Journal of Great Lakes Research xxx (2017) xxx–xxx

Contents lists available at ScienceDirect

Journal of Great Lakes Research

journal homepage: www.elsevier.com/locate/jglr

A population on the rise: The origin of deepwater sculpin in Lake Ontario

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ARTICLE INFO

Article history:
Received 29 September 2016
11 April 2017
Accepted 27 April 2017
Available online xxxx

Keywords:
Deepwater sculpin
Larval drift
Lake Ontario
Recolonization
Resurgence

ABSTRACT

Deepwater sculpin, *Myoxocephalus thompsonii*, were thought to have been extirpated from Lake Ontario. However, in recent years, abundance has increased and recruitment has been documented. There are two hypotheses concerning the origin of the current Lake Ontario deepwater sculpin population. First, individuals from the upper Great Lakes may have recolonized Lake Ontario. Alternatively, the Lake Ontario population may have not been extirpated, and the remnant population has recovered naturally. To test these hypotheses, eight microsatellite loci were used to analyze samples from the current Lake Ontario population, museum specimens from the historic Lake Ontario population, and current upper Great Lakes populations. The genetic data suggest that historically throughout the Great Lakes, deepwater sculpin exhibited low levels of spatial genetic structure. Approximate Bayesian Computation analyses support the hypothesis that the current Lake Ontario population is more closely related to populations in the upper Great Lakes than to the historic Lake Ontario samples, indicating that the current Lake Ontario population likely resulted from recolonization from the Upper Great Lakes. The current Lake Ontario population has reduced allelic diversity relative to upper Great Lakes populations, indicating a possible founder effect. This study demonstrates the role life history variation can play in recolonization success. The pelagic larval phase of the deepwater sculpin allowed recolonization of Lake Ontario via passive larval drift.
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Introduction

Deepwater sculpin (*Myoxocephalus thompsonii*) are an important part of deepwater ecosystems of the Laurentian Great Lakes. As a native fish in deepwater food webs, the species helps to maintain a functional and resilient ecosystem. Deepwater sculpin are most abundant at depths exceeding 90 m (Kraft and Kitchell, 1986; Madenjian and Bunnell, 2008; Wells, 1968), and it appears that differences in depth preference allow the deepwater sculpin to coexist with the slimy sculpin (*Cottus cognatus*) (Madenjian and Bunnell, 2008). Most of the Great Lakes have experienced a decline in deepwater sculpin abundance in the recent past (Bunnell et al., 2006; Lantry et al., 2007; Roseman and Riley 2009). Several hypotheses have been proposed to describe the mechanism(s) contributing to deepwater sculpin population declines. These include competition and predation by slimy sculpin (Brandt 1986) and declines of their prey, the benthic amphipod *Diporeia* spp. which would limit any recovery potential in areas where population declines may occur (Hondorp et al., 2005; Owens and Dittman, 2003). Deepwater sculpin in Lake Michigan were found to have a low energy density, which may be due to increased foraging effort for *Diporeia* or the need to eat alternative prey with lower energy content (Hondorp et al., 2005). Reduced abundance of native forage fishes like the deepwater sculpin has also contributed to nutritional effects on important predators, such as the lake trout (*Salvelinus namaycush*; Roseman and Riley, 2009).

An alternate hypothesis suggests deepwater sculpin population declines are best explained by predation on larval deepwater sculpin by alewives, nonnative planktivores that are capable of feeding on the pelagic larval phase of deepwater sculpin (Bunnell et al., 2006; Madenjian and Bunnell, 2008). There is substantial spatial overlap between deepwater sculpin larvae and alewives, making this life stage vulnerable to predation (Madenjian and Bunnell, 2008). After deepwater sculpin eggs hatch in March, larvae inhabit the entire water column for the next three months before they settle on the bottom in July (Geffen and Nash, 1992). In Lake Ontario, the timing of deepwater sculpin loss from the ecosystem did coincide with high alewife abundance (Madenjian and Bunnell, 2008; Walsh et al. 2016), but the more recent apparent increase in deepwater sculpin documented by Lantry et al. (2007) occurred as alewife abundance was still high. Weidel et al. (in this issue) documented post-larval (≥30 mm TL) demersal deepwater

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http://dx.doi.org/10.1016/j.jglr.2017.04.009
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sculpin in May at depths of 35–55 m in Lake Ontario, and suggested that predation on larval deepwater sculpin (by alewives and other species) was reduced not by a decrease in abundance, but by a decrease in habitat overlap in these vulnerable stages of deepwater sculpin early life history.

