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RESEARCH ARTICLE

Two decades of genetic consistency in a reproductive population in the face of exploitation: patterns of adult and larval walleye (*Sander vitreus*) from Lake Erie's Maumee River

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Abstract Analyses of genetic variability and allelic composition in a species exhibiting reproductive fidelity to natal sites may provide important ecological indication of temporal population dynamics, facilitating understanding responses to past disturbances and future climate change. The walleye is an ecologically and economically valuable species, whose largest fishery centers in Lake Erie of the Laurentian Great Lakes; it exhibits reproductive site fidelity, despite otherwise wide-ranging dispersal. We tested whether genetic composition and diversity have remained temporally stable in Lake Erie's Maumee River, which is the largest and most highly fished spawning run. This population has experienced over a century of exploitation, habitat alterations, and pollution, which may have affected genetic structure and might influence future sustainability. Fourteen nuclear DNA microsatellite loci were analyzed from 744 spawning run walleye to test genetic patterns across: (1) years ($N = 12$, spanning 1995–2013), (2) birth year cohorts, (3) the sexes, (4) those reproducing earlier (ages 2–6) versus later (7 or older) in life, and (5) the adults versus larvae. Results indicated stability in genetic diversity levels (mean $H_O = 0.76 \pm 0.03$) and allelic composition across years ($F_{ST} = 0.000$–0.006, NS), cohorts ($F_{ST} = 0.000$–0.013, NS), sexes ($F_{ST} = 0.000$, NS), earlier versus later reproduction ($F_{ST} = 0.000$, NS), and between the larvae and adults ($F_{ST} = 0.000$–0.004, NS). Number of breeders and effective population size were substantial and consistent. This reproductive population thus has maintained genetic stability and high diversity, despite intensive anthropogenic pressures.

Keywords Lake Erie · Maumee River · Microsatellites · Percidae · *Sander vitreus* · Walleye

Introduction

An understanding of the temporal dynamics of genetic variability and composition is critically important to manage and maintain populations in the face of anthropogenic stressors, such as exploitation and habitat alterations. Population genetic changes may occur—resulting from a number of factors—including genetic drift, differential survival of offspring, and/or recruitment. However, many studies solely rely on results from single sampling years or on samples separated by long time periods, which may not adequately characterize the micro-evolutionary processes acting on populations (see Crispo and Chapman 2010; Charlier et al. 2012; Holmes 2015).

Large populations frequently possess greater resilience to genetic drift, undergoing limited or no discernable changes in allele frequencies and composition from generation to generation (Waples 1990; Allendorf et al. 2013; Peters et al. 2014), whereas smaller ones often decline in genetic variation. These principles have been demonstrated in a variety of taxa, including fishes (Ozerov et al. 2013; Ruzzante et al. 2016), ducks (Liu et al. 2013), and

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mammals (Ortego et al. 2011). For example, analyses of 14 microsatellite (μsat) loci by Ozerov et al. (2013) in Atlantic salmon *Salmo salar* populations spawning in the Russian White Sea Basin showed two temporal trends: smaller populations diverged over time, mainly due to drift, whereas larger populations remained genetically consistent. Similarly, Liu et al. (2013) found genetic stability at 11 μsat loci in a large population of the tufted duck *Aythya fuligula* that was overwintering at Lake Sempach, Switzerland, from 2007 to 2009. In contrast, a small population of the mountain goat *Oreamnos americanus* in west-central Alberta, Canada exhibited high temporal genetic variability at 28 μsat loci, declining in diversity over 14 years (Ortego et al. 2011).

Population genetic structure also may be influenced by variable recruitment to adult populations (see Ruzzante et al. 1996; Gilg and Hilbish 2003; Owen and Rawson 2013; Yednock and Neigel 2014). For many fish and aquatic invertebrate populations, differential production and survival of larvae lead to marked variations in year class representation, recruitment, and adult population abundances (summarized by Letcher et al. 1996; Ludsin et al. 2014), which likely impact genetic diversity and composition (see Owen and Rawson 2013; Yednock and Neigel 2014). Planktonic larval fishes frequently experience very high mortality rates due to predation, asynchrony of hatch timing with food availability, and/or stochastic weather events (see Mion et al. 1998; Ludsin et al. 2014). An estimated ~5–25 % of individual planktonic fish larvae die per day (reviewed by Dahlberg 1979; Kalff 2002). For example, ~84 % of yellow perch *Perca flavescens* in Oneida Lake, NY that hatched in the spring died within 2 months (Mills et al. 1989). Similarly, ~87–95 % of hatched walleye *Sander vitreus* in Oneida Lake, NY perished within a few months (Forney 1976). Notably, Mion et al. (1998) found that survival of larval walleye was highly variable in different years, attributed to differences in discharge levels of the rivers in which the adults spawned during the spring. Strong discharges often kill delicate larvae—subjecting them to collisions with debris and the benthos, and washing them away from suitable nursery grounds. Suspended sediments tend to clog the gills of larvae and impede their ability to feed. During springs with large storm events, high water discharge, and marked turbidity, fewer walleye larvae hatched and survived, resulting in poor year class recruitment (Mion et al. 1998). Such high mortality—over the course of several years—can alter the genetic composition of a population, leaving it represented by fewer surviving individuals and may have long-term effects (see Hedgecock 1994). However, there have been limited evaluations of the genetic effects of variable larval walleye recruitment, which served as the focus of the present investigation.

Lake Erie is known as the "walleye capital of the world" and supports substantial commercial and recreational fisheries worth ~$2 billion U.S. (Gentner and Bur 2009). Eleven primary walleye spawning group locations are known in Lake Erie's shallow reefs and rivers (Fig. 1; Walleye Task Group of the Lake Erie Committee (WTG 2016)), with the largest reported annual run occurring in the western basin's Maumee River (Trautman 1981). The present study analyzed the temporal genetic patterns of this spawning run.

When water temperatures reach 5–11 °C during spring to early summer, adult walleye (beginning at about three years of age) migrate to reproduce at the Maumee River and other spawning grounds; these appear to be their birth sites, according to tagging (Wang et al. 2007) and genetic data (Stepien and Faber 1998; Stepien et al. 2009, 2015a). Walleye typically spawn in small groups, with the females broadcasting their eggs over the substrate for several days, in multiple clutches (Scott and Crossman 1973; Craig 2000). Groups of several males follow each female to externally fertilize the eggs, which have a sticky outer coating that adheres them to the substrate (Collette et al. 1977; Barton and Barry 2011). Past research by our laboratory has shown that these spawning groups are genetically distinguishable (Strange and Stepien 2007; Stepien et al. 2009, 2010, 2012, 2015a; Haponski and Stepien 2014). These annual spawning runs thus provide a unique opportunity to evaluate the temporal consistency of genetic patterns from year to year and generation to generation.

The Maumee River walleye spawning group has been subjected to high exploitation each year, with thousands of individuals removed by sport fishing during the annual spring spawning runs (Ohio Division of Wildlife (ODW 2014)). Moreover, Maumee River and other Lake Erie tributaries and nearshore areas steadily lost fish habitat from the 1900–1970s due to draining of wetlands, armoring of shorelines, channelization, dredging, and increased industrialization (Hartig et al. 2009). The Maumee River experienced increased siltation and water level fluctuations from drainage and land development (Trautman 1981), and is the major conduit of run-off and phosphorous loadings from agricultural fields to Lake Erie (see Bridgeman et al. 2012; Stepien et al. 2016). Reduction of point-source pollution and implementation of some best management practices, such as no-till farming, reduced phosphorus levels in the Maumee River and Lake Erie during the 1980s until ~1995, but phosphorus levels stemming from non-point sources have been increasing during the last decade, fueling harmful algal blooms of cyanobacteria (summarized by Bridgeman et al. 2012). The present study evaluates the temporal genetic composition of the economically and ecologically important spawning run occurring in the Maumee River in light of these anthropogenic pressures.

