hypotenuse, c, which represents the fine-point-dividers

length, is fixed and b/c (sine angle B) is the factor for converting caliper length to dividers length. Where necessary, the distal ends of bony structures that were obscured in dorsal view were located in side view by referencing a landmark, such as a pigment spot. Measures of a, b, and c were made from digital images of three specimens each of thawed *artedi*, *hoyi*, *kiyi*, and *zenithicus* collected in 2014 from various locations in Lake Superior. The resulting correction factors (b/c; Table 4) varied little between forms (HLL/POL = 0.95, range 0.93-0.96; HLL/MXL = 0.84, range 0.82-0.86), negating a need for form-specific factors. Both correction factors were very close to the ideal factors that align the average measurements made by Koelz with those made contemporaneously on Lake Superior forms (HLL/POL = 0.94; HLL/MXL = 0.83; Appendix Tables 2B and 13), indicating that the geometric method mimics closely Koelz's measurement of these head parts. Correction factors were also calculated for OOL (Fig. 6), but the overall factor of 0.99, if applied, would be inconsequential.

Table 4. Rows 1-2: Correction factors for converting HLL/POL and HLL/MXL of Koelz (subscript k = Koelz method; Appendix Tables 1B-7B) to contemporary HLL/POL and HLL/MXL (subscript c = contemporary method; Appendix Tables 13-18), all forms combined (see text). Rows 3-12: equations for estimating PPD and PAD from STL for five forms of cisco. The ratios for paired-fin length based on standard length (STL/PCL and STL/PVL; Appendix Tables 8-17) can be converted to ratios based on pectoral-pelvic and pelvic-anal distances (PPD/PCL and PAD/PVL) by multiplying them by the appropriate factor (see text). Abbreviations defined in Table 3.

Forms	Size Range (mm)	Character	Relationship	Correction ± SD
All	207-351	POL	$HLL/POL_k = 0.95 \cdot HLL/POL_c$	0.95
		MXL	$HLL/MXL_k = 0.84 \cdot HLL/MXL_c$	0.84
<i>artedi</i>	176-387	PPD	$PPD = 0.3564 \cdot STL - 8.8974, r^2 = 0.96, n = 12$	0.32 ± 0.01
		PAD	$PAD = 0.2574 \cdot STL - 1.9884, r^2 = 0.94, n = 12$	0.25 ± 0.00
<i>hoyi</i>	128-200	PPD	$PPD = 0.2675 \cdot STL + 10.794, r^2 = 0.81, n = 12$	0.32 ± 0.01
		PAD	$PAD = 0.2755 \cdot STL - 1.6043, r^2 = 0.67, n = 12$	0.27 ± 0.00
<i>kiyi</i>	136-175	PPD	$PPD = 0.2326 \cdot STL + 13.143, r^2 = 0.47, n = 12$	0.31 ± 0.00
		PAD	$PAD = 0.2474 \cdot STL - 1.7588, r^2 = 0.51, n = 12$	0.24 ± 0.00
<i>nigripinnis</i>	243-319	PPD	$PPD = 0.3363 \cdot STL - 8.911, r^2 = 0.81, n = 11$	0.31 ± 0.00
		PAD	$PAD = 0.2533 \cdot STL + 7.5859, r^2 = 0.89, n = 11$	0.28 ± 0.00
<i>zenithicus</i>	174-283	PPD	$PPD = 0.3207 \cdot STL - 4.1711, r^2 = 0.94, n = 12$	0.30 ± 0.00
		PAD	$PAD = 0.2903 \cdot STL - 10.169, r^2 = 0.93, n = 12$	0.24 ± 0.01

Fig. 6. Diagrammatic representation of morphological characters of the head of a cisco in dorsal perspective. Characters shown are head length (HLL), maxillary length (MXL), preorbital length (POL), and orbital length (OOL). Right triangle components shown are angles A, B, C, and legs a, b, c. Leg b is in the plane of a photographic image and depicts uncorrected measurements as made for contemporary samples. Leg c is in the actual plane of orientation of the morphological character and depicts measurements as made by Koelz and Smith.



MEASUREMENT CONVERSIONS FOR PAIRED-FIN LENGTHS

In a further complication of comparability, the ratios used to quantify paired-fin lengths used a different ratio in the middle and contemporary periods than in the early period. Koelz quantified paired-fin length using a ratio of the distance between fin insertions (called fin bases, but not the bases of individual fins) and pectoral fin length (PPD/PCL) and pelvic fin length (PAD/PVL). In contrast, during the middle and contemporary periods, fin-length ratios were based on standard length (STL), although PPD and PAD (fin bases) were occasionally recorded in the middle period. As Koelz (1929) provided only ratios (not actual fin lengths), paired-fin-length ratios from the middle and contemporary periods cannot be compared directly to those of the early period.

To provide factors for conversion of STL/PCL to PPD/PCL and of STL/PVL to PAD/PVL, measurements of STL, PPD, and PAD were taken from University of Michigan Museum of Zoology (UMMZ) archival *artedi*, *kiyi*, *hoyi*, and *zenithicus* of Lake Superior and *nigripinnis* of Lake Nipigon, all collected by Koelz. Measurements were made with a jawed caliper after determining that both methods of measurement (the other being dividers) gave the same results. These measurements were then used to quantify the relationships of PPD and PAD to STL for each form (Table 4). These relationships allowed for estimation of PPD and PAD from the raw contemporary data used to produce Appendix Table 13 (all species, except *nigripinnis*) and Appendix Table 18 (*nigripinnis*). The conversion factors are the simple means of PPD/STL and PAD/STL; they allow for the conversion of STL/PCL and STL/PVL (Appendix Tables 8-17) to PPD/PCL and PAD/PVL, the ratios used by Koelz (1929) to compare fin lengths among forms and lakes (Appendix Tables 1A-7A).

The conversion factors (Table 4) used to estimate STL/PPD and STL/PAD from STL allow for estimation of contemporary PPD/PCL and PAD/PVL that compare well with Koelz (Appendix Tables 1A-7A), except for PAD/PVL of *hoyi* in Lakes Superior, Michigan, and Nipigon (*hoyi* of Lake Huron revised to hybrid-swarm cisco; see *Lake Accounts* section). Estimated PAD/PVL of all contemporary *hoyi* imply that its pelvic fins are, on average, 25% shorter than when Koelz made his measurements. Have *hoyi* pelvic fins actually become shorter or is this change due to measurement error?

Three observations bear on this question. First, if the cause is measurement error, why does the error only express in *hoyi* and not in its four sister forms, which were measured in the same manner? Second, the differences between PAD/PVL of Koelz and contemporary (converted) PAD/PVL do not differ systematically among the sister forms, and most measurements of the sister forms are close to what Koelz estimated. Third, Stanford Smith's measurements of *hoyi* STL/PVL (excluding Lake Nipigon) during the middle period (Appendix Tables 8-10) also indicate shorter pelvic fins compared to measurements made by Koelz (1929), only slightly less so than in the contemporary period. In Lake Nipigon, however, PVL in 1973 did not differ from measurements made by Koelz in 1922 (T.N. Todd, retired, USGS, unpublished data). These observations imply that the unexplained reduction in PVL of *hoyi* is real and began before the early 1950s in Lakes Superior and Michigan and after 1973 in Lake Nipigon. Collectors should account for this anomaly when identifying putative *hoyi* based on PVL.

SIZE EFFECTS ON BODY METRICS

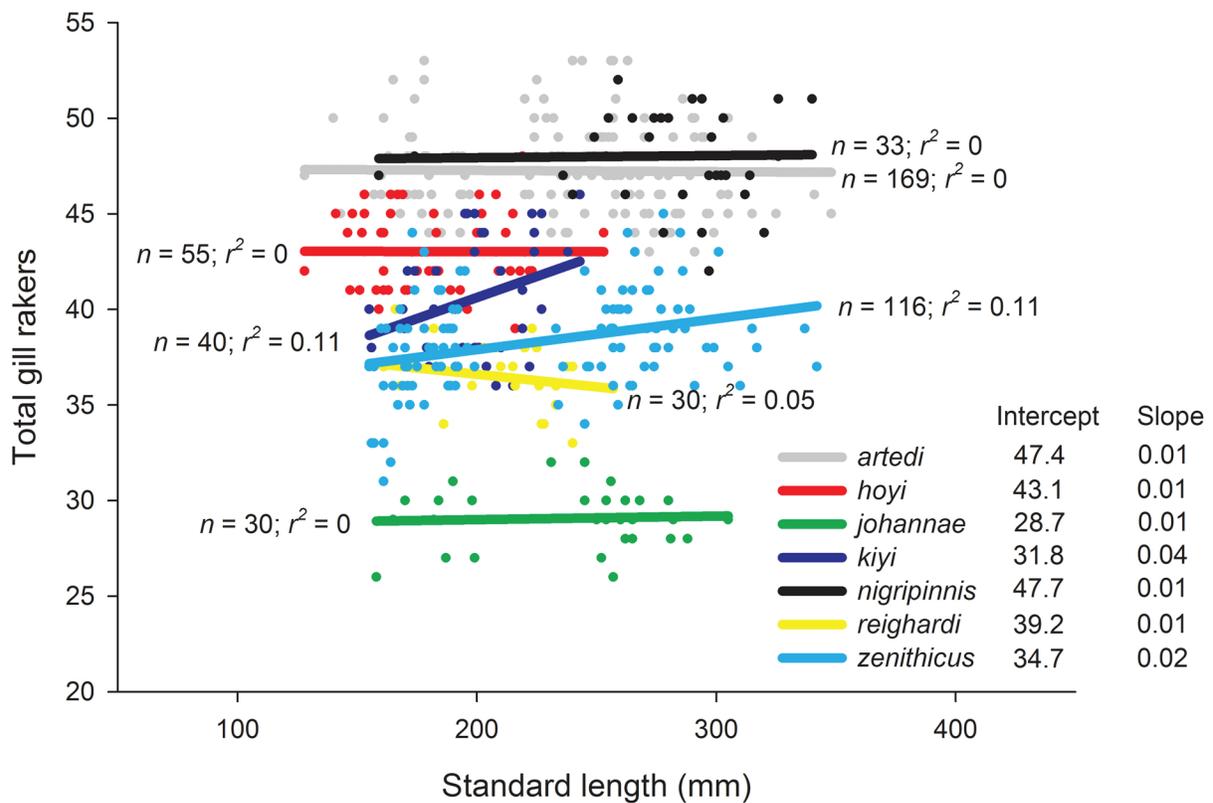
As ciscoes grow, allometric changes can occur that affect accurate use of morphometrics and meristics. Of particular interest, as body size increases, the number of gill rakers increases, and the length of the head as a proportion of body length decreases (Koelz 1929). To provide insights on allometry, regressions of TGR on STL are provided in Fig. 7, and a method of assessing whether a ratio for a given body metric is questionable is explained. In general, this publication is intended for identification of adult-sized fish within the size ranges of the regressions shown in Fig. 7. Juveniles and exceptionally large specimens should be identified with caution.

Regressions of TGR on STL for each form were, in general, statistically weak (low r^2); most had zero slopes (Fig. 7). These regressions are based on Koelz's "representative fish," lakes combined (Appendix Table 1A). Only data with undisputed taxonomy within forms were used (see footnotes in Appendix Table 1A). The regressions for *artedi*, *hoyi*, *johannae*, *nigripinnis*, and *reighardi* were flat ($r^2 = 0.00-0.02$) while those for *alpenae*, *kiyi*, and *zenithicus* were positive but weak ($r^2 = 0.11-0.16$; Fig. 7). Lake-specific regressions may have been more predictive as indicated for *artedi* of Great Slave Lake (Muir et al. 2013), but their sample size ($n = 236$) and size range (~77-400 mm) were large. The representative-fish samples of Koelz, however, are too few to allow for regressions by lake.

A coarse estimate of the effect of allometry on a particular body-metric ratio can be determined rapidly by referral to the “representative fish” tables in Koelz (1929). In the table for the lake of capture and suspected form, the STL of the table entry that best matches the ratio being checked can be readily located. If the size of the specimen being identified and sizes of representative

fish with the same ratio match poorly, the specimen may be misidentified, barring documentation of a change in morphotype for that form and lake (see *Lake Accounts* section). Koelz typically organized his representative fish by size groups (<200 mm and >200 mm), which facilitates this procedure.

Fig. 7. Linear regressions of total gill raker number (TGR) on standard length (STL) for eight forms of ciscoes based on “representative fish” enumerated in Koelz (1929). Data comprise all lakes of occurrence as shown in Appendix Table 1A with these exceptions: *artedi* includes typical *artedi*, *albus*, and *manitoulinus* (excludes *artedi* all); *nigripinnis* includes only Lakes Michigan and Huron; *reighardi* includes only Lakes Michigan and Ontario; and *zenithicus* includes *alpenae*.



TEMPORAL DIFFERENCES IN BODY METRICS

A key feature of this publication is identification of “notable” temporal changes in body metrics between time periods within the same form and lake and between a particular form and a composite of that form involving two or more lakes. Of special interest is identification of contemporary morphologies inconsistent with the descriptions of Koelz. Where data are available, the morphologies recorded by Stanford Smith from the 1950s to the early 1970s (Appendix Tables 8-12) are used to determine whether a nonconforming morphology expressed before or after Smith collected, i.e., in or before the last half century. Notable differences are defined as those that appear to reflect actual changes in morphology, and the problem is separating those from variations resulting from sampling and measurement error. An examination of the data sets in the appendix, comprising means, SDs, and ranges, indicates that, for gill rakers, a separation between means of two SDs (using the smallest SD) is too large to be used as a threshold for what constitutes a notable difference. This amount of separation would not allow for distinguishing between some forms, much less populations within forms.

As an alternative, one SD was tested by contrasting 12 pairings of raker number in populations found to be significantly different with eight pairings of populations found not to differ significantly by Todd and Stedman (1989) and Todd (1998). These pairings resulted from either experiments where progeny were reared from wild parents or from a need to compare one wild population with another. The significant pairings had a mean difference of 2.9 gill rakers, and the non-significant pairings had a mean difference of 1.1 gill rakers. If *kiyi*, which grew little in the rearing experiments, is eliminated, the significantly different pairings had a mean raker difference of 2.2. The population mean SDs for each of the two groups were nearly identical (2.2 and 2.1, respectively). From these results, a threshold of one SD, although coarse, appears to be conservative as a simple means for identifying changes in gill raker number consistent with the concept of being notable.

Although a one-SD threshold for distinguishing between means appears suitable for identifying temporal changes in gill raker number, it is too small for comparisons of body-metric ratios, especially those involving head anatomy. Ratios involving the head may have a population SD of only 0.1. A threshold that small may result from differences in measurement and rounding error. To achieve simplicity across all ratios yet provide for a reasonable level of detection, a threshold of two SDs is used throughout for determining whether the means of body metric ratios are notably different. Differences in gill raker counts and ratios that fall just short of these thresholds may still be identified, but will be described as “marginally” different. In all paired comparisons, the smaller of the two SDs is taken as the threshold for detection of a notable difference between means. Researchers are expected to go back to the original data www.glf.org/pubs/misc/Digital_data_for_Ciscoes_of_the_Laurentian_Great_Lakes_and_Lake_Nipigon.acedb using actual statistical tests rather the approximations used here. The inferences regarding nonconforming morphotypes identified here can be considered hypotheses that would benefit from further analysis.

COLLECTION AND PRESERVATION

Ciscoes may be encountered that appear unique or that are not identified readily using this publication. Such a specimen could be a hybrid, a member of a rare or considered-extirpated form, or simply an anomalous morphological variant of a common form. Specimens in good physical condition (i.e., minimal damage from capture) but not identifiable should be retained and prepared for submission to an expert. Specimen collection information should be recorded on waterproof paper using pencil or indelible ink. Detailed specimen collection procedures are given by Zale et al. (2012) and include the following:

1. Fish identification number: Each specimen in an agency collection should have a unique identification number to allow for tracing a preserved specimen back to the agency's database.
2. Capture data: The following information should be recorded for each specimen or group of specimens in the same collection:
 - Date and time: Date (e.g., 11 September 2013) and time (24-hour clock) of capture
 - Location: County, state/province
 - Water body: Proper name
 - Geographic coordinates: Latitude and longitude
 - Water depth: Bottom depth and depth at capture, if different
 - Capture method: Gear used, including mesh size, where appropriate

3. Supporting environmental information: Climatic and available physical (e.g., depth of thermocline) and chemical (e.g., dissolved oxygen concentration) data associated with the sampling event should be recorded.
4. Sample handling methods: State of the specimen should be indicated (fresh, frozen whole, fixed in 10% formalin, or other); this information allows for safe handling once the specimen is received from the field.
5. Collector: First and last name and contact information (e.g., agency, e-mail, phone number, postal address) of the person who collected the specimen.

Often anglers or commercial operators do not have the means or equipment to retain, store, or submit specimens to an expert. In this situation, precise information and a high-quality digital image can be collected and submitted to an authority. Biologists are also encouraged to digitally archive samples using the imaging protocol in Muir et al. (2012). If the full protocol cannot be followed, a suitable image may be made as follows: the specimen should lie on a flat, light-colored surface with its head and tail slightly elevated to produce a flat, lateral profile with respect to the camera lens; an imaginary line following the middle of the carcass from the tip of the snout through the middle of the tail should be straight; and a scaling object, such as a rule (preferred) or coin, should be included. Images should be captured using a normal (i.e., >50-mm focal length) rather than a wide-angle-lens setting (Fig. 8).

Fig. 8. Lateral view of a Shortjaw Cisco, *C. zenithicus*, with pinned fins and jaw, collected from Lake Nipigon (image by AMM).



Paretyphus

COLLECTION OF FISHES
UNIV. MICH. MUS. ZOOLOGICAL

Tank 9^N

GROUP 9

SPECIES *Coregonus alpenae*

CAT. NO.	SP.	LOCALITY	COLLECTOR	DATE
59406, 59411-413	4	MICHIGAN Lake Huron, off Alpena	W. Koelz	VII: 2: 1923
59502-59503 59504-59505 59523-28 59531	12	" "	"	VII: 7: 1923
5468-5-691, 54693-697, 54698-702, 54704-707	12	Lake Huron, off Cheboygan	"	VII: 2: 1919
54710	1	" off Rogers	"	VII: 24: 1919
54712-717	6	" off Alpena	"	IX: 10: 1917
54719	1	" " "	"	IX: 18: 1917
54720	1	" " "	"	IX: 17: 1917
54722	1	" " "	"	IX: 19: 1917
54725	1	" " "	"	IX: 26: 1917
58703	1	Michigan, 13 mi. SE 1/2 E of Manistiquette	"	VIII: 11: 1920
58730-35	6	" 9 mi. N. P. Retire	"	X: 4: 1920
58748-53	6	" 15 mi. SE by S. 1/2 S. of Manistiquette	"	VIII: 12: 1920
62993	80	Mich: Lake Huron, 15 mi. N.E. of Thunder Bay Co.	W. Koelz	IX: 18: 1919

Form 2500

University of Michigan Museum of Zoology
Accession Summary List for *Coregonus alpenae*
Collected by Walter Koelz from Lakes
Michigan and Huron

Image by AMM.

Specimens should be bagged individually with a waterproof label on the inside and outside of the package. Specimen labels should minimally contain a specimen identification number, collection date, and the identity of the collector printed in pencil or indelible ink. If possible, bagged specimens should be kept on ice until they can be transferred to a freezer (i.e., -20° C).

Specimens intended for museum archiving or for retention as vouchers for expert identification may be fixed. Fixation is the process of stopping cell degradation and protein coagulation, thereby preventing tissue breakdown. Formalin, the preferred fixative, is a buffered 10% dilution of formaldehyde (CH₂O) with water. Specimens should be retained in formalin until the tissues are fully penetrated and hardened. This process can be accelerated by injecting muscle and organs with formalin or by opening the coelomic cavity, procedures typically necessary for specimens >25 cm long. The duration of tissue fixation varies with fish size, temperature, and a host of other variables. In general, formalin penetrates tissues at approximately 1 mm per hour (Medawar 1941). Once the specimen is fixed, it can be rinsed in water and then transferred to isopropanol (C₃H₈O) or ethanol (C₂H₆O) for long-term preservation. If the specimen is removed from formalin slightly prematurely, it will continue to be fixed by the alcohol; therefore, the exact timing of transfer from the fixative to the preservative is not critical. Fixed and preserved specimens can be stored in plastic or glass jars or plastic bags that form a tight seal and do not leak. Consult the Material Safety Data Sheets for proper formalin- and alcohol-handling information. Once a specimen is collected, it should be submitted to an appropriate authority. Local fish and wildlife resource agencies can aid in handling specimens and contacting appropriate authorities. Alternatively, contact information for the authors of this publication is provided on the title page.

ILLUSTRATIONS

This publication contains three types of fish illustrations, all made by Paul Vecsei. Black-ink line drawings were made by placing a sheet of tracing paper (25 lb/41 gsm) over a morphometrically correct lateral-view photograph. Using a Pilot Fineliner™ ink pen, the contours and outlines of all details were traced. These illustrations are featured in the *Main Forms* section and are intended to provide a depiction of gross anatomical features.

One type of color illustration was created from enhanced digital images of live or freshly caught fish. Here, printed color images were placed on a light table, and body outlines were transferred to cotton archival two-ply vellum (Strathmore™ Artist Papers). Anatomical features (meristic and morphometric variables) were drawn to scale on these outlines. Using the digital images as a reference, a combination of graphite and polychromos color pencils (Faber-Castell) were used to color the illustrations, which were finished with multiple wash-layers of watercolor pencil.

A second type of color illustration was necessitated by a lack of quality color images for extirpated and extinct ciscoes. Here, museum specimens were used to make the outlines as per above, while coloring was based on the very-detailed descriptions provided by Koelz (1929).

Both types of color illustrations are featured in the *Lake Accounts* section and are intended to depict details of pigmentation, coloration in life and death, and, where possible, variation within forms. Color illustrations are not provided for all forms in all lakes. Omissions result from unavailable specimens, from inadequate color descriptions for a particular form, or from similarity to an extant form illustrated elsewhere within this publication.

Body coloration can be helpful in differentiating among ciscoes, but caution should be exercised because coloration may change with ontogeny and is lost rapidly postmortem. All of the digital images of live or freshly caught specimens used here for making illustrations of extant forms were taken in direct sunlight (referred to as color in life) as greens appear blue or black when not in direct sunlight and postmortem (Fig. 9). Koelz's descriptions of coloration are so vivid that he likely made them while viewing his specimens in direct sunlight, too. Because identification will often be based on color in death, side-by-side swatches of color in life and color in death are provided for selected forms collected by Koelz and for all extant forms.

Fig. 9. Macro (Nikon 60 mm) of dorsal lateral scales of *nigripinnis* from Lake Nipigon (left) and *artedi* from Lake Ontario (right). Images taken in direct light from fresh fish to show how iridescence and coloration can differ among ciscoes. Note differences in scale shape between these two forms (images by AMM).



GEOGRAPHIC DISTRIBUTIONS

Figures depicting geographic distributions are given for each of the main forms as indicated by red (widespread and abundant) and pink (reduced and patchy) shading and are intended to illustrate two points: local or lakewide extirpations and potential available habitat in lakes currently supporting those forms. Interpretation of distributions beyond these two points is tenuous due to differences in sampling gear and incomplete sampling within and among lakes and time periods. Historical distributions (pre-2000) were generated in a synthesis of published fishery and fishery-independent catch data (Table 5). Contemporary distributions (post-2000) for Lakes Ontario, Michigan, Huron, and Superior were generated using published data on extirpations and supplemented by recent fishery-independent survey data

generated by the USGS (Table 5). The percentage of trawls containing each form was plotted for 20-m depth bins (0-340 m). For rarely captured forms, minimum depth of the distribution was identified as the shallow end of the depth range in which a particular form was caught in 1% of all trawl tows conducted within that bin. Likewise, the maximum depth of the distribution was identified as the deep end of the depth range in which 1% of all trawls within that bin caught that particular form. For common forms, the same rationale applied, but a less-conservative cut-off of 10% was implemented. Using these rules eliminated depth zones where a form was only occasionally caught and produced depth ranges roughly consistent with published data.



Lake Huron Swarm Cisco (*Hybrida*) Depicting Extended Jaw

Image by AMM.

Table 5. Sources used to generate historical (pre-2000) and contemporary (post-2000) Great Lakes cisco distributions.

Cisco Form	Historical	Contemporary
<i>artedi</i>	Superior, Huron, Michigan, and Ontario expanded from historical reports on the basis of Yule et al. (2013) and unpublished U.S. Geological Survey (USGS) trawl data. Data for Lake Nipigon from Ontario Ministry of Natural Resources and Forestry (OMNRF) bottom-set gillnets.	Superior (Yule et al. 2013; USGS, unpublished trawl data); Nipigon (OMNRF, bottom-set gillnet data); Huron, Michigan, and Ontario (USGS, unpublished trawl data).
<i>hoysi/hybrida</i>	Superior, Michigan, and Huron (Koelz 1929; Selgeby and Hoff 1996); Ontario (Koelz 1929; Stone 1947; Selgeby and Hoff 1996); Nipigon (OMNRF, gillnet data).	Superior (Gorman and Todd 2007; Gorman et al. 2012a; USGS, unpublished trawl data); Michigan (USGS, unpublished trawl data); Nipigon (OMNRF, bottom-set gillnet data); Huron (Harford et al. 2012; USGS, unpublished trawl data).
<i>johanna</i>	Koelz (1929).	Extinct.
<i>kiyi</i>	Koelz (1929).	Superior (Gorman and Todd, 2007; Gorman et al. 2012a; USGS, unpublished trawl data).
<i>nigripinnis</i>	Superior and Huron (Koelz 1929); Michigan (Koelz 1929; Bunnell et al. 2012a); Nipigon (Dymond 1943; Turgeon et al. 1999).	Superior (USGS, unpublished trawl data); Nipigon (OMNRF, bottom-set gillnet data).
<i>reighardi</i>	Superior and Nipigon (Koelz 1929); Huron (Webb and Todd 1995); Michigan (Koelz 1929; Jobs 1943); Ontario (Pritchard 1931).	Extinct.
<i>zenithicus</i>	All lakes (excludes Ontario), except Erie (Koelz 1929); Erie (Scott and Smith 1962).	Superior (Gorman and Todd 2007; Pratt 2012; USGS, unpublished trawl data); Nipigon (OMNRF, bottom-set gillnet data).

During the historical time period, catch data were primarily limited to water depths <200 m due to gear limitations and catchability; therefore, historical distributions are biased. For example, *artedi* occurs throughout the pelagia of Lake Superior. We assume pelagic distribution occurred historically, as suspected by Koelz, but was not detected by him due to sampling limitations.

Contemporary data show that the distribution of *kiyi* extends to the deepest waters of Lake Superior—this distribution was probably true historically, too. Refer to the *Succession in the Cisco Fisheries* section to determine when changes in distribution actually occurred, which in most cases was well before 2000.



Seining

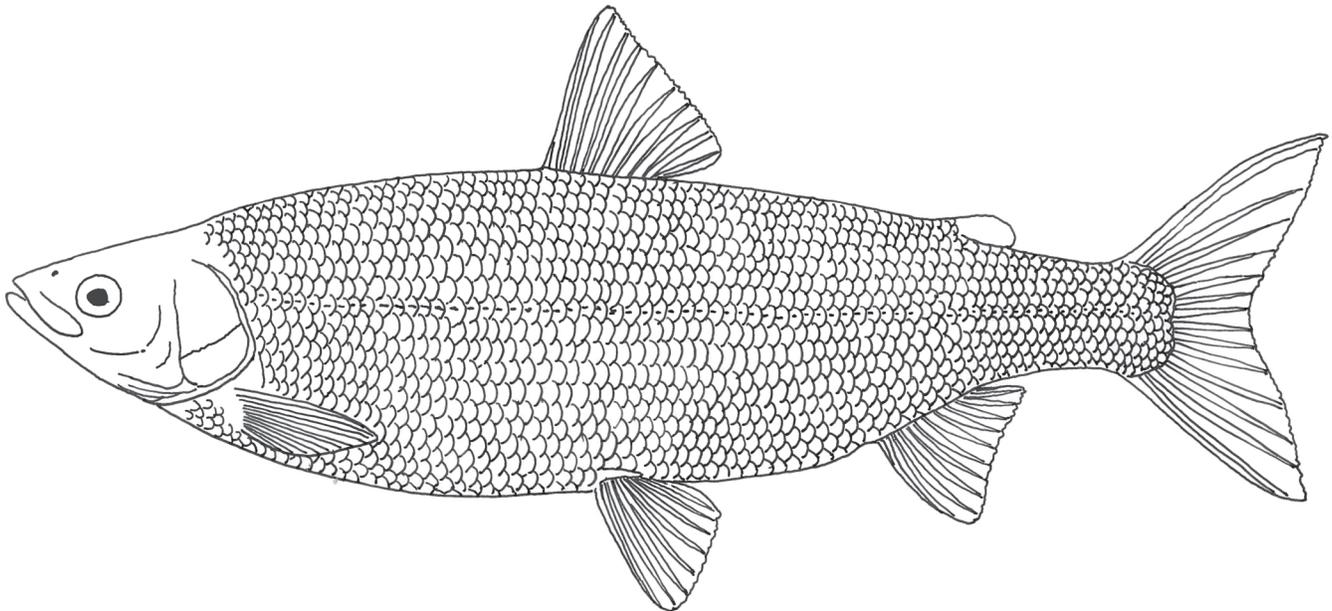
Reprinted with permission from the artist, Howard Sivertson.

MAIN FORMS

Here, in the style of Scott and Crossman (1998), Becker (1983), and others, a synthetic, broad-brush overview of the taxonomy, distribution, description, and ecology of the major forms is provided. To minimize redundancy with material in the following *Lake Accounts* section, this section focuses on information relevant to populations across lakes. Here, the taxonomy subsections are comprehensive, whereas the taxonomy subsection at the beginning of each lake account pertains just to that lake. Likewise, the information on distribution is comprehensive, being depicted in maps of the Great Lakes and Lake Nipigon for historical (pre-2000) and contemporary (post-2000) time periods. Distributions highlighted in red denote widespread and abundant and those in pink denote patchy and reduced.

To avoid repetition with the lake accounts, the descriptions here are based solely on a composite of each form using data from Koelz (1929) (Appendix Tables 1A,B). Therefore, these descriptions do not account for changes in morphology that occurred after Koelz collected or for differences among lakes and should not be used for identification. Temporal changes in morphotype, though, are given in the *Lake Accounts* section and tabulated by lake in Table 6. The information in the ecological sketch subsections is intended to provide the range of variation for a trait and, again, may not be applicable to a specific lake.

CISCO *Coregonus artedii* (Lesueur)



TAXONOMY

Coregonus artedii was described by Lesueur (1818) using specimens collected from Lakes Erie and Ontario (Scott and Crossman 1998). The variability in morphometry, meristics, and general appearance across the species range led to a large number of common names, including Cisco, shallow-water cisco, lake herring, tullibee,

freshwater herring, blueback herring, and grayback Tullibee (Scott and Crossman 1998). Taxonomists had previously classified *C. artedii* in *Salmo*, *Argyrosomus*, and *Leucichthys*, in that order. More recently, Hubbs and Lagler (1958) placed the species, along with all of the Great Lakes ciscoes, in *Coregonus*.

Several authors have described the morphological diversity associated with *C. artedi* by defining subspecies (Koelz 1929, 1931; Hubbs and Lagler 1958). Koelz (1925) described a tullibee-like species in Lake Nipigon (*L. nipigon*) that was later renamed *C. nipigon* and synonymized with Great Lakes *C. artedi* (Scott and Crossman 1998). Koelz (1929) identified three *C. artedi* subspecies, including a “slim terete” form based on Lake Michigan specimens (*L. a. artedi*), a “deep compressed” form (*L. a. albus*), and a deep-bodied form resembling tullibee in western Canada lakes (*L. a. manitoulinus*). Smith and Todd (1992) reported that Great Lakes *C. artedi* have basibranchial teeth that *C. artedi* outside the Great Lakes lack. They thereby made Great Lakes *C. artedi* a distinct form while reserving the common name tullibee for inland *C. artedi*.

Typical *artedi* (excludes *albus*) was the most-abundant form in all of the Great Lakes, except Lake Erie where *albus* was predominant (Koelz 1929). *Albus* was also present, although rare, in Lake Ontario and the northern bays of Lake Superior. *Manitoulinus* occurred only in the North Channel of Lake Huron and closely resembled *nigripinnis*. Koelz (1929) observed that Lake Nipigon contained a somewhat distinct form resembling *albus* and *artedi*, but he did not classify it as a subspecies.

Scott and Crossman (1998) stated that the development of long lists of subspecies was “regrettable for many reasons,” but mainly because it led to widespread confusion about the taxonomy of the species. Subsequent authors began to refer to *C. artedi* as a species complex (e.g., *Coregonus artedi* complex; McPhail and Lindsey 1970). Others have gone so far as to drop specific epithets altogether, defining forms by letters (Turgeon et al. 1999).

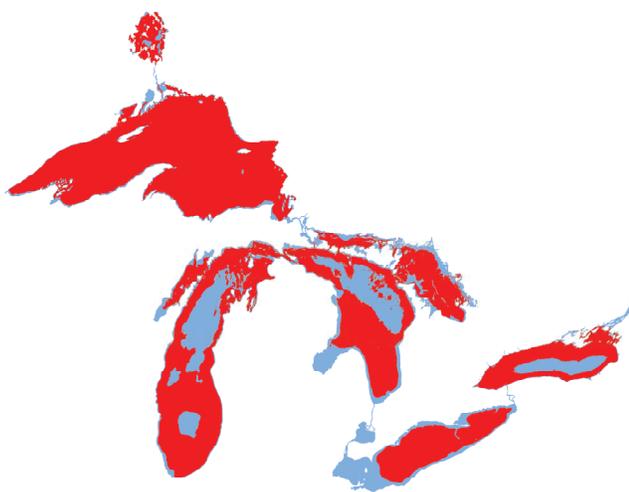
Evidence is growing that similarly shaped forms in each Great Lake are not monophyletic, leading Turgeon and Bernatchez (2003) to argue against subspecies-level taxonomic assignments (see *The Coregonine Problem* section) in lieu of *C. artedi* as the sole legitimate taxon.

GEOGRAPHICAL DISTRIBUTION

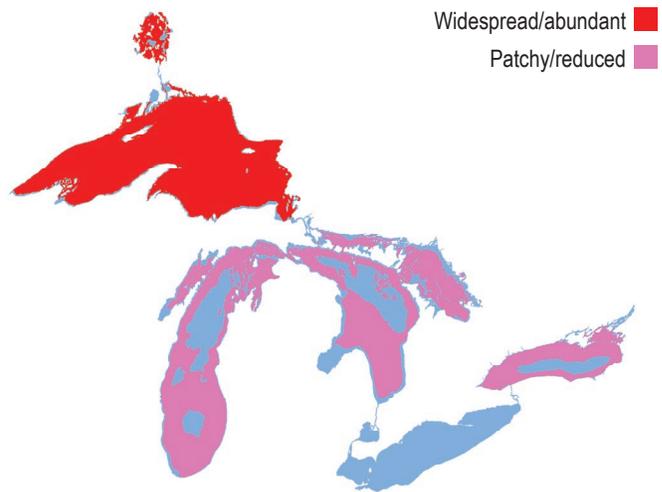
Coregonus artedi is the most widespread of the North America ciscoes, ranging in the north from the Northwest Territories to eastern Quebec and in the south from southern Alberta to Lake Erie (Scott and Crossman 1998). Smith (1995) wrote “...early descriptions and catch records indicate that the lake herring (Cisco) must have been the most-abundant individual species in each of the Great Lakes.” Populations collapsed during the middle of the 20th century because of overfishing, interactions with invasive species, such as Alewife and Rainbow Smelt, and loss of spawning and rearing habitat (Christie 1973; Wells and McLain 1973; Egerton 1985; Madenjian et al. 2011). At present, typical *artedi* abundance is high in Lake Superior, but well below historical levels; low and stable in Lake Huron (Ebener 2013); extremely low in Lakes Michigan and Ontario (Stockwell et al. 2009); and extirpated from Lake Erie (see *Lake Accounts* section, Ciscoes of Lake Erie subsection).

DESCRIPTION (See Appendix)

Typical *artedi* is subterete and more elongate appearing than *albus*, which is more terete, and *manitoulinus*, which in its extreme form is more ovate. Shape elliptical in side view with ventral outline having greater curvature than dorsal outline. Standard-length-to-body-depth ratio



Artedi historical distribution.



Artedi contemporary distribution.

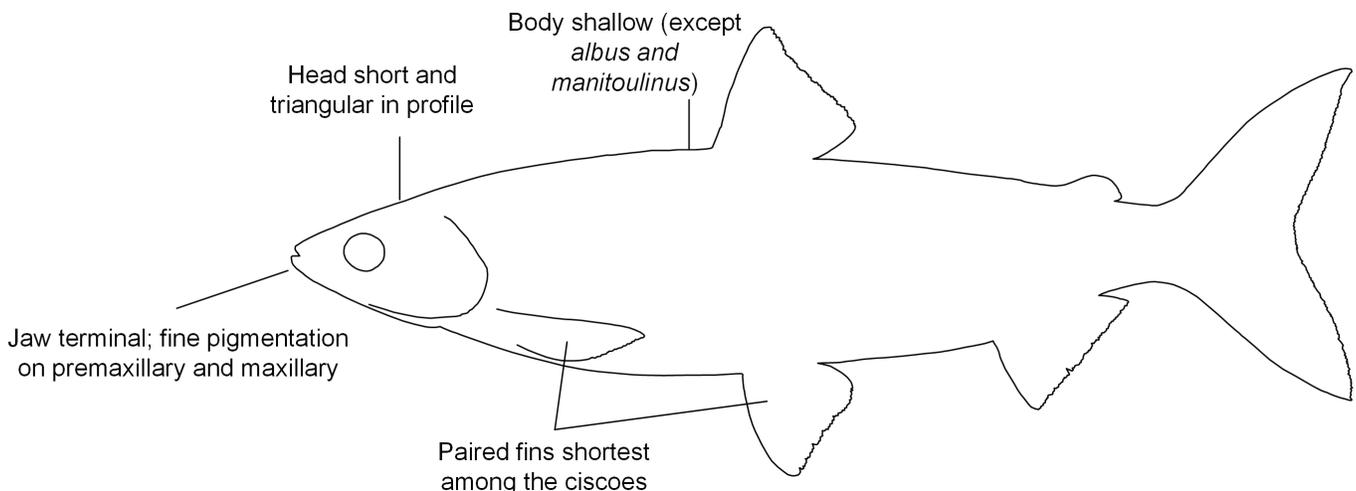
(STL/BDD) is 4.4 ± 0.4 , range 3.6-5.4 (mean \pm SD throughout), making it and *zenithicus* the most shallow-bodied forms. *Albus* and *manitoulinus* deeper bodied and more laterally compressed; both have STL/BDD of 3.6. Head triangular but sloping in side view and short except *manitoulinus* (Fig. 3), length-to-head-length ratio (STL/HLL) all forms combined 4.4 ± 0.2 (range 3.7-5.2). Snout (preorbital length, POL) short in typical *artedi*, HLL/POL 4.1 ± 0.2 (range 3.4-4.7). Orbital length (OOL) medium in typical *artedi*, HLL/OOL 4.1 ± 0.2 (range 3.4-4.7) and long in *manitoulinus*, 3.4 ± 0.1 (range 3.4-3.8). Jaw usually terminal with 8% extended in Lake Michigan and 11% extended in Lake Huron (Koelz 1929). Among ciscoes, typical *artedi* and *albus* have shortest maxillary, HLL/MXL both 2.8 ± 0.1 (range 2.5-3.2). Koelz (1929) grouped *artedi* with *hoyi*, *johanna*, *kiyi*, and *nigripinnis* in having a premaxillary angle (PMA) of 45-60°, whereas *zenithicus* and *reighardi* have a PMA of 60-75°.

Among ciscoes, typical *artedi* has shortest dorsal fin, STL/DOH, 7.1 ± 0.7 (range 5.8-8.9). All *artedi* (except *manitoulinus*) have short paired fins, pectoral-ventral-distance-to-pectoral-length ratio (PPD/PCL) 2.0 ± 0.2 (range 1.4-2.8) and pelvic-to-anal-fin-distance-to-pelvic-length ratio (PAD/PVL) 1.6 ± 0.2 (range 1.1-2.3). Gill raker length not reported. Koelz (1929) placed all typical *artedi* in his highest-rakered group (TGR commonly >43). TGR in all *artedi* forms combined 47.4 ± 2.5 (range 38-55). Rakers in *manitoulinus* at low end of range, TGR 45.7 ± 1.3 (range 43-47). In life, appearance silvery with iridescent hues of pink and purple on sides. Back blue green to pea green (*albus*) or deep blue green (typical *artedi*, the blueback); colors extend on the sides to about halfway to the lateral line and then pale gradually to the underside, which is whitish. Back finely pigmented; pigment is abundant in the preorbital area and on maxillary and mandible. Dorsal and caudal fins

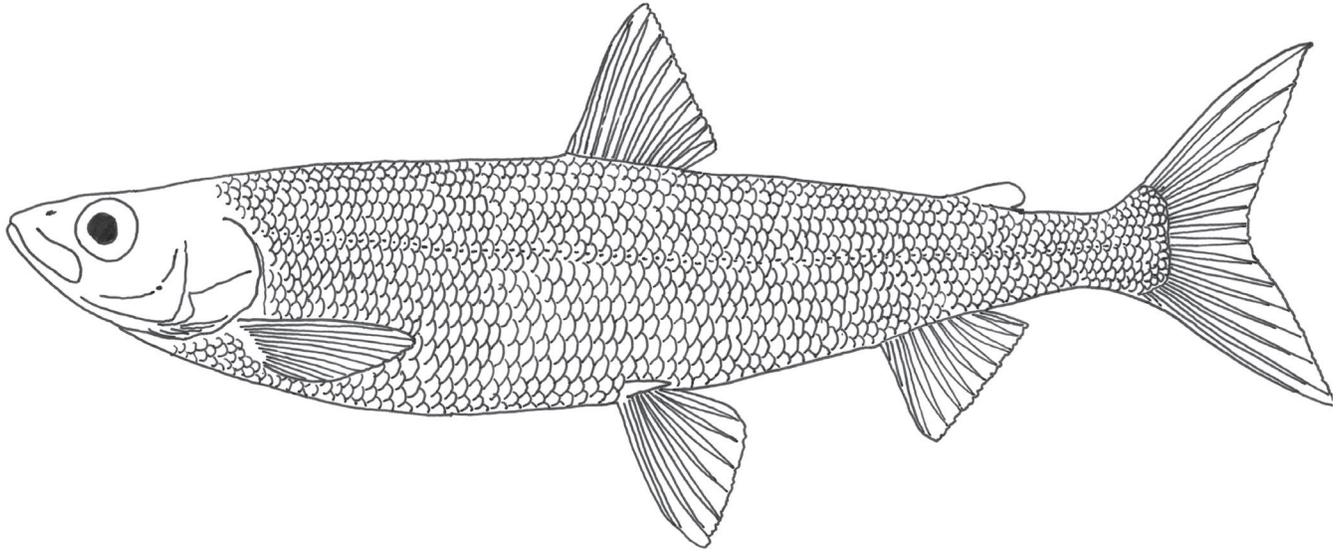
sprinkled with pigment with darker distal ends. Paired fins typically whitish and lack conspicuous pigmentation (i.e., immaculate), except nearshore-shoal-spawning fish from Lakes Ontario, Huron, and Michigan moderately pigmented. All color fades with preservation (condensed from Koelz 1929).

ECOLOGICAL SKETCH

Spawning occurs from mid-November to mid-December depending on latitude and year-to-year climatic variations (Koelz 1929). Spawning starts when water temperatures drop to 4-5°C and peaks at 3°C (Cahn 1927; Pritchard 1931). Depth of spawning typically ranges from 1-3 m (Lake Ontario; Pritchard 1930) to 64 m (Lake Superior; Dryer and Beil 1964), although Smith and Todd (1984) reported a very-unusual spring-spawning event in Lake Superior at depths of 130-140 m. Males while spawning may be more bottom oriented (Yule et al. 2006), and females may become more bottom oriented as spawning progresses (Dryer and Beil 1964). Spawning occurs over no specific type of substrate (Smith 1956; Selgeby 1982; Fielder 2000), but shoal-spawning populations are common in Lake Huron (Loftus 1980) and in Grand Traverse Bay, Lake Michigan (see *Lake Accounts* section). Maximum bottom-depth occupied, when not spawning, ranges typically from 90 m (Koelz 1929; Dryer 1966) to 150 m (Selgeby and Hoff 1996). Beginning in late spring, *artedi* is reported to descend from surface waters to just below the metalimnion (Scott 1951; Stockwell et al. 2006). During stable stratification, adults typically occupy the hypolimnion during daylight and the metalimnion at night (Stockwell et al. 2010a; Ahrenstorff et al. 2011). *Artedi* consumes a wide range of prey, including cyclopoid and calanoid copepods, *Daphnia*, *Mysis diluviana*, and *Bythotrephes* (Anderson and Smith 1971a; Selgeby 1982; Stockwell et al. 2010b; Ahrenstorff et al. 2011; Gamble et al. 2011a; Gamble et al. 2011b).



BLOATER *Coregonus hoyi* (Milner)

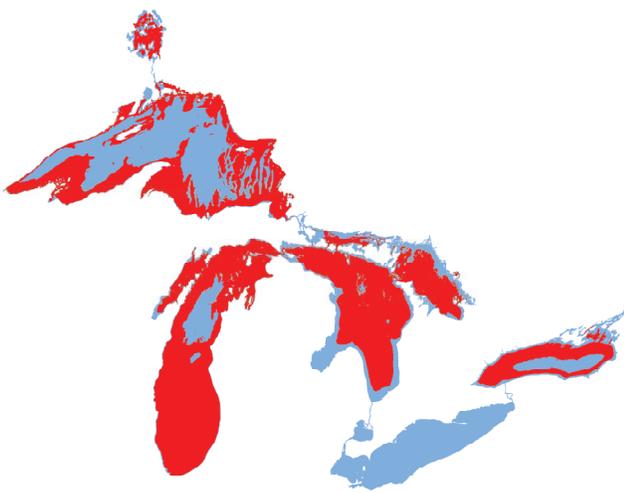


TAXONOMY

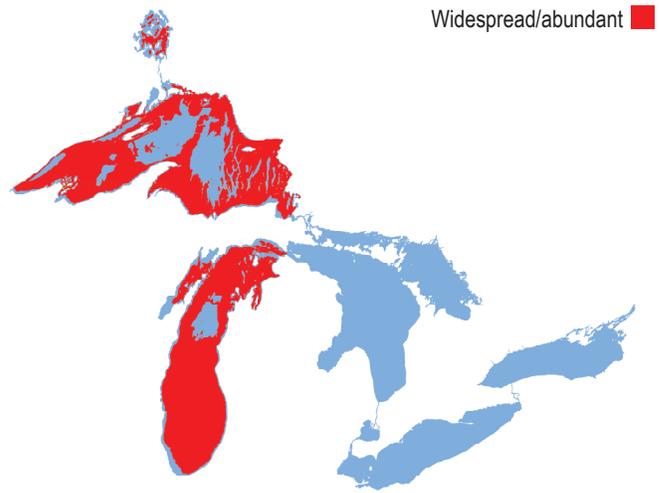
Gill named, but did not describe, two ciscoes collected by Hoy (1872), who obtained them from a commercial operation on Lake Michigan out of Racine, Wisconsin (Koelz 1929). Milner (1874) is now credited with the description, although Koelz (1929) produced what came to be the accepted description based on one of the two specimens collected by Hoy. Following Jordan and Evermann (1911), Koelz changed the genus to *Leucichthys*, which held until Hubbs and Lagler (1958) placed all of the Great Lakes ciscoes in *Coregonus*. *Hoyi* is considered a Great Lakes endemic (Bailey and Smith 1981).

GEOGRAPHICAL DISTRIBUTION

Koelz (1929) recognized that *hoyi* was widespread, occurring in Lake Nipigon and all of the Great Lakes except Erie. In Lake Huron, it occurred in all three basins. *Hoyi* has proved to be the most resilient of the deepwater ciscoes, having been extirpated from Lake Huron through introgression with other deepwater ciscoes (see *Lake Accounts* section, Ciscoes of Lake Huron subsection) and likely extirpated from Lake Ontario (Fave and Turgeon 2008). Elsewhere in its native range, it remains abundant.



Hoyi historical distribution.



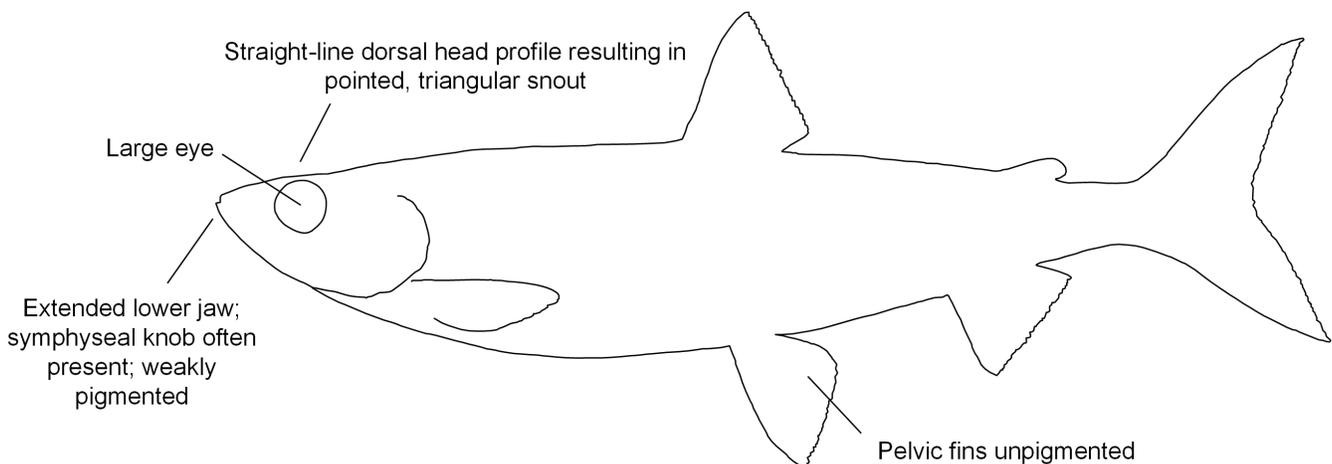
Hoyi contemporary distribution.

