Evidence for Migratory Spawning Behavior by Morphologically Distinct Cisco (Coregonus artedi) from a Small Inland Lake

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ABSTRACT.—Conservation and management of rare fishes relies on managers having the most informed understanding of the underlying ecology of the species under investigation. Cisco (*Coregonus artedi*), a species of conservation concern, is a cold-water pelagic fish that is notoriously variable in morphometry and life history. Published reports indicate, at spawning time, Cisco in great lakes may migrate into or through large rivers, whereas those in small lakes move inshore. Nonetheless, during a sampling trip to Follensby Pond, a 393 ha lake in the Adirondack Mountains, New York, we observed gravid Cisco swimming over an outlet sill from a narrow shallow stream and into the lake. We opportunistically dip-netted a small subsample of 11 individuals entering the lake from the stream (three female, eight male) and compared them to fish captured between 2013 and 2015 with gillnets in the lake. Stream-captured Cisco were considerably larger than lake-captured individuals at a given age, had significantly larger asymptotic length, and were present only as mature individuals between age of 3 and age 5. These results could suggest either Cisco are migrating from a nearby lake to spawn in Follensby Pond, or that a distinct morphotype of Cisco from Follensby Pond migrates out to the stream and then back in at spawning time. Our results appear to complement a handful of other cases in which Cisco spawning migrations have been documented and to provide the first evidence for such behavior in a small inland lake.

INTRODUCTION

Cisco (*Coregonus artedi*) are broadly distributed across North America, with populations extending from the north-central and eastern United States, northward through most of Canada to the Arctic Ocean (Scott and Crossman, 1973). They are common to pelagic areas of coldwater lakes, in addition to estuaries of Hudson Bay (Cahn, 1927; Scott and Crossman, 1973). It is only during annual spawning migrations that Cisco move near-shore in the lake they reside, or up large rivers from the great lakes or estuaries they inhabit (Dymond, 1943; Morin *et al.*, 1981, Fielder, 1998). Cisco prey upon a variety of zooplankton, larval insects, and midges and are preyed upon in turn by predators such as Lake Trout (*Salvelinus namaycush*; Scott and Crossman, 1973; Engel, 1976; Eshenroder *et al.*, 2016).

Despite their extensive geographic range, Cisco are a species of conservation concern in many regions, including New York State where the present study takes place (NYSDEC,

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2015). Current threats to Cisco populations include nutrient-induced eutrophication, competition with invasive species like Rainbow Smelt (*Osmerus mordax*), warming summer water temperature and extended thermal stratification, and overharvesting (Latta, 1995; Hrabik, *et al.*, 1998; Stockwell *et al.*, 2009; Jacobson *et al.*, 2012). Because Cisco and its congeners were historically important pelagic prey species, there is substantial conservation interest in their ecological and phylogenetic diversity within the Laurentian Great Lakes basin (Dymond, 1943; Zimmerman and Krueger, 2009) and inland lakes across their range (Jacobson *et al.*, 2011; Fang *et al.*, 2012).

Although Cisco generally spawn in the lake in which they reside, migratory spawning behavior has been reported for a handful of populations (Cahn, 1927). Anadromous runs of Cisco have been documented from James Bay (Ontario/Quebec, Canada) to some of its tributary rivers (Morin *et al.*, 1982; Lambert and Dodson, 1990). In addition, a large spawning aggregation of Cisco exists in the St. Mary's River between Lake Huron and Lake Superior, which may consist of Lake Huron fish that have migrated upriver to spawn (Fielder, 1998); ancillary populations with this behavior may have historically existed elsewhere in the Laurentian Great Lakes (Muir *et al.*, 2013). Most recently, work in Great Slave Lake (Northwest Territories, Canada) has documented the occurrence of separate lacustrine and riverine morphotypes of Cisco and suggested the riverine type exhibits an "adfluvial" spawning migration from the lake to its tributary rivers (Blackie *et al.*, 2012; Muir *et al.*, 2013). Adfluvial behavior has also been reported anecdotally for Cisco in small Wisconsin lakes in the Great Lakes basin (Cahn, 1927) and documented in Eurasian populations of other *Coregonus* species (Naesje *et al.*, 1986; Bronte *et al.*, 1999).

