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Genetic connectivity and diversity of walleye (*Sander vitreus*) spawning groups in the Huron–Erie Corridor

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ABSTRACT

The Huron–Erie Corridor (HEC) connects the upper and lower Great Lakes, providing key fish passage. A century of channelization, dredging, and pollution has led to habitat loss and declining fish numbers. Since 2004, the multi-agency HEC initiative augmented fish spawning habitat at Belle Isle and Fighting Island in the Detroit River, whose populations are examined here. We analyze genetic patterns among seven spawning groups ($N = 311$) of walleye *Sander vitreus*, a key fishery species, using nine nuclear DNA microsatellite loci and mitochondrial DNA control region sequences. Results reveal that all spawning groups contained appreciable genetic diversity (microsatellites: $H_O = 0.72$; mtDNA: $H_D = 0.73$) and showed a mixture of connectivity and divergence. Genetic relationships did not fit an isolation by geographic distance hypothesis, with some closely spaced populations being very different. Notably, the Flint River–Lake Huron spawning group was the most divergent, showing no genetic exchange. The Belle Isle and Fighting Island populations markedly differed, with the latter showing some genetic exchange with the Grosse Ile (Detroit River) and the Huron River (northwest Lake Erie) populations to the south. Walleye spawning at Fighting Island experienced no significant change in overall genetic diversity pre- versus post-habitat augmentation, but the allelic frequency changed. Our results comprise an important baseline for future population analyses and habitat assessment of these habitat augmentation areas. Despite habitat degradation and pollution, it appears that historic walleye spawning groups have persisted along the HEC, meriting continued genetic monitoring and further restoration efforts to conserve and enhance this important and diverse fishery.

Introduction

Understanding the genetic connectivity (i.e., gene flow) and divergence of populations is fundamental to develop appropriate management strategies for ecologically and economically valuable species. Notably, identifying barriers to gene flow reveals important ecological information on species movement, dispersal, behavior, survival, and reproduction patterns that may be used to identify evolutionary significant units or other conservation management designations (see Sork and Waits, 2010; Waples, 1995; Wofford et al., 2005).

Aquatic populations may maintain gene flow through connecting channels that serve as migration corridors among watersheds (LeClerc et al., 2008; Robinson et al., 2002). Vagile fishes use such avenues to disperse to spawning sites, nursery habitats, and feeding grounds (Meeuwig et al., 2010; Sheer and Steel, 2006). Some widely distributed species may exhibit high gene flow across their connected range, with low overall population structure and little specialization (Boulet et al., 2007; Hughes, 2007). On the other hand, species having spawning site fidelity may show marked genetic structure and local adaptedness, despite apparent ample opportunity for migration and gene flow among adjacent locations. Notably, populations of salmonid fishes and other species, including walleye *Sander vitreus* (Percidae: Teleostei) are genetically structured due to spawning site philopatry and natal homing (Banks et al., 2000; Jennings et al., 1996; Nielsen and Fountain, 1999; Stepien and Faber, 1998; Utter et al., 1989). Throughout most of the year, walleye move widely and intermingle within and among bodies of water, with some individuals traveling 50–300 km (Colby et al., 1979). In the spring walleye return to spawn at rocky shoals believed to be their natal sites (Jennings et al., 1996; Stepien and Faber, 1998; Wang et al., 2007).

Anthropogenic activities, such as exploitation, stocking, and habitat fragmentation and channelization may disrupt or increase genetic exchange across migration corridors, changing relationships among sub-populations. Such factors may lower genetic diversity and increase genetic drift, or may act to homogenize formerly different groups (Laroche and Durand, 2004; Wofford et al., 2005) and lead to declines in adaptedness and fitness (Leberg, 1992; Schindler et al., 2010).

