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ARTICLE

Egg and Larval Collection Methods Affect Spawning Adult Numbers Inferred by Pedigree Analysis

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Abstract

Analytical methods that incorporate genetic data are increasingly used in monitoring and assessment programs for important rate functions of fish populations (e.g., recruitment). Because gear types vary in efficiencies and effective sampling areas, results from genetic-based assessments likely differ depending on the sampling gear used to collect genotyped individuals; consequently, management decisions may also be affected by sampling gear. In this study, genetic pedigree analysis conducted on egg and larval Lake Sturgeon *Acipenser fulvescens* collected from the St. Clair–Detroit River system using three gear types was used to estimate and evaluate gear-specific differences in the number of spawning adults that produced the eggs and larvae sampled (N_s), the effective number of breeding adults (N_b), and individual reproductive success. Combined across locations and sampling years, pooled estimates were 334 (N_s; point estimate) and 317 (N_b; 95% CI = 271–372). Mean reproductive success was 4.41 with a variance of 5.13 individuals/spawner. Mean ± SE estimated numbers of unique parents per genotyped egg or larva (i.e., adult detection rate) from 2015 samples were 1.140 ± 0.003 for vertically stratified conical nets, 0.836 ± 0.002 for D-frame nets, and 0.870 ± 0.002 for egg mats. Using samples from 2016, adult detection rates were 0.823 ± 0.001 for D-frame nets and 0.708 ± 0.001 for egg mat collections. Coancestry values were negatively correlated with adult detection rate. Although genetic pedigree analyses can improve the understanding of recruitment in fish populations, this study demonstrates that estimates from genetic analyses can vary with the targeted life stage (a biologically informative

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outcome) and sampling methodology. This study also highlights the influence of sampling methods on the interpretation of genetic pedigree analysis results when multiple gear types are used to collect individuals. Development of standardization approaches will facilitate spatial and temporal comparisons of genetic-based assessment results.

In recent years, genetic data have been increasingly used to assess population recruitment (Jay et al. 2014; Tsehaye et al. 2016; Brenden et al. 2018). Accurate and precise understanding of recruitment in natural fish populations is fundamental to management because of its importance for a population's long-term sustainability (Houde 2008; Jay et al. 2014; Ludsin et al. 2014). Recruitment estimates can be obtained from samples collected using many different gear types, the selection of which is contingent on a species' life history (Casselman et al. 1990) and habitat-imposed constraints on gear sampling effectiveness (Casselman et al. 1990; Erős et al. 2009). Efficiencies of different gear types vary (Casselman et al. 1990), and sampling events typically involve varying levels of effort (Jackson and Harvey 1997). Consequently, analytical approaches have been proposed to standardize traditional fisheries data to allow comparisons among samples collected at different times and locations, for different sampling durations, and with different gear types (Maunder and Punt 2004; Lee et al. 2010).

The sampling properties of different gears with respect to estimated genetic diversity of sampled individuals have not been thoroughly evaluated for different collection methodologies and species, and this may influence resulting measures of recruitment. Specimens from which genetic data are extracted are often obtained as part of standardized fisheries assessments or with the same suite of gears used during standardized assessments. As a result, genetic-based assessments of population recruitment could be improved if differences among gear types can be quantified and new relative metrics can be developed to account for differences in parameter estimates among collection methodologies; such metrics would facilitate spatial and temporal comparisons of recruitment estimates.

In this study, we focus on the genetic assessment of population recruitment in Lake Sturgeon *Acipenser fulvescens* of the St. Clair–Detroit River system (SCDRS). The Lake Sturgeon is a species of conservation concern that was once abundant throughout the Laurentian Great Lakes (Auer 1999). However, due in part to habitat modifications and overexploitation (Manny et al. 1988; Auer 1996; Bennion and Manny 2011; Hondorp et al. 2014), Lake Sturgeon populations have declined and not fully recovered despite implementation of more restrictive harvest regulations (Auer 1996) and improvements in water quality (Hartig et al. 2009). Recent habitat remediation efforts in the SCDRS included the construction of spawning reefs with the intent of increasing spawning habitat availability and ultimately the recruitment of lithophilic fishes (Roseman et al. 2011b; Hondorp et al. 2014; Manny et al. 2015).

Prior research conducted in the SCDRS immediately after construction of spawning reefs found that adult Lake Sturgeon successfully spawned over the reefs (Roseman et al. 2011b; Bouckaert et al. 2014; Manny et al. 2015; Prichard et al. 2017). Assessments also showed that eggs deposited at constructed reef sites survived to the larval drift stage (Roseman et al. 2011b; Bouckaert et al. 2014).

Despite evidence of successful spawning, questions remained as to how many spawning adults contributed the eggs or larvae that were sampled (N_s), the effective number of breeders (N_b), and the variance in individual reproductive success of Lake Sturgeon associated with the constructed reef sites. Genetic pedigree analysis is a useful method by which to characterize adult contributions to recruitment associated with remediation efforts (Christie et al. 2010; Sard et al. 2015). Information on how spawner abundance and reproductive success may affect cohort levels of genetic diversity is provided by estimates of N_b (i.e., the effective breeding population size for a spawning period). The N_b is usually smaller than the population abundance because of sex ratio skew (Frankham 1995; Charlesworth 2009; Waples 2010). High levels of variation in adult reproductive success also result in reduced N_b (Araki et al. 2007; Duong et al. 2013). Estimates of N_s, N_b, and variance in adult reproductive success generated using sibship reconstruction methods based on genetic data further inform managers of the benefits of constructed spawning habitat for lithophilic-spawning fishes. However, estimates based on traditional assessments (e.g., abundance estimates from eggs and larvae collected with egg mats and nets) as well as genetic data may be affected by the methodologies used to collect samples and the biology of the species of interest.

The number of larvae collected in individual sampling events is often highly variable due to spatially and temporally heterogeneous distributions of individuals in the environment (Cyr et al. 1992; D'Amours et al. 2001). Because of the potential for passive and active dispersal during early (egg and larval) ontogenetic stages, measures of spawning success generated using genetic pedigree analysis may be influenced by specific sampling methodologies. In the case of Lake Sturgeon in the SCDRS, large numbers of eggs or larvae collected from sampling conducted at a reef site does not necessarily indicate a large number of spawning adults. Lake Sturgeon are highly fecund (Bruch et al. 2006), and a single adult pair ostensibly could produce all of the eggs or larvae collected in a sample. For example, sampling gear such as small (38- × 24- × 0.5-cm) egg mats positioned directly on a constructed reef may sample offspring from many males because females mate with multiple males (Bruch and Binkowski 2002).

However, it is possible that the offspring were contributed by an individual female due to heterogeneous dispersal of eggs and dispersion of egg mats during spawning. Additionally, if eggs from individual females are not evenly distributed across a spawning site, positioning the sampling gear, such as D-frame nets, directly downstream of constructed spawning reefs may collect larvae dispersing from small proportions of the reef and thus underestimate adult spawning number when collected larvae are used for genetic pedigree analysis. Gear types such as vertically stratified conical nets positioned further away from constructed reefs may be more likely to sample larvae from proportionately more spawning adults because of the potential for larvae to mix in the water column during dispersal. Additionally, the sampling efficiency of each gear type in terms of the number of eggs and larvae collected per sampling event can lead to potential differences in N_s and N_b estimated from genetic pedigree analysis.

The objective of this study was to examine the effects of early life stage collection methods on estimates of N_s and N_b obtained using genetic pedigree analysis. We hypothesized that estimates of N_s, N_b, and measures of reproductive success would differ among sampling methods due to unequal sample sizes, per-net or per-egg-mat frequency of egg and larva collection, and within-sample relatedness of collected individuals.