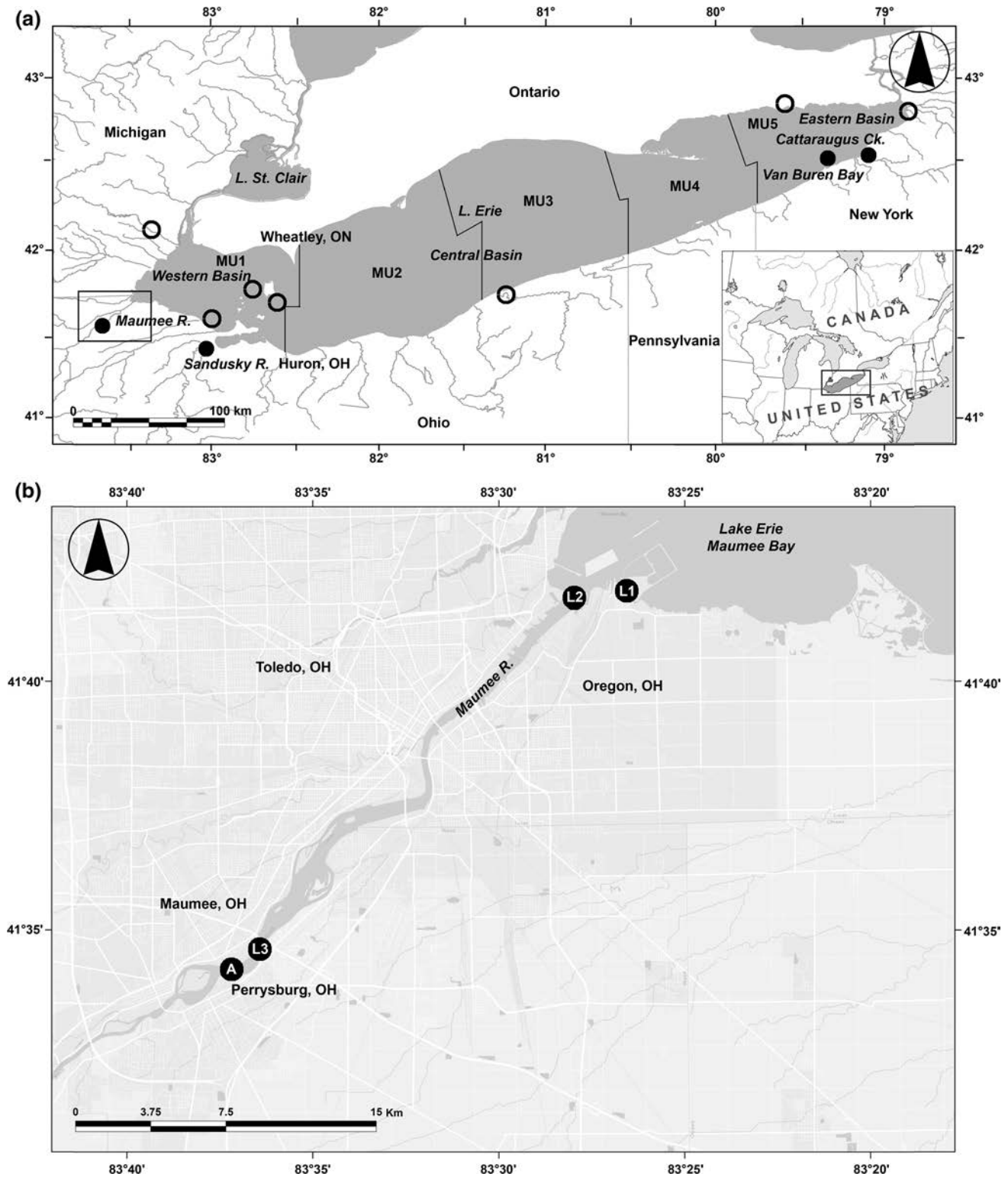

Fig. 1 Map showing locations of **a** Lake Erie walleye spawning groups and management units (MUs) and **b** enlarged view of sampling locations in the Maumee River (Ohio), a western Lake Erie tributary (*box in panel* **a**). In **a**, *closed circles* represent locations discussed in this study and *open circles* denote the other primary walleye spawning locations. In **b**, labels are sampling locations for walleye adults (*A*) and larvae (*L1–L3*), at the spawning grounds (*A, L3*), river mouth (*L2*), and the intake channel of FirstEnergy's Bay Shore Power Plant (*L3*)

Neither sex exhibits parental care and post-spawning walleye often disperse across a wide geographic range (Collette et al. 1977; Barton and Barry 2011), traveling from 50 to 300 km (Colby et al. 1979). Thus, population structure primarily is apparent at the time of spawning (Stepien et al. 2012, 2015a; Haponski and Stepien 2014).

Relation of population genetics to conservation management

The Lake Erie walleye fishery is managed under the jurisdiction of the bi-national Great Lakes Fishery Commission's (GLFC) Lake Erie Committee (LEC), applying recommendations from the Walleye Task Group (WTG) subcommittee that comprises representative agencies from the U.S. states of Michigan, Ohio, Pennsylvania, and New York and the province of Ontario, Canada (see Locke et al. 2005; Kayle et al. 2015). Fish community goals and objectives for the maintenance of Lake Erie walleye include self-sustaining populations, sustainable harvests, and genetic diversity (see Ryan et al. 2003; Locke et al. 2005; Kayle et al. 2015). To meet these goals, the LEC employs a management unit (MU) framework, which is used to set annual quotas and recommend annual walleye harvest numbers. The designation of MUs constitutes a common conservation approach for assessing and managing sustainable harvests of populations in given locations (Begg et al. 1999; Schwartz et al. 2007). However, MUs—such as the ones used in Lake Erie—that are based primarily on geography may not be biologically relevant (Waples and Gaggiotti 2006; Palsboll et al. 2007), and population genetic data offer important criteria to evaluate their composition, diversity, and consistency (Reiss et al. 2009; Sullivan and Stepien 2015). The Maumee River spawning group of walleye is located in MU1 of Lake Erie, which encompasses the entire Western Basin, ending on the northern shore near Wheatley, ON and Huron, OH along the southern shore (see Fig. 1). MU1 contains a number of genetically separable walleye spawning groups, including the Maumee River (summarized in Stepien et al. 2015a), which are managed together as a single unit (Fig. 1).

Numbers of Lake Erie walleye have fluctuated during the past decade as a result of exploitation and variable recruitment (Locke et al. 2005; Kayle et al. 2015; WTG 2016). For example, two larger birth year cohorts (hereafter cohorts) from 2003 to 2010, and moderate-sized cohorts from 2007 to 2009 dominated walleye catches, whereas others had low recruitment (WTG 2015). Stochasticity in survival and recruitment has raised concern for sustainability of local populations and the fishery. Understanding the genetic patterns of Lake Erie walleye at spawning locations and whether these have remained stable over time, in relation to factors that underlie population fluctuations may provide important information for conservation, including (a) identification of population groups with localized adaptations, (b) linkages (gene flow) or divergence among spawning groups, and (c) temporal changes and (d) the possible effects of stochastic recruitment. For example, designated no-catch areas and/or ecological preserves may conserve the overall genetic diversity of a population group, providing a reservoir for surrounding groups (e.g., Munguía-Vega et al. 2015).

Study objective and questions

The objective was to test whether genetic diversity and allelic composition of walleye spawning in Lake Erie's Maumee River have been temporally stable over the past two decades. We expanded and extended a prior temporal sampling by Stepien et al. (2012) to more rigorously evaluate the genetic consistency of spawning runs from 1995 to 2013, including every annual run from 2005 to 2013 and uniquely evaluating the cohorts within the runs. This new investigation increased the number of nuclear μsat loci analyzed from nine to 14. We additionally compared the genetic composition of the larvae with the adults, in order to examine whether the offspring represented the overall genetic composition of the adults reproducing at the site, and the possible influence of larval survival on the gene pool. Lastly, we evaluated the kin relationships of walleye from the annual spawning runs, cohorts, the sexes, and larvae versus spawning adults.

Micro-evolutionary processes, including genetic drift and inbreeding, may affect walleye populations, as measured by the effective population size (N_e) and effective number of breeders (N_b). Briefly, N_e is the size of an ideal population that loses genetic diversity at the same rate as the one being observed (Wright 1931; Allendorf et al. 2013; Ruzzante et al. 2016). The metric N_b is the number of breeders contributing to a single reproductive event (summarized by Perrier et al. 2016). Changes in N_e and N_b also can provide insights into the risk of extirpation for the population of interest (summarized by Perrier et al. 2016). Larger estimates indicate stability, little genetic drift, low inbreeding, and little risk of extinction. In contrast, lower estimates may identify populations in need of immediate conservation action (see Perrier et al. 2016; Ruzzante et al. 2016). Thus, we estimated N_e and N_b for the Maumee River walleye resource.

Specific questions were: (1) have the genetic diversity and allelic composition of the walleye population reproducing in the Maumee River changed or remained consistent (a) among annual spawning runs, (b) among cohorts, (c) between the sexes, (d) those reproducing earlier (ages 2–6) versus later in life (ages 7 or greater), and (e) between

the larvae versus adults? (2) What were the kin relationships among walleye spawning runs and cohorts? (3) Did the numbers of breeders and effective population size change or remain consistent?