Of all the Great Lakes, Lake Ontario experienced the most drastic decline of deepwater sculpin. In the 1920s, large numbers of deepwater sculpin resided in the lake (Wells, 1969), and diets of predators during that time period also confirmed these high numbers (Dymond 1928), which seemed to persist through the 1940s (reviewed in Lantry et al., 2007). Some researchers considered the population to be extirpated by the 1960s (Brandt, 1986; Christie, 1973; Smith, 1985); however, isolated individuals continued to be captured until 1972. Deepwater sculpin were not collected in any standard bottom trawling between 1973 and 1996 (Lantry et al., 2007). In 1996, three deepwater sculpin collections marked the first time the species had been seen since 1972, and sporadic captures continued until more consistent catches starting in 2005 led researchers to question the source, dynamics, and future of this population (Lantry et al., 2007).

The origin of the recovering deepwater sculpin population has been a question of interest to researchers and managers given the need to understand relationships among extant populations for native species restoration in Great Lakes ecosystems (Zimmerman and Krueger, 2009). Since 2005, the Lake Ontario deepwater sculpin population has continued to increase in abundance and density, and in recent years, small (30–60 mm TL) individuals have been captured, indicating that recruitment is occurring in the population (Weidel et al., in this issue). Based on the species' summary and status in 2005 (Lantry et al., 2007), there were two possible scenarios offered to explain the source of the rebounding deepwater sculpin population. One hypothesis is that the Lake Ontario population was never extirpated. Instead, the population may have continued to survive in low numbers in areas that were not sampled during ongoing trawling programs. Weidel et al. (in this issue) show catches of deepwater sculpin at depths >200 m, which were not sampled by trawling until 2013, so it is plausible that a greatly decreased population existed in unsampled habitat. An alternative hypothesis is that the Lake Ontario population may have been extirpated, and the lake was more recently recolonized by larvae that drifted from the Upper Great Lakes. The two hypotheses are not mutually exclusive. Either explanation would result in the current population likely being founded by a small number of individuals, which could result in reduced genetic diversity relative to source populations or the previous Lake Ontario population.

Determining the source of a recovering population can provide insight into how a population can recover from the brink of extirpation and the genetic consequences of that recovery. Genetic data have been used to determine whether species restoration resulted from natural recruitment or hatchery supplementation in lake trout (*Salvelinus namaycush*) (Guinand et al., 2003; Piller et al., 2005). A similar approach has been used to differentiate a cryptic refugial population from rapid postglacial recolonization in the three-spined stickleback (*Gasterosteus aculeatus*) (Ravinet et al., 2014). Changes in genetic composition due to range expansion and recolonization can be observed in as little as 1.5 generations (Hagen et al., 2015). In this study, our objectives were to 1) assess the genetic diversity of the current Lake Ontario population and 2) determine the most likely source of recently-captured deepwater sculpin individuals in Lake Ontario.