METHODS

Study area.— The SCDRS is a 145-km, barrier-free connecting channel between Lake Huron and Lake Erie (Figure 1). The head of the SCDRS, located near the city of Port Huron, Michigan, is a known natural spawning site for Lake Sturgeon (Manny and Kennedy 2002). Sites included in this study were located downstream of this natural spawning area. The 1.7-ha (~56.4- × 306.6-m) Harts Light Reef was located approximately 35 km downstream from the head of the St. Clair River, near East China, Michigan (Figure 1), and was constructed from 10- to 15-cm sorted limestone in 2014. Water depth was approximately 16 m, with a discharge of 1.35 m^3/s. Further downstream (28 km) in the St. Clair River was the 0.6-ha (~32.9- × 184.4-m) Pointe Aux Chenes Reef (Figure 1), which was constructed in 2014 from 10- to 15-cm sorted limestone; water depth was approximately 15 m, with a discharge of 1.03 m^3/s. Finally, in the Detroit River, the 1.6-ha (~43.6- × 371.6-m) Grassy Island Reef (Figure 1) was constructed in 2015 from 10- to 15-cm sorted limestone. Water depth at Grassy Island Reef was approximately 12 m, with a discharge of 0.80 m^3/s.

Egg and larval collection methods.— Egg- and larval-stage Lake Sturgeon were collected using egg mats (egg stage: Roseman et al. 2011a), D-frame nets (larval stage: Roseman et al. 2011a), and vertically stratified conical nets (larval stage: Bouckaert et al. 2014) at Harts Light and Pointe Aux Chenes reefs and two additional spawning sites in the North Channel and Middle Channel, St. Clair River, during 2015 and 2016; and at Grassy Island Reef in the Detroit River, during 2016 (Figure 1). Egg mats consisted of a furnace filter surrounding a 38- × 24- × 0.5-cm steel frame secured using 5- × 2.5-cm binder clips. Egg

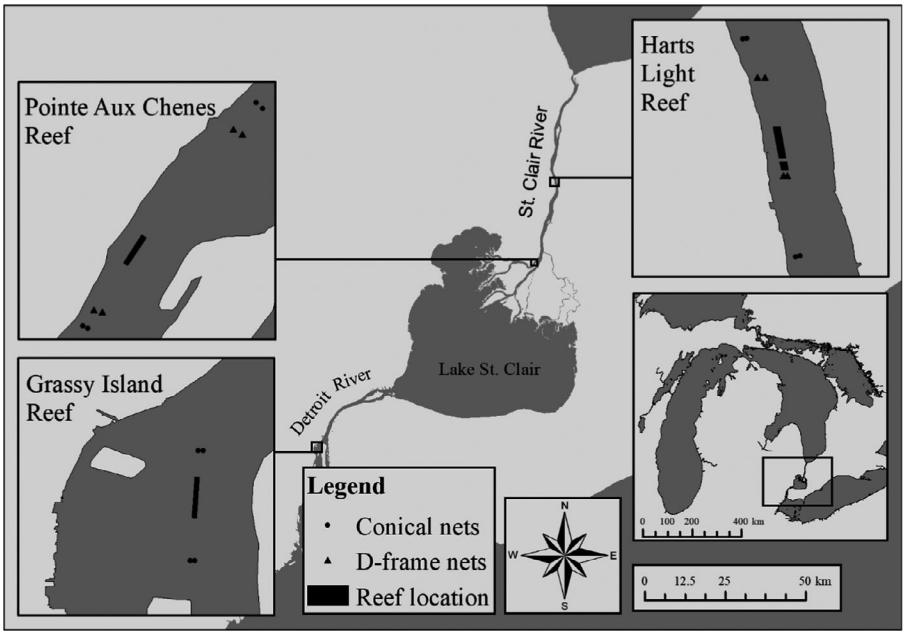

FIGURE 1. Map of the St. Clair–Detroit River system. Locations of constructed reef sites are highlighted, and net locations are indicated by triangles for D-frame nets and by circles for vertically stratified conical nets. Egg mats were deployed on the constructed reefs.

mats were deployed on constructed reefs in sets of three mats separated by 1 m (Manny et al. 2010; Roseman et al. 2011a). Two sets of egg mats were deployed on each reef. One egg mat set was placed on the upstream portion of the reef, and one egg mat set was placed on the downstream portion. Egg mats were retrieved weekly, and eggs were identified to species and enumerated. Each egg mat retrieved was treated as a separate sample. In total, 363 (2015) and 322 (2016) egg mats were retrieved across all study sites and checked for Lake Sturgeon eggs during the spawning period. Numbers of Lake Sturgeon eggs collected on upstream egg mats compared to downstream egg mats were similar for Harts Light Reef and Pointe Aux Chenes Reef. However, Lake Sturgeon eggs were collected only on the downstream egg mats at Grassy Island Reef (Craig et al. 2017). A subset of Lake Sturgeon eggs from each egg mat was selected at random and reared (Sutherland et al. 2014) until the yolk sac was absorbed to allow for DNA extraction.

The D-frame nets were 76 cm at the base × 54 cm high and were made of 1,600-μm mesh. They were deployed as paired sets of two nets on the river bottom directly upstream and two nets directly downstream of each constructed reef. The D-frame nets were fished at depths of approximately 14.5 m (upstream) and 17.3 m (downstream) at Harts Light Reef; 15.7 m (upstream) and 16.2 m (downstream) at Pointe Aux Chenes Reef; and 9.8 m (upstream) and 10.2 m (downstream) at Grassy Island Reef. Nets were deployed at each reef from approximately 2000 to 0400 hours, during the peak larval drift period for Lake Sturgeon in the SCDRS as identified by Bouckaert et al. (2014). In 2015, 91 D-frame nets were deployed and retrieved in the SCDRS. In 2016, 181 D-frame nets were deployed and retrieved.

Vertically stratified conical nets were deployed in paired sets with two groups of nets (3 nets/group) directly upstream and two groups of nets directly downstream of each constructed reef. A group consisted of three conical nets that were 0.3 m in diameter with 750-μm mesh. Nets were suspended on a buoy line in the water column; one net was set 1 m below the surface, one net was set in the middle of the water column, and one net was set 1 m off the river bottom (D'Amours et al. 2001; McCullough et al. 2015). Vertically stratified conical nets were deployed at sunset and retrieved at sunrise. In total, 211 vertically stratified conical nets were deployed and retrieved in 2015 and 240 were deployed and retrieved in 2016. Each conical net deployed on each night was treated as a separate sample.

Extraction and amplification of DNA.— Caudal fin tissue was sampled from collected larvae, and DNA was extracted using Qiagen DNeasy kits (Qiagen, Valencia, California) according to the manufacturer's protocol. A NanoDrop spectrophotometer was used to determine the DNA concentration, and DNA was diluted to a concentration of 20 ng/μL.

Polymerase chain reaction was used to amplify DNA for each of 13 disomic loci: *LS-68* (May et al. 1997); *Afu68b* (McQuown et al. 2002); *Spl120* (McQuown et al. 2000); *Aox27* (King et al. 2001); *AfuG9*, *AfuG56*, *AfuG63*, *AfuG74*, *AfuG112*, *AfuG160*, *AfuG195*, and *AfuG204* (Welsh et al. 2003); and *Atr113* (Rodzen and May 2002). Analyses also included five polysomic loci adapted from Jay et al. (2014): *Atr100*, *Atr114*, *Atr117*, *AciG35*, and *AciG110* (Rodzen and May 2002). The PCR conditions for each of the 13 disomic loci were as described by Duong et al. (2013), and those for the five polysomic loci were as described by Jay et al. (2014).

