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Retention of morphological and ecological traits of Lake Superior cisco *Coregonus artedi* after translocation into inland lakes

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ABSTRACT

Introductions of *Coregonus artedi* from Lake Superior into several inland lakes in Minnesota in the 1920s and 1930s constituted a natural experiment of how phenotypic plasticity and adaptation can shape cisco diversity. Genetic data were consistent with a Lake Superior origin for the introduced populations, which resembled contemporary Lake Superior cisco in possessing large, elongated bodies and short fins, and in maturing at older ages. Native inland cisco had smaller, deeper bodies, longer fins, and matured at younger ages. Introduced populations also retained the Lake Superior characteristic of inhabiting the upper portion of the water column and showed a high degree of planktivory. However, introduced cisco exhibited small but measurable shifts in body shape and fin lengths toward native inland forms. These morphological shifts were possibly associated with greater benthivory after translocation. Assuming that native inland populations were well adapted to inland lakes and that selective pressures on native and introduced populations were similar, these results indicated that substantial further phenotypic, behavioral, and life history change is required before the introduced populations become similarly adapted to their new environments. The findings suggest that anthropogenic environmental alterations such as climate change and eutrophication might occur at a faster pace than adaptive evolutionary responses. In addition, translocated Great Lakes coregonines could possibly maintain traits exhibited in their source lake, and may not fully restore ecological functions of extirpated populations.

Introduction

Coregonine fishes exhibit remarkable phenotypic variation in lakes across the northern hemisphere (Koelz, 1931; Vonlanthen et al., 2012). The diversity is manifested in sympatric and allopatric populations of European whitefish (*Coregonus lavaretus* and related taxa) and North American ciscoes (*C. artedi* and related taxa) that exhibit a wide variation in body morphometry (slender “dwarfs” and large, deep-bodied forms), trophic ecology (e.g. pelagic planktivores and benthic invertivores), gill raker number and morphology, jaw and head anatomy, depth preferences, and spawning times (Kahilainen and Østbye, 2006; Muir et al., 2014). Much of the coregonine diversity has likely arisen from recent adaptive radiations (Bernatchez, 2004; Østbye et al., 2006) since the last glacial maxima (8–12,000 ybp), and repeated, parallel evolution of sympatric morphotypes of North American ciscoes has occurred in a number of lakes (Turgeon and Bernatchez, 2003).

The Laurentian Great Lakes present an especially high genetic and ecological diversity of North American ciscoes (Koelz, 1927), with at least seven species recognized (Todd and Smith, 1992), although many forms have been extirpated. Lake Superior has a relatively intact assemblage of native ciscoes with *C. artedi*, *C. hoyi*, *C. kiyi*, and *C. zenithicus* still extant (Eshenroder et al., 2016). Lake Superior *C. artedi* are pelagic planktivores (Johnson et al., 2004; Gamble et al., 2011; Isaac et al., 2012) while *C. hoyi*, *C. kiyi*, and *C. zenithicus* dominate deep-water habitats (Eshenroder et al., 2016). While most inland lakes in Minnesota have one morphotype (planktivorous *C. artedi* with large numbers of gill rakers; Eddy and Underhill, 1974), sparsely rakered *C. zenithicus* is occasionally found sympatrically with *C. artedi*, as is another highly rakered, planktivorous form, *C. nipigon* (Etnier et al., 2003). Zooplankton are important in *C. artedi* diets in inland lakes, but larger, benthic-orientated prey such as *Chaoborus* and *Hexagenia* can also constitute over half their diet (Ahrenstorff et al., 2013). The origin and timing of coregonine diversification is of great interest to evolutionary ecologists and fisheries managers responsible for protecting that diversity (Bernatchez et al., 2010).

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In the face of rapid environmental change (Merilä and Hendry, 2014), it is important to understand both the factors that generate coregonine diversity (Lundsgaard-Hansen et al., 2013) and the rates of phenotypic change in individual populations. Environmentally-induced differences based on phenotypic plasticity are common in coregonines (Hile, 1936; Todd et al., 1981) and reaction norms are possibly large (Lindsey, 1981). However, if rapidly changing environmental conditions (such as those produced by anthropogenic climate change) overwhelm reaction norms (Visser, 2008), cisco populations could decline. Moreover, although coregonines are suspected to have rapidly and repeatedly evolved into multiple forms (Praebel et al., 2013; Turgeon et al., 2016), the capacity of evolution to keep pace with the effects of climate change remains an open question (Hoffman and Sgrò, 2011; Kopp and Matuszewski, 2014). Indeed, environmental change associated with recent eutrophication significantly reduced coregonine diversity in European alpine lakes (Vonlanthen et al., 2012). Thus, understanding the capacity of populations to adapt to or compensate for environmental stressors such as climate change and eutrophication is of critical importance for coregonine conservation.

Translocations of fish into novel environments allow for the examination of rates of phenotypic and genetic change, some of which may be adaptive, over relatively short time scales (Hutchings, 2014). Such changes have been reported for several translocated populations of coregonines. For example, some traits of lake whitefish *C. clupeaformis* (fin length, head morphology, and body shape), but not others (gill raker number, lateral line scale count, and interorbital width) changed after translocation to lakes within Manitoba, Canada (Loch, 1974). Shields and Underhill (1993) observed that some traits (growth rates and ultimate body size) changed immediately after translocation of cisco in Minnesota lakes, but others (pigmentation and spawning season) remained stable. Significant changes in morphology of powan (*C. lavaretus*) occurred after translocation in Scotland (Etheridge et al., 2010). Although founder effects are possible after translocation, the stocking of 90,000 vendace, *C. albula*, fry provided substantial genetic variation that was maintained in the population 92 years after introduction (Vuorinen et al., 1991). Potential phenotypic and genetic changes are of considerable interest to conservationists who are attempting to reintroduce populations that have been extirpated, to supplement declining populations, or to protect imperiled populations by translocating them to other bodies of water.

