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Compositions of lake sturgeon (*Acipenser fulvescens*) mixtures in Lake Michigan: hierarchical spatial heterogeneity and evidence of improving recruitment in Wisconsin spawning populations

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Abstract

Information regarding site occupancy of fish that migrate long distances during non-spawning periods together with estimates of recruitment trends for individual populations can be informative for management, especially when individuals from different spawning populations intermix and are sampled/harvested together. Tendencies for individuals from different populations to preferentially occupy specific regions increases vulnerability to anthropogenic and natural disturbances. Using mixed stock analysis (MSA), we estimated population-specific occupancy of lake sturgeon in open-water and nearshore regions of Lake Michigan across a hierarchy of spatial scales. Open-water mixture composition differed between Lake Michigan's eastern and western basins. Significant heterogeneity in habitat occupancy was also observed at microgeographic scales throughout open-water regions of Green Bay, indicating non-random occupancy to regions proximal to natal streams. Estimates of relative recruitment levels determined from MSA extensions indicated increasing recruitment trends for spawning populations associated with Wisconsin tributaries (Oconto/Peshtigo, Fox, and Menominee Rivers). Our lake sturgeon results demonstrate the utility of genetic data for informing management efforts for spatially-structured, highly migratory species. Similar analyses could prove beneficial for species with similar characteristics.

Introduction

Habitat occupancy and movements among habitats have been major focal areas in aquatic resource management (Cooke et al. 2016; Brooks et al. 2019) due to their importance for quantifying spatial biodiversity patterns and metapopulation connectivity, which improves understanding of community dynamics and ecosystem function (Bauer and Hoye 2014). Many fish species migrate seasonally for reproduction (Naiman et al. 2002; Cook et al. 2005; Forsythe et al. 2012; Brenden et al. 2017; Li et al. 2017). Among such species, highly vagile fish, especially those with delayed sexual maturity and multi-annual inter-spawning intervals, can disperse considerable distances from natal habitats during non-spawning periods. Consequently, in large systems, fish from multiple spawning populations frequently intermix during non-spawning seasons and form stock mixtures (e.g., pre-reproductive oceanic life stage of Pacific salmonids, *Oncorhynchus spp.*; Beacham et al. 2005, 2006). The occurrence of mixed stocks comprised of individuals from genetically-distinct spawning populations can result in less productive populations being vulnerable to overharvest or other disturbances. Accordingly, movement tendencies and non-random habitat occupancy have been identified as significant knowledge gaps for effective fisheries management in all aquatic ecosystems, including the North American Laurentian Great Lakes (Landsman et al. 2011).

Traditional methods used to document movements and habitat occupancy of fishes include direct methods such as tagging/marking (Labonne and Gaudin 2005; Schwartz et al. 2007), direct observation (Trenham et al. 2000), telemetry (Rogers and White 2007) and morphometrics (Cadrin 2000). Some studies have combined methods (tagging, marking, direct observation) to characterize movements (see review in Fabrizio 2005). Despite their utility, traditional methods can be challenging to implement in large systems because of meta-population structure and difficulties in sustained tagging and monitoring of large numbers of fish across the full complement of spawning populations (Vandergoot and Brenden 2014).

Genetic methods, including the use of mixed stock analysis (MSA) (e.g., Pella and Masuda 2001; Bradbury et al. 2016), have also been widely used to quantify population-specific habitat occupancy and movements. Many fish species exhibit a high degree of natal philopatry, which can give rise to spatial genetic structuring (i.e., spatial heterogeneity in allele frequency) among spawning populations. Traditional MSA examines a mixture of individuals from unknown origins and estimates the proportional contributions of putative spawning populations to the mixture (i.e., many-to-one analysis) based on genotypes of mixture individuals and genetic characteristics (i.e., allele frequencies) of the spawning populations. This method has been routinely applied in marine fisheries (e.g., Shaklee et al. 1999; Beacham et al. 2006, 2020), and has been increasingly used to examine fish movements and mixture compositions in Great Lakes fisheries (e.g., Bott et al. 2009; Brenden et al. 2015; Andvik et al. 2016; Scribner et al. 2018; Euclide et al. 2020).

In traditional MSA, stock composition estimation is made without consideration to ages or sizes of fish in the mixture, time periods of collection, or regions where fish were collected. Recently, changes have been made due in part to wider recognition that mixture composition integrates numerous factors, including population-specific recruitment, mortality, and movement rates (Bjorndal and Bolten 2008). Consequently, more detailed information on some of these important rates can be obtained by parsing mixture data into different components (e.g., fish ages or sizes, different mixture sub-regions). For example, MSA applied to different season and age components of walleye (*Sander vitreus*) collected from Saginaw Bay, Lake Huron potentially identified differences in migration patterns of young fish originating from Lakes Erie and St. Clair (Brenden et al. 2015). Similarly, individual assignment and MSA were used to elucidate differences in length distributions of Atlantic salmon (*Salmo salar*) produced from different

Baltic Sea tributaries and between hatchery- and wild-produced fish (Koljonen et al. 2021). Bolker et al. (2007) used hierarchical modeling to expand MSA to estimate population contributions to multiple mixtures (i.e., many-to-many analysis), which was capable of providing more detailed information on the spatial ecology of individual spawning populations.

The wealth of information encompassed in mixture compositions has also resulted in genetic data and MSA methodologies being included in integrated population models (Abadi et al. 2010; Chandler and Clark 2014) to improve estimation of population demographics and important dynamic rates. For example, mixture composition and MSA methodologies were incorporated in an integrated population model for Atlantic salmon from the Baltic Sea, which permitted joint inferences on abundance, movement, and stock composition of multiple populations in the region (Whitlock et al. 2018). Likewise, MSA has been extended to incorporate age or length information of individuals collected from the mixtures to estimate important dynamic rates, such as recruitment, mortality, or movement, of spawning population contributing to mixtures (Tsehaye et al. 2016; Brenden et al. 2018). These extensions parameterize expected mixture compositions as functions of population-, year-, and/or region-specific recruitment, mortality, and movement rates (Tsehaye et al. 2016; Brenden et al. 2018). The extended MSA then is used to estimate dynamic rates of interest, consistent with population compositions that are evident in the mixtures.

The ability to use extended MSA methods to quantify relative recruitment levels of spawning populations contributing to mixed fisheries may be the greatest utility of MSA model extensions that incorporate age- or length information. Fish population abundance is strongly affected by recruitment rates, and recruitment typically varies spatially and temporally (Fogarty 1993; Myers et al. 1997) due to variation in spawning population size (Ricker 1954), survival during early life stages (Ludsin et al. 2014), adult fecundity (Hilborn and Walter 1992; Quinn and Deriso 1999), habitat limitations (Walters and Juanes 1993), and predation (Walters and Juanes 1993). Science-based adaptive management of mixed stocks would benefit from understanding the recruitment dynamics of constituent populations to identify which spawning populations may be most susceptible to natural or anthropogenic stressors (Stephenson 1999), which in turn could protect the resilience of the entire population complex (DuFour et al. 2015). Recruitment levels for populations contributing to mixtures are difficult to estimate when sampling is not conducted during the spawning season (Li et al. 2015). Sampling of mixtures during non-reproductive periods can incorporate sampling of sub-adults that would not otherwise be available for sampling of spawning populations. The ability to quantify population recruitment from collections made during the non-spawning season would allow managers to better assess whether current efforts can achieve management goals for a species (Hayes and Caroffino 2010).

Lake sturgeon (*Acipenser fulvescens*) is a species of conservation focus throughout its native range including the Laurentian Great Lakes region (Peterson et al. 2007; Bruch et al. 2017). Despite conservation efforts, seasonal or age-specific information on lake sturgeon movements and site occupancy during their prolonged non-spawning periods is lacking. Lake sturgeon are adfluvial, migrating from open-water areas to rivers for spawning, and are long-lived, with onset of sexual maturity occurring at between 12 and 25 years of age depending on sex (Baker 1980; Houston 1987; Auer 1996; Harris et al. 2017). After maturation, the interval between spawning events is sex- and location-dependent, with males spawning every one to four years and females spawning every three to seven years (Auer 1999b; Beamish et al. 1996; Forsythe et al. 2012). Prior to sexual maturity and during extended non-spawning periods, individuals from different tributary populations can disperse considerable distances and form mixed stocks (Auer 1999a; Gunderman and Elliott 2004).

Since European colonization of the Great Lakes region, lake sturgeon abundance has declined markedly, especially since the last half of the 19th century (Hay-Chmielewski and Whelan 1997). Declines in abundance have been attributed to several factors, including habitat loss and degradation, pollution, loss of habitat connectivity, and over-exploitation (Holey et al. 2000). Although harvest has been substantially reduced or entirely eliminated in many areas of the Great Lakes, and water quality has been greatly improved, lingering threats to remnant populations include by-catch harvest and non-point-source pollution, both of which are likely to occur at local scales during non-reproductive periods. The effects of biotic and physical features on reproductive success (Dammerman et al. 2019) and recruitment levels in natal streams also are issues affecting lake sturgeon populations. These threats are likely to affect populations differently depending on where events occur, and as a consequence of heritable differences in population life-histories or sensitivities to environmental factors [e.g., timing of spawning (Prince et al. 2017), growth associated with temperature, or flow regimes in natal stream environments (Dammerman et al. 2015; Dammerman et al. 2016)].

Given the potential for long-range movements by lake sturgeon within the Great Lakes, the occurrence of stock mixtures, and spatial variation in threats to individual spawning populations, successful restoration efforts and assessment of future risk requires a fundamental understanding of areas and habitats occupied by individuals from different lake sturgeon populations during non-spawning periods. There is also considerable interest in obtaining information pertaining to distributions of young lake sturgeon cultured in streamside rearing facilities (Holtgren et al. 2007) and stocked in the Great Lakes to rehabilitate/restore wild populations.

Traditional techniques for monitoring fish movement and habitat use, such as tagging and telemetry have provided valuable information on seasonal variation in lake sturgeon movement and habitat use (Colborne et al. 2020), and have identified focal areas and habitats associated with foraging, reproduction, or avoidance of unfavorable environmental conditions (Auer 1999b). Studies have also found considerable plasticity in lake sturgeon movement behavior. For example, Colborne et al. (2020) and Kessel et al. (2018) used acoustic telemetry to document multiple migratory behaviors of lake sturgeon in the Huron-Erie Corridor, which comprises Lake St. Clair and Detroit and St. Clair Rivers. Similarly, Larson et al. (2020) used PIT tag antennas to document multiple migratory events by male lake sturgeon in a single season in Michigan's Upper Black River.

Despite valuable contributions from past studies that have used traditional fisheries methods, data on lake sturgeon movements and habitat occupancy are lacking in most open-water areas of the Great Lakes, including Lake Michigan, which contains a large portion of the remnant tributary spawning populations in the Great Lakes (Holey et al. 2000). Such information on habitat use is particularly important for understanding risks and threats to remnant populations. Given the large spatial scales and mixing of many source populations, genetic approaches have much to contribute to understanding habitat use dynamics by lake sturgeon in the Great Lakes. Comprehensive information on trends in recruitment across populations also are generally lacking for lake sturgeon, and are not available from previous studies on Lake Michigan populations. Management decisions for species of conservation concern such as lake sturgeon can greatly benefit from knowledge of historical and contemporary patterns of recruitment for remnant populations (Holey et al. 2000; Bruch et al. 2017) by assessing relative population demographic trends in the context of population management.

This study used genetic information and MSA to quantify habitat occupancy of lake sturgeon in Lake Michigan using mixture samples from open-water and nearshore sites collected throughout the lake over multiple years. The primary objective of this study was to quantify population contributions for each Lake Michigan tributary spawning population to mixtures collected in a spatially hierarchical fashion at individual sampling locations within different open-water and nearshore regions of the lake. In situations where sample sizes were sufficient, differences in mixture composition were characterized between sub-adult and adult age groups and between collections made during different seasons (spring vs fall). Our secondary objective was to use the MSA extension of Tsehaye et al. (2016) to estimate relative recruitment rates for Lake Michigan tributary-spawning source populations contributing to mixed population samples in open-water and nearshore areas of Green Bay to assess the recovery status of individual populations.

Materials and Methods

Sampling of baseline spawning populations

From 1999 to 2015, cooperating agencies and institutions captured adult lake sturgeon during the spawning season (late April to early June) from seven remnant tributary spawning populations throughout Lake Michigan (Fig. 1A and B). Fish were designated as belonging to a particular spawning population based on time and location of collection, and whether individuals could express gametes. Individuals were collected using long-handled dip nets, gill nets, and electrofishing. Total length, girth, and weight of each captured individual were recorded. Individuals were sexed based on expression of gametes and visual inspection of the vent. Prior to release, a tissue sample (≈1-cm^2 clip of the dorsal fin) was collected and dried in a scale envelope at ambient temperature (DeHaan et al. 2006).

Sampling mixtures of unknown population composition

During non-spawning seasons, lake sturgeon were collected from open-water areas of Green Bay, as well as open-water areas in the Northern, East-Central, and Southeastern regions of Lake Michigan (Fig. 1A and B). Lake sturgeon were also collected during non-spawning seasons from nearshore areas in Green Bay at the mouths of the Oconto, Peshtigo, and Menominee Rivers. Because lake sturgeon density in areas proximal to spawning locations is low during non-spawning periods, sampling was conducted over several years (Supplemental Table S1). Samples included a mixture of age groups based on total length data collected from the majority of individuals captured.

Open-water samples were collected from 1996 to 2018 by U.S. Fish and Wildlife Service (USFWS), Michigan Technological University, Grand Valley State University, Central Michigan University, Michigan Department of Natural Resources (MiDNR), Wisconsin Department of Natural Resources (WiDNR), and Little Traverse Bay Band of Odawa Indians staff, often working in cooperation with commercial fishers. Most open-water samples in Green Bay (2001 to 2009 sampling years) and the northern portion (2002 to 2007 sampling years) of the main basin were collected using gill nets and large commercial trap nets. Nets varied in mesh size and dimensions depending on the targeted species. Commercial gill nets targeting lake whitefish (*Coregonus clupeaformis)* and yellow perch (*Perca flavescens)* were 11.3-cm and 6.3-cm stretch mesh, respectively. Graded-mesh research gill nets targeting lake sturgeon were 15- to 35-cm stretch mesh. Commercial trap nets targeting lake whitefish had leads approximately 305 m in length connected to pots approximately 6.1 × 9.1 × 10.7-m, with pot mesh of 11.3-cm stretch mesh. Samples from the east-central (1996 to 2018 sampling years) and southeastern regions (2001 to 2009 sampling years) of the main basin were collected using multiple approaches including graded-mesh gill nets targeting lake sturgeon.

Nearshore lake sturgeon were collected from the mouths of the Oconto and Peshtigo Rivers in Wisconsin from 2002 to 2009 using electrofishing and large mesh gill nets. Sampling in the Menominee River was conducted from 2001 to 2009 using electrofishing and hook and line angling during an annual harvest season (details in Bott et al. 2009).

Lake sturgeon from open-water and nearshore areas were collected throughout the calendar year. However, the majority of open-water samples were collected in the spring and early summer whereas the majority of nearshore samples were collected in the spring and fall. Fish captured in open-water or nearshore areas were not sexed because external sex-diagnostic morphological features are not a reliable indicator of sex outside the period of active spawning (Webb et al. 2019).