DESCRIPTION (See Appendix)

Elliptical (terete) body form in side view and straight-line dorsal head profile (i.e., flat), resulting in pointed, triangular snout (Fig. 3; Koelz 1929). Body depth (BDD) slightly less than in *kiyi*, STL/BDD 4.1 ± 0.3 (range 3.6-4.8). Atypically thin body wall, resulting in severe bloating and scale shedding when hauled from deep water—a trait less pronounced in other ciscoes. Head long, STL/HLL 4.0 ± 0.2 (range 3.4-4.6). Snout length medium, HLL/POL 3.8 ± 0.2 (range 3.4-4.3). Orbital length (OOL) long, HLL/OOL 3.8 ± 0.2 (range 3.1-4.7). Mandible typically extended and symphyseal knob often present (Becker 1983), one-third with terminal jaws, included jaw rare. Maxillary very long as in *kiyi* and *zenithicus*, HLL/MXL 2.5 ± 0.1 (range 2.2-2.8). Premaxillary angle (PMA) ~ 40 degrees. Dorsal fin tall, HLL/DOH 5.7 ± 0.5 (range 4.7-6.8). Paired fins medium-long, pectoral-pelvic-distance-to-pectoral-length ratio (PPD/PCL) 1.8 ± 0.2 (range 1.2-2.2) and pelvic-to-anal-fin-distance-to-pelvic-length ratio (PAD/PVL) 1.3 ± 0.1 (range 0.9-1.7). Gill rakers long, longest usually longer than longest gill raker filament (Becker 1983). Mean total gill rakers (TGR) medium, 42.4 ± 2.1 (range 37-50). In life, silvery with faint pinkish to purplish iridescence, especially above the lateral line, but absent from ventral surface. Silvery appearance overall with faint pinkish to purplish iridescence strongest above lateral line; dorsally, particularly forward of dorsal fin, slate bluish to pea green. Pelvic fins often vividly pale yellow. Pigmentation weak on fins and head, including cheeks and tip of lower jaw. Dorsal and caudal fins with darkly pigmented edges, pelvic fins unpigmented (Koelz 1929).

ECOLOGICAL SKETCH

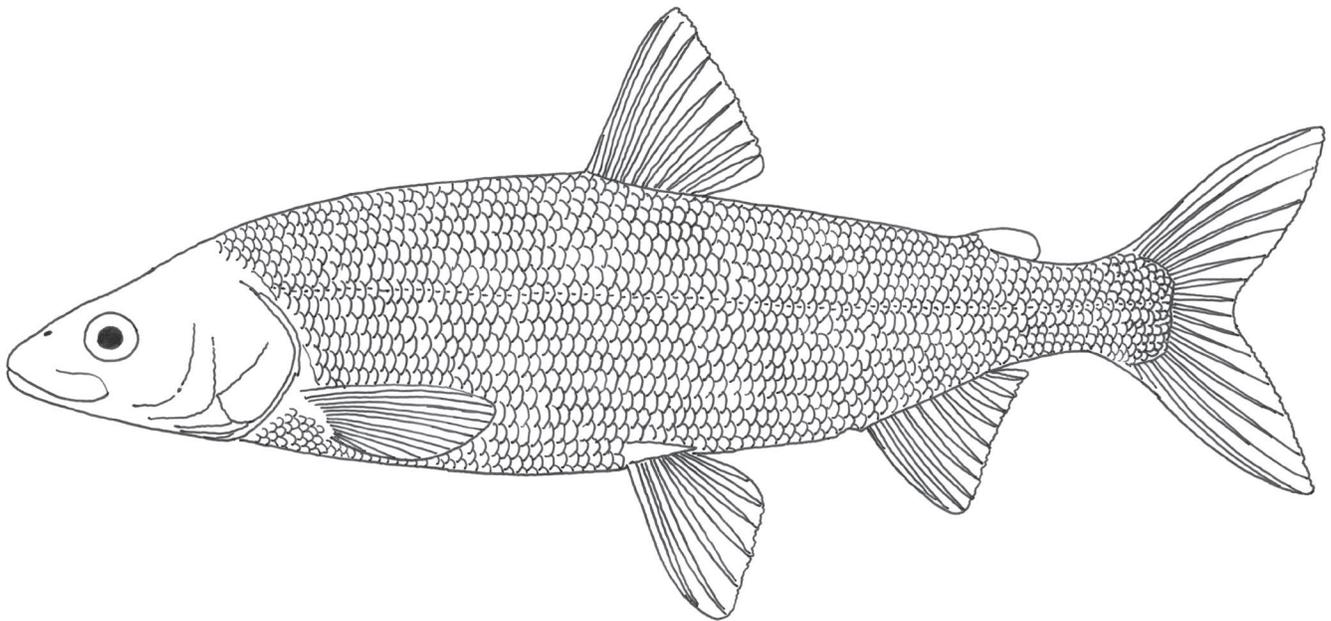
Koelz (1929) reported that southern Lake Michigan *hoyi* spawned from late February through March at depths of around 55 m. His two lifts of record, both off Michigan City, Indiana, comprised 81% and 96% *hoyi*—high percentages then, indicating a spawning aggregation. The bottom contours, where these lifts were made, slope gradually over a sand and silt bottom. Owing to much-reduced fishing effort in winter, Koelz (1929) had little else to report on time of spawning, but increased winter fishing for *hoyi* in succeeding years resulted in a belief that the spawning period is protracted. The larval life history of *hoyi* is illustrative of adaptations for deepwater spawning in large lakes. In southeastern Lake Michigan, yolk-sac larvae measuring ~ 10 mm were abundant from late May to early July near bottom at depths of 90-110 m (Wells 1966). Advanced larvae, measuring 17-53 mm, were taken in neuston nets fished at the surface in southwestern Lake Michigan during late August-early September (Crowder and Crawford 1984). These studies suggest that, in southern Lake Michigan, *hoyi* spawning was concentrated on depths of ~ 100 m, the embryos hatched over a protracted period lasting from April to August, and, larvae, once developed, migrated throughout the summer months from hypolimnetic to surface waters. The depth distribution of *hoyi* is unusual in that it was the most-abundant deepwater cisco in shallow waters, while at the same time it occupied waters as deep as those inhabited by its sister species. In Lake Superior, *hoyi* was consistently found at depths < 40 m to depths of 121-160 m with peak occurrence at depths of 41-120 m (Koelz 1929; Dryer 1966; Selgeby and Hoff 1996; Gorman and Todd 2007). In Lake Huron, “large” *hoyi* were abundant



at a depth of only 24 m in outer Saginaw Bay (R/V *Cisco*, cruise report I, 1956) just before the great extirpation of Lake Huron ciscoes (Eshenroder and Burnham-Curtis 1999; Dobiesz et al. 2005), yet Koelz (1929) inferred that *hoyi* occurred at depths greater than 183 m. In Lake Ontario, *hoyi* occupied depths of 55-145 m according to Stone (1947), although Koelz (1929) caught *hoyi* at depths as shallow as 27 m. In Lake Nipigon, *hoyi* occupied a depth range of 27-100 m (Dymond 1926). In Lake Michigan from 1930 to 1961, *hoyi* extended its range to deeper waters in response to depletion of its sister forms

and release from Lake Trout predation (Smith 1964). *Hoyi* makes a shoreward migration in summer (Wells 1968; Harford et al. 2012). In Lake Michigan during 1954-1962, small *hoyi* (<178 mm) fed mainly on zooplankton while large *hoyi* (>178 mm) fed mainly on *Diporeia* spp. and *M. diluviana* (formerly *M. relicta*; Wells and Beeton 1963). In Lake Superior, which has fewer habitats for *Diporeia* spp., copepods dominate the diet (Anderson and Smith 1971b), whereas the diet in Lake Ontario in the past appears to have been similar to that of Lake Michigan (Clemens and Crawford 2009).

DEEPWATER CISCO *Coregonus johanna*e (Wagner)



TAXONOMY

Wagner (1910) named *Argyrosomus johanna*e from a collection taken commercially in Lake Michigan approximately 30 km east of Racine, Wisconsin. The type specimen, a male 269-mm standard length, was taken at a depth of 47 m. Jordan and Evermann (1911) substituted the name *Leucichthys* for *Argyrosomus* and named this form the “chub” as Wagner had not provided a common name. *Leucichthys* became a subgenus when Hubbs and Lagler (1958) placed all of the Great Lakes ciscoes in *Coregonus*. They also created its accepted common name, Deepwater Cisco even though it can be confused with the general name, deepwater cisco. *C. johanna*e was endemic to the Great Lakes and considered extinct (Todd and Smith 1992; Webb and Todd 1995).

GEOGRAPHICAL DISTRIBUTION

*Johanna*e occurred only in Lakes Michigan and Huron (excludes the North Channel) and was widespread at depths of 55-82 m, although Koelz (1929) indicated it was not found in all lifts of “chub” nets set in the deep waters of Lake Michigan. *Johanna*e apparently was depleted in Lake Michigan by the time Koelz was conducting his field studies (Moffett 1957). Koelz (1964) noted that by the end of the 19th century this lake could no longer keep up with market demand for large-bodied ciscoes (commercially, chubs). Chub fishing began later in Lake Huron, around 1910, and Koelz (1929) reported that *johanna*e was more widely distributed there than in Lake Michigan. These findings suggest that *johanna*e once was more widely distributed in Lake Michigan than indicated by Koelz’s (1929) field records. Stanford Smith identified in 1951



Johannaea historical distribution.



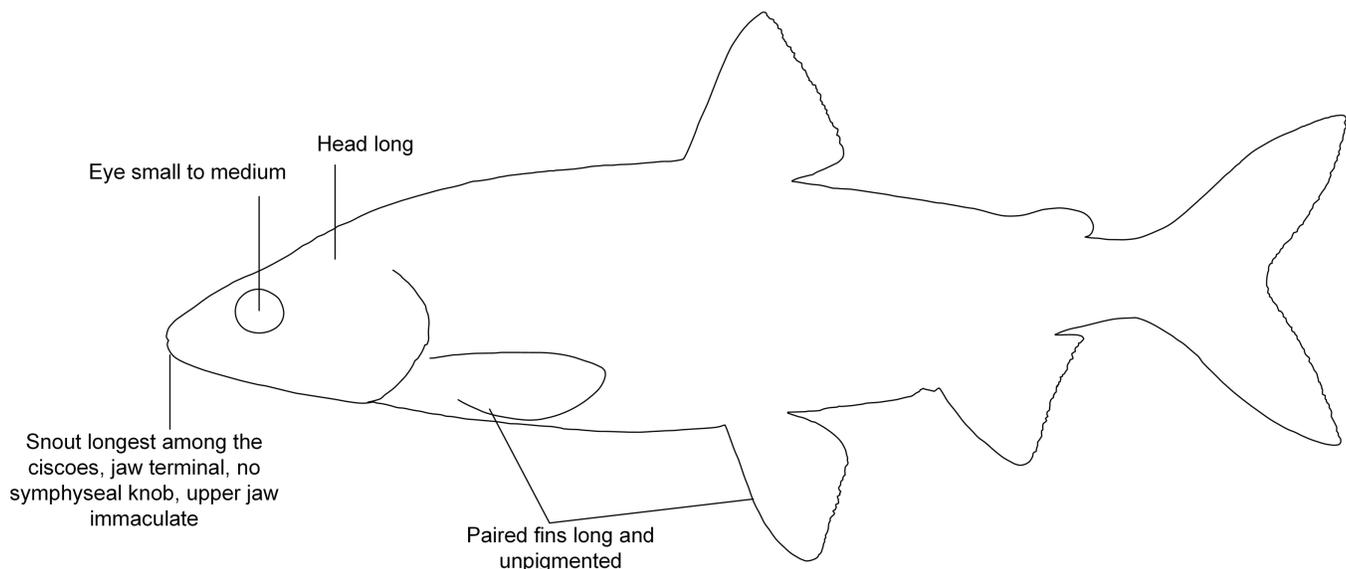
Johannaea contemporary distribution.

the last *johannaea* from Lake Michigan (Moffett 1957), and the last identifications from Lake Huron were made by Koelz (1929) in 1923, although the form was still abundant at that time.

DESCRIPTION (See Appendix)

Smith (1964) considered *johannaea* to be the second largest of the deepwater ciscoes. As of 1930, when large-bodied ciscoes were already becoming scarce in Lake Michigan, *johannaea* averaged 290-mm standard length (Smith 1964). Nine specimens taken in 2.50-2.75-inch (63.5-69.9 mm) -mesh gillnets from Lake Michigan, for which lengths were given by Koelz (1929), varied from 231 to 288 mm standard length (STL); Lake Huron specimens from the same mesh sizes varied from 170-305 mm. *Johannaea* is slightly ovate in shape, moderately

compressed, and elongate (Koelz 1929). Greatest body depth just in front of dorsal fin. Body depth intermediate, STL/BDD 4.1 ± 0.4 (range 3.6-4.9). Head long (Fig. 3), STL/HLL 3.9 ± 0.2 (range 3.4-4.4). Snout longest among ciscoes, HLL/POL 3.5 ± 0.1 (range 3.3-3.8). Eye small to medium, HLL/OOL 4.4 ± 0.3 (range 3.6-5.3). Jaws usually terminal although lower jaw can be shorter. Gill rakers short, longest generally shorter than longest gill filament (Becker 1983); no symphyseal knob. Premaxillary angle (PMA) $50-60^\circ$. Maxillary length intermediate, HLL/MXL 2.6 ± 0.1 (range 2.4-2.8). Dorsal fin tall, HLL/DOH 6.1 ± 0.5 (range 4.4-7.2). Paired fins long, pectoral-pelvic-distance-to-pectoral-length ratio (PPD/PCL) 1.7 ± 0.2 (range 1.2-2.1), pelvic-anal-fin-distance-to-pelvic-length ratio (PAD/PVL) 1.3 ± 0.1 (range 0.8-1.6). Gill rakers (TGR) 29.3 ± 1.8 (range 25-36). *Johannaea* distinguishable from other ciscoes by almost always having fewer than



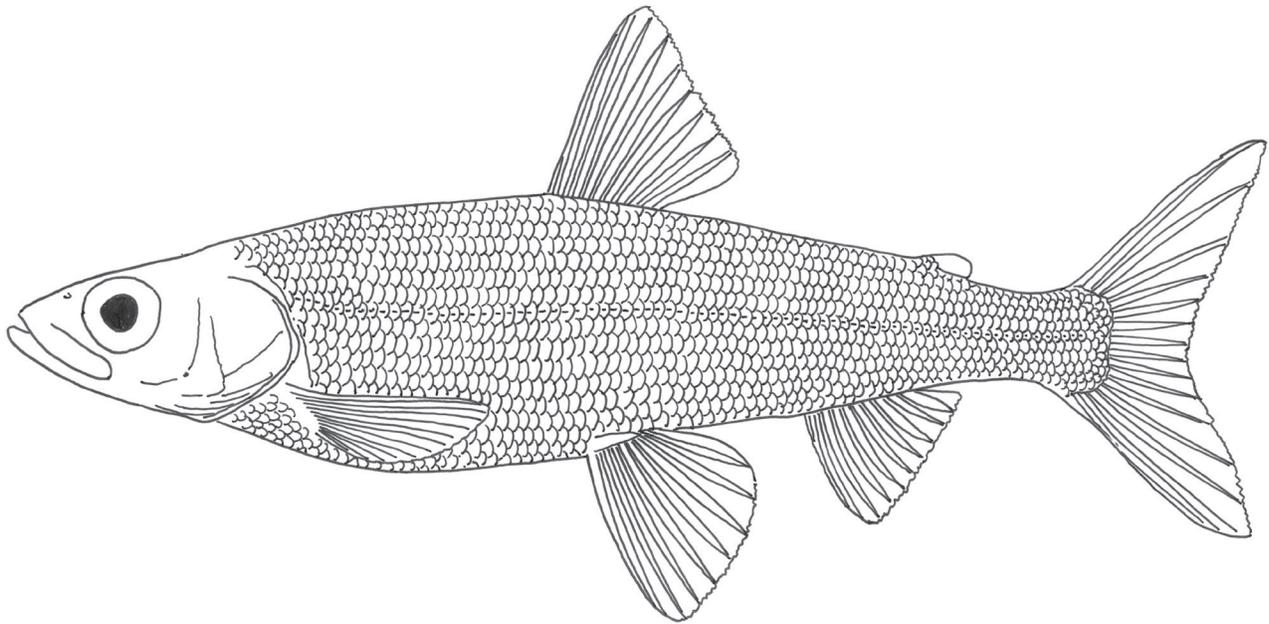
35 gill rakers on the first branchial arch, although a few *zenithicus* and *reighardi* may have 32 or fewer rakers. Paired fins unpigmented. Upper jaw unpigmented, whereas those of *zenithicus* and *reighardi* pigmented (Koelz 1929), allowing for identification of putative *johanna*e having 32-35 rakers. Color in life silvery, with a more or less faint pinkish to purplish iridescence, strongest above the lateral line and absent on the belly; colors fade after death exposing diminished amounts of pigment above the lateral line in preserved specimens (Koelz 1929).

ECOLOGICAL SKETCH

According to Koelz (1929), the spawning period was from mid-August to the end of September, but the spawning grounds were unknown. Most females with ripening ova disappeared from their feeding grounds in late August, suggesting that the feeding and the unidentified spawning grounds were disjunct. In Lake Michigan, adult-sized

*johanna*e typically occupied depths of 55-165 m. No juveniles of a size vulnerable to 1.5-inch (38-mm) -mesh gillnets (“bait nets”) were recorded, even at depths as great as 90 m (Koelz 1929). Gillnets of this mesh size were efficient for 150-275-mm standard length *C. hoyi* in Lake Huron in 1938 (Dobiesz et al. 2005). The “extreme” depth range for *johanna*e in Lake Huron given by Koelz (1929) was from 29 to 183 m, although he suspected this form occupied the deepest waters of the lake. Peak abundance in Lake Michigan occurred around 150 m in spring and summer and around 50 m in autumn (Bunnell et al. 2011). Thirty-four specimens from Lake Huron taken at depths of around 120 m had diets dominated by *Mysis diluviana* (Koelz 1929). Stable isotope analysis indicated the trophic position ($\delta^{15}\text{N}$) of *johanna*e was very similar to that of three congeners (*nigripinnis*, *zenithicus*, and *reighardi*). Its $\delta^{13}\text{C}$ signature was not as depleted as were those of *nigripinnis* and *kiiyi*, forms more deeply distributed in Lakes Michigan and Huron (Schmidt et al. 2011).

KIIYI *Coregonus kiiyi* (Koelz)



TAXONOMY

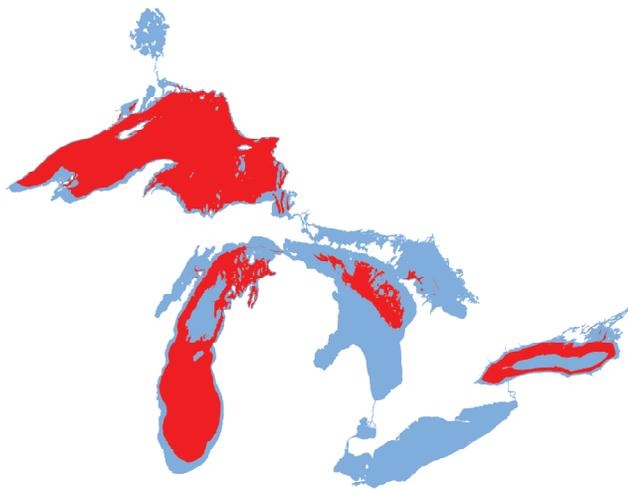
Leucichthys kiiyi was described by Koelz (1921) based on a specimen from Lake Michigan, but was later revised to *C. kiiyi* by Hubbs and Lagler (1958). Koelz (1929) grouped *C. kiiyi* of Lakes Michigan, Huron, and Superior into the subspecies *L. kiiyi kiiyi*. Because Lake Ontario specimens differed from those in the other three lakes

(“many more gill rakers on the first branchial arch, much-shorter paired fins, and a somewhat shorter head”), Koelz assigned this form to the subspecies *L. kiiyi orientalis*. The common name Kiiyi was given by the “chub” fishermen of Lake Michigan.

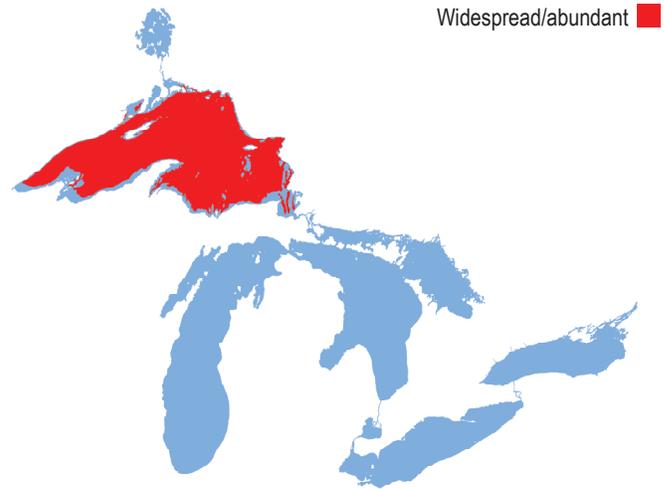
GEOGRAPHICAL DISTRIBUTION

Kiyi is endemic to and was widespread in the deep waters (>110 m) of all Laurentian Great Lakes except Erie and Nipigon (Koelz 1929). *Kiyi* is currently considered extant only in Lake Superior (Todd 1980; Miller et al. 1989).

Kiyi was last recorded in Lake Ontario in 1964, Lake Huron in 1973, and Lake Michigan in 1974 (Parker 1989; T. Todd, retired, USGS, personal communication, 2015).



Kiyi historical distribution.



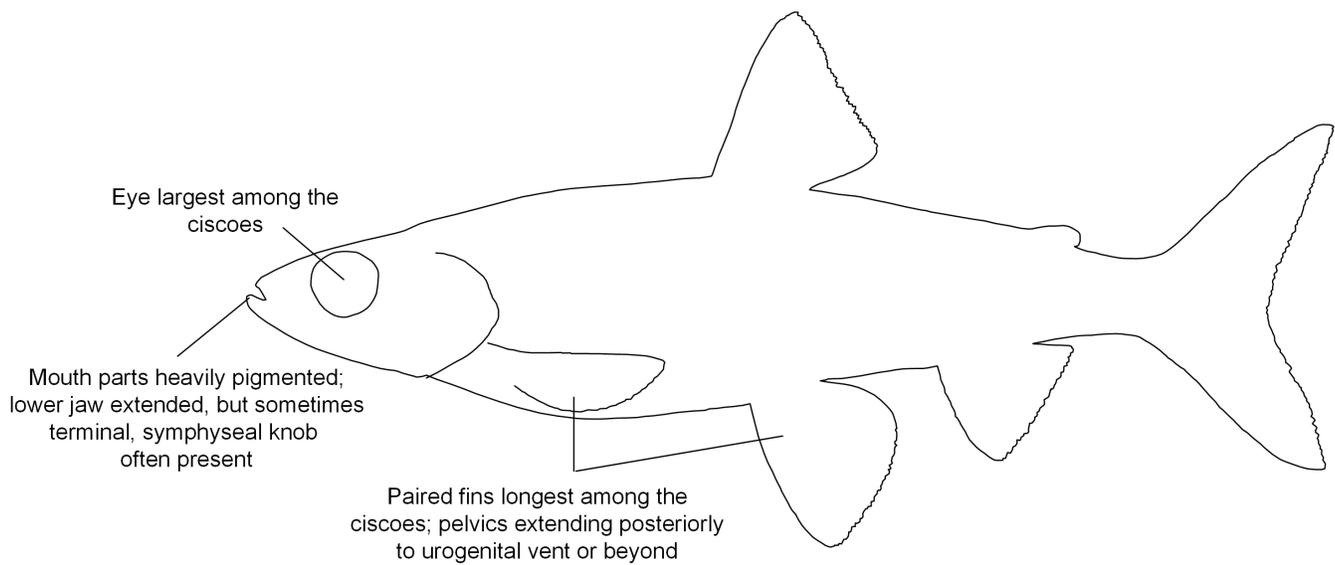
Kiyi contemporary distribution.

DESCRIPTION (See Appendix)

Koelz (1929) distinguished *kiyi* from other deepwater ciscoes by its relatively small size, laterally compressed body, and long paired fins. In the early 20th century, *kiyi* along with *hoyi* was the smallest of the Great Lakes ciscoes (<245 mm; Koelz 1921; Smith 1964). In contemporary times, mean standard length (STL) of *kiyi* sampled in a bottom-set, multi-mesh gillnet survey of the Canadian waters of Lake Superior was only 174 mm (range 131-265 mm), and mean weight was 67.0 ± 23.7 g (mean \pm SD throughout; Pratt and Chong 2012). Unlike in previous descriptions, mean STL of *kiyi* was shorter than that of *hoyi* (188 mm).

The body of *kiyi* is short, distinctly compressed laterally, and more ovate in side view compared with its closest conspecific, *hoyi*, which is more elliptical (terete) laterally (Koelz 1929; Pritchard 1931). Other characteristics that distinguish *kiyi* from *hoyi* include a larger eye, longer paired fins, and more heavily pigmented mouth parts (Todd 1980). Body depth distinctly greatest in front of dorsal fin at a point comprising 20-30% of STL (Scott and Crossman 1998). STL/BDD 3.9 ± 0.4 (range 3.1-5.3).

Deepest-bodied cisco except for *nigripinnis*. Head long (Fig. 3), STL/HLL 3.9 ± 0.2 (range 3.5-4.4). Snout long, HLL/POL 3.6 ± 0.2 (range 3.3-4.1). Eye exceptionally large, HLL/OOL 3.9 ± 0.2 (range 3.3-4.4). Mouth can be terminal, but weak lower jaw typically projects beyond upper jaw. Distinct symphyseal knob often on lower jaw (Scott and Crossman 1998), but observed in few contemporary specimens and may no longer be prominent. Maxillary long extending posteriorly to below anterior half of eye, HLL/MXL 2.5 ± 0.1 (range 2.3-2.7). Premaxillaries directed forward, premaxillary angle (PMA) $\sim 50^\circ$. Among ciscoes, tallest dorsal fin, STL/DOH 5.6 ± 0.4 (range 4.9-6.4). Longest paired fins among ciscoes, pectoral-pelvic-distance-to-pectoral-length ratio (PPD/PCL) 1.6 ± 0.2 (range 1.1-2.2) and pelvic-anal-fin-distance-to-pelvic-length ratio (PAD/PVL) 1.2 ± 0.1 (range 0.9-1.6). Only in *kiyi* do pelvic fins reach posteriorly to urogenital vent (Todd 1980). Gill rakers medium long, longest approximately equal to longest gill filament (Becker 1983). Total gill rakers (TGR) low end of range for ciscoes (39.7 ± 3.0 , range 34-48). Color in life silvery with pink, purple, or navy blue iridescence



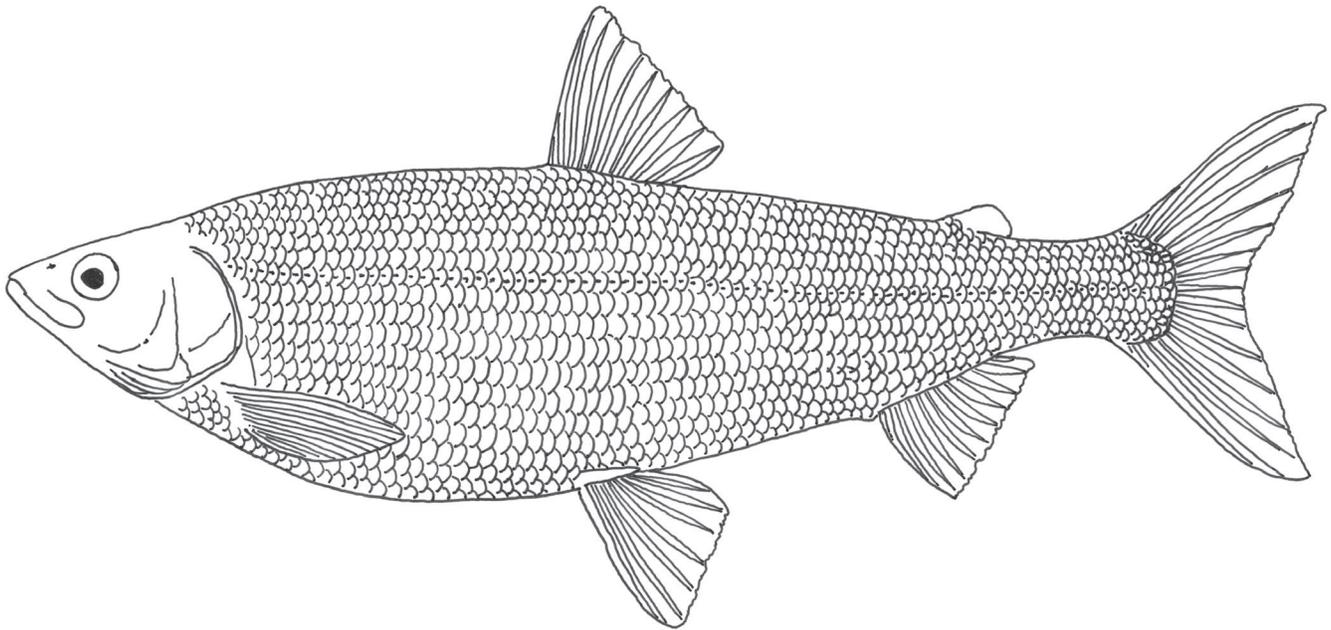
(Scott and Crossman 1998). Heavy pigmentation along entire dorsal surface above lateral line and extending to head with especially dark preorbital area. Minimal pigmentation (appears white) from below lateral line to ventral surface. Tip of mandible often densely pigmented. Dorsal and caudal fins black around margins, fins “sparingly sprinkled with pigment,” and ventral fins unpigmented (Koelz 1929).

ECOLOGICAL SKETCH

Putative timing of spawning differs among lakes and, to some extent, studies. In Lake Ontario, Koelz (1929) reported August spawning, whereas Pritchard (1931) reported October to January spawning. In Lake Michigan, Koelz (1929) reported October spawning, which is generally consistent with the September to November spawning reported by Hile and Deason (1947). Koelz (1929) reported that *kiyi* spawned as late as November in Lake Superior. *Kiyi* historically had the deepest depth distribution among the ciscoes, overlapping at the greatest depths only with *C. nigripinnis* (Koelz 1929; Hile and Deason 1947; Bunnell et al. 2012a). Across all studies, depth of capture ranged from 35 to >390 m, peak abundance occurred at depths ≥ 125 m, and *kiyi* was rare at ≤ 100 m (Koelz 1929; Pritchard 1931; Smith 1964; Dryer 1966; Scott and Crossman 1998; Sitar et al. 2008; Bunnell et al. 2012a). Koelz (1929) reported *kiyi* associated with clay or silt substrates. It comprised $\sim 53\%$ of all deepwater ciscoes caught in experimental gillnets in Lake Ontario during 1927 (Pritchard 1931) but only 0.01% in 1942

(Stone 1947). In Lake Michigan, the percentage of *kiyi* among all deepwater ciscoes taken in experimental gillnets in the northern basin declined from 7.8% in 1932 to 3.8% in 1955 to 1.0% in 1961, and, in the southern basin in comparable time periods, the declines were from 24.3% to 14.0% to 4.9% (Smith 1964). In Lake Superior in 2001-2003, *kiyi* represented $\sim 40\%$ of the deepwater ciscoes at depths of 121-160 m and $>90\%$ at depths of 161-300 m (Gorman and Todd 2007). On the basis of contemporary sagittal otolith sections, *kiyi* was the youngest among the Lake Superior ciscoes—female mean age was 9.1 ± 2.8 years (range 4-22); male mean age was 8.4 ± 2.3 years (range 5-16). *Kiyi* is the slowest growing and has the lowest rate of annual survival ($\sim 62\%$) among the Lake Superior ciscoes (Pratt and Chong 2012). In Lakes Michigan and Ontario historically, *kiyi* fed on *Diporeia* spp. near the lakebed during the day (Pritchard 1931; Bersamin 1958). In Lake Superior, *Mysis* consistently comprised $>90\%$ of the diet (Anderson and Smith 1971b; Gamble et al. 2011a). A comparison of stable isotopes of ciscoes preserved during the 1920s indicated that in Lake Michigan the trophic niche of *kiyi* was separated significantly from, but was most similar to, the trophic niche of *C. nigripinnis*. By contrast, in Lakes Superior and Huron, the historical trophic niche of *kiyi* was most similar to that of *hoyi*, particularly in Lake Superior (Schmidt et al. 2011). Contemporary stable isotopes show *Mysis diluviana* is consumed more by *kiyi* than by *hoyi* (Sierszen et al. 2014).

BLACKFIN CISCO *Coregonus nigripinnis* (Milner)



TAXONOMY

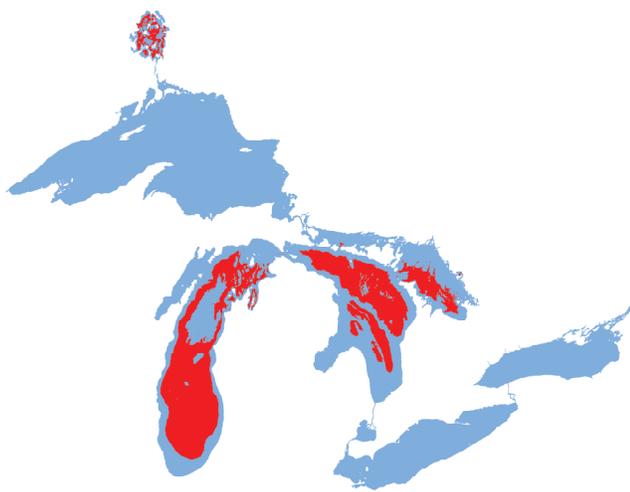
Milner (1874) named the Blackfin Cisco (*Argyrosomus nigripinnis nigripinnis*) in the first report on Great Lakes fisheries published by the U.S. Fish Commission. Although Gill (in Hoy 1872) had been credited previously as the author of the Blackfin Cisco, Page et al. (2013) revised authorship to Milner owing to Gill's paper not having been published formally. Milner (1874) identified the Blackfin Cisco only in connection with it being an important commercial species in Grand Traverse Bay, Lake Michigan. After Jordan and Evermann's (1911) revision of *Argyrosomus* to *Leucichthys*, Koelz (1929) described *Leucichthys nigripinnis* of the Great Lakes,

recognizing four subspecies: *cyanopterus* in Lake Superior, *nigripinnis* in Lakes Michigan and Huron, *prognathus* in Lake Ontario, and *regalis* in Lake Nipigon. Hubbs and Lagler (1958) made *Leucichthys* a subgenus of *Coregonus*, which remains current. Todd and Smith (1980) synonymized *cyanopterus* with *C. zenithicus*, and Todd (1981) recommended *prognathus* not be considered a valid taxon owing to the "poor condition and uncertain identity of the holotype." The affinity between *regalis* and *C. n. "nigripinnis"* remains uncertain (Todd and Smith 1980).

GEOGRAPHICAL DISTRIBUTION

Within the Great Lakes, *C. nigripinnis nigripinnis* occupied only Lakes Michigan and Huron (excluding the North Channel); the *regalis* form remains in Lake Nipigon (Clarke and Todd 1980; Todd and Smith 1992; Turgeon et al. 1999). *Nigripinnis* is reported to occur in various western Canadian lakes, but these forms may be variants of *C. artedi* (Clarke and Todd 1980; Scott and Crossman 1998; Mellow 2007). Very recently, a *nigripinnis*-like form was reported from inland lakes in Algonquin Park, Ontario (M. Ridgeway, OMNRF, personal communication, 2014), but inland lake forms are not addressed in this publication.

Formerly, *nigripinnis* occurred throughout Lake Michigan, Lake Huron’s main basin, and Georgian Bay at suitable depths (Koelz 1929). Koelz (1929) did not observe *nigripinnis* while sampling the North Channel and was skeptical that it occurred in this relatively shallow embayment. The last specimen from Lake Michigan was seen in 1955 (Smith 1964) and none were taken in Lake Huron during investigations conducted during 1956 (Eshenroder and Burnham-Curtis 1999), making 1923 the last record for Lake Huron (Koelz 1929). In Lake Nipigon, *nigripinnis* remains abundant (Koelz 1929; Turgeon et al. 1999).



Nigripinnis historical distribution.



Nigripinnis contemporary distribution.

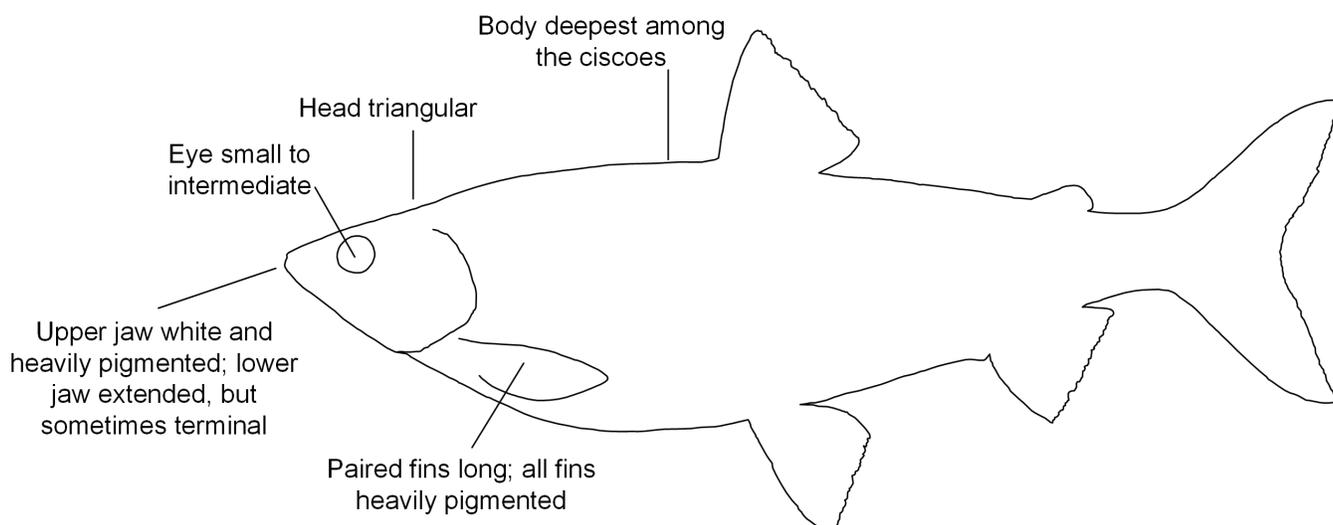
Widespread/abundant ■

DESCRIPTION (See Appendix)

Nigripinnis was the largest of the deepwater ciscoes inhabiting Lake Michigan (Smith 1964). The size range of specimens from Lake Michigan given by Koelz, 252-300 mm, likely is biased low for fish vulnerable to bottom-set gillnets fished in waters deeper than 64 m. His gillnet-mesh sizes (stretch mesh) ranged from 2.50-2.75 inch (63.5-69.9 mm), whereas he noted that the commercial fishery formerly targeted this species using mesh sizes of 3.5-4.0 inch (88.9-101.6 mm). He also noted that *nigripinnis* “not infrequently” attained a standard length (STL) of 350 mm and a weight exceeding 680 g. Koelz (1929) saw even larger specimens in Lake Nipigon, the largest recorded having an STL of 330 mm, but this difference likely owes to the Lake Michigan population being commercially extinct by the early 1920s (Koelz 1926), whereas the Lake Nipigon population was

essentially unfished at the time Koelz was conducting his field work (Dymond 1943).

Body ovate, deepest in front of dorsal fin and of nearly uniform depth from back of head to insertion of dorsal and ventral fins. Head triangular in side view. Body depth deepest among deepwater ciscoes, STL/BDD 3.8 ± 0.3 (range 3.4-4.2). Head moderately long (Fig. 3), STL/HLL 4.1 ± 0.2 (range 3.7-4.7). Snout blunt and moderately long, HLL/POL 3.7 ± 0.1 (range 3.5-4.1). Orbital length (OOL) short to intermediate, HLL/OOL 4.1 ± 0.3 (range 3.6-4.6). Lower jaw usually extended but sometimes terminal without symphyseal knob (Scott and Crossman 1998). Maxillary length intermediate, HLL/MXL 2.6 ± 0.1 (range 2.4-2.7). Premaxillary angle (PMA) 45-60°. Dorsal fin tall, STL/DOH 5.9 ± 0.3 (range 5.5-6.9). Paired fins long,



pectoral-pelvic-distance-to-pectoral-length ratio (PPD/PCL) 1.6 ± 0.2 (range 1.2-2.2), and pelvic-anal-fin-distance-to-pelvic-length ratio (PAD/PVL) 1.3 ± 0.1 (range 1.0-1.6). Gill rakers long, longest gill filament shorter than longest raker (Becker 1983). Gill rakers (TGR) numerous (47.1 ± 2.4 , range 40-52). In life, *nigripinnis* of Lakes Michigan, Huron, and Nipigon varied little in color, all being generally silvery in tone and having a blue-black dorsal surface with pea-green and blue-green hues. Below the lateral line, a pale blue green is evident beneath the silvery layer. Sides and cheeks suffused with a purplish iridescence, which is strongest above lateral line. Upper jaw white and heavily pigmented. Fins whitish, all usually so heavily pigmented the effect is blue black. Preserved *nigripinnis* appear heavily pigmented above lateral line, including top of head and distal portions of all fins (Koelz 1929).

ECOLOGICAL SKETCH

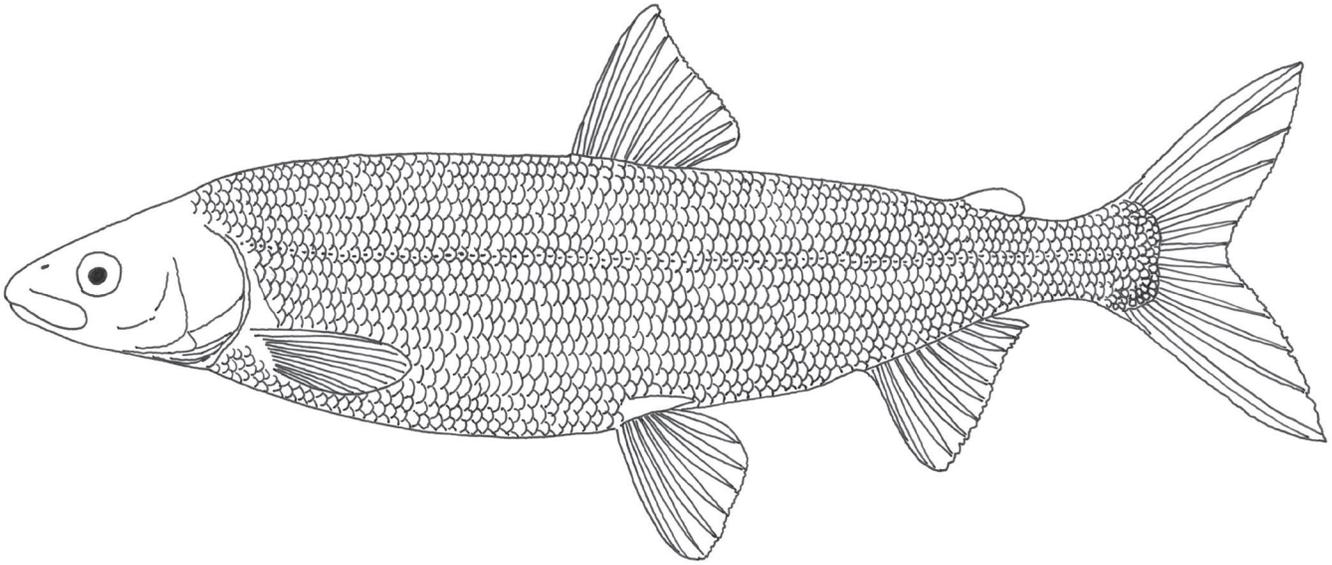
Lake Michigan fishermen claimed to have taken spawning *nigripinnis* at depths of 73-165 m east of Milwaukee during late December-early January, according to Koelz (1929). He thought the spawning season occurred sometime between October and March in Lake Michigan and after December in Lake Huron, but as *nigripinnis* was already scarce during his study (1917-1925), his bathymetric distributions and spawning times in these two lakes are approximations.

No information on spawning season has been published for the Lake Nipigon form. For Lake Huron, Koelz (1929) reported a maximum fishing depth of 183 m, while recognizing that *nigripinnis* likely occupied even deeper waters. For Lake Nipigon, Dymond (1943)

reported that *nigripinnis* occupied depths as great as ~100 m, more than any other species of fish in the lake, including three other species of deepwater ciscoes. Lake Nipigon *nigripinnis*, however, was commonly found in shallow waters, too, and was said by Dymond (1943) to have had an optimum summer depth of only 33-37 m, indicating a substantial behavioral divergence from the Great Lakes form. Koelz (1929) recorded *nigripinnis* in Lake Nipigon from the shallowest (~60 m) and deepest (102 m) depths sampled, and almost all lifts were made during June-September. This finding is consistent with Dymond (1943) in that the recent collections were made in August, a month when *nigripinnis* was reported to occupy shallow water. Based on few samples, *nigripinnis* of Lake Huron fed on *Mysis diluviana* (Koelz 1929). Those collected in Lake Nipigon in August in shallow water (<60 m) fed on *M. diluviana* and copepods (Turgeon et al. 1999), indicating some overlap with what Koelz (1929) reported for Lake Huron.

SHORTNOSE CISCO *Coregonus reighardi* (Koelz)

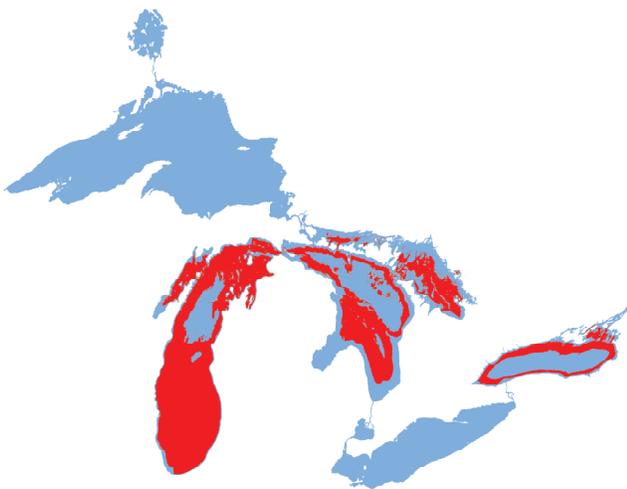
MAIN FORMS



TAXONOMY

The Shortnose Cisco (*Coregonus reighardi* Koelz) was described from Lake Michigan (Koelz 1924), named after Dr. Reighard, and subsequently identified in Lake Nipigon (Dymond 1926), Lakes Ontario and Superior (Koelz 1929), and Lake Huron (Scott and Smith 1962). Koelz (1929) identified two subspecies: *C. r. reighardi* of Lakes Michigan and Ontario and *C. r. dymondi* of Lakes Nipigon and Superior. Todd and Smith (1980) concluded that the subspecies *C. r. dymondi* was a synonym of

C. zenithicus, even though *C. r. dymondi* spawned in spring (Koelz 1929; Pritchard 1931; Jobes 1943). Schmidt et al. (2011), however, reported significant isotopic differences between *r. dymondi* and *zenithicus* of Lake Superior, suggesting that *r. dymondi* was a distinct form. Webb and Todd (1995) inferred that *reighardi* in each of the Great Lakes may not share a recent, common ancestor, making each a separate evolutionary entity.



Reighardi historical distribution.



Reighardi contemporary distribution.

GEOGRAPHICAL DISTRIBUTION

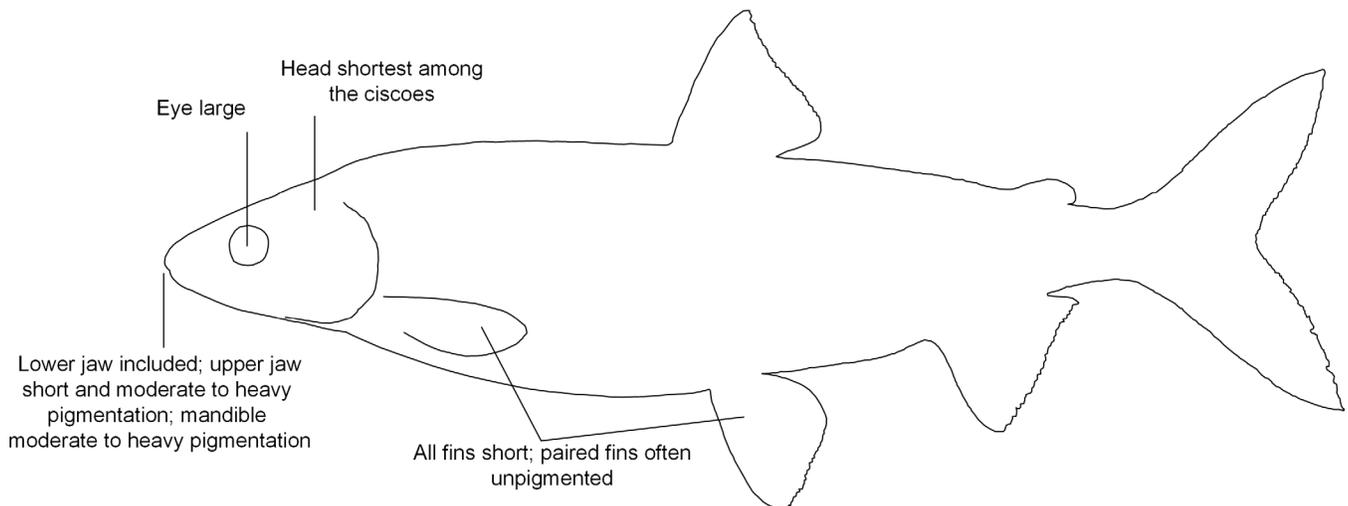
Reighardi was endemic to Lakes Huron, Michigan, and Ontario (Koelz 1929; Scott and Crossman 1998). Despite more-recent sampling using appropriate gear at suitable locations and depths, *reighardi* was last recorded in Lake Ontario in 1964, Lake Michigan in 1982, and Lake Huron in 1985 and is currently believed to be extinct (Webb and Todd 1995).

DESCRIPTION (See Appendix)

The body in side view tapers smoothly and regularly to the head and tail from the deepest point of the body, located just in front of the dorsal fin, and comprising 22-26% of standard length (STL; Koelz 1929). Body only slightly laterally compressed, almost cylindrical in cross section (Scott and Crossman 1998). Body shallow, STL/BDD 4.3 ± 0.3 (range 3.7-4.7). Head short (shortest in Lake Ontario; Fig. 3), STL/HLL 4.3 ± 0.2 (range 3.9-5.0). Snout truncate in side view, because of near vertical position of premaxillaries, and medium in length, HLL/POL 3.8 ± 0.2 (range 3.4-4.3). Eye relatively small, HLL/OOL 4.0 ± 0.2 (range 3.5-5.0). Lower jaw included without symphyseal knob. Maxillary short for deepwater cisco, HLL/MXL 2.7 ± 0.1 (range 2.5-2.9). Premaxillary angle (PMA) 60-70°, tip of maxillary usually at or below lower edge of pupil (Koelz 1929).

Dorsal fin height medium, STL/DOH 7.0 ± 0.4 (range 5.7-8.0). All fins rather short, pectoral-pelvic-distance-to-pectoral-length ratio (PPD/PCL) 2.2 ± 0.2 (range 1.5-2.9) and pelvic-anal-fin-distance-to-pelvic-length ratio (PAD/PVL) 1.5 ± 0.1 (range 1.2-2.1). Gill rakers short, longest shorter than longest gill filament (Becker 1983). Gill rakers few in number, TGR 36.2 ± 2.1 (range 30-43). Scott and Crossman (1998) reported a more compressed gill raker range (32-38) for *reighardi* of Lakes Huron, Michigan, and Ontario. Nuptial tubercles present on mature males and at least some females (Scott and Crossman 1998). Its $\delta^{15}\text{N}$ signature in Lakes Michigan and Huron suggests that, among deepwater ciscoes, it occupied an intermediate trophic level. Its $\delta^{13}\text{C}$ signature in these lakes indicated a more inshore carbon supply (Schmidt et al. 2011), consistent with its occupancy of relatively shallow water.