Materials and methods

Sample collection

Fin clips (1–2 cm^2 of pectoral or caudal fins) from 600 Maumee River spawning-condition walleye were sampled during 12 annual runs (1995–2013) by the Ohio Department of Natural Resources (ODNR) or by our laboratory (site A; Table 1; Fig. 1), labeled, and preserved in 95 % EtOH. Sex, length, and age data were recorded when possible. Sex data were available for all collection years except for 2003 (in that year, sex data were not collected by ODNR). Age data for adults from the 2007–2013 spawning runs were calculated by ODNR using annual rings from sectioned otoliths and site-specific age-length plots (Travis Hartman, pers. comm.), allowing us to test for possible genetic differences among the cohorts. We restricted our analyses to aged cohort samples containing four or more individuals. We additionally evaluated individuals spawning earlier in life (ages 2–6) versus later (ages 7 or older) to test for possible genetic differences.

We also compared the genetic composition of adults with larvae sampled from the Maumee River during spring 2010 ($N = 96$) and spring 2011 ($N = 48$). DuFour et al. (2014) obtained the samples for us from three sites (labeled L1–L3 on Fig. 1), including close to the walleye spawning grounds (L3), near the River's mouth (L2), and at the intake channel to FirstEnergy's Bay Shore Power Plant (L1; https://www.firstenergycorp.com/content/dam/corporate/generationmap/files/Bay%20Shore%20Plant%20Facts.pdf). Larvae were sampled from the Power Plant's intake (L1) and the Maumee River's mouth (L2) during two peak hatches in 2010 (labeled a and b; Table S1), and in 2011 from the River's mouth (L2) and near the spawning grounds (L3). DuFour et al. (2014) used paired ichthyoplankton Bongo net tows fitted with 350 and 500 µm mesh conical nets and 0.5 m diameter openings, which were towed horizontally against the current, at surface and mid-depth. Larvae then were stored in vials containing 95 % EtOH at room temperature and archived in the Great Lakes Genetics/Genomics Laboratory at the University of Toledo's Lake Erie Center (Oregon, OH). Larvae were identified and enumerated by DuFour et al. (2014) using the Auer (1982) taxonomic key with a Leica Microsystems dissecting microscope (Buffalo Grove, IL) at the Lake Erie Center. We then tested for genetic differences among the larvae taken within a given year, and found high similarity among them (2010: $F_{ST} = <0.001–0.005$, NS, $\chi^2 = 24.33–35.14$, NS; 2011: $F_{ST} = <0.001$, NS, $\chi^2 = 14.68$, NS; Table S1); these thus were pooled into two collection year groups: 2010 and 2011.

DNA extraction and amplification

Genomic DNA was extracted using Qiagen DNeasy extraction kits (Qiagen Inc., Valencia, CA), and then assessed for quality and quantity on 1 % agarose mini-gels stained with ethidium bromide and with a Thermo Scientific (Waltham, MA) Nanodrop 2000 spectrophotometer. We analyzed allelic variation at 14 µsat loci for 744 individuals (Tables 1, S2). The present study added 345 adult individuals from the 2005, 2006, and 2009–2013 run samples, conducted a unique analysis of 144 larval walleye, and added five more loci to results reported by Stepien et al. (2012). The latter analyzed nine loci and 250 spawning-condition walleye from the 1995, 1998, 2003, and 2007–2008 spawning runs. We further increased the sample size for the 2007 spawning run by five individuals.

Polymerase chain reaction (PCR) amplifications were conducted in 48 well plates with 10 µl reactions of 0.6 U *Taq* polymerase, 50 µM dNTPs, 50 mM KCl, 1.5 mM $MgCl_2$, 10 mM Tris–HCl, 0.5 µM of each primer, and ~80 ng template. A positive control (sample AZE31 spawning in 2010 in the Maumee River) and a negative control (no template) were included in all reaction runs. PCR cycling parameters were 2 min at 94 °C for initial denaturation, followed by 35 cycles of denaturation (94 °C, 30 s), primer annealing (1 min) at specific temperatures (Table S2), and polymerase extension at 72 °C for 30 s, capped by a final 72 °C 5 min extension.

Four sets of loci were multiplexed as single PCR reactions: (1) *Svi*4 and 33, (2) *Svi*2, 6, and 7, (3) *Svi*L2 and L3, and (4) *Svi*L6 and L7. Loci *Svi*14, 17, 18, 20, and L4 were run individually. Amplification products were diluted 1:50, of which 1 µl was added to 13 µl of formamide and Applied Biosystems (ABI, Fullerton, CA) Gene Scan 500 size standard in 96-well plates, denatured for 2 min at 95 °C, and analyzed on an ABI 3130xl Genetic Analyzer with GENEMAPPER v3.7. Output profiles were checked manually to confirm allelic size variants.

Data analyses

Each locus, spawning year, and sample was tested for conformance to Hardy–Weinberg equilibrium (HWE) and linkage disequilibrium (LD) expectations with 10,000 Markov chain Monte Carlo (MCMC) dememorizations, 1000 batches, and 10,000 iterations in GENEPOP v4.0 (Rousset 2008). HWE and LD tests were adjusted using sequential Bonferroni corrections (Rice 1989). Loci were

Table 1 Composition and genetic variation in the Maumee River walleye population among samples for spawning years, birth year cohorts, the sexes, early (ages 2–6) versus later (7 or older) reproducers, and larvae determined from 13 nuclear DNA μsat loci

Sample	N	$H_O \pm$ SE	N_A	N_{PA}	P_{PA}	$A_R \pm$ SE	$F_{IS} \pm$ SE	Full sibs	Half sibs
Adult spawning years									
1995-A	53	0.74 ± 0.04	144	0	0.00	7.72 ± 0.71	0.039 ± 0.033	0.00	0.72
1998-A	28	0.76 ± 0.04	126	1	0.01	7.87 ± 0.79	0.006 ± 0.027	0.00	0.50
2003-A	76	0.75 ± 0.03	154	1	0.01	7.83 ± 0.77	0.024 ± 0.025	0.03	0.75
2005-A	56	0.76 ± 0.04	143	3	0.02	7.71 ± 0.84	0.001 ± 0.017	0.04	0.77
2006-A	51	0.76 ± 0.04	141	2	0.01	7.74 ± 0.79	0.017 ± 0.036	0.00	0.75
2007-A	48	0.74 ± 0.03	140	4	0.03	7.66 ± 0.84	0.035 ± 0.024	0.04	0.60
2008-A	50	0.74 ± 0.02	135	0	0.00	7.48 ± 0.80	0.027 ± 0.018	0.04	0.64
2009-A	48	0.78 ± 0.03	138	3	0.02	7.74 ± 0.79	−0.014 ± 0.020	0.00	0.60
2010-A	48	0.76 ± 0.04	137	1	0.01	7.65 ± 0.75	0.018 ± 0.030	0.00	0.58
2011-A	48	0.78 ± 0.03	142	1	0.01	7.88 ± 0.74	0.009 ± 0.020	0.04	0.69
2012-A	46	0.75 ± 0.03	147	7	0.05	8.07 ± 0.78	0.045 ± 0.019	0.00	0.54
2013-A	48	0.76 ± 0.03	150	7	0.05	7.91 ± 0.82	0.015 ± 0.014	0.00	0.67
Mean	50	0.76 ± 0.03	141	3	0.02	7.77 ± 0.79	0.019 ± 0.022	0.02	0.65
Adult birth year cohorts									
1996-A	25	0.78 ± 0.04	127	2	0.02	8.15 ± 0.77	0.029 ± 0.028	0.00	0.32
1998-A	15	0.75 ± 0.03	99	1	0.01	7.45 ± 0.88	0.031 ± 0.037	0.00	0.00
1999-A	34	0.78 ± 0.04	134	2	0.01	7.89 ± 0.83	0.006 ± 0.021	0.00	0.50
2001-A	14	0.78 ± 0.03	98	0	0.00	7.54 ± 0.81	−0.011 ± 0.042	0.00	0.00
2003-A	95	0.75 ± 0.03	158	5	0.03	7.68 ± 0.79	0.021 ± 0.013	0.00	0.87
2005-A	19	0.79 ± 0.02	118	2	0.02	8.21 ± 0.88	0.003 ± 0.024	0.00	0.11
2007-A	21	0.77 ± 0.04	116	1	0.01	7.93 ± 0.80	−0.003 ± 0.029	0.00	0.19
2008-A	27	0.76 ± 0.03	115	1	0.01	7.44 ± 0.73	0.016 ± 0.029	0.00	0.30
2010-A	16	0.77 ± 0.03	111	10	0.09	8.11 ± 0.79	0.010 ± 0.034	0.00	0.00
Mean	30	0.77 ± 0.03	120	3	0.02	7.82 ± 0.81	0.011 ± 0.029	0.00	0.25
Adult sexes									
Males	311	0.75 ± 0.03	201	40	0.18	7.77 ± 0.79	0.028 ± 0.010	0.00	0.09
Females	186	0.77 ± 0.03	179	18	0.10	7.85 ± 0.77	0.005 ± 0.010	0.03	0.03
Mean	249	0.76 ± 0.03	190	29	0.14	7.81 ± 0.78	0.017 ± 0.010	0.02	0.06
Early versus later reproduction									
Early (ages 2–6)	128	0.76 ± 0.03	173	25	0.14	7.79 ± 0.77	0.008 ± 0.013	0.00	0.02
Later (7 or older)	138	0.76 ± 0.03	180	18	0.10	7.83 ± 0.79	0.020 ± 0.010	0.03	0.04
Mean	133	0.76 ± 0.03	177	22	0.12	7.81 ± 0.78	0.014 ± 0.012	0.02	0.03
Early versus later reproduction for the 2003 cohort									
Early	41	0.74 ± 0.04	135	17	0.13	7.48 ± 0.78	0.011 ± 0.020	0.00	0.00
Later	54	0.75 ± 0.03	141	23	0.16	7.77 ± 0.80	0.025 ± 0.022	0.00	0.00
Mean	48	0.75 ± 0.04	138	20	0.15	7.63 ± 0.79	0.018 ± 0.021	0.00	0.00
Larvae									
2010-L	96	0.75 ± 0.04	168	5	0.03	7.94 ± 0.82	0.024 ± 0.021	0.00	0.86
2011-L	48	0.75 ± 0.03	145	0	0.00	7.87 ± 0.85	0.031 ± 0.023	0.00	0.60
Mean	72	0.75 ± 0.04	157	3	0.02	7.91 ± 0.84	0.028 ± 0.022	0.00	0.73