In this paper, we present initial evidence of migratory spawning behavior by Cisco entering a small inland lake from a narrow and shallow outlet stream. While we were conducting research on this lake (Lenker *et al.*, 2016), the long-time caretaker of the property informed us Cisco routinely enter the lake from its outlet stream in late autumn, just prior to the occurrence of Cisco spawning aggregations (Tom Lake, Adirondack Chapter of The Nature Conservancy, Tupper Lake, NY, pers. comm.). In response to this information, we opportunistically captured Cisco as they staged to swim into the lake and compared their size-at-age, growth rate, and sex ratio to Cisco captured in the lake. Our results provide limited but intriguing evidence that two distinct morphotypes of Cisco may be spawning in this system.

METHODS

STUDY SITE

Follensby Pond (44.17°N, 74.37°W) is located in the St. Lawrence River watershed in the Adirondack Mountains of New York State. The lake is 393 ha in area, reaches a maximum depth of 33 m, and is hydrologically connected to the Raquette River lake-chain through an outlet at its north end (Fig. 1). A man-made sill at the lake outlet controls discharge and acts as an impediment but not a complete barrier to fish movement in and out of the lake. The lake sustains naturally reproducing populations of several fish species including Cisco, Lake Trout, Largemouth and Smallmouth Bass (*Micropterus salmoides* and *M. dolomieu*), Yellow Perch (*Perca flavescens*), sunfishes (*Lepomis* spp.), and others (Solomon, unpub. data). Cisco may have been introduced to the Raquette watershed prior to the 1930s; however, no recorded stocking in Follensby Pond has occurred since that time (Greeley, 1934). A recent hydroacoustic survey indicates Cisco abundance in Follensby Pond is high for a lake of its size with an estimated population of 220,000 individuals, or 560 individuals ha^{-1} (Rudstam *et al.*, 1987; Weidel and Solomon, unpubl. data).
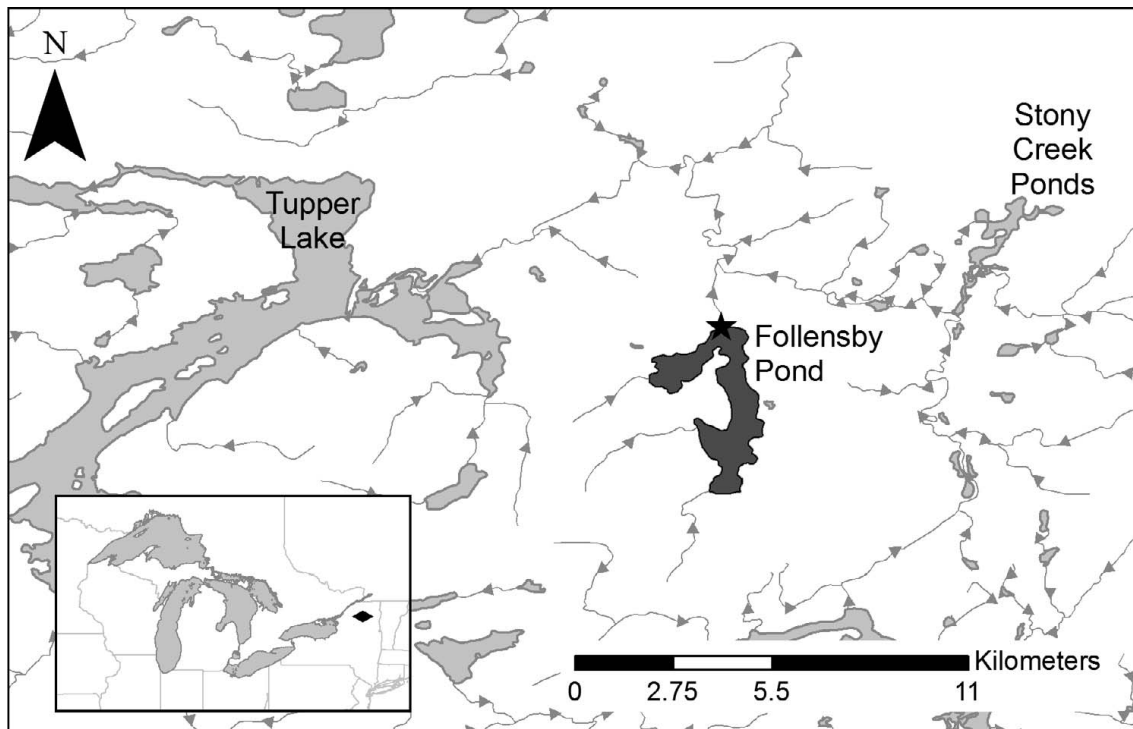
Fig. 1.—Follensby Pond is indicated in dark grey, with a star denoting the location of the outlet sill and area of stream-capture. Other streams and waterbodies are shown in light gray, with arrows indicating direction of streamflow. The inset indicates the approximate location of Follensby Pond within New York State and the Laurentian Great Lakes region