Walleye distribution and genetic patterns

The walleye is one of the most ecologically and economically valuable fishes in the Great Lakes, constituting a keystone species as a primary predator (Locke et al., 2005; Nate et al., 2011; Roseman et al., 2010)

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and supporting large sport and commercial fisheries (Schmalz et al., 2011). Its native distribution ranges from the Mackenzie River in the Northwest Territories of Canada, south to the US Gulf Coast, and northeastward to New Hampshire and Quebec (Page and Burr, 2011). Over the past century, stocking transplants – many originating from western Lake Erie in the Great Lakes – introduced walleye throughout most of the continental US and southern Canada (summarized by Billington et al., 2011).

Broad and fine-scale spatial genetic patterns of walleye spawning groups have been defined across North America using mitochondrial (mt) DNA (Billington et al., 1992; Gatt et al., 2000, 2002; Stepien and Faber, 1998) and nuclear DNA microsatellite (μsat) loci (Stepien et al., 2009, 2010, 2012; Strange and Stepien, 2007). Results have shown that many walleye spawning groups exhibited little genetic connectivity (e.g., gene flow) and significantly diverged in genetic composition, including between and within lakes, their basins, and connected tributaries (Stepien et al., 2009, 2010). The largest genetic divisions across their native range separated populations outside of the Great Lakes region from those within (Stepien et al., 2009). The Great Lakes region was colonized by walleye originating in three Pleistocene glacial refugia: the Atlantic coastal, Mississippian, and Missourian (Billington et al., 1992; Gatt et al., 2000; Stepien and Faber, 1998; Ward et al., 1989). Primary population demarcations within the Great Lakes separate the upper Lakes (Lakes Superior, Michigan, and Huron) from the lower Lakes (Lakes Erie and Ontario), with significant genetic barriers between most of the lakes and some within them (Stepien et al., 2009, 2010; Strange and Stepien, 2007). The genetic patterns of the upper Great Lakes are likely a result of fish colonizing from the Mississippian and Missourian glacial refugia. The lower Great Lakes populations also were largely founded by the Mississippian refugium, with some contribution from the Atlantic Coastal refugium (Billington et al., 1992; Gatt et al., 2000; Stepien and Faber, 1998; Ward et al., 1989). A recent investigation evaluated three closely-related Lake Erie spawning runs over 15 years, showing overall within-site genetic consistency, and some genetic connectivity and divergence among them (Stepien et al., 2012).

Little is known of the genetic connectivity or divergence among walleye spawning groups in connecting channels, such as the HEC. Those spawning groups may be locally adapted, with unique ecological and physiological variations that may aid their response to external pressures such as spawning habitat loss, exploitation, invasive species, and climate change (Kerr et al., 2010; Stepien and Faber, 1998). Such perturbations likely have impacted walleye populations across the Great Lakes for more than a century, especially along fragile and degraded connecting channels, including the HEC. Defining the patterns of genetic connectivity and divergence of HEC walleye spawning groups may aid managers to maintain and enhance the fishery across this highly impacted system.

Degradation and augmentation of fish habitat along the Huron–Erie Corridor

The HEC is one of four connecting channels within the Great Lakes; it links Lakes Huron and Erie via the St. Clair River, Lake St. Clair, and the Detroit River (Fig. 1). The HEC constitutes a major international shipping route, supporting over $80 billion USD in annual trade (USGS, 2010). It once housed productive spawning and nursery habitats for many ecologically and economically important fish species, including lake trout *Salvelinus namaycush*, lake sturgeon *Acipenser fulvescens*, and walleye (Manny et al., 2010). The first reported habitat modifications began in 1874 with the construction of a shipping channel (914 m long, 91 m wide, and 6 m deep) near Bois Blanc Island in the Detroit River, which eliminated fish spawning habitat in that area. Since that time, the HEC underwent a series of detrimental habitat modifications and fragmentation, including loss of coastal wetlands, armoring of shorelines, channelization, dredging, and industrialization (Bennion and Manny, 2011; Hartig et al., 2009; USGS, 2010).

