Journal of Great Lakes Research 41 (2015) 1131–1137

Contents lists available at ScienceDirect

Journal of Great Lakes Research

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

Spatial genetic structure of suspected remnant and naturalized populations of muskellunge and evidence for introgression between stocked and native strains

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ARTICLE INFO

Article history:
Received 25 March 2015
Accepted 21 August 2015
Available online 11 September 2015

Communicated by Stephen Charles Riley

Index words:
Muskellunge
Esox masquinongy
Genetic structure
Stocking
Introgression
Management

ABSTRACT

Achievement of management goals to maintain, enhance, or re-establish fish species of management importance in the Great Lakes often relies on hatchery supplementation. Issues may arise when individuals of hatchery origin are super-imposed upon natural stocks, particularly when resident species are naturally in low abundance such as with most Muskellunge (*Esox masquinongy*) populations. We used 12 microsatellite loci to survey 450 individuals from 13 populations to quantify the contributions of stocked individuals to the current Muskellunge stock structure in Michigan and document evidence of inter-strain hybridization. Genetic differentiation among populations based on variance in allele frequency was moderately high (mean $F_{st} = 0.18$), and was largely attributed to stocking history. The major genetic discordance was found among populations inhabiting waters with native Great Lakes and native and introduced Northern Muskellunge strains. We identified five genetic lineages, corresponding to native stocks (one Great Lake and two Northern strains) and two Northern Muskellunge strains obtained from other states and stocked across Michigan. Analyses revealed that the majority of populations sampled were composed of multiple hatchery strains of Northern Muskellunge, including waters connected to the Great Lakes and in waters with remnant native stocks. Admixtures of stocked strains and evidence of inter-strain hybridization were widespread. Collectively, data reveal that hatchery programs have the potential to restructure native fish populations on a statewide basis. Greater attention to current genetic stocks of both donor and recipient populations is advised to ensure that future supplementation efforts do not further erode the integrity of native stocks.

Introduction

Muskellunge (*Esox masquinongy*) are native to the Great Lakes and northern Mississippi River drainages in North America (Scott and Crossman, 1973; Crossman, 1978). Several strains or subspecies of muskellunge are recognized (Becker, 1983) including northern muskellunge from inland waters in the Mississippi drainage and Great Lakes muskellunge from the five Great Lakes and the St. Lawrence River. Great Lakes muskellunge were once abundant enough in Michigan to support a limited commercial fishery (Schrouder, 1973) and were highly valued in the commercial fishery in the late 1800s (Kerr, 2011). The natural range of Great Lakes muskellunge in Michigan waters is believed to include: Brevoort and Indian lakes (Upper Peninsula); the Cheboygan River drainage including the Burt, Black, and Mullet Lake chain; the intermediate chain of lakes including Elk, Skegemog, and Torch lakes; the St. Mary's River (Upper Peninsula); the lower Menominee River (Upper Peninsula); Green Bay and its tributaries; Saginaw Bay; St. Clair-Detroit River system; and potentially drowned river mouths associated with tributaries to Lake Michigan. Limited information is available pertaining to current distribution and abundance for populations of Great Lakes muskellunge. Northern muskellunge in Michigan waters were believed to be restricted to a few water bodies in the western Upper Peninsula as the Wisconsin River system headwaters are in Michigan, and this strain is native to this river system.

Until 2012, the Michigan Department of Natural Resources (MDNR) annually stocked non-native strains of northern muskellunge (*E. masquinongy*) into inland waters of the State, including impoundments upstream of dams on Great Lakes tributaries. Little

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http://dx.doi.org/10.1016/j.jglr.2015.08.011
0380-1330/

current information is available on the genetic characteristics of suspected remnant muskellunge populations, spatial genetic structure among these populations, or whether inter-breeding has occurred between individuals from resident stocks and hatchery strains. There are concerns that stocking efforts that have been ongoing since the 1950s may not be compatible with management goals to maintain the genetic integrity or sustainability of remnant populations of a native muskellunge (Great Lakes or northern) that are believed to have historically occurred in watersheds associated with the Great Lakes basin and Mississippi River drainage, respectively.

The management objectives for muskellunge in Michigan include management of waters to preserve the natural range of native species, to rehabilitate or establish populations where natural reproduction is likely, and to establish populations in waters where stocked fish have been shown to provide a trophy fishery (Smith et al., in press). Since the inception of the Michigan program, muskellunge were generally stocked into larger lakes on the premise that these fish would add variety and quality to the states' fisheries program along with meeting the needs of anglers for a trophy fish experience. Data on the effects from stocking of northern muskellunge on remnant Great Lakes muskellunge populations are lacking. Identification of Great Lakes muskellunge populations with low levels of genetic diversity (inferentially attributed to low population abundance) is important for conservation and management planning. Identification of potential areas of high genetic differentiation, for example among populations from different Great Lakes basins, would be important to identify and reduce introgression risks (Kapuscinski et al., 2013), and potential negative effects of inter-strain outbreeding to future recruitment and population viability (McClelland and Naish, 2007; Naish et al., 2008).