Genetic Analyses

DNA was extracted from lake sturgeon fin tissue samples using QIAGEN DNeasy® kits (QIAGEN Inc.) according to manufacturer's protocols. All samples were diluted to a consistent DNA concentration of 20 ng/ml for PCR reactions. Individuals were genotyped at 12 disomically-inherited microsatellite loci including Spl 120 (McQuown et al. 2000); AfuG 68B (McQuown et al. 2002); Aox 27 (King et al. 2001); AfuG 68, AfuG 9; AfuG 63, AfuG 74, AfuG 112, AfuG 56, AfuG 160, AfuG 195 and AfuG 204 (Welsh et al. 2003). For polymerase chain reactions (PCR), 100-ng DNA was amplified in 25-µl reaction mixtures containing 2.5 µl of 10 X PCR buffer (1 M tris-HCl, 1 M $MgCl_2$, 1 M KCl, 10% gelatin, 10% NP-40, and 10% triton X); 1-mM or 1.5-mM $MgCl_2$ (for AfuG 9), but no $MgCl_2$ for AfuG 63, Aox 27 and AfuG 74; 0.8-mM deoxy-nucleotide-triphosphate (dNTP); 10-pm fluorescently labeled forward and unlabeled reverse primers and 0.25 units of Taq polymerase.

All PCR reactions were conducted using a Robocyler 96 thermal cycler. The PCR conditions were 94°C for 2 min, followed by 30 cycles of 1 min for primer-specific annealing temperatures, 72°C for 1 min, and the final extension for 2.5 min at 72°C. PCR products were run on 6% denaturing polyacrylamide gels and visualized on a Hitachi FMBIOII scanner. Allele sizes were determined using commercially available size standards (MapMarkerTM, BioVentures Inc.) and based on standard samples of known genotype. To minimize error, all genotypes were independently scored by two experienced individuals and verified again after data were entered into electronic databases. Ten percent of all individuals were blindly genotyped for all loci a second time as a quality control measure.

Statistical analyses

Previous studies have genetically characterized spawning lake sturgeon populations in Lake Michigan (DeHaan et al. 2006; Bott et al. 2009 based on 8 loci) and (Homola et al. 2012 based on 12 loci) and found populations to be genetically differentiated in allele frequency. In addition to data from new samples obtained for this study, we reanalyzed data for Lake Michigan populations using 12 loci and based on larger spawning adult samples sizes than used in previous research. We additionally added data from samples from the Kalamazoo River, Michigan population that had previously been characterized genetically based on a small sample size (Homola et al. 2012).

Estimates of allele frequencies and Hardy-Weinberg equilibrium tests for spawning baseline populations were conducted using program GenePop (Rousset 2008). Estimates of deviations from Hardy-Weinberg equilibrium were quantified using Wright's inbreeding coefficient (F_{is}; Weir and Cockerham 1984). Measures of genetic diversity, including observed (H_o) and expected (H_e) heterozygosity and allelic richness were estimated using program FSTAT (Goudet 2001). Estimates of inter-population variance in allele frequency (F_{st}) were estimated using program FSTAT. A Bonferroni correction was used to adjust significance to account for multiple testing.

Pairwise Kolmogorov-Smirnov tests were conducted in R (R Core Team 2018) and used to compare total length (TL) distributions of lake sturgeon collected from the different regions (i.e., East Central Lake Michigan, Open-water Green Bay, Nearshore Green Bay, Northern Lake Michigan, and Southeastern Lake Michigan). Using a Bonferroni correction, a *P*-value less than 0.005 was necessary to reject the null hypothesis that length distributions were drawn from a common distribution.

Analyses of stock mixtures

We used MSA to quantify the proportional contributions of spawning populations to the sampled mixtures. MSA was conducted using the Statistical Program for the Analysis of Mixtures, version 3.7b (SPAM; Debevec et al. 2000, Alaska Department of Fish and Game 2003). SPAM implements a maximum likelihood-based approach for conducting the MSA. However, SPAM does accommodate Bayesian-based options for estimating allele frequencies at individual loci for the baseline spawning populations, which is beneficial when alleles are observed in mixture samples that are not observed in the spawning population samples. For our analyses, we used the Rannala-Mountain approach (Rannala and Mountain 1997) for calculating allele frequencies for spawning populations. Uncertainty in spawning population contribution estimates was determined by bootstrapping (number of bootstrap samples = 1000) the mixture data but leaving baseline allele frequencies fixed at the mean of the Dirichlet posterior distributions from the Rannala-Mountain approach for calculating allele frequencies.

Analyses of stock mixtures: simulation analyses

Simulations were initially conducted to determine MSA accuracy, precision, and allocation bias based on genetic data for the Lake Michigan lake sturgeon spawning populations. Data from each spawning population were used to simulate mixtures composed entirely of individuals from that population (i.e., 100% mixture simulations). The size of the simulated mixtures was 200 fish. SPAM was then used to conduct a MSA including all spawning populations to determine whether the MSA procedure identified that most of the mixture came from the correct spawning populations for that simulation. For each spawning population, a total of 1,000 simulations was conducted. In a dataset with completely accurate population allocation, the contribution from the spawning population that was used to simulate the mixture would be estimated at 100% whereas the contributions from the other spawning populations would be 0% across all the iterations. Deviations from 100% allocation indicate where, and of what magnitude, misallocations are likely to occur in empirical mixtures of unknown composition.

In addition to the 100% mixture simulations, we conducted leave-one-out cross validation simulations (Anderson et al. 2008) to assess the potential accuracy of MSA applied to the Lake Michigan lake sturgeon spawning populations. The analysis was performed in R using the rubias package (Moran and Anderson 2018) and the assess_reference_loo() function. Unlike the 100% mixture simulations, simulations for the leave-one-out cross validation consisted of simulating mixtures with stochastic composition and then evaluating how closely estimated population contributions aligned with true contributions. Mixture composition was generated randomly from Dirichlet distributions with the concentration parameter for each spawning population set at 1.5. As with the 100% mixture simulations, size of the mixture was set at 200 fish and 1,000 simulations were conducted. Accuracy for the leave-one-out cross validation accuracy was determined by calculating the mean absolute deviation between estimated and true contribution for each of the spawning populations.

Analyses of mixture composition: estimation analyses

Using multilocus genotypes of individuals from open-water samples, we conducted MSA at several spatial extents. First, at a local scale, we generated compositional estimates of lake sturgeon mixtures from different sampling locations within Green Bay (Fig. 1A). These sampling locations were then aggregated into four open-water regions of Green Bay (South, Central A, Central B, and North) for estimating mixture compositional estimates. Lake sturgeon of certain ages may be more predisposed to remain closer to natal tributaries, or to utilize larger areas of open-water habitats. Accordingly, we were interested in whether mixture compositions differed as a function of age (adult vs sub-adult) for the Green Bay aggregated regions. Fish were characterized as adults or subadults based on total length, with 110 cm used as the threshold length.

The Green Bay open-water samples were combined and used along with the Northern, East-Central, and Southeastern samples to estimate spawning population contributions to different Lake Michigan regions (Fig. 1B). Finally, all samples were combined to estimate spawning population contributions to all Lake Michigan open-water samples for the entire basin. We used the Reynolds and Templin (2004) approach to test whether spawning population contributions were consistent among the four Green Bay open-water regions (South, Central B, Central A, North; Fig. 1A) and the four Lake Michigan open-water regions (Green Bay (GB), North (N), East-Central (EC), Southeastern (SE); Fig. 1B). We used the asymptotic theory approach rather than the resampling approach for conducting the likelihood ratio tests (Reynolds and Templin 2004).

For the nearshore analyses, we quantified spawning population contributions to the Menominee and Oconto/Peshtigo river mouths overall and separately by spring (April-June) and fall (September-November) seasons. Our hypothesis was that spawning population contributions would differ seasonally with higher contributions from the spawning population associated with those particular rivers during the spring when spawning individuals would be expected to return to natal streams to spawn. The Reynolds and Templin (2004) asymptotic approach was used to conduct likelihood ratio tests of population compositional heterogeneity for river mouth collections between seasons for each river.

Estimation of relative stock recruitment

Trends in relative recruitment of the lake sturgeon spawning populations contributing to the Green Bay samples were assessed using the methodology of Tsehaye et al. (2016), which is a generalization of a method described in Brenden et al. (2018). In describing their methodology, Tsehaye et al. (2016) included an application of their method to lake sturgeon samples from Lake Michigan. Analyses conducted here differ from that of Tsehaye et al. (2016) in that a much larger mixture sample size is analyzed that includes both nearshore and open-water areas of Green Bay; additionally, this analysis includes one additional lake sturgeon spawning population (i.e., the Kalamazoo River). Our analyses also differ from that of Tsehaye et al. (2016) in that we account for age-based selectivity of the sampling gear used to collect lake sturgeon from the mixture region, and sensitivity analyses are conducted to determine how violations in assumptions may affect relative recruitment estimates (see details below). We chose to not include samples from the other Lake Michigan regions due to small sample sizes and inconsistencies in lengths of sampled individuals and the years from which samples were obtained, which could influence the results of the relative recruitment analysis.

For lake sturgeon, the critical time period (i.e., early life when mortality is high; Hjort 1914) is believed to be the first several months after hatching. During this larval-phase period, survival of lake sturgeon can be highly variable and depend on a variety of factors, including environmental conditions, availability of prey and/or habitat, and presence of predators (Caroffino et al. 2010). After the larval period, lake sturgeon transition to an age-0 juvenile state during which they develop protective scutes and reach large enough sizes that they are fairly invulnerable to predation (Caroffino et al. 2010). The point of recruitment we attempted to index was when fish had attained the age-0 juvenile state (approximately 4 months of age and 150 mm total length). Indexing recruitment to an earlier life history point would not be possible without detailed information on the mortality rates experienced by individual year classes during egg or larval stages.

Under the Tsehaye et al. (2016) approach, the expected proportional contributions to a mixture from the *i*-th source for the *a*-th age class in the *s*-th sampling year is

$$(1) \qquad P_{i,a}^{s} = \frac{sel_a \ddot{N}_{i,a}^{s-a}}{\sum_{i=1}^{I} \sum_{o=\min(\text{age})}^{\max(\text{age})} se\ddot{l}_o N_{i,o}^{s-o}},$$

where min(age) and max(age) reference the minimum and maximum age in the mixture, *s-o* and *s-a* index the correct year class for calculating the proportional contributions, *I* is the total number of spawning populations, sel_a is the relative vulnerability of the *a*-th age class to the sampling gear used to collect individuals from the mixture, and $\ddot{N}$ is the expected relative abundances at age for the spawning populations contributing individuals to the assessed mixture. Although Tsehaye et al. (2016) did not evaluate the ability of the proposed model to estimate age-specific selectivities, preliminary evaluations that we conducted as part of this research suggested that the model could accurately estimate selectivities at least in some situations. The approach for estimating selectivities is described below. The true age-specific relative abundances of the spawning populations for the *y*-th year class is

$$(2) \qquad N_{i,a}^{y} = \frac{\ddot{N}_{i,a}^{y}}{d_{i,a}}$$

where $d_{i,a}$ is the fraction of fish from the *i*-th spawning population and *a*-th age class that move into the mixture region (Brenden et al. 2018). An estimate of $d_{i,a}$ is not required for the analysis; however, it is necessary to assume that $d_{i,a}$ is constant over time and age although we did conduct sensitivity analyses to determine the effect that deviations from this assumption had on recruitment estimates (see below). The Tsehaye et al. (2016) method for estimating trends in relative recruitment decomposes age-specific relative abundances into recruitment and mortality components

$$(3) \qquad \log_e\left(N_{i,a}^{y}\right) = \log_e\left(N_{i,0}^{y}\right) - \sum_{o=1}^{a} Z_{i,o-1}$$

with recruitment modeled through a standard population growth function

$$(4) \ \log_e\left(N_{i,0}^{y}\right) = \log_e\left(\alpha_i + \beta_i \cdot y\right).$$

In the above equations, $\sum_{o=1}^{a} Z_{i,o-1}$ is the cumulative instantaneous total mortality experienced by the *i*-th spawning population up to the *a*-th age class, $N_{i,0}^{y}$ is the abundance at age 0 (or some other specified age of recruitment) for the *i*-th spawning population and *y*-th year class, α_i is the recruitment level for the *i*-th spawning population for the first assessed year class, which is a function of the years that samples are collected and the age range of individuals collected from the mixture, and β_i is the instantaneous rate of change in recruitment for the *i*-th spawning population. The estimation of actual abundance is not possible based simply on mixture composition data; consequently, it is necessary to impose a constraint that the α_i on a $\log_e$ scale sum to 0 (i.e., $\sum_{i=1}^{I} log_e(\alpha_i) = 0$) for the model to be estimable (Tsehaye et al. 2016). This constraint is necessary because otherwise multiple solutions exist (i.e., multiple sets of α_i can produce the same mixed stock compositions). Additionally, to reduce parameter correlations it is beneficial to estimate the rates of change in recruitment as

$$(5) \qquad \beta_i = \overline{\beta} + \delta_i,$$

where $\overline{\beta}$ is the overall mean instantaneous rate of change in year-class strength of the sources and $\delta_i \left(\sum_{i=1}^{I} \delta_i = 0\right)$ are the spawning population specific deviations from the overall mean (Tsehaye et al. 2016). We assumed an annual instantaneous total mortality rate of 0.05 for lake sturgeon past the point of recruitment (Elliott and Gunderman 2008) although sensitivity analyses were conducted to determine the effect that deviations from this assumption had on recruitment estimates (see below).

Age estimates were not available for Lake Michigan lake sturgeon. Consequently, we used the length-as-a-surrogate-for-age approach for estimating trends in relative recruitment (Tsehaye et al. 2016). Based on existing age-length data for Lake Michigan lake sturgeon (Elliott and Gunderman 2008), a single von Bertalanffy growth model with parameter estimates of L_∞= 181.46 cm, k = 0.079, t_0= −2.023 yrs, and σ= 0.109 (assuming a multiplicative error structure) was used to convert lengths of fish in mixture samples to ages. We assumed growth rates were comparable across the lake basin, although we did conduct sensitivity analyses to determine the effect that deviations from this assumption had on recruitment estimates (see below). Based on the resulting ages, we used an age range of 0–37 years for assessing recruitment changes. Given this age range and that samples from Green Bay were largely restricted to collections from 2001 to 2009, the first modeled year class corresponded to 1964 whereas the last modeled year class corresponded to 2009.

Age-specific selectivities of the sampling used to collect individuals from the mixture were estimated using an additive combination of logistic and normal selectivity functions

$$(6) \quad sel_a = \gamma \cdot exp\left(-\frac{(a-\theta_1)^2}{2.0 \cdot \theta_2^2}\right) + \frac{1}{1 + exp(\theta_3 \cdot (a-\theta_4))}$$

where θ_1 and θ_2 are parameters for the normal component of the function, θ_3 and θ_4 are parameters for the logistic component of the function, and γ determines the relative contribution of the normal component of the function to the logistic component. When estimating this function, γ was constrained to be between 0 and 1, meaning that the normal component of the selectivity function was constrained to be less than or equal to the logistic component of the function. The estimated selectivity values were scaled to a range of 0 to 1. This additive logistic and normal function was chosen because it yielded a better fit to observed data than simpler selectivity functions (e.g., logistic function alone, normal function alone, lognormal function, gamma function; Supplemental Table S3).