Polymerase chain reaction was performed in 25-μL reactions with 100 ng of genomic DNA. Based on optimizations described by K. T. Scribner, G. Uhrig, and J. Kanefsky (unpublished data), reactions used 10 × PCR buffer (0.1-M Tris-HCl, 15-mM $MgCl_2$, 0.5-M KCl, 0.1% gelatin, 0.1% NP-40, and 0.1% Triton-X), $MgCl_2$, 2-mM each dNTP, 10 pmol of forward and reverse primers, and Denville *Taq* polymerase (Denville Scientific, Metuchen, New Jersey). After multiplexing and dilution to concentrations optimized for analysis, PCR product was analyzed on an ABI 3730xl DNA analyzer (Applied Biosystems, Foster City, California) at the Michigan State University Research Technology Support Facility. All allele sizes were analyzed with MapMarker size standards (BioVentures, Murfreesboro, Tennessee) and included three Lake Sturgeon samples of known genotype and a negative sample (no DNA). Results were visualized using GeneMarker (Softgenetics, State College, Pennsylvania). Alleles were scored independently and confirmed by two experienced laboratory personnel. Approximately 10% of all individuals were selected randomly and re-genotyped as a further quality control check, resulting in empirical scoring error rates of 0.5% in 2015 and 1.8% in 2016.

Pedigree analysis.— Allele scores (bp) were assigned using the method of Rodzen et al. (2004) and Wang and Scribner (2014). This method treats individual alleles as pseudo-disomic loci, resulting in a score reflecting presence (score = 1), absence (score = 2), or missing data (score = 0) for each individual and locus. Data were recorded as missing if an individual failed to amplify at a locus despite two separate amplification attempts. Overall, 741 larvae collected in nets or reared from eggs collected on egg mats were analyzed using 164 alleles (pseudo-disomic loci) in 2015 and 2016; the total sample size was 741 eggs and larvae. The program COLONY was used to assign larvae to full-sibling and half-sibling groups and to infer N_s and N_b contributing to offspring sampled by using a full maximum likelihood approach (Wang 2004). The COLONY parameters included polygamy for males and females, high

likelihood precision, unique random number seeds for each run, and no prior sibship knowledge. All other COLONY parameters were run at default settings.

Accuracy in pedigree analysis is dependent on the number of loci analyzed and the amount of information provided by the markers (Wang and Scribner 2014). Wang and Scribner (2014) found that treating polysomic markers as pseudo-disomic loci allowed for accurate assessment of full-sibling and half-sibling relationships. Simulations from Hunter et al. (in press) demonstrated sufficient power to accurately assign larvae to full-sibling and half-sibling groups and to infer N_s.

Pedigrees were generated in COLONY and consisted of each unique larval identity, a putative mother identity, and a putative father identity. Using only larval genotypes to generate the pedigree provides no information on the actual sex of the putative parents, so further analysis considered only unique parent identities.

Statistical analysis.—To account for potential within-sample variation as well as variation in results due to the order that larvae were included in the pedigree, each collection method and location-specific pedigree underwent bootstrap resampling (total number of iterations = 1,000). Resampling resulted in bootstrapped pedigrees for which the cumulative sums of unique parents per larva genotyped were generated. A simple linear regression model (equation 1) was fit to each bootstrapped pedigree for each collection method,

$$\mathrm{Sum}_{par} = \beta_0 + \beta_1 N_{off}, \tag{1}$$

where Sum_{par} is the cumulative sum of unique parents detected, β_0 is the intercept, β_1 is the model slope (i.e., the rate of detection of unique parents per larva genotyped), and N_{off} is the number of larvae genotyped. The mean slope was calculated as the mean of all slopes estimated from 1,000 bootstrapped pedigrees. Regressing the cumulative sum of unique parents detected per larva genotyped for each collection method yielded an estimate of the rate of detection of unique parents per larva genotyped for a particular sampling method (i.e., a measure of gear sampling efficiency with respect to adult numbers represented in the progeny sampled). These slopes were hypothesized to differ between collection methods due to within-sample variation or due to the sequential order in which larvae—and subsequently the parents that contributed them—were included in the analysis. Differences in numbers of parents detected per larva genotyped between gear types were examined for each bootstrap sample for each sampling gear using a varying slope and varying intercept linear model (equation 2),

$$\mathrm{Sum}_{par_t} = \beta_{0_t} + \beta_{1_t} N_{off_t} + \varepsilon, \tag{2}$$

where Sum_{par} is the cumulative sum of unique parents detected by sampling gear t; β_{0_t} is the model intercept for sampling gear t; β_{1_t} is the model slope for sampling gear t; and N_{off_t} is the number of larvae genotyped for sampling gear t. Error (ε) was assumed to be normally distributed with a mean of zero and a variance of σ^2. The varying-intercept and varying-slope linear model was fit in R version 3.4.3 (R Core Team 2017) using the lm function from the "stats" package. After fitting the linear model, we tested whether slopes for the sampling gears were significantly different ($\alpha = 0.05$) by using the linearHypothesis function from the "CAR" package (Fox and Weisberg 2011). Testing the differences in slopes effectively tested for significant differences in the rate of detection of unique parents per larva genotyped for the sampling methods for each pair of bootstrapped pedigrees. Repeating this across all bootstrapped samples resulted in 1,000 significance test results as to whether model slopes differed between the sampling gears. To conclude that there were significant differences in the rate of detection of unique parents per larva genotyped for two sampling methods, the test for slope equality had to be rejected for more than 950 ($\alpha = 0.05$) of the bootstrap draws. Because of small sample sizes, captures from vertically stratified conical nets in 2016 were not included in the slope comparisons.

In addition to rates of detection of unique parents per larva genotyped, we also examined coancestry (θ) as a measure of relatedness among individuals sampled. Coancestry was calculated for each bootstrapped pedigree according to the methods described by Bartron et al. (2018). Individual θ values were calculated for each of 1,000 bootstrapped pedigrees as (equation 3)

$$\theta = \frac{n_{fs}(0.25) + n_{hs}(0.125) + n_u(0)}{n_t}, \tag{3}$$

where n_{fs} is the number of full-sibling dyads, n_{hs} is the number of half-sibling dyads, and n_u is the number of unrelated dyads identified in each bootstrapped pedigree (Cockerham 1969; Crossman et al. 2011; Bartron et al. 2018). Mean coancestry was calculated as the sum of all individual θ values for 1,000 bootstrapped pedigrees divided by the number of bootstrapped iterations. Standard errors for mean θ, the number of unique parents included in bootstrapped pedigrees (N_s), and the slope (rate of detection of unique parents genotyped) were also calculated from the bootstrapped results.

Two-sided Student's *t*-tests based on the bootstrap results were used to test for significant differences between θ for each gear type by location and year. Pearson's product-moment correlation was used to examine correlations between θ, N_s, and the rate of detection of unique parents per larva genotyped.

RESULTS

Sample Sizes Varied by Gear Type

Collections of egg-stage and larval Lake Sturgeon were generally low for all gear types (Table 1). Egg mats had the highest mean catch at approximately 7 individuals/mat in 2015 and 6.5 individuals/mat in 2016. Catches in D-frame nets were substantially lower at 3.8 individuals/net in 2015 and 4.3 individuals/net in 2016. The mean number of individuals captured per conical net was far lower than the number captured per egg mat or D-frame net, with only 6.0% (in 2015) and 0.4% (in 2016) of the mean number of individuals captured per egg mat. Comparison of nonzero catches showed even greater disparity among gear types. In 2015, the mean nonzero catch was only 6.3% (D-frame net) and 2.4% (conical net) of the mean nonzero catch per egg mat. Similarly, in 2016 the mean nonzero catch was 13.9% (D-frame net) and 1.2% (conical net) of the mean nonzero catch per egg mat. However, averaged across years, over 90% of egg mats and conical net sets had a catch of zero (Table 1). In contrast, 57.3% of D-frame net sets collected one or more larval Lake Sturgeon when averaged across years. The three gear types frequently collected zero individuals, with D-frame nets collecting individuals more often than egg mats and conical nets. However, when egg mats did collect individuals they tended to collect more individuals than D-frame nets or conical nets.