Stocking in general has been shown to significantly affect levels of genetic diversity within and among populations (Hindar et al., 1991; Reisenbichler and Rubin, 1999; Miller and Kapuscinski, 2003). For muskellunge, the effects of supplementation programs have been widely documented (Jennings et al., 2010). For example, the genetic composition of individual water bodies, spatial stock structure over large scales, and population-level changes in heritable traits (Miller et al., 2009, 2012) have been observed. In light of these and other studies (e.g., Clapp and Wahl, 1996; Margenau and Hanson, 1996; Wahl, 1999) along with prevailing views that populations in tributaries from Lakes Superior and Michigan are highly differentiated relative to the current northern broodstock source(s) and future sources of Great Lakes broodstock production (St. Clair-Detroit River system), development of genetic stocking guidelines is warranted.

Background and history of muskellunge management in Michigan

The Michigan Department of Natural Resources (DNR) initiated a lake resident feral broodstock program in 1954 (Williams, 1954) using gametes taken from a putative northern muskellunge population source from Lac Vieux Desert in Gogebic County in the western Upper Peninsula (UP) (Fig. 1). For a period of 18 years, fingerlings from gametes taken from Lac Vieux Desert were used to stock Murphy Lake in Tuscola County and Bankson Lake in Van Buren County, in the east-central region of Michigan's Lower Peninsula (Fig. 1). Fish from Murphy Lake were subsequently used to populate two additional broodstock lakes that are currently used for gamete collections for northern muskellunge culture and stocking (Thornapple Lake in Barry County and Hudson Lake in Lenawee County; Fig. 1). Thus, initially, it appears that a single Michigan resident northern muskellunge strain was used for artificial propagation although Hubbs (1933) believed Thornapple Lake supported a native strain of muskellunge.

Subsequently, strains of muskellunge were brought into the Michigan state fish hatchery system from numerous sources as the result of below required production of fish from Michigan broodstock sources. During an 11 year period (1998–2009) fingerlings were obtained from Iowa. In 1997, 2003 and 2011, additional fingerlings were obtained from Indiana Department of Natural Resources state fish hatchery system. Gametes were also obtained from Wisconsin Department of Natural Resources which is the source of the Iowa Department of Natural Resources' state fish hatchery system muskellunge. Thus, given the geographic range and large numbers of the gametes, eyed embryos, or fingerlings obtained from other states and stocked widely throughout Michigan, if survival of stocked fish was relatively high and if stocked fish mated randomly with native fish, there is high potential for admixture and inter-strain introgression based on super-imposition of multiple hatchery strains from multiple sources.

The MDNR recognizes 116 inland and Great Lakes muskellunge waters across the state. Seventy-seven of these waters have self-sustaining populations and the others are maintained with stocking. Over the period 1933–1979, 1,581,000 muskellunge were stocked throughout Michigan. Based on the stocking history described above, it is likely that fish stocked during the early period were all descended from the Lac Vieux Desert population. From 1980–present, at least 1,190,000 have been stocked. Given the large numbers and numerous strains used for supplementation, our working hypothesis was that population levels of genetic diversity and inter-population relationships largely reflect stocking history and not natural (e.g., vicariance and gene flow) processes.

Currently, the MDNR is initiating a Great Lakes muskellunge broodstock program that will replace northern strain muskellunge as the source of gametes for production and release into most Michigan inland waters. Some waters in the western Upper Peninsula (UP) will continue to be stocked with northern strain muskellunge directly from the Wisconsin Department of Natural Resources state fish hatchery system. Production from this new broodstock may also be useful for supplementation activities for remnant Great Lakes muskellunge in Great Lakes waters and their tributaries. Given the objectives of the MDNR Esocid Management Plan (Smith et al., in press), the knowledge of existing stock structure of remnant populations across waters associated with each of the Great Lakes (Superior, Michigan, Huron/ St. Clair-Detroit River system) will be critical to the plan's successful implementation.

The primary objectives of this study were: 1) to genetically characterize levels of diversity within and among populations of suspected Great Lakes muskellunge and 2) quantify evidence for mixing and introgression between native Great Lakes and stocked northern muskellunge.

Methods

Sample collection

Fin clips from 450 muskellunge were sampled from 13 Michigan lakes and rivers by MDNR personnel (see Table 1 for sample sizes and Fig. 1 for locations). Stocking histories of water bodies surveyed represent a range of supplementation regimes (Table 1). Populations from several rivers (e.g., St. Mary's, Tahquamenon, Cheboygan, Tittabawassee, and Huron) were of particular interest because of connectivity with the Great Lakes. The Huron River was also of interest because it is a large Michigan tributary to Lake Erie near lower Detroit River and Lake St. Clair. Because Northern Pike (*Esox lucius*) and northern muskellunge hybrids (Tiger muskellunge) were historically stocked throughout Michigan, we also genotyped northern pike from one natural population (Gunn Lake; $N = 40$).

Laboratory analysis

DNA was extracted from fin tissue and scales using QIAGEN DNeasy kits (Qiagen, Inc., Valencia, CA). DNA was quantified using a Nanodrop spectrophotometer (NanoDrop Technologies, Thermo Scientific, Wilmington, DE) and diluted to a concentration of 20 ng/μL. All individuals were genotyped at twelve microsatellite loci including: EmaA5, EmaA10, EmaA104, EmaC1, EmaD12a (Sloss et al., 2008), EluB108, EluB118, EluBe (Launey et al., 2006), Ema15, Ema30 (Reading et al.,