Under the length-as-a-surrogate-for-age approach for estimating trends in relative recruitment, the conditional likelihood ($\mathcal{L}$) of observing mixture genotype samples for a particular sample given model parameters is specified as

$$(7) \quad \mathcal{L}(\mathbf{Q},\boldsymbol{\alpha},\overline{\beta},\boldsymbol{\delta},\boldsymbol{\theta},\gamma,\mathbf{Y}|\mathbf{X}) = \prod_{m=1}^{M}\sum_{i=1}^{I}\sum_{j=\min(\mathrm{age})}^{\max(\mathrm{age})} T_{i,L_m,j}\left[P_{i,j}^{s}(\boldsymbol{\alpha},\overline{\beta},\boldsymbol{\delta},\boldsymbol{\theta},\gamma)\right] f(\mathbf{X}_m|\mathbf{Q}_i)\pi(\mathbf{Q}|\mathbf{Y})$$

,

where **Q** are the allele relative frequencies at each locus for each source which is determined from the collection and genotyping of individuals collected from the spawning populations (**Y**), M is the total number of samples from the mixture, $\mathbf{X}_m$ is the observed allele count for all loci for the m-th individual, $f(\mathbf{X}_m|\mathbf{Q}_i)$ is the probability of an individual from the i-th spawning population having the same genotype as the m-th individual from the mixture, which is determined from the allele relative frequencies for the i-th population under an assumption of Hardy-Weinberg equilibrium (Pella and Milner 1987; Pella and Masuda 2001), $T_{i,L_m,j}$ is the probability that the m-th individual of length L_m from the mixture is age j given that it is from the i-th spawning population, and $P^{s}_{i,j}(\boldsymbol{\alpha},\overline{\beta},\boldsymbol{\delta},\boldsymbol{\theta},\gamma)$ simply denotes that P^{s}_{ij} is a function of $\boldsymbol{\alpha}$,$\overline{\beta}$,$\boldsymbol{\delta}$, $\boldsymbol{\theta}$, and γ. The likelihood specified in equation 7 does not include parameters for mortality or growth as these are treated as pre-specified constants. In Equation 7, $\pi(\mathbf{Q}|\mathbf{Y})$ is the posterior probability distribution for allele frequencies of the spawning populations (**Q**) given the collection and genotyping of individuals collected from the spawning population (**Y**) calculated following Rannala and Mountain (1997) with a Dirichlet probability density function assumed as the prior. **Q** is not updated as part of the model fitting process, which is why the likelihood in Equation 7 is referred to as a conditional likelihood.

We fit the relative recruitment model to our Lake Michigan lake sturgeon spawning population and mixture data using AD Model Builder (Fournier et al. 2012). Model parameters were estimated by highest posterior density estimation (also referred to as maximum penalized likelihood) using the quasi-Newton optimization algorithm implemented in AD Model Builder. Penalties that were assigned to parameters to help regularize the model and achieve estimation convergence included assuming the αs and $\overline{\beta}$ were from normal distributions with means of 0 and standard deviations of 12 and 8, respectively. For other parameters, upper and lower bounds were specified to help keep the optimization algorithm from flat parts of the likelihood surface. Uncertainty in recruitment parameters from Equation 4 (i.e., *α*s, *β*s) and in the relative recruitment values for the final assessed year (i.e., 2009) was assessed by likelihood profiling as implemented in AD Model Builder.

Sensitivity of relative recruitment estimates

We assessed sensitivity of relative recruitment estimates to potential violations in assumptions about mortality, growth, and movement. To evaluate sensitivity to assumptions about growth, we generated 100 random sets of population-specific von Bertalanffy growth model parameters and then refit the relative recruitment model for each of these sets of new growth parameters to determine how sensitive relative recruitment estimates were to the specified growth parameters. Thus, for these 100 sets of population specific parameters, it was assumed that growth varied among fish from the different source populations. The random growth model parameters were generated from a multivariate normal probability distribution, with the mean vector and covariance matrix set equal to the estimates from fitting a von Bertalnaffy growth model to existing age-length data for Lake Michigan lake sturgeon (Elliott and Gunderman 2008). To evaluate sensitivity to mortality assumptions, we conducted two sets of simulations. For the first set, we randomly generated population-specific total mortality rates from uniform distributions with lower and upper bounds of 0.01 and 0.10, respectively and then refit the relative recruitment model. For the second set of simulations, we randomly generated age-specific mortality estimates for the different spawning populations and then refit the relative recruitment model. For fish younger than age 10, age-specific mortality rates for each of the populations were randomly generated from uniform distributions with lower and upper bounds of 0.05 and 0.10, respectively. For fish age 10 and older, age-specific mortality rates were randomly generated from uniform distributions with lower and upper bounds of 0.005 and 0.045, respectively. As with the simulations for evaluating sensitivity to assumed growth, we repeated this 100 times, generating new mortality rates for each iteration and refitting the relative recruitment model. While the range of mortality rates that was considered was small, the life span for lake sturgeon ranges from 50 to 150 years depending on sex, which would be highly improbable with mortality levels much greater than 0.1, especially in light of major reductions in harvest and by-catch of lake sturgeon that has occurred on the Great Lakes. To assess sensitivity to assumptions about movement, we refit the relative recruitment model under an assumption that the movement rate for age-5 and younger lake sturgeon to the mixture for all spawning populations was lower than the movement rate for age-6 and older lake sturgeon. Such lower movement rates could arise from young lake sturgeon initially residing in tributaries or near river mouth areas where they were spawned before migrating out to open-water areas of Green Bay or Lake Michigan (Caroffino et al. 2010). We believe this is the most likely scenario for age-related differences in movement for lake sturgeon and believe it to be highly unlikely that older lake sturgeon would have lower movement rates to mixture regions than younger fish. For each age and spawning-population, we randomly generated movement rates from uniform distributions with lower and upper bounds of 0.25 and 0.75. As with the other sensitivity scenarios, we generated these age- and spawning-population-specific movement rates 100 times and refit the relative recruitment model to determine how recruitment estimates changed across the simulations.

Results

Genetic differentiation within and among spawning populations

Expected heterozygosity (H_e) in the spawning populations ranged from 0.49 to 0.61 whereas mean allelic richness (A) ranged from 4.42 to 5.00 (Supplemental Table S2) suggesting that the populations had similar levels of genetic diversity despite large historical differences in spawning population abundance (Holey et al. 2000; DeHaan et al. 2007). Genotypic frequencies deviated modestly from Hardy-Weinberg expectations (population mean inbreeding coefficient F_{is} range -0.01 to 0.059); frequencies were significantly different from Hardy-Weinberg expectations in just one of the spawning populations [Manistee River (0.059), Supplemental Table S2].

Spawning populations of lake sturgeon from tributaries of Lake Michigan were genetically differentiated in microsatellite allele frequency. Pair-wise estimates of inter-population variance in allele frequency (F_{st}) were significantly different for all population pairs (Table 1), with the exception of the Oconto and Peshtigo Rivers (F_{st}=0.009, where the type-1 error rate for the pairwise tests was 0.0034 after Bonferroni correction). Based on insignificant allele frequency differentiation, lake sturgeon from the Oconto and Peshtigo Rivers were combined for mixture analyses. Estimates of inter-population F_{st} ranged from 0.017 (Fox River to nearby Oconto/Peshtigo Rivers; Fig. 1, Table 1) to 0.148 (Kalamazoo River vs Menominee River; Fig. 1, Table 1), with overall patterns of differentiation similar to a previous study of these populations based on smaller sample sizes (Homola et al. 2012). Generally, inter-population variation in allele frequency among spawning populations of lake sturgeon was greater between eastern and western basin tributaries than between tributary spawning populations within the eastern or western basin. The Kalamazoo River population was more divergent in allele frequency than other Lake Michigan populations (Table 1, Supplemental Table S2).

Analysis of baseline populations: mixture simulation analyses

Results from simulated mixtures based on leave-one-out analyses (Fig. 2) suggested that on average there was sufficient genetic differentiation among the spawning populations using 12 disomic microsatellite loci to estimate mixture contribution within 3% of true contributions.

Based on the leave-one-out cross validation simulations, the mean absolute deviation between estimated and simulated population contributions ranged from 2.1 to 3.2% for the different spawning populations, with the highest deviance for the Fox and Oconto/Peshtigo spawning populations and the lowest deviance for the Kalamazoo and Muskegon populations (Fig. 2). This means on average across the simulations, estimated spawning population contributions were within approximately ±3% of the simulated population contributions. The maximum absolute deviation from the leave-one-out cross validation simulations ranged from 9.3 to 16.4% for the different spawning populations, with the highest deviance again observed for the Fox and Oconto/Peshtigo spawning populations (Fig 2).

The results from the 100% mixture simulations also indicated that proportional contributions of tributary spawning populations could be assigned with high confidence (Supplemental Table S4). The estimated proportional contributions for the population of origin (i.e., diagonal values of the misclassification matrix) ranged from 93.1% to 96.9%; Supplemental Table S4). For all simulations, the upper 95% confidence limit for the proportional contribution estimate for the population of origin was 100%. Most misallocations were to streams in close geographic proximity (within the eastern or western lake basin), and to populations which had similar allele frequencies (i.e., as reflected in inter-population F_{st} values; Table 1).

Hierarchical analyses of mixture composition for open-water collections

Compositional estimates of population mixtures from individual sampling locations within open-water areas of Green Bay (Fig. 1A) revealed considerable spatial variation in population contributions from southern to northern locations with compositions generally reflecting proximity of sampling locations to natal steams (see Supplemental Table S5 for point estimates and upper and lower 95% CIs). Samples from the southern portion of Green Bay [e.g., Southern Green Bay (SGB), Pensaukee (PEN), Dykesville (DYK), and Oconto River Area (ORA)] included higher percentages from the Oconto/Peshtigo and Fox Rivers than samples further north in Green Bay (Fig. 1A; Supplemental Table S5). Contributions from the Menominee River spawning population increased in sampling locations north of the Peshtigo Reef (PRF) area (Fig. 1A; Supplemental Table S5) except for samples from around Chambers Island (CHI) that were composed almost entirely of individuals from the Oconto/Peshtigo River. The contributions from lake sturgeon spawning populations in Michigan tributaries to Green Bay mixtures were generally low. The Muskegon, Kalamazoo, and Manistee spawning populations composed approximately 26% and 21% of the mixture from the Washington Islands and Door County sampling locations, respectively, both on the outer edge or just outside of Green Bay. For the other Green Bay sampling locations, however, the Muskegon, Kalamazoo, and Manistee spawning populations composed between 0 and 10% of the mixtures with the lower 95% confidence limit for the contribution estimates generally at 0% (Supplemental Table S5).

When the open-water Green Bay sampling locations were combined into regions, the Oconto/Peshtigo River spawning population composed between 60 and 70% of the mixtures in the Southern, Central A, and Central B areas of Green Bay (Fig. 1A; Supplemental Table S6). The second greatest contributor in the Southern and Central A regions of Green Bay was the Fox River spawning population; however, in the Central B region the second greatest contributor was the Menominee River spawning population. In Northern Green Bay, the Menominee River and Oconto/Peshtigo River spawning populations composed 37 and 31% of the mixture, respectively, whereas the Fox River population composed 19% of the mixture. Point estimates for contributions to Green Bay mixtures from eastern basin populations (Manistee, Muskegon, Kalamazoo Rivers) were near zero for every region in Green Bay except the Northern region (Fig. 1A; Supplemental Table S6).

At a lake-wide spatial scale, mixture compositions varied across the regions (Fig. 1B; Supplemental Table 7). Overall, Michigan spawning populations were estimated to have contributed approximately 14% of the fish in the mixtures, with fairly equal contributions from the Manistee and Muskegon River populations. The Menominee River spawning population composed the majority of the mixture for the entire lake basin scale (65%) and in Green Bay (77%), followed by the Oconto/Peshtigo River spawning population (entire lake basin:16%; Green Bay: 17%). The large contribution of Menominee River fish was in part attributed to the large number of fish from nearshore habitats estimated to have originated from this tributary (see river-mouth results below). For the entire lake basin, the Manistee (7%) and Muskegon River (7%) spawning population composed the next highest proportions of the mixture, whereas in Green Bay the Fox River spawning population provided the next highest proportion of the mixture (4%). In the north region which included both northern Green Bay and the north end of Lake Michigan's main basin, the Menominee, Oconto/Peshtigo, and Fox River spawning populations composed approximately 91% of the mixture, with the rest of the mixture composed of the Manistee (5%) and Muskegon (4%) River spawning populations. For the East-Central region of the lake, the Manistee River population composed the greatest amount of the mixture (48%) followed by the Muskegon (44%) and Fox (6%) River spawning populations. For the Southeast region, the Muskegon River spawning population composed the majority (58% of the mixture), followed by the Manistee (22%) and Menominee (12%) River spawning populations. The Kalamazoo River spawning population overall was a minor contributor of fish to the assessed mixtures and was estimated to compose no more than 2% of the mixtures in any of the regions.

For both the open-water Green Bay and Lake Michigan regions, the null hypothesis that each of the regions had equal spawning population contributions was rejected (Table 2). Based on pairwise testing of the regions, spawning population contributions to the Northern region of Green Bay were significantly different from the contributions to the South and Central A regions; however, we were unable to detect contribution differences between the Northern and Central B regions (Table 2). We also did not detect contribution differences between the Southern, Central A, and Central B regions (Table 2). For the whole lake regions, spawning population contributions to the East Central and Southeastern regions were significantly different from the contributions to the Green Bay and North Regions (Table 2). We were unable to detect differences between any of the other regions (Table 2).

Compositional variation between ages and seasons

When sampling locations in Green Bay were combined into groups, sample sizes were sufficient to estimate proportional contributions of tributary baseline populations to mixture portions comprised of adult ($\geq$110 cm TL) and sub-adult (<110 cm TL) age groups (Table 3). Mixture composition point estimates for western basin (Wisconsin) populations often varied by 10% or more between age groups within a location. However, sample sizes were comparatively small, 95% confidence intervals were concomitantly larger, and thus no significant difference in the compositions between the length-based groups was detected in any Green Bay region (likelihood ratio tests (P>0.05, data not shown). As with the grouped open-water Green Bay data with combined ages (Supplemental Table S6), we observed no statistical support for contributions of any eastern basin tributary population to mixtures of either age group in Green Bay.

Fish from different natal tributaries may utilize river-mouth habitats in different frequencies during different seasons (Donofrio et al. 2018). Extensive sampling in nearshore river-mouth habitats allowed compositional comparisons to be made between spring and fall mixtures. Samples were combined across ages and years to increase sample size. Simulation analyses (Supplemental Table S4) indicated that samples could be assigned to their true population with high accuracy (96.96% for Menominee River fish and 95.92% for Oconto/Peshtigo fish). Mixture compositional estimates for both spring and fall were considerably lower than 100% indicating that the aggregations even during the spring season outside the rivers proper, were comprised of fish from several tributaries (Table 4). This was particularly evident for the Oconto/Peshtigo River where a considerable proportion of the spring and fall mixtures were estimated to have come from the Menominee River. The large proportions of Menominee River fish captured in mixtures in nearshore waters contrasts with results from open-water regions of Green Bay (Supplemental Table S6). Compositions were not statistically different between spring and fall collections for either river (likelihood ratio tests, P>0.05).