Values include number of samples (N), observed heterozygosity (H_O) ± standard error (SE), number of alleles (N_A), number of private alleles (N_{PA}), proportion of private alleles (P_{PA}), allelic richness (A_R) ± SE, and inbreeding coefficient (F_{IS}) ± SE from GENEPOP v4.2 (Rousset 2008) and *F*STAT v2.9.3.2 (Goudet 2002). Estimated proportion of full (Full) and half (Half) siblings calculated using COLONY v2.0.5.0 (Jones and Wang 2009) analyses

evaluated with MICRO-CHECKER v2.2.3 (van Oosterhout et al. 2004) for heterozygote deficiency or excess, and for possible occurrence of null alleles. Per-locus calculations also included: number of alleles (N_A), inbreeding (F_{IS}), overall genetic deviation across all samples (F_{IT}), and divergences (F_{ST}); all were determined in *F*STAT v2.9.3.2

(Goudet 2002; Table S2). We tested for outlier loci and possible evidence of selection with the programs LOSITAN (Beaumont and Nichols 1996; Antao et al. 2008) and BAYESCAN (Foll and Gaggiotti 2008). LOSITAN identifies loci having higher or lower F_{ST} values than expected under neutrality (see Antao et al. 2008). Since that method has been found to be prone to Type I error (Narum and Hess 2011), we also used the Bayesian approach in BAYESCAN, which compares differences in allele frequencies at each locus (Foll and Gaggiotti 2008). For any loci exhibiting possible selection, allele frequencies were graphed in Microsoft Office Excel 2008 and results compared to those from neutral loci; the former then were removed from subsequent analyses. We also tested whether increasing the number of loci from nine (Stepien et al. 2012) to 14 increased our discrimination power, with the program POWSIM v4.1 (Ryman and Palm 2006).

Diversity metrics included: observed (H_O) and expected (H_E) heterozygosities in GENEPOP, and F_{IS}, N_A, and allelic richness (A_R) values in *F*STAT. For A_R calculations, *F*STAT used rarefaction to standardize sample size across spawning years, cohorts, sexes, early versus later reproduction, and larvae. We tested for possible significant differences in diversity values (H_O and A_R) using Wilcoxon and Friedman rank sum tests (Zar 1999) with the R statistical analysis software suite v3.1.1 (R Development Core Team 2014). Significant differences with and without inclusion of any loci exhibiting possible evidence of selection were compared using Analysis of Variance (ANOVA) and Wilcoxon rank sum tests (Zar 1999) in R. Number and proportion of private alleles (N_{PA}), i.e., those that were unique to a given spawning year, cohort, sex, or larval sample, were determined using CONVERT v1.31 (Glaubitz 2004). Standard errors were calculated with Microsoft Office Excel 2008.

Genetic consistency among samples was evaluated using unbiased F_{ST} estimates (Weir and Cockerham 1984) in *F*STAT. Since *F*-statistic estimates assume a normally distributed data set (Weir and Cockerham 1984) and may be affected by small sample sizes and rare alleles (Raymond and Rousset 1995), pairwise exact tests of differentiation (χ^2) also were calculated with GENEPOP. Those used a MCMC procedure with a chain of 10,000, 1000 batches, and 10,000 iterations to randomly sample allele frequencies—a procedure that was not dependent upon sample size or a normal distribution (Raymond and Rousset 1995). Probability values for both types of pairwise comparisons were adjusted using sequential Bonferroni correction (Rice 1989).

Relationships within and among the samples were examined with 3-dimensional Factorial Correspondence Analyses (3d-FCA, Benzecri 1973) in GENETIX v4.05 (Belkhir et al. 2004). We additionally tested the hierarchical partitioning of genetic variation among various possible groupings with Analysis of Molecular Variance (AMOVA; Excoffier et al. 1992) in ARLEQUIN v3.5.1.3 (Excoffier and Lischer 2010). Scenarios that were evaluated included comparisons of the relative amount of variation distributed among the spawning years, cohorts, between the sexes, and spawning earlier (ages 2–6) versus later in life history (age 7 or greater). We also tested the influence of kin relationships on Maumee River population sub-structuring with COLONY v2.0.5.4 (Jones and Wang 2009), which used a maximum likelihood approach to assign full and half sib-ships from multi-locus genotype data. Sibling relationships identified with a probability of 0.95 or higher were recorded.

The overall effective population size (N_e) was estimated for data across all spawning run years, cohorts, and larval samples. The effective number of breeders (N_b) was estimated for each individual spawning year and cohort. Comparisons were made between males and females and between individuals spawning earlier (ages 2–6) and later (>7 years) in their lives, using the entire dataset and the 2003 cohort alone. Effective population size and N_b were calculated using the linkage-disequilibrium method (LD; Waples and Do 2008) with NEESTIMATOR v2.0.1 (Do et al. 2014). This method is useful for multi-locus datasets with sample sizes of ~30–50 individuals (see Luikart et al. 2010; Waples and Do 2010), providing greater precision than single or two-sample estimators (Waples 2010; Gilbert and Whitlock 2015). Reported estimates excluded rare alleles less than $p = 0.02$ (see Do et al. 2014).

Results

The 14 nuclear μsat loci, spawning year, cohort, and larval samples all conformed to HWE expectations following sequential Bonferroni correction and showed no evidence of LD. Locus *Svi*20 was identified by both LOSITAN and BAYESCAN as an outlier locus potentially under positive selection (Table S2); it thus was excluded from further analyses. Allele frequency bar graphs showed *Svi*20 had high allele frequency fluctuations compared to the neutral loci (e.g., *Svi*L4; Fig. S1). However, genetic diversity and composition values were similar with and without its inclusion. Its overall F_{ST} value was 0.011 (Table S2), which was much higher than any other locus. POWSIM analyses (Ryman 2011) comparing the 9 versus 13 locus datasets showed that the former dataset was more prone to Type I errors (Fisher's exact test *p* value 9 loci = 0.06; 13 loci = 0.05). Increasing the number of loci to 13 thus reduced the number of false positives among our comparisons.

MICRO-CHECKER suggested null alleles with slight homozygote excess at six loci for a few selected samples,

including: *Svi*14 (2008 and 2012 spawning years), *Svi*18 (1995, 2003, 2006, and 2010 spawning years, 1996 cohort, 2010 larvae), *Svi*L2 (2003 cohort), *Svi*L4 (1995, 2003, and 2007 spawning years, 2008 cohort), *Svi*L6 (2011 spawning year), and *Svi*L7 (2006 spawning year). For *Svi*18 alone, homozygous excess in samples from 1995 and 2003 may have been due to some stuttering. We manually rechecked all electropherograms and found those allele peaks to be clear and high in amplitude; thus no data adjustments were made. Our analyses were based on 13 of the loci, since (1) there was no indication of null alleles at those loci in the other samples, (2) all loci and samples were in HWE, and there were no signs of (3) heterozygote deficiency, (4) scoring error, or (5) other stuttering (see van Oosterhout et al. 2004).