SAMPLE COLLECTION

Lake-caught fish were captured in 2013 (May 11–13), 2014 (Aug. 26), and 2015 (Aug. 18–19; Nov. 03–04), and stream caught fish were captured in 2015 (Nov. 03, 05). Lake-caught Cisco were sampled using horizontal gillnets (experimental gillnet: 1.8 m high with two panels each of 19 mm, 25.4 mm, and 32 mm bar mesh; fished for ~1.5 h sets in littoral and pelagic habitats), and vertical gillnets (seven unconnected gillnet panels 20 m deep and 3 m wide with mesh sizes of 6 mm, 8 mm, 10 mm, 12.5 mm, 15.5 mm, 18.75 mm, and 26 mm bar mesh; fished for ~6 h sets in pelagic habitats). Stream-caught Cisco were captured opportunistically with a few minutes of dip-netting on Nov. 2–5 2015 as they swam into Follensby Pond. We dip-netted fish while standing in the middle of a sill spanning the outlet stream. Just below the sill, Cisco were aggregated in a pool of approximately 0.5 m of water. In total 11 individuals were removed from the stream, representing a small percentage of the individuals actually present in the stream. Total length (mm) was recorded for each individual fish, and sex, and body mass (g), and were identified for all fish captured in November of 2015. Maturity was assessed for stream-caught Cisco by gonad removal and visually assessing ovaries/testes.

SAMPLE PROCESSING AND DATA ANALYSIS

We determined the age of captured Cisco by examining sagittal otoliths. One otolith from each individual was cast in a mold using a two-part epoxy resin, sectioned transversely through the origin using a low-speed precision saw, polished with abrasive discs, and
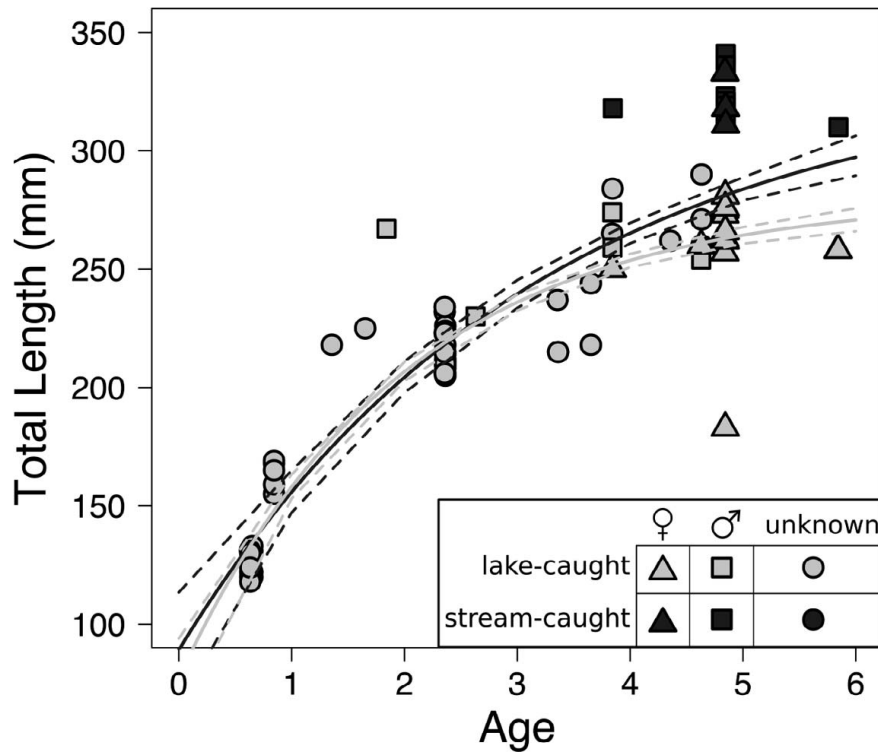
FIG. 2.—Length-age relationship for Follensby Pond Cisco. Black points indicate fish captured by dip-net as they swam into the lake from the outlet stream. A von Bertalanffy growth model was fit to the lake-caught individuals only (solid gray line; $K = 0.51 \pm 0.05$, $L_\infty = 280 \pm 5$, $t_0 = -0.64 \pm 0.13$) and to all fish including lake- and stream-caught individuals (solid black line; $K = 0.32 \pm 0.05$, $L_\infty = 333 \pm 17$, $t_0 = -0.98 \pm 0.27$). Dashed lines indicate 95% confidence intervals for the two growth models