Relative recruitment for spawning populations

The demographic composition of stock mixtures as evidenced by differences in lake sturgeon size distributions varied considerably across regions of Lake Michigan (Fig. 3). Size distributions for fish in the western portion of the basin, including Green Bay waters and waters of the northern Lake Michigan were generally unimodal with median sizes at or slightly above the size of sexual maturity used in analyses (~110 cm). Mean and standard deviation in total length was 115.4 and 35.78 cm (open-water Green Bay), 132.6 and 16.49 cm (Green Bay River mouth), and 129.80 and 29.23 cm (Northern). Samples from regions of the eastern basin including EastCentral (EC) (mean and SD: 74.61 and 38.90 cm) and SouthEast (SE) (mean and SD: 70.64 and 44.46 cm) were generally smaller on average and more uniformly distributed and exhibited a larger range of sizes (Fig. 3). All pairwise inter-regional Kolmogorov-Smirnov test comparisons for size distributional heterogeneity were found to be significantly different, with the exception of EC vs SE and Northern vs Green Bay regions (Supplemental Table S8). Because of the heterogeneity in size (and therefore age) distributions among regions, and the large disparities in sample size across regions in the basin, only relative stock recruitment estimates for Green Bay were estimated based on combined samples from all nearshore river-mouth and open-water collections (combined N=1732).

The combined normal and logistic selectivity function that was estimated as part of the relative recruitment model indicated that the contribution of the normal component of the model was equal to that of the logistic component (i.e., $\gamma = 1.0$). The estimated age-specific selectivities peaked at approximately 14 years (Fig. 4), which based on the assumed growth model corresponded to an expected length of approximately 130 cm, and was the approximate length for the mode of the length-frequency distribution for the combined Green Bay sample (Fig. 3). The inflection point for the logistic component of the selectivity function was at approximately 17 years of age, and selectivities reached an asymptote of approximately 83% at around 25 years of age (Fig. 4)

For lake sturgeon populations associated with Michigan tributaries, there was considerable uncertainty in each of the recruitment parameter estimates, which likely was due to these spawning populations contributing less than 1% of the fish collected from the Green Bay mixture (Supplemental Table S7). As a result, there were insufficient data to estimate how recruitment levels for the spawning populations from these tributaries were changing over time. Consequently, we do not discuss the results for the eastern basin spawning populations further.

Of the assessed Wisconsin spawning populations, the initial (first assessed year class) estimates of recruitment to the Green Bay populations (log $\boldsymbol{\alpha}$) were highest for the Fox River, followed by the Menominee and Oconto/Peshtigo Rivers (Table 5). However, as pointed out by Tsehaye et al. (2016), comparisons of the initial recruitment values are only valid if movement rates are equal among the spawning populations. Otherwise, differences in these initial recruitment values could just be indicative of populations differing in movement rates to the mixture area. With respect to changes in recruitment levels, the Fox, Menominee, and Oconto/Peshtigo had positive β estimates suggesting their recruitment levels were increasing over time (Table 5). The Oconto/Peshtigo Rivers has the largest β estimate*,* suggesting that recruitment for this spawning population had increased the most over the assessed time period, followed by the Menominee and Fox Rivers. The likelihood profile confidence intervals for the β estimates for the Oconto/Peshtigo and Fox Rivers did not overlap, suggesting that the increase in recruitment for the Oconto/Peshtigo population was significantly better than the Fox population. Conversely, the confidence interval for the β estimate for the Menominee River overlapped those of the Oconto/Peshtigo and Fox Rivers, suggesting there were not statistically significant differences in the recruitment trends for those populations.

Sensitivity of relative recruitment estimates

The sensitivity analyses suggested that the estimates of the rate of change in recruitment levels (β) for the Wisconsin lake sturgeon populations were fairly robust to deviations in assumptions about growth, mortality, and movement (Fig. 5). Results for the Michigan lake sturgeon populations were more sensitive to violations in assumptions, although as indicated above the relative recruitment estimates for Michigan populations were uncertain to begin with due to low contributions to the Green Bay mixtures. Point estimates for the *β*s for the Wisconsin populations were typically, although not always, encompassed within the range of the 95% confidence intervals shown in Table 5. Estimates for all Wisconsin lake sturgeon populations were greater than 0.0 suggesting that relative recruitment has indeed increased in most recent year classes although for the Fox River spawning population some point estimates neared 0.0. Results were most sensitive to differences in assumptions about growth rates of individual spawning populations. Assumptions about mortality rates had little influence on estimates of the *β*s and in many cases resulted in larger estimates for the spawning populations, although this was directly influenced by the range of mortality rates that were considered and the assumption that mortality rates of younger fish was greater than older fish. Likewise, assumptions about movement rates quite often resulted in higher estimates of *β*s for the Wisconsin spawning populations again likely due to the assumption that movement rates were lower for younger fish.

Discussion

Results of this study tie together estimates of mixed stock composition and relative stock-specific recruitment trends from the same dataset, which we hope will inspire other researchers with large-scale genotyping datasets to apply our approach as a means to improve understanding of metapopulation demographics and dynamics (Cadrin 2020; Koljonen et al. 2021). The concept that the co-occurrence of locally distinct spawning populations improves overall population stability and resiliency at larger spatial scales has been referred to as portfolio theory or portfolio effects (Schindler et al. 2010; DuFour et al. 2015). The premise of the portfolio theory is that distinct spawning populations have intrinsic differences in reproductive efforts due to regional differences in control mechanisms (DuFour et al. 2015). Consequently, populations that are part of metapopulations can have greater stability than individual populations or degraded populations. However, protecting metapopulations from natural or anthropogenic disturbances can be difficult. The methodologies presented in this paper provide a means to better understand demographics (e.g., recruitment) of individual populations, and a way to assess overall recruitment health, which should improve management efforts.

Our study results provide compelling evidence for non-random open-water and nearshore habitat use by adult and sub-adult lake sturgeon from different tributary spawning populations. While other studies (e.g., Stabile et al. 1996; Rusak and Mosindy 1997; Auer 1999a; Knights et al. 2002) have examined patterns of lake sturgeon movements, the methods used in this study allowed analyses based on sample sizes far greater than those possible via direct capture-mark-recapture or telemetry methods. In total, we genotyped 1,907 lake (open-water and nearshore) and 533 baseline (river-spawning) fish, which considering the species' depressed abundance in Lake Michigan (Holey et al. 2000), likely constitutes a substantial proportion of the lake's total lake sturgeon population. For example, Elliott and Gunderman (2008) estimated the total abundance of lake sturgeon > 112 cm in open-waters of central and southern Green Bay to be around 5,600 fish from 2002 to 2006. Given the lake sturgeon's conservation status, it likely would have been too risky to physically tag this number of lake sturgeon with internal or external transmitters to obtain comparable movement information.

Our study results have significant management implications in terms of risk assessment for Lake Michigan lake sturgeon populations. For example, if a portion of habitat (e.g., different areas within Green Bay) were to become degraded through either point or non-point pollution events, our results indicate that effects to specific populations would be non-random. Similarly, if new fisheries developed or existing fisheries shifted gear types that resulted in significant by-catch of lake sturgeon in particular areas, specific lake sturgeon populations could be particularly vulnerable to harvest (e.g., Bott et al. 2009). Importantly, using data described here, effects to specific tributary populations could be predicted based on high probabilities of habitat occupancy of open-water and nearshore regions in close proximity to natal rivers.

Genetic structure of mixtures exists at multiple hierarchical scales

Hierarchical spatial sampling indicated non-random occupancy by lake sturgeon in Lake Michigan waters at microgeographic, regional, and basin-wide scales across the lake basin. At the lowest scale of analysis, results indicated a high level of heterogeneity in the population composition of mixtures collected from different portions of Green Bay, which has a total surface area in excess of 2400 km^2. One example of compositional differences over a microgeographical scale were 12% and 14% differences in mixture compositional point estimates originating from the Oconto/Peshtigo and Menominee River populations from open-water sampling locations MAR and PRA (Fig. 1, Supplemental Table S5) that were within 20 km of each other, and separated by a very shallow shoal extending out from land. Data exemplify the potential spatial heterogeneity in areas occupied by members of different spawning populations. Findings of significant spatial heterogeneity at small spatial scales even though samples were collected over multiple years, suggest temporal consistency in open-water habitat occupancy.

To interpret patterns across Green Bay, the contribution of particular spawning populations to mixtures can be examined on a north-south gradient. The estimated contribution from each population changed directionally in terms of population rank order of contribution to mixtures from southern-most to northern most sampling locales. For example, contributions from the eastern basin (Michigan tributaries) in the southern most sampling sites (SGB, DYK, PEN, ORA collection sites within Green Bay) were absent. Southern Green Bay sampling locations also lacked appreciable contributions from the Menominee River population, while being dominated by individuals from the Oconto/Peshtigo River and Fox River tributaries.

The Menominee River lake sturgeon population has been identified as the most abundant population in the Lake Michigan basin (Holey et al. 2000). However, fish originating from the Menominee River were not the most widely distributed in terms of open-water areas within Green Bay but did dominate nearshore (river mouth) areas. Fish from nearshore areas were generally larger, which is consistent with prevalence of sexually mature adults prior to spring or staging the fall before spawning events. Mixture compositional differences between open-water (generally smaller) and nearshore (generally larger) individuals could indicate individuals are spatially structured differently as a function of age. This was suggested in mixture compositional comparisons between sub-adult and adult individuals in different regions of Green Bay.

Within the central region of Green Bay (sampling locations YRA/PRA, PRF/MAR, LSS/LSN), mixture compositional differences were documented among sites that are in relatively close geographic proximity. For example, the PRA/YRA open-water mixture included a low proportional contribution of individuals originating from the Menominee River. The neighboring PRF/MAR open-water sampling sites were dominated by fish of Menominee River origin. Significant north to south heterogeneity in population contributions to mixtures were further seen when sampling locations were aggregated into 'groups'.

Significant differences in mixture composition were likely dictated by physical features (e.g., Peshtigo shoal on the western shore of Green Bay, near collection sites PRA and PRF), and water circulation patterns (counter-clockwise within the bay, US EPA 1990). Significant variation in population composition within areas as close as 20 km suggests that habitat use may be dictated by bathymetric features or other aspects of lake habitat. For example, descriptions of the species' depth limitations (approximately 18.2 m; Harkness and Dymond 1961) suggests that benthivores such as lake sturgeon would be less likely to suspend and traverse deep-water areas but rather would travel along shallow water areas.

The mixture compositional estimate for the Door County sampling site is not consistent with mixture compositional trends at other nearby sampling locales. There are several likely explanations. As above, Door County is really the only open lake site sampled outside (east) of Green Bay proper, and physical barriers may cause unusual mixing of populations. Secondly, there is a man-made channel through the Door County peninsula that could feasibly provide a corridor for Fox River lake sturgeon to pass into the open lake. The other and perhaps more likely scenario is that Wolf River (genetically indistinguishable from Fox River; DeHaan et al. 2007) have been stocked into two Wisconsin Lake Michigan tributaries south of the Door County sampling site (Milwaukee and Kewanee Rivers). Hatchery-origin fish of Fox (or Wolf) River origin could be represented in fish captured. We make a similar argument explaining Wisconsin-origin baseline populations present in the SE portion of Lake Michigan (Fig. 1B).

At the eastern (Michigan) and western (Wisconsin) basin level, genetic data indicated large and significant compositional heterogeneity in population contributions to open-water mixtures. Results indicate there is limited trans-basin movements of individuals from different sub-basin tributaries except to the northern portion of Green Bay and to the basin's Southeastern region. Limited trans-basin movement of lake sturgeon in Lake Michigan is also supported by genetic studies that found far greater variance in allele frequency between populations from different sides of the Lake Michigan basin (DeHaan et al. 2006, Table 1 this study) and estimates of inter-population straying of adults into non-natal rivers (Homola et al. 2012).

Within mixtures collected along the eastern shore of Lake Michigan (EC and SE regions), point estimates of western basin population contributions were non-zero and higher than estimates of eastern basin populations contributing to GB and N region mixtures. The lack of reciprocity in assignments across northern Lake Michigan was surprising because Green Bay offers shallow and productive habitat. Given that lake sturgeon are benthivores, habitat productivity or other characteristics may be a significant factor influencing movements. The contributions of small (Fig. 3) lake sturgeon in the SE region of Lake Michigan assigned to Green Bay tributary populations could indicate that fish raised in stream-side hatcheries in central and southern tributaries in Wisconsin, and stocked into the lake during the past decade could be dispersing around the southern basin and into Michigan waters. Approximately 30% of the Southeastern region collections was composed of fish <40 cm in length, which is consistent with the expected size of fish from past stocking events. If smaller Southeastern region Lake Michigan lake sturgeon are of hatchery origin, these findings could corroborate other findings that some hatchery fish disperse considerable distances from release sites (Eggold et al. 2012). It should be noted that point estimates of mixture contributions by trans-basin populations tended to have large confidence intervals based on small sample sizes, particularly for eastern basin mixtures. The magnitude and direction of non-zero trans-basin movements, while not large are worthy of further study.

Studies of adult lake sturgeon habitat occupancy in other regions have documented a variety of spatial patterns. Rusak and Mosindy (1997) use telemetry data to document evidence for two subpopulations of lake sturgeon within a relatively restricted area of the Rainy River and Lake of the Woods that were differentiated in part on movement patterns and rates. The data indicated occupancy of different habitats in close proximity. Seasonal differences in movement rates were also documented. Auer (1999a) examined habitat use and movement by 25 adult (ranges in total length 130-174 cm) lake sturgeon in Lake Superior after spawning in the Sturgeon River. Individuals inhabited a variety of water depths throughout the lake and traveled throughout the southern portion of the lake (70-280 km). The lack of concordance across studies suggests that any observed patterns of habitat use and movement may not be generalizable to all populations of lake sturgeon inhabiting such different habitats (i.e. riverine vs. lacustrine populations). Findings in this study indicating that lake sturgeon are more likely to remain near natal streams during non-spawning periods also differs from studies in other sturgeon species. For example, a recent study by Kazyak et al. (2021) found subadult and adult Atlantic sturgeon (*Acipenser oxyrinchus*) migrate extensively and are found in mixed-stock groups in non-natal habitats hundreds of kilometers from natal streams in estuarine and marine environments.

Characteristics of habitat may be driving dispersal patterns, rather than dispersal occurring in similar patterns irrespective of habitat. For example, Knights et al. (2002) observed movement among lake sturgeon populations in the upper Mississippi River. Individual fish were observed returning to certain habitat areas with common characteristics, which the authors hypothesized might provide optimal feeding habitat. Also, groups of fish tended not to overlap in the geographic range of their movements, suggesting that even when movements occurred, all available habitats were not used equally by all individuals.

Habitat characteristics have been found to affect sturgeon movement in other species and other regions. Researchers working in the Rainy River/Lake of the Woods system (Ontario, CA/Minnesota, USA) tracked movements of individual lake sturgeon within both riverine and lacustrine habitats over a three-year period (Rusak and Mosindy 1997). Results suggested that movements were dictated by foraging behavior, as fish congregated at appropriate feeding habitat areas. Similarly, work with the Gulf sturgeon, *Acipenser oxyrhynchus desotoi*, found that individuals tended to prefer specific microhabitats within rivers (Wooley and Crateau 1985). Results from a study of sub-adult Atlantic sturgeon, *Acipenser oxyrinchus*, suggested that non-natal habitats are important for the persistence of sturgeon populations, although the function of these habitats (feeding, protection, staging) was unknown (Savoy and Pacileo 2003).

Estimates of uncertainty in compositional estimates varied across the mixtures analyzed. Results from leave-one-out analyses (Fig. 2) and 100% simulations (Supplemental Table S4) revealed that mixture composition can be apportioned with high accuracy and minimal bias. The large confidence intervals about estimates for several samples is likely due to the sample sizes employed **(**Kalinowski 2004). Examination of mixtures of different sizes revealed a demonstrable trend toward smaller confidence intervals when mixture sizes were larger.