Overall, 229 alleles were recovered from 600 adult and 144 larval walleye for the 13 nuclear μsat loci (Table S2). Yearly samples of spawning-condition walleye had high numbers of alleles, with the most occurring in 2003 (154; Table 1). Allelic richness values showed year to year consistency based on a Friedman rank sum test ($\chi^2 = 12.31$, df = 11, NS). The 2012 and 2013 samples contained the most private alleles, which were nearly twice the number recovered in other years. The overall proportion of private alleles was low for individual spawning year samples (ranging from 0.00–0.05), cohorts (0.00–0.09), and larvae (0.00–0.03).

Individual cohort samples consistently possessed high numbers of alleles and allelic richness values; there were no significant differences among them (Friedman rank sum test: $\chi^2 = 11.26$, df = 8, NS). The 2010 cohort contained the most private alleles, ranging from 2 to 10× more than other cohorts. Likewise, both sexes and individuals reproducing early versus later had similar values, as indicated by Wilcoxon rank sum tests (sexes: W = 88.0, NS, early versus late: overall: W = 85.0, NS, 2003 cohort: W = 83.0, NS). Samples of larvae from 2010 to 2011 possessed similarly high numbers of alleles and consistent allelic richness values (W = 86.0, NS), which did not differ from the spawning adults (Friedman test: $\chi^2 = 15.93$, df = 13, NS) or cohorts (Friedman: $\chi^2 = 11.97$, df = 10, NS).

Heterozygosity values were consistent among walleye samples from different spawning years (Friedman test: $\chi^2 = 7.27$, df = 11, NS), cohorts (Friedman: $\chi^2 = 13.66$, df = 8, NS; Table 1), between the sexes (Wilcoxon: W = 97.0, NS), those reproducing early versus later in life (overall Wilcoxon: W = 83.0, NS, 2003 cohort: W = 89.0, NS), and between the two years of sampled larvae (Wilcoxon: W = 88.5, NS; Table 1). Heterozygosity also did not differ between the larvae versus the spawning adults (Friedman test: $\chi^2 = 9.24$, df = 13, NS) or among the cohorts (Friedman: $\chi^2 = 7.07$, df = 10, NS).

Adult and larval samples both showed some indication of inbreeding, whereas some outbreeding was indicated for the 2009 spawning year alone (Table 1). Samples from spawning years, cohorts, sexes, early versus later reproduction, and larvae overall contained low numbers of full siblings, with most having none, according to the COLONY analyses. Higher proportions of half-siblings were estimated across all samples, with the most occurring in the 2005 spawning year, 2003 cohort, and the 2010 larval sample (Table 1).

Samples of spawning-condition walleye possessed consistent genetic composition from year to year, as indicated in pairwise comparisons (Table 2a). F_{ST} tests also showed no significant differences among the cohorts (Table 2b), for which the exact tests recovered a single significant difference between 2003 and 2010. The larvae from 2010 to 2011 were indistinguishable in genetic composition with both types of tests. No significant differences were found between the larvae and the adult cohorts with the F_{ST} tests, but the 2010 larvae significantly differed from the 2003 and 2010 cohorts according to the exact tests of differentiation (Table 2b). Variation between the results of the two types of pairwise comparisons may have been due to violation of one or more of the assumptions for $F_{ST,}$ compared to the more robust exact tests of differentiation (see Raymond and Rousset 1995). Larvae from 2011 were genetically consistent with the adults spawning in 2011, and with the 2011 cohort, in both types of pairwise comparisons (Table 2).

Overall, there was no significant difference in genetic composition between males and females spawning in the Maumee River ($F_{ST} = 0.000$, NS; $\chi^2 = 15.90$, NS) or when analyzed within annual spawning runs (Table S3, except for 2008, which likely was due to chance alone). Exact tests of differentiation suggested some allele frequency fluctuations between the sexes in 2005, 2008, 2010, and 2013; this likely was due to sample size. Male and females in cohorts did not differ in genetic composition (Table S4). Additionally, genetic compositions were similar for individuals spawning earlier (ages 2–6) versus later in life (age 7 or older; $F_{ST} = 0.000$, NS; $\chi^2 = 19.68$, NS). When analyzed for the 2003 cohort alone, there was slight difference between them ($F_{ST} = 0.004$, $p = 0.04$; $\chi^2 = 38.15$, $p = 0.06$).

Genetic similarities among walleye from different sampling years, cohorts, sexes, and spawning earlier versus later in life likewise were supported by AMOVA (Table 3). Hierarchical relationships in AMOVA indicated some genetic structure between the sexes when classified by spawning years (scenario 2) and among spawning year samples when grouped as male or female in scenario 5 (Table 3). The 3d-FCA likewise showed little division among sampling years or cohorts (Fig. 2). Individuals

Table 2 Pairwise divergences of allelic composition from 13 nuclear μsat loci, between (a) spawning year adults (A) or larvae (L) and (b) birth year cohorts of adults (A) or larvae born in that year (L)

Panel (a)

Spawning year (sample size)	1995-A	1998-A	2003-A	2005-A	2006-A	2007-A	2008-A	2009-A	2010-A	2010-L	2011-A	2011-L	2012-A	2013-A
1995-A ($N = 53$)	–	28.28	18.28	33.02	19.10	23.47	21.23	22.90	23.97	39.55	20.89	26.02	32.61	37.05
1998-A ($N = 28$)	0.000	–	24.45	40.39	35.40	25.96	32.68	35.54	30.19	44.57	28.13	37.26	33.32	45.68
2003-A ($N = 76$)	0.000	0.000	–	26.03	15.74	24.11	18.77	22.86	26.09	40.44	29.53	30.72	37.59	50.58
2005-A ($N = 56$)	0.003	0.002	0.000	–	21.56	27.43	34.52	23.80	28.11	33.21	32.74	42.63	28.00	55.62
2006-A ($N = 51$)	0.000	0.001	0.000	<0.001	–	16.12	29.26	34.17	22.68	39.21	28.07	26.52	25.81	37.84
2007-A ($N = 48$)	0.000	0.000	0.000	0.000	0.000	–	22.90	26.37	24.12	38.72	23.30	28.86	30.29	42.87
2008-A ($N = 50$)	0.000	0.001	0.000	0.000	0.000	0.000	–	22.56	30.77	51.21	34.76	40.94	45.43	47.66
2009-A ($N = 48$)	0.000	0.004	0.000	0.001	0.002	0.000	0.000	–	32.53	44.08	37.00	31.77	27.15	45.71
2010-A ($N = 48$)	<0.001	0.002	0.002	0.001	0.001	0.000	<0.001	0.002	–	42.72	34.78	27.02	15.53	47.42
2010-L ($N = 96$)	0.001	0.005	0.000	0.001	0.003	0.002	0.001	0.000	0.004	–	53.16	47.80	47.61	65.05*
2011-A ($N = 48$)	0.000	0.001	0.001	<0.001	0.001	0.000	0.000	<0.001	<0.001	0.002	–	28.11	22.32	25.73
2011-L ($N = 48$)	0.000	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.000	–	16.76	32.98
2012-A ($N = 46$)	0.001	0.003	0.001	0.000	0.002	<0.001	0.002	<0.001	0.000	0.003	0.000	0.000	–	20.91
2013-A ($N = 48$)	0.004	0.006	0.004	0.005	0.003	0.005	0.003	0.005	0.005	0.005	0.001	0.002	<0.001	–

Panel (b)

Birth year cohort (sample size)	1996-A	1998-A	1999-A	2001-A	2003-A	2005-A	2007-A	2008-A	2010-A	2010-L	2011-L
1996-A ($N = 25$)	–	14.45	9.86	18.54	20.66	18.78	18.76	22.18	29.44	33.35	17.05
1998-A ($N = 15$)	0.000	–	19.70	24.12	17.70	22.13	21.01	17.44	42.78	15.85	18.91
1999-A ($N = 34$)	0.000	0.000	–	25.88	39.69	34.72	28.01	29.76	47.46	43.36	21.71
2001-A ($N = 14$)	0.000	0.000	0.001	–	21.00	34.16	39.20	30.70	27.22	29.22	32.35
2003-A ($N = 95$)	0.000	0.000	0.002	0.004	–	29.28	20.43	16.98	56.45*	62.77*	30.89
2005-A ($N = 19$)	0.000	0.000	0.001	0.004	0.000	–	25.73	26.62	39.41	39.07	31.18
2007-A ($N = 21$)	0.000	0.000	0.003	0.011	0.000	0.000	–	28.65	40.27	34.52	27.92
2008-A ($N = 27$)	0.000	0.000	0.000	0.001	0.000	0.000	<0.001	–	32.75	26.40	18.02
2010-A ($N = 16$)	<0.001	0.006	0.005	<0.001	0.007	0.004	0.007	0.002	–	76.85*	50.02
2010-L ($N = 96$)	0.003	0.000	0.001	0.005	0.001	0.001	0.005	0.000	0.013	–	49.60
2011-L ($N = 48$)	0.000	0.000	0.000	0.004	0.000	0.000	0.000	0.000	0.007	0.002	–

Below diagonal = F_{ST} values (Weir and Cockerham 1984). Above diagonal = exact tests of differentiation (χ^2)

* Significant with sequential Bonferroni correction (Rice 1989)

spawning in 2013 clustered separately from the others and the 2010 cohort also appeared more distinct.