Number of Spawning Adults Contributing Eggs and Larvae

Point estimates of N_s were sample size dependent and increased linearly with the number of larvae that were genotyped (Figure 2). To account for sample size dependence and to compare N_s point estimates between gear types and across locations, the N_s values were divided by the total number of larvae genotyped in each sample and averaged across years. There was a 4.8% difference in average point estimates of N_s per larva genotyped across all reefs and years between egg mats (0.577 N_s per larva genotyped) and D-frames (0.550 N_s per larva genotyped). However, vertically stratified conical nets had a 73% larger estimate of N_s per larva genotyped (1.00 N_s per larva genotyped) compared to egg mats and a 82% larger estimate than D-frame nets. At Harts Light Reef, the average N_s per larva genotyped for vertically stratified conical nets (1.259 N_s per larva genotyped) was 85% larger than the average for egg mats (0.682 N_s per larva genotyped) and 61% larger than the average for D-frame nets (0.784 N_s per larva genotyped). At Pointe Aux Chenes Reef, the average estimate of N_s for egg mats (1.085 N_s per larva genotyped) was 26% larger than that for D-frame nets (0.859 N_s per larva genotyped), but the average for vertically stratified conical nets (1.60 N_s per larva genotyped) was 86% larger than that for D-frame nets and 47% larger than that for egg mats. Finally, the average estimate of N_s at Grassy Island Reef in 2016 for D-frame nets (0.554 N_s per larva genotyped) was 43% larger than the average for egg mats (0.789 N_s per larva genotyped). Between-year variation in detection of unique parents per larva genotyped for each of the sampling methods was generally low for individual reefs and when reefs were combined (Table 2).

Effective Number of Breeders

Estimates of N_b were also sample size dependent (Figure 2). When we accounted for the effect of sample size, vertically stratified conical nets consistently had greater N_b values estimated compared to egg mats and D-frame nets. Egg mats and D-frame nets had similar point estimates for N_b per larva genotyped, but generally D-frame nets had larger values of N_b per larva genotyped than did egg mats. However, 95% CIs around N_b estimates for all gear types overlapped across all constructed reef sites for all years (Table 2).

Rates of Detection of Unique Parents

Mean slopes between years were similar within collection methods over all locations (Figure 3). Trends for differences in mean slope remained consistent between reefs and years. Vertically stratified conical nets detected unique parents at a higher rate per larva genotyped (range = 1.140–1.220), followed by D-frame nets (range = 0.823–1.182) and then egg mats (range = 0.555–1.000; Table 3). Significant differences in the rates of unique

TABLE 1. Trends in egg and larval Lake Sturgeon capture rates by year and gear type. Mean catch (±SD) is the mean for each gear type by year, including egg mats or nets that collected zero eggs or larvae. Mean nonzero catch (±SD) is the mean for each gear type by year for only egg mats or nets that collected at least 1 egg or larva. Percent zero catch is the percentage of egg mats or nets that caught zero eggs or larvae by year.

	Egg mats		D-frame nets		Conical nets	
Variable	2015	2016	2015	2016	2015	2016
Mean catch	7.02 ± 42.11	6.49 ± 37.80	3.75 ± 9.17	4.30 ± 13.38	0.42 ± 1.15	0.03 ± 0.16
Mean nonzero catch	110.74 ± 131.03	83.08 ± 111.18	6.96 ± 11.62	11.61 ± 20.05	2.62 ± 2.74	1.00 ± 0.00
Percent zero catch	93.66	92.19	46.15	62.98	83.89	97.50

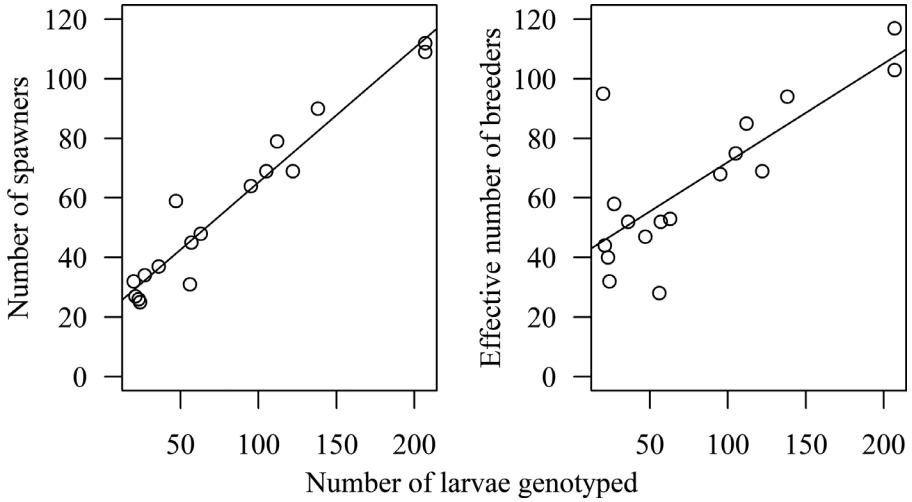

FIGURE 2. Plots of the number of spawning adult Lake Sturgeon that produced the eggs and larvae sampled (N_s) and the effective number of breeding adults (N_b) by the number of larvae genotyped in the pedigree used to generate the estimate. The N_s and N_b values are positively correlated with sample size. Points are parameter estimates for individual reefs and all reefs combined in 2015 and 2016.

parents detected per larva genotyped were observed between vertically stratified conical nets and either D-frame nets ($P = 0.012$) or egg mats ($P = 0.022$) in 2015 pooled across all sites (Table 4). No significant difference was found between D-frame nets and egg mats ($P = 0.156$) in 2015 across all reef sites. However, a significant difference in the rates of detection of unique parents per larva genotyped was observed between egg mats and D-frame nets ($P = 0.018$) in 2016 for eggs and larvae pooled across all reef sites, with D-frame nets detecting unique parents at a slightly higher rate. Trends in rates of detection of unique parents per larva genotyped were relatively similar across locations and between years (Table 3). No significant differences were observed for the rate of detection of unique parents per larva genotyped at individual reef sites between any of the collection methods in 2015 (Table 4). Differences were not always significant, but for each location and year vertically stratified conical nets generally had the highest rate of detection, followed by D-frame nets and finally egg mats (Table 3).

Levels of Coancestry in Bootstrap Resampled Pedigrees

Mean θ was generally lower for pedigrees generated using samples collected with vertically stratified conical nets compared to pedigrees generated using samples

TABLE 2. Empirical results from genetic pedigree analysis for each gear in 2015 and 2016 using Lake Sturgeon larvae pooled across all reefs and at each reef location ($N_{individuals}$ = number of larvae genotyped; N_s = estimated number of spawning adults; N_b = effective number of breeders, with 95% CIs shown in parentheses; NA = data not available).

		2015			2016	
Location	Variable	Conical nets	D-frame nets	Egg mats	D-frame nets	Egg mats
All reefs	$N_{individuals}$	47	122	138	207	207
	N_s	47	69	90	112	109
	N_b	59 (40, 93)	69 (50, 98)	94 (69, 127)	117 (91, 152)	103 (77, 137)
Harts Light Reef	$N_{individuals}$	27	21	112	95	105
	N_s	34	27	79	64	69
	N_b	58 (36, 106)	44 (25, 91)	85 (63, 122)	68 (48, 99)	75 (55, 106)
Pointe Aux Chenes Reef	$N_{individuals}$	20	63	23	36	24
	N_s	32	48	26	37	25
	N_b	95 (51, 352)	53 (36, 82)	40 (23, 82)	52 (33, 87)	32 (18, 61)
Grassy Island Reef	$N_{individuals}$	NA	NA	NA	57	56
	N_s	NA	NA	NA	45	31
	N_b	NA	NA	NA	52 (34, 78)	28 (17, 48)