Given the amount of time lake sturgeon spend in open-water habitats, certain habitats may be occupied by a relatively high density of lake sturgeon while other habitat is vacant. Based on results from Green Bay and across the Lake Michigan basin, differences in mixture composition may be partially explained by physical features. A pattern of non-random habitat occupancy may help managers prioritize habitats for restoration or protection, particularly if the reasons for the pattern can be explained.

Estimated relative recruitment parameters for Lake Michigan tributary populations

For all Wisconsin spawning populations, our results suggest recruitment to the nearshore and open-waters of Green Bay have increased over time for the assessed year classes (roughly 1964 to 2009). Elliott and Gunderman (2008) also concluded that recruitment observed in the early

2000s (2003 to 2006) was likely higher than during the preceding 10 to 40 years, although they were not able to provide estimates for years prior to their study. Historically, Lake Michigan lake sturgeon population abundance was suppressed due to a combination of overharvest and poor recruitment attributed to habitat loss and degradation caused by dams and poor spawning habitat quality (Hayes and Caroffino 2012). Commercial harvest of lake sturgeon in the US waters of the Great Lakes was suspended in the late 1970s. While recreational and tribal fishing still occurs in some rivers, tribal harvest in particular is limited, and these fisheries are highly regulated and monitored. As a result, there has been an ostensible increase in spawning stock biomass in all the Great Lakes, including Lake Michigan, where there is no recreational or tribal harvest, which could be a factor contributing to improvements in recruitment for Wisconsin spawning populations. Elliott and Gunderman (2008) estimated the annual spawning run size in the Menominee, Oconto, Peshtigo, and Fox Rivers through mark-recapture analysis. They estimated the Lower Menominee River to have a spawning run size of 340 fish, followed by the Oconto/Peshtigo and Fox Rivers with spawning run sizes of 225 and 50 fish, respectively (Elliott and Gunderman 2008). More recently, observations for some of these rivers suggest significant increases in spawner numbers (Tucker et al. 2021). This suggests a positive relationship between spawning stock size and trends in recruitment, although it is important to note that this is based on the assessment of only 4 river systems. Additionally, two of these rivers have additional sources of potential recruitment from upriver populations that occur in Lake Winnebago, upstream of the Lower Fox River, and occur in the Upper Menominee River, upstream of the dam in the lower Menominee River. Both the Winnebago population and the Upper Menominee River are known to contribute fish to the Fox River and Menominee River populations, respectively described in this study.

Curtailment of most directed fishing for lake sturgeon in Lake Michigan means that remaining impediments to lake sturgeon rehabilitation include factors such as habitat loss (including effects of dams) and degradation leading to reduced recruitment or poor early life (i.e., pre-juvenile stage) survival. The Menominee, Oconto, Peshtigo, and Fox Rivers have all been dammed for extended periods of time, certainly periods longer than the age of the largest/oldest fish in the data set. The rivers had been significantly impacted by anthropogenic stressors including surrounding land use practices (urban and agriculture) and non-point source pollution. Point source pollution abatement as mandated by the Clean Water Act of 1972 is widely believed to have reduced point source pollution and improved opportunities for successful reproduction, which also could be a factor contributing to positive recruitment trends for the Wisconsin Rivers.

Although we had to make numerous assumptions about mortality, movement, and growth to index relative recruitment levels for the Wisconsin spawning populations, we found that our findings of improved recruitment were fairly insensitive to deviations from these assumptions (Fig. 5). Under some sensitivity simulations, the rate of recruitment change approached 0 for the Fox River spawning population, so additional investment of resources to assess the health of that population that occurred during 2017-2020 were warranted (Tucker et al. 2021). If a decision was made to use the relative recruitment model of Tsehaye et al. (2016) as a framework to gauge the health of individual spawning populations, it would be beneficial to enact assessment programs that could provide information on factors such as growth, mortality, and movement for individual spawning populations. Additionally, it would be beneficial for estimation purposes to use standardized methods to collect lake sturgeon rather than having to rely on a multitude of sampling gears to obtain samples from the mixture fishery.

At the outset of this project, we had initially wanted to combine mixtures sampled from throughout the entire Lake Michigan basin so that we could index for recruitment levels for all spawning populations rather than just Wisconsin spawning populations. However, we had to abandon these plans because of differences in length frequencies and sample sizes among the regions, which led to concerns about inconsistent results if we combined samples. A coordinated and consistent sampling protocol would allow this type of an analysis to be performed.

In spite of the need to make some strong assumptions, we believe that in the absence of comparable population recruitment estimates from other sources, data presented here constitute a credible first step toward developing assessment programs to further address indicators of low and declining recruitment. A strength of our analysis was the large sample sizes involved, with relative recruitment estimate based on collections of 1907 open-water and nearshore captured individuals of a range of ages that included representation of individuals from eastern basin populations. The large sample sizes and comprehensive sampling of the region allowed us to evaluate recruitment trends despite the compositional heterogeneity of the open-water mixtures and larger area involved.

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References

Abadi, F., Gimenez, O., Arlettaz, R., and Schaub, M. 2010. An assessment of integrated population models: bias, accuracy, and violation of the assumption of independence. Ecology, 91:7–14. doi:10.1890/08-2235.1.

Alaska Department of Fish and Game. 2003. SPAM Version 3.7: User's Guide Addendum. Addendum II to Special Publication 15, Alaska Department of Fish and Game, Commercial Fisheries Division, Gene Conservation Lab, 333 Raspberry Road, Anchorage, Alaska, 99518. 22 pp.

Anderson E.C., Waples, R.S., and Kalinowski, S.T. 2008. An improved method for predicting the accuracy of genetic stock identification. Can. J. Fish. Aquat. Sci. 65:1475–1486. doi:10.1139/F08-049.

Andvik R.T., Sloss B.L., VanDeHey J.A., Claramunt R.M., Hansen S.P., and Isermann D.A. 2016. Mixed stock analysis of Lake Michigan's lake whitefish *Coregonus clupeaformis* commercial fishery. J. Great Lakes Res. 42: 660–667. doi:10.1016/j.jglr.2016.02.005.

Auer, N.A. 1996. Importance of habitat and migration to sturgeons with emphasis on lake sturgeon. Can. J. Fish. Aquat. Sci. 53: 152-160. doi:10.1139/cjfas-53-S1-152.

Auer, N.A. 1999a. Lake sturgeon: a unique and imperiled species in the Great Lakes. In: *Great Lakes Fisheries Policy and Management: A Binational Perspective* (ed. C.P.Ferreri and W.W. Taylor), pp. 515-538. Michigan State University Press, East Lansing, MI.

Auer, N.A. 1999b. Population characteristics and movements of Lake Sturgeon in the Sturgeon River and Lake Superior. J. Great Lakes Res. 25: 282- 293. doi:10.1016/S0380-1330(99)70737-9.

Baker, J.P. 1980. The distribution, ecology, and management of the lake sturgeon (*Acipenser fulvescens* Rafinesque) in Michigan. Michigan Department of Natural Resources, Fisheries Research Report no. 1883, Ann Arbor, Michigan.

Bauer, S., and Hoye, B.J. 2014. Migratory animals couple biodiversity and ecosystem functioning worldwide. Science: 344: 1242552. doi:10.1126/science.1242552

Beacham, T. D. Candy, J. R., McIntosh, B., MacConnachie, C., Tabata, A., Kaukinen, K., Varnavskaya, N. 2005. Estimation of stock composition and individual identification of sockeye salmon on a Pacific Rim basis using microsatellite and major histocompatibility complex variation. Trans. Amer. Fish. Soc. 134: 1124–1146. doi:10.1577/T05-005.1.

Beacham, T.D., McIntosh, B., MacConnachie, C., Miller, K.M., Withler, R.E., and Varnavskaya, N. 2006. Pacific Rim population structure of sockeye salmon as determined from microsatellite analysis. Tran. Amer. Fish. Soc. 135; 174-187. doi:10.1577/T05-149.1.

Beacham, T. D., K. Jonsen, B. McIntosh, B. J. G. Sutherland, D. Willis, C. Lynch, and C. Wallace. 2020. Large-scale parentage-based tagging and genetic stock identification applied in assessing mixed-stock fisheries and hatchery brood stocks for coho salmon in British Columbia, Canada. Can. J. Fish. Aquat. Sci. 77: 1505-1517. doi:10.1139/cjfas-2020-0035.

Beamish, F.W.H, Jebbink, J.A., Rossiter, A., and Noakes, D.I.G. 1996. Growth strategy of juvenile lake sturgeon (*Acipenser fulvescens*) in a northern river. Can. J. Fish. Aquat. Sci. 53: 481-489. doi:10.1139/f95-222.

Bjorndal, K.A., and Bolten, A.B. 2008. Annual variation in source contributions to a mixed stock: implications for quantifying connectivity. Mol. Ecol. 17: 2185–2193. doi:10.1111/j.1365-294X.2008.03752.x.

Bolker, B.M., Okuyama, T., Bjorndal, K.A., Bolten, A.B. 2007. Incorporating multiple mixed stocks in mixed stock analysis: “many -to-many” analyses. Mol. Ecol. 16: 685–695. doi.org/10.1111/j.1365-294X.2006.03161.x.

Bott, K., Scribner, K.T., Kornely, G.,Donofrio, M., and Elliott, R.F. 2009. Mixed-stock analysis of lake sturgeon harvest mixtures and from adjoining open-waters of western Lake Michigan. N. Amer. J. Fish. Manage. 29: 1636-1643. doi:10.1577/M08-211.1.

Bradbury, I.R., Hamilton, L.C., Sheehan, T.F., Chaput, G., Robertson, M.J., Dempson, J.B.,Reddin, D., Morris, V., King, T., and Bernatchez, L. 2016. Genetic mixed-stock analysis disentangles spatial and temporal variation in composition of the West Greenland Atlantic Salmon fishery. ICES J. Mar. Sci. 73: 2311-2331. doi: 10.1093/icesjms/fsw072

Brenden, T.O., Scribner, K.T., Bence, J.R., Tsehaye, I., Kanefsky, J., Vandergoot, C.S., and

Fielder, D.G. 2015. Genetic stock identification of spawning populations contributing to the Saginaw Bay, Lake Huron recreational walleye fishery. N. Amer. J. Fish. Manage. 35: 567-577. doi:10.1080/02755947.2015.1020079.

Brenden, T.O., Tsehaye, I., Bence, J.R., Kanefsky, J., and Scribner, K.T. 2018. Indexing recruitment for source populations contributing to mixed fisheries by incorporating age in genetic stock identification models. Can. J. Fish. Aquat. Sci. 75; 934-954. doi:10.1139/cjfas-2016-0525.

Brooks, J.L., Chapman, J.M., Barkley, A.N., Kessel, S.T., Hussey, N.E., Hinch, S.G., Patterson, D.A., Hedges, K.J., Cooke, S.J., Fisk, A.T., Gruber, S.H., and Nguyen, V.M. 2019. Biotelemetry informing management: case studies exploring successful integration of biotelemetry data into fisheries and habitat management. Can. J. Fish. Aquat. Sci. 1238-1252. doi:10.1139/cjfas-2017-0530.

Bruch, R.M., Haxton, T.J., Koenigs, R., Welsh, A. and Kerr, S.J. 2017. Status of lake sturgeon (*Acipenser fulvescens* Rafinesque 1817) in North America. J. Appl. Ichth. 32: 162-190. doi:10.1111/jai.13240.

Cadrin, S. X. 2000. Advances in morphometric identification of fishery stocks. Rev. Fish Biol. Fish. 10: 91–112. doi:10.1023/A:1008939104413.

Cadrin, S. X. 2020. Defining spatial structure for fishery stock assessment. Fish. Res. 221, 105397. doi:10.1016/j.fishres.2019.105397.

Caroffino, D.C., Sutton, T.M., Elliott, R.F., and Donofrio, M.C. 2010. Early life stage mortality rates of lake sturgeon in the Peshtigo River, Wisconsin. N. Amer. J. Fish. Manage. 30, 295-304. https://doi.org/10.1577/M09-082.1.

Chandler, R.B., and Clark, J.D. 2014. Spatially explicit integrated population models. Methods Ecol. Evol. 5: 1351–1360. doi:10.1111/2041-210X.12153.

Colborne, S.F., Hondorp, D.H., Holbrook, C.M., Lowe, M.R., Boase, J.C., Chiotti, J.A., Wills, T.C., Roseman, E.F., and Krueger, C.C. 2020. Sequence analysis and acoustic tracking of individual lake sturgeon identify multiple patterns of river–lake habitat use. Ecosphere doi: 10.1002/ecs2.2983.

Cooke S.J., Bunt C.M., Hamilton S.J., Jennings C.A., Pearson M.P., and Cooperman M.S. 2005. Threats, conservation strategies, and prognosis for suckers (Catostomidae) in North America: insights from regional case studies of a diverse family of non-game fishes. Biol. Cons. 121: 317– 331. doi:10.1016/j.biocon.2004.05.015.

Cooke, S.J., Martins, E.G., Struthers, D.P., Gutowsky, L.F.G., Power, M., Doka, S.E., Dettmers, J.M., Crook, D.A., Lucas, M.C., Holbrook, C.M, and Krueger, C.C. 2016. A moving target – incorporating knowledge of the spatial ecology of fish into the assessment and management of freshwater fish populations. Environ. Monit. Assess. 188: 239-257. doi:10.1007/s10661-016-5228-0.

Dammerman, K.J., Steibel, J.P. and Scribner, K.T. 2015. Genetic and environmental components of phenotypic and behavioral trait variation during lake sturgeon (*Acipenser fulvescens*) early ontogeny. Environ. Biol. Fish. 98: 1659-1670. doi:10.1007/s10641-015-0392-6.

Dammerman, K.J., Steibel, J.P., and Scribner, K.T. 2016. Increases in the mean and variability of thermal regimes result in differential phenotypic responses among genotypes during early ontogenetic stages of lake sturgeon (*Acipenser fulvescens*). Evol. Appl. 9: 1258-1270. doi:10.1111/eva.12409.

Dammerman, K., Webb, M., and Scribner, K.T. 2019. The influence of reproductive timing on female reproductive success and ovarian quality determined using plasma testosterone concentrations in lake sturgeon (*Acipenser fulvescens*). Can. J. Fish. Aquat. Sci. 76: 1147-1160. doi.org/10.1139/cjfas-2018-0141.

Debevec, E.M., Gates, R.B.,Masuda, M., Pella, J.,Reynolds, J., and Seeb, L.W. 2000. SPAM (version 3.2): Statistics program for analysis of mixtures. J. Hered. 91: 509- 510. doi: 10.1093/jhered/91.6.509.

DeHaan, P.W, Libants, S.V., Elliott, R.F., and Scribner, K.T. 2006. Genetic population structure of remnant lake sturgeon populations in the upper Great Lakes basin. Trans. Amer. Fish. Soc.. 135**:** 1478-1492. doi:10.1577/T05-213.1.

Donofrio, M.C., Scribner, K.T., Baker, E.A., Kanefsky, J., Tsehaye, I. and Elliott, R.F. 2018. Telemetry and genetic data characterize lake sturgeon breeding ecology and spawning site fidelity in Green Bay rivers of Lake Michigan. J. Appl. Ichthy. 34: 302-313. doi: 10.1111/jai.13561.

DuFour, M.R., May, C.J., Roseman, E.F., Ludsin, S.A., Vandergoot, C.S., Pritt, J.J., Fraker, M.E., Davis, J.J., Tyson, J.T., Miner, J.G., Marschall, E.A., and Mayer, C.M. 2015. Portfolio theory as a management tool to guide conservation and restoration of multi-stock fish populations. Ecosphere 6: 296. https://doi.org/10.1890/ES15-00237.1.