The overall estimate of N_e for adult Maumee River walleye was similar between the samples from different spawning years, cohorts, and earlier versus later reproduction (Table 4). The overall range was 5021 individuals through infinity, i.e., N_e was large enough that sampling error obscured genetic signal. Estimates based on the 2003

Table 3 Relative distribution of genetic variation among walleye spawning in the Maumee River per year, birth year cohort, sex, and those reproducing earlier (ages 2–6) versus later (7 or older) in life using Analysis of Molecular Variance (Excoffier et al. 1992), calculated from 13 nuclear μsat loci in ARLEQUIN v3.5.1.3 (Excoffier and Lischer 2010)

Source of variation	% variation	Φ value
1. Among annual spawning years	0.00	0.000
Among birth year cohorts within spawning years	0.36	0.004
Within samples	99.64	0.004
2. Among annual spawning years	0.00	0.000
Between sexes within spawning years	0.29	0.003*
Within samples	99.71	0.002*
3. Among birth year cohorts	0.00	0.000
Among spawning years per cohort	0.46	0.005
Within samples	99.54	0.003
4. Among birth year cohorts	0.24	0.002
Between sexes per cohort	0.00	0.000
Within samples	99.76	0.000
5. Between sexes	0.00	0.000
Among spawning years per sex	0.24	0.002*
Within samples	99.76	0.001*
6. Between sexes	0.00	0.000
Among cohorts per sex	0.00	0.000
Within samples	100.00	0.000
7. Spawning early (ages 2–6) versus later (7 or older) in life	0.00	0.000
Early versus later among spawning years	0.11	0.001
Within samples	99.89	0.001
8. Spawning early (ages 2–6) versus late (7 or older) in life	0.00	0.000
Early versus late among birth year cohorts	0.02	0.001
Within samples	99.98	0.001

* Significant

cohort spawning earlier versus later in life and the larval walleye yielded the largest N_e values (infinity; Table 4). Estimates of N_b were high for most samples (Table 4). Individuals spawning later in life tended to show lower N_b compared to those reproducing at ages 2–6. This pattern remained consistent for the estimates from the 2003 cohort.

Discussion

Walleye temporal genetic patterns

Our study shows that despite intense fishing pressure and habitat degradation, the gene pool of walleye reproducing in the Maumee River has remained genetically stable, likely due to consistently large population sizes over the past two decades. Levels of genetic diversity, allelic composition, and allelic richness have remained similar among annual spawning runs, cohorts, and between the sexes.

There appeared to be some slight divergence of the 2013 spawning year individuals, and for the 2003 and 2010 cohorts, which is attributed to allele frequency fluctuations. These variations might stem from the preponderance of the very successful 2003 cohort in the samples (Fig. 3), which subsequently dominated the numbers of walleye in Lake Erie (WTG 2015). The 2003 cohort recruited to the fishery in 2005, and represented as much as 81 % of the 2007 catch in Lake Erie's Western Basin (WTG 2008). In 2014, the 2003 cohort still composed ~27 % of all Western Basin walleye (WTG 2015). Individuals born in 2007 and later predominantly were offspring of the 2003 cohort. In the later spawning years sampled here (2010–2013; see Fig. 3), fewer individuals born in 1992–1998 were present, and the genetic composition of the population likely was dominated by the 2003 cohort and its offspring. As this abundant cohort and its offspring continue to successfully reproduce, its genetic composition likely will continue, with the signatures of older cohorts (e.g., 1992–1998) disappearing. Thus, abundant cohorts may differentially affect the genetic composition of populations. Additional samples from later years should be tested to determine if this genetic trend continues. It would be interesting to analyze whether the two strong larval hatches in 2014 and 2015 (WTG 2016) affect the genetic composition of Maumee River walleye.

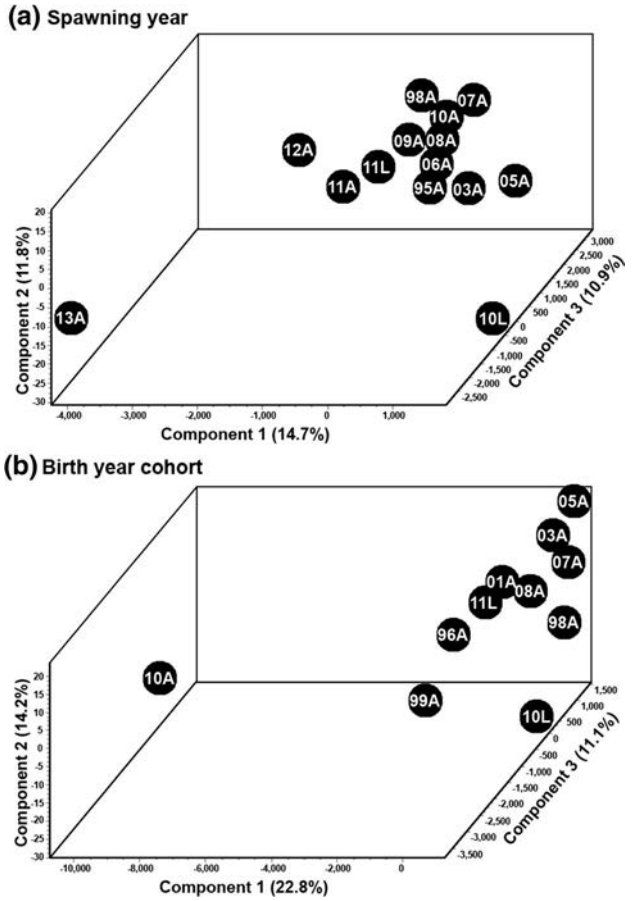

Fig. 2 Genetic relationships among Maumee River spawning adult and larval walleye samples, as depicted by 3d-FCA (Benzecri 1973) for: **a** sampling years and **b** birth year cohorts. *Circles* represent the centroids for the individuals per sample. Labels include adult (*A*) and larval (*L*) sample designations for spawning year in **a**, and birth year cohort in **b**

Our results significantly further those reported by Stepien et al. (2012) and Haponski et al. (2014) for walleye sampled from four Lake Erie spawning sites, including Van Buren Bay and Cattaraugus Creek in the Eastern Basin, and the Sandusky and Maumee rivers in the Western Basin. The temporal stability observed in today's Lake Erie walleye reproductive populations likely is the result of their large population sizes counteracting potential influences of genetic drift. Thus, it appears that the current GLFC's LEC management practices are meeting the Fish Community Objective to maintain high levels of genetic diversity in Lake Erie's walleye spawning groups (see Ryan et al. 2003; Locke et al. 2005; Kayle et al. 2015), with populations showing temporal consistency. Additionally, since genetic diversity and composition are stable, local adaptations of this valuable fishery likely are being preserved.