The body has a silver iridescence on the sides and is white below; upper jaw, mandible, dorsal fin, and caudal fin are pigmented. Paired fins often unpigmented (Scott and Crossman 1998). *Reighardi* can be distinguished from other ciscoes by the distinctive dark pigmentation of the snout and upper jaw, but less so over the maxillary bone (Scott and Crossman 1998). Pritchard (1931) noted that Lake Ontario specimens had a light greenish straw-colored dorsum.



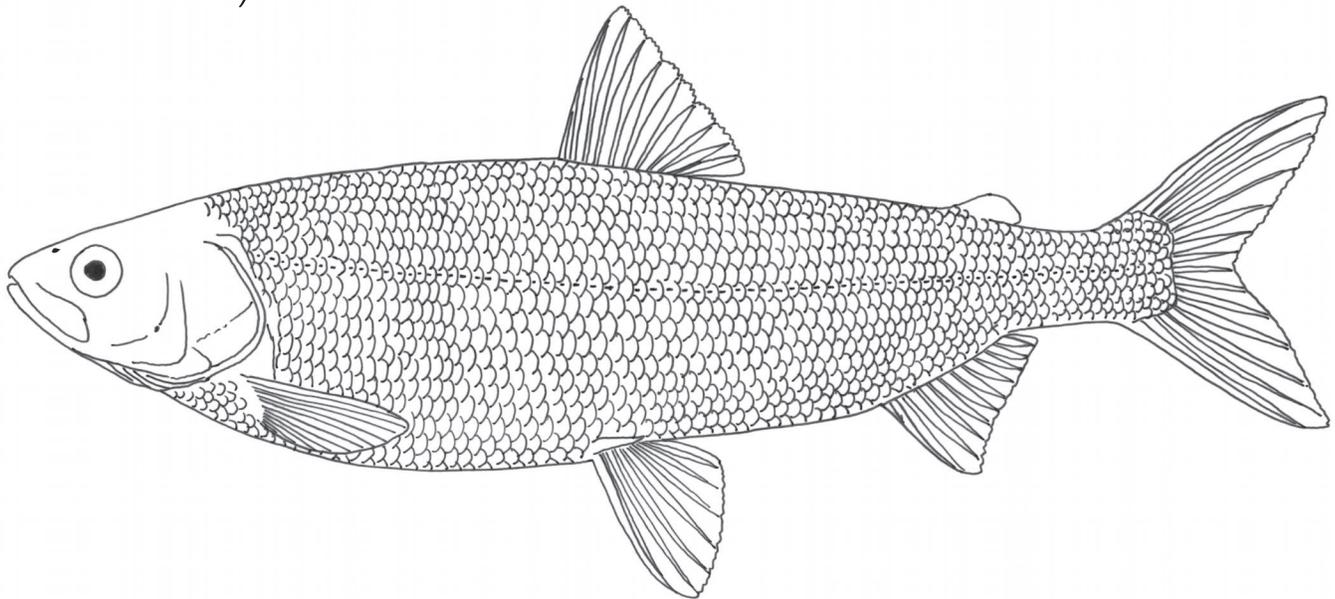
ECOLOGICAL SKETCH

Reighardi inhabited depths of 37 to 92 m in Lake Huron (Webb and Todd 1995) and 22 to 92 m in Lake Ontario (Pritchard 1931). In Lake Michigan during the early 1930s, *reighardi*, along with *hoyi*, typically was most abundant at relatively shallow depths (50-68 m) compared to other deepwater ciscoes (Bunnell et al. 2012a).

Reighardi was the only cisco that typically spawned in spring (Webb and Todd 1995). Spawning occurred from May to June in Lakes Huron and Michigan (Koelz 1929; Jobs 1943; Scott and Crossman 1998) and in April to May in Lake Ontario (Pritchard 1931). Spawning occurred at depths of 52-146 m in Lake Michigan (Jobs

1943), and predominantly at 73 m in Lake Ontario (Pritchard 1931). Spawning depths in Lake Huron are unknown (Scott and Crossman 1998). Smith (1964) noted a large number of individuals in spawning condition in autumn in an area of Lake Michigan where spawning had occurred the previous spring, indicating a change in spawning behavior and increasing the possibility of hybridization with other autumn-spawning ciscoes. Prey items in Lakes Huron and Ontario were predominantly the freshwater crustaceans *Mysis diluviana* and *Diporeia* spp. (Koelz 1929; Pritchard 1931).

SHORTJAW CISCO *Coregonus zenithicus* (Jordan and Evermann)



TAXONOMY

Argyrosomus zenithicus was described from a Lake Superior specimen captured off Duluth, Minnesota (the “Zenith” city), by Jordan and Evermann (1909). It was revised to *Leucichthys zenithicus* by (Dymond 1926) and ultimately named *Coregonus zenithicus* by Hubbs and Lagler (1958). Koelz (1929) identified *C. alpenae* from Lakes Michigan and Huron, *C. nigripinnis cyanopterus* from Lake Superior, and *C. reighardi dymondi* from Lakes Superior and Nipigon. It was subsequently reported from

Lake Erie by Scott and Smith (1962). All of these forms were synonymised with *zenithicus* (Todd and Smith 1980; Todd et al. 1981). Further, Clarke (1973) suggested that *C. nigripinnis prognathus* and *C. reighardi reighardi* in Lake Ontario also may be synonymous with *zenithicus* (see also Todd 1981). Identifications of *zenithicus* outside of the Great Lakes should be viewed with caution due to taxonomic uncertainty (Scott and Crossman 1998; Todd 2003).

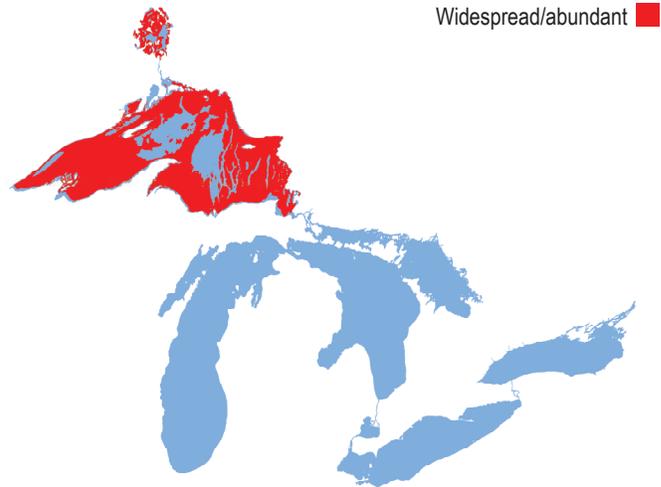
GEOGRAPHICAL DISTRIBUTION

Zenithicus was described from all the Great Lakes and Lake Nipigon, with the exception of Lake Ontario. It was last verified in Lake Michigan in 1975 and was believed extirpated in Lake Huron after 1982 (Todd 2003). Occasional, more-recent recoveries of putative *zenithicus* from Lake Huron (Mandrak et al. 2014) have been reclassified as hybrids, implying that *zenithicus* is extirpated from this lake (see *Lake Accounts* section, Ciscoes of Lake Huron subsection). Seven *alpenae*,

collected in 1946-1947, originally identified as *johanna* and now synonymized as *zenithicus*, were recognized as the first *alpenae* collected from Lake Erie (Scott and Smith 1962). An additional 26 *alpenae* were collected in 1957, and these were the last recorded (Scott and Smith 1962). *Alpenae* was also identified among the last *zenithicus* netted from Lakes Michigan and Huron. *Zenithicus* remains widely dispersed in Lakes Superior and Nipigon (Todd 2003).



Zenithicus historical distribution.



Zenithicus contemporary distribution.

DESCRIPTION (See Appendix)

Maximum standard lengths (STL) from (Koelz 1929) were: Lake Superior 332 mm, Lake Michigan 312 mm, Lake Huron 318 mm, and Lake Nipigon 308 mm. These maximums would not change if the now synonymized *reighardi dymondi* of Lakes Superior and Nipigon were included with *zenithicus* in those lakes, but, if the now synonymized *nigripinnis cyanopterus* were included with Lake Superior *zenithicus*, the maximum would increase substantially, to 375 mm. The maximum STL for Lakes Michigan and Huron would increase considerably if the now synonymized *alpenae* was included with *zenithicus* in those lakes (386 and 368 mm, respectively). In Lake Michigan, mean STL of *alpenae* captured in 2.38-3.00-inch (60.3-76.2 mm) -stretch-mesh gillnets varied little over time: 1923 = 227 mm, 1928 = 212 mm, 1930-1932 = 231 mm (Jobs 1949). Similarly, in 1922, Van Oosten (1929) recorded a mean standard length of 220 mm for *zenithicus* collected in Lake Superior with 2.63-inch

(66.7 mm) -stretch-mesh gillnets. *Alpenae* from Lake Erie captured in commercial and experimental gillnets and in bottom trawls (245 mm, range 219-268, Scott and Smith 1962) were smaller than those reported by Koelz (1929) from Lakes Huron and Michigan.

Body elongate, subterete, laterally compressed, and of moderate size. Body deepest just before dorsal fin. STL/BDD 4.4 ± 0.4 (range, 3.5-5.3), same as typical *artedi*. Head long (Fig. 3); STL/HLL 4.0 ± 0.2 (3.5-4.5). Snout very long; HLL/POL 3.5 ± 0.1 (range 3.2-4.0). Eye small to medium; HLL/OOL 4.3 ± 0.3 (range 3.5-5.2). Mouth inferior and small in *zenithicus* and superior in *alpenae* (see *Epilogue* section). Maxillary relatively long; HLL/MXL 2.5 ± 0.1 (range 2.3-2.8). Mandible without symphyseal knob, typically included *zenithicus* and extended *alpenae*. Premaxillaries typically make distinct angle on snout (PMA = 60-75°), whereas in other ciscoes (excluding *reighardi*), premaxillaries in line with slope of head or make only very minor

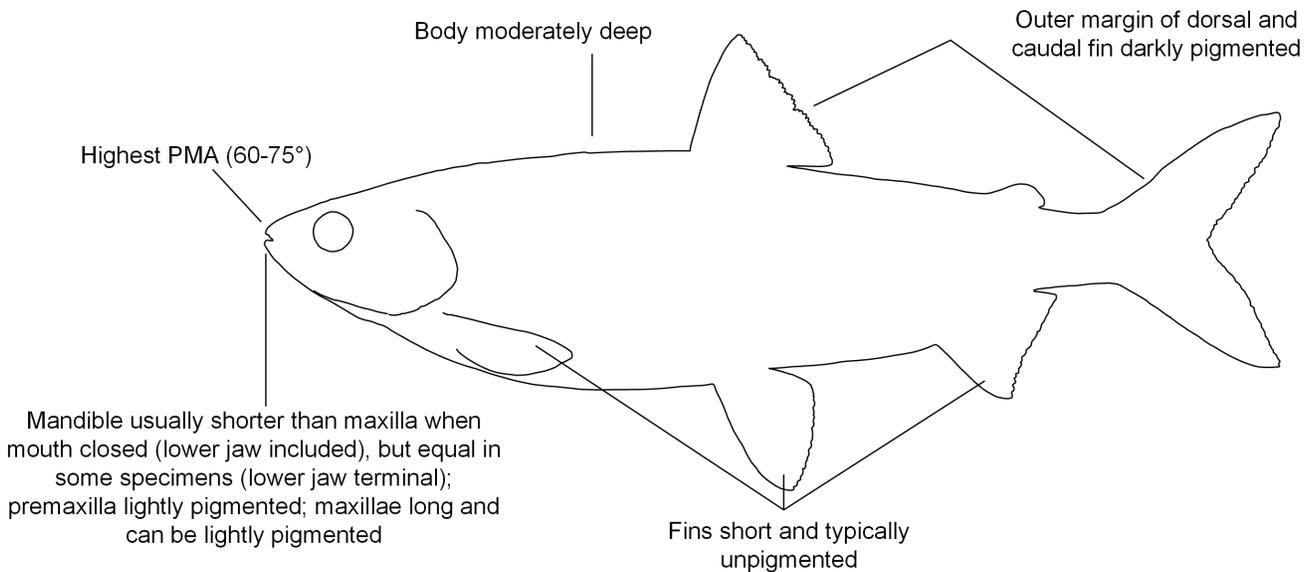
angle at snout. Dorsal fin height medium; STL/DOH 6.4 ± 0.6 (range 5.2-7.9). Paired fins medium-short; pectoral-ventral-distance-to-pectoral-length ratio (PPD/PCL) 1.8 ± 0.2 (range 1.3-2.6) and pelvic-anal-distance-to-pelvic-fin-length ratio (PAD/PVL) 1.4 ± 0.1 (range 1.0-2.0). Gill rakers medium long; longest equals length of longest gill filament (Becker 1983). Gill rakers (TGR) low in number; TGR exclusive of synonymised forms 39.5 ± 2.3 (range 32-46). Generally silver in color. Greenish, olive, or tan dorsally shading to white ventrally. Premaxillary and tissue over maxillary bone usually pigmented in *zenithicus*. Premaxillary unpigmented in half of *alpenae* specimens and faintly pigmented in other half but flesh over maxillary bone almost always unpigmented. Specimens preserved for long periods lose all color while pigments become pronounced on back and diffused elsewhere (Koelz 1929; Clarke and Todd 1980; Todd 2003).

ECOLOGICAL SKETCH

Koelz (1929) did not observe any *zenithicus* in spawning condition in Lake Superior, but, in Whitefish Bay during June, he saw several females that were approaching ripeness. Todd and Smith (1980) reported spring spawning along the south shore of Lake Superior at three locations: Apostle Islands, Keweenaw Peninsula, and Grand Marais. Spring spawning was considered unusual, however, as *zenithicus* in Lakes Michigan, Huron, and Erie spawned solely in autumn (Koelz 1929; Scott and Smith 1962). In Lake Michigan, spawning occurred over clay at depths

of 18-55 m (Koelz 1929). *Zenithicus* in the Great Lakes generally inhabited depths of 45-144 m (Todd 2003), with capture depths of 18-183 m (Scott and Crossman 1998). Seasonal differences were noted in Lake Superior with movement into deeper water in spring (110-144 m) and shallower water in summer (55-71 m) and winter (73-90 m) (Dryer 1966). *Zenithicus* of Lake Superior constituted over 90% of cisco samples in the early 1920s (Koelz 1929), 34% in the late 1950s (unpublished data cited in Hoff and Todd 2004), and around 11% in the early 1970s (Peck 1977).

Deepwater macroinvertebrates, primarily *Mysis diluviana* and to a lesser extent *Diporeia* spp., and limnetic crustaceans, mostly copepods and cladocerans, are the primary diet items consistent with the depth distribution of *zenithicus* (Koelz 1929; Anderson and Smith 1971b; Turgeon et al. 1999; Pratt 2013). Some seasonality in diet was apparent in Lake Superior with Chironomidae appearing in September and coregonine eggs appearing in May, indicating some opportunistic foraging (Anderson and Smith 1971b). Stable isotope analysis indicated a trophic niche in Lakes Huron, Michigan, Nipigon, and Superior distinct from other deepwater ciscoes, except for *C. nigripinnis cyanopterus* in Lake Superior (Schmidt et al. 2011). The relatively consistent trophic positioning of *zenithicus* indicates that it feeds at a lower trophic level than other ciscoes (Schmidt et al. 2009; Schmidt et al. 2011).



LAKE ACCOUNTS

The preceding *Main Forms* section is intended to provide a broad-brush perspective of each of the main forms and is not intended to be used alone for identification of specimens. High variation within forms among lakes calls for more-targeted descriptions. For example, contemporary shoal-spawning *artedi* from Lake Michigan has, on average, 4.0 fewer gill rakers than its counterpart in Lake Huron. Accordingly, lake accounts discuss morphological and ecological data specific to a lake and form. The description of each form within a lake account begins with a documentation of maximum size. Then, using nine body metrics, the morphotype described by Koelz (Appendix Tables 2-7) is compared with an across-lake composite of that same morphotype, also based on Koelz (Appendix Table 1). Next, the morphotype described by Koelz is compared to the contemporary morphotype (Appendix Tables 13-18). If the contemporary morphotype differs from the Koelz morphotype (see *Morphology of Ciscoes* section, Temporal Differences in Body Metrics subsection), a further comparison of a diverged body metric(s) is made with the same metric(s) recorded by Stanford Smith (Appendix Tables 8-12). This secondary comparison allows for determination of when the morphological divergence occurred, before or after Smith collected.

To enable more-rapid identification, each lake account contains a quick key that provides a weighted system for assessing the importance of nine characteristics: body shape, orbital length, lower jaw position, premaxillary angle, paired-fin lengths, gill raker number, upper jaw pigmentation, and paired-fin pigmentation. The degree to which each form expresses a particular trait is represented by three sizes of circle—large black circles represent a main character state, medium striped circles represent a moderate or occasional character state, and small white circles represent a rare character state. Intended mainly for use in making identifications of contemporary specimens, the quick keys for extant forms are based solely on contemporary body metrics (Appendix Tables 13-18) and patterns of pigmentation, the latter of which have not changed perceptibly from the descriptions of Koelz (1929). Historical data for extirpated/extinct forms are, however, included in the quick keys to provide perspective. The lake accounts are data rich, drawing heavily on appendix data, and are intended to be used mainly as a laboratory resource to further narrow field identifications and to facilitate quantitative comparisons among lakes and forms.



Setting Gillnets from a Small Boat

Image by AMM.

CISCOES OF LAKE SUPERIOR

TAXONOMY

Bailey and Smith (1981) and Todd and Smith (1992) recognized four species (here forms) of ciscoes from Lake Superior (*Coregonus artedi*, *C. hoyi*, *C. kiyi*, and *C. zenithicus*), although Koelz (1929) recognized additional species and subspecies (*C. artedi albus*, *C. nigripinnis cyanopterus*, and *C. reighardi dymondi*). *Albus* is recognized as a deep-bodied form of *artedi* (Yule et al. 2013), but Todd and Smith (1980) synonymized *C. r. dymondi* and *C. n. cyanopterus* with *C. zenithicus*. More recently, Schmidt et al. (2011) found, based on fish preserved by Koelz (1929), that *C. reighardi* was isotopically distinct from *C. zenithicus*, suggesting it was ecologically distinct too and therefore a valid form. Schmidt et al. (2011), though, did support Todd and Smith's (1980) synonymizing of *C. n. cyanopterus* with *C. zenithicus*, as the two forms had nearly identical isotopic signatures. *Dymondi* and *cyanopterus* may be environmentally induced (polyphenic) forms of *zenithicus*, as proposed by Todd and Smith (1980). Nonetheless, their morphotypes require recognition so as to determine their range and to account for morphotypic variation in *zenithicus*.

IDENTIFICATION OF EXTANT FORMS

Three of the four accepted forms differ in body shape. Typical *artedi* is subterete (*albus* is terete), *zenithicus* is also subterete, but one of its phenotypes is ovate (see below), *hoyi* is terete, and *kiyi* is ovate. *Hoyi* and *kiyi* typically have extended lower jaws whereas *zenithicus* and one of its phenotypes typically have an included lower jaw. *Artedi* may have an extended lower jaw, but has a high gill raker count (TGR, 43.9 ± 2.5), especially when compared to *kiyi* (40.6 ± 2.8) and *zenithicus* (40.7 ± 2.7 ; Appendix Table 13). *Kiyi* is the only form with pelvic fins long enough to extend to the urogenital vent. *Hoyi*, having an intermediate number of gill rakers (41.9 ± 2.6), has a triangular-shaped, flat head profile (Fig. 3), which is diagnostic, and also has a large eye (HLL/OOL, 4.2 ± 0.3), much like *kiyi* (3.9 ± 0.3). The premaxillaries in *zenithicus*, including its *r. dymondi* (putative) phenotype, diverge downward from the slope of the head (steep PMA, Figs. 3, 5), whereas the premaxillaries tend to follow the curvature of the head in *artedi*, *hoyi*, and *kiyi* (Fig. 3). This trait is not as pronounced now in *zenithicus* and *r. dymondi* as it was when Koelz collected (see illustrations below) but is still diagnostic. *Artedi*, *hoyi*, and *kiyi* are abundant

and relatively easy to distinguish upon capture. Field identification of the relatively uncommon *zenithicus* has been problematic because collectors are less familiar with this form, and specimens in recent years have tended to be smaller and confused with *hoyi* or *artedi*. Older, larger *zenithicus*, including the *dymondi* and *nigripinnis*-like phenotypes, are relatively easy to distinguish from *hoyi* or *kiyi* because *zenithicus* attains a noticeably larger body size (see below).

Identification of what Koelz classified as *n. cyanopterus* is unresolved. An extant, but uncommon, phenotype is large bodied and *nigripinnis*-like (ovate) in shape but with premaxillaries that follow the slope of the head (see Fig. 3 and illustration below), but museum specimens that Koelz classified as *n. cyanopterus* have steep premaxillary angles (not illustrated; personal observation, RLE and AMM). Both forms have gill raker numbers similar to *zenithicus* (TGR 40.7 ± 2.7 ; Appendix Table 2A,13). To provide names for these phenotypes, *cyanopterus* is retained for specimens with steep PMAs while *nigripinnis*-like ciscoes with low PMAs are referred to as “*nigripinnis* unnamed.” Distinguishing among *zenithicus* phenotypes remains challenging and would benefit from additional research.

Although Koelz identified *r. dymondi* as common in Lake Superior, particularly in northern bays, it was rare in gillnet and trawl surveys conducted from 1958 to 1974 by the USGS (OTG, unpublished data). More-recent studies by Gorman and Todd (2007) and Pratt and Chong (2012) failed to find *dymondi*, although USGS trawl surveys conducted in the eastern basin of Lake Superior in 2010-2013 produced seven individuals that were provisionally identified as *reighardi* (OTG, unpublished data). Given the distinctive character suite for this form in Lake Superior (compressed body, small eye, included lower jaw, and short pectoral fins; see quick key) and the finding that this form was isotopically distinct (Schmidt et al. 2011), the *reighardi* phenotype may be absent or nearly so in Lake Superior. However, this form may have been confused in recent collections with *zenithicus* as the differences between *zenithicus* and *reighardi* are subtle (Todd and Smith 1980).





Archived Ciscoes in the Walter Koelz Collection at the University of Michigan Museum of Zoology

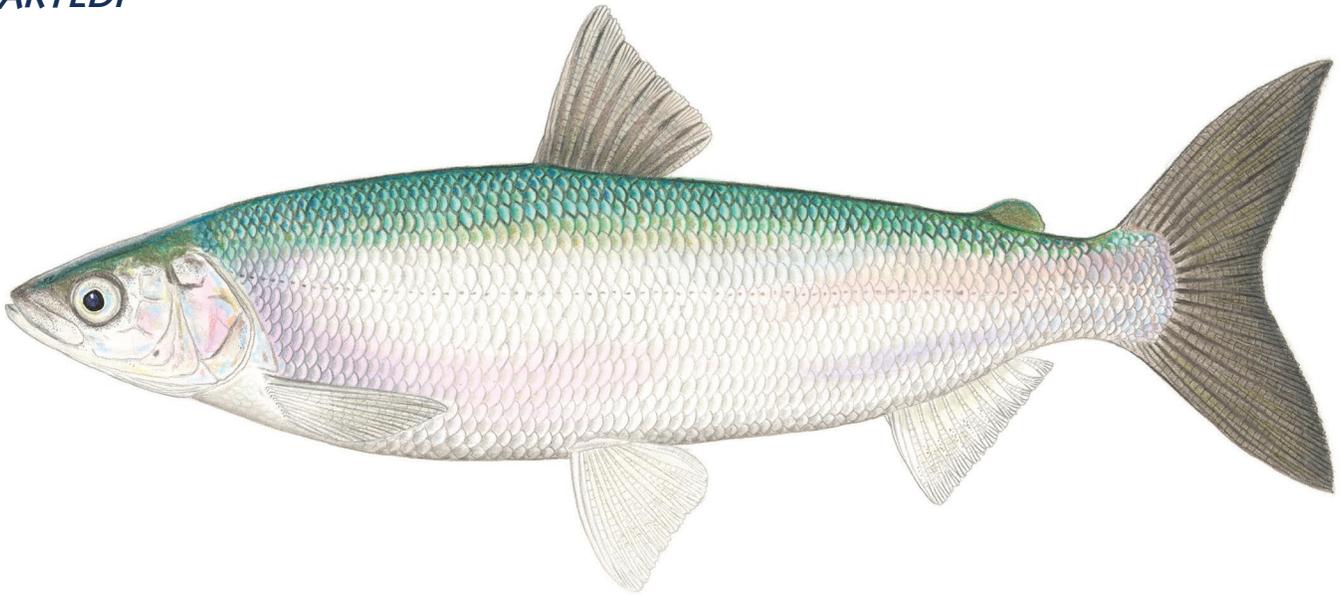
Image by AMM.

Low numbers of *nigripinnis*-like forms were identified in USGS gillnet and trawl surveys made during 1958-1971. The investigators at the Lake Superior Biological Station identifying these fish would have been influenced by Stanford Smith, whose summary of characteristics for separating ciscoes was based on Lake Michigan forms (Chart 1 in Hubbs and Lagler 1958). As a result, early investigators working in Lake Superior may have been looking for *n. nigripinnis* (a high-rakered form; Appendix Table 3A) and not *n. cyanopterus* (a low-rakered form; Appendix Table 2A). In the late 1970s, Stanford Smith provided a revised set of characters for Lake Superior ciscoes, which was largely concordant with Koelz's characters.

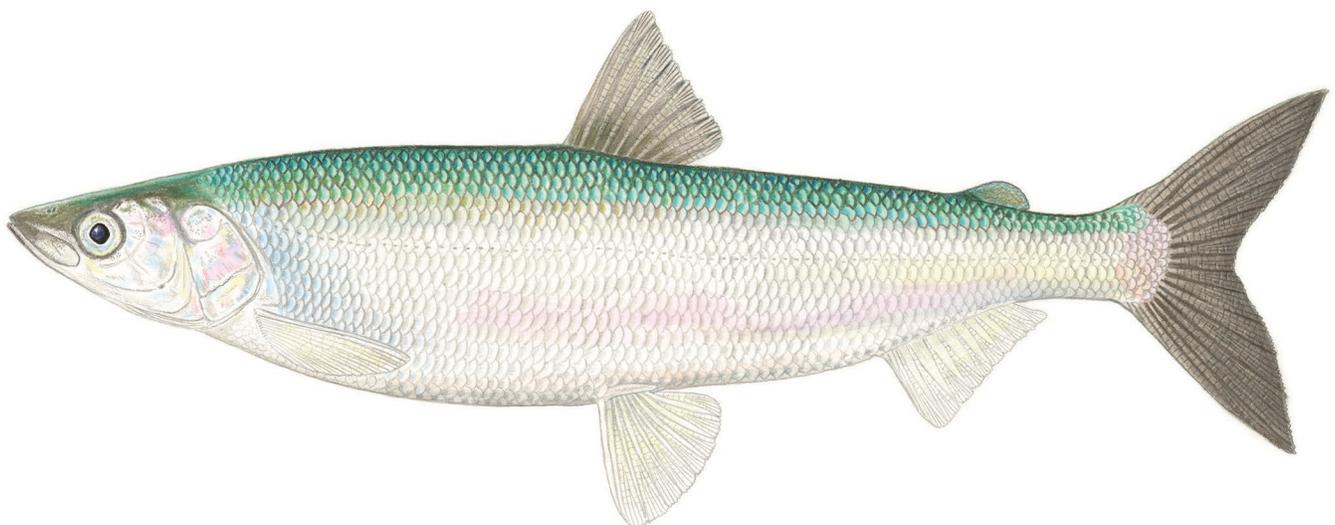
Bottom-trawl surveys conducted during 2007-2015 by the USGS yielded 15 putative *n. nigripinnis*, but whether these fish are *n. cyanopterus* is uncertain. These fish were described as medium to large chubs with *artedi*-like heads, deep ovate bodies, and medium-length fins, quite distinct from *artedi* and often with conspicuous black pigmentation. A subsample of seven had high gill raker counts (mean 43.7 ± 2.1), similar to contemporary *artedi*. *Nigripinnis* unnamed appears to be a common *zenithicus* phenotype in northwestern waters, although its distribution remains to be determined.



ARTEDI



Albus form of *C. artedi* collected by AMM and TCP 5.5 km east of Pie Island, 21 June 2010, GLFC specimen 70003, STL 277 mm.



Typical *artedi* collected by AMM and TCP off Thompson Island, 21 June 2010, GLFC specimen 60024, STL 255 mm.



Color in life



Color in death



Distinctive Taxonomic Traits

The maximum STL (standard length) of *artedi* reported by Koelz (1929) was 435 mm, but whether this individual was typical *artedi* or the deeper-bodied *albus* is uncertain. *Albus* was relatively rare in Koelz's collections; he enumerated only four specimens among his "representative fish." *Albus* occurred only in northern bays (Thunder, Black, and Nipigon) where it resembled *albus* of Lake Erie (Koelz 1929). Applying a discriminate function model based on Koelz's (1929) measurements to 2007-2011 collections, Yule et al. (2013) concluded that two forms of *artedi*, similar to the those described by Koelz (1929), existed in Lake Superior. *Albus* (the second form) comprised 24% of the individuals sampled in Black Bay and 31% of those in Nipigon Bay. In Canadian waters in 2004-2008, maximum size of all *artedi* from gillnets was 394 mm (Pratt and Chong 2012). In a comparison of nine metrics between typical *artedi* collected by Koelz (Appendix Tables 2A,B) and a composite typical *artedi* representing all lakes (Appendix Tables 1A,B), typical *artedi* from Lake Superior had a shallower body depth (STL/BDD, 4.8 ± 0.2 vs. 4.4 ± 0.4) and longer snout (HLL/POL, 3.7 ± 0.2 vs. 4.1 ± 0.2). The seven remaining body metrics differed little between typical *artedi* and the composite across all lakes.

Contemporary *artedi* (Appendix Table 13) differed notably from *artedi* collected by Koelz only in one out of nine metrics. This comparison was based on corrected HLL/POL and HLL/MXL, on conversion of the ratios used to assess paired-fin length (see Morphometrics and Meristics subsection), and on a contemporary dorsal fin height (DOH) of 6.6 ± 1.0 (not given in Appendix Table 13). Contemporary *artedi* had 3.0 fewer gill rakers than *artedi* collected by Koelz (TGR, 43.9 ± 2.5 vs. 46.9 ± 2.2). This decline in raker number does not result from contemporary *artedi* being smaller (mean STL = 240 mm). The regression of raker number on length is flat over the sizes of concern here (Fig. 6). Stanford Smith's raker count (46.7 ± 2.6 ; Appendix Table 8) was almost identical to that of Koelz, implying that the decline in raker number occurred after 1959-1961. Link and Hoff's (1998) regression of raker number on length based on a 1995 collection from southwestern Lake Superior does not provide insights. Their regression appears to be biased low such that contemporary *artedi* should have had a mean raker count of only 38.3 instead of 43.9, a 5.6 raker shortfall. Why gill raker number appears to have declined by three in *artedi* is unclear.

The appearance in 1987 of *Bythotrephes longimanus*, a relatively large zooplankton, represents a new selection pressure as would larger populations of zooplankton

resulting from increased top-down control by lake trout (Pratt et al. 2016). *Artedi* of Lake Superior appears to have remained fairly stable morphologically for around 90 years, except for the decline in gill raker number.

Local Ecological Characteristics

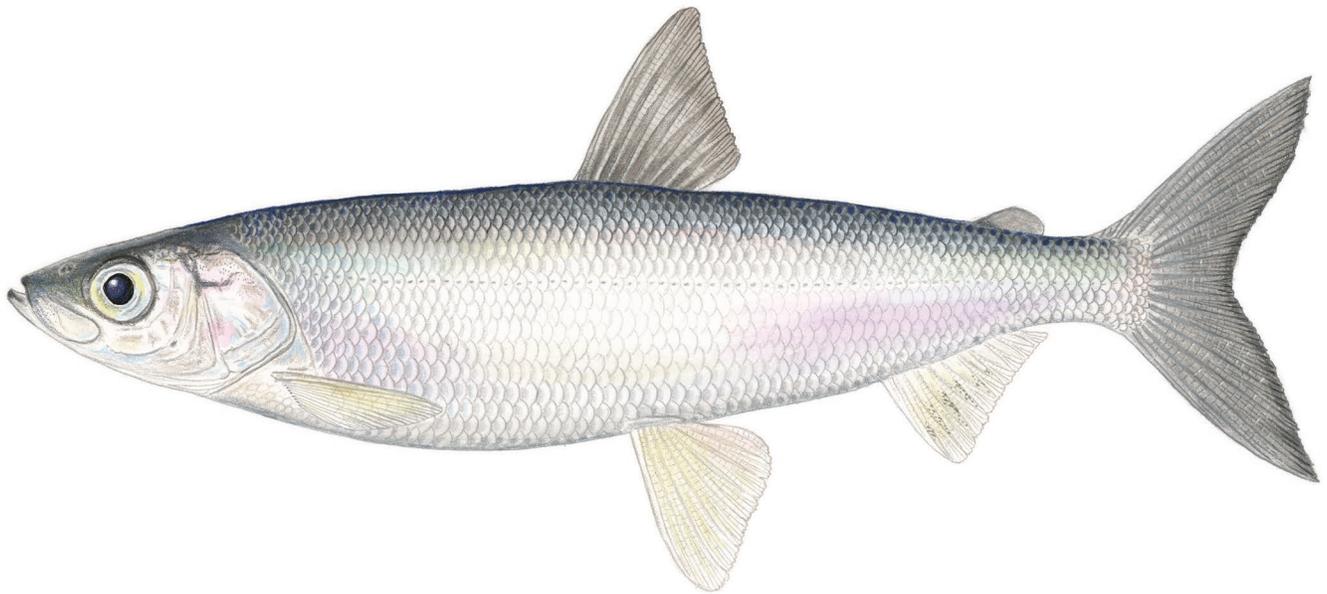
Coregonus artedi is the most-abundant cisco in biomass in Lake Superior (Stockwell et al. 2009; Yule et al. 2013) and was estimated to represent 61% of the total fish community in 2008 (Gorman et al. 2012b). As of 2015, populations were dominated by age-12 fish from the 2003 (last strong) year-class. Juveniles (≤ 4 years) occupy nearshore waters (≤ 80 -m depth) while adults occupy nearshore and deep (> 80 -m depth) offshore waters (Stockwell et al. 2009; Stockwell et al. 2010a; Gorman et al. 2012a; Pratt 2012). Adults are conspicuously pelagic and under-represented in bottom-set gillnet and bottom trawl surveys (Stockwell et al. 2006; Yule et al. 2007; Yule et al. 2008a), and express a pattern of shallow diel vertical migration (DVM) from depths of 50-80 m during the day to 10-40 m at night (Stockwell et al. 2010a; Ahrenstorff et al. 2011). Juveniles are demersal during the day and undergo DVM at night (Yule et al. 2007; Gorman et al. 2012a). Most individuals > 229 -mm STL and at least age 5 are mature (Yule et al. 2008b). Females reach a larger maximum size than males, exceeding 347 mm (Stockwell et al. 2009), and males exhibit higher mortality than females such that by age 10, 70% of the population is female (Yule et al. 2008b; Gorman 2012). Maximum age of *artedi* exceeds 20 years, but individuals > 15 years represented less than 10% of the Thunder Bay population in 2005 (Yule et al. 2008b). In Canadian waters in 2004-2008, maximum age was 30 years and females survived better, resulting in the population being 59% female (Pratt and Chong 2012).

Adults undergo seasonal migration from nearshore to offshore waters during spring and summer and return to nearshore waters during autumn, forming large spawning aggregations (Yule et al. 2006; Yule et al. 2009; Stockwell et al. 2010a). Spawning in the Apostle Islands occurs typically in nearshore waters 15-35-m deep in late November through early December, when *artedi* concentrate in the upper 20 m (Yule et al. 2006). Larval *artedi* hatch in late March through mid-May depending on weather conditions and ice-out with peak hatching usually occurring in early May (John and Hasler 1956; Oyadomari and Auer 2004, 2008). In spring, calanoid copepods dominated the diet, but during summer and autumn, cladocerans, including *B. longimanus*, became important (Johnson et al. 2004; Isaac et al. 2012). Adults

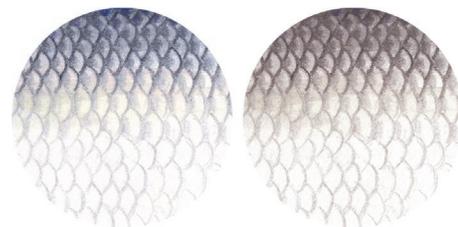
are known to feed on Rainbow Smelt during winter (Hoff et al. 1997). Analysis of stable carbon and nitrogen isotopes indicated that, in spring and summer of 2005-2006, *artedi* obtained ~78% of its nutrition from pelagic sources (Sierszen et al. 2014). In this same study, *Mysis diluviana* and zooplankton each comprised 39% of the diet, while Rainbow Smelt comprised 22%. Among Lake

Superior ciscoes, historically, *artedi* occupied a lower trophic level and tended to be intermediate in its use of respired carbon (Schmidt et al. 2011). When juveniles were abundant in Lake Superior, during 2005-2006, they represented 24% of the diet of lean Lake Trout (Sierszen et al. 2014).

HOYI



Collected by AMM and TCP off Sleeping Giant, 21 June 2010, GLFC specimen 80006, STL 175 mm.



Color in life

Color in death



Distinctive Taxonomic Traits

Maximum STL (standard length) reported by Koelz (1929) was 251 mm ($n = 335$), whereas in 2001-2005 maximum STL from a much-larger sample ($n = 1,762$) was 298 mm, but only 1% of these exceeded 227 mm (OTG, unpublished data). No notable differences were found in a comparison of nine metrics between Lake Superior *hoyi* (Appendix Tables 2A,B) and a composite *hoyi* (Appendix Tables 1A,B), all collected by Koelz, indicating that *hoyi* was remarkably similar basinwide. Of the nine metrics comparable between *hoyi* collected by Koelz and *hoyi* collected contemporaneously (Appendix Table 13; STL/DOH = 5.4 ± 0.4 (not in table)), contemporary *hoyi* had a smaller eye (HLL/OOL, 4.2 ± 0.3 vs. 3.7 ± 0.2) and a shorter pelvic fin (PAD/PVL, 1.6 ± 0.1 vs. 1.2 ± 0.1). This comparison was based on corrected HLL/POL and HLL/MXL and on conversion of STL/PCL and STL/PVL to PPD/PCL and PAD/PVL (see Morphometrics and Meristics subsection). Some small fraction of the reduction in orbital length likely results from measurement error (see Morphometrics and Meristics subsection), but most appears to be real in that *hoyi* now has a smaller eye than *kivi* (HLL/OOL, 3.9 ± 0.3 ; Appendix Table 13), whereas Koelz found them equal (Appendix Table 2A). Stanford Smith did not record HLL/OOL (Appendix Table 8) so whether this change in morphology occurred before or after the mid-1900s is unknown. As noted in the appendix, the reduction in pelvic fin length appears to be real, not the result of measurement error, and occurred during or before the mid-1900s.

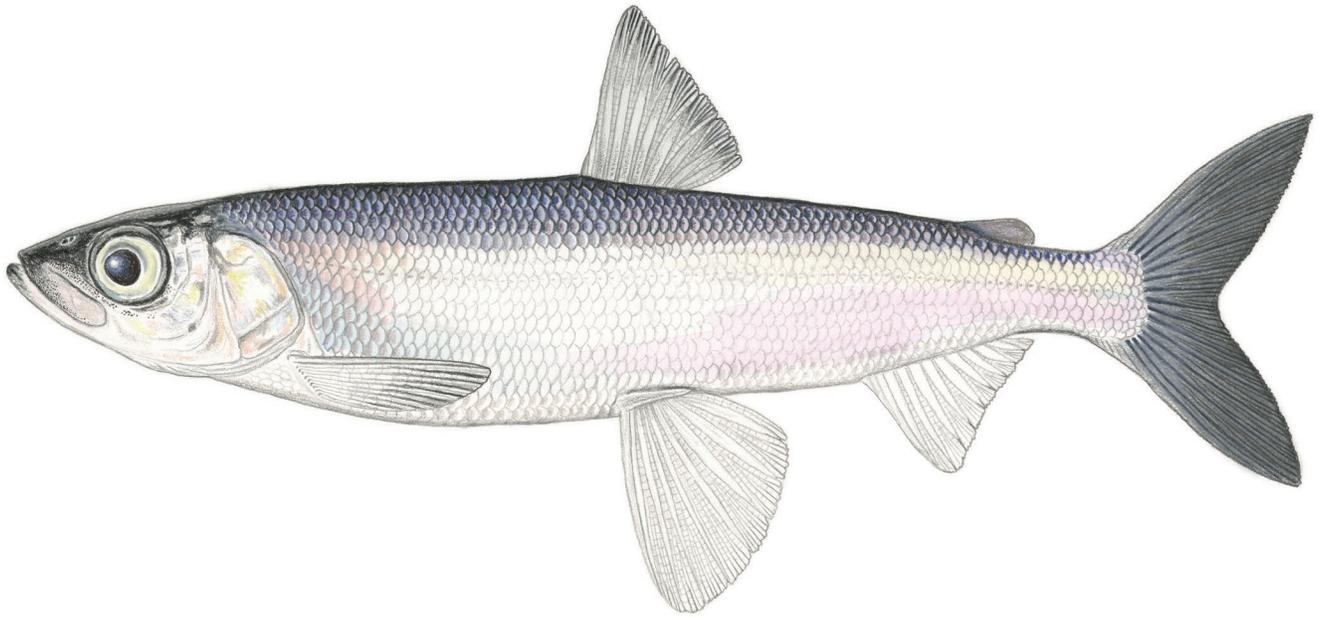
Local Ecological Characteristics

Hoyi is currently the most-abundant deepwater cisco in nearshore waters (<80-m depth) (Gorman and Todd 2007) and represented 2% of fish community biomass in 2008 (Gorman et al. 2012b). Adults and juveniles occupy demersal habitats during the day within 5-10 km of the shore at depths of 40 to 160 m (Gorman and Todd 2007; Gorman et al. 2012a; Pratt 2012). Smaller *hoyi* (<195 mm) are associated with depths <90 m, whereas larger fish are associated with depths of 60-160 m (Gorman et al. 2012b).

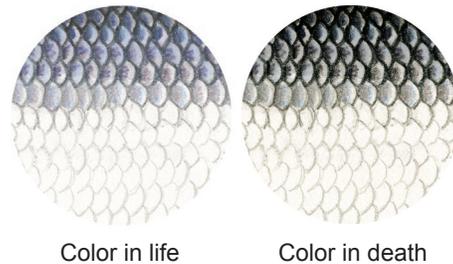
Hoyi undertake DVM at night, although not to the extent of *artedi* or *kivi* (Yule et al. 2007; Ahrenstorff et al. 2011; Gorman et al. 2012a). Based on a sample of 1,735 *hoyi* collected in bottom trawls in 2000-2005, growth was not sexually dimorphic, although by age 10 nearly 80% of the population was female, resulting in females attaining larger maximum sizes than males (Gorman 2012; OTG, unpublished data). The oldest individual was 21 years (otolith age) and >90% of the individuals were ≤ 8 years (OTG, unpublished data). In Canadian waters in 2004-2008, maximum age was 24 years, mean age was 10 years, and 75% ($n = 1,609$) were female (Pratt and Chong 2012). Most individuals >166 mm STL and at least age 4 are mature (Gorman 2012). In the Apostle Islands region of Lake Superior, most spawning appears to occur in the months of February and March close to bottom depths of 37-91 m over various bottom types (Dryer and Beil 1968), which is consistent with accounts of spawning in Lake Michigan by Koelz (1929) and Jobes (1949).

Adult diet varies regionally and by depth. In the Apostle Islands region, diet was dominated by calanoid copepods during spring and by *Mysis diluviana* supplemented with *Diporeia* spp. and copepods during summer and autumn (Anderson and Smith 1971b). In the Duluth region, diet was more diverse in spring and included a mix of *M. diluviana*, *Diporeia* spp., and calanoid copepods; this diet continued into the summer and autumn except that cladocerans were added during autumn (Anderson and Smith 1971b). In a more-recent diet study in nearshore waters (<80 m), *Diporeia* spp. and calanoid copepods were dominant in spring and cladocerans were added in summer and autumn (Gamble et al. 2011b). In offshore waters (>80 m) during spring, *Diporeia* spp. were dominant and supplemented by calanoid copepods; *M. diluviana* and calanoid copepods were dominant in summer and autumn (Gamble et al. 2011a). Based on stable isotopes, *hoyi* historically occupied a relatively high trophic level, which was almost identical to that of *kivi* and, like *kivi*, was, in comparison to other ciscoes, more dependent on pelagic food sources (Schmidt et al. 2011).

KIYI



Collected by AMM and TCP 3.7 km west of Pie Island, 21 June 2010, GLFC specimen 65023, STL 153 mm.



Distinctive Taxonomic Traits

Maximum STL (standard length) reported by Koelz (1929) was 204 mm, a length comparable to that observed in 1994-2010, when only 1% of a sample of 1,282 *kiyi* exceeded 205 mm, the largest being 269 mm (OTG, unpublished data). Pratt and Chong (2012) recorded from Canadian waters a *kiyi* of 265 mm from a sample of 420 individuals. In a comparison of nine metrics between Lake Superior *kiyi* (Appendix Tables 2A,B) and a composite *kiyi* (Appendix Tables 1A,B), all collected by Koelz, Lake Superior *kiyi* and the composite were essentially identical. No notable differences were detected in a comparison of nine metrics (includes correction of HLL/POL and HLL/MXL and conversion of paired-fin-length ratios; see Morphometrics and Meristics subsection) between *kiyi* collected by Koelz (Appendix Tables 2A,B) and contemporary *kiyi* (Appendix Table 13; STL/DOH = 5.0 ± 0.4 (not in table)). These comparisons indicate that the morphology of *kiyi* has been more stable than that of *hoi* for the same 90-year period.

Local Ecological Characteristics

Kiyi is the most-abundant deepwater cisco in offshore waters (>80-m deep) (Gorman and Todd 2007) and was estimated to represent 7% of the total fish biomass in 2008 (Gorman et al. 2012b). Adults and juveniles occupy demersal habitats during the day at depths ranging from 80 to >200 m in waters more than 5-10 km from shore (Gorman and Todd 2007; Gorman et al. 2012a; Pratt 2012). *Kiyi* undertakes strong DVM at night, ascending to water-column depths of <80 m at sunset and returning to deeper waters at sunrise (Stockwell et al. 2010a; Ahrenstorff et al. 2011). Maximum age during 2004-2008 was 22 years, though *kiyi* had the youngest mean age (8.9 years) among all ciscoes. Growth was similar between males and females, and, by age 7, females comprised 77% of the catch (Pratt and Chong 2012). Nearly all individuals >133 mm (STL) and at least age 4 were mature (Gorman 2012). Based on fish in ripe condition collected in waters off Marquette, Michigan, Koelz (1929) concluded that *kiyi* spawn in late November

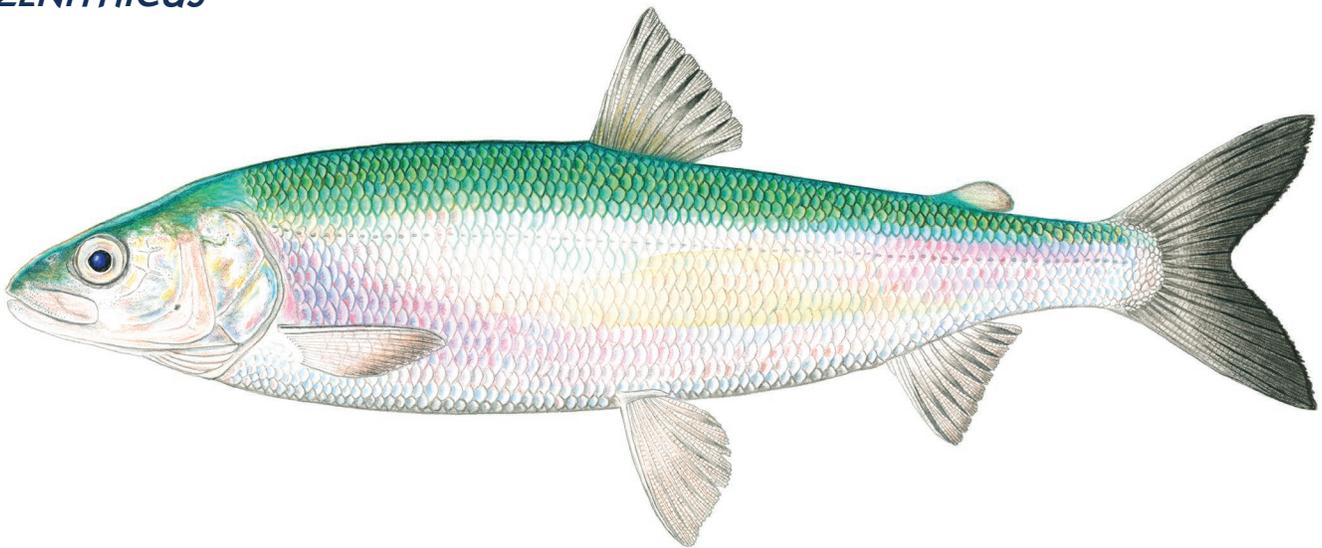


or early December. These fish were collected in gillnets set on the bottom at a depth of approximately 128 m. No other records of *kivi* spawning are known.

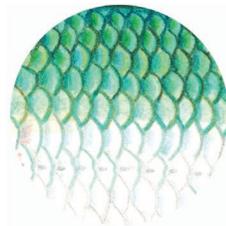
In the Apostle Islands region, the diet of *kivi* was dominated by *Mysis diluviana* during spring, summer, and late autumn and supplemented by copepods and cladocerans during early autumn (Anderson and Smith 1971b). Similarly, Gamble et al. (2011a, 2011b) found that the diet in nearshore (<80 m) and offshore (>80 m)

waters was dominated by *M. diluviana* in all seasons, but cladocerans appeared in the diet during summer and autumn. In offshore waters in 2007-2008, *M. diluviana* was nearly the sole diet item (Ahrenstorff et al. 2011). In an isotopic study of Lake Superior ciscoes, *kivi* historically occupied an intermediate trophic level and tended to be more dependent on pelagic than benthic food sources (Schmidt et al. 2009), a pattern that appears to have persisted (Sierszen et al. 2014).

ZENITHICUS



Zenithicus collected by W. Koelz off Alona Bay, Ontario, 26 June 1922, Univ. Mich. Mus. Zool. specimen 57139, STL 261 mm.