Eggold, B., Baumgartner, M., Fajfer, S., Holtgren, M., Baker, E., Elliott, R., and Holleback, M. 2012. Lake sturgeon rehabilitation using streamside rearing facilities [online]. Available from https://www.glft.org/documents/671-glft_final_-_proj_2005-671.

Elliott, R.F., and Gunderman, B. 2008. Assessment of Remnant Lake Sturgeon Populations in the Green Bay Basin, 2002-2006. Final Report to the Great Lakes Fishery Trust. Project No.

2001.113/2004.610.

Euclide, P.T., MacDougall, T., Robinson, J.M., Faust, M.D., Wilson, C.C., Chen, K-U., Marschall, E.A., Larson, W., and Ludsin, S.A. 2020. Mixed-stock analysis in the age of genomics: Rapture genotyping enables evaluation of 1 stock-specific exploitation in a freshwater fish population with weak genetic structure. bioRvix doi:10.1101/2020.11.10.376350.

Fabrizio, M.C. 2005. Experimental design and sampling strategies for mix-stock analysis. pp 467-498 in Cadrin, S.X., Friedland, K.D., and Waldman, J.R. (eds.). Stock Identification Methods: Applications in Fishery Science. Elsevier, Academic Press, NY. doi: 10.1016/B978-012154351-8/50024-1.

Fogarty, M.J. 1993. Recruitment in randomly varying environments. ICES J. Mar. Sci. 50: 247–260. doi:10.1006/jmsc.1993.1027.

Fournier, D.A., Skaug, H.J., Ancheta, J., Ianelli, J., Magnusson, A., Maunder, M.N., Nielsen, A., and Sibert, J. 2012. AD Model Builder: using automatic differentiation for statistical inference of highly parameterized complex nonlinear models. Optim. Methods Softw. 27:233-249. doi.org/10.1080/10556788.2011.597854.

Forsythe, P.S., Crossman, J.A., Bello, N.M., Baker, E.A., and Scribner, K.T. 2012. Individual-based analyses reveal high repeatability in timing and location of reproduction in lake sturgeon. Can. J. Fish. Aquat. Sci. 69: 60-72. doi:10.1139/f2011-132.

Goudet, J. 2001. FSTAT, a program to estimate and test gene diversities and fixation indices (version 2.9.3). http://www.unil.ch/izea/softwares/fstat.html.

Gunderman, B.J., and Elliott, R.F. 2004. Assessment of Remnant Lake Sturgeon Populations in the Green Bay Basin, 2002-2003, pp. 1-105. Great Lakes Fishery Trust Final Report.

Harkness, W.J.K., and Dymond, J.R. 1961. The lake sturgeon: the history of its fishery and problems of conservation. Ontario Department of Lands and Forests, Fish and Wildlife Branch, Toronto.

Harris, B.S., Ruetz III, C.R., Wieten, A.C., Altenritter, M.E., and Smith, K.M. 2016. Characteristics of lake sturgeon Acipenser fulvescens Rafinesque, 1817 in a tributary of Lake Michigan: Status of the Muskegon River population. J. Appl. Ichthyol. 36: 547-558. doi.org/10.1111/jai.14076.

Hay-Chmielewski, E.M., and Whelan, G.E. 1997. Lake Sturgeon Rehabilitation Strategy. 51 pp. Michigan Department of Natural Resources, Fisheries Division.

Hayes, D., and D. Caroffino. 2010. Michigan DNR Lake Sturgeon Rehabilitation Strategy. Final Report.

Hilborn, R., and Walters, C.J. 1992. Quantitative fisheries stock assessment: choice, dynamics, and uncertainty. Chapman and Hall, New York.

Hjort J. 1914. Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. Rapp. Proc. V. Reun. Cons. Int. Explor. Mer, 20: 1–228.

Holey, M., Baker, E.A., Thuemler, T., and Elliott, R.F. 2000. Research and assessment needs to restore lake sturgeon in the Great Lakes. Workshop Results, Muskegon, Michigan. Tech. Report, Great Lakes Fishery Trust.

Holtgren, J.M., Ogren, S.A., Paquet, A.J., and Fajfer, S. 2007. Design of a portable streamside rearing facility for lake sturgeon. N. Amer. J. Aqua. 69: 317-323. doi:10.1577/A06-013.1.

Homola, J.J., Scribner, K.T., Elliott, R.F., Donofrio, M.C., Kanefsky, J., Smith, K.M., and McNair, J.N. 2012. Genetically-derived estimates of contemporary natural straying rates and historical gene flow among Lake Michigan lake sturgeon populations. Tran. Amer. Fish. Soc. 141: 1374-1388. doi:10.1080/00028487.2012.694829.

Houston, J.J. 1987. Status of the Lake Sturgeon *Acipenser fulvescens* in Canada. Can. Field Nat. 101: 171-185.

Kalinowski, S.T. 2004. Genetic polymorphism and mixed-stock fisheries analysis. Can. J. Fish. Aquat. Sci. 61: 1075-1082. doi:10.1139/f04-060.

Kazyak, D.C., White, S.L., Lubinski, B.A., Johnson, R., and Eackles, M. 2021. Stock composition of Atlantic sturgeon (*Acipenser oxyrinchus oxyrinchus*) encountered in marine and estuarine environments on the U.S. Atlantic Coast. Cons. Gen. doi:10.1007/s10592-021-01361-2.

Kessel, S.T., Hondorp, D.W., Holbrook, C.M., Boase, J.C., Chiotti, J.A., Thomas, M.V., Wills, T.C., Roseman, E.F., Drouin, R., and Krueger, C.C. 2018. Divergent migration within lake sturgeon (*Acipenser fulvescens*) populations: multiple distinct patterns exist across an unrestricted migration corridor. J. Anim. Ecol. 87: 259-273. doi: 10.1111/1365-2656.12772.

King, T.L., Lubinksi, B.A., and Spidle, A.P. 2001. Microsatellite DNA variation in Atlantic sturgeon (*Acipenser oxyrinchus oxyrinchus*) and cross-species amplification in the Acipenseridae. Con. Gen. 2: 103-119. doi:10.1023/A:1011895429669.

Knights B.C., Vallazza, J.M., Zigler, S.J., and Dewey, M.R. 2002. Habitat and movement of lake sturgeon in the upper Mississippi River system, USA. Tran. Amer. Fish. Soc. 131: 507-522. doi: 10.1577/1548-8659(2002)131<0507:HAMOLS>2.0.CO;2.

Koljonen, M-L., Masuda, M., Kallio-Nyberg, I., Koskiniemi, J., and Saloniemi, I. 2021. Large inter-stock differences in catch size-at-age of mature Atlantic salmon observed by using genetic individual origin assignment from catch data. PlosOne 16(4): e0247435. doi:10.1371/journal.pone.0247435.

Labonne, J., and Gaudin, P. 2005. Exploring population dynamics patterns in a rare fish, *Zingel asper*, through capture-mark-recapture methods. Con. Biol. 19: 463- 472. doi:10.1111/j.1523-1739.2005.00013.x.

Landsman, S.J., Nguyen, V.M, Gutowsky, L.F.G., Gobin, J., Cokk, K.V., Binder, T.R., Lower, N., McLaughlin, R.L., and Cooke, S.J. 2011. Fish movement and migration studies in the Laurentian Great Lakes: research trends and knowledge gaps. J. Great Lakes Res. 37: 365-379. doi:10.1016/j.jglr.2011.03.003.

Larson, D.L., Kimmel, J.G., Hegna, J., Riedy, J., Baker, E.A., and Scribner, K.T. 2020. Male lake sturgeon (*Acipenser fulvescens*) migratory and spawning behaviors are associated with sperm quality and reproductive success. Can. J. Fish. Aquat. Sci. 77: 1943-1959. doi:10.1139/cjfas-2020-0124.

Li, Y., Bence, J.R., and Brenden, T.O. 2015. An evaluation of alternative assessment approaches for intermixing fish populations: a case study with Great Lakes lake whitefish. ICES J. Mar. Sci. 72: 70–81. doi:10.1093/icesjms/fsu057.

Li, Y., Bence, J.R., Zhang, Z., and Ebener, M.P. 2017. Why do lake whitefish move long distances in Lake Huron? Bayesian variable selection of factors explaining fish movement distance. Fish. Res. 195: 169-179. doi:10.1016/j.fishres.2017.07.014.

Ludsin, S.A., DeVanna, K.M., and Smith, R.E.H. 2014. Physical–biological coupling and the challenge of understanding fish recruitment in freshwater lakes. Can. J. Fish. Aquat. Sci. 71:775–794. doi:10.1139/cjfas-2013-0512.

McQuown, E.C., Sloss, B.L., Sheehan, R.J., Rodzen, J., Tranah, G.J., and May, B. 2000. Microsatellite analysis of genetic variation in sturgeon: new primer sequences for *Scaphirhynchus* and *Acipenser*. Tran. Amer. Fish. Soc. 129: 1380-1388. doi: 10.1577/1548-8659(2000)129<1380:MAOGVI>2.0.CO;2.

McQuown, E., Graham, G.A.E., and May, B. 2002. Characterization and inheritance of six microsatellite loci in lake sturgeon. Tran. Amer. Fish. Soc. 131: 299-307. doi: 10.1577/1548-8659(2002)131<0299:CAIOSM>2.0.CO;2.

Moran, B.M., and Anderson, E.C. 2018. Bayesian inference from the conditional genetic stock identification model. Can. J. Fish. Aquat. Sci. 76, 551-560. https://doi.org/10.1139/cjfas-2018-0016

Myers, R., Mertz, A.G., and Bridson, J. 1997. Spatial scales of interannual recruitment variations of marine, anadromous, and freshwater fish. Can. J. Fish. Aquat. Sci. 54: 1400–1407. doi:10.1139/f97-045.

Naiman, R.J., Bilby, R.E., Schindler, D.E., and Helfield, J.M. 2002. Pacific salmon, nutrients, and the dynamics of freshwater and riparian ecosystems. Ecosystems 5:399–417. doi: 10.1007/s10021-001-0083-3.

Pella, J., and Masuda, M. 2001. Bayesian methods for analysis of stock mixtures from genetic characters. Fish. Bull. 99: 151-197.

Peterson, D.L., Vecsei, P., and Jennings, C.A. 2007. Ecology and biology of the lake sturgeon: a synthesis of current knowledge of a threatened North American Acipenseridae. Rev. Fish Biol. Fish. 17: 59–76. doi:10.1007/s11160-006-9018-6.

Prince, D.J., O'Rourke, S.M., Thompson, T.Q., Ali, O.A. Lyman, H.S., Saglam, I.K.,Hotaling, T.J., Spindle, A.P., and Miller, M.R. 2017. The evolutionary basis of premature migration in Pacific salmon highlights the utility of genomics for informing conservation. Sci. Adv. 3, e1603198. doi:10.1126/sciadv.1603198.

Quinn, T.J., II, and Deriso, R.B. 1999. Quantitative Fish Dynamics. Oxford University Press, New York.

R Core Team. 2018. R: A language and environment for statistical computing. Vienna, Austria.

Rannalla, B., and Mountain, J. 1997. Detecting immigration by using multilocus genotypes. Proc. Natl. Acad. Sci. U.S.A. 94: 9197–9201. doi:10.1073/pnas.94.17.9197

Reynolds, J.H., and Templin, W.D. 2004. Detecting specific populations in mixtures. Envir. Biol. Fish. 69: 233-243. doi:10.1023/B:EBFI.0000022877.38588.f1.

Ricker, W.E. 1954. Stock and recruitment. J. Fish. Res. Board Canada 11: 559-623. doi:10.1139/f54-039.

Rousset, F. 2008. GENEPOP'007: A complete re-implementation of the GENEPOP software for Windows and Linux. Mol. Ecol. Res. 8, 103–106. doi:10.1111/j.1471-8286.2007.01931.x.

Rogers, K.B., and G.C. White. 2007. Analysis of movement and habitat use from telemetry data. Pp 625-676, in Analysis and Interpretation of Freshwater Fisheries Data C.S. Guy and M.L. Brown (eds). American Fisheries Society. Bethesda, MD.

Rusak, J.A. and, Mosindy, T. 1997. Seasonal movements of lake sturgeon in Lake of the Woods and the Rainy River, Ontario. Can. J. Zool. 75: 383-395. doi:10.1139/z97-048.

Savoy, T., and Pacileo, D. 2003. Movements and important habitats of subadult Atlantic sturgeon in Connecticut waters. Tran. Amer. Fish. Soc. 132: 1-8. doi: 10.1577/1548-8659(2003)132<0001:MAIHOS>2.0.CO;2.

Schwartz, M.K., Luikart, G., and Waples, R.S. 2007. Genetic monitoring as a promising tool for conservation and management. Trends Ecol. Evol. 22: 25-33. doi:10.1016/j.tree.2006.08.009.

Schindler, D.E., Hilborn, R., Chasco, B., Boatright, C.P., Quinn, T.P., Rogers, L.A., and Webster, M.S. 2010. Population diversity and the portfolio effect in an exploited species. Nature 465, 609-612. https://doi.org/10.1038/nature09060.

Scribner, K.T., Tsehaye, I., Brenden, T., Stott, W., Kanefsky, J., and Bence, J. 2018. Hatchery strain contributions to emerging wild lake trout populations in Lake Huron. J. Hered. 109: 675–688. doi.org/10.1093/jhered/esy029.

Seeb, L.W., Habicht, C., Templin, W.D., Tarbox, K.E., Davis, R.Z., Brannian, L.K., and Seeb, J.E. 2000. Genetic diversity of sockeye salmon of Cook Inlet, Alaska, and its application to management of populations affected by the *Exxon Valdez* oil spill. Tran. Amer. Fish. Soc, 129: 1223–1249. doi:10.1577/1548-8659.

Shaklee, J.B., Beacham, T.D., Seeb, L.W., and White, B.A. 1999. Managing fisheries using genetic data: case studies from four species of Pacific salmon. Fish. Res. 43: 45- 78. doi: 10.1016/S0165-7836(99)00066-1.

Stabile J, Wildman, J.R., Parauka, F., and Wirgin, I. 1996. Stock structure and homing fidelity in Gulf of Mexico sturgeon (*Acipenser oxyrhinchus desotoi*) based on restriction fragment length polymorphism and sequence analysis of mitochondrial DNA. Genetics. 144: 767-775. doi:10.1093/genetics/144.2.767.

Stephenson, R.L. 1999. Stock complexity in fisheries management: a perspective of emerging issues related to population sub-units. Fish. Res. 43: 247–249. doi:10.1016/S0165-7836(99)00076-4.

Trenham, P.C., Shaffer, H.B., Koenig, W.D. and Stromberg, M.R. 2000. Life history and demographic variation in the California tiger salamander *(Ambystoma californiense).* Copeia*,* 2000: 365-377. doi:10.1643/0045-8511.

Tsehaye, I., Brenden, T.O., Bence, J.R., Liu, W., Scribner, K.T., Kanefsky, J., Bott, K., and Elliott, R.F. 2016. Combining genetics with age/length data to estimate consistent changes in year-class strength of spawning populations contributing to admixtures, with application to Lake Michigan lake sturgeon. Fish. Res. 173: 236-249. doi:10.1016/j.fishres.2015.09.004.

Tucker, S.R., Houghton, C.J., Harris, B.S., Elliott, R.F., Donofrio, M.C., and Forsythe, P.S. 2021. Reproductive status of a remnant Lake sturgeon (Acipenser fulvescens) population: Spawning and larval drift in the lower Fox River, Wisconsin. River Res Appl. doi.org/10.1002/rra.3836.