Other walleye spawning groups outside of Lake Erie displayed temporal variation in genetic composition resulting from population declines from exploitation and habitat degradation (Gatt et al. 2002; Garner et al. 2013). For example, walleye spawning in Georgian Bay, Lake Huron experienced significant declines in genetic diversity from $H_O = 0.50$ in 1965 to 0.15 in 1998, according to mtDNA restriction fragment length polymorphisms (Gatt

Table 4 Estimates of the effective number of breeders (N_b) and the overall effective population size (N_e) for Maumee River walleye spawning years, birth year cohorts, sexes, those reproducing earlier (ages 2–6) versus later (7 or older) in life, and larval samples determined from 13 nuclear DNA μsat loci using the linkage disequilibrium method (LD; Waples and Do 2008) in NEESTIMATOR v2.0.1 (Do et al. 2014)

Sample	*N*	LD
Adults spawning		
1995	53	707 (245–∞)
1998	28	361 (110–∞)
2003	76	∞ (1244–∞)
2005	56	575 (231–∞)
2006	51	536 (211–∞)
2007	48	644 (230–∞)
2008	50	453 (205–∞)
2009	48	2157 (327–∞)
2010-A	48	∞ (765–∞)
2011-A	48	329 (174–1964)
2012	46	16,762 (357–∞)
2013	48	∞ (20,117–∞)
Overall N_e	600	12,744 (3530–∞)
Adult birth year cohorts		
1996	25	∞ (206–∞)
1998	15	∞ (122–∞)
1999	34	5418 (223–∞)
2001	14	409 (57–∞)
2003	95	∞ (1029–∞)
2005	19	∞ (197-∞)
2007	21	1054 (118–∞)
2008	27	∞ (247–∞)
2010-A	16	∞ (122–∞)
Overall N_e	266	11,612 (1826–∞)
Early versus later reproduction		
Early (ages 2–6)	128	∞ (1066–∞)
Later (7 or older)	138	2204 (722–∞)
Overall N_e	266	11,612 (1826–∞)
Early versus later reproduction for the 2003 cohort		
Early	41	∞ (421–∞)
Later		1110 (287–∞)
Overall N_e	95	∞ (1029–∞)
Larvae		
2010-L	96	3357 (667–∞)
2011-L	48	∞ (469–∞)
Overall N_e	144	∞ (1342–∞)

∞ = infinity

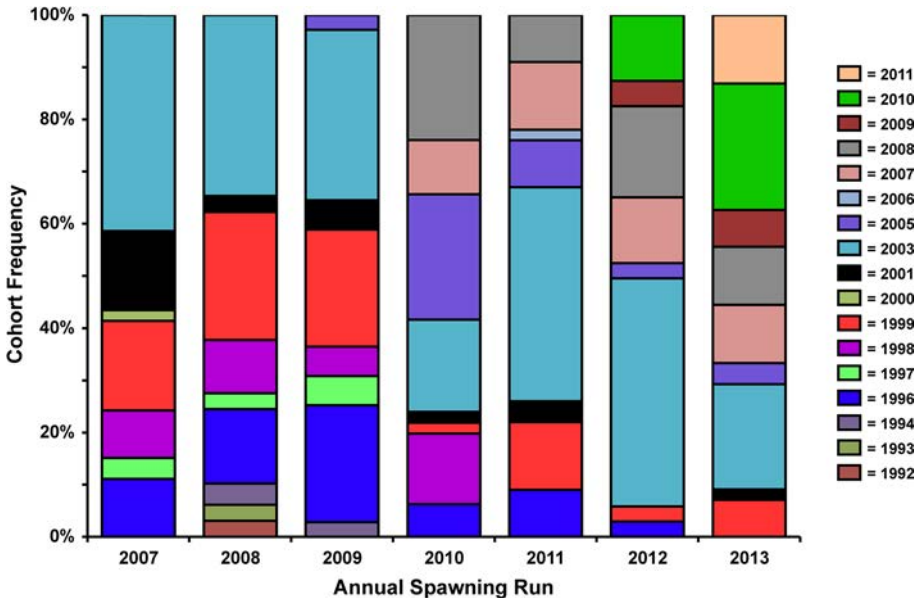

Fig. 3 Bar graph showing frequencies for walleye birth year cohort individuals spawning in the Maumee River for each year sampled where age data were available

et al. 2002). Garner et al. (2013) described significant changes in genetic composition for walleye spawning in Black Bay, Lake Superior from 1966 to 2010. Both the Georgian and Black Bay walleye populations are much smaller in size (Gatt et al. 2002; Garner et al. 2013) than those in Lake Erie (WTG 2015). Such temporal genetic fluctuations may be attributable to smaller population sizes and their greater susceptibility to genetic drift (summarized by Allendorf et al. 2013). As long as Lake Erie walleye spawning groups maintain their large population sizes (currently ~33 million fish; WTG 2016), significant loss of genetic diversity and changes in genetic composition appear unlikely. However, given that Lake Erie walleye populations have declined over recent years—from ~100 million in 2005 to 33 million in 2016 (WTG 2016)—continued exploitation and/or habitat degradation might impact their genetic composition and diversity, and thus warrants management attention.

Temporal patterns of walleye in comparison with other species

Other fishery species have shown variable patterns of relative stability or stochasticity in genetic diversity and composition. For example, populations of Atlantic cod *Gadus morhua* in the Gulf of St. Lawrence displayed temporal genetic stability and large effective population sizes over an 80-year period (1928–2008), according to nine μsat loci, despite intensive fishing pressure and decline in population abundance (Therkildsen et al. 2010). Notably, similar genetic diversity and allelic richness values were recovered between samples from 1928 to 2008, congruent with the pattern found here for Maumee River walleye. As in our results for walleye, Therkildsen et al. (2010) noted that those Atlantic cod populations had relatively large population sizes, according to N_e estimates.

In contrast to the stability we discerned for Lake Erie walleye and found for Gulf of St. Lawrence Atlantic cod (Therkildsen et al. 2010), brown trout *Salmo trutta* in a small Scandinavian lake displayed temporal allele frequency fluctuations among annual samples and cohorts spanning a 30-year period according to 14 allozyme loci, indicating genetic drift (Charlier et al. 2012). Lake Erie yellow perch also showed high temporal genetic divergence between spawning groups sampled in 2001–2005 versus 2009 using 14 μsat loci (Sullivan and Stepien 2015). Lake Erie houses a large population of yellow perch numbering ~151 million fish (Yellow Perch Task Group of the Lake Erie Committee (YPTG 2016)). Yellow perch, similar to walleye, exhibits natal homing and segregates each spring into small spawning groups (Sullivan and Stepien 2015 and references therein). This suggests the potential for a greater influence of genetic drift on these smaller yellow perch spawning groups compared to walleye.

Yellow perch also showed a higher association of kin groups than walleye. Kinship tests by our laboratory revealed higher proportions of full siblings in yellow perch spawning groups (mean 0.18, ranging to 0.75; Sullivan and Stepien 2015), which are 4× greater than those discerned here for walleye (mean 0.02, ranging to 0.04). The temporal genetic stochasticity reported for Lake Erie yellow perch likely was the result of a combination of genetic drift and inbreeding. Yellow perch may be able to reduce inbreeding by recognizing their close relatives and avoiding reproducing with them (see Stepien et al. 2015b); this

has been indicated for the closely related European perch *Perca fluviatilis* (Gerlach et al. 2001; Behrmann-Godel and Gerlach 2008). It appears likely that stability or stochasticity of temporal genetic patterns largely result from the effects of reproductive population size and behavior of spawning groups.

Relation of findings to history of Lake Erie walleye

In contrast to the genetic consistency found in the present study over the past two decades, Haponski and Stepien (2014) found that Lake Erie walleye populations sampled in 1923–1949 significantly differed from those sampled in this study from 1995 through the present. The earlier walleye samples had lower genetic diversity, different proportions of predominant alleles, and differences in allelic frequencies, in contrast to those examined here. The lower genetic diversity of the earlier populations likely stemmed from poorer environmental conditions and consequential population declines of walleye (and other fishes) due to the pronounced development, industrialization, exploitation, habitat loss, and pollution of Lake Erie during the early part of the twentieth Century (summarized by Hartig et al. 2009).

Other fish species from that time period likewise exhibited lower genetic diversity, attributed to population declines from polluted environmental conditions and overexploitation. For example, genetic diversity of the lake whitefish *Coregonus clupeaformis* in Lake Erie was lower in 1927 ($H_O = 0.60$) than in 1997–2005 (0.65) (Stott et al. 2013). Additionally, lake trout *Salvelinus namaycush* populations in Lakes Superior, Michigan, and Huron were less variable in 1940–1959 (0.47) than in 1995–1999 (0.51), based on analysis of five μsat loci (Guinand et al. 2003). As in walleye, those fish species also exhibited greater genetic diversity in more recent years, lending support for successful management strategies by the GLFC across the Great Lakes.