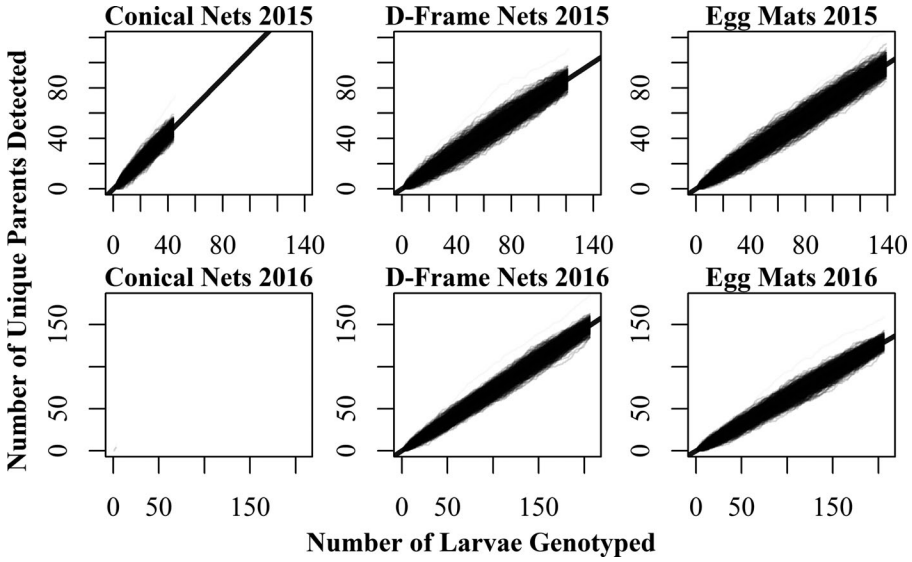

FIGURE 3. Plots of the rate of detection of unique Lake Sturgeon parents per additional larva genotyped by each collection method in 2015 and 2016 for each of 1,000 bootstrapped gear- and year-specific pedigrees. Mean slope (solid line) represents the mean rate of detection of unique parents for each collection method in each year. The cloud of lines surrounding the mean slope represents the cumulative number of unique parents detected per larva genotyped for each of 1,000 pedigrees bootstrapped with replacement.

from D-frame nets and egg mats in 2015 (Table 3). In 2016, pedigrees from samples collected using D-frame nets resulted in significantly lower θ values than egg mats across all sites ($P < 0.001$). However, this pattern was not always consistent in 2015, as higher θ was observed in D-frame collections using samples from all reefs (Table 3). Student's *t*-tests indicated significant differences in levels of θ among all gear types ($P < 0.001$; Table 5). Significant negative correlations were observed between θ and N_s and between θ and the slope (rate of detection of unique parents per larva genotyped) in 2015 (Table 6) and at most locations in 2016 (Table 7). There were significant ($P < 0.001$) positive correlations between mean slope and N_s in 2015 (Table 6) and at most locations in 2016 (Table 7).

DISCUSSION

The study focus was to evaluate sampling gear effects on estimates of adult Lake Sturgeon use of constructed spawning reefs as measured by N_s and N_b. Critical assessment of the effects of sampling methodology on the number of spawning adults contributing offspring for traditional assessment and genetic pedigree analysis will afford opportunity for statistical comparison and allow proper interpretation of results to inform management. Cyr et al. (1992) demonstrated that the number of replicate samples required for precise estimates of larval abundance using traditional sampling methods rises rapidly as the mean number of larvae captured per sample decreases. Pritt et al. (2014) similarly found evidence for differences in detection probabilities among species with differing early life history traits that impact site occupancy and abundance estimates. Additionally, Bacles et al. (2018) demonstrated that estimates of N_b are affected by spatial and temporal differences in collection methodologies as well as sibship reconstruction methods for Atlantic Salmon *Salmo salar* in the River Nivelle, France. Similarly, results of this study demonstrate that precision in parameters estimated based on genetically reconstructed pedigrees may be improved by sampling sufficient numbers of individuals and by conducting more spatially and temporally intensive sampling. Findings here indicate that the selection of sampling methods with high sampling efficiencies is important. Parameters that were estimated (N_s and N_b) via reconstructed pedigrees were sample size dependent, and each gear collected different numbers of eggs and larvae per sampling event. Additionally, the relationship between sample size and the accuracy of N_b estimates has been previously established (England et al. 2006; Ackerman et al. 2017). Ackerman et al. (2017) used COLONY to estimate N_b and suggested that the desired sample size to produce accurate estimates should equal or exceed the true N_b for the sampled population. Sample sizes that generate accurate N_b estimates are dependent on the population being sampled, and populations with a small true N_b may not require large sample sizes to generate reliable estimates (Bacles et al. 2018). Additionally, Bacles et al. (2018) demonstrated that N_b estimates generated with juvenile sample sizes 10 times greater than the true

TABLE 3. Mean (±SE) number of spawning adult Lake Sturgeon (N_s) included in each simulation, the slope (rate of detection of unique parents per larva genotyped), and coancestry (θ) for 1,000 pedigrees bootstrapped with replacement for each gear type and reef site in 2015 and 2016 (NA = data not available).

		2015			2016	
Location	Variable	Conical nets	D-frame nets	Egg mats	D-frame nets	Egg mats
All reefs	N_s	53 ± 0.124	101 ± 0.152	119 ± 0.176	101 ± 0.152	119 ± 0.176
	Slope	1.140 ± 0.003	0.836 ± 0.002	0.870 ± 0.002	0.823 ± 0.001	0.709 ± 0.001
	θ	0.006 ± 0.0002	0.013 ± 0.0001	0.011 ± 0.0001	0.007 ± 0.0001	0.013 ± 0.0001
Harts Light Reef	N_s	28 ± 0.096	25 ± 0.087	103 ± 0.177	96 ± 0.161	67 ± 0.137
	Slope	1.180 ± 0.005	1.122 ± 0.005	0.927 ± 0.002	1.022 ± 0.002	1.00 ± 0.003
	θ	0.007 ± 0.0004	0.002 ± 0.0002	0.011 ± 0.0002	0.007 ± 0.0001	0.012 ± 0.0002
Pointe Aux Chenes Reef	N_s	23 ± 0.086	60 ± 0.122	20 ± 0.080	41 ± 0.110	23 ± 0.090
	Slope	1.220 ± 0.006	0.960 ± 0.003	0.930 ± 0.005	1.182 ± 0.004	0.982 ± 0.005
	θ	0.002 ± 0.0002	0.014 ± 0.0002	0.057 ± 0.0015	0.005 ± 0.0002	0.034 ± 0.0010
Grassy Island Reef	N_s	NA	NA	NA	58 ± 0.124	31 ± 0.078
	Slope	NA	NA	NA	1.039 ± 0.003	0.555 ± 0.002
	θ	NA	NA	NA	0.011 ± 0.0002	0.072 ± 0.0010

population N_b without including parent genotypes in the sibship reconstruction analysis tended to overestimate N_b. However, parameter estimates generated using genetic pedigree analysis are dependent not only on sample size, replicate sampling, and species early life history traits but also on different levels of relatedness among individuals collected with different gear types.

Sample coancestry (θ) was correlated with the rate at which unique parents were detected and generally differed between collections obtained using different gear types. Results may be due to the fact that eggs deposited by Lake Sturgeon are clustered by family group across a spawning site. Consequently, sample collection using egg mats may generate pedigrees with high θ and a lower

TABLE 4. *P*-values for tests of significant differences in the rate of detection of unique Lake Sturgeon parents per larva genotyped between gear types across all reefs and at each reef in 2015 and 2016. Asterisks represent significant differences in the rate of detection of unique parents between gear types (α = 0.05; NA = data not available; vs. = versus).