In addition to habitat loss, industrial outputs along the HEC resulted in heavy metal contamination and declining fish health and numbers throughout the mid to late 20th century (Hartig et al., 2009). Fish health problems included neoplasms, tumors, and lesions on walleye, brown bullhead *Ameirus nebulosis*, white sucker *Catostomus commersonii*, and other species (Manny and Kenaga, 1991). During the 1970s, walleye populations crashed and the entire fishery (commercial and recreational) was closed along the HEC due to high mercury levels in fish tissues.

In 2004, the HEC Initiative partnered 27 federal, state, and provincial agencies and local groups with the goal of restoring aquatic habitat (USGS, 2010). Two artificial reefs were installed in the Detroit River in waters ≥ 6 m deep: one in 2004 off the northeastern corner of Belle Isle (site C in Fig. 1) and another in 2008 at Fighting Island offshore from LaSalle, Ontario (site D in Fig. 1) (HTG, 2009, 2011; Habitat Task Group of the Lake Erie Committee, Great Lakes Fishery Commission). Pre-construction assessment of spawning habitat revealed that walleye spawned at the Belle Isle site (Manny et al., 2007) and walleye and lake whitefish *Coregonus clupeaformis* spawned on suboptimal substrates at Fighting Island (HTG, 2009; Roseman et al., 2011). Prior to installation of these artificial reefs, the Belle Isle and Fighting Island sites contained suboptimal habitat for walleye spawning with thin patches (<8 cm thick) of sand and small-diameter gravel on hardpan clay, lacking interstitial spaces to protect fish eggs from predation or dislodgement (Manny, 2006; Roseman et al., 2011). In 2004, 1080 m^2 of broken limestone (41–61 cm diameter), metamorphic cobble and gravel (20–30 cm), and coal cinders (2–8 cm) were deposited at the Belle Isle reef site to augment the spawning substrate (Manny et al., 2005). In 2008, 3300 m^2 of four different bed materials were deposited at the Fighting Island site, including a wide size range of broken limestone (5–50 cm) and rounded rock (10–25 cm; HTG, 2009, 2011) to provide an interstitial space gradient so that fish eggs would not be swept away by the current (Roseman et al., 2011). Prior to our study, it was unknown if walleye spawning at Belle Isle and Fighting Island belonged to historical spawning groups or were migrants from other locations.

Use of the Huron–Erie Corridor by walleye

Ripe walleye have been tagged and recorded to travel through the HEC in the spring to reach their spawning grounds (Ferguson and Derkson, 1971; Wang et al., 2007). Historically, walleye were known to spawn at sites along the HEC, most of which were sampled in the present study, with major runs occurring in Lake Huron's Saginaw Bay, the Thames River of Lake St. Clair (site B; Fig. 1), and the Hen Island shoals in northwestern Lake Erie (site G; Goodyear et al., 1982; Wolfert, 1963; known spawning sites are marked with Xs in Fig. 1). Along the remainder of the HEC, smaller walleye spawning runs were located in the Flint River (site A), St. Clair River (including at its connection to Lake Huron), Detroit River (sites C–E), including its lower reaches and mouth, and the Huron River (site F; Fielder et al., 2006; Goodyear et al., 1982). Historical walleye spawning runs likely occurred at Belle Isle (site C) and Fighting Island (site D), where the artificial reefs were constructed (HTG, 2009; Manny et al., 2007).

Walleye spawning in the HEC have experienced varying degrees of habitat degradation, exploitation, and stocking (Thomas and Haas, 1994). Saginaw Bay comprises the largest commercial walleye fishery in Lake Huron (Fielder and Baker, 2004). This population experienced spawning habitat loss in the Saginaw River and its tributaries, including the Flint River (site A), due to construction of several dams. The walleye run in the Flint River is relatively small and provides one of the sole sources of natural recruitment to Saginaw Bay (Leonardi and Gruhn, 2001). The lower reaches of the Flint River were stocked with walleye in 1976 (Leonardi and Gruhn, 2001) and the Saginaw River and Bay have been stocked on a regular basis since 1989 (USFWS/GLFC, 2010) from a western Lake Erie source. There thus is