Historical introductions of *C. artedi* from Lake Superior into several inland lakes in Minnesota constituted a natural experiment to investigate how phenotypic plasticity and adaptation can shape cisco diversity. The lakes were stocked with fry, hatched from eggs of cisco captured in Lake Superior commercial nets during fall spawning periods in the 1920s and 1930s (Minnesota Department of Natural Resources files, Peter C. Jacobson, 10 July 2015). Cisco were likely absent from the lakes at the time of introduction. The lake locations near the heads of watersheds in rugged terrain apparently presented significant barriers for post-glacial colonization by fish, and the lakes contain low species diversity. This study compares morphological and ecological traits of contemporary Lake Superior cisco to introduced inland populations, relative to native inland populations. Examination of how these traits changed in the ~80 years since translocation provided insight into the rates of phenotypic change (Ellner et al., 2011) within this characteristically plastic taxon (Lindsey, 1981). Because native inland lakes were physically and chemically similar to those occupied by the introduced populations, meaningful comparisons were possible. Two contrasting predictions were considered, based on different assumptions about the potential for phenotypic change. If the introduced populations were capable of rapid adaptive evolutionary or phenotypically plastic change, contemporary samples of those fish should resemble native inland populations. In contrast, if the potential for phenotypic change was strongly constrained (due to narrow reaction norms, limited genetic diversity, weak selection gradients, or insufficient time in the new habitat), introduced populations should still resemble contemporary fish from their original source population in Lake Superior. This information should prove useful for fisheries managers considering reestablishment of depleted or lost cisco forms in the Laurentian Great Lakes (Zimmerman and Krueger, 2009). Morphological and ecological changes after introduction into a novel environment should also provide insight into the capacity of cisco to evolutionarily adapt, or to show adaptive plastic responses, to rapidly changing environments such as those driven by climate change and eutrophication.

Methods

Study area

Cisco were collected from sites in Lake Superior, four inland lakes that received introductions from Lake Superior, and five inland lakes with native cisco (Table 1). All nine inland lakes are on the Precambrian Shield in northeastern Minnesota, a region with large expanses of exposed igneous rock and shallow soils. Lakes on the Shield are often deep, with few dissolved solids, and low productivities. The five lakes with native cisco and the four with introduced populations were similar in size, depth, productivity, alkalinity, and transparency. The inland lakes were different in size and depth than Lake Superior, which also had the lowest productivity and highest transparency and alkalinity. All lakes had well oxygenated hypolimnia with TDO_3 values (vertical profile temperature associated with a dissolved oxygen concentration of 3 mg/L) <10 °C, considered to be good coldwater habitat for summer hypolimnetic dwellers such as cisco in Minnesota (Jacobson et al., 2010). The inland lakes with native cisco contained a single taxon of cisco (*C. artedi*).

Introductions of *C. artedi* fry from the Minnesota waters of Lake Superior into the four inland lakes occurred in the 1920s and 30s (60,000 fry into Clearwater Lake in 1936, 140,000 fry into Flour Lake in 1938, 90,000 fry into Greenwood Lake in 1926, 30,000 fry in 1926 and 260,000 fry in 1938 into Loon Lake). Several million hatchery-reared fry from these lakes were subsequently restocked back into Lake Superior in the 1970s and 80s. The contribution of the restocked fry to the existing Lake Superior cisco population is unknown, but was likely small (Todd, 1986). Native cisco inland lakes in this study are located in the Hudson Bay drainage. Of the inland lakes with introduced cisco, (for brevity, hereafter referred to as introduced without the term inland), Loon Lake is in the Hudson Bay drainage and the remainder are in the Atlantic drainage.

Field collection

Cisco from native and introduced inland lakes were collected with vertical gill nets used by the Minnesota Department of Natural Resources to sample pelagic fish in deep lakes. The nets consisted of seven 61 m deep panels of monofilament webbing (bar measure mesh size × panel width: 10 mm × 0.9 m, 13 mm × 0.9 m, 19 mm × 1.8 m, 25 mm × 1.8 m, 32 mm × 3.0 m, 38 mm × 3.0 m, 44 mm × 3.0 m). The 10 mm and 13 mm panels were sewn together vertically into one net, as were the 19 mm and 25 mm panels. The 32 mm, 38 mm, and 44 mm panels each comprised individual nets for a total of five separate vertical nets. Each net was ganged together by a 2 m connecting rope and the gang (5 nets with 7 total individual mesh panels) was set as a unit in the deepest basins of a lake. One gang was set in simple lake basins that have a single deep area. A maximum of three gangs were set in complex lake basins with multiple deep areas. Each net was deployed to cover the entire water column and set overnight. Temperature and dissolved oxygen profiles were collected at each gang location. Depth of capture was recorded for each specimen and relative water column position was calculated as (bottom depth − capture depth)/(bottom depth − thermocline depth) for fish below the thermocline, and as ((thermocline depth − capture depth)/thermocline depth) + 1 for fish above the thermocline. Determination of relative water column

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