	2015			2016
Location	Conical nets vs. D-frame nets	Conical nets vs. egg mats	D-frame nets vs. egg mats	D-frame nets vs. egg mats
All reefs	0.012*	0.022*	0.156	0.008*
Harts Light Reef	0.609	0.214	0.220	0.226
Pointe Aux Chenes Reef	0.221	0.277	0.467	0.230
Grassy Island Reef	NA	NA	NA	0.000*

TABLE 5. *P*-values calculated using Student's *t*-test comparing coancestry for 1,000 Lake Sturgeon pedigrees bootstrapped with replacement between gear types across all reefs and at each reef in 2015 and 2016. Asterisks represent differences in coancestry between gear types (α = 0.05; NA = data not available; vs. = versus).

	2015			2016
Location	Conical nets vs. D-frame nets	Conical nets vs. egg mats	D-frame nets vs. egg mats	D-frame nets vs. egg mats
All reefs	<0.001*	<0.001*	<0.001*	<0.001*
Harts Light Reef	<0.001*	<0.001*	<0.001*	<0.001*
Pointe Aux Chenes Reef	<0.001*	<0.001*	<0.001*	<0.001*
Grassy Island Reef	NA	NA	NA	<0.001*

TABLE 6. Results of Pearson's product-moment correlation tests, indicating significant negative correlations between coancestry (θ) and the number of unique Lake Sturgeon parents detected in the pedigree (N_s), significant negative correlations between θ and slope (i.e., rate of detection of unique parents per larva genotyped), and significant positive correlations between slope and N_s in 2015. Asterisks represent significant correlations ($\alpha = 0.05$; vs. = versus).

		Conical nets			D-frame nets			Egg mats		
Location	Statistic	θ vs. N_s	Slope vs. N_s	θ vs. slope	θ vs. N_s	Slope vs. N_s	θ vs. slope	θ vs. N_s	Slope vs. N_s	θ vs. slope
All reefs	*t*	−9.88	41.75	−7.78	−13.81	38.32	−10.68	−16.13	37.75	−12.26
	P	<0.001*	<0.001*	<0.001*	<0.001*	<0.001*	<0.001*	<0.001*	<0.001*	<0.001*
	r	−0.30	0.80	−0.24	−0.40	0.77	−0.32	−0.45	0.77	−0.36
Harts Light Reef	*t*	−7.97	43.85	−6.17	−3.33	42.96	−3.37	−14.62	43.38	−11.70
	P	<0.001*	<0.001*	<0.001*	<0.001*	<0.001*	<0.001*	<0.001*	<0.001*	<0.001*
	r	−0.24	0.81	−0.19	−0.10	0.81	−0.11	−0.42	0.81	−0.35
Pointe Aux Chenes Reef	*t*	−4.41	43.03	−3.83	−14.21	41.56	−11.44	−16.17	41.90	−12.90
	P	<0.001*	<0.001*	<0.001*	<0.001*	<0.001*	<0.001*	<0.001*	<0.001*	<0.001*
	r	−0.14	0.81	−0.12	−0.41	0.80	−0.34	−0.46	0.80	−0.38

TABLE 7. Results of Pearson's product-moment correlation tests, indicating significant negative correlations between coancestry (θ) and the number of unique Lake Sturgeon parents detected in the pedigree (N_s), significant negative correlations between θ and slope (i.e., rate of detection of unique parents per larva genotyped), and significant positive correlations between slope and N_s in 2016. Asterisks represent significant correlations ($\alpha = 0.05$; vs. = versus).

		D-frame nets			Egg mats		
Location	Statistic	θ vs. N_s	Slope vs. N_s	θ vs. slope	θ vs. N_s	Slope vs. N_s	θ vs. slope
All reefs	*t*	−1.19	2.02	−11.00	−0.45	0.81	−9.77
	P	0.232	0.046*	<0.001*	0.652	0.418	<0.001*
	r	−0.04	0.06	−0.33	−0.01	0.03	−0.30
Harts Light Reef	*t*	−13.25	42.79	−10.51	−12.44	39.95	−9.22
	P	<0.001*	<0.001*	<0.001*	<0.001*	<0.001*	<0.001*
	r	−0.39	0.80	−0.32	−0.37	0.78	−0.28
Pointe Aux Chenes Reef	*t*	−9.84	42.36	−7.72	−14.76	44.08	−10.92
	P	<0.001*	<0.001*	<0.001*	<0.001*	<0.001*	<0.001*
	r	−0.30	0.80	−0.24	−0.42	0.81	−0.33
Grassy Island Reef	*t*	−12.40	39.43	−9.60	−12.78	28.66	−7.36
	P	<0.001*	<0.001*	<0.001*	<0.001*	<0.001*	<0.001*
	r	−0.37	0.78	−0.29	−0.37	0.67	−0.23

rate of detection of unique parents per larva genotyped. The heterogeneous spatial distribution of fish larvae (Cyr et al. 1992; D'Amours et al. 2001) may also affect levels of relatedness within samples based on gear type and placement, and variance in detection probability for each gear type may vary based on the early life history traits of the species (Pritt et al. 2014). For example, fewer family groups of larvae may have been collected by D-frame nets positioned close to the constructed spawning reefs. In contrast, vertically stratified conical nets positioned further from the spawning site may have collected individuals after mixing in the water column as individuals dispersed from a spawning site. Differences in measures of coancestry and the rate of detection of unique parents among collections made using different gear types support the hypothesis that each gear type samples full-sibling, half-sibling, and unrelated eggs and larvae at different rates. Coancestry measurement differences may be due to spatial and temporal (ontogenetic) differences in the degree of clustering of offspring within family groups at spawning sites.

Collection methodology influenced the estimates of θ and detection rates of unique spawning adults; however, each methodology can answer critical questions for the assessment of constructed spawning habitat use. Egg mat collections allowed for quantification of spawning effort after reef construction based on the enumeration of eggs deposited on the reef relative to sampling effort. Benthic

D-frame nets allowed for the quantification of larvae that dispersed from constructed spawning reef sites, and vertically stratified conical nets allowed insight into larval position in the water column during dispersal. When used in combination with genetic pedigree analysis, egg mats on constructed spawning reefs provided the location at which unique parents contributed offspring, allowing estimates of N_s and N_b at a specific location and the point of origin to subsequently estimate larval dispersal (e.g., Derosier et al. 2007). However, differences in gear collection rates and between parameter estimates from the methodologies presented in this study suggest further consideration of differences between parameter estimates generated using genetic pedigree analysis from different gear types to improve interpretation of the results used to inform management decisions.

It is important to consider the differences among collection methodologies and inherent differences in gear sampling properties relative to sample size and the genetic makeup of the samples collected. However, this study does not offer direct insight into the best strategy by which to fully account for these differences; rather, we provide evidence for the importance of considering new methods to address differences inherent in sampling methodologies when the collected individuals are used with genetic pedigree analysis. One possibility to account for differences between collection methodologies may be to use samples collected with a single gear type (e.g., egg mats) that collects the most individuals per mat or net.

The importance of standardized field sampling and analytical techniques has long been recognized for traditional assessment and monitoring efforts (Bonar and Hubert 2002; Hayes et al. 2003; Maunder and Punt 2004). Bonar and Hubert (2002) called for standardization of sampling methods used in the assessment of inland fishes, citing benefits such as improved comparisons between sampling locations and improved communication of results, particularly for large systems where multiple agencies participate in sampling and management efforts. Likewise, Hayes et al. (2003) described the development of standardized sampling procedures for statewide monitoring and assessment to inform management of Michigan's aquatic resources and listed the advantages that such an approach affords. Additionally, Bacles et al. (2018) called for sampling at the same times of year, identical collection methodologies, and identical sampling intensity between sampling years and locations to generate reliable data for population monitoring.

Increasingly, molecular methods are being combined with traditional sampling protocols to further inform management decisions (Schwartz et al. 2007). Although the emergence of this technology provides unique insights into the reproductive ecology of fishes, a need has also emerged to develop analytical methods that allow for standardization or adjustments in results obtained with sampling gear differing in the coancestry of individuals captured. Future research may facilitate development of new analytical methods that account for variation in the rate of detection of unique parents per larva genotyped between collection methodologies. Such analytical methods may improve thereby improving interpretation of parameter estimates (e.g., N_s and N_b) generated by genetic pedigree analysis.