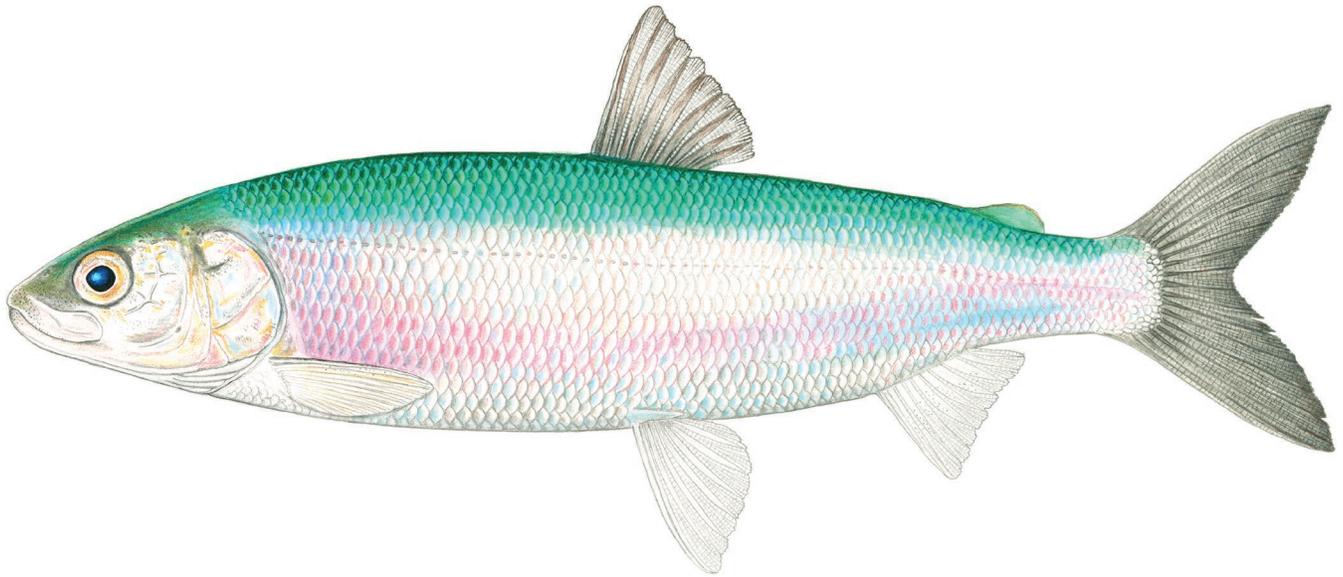
Color in life



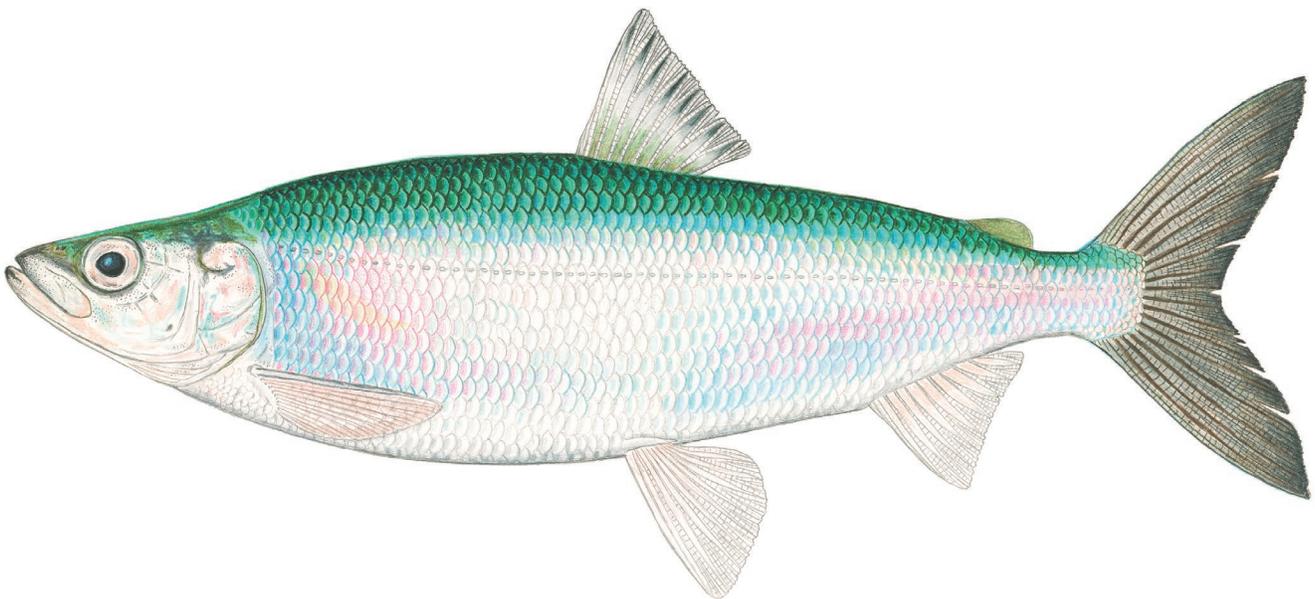
Color in life variant



Color in death



Dymondi form of *zenithicus* collected by W. Koelz off Pie Island, Thunder Bay, Ontario 25 November 1922, Univ. Mich. Mus. Zool. specimen 59279, STL 219 mm.



Nigripinnis unnamed form of *zenithicus* collected by AMM and TCP 4 km northwest of Sleeping Giant, 21 June 2010, GLFC specimen 80047, STL 251 mm.



Distinctive Taxonomic Traits

Maximum STL (standard length) of *zenithicus* reported by Koelz (1929) was 332 mm ($n = 787$). During 1997-2010, maximum STL (all phenotypes combined in contemporary samples) from lakewide bottom trawling was less, 296 mm, and only 1% of 569 individuals exceeded 239 mm (OTG, unpublished data). In Canadian waters during 2004-2008, maximum size in a sample of 364 individuals taken from gillnets was 308 mm (Pratt and Chong 2012). Contemporary *zenithicus* appear to be no larger than *zenithicus* at the time of Koelz and may well be smaller. No notable differences were found in a comparison of nine body metrics between Lake Superior *zenithicus* (Appendix Tables 2A,B) and a composite *zenithicus* (Appendix Tables 1A,B), all collected by Koelz. Also, no notable differences were found in a comparison of nine metrics (includes correction of HLL/POL and HLL/MXL and conversion of paired-fin-length ratios; see Morphometrics and Meristics subsection) between *zenithicus* collected by Koelz and contemporary *zenithicus* (all phenotypes combined; Appendix Table 13), although the dorsal fin was marginally taller in contemporary fish (STL/DOH, 5.5 ± 0.5 vs. 6.2 ± 0.4 ; not included in Appendix Table 13).

From the body-metric ratios used here, *zenithicus* appears to have changed little morphologically from when Koelz collected in Lake Superior, but, as noted in the Identification of Extant Forms subsection, the premaxillaries appear to be less prominent now than when Koelz collected. The *nigripinnis* unnamed form (see Identification of Extant Forms above) was nearly identical to the *zenithicus* form in all but one of the eight metrics in a mixed subsample of 24 *zenithicus* enumerated in Appendix Table 13, hinting at polyphenism in that these forms differ markedly in body shape (see illustrations). Maxillary length was notably greater in *nigripinnis* unnamed (HLL/MXL, 2.7 ± 0.1 vs. 3.0 ± 0.3), which may result from its shallow premaxillary angle, i.e., an artifact of how maxillary length is measured (see Morphometrics and Meristics subsection in *Morphology of Ciscoes* section).

Local Ecological Characteristics

In 1921-1922, Koelz (1929) found *zenithicus* to be the dominant deepwater cisco in Lake Superior, representing >90% of ciscoes captured by bottom-set gillnets. In nearshore and offshore bottom-trawl surveys conducted in 2001-2003, *zenithicus* represented <4% of deepwater ciscoes (Gorman and Todd 2007) and in 2008 represented just 0.2% of total fish biomass (Gorman et al. 2012b). Pratt and Chong (2012), though, reported that *zenithicus* represented 13% of the cisco assemblage taken in graded-mesh gillnets in Canadian waters of Lake Superior during 2004-2008, suggesting a modest recovery in recent years. Abundance of the *cyanopterus* form is less certain in that it has been grouped with *zenithicus* in assessments. Six out of a subsample of 24 ciscoes from northwestern waters originally classified as *zenithicus* were reclassified from images by RLE and OTG as *nigripinnis* unnamed. Adults occupy demersal habitats during the day at depths of 80-160 m in waters <5-10 km from shore (Gorman and Todd 2007; Gorman et al. 2012a, 2012b; Pratt 2012). *Zenithicus* undertakes moderate DVM at night, ascending to within 40 m of the surface (Gorman et al. 2012a). Sexual dimorphism in growth through age 6 is not evident, but, thereafter, males grew more slowly than females such that by age 20 the average size of males was 220 mm and of females 244 mm (OTG, unpublished data). Because female *zenithicus* showed higher survivorship than males, the proportion of females increased from 55% at ages 3-5 years to 81% at ages 16-24 years (OTG, unpublished data). In Canadian waters, maximum age in a sample of 302 individuals was 25 years, and mean age was 11.4 years, making contemporary *zenithicus* the oldest of the lake's ciscoes. Females grew to a larger size than males and comprised 62% of captures (Pratt and Chong 2012). Nearly all individuals >183 mm (STL) and at least age 5 were mature (Gorman 2012). Based on ripe fish collected in waters off Marquette, Michigan, in 1922, Koelz (1929) concluded that *zenithicus* spawns in late November or early December. These fish were collected in bottom-set gillnets over clay substrates at depths of 37-73 m, implying *zenithicus* spawns in nearshore waters at depths <80 m near the lake bottom. More-recent records of spawning are lacking. In the Apostle Islands region, *Mysis diluviana* was the dominant prey during spring through autumn, while copepods and *Diporeia* spp. made lesser contributions (Anderson and Smith 1971a). More-recent diet studies are lacking. Among ciscoes, *zenithicus* historically occupied a lower trophic position and was intermediate in use of pelagic food sources (Schmidt et al. 2011).

CISCOES OF LAKE MICHIGAN

TAXONOMY

Bailey and Smith (1981) and Todd and Smith (1992) recognized seven species of ciscoes from Lake Michigan (*Coregonus artedi*, *C. hoyi*, *C. johanna*, *C. kiyi*, *C. nigripinnis*, *C. reighardi*, and *C. zenithicus*) and in doing so synonymized *C. alpenae*, a species recognized by Koelz (1929), with *zenithicus*. The elimination of *alpenae* was based on an unpublished report by T. Todd (USGS) and G. Smith (University of Michigan), which concluded that morphometric differences among geographically distant *alpenae* populations were no greater than the differences between *alpenae* and *zenithicus*. *Alpenae* and *zenithicus*, however, were recently shown to have been isotopically distinct in Lakes Michigan and Huron in the 1920s (Schmidt et al. 2011) despite occupying similar depth distributions in Lake Michigan in the 1930s (Bunnell et al. 2012a). Owing to uncertainty in taxonomy, *alpenae* is included here in the subsection on *zenithicus*.

IDENTIFICATION OF EXTANT FORMS

Although Lake Michigan once contained in great abundance all seven of the main forms, only two, *artedi* and *hoyi*, are extant (Todd and Smith 1992). Of these two, *hoyi* is by far the most common, making it likely that

any capture in the near future of an unidentified cisco from Lake Michigan is a *hoyi*. *Hoyi* is distinguished by a terete body shape in side view with a straight-line head profile dorsally, resulting in a pointed, triangular head (Fig. 3). *Artedi* has a subterete (less deep) body profile, curving more gently with less change in depth from the end of the head to the beginning of the caudal peduncle. The head profile is triangular, too, but is curved and not pointed. See illustrations and the *Main Forms* section for differences in color and pigmentation. Although Koelz (1929) noted for Lake Michigan that *hoyi* almost always has an extended lower jaw, he also found that 35% of *artedi* >225-mm standard length (STL) had an extended jaw (see quick key). Of eight metrics comparable between contemporary *artedi* and *hoyi* (Appendix Table 14), five were notably different. In comparison to *hoyi*, *artedi* has a shorter head (STL/HLL, 5.2 ± 0.3 vs. 4.1 ± 0.2), a smaller eye (HLL/OOL, 5.2 ± 0.4 vs. 3.9 ± 0.2), a shorter pectoral fin (STL/PCL, 7.5 ± 0.4 vs. 5.9 ± 0.3), a shorter pelvic fin (STL/PVL, 7.7 ± 0.5 vs. 6.4 ± 0.4), and more gill rakers (TGR, 46.0 ± 1.8 vs. 41.9 ± 2.0). The *artedi* for this comparison comprise one collection from a spawning run in the east arm of Grand Traverse Bay. Lakewide representativeness of this population remains to be determined. These *artedi* have *albus*-like features, which accounts for body depth being similar to that of *hoyi* (STL/BDD, 4.1 ± 0.3 vs. 4.0 ± 0.3).



Hauling Bottom Trawl Aboard R/V *Grayling*

Image by AMM.

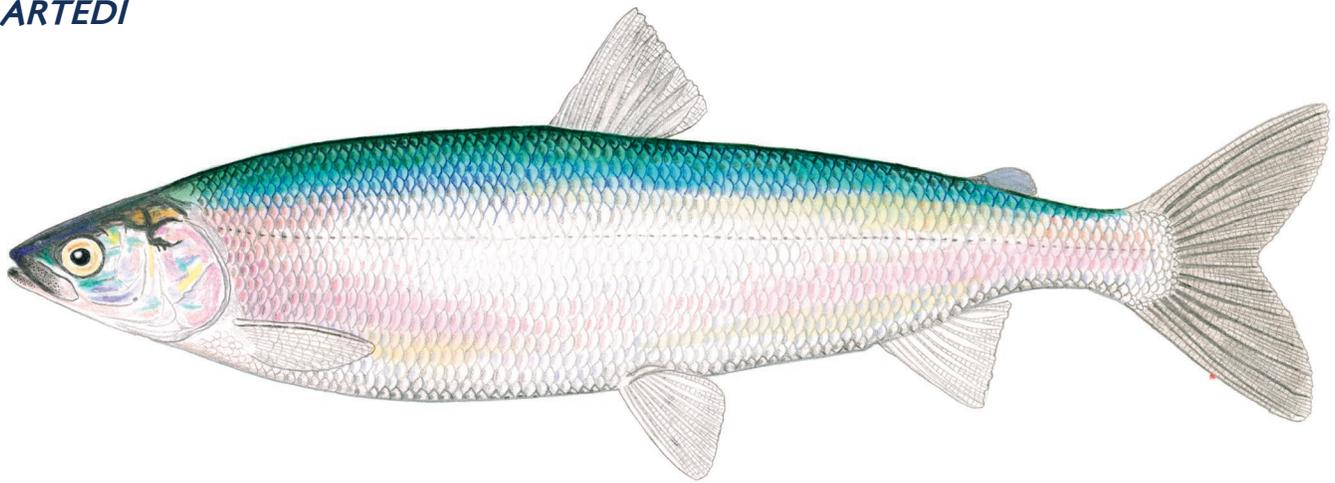


LAKE MICHIGAN QUICK KEY

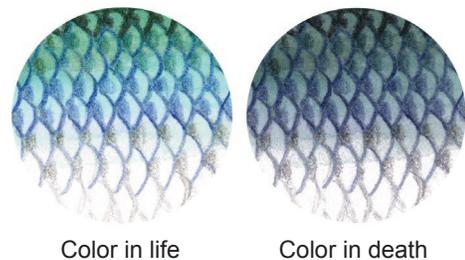
Form	Body Shape			Orbital Length (HLL/OOL)			Lower Jaw Position			PMA	Pectoral Fin Length (STL/PCL)			Pelvic Fin Length (STL/PVL)			Gill Raker Number				Upper Jaw Pigmentation		Paired-Fin Pigmentation			
	Terete	Subterete	Ovate	Small >4.2	Medium 4.2-4.0	Large <4.0	Included	Terminal	Extended		Short >5.6	Medium 5.6-5.4	Long <5.4	Short >6.5	Medium 6.5-6.0	Long <6.0	Low <35	35-40	Medium 41-45	46-50	High 51+	Low	High	Low	High	
<i>Albus</i> ¹	●			●	○			●	●	45-55°			●					●	●	○	●	○	●	○	●	
<i>Hoyi</i>	●			○	○	●	○	●	●	~40°	●	○	○	●		●	○	●	○	○	○	○	○	○	○	
<i>Johannae</i>	●			●	●		○	○	○	50-60°	●		●		●		●				●					
<i>Kiyi</i>			●	●	●	●	○	○	○	~50°	○	●	○	○	○		○	○			○	○	○	○	○	○
<i>Nigripinnis</i>			●	●	●	○	○	○	○	45-60°	●		●		●		●				○	○	○	○	○	○
<i>Reighardi</i>					●	●	○	○	○	60-70°			●				○									
<i>Zenithicus</i>		●		●	●		○	○	○	60-75°	●		●		○		○									

Main character state
 Moderate or occasional character state
 Extrinsic/extinct forms
 Rare character state
 East Arm Grand Traverse Bay population

ARTEDI



Albus-like form collected by R. Claramunt (Michigan DNR) ~0.5 km north of Elk Rapids Harbor, 16 November 2009, Michigan DNR specimen 9325-28, STL 473 mm.



Distinctive Taxonomic Traits

Maximum STL (standard length) of Lake Michigan *artedi* examined by Koelz (1929) was 367 mm ($n = 391$), but the maximum for contemporary *artedi* was much greater, 475 mm ($n = 24$), although more sampling would likely produce larger fish. Koelz (1929) grouped all *artedi* of Lake Michigan with *C. artedi artedi* of Lake Erie, both being slender blue-back (bluish-green) forms. Yule et al. (2013), surprisingly, detected *albus*-like forms in addition to typical *artedi*-like forms in samples collected between 2007 and 2011 from Grand Traverse Bay. Although Koelz collected in Grand Traverse Bay, he did not recognize *albus* from Lake Michigan. Koelz's measurements of nine body metrics for Lake Michigan typical *artedi* (Appendix Tables 3A,B) varied little from a basinwide composite for typical *artedi* (Appendix Tables 1A,B). All metrics were within one standard deviation of the mean and most were nearly identical to the composite. However, seven of nine body metrics for contemporary *artedi* of Grand Traverse Bay (Appendix Table 14) diverged notably from those computed by Koelz for typical *artedi*, and one metric diverged marginally (HLL/POL and HLL/MXL corrected and PVD/PCL and PAD/PVL converted to STL/PCL and STL/PVL; see Morphometrics and Meristics subsection). Of the seven

metrics that diverged notably, contemporary *artedi* had a shorter head (STL/HLL, 5.2 ± 0.3 vs. 4.4 ± 0.2), shorter snout (4.7 ± 0.4 vs. 3.9 ± 0.2), shorter maxillary (3.3 ± 0.2 vs. 2.8 ± 0.1), shorter dorsal fin (STL/DOH, 8.3 ± 1.6 vs. 7.2 ± 0.5 ; contemporary DOH not tabled), shorter pectoral fins (PPD/PCL, 2.4 ± 0.1 vs. 2.0 ± 0.2), shorter pelvic fins (PAD/PVL, 1.9 ± 0.1 vs. 1.7 ± 0.1), and 2.3 fewer gill rakers (46.0 ± 1.8 vs. 48.3 ± 2.6). In addition to these notable differences, contemporary *artedi* had a marginally deeper body (STL/BDD, 4.1 ± 0.3 vs. 4.6 ± 0.4). Lake Erie *albus* had a body depth (STL/BDD) of 3.6 ± 0.3 (Appendix Table 5B), indicating that, in terms of body depth, contemporary *artedi* is only somewhat *albus*-like. Its apparent preference for bays though implies that it is a type of *albus*. Stanford Smith did not sample anywhere near Grand Traverse Bay. His measurements (Appendix Table 9; paired-fin length ratios converted) mirror closely those of Koelz except for 3.0 fewer gill rakers (STL, 45.3 ± 1.4 vs. 48.3 ± 2.6), suggesting that he was unaware of *albus*-like ciscoes. The similarity between the Koelz and Smith samples implies that the *albus*-like form is not a recent derivative of typical *artedi*. Otherwise, it expressed only after 1972, when Smith last collected.



Local Ecological Characteristics

Artedi was the most-abundant fish in the early Lake Michigan fishery with some landings in the late 1800s exceeding 10,000 tonnes. From the early 1900s to 1940, the catch was much reduced, staying at around 2,000 tonnes. A brief dip in the catch in the 1940s was followed by a short-lived surge that peaked in 1952 at 4,000 tonnes and plummeted to near nothing in 1960 (Wells and McLain 1973), where it still remains. Nonetheless, the spawning run in Grand Traverse Bay has increased each year from 2007 to 2013 (R. Claramunt, Michigan DNR, personal communication, 2015), suggesting that whatever heretofore impeded population abundance has lessened. In Green Bay in early May 1952, *artedi* was distributed from the surface to the bottom over depths of 27 m, the maximum depth sampled (Smith 1956). By mid-May, these fish were entirely pelagic and within 9 m of the surface. With warming in June and July, *artedi* was partially pelagic, occupying depths of 9 to 27 m. In October, *artedi* again tended to be pelagic and was most abundant from the surface down to 9 m. Ages based on otoliths have not been published for Lake Michigan *artedi*, but scale ages from Smith (1956) may

be reasonable approximations as scale aging was shown to be fairly accurate for Lake Superior *artedi* up to age 5 (Yule et al. 2008b). Smith (1956) showed that the fishery was consistently dominated by age-3 fish while age-5 fish were rare, indicating that the population at that time was fast growing and young. The three immature males for which Koelz (1929) provided individual data ranged in STL from 174 to 178 mm; similarly, three immature females were 157-248 mm. In Green Bay, all fish age 3+ and the great majority of those age 2 were mature (Smith 1956). Spawning in Lake Michigan occurred from late November to early December with fish migrating into shallow water (3-8 m) usually over sand bottoms (Koelz 1929). Most of the spawning occurred in Green Bay, but spawning was widespread in the lake (Koelz 1929). Smith (1956) reported that, in Green Bay, the species spawned mostly at depths of 3-20 m over virtually all substrates; some spawning occurred down to at least 37 m. Diet data for Lake Michigan *artedi* are scant, but its isotopic signature shows that, among ciscoes during the 1920s, *artedi* occupied the most-unique trophic niche, likely differentiating itself by occupying the shallower areas of the lake (Schmidt et al. 2011).

HOYI



Collected by W. Koelz off Charlevoix, Michigan, 3 November 1920, Univ. Mich. Mus. Zool. specimen 8009.



Color in life

Color in death

Distinctive Taxonomic Traits

Koelz (1929) did not recognize racial differences among his extensive collections of *hoi* from Lake Michigan. Of the 1,161 *hoi* he examined, maximum STL (standard length) was only 265 mm, and most were <200 mm. *Hoi* size has increased since Koelz collected in 1920-1923. During 1973-1982, mean STL of fish >95 mm (age 1+) was 165 mm, and maximum STL was 350 mm, although during 1983-1997, mean and maximum STL decreased to 158 and 342 mm, respectively. During 1998-2013, mean STL reached record levels, 171 mm, although the maximum STL of 310 mm was not a record (data per Bunnell et al. 2012a). In nine comparisons of body metrics, Lake Michigan *hoi* during 1920-1923 (Appendix Tables 3A,B) resembled closely a basinwide composite from the same period (Appendix Tables 1A,B). Deviations from the composite never exceeded one SD. In eight comparisons of body metrics between *hoi* of 1920-1923 and contemporary *hoi* collected in 2008 and 2011 (Appendix Table 14; excludes height of dorsal fin and includes correction of HLL/POL and HLL/MXL and conversion of paired-fin-length ratios; see Morphometrics and Meristics subsection), only pelvic fin length differed notably and was 24% shorter in contemporary *hoi* (PAD/PVL, 1.7 ± 0.1 vs. 1.3 ± 0.1). The apparent reduction in length of the pelvic fin is unexplained and is evident in all contemporary *hoi* populations (see Morphometrics and Meristics subsection). Collections of *hoi* made by Stanford Smith in 1950 and 1972 (Appendix Tables 9A,B) are of interest here because he reported hybridization among ciscoes in 1960-1961 and in 1963 (Smith 1964). His 1950 collection differs from *hoi* collected in 1920-1923 in only one of eight body metrics. Pelvic fins were shorter in 1950 as noted above for contemporary *hoi* (STL/BDD not recorded by Smith; includes conversion of paired-fin-length ratios). Smith's 1972 collection diverges more than his 1950 collection from *hoi* collected in 1920-1923. As compared to 1920-1923, *hoi* collected in 1972 had a shorter head (STL/HLL, 4.3 ± 0.1 vs. 4.1 ± 0.2), the same short-pelvic fin anomaly as seen in 1950, and fewer gill rakers (discussed below).

Over a 40-year period, total gill raker number (TGR) in *hoi* went through a cycle of change from the nearly identical values reported by Koelz for 1920-1924 (42.6 ± 0.1 ; Appendix Table 3A; all SE this section only) and by Stanford Smith for 1950 (42.7 ± 0.5 ; Appendix Table 9). Taking Koelz as the historical average, TGR by 1960 had increased by 1.4 rakers (44.0 ± 0.3) as evidenced by a collection made by Stanford Smith from southern Lake Michigan (Crowder 1984; raw data since lost).

This increase is supported somewhat by Todd and Stedman (1989), who obtained only 0.1 raker less (43.9 ± 0.2) in *hoi* collected from northern, not southern, Lake Michigan in 1972-1974. By this same time (1972), however, raker number in southern Lake Michigan, based on a small sample ($n = 14$) of Smith's, appears to have declined by 4.8 (39.2 ± 0.1 ; Appendix Table 9) from the value reported by Crowder (1984) for southern waters in 1960 (Smith's value). After 1972, raker number in southern waters began to return to historical levels, assuming Smith's small sample from 1972 was not anomalous. Crowder (1984) reported a 1979 count for southern waters (41.9 ± 0.2) that was only 0.7 rakers less than the historical average, a value that apparently persisted in contemporary *hoi* collected in 2008 and 2011 (41.9 ± 0.2) from northern waters. By 1960-1961, hybridization among deepwater ciscoes was advanced at least in southern waters (Smith 1964), which provides the most-straightforward explanation for the apparent cycle in gill raker number. In retrospect, Crowder's raker estimate for 1979 does not appear to be biased low as suggested by Todd and Stedman (1989), and Crowder's hypothesis of character displacement to account for the decline in raker number from 1960 to 1979 seems unlikely in that, by the time he sampled, raker number may have increased, not decreased. Although *hoi* morphology appears to be unchanged from the early 1920s to 2011, except for the decline in pelvic fin length (see above), its genome may have been altered by hybridization in the 1960s and early 1970s.

If raker number in *hoi* increased around 1960 and then decreased around 1972, owing to hybridization, why did raker number subsequently return to historical values? *Hoi* was very abundant as hybridization was ongoing, representing 76% of the assessment catch of deepwater ciscoes in 1954-1955 and 94% in 1960-1961 (Smith 1964). The reduction in abundance of the other deepwater ciscoes began sooner in northern waters than in southern waters, suggesting that hybridization was more severe in the north. Despite these longitudinal differences in population declines, *hoi* does not appear to be genetically structured by basin (Fave and Turgeon 2008), which implies that the changes in raker numbers do not owe to sampling location. Natural selection may have driven raker number back to its historical value.



Local Ecological Characteristics

Based on bottom trawling, *hoyi* biomass averaged 2.4 kg/ha during 2005-2011, only 9% of the mean since this assessment began in 1979 (Claramunt et al. 2012). Juvenile *hoyi*, sampled with mid-water trawls during autumn, were pelagic and widely distributed in waters $>7.5^{\circ}\text{C}$ (Eshenroder et al. 1998). From 1930 to 1961, *hoyi* extended its range to deeper waters in response to depletion of its sister forms and to release from Lake Trout predation (Smith 1964). In the northern waters of Lake Michigan, peak catch-per-effort (CPUE) in bottom trawls occurred at 62 m during 1974-1977, at 70 m during 1988-1991, and at 110 m during 2004-2007. In southern waters, peak CPUE during the first two periods occurred at 52 m but occurred at 85 m during the third period (Bunnell et al. 2012a). Correspondence between scale and otolith ages for Lake Michigan *hoyi* has been unsatisfactory so growth data are not provided here. Both sexes of *hoyi* reach 50% maturity at an STL of 162 mm (Bunnell et al. 2012b). Koelz (1929) reported that southern Lake Michigan *hoyi* spawned from late February through March at depths of around 55 m. His two lifts of record comprising mostly spawning or ripe fish made on March 2, both off Michigan City, Indiana, comprised 81 and 96% *hoyi*—high percentages, indicating spawning aggregations. The bottom contours where these lifts were made slope gradually, and the lakebed is sand and silt.

By 1964, when *hoyi* was essentially the only deepwater cisco in Lake Michigan, spawning in southeastern waters was most common at depths of ~75-110 m, an inference based on the distribution of yolk-sac larvae (Wells 1966). The diet of *hoyi* >141 -mm STL during the late 1950s to early 1960s comprised mostly *Diporeia* spp. and *Mysis diluviana* with a greater proportion of *M. diluviana* in deeper waters; *hoyi* <141 mm consumed mostly zooplankton (Wells and Beeton 1963). With the recent population collapse of the *Diporeia* spp. population, *M. diluviana* has become even more important in the diet of larger *hoyi* (Hondorp et al. 2005) as has *Limnocalanus macrurus* (Bunnell et al. 2015). Notwithstanding these adaptations and a greatly reduced density of *hoyi* during 2009-2011 as compared to 1993-1996, consumption by *hoyi* did not increase, suggesting that the capacity of the lake to support this form has diminished (Pothoven and Bunnell 2016). Based on its isotopic signature, *hoyi* during the 1920s occupied relatively shallow depths in comparison to other deepwater ciscoes in Lake Michigan (Schmidt et al. 2011).

JOHANNAE

Distinctive Taxonomic Traits

Koelz's (1929) few samples did not indicate racial differences within Lake Michigan. Smith (1964) considered *johanna*e to be the second largest of the deepwater ciscoes (see *Lake Huron Account* for illustration). As of 1930, when large-bodied ciscoes were already becoming scarce in Lake Michigan, *johanna*e averaged 252 mm standard length (STL) (Smith 1964). Nine specimens taken in 2.50-2.75-inch (63.5-69.9 mm) -mesh gillnets from Lake Michigan, for which STLs were given by Koelz (1929), varied from 231-288 mm. Because *johanna*e occurred only in two lakes, Michigan and Huron, the Michigan form will be compared with the Lake Huron form rather than a basinwide composite. *Johanna*e of Lake Michigan (Appendix Tables 3A,B) varied little morphologically from its counterpart in Lake Huron (Appendix Tables 4A,B) during the 1920s. Just two of nine body metrics differed, the Lake Michigan form having a slightly shorter head (STL/HLL, 4.1 ± 0.2 vs. 3.9 ± 0.1) and a slightly shorter snout (HLL/POL, 3.6 ± 0.1 vs. 3.4 ± 0.1). No further comparative data on morphology are available as *johanna*e was commercially extinct by the time Stanford Smith conducted his surveys of Lake Michigan during 1950-1972.

Local Ecological Characteristics

*Johanna*e, as its former common name (the Chub) implies, had been the target of the chub fishery and was already much reduced in abundance in Lake Michigan when Koelz (1929) conducted his surveys during 1919-1923. He listed this form as rare in 11 out of 13 lifts examined for composition. By 1930-1932, when surveys were next undertaken in Lake Michigan, *johanna*e was poorly represented in catches, and, by 1954-1955, none were seen (Smith 1964). Adult-sized *johanna*e occupied depths of 55-165 m and may have occupied even deeper waters. Juveniles of a size vulnerable to 1.5-inch (38-mm) -mesh gillnets ("bait nets") were not captured, even at depths as great as 90 m (Koelz 1929). Juveniles may have inhabited (shallower) depths avoided by adults or were pelagic and not available to bottom-set gillnets. Size at maturity is unknown. All 10 of the individual fish enumerated by Koelz (1929) were mature, and the smallest of these measured 231 mm. According to Koelz (1929), the spawning period in Lake Michigan was from mid-August to the end of September, but the spawning grounds were unknown. No diet data are available from

Lake Michigan, but 34 specimens from Lake Huron taken at depths of around 120 m fed predominately on *Mysis diluviana* (Koelz 1929). Stable isotope analysis indicated that, among Lake Michigan ciscoes, *johannae* occupied an intermediate trophic position with respect to depth (Schmidt et al. 2011).

KIYI

Distinctive Taxonomic Traits

Koelz (1929) had too few specimens to detect racial differences in Lake Michigan, even though his samples came from all ports visited. His subsample (all adults) of 174 *kiyi* ranged in standard length (STL) from 122-245 mm. Deason and Hile (1947) reported that adult females in the early 1930s averaged 192 mm and adult males 185 mm, and they inferred fishing was causing the maximum length to plateau. Mean STL of a sample from 1950 was 199 mm (range 151-222), only slightly greater than in the early 1930s. No notable differences were evident in a comparison of nine body metrics between Lake Michigan *kiyi* of 1920-1923 (Appendix Tables 3A,B) and a basinwide composite from the same period (Appendix Tables 1A,B), suggesting that the Lake Michigan form was typical of *kiyi* across the Great Lakes. The last morphological data for *kiyi* of Lake Michigan were recorded in 1950 off Algoma, Wisconsin. This collection (Appendix Table 9) indicates two metrics had changed from when Koelz collected in 1920-1923. Pelvic fin length (PVL; STL/PVL converted to PAD/PVL) had become shorter (1.4 ± 0.2 vs. 1.1 ± 0.1) and total gill rakers (TGR) had increased (41.0 ± 2.1 vs. 38.5 ± 1.9). These changes were occurring at a time when the *kiyi* population was in decline. In northern waters, CPUE had declined 65% from 1932 to 1961 and in deep central and southern waters it had declined 74% between 1930-1931 and 1960-1961 (Smith 1964). Six of the 27 *kiyi* collected in 1950 were identified as *kiyi-zenithicus*, suggesting possible hybridization with *zenithicus*, which had declined even more (see *Zenithicus* subsection below). However, hybridization between *kiyi* and *zenithicus* would not be expected to result in increased TGR, but hybridization with *hoi*, the dominant deepwater cisco in 1954-1955 (Smith 1964) could account for it. *Hoi* at this time had already expressed shorter pelvic fins (see *Hoi* subsection above), so hybridization with *hoi* could account for the gill raker anomaly too.

Local Ecological Characteristics

Of the six forms of deepwater ciscoes in Lake Michigan, *kiyi* may have been the most abundant historically, but it was likely under-sampled in early surveys owing to its deep depth distribution. Peak CPUEs of *kiyi* modeled from catches taken in experimental gillnets during 1930-1932 occurred at a depth of 150 m, the deepest depth fished, in all seasons (except winter) for northern waters and at 125-150 m for southern waters, also all seasons (Bunnell et al. 2012a). From 1932 to 1961, *kiyi* underwent a population decline of 65% in northern waters and of 74% in east-central waters (Smith 1964), although these estimates are based on waters of intermediate depth (<60 m). By 1975, all six *kiyi* taken in Stanford Smith's survey were identified as *kiyi-zenithicus*, suggesting that hybridization, which would result in the eventual disappearance of this form from Lake Michigan, was well underway. The smallest female examined by Deason and Hile (1947) measured 143 mm and the smallest male 146 mm. Both were mature as were essentially all of their 6,000+ samples, which were collected in experimental gillnets (minimum mesh size of 2.38 inch, (60 mm)) fished from the R/V *Fulmar* in 1930-1932. Koelz (1929) "supposed" that Lake Michigan *kiyi* spawned in October. Deason and Hile (1947) reported spent fish taken as early as late September 1931 with spawning continuing in southern waters through the first two weeks of November. Spawning appeared to have little effect on depth distribution. Deason and Hile (1947) suggested that *kiyi* spawned throughout Lake Michigan at suitable depths (90-165+ m), indicating no preference for bottom type. The diet of Lake Michigan *kiyi* has gone unreported. On the basis of stable carbon and nitrogen isotopes, *kiyi* (and *nigripinnis*) occupied a somewhat unique trophic niche in the deepest waters of the lake (Schmidt et al. 2011).



NIGRIPINNIS

Distinctive Taxonomic Traits

Nigripinnis was the largest of the deepwater ciscoes inhabiting Lake Michigan (Smith 1964). The size range of specimens selected by Koelz (1929) as “representative,” 254-300 mm, likely is biased low for fish vulnerable to bottom-set gillnets. His gillnet-mesh sizes (stretch mesh) ranged from 2.50-2.75 inch (63.5 to 69.9 mm), whereas he noted that the commercial fishery formerly targeted this species using mesh sizes of 3.5-4.0 inch (88.9-101.6 mm). Koelz (1929) also noted that *nigripinnis* “not infrequently” attained a standard length (STL) of 350 mm and a weight exceeding 680 g, and he reported a maximum size of 360 mm among his sample of 52. None of nine body metrics comparable between Lake Michigan *nigripinnis* (Appendix Tables 3A,B) and a composite based on Lakes Huron and Nipigon *nigripinnis* (Appendix Tables 1A,B) differed notably (*n. cyanopterus* of Lake Superior excluded), indicating the integrity of this phenotype across lakes. No further comparisons of body metrics can be made—*nigripinnis* was not taken in subsequent assessments of body morphology.

Local Ecological Characteristics

Nigripinnis was becoming scarce in Lake Michigan during 1917-1924, when Koelz was conducting field work. He was able to collect only 52 specimens. Moffet (1957) reported that *nigripinnis* was not taken in surveys conducted in 1954-1955, and none were taken during the Stanford Smith surveys. Koelz (1929) reported that fishing occurred as deep as 165 m and that this form was rarely taken in less than ~75 m. Based on surveys conducted in 1930-1932, *nigripinnis* was predicted to reach peak abundance at depths of 122-138 m in northern waters and 150 m in southern waters (Bunnell et al. 2012a). Lake Michigan fishermen claimed to have taken spawning *nigripinnis* at depths of 73-165 m east of Milwaukee during late December-early January, according to Koelz (1929). He quoted a commercial fisherman as saying *nigripinnis* spawned off Manistee at depths of 73-146 m over a clay bottom. Evermann and Smith (1896) examined ripe and partially spent *nigripinnis* off Milwaukee in mid-November, which is the only authoritative account of a spawning event in Lake Michigan. The diet in Lake Michigan has gone unreported. Its isotopic signature from the 1920s suggests foraging (along with *kīyi*) in the deepest waters of the lake (Schmidt et al. 2011).

REIGHARDI

Distinctive Taxonomic Traits

Koelz (1929) described *reighardi* as “one of the smaller chubs.” His largest specimen measured 278 mm standard length (STL), but most were <240 mm. Koelz noted that *reighardi* from northern waters had longer snouts and upper jaws than those from southern waters, although the differences were not definitive. Neither of two composite *reighardi*, one that includes synonymized populations (four lakes) or one based on currently accepted taxonomy but consisting of only Lakes Ontario and Michigan (Appendix Tables 3A,B; see footnote 2 in tables), are suitable for comparison of body metrics with Lake Michigan *reighardi*. Therefore, Lake Michigan *reighardi* is compared only with Lake Ontario *reighardi*, all collected by Koelz (Appendix Tables 3A,B and 6A,B). This comparison shows that these two populations were quite similar in morphology across nine metrics. The morphology of Lake Michigan *reighardi* persisted into 1950 when Stanford Smith collected (Appendix Table 9). None of six body metrics available for comparison (excludes body depth and paired-fin lengths; no conversion for *reighardi* paired-fin-length ratios available) differed notably, and most were nearly identical. The 1950 collection was made just 13 years before Smith (1964) reported that ciscoes had become difficult to identify. He also observed that *reighardi* was spawning during autumn where it had spawned the previous spring (*reighardi* was known as a spring spawner).

Local Ecological Characteristics

Reighardi was one of the more-abundant ciscoes in Lake Michigan based on Koelz’s (1929) records (his Table 2). Subsequently, this form became one of the small-bodied ciscoes favored by the extirpation of the Lake Trout and possibly of the larger-bodied ciscoes. Nonetheless, CPUE of *reighardi* in deeper waters declined from 60.5 in 1931-1932 to 4.0 in 1960-1961 (Smith 1964), and it was soon extirpated (Webb and Todd 1995). Koelz (1929) gave a depth distribution of 11-165 m. During the early 1930s, *reighardi*, along with *hoyi*, typically was most abundant at relatively shallow depths (50-68 m) as compared to other deepwater ciscoes (Bunnell et al. 2012a). Jobs (1943) reported a depth distribution ranging from 37 to 110 m. The smallest gravid and spent females seen by Jobs (1943) were in his 178-181-mm size group. The smallest mature male taken in Koelz’s (1929) 1.5-inch (38 mm) -mesh “bait net” was 172 mm. Otherwise, the size at maturity for males is unknown. Koelz (1929)

reported that Lake Michigan *reighardi* spawned sometime between the end of March and the last of June. Jobes (1943), having more data, narrowed the spawning period to the months of May and June. He indicated the species spawned over a wide range of bottom types, typically at

depths of 37-144 m in southern waters and 55-108 m in northern waters. The diet of *reighardi* in Lake Michigan has gone unreported. The isotopic signature of the form in the 1920s places it at an intermediate trophic level with respect to its depth preference (Schmidt et al. 2011).

ZENITHICUS



Collected by W. Koelz 27 km NNW of Michigan City, 19 November 1920, Univ. Mich. Mus. Zool. specimen 58744, STL 252 mm, specimen identified by W. Koelz as *C. alpenae* and later re-catalogued by G. Smith (Univ. Mich.) as *C. zenithicus*.

Distinctive Taxonomic Traits

Maximum STL (standard length) recorded by Koelz (1929) was 312 mm, although, if *alpenae* is synonymized with *zenithicus*, maximum size would be 386 mm, *alpenae* being larger than *zenithicus*. Koelz noted, too, that *zenithicus* rarely exceed an STL of 300 mm whereas *alpenae* >300 mm “are met frequently.” The *zenithicus* and *alpenae* basinwide composites based on Koelz (Appendix Tables 1A,B) were alike morphologically with the *zenithicus* composite having marginally more gill rakers (TGR, 39.5 ± 2.3 vs. 38.2 ± 3.0). Lake Michigan *zenithicus* collected by Koelz (Appendix Tables 3A,B) conformed well to the composite *zenithicus* except that it had a shorter head (STL/HLL, 4.2 ± 0.1 vs. 4.0 ± 0.2). *Alpenae* during the 1920s was also similar to its composite having 0.8 fewer gill rakers (37.4 ± 2.2 vs. 38.2 ± 3.0) whereas *zenithicus* had 0.2 more rakers than its composite (39.7 ± 1.9 vs. 39.5 ± 2.3). Body morphology of *zenithicus* remained relatively stable from the 1920s until 1950 and 1960 when Stanford Smith collected these two forms (Appendix Table 9). Of eight body metrics comparable between these periods

(Smith did not record body depth; STL/PCL and STL/PVL of Smith converted to PPD/PCL and PAD/PVL; see Morphometrics and Meristics subsection), gill raker number differed most, increasing in *zenithicus* by 2.0 rakers, from 39.7 ± 1.9 to 41.7 ± 2.0 . Body morphology of *alpenae* during this same period was also stable except for gill raker number, which increased from 37.4 ± 2.2 to 41.5 ± 2.2 ; i.e., by 4.1 rakers. Most of this increase owes to a 1960 collection (TGR, 42.2, $n = 20$) from southeastern waters as opposed to a 1950 collection (TGR, 40.3, $n = 10$) from northwestern waters. The initial difference in gill raker number between *zenithicus* and *alpenae* of 2.3 rakers as reported by Koelz (1929) decreased to a difference of only 0.2 rakers in Smith’s collections. *Zenithicus* and *alpenae* became more alike as cisco populations were undergoing depletion in Lake Michigan (Smith 1964). This anomaly does not owe to differences in fish size as *alpenae* should have had more, not fewer rakers, when Koelz collected because it was “generally” larger than *zenithicus*. The slope of the relationship between raker number and STL was



positive for *zenithicus* (Fig. 7), and both forms in Smith's collections were of the same size. Smith's raker counts, being nearly identical, could be taken as supportive of synonymy, but the histories of the differences in raker number are unlike, hinting that the two forms were distinct.

Koelz distinguished *zenithicus* from *alpenae* mainly on jaw position and jaw pigmentation. The mandible of *zenithicus* was typically included, whereas it was typically extended in *alpenae*. *Alpenae* was usually less pigmented around the premaxillaries, and the tissue over the maxillary bone was unpigmented in *alpenae* but lightly pigmented in *zenithicus* (Koelz 1929). In collections of both forms made by Stanford Smith in 1950 and 1960, mandible length (MDB) was identical (HLL/MDB, 2.0 ± 0.1), suggesting that jaw position was not a function of its length. Of 59 *zenithicus* collected by Stanford Smith off Grand Haven, Michigan, in 1960, none were identified as being possible hybrids. However, 17 out of 52 *zenithicus* collected in 1950 off Algoma, Wisconsin, were identified as *zenithicus-alpenae* and six were identified as *kiyi-zenithicus*. Likewise, five ciscoes collected in northwestern waters in 1950 were identified as *alpenae-kiyi*. These unusual entries indicate hybridization among ciscoes was ongoing a decade earlier in northwestern waters than in southeastern waters. Consistent with this disparity between locations, *zenithicus* and *alpenae* populations in northern waters had declined by approximately 90% from 1932 to 1955, whereas the decline in deeper southern waters over nearly the same period (from 1930-1931 to 1954-1955) was approximately 50% (Smith 1964). No further study of the body morphology of Lake Michigan *zenithicus* or *alpenae* was undertaken.

Local Ecological Characteristics

Alpenae (see *The Coregonine Problem and Main Forms* sections) was approximately three times as abundant as *zenithicus* in shallow and deep water in 1931-1932 and in 1954-1955 (Smith 1964). *Zenithicus* in 1931-1932 was also less abundant than *hoi* and *reighardi*. According to Koelz (1929), during the non-spawning season, *zenithicus* >200-mm STL were gillnetted at depths of 51-165 m, although very few were taken at depths >128 m; juveniles were scarce in "bait nets" set at depths of 48-73 m. Koelz reported too that *alpenae* was more widely distributed in Lake Michigan than *zenithicus*, area- and depth-wise, with adult *alpenae* taken in almost every gillnet set and even in pound nets. These depths ranged from 9-165 m (the deepest waters fished). A few juveniles (<200 mm) were taken in "bait nets" at depths of 9-46 m. Otolith-based ages are not available for Lake Michigan *zenithicus* or *alpenae*. *Zenithicus* males matured at an STL of roughly 185-240 mm and females at 175-252 mm, and all *alpenae* >206-mm STL were mature (Koelz 1929). Pre-spawning *zenithicus* were said to be aggregated typically from mid-October to the first of November at depths of 18-55 m over clay and sand bottoms. Koelz (1929) observed spawning in shallow water in mid-November off Michigan City and Milwaukee and suspected that spawning was widespread in west-central waters. Of particular interest, spawning aggregations of *zenithicus* at these two locations contained virtually no *alpenae*, implying *zenithicus* was reproductively isolated from *alpenae*. *Alpenae* was thought to spawn in November, although Koelz (1929) saw none in spawning condition. No diet information is available. Based on isotopic signatures of all Lake Michigan ciscoes, *zenithicus* occupied the lowest trophic level while *alpenae* occupied an intermediate level. Both forms tended to feed more on benthic prey than did other ciscoes (Schmidt et al. 2011).



CISCOES OF LAKE HURON

TAXONOMY

Koelz (1929) and Bailey and Smith (1981) recognized seven forms of ciscoes from Lake Huron, agreeing on six (*Coregonus artedi* (includes *C. artedi manitoulinus*), *C. hoyi*, *C. johanna*, *C. kiyi*, *C. nigripinnis*, and *C. zenithicus*), but not on *C. reighardi* and *C. alpenae*. Koelz simply did not recognize *reighardi* from Lake Huron, even though it must have been present. In fact, Webb and Todd (1995) discovered one *reighardi* in a March 1919 collection of Koelz's archived at the UMMZ. Koelz (1929) recognized *alpenae*, whereas Bailey and Smith (1981) and Todd and Smith (1992) synonymized *alpenae* with *zenithicus* based on an unpublished report by T. Todd (USGS) and G. Smith (University of Michigan). This report concluded that morphometric differences among geographically distant *alpenae* populations were no greater than the differences between *alpenae* and *zenithicus*. *Alpenae* and *zenithicus*, however, were recently shown to have been isotopically distinct in Lakes Michigan and Huron (Schmidt et al. 2011) despite overlapping depth distributions in Lake Michigan in the 1930s (Bunnell et al. 2012a). Owing to uncertainty in taxonomy, *alpenae* is included here provisionally in the subsection on *zenithicus*. In a further revision, *alpenae*, *hoyi*, *kiyi*, *reighardi*, and *zenithicus* are hypothesized to have introgressed sometime after 1956, coalescing into a hybrid swarm with a distinct suite of morphological traits. For convenience, the members of this swarm are named *hybrida* (see below).

IDENTIFICATION OF EXTANT FORMS

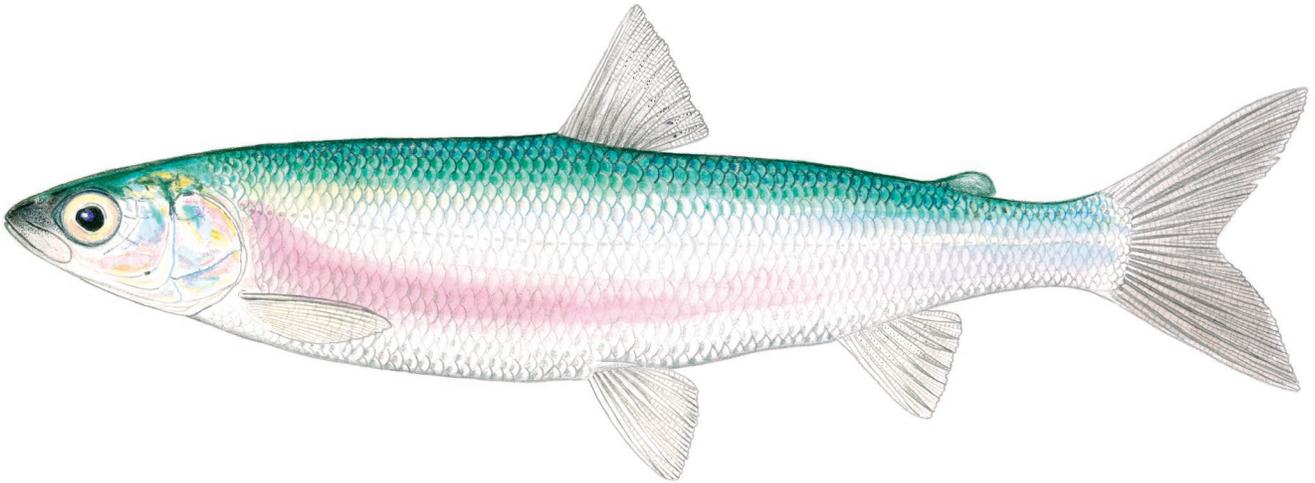
When this project started, only *artedi*, *hoyi*, and *zenithicus* were considered extant, and, of these, *zenithicus* was considered rare (Mandrak et al. 2014). Now, *hoyi* and *zenithicus* along with three other deepwater ciscoes (*alpenae*, *kiyi*, and *reighardi*) extant in 1956 (Eshenroder and Burnham-Curtis 1999) are hypothesized to have introgressed and formed a hybrid swarm (Seehausen 2004) that expresses variable morphology among the lake's three basins (see discussion in *Hoyi* subsection). Introgression has reduced diversity such that only one deepwater cisco (named *hybrida* for convenience) and various forms of *artedi* are candidates for identification.