United States Environmental Protection Agency, Office of Water. 1990. The Green Bay Mass Balance Project.

Vandergoot, C.S., and Brenden, T.O. 2014. Spatially-varying population demographics and fishery characteristics of Lake Erie walleye (*Sander vitreus*) inferred from a long-term tag-recovery study. Tran. Amer. Fish. Soc. 143: 188-204. doi:10.1080/00028487.2013.837095.

Walters C.J., and Juanes, F. 1993. Recruitment limitation as a consequence of natural selection for use of restricted feeding habitats and predation risk taking by juvenile fishes. Can. J. Fish. Aquat. Sci. 50: 2058-2070. doi:10.1139/f93-229.

Webb, M.A.H., Van Eenennaam, J.P., Crossman, J.A., and Chapman, F.A. 2019. A partial guide for assigning sex and stage of maturity in sturgeons and paddlefish. J. Appl. Ichthy. 35: 169-186. doi:10.1111/jai.13582.

Welsh, A.B., Blumberg, M., and May, B. 2003. Identification of microsatellite loci in lake sturgeon, *Acipenser fulvescens*, and their variability in green sturgeon, *A. medirostris*. Mol. Ecol. Notes. 3: 47-55. doi:10.1046/j.1471-8286.2003.00346.x.

Weir, B.S., and Cockerham, C.C. 1984. Estimating *F*-statistics for the analysis of population structure. Evolution 38: 1358-1370. doi:10.2307/2408641.

Whitlock, R., Mäntyniemi, S., Palm, S., Koljonen, M.-L., Dannewitz, J., and Östergren, J. 2018. Integrating genetic analysis of mixed populations with a spatially explicit population dynamics model. Methods Ecol. Evol. 9: 1017-1035. doi:10.1111/2041-210X.12946.

Wooley, C.M., and Crateau, E.J. 1985. Movement, microhabitat, exploitation, and management of Gulf of Mexico sturgeon, Apalachicola River, Florida. N. Amer. J. Fish. Manage. 5: 590–605. doi:10.1577/1548-8659.

Figure Legends

Figure 1. Map presented on a hierarchical scale showing Lake Sturgeon open-water sampling locations and regions in (A) Green Bay, (B) regional sampling locations across the Lake Michigan basin including Green Bay (GB), EastCentral (EC), SouthEast (SE), Northern (N), and the (C) Great Lakes.

Figure 2. Results from leave-one-out cross-validation simulations evaluating the expected accuracy in estimated spawning population contributions for mixtures composed of lake sturgeon from the Lake Michigan spawning populations evaluated in this study. Mixture compositions were generated randomly from Dirichlet populations with concentration parameters set to 1.5. Accuracy was evaluated by calculated mean (Mean AD) and maximum (Max. AD) absolute deviations between estimated and simulated contributions.

Figure 3. Frequency histograms characterizing distributions of total body length (cm) for lake sturgeon sampled in different regions in the Lake Michigan basin.

Figure 4. Estimated age-specific selectivities (i.e., relative vulnerabilities) to the sampling gear of lake sturgeon in Green Bay open-water and nearshore areas. Selectivities were estimated using an additive combination of logistic and normal selectivity functions (equation shown). Point estimates of the selectivity function parameters are provided as are the 95% profile likelihood confidence intervals for the parameters (values in parenthesis).

Figure 5. Results from sensitivity analyses assessing how estimates of the relative recruitment change (*b*) parameter were affected by deviations from assumptions about growth, mortality, and movement.

Table 1. Pair-wise estimates of inter-population variance in allele frequency (F_{st}) for baseline adult spawning populations of lake sturgeon in tributaries to Lake Michigan.

	Western Basin Tributaries (Wisconsin)			(Eastern Basin Tributaries (Michigan)		
	Fox River	Oconto/Pestigo Rivers	Menomenee River	Manistee River	Muskegon River	Kalamazoo River
Tributary	72[a]	122[a]	65[a]	106[a]	98[a]	70[a]
Fox River		0.017	0.044	0.044	0.052	0.136
Oconto/Pestigo Rivers			0.033	0.043	0.061	0.139
Menomenee River				0.059	0.081	0.148
Manistee River					0.047	0.128
Muskegon River						0.066
Kalamazoo River						

[a] Baseline sample size.

All pair-wise F_{st} estimates signficant at $P<0.01$ following Bonferroni correction for multiple testing.

Table 2. Likelihood estimates of mixture heterogeniety (Reynolds and Templin 2004) for regional mixture composition comparisons (A) and among groups from within Green Bay (B). Locations shown in Figure 1.

A. Regions of the entire Lake Michigan Basin

Mixture comparison	Null Likelihood	General Likelihood	Likelihood Ratio	No. Groups Compared	df	P-value	Conclusion: mixture compositional comparison	Interpretation
All regions pooled	-19300.3	-19086.798	213.502	4	15	0	Reject	All regions do not have the same population contributions
Ecentral (EC) vs Green Bay (GB)	-17246.8	-17080.8	166	2	5	0	Reject	Ecentral and GB do not have the same population contributions
Ecentral (EC) vs Northern (N)	-3235.79	-3187.08	48.71	2	5	2.54E-09	Reject	Ecentral and Northern do not have the same population contributions
Ecentral (EC) vs SE	-2920.43	-2915.718	4.712	2	5	4.52E-01	Fail to Reject	Cannot say that Ecentral and SE do not have the same population contributions
Green Bay (GB) vs Northern (N)	-16183.3	-16171.08	12.22	2	5	3.19E-02	Fail to Reject	Cannot say that GB and Northern do not have the same population contributions
GB vs SE	-15967.3	-15899.718	67.582	2	5	3.26E-13	Reject	GB and SE do not have the same population contribution
Northern (N) vs SE	-2027.5	-2005.998	21.502	2	5	6.51E-04	Reject	Northern and SE do not have the same population contributions

Bonferonni corrected alpha = 0.007

B. Aggregated Groups within Green Bay, WI

Mixture Comparision	Null Likelihood	General Likelihood	Likelhood Ratio	No. Groups Compared	df	P-value	Conclusion	Interpretation
Pooled	-14452.4	-14420.64	31.76	4	15	0.0069	Reject	All regions do not have the same population contributions
North vs South	-6074.24	-6048.98	25.26	2	5	0.0001	Reject	North and South do not have the same population contributions
North vs CentralA	-9367.64	-9349.53	18.11	2	5	0.0028	Reject	North and CentralA do not have the same population contributions
North vs CentralB	-4184.32	-4177.51	6.81	2	5	0.2352	Fail to Reject	Cannot say that North and CentralB do not have the same population contributions
South vs CentralA	-10248.6	-10243.13	5.47	2	5	0.3612	Fail to Reject	Cannot say that South and CentralA do not have the same population contributions
South vsCentralB	-5078.72	-5071.11	7.61	2	5	0.1791	Fail to Reject	Cannot say that South and CentralB do not have the same population contributions
CentralA vs CentralB	-8373.14	-8371.66	1.48	2	5	0.9154	Fail to Reject	Cannot say that CentralA and CentralB do not have the same population contributions

Bonferonni corrected alpha = 0.007

Table 3. Estimates and 95% confidence intervals of proportional population contributions to mixtures in different regions of Green Bay. Estimates are derived for all samples and according to body size categories generally corresponding to sub-adults (<110cm) and adults (≥110cm) based on total length. Locations are described in Figure 1.

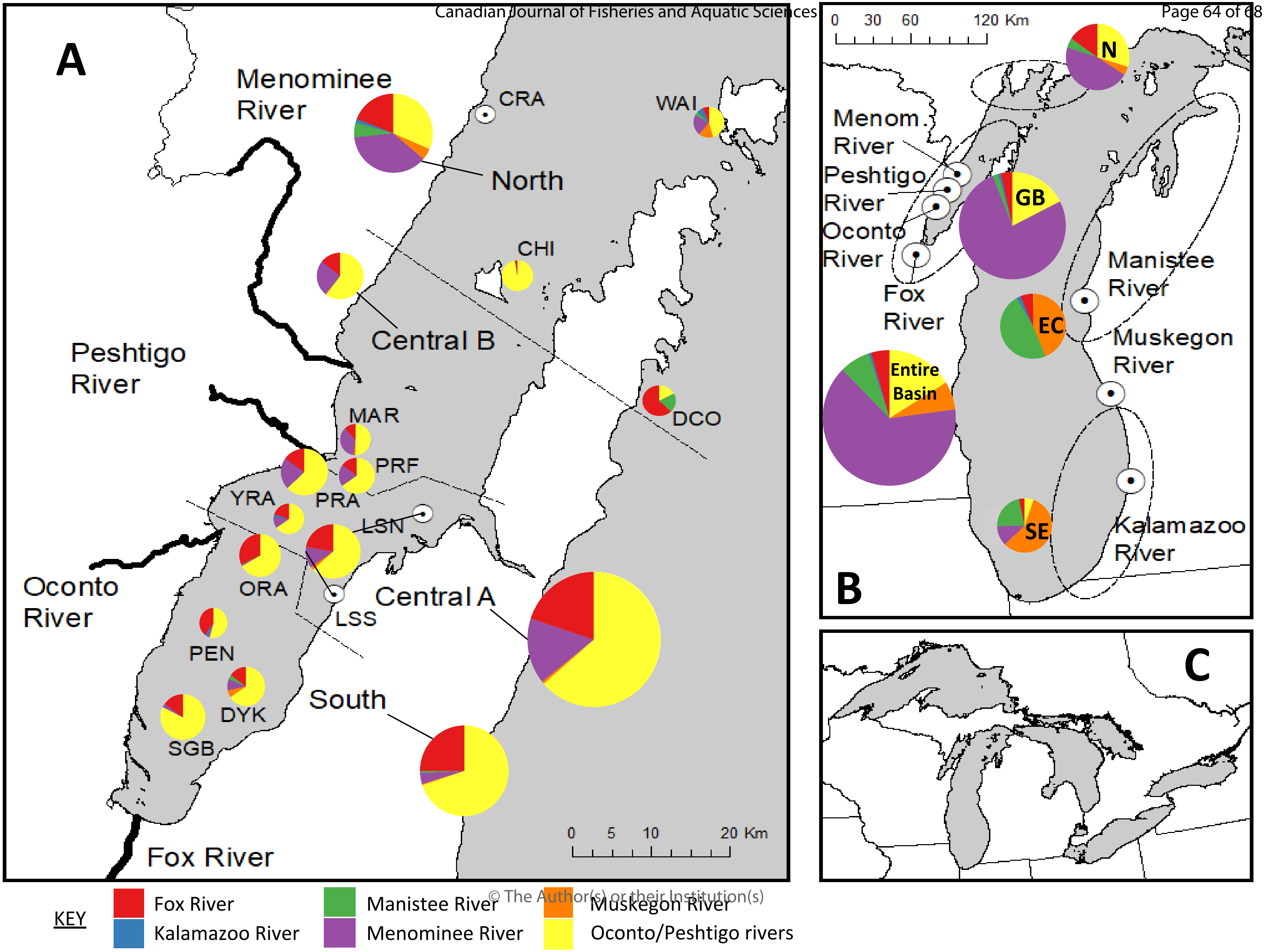
		Population					
		Western Basin Tributaries (Wisconsin)			Eastern Basin Tributaries (Michigan)		
Aggregate Group	Size group	Fox	Menomenee	Oconto/Pesh	Manistee	Muskegon	Kalamazoo
South	All	0.252	0.039	0.699	0.007	0.004	0.000
		(0.158 - 0.345)	(0.0 - 0.078)	(0.606 - 0.797)	(0.0 - 0.013)	(0.0 - 0.007)	(0.0 - 0.0)
	≥110mm	0.382	0.058	0.558	0.001	0.000	0.000
		(0.226 - 0.543)	(0.0 - 0.116)	(0.385 - 0.758)	(0.0 - 0.0026)	(0.0 - 0.0)	(0.0 - 0.0)
	<110 mm	0.157	0.036	0.787	0.009	0.012	0.000
		(0.041 - 0.269)	(0.0 - 0.071)	(0.671 - 0.912)	(0.0 - 0.018)	(0.0 - 0.023)	(0.0 - 0.0)
CentralA	All	0.200	0.157	0.637	0.000	0.006	0.000
		(0.141 - 0.253)	(0.111 - 0.201)	(0.568 - 0.708)	(0.0 - 0.0)	(0.0 - 0.012)	(0.0 - 0.001)
	≥110mm	0.201	0.177	0.621	0.000	0.000	0.002
		(0.130 - 0.266)	(0.110 - 0.232)	(0.539 - 0.703)	(0.0 - 0.0)	(0.0 - 0.0)	(0.0 - 0.003)
	<110 mm	0.194	0.106	0.655	0.002	0.044	0.000
		(0.070 - 0.301)	(0.028 - 0.182)	(0.522 - 0.788)	(0.0 - 0.004)	(0.0 - 0.086)	(0.0 - 0.0)
CentralB	All	0.141	0.251	0.603	0.000	0.005	0.000
		(0.029 - 0.254)	(0.134 - 0.363)	(0.463 - 0.759)	(0.0 - 0.0)	(0.0 - 0.009)	(0.0 - 0.0)
	≥110mm	0.171	0.283	0.519	0.000	0.027	0.000
		(0.002 - 0.320)	(0.136 - 0.420)	(0.326 - 0.727)	(0.0 - 0.0)	(0.0 - 0.054)	(0.0 - 0.0)
	<110 mm	0.089	0.188	0.723	0.000	0.000	0.000
		(0.0 - 0.1781)	(0.0 - 0.371)	(0.523 - 0.959)	(0.0 - 0.0)	(0.0 - 0.0)	(0.0 - 0.0)
North	All	0.194	0.377	0.304	0.069	0.039	0.017
		(0.083 - 0.288)	(0.272 - 0.479)	(0.188 - 0.417)	(0.003 - 0.136)	(0.0 - 0.078)	(0.0 - 0.034)
	≥110mm	0.285	0.433	0.193	0.051	0.039	0.000
		(0.1434 - 0.421)	(0.280 - 0.566)	(0.035 - 0.336)	(0.0 - 0.101)	(0.0 - 0.077)	(0.0 - 0.0)
	<110 mm	0.036	0.305	0.486	0.098	0.029	0.046
		(0.0 - 0.071)	(0.139 - 0.462)	(0.299 - 0.697)	(0.0 - 0.196)	(0.0 - 0.057)	(0.0 - 0.092)

Table 4. Estimates and 95% confidence intervals of proportional population contributions to mixtures collected during the spring and fall in the river mouths and adjacent areas of the Menominee River and Pestigo/Oconto Rivers during the spring and fall over the period 2001-2008.