Methods

Sample collection

As part of both standard Lake Ontario fisheries assessment programs and occasional targeted deepwater sampling efforts, the USGS Great Lakes Science Center's Lake Ontario Biological Station (LOBS), New York State Department of Environmental Conservation's Cape Vincent Fisheries Unit (NYSDEC), Environment Canada's Water Quality Monitoring and Surveillance Division (EC), and Ontario Ministry of Natural Resources (OMNR) have collected deepwater sculpin in recent years with bottom trawls (Lantry et al. 2007). Genetic samples were taken from numerous individuals collected by LOBS, NYSDEC, and EC, and were stored at LOBS. Upon capture of a deepwater sculpin, the live length (mm TL), weight (g), and location and depth of capture were recorded. If the animal was alive, a fin clip was taken and preserved in 95% ethanol. In cases where mortality occurred, the whole body was preserved in 95% ethanol. Most samples were from individuals collected from southern waters of Lake Ontario, although some collections have been made by EC in northern waters near Cobourg, Ontario (Fig. 1; Table 1). Samples were grouped into ecoregions, based on geologic basins (Missisauga: n = 80; Rochester: n = 28). Historical collections from the south shore of Lake Ontario near Oswego, NY in 1936 and 1942 (n = 60) were also analyzed (samples supplied by Cornell University Museum of Vertebrates; CU# 10362, 10389, 27693, 27695, 28010, 54421).

Samples from lakes Superior, Michigan, and Huron (Upper Great Lakes) were collected from multiple sampling locales during the USGS Great Lakes Science Center's (USGS-GLSC) spring bottom trawl forage fish assessment surveys between 2002 and 2004 (Fig. 1; Table 1). The sampling locations in Lake Superior correspond to ecoregions (Gorman and Todd, 2007), which were delineated primarily based on slope and geology, and samples were grouped from several assessment stations within each ecoregion because of small sample sizes. Samples in Lakes Michigan and Huron were grouped by sampling location. Sample site and ecoregion names and abbreviations for all four lakes are summarized in Table 1 and Fig. 1.

Laboratory procedures

For the recent Lake Ontario samples, genomic DNA was extracted using the Promega Wizard® SV 96 Genomic DNA Purification System and DNA was eluted in 50 μl. For samples from the Upper Great Lakes, DNA was extracted from fin tissue using QIAGEN DNeasy kits (Qiagen, Inc., Valencia, CA) according to manufacturer's specifications. Extracted DNA was quantified using a ThermoScientific NanoDrop 2000c spectrophotometer. All samples were analyzed at two previously-used microsatellite loci (*Cgo*33 and *Cgo*05ZIM; Englbrecht et al. 1999) and eight newly-developed loci (*Mth*-256, 263, 286, 287, 314, D11a, E10, G10; W. Stott, USGS-GLSC, unpublished data). PCR reactions (15 μl) consisted of: 50 ng DNA, 1 × PCR buffer, 0.2 mM dNTPs, varying concentrations of a fluorescently-labeled forward primer, reverse primer, $MgCl_2$, and Taq polymerase (Table S1). Thermal cycling conditions for the newly-developed loci consisted of: 1) an initial 3 min 95 °C denaturation, 2)15 cycles of 94 °C for 1 min, annealing (see Electronic Supplementary Material (ESM) Table S1 for temperature) for 45 s, 72 °C for 10 s, 3) 20 cycles of 94 °C for 30 s, annealing for 30 s, and 72 °C for 10 s, and 4) 72 °C final extension for 5 min. Thermal cycling conditions for *Cgo*33 and *Cgo*05ZIM were: 1) an initial 2-minute denaturation, 2) 35 cycles of 94 °C for 1 min, 50 °C for 1 min 30 s, 72 °C for 1 min 30 s, and 3) 72 °C final extension for 5 min. For the Lake Ontario samples, amplified fragments were visualized on a Beckman Coulter CEQ8000 capillary electrophoresis system. For the upper Great Lakes samples, amplified PCR products were visualized on 6% denatured polyacrylamide gels using an FMBIO II scanner (Hitachi Software Engineering Co., Ltd., Yokohama, Japan). Current and historic Lake Ontario samples were processed at one laboratory and Upper Great Lakes populations were processed at another laboratory. Allele sizes were standardized between the two electrophoresis systems using 24 deepwater sculpin samples of known genotype.

The Lake Ontario deepwater sculpin samples from 1936 and 1942 had been fixed in formalin and subsequently stored in ethanol. Genomic DNA was extracted using the Gentra Puregene Tissue Kit, using the manufacturer's protocol for formalin-fixed specimens. Modifications to the protocol included increasing the amount of proteinase K to 60

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