Manitoulinus, considered a subspecies of *artedi* by Koelz (1929) and here considered a minor form, may no longer occur in the North Channel, although ciscoes with morphometrics characteristic of *manitoulinus* were reported from the St. Marys River and the north shore of the main basin (Yule et al. 2013). Likewise, the same study reported *albus*-like ciscoes, not recognized from Lake Huron by Koelz, from both locations (Yule et al. 2013).

Typical *artedi* has a subterete profile (*albus* is terete) curving gently from the snout to the occiput dorsally and ventrally but less so ventrally in fish >300 mm standard length. The body is of relatively uniform depth from the occiput to the beginning of the caudal peduncle at which point the body curves gradually to the end of the caudal peduncle, creating a symmetrical appearance overall. *Albus*- and *manitoulinus*-like *artedi*, being deeper bodied, lack the gentle recurving dorsal profile after the pelvic fins. *Hybrida* tends to be *hoyi*-like overall, but with morphology intermediate among all deepwater ciscoes extant in 1956. It tends to reflect a mixture of character states shown in the quick key for extirpated forms (excludes *johanna* and *nigripinnis*) but with *hoyi* traits predominant. Considerable variation occurs among *hybrida* samples (note high SDs for body metrics in Appendix Table 15). The lateral profile is terete with greatest body depth (BDD) well forward of insertion of dorsal fin. The dorsal profile of the head is straight for a much-shorter distance than in *hoyi* (Fig. 3). Mandible typically extended (like *hoyi*) and symphyseal knob occasionally present. Head and dorsal body surface lightly pigmented. Tip of mandible, premaxillary, and flesh over anterior half of maxillary bone lightly pigmented. Pectoral fins ranging from translucent and unpigmented to yellow with light pigmentation on distal margins. Pelvic and anal fins translucent to yellow, typically unpigmented. Margin of dorsal lightly pigmented; caudal light to moderate pigmentation. In life, dorsal body coloration varying widely from emerald green to gray with pink, blue, or yellow hues. In death, color fades to gray or tan.



ARTEDI



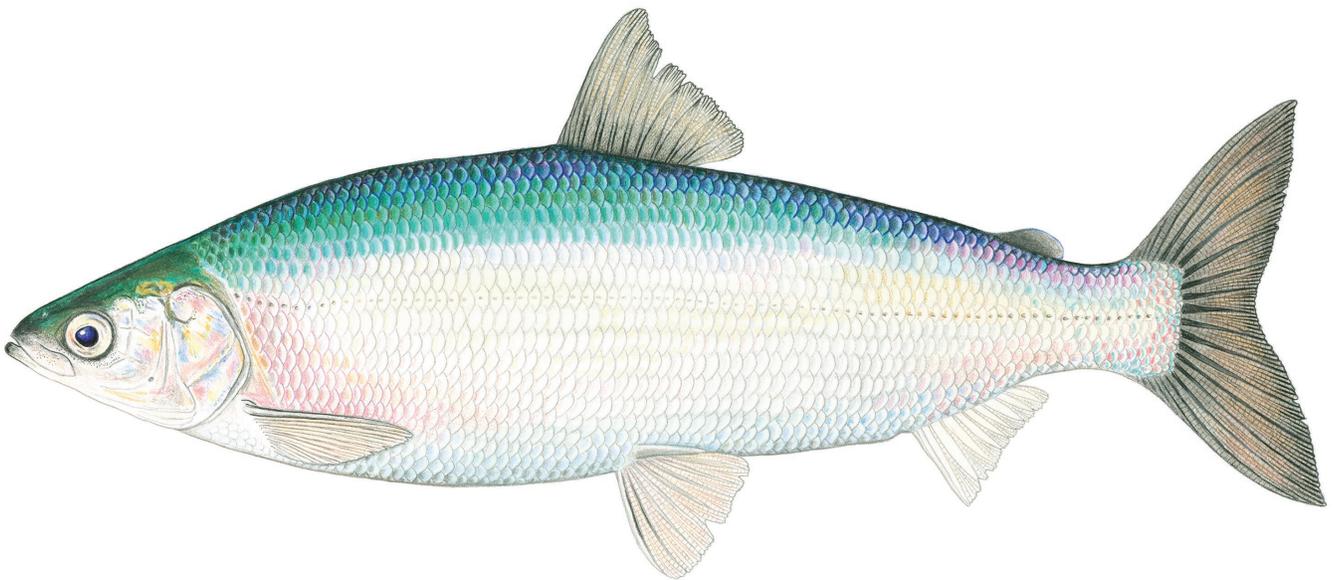
Typical form collected by W. Koelz from Colpoys Bay, Ontario, 5 November 1917, Univ. Mich. Mus. Zool. specimen 52308.



Color in life



Color in death



Albus form collected by C. Olds, USFWS, Government Bay, Les Cheneaux Islands, November 2015, USFWS specimen 2407-011, STL 300 mm.

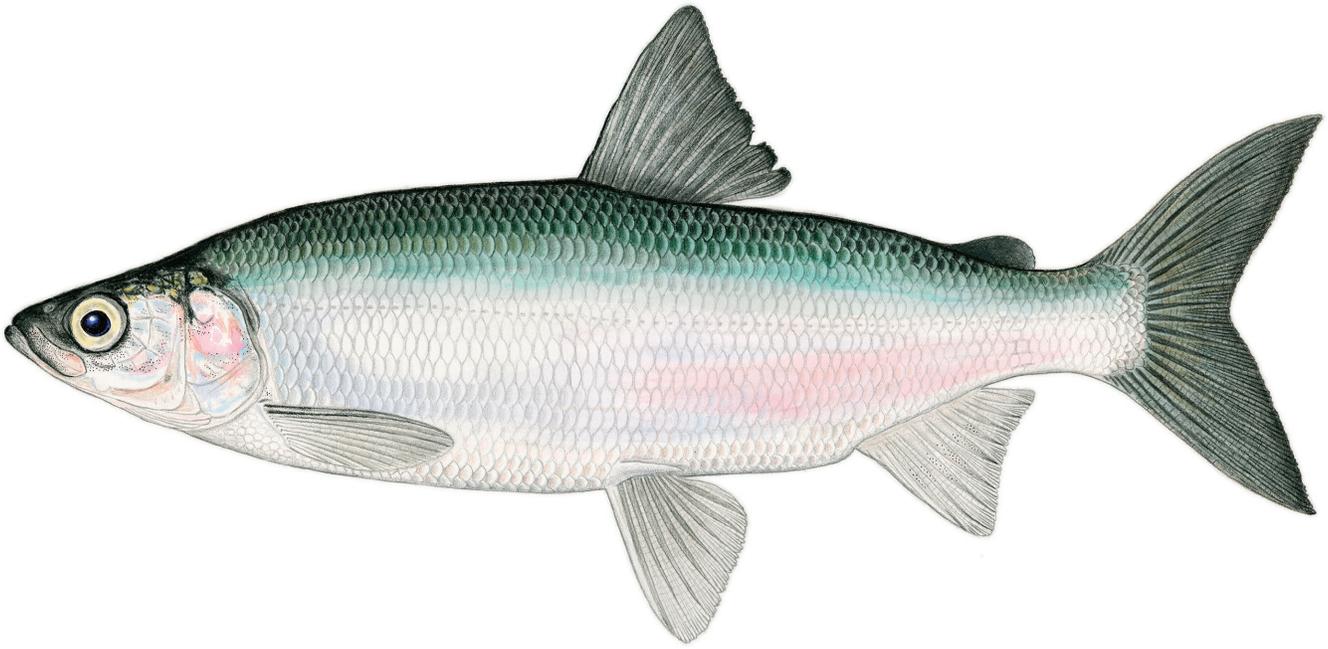


Color in life



Color in death





Manitoulinus form collected by W. Koelz off Cutler Bay, North Channel, 11 November 1917, Univ. Mich. Mus. Zool. specimen 52423, STL 238 mm.

Distinctive Taxonomic Traits

Maximum STL (standard length) of 343 *artedi* examined lakewide by Koelz (1929) was 371 mm, close to what Stanford Smith observed in the main basin in 1956 (STL = 333 mm, $n = 42$). Maximum STLs of contemporary *artedi* (form not determined) from the main basin, Georgian Bay, and the North Channel were 410, 400, and 414 mm, respectively (C. Davis, OMNRF, unpublished data). Morphology of Lake Huron typical *artedi* collected by Koelz (Appendix Tables 4A,B) conformed well to a basinwide composite also based on Koelz (Appendix Tables 1A,B) over all nine metrics. Koelz noted that Lake Huron typical *artedi* closely resembled typical *artedi* of Lake Michigan as well as the slender “blue back” of Lake Erie. Koelz (1929) considered *manitoulinus* to be a “local race” because it intergraded with typical *artedi*. *Manitoulinus* was morphologically diverged from typical *artedi* in that typical *artedi* had a shallower body (STL/BDD, 4.4 ± 0.4 vs. 3.6 ± 0.2), shorter head (STL/HLL, 4.4 ± 0.2 vs. 4.1 ± 0.1), smaller eye (HLL/OOL, 4.0 ± 0.2 vs. 3.7 ± 0.1), and shorter paired fins (PPD/PCL, 2.0 ± 0.2 vs. 1.7 ± 0.1 ; PAD/PVL, 1.7 ± 0.1 vs. 1.4 ± 0.2 ; Appendix Tables 4A,B). These notable differences suggest that Koelz may have avoided intergrades when sorting *manitoulinus* from typical *artedi*.

Four of nine body metrics comparable between contemporary *albus*-like ciscoes and typical *artedi* collected by Koelz differed notably (Appendix Table 15, excluding STL/DOH of 7.0 ± 0.4 ; includes correction of HLL/POL and HLL/MXL and conversion of paired-fin length ratios; see Morphometrics and Meristics subsection). The *albus*-like form had a much-deeper body (STL/BDD, 3.7 ± 0.1 vs. 4.4 ± 0.4), a shorter head (STL/HLL, 5.0 ± 0.2 vs. 4.4 ± 0.2), a shorter snout (HLL/POL, 4.7 ± 0.3 vs. 3.9 ± 0.2), and 3.9 more gill rakers (TGR, 51.0 ± 2.2 vs. 47.1 ± 2.2). These metrics indicate that contemporary *artedi* is an *albus* form, although considerably more diverged from typical *artedi* of the same lake than was *albus* of Lake Erie (see *Lake Accounts* section, Ciscoes of Lake Erie subsection). Only one of eight body metrics comparable between Koelz and Stanford Smith’s main basin collection of 1956 differed (excludes body depth; Appendix Table 10); the dorsal fin was taller in 1956 (6.5 ± 0.5 vs. 7.5 ± 0.7). The similarity between the body metrics of Koelz and Stanford Smith suggest that the apparent changes in body morphology in the contemporary *albus*-like form occurred after 1956 (an unlikely proposition) or that Koelz and Smith sampled a different population than that sampled in 2015, which spawned at Boot Island in the Les Cheneaux Islands complex. Smith sampled



mainly the spawning run in Saginaw Bay, and most of Koelz's samples came from the main basin too, but this population apparently no longer exists. As shown just above and in Yule et al. (2013), contemporary *albus*, including the populations spawning off the south side of Drummond Island (Ebener 2013), in the St. Marys River (Ebener 2013), and in the North Channel differ markedly from the typical *artedi* described by Koelz (1929) or by Stanford Smith. Instead, all of these contemporary populations are *albus*-like, a form not observed by Koelz, but that likely existed when he collected. The morphology of the typical *artedi* form appears to have been associated with a wide ranging, mostly offshore existence, whereas that of the *albus* type appears to be associated with a nearshore existence around bays. This inference is buttressed by the fact that the morphologies of typical *artedi* in Lakes Huron and Michigan as described by Koelz were very similar with five of their nine body metrics being identical (Appendix Tables 3A,B and 4A,B), suggesting selection for the same offshore morphotype in both lakes.

Local Ecological Characteristics

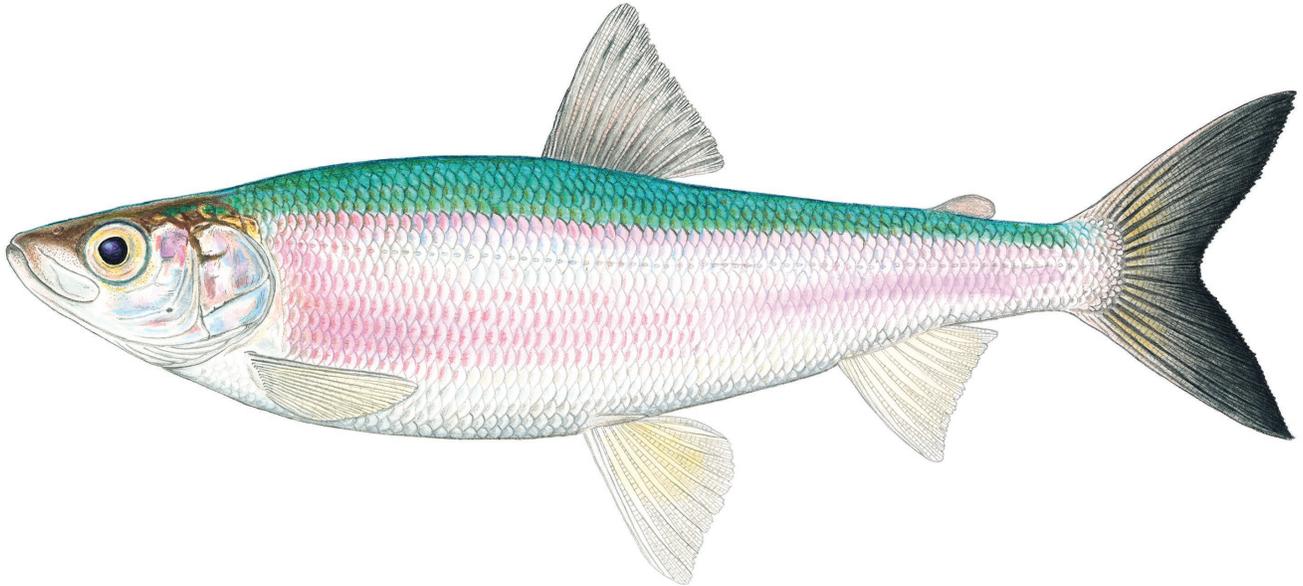
From the late 1800s to 1902, a period encompassing the heyday of the cisco fishery, catch records for *artedi* and deepwater ciscoes were combined as lake herring. Thereafter, deepwater ciscoes were marketed in the aggregate as chubs, obscuring which forms were most abundant historically. From 1912-1921, the first 10-year period of complete records, annual landings of what would have been mostly typical *artedi* averaged 2,000 tonnes, whereas landings of chubs averaged only 400 tonnes (Baldwin et al. 2009). Although landing of chubs during an unsustainable, short period of intensified fishing in the 1950s also reached 2,000 tonnes, landings of *artedi* were high for a much-longer period, through about 1950, suggesting that *artedi* always had been the most-abundant cisco. *Artedi* now is only widespread in Georgian Bay (form undetermined) and the North Channel (*albus*-like forms, Yule et al. 2013). The formerly dominant main basin population of typical *artedi* that spawned in Saginaw Bay (Dobiesz et al. 2005) appears to be extirpated while *albus*-like forms continue to spawn along the north shore (Ebener 2013; Yule et al. 2013).

Artedi was fished mostly in shallow water at depths under 10 m in spring and autumn, especially in November during the spawning run. In summer, *artedi* was pelagic and offshore making it unavailable to the fishery (Koelz 1929). Van Oosten (1929) reported for Saginaw Bay a maximum age of 8 years, which, based on scales, may be an underestimate. His findings that age-4 fish dominated the fishery and that fishing mortality was high were likely correct. He critiqued the scale method for aging *artedi* used by Scott (1951), who appears to have correctly aged the young fish that supported the Lake Erie fishery (see *Lake Accounts* section, Ciscoes of Lake Erie subsection). Maximum otolith age of contemporary *artedi* from the north shore of the main basin was 23 years (M. Ebener, Chippewa-Ottawa Resource Authority, personal communication, 2015). Size at maturity in the past is uncertain. Koelz's (1929) specimens >200 mm ($n = 50$), regardless of basin, were all mature. The only immature male had an STL of 161 mm and the largest of two immature females had an STL of 180 mm. Van Oosten (1929) suggested that females matured before males as females dominated his youngest age groups during the spawning run. Maximum STLs of immature contemporary *artedi* in the main basin, Georgian Bay, and the North Channel were 298, 243, and 386 mm, respectively (C. Davis, OMNRF, unpublished data).

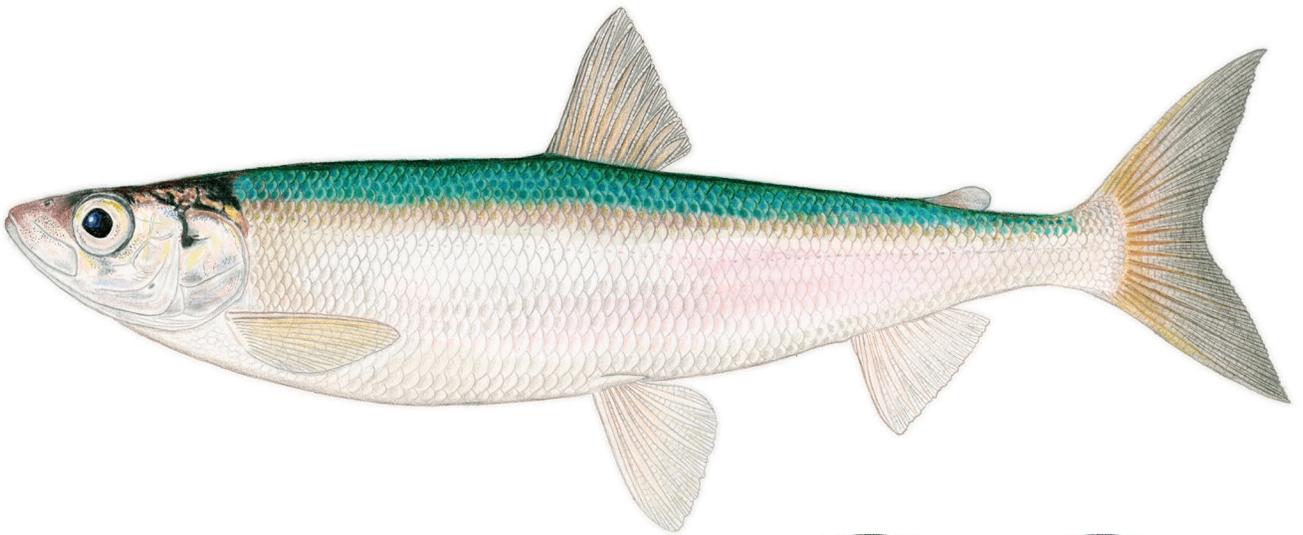
Van Oosten (1929) believed that the sandy-gravelly bottom of Saginaw Bay was ideal for spawning and had been told that *artedi* spawned in the Saginaw River before it became polluted. Although his collections of 1921-1924 occurred from as early as October 26 to as late as December 4, when spawning actually occurred is unclear; he did not document when spent fish were present. Spawning in the lower St. Marys River (Lake Nicolet) now occurs around November 19 over a sand bottom at a depth of ~6 m, while spawning along the south shore of Drummond Island occurs at the end of October over rock, again at ~6 m. The diet in inshore waters in autumn 1917 comprised crustaceans and *Hexagenia* (Koelz 1929). More-specific diet data are lacking. Isotopically, *artedi*, among Lake Huron ciscoes, occupied the most-unique trophic position, relying more on nearshore carbon sources than did other ciscoes (Schmidt et al. 2011).



HOYI AND HYBRIDA



Hoyi collected by W. Koelz off Alpena, Michigan, 16 September 1919, Univ. Mich. Mus. Zool. specimen 52881, STL 253 mm.



Hybrida (hybrid swarm cisco) collected by AMM and DBB off Hammond Bay, Michigan, 29 July 2014.



Color in life



Color in death



Distinctive Taxonomic Traits

Koelz (1929) noted that *hoyi* of Lake Huron was very much like *hoyi* of Lake Michigan except that the Huron form was smaller, having a maximum STL (standard length) of 221 vs. 265 mm in Lake Michigan. He also noted that *hoyi* of Lake Huron from depths <55 m and >110 m were morphologically different, the deeper-water *hoyi* having a longer head, longer paired fins, and a tendency to have an extended mandible. During 1976-2014, mean size of bottom-trawl-caught putative *hoyi* from the main basin peaked in 1997 (maximum STL, 286 mm) and then declined to only 201 mm in 2014 (DBB, unpublished data). Based on Koelz's data, Lake Huron *hoyi* was similar morphologically to a composite *hoyi* from all lakes of occurrence over all nine body metrics (Appendix Tables 1A,B and 4A,B). Four of eight body metrics comparable between *hoyi* described by Koelz and contemporary *hoyi*-like ciscoes (putative *hoyi*) identified by Mandrak et al. (2014) were notably different (contemporary dorsal fin height not recorded; Appendix Table 15). Putative *hoyi* had a shallower body depth (STL/BDD 4.8 ± 0.7 vs. 4.1 ± 0.3), a smaller eye (HLL/OOL, 4.0 ± 0.5 vs. 3.7 ± 0.2), a shorter maxillary (HLL/MXL, 3.0 ± 0.2 vs. 2.5 ± 0.1), and a shorter pelvic fin (PAD/PVL, 1.8 ± 0.2 vs. 1.3 ± 0.1 ; STL/PVL converted to PAD/PVL; see Morphometrics and Meristics subsection). Moreover, the standard deviations of body depth, snout length, maxillary length, orbital length, and pelvic fin length were 100% or more higher in putative *hoyi* as compared to *hoyi* collected by Koelz, suggesting profound changes. A shortened pelvic fin (PAD/PVL, 1.6 ± 0.1) is the only one of eight body metrics from Stanford Smith's survey of the main basin in 1956 (BDD was not recorded in 1956; Appendix Table 10) that differed from those of Koelz, indicating that the morphological changes implied in contemporary (putative) *hoyi* occurred after 1956.

Also peculiar, *artedi* and *hoyi* in 1956 differed substantially in head length, paired-fin lengths, and total gill rakers (TGR), but these body metrics in contemporary *artedi*-like ciscoes (putative *artedi*) and putative *hoyi* identified by Mandrak et al. (2014), especially pelvic fin length and total gill rakers, became more alike (i.e., converged; Appendix Tables 10 and 15). Head lengths (STL/HLL) of *artedi* and *hoyi* in 1956 were 4.4 ± 0.2 and 4.1 ± 0.3 , respectively, but, in contemporary (putative) *artedi* and *hoyi*, head lengths became 4.2 ± 0.3 and 4.1 ± 0.3 , respectively. Even more striking, pectoral fin lengths (STL/PCL) in *artedi* and *hoyi*, which in 1956 were 6.6 ± 0.5 and 5.6 ± 0.4 , respectively, were identical in contemporary (putative) *artedi* and *hoyi* (5.9 ± 0.6 and 5.9 ± 0.4 , respectively). Likewise, pelvic fin lengths

(STL/PVL) in *artedi* and *hoyi*, which in 1956 were 7.1 ± 0.5 and 5.8 ± 0.5 , respectively, converged to 6.3 ± 0.7 and 6.5 ± 0.7 , respectively. The convergence of total gill rakers in *artedi* and *hoyi* was also dramatic, declining from a difference of 4.5 rakers in 1956 to 2.4 rakers in 2003-2012. Differences in body metrics over time, especially that of gill rakers, may owe to differences in fish size with larger ciscoes having more rakers (Koelz 1929). The mean STL of *hoyi* collected in 1956, however, was essentially the same (214 mm) as that of contemporary (putative) *hoyi* (210 mm), yet contemporary (putative) *hoyi* had 2.2 fewer rakers (main basin samples) than *hoyi* collected during 1956 by Smith.

While four metrics for contemporary putative *artedi* and contemporary putative *hoyi* appeared to have converged, two metrics, snout length (HLL/POL) and orbital length (HLL/OOL), appeared to have diverged (Appendix Tables 10 and 15). Snout length in *artedi* and *hoyi* in 1956 was 4.0 ± 0.2 and 3.9 ± 0.2 , respectively, but became 4.2 ± 0.4 and 3.7 ± 0.5 (contemporary HLL/POL corrected; see Morphometrics and Meristics subsection). Orbital length of these two forms diverged to the point of reversing—putative *artedi* now has a larger eye than putative *hoyi*; HLL/OOL was 4.3 ± 0.3 and 4.0 ± 0.3 but became 3.8 ± 0.6 and 4.0 ± 0.5 , respectively). The above observations cast doubt on whether contemporary ciscoes classified as *artedi*, *hoyi*, and *zenithicus* by Mandrak et al. (2014) (Appendix Table 15) were the same forms sampled by Stanford Smith in 1956 or by Koelz (1929).

The preceding analysis supports an alternative view to the finding by Mandrak et al. (2014) that *artedi*, *hoyi*, and *zenithicus*, as described generally by Koelz (1929), still occurred in the deep waters of Lake Huron. This alternative states that the ciscoes of Lake Huron (less *albus*) now comprise a hybrid swarm (as per Seehausen 2004) resulting from introgressive hybridization caused by size-selective overfishing, especially two bouts of chub fishing that occurred during the late 1950s to early 1960s (Dobiesz et al. 2005), the near extirpation of their primary predator (Lake Trout) during the 1940s, and the introduction of the Sea Lamprey in 1937 (Smith 1968; Eshenroder et al. 1995), which fed on large individuals. These events, which reduced population sizes, appear to have eliminated the reproductive barriers that had separated the then remaining deepwater forms (*alpenae*, *hoyi*, *kiyi*, *reighardi*, and *zenithicus*) (Eshenroder and Burnham-Curtis 1999) as proposed for Lake Michigan by Smith (1964). Substantial numbers (up to 21% of total samples) of contemporary ciscoes not identifiable or having characteristics of more than one form (Todd and



Stedman 1989; Mandrak et al. 2014) suggest a single hybridized form.

Further evidence of a hybrid swarm can be found in the depth distributions of what had been classified as contemporary *hoyi* and *artedi* (Mandrak et al. 2014). Koelz found *artedi* uncommon in bottom-set gillnets at depths >22 m, whereas contemporary ciscoes classified as *artedi*, along with putative *hoyi* and *zenithicus*, were reported to be abundant in 2012 in Georgian Bay at depths of 77-93 m (Mandrak et al. 2014). Spangler and Collins (1992) detected an abundance of *artedi* in deep water in Lake Huron as early as 1958-1963 (first record). In their study, *artedi* was taken in Georgian Bay in bottom-set gillnets at 2-37 m and 55-91 m but not at intermediate depths, an improbable distribution for adults. In the North Channel, *artedi* was not taken at intermediate or deep depths in 1964, the only year sampled, or in the main basin in 1967-1968. Likewise, when Stanford Smith surveyed the main basin in 1956, *artedi* was found predominately in shallow water. Only two of his 47 *artedi* samples were taken in deep water (91 m), while 91% came in mid-November from a spawning run in outer Saginaw Bay mentioned by Carr (1962). These observations suggest that introgression was well underway in Georgian Bay by the 1950s. This inference is consistent with Webb and Todd (1995) finding small numbers of what appeared to be *hoyi* x *reighardi* hybrids in Georgian Bay in 1992-1993.

Deepwater ciscoes in the main basin appear to have introgressed into a hybrid swarm sometime after 1956, when Stanford Smith collected, and before 1984-1985, when Todd and Stedman (1989) collected. Based on trawl samples, Todd and Stedman (1989) reported hybridization between *hoyi* and *artedi* throughout the main basin at depths of 43-73 m. These two forms were said to differ by only 2.7 gill rakers, nearly identical to the lakewide 2.4 raker difference between contemporary swarm ciscoes identified as *hoyi* and *artedi* (Appendix Table 15) and much less than the 5.7 raker difference reported by Koelz (Appendix Table 4B) or the 4.5 raker difference observed by Stanford Smith (Appendix Table 10). These small differences in contemporary raker numbers between putative *artedi* and *hoyi* may result from observer bias (Todd and Smith 1980) in that gill raker number was used in identification. The raker data suggest that Todd and Stedman (1989) were sampling from the hypothesized hybrid swarm rather than from hybridized *artedi* and *hoyi*. *Artedi* was unlikely plentiful enough in the main basin just before 1984-1985 to produce observable numbers of *artedi* x *hoyi* hybrids. The dominant Saginaw Bay population had been

extirpated three decades earlier (Baldwin et al. 2009). One author of this report (RLE) saw only a handful of *artedi* south of the north shore during the entire 1970s and then only in spawning aggregations of Lake Whitefish (*C. clupeaformis*). The problem appears to be that some fraction of the ciscoes collected in deep water resemble *artedi* in shape although not, as shown above, in body metrics.

If the hybrid swarm hypothesis is correct, *hoyi* and *zenithicus* no longer exist in Lake Huron as distinct forms but rather have introgressed into aggregations whose origin also includes the other three deepwater ciscoes extant in 1956. Whether each aggregation coalesced into a single breeding population is uncertain. Genetic structuring by basin within Lake Huron is not evident (Fave and Turgeon 2008). The morphology of swarm ciscoes in each of Lake Huron's basins is relatively similar and *hoyi*-like across eight body metrics, although the North Channel population is most diverged (Appendix Table 15). As compared to the lakewide swarm, the North Channel population has a deeper body (HLL/BDD, 4.2 ± 0.4 vs. 4.9 ± 0.7) and 2.3 more gill rakers (TGR, 43.3 ± 1.6 vs. 41.0 ± 2.2). The Georgian Bay population is distinctive in having a larger eye (STL/OOL, 3.6 ± 0.5) than the North Channel (4.3 ± 0.3) or main basin populations (4.2 ± 0.4). Selection may favor specializations along ecological gradients. Regressions of gill raker number on standard length for contemporary swarm ciscoes yielded a weak negative relationship ($r^2 = 15\%$) for the main basin but not for the North Channel and Georgian Bay (TCP and NEM, unpublished data).

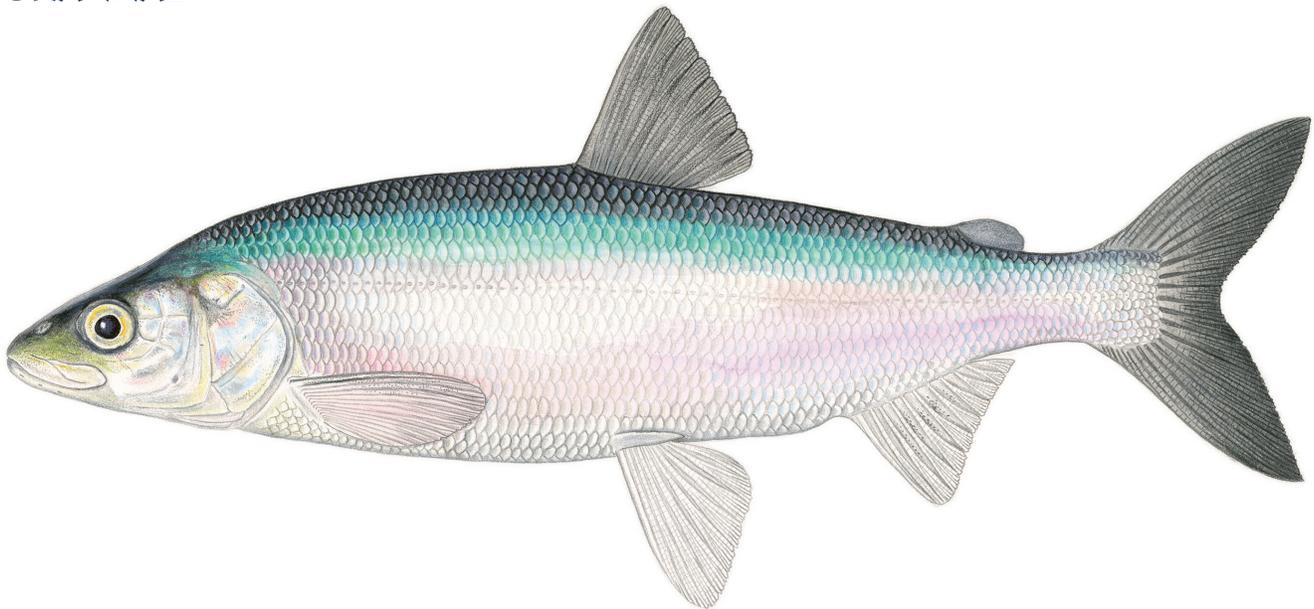
Why the deepwater ciscoes of Lake Michigan, which went through size-selective overfishing similar to what occurred in Lake Huron, do not appear to have coalesced into a hybrid swarm is a challenging question. The greater relative abundance of Lake Michigan *hoyi* during the period of hybridization may have made its morphotype more resilient. *Hoyi* comprised 76% of all deepwater ciscoes in 1954-1955 and 91% in 1960-1961 (Smith 1964), whereas Lake Huron *hoyi* in the main basin in 1956, when the effects of hybridization were already apparent, comprised a lesser amount, 56% (R/V *Cisco* cruise reports). Whether or not the swarm hypothesis proves correct, contemporary ciscoes are so diverged from the forms described by Koelz (1929) that, at the minimum, a new classification is required, a need anticipated by Smith (1964) when he observed hybridization among the ciscoes of Lake Michigan (see *Lake Accounts* section, Ciscoes of Lake Michigan subsection).

Local Ecological Characteristics

When Koelz (1929) conducted his survey of Lake Huron in 1917-1924, *hoyi*, due to its small size, was not targeted by the fishery except for bait, which obscured its relative abundance. The extirpation of the Lake Trout, its main predator, the introduction of the Sea Lamprey, which preyed selectively on larger ciscoes, and overfishing of larger-bodied ciscoes likely allowed *hoyi* to become dominant just before the 1956 survey (Smith 1968). Landings of deepwater ciscoes, in various stages of hybridization, reached an unsustainable peak of 2,500 tonnes in 1961, considerably above mean landings during 1912-1956 of 376 tonnes for all deepwater ciscoes (chubs) combined. Current landings, being negligible (Ebener 2013) owing to weak market demand, underestimate abundance. Assuming that the assessment catch of what had been classified as *hoyi* during 1973-1999 was actually *hybrida*, abundance of the swarm in the main basin peaked in 1990 as part of a cycle associated with changes in sex ratio and recruitment (Dobiesz et al. 2005). Koelz (1929) reported that *hoyi* had a depth range of 18-183 m and was most abundant at 55 m. Of the two most-common depths fished in 1956 (46 and 91 m), *hoyi* was the most-abundant cisco by far at 46 m, yet was found as deep as 91 m and as shallow as 24 m (R/V *Cisco* cruise reports).

Otolith ages of Lake Huron *hoyi* have gone unreported. During 2004-2014, maximum age of *hybrida* was 10 in the North Channel, 15 in Georgian Bay, and 14 in the main basin. In these same years, maximum size of immature males in Georgian Bay and the main basin was 202 mm and of immature females was 193 mm (C. Davis, OMNRF, unpublished data). In contrast, all of Koelz's representative *hoyi* (minimum STL, 151 mm) were mature, suggesting that introgression resulted in an increase in size at maturity. *Hoyi* collected by Koelz (1929) from the main basin at <55 m depths had eaten 60-98% *Diporeia* spp. and in >110 m had eaten *Mysis diluviana* exclusively. Historically, among the deepwater ciscoes of Lake Huron, *hoyi* occupied the highest trophic level along with *kiyi*. Analysis of stable isotopes from *hoyi* archived from the Koelz era indicated a relatively unique trophic niche (Schmidt et al. 2011). Among *Coregonus* it had the second-highest enrichment of nitrogen, suggestive of feeding at a higher trophic level. Diet composition of *hybrida* taken from the northern main basin at a depth of 91 m in 2007 indicated lower reliance on *M. diluviana* (23% of diet volume between May and September) and *Diporeia* spp. (3% by volume) and increased feeding on calanoid copepods (58%) (Bunnell et al. 2011).

JOHANNAE



Collected by W. Koelz ~29 km NNW of Thunder Bay, Michigan, 5 July 1923, Univ. Mich. Mus. Zool. specimen 59465, STL 224 mm.



Distinctive Taxonomic Traits

The last records of *johannae* from Lake Huron are those of Koelz (1929); maximum STL (standard length) then was 332 mm. As noted in the *Lake Accounts* section, Ciscoes of Lake Michigan subsection, this form varied little morphologically from the Lake Michigan form, which was the only other occurrence. Just two of nine body metrics differed between these populations, the Lake Huron form having a slightly longer head (STL/HLL, 3.9 ± 0.1 vs. 4.1 ± 0.1) and a slightly longer snout (HLL/POL, 3.4 ± 0.1 vs. 3.6 ± 0.1 ; Appendix Tables 3A,B and 4A,B). Koelz (1929) reported that the Lake Michigan form appeared to have a smaller eye, but the ratios were identical (HLL/OOL, 4.4). No further comparative data on morphology are available as *johannae* was commercially extinct by the time Stanford Smith conducted his 1956 survey.

Local Ecological Characteristics

Johannae was commercially important in Lake Huron during Koelz's 1917-1923 surveys as evidenced by individual lifts containing up to 90% of this form. Its extirpation from Lake Huron was swift when considering that, in 1920, a lift of 1,400 kg was witnessed, but, by 1956, none could be found. An "extreme" depth range from Koelz (1929) was 29 to 183 m, although he suspected this form occupied the deepest waters of the lake. All individuals <165 mm were immature and most of those >195 mm were mature (Koelz 1929). He noted, however, that *johannae* as large as 240-320 mm were immature, although other fish of the same size were in spawning condition, leading him to suggest that spawning may be intermittent, occurring every other year. Although Koelz was not able to determine exactly when or where spawning occurred, he did note that the population migrated away from "feeding grounds" at the end of August and into September and observed ripe fish landed at Alpena, Michigan, in late August-early September that came from depths of 110-117 m over clay bottoms. Stomachs examined from Koelz's collections were dominated by *M. diluviana*. Among Lake Huron ciscoes, *johannae* was nearly identical isotopically to *reighardi*, occupying an intermediate trophic niche (Schmidt et al. 2011).

KIYI

Distinctive Taxonomic Traits

Kiyi of Lake Huron was small in size for this form across its range (Koelz 1929). Maximum STL (standard length) was 249 mm ($n = 226$), slightly larger than recorded by Stanford Smith in 1956 (233 mm, $n = 27$). Lake Huron *kiyi* conformed well to the basinwide composite across all nine body metrics (Appendix Tables 1A,B and 4A,B). Koelz (1929) inferred that Lake Huron *kiyi* were quite similar in morphology to Lake Michigan *kiyi* with only minor differences in head length and orbital length owing to the smaller size of his Lake Huron specimens. The *kiyi* collected by Stanford Smith in 1956 from the main basin (Appendix Table 10) varied morphologically from those collected by Koelz lakewide, suggesting that reproductive barriers between Lake Huron forms had been deteriorating. *Kiyi* in 1956 differed in having a smaller eye (HLL/OOL, 4.0 ± 0.2 vs. 3.7 ± 0.2), shorter pelvic fin (PAD/PVL, 1.3 ± 0.2 vs. 1.1 ± 0.1 ; paired-fin lengths converted; see Morphometrics and Meristics subsection), and more gill rakers (41.0 ± 2.6 vs. 38.2 ± 1.9). Although these changes in body metrics are not dramatic individually, together they indicate profound change when considering that the morphology of Lake Huron *kiyi* was previously indistinguishable from Lake Michigan *kiyi* even though these populations were separated spatially for thousands of years. Except for the change in orbital length, the two remaining shifts in body metrics are consistent with hybridization with *hoyi*, which remained abundant after 1956 (Dobiesz et al. 2005).

Local Ecological Characteristics

Because of its small size, *kiyi* was infrequently caught in the commercial gillnets monitored by Koelz, and, being of little commercial value then, its abundance in relation to its sister forms is uncertain. *Kiyi* was better represented in Stanford Smith's 1956 survey likely owing to the differences in gillnet-mesh size. Koelz typically sampled 2.75-inch (69.9 mm) -mesh gillnets, whereas Smith included various panels with meshes as small as 1.0 inch (25.4 mm) (R/V *Cisco*, cruise reports of 1956). One lift of Koelz's "bait net" (1.5-inch (38-mm) mesh) yielded eight *kiyi*, his best catch, indicating that this form was reasonably abundant in 1919. *Kiyi* inhabited the deeper waters of Lake Huron mostly beyond 110 m (Koelz 1929). Smith's surveys of the main basin focused on depths of 46 and 91 m, and *kiyi* was only abundant in the deep sets. All 10 of Koelz's "representative" *kiyi* (minimum STL, 155 mm) were mature females. Eggs were approaching maturity by mid-October, but Koelz was unable to

determine when and where spawning occurred. A sample of 20 *kiyi* taken from a depth of more than 110 m fed almost exclusively on *M. diluviana* (Koelz 1929). Among Lake Huron ciscoes, *kiyi* and *hoyi*, on the basis of stable isotopes, occupied a very-similar trophic position, having the highest enrichment of nitrogen (Schmidt et al. 2011).

NIGRIPINNIS

Distinctive Taxonomic Traits

Historically one of the two largest forms of deepwater cisco in Lake Huron, the other being *johanna*, *nigripinnis* reached a maximum STL (standard length) of 371 mm (Koelz 1929). *Nigripinnis* was essentially identical across nine body metrics when compared to a composite *nigripinnis* based on four lakes (Appendix Tables 1A,B and 4A,B). In a comparison with only the Lake Michigan form, Koelz (1929) saw that the Lake Huron form had a slightly larger head, larger eye, and longer paired fins. These metrics differed little between lakes, however, except that the Lake Huron form had a slightly longer pectoral fin (PPD/PCL, 1.5 ± 0.1 vs. 1.7 ± 0.2 ; Appendix Tables 3A,B). Koelz (1929) also noted that occasional individuals within a catch from Georgian Bay lacked the “characteristic bright-blue body color and the reduction of the usual pigmentation of the fins, especially of the ventrals.”

Local Ecological Characteristics

Nigripinnis of Lake Huron was not as overfished as was the Lake Michigan form when Koelz was conducting field work. Koelz saw heavy catches in the main basin as late as 1923, while, during the same period, he collected only 52 from all of Lake Michigan. Nonetheless, the Stanford Smith survey of 1956 did not collect any *nigripinnis* from Lake Huron’s main basin, so this form was extirpated in a matter of decades. Koelz (1929) gave a depth distribution for Lake Huron of 64-183 m and suggested that *nigripinnis* likely inhabited even deeper waters. No specimens less than 220-mm STL were found to be mature, and spawning was said, based on appearance of ovaries, to occur after November and even into January, although Koelz did not observe spawning. Isotopically, *nigripinnis* occupied an intermediate trophic niche similar to that of *johanna* and *reighardi* (Schmidt et al. 2011).

REIGHARDI

Distinctive Taxonomic Traits

The 1956 collection of Stanford Smith is the first for Lake Huron *reighardi* and the sole source of morphological data (Appendix Table 10). Maximum STL (standard length) of main basin *reighardi* was 219 mm ($n = 64$); maximum size reported by Webb and Todd (1995) was slightly larger, 229 mm; whereas maximum STLs in Lakes Michigan and Ontario were 278 and 295 mm, respectively (Koelz 1929). In a comparison of six body metrics (excludes BDD and paired-fin lengths), *reighardi* of Lake Huron in 1956 was nearly identical to a composite *reighardi* comprising Lakes Michigan and Ontario specimens collected by Koelz (Appendix Tables 1A,B). Dorsal height (DOH) differed most and was marginally taller in Lake Huron *reighardi* (STL/DOH, 6.3 ± 0.4 vs. 7.0 ± 0.4). These limited data indicate that *reighardi* in the main basin, when discovered, had not begun to introgress with other deepwater ciscoes (see *Hoyi* and *Hybrida* subsection above).

Local Ecological Characteristics

Based on R/V *Cisco* cruise reports of 1956, *reighardi* was more plentiful at depths of 46 m than at 91 m (only two depths were fished). At 46 m, it appeared to be second in abundance among the six remaining ciscoes (includes *alpenae*), and, at 91 m, it was the least-abundant cisco. *Reighardi* was very scarce in the main basin following a bout of intense fishing during the late 1950s through the 1960s and disappeared in Georgian Bay following a similar bout of fishing in the mid-1970s (Webb and Todd 1995; Dobiesz et al. 2005). Being of small size, *reighardi*, like *kiyi*, may not have succumbed to excessive fishing mortality directly, but to a fishery-induced breakdown of reproductive barriers between the forms, which had kept them reproductively isolated. In fact, Webb and Todd (1995) reported what appeared to be *hoyi* x *reighardi* hybrids. Size at maturity has not been reported for Lake Huron *reighardi*. Webb and Todd (1995) reported that spawning occurred in May-June at depths similar (52-146 m) to those used by *reighardi* of Lake Michigan. Its diet in Lake Huron is unknown, but, isotopically, among Lake Huron ciscoes, it occupied an intermediate niche very similar to that of *johanna* (Schmidt et al. 2011).



ZENITHICUS

Distinctive Taxonomic Traits

Maximum STL (standard length) was 318 mm ($n = 91$) in 1917-1923 (Koelz 1929) and 267 mm ($n = 4$) in 1956 (Stanford Smith's collection). *Alpenae* in 1956 apparently was more plentiful than *zenithicus* in the main basin and had a smaller maximum STL (255 mm, $n = 20$), suggesting that, in 1956, identification of these now synonymized forms was not based on *alpenae* being larger. The *zenithicus* and *alpenae* composites based on Koelz's collections were remarkably similar (Appendix Tables 1A,B). Neither *zenithicus* nor *alpenae* collected by Koelz differed notably from their composites (Appendix Tables 4A,B). Koelz separated these two forms based mainly on the position of the mandible, which was typically extended in *alpenae* and included in *zenithicus* (body depth, head depth, and pigmentation of the jaws were also important). Based on Tables 23 and 31 of Koelz (1929), mandible length (MDB) was longer in *alpenae* than in *zenithicus* (HLL/MDB, 1.9 ± 0.1 vs. 2.1 ± 0.1), although HLL/MDB of both forms was identical in 1956 (2.0 ± 0.1 ; Stanford Smith data not in appendix). In a comparison of eight body metrics (Appendix Tables 4A,B and 10; excludes STL/BDD and includes conversion of paired-fin lengths; see Morphometrics and Meristics subsection), *zenithicus* of 1917-1923 and 1956 were quite similar except for dorsal fin height (DOH), which was taller in 1956 (STL/DOH, 5.9 ± 0.3 vs. 6.8 ± 0.6). Likewise, *alpenae* of 1917-1923 was nearly identical to *alpenae* of 1956 except for DOH, which also was taller in 1956 (STL/DOH, 5.8 ± 0.3 vs. 6.7 ± 0.6). *Zenithicus* and *alpenae* of the main basin appear to have been more resistant to introgression than was *kiyi* (see above), both remaining stable morphologically through 1956.

In contrast to *zenithicus* of 1956, putative contemporary *zenithicus* (contemporary *alpenae* not recognized) differed morphologically in four out of eight body metrics from *zenithicus* collected by Koelz (dorsal height not compared; Appendix Table 15). As compared to Koelz's samples, contemporary *zenithicus* (snout length and maxillary length corrected and paired-fin lengths converted; see Morphometrics and Meristics subsection) had a shallower body (STL/BDD, 5.1 ± 0.7 vs. 4.3 ± 0.5), a shorter snout (HLL/POL, 4.1 ± 0.6 vs. 3.5 ± 0.2), a larger eye (HLL/OOL, 3.8 ± 0.6 vs. 4.2 ± 0.3), and 1.9 more gill rakers (TGR, 39.3 ± 1.9 vs. 37.4 ± 2.2). The mean STL of Koelz's "representative" *zenithicus* >200 mm was 267 mm, which suggests that his net-run fish were typically far larger than contemporary samples, which averaged only 192 mm (all basins

combined). Although some of the apparent decline in body depth relates to contemporary *zenithicus* being smaller, none of 10 small (range 167-191) *zenithicus* individually enumerated by Koelz was as shallow bodied as contemporary *zenithicus*. Likewise, being larger in size, *zenithicus* collected by Koelz should have had more rakers, not fewer, than contemporary *zenithicus*. Thus, the apparent increase in raker count was likely greater than 1.9. These findings suggest, as was the case above for *hoyi*, that contemporary *zenithicus* is no longer extant in Lake Huron; rather it appears to be introgressed into a hybrid swarm, previously discussed, having mainly *hoyi* features.

Local Ecological Characteristics

The historical abundance of *zenithicus* in relation to that of the other deepwater ciscoes of Lake Huron is obscure in that this form was only observed to be plentiful while spawning (Koelz 1929). In Stanford Smith's survey of the main basin in 1956, *zenithicus* was uncommon and seen only at the deeper of the two stations fished (46 and 91 m; R/V *Cisco* cruise reports). If *alpenae* was synonymous with *zenithicus*, then *zenithicus* occupied depths of 26-183 m when not spawning and reached peak abundance at ~90 m (Koelz 1929). Regarding maturity of Koelz's representative fish, standard length of the largest immature male was 190 mm (an anomalous 287-mm male was listed as immature) and the largest immature female was 188 mm. Koelz (1929) collected *zenithicus* in spawning condition on September 28-29 and October 14 from northwestern Lake Huron between Spectacle Reef and 40 Mile Point over clay bottoms at depths of 64-91 m. Each lift yielded 700-800 kg comprising 99% *zenithicus*. In contrast, the only known spawning location of *alpenae* was in Georgian Bay (Colpoys Bay). There, Koelz observed spawning on November 19 and December 3 over mud and rock bottoms at depths of 18-46 m. Yield was 170-350 kg of 100% *alpenae*. These records suggest that *alpenae* and *zenithicus* were reproductively isolated. Only seven *zenithicus* stomachs, all collected off Cheboygan, Michigan, in September, were examined by Koelz; 95% of the diet comprised *Diporeia* spp. and *Mysis diluviana*. Thirty *alpenae* stomachs collected off Alpena, Michigan, also in September contained only *M. diluviana*. Based on isotopic signatures of all Lake Huron ciscoes, *zenithicus* and *alpenae* occupied different trophic niches. *Zenithicus* occupied a higher trophic position than *alpenae*, but both used similar carbon sources. Niche partitioning also occurred between *zenithicus* and *alpenae* of Lake Michigan, but the relative trophic positions were reversed (Schmidt et al. 2011).



CISCOES OF LAKE ERIE

TAXONOMY

In recognizing only *artedi* and *zenithicus* from Lake Erie, Todd and Smith (1992) synonymized *zenithicus* and *alpenae*, the latter being a form described for this lake by Scott and Smith (1962) but not observed by Koelz (1929). Their synonymizing likely was based on rearing experiments conducted by Todd et al. (1981) but was inadvertently referenced as Todd and Smith (1980), which does not mention *alpenae*. Both the *albus* and typical forms of *artedi* occurred in Lake Erie, but *albus* was far more abundant. Because *alpenae* is considered a distinct form elsewhere in this report, *alpenae* and *zenithicus* are treated here as *zenithicus/alpenae*.