			Populations					
			Western Basin Tributaries (Wisconsin)			Eastern Basin Tributaries (Michigan)		
Near-shore and river mouth sampled	Season sampled	Sample size	Fox River	Menomenee River	Oconto/Peshtigo Rivers	Manistee River	Muskegon River	Kalamazoo River
Menominee	Combined	758	0.032	0.850	0.108	0.002	0.000	0.009
			(0.008 - 0.050)	(0.816 - 0.887)	(0.079 - 0.143)	(0.0 - 0.004)	(0.0 - 0.0)	(0.0 - 0.018)
	Spring	73	0.006	0.856	0.104	0.000	0.014	0.021
			(0.0 - 0.011)	(0.766 - 0.950)	(0.017 - 0.189)	(0.0 - 0.0)	(0.0 - 0.028)	(0.0 - 0.041)
	Fall	685	0.035	0.848	0.107	0.003	0.000	0.007
			(0.009 - 0.056)	(0.812 - 0.884)	(0.069 - 0.141)	(0.0 - 0.006)	(0.0 - 0.0)	(0.0 - 0.014)
Oconto/Peshtigo	Combined	210	0.054	0.408	0.533	0.006	0.000	0.000
			(0.0 - 0.104)	(0.327 - 0.492)	(0.440 - 0.627)	(0.0 - 0.011)	(0.0 - 0.0)	(0.0 - 0.0)
	Spring	51	0.051	0.428	0.510	0.012	0.000	0.000
			(0.0 - 0.101)	(0.326 - 0.523)	(0.397 - 0.618)	(0.0 - 0.023)	(0.0 - 0.0)	(0.0 - 0.0)
	Fall	159	0.058	0.345	0.597	0.000	0.000	0.000
			(0.0 - 0.115)	(0.176 - 0.509)	(0.423 - 0.775)	(0.0 - 0.0)	(0.0 - 0.0)	(0.0 - 0.0)

Table 5. Estimates of relative recruitment parameters for baseline tributary spawning populations of lake sturgeon from Green Bay in the Lake Michigan Basin.

Basin Region	Baseline Population	Log alpha	95% LCL	95% UCL	Beta	95% LCL	95% UCL	Final Year Recruitment	95% LCL	95% UCL
Western Basin	Fox	7.201	3.698	9.853	0.084	0.005	0.196	10.983	7.010	15.316
	Menominee	4.328	1.731	6.556	0.266	0.186	0.369	16.276	11.821	21.035
	Oconto/Peshtigo	1.804	-0.983	4.140	0.350	0.258	0.464	17.542	12.961	22.510
Eastern Basin	Manistee	-0.630	-6.720	8.000	0.302	-0.342	0.543	12.963	-5.178	17.909
	Muskegon	-7.549	-11.235	5.945	0.519	-0.020	0.634	15.796	6.175	18.684
	Kalamazoo	-5.154	-11.438	3.408	0.437	-0.027	0.664	14.522	3.997	18.755


A
Menominee River
CRA
WAI
North
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DCO
MAR
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LSN
ORA
Oconto River
Central A
LSS
PEN
DYK
SGB
South
0 5 10 20 Km
Fox River
B
0 30 60 120 Km
N
Menom. River
Peshtigo River
Oconto River
Fox River
GB
Manistee River
EC
Muskegon River
Entire Basin
Kalamazoo River
SE
C
KEY
🟥 Fox River
🟦 Kalamazoo River
🟩 Manistee River
🟪 Menominee River
🟧 Muskegon River
🟨 Oconto/Peshtigo rivers

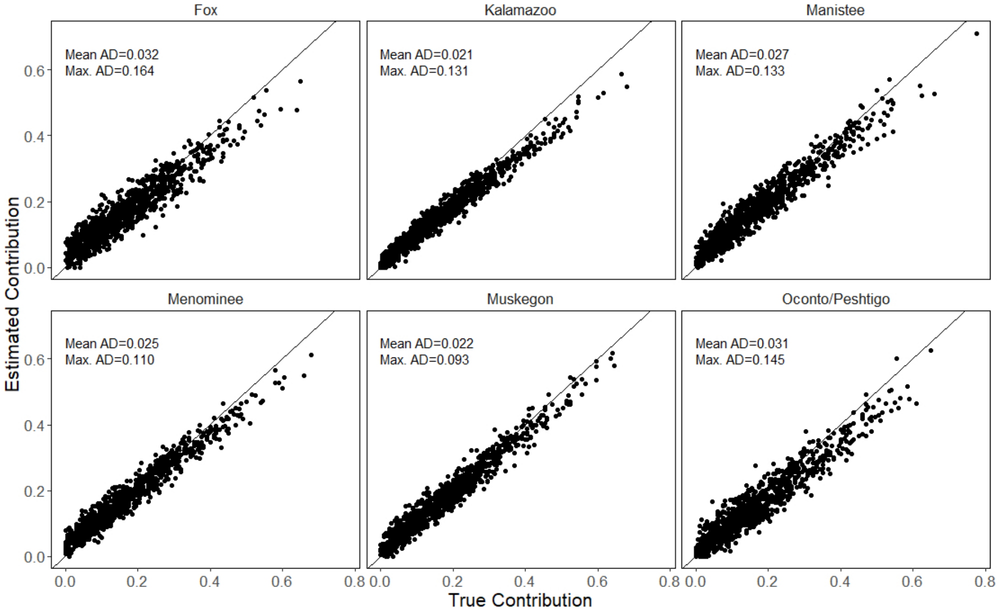


Figure 2. Results from leave-one-out cross-validation simulations evaluating the expected accuracy in estimated spawning population contributions for mixtures composed of lake sturgeon from the Lake Michigan spawning populations evaluated in this study. Mixture compositions were generated randomly from Dirichlet populations with concentration parameters set to 1.5. Accuracy was evaluated by calculated mean (Mean AD) and maximum (Max. AD) absolute deviations between estimated and simulated contributions.

392x245mm (72 x 72 DPI)

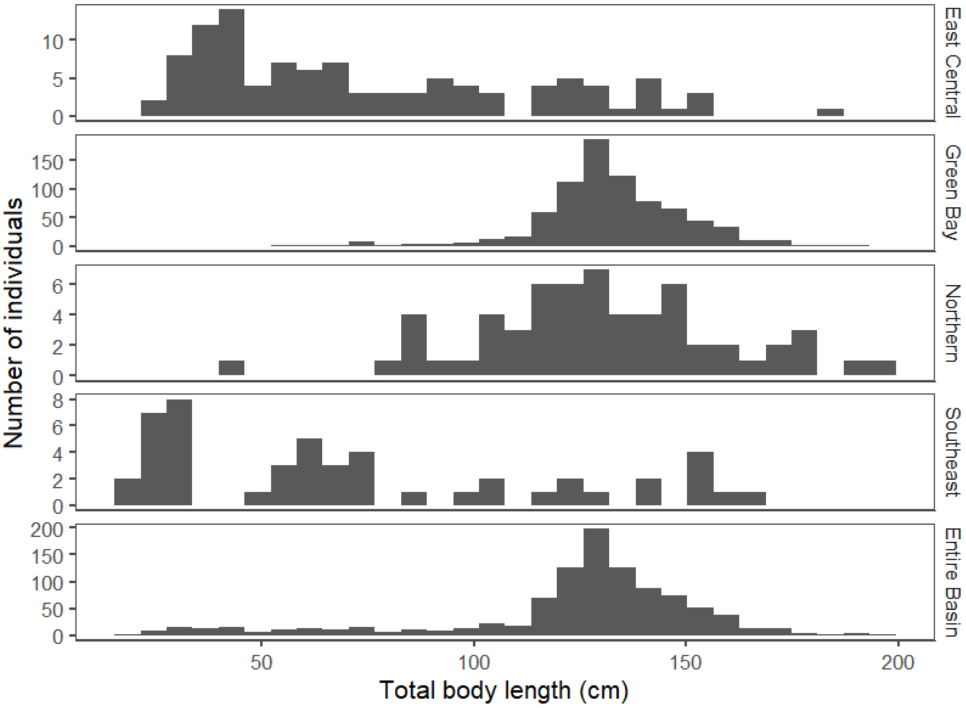
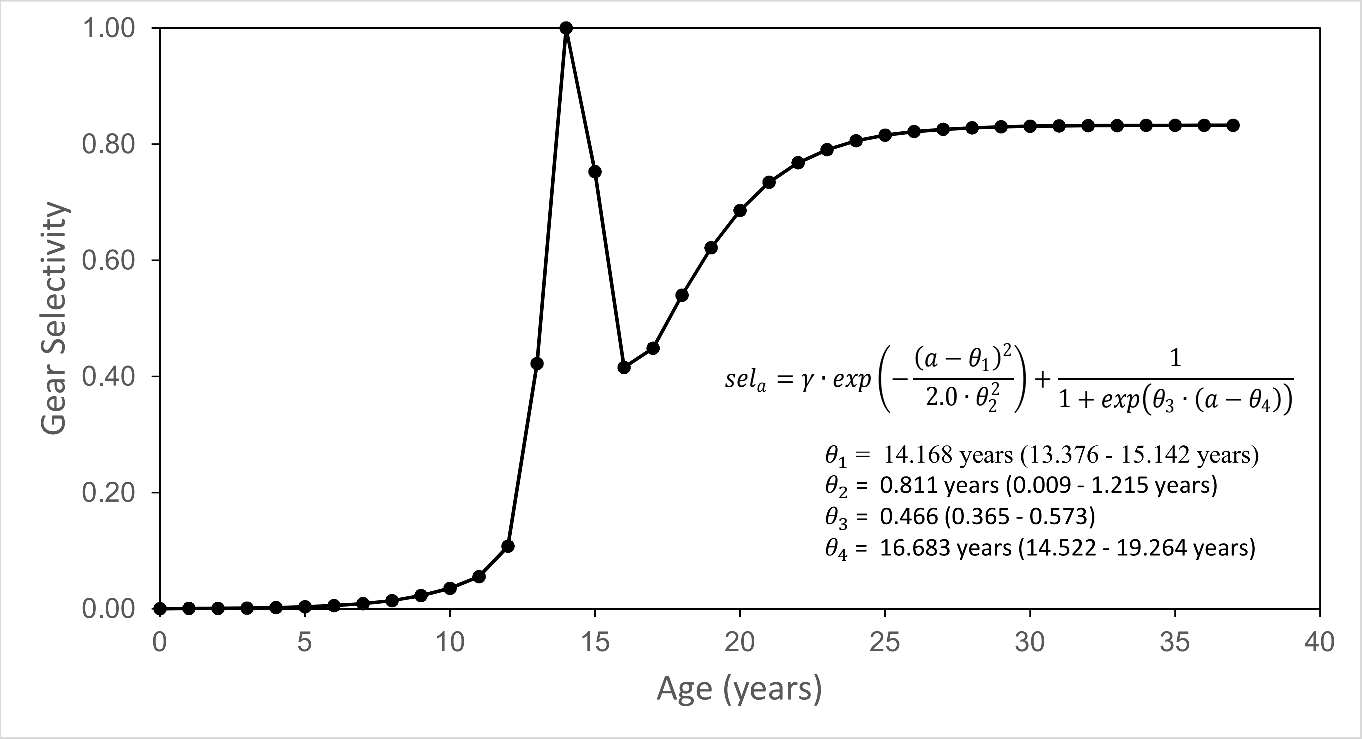
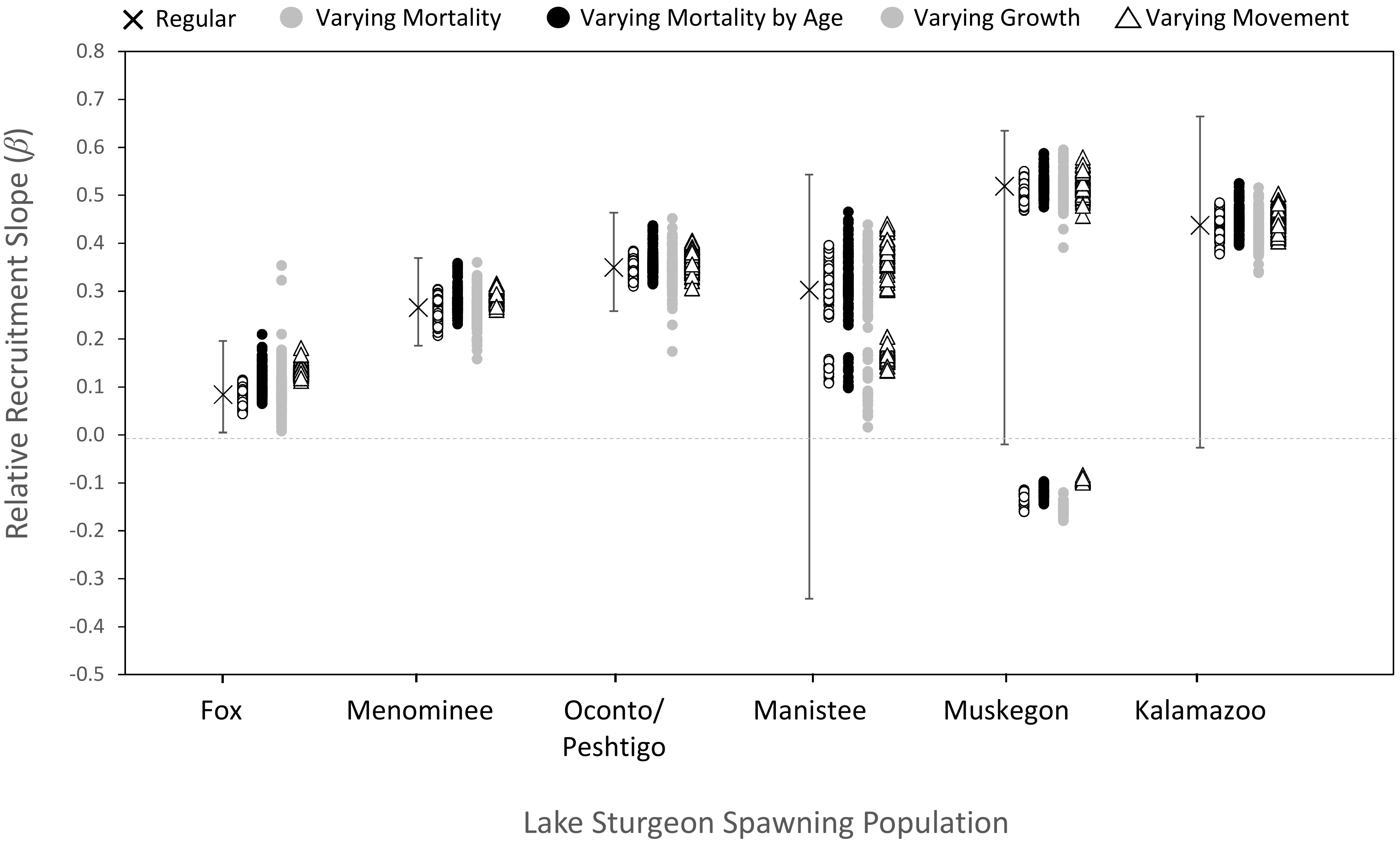


Figure 3. Frequency histograms characterizing distributions of total body length (cm) for lake sturgeon sampled in different regions in the Lake Michigan basin.

549x397mm (38 x 38 DPI)


1.00
0.80
0.60
0.40
0.20
0.00
Gear Selectivity
0
5
10
15
20
25
30
35
40
Age (years)
$sel_a = \gamma \cdot exp\left(-\frac{(a-\theta_1)^2}{2.0 \cdot \theta_2^2}\right) + \frac{1}{1+exp\big(\theta_3 \cdot (a-\theta_4)\big)}$
θ_1 = 14.168 years (13.376 - 15.142 years)
θ_2 = 0.811 years (0.009 - 1.215 years)
θ_3 = 0.466 (0.365 - 0.573)
θ_4 = 16.683 years (14.522 - 19.264 years)


× Regular
● Varying Mortality
● Varying Mortality by Age
● Varying Growth
△ Varying Movement
Relative Recruitment Slope (β)
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
-0.1
-0.2
-0.3
-0.4
-0.5
Fox
Menominee
Oconto/ Peshtigo
Manistee
Muskegon
Kalamazoo
Lake Sturgeon Spawning Population