Early life history sampling techniques combined with genetic pedigree analysis allow for quantification of adult numbers that are otherwise difficult to attain due to species ecology and effort required to sample large study systems. Sampling of eggs and larvae can be relatively noninvasive on the population level (e.g., species that are known to exhibit high natural early life mortality) and is of particular importance for threatened and endangered species, such as the Lake Sturgeon. In combination with genetic pedigree analysis, use of multiple gear types allows insight into a suite of critical ecological questions surrounding adult spawning numbers and recruitment. Better understanding of the effects of these collection methods on pedigree analysis parameter estimates can improve management decisions by increasing the precision of estimated adult spawning population numbers and levels of recruitment. This study demonstrates the importance of considering collection methodology given the observed differences in coancestry between samples obtained using varied collection methodologies. Results indicate the need for further pursuit of analytical methods that may account for variation in parameter estimates generated using genetic pedigree analysis.

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REFERENCES

Ackerman, M. W., B. K. Hand, R. K. Waples, G. Luikart, R. S. Waples, C. A. Steele, B. A. Garner, J. McCane, and M. R. Campbell. 2017. Effective number of breeders from sibship reconstruction: empirical evaluations using hatchery steelhead. Evolutionary Applications 10:146–160.

Araki, H., R. S. Waples, W. R. Ardren, B. Cooper, and M. S. Blouin. 2007. Effective population size of steelhead trout: influence of

variance in reproductive success, hatchery programs, and genetic compensation between life-history forms. Molecular Ecology 16:953–966.

Auer, N. A. 1996. Importance of habitat and migration to sturgeons with emphasis on Lake Sturgeon. Canadian Journal of Fisheries and Aquatic Sciences 53:152–160.

Auer, N. A. 1999. Population characteristics and movements of Lake Sturgeon in the Sturgeon River and Lake Superior. Journal of Great Lakes Research 25:282–293.

Bacles, C. F. E., C. Bouchard, F. Lange, A. Manicki, C. Tentlier, and O. Lepais. 2018. Estimating the effective number of breeders from single parr samples for conservation monitoring of wild populations of Atlantic Salmon *Salmo salar*. Journal of Fish Biology 92:699–726.

Bartron, M. L., N. M. Sard, and K. T. Scribner. 2018. Evaluation of effective number of breeders and coancestry among progeny produced using common hatchery mating strategies. Transactions of the American Fisheries Society 147:185–194.

Bennion, D. H., and B. A. Manny. 2011. Construction of shipping channels in the Detroit River: history and environmental consequences. U.S. Geological Survey, Scientific Investigations Report 2011-5122, Reston, Virginia.

Bonar, S. A., and W. A. Hubert. 2002. Standard sampling of inland fish: benefits, challenges, and a call for action. Fisheries 27(3):10–16.

Bouckaert, E. K., N. A. Auer, E. F. Roseman, and J. Boase. 2014. Verifying success of artificial spawning reefs in the St. Clair–Detroit River system for Lake Sturgeon (*Acipenser fulvescens* Rafinesque, 1817). Journal of Applied Ichthyology 30:1393–1401.

Brenden, T. O., I. Tsehaye, J. R. Bence, J. Kanefsky, and K. T. Scribner. 2018. Indexing recruitment for source populations contributing to mixed fisheries by incorporating age in genetic stock identification models. Canadian Journal of Fisheries and Aquatic Sciences 75:934–954.

Bruch, R. M., and F. P. Binkowski. 2002. Spawning behavior of Lake Sturgeon (*Acipenser fulvescens*). Journal of Applied Ichthyology 18:570–579.

Bruch, R. M., G. Miller, and M. J. Hansen. 2006. Fecundity of Lake Sturgeon (*Acipenser fulvescens*, Rafinesque) in Lake Winnebago, Wisconsin, USA. Journal of Applied Ichthyology 22(Supplement 1):116–118.

Casselman, J. M., T. Penczak, L. Carl, R. H. Mann, J. Holcik, and W. A. Woitowich. 1990. An evaluation of fish sampling methodologies for large river systems. Polskie Archiwum Hydrobiologii 37:521–551.

Charlesworth, B. 2009. Effective population size and patterns of molecular evolution and variation. Nature Reviews Genetics 10:195–205.

Christie, M. R., D. W. Johnson, C. D. Stallings, and M. A. Hixon. 2010. Self-recruitment and sweepstakes reproduction amid extensive gene flow in a coral-reef fish. Molecular Ecology 19:1042–1057.

Cockerham, C. C. 1969. Variance of gene frequencies. Evolution 23:72–84.

Craig, J. M., G. W. Kennedy, and E. F. Roseman. 2017. Fish eggs collected in the St. Clair and Detroit rivers, 2005–2016. U.S. Geological Survey data release. Available: https://www.sciencebase.gov/catalog/item/5c9b8968e4b0b8a7f62c28ce. (February 2020).

Crossman, J. A., K. T. Scribner, D. T. Yen, C. A. Davis, P. S. Forsythe, and E. A. Baker. 2011. Gamete and larval collection methods and hatchery rearing environments affect levels of genetic diversity in early life stages of Lake Sturgeon (*Acipenser fulvescens*). Aquaculture 310:312–324.

Cyr, H., J. A. Downing, S. Lalonde, S. B. Baines, and M. L. Pace. 1992. Sampling larval fish populations: choice of sample number and size. Transactions of the American Fisheries Society 121:356–368.

D'Amours, J., S. Thibodeau, and R. Fortin. 2001. Comparison of Lake Sturgeon (*Acipenser fulvescens*), *Stizostedion* spp., *Catostomus* spp., *Moxostoma* spp., Quillback (*Carpiodes cyprinus*), and Mooneye (*Hiodon tergisus*) larval drift in Des Prairies River, Quebec. Canadian Journal of Zoology 79:1472–1489.

Derosier, A. L., M. L. Jones, and K. T. Scribner. 2007. Dispersal of Sea Lamprey larvae during early life: relevance for recruitment dynamics. Environmental Biology of Fishes 78:271–284.

Duong, T. Y., K. T. Scribner, P. S. Forsythe, J. A. Crossman, and E. A. Baker. 2013. Inter-annual variation in effective number of breeders and estimation of effective population size in long-lived iteroparous Lake Sturgeon (*Acipenser fulvescens*). Molecular Ecology 22:1282–1294.

England, P. R., J. M. Cornuet, P. Berthier, D. A. Tallmon, and G. Luikart. 2006. Estimating effective population size from linkage disequilibrium: severe bias in small samples. Conservation Genetics 7:303.

Erős, T., A. Specziár, and P. Bíró. 2009. Assessing fish assemblages in reed habitats of a large shallow lake: a comparison between gillnetting and electric fishing. Fisheries Research 96:70–76.

Fox, J., and S. Weisberg. 2011. An R companion to applied regression, 2nd edition. Sage, Thousand Oaks, California.

Frankham, R. 1995. Effective population-size adult-population size ratios in wildlife—a review. Genetics Research 66:95–107.

Hartig, J. H., M. A. Zarull, J. J. Ciborowski, J. E. Gannon, E. Wilke, G. Norwood, and A. N. Vincent. 2009. Long-term ecosystem monitoring and assessment of the Detroit River and western Lake Erie. Environmental Monitoring and Assessment 158:87–104.

Hayes, D., E. Baker, R. Bednarz, D. Borgeson Jr., J. Braunscheidel, A. Harrington, R. Hay, J. Waybrant, J. Breck, A. Nuhfer, and M. Bremigan. 2003. Developing a standardized sampling program: the Michigan experience. Fisheries 28(7):18–25.