IDENTIFICATION OF EXTANT FORMS

Even though no *alpenae*-like form has been reported since Scott and Smith (1962) surveyed in 1957, any new recovery of a cisco could be a deepwater (hybrid swarm) cisco (*hybrida*) from Lake Huron's main basin. *Hybrida*

from the main basin of Lake Huron (Appendix Table 15) has a mean gill raker count of 40.7 ± 2.4 (range 32-52), whereas, in 1957, Lake Erie *albus* had a mean count of 45.8 ± 2.7 (range 42-50; Appendix Table 11), close to what Koelz reported in the 1920s (46.5 ± 2.1 , range 41-53; Appendix Table 5A). A contemporary specimen identified as *artedi* could be *albus*, which had been dominant in Lake Erie, or typical *artedi*.

Typical *artedi* is distinctive in having a subterete profile curving gently from the snout to the occiput dorsally and ventrally. The body is of relatively uniform depth from the occiput to the beginning of the caudal peduncle where it curves gradually to the end of the caudal peduncle, creating a symmetrical appearance overall. *Albus* is similar in shape but deeper bodied, hence *albus* is described in the Lake Erie Quick Key as having a terete profile. For a description of *hybrida*, see *Lake Accounts* section, Lake Huron subsection, *Hoyi* and *Hybrida* subsection.

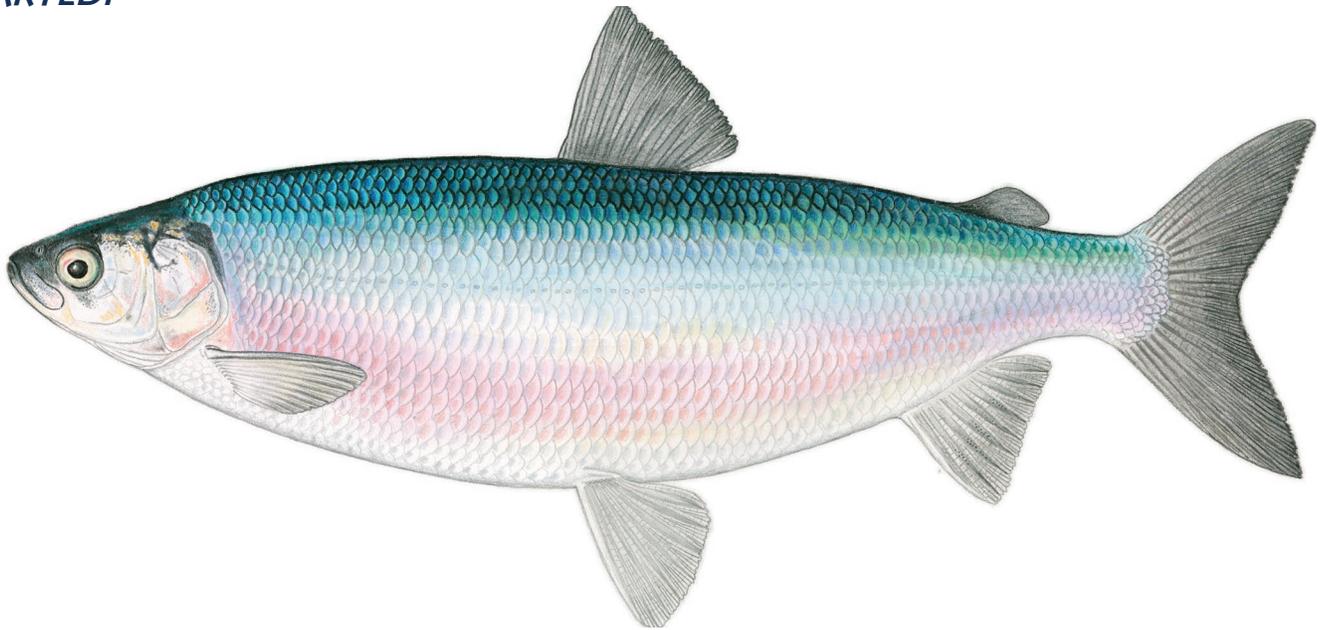


Lake Erie, 17 March 2005, Satellite Imagery

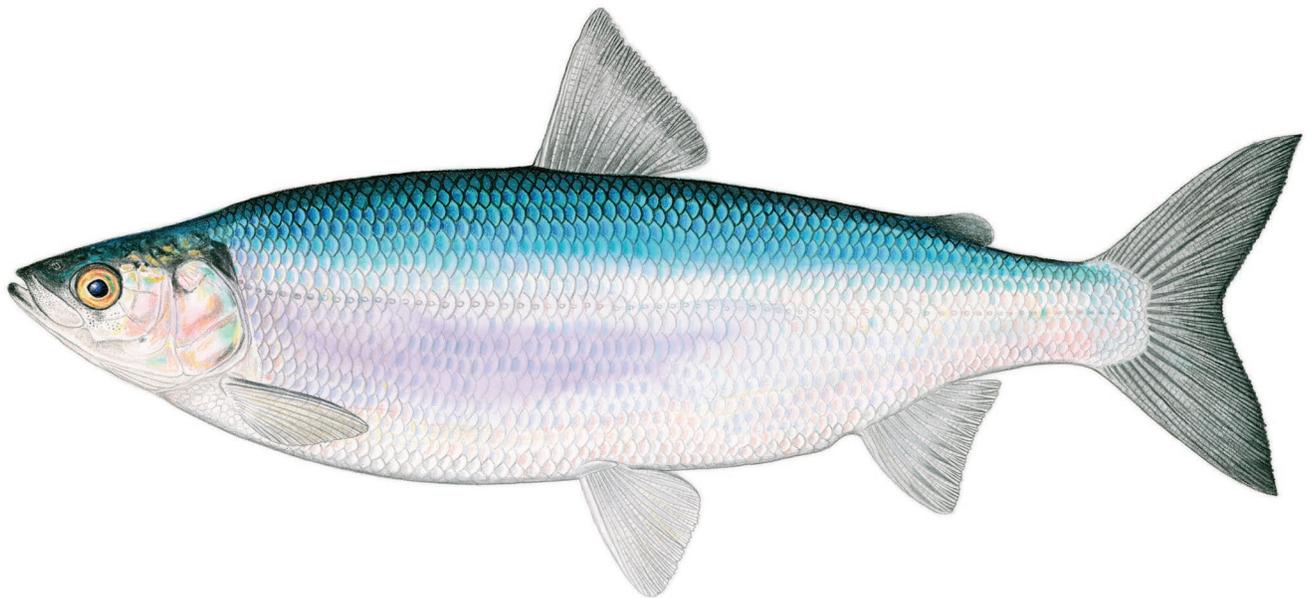
Image from U.S. National Weather Service.



ARTEDI



Albus form collected by W. Koelz west of Port Stanley, Ontario, 16 December 1922, Univ. Mich. Mus. Zool. specimen 59375, STL 322 mm.



Albus form collected by W. Koelz west of Port Stanley, Ontario, 16 December 1922, Univ. Mich. Mus. Zool. specimen 59364, STL 263 mm.



Distinctive Taxonomic Traits

Maximum STL (standard length) observed by Koelz (1929) was 402 mm ($n = 163$), far greater than the maximum STL of 234 mm reported by Stanford Smith for 1957, but Smith's sample size was only 13 owing to the depleted state of that population at that time. Lake Erie *albus* differed morphologically from the composite typical *artedi* only in body depth (BDD) with *albus* being deeper bodied (STL/BDD, 3.6 ± 0.3 vs. 4.4 ± 0.4 ; Appendix Tables 1B and 5B). The few ($n = 10$) typical *artedi* from Lake Erie enumerated by Koelz also had relatively deep bodies (4.1 ± 0.3 ; Appendix Table 5B) as compared to the composite *artedi*, which is why Koelz considered *albus* and typical *artedi* to be races as opposed to species. *Albus* and typical *artedi* of Lake Erie in 1920-1924 differed in two metrics with *albus* being marginally deeper bodied (STL/BDD, 3.6 ± 0.3 vs. 4.1 ± 0.3) and having longer paired fins (PPD/PCL, 1.9 ± 0.2 vs. 2.3 ± 0.2 ; PAD/PVL, 1.6 ± 0.2 vs. 1.8 ± 0.1 ; Appendix Tables 5A,B). Smith did not record body depth, but his samples had long paired fins (PPD/PCL, 1.9 ± 0.1 ; PAD/PVL, 1.5 ± 0.1), more like *albus* than typical *artedi* (Appendix Table 11; fin-length ratios converted; see Morphometrics and Meristics subsection). Of the eight body metrics comparable between *albus* of Koelz and Stanford Smith's presumed *albus*, none differed notably. Smith's limited data suggest that *albus* of Lake Erie remained morphologically stable from 1920-1924 through 1957, even though by then the population was commercially extirpated (see below).

Contemporary ciscoes are collected from Lake Erie infrequently. Two groups of specimens collected by commercial operators were available for analysis—nine collected during 1995-1999 and 22 collected during 2003-2015. Morphological measurements from the 1995-1999 collection, archived at the Royal Ontario Museum, were made by Beverly Scott; NEM worked up the 2003-2015 collection (Appendix Table 16). The 1995-1999 collection contained six small (112-171 mm) and three large ciscoes (268-410 mm). This distribution limits comparisons involving ratios as most of the specimens are of a size poorly represented (too small, too large) in the appendix. Despite this caveat, the gill raker counts of the three larger fish collected in 1995-1999, varying from 44-47, indicate they were a form of *artedi*. The largest high-rakered cisco, having short fins, appeared to be typical *artedi*, whereas the other two, having fins of intermediate length, were difficult to place. The six smaller ciscoes, having gill raker counts of 41-42, did not appear to be a form of *artedi*.

The 2003-2015 collection appeared to contain more than one form, so groupings were made after each individual was classified. Individual body metrics and images were

compared against images of Lake Huron swarm ciscoes (*hybrida*) and against the means of body metrics of Stanford Smith's *albus*-like collection of 1957 and of Koelz's *albus* and typical *artedi* of Lake Erie (tables as above). Of the 22 individuals, RLE classified one as typical *artedi*, two as hybrids of *C. clupeaformis* and an unknown cisco, and the remaining 19 as *hybrida*. The individual classified as typical *artedi* had 49 gill rakers, a shallow body (STL/BDD, 4.9), and short paired fins (STL/PCL, 7.1; STL/PVL, 7.1), distinguishing it from *albus*. The two individuals classified as *C. clupeaformis* of uncertain ancestry had short, widely spaced gill rakers typical of this species (see Fig. 13 in Koelz 1929). The remaining individuals, ovate in body shape, grouped surprising well in having long heads (STL/HLL, 4.1 ± 0.2), small eyes (HLL/OOL, 5.2 ± 0.5), long paired fins (STL/PCL, 5.6 ± 0.5 ; STL/PVL, 5.9 ± 0.4), and an intermediate number of gill rakers (TGR, 38.4 ± 3.6). *Hybrida* of Lake Huron and putative *hybrida* of Lake Erie differed notably only in orbital length, Lake Erie putative *hybrida* having a smaller eye (HLL/OOL, 5.2 ± 0.5 vs. 4.2 ± 0.4). As noted in the *Lake Accounts* section, Ciscoes of Lake Huron subsection, *Hoyi* subsection, the standard deviations of *hybrida* body metrics are somewhat large such that comparisons of *hybrida* between lakes are relatively imprecise. Comparisons of *hybrida* with other cisco forms are more precise in that the cutoff is based on the sample with the lowest standard deviation. That said, the images and body metrics are convincing that, among ciscoes, *hybrida* was dominant but rare in Lake Erie, and this form most-likely originated from Lake Huron. Both typical *artedi* and *albus* appear to be so scarce in Lake Erie that *artedi* was classified in Table 2 as extirpated.

Local Ecological Characteristics

The Lake Erie fishery for *albus* was the largest of any in the Great Lakes and was once said to be the largest freshwater fishery in the world. A record of landings was not complete across jurisdictions until 1914 (Baldwin et al. 2009), even though the fishery was fully developed by 1870 (Koelz 1926). Abundance remained high only through the first 11 years of complete records, 1914-1924, when landings averaged 12,000 tonnes. Thus, the fishery was already at the end of its heyday when Koelz was conducting his field studies in 1920-1924. Koelz (1926) recognized that abundance was far less than in earlier years and that the population was seriously overfished. One year after Koelz completed his field work, landings declined sharply, amounting to only 22% of the 1914-1924 mean. Landings continued downward reaching economic insignificance in 1928 (Van Oosten

1930), proving Koelz to be insightful. *Albus* was primarily pelagic, except while spawning and during spring, as evidenced by the high efficiency of deep gillnets (~6 m deep) suspended from the surface (bull nets). These nets were introduced late, apparently around 1910, and appear to have hastened the fishery collapse (Koelz 1926). No otolith-based ages are available for *albus*, but the correspondence of Scott's (1951) scale ages with the appearance of the exceptionally strong 1943 year-class in 1946-1948 is convincing that his aging of young *albus* was correct. *Artedi* <6 years of age can be aged with reasonable accuracy using scales (Yule et al. 2008b), and age-3 fish dominated the fishery. The 1943 year-class was famous for its massiveness in various disjunct populations of Cisco, Lake Whitefish, and Walleye (*Sander vitreus*) in Lakes Michigan and Huron (Hile et al. 1953; Cucin and Regier 1966). The smallest mature male recorded by Koelz (1929) had a standard length of 181 mm, and the standard length of the smallest mature female was 185 mm. Spawning occurred from late November through early December, occurring later in eastern waters, over clay and gravel bottoms at depths of around 40 m in eastern waters and 20 m in western waters and off "virtually every port on the lake" (Koelz 1929). The diet of *artedi* or *albus* in Lake Erie has not been reported. Putative *hybrida* were widely dispersed at bottom depths of 7-38 m during 2003-2015.

ZENITHICUS

Distinctive Taxonomic Traits

The largest *zenithicus/alpenae* reported by Scott and Smith (1962) from a sample of 26 measured 268 mm standard length (STL). Lake Erie *zenithicus/alpenae* differed from their respective composites in similar ways except for snout length and pectoral fin length (Appendix Tables 1A,B and 11; paired-fin lengths converted; see Morphometrics and Meristics subsection). As compared to the *zenithicus* composite, Lake Erie *zenithicus/alpenae* had a shorter head (STL/HLL, 4.3 ± 0.1 vs. 4.0 ± 0.2), a shorter snout (HLL/POL, 3.7 ± 0.1 vs. 3.5 ± 0.1), a shorter maxillary (HLL/MXL, 2.7 ± 0.1 vs. 2.5 ± 0.1), a taller dorsal fin (STL/DOH, 5.8 ± 0.3 vs. 6.4 ± 0.5), and fewer gill rakers (TGR, 35.6 ± 1.6 vs. 39.5 ± 2.3). Compared to the *alpenae* composite, Lake Erie *zenithicus/alpenae* had a shorter head (STL/HLL, 4.3 ± 0.1 vs. 4.1 ± 0.2), a shorter maxillary (HLL/MXL, 2.7 ± 0.1 vs. 2.5 ± 0.1), a taller dorsal fin (STL/DOH, 5.8 ± 0.3 vs. 6.7 ± 0.5), a longer pectoral fin (PPD/PCL, 1.7 ± 0.1 vs. 2.0 ± 0.2), and fewer gill rakers (TGR, 35.6 ± 1.6 vs. 38.2 ± 3.0).

These comparisons reflect the similarity of *zenithicus* and *alpenae* across all three lakes. Snout length and pectoral fin length were outliers, but the differences between these body metrics and the composites were relatively small and, to some extent, result from precise body measurements (small standard deviations). The key characters separating *alpenae* from *zenithicus* were mandible position, mouth pigmentation, and premaxillary angle, with mandible position being particularly important. The mandible (jaw) is typically extended in *alpenae* and included in *zenithicus*, hence their common names, Longjaw Cisco and Shortjaw Cisco, respectively (Koelz 1929; Scott and Smith 1962). Mandible lengths of *alpenae* and *zenithicus*, however, were nearly identical in both forms across all three lakes (HLL/MBD, 2.0 ± 0.1 ; same authors). Surprisingly, jaw position does not appear to depend on jaw length. This finding is certainly one of the most intriguing paradoxes relating to the taxonomy of these two forms (see *Epilogue* section).

Local Ecological Characteristics

Zenithicus/alpenae of Lake Erie was not recognized as being commercially important. It may have been more important before complete records were kept (see above) and marketed with the much more-abundant *albus*. Possibly, samples collected in 1946-1947 and in 1957 (Scott and Smith 1962) represented a residual population exploited minimally in the 1800s due to weak markets for a deepwater cisco. Little is known about depth distribution, although most of the 1957 samples were taken by bottom trawl in 60-62-m depths, comparatively deep for Lake Erie (maximum depth, 64 m). No information is available on otolith ages. All fish >219 mm standard length sampled by Smith were mature (Scott and Smith 1962). Specimens taken on November 13 had well-developed gonads and one male was partially spent. According to fishermen, spawning occurred during the "stormy period" in November and December (Scott and Smith 1962). Bottom type, spawning location, and diet are unknown.



CISCOES OF LAKE ONTARIO

TAXONOMY

Bailey and Smith (1981) and Todd and Smith (1992) recognized four species of ciscoes from Lake Ontario: *C. artedi*, *C. hoyi*, *C. kiyi orientalis*, and *C. reighardi* (the listing of *C. zenithicus* in Todd and Smith is a typesetting error). *Orientalis* was described as a new subspecies by Koelz (1929). He also described an additional species, *C. prognathus*, which he deemed a blackfin, and recognized a subspecies of *artedi*, *C. a. albus*. Todd (1981) declared *prognathus* an invalid species not resolvable owing to the poor condition of the holotype and to misidentifications of other archived specimens. Koelz considered *albus* to be a deepwater form distinct from typical *artedi*, which he considered a shallow-water form. Stone (1947) questioned whether *albus* deserved a subspecific classification owing to the many intergrades between typical *artedi* and *albus*, although he was able to sort most of his specimens. Therefore, the taxonomic status of *albus* remains uncertain, although an *albus*-like cisco was collected in

2013 and is illustrated below. All forms except *artedi* are considered extirpated from the lake (Bailey and Smith 1981; Todd and Smith 1992). The status of *hoyi* is uncertain. It is being reintroduced (Fave and Turgeon 2008) from Lake Michigan donors.

IDENTIFICATION OF EXTANT FORMS

As relatively few *hoyi* have been reintroduced, in the near term, an unidentified cisco will most likely be *artedi*, although all ciscoes should be examined carefully to document any reintroduced *hoyi*. *Artedi* can most readily be separated from *hoyi* by body shape. *Artedi* is subterete in side view, while *albus* and *hoyi* are terete, and *hoyi* has a straight-line dorsal head profile resulting in a pointed, triangular snout, whereas the head of *artedi* is elliptical in side view (Fig. 3; Koelz 1929). The descriptions in the *Main Forms* section, illustrations, quick key, and other material in this section should be consulted for identification.

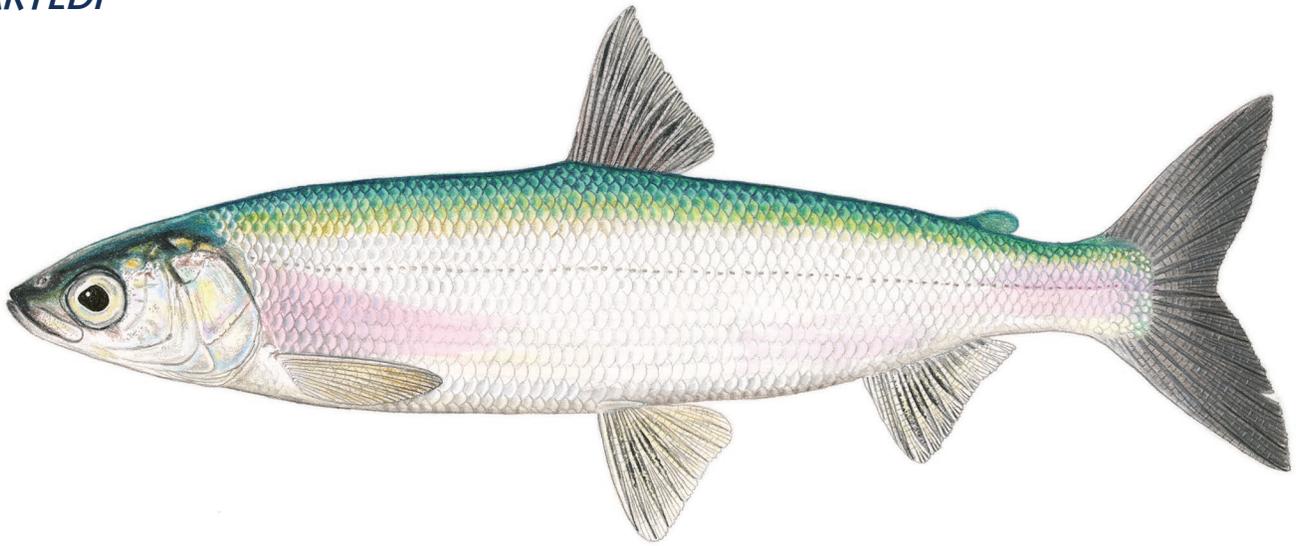


Anterior View of *Coregonus Artedi* from Lake Ontario

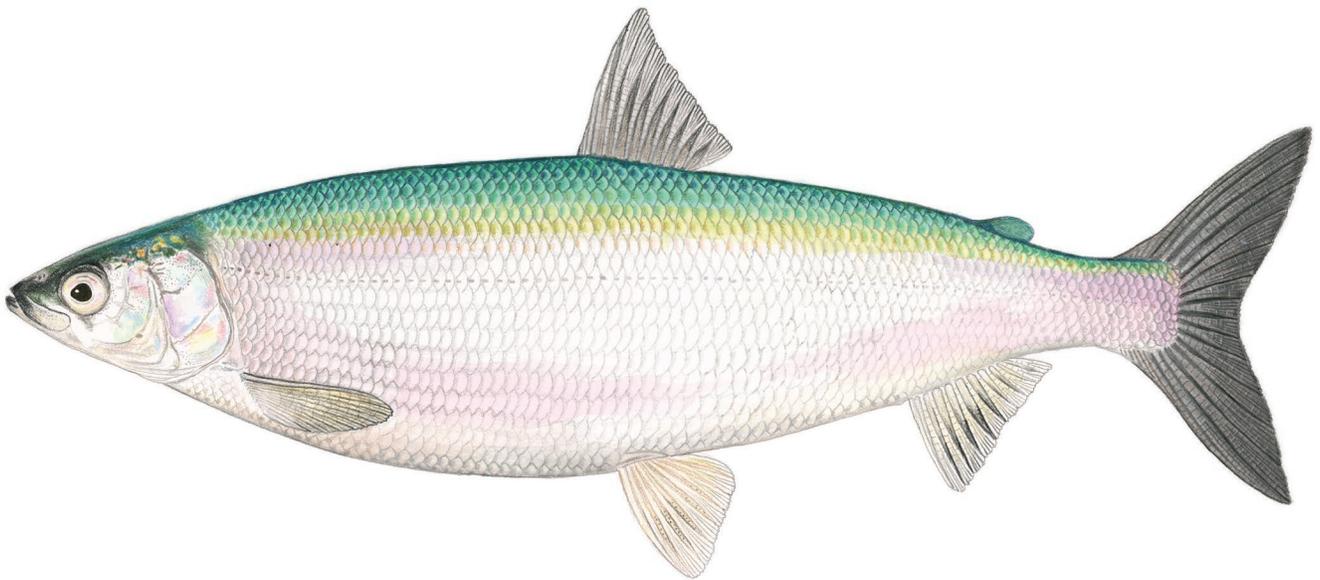
Image by AMM.



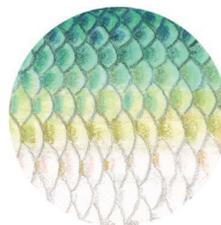
ARTEDI



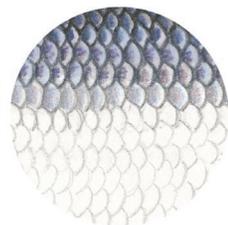
Typical *artedi* collected by AMM off Big Island, Bay of Quinte, Ontario, 06 November 2013, GLFC specimen 501, STL 250 mm.



Albus-like form collected by AMM off Big Island, Bay of Quinte, Ontario, 06 November 2013, GLFC specimen 509, STL 312 mm.



Color in life



Color in death



Distinctive Taxonomic Traits

Pritchard (1927) noted two races of *artedi* in Lake Ontario, a subterete, laterally compressed form that spawned in shallow water in the Bay of Quinte and a deeper-bodied form that spawned in deeper waters along open shorelines. Pritchard did not refer to the deeper-bodied type as *albus*, even though he likely was in contact with W. Koelz. Nevertheless, these two types are apparently what Koelz (1929) referred to as typical *artedi* and *albus* although, unlike Pritchard (1927), Koelz noted that typical *artedi* spawned in locations other than the Bay of Quinte. Koelz (1929) gave a maximum STL (standard length) of 366 mm for combined typical *artedi* and *albus*, all collected in 1917-1923. The 20 specimens he selected as representative of these two forms, all large in size, do not suggest any difference in maximum size between *albus* and typical *artedi*. The largest *artedi* collected in 1926 by Pritchard (1927) was 321 mm, small compared with Koelz's collection, but Koelz had a larger sample size, 254 vs. 100. Pritchard (1928) referred to these same *artedi* as "blue backs," i.e., typical *artedi*, implying the shallow-water form. Contemporary *artedi* collected in 2012 had a maximum STL of 414 mm, somewhat large, but not atypical for depleted populations (Selgeby 1982). Other than slight differences in color and body depth (BDD) (*albus* was paler and deeper bodied), the two forms were morphologically indistinguishable (Koelz 1929). STL/BDD was 3.5 ± 0.2 for *albus* and 3.9 ± 0.2 for typical *artedi* (Appendix Table 6B). Pritchard (1927) gave an estimate of 4.1 for STL/BDD, which suggests he was sampling typical *artedi*. Body measurements of *albus* (Appendix Tables 6A,B) were similar to composites of typical *artedi* and *albus* collected by Koelz from across the Great Lakes (Appendix Tables 1A,B) except that the typical *artedi* composite had, as would be expected, a shallower body depth (STL/BDD, 4.4 ± 0.4).

All eight body metrics from a sample of only 12 *artedi* (form not specified) collected from Lake Ontario in 1972 (Appendix Table 12; paired-fin-length ratios STL/PCL and STL/PVL converted to PPD/PCL and PAD/PVL, respectively; see Morphometrics and Meristics subsection) conformed well to those estimated in 1917-1923 by Koelz (Appendix Tables 6A,B; although body depth was not recorded in 1972). These metrics indicate little change in the body morphology of *artedi* over this 50-year period.

Further, none of nine body metrics (HLL/POL and HLL/MXL corrected and paired-fin-length ratios converted; see Morphometrics and Meristics subsection) comparable between 1921-1923 and 2012 (Appendix Table 17; STL/DOH, 6.4 ± 0.7 , not in table) changed notably over this 90-year period. Of interest, a body depth (STL/BDD) of 4.0 ± 0.3 (Appendix Table 17) indicates that the contemporary samples were predominately typical *artedi*, not *albus*. Overall, the contemporary data suggest that *artedi* morphology remained remarkably stable in Lake Ontario despite depletion of the population, although the *albus* form may be rare.

Local Ecological Characteristics

Exactly how important *artedi* was in the early commercial fishery is complicated by the past practice of compiling the catch of deepwater ciscoes with that of *artedi*. Combined landings peaked in 1889 at 2,250 tonnes (Baldwin et al. 2009), but peak landings may have occurred before then (Smith 1995). Both fisheries collapsed around 1950 (Christie 1973), and only *artedi* persists, but at low numbers. Catches in the past were made typically in the spring and autumn during inshore migrations, suggesting these forms were otherwise pelagic in the open surface waters of the lake. Individuals, however, could be caught as deep as 122 m (Pritchard 1928). Unlike in Lake Erie, *albus* was less abundant in Lake Ontario than typical *artedi*, but *albus* was much more prominent in Lake Ontario than was typical *artedi* in Lake Erie (Koelz 1929). All 20 of the typical *artedi* and *albus* detailed by Koelz were mature; the smallest male measured 200 mm and the smallest female 220 mm. Spawning along open shorelines occurred in October and in the Bay of Quinte in November (Pritchard 1927). *Albus* was said by Koelz (1929) to have spawned in relatively deep water, 27-55 m, whereas typical *artedi* spawned in shallow bays (Pritchard 1928; Koelz 1929). More recently (November 6, 2012), a pre-spawning aggregation of *artedi* was sampled at a depth of 6 m on a rocky shoal in Big Bay within the Bay of Quinte (Appendix Table 18). Diet data are lacking.



HOYI

Distinctive Taxonomic Traits

The maximum STL (standard length) of *hoi* sampled by Pritchard (1927) and Koelz (1929) were nearly identical, 258 and 255 mm, respectively. Stone (1947), sampling later (1942), when *hoi* had come to comprise 93% of the catch of deepwater ciscoes, reported a larger maximum size, 293 mm, suggesting release of *hoi* from competition with the reduced populations of *kiyi* and *reighardi*. Body measurements of Lake Ontario *hoi* are similar to those of a composite *hoi* for the Great Lakes and Lake Nipigon except that Lake Ontario *hoi* had a smaller eye (HLL/OOL, 4.2 ± 0.2 vs. 3.8 ± 0.2) and 2.2 more gill rakers (TGR, 44.6 ± 2.0 vs. 42.4 ± 2.1 ; Appendix Tables 1A,B and 6A,B). Both deviations were noted by Koelz (1929) in his comparison of Lakes Ontario and Michigan *hoi*. Pritchard's measurements for head length, orbital length, snout length, maxillary length, and gill raker number were very close to those of Koelz (1929). No body measurements have been published subsequently.

Local Ecological Characteristics

The *hoi* population of Lake Ontario, once vast, was represented by only 10 specimens, taken by gillnets, in a lakewide survey conducted in 1964 (Wells 1969). The next survey, conducted in 1972 as part of the International Field Year for the Great Lakes, found one (O'Gorman et al. 1989), and the last seen was in 1983 (Owens et al. 2003). Pritchard (1928) reported *hoi* was most abundant at depths of 76-91 m; Koelz (1929) found *hoi* at depths of 29-137 m, which was close to what Stone (1947) reported (55-146 m). Almost all of the 2,200 *hoi*, the smallest being in the 190-194-mm size-class, collected by Stone (1947) were mature. The population then was 82% female, a phenomenon reported for Lakes Michigan and Huron (Dobiesz et al. 2005). Information on spawning is limited. Koelz (1929) thought that spawning occurred sometime between November and March, but where and at what depths went unreported.

KIYI

Distinctive Taxonomic Traits

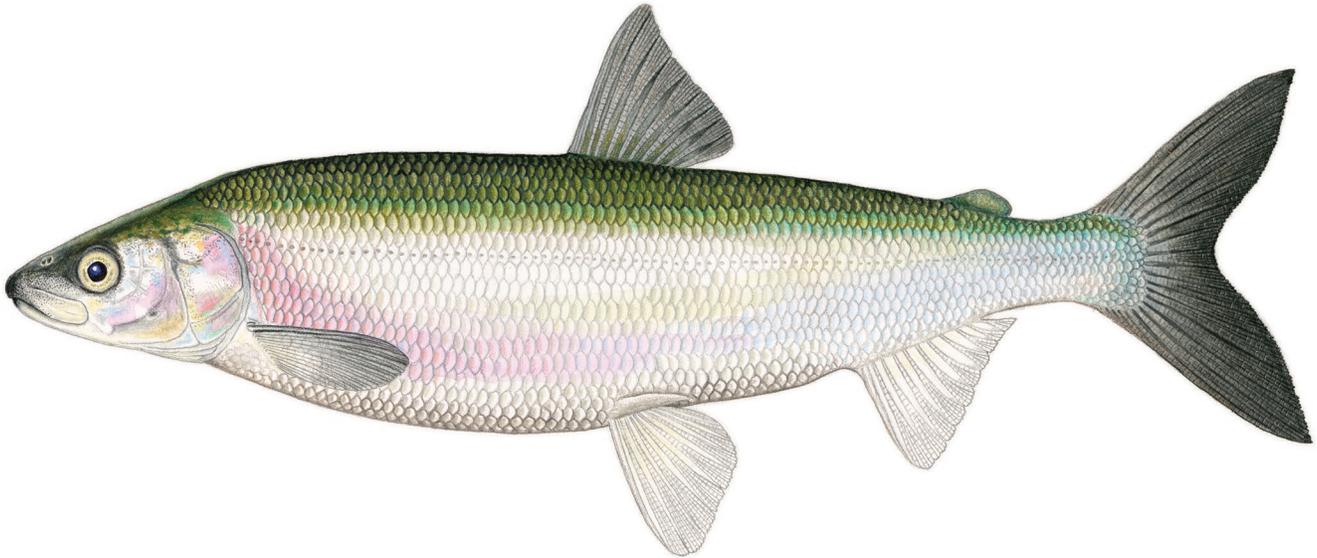
Kiyi of Lake Ontario was slightly larger in size than *kiyi* from the upper Great Lakes. Maximum STL (standard length) was 263 mm in 1921 (Koelz 1929) and 255 mm in 1926 (Pritchard 1927). Stone (1947) did not give any summary statistics for *kiyi* because this form comprised only 0.5% of his sample of deepwater ciscoes. Koelz (1929) found that *kiyi* of Lake Ontario differed enough in body measurements from the typical (upper lakes) form to warrant subspecies rank: these differences were mainly a shorter head (STL/HLL, 4.2 ± 0.1 vs. 3.9 ± 0.2), shorter pectoral fin (PPD/PCL, 1.9 ± 0.1 vs. 1.6 ± 0.2), and more gill rakers (TGR, 44.4 ± 1.8 vs. 39.7 ± 3.0) (Appendix Tables 1A,B and 6A,B). Koelz (1929) suggested that the pelvic fins were shorter, too, but the statistical means do not bear this out (PAD/PVL, 1.3 ± 0.1 Lake Ontario form vs. 1.2 ± 0.1 typical form). Still, Koelz appears to have been justified at the time in making *orientalis* a subspecies. Those six body measurements (STL/BDD, STL/HLL, HLL/POL, HLL/OOL, HLL/MXL, and TGR) comparable between Pritchard (1927, 1928) and Koelz (1929) were all in agreement. A nonconforming STL/BDD in Pritchard (1927) was corrected in Pritchard (1928). No subsequent body measurements of *kiyi* have been published.

Local Ecological Characteristics

The former abundance of *kiyi* is unknown, in part, because it, along with *hoi*, was not considered commercially important (Pritchard 1927) until *reighardi* became scarce (Stone 1947). The last *kiyi* was taken from Lake Ontario in 1964 (Wells 1969). Koelz (1929) inferred a depth range of 37-137 m, similar to that of *hoi*, and, according to Pritchard (1927), *kiyi* was most prevalent at depths of 76-84 m. Of the 10 representative *kiyi* enumerated by Koelz (1929), all were mature; the smallest male measured 199 mm and the smallest female 227 mm. Spawning occurred in August (Koelz 1929). Little else is known of its breeding habits or diet.



REIGHARDI



Collected by W. Koelz 14 km NNW off Sodus Point, New York, 12 July 1921, Univ. Mich. Mus. Zool. specimen 54144, STL 290 mm.

Distinctive Taxonomic Traits

Maximum STL (standard length) reported by Pritchard (1927) was 267 mm. Koelz (1929) sampled one specimen that had an STL of 295 mm and noted it was exceptional in size. Body measurements of *reighardi* of Lake Ontario conformed well to those of *reighardi* of Lake Michigan (Appendix Tables 3A,B and 6A,B) and to those reported by Pritchard (1927). Koelz recognized that the Lake Ontario form had a slightly shorter head and a smaller eye than the Lake Michigan form, but the means of STL/HLL (4.5 ± 0.2 vs. 4.3 ± 0.2) and HLL/OOL (4.3 ± 0.2 vs. 4.0 ± 0.2) for each form were not notably different. That these two geographically disjunct forms could be so similar in morphology is remarkable. No subsequent body measurements of *reighardi* were reported.

Local Ecological Characteristics

Pritchard (1928) noted that *reighardi* was considered by fishermen to be the “best” of the ciscoes, owing to its larger size and higher fat content. Accordingly, it was fished preferentially over *kiyi* and *hoyi*. It was already less abundant than *kiyi* and *hoyi* when Koelz (1928) sampled in 1921-1922. By 1942, when Stone (1947) was conducting his study, *reighardi* amounted to only 0.2% of his samples. The last *reighardi* taken from Lake Ontario, two specimens, were caught in 1964 (Wells 1969). Koelz reported that *reighardi* was found most commonly at depths of 37-91 m, and Pritchard (1928) said it was most abundant at a depth of 76 m, which he also gave as its spawning depth. Even the smallest female (203 mm) of the “representative” specimens enumerated by Koelz (1928) was mature. Spawning occurred from about 15 April-15 May (Pritchard 1928). The diet has gone unreported.



CISCOES OF LAKE NIPIGON

TAXONOMY

Bailey and Smith (1981) and Todd and Smith (1992) recognized four species of ciscoes from Lake Nipigon: *C. artedi*, *C. hoyi*, *C. nigripinnis*, and *C. zenithicus* (the listing of *C. reighardi* in Todd and Smith is a typesetting error). Koelz (1929) recognized an additional species and subspecies, *C. nipigon* and *C. reighardi dymondi*, and had considered *nigripinnis* a subspecies, *n. regalis*. Scott and Crossman (1998) synonymized *nipigon* with *artedi*, saying that *nipigon* was simply an *artedi* of exceptional size. Further, Todd and Smith (1980) synonymized *r. dymondi* with *zenithicus*, and Todd and Smith (1992) questioned the affinity of *regalis* with *C. n. nigripinnis*, leaving the status of *regalis* uncertain. More recently, Schmidt et al. (2011) found, based on fish archived by Koelz (1929), that *dymondi* was isotopically distinct from *zenithicus*. Turgeon and Bernatchez (1999), using microsatellite markers, reported that *zenithicus* was the most distinctive of the four forms, although they were not genetically differentiated. Moreover, these authors could not get correspondence between morphological traits and ecological traits. As an interim approach, until the taxonomy of Lake Nipigon ciscoes is better resolved, this publication assumes four forms, all extant, as per Todd and Smith (1992).

IDENTIFICATION OF FORMS

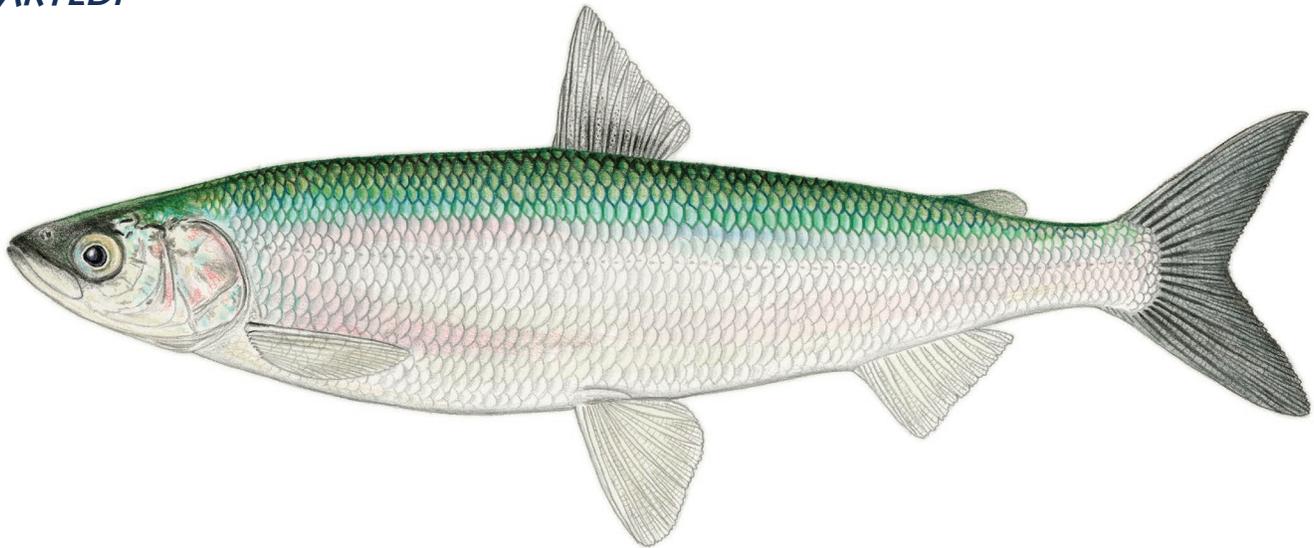
The dark pigmentation of *nigripinnis* and ovate body shape in side view define this form allowing for an initial separation into two groups: *nigripinnis* or non-*nigripinnis*. Non-*nigripinnis* should be assessed first by body shape. In side view, *hoyi* is terete (deeper), and the head is triangular, whereas *artedi* and *zenithicus* are subterete, with *zenithicus* being slightly more terete and both having elliptically shaped heads (Fig. 3). Larger *artedi* are deeper bodied (Dymond 1926) and may be confused with *zenithicus* based on body shape alone. Gill raker numbers are diagnostic for separating *artedi* from *zenithicus*. Mean gill raker number in contemporary *artedi* is 46.3 ± 2.1 and in *zenithicus* 37.5 ± 2.6 , although a few specimens of either form with aberrant counts were seen in recent collections (Appendix Table 16). The descriptions in the *Main Forms* section, illustrations, quick key, and other material in this section should be consulted for further identification.



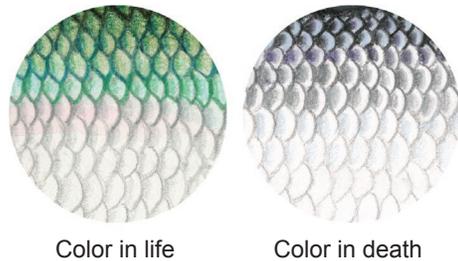
Ontario Ministry of Natural Resources and Forestry Research Craft Moored at MacDiarmid, Lake Nipigon

Image by AMM.

ARTEDI



Collected by AMM off Jackfish Island, 28 July 2013, GLFC specimen 102040, STL 175 mm.



Color in life

Color in death

Distinctive Taxonomic Traits

Maximum STL (standard length) reported by Koelz (1929) was relatively small (253 mm) compared to maximum STL in samples collected in 2008-2009 (345 mm; TCP, unpublished data). The absence of large *artedi* (≤ 400 mm) in recent collections raises the question of whether *nipigon*, having a maximum STL of 447 mm in 1922 samples, was a distinct form that is now rare or absent from Lake Nipigon. *Artedi* exceeding an STL of 400 mm should be saved and submitted to an expert (see *Collection and Preservation* section). Koelz (1929) distinguished *nipigon* from *artedi* mainly by size, but gill raker number was markedly different, too, with *nipigon* having >54 and *artedi* having <53 . Koelz (1929) recognized that larger members of a cisco population tend to have more gill rakers than smaller members, but he apparently thought the difference in *nipigon* was exceptional. The absence of any small *nipigon* with >54 rakers led Scott and Crossman (1998) to reject *nipigon*

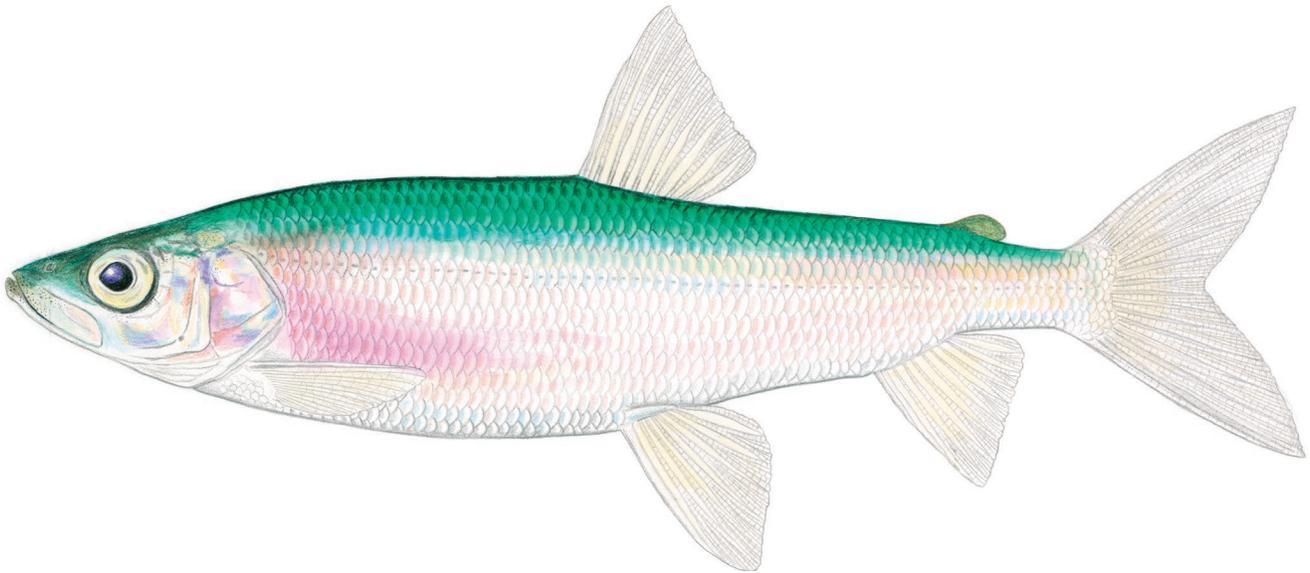
as a distinct form. In a comparison of nine body metrics, *artedi* of Lake Nipigon in 1922 (Appendix Tables 7A,B) differed notably from the composite typical *artedi* from across the Great Lakes (Appendix Tables 1A,B) in having a taller dorsal fin (STL/DOH, 5.8 ± 0.4 vs. 7.1 ± 0.7), longer pectoral fin (PVD/PCL, 1.7 ± 0.1 vs. 2.1 ± 0.2), and longer pelvic fin (PAD/PVL, 1.5 ± 0.1 vs. 1.7 ± 0.1 ; Appendix Tables 7A,B). In a comparison of eight metrics (excludes DOH and includes, for contemporary samples, corrected snout length, corrected maxillary length, and converted paired-fin lengths; see Morphometrics and Meristics subsection) between contemporary *artedi* (Appendix Table 18) and *artedi* collected by Koelz, two metrics, body depth and total gill rakers, differed, but only marginally, over this 90-year period. Contemporary *artedi* had a shallower body depth (STL/BDD, 4.6 ± 0.4 vs. 4.0 ± 0.4) and 1.5 fewer gill rakers (TGR, 46.3 ± 2.1 vs. 47.8 ± 2.2).

Local Ecological Characteristics

The CPUE of *artedi* in Lake Nipigon surveys declined 87% from 1998-1999 to 2008-2009 (TCP, unpublished data). The causes of such a severe decline are unclear, although the introduction of Rainbow Smelt in the early 1970s and *Bythotrephes longimanus* in 2001 may be involved. Both species could affect zooplankton availability for *artedi*, thus explaining the reduction in its body depth and the apparent loss of 1.5 gill rakers. During summer 1921-1923, *artedi* was not taken at depths greater than 27 m, and schools were observed on the lake's surface (Koelz 1929). Likewise, Dymond (1926) reported *artedi* uncommon at depths >30 m. Maximum otolith age in 2008-2009 was 26 years (TCP, unpublished data). Of 10 *artedi* detailed by Koelz (1929), neither the smallest

male (160-mm STL) nor the smallest female (222 mm) were designated as immature. Likewise, the smallest male (139 mm) sampled in 2008-2009 ($n = 121$) was mature as was the smallest female (156 mm; TCP, unpublished data). The time, bottom type, and location of spawning for *artedi* in Lake Nipigon have not been reported. Cladocerans and copepods were the main diet items in a 1997 study conducted in August (Turgeon et al. 1999). Stable isotopes indicated that, from 1922 through 2005, *artedi* maintained a distinct feeding niche among ciscoes characterized by a surprisingly high trophic position and a dependence on benthic as compared to pelagic carbon sources (Schmidt et al. 2011).

HOYI



Collected by J. Dymond from Orient Bay, 10 September 1923, Univ. Mich. Mus. Zool. specimen 54346, STL 205 mm.



Color in life



Color in death



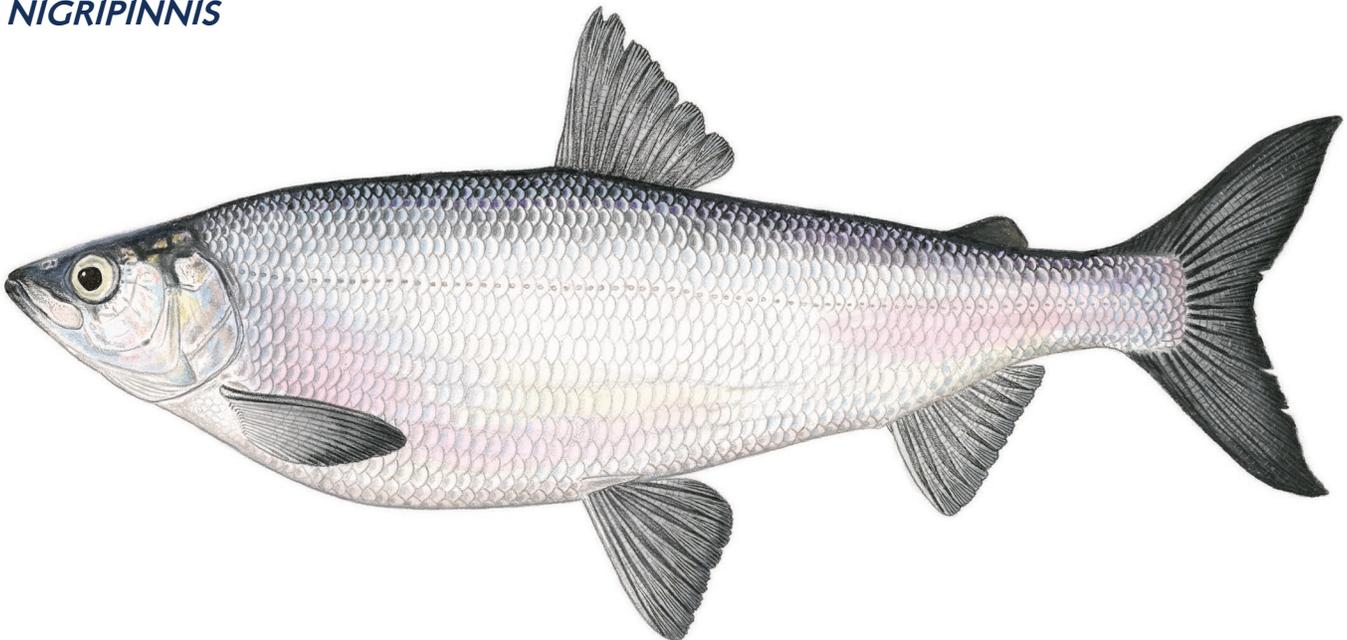
Distinctive Taxonomic Traits

Maximum STL (standard length), 327 mm, in 2008-2009 (TCP, unpublished data) was considerably larger than the 231 mm reported for 1922 by Koelz (1929). All nine body metrics for *hoyi* of 1922 (Appendix Tables 7A,B) were similar to those of the composite for the same period (Appendix Tables 1A,B), which is of interest in that the Lake Nipigon ciscoes are part of a distinct western microsatellite group, whereas the Great Lakes forms belong to an eastern group (Turgeon and Bernatchez 2001b). Of eight metrics (Appendix Table 18) that can be compared between 1922 and 2009-2012 (excludes dorsal height and includes, for contemporary samples, corrected snout length, corrected maxillary length, and converted paired-fin lengths; see Morphometrics and Meristics subsection), notable differences were found for three metrics: head length, orbital length, and pelvic length. In comparison to *hoyi* in 1922, contemporary *hoyi* had a shorter head (STL/HLL, 4.3 ± 0.2 vs. 3.9 ± 0.1), a smaller eye (HLL/OOL, 4.2 ± 0.3 vs. 3.7 ± 0.2), and a shorter pelvic fin (PAD/PVL, 1.6 ± 0.1 vs. 1.2 ± 0.1). The apparent reduction in length of the pelvic fin, but not the pectoral fin, is unexplained and is evident in all contemporary *hoyi* populations (see Morphometrics and Meristics subsection).