examined microscopically to identify and count annuli (Jenke, 2002). Two observers independently interpreted each otolith and then agreed on a consensus age.

We fit age-at-length data for all the fish and for lake-caught fish only, to a standard von Bertalanffy growth model to describe somatic growth rates. Growth rates were considered significantly different if 95% confidence intervals did not overlap. To account for small sample size, a Fisher exact test was used to assess differences in sex ratios for stream-caught and lake-caught Cisco.

To investigate differences in length-weight relationships for age 4+ stream- and lake-caught Cisco, we calculated a Relative Condition Factor (K; Le Cren, 1951) and used a two-sample t-test to test for differences based on capture-location. Only age 4+ fish were used in the analysis; there was only one 3+ and one 5+ stream-caught individual so stream/lake comparisons could not be made for these age classes.

RESULTS

Stream-caught Cisco captured as they staged to swim into Follensby Pond were considerably larger at a given age than lake-caught Cisco (Fig. 2); however, these fish were not different in relative condition (K); $t = -0.057$, $P = 0.95$). Age structure of lake-caught Cisco spanned a gradient of juvenile to mature individuals (range: age 0 to 5; median age = 2), whereas stream-caught Cisco ranged only from age 3 to age 5 (median age = 4). At the time of capture, all stream-caught individuals were sexually mature, with fully developed

TABLE 1.—Proportion (sample size in brackets) of male and female fish for lake-caught and stream-caught Cisco in Follensby Pond, NY, during the spawning period of November 2015

| | Capture location | |
	Lake	Stream
Female	0.75 (15)	0.27 (3)
Male	0.25 (5)	0.73 (8)

testes or ovaries. The sex ratio differed significantly between stream- and lake-caught Cisco; 73% of the stream-caught individuals were male, compared to only 25% of those caught in the lake (Fisher exact test, $P = 0.021$; Table 1).

Because of differences in size-at-age between stream- and lake-caught fish, the estimated von Bertalanffy growth model differed depending on whether stream-caught fish were included in the dataset (Fig. 2). When the model was fit only to the lake-caught fish, the estimated initial growth rate and asymptotic length were $K = 0.51$ yr^{-1} [95% CI: 0.41–0.60] and $L_\infty = 280.4$ mm [95% CI: 270.4–290.4], respectively. When stream-caught fish were also included, the estimated initial growth rate was slower ($K = 0.32$ yr^{-1} [95% CI: 0.20–0.43]) and the asymptotic length was significantly longer ($L_\infty = 333.2$ mm [95% CI: 299.0–367.5]).

DISCUSSION

The capture of large gravid Cisco swimming into Follensby Pond from its outlet stream presents intriguing evidence of a unique Cisco morphotype entering a small inland lake to spawn, therefore suggesting two possible scenarios. First, it could be that stream-caught individuals are making spawning migrations to Follensby Pond from other lakes in the Raquette system. Nearby Stony Creek Pond and Tupper Lake (Fig. 1; ~10 and 17 km by run-of-river, respectively) contain populations of Cisco, making them possible sources of such individuals. Similar behavior has been described for Cisco traveling through channel connections in southeastern Wisconsin (Cahn, 1927), although the migration distance in that case was considerably shorter (~3.5 km) and the details reported in the paper were sparse. Furthermore, a recent genetic analysis of Lake Trout population structure along the Raquette River chain indicates admixture of disparate fish populations within this system, with Raquette Lake (~65km by run-of-river) genes present in Follensby Pond Lake Trout stocks (Solomon et al., unpubl. data). Alternatively, it could be that Follensby Pond Cisco exhibit complex and diverse life history strategies, wherein at least two distinct morphotypes exist in sympatry and one type performs a partial migration into lotic habitats. In this partial migration, the larger of the two morphotypes enters the outlet stream when physical and limnological conditions allow, and return to the lake to spawn.