Hondorp, D. W., E. F. Roseman, and B. A. Manny. 2014. An ecological basis for future fish habitat restoration efforts in the Huron–Erie corridor. Journal of Great Lakes Research 40(Supplement 2):23–30.

Houde, E. D. 2008. Emerging from Hjort's shadow. Journal of Northwest Atlantic Fishery Science 41:53–70.

Hunter, R. D., E. F. Roseman, N. M. Sard, R. L. DeBruyne, J. Wang, and K. T. Scribner. In press. Genetic family reconstruction characterizes Lake Sturgeon use of newly constructed spawning habitat and larval dispersal. Transactions of the American Fisheries Society. DOI: 10.1002/tafs.10225.

Jackson, D. A., and H. H. Harvey. 1997. Qualitative and quantitative sampling of lake fish communities. Canadian Journal of Fisheries and Aquatic Sciences 54:2807–2813.

Jay, K., J. A. Crossman, and K. T. Scribner. 2014. Estimates of effective number of breeding adults and reproductive success for White Sturgeon. Transactions of the American Fisheries Society 143:1204–1216.

King, T. L., B. A. Lubinski, and A. P. Spidle. 2001. Microsatellite DNA variation in Atlantic Sturgeon (*Acipenser oxyrinchus oxyrinchus*) and cross-species amplification in the Acipenseridae. Conservation Genetics 2:103–119.

Lee, J., A. B. South, and S. Jennings. 2010. Developing reliable, repeatable, and accessible methods to provide high-resolution estimates of fishing-effort distributions from vessel monitoring system (VMS) data. ICES Journal of Marine Science 67:1260–1271.

Ludsin, S. A., K. M. DeVanna, and R. E. Smith. 2014. Physical–biological coupling and the challenge of understanding fish recruitment in freshwater lakes. Canadian Journal of Fisheries and Aquatic Sciences 71:775–794.

Manny, B. A., T. A. Edsall, and E. Jaworski. 1988. The Detroit River, Michigan: an ecological profile. U.S. Fish and Wildlife Service Biological Report 85(7.17).

Manny, B. A., and G. W. Kennedy. 2002. Known Lake Sturgeon (*Acipenser fulvescens*) spawning habitat in the channel between Lakes Huron and Erie in the Laurentian Great Lakes. Journal of Applied Ichthyology 18:486–490.

Manny, B. A., G. W. Kennedy, J. C. Boase, J. D. Allen, and E. F. Roseman. 2010. Spawning by Walleye (*Sander vitreus*) and White Sucker

(*Catostomus commersoni*) in the Detroit River: implications for spawning habitat enhancement. Journal of Great Lakes Research 36:490–496.

Manny, B. A., E. F. Roseman, G. Kennedy, J. C. Boase, J. M. Craig, D. H. Bennion, J. Read, L. Vaccaro, J. Chiotti, R. Drouin, and R. Ellison. 2015. A scientific basis for restoring fish spawning habitat in the St. Clair and Detroit rivers of the Laurentian Great Lakes. Restoration Ecology 23:149–156.

Maunder, M. N., and A. E. Punt. 2004. Standardizing catch and effort data: a review of recent approaches. Fisheries Research 70(2–3):141–159.

May, B., C. C. Krueger, and H. L. Kinkaid. 1997. Genetic variation at microsatellite loci in sturgeon: primer sequence homology in *Acipenser* and *Scaphirhynchus*. Canadian Journal of Fisheries and Aquatic Sciences 54:1542–1547.

McCullough, D. E., E. F. Roseman, K. M. Keeler, R. L. DeBruyne, J. J. Pritt, P. A. Thompson, S. Ireland, J. E. Ross, D. Bowser, R. D. Hunter, and D. Castle. 2015. Evidence of the St. Clair–Detroit River system as a dispersal corridor and nursery habitat for transient larval Burbot. Hydrobiologia 757:21–34.

McQuown, E. C., G. A. Gall, and B. May. 2002. Characterization and inheritance of six microsatellite loci in Lake Sturgeon. Transactions of the American Fisheries Society 131:299–307.

McQuown, E. C., B. L. Sloss, R. J. Sheehan, J. Rodzen, G. J. Tranah, and B. May. 2000. Microsatellite analysis of genetic variation in sturgeon: new primer sequences for *Acipenser* and *Scaphirhynchus*. Transactions of the American Fisheries Society 129:1380–1388.

Prichard, C. G., J. M. Craig, E. F. Roseman, J. L. Fischer, B. A. Manny, and G. W. Kennedy. 2017. Egg deposition by lithophilic-spawning fishes in the Detroit and St. Clair rivers, 2005–2014. U.S. Geological Survey, Scientific Investigations Report 2017-5003, Reston, Virginia.

Pritt, J. J., M. R. DuFour, C. M. Mayer, E. F. Roseman, and R. L. DeBruyne. 2014. Sampling little fish in big rivers: larval fish detection probabilities in tow Lake Erie tributaries and implications for sampling effort and abundance indices. Transactions of the American Fisheries Society 143:1011–1027.

R Core Team. 2017. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.

Rodzen, J. A., T. R. Famula, and B. May. 2004. Estimation of parentage and relatedness in the polyploid White Sturgeon (*Acipenser transmontanus*) using a dominant marker approach for duplicated microsatellite loci. Aquaculture 232:165–182.

Rodzen, J. A., and B. May. 2002. Inheritance of microsatellite loci in White Sturgeon (*Acipenser transmontanus*). Genome 45:1064–1076.

Roseman, E. F., J. Boase, G. W. Kennedy, and J. Craig. 2011a. Adaptation of two techniques for sampling fish eggs and larvae in deep rivers. Journal of Applied Ichthyology 27(Supplement 2):89–92.

Roseman, E. F., B. A. Manny, J. Boase, M. Child, G. W. Kennedy, J. Craig, K. Soper, and R. Drouin. 2011b. Lake Sturgeon response to a spawning reef constructed in the Detroit River. Journal of Applied Ichthyology 27:66–76.

Sard, N. M., K. G. O'Malley, D. P. Jacobson, M. J. Hogansen, M. A. Johnson, and M. A. Banks. 2015. Factors influencing spawner success in a spring Chinook Salmon (*Oncorhynchus tshawytscha*) reintroduction program. Canadian Journal of Fisheries and Aquatic Sciences 72:1390–1397.

Schwartz, M. K., G. Luikart, and R. S. Waples. 2007. Genetic monitoring as a promising tool for conservation and management. Trends in Ecology and Evolution 22:25–33.

Sutherland, J. L., B. A. Manny, G. A. Kennedy, E. F. Roseman, J. Allen, and M. G. Black. 2014. A portable freshwater closed-system fish egg incubation system. North American Journal of Aquaculture 76:391–398.

Tsehaye, I., T. O. Brenden, J. R. Bence, W. Liu, K. T. Scribner, J. Kanefsky, K. Bott, and R. F. Elliott. 2016. Combining genetics with age/length data to estimate temporal changes in year-class strength of source populations contributing to mixtures. Fisheries Research 173:236–249.

Use of Fishes in Research Committee (joint committee of the American Fisheries Society, the American Institute of Fishery Research Biologists, and the American Society of Ichthyologists and Herpetologists). 2014. Guidelines for the use of fishes in research. American Fisheries Society, Bethesda, Maryland.

Wang, J. 2004. Sibship reconstruction from genetic data with typing errors. Genetics 166:1963–1979.

Wang, J., and K. T. Scribner. 2014. Parentage and sibship inference from markers in polyploids. Molecular Ecology Resources 14:541–553.

Waples, R. S. 2010. Spatial–temporal stratifications in natural populations and how they affect understanding and estimation of effective population size. Molecular Ecology Resources 10:785–796.

Welsh, A. B., M. Blumberg, and B. May. 2003. Identification of microsatellite loci in Lake Sturgeon, *Acipenser fulvescens*, and their variability in Green Sturgeon, *A. medirostris*. Molecular Ecology Notes 3:47–55.