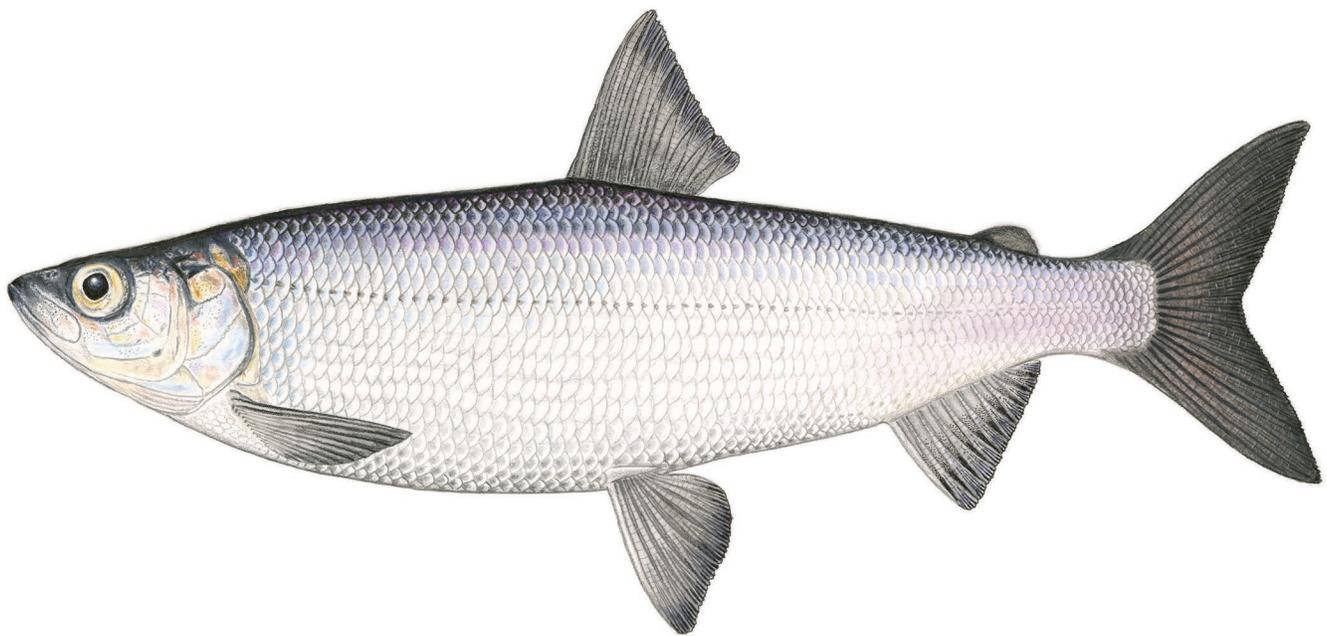
Local Ecological Characteristics

The CPUE of *hoyi* in Lake Nipigon surveys has declined 60% from 1998-1999 to 2008-2009 (TCP, unpublished data). During July-September 1921-1923, *hoyi* occupied a depth range of 27-100 m, and was more constrained thermally than the lake's other ciscoes (Dymond 1926). Maximum otolith age in 2008-2009 was 27 years (TCP, unpublished data). Of 10 *hoyi* tabulated individually by Koelz (1929), neither the smallest male (153-mm STL) nor the smallest female (164 mm) were designated as immature. The smallest male (206 mm) sampled in 2008-2009 ($n = 184$) was mature as was the smallest female (200 mm; TCP, unpublished data). *Hoyi* of a size likely to be immature have not been reported. The time, bottom type, and location of spawning in Lake Nipigon are unknown. In August 1997, *hoyi* consumed *M. diluviana* and *Diporeia* spp. almost exclusively (Turgeon et al. 1999). Its trophic position in Lake Nipigon placed *hoyi* midway among ciscoes in utilization of pelagic-based food sources (Schmidt et al. 2011).

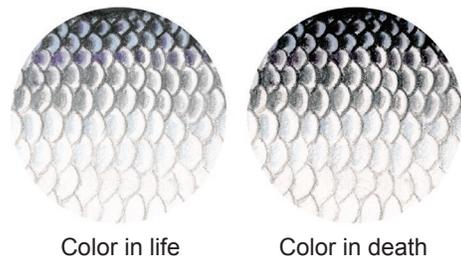
NIGRIPINNIS



Collected by AMM off Jackfish Island, 27 July 2013, GLFC specimen 102029, STL 339 mm.



Collected by AMM off Jackfish Island, 25 July 2013, GLFC specimen 102001, STL 323 mm.



Distinctive Taxonomic Traits

Maximum STL (standard length) in 2008-2009 (436 mm, $n = 341$; TCP, unpublished data) was greater than Koelz (1929) observed in 1922 (355 mm, $n = 230$), a change also seen in *artedi* and *hoi* (see above). Koelz (1929) believed that *nigripinnis* of Lake Nipigon was distinctive enough from *nigripinnis* of Lake Michigan (the species type) to warrant a subspecies classification. However, the nine metrics for *nigripinnis* of Lakes Huron and Michigan combined (Appendix Tables 1A,B) differ little from those for *nigripinnis* of Lake Nipigon (Appendix Tables 7A,B). Koelz (1929) used scale and scale-row counts in his classification of *nigripinnis regalis*, which are not considered here, and the appendix metrics are statistical estimates, whereas Koelz (1929) used a notation much less precise for assessing differences (see Navigating Koelz subsection). Of eight metrics (Appendix Table 18) comparable between 1922 and 2009-2012 (excludes dorsal height and includes, for contemporary samples, corrected snout length, corrected maxillary length, and converted paired-fin lengths; see

Morphometrics and Meristics subsection), only the length of the paired fins differ notably, both being shorter in contemporary samples (PPD/PCL, 1.9 ± 0.1 vs. 1.5 ± 0.1 ; PAD/PVL, 1.8 ± 0.1 vs. 1.4 ± 0.1). The apparent reduction in length of the pectoral fin is an outlier. All other such comparisons, regardless of lake and form, showed essentially no change in length of the pectoral fin between contemporary samples and those made by Koelz. A reduction in length of the pelvic fin, as seen in *nigripinnis* of Lake Nipigon, was observed across lakes in *hoi* (see Morphometrics and Meristics subsection). However, paired-fin lengths measured by Dymond (1926) were closer to the converted contemporary values (PPD/PCL = 1.7; PAD/PVL = 1.6). These numbers required transformation of ratios based on head length (Dymond assessed paired-fin length in relation to head length) to ratios based on standard length, which were then converted to ratios based on PPD and PAD, creating opportunities for amplification of rounding error. An assessment of paired-fin lengths in 1973, approximately



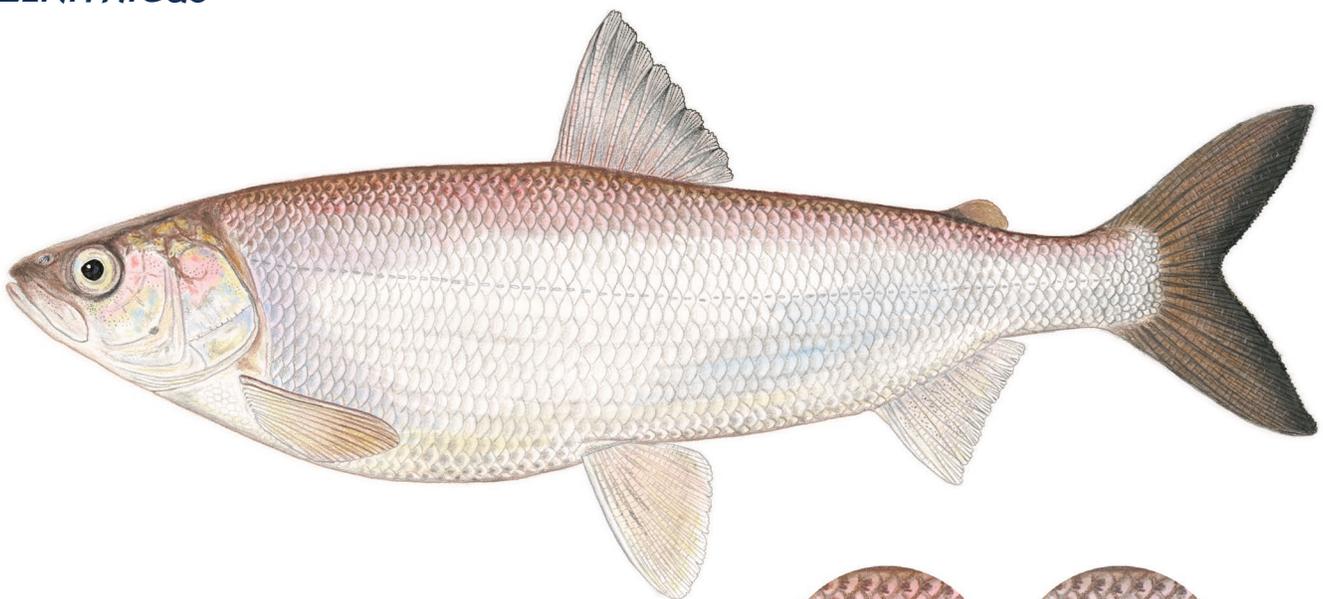
midway between the early and contemporary periods, indicated that neither pectoral fin length (PPD/PCL, 1.5 ± 0.1) nor pelvic fin length (PAD/PVL, 1.3 ± 0.2) had changed whatsoever from Koelz (T.N. Todd, retired, USGS, unpublished data). In aggregate, these data indicate that pectoral fin length is now only slightly shorter than in the past, but pelvic fin length underwent a substantial reduction after 1973.

Local Ecological Characteristics

The CPUE of *nigripinnis* in Lake Nipigon surveys declined 41% from 1998-1999 to 2008-2009 (TCP, unpublished data), a less-severe decline than witnessed for *artedi* and *hoyi* over the same time period. Dymond (1943) reported that *nigripinnis* occupied depths as great as ~100 m, more than any other species of fish in Lake Nipigon. *Nigripinnis*, however, was commonly found in shallow waters too, and was said by Dymond (1943) to have had an optimum summer depth of only 33-37 m, indicating a substantial behavioral divergence from *nigripinnis* of Lakes Michigan and Huron. Koelz (1929) recorded *nigripinnis* from the shallowest (~60 m) and deepest (102 m) depths sampled in Lake Nipigon with almost all surveys made during June-September. In a more-recent study of Lake Nipigon, Turgeon et al. (1999)

reported that *nigripinnis* (labeled as morph C) was rare in its deepest (>60 m) depth stratum, which was dominated by *hoyi*. This finding is consistent with Dymond (1943) in that the recent collections were made in August, a month when *nigripinnis* occupied shallow water. Maximum age in 2008-2009 was 27 years (TCP, unpublished data). The smallest male (174 mm) and female (249 mm) tabulated individually ($n = 10$) by Koelz (1929) were immature. In 2008-2009 collections ($n = 341$), the smallest male (202 mm) was mature, but the smallest female (156 mm) was immature (TCP, unpublished data). Koelz (1929) reported that as of October 26 no mature (ripe) sex organs were visible, implying to him winter spawning. The observed time, bottom type, and location of spawning in Lake Nipigon have gone unreported. The diet in August consisted of *Mysis diluviana* and copepods with *M. diluviana* dominant at depths <60 m (Turgeon et al. 1999). An abundance of *M. diluviana* in relatively shallow water in Lake Nipigon during August may account in part for the unusual depth preference of *nigripinnis* of Lake Nipigon as compared to *nigripinnis* of Lakes Michigan and Huron. Stable isotopes indicated that among the lake's ciscoes in the 1920s, *nigripinnis* occupied an intermediate trophic level while consuming somewhat more depleted (benthic) carbon sources (Schmidt et al. 2011).

ZENITHICUS



Collected by AMM off Jackfish Island, 25 July 2013, GLFC specimen 102000, STL 320 mm.

Color in life

Color in death

Distinctive Taxonomic Traits

Maximum STL (standard length) in 2008-2009 (342 mm; TCP, unpublished data) was similar to what Koelz (1929) observed in 1922 (332 mm). In comparisons of nine metrics, Lake Nipigon *zenithicus* in 1922 varied little from a composite from across the Great Lakes, except the Nipigon form had a longer head (STL/HLL, 3.9 ± 0.1 vs. 4.4 ± 0.2 ; Appendix Tables 1A,B and 7A,B). In a comparison of eight metrics (Appendix Table 18) between 2009-2012 and 1922 (excludes dorsal height and includes, for contemporary samples, corrected snout length, corrected maxillary length, and converted paired-fin lengths; see Morphometrics and Meristics subsection), three metrics were notably different. Contemporary *zenithicus* had a deeper body (STL/BDD, 3.9 ± 0.2 vs. 4.5 ± 0.4), a shorter head (STL/HLL, 4.3 ± 0.2 vs. 3.9 ± 0.1), and a smaller eye (HLL/OOL, 4.6 ± 0.3 vs. 4.2 ± 0.2). Head length now more closely resembles that of the composite.

Local Ecological Characteristics

The CPUE of *zenithicus* in Lake Nipigon surveys declined 73% from 1998-1999 to 2008-2009 (TCP, unpublished data), a decrease almost as severe as that observed for *artedi*, which, among the lake's ciscoes, suffered the largest decline over that period. Dymond (1926) reported that *zenithicus* occupied deep waters, sometimes as deep as 91 m. Koelz (1929), referring to collections archived at the University of Toronto by Dymond, stated that most specimens came from depths <55 m. More-recent surveys in summer show that *zenithicus* occupies depths mainly <30 m but is also prominent at 30-55 m (Turgeon et al. 1999). Maximum otolith age in recent collections was 27 years (TCP, unpublished data). Of 10 specimens <200 mm tabulated individually by Koelz (1929), the only immature male was 161 mm and all five females, the largest being 186 mm, were immature. All specimens in a collection made in 2008-2009 ($n = 109$) were mature; the smallest was 215 mm (TCP, unpublished data). Based on only a few specimens, Koelz (1929) thought that spawning occurred around the first of November. Bottom type and location of spawning are unknown. *M. diluviana* was dominant in the diet even at depths <30 m (Turgeon et al. 1999). Stable isotope analysis indicated that, compared to other ciscoes in Lake Nipigon, *zenithicus* fed at a lower trophic level, but its prey originated more from the pelagic food web (Schmidt et al. 2011).



EPILOGUE

Three topics involving more than one lake were reserved for this section as follows: discrimination of *zenithicus* from *alpenae*, the *reighardi* paradox, and temporal variations in morphology. The first two of these topics, synonymizing *alpenae* and the *reighardi* paradox, are based on an examination by AMM and RLE of *zenithicus* ($n = 18$) and *alpenae* ($n = 15$) collected by Koelz from northern Lake Huron's main basin off the ports of Cheboygan and Alpena during 1917-1923 and archived at the University of Michigan Museum of Zoology (UMMZ). The objective of this examination was to better determine how Koelz and Stanford Smith separated these two forms. Koelz (1929) identified four characteristics for differentiating the two forms: jaw position, *alpenae* having an extended jaw and *zenithicus* having an included jaw; pigmentation on the tip of the mandible and upper jaw; depth of head and body; and maximum size attained (Smith likely used the same features). In Lake Huron, head-length-to-mandible-length ratios (HLL/MBD) from Koelz (1929) were similar for *zenithicus* (2.1 ± 0.1) and *alpenae* (1.9 ± 0.1 ; see his Tables 23, 31). Even more perplexing, Smith's ratios for Lake Huron (raw data not given here) were identical (2.0 ± 0.1). Yet, 67% of museum specimens identified as *alpenae* had an extended mandible and 89% of specimens identified as *zenithicus* had an included jaw. As regards pigmentation, the flesh over the maxillary bone of *alpenae* was consistently unpigmented, whereas *zenithicus* was most-often pigmented, consistent with the description by Koelz (1929). Close examination of these forms side by side revealed that the mouth of *alpenae* opened upward (superior) as if for feeding above the body plane, whereas the mouth of *zenithicus* opened straight ahead (inferior) as if for feeding in the plane of the body (Fig. 10). Koelz and Smith may have taken this anatomical difference into account without realizing it. The difference is depicted but not flagged in an illustration (Chart 1) in Hubbs and Lagler (1958), which was contributed by Stanford Smith. The differences in orientation of the mouth explain how such small differences in jaw lengths could have been diagnostic. A superior orientation of the mouth makes a mandible of a given length more likely to extend past the premaxillaries, whereas a mandible of the same length in an inferior mouth is more likely to be included.

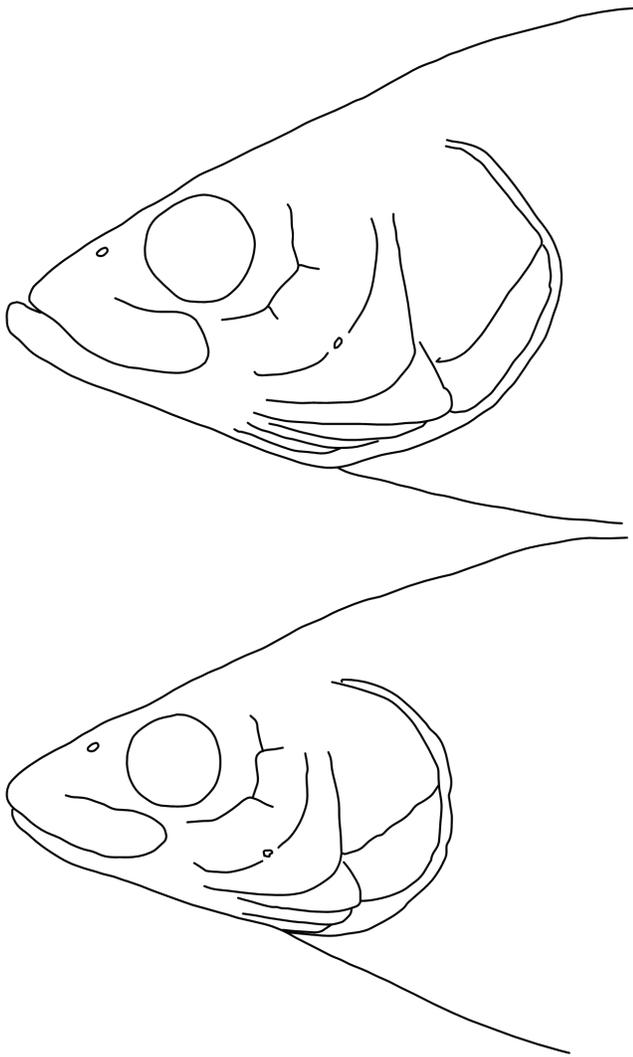
As noted in the *Lake Accounts* section, Ciscoes of Lake Huron subsection, Taxonomy subsection, Koelz (1929) did not recognize *reighardi* from Lake Huron but, surprisingly, Stanford Smith in 1956 found this form plentiful—this is the *reighardi* paradox. Based on the above examination of *zenithicus* specimens archived at the UMMZ, Smith and

Koelz appear to have been using different snout criteria when distinguishing between *zenithicus* and *reighardi*. These specimens had unusually blunt snouts reminiscent of *reighardi*. In fact, some of these specimens had premaxillary angles (see Morphometrics and Meristics subsection) much greater than the 60-70° noted by Koelz as being typical for Lake Michigan *reighardi* (e.g., see *zenithicus* head illustration in Fig. 10). Apparently, Smith named *reighardi* what Koelz would have named *zenithicus*. In identifying Lake Huron *zenithicus*, Koelz and Smith may have been influenced by other features that to them overruled a *reighardi* classification. What these features were is conjectural. Both recorded essentially only one of these two forms from Lake Huron. Although Smith did collect four *zenithicus*, this small sample size precludes an accurate comparison of his *zenithicus* with his *reighardi* (Appendix Table 10). Smith's extensive collection of ciscoes lack UMMZ accession numbers making retrieval of his specimens arduous.

The *Lake Accounts* section documents 22 instances overall where a notable difference (≥ 2 SD for ratios and ≥ 1 SD for gill rakers; see *Morphology of Ciscoes* section, Temporal Differences in Body Metrics subsection) in the value of a morphometric or meristic trait was observed between when contemporary and Koelz's samples were collected. Notable differences occurred in 23% of the comparisons, but these were not distributed evenly across lakes or forms (Table 6). Comparisons among lakes are constrained by the differences in the diversity of extant forms owing to extirpations or extinctions or both. Lakes Superior and Nipigon now have by far the greatest diversity; each has four forms, three of which are the same (Table 2), making for the best comparison. Only three notable differences were tallied among Lake Superior forms, whereas eight were tallied for Nipigon forms, a finding that seems counterintuitive in that Lake Nipigon is considered less disturbed than Lake Superior (see *Lake Accounts* section). One explanation for this anomaly is that the much-larger size of Lake Superior (47 times larger by volume) makes its fauna more resistant to perturbation.

As regards differences among forms, *artedi* accounted for half of the notable differences. It is more widespread than any of the other forms so would be expected to accumulate more differences across lakes. When the number of notable differences is expressed as a rate (differences per form), *artedi*, *hoyi*, and *zenithicus* were similar (0.23, 0.25, and 0.19, respectively). That said, this comparison reflects mainly the high number of notable

Fig. 10. Illustrations of the heads of *alpenae* (top) and *zenithicus* traced from images of specimens collected by W. Koelz from the main basin of northern Lake Huron in 1919 and 1917, respectively; University of Michigan Museum of Zoology accession numbers 54717 and 52746 .



differences in *hoi* and *zenithicus* of Lake Nipigon, which again indicates a negative effect of lake size on morphotypic stability. Based on the method used here to assess temporal change in morphotype, *zenithicus* of Lake Superior was deemed stable morphologically, but the head profiles of *zenithicus* and *r. dymondi* are not as distinctive now as they were at the time Koelz sampled (see *Lake Accounts* section, Ciscoes of Lake Superior subsection, Identification of Extant Forms subsection). Moreover, Smith found that *r. dymondi* had 4.9 more gill rakers than reported by Koelz, indicating morphological instability and convergence in *zenithicus* and *r. dymondi* by 1959-1961 (Appendix Tables 2B and 8). These results suggest that relatively modest shifts in the diversity of ciscoes, including

a decline in *zenithicus* abundance that was evident by the 1950s (Gorman 2012), were accompanied by greatly reduced expression of the *dymondi* and *cyanopterus* phenotypes, or, if these forms were not polyphenic, by their diminishment. At the same time, a previously, apparently unrecognized form, labeled here “*nigripinnis* unnamed,” appeared (see Identification of Extant Forms above).

Given the above, the high number of notable body-metric differences in contemporary *albus*-like forms of Lakes Michigan and Huron as compared to historical *artedi* from these same lakes invites further analysis. Together they accounted for ten of the eleven notable differences in *artedi*. Otherwise, *artedi* appears to have been a relatively stable form except for a decline in gill raker number in Lake Superior. The temporal differences in morphology in *artedi* in Lakes Michigan and Huron may not reflect recent divergence. The *artedi* sampled by Koelz (1929) from Lake Michigan and from Lake Huron’s main basin came from all sectors, including offshore areas (see his Figs. 4, 5). *Artedi* in Lake Michigan and the main basin of Lake Huron was dominated by single spawning populations (Van Oosten et al. 1946; Hile et al. 1953; Smith 1956), now extirpated. Koelz (1929) typically did not obtain *artedi* samples from spawning aggregations except in Green and Saginaw Bays (see his Tables 2, 3), which suggests his metrics describe fish that originated from (or were in) Green and Saginaw Bays. That so, the morphological differentiation evident now between the contemporary samples, which came from the East Arm of Grand Traverse Bay (Lake Michigan) and the outer Les Cheneaux Islands (Lake Huron), and those of Koelz may be long established. Joukhadar et al. (2002), using oxygen isotopes, showed that contemporary *artedi* from the St. Marys River (Lake Nicolet) inhabited warmer water than did museum-archived *artedi* collected by Koelz off the main basin ports of Cheboygan and Alpena, indicating population structure in northern waters. These insights and the minor amount of morphological change observed in *artedi* of Lakes Superior and Ontario favor the hypothesis that the morphological differentiation between contemporary *albus* of Lakes Michigan and Huron and *artedi* collected by Koelz from these same lakes occurred long ago.

Table 6. Tally of cisco body metrics by (a) lake and form and (b) form only that differed notably (≥ 2 SD for ratios and ≥ 1 SD for gill rakers) from when Koelz collected (1917-1924; Appendix Tables 1-7) to when contemporary samples were collected (2003-2015; Appendix Tables 13-18). The values of the metrics are given in the *Lake Accounts* section. STL = standard length, BDD = body depth, HLL = head length, POL = preorbital length, OOL = orbital length, MXL = maxillary length, PCL = pectoral fin length, PVL = pelvic fin length, and TGR = total gill rakers (see Fig. 5). Contemporary dorsal fin height not included owing to incomplete records.

(a)

Lake/Form	Morphometrics and Meristics							TGR	Total
	STL/ BDD	STL/ HLL	HLL/ POL	HLL/ OOL	STL/ MXL	STL/ PCL	STL/ PVL		
Superior									
<i>artedi</i>								x	1
<i>hoyi</i>				x			x		2
<i>kiyi</i>									0
<i>zenithicus</i>									0
Michigan									
<i>artedi</i>		x	x		x	x	x	x	6
<i>hoyi</i>							x		1
Huron									
<i>artedi</i>	x	x	x					x	4
Ontario									
<i>artedi</i>									0
Nipigon									
<i>artedi</i>									0
<i>hoyi</i>		x		x			x		3
<i>nigripinnis</i>						x	x		2
<i>zenithicus</i>	x	x		x					3

(b)

Form	Morphometrics and Meristics							TGR	Total
	STL/ BDD	STL/ HLL	HLL/ POL	HLL/ OOL	STL/ MXL	STL/ PCL	STL/ PVL		
<i>artedi</i>	1	2	2	0	1	1	1	3	11
<i>hoyi</i>	0	1	0	2	0	0	3	0	6
<i>kiyi</i>	0	0	0	0	0	0	0	0	0
<i>nigripinnis</i>	0	0	0	0	0	1	1	0	2
<i>zenithicus</i>	1	1	0	1	0	0	0	0	3

GLOSSARY

allopatric	Populations or taxa whose ranges do not overlap; geographically separated (Coad and McAllister 2015).
benthic	Bottom dwelling; pertaining to the sea, lake, or riverbed (Coad and McAllister 2015).
conspecific	Belonging to the same species (Coad and McAllister 2015).
extended jaw	Lower jaw extends beyond the upper jaw (Coad and McAllister 2015).
gill raker	One of a series of variously shaped bony or cartilaginous projections on the inner side of the branchial arch (Coad and McAllister 2015).
hybrid swarm	Population of hybrids that has survived beyond the initial hybrid generation with interbreeding between hybrid individuals and backcrossing with parental types.
included jaw	Lower jaw shorter than upper jaw (also contained within upper jaw; Coad and McAllister 2015).
interspecific	Between two or more species (Coad and McAllister 2015).
intraspecific	Within a species (Coad and McAllister 2015).
introgressed	Progeny resulting from crosses between hybrids with their parental type(s).
immaculate	Lacking pigmentation and appearing white or translucent in fresh specimens.
meristics	Pertaining to serially repeated structures (e.g., scales, fin rays, and other structures) that can be counted but here limited to gill rakers. The study and comparison of body-part counts (Coad and McAllister 2015).
morphology	Appearance, form, and structure of an organism, especially based on external characters (Coad and McAllister 2015).
morphometrics	Measurement of a body part (e.g., head length). More broadly, the study and comparison of body-part measurements (Coad and McAllister 2015).
occiput	Back end of the top of the head marked by a line separating scaly and scaleless portions of skin (Coad and McAllister 2015).
ontogenetic	Adjective for ontogeny. Ontogeny is the development from embryo to adult (Coad and McAllister 2015).
operculum	Principal and largest paired dermal bone comprising the upper part of the gill cover above the suboperculum (also called opercle) (Coad and McAllister 2015).
ovate	Having an egg-shaped lateral profile.
paired fins	Collectively referring to the pectoral and pelvic fins.
pelagic	Waters occurring above the bottom; non-benthic (Coad and McAllister 2015).
phenotypic plasticity	Environmentally induced variation in morphology, physiology, or behavior within a genotype.
polyphenism	An extreme form of phenotypic plasticity in which two or more distinctively different adaptive phenotypes arise from the same individual.
race	Colloquial term for a distinctive population.
subterete	In profile, a gently tapering elliptical shape dorsally and ventrally, ideally with the dorsal and ventral halves being mirror images (see terete below).
sympatric	Sharing, at least in part, the same geographical range (Coad and McAllister 2015).
symphyseal knob	Swelling on the tip of the lower jaw (Coad and McAllister 2015).
terminal jaw	Tips of upper and lower jaws meet.
terete	In profile, a more rapidly tapering elliptical shape dorsally and ventrally, typically with the ventral half somewhat distorted posteriorly by a flatter midsection (see subterete above).
zooplanktivore	Animal that feeds on zooplankton.



Salting Down the Catch

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APPENDIX: MORPHOMETRIC AND MERISTIC DATA

NAVIGATING KOELZ

Koelz's (1929) monograph, totaling 349 pages, was a monumental work on the coregonines of the Great Lakes, especially of the ciscoes, and remains the foremost repository of information on this taxonomically challenging group of fishes. By necessity, much of the material in this publication owes to Koelz—for some forms of cisco he is the original source.

Accordingly, we anticipate and encourage those using this publication to refer to Coregonid Fishes of the Great Lakes for more-complete descriptions of the forms than we are able to provide here (http://docs.lib.noaa.gov/rescue/Fish_Commission_Bulletins/BFC1927-v43-pt2.PDF [begins PDF page 338/document page 297]). Here we discuss those of his methods and conventions that may be unfamiliar or confusing to the casual reader.

CHUB/CHUBS

Use of the words chub/chubs in Koelz can be confusing. *Coregonus hoyi* and *C. kiyi*, because of their small size, were not considered “chubs” in the commercial sense. At the same time, chub was the common name for *C. johanna*. In particular, in his chapters on *johanna*, Koelz referred only to this form in his use of chubs/the chub, e.g., “Out of the 174 chubs examined...”

COLLECTING GEAR

Koelz collected all of his ciscoes from commercial fishing boats using commercial nets fished on the lakebed. Most were taken in gillnets of 2.50-2.75-inch (63.5-69.9-mm) stretch mesh. Larger ciscoes also were taken in 3.25-inch (82.6-mm) gillnets and in 4.0-4.5-inch (101.6-114.3-mm) gillnets fished for Lake Whitefish and Lake Trout. Occasionally, a 1.5-inch (38.1-mm) gillnet (Koelz's bait net) was fished for small-bodied forms and for juveniles of larger forms, and a few specimens were taken in shallow water from pound nets. The locations, dates, and collecting gear of Koelz's collections are given in tables, but summary data are composites based on multiple collections often spanning a whole lake. Koelz typically provided extensive data for a “representative” (non-random) sample of 10 large (>200 mm) and, when

available, 10 small (<200 mm) ciscoes for each form and lake. These fish are identified with particular collections and have University of Michigan Museum of Zoology collection numbers that can be searched in the Fish Division archive: http://fms02.lsa.umich.edu/fmi/webd/ummz_fish.

SUMMARY STATISTICS

Koelz needed to discuss the frequency distributions of the many measurements and ratios that he presented, but, at that time, conventional statistics were not in wide use. He resolved this problem by using a notational framework in use at the time. With this method the extremes are placed in parentheses at the beginning and end of the expression while values denoting the extremes of the middle two-thirds (estimated by eye) are placed in the middle and separated by a dash—hence, they were described as “roughly two-thirds.” An example of this notation for a gill raker count for *johanna* of Lake Michigan follows: 10 + 19 [(9) 10-12 (14) + (16) 17-20 (22)] = (25) 27-32 (36). In this example, the medial values for the upper and lower arches are 10 and 19 (medial values used only for gill rakers), respectively, which added together are seen to fall near the middle of the central two-thirds of the combined distribution (27-32). Note further that the lower extremes for the upper and lower arches are (9) and (16), respectively, which together equal the lower extreme (25) for the entire arch. This notation, especially for gill rakers, is so difficult that the preceding example contained an error. We do not use this notation.

Koelz's text descriptions of counts for scales of the lateral line and scale rows remain partly unexplained. For example, for *johanna* of Lake Michigan, he described the frequency distribution of the number of scales in the lateral line as 82 [(74) 80-90 (95)]. Referring to his Table 7, the extremes of this distribution are 74 and 95 and roughly two-thirds of his 74 samples had 80-90 lateral-line scales (actually these counts were those having a frequency of three or more), so the notation between the brackets is clear. The problem is determining what the number preceding the brackets, in this example, 82, represents; the midpoint of the frequency is 84, the

median is 84, and means would typically not be whole numbers. We advise ignoring the number preceding the brackets in Koelz's text descriptions of lateral-line scales. Instead, we direct the reader interested in this metric to use the modal groups for comparisons. This publication does not incorporate counts of lateral-line scales as their power to discriminate among forms is marginal. Most of the counts between forms differ by less than one SD. Koelz did not provide tabled data for scale rows, and this publication does not use this characteristic.

MEASUREMENTS AND RATIOS

Koelz used standard length throughout, but confusion may arise in that this term was not then in wide use. He referred to "length" and "total length" interchangeably, but defined length unambiguously as the distance from the junction of the premaxillaries to the end of the last vertebra. This publication also uses standard length exclusively, which necessitated conversion from total and fork lengths for all forms as follows: $SL = 0.8677 TL$ and $0.9146 FL$ (Pratt and Chong 2012). Ratios involving body length from Scott and Crossman (1998), which are based on total length, need to be divided by 0.867 for comparison with ratios in Koelz (1929) or in this publication. Ratios involving the paired fins in Scott and Crossman (1998), Appendix Tables 8-12 (Stanford Smith data), and Appendix Tables 13-18 (contemporary data) cannot be compared directly to those of Koelz without conversion (see Morphometrics and Meristics subsection; Table 4). Likewise, snout and maxillary measurements in Koelz are point to point measured on a diagonal, whereas contemporary fish were measured on a horizontal, making them shorter and requiring correction for comparisons with Koelz and Smith (see Morphometrics and Meristics subsection; Table 4).

NOTES

Appendix Tables 1A-7B are based on statistical treatments of Koelz's (1929) data. The "A" tables comprise five metrics calculated from his frequency distributions (his Tables 6 and 8-11), which combined "large" and "small" fish, except for the forms of *C. artedi* (typical *artedi*, *albus*, and *manitoulinus*). The forms of *artedi* in contrast are based on "representative" (smaller) samples selected by Koelz for more expansive

treatment. Lumping small and large fish together likely biases gill raker counts and ratios involving the length of the head. The "B" tables comprise four metrics based entirely on Koelz's representative fish with large and small fish combined. Two rows of values are given for *nigripinnis* and *reighardi* in Appendix Tables 1A,B. Those rows identified as "all" include samples from lakes where each species was subsequently synonymized with *zenithicus*. Therefore, the "all" data (Appendix Tables 1A,B) are as Koelz saw these species. The second row of values for *nigripinnis* and *reighardi* comprise just those lakes identified in footnotes. The *zenithicus* data in Tables 1-7 do not include samples of synonymized fish (*C. alpenae*, *C. nigripinnis cyanopterus*, and *C. reighardi dymondi*). Were they included, they would contribute twice to the tables.

Appendix Tables 8-12 were compiled from data archived at the Great Lakes Science Center, having been collected during 1950-1972 under what was called the Great Lakes Cisco Project. The collections were made mostly from the R/Vs *Cisco* and *Kaho* under the direction of Stanford Smith, except that the 1950 collection from Lake Michigan was of commercially caught fish from northern Wisconsin. For the most part, Smith employed Koelz's methodology. Koelz (1929), however, computed paired-fin-length ratios based on the distance between the insertion of the pectoral and pelvic fins or the insertion of the pelvic and anal fins (see Morphometrics and Meristics subsection), whereas Smith measured these so-called bases on only a few specimens. Therefore, to make comparisons of paired-fin lengths, Smith's STL/PCL and STL/PVL must first be converted to PPD/PCL and PAD/PVL (see Morphometrics and Meristics subsection; Table 4). Also, Smith typically did not measure body depth; thus, the tables based on Koelz's collections contain one more metric than those based on Smith.

Appendix Tables 13-18, featuring contemporary data, were produced from ciscoes collected during 2003-2015 by various authors of this publication as noted in the captions and by their collaborators as noted in the acknowledgements. These tables contain the same eight metrics as in the Stanford Smith tables except that dorsal fin height was recorded only for Lakes Superior and Ontario. The ratios concerning paired-fin length are directly comparable to those in Appendix Tables 8-12 but not Appendix Tables 1A-7B.



Fishing the North Shore, ca. 1940

Gallagher Studio (courtesy of the Minnesota Historical Society).

TABULAR DATA

WALTER KOELZ TABULAR DATA

Table IA. All Lakes—Head, Orbit, Paired Fins, Gill Rakers

Mean (\bar{x}), standard deviation (SD), and range of four morphological and one meristic characteristic (gill rakers) for 10 forms of cisco combined from across the Great Lakes and Lake Nipigon (see Notes subsection) based on “representative” specimens (typical *artedi*, *albus*, and *manitoulinus*) or frequency distributions (all other forms) in Koelz (1929) (see Appendix Tables 2-7 for collection years). STL = standard length, HLL = head length, OOL = orbital length, PPD = Pectoral-pelvic distance, PCL = pectoral fin length, PAD = pelvic-anal distance, PVL = pelvic fin length, and TGR = total gill rakers; *n* is sample size for TGR only; refer to Koelz (1929) for sample sizes of other characteristics.

Form	STL/HLL			HLL/OOL		PPD/PCL		PAD/PVL		TGR	
	<i>n</i>	$\bar{x} \pm SD$	Range	$\bar{x} \pm SD$	Range						
<i>alpenae</i>	770	4.1 ± 0.2	3.4-4.6	4.3 ± 0.3	3.6-5.2	2.0 ± 0.2	1.6-2.5	1.5 ± 0.2	1.1-1.9	38.2 ± 3.0	31-46
<i>artedi</i> (all)	1516	4.4 ± 0.2	3.7-5.2	4.1 ± 0.3	3.4-5.2	2.0 ± 0.2	1.4-2.8	1.6 ± 0.2	1.1-2.3	47.4 ± 2.5	38-55
typical	115	4.4 ± 0.2	4.0-5.2	4.1 ± 0.2	3.4-4.7	2.1 ± 0.2	1.5-2.5	1.7 ± 0.1	1.4-2.1	47.6 ± 2.5	43-53
<i>albus</i>	44	4.4 ± 0.2	4.1-4.7	4.3 ± 0.3	3.6-4.9	2.0 ± 0.2	1.7-2.4	1.6 ± 0.2	1.3-2.0	46.8 ± 2.0	43-53
<i>manitoulinus</i>	10	4.1 ± 0.1	4.0-4.3	3.4 ± 0.1	3.4-3.8	1.7 ± 0.1	1.6-1.8	1.4 ± 0.2	1.1-1.6	45.7 ± 1.3	43-47
<i>hoyi</i>	2,706	4.0 ± 0.2	3.4-4.6	3.8 ± 0.2	3.1-4.7	1.8 ± 0.2	1.2-2.2	1.3 ± 0.1	0.9-1.7	42.4 ± 2.1	37-50
<i>johannae</i>	563	3.9 ± 0.2	3.4-4.4	4.4 ± 0.3	3.6-5.3	1.7 ± 0.2	1.2-2.1	1.3 ± 0.1	0.8-1.6	29.3 ± 1.8	25-36
<i>kiyi</i>	621	3.9 ± 0.2	3.5-4.4	3.9 ± 0.2	3.3-4.4	1.6 ± 0.2	1.1-2.2	1.2 ± 0.1	0.9-1.6	39.7 ± 3.0	34-48
<i>nigripinnis</i> (all)	547	4.1 ± 0.2	3.6-4.7	4.1 ± 0.3	3.2-5.2	1.6 ± 0.2	1.2-2.2	1.4 ± 0.1	1.0-1.7	46.1 ± 4.3	36-54
<i>nigripinnis</i> ¹	182	4.1 ± 0.2	3.7-4.7	4.1 ± 0.3	3.6-4.6	1.6 ± 0.2	1.2-2.2	1.3 ± 0.1	1.0-1.6	47.1 ± 2.4	40-52
<i>reighardi</i> (all)	813	4.2 ± 0.3	3.5-5.0	4.0 ± 0.2	3.5-5.0	2.1 ± 0.3	1.4-2.9	1.5 ± 0.1	1.1-2.1	36.0 ± 2.0	30-43
<i>reighardi</i> ²	482	4.3 ± 0.2	3.9-5.0	4.0 ± 0.2	3.5-5.0	2.2 ± 0.2	1.5-2.9	1.5 ± 0.1	1.2-2.1	36.2 ± 2.1	30-43
<i>zenithicus</i> ³	1,322	4.0 ± 0.2	3.5-4.5	4.3 ± 0.3	3.5-5.2	1.8 ± 0.2	1.3-2.6	1.4 ± 0.1	1.0-2.0	39.5 ± 2.3	32-46

¹Lakes Michigan and Huron; ²Lakes Michigan and Ontario; ³Lakes Superior, Michigan, Huron, and Nipigon.

Table IB. All Lakes—Body Depth, Snout, Maxillary, Dorsal Fin

Mean (\bar{x}), standard deviation (SD), and range of three morphological and one meristic characteristic (gill rakers) for 10 forms of cisco combined from across the Great Lakes and Lake Nipigon (see Notes subsection) based on “representative” specimens selected by Koelz (1929). STL = standard length, BDD = body depth, HLL = head length, POL = preorbital length, MXL = maxillary length, and DOH = dorsal fin height; n = sample size.

Form	STL/BDD			HLL/POL		HLL/MXL		STL/DOH	
	n	$\bar{x} \pm SD$	Range						
<i>alpenae</i>	39	4.3 ± 0.4	3.5-5.1	3.6 ± 0.2	3.0-4.0	2.5 ± 0.1	2.3-2.7	6.7 ± 0.5	6.1-7.8
<i>artedi</i> (typical)	115	4.4 ± 0.4	3.6-5.4	4.1 ± 0.2	3.4-4.7	2.8 ± 0.1	2.5-3.2	7.1 ± 0.7	5.8-8.9
<i>albus</i>	44	3.6 ± 0.3	2.8-4.2	4.0 ± 0.2	3.7-4.5	2.8 ± 0.1	2.5-3.1	6.3 ± 0.5	5.3-7.7
<i>manitoulinus</i>	10	3.6 ± 0.2	3.4-4.0	3.9 ± 0.2	3.7-4.2	2.7 ± 0.1	2.5-2.8	5.7 ± 0.8	4.9-7.7
<i>hoi</i>	55	4.1 ± 0.3	3.6-4.8	3.8 ± 0.2	3.4-4.3	2.5 ± 0.1	2.2-2.8	5.7 ± 0.5	4.7-6.8
<i>johannae</i>	30	4.1 ± 0.4	3.6-4.9	3.5 ± 0.1	3.3-3.8	2.6 ± 0.1	2.4-2.8	6.1 ± 0.5	4.4-7.2
<i>kïyi</i>	40	3.9 ± 0.4	3.1-5.3	3.6 ± 0.2	3.3-4.1	2.5 ± 0.1	2.3-2.7	5.6 ± 0.4	4.9-6.4
<i>nigripinnis</i> (all)	43	3.8 ± 0.3	3.1-4.6	3.7 ± 0.2	3.5-4.1	2.6 ± 0.1	2.4-2.7	5.9 ± 0.4	4.9-6.9
<i>nigripinnis</i> ¹	21	3.8 ± 0.3	3.4-4.2	3.7 ± 0.1	3.5-4.1	2.6 ± 0.1	2.4-2.7	5.9 ± 0.3	5.5-6.9
<i>reighardi</i> (all)	58	4.1 ± 0.3	3.7-4.8	3.7 ± 0.2	3.4-4.3	2.6 ± 0.2	2.3-2.9	6.5 ± 0.7	5.2-8.0
<i>reighardi</i> ²	30	4.3 ± 0.3	3.7-4.7	3.8 ± 0.2	3.4-4.3	2.7 ± 0.1	2.5-2.9	7.0 ± 0.4	5.7-8.0
<i>zenithicus</i> ³	77	4.4 ± 0.4	3.5-5.3	3.5 ± 0.1	3.2-4.0	2.5 ± 0.1	2.3-2.8	6.4 ± 0.6	5.2-7.9

¹Lakes Michigan and Huron; ²Lakes Michigan and Ontario; ³Lakes Superior, Michigan, Huron, and Nipigon.

Table 2A. Lake Superior—Head, Orbit, Paired Fins, Gill Rakers

Mean (\bar{x}), standard deviation (SD), and range of four morphological and one meristic characteristic (gill rakers) based on “representative” specimens (*albus* only) or frequency distributions (all others) for seven forms of cisco compiled by Koelz (1929) from Lake Superior, 1917-1925. STL = standard length, HLL = head length, OOL = orbital length, PPD = Pectoral-pelvic distance, PCL = pectoral fin length, PAD = pelvic-anal distance, PVL = pelvic fin length, and TGR = total gill rakers; n = sample size for TGN; sample sizes for other characteristics vary slightly from TGR, except for *albus*.

Form	STL/HLL			HLL/OOL		PPD/PCL		PAD/PVL		TGR	
	n	$\bar{x} \pm \text{SD}$	Range	$\bar{x} \pm \text{SD}$	Range						
<i>artedi</i> (typical)	248	4.5 ± 0.2	4.0-5.1	4.2 ± 0.3	3.4-5.1	2.1 ± 0.2	1.6-2.8	1.7 ± 0.1	1.3-2.3	46.9 ± 2.2	38-53
<i>albus</i>	4	4.3 ± 0.1	4.1-4.4	3.8 ± 0.1	3.6-3.9	1.9 ± 0.1	1.8-2.0	1.6 ± 0.0	1.6-1.6	49.8 ± 2.4	48-53
<i>hoyi</i>	333	3.9 ± 0.2	3.4-4.3	3.7 ± 0.2	3.2-4.3	1.7 ± 0.2	1.4-2.2	1.2 ± 0.1	0.9-1.6	42.1 ± 1.9	37-49
<i>kiyi</i>	78	3.8 ± 0.1	3.5-4.1	3.7 ± 0.1	3.4-4.1	1.4 ± 0.1	1.1-1.7	1.1 ± 0.1	0.9-1.4	39.6 ± 1.9	36-45
<i>nigripinnis</i>	162	4.1 ± 0.1	3.7-4.4	4.5 ± 0.2	4.0-5.2	1.7 ± 0.1	1.4-2.2	1.4 ± 0.1	1.1-1.7	40.4 ± 1.9	36-48
<i>reighardi</i>	233	4.0 ± 0.1	3.7-4.4	4.1 ± 0.2	3.6-5.0	1.9 ± 0.2	1.5-2.4	1.5 ± 0.1	1.2-1.9	36.2 ± 1.9	32-42
<i>zenithicus</i>	956	3.9 ± 0.1	3.5-4.4	4.3 ± 0.3	3.6-5.1	1.8 ± 0.2	1.3-2.4	1.4 ± 0.1	1.0-1.9	40.2 ± 2.1	32-46

Table 2B. Lake Superior—Body Depth, Snout, Maxillary, Dorsal Fin

Mean (\bar{x}), standard deviation (SD), and range of four morphological characteristics based on “representative” specimens for seven forms of cisco compiled by Koelz (1929) from Lake Superior, 1917-1925. STL = standard length, BDD = body depth, HLL = head length, POL = preorbital length, MXL = maxillary length, and DOH = dorsal fin height; n = sample size.

Form	STL/BDD			HLL/POL		HLL/MXL		STL/DOH	
	n	$\bar{x} \pm \text{SD}$	Range						
<i>artedi</i> (typical)	16	4.8 ± 0.2	4.5-5.1	3.7 ± 0.2	3.4-4.1	2.8 ± 0.1	2.6-3.0	7.1 ± 0.4	6.3-8.0
<i>albus</i>	4	3.9 ± 0.1	3.8-4.0	3.9 ± 0.3	3.7-4.3	2.9 ± 0.1	2.7-3.0	6.7 ± 0.3	6.4-7.1
<i>hoyi</i>	10	4.0 ± 0.2	3.7-4.3	3.8 ± 0.2	3.6-4.3	2.4 ± 0.1	2.3-2.6	5.4 ± 0.4	4.7-6.0
<i>kiyi</i>	10	4.0 ± 0.3	3.7-4.8	3.7 ± 0.2	3.4-4.1	2.5 ± 0.1	2.3-2.6	5.3 ± 0.3	4.9-6.0
<i>nigripinnis</i>	10	3.9 ± 0.2	3.5-4.2	3.7 ± 0.1	3.6-3.9	2.6 ± 0.1	2.5-2.7	6.2 ± 0.3	5.5-6.6
<i>reighardi</i>	10	4.1 ± 0.2	3.7-4.4	3.8 ± 0.2	3.5-4.1	2.5 ± 0.1	2.4-2.6	6.2 ± 0.4	5.6-6.8
<i>zenithicus</i>	20	4.4 ± 0.3	4.0-5.3	3.5 ± 0.1	3.3-3.7	2.5 ± 0.1	2.3-2.6	6.2 ± 0.4	5.6-7.0

Table 3A. Lake Michigan—Head, Orbit, Paired Fins, Gill Rakers

Mean (\bar{x}), standard deviation (SD), and range of four morphological and one meristic characteristic (gill rakers) based on frequency distributions in Koelz (1929) for eight forms of cisco collected from Lake Michigan, 1920-1924. STL = standard length, HLL = head length, OOL = orbital length, PPD = Pectoral-pelvic distance, PCL = pectoral fin length, PAD = pelvic-anal distance, PVL = pelvic fin length, and TGR = total gill rakers; n = sample size for TGR; sample sizes for other characteristics vary slightly from TGR.