Dissimilarities in somatic growth rate, and body length between stream-caught and lake-caught individuals may indicate underlying differences in life history traits between the two potential morphotypes. While Cisco typically inhabit pelagic areas of cool, well-oxygenated, deep lakes (Rudstam and Magnusson, 1985), variation in habitat preference has been noted (Ahrenstorff et al., 2013; Muir et al., 2013) and various life-histories for members of the subfamily Coregoninae is common (Morin et al., 1982; Muir et al., 2013). Our current state of knowledge for Cisco migration is that horizontally migrating individuals are smaller, have a more fusiform body shape, and fewer gill rakers than their nonmigrating counterparts, (Blackie et al., 2012; Muir et al., 2013) and Cisco that migrate vertically in the water column

also have a smaller body size than those who do not migrate (Ahrenstorff *et al.*, 2013). In the two cases above, changes in life history traits have been attributed to prey choice or habitat selectivity. Interestingly, we observed the opposite relationship with stream occupancy for Cisco, wherein stream-caught individuals entering Follensby Pond were substantially larger at a given age than their lake-caught conspecifics. The individual decision to migrate or stay resident in other salmonids is complex; however, there is evidence that it is energetically advantageous for large individuals to have a migratory life history (Jonsson and Jonsson, 1993; Dodson *et al.*, 2013). For a variety of partial-migrant salmonid species, individuals that experience fast growth are more likely to migrate to richer and more productive habitats to avoid the energetic constraints of a lower-productivity, resident habitat (Taborsky, 2008). Additionally, the migrants that take advantage of more productive spawning environments are typically large, dominant males that are able to monopolize mating opportunities due to their size (Taborsky, 2008).

While we detected habitat-dependent differences in sex ratios, these differences, despite their statistical significance, should be interpreted with some care. Cisco population structure is typically comprised of an even ratio of males to females in relatively undisturbed populations and a dominance of females in exploited populations (Bowen *et al.*, 1991; Pratt and Chong, 2012). Because male Cisco move onto spawning beds 2 to 4 d prior to females (Cahn, 1927; Scott and Crossman, 1973), and our stream sampling occurred over a 3-d period near the beginning of the 2015 spawning season, the calculated sex ratio may be influenced by limited capture dates, in addition to small sample size.

Identifying unique life history strategies for Cisco will be important for improving our understanding of population dynamics across their range. Within the Saint Lawrence watershed of the Great Lakes Basin, morphological, genetic, and life history variants of Cisco remain largely undocumented. However, records from the companion database to the Atlas of Inland Fishes of New York show Cisco have been captured in the Chateauguay River, Saranac River, and Saint Lawrence River (Carlson *et al.*, 2016), indicating the possibility of other fluvial-run populations in the Saint Lawrence watershed. Cisco have also been captured in nearby lakes too shallow to support coldwater fish year-round (*e.g.*, Lake Flower in Saranac Lake, mean depth 1.5m; NYSDEC, 2016); their presence suggests Cisco may be seasonally traveling not just through large riverine complexes but through smaller tributary systems as well. Our findings, along with those reported above, suggest the behavior witnessed at Follensby Pond may occur with some frequency within the Saint Lawrence watershed and potentially more broadly across the species' range.

Determining where and why this life history strategy exists and how to best manage for alternate life history strategies within Cisco populations will be important for reducing population declines, creating resilience in remaining stocks, and informing management decisions for Cisco re-establishment programs. Threats to Cisco are well known: warming water temperatures have reduced optimal thermal habitat (Jacobson *et al.*, 2012; Herb *et al.*, 2014), land-use changes have increased incidents of hypoxic conditions within the hypolimnion of lakes (Latta, 1995; Honsey *et al.*, 2016), and invasive species such as Rainbow smelt have displaced Cisco through competition (Hrabik *et al.*, 1998; Sharma *et al.*, 2011). Given the interaction of several stressors leading to Cisco decline, the maintenance of biocomplexity within aggregate populations may encourage stock vitality at a regional-scale, despite changes within local Cisco environments (Hilborn *et al.*, 2003). By cataloguing the standing variation in Cisco life history strategies and genotypes, management decisions for re-establishment and conservation of coregonines within inland lakes and the Laurentian Great Lakes can be further refined (Zimmerman and Krueger, 2009; Jacobson *et al.*, 2011).

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