Lake Erie walleye recovered from population declines, reaching ~10 million in 1978, following the fishery's closure from 1970–1976 in response to mercury contamination and overfishing (Haas and Thomas 2007). Other factors leading to improved environmental conditions and population sizes, included implementation of the 1970 Canada Water Act, the 1972 U.S. Clean Water Act, and the 1972 Canada-US. Great Lakes Water Quality Agreement (Hartig et al. 2009). Increases in water temperature—especially in the shallow western basin—then shifted the Lake Erie fish community from predominantly cold-water species (e.g., lake trout) to warmer water species, favoring walleye and yellow perch during the past four decades. Declining numbers of colder water competitors presumably have enhanced walleye abundance (Ryan et al. 2003). By 1984, Lake Erie walleye had rebounded to ~90 million, which is nine times the 1978 population; these numbers then decreased to ~33 million in 2016 (WTG 2016). Large larval hatches were reported for 2014 and 2015 (WTG 2016). Their effects and contributions to the walleye population will be revealed in 2016 and 2017, when they recruit to the fishery.

The recovery and past 20 years of consistency in population size and genetic diversity of Lake Erie walleye that we observed likely was aided by migration of individuals from other locations. Notably, walleye spawning to the north of Lake Erie and the Maumee River in Lake St. Clair showed high genetic similarity to walleye in the western basin, indicating a potential source (see Stepien et al. 2009, 2010; Haponski and Stepien 2014). Our genetic analyses of Lake Erie walleye spawning groups have revealed overall temporal stasis in genetic diversity and allelic composition from 1995 to the present day. This should persist in concert with management strategies that continue to maintain large population sizes.

Comparisons of walleye kin relationships with other exploited species

We found that the population of walleye spawning in the Maumee River contained few full-siblings (mean 2 %), yet had substantial proportions (mean 25–73 %) of half-siblings. Similar to this pattern in walleye, Welsh et al. (2015) discerned few full-siblings in lake sturgeon *Acipenser fulvescens* spawning in the Kaministiquia River of Lake Superior, based on 12 μsat loci. Walleye are iteroparous (Johnston and Leggett 2002) and return to spawn at their natal sites each spring. During spawning a single female is surrounded by a group of 5–6 males, with females laying multiple clutches over several days and multiple males fertilizing these eggs as both eggs and sperm are broadcast into the water column (Collette et al. 1977; Barton and Barry 2011). This behavior creates ample opportunity for the mixing of gametes from multiple individuals from multiple cohorts, alleviating the potential genetic consequences of inbreeding, but potentially leading to high numbers of half-siblings. Discerning the relative proportions of half- and full-siblings in other walleye spawning groups would be an interesting avenue for further study.

In comparison, samples of yellow perch spawning groups from Lake Erie had consistently higher numbers of full-siblings (mean 18 %; Sullivan and Stepien 2015), which may indicate more inbreeding than in walleye. Yellow perch may avoid substantial inbreeding by recognizing their kin, perhaps by olfactory cues, and preferring to spawn with non-related individuals (see Stepien et al. 2015b). Walleye also may recognize their close kin, and choose non-related individuals to spawn with thereby

maintaining high genetic diversity and temporal genetic consistency. This scenario remains to be empirically tested.

Early life history of walleye and other species, and its possible influence on the gene pool

Broadcast spawning is a common reproductive strategy among fishes (including walleye) and many aquatic invertebrates (see Ruzzante et al. 1996; Gilg and Hilbish 2003; Welsh et al. 2015; Yednock and Neigel 2014). Broadcast spawners tend to have high fecundity and may undergo "sweepstakes" reproduction (see Hedgecock 1994)—with their reproductive success, larval survival, and recruitment being highly stochastic. This can result in fluctuations of genetic diversity and composition of the population, with a small minority of surviving individuals contributing a majority of the alleles. Notably, Ruzzante et al. (1996) examined the influence of larval recruitment on genetic structure of Atlantic cod. In analyzing multiple cohorts from a large aggregation comprising multiple spawning events, they found that just a single larval cohort survived and recruited, attributed to match in timing with environmental conditions.

Welsh et al. (2015) found no evidence for "sweepstakes" reproduction in lake sturgeon, with the larvae and spawning adults having similar diversity levels. Likewise, "sweepstakes" reproduction was not supported in the present study, since genetic diversity and composition of larval and adult walleye samples matched, and overall were temporally consistent over 20 years. However, comparison of the 2010 larval sample to adults that were born in 2010 and recruited to the fishery (i.e., the 2010 cohort), revealed a possible difference in genetic composition.

Survival of larval walleye in the Maumee River is highly variable from year to year, and is regulated by physical river conditions (see Mion et al. 1998; DuFour et al. 2014). During periods of high temperatures, numbers of larvae were low due to high mortality (Mion et al. 1998). In late spring 2010, 73 % of the days in May–June had above average air temperatures (by 4–16 °C, WeatherSpark 2014). Those temperatures coincided with the peak of the larval walleye hatch (see DuFour et al. 2014), which likely affected their survival and may have influenced recruitment in 2012 and later, resulting in some slight allele fluctuations in the cohorts. Thus our results suggest that variable recruitment has the potential to affect the genetic composition of adult cohorts, especially if numbers of walleye decline.

Effective population size and number of breeders

The Maumee River houses a sizeable walleye population, whose large number of breeding adults consistently have genetically contributed to high overall diversity, based on our estimates of N_e and N_b. These results additionally support that genetic drift and inbreeding have had little recent influence on this population (see Do et al. 2014) and that extirpation risk is low. The temporal genetic stability of walleye spawning in the Maumee River over the past 20 years is attributed to its large population size.

Pritt et al. (2013) estimated Maumee River walleye census abundance at 431,000–1,446,000 in 2011 and 386,400–857,200 in 2012 using a combination of hydroacoustic and gill net sampling, along with modeling. Those abundances were much higher than our estimates of overall N_e (12,744 among all spawning runs, 11,612 for all cohorts) and N_b for these two years (329 in 2011, 16,762 in 2012), with our values reflecting the number of reproducing adults contributing to the next generation.

The large population size of walleye may have exceeded the ability of estimators to distinguish "true" N_e and N_b values in the LD method, leading to our lower values (see Luikart et al. 2010; Waples and Do 2010). Lower estimates also could be the result of LD method assumptions violations, which include the use of neutral genetic markers, populations that are isolated, and have discrete generations (Waples and Do 2008). Our study solely analyzed loci exhibiting selective neutrality. Spawners in the Maumee River showed slight genetic divergence from other Lake Erie spawning groups (see Strange and Stepien 2007; Stepien et al. 2012), with some indication of migration (and gene flow) with nearby spawning groups. In violation of LD assumptions, walleye spawning groups comprise several generations. Since we sampled multiple ages (2–16), and also found no differences between those spawning at younger versus older ages, this may not have greatly affected our estimates (see Welsh et al. 2015). Overall, the results from walleye abundance estimates and our genetic data indicate that current GLFC LEC management practices are maintaining a large and genetically diverse walleye population. This could change if Lake Erie walleye numbers continue to decline. The large cohort born in 2015 (WTG 2016) may continue to stabilize the population, pending successful recruitment.

Franckowiak et al. (2009) calculated N_e and N_b for walleye spawning in Escanaba Lake, WI, finding that the average N_e ranged from 125–185 individuals and values of N_b from 159–852. The smaller N_e and N_b values compared to our study likely stems from this population occurring in a small isolated lake with just $\sim$3700 walleye, compared to the much larger population sizes and potential for migration in Lake Erie walleye.

Our N_e estimates for larval walleye also indicate possible effects of mortality on recruitment in 2010 and 2011. Notably, the N_e estimate from the larvae was much higher (although confidence intervals overlapped) than that for the

adult cohorts. This might account for the observed allelic frequency fluctuations between the 2010 larvae and its adult cohort. Further analysis of these patterns is warranted with additional larval samples, since our calculations were based on just two years.

Conclusions

This investigation increases our understanding of the fine-scale temporal genetic patterns of walleye, revealing large population size and remarkable consistency in genetic composition and diversity over the past two decades. This markedly contrasts with findings of lower diversity and different genetic composition in 1923–1949 (Haponski and Stepien 2014). Here we find that walleye spawning in the Maumee River are genetically consistent among yearly runs, cohorts, between the sexes, reproduction timing early versus later in life, and between the larvae and spawning adults despite a history of intensive exploitation and habitat degradation. There appears to have been little genetic drift, as indicated by the large number of breeders and substantial effective population sizes. There are some slight allele frequency fluctuations in recent spawning years, which may be due to the preponderance of the 2003 year class and its offspring as well as overall changes in year class composition from earlier decades. In the future, such fluctuations may increase due to genetic drift, if walleye population abundances further decline. It is possible that with extreme weather events and declining population sizes, "sweepstakes" reproduction might occur, leading to possible genetic changes. Future research is recommended that employs genomics to discern the adaptations of this large spawning group. Such applied knowledge will aid management efforts to sustain this valuable population in the face of further exploitation, habitat degradation, ongoing climate change, and/or new anthropogenic stressors.

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