Form	STL/HLL			HLL/OOL		PPD/PCL		PAD/PVL		TGR	
	n	$\bar{x} \pm SD$	Range	$\bar{x} \pm SD$	Range						
<i>alpenae</i>	383	4.2 ± 0.1	3.8-4.6	4.4 ± 0.2	3.7-5.2	2.0 ± 0.2	1.6-2.5	1.6 ± 0.1	1.2-1.9	37.4 ± 2.2	33-46
<i>artedi</i> (typical)	391	4.4 ± 0.2	4.0-5.0	4.0 ± 0.2	3.5-4.7	2.0 ± 0.2	1.6-2.6	1.7 ± 0.1	1.3-2.3	48.3 ± 2.6	41-55
<i>hoyi</i>	1,100	4.1 ± 0.2	3.6-4.6	3.8 ± 0.2	3.3-4.5	1.9 ± 0.2	1.3-2.5	1.3 ± 0.1	1.0-1.7	42.6 ± 1.9	37-48
<i>johannae</i>	122	4.1 ± 0.1	3.8-4.4	4.4 ± 0.2	4.0-4.9	1.7 ± 0.2	1.5-2.1	1.4 ± 0.1	1.1-1.6	30.1 ± 2.1	26-36
<i>kiyi</i>	212	4.0 ± 0.1	3.7-4.3	4.0 ± 0.2	3.6-4.3	1.6 ± 0.2	1.1-2.1	1.1 ± 0.1	0.9-1.4	38.5 ± 1.9	34-45
<i>nigripinnis</i>	53	4.3 ± 0.2	3.8-4.7	4.3 ± 0.2	4.0-4.6	1.7 ± 0.2	1.5-2.2	1.4 ± 0.1	1.2-1.6	47.6 ± 2.5	41-52
<i>reighardi</i>	406	4.3 ± 0.2	3.9-4.8	4.0 ± 0.2	3.5-4.6	2.2 ± 0.2	1.5-2.8	1.5 ± 0.1	1.2-1.9	36.2 ± 2.2	30-43
<i>zenithicus</i>	122	4.2 ± 0.1	3.9-4.5	4.3 ± 0.2	3.8-5.0	2.1 ± 0.2	1.7-2.4	1.5 ± 0.1	1.2-2.0	39.7 ± 1.9	35-44

Table 3B. Lake Michigan—Body Depth, Snout, Maxillary, Dorsal Fin

Mean (\bar{x}), standard deviation (SD), and range of four morphological characteristics based on “representative” specimens in Koelz (1929) for eight forms of cisco collected from Lake Michigan, 1920-1924. STL = standard length, BDD = body depth, HLL = head length, POL = preorbital length, MXL = maxillary length, and DOH = dorsal fin height; n = sample size.

Form	STL/BDD			HLL/POL		HLL/MXL		STL/DOH	
	n	$\bar{x} \pm SD$	Range						
<i>alpenae</i>	19	4.4 ± 0.5	3.5-5.1	3.5 ± 0.4	6.2-7.4	2.6 ± 0.1	4.0-4.9	6.6 ± 0.4	6.2-7.3
<i>artedi</i> (typical)	29	4.6 ± 0.4	3.6-5.4	3.9 ± 0.2	3.6-4.2	2.8 ± 0.1	2.5-3.1	7.2 ± 0.5	6.4-8.5
<i>hoyi</i>	10	4.1 ± 0.4	3.6-4.8	3.8 ± 0.1	3.6-4.0	2.6 ± 0.1	2.4-2.8	5.8 ± 0.5	5.2-6.5
<i>johannae</i>	10	3.9 ± 0.2	3.6-4.3	3.6 ± 0.1	3.4-3.8	2.7 ± 0.1	2.5-2.8	6.2 ± 0.4	5.6-7.2
<i>kiyi</i>	10	3.9 ± 0.3	3.5-4.4	3.6 ± 0.1	3.4-3.8	2.5 ± 0.1	2.3-2.7	5.4 ± 0.4	5.0-6.1
<i>nigripinnis</i>	10	3.8 ± 0.3	3.4-4.2	3.8 ± 0.2	3.5-4.1	2.7 ± 0.1	2.6-2.7	5.9 ± 0.2	5.4-6.3
<i>reighardi</i>	20	4.3 ± 0.3	3.8-4.7	3.8 ± 0.2	3.6-4.3	2.7 ± 0.1	2.5-2.8	6.9 ± 0.4	6.0-7.5
<i>zenithicus</i>	17	4.5 ± 0.4	3.8-5.3	3.5 ± 0.1	3.2-3.6	2.5 ± 0.1	2.3-2.7	6.8 ± 0.5	6.0-7.9

Table 4A. Lake Huron—Head, Orbit, Paired Fins, Gill Rakers

Mean (\bar{x}), standard deviation (SD), and range of four morphological and one meristic characteristic (gill rakers) based on “representative” specimens (*manitoulinus* only) or frequency distributions (all others) in Koelz (1929) for eight forms of cisco collected from Lake Huron, 1917-1924. STL = standard length, HLL = head length, OOL = orbital length, PPD = Pectoral-pelvic distance, PCL = pectoral fin length, PAD = pelvic-anal distance, PVL = pelvic fin length, and TGR = total gill rakers; *n* = sample size for TGR; sample sizes for other characteristics vary slightly from TGR, except for *manitoulinus*.

Form	STL/HLL			HLL/OOL		PPD/PCL		PAD/PVL		TGR	
	<i>n</i>	$\bar{x} \pm SD$	Range	$\bar{x} \pm SD$	Range						
<i>alpenae</i>	387	4.0 ± 0.2	3.4-4.4	4.3 ± 0.4	3.6-5.2	1.9 ± 0.1	1.6-2.4	1.5 ± 0.2	1.1-1.9	36.8 ± 2.7	31-44
<i>artedi</i> (all)	302	4.4 ± 0.2	3.9-5.0	4.0 ± 0.2	3.4-5.1	2.0 ± 0.2	1.5-2.6	1.7 ± 0.1	1.1-2.1	47.1 ± 2.2	40-53
<i>manitoulinus</i>	10	4.1 ± 0.1	4.0-4.3	3.7 ± 0.1	3.4-3.8	1.7 ± 0.1	1.6-1.8	1.4 ± 0.2	1.1-1.6	45.7 ± 1.3	43-47
<i>hoyi</i>	870	4.0 ± 0.2	3.5-4.5	3.7 ± 0.2	3.3-4.2	1.8 ± 0.2	1.4-2.2	1.3 ± 0.1	1.0-1.7	41.4 ± 1.7	37-47
<i>johannae</i>	441	3.9 ± 0.1	3.4-4.3	4.4 ± 0.3	3.6-5.3	1.6 ± 0.2	1.2-2.1	1.3 ± 0.1	0.8-1.6	29.1 ± 1.7	25-35
<i>kiyi</i>	212	3.8 ± 0.1	3.5-4.1	3.7 ± 0.2	3.3-4.3	1.5 ± 0.1	1.1-1.9	1.1 ± 0.1	0.9-1.4	38.2 ± 1.9	34-44
<i>nigripinnis</i>	129	4.1 ± 0.1	3.7-4.4	4.1 ± 0.2	3.6-4.6	1.5 ± 0.1	1.2-1.9	1.3 ± 0.1	1.0-1.6	46.9 ± 2.4	40-52
<i>zenithicus</i>	157	4.1 ± 0.1	3.7-4.5	4.2 ± 0.3	3.5-5.2	2.0 ± 0.2	1.6-2.6	1.5 ± 0.1	1.1-1.8	37.4 ± 2.2	32-41

Table 4B. Lake Huron—Body Depth, Snout, Maxillary, Dorsal Fin

Mean (\bar{x}), standard deviation (SD), and range of four morphological characteristics based on “representative” specimens selected by Koelz (1929) for seven forms of cisco collected from Lake Huron, 1917-1924. STL = standard length, BDD = body depth, HLL = head length, POL = preorbital length, MXL = maxillary length, and DOH = dorsal fin height; *n* = sample size.

Form	STL/BDD			HLL/POL		HLL/MXL		STL/DOH	
	<i>n</i>	$\bar{x} \pm SD$	Range	$\bar{x} \pm SD$	Range	Form	<i>n</i>	$\bar{x} \pm SD$	Range
<i>alpenae</i>	20	4.1 ± 0.2	3.7-4.6	3.6 ± 0.2	3.4-4.0	2.5 ± 0.1	2.3-2.7	6.7 ± 0.6	6.0-7.9
<i>artedi</i> (typical)	40	4.4 ± 0.4	3.7-5.4	3.9 ± 0.2	3.5-4.3	2.9 ± 0.2	2.6-3.2	7.5 ± 0.7	6.3-8.9
<i>manitoulinus</i>	10	3.6 ± 0.2	3.4-4.0	3.9 ± 0.2	3.7-4.2	2.7 ± 0.1	2.5-2.8	5.7 ± 0.8	4.9-7.7
<i>hoyi</i>	15	4.1 ± 0.3	3.7-4.6	3.8 ± 0.1	3.5-4.1	2.5 ± 0.1	2.3-2.7	6.0 ± 0.3	5.3-6.6
<i>johannae</i>	20	4.2 ± 0.3	3.6-4.9	3.4 ± 0.1	3.3-3.6	2.6 ± 0.1	2.4-2.8	6.0 ± 0.5	4.4-6.4
<i>kiyi</i>	10	4.0 ± 0.6	3.5-5.3	3.5 ± 0.1	3.3-3.7	2.5 ± 0.1	2.4-2.7	5.5 ± 0.4	5.1-6.2
<i>nigripinnis</i>	10	3.8 ± 0.3	3.4-4.2	3.7 ± 0.1	3.5-3.8	2.6 ± 0.1	2.4-2.7	6.0 ± 0.3	5.7-6.8
<i>zenithicus</i>	20	4.3 ± 0.5	3.5-5.1	3.5 ± 0.2	3.3-4.0	2.5 ± 0.1	2.3-2.8	6.8 ± 0.3	6.5-7.4

Table 5A. Lake Erie—Head, Orbit, Paired Fins, Gill Rakers

Mean (\bar{x}), standard deviation (SD), and range of four morphological and one meristic characteristic (gill rakers) based on frequency distributions in Koelz (1929) for *Coregonus artedi* (predominately *albus*) collected from Lake Erie, 1920-1924. STL = standard length, HLL = head length, OOL = orbital length, PPD = Pectoral-pelvic distance, PCL = pectoral fin length, PAD = pelvic-anal distance, PVL = pelvic fin length, and TGR = total gill rakers; n = sample size for TGR; sample sizes for other characteristics vary slightly from TGR.

Form	STL/HLL			HLL/OOL		PPD/PCL		PAD/PVL		TGR	
	n	$\bar{x} \pm SD$	Range	$\bar{x} \pm SD$	Range						
<i>albus</i>	313	4.4 ± 0.2	3.9-5.2	4.2 ± 0.3	3.7-4.9	1.9 ± 0.2	1.6-2.5	1.6 ± 0.2	1.3-2.1	46.5 ± 2.1	41-53
<i>artedi</i> (typical)	10	4.7 ± 0.2	4.5-5.2	4.3 ± 0.1	4.1-4.5	2.3 ± 0.2	2.1-2.5	1.8 ± 0.1	1.7-2.1	47.5 ± 1.8	45-50

Table 5B. Lake Erie—Body Depth, Snout, Maxillary, Dorsal Fin

Mean (\bar{x}), standard deviation (SD), and range of four morphological characteristics based on “representative” specimens selected by Koelz (1929) for two forms of cisco collected from Lake Erie, 1920-1924. STL = standard length, BDD = body depth, HLL = head length, POL = preorbital length, MXL = maxillary length, and DOH = dorsal fin height; n = sample size.

Form	STL/BDD			HLL/POL		HLL/MXL		STL/DOH	
	n	$\bar{x} \pm SD$	Range	$\bar{x} \pm SD$	Range	Form	n	$\bar{x} \pm SD$	Range
<i>albus</i>	30	3.6 ± 0.3	2.8-4.2	4.0 ± 0.2	3.7-4.5	2.8 ± 0.1	2.5-3.1	6.1 ± 0.4	5.3-6.7
<i>artedi</i> (typical)	10	4.1 ± 0.3	3.7-4.8	3.8 ± 0.2	3.6-4.2	2.9 ± 0.2	2.6-3.1	6.4 ± 0.6	6.7-8.0

Table 6A. Lake Ontario—Head, Orbit, Paired Fins, Gill Rakers

Mean (\bar{x}), standard deviation (SD), and range of four morphological and one meristic characteristic (gill rakers) based on frequency distributions in Koelz (1929) for four forms of cisco collected from Lake Ontario, 1917-1923. STL = standard length, HLL = head length, OOL = orbital length, PPD = Pectoral-pelvic distance, PCL = pectoral fin length, PAD = pelvic-anal distance, PVL = pelvic fin length, and TGR = total gill rakers; n = sample size for TGR; sample sizes for other characteristics vary slightly from TGR.

Form	STL/HLL			HLL/OOL		PPD/PCL		PAD/PVL		TGR	
	n	$\bar{x} \pm SD$	Range	$\bar{x} \pm SD$	Range						
<i>artedi</i> (all)	191	4.4 ± 0.2	3.7-5.0	4.3 ± 0.2	3.8-4.9	2.0 ± 0.2	1.6-2.5	1.6 ± 0.1	1.2-1.9	47.7 ± 2.7	41-54
<i>hoi</i>	243	4.1 ± 0.1	3.7-4.6	4.2 ± 0.2	3.7-4.7	1.8 ± 0.2	1.4-2.2	1.4 ± 0.1	1.1-1.6	44.6 ± 2.0	39-50
<i>kiyi</i>	120	4.2 ± 0.1	3.8-4.4	4.0 ± 0.1	3.6-4.4	1.9 ± 0.1	1.5-2.2	1.3 ± 0.1	1.0-1.6	44.4 ± 1.8	41-48
<i>reighardi</i>	76	4.5 ± 0.2	4.0-5.0	4.3 ± 0.2	4.0-5.0	2.4 ± 0.2	1.7-2.9	1.6 ± 0.1	1.3-2.1	36.4 ± 1.9	33-42

Table 6B. Lake Ontario—Body Depth, Snout, Maxillary, Dorsal Fin

Mean (\bar{x}), standard deviation (SD), and range of four morphological characteristics based on “representative” specimens selected by Koelz (1929) for five forms of cisco collected from Lake Ontario, 1917-1923. STL = standard length, BDD = body depth, HLL = head length, POL = preorbital length, MXL = maxillary length, and DOH = dorsal fin height; n = sample size.

Form	STL/BDD			HLL/POL		HLL/MXL		STL/DOH	
	n	$\bar{x} \pm SD$	Range	$\bar{x} \pm SD$	Range	Form	n	$\bar{x} \pm SD$	Range
<i>artedi</i> (typical)	10	3.9 ± 0.2	3.7-4.4	4.0 ± 0.3	3.7-4.5	2.8 ± 0.2	2.6-3.1	6.5 ± 0.4	5.8-7.1
<i>albus</i>	10	3.5 ± 0.2	3.1-3.8	4.0 ± 0.2	3.7-4.3	2.8 ± 0.1	2.6-2.9	6.7 ± 0.5	6.1-7.7
<i>hoi</i>	10	4.0 ± 0.3	3.6-4.5	3.7 ± 0.2	3.5-4.1	2.6 ± 0.1	2.4-2.8	6.2 ± 0.4	5.5-6.8
<i>kiyi</i>	10	3.7 ± 0.3	3.1-4.0	3.6 ± 0.1	3.4-3.7	2.5 ± 0.1	2.4-2.7	6.1 ± 0.3	5.4-6.4
<i>reighardi</i>	10	4.2 ± 0.3	3.7-4.6	3.8 ± 0.2	3.4-4.2	2.8 ± 0.1	2.6-2.9	7.2 ± 0.4	6.5-8.0

Table 7A. Lake Nipigon—Head, Orbit, Paired Fins, Gill Rakers

Mean (\bar{x}), standard deviation (SD), and range of four morphological and one meristic character (gill rakers) based on frequency distributions in Koelz (1929) for five forms of cisco collected from Lake Nipigon, 1922. *Coregonus nipigon* included with “*artedi* (all).” STL = standard length, HLL = head length, OOL = orbital length, PPD = Pectoral-pelvic distance, PCL = pectoral fin length, PAD = pelvic-anal distance, PVL = pelvic fin length, and TGR = total gill rakers; n = sample size for TGR; sample sizes for other characteristics vary slightly from TGR.

Form	STL/HLL			HLL/OOL		PPD/PCL		PAD/PVL		TGR	
	n	$\bar{x} \pm SD$	Range	$\bar{x} \pm SD$	Range						
<i>artedi</i> (all)	71	4.2 ± 0.2	3.8-4.6	4.1 ± 0.4	3.5-5.2	1.7 ± 0.1	1.4-2.0	1.5 ± 0.1	1.3-1.7	47.8 ± 2.2	41-53
<i>hoi</i>	146	3.9 ± 0.1	3.6-4.2	3.7 ± 0.2	3.1-4.2	1.6 ± 0.1	1.2-1.9	1.2 ± 0.1	1.0-1.5	43.8 ± 1.8	40-48
<i>nigripinnis</i> (<i>regalis</i>)	183	4.0 ± 0.1	3.6-4.4	3.9 ± 0.2	3.2-4.3	1.5 ± 0.1	1.2-1.9	1.4 ± 0.1	1.1-1.7	49.4 ± 2.0	44-54
<i>reighardi</i> (<i>dymondi</i>)	86	3.8 ± 0.1	3.5-4.1	4.1 ± 0.3	3.6-4.8	1.7 ± 0.1	1.4-2.0	1.4 ± 0.1	1.1-1.7	34.7 ± 1.4	32-38
<i>zenithicus</i>	147	3.9 ± 0.1	3.5-4.2	4.2 ± 0.2	3.6-4.6	1.7 ± 0.1	1.5-2.1	1.4 ± 0.1	1.1-1.7	37.7 ± 1.7	33-42

Table 7B. Lake Nipigon—Body Depth, Snout, Maxillary, Dorsal Fin

Mean (\bar{x}), standard deviation (SD), and range of four morphological metrics based on “representative” specimens selected by Koelz (1929) for six forms of cisco collected from Lake Nipigon, 1922. STL = standard length, BDD = body depth, HLL = head length, POL = preorbital length, MXL = maxillary length, and DOH = dorsal fin height; n = sample size.

Form	STL/BDD			HLL/POL		HLL/MXL		STL/DOH		
	n	$\bar{x} \pm SD$	Range	$\bar{x} \pm SD$	Range	Form	n	$\bar{x} \pm SD$	Range	
<i>artedi</i> (typical)	20	4.0 ± 0.4	3.3-4.8	3.8 ± 0.2	3.6-4.2	2.7 ± 0.1	2.5-2.9	5.8 ± 0.4	5.1-6.3	
<i>nipigon</i>	10	3.7 ± 0.3	3.3-4.1	3.7 ± 0.1	3.6-4.0	2.6 ± 0.1	2.5-2.7	5.5 ± 0.4	5.1-6.2	
<i>hoi</i>	10	4.3 ± 0.2	4.0-4.6	3.6 ± 0.2	3.4-3.8	2.3 ± 0.1	2.2-2.4	5.2 ± 0.3	4.9-5.7	
<i>nigripinnis</i> (<i>regalis</i>)	12	3.9 ± 0.4	3.1-4.6	3.8 ± 0.2	3.6-4.0	2.6 ± 0.1	2.5-2.7	5.4 ± 0.4	4.9-6.1	
<i>reighardi</i> (<i>dymondi</i>)	18	4.0 ± 0.3	3.7-4.8	3.6 ± 0.2	3.4-4.0	2.5 ± 0.1	2.3-2.6	5.7 ± 0.3	5.1-6.3	
<i>zenithicus</i>	20	4.5 ± 0.4	3.9-5.1	3.4 ± 0.1	3.2-3.7	2.4 ± 0.1	2.3-2.6	5.8 ± 0.4	5.1-6.5	

STANFORD SMITH TABULAR DATA

Table 8. Lake Superior—Head, Snout, Orbit, Maxillary, Dorsal Fin, Paired Fins, Gill Rakers

Mean (\bar{x}), standard deviation (SD), and range for seven morphological and one meristic characteristic (gill rakers) of six forms of Lake Superior ciscoes collected and measured under the direction of Stanford Smith during 1959-1961 (see Notes subsection). STL = standard length, HLL = head length, POL = preorbital length, OOL = orbital length, MXL = maxillary length, DOH = dorsal fin height, PCL = pectoral fin length, PVL = pelvic fin length, and TGR = total gill rakers; and n = sample size.

Form	STL/HLL			HLL/POL			HLL/OOL			HLL/MXL		
	n	$\bar{x} \pm SD$	Range									
<i>artedi</i>	84	4.4 ± 0.4	4.0-7.1	-	-	-	-	-	-	84	2.7 ± 0.2	1.8-3.1
<i>hoi</i>	216	4.0 ± 0.1	3.6-4.4	1	2.2	-	-	-	-	215	2.5 ± 0.1	2.3-2.8
<i>kiyi</i>	195	3.8 ± 0.1	3.5-4.3	-	-	-	-	-	-	195	2.5 ± 0.1	2.2-3.1
<i>nigripinnis</i>	43	4.1 ± 0.1	3.8-4.4	37	3.6 ± 0.1	3.4-3.8	37	4.7 ± 0.4	2.7-5.2	43	2.6 ± 0.1	2.4-2.8
<i>reighardi</i>	118	4.1 ± 0.2	3.6-4.7	-	-	-	-	-	-	118	2.6 ± 0.1	2.4-3.0
<i>zenithicus</i>	184	3.9 ± 0.2	3.5-4.3	26	3.7 ± 0.1	3.4-4.0	26	4.4 ± 0.4	3.7-5.2	184	2.5 ± 0.1	2.3-2.8
	STL/DOH			STL/PCL			STL/PVL			TGR		
<i>artedi</i>	84	7.0 ± 0.9	5.5-9.2	84	6.2 ± 0.6	4.7-7.5	84	6.9 ± 0.7	5.5-8.7	84	46.7 ± 2.6	40-52
<i>hoi</i>	216	5.7 ± 0.4	4.7-7.1	216	5.2 ± 0.4	4.3-6.3	216	5.7 ± 0.4	4.7-6.9	216	43.6 ± 2.2	38-49
<i>kiyi</i>	195	5.4 ± 0.5	4.5-9.4	195	4.7 ± 0.4	3.9-6.0	195	5.4 ± 0.4	4.2-6.6	195	42.0 ± 2.4	34-48
<i>nigripinnis</i>	43	6.4 ± 0.5	5.4-7.3	43	5.7 ± 0.5	4.9-6.5	43	6.4 ± 0.4	5.5-7.3	43	42.1 ± 2.5	36-48
<i>reighardi</i>	118	6.1 ± 0.5	4.7-7.1	118	5.6 ± 0.5	4.5-6.6	118	6.1 ± 0.5	4.7-7.2	118	41.1 ± 3.3	32-49
<i>zenithicus</i>	184	6.2 ± 0.4	4.9-7.3	184	5.5 ± 0.4	4.2-6.7	184	6.6 ± 0.4	4.9-7.1	184	40.5 ± 1.9	36-49

Table 9. Lake Michigan—Head, Snout, Orbit, Maxillary, Dorsal Fin, Paired Fins, Gill Rakers

Mean (\bar{x}), standard deviation (SD), and range for seven morphological and one meristic characteristic (gill rakers) of six forms of Lake Michigan ciscoes collected and measured under the direction of Stanford Smith during 1950, 1960 (*zenithicus*), and 1972 (*artedi* and *hoyi*). STL = standard length, HLL = head length, POL = preorbital length, OOL = orbital length, MXL = maxillary length, DOH = dorsal fin height, PCL = pectoral fin length, PVL = pelvic fin length, TGR = total gill rakers; *n* = sample size.

Form	STL/HLL			HLL/POL			HLL/OOL			HLL/MXL		
	<i>n</i>	$\bar{x} \pm \text{SD}$	Range									
<i>alpenae</i>	35	4.1 ± 0.1	3.9-4.5	35	3.6 ± 0.1	3.3-3.9	35	4.4 ± 0.2	4.0-4.7	35	2.6 ± 0.1	2.4-2.7
<i>artedi</i>	10	4.6 ± 0.3	4.3-5.2	10	3.7 ± 0.3	3.3-4.1	10	4.2 ± 0.3	3.5-4.6	10	2.9 ± 0.2	2.5-3.2
<i>hoyi</i> (all)	30	4.2 ± 0.1	3.9-4.5	30	3.8 ± 0.2	3.3-4.2	30	4.1 ± 0.2	3.7-4.6	30	2.6 ± 0.1	2.5-2.8
<i>hoyi</i> (1950)	16	4.1 ± 0.1	3.9-4.3	16	3.9 ± 0.2	3.6-4.2	16	4.0 ± 0.2	3.7-4.5	16	2.6 ± 0.1	2.5-2.8
<i>hoyi</i> (1972)	14	4.3 ± 0.1	4.0-4.5	14	3.7 ± 0.2	3.3-4.0	14	4.2 ± 0.3	3.8-4.6	14	2.7 ± 0.1	2.5-2.8
<i>kiyi</i>	27	4.0 ± 0.1	3.7-4.3	27	3.6 ± 0.1	3.4-3.9	27	4.1 ± 0.2	3.9-4.5	27	2.5 ± 0.1	2.4-2.9
<i>reighardi</i>	33	4.4 ± 0.2	4.2-4.8	33	3.8 ± 0.1	3.5-4.1	33	4.0 ± 0.2	3.5-4.2	33	2.7 ± 0.1	2.3-3.0
<i>zenithicus</i>	107	4.2 ± 0.5	3.6-9.1	107	3.6 ± 0.2	3.4-4.1	107	4.4 ± 0.3	2.2-5.0	107	2.5 ± 0.2	1.0-2.8
	STL/DOH			STL/PCL			STL/PVL			TGR		
<i>alpenae</i>	35	6.5 ± 0.4	5.6-7.1	35	6.4 ± 0.4	5.5-7.2	35	6.6 ± 0.3	5.8-7.1	35	41.5 ± 2.2	37-47
<i>artedi</i>	10	8.0 ± 0.8	6.6-9.2	10	7.3 ± 0.8	5.6-8.2	10	8.0 ± 0.7	6.5-8.9	10	45.3 ± 1.4	43-48
<i>hoyi</i> (all)	30	5.9 ± 0.4	5.3-6.6	30	6.0 ± 0.3	5.2-6.5	30	6.0 ± 0.3	5.5-6.6	30	41.1 ± 2.5	35-46
<i>hoyi</i> (1950)	16	6.1 ± 0.3	5.5-6.6	16	6.0 ± 0.2	5.5-6.4	16	6.0 ± 0.2	5.6-6.4	16	42.7 ± 0.2	38-46
<i>hoyi</i> (1972)	14	5.7 ± 0.3	5.3-6.4	14	5.9 ± 0.4	5.2-6.5	14	6.0 ± 0.3	5.5-6.6	14	39.2 ± 1.5	35-41
<i>kiyi</i>	27	5.7 ± 0.6	4.8-6.9	27	5.4 ± 0.8	4.5-7.5	27	5.7 ± 0.7	4.9-7.1	27	41.0 ± 2.1	37-46
<i>reighardi</i>	33	7.3 ± 0.5	6.5-8.8	33	7.3 ± 0.5	6.5-8.8	33	7.0 ± 0.4	6.3-7.8	33	37.5 ± 1.9	34-43
<i>zenithicus</i>	107	6.6 ± 0.4	5.5-7.6	107	6.4 ± 0.5	5.1-8.1	107	6.6 ± 0.4	5.5-7.7	107	41.7 ± 2.0	37-47

Table 10. Lake Huron—Head, Snout, Orbit, Maxillary, Dorsal Fin, Paired Fins, Gill Rakers

Mean (\bar{x}), standard deviation (SD), and range for seven morphological and one meristic characteristic (gill rakers) for six forms of Lake Huron ciscoes collected and measured under the direction of Stanford Smith during 1956 (see Notes subsection). STL = standard length, HLL = head length, POL = preorbital length, OOL = orbital length, MXL = maxillary length, DOH = dorsal fin height, PCL = pectoral fin length, PVL = pelvic fin length, TGR = total gill rakers; n = sample size.

Form	STL/HLL			HLL/POL			HLL/OOL			HLL/MXL		
	n	$\bar{x} \pm SD$	Range	n	$\bar{x} \pm SD$	Range	n	$\bar{x} \pm SD$	Range	n	$\bar{x} \pm SD$	Range
<i>alpenae</i>	33	4.0 ± 0.2	3.7-4.4	33	3.6 ± 0.1	3.3-3.9	33	4.3 ± 0.1	3.9-4.5	33	2.5 ± 0.1	2.3-2.8
<i>artedi</i>	42	4.4 ± 0.2	4.0-8.0	42	4.0 ± 0.2	3.5-4.7	42	4.3 ± 0.3	3.7-5.1	42	2.9 ± 0.1	2.6-3.2
<i>hoi</i>	29	4.1 ± 0.3	3.3-4.5	29	3.9 ± 0.2	3.5-4.4	29	4.0 ± 0.3	3.6-4.8	29	2.6 ± 0.1	2.4-3.0
<i>kiyi</i>	27	3.9 ± 0.1	3.6-4.1	27	3.7 ± 0.2	3.3-4.2	27	4.0 ± 0.2	3.6-4.4	27	2.6 ± 0.1	2.4-2.9
<i>reighardi</i>	65	4.3 ± 0.2	3.9-5.1	65	3.8 ± 0.3	3.0-4.3	65	4.0 ± 0.2	3.0-4.5	65	2.8 ± 0.1	2.2-3.0
<i>zenithicus</i>	4	3.9 ± 0.3	3.7-4.2	1	3.4	-	4	4.2 ± 0.1	4.1-4.3	4	2.6 ± 0.1	2.5-2.7
Form	STL/DOH			STL/PCL			STL/PVL			TGR		
	n	$\bar{x} \pm SD$	Range	n	$\bar{x} \pm SD$	Range	n	$\bar{x} \pm SD$	Range	n	$\bar{x} \pm SD$	Range
<i>alpenae</i>	33	5.8 ± 0.3	5.2-6.6	33	6.4 ± 0.8	5.2-10.2	33	6.4 ± 0.4	5.6-7.1	33	36.9 ± 2.3	33-42
<i>artedi</i>	42	6.5 ± 0.5	5.3-7.4	42	6.6 ± 0.5	5.8-7.5	42	7.1 ± 0.5	5.9-8.3	42	47.2 ± 3.8	41-61
<i>hoi</i>	29	5.5 ± 0.5	4.1-6.5	29	5.6 ± 0.4	4.6-6.3	29	5.8 ± 0.5	4.4-7.0	29	42.7 ± 2.1	39-45
<i>kiyi</i>	27	5.2 ± 0.4	4.4-5.8	27	5.1 ± 0.4	4.4-5.8	27	5.5 ± 0.3	4.7-6.0	27	41.0 ± 2.6	36-46
<i>reighardi</i>	65	6.3 ± 0.4	5.4-7.3	65	6.5 ± 0.5	5.3-7.9	65	6.6 ± 0.4	5.5-7.3	65	36.5 ± 2.2	31-44
<i>zenithicus</i>	4	5.9 ± 0.3	5.5-6.2	4	6.2 ± 0.4	5.6-6.6	4	6.5 ± 0.3	6.1-6.8	4	37.0 ± 2.0	36-40

Table 11. Lake Erie—Head, Snout, Orbit, Maxillary, Dorsal Fin, Paired Fins, Gill Rakers

Mean (\bar{x}), standard deviation (SD), and range for seven morphological and one meristic characteristic (gill rakers) of two forms of Lake Erie ciscoes collected and measured under the direction of Stanford Smith during 1957 (see Notes subsection). STL = standard length, HLL = head length, POL = preorbital length, OOL = orbital length, MXL = maxillary length, DOH = dorsal fin height, PCL = pectoral fin length, PVL = pelvic fin length, TGR = total gill rakers; n = sample size.

Form	STL/HLL			HLL/POL			HLL/OOL			HLL/MXL		
	n	$\bar{x} \pm SD$	Range									
<i>alpenae</i>	26	4.3 ± 0.1	4.0-4.5	26	3.7 ± 0.1	3.5-4.1	26	4.5 ± 0.2	4.0-4.8	26	2.7 ± 0.1	2.4-3.0
<i>albus</i>	13	4.4 ± 0.3	3.6-4.8	13	4.0 ± 0.2	3.6-4.5	13	4.5 ± 0.2	4.3-4.9	13	2.9 ± 0.1	2.7-3.2
Form	STL/DOH			STL/PCL			STL/PVL			TGR		
	n	$\bar{x} \pm SD$	Range									
<i>alpenae</i>	26	5.8 ± 0.3	5.4-6.6	26	5.8 ± 0.3	5.4-6.3	26	5.8 ± 0.3	5.4-6.8	26	35.6 ± 1.6	33-39
<i>albus</i>	13	5.7 ± 0.5	4.7-6.4	13	5.8 ± 0.3	5.3-6.3	13	5.8 ± 0.4	4.9-6.6	13	45.8 ± 2.7	42-50

Table 12. Lake Ontario—Head, Snout, Orbit, Maxillary, Dorsal Fin, Paired Fins, Gill Rakers

Mean (\bar{x}), standard deviation (SD), and range for seven morphological and one meristic characteristic (gill rakers) of *Coregonus artedi* (form not specified) from Lake Ontario collected and measured under the direction of Stanford Smith in 1972 (see Notes subsection). STL = standard length, HLL = head length, POL = preorbital length, OOL = orbital length, MXL = maxillary length, DOH = dorsal fin height, PCL = pectoral fin length, PVL = pelvic fin length, and TGR = total gill rakers; n = sample size.

Form	STL/HLL			HLL/POL			HLL/OOL			HLL/MXL		
	n	$\bar{x} \pm SD$	Range									
<i>artedi</i>	12	4.5 ± 0.2	4.2-4.7	12	4.1 ± 0.5	3.3-5.2	12	4.2 ± 0.2	3.8-4.6	12	3.1 ± 0.2	2.9-3.5
<i>artedi</i>	STL/DOH			STL/PCL			STL/PVL			TGR		
	n	$\bar{x} \pm SD$	Range									
	8	6.3 ± 0.4	5.8-6.8	12	6.4 ± 0.3	5.9-6.9	12	6.9 ± 0.5	6.0-7.7	12	46.8 ± 2.3	43-51

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Table 13. Lake Superior—Body Depth, Head, Snout, Orbit, Maxillary, Paired Fins, Gill Rakers

Mean (\bar{x}), standard deviation (SD), and range of seven morphological and one meristic characteristic (gill rakers) for four forms of cisco collected from Lake Superior by TCP (2004 and 2006-2010) and AMM (2009-2010). STL = standard length, BDD = body depth, HLL = head length, POL = preorbital length, OOL = orbital length, MXL = maxillary length, PCL = pectoral fin length, PVL = pelvic fin length, and TGR = total gill rakers; n = sample size.

Form	STL/BDD			STL/HLL			HLL/POL			HLL/OOL		
	n	$\bar{x} \pm SD$	Range									
<i>artedi</i>	241	4.5 ± 0.5	3.2-5.7	242	4.5 ± 0.3	3.6-5.4	244	3.9 ± 0.2	2.9-4.7	244	4.5 ± 0.3	3.4-5.3
<i>hoi</i>	256	4.1 ± 0.5	3.0-5.6	257	4.2 ± 0.2	3.6-4.8	259	3.9 ± 0.3	3.2-5.0	259	4.2 ± 0.3	3.5-5.2
<i>kiyi</i>	89	4.3 ± 0.3	3.6-5.0	89	4.0 ± 0.2	3.5-4.6	91	3.9 ± 0.2	3.3-4.4	91	3.9 ± 0.3	3.5-5.0
<i>zenithicus</i>	188	4.0 ± 0.4	3.1-5.1	188	4.2 ± 0.2	3.3-4.8	189	3.8 ± 0.3	3.2-4.8	189	4.3 ± 0.3	3.4-5.1
Form	HLL/MXL			STL/PCL			STL/PVL			TGR		
	n	$\bar{x} \pm SD$	Range									
<i>artedi</i>	244	3.1 ± 0.3	2.4-4.0	242	6.2 ± 0.7	4.5-7.9	242	6.6 ± 0.7	4.9-8.5	240	43.9 ± 2.5	36-52
<i>hoi</i>	258	3.0 ± 0.3	2.3-3.9	257	5.6 ± 0.5	4.4-7.0	257	5.9 ± 0.5	4.7-8.0	258	41.9 ± 2.6	33-49
<i>kiyi</i>	91	2.9 ± 0.2	2.4-4.0	89	5.0 ± 0.5	4.2-6.3	89	5.5 ± 0.4	4.7-6.9	90	40.6 ± 2.8	34-47
<i>zenithicus</i>	189	2.9 ± 0.3	2.4-3.8	188	5.6 ± 0.5	4.5-7.4	188	6.0 ± 0.6	4.8-8.0	187	40.7 ± 2.7	33-48

Table 14. Lake Michigan—Body Depth, Head, Snout, Orbit, Maxillary, Paired Fins, Gill Rakers

Mean (\bar{x}), standard deviation (SD), and range of seven morphological and one meristic characteristic (gill rakers) for two forms of Lake Michigan ciscoes. *Albus*-like collected by R. Claramunt, Charlevoix Great Lakes Fishery Office, from 2007 to 2015 and *hoi* collected by AMM (2008) and SMR (2011). STL = standard length, BDD = body depth, HLL = head length, POL = preorbital length, OOL = orbital length, MXL = maxillary length, PCL = pectoral fin length, PVL = pelvic fin length, TGR = total gill rakers; n = sample size.

Form	STL/BDD			STL/HLL			HLL/POL			HLL/OOL		
	n	$\bar{x} \pm SD$	Range									
<i>albus</i> -like	25	4.1 ± 0.3	3.6-4.5	20	5.2 ± 0.3	4.8-5.8	20	4.7 ± 0.4	4.2-5.5	20	4.2 ± 0.3	3.7-4.8
<i>hoi</i>	160	4.0 ± 0.3	3.3-4.9	160	4.1 ± 0.2	3.8-4.6	160	4.1 ± 0.2	3.6-4.8	160	3.9 ± 0.2	3.5-4.7
Form	HLL/MXL			STL/PCL			STL/PVL			TGR		
	n	$\bar{x} \pm SD$	Range									
<i>albus</i> -like	24	3.3 ± 0.2	3.0-3.7	24	7.5 ± 0.4	6.7-8.4	25	7.7 ± 0.5	6.9-8.6	25	46.0 ± 1.8	43-50
<i>hoi</i>	160	3.0 ± 0.2	2.6-3.8	160	5.9 ± 0.3	5.1-7.1	160	6.4 ± 0.4	5.4-7.7	159	41.9 ± 2.0	36-48

Table 15. Lake Huron—Body Depth, Head, Snout, Orbit, Maxillary, Paired Fins, Gill Rakers

Mean (\bar{x}), standard deviation (SD), and range of seven morphological and one meristic characteristic (gill rakers) for *albus*-like and swarm ciscoes (*hybrida*) of Lake Huron. *Albus* collected 2015, Les Cheneaux Islands (specifically Boot Island and Government Bay), north main basin, courtesy Alpena Fish and Wildlife Conservation Office. *Artedi*-like, *hoyi*-like, and *zenithicus*-like collected and identified as per Mandrak et al. (2013) during 2003-2012. STL = standard length, BDD = body depth, HLL = head length, POL = preorbital length, OOL = orbital length, MXL = maxillary length, PCL = pectoral fin length, PVL = pelvic fin length, TGR = total gill rakers; *n* = sample size.

Form	STL/BDD			STL/HLL			HLL/POL			HLL/OOL		
	<i>n</i>	$\bar{x} \pm SD$	Range									
<i>albus</i> -like	19	3.7 ± 0.1	3.5-4.0	24	5.0 ± 0.2	4.7-5.3	28	4.7 ± 0.3	4.0-5.4	28	4.0 ± 0.2	3.6-4.3
swarm ciscoes												
all	326	4.9 ± 0.7	3.4-6.6	761	4.1 ± 0.3	2.7-6.2	762	3.8 ± 0.5	2.5-6.2	763	4.0 ± 0.6	2.7-5.9
main basin	78	4.4 ± 0.4	3.4-5.3	392	4.2 ± 0.3	2.7-5.2	393	3.6 ± 0.4	2.6-5.2	393	4.2 ± 0.4	2.9-5.9
Georgian Bay	200	5.2 ± 0.5	4.1-6.6	321	4.1 ± 0.3	3.3-6.2	321	4.1 ± 0.6	2.5-6.2	322	3.6 ± 0.5	2.7-5.5
North Channel	48	4.2 ± 0.4	3.5-5.4	48	4.4 ± 0.2	4.0-5.1	48	3.9 ± 0.2	3.5-4.4	48	4.3 ± 0.3	3.7-4.9
<i>artedi</i> -like	134	4.9 ± 0.6	3.8-6.6	144	4.2 ± 0.3	3.6-5.2	144	4.2 ± 0.4	3.1-5.5	144	3.8 ± 0.6	2.7-4.9
<i>hoyi</i> -like	167	4.8 ± 0.7	3.4-6.6	582	4.1 ± 0.3	2.7-6.2	583	3.7 ± 0.5	2.5-6.2	584	4.0 ± 0.5	2.9-5.9
<i>zenithicus</i> -like	25	5.1 ± 0.7	3.9-6.3	35	4.1 ± 0.2	3.7-5.0	35	4.1 ± 0.6	3.2-5.5	35	3.8 ± 0.6	3.0-4.9
	HLL/MXL			STL/PCL			STL/PVL			TGR		
<i>albus</i> -like	19	3.1 ± 0.2	2.9-3.6	24	6.4 ± 0.3	5.9-7.0	24	6.5 ± 0.4	5.9-7.5	24	51.0 ± 2.0	48-54
swarm ciscoes												
all	326	3.1 ± 0.2	2.5-4.5	326	5.9 ± 0.5	4.6-8.7	569	6.5 ± 0.7	5.1-9.8	746	41.0 ± 2.2	32-52
main basin	78	3.1 ± 0.3	2.7-4.5	78	6.2 ± 0.5	5.2-7.7	273	6.7 ± 0.7	5.4-9.3	383	40.7 ± 2.4	32-52
Georgian Bay	200	3.0 ± 0.2	2.5-3.4	200	5.8 ± 0.4	4.6-7.1	248	6.2 ± 0.6	5.1-9.8	315	41.0 ± 1.8	36-47
North Channel	48	3.2 ± 0.3	2.7-3.8	48	6.0 ± 0.7	5.1-8.7	48	6.3 ± 0.6	5.6-8.9	48	43.3 ± 1.6	41-49
<i>artedi</i> -like	134	3.1 ± 0.3	2.5-4.5	134	5.9 ± 0.6	4.8-8.7	139	6.3 ± 0.7	5.1-9.8	143	43.0 ± 1.9	38-52
<i>hoyi</i> -like	167	3.0 ± 0.2	2.5-3.7	167	5.9 ± 0.4	4.6-7.3	397	6.5 ± 0.7	5.2-9.3	568	40.6 ± 1.9	32-47
<i>zenithicus</i> -like	25	2.9 ± 0.2	2.7-3.3	25	6.0 ± 0.6	5.3-8.4	33	6.4 ± 0.5	5.5-8.0	35	39.3 ± 1.9	36-45

Table 16. Lake Erie—Body Depth, Head, Snout, Orbit, Maxillary, Paired Fins, Gill Rakers

Mean (\bar{x}), standard deviation (SD), and range of seven morphological and one meristic characteristic (gill rakers) for Lake Erie swarm ciscoes collected by Ontario Ministry Natural Resources and Forestry (2003-2015). STL = standard length, BDD = body depth, HLL = head length, POL = preorbital length, OOL = orbital length, MXL = maxillary length, PCL = pectoral fin length, PVL = pelvic fin length, and TGR = total gill rakers; n = sample size.

Form	STL/BDD			STL/HLL			HLL/POL			HLL/OOL		
	n	$\bar{x} \pm SD$	Range									
Swarm ciscoes	19	4.1 ± 0.4	3.5-5.1	19	4.1 ± 0.2	3.6-4.4	19	3.9 ± 0.3	3.4-4.5	19	5.2 ± 0.5	4.4-6.5
	HLL/MXL			STL/PCL			STL/PVL			TGR		
Swarm ciscoes	19	2.9 ± 0.2	2.7-3.3	19	5.6 ± 0.5	4.4-6.3	19	5.9 ± 0.4	4.8-6.5	7	38.4 ± 3.6	33-44

Table 17. Lake Ontario—Body Depth, Head, Snout, Orbit, Maxillary, Paired Fins, Gill Rakers

Mean (\bar{x}), standard deviation (SD), and range of seven morphological and one meristic characteristic (gill rakers) for Lake Ontario *Coregonus artedii* collected by SMR (2011) and AMM (2013). STL = standard length, BDD = body depth, HLL = head length, POL = preorbital length, OOL = orbital length, MXL = maxillary length, PCL = pectoral fin length, PVL = pelvic fin length, TGR = total gill rakers; n = sample size.

Form	STL/BDD			STL/HLL			HLL/POL			HLL/OOL		
	n	$\bar{x} \pm SD$	Range	n	$\bar{x} \pm SD$	Range	n	$\bar{x} \pm SD$	Range	n	$\bar{x} \pm SD$	Range
<i>artedii</i>	147	4.0 ± 0.3	3.1-4.7	147	4.7 ± 0.2	4.0-5.5	147	4.3 ± 0.3	3.5-6.0	147	4.0 ± 0.2	3.5-4.7
	HLL/MXL			STL/PCL			STL/PVL			TGR		
<i>artedii</i>	147	3.5 ± 0.3	2.6-4.3	147	6.8 ± 0.5	5.6-8.9	147	7.3 ± 0.7	5.8-10.1	143	48.5 ± 2.1	43-55

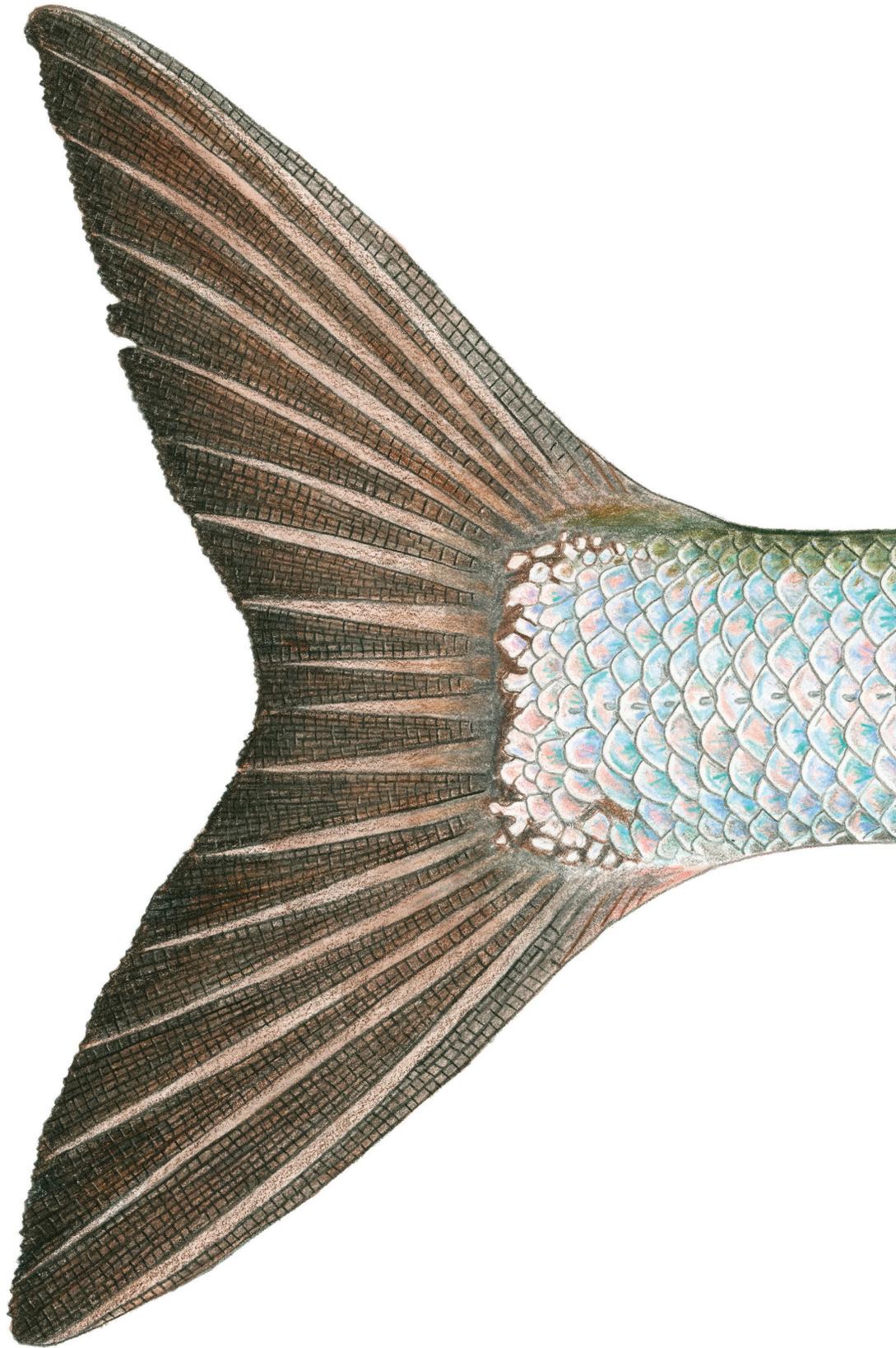
Table 18. Lake Nipigon—Body Depth, Head, Snout, Orbit, Maxillary, Paired Fins, Gill Rakers

Mean (\bar{x}), standard deviation (SD), and range of seven morphological and one meristic characteristic (gill rakers) for four forms of Lake Nipigon ciscoes collected by TCP (2007-2010) and AMM (2013). STL = standard length, BDD = body depth, HLL = head length, POL = preorbital length, OOL = orbital length, MXL = maxillary length, PCL = pectoral fin length, PVL = pelvic fin length, TGR = total gill rakers; n = sample size.

Form	STL/BDD			STL/HLL			HLL/POL			HLL/OOL		
	n	$\bar{x} \pm SD$	Range									
<i>artedii</i>	68	4.6 ± 0.4	3.1-6.0	68	4.4 ± 0.3	4.0-5.2	68	4.0 ± 0.2	3.6-4.5	68	4.2 ± 0.3	3.6-4.9
<i>hoi</i>	122	4.1 ± 0.4	3.0-5.4	123	4.3 ± 0.2	3.8-4.9	124	3.9 ± 0.2	3.4-4.6	124	4.2 ± 0.3	3.7-4.9
<i>nigripinnis</i>	189	3.8 ± 0.4	2.7-5.4	190	4.4 ± 0.3	3.1-5.6	191	4.0 ± 0.3	3.4-5.5	191	4.1 ± 0.3	3.5-5.0
<i>zenithicus</i>	57	3.9 ± 0.2	3.1-4.6	57	4.3 ± 0.2	4.0-4.7	57	3.9 ± 0.2	3.4-4.5	57	4.6 ± 0.3	3.8-5.4
	HLL/MXL			STL/PCL			STL/PVL			TGR		
<i>artedii</i>	134	3.2 ± 0.3	2.7-4.0	68	5.9 ± 0.5	3.4-7.2	68	6.2 ± 0.5	5.3-7.3	68	46.3 ± 2.1	40-51
<i>hoi</i>	122	3.0 ± 0.3	2.2-4.1	123	5.6 ± 0.4	4.5-7.0	123	5.9 ± 0.4	4.9-7.5	124	44.8 ± 1.8	40-49
<i>nigripinnis</i>	190	3.4 ± 0.3	2.6-4.4	188	6.0 ± 0.5	4.5-7.3	190	6.4 ± 0.5	4.6-7.7	191	50.0 ± 2.5	42-56
<i>zenithicus</i>	57	3.1 ± 0.3	2.6-3.7	57	6.1 ± 0.4	5.2-7.3	57	6.5 ± 0.4	5.6-7.5	57	37.5 ± 2.6	33-48

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