Fisheries Research 173 (2016) 236–249

Contents lists available at ScienceDirect

Fisheries Research

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

Combining genetics with age/length data to estimate temporal changes in year-class strength of source populations contributing to mixtures

Iyob Tsehaye[a,*], Travis O. Brenden[a], James R. Bence[a], Weihai Liu[a], Kim T. Scribner[b], Jeannette Kanefsky[b], Kristin Bott[b], Robert F. Elliott[c]

[a] *Quantitative Fisheries Center, Department of Fisheries and Wildlife, Michigan State University, 293 Farm Lane, Room 153, East Lansing, MI 48824, USA*
[b] *Department of Fisheries and Wildlife, Michigan State University, 480 Wilson Road, Room 13, East Lansing, MI 48824, USA*
[c] *U.S. Fish and Wildlife Service, Green Bay Fish and Wildlife Conservation Office, 2661 Scott Tower Drive, New Franken, WI 54229, USA*

ARTICLE INFO

Article history:
Received 29 April 2015
Received in revised form 1 September 2015
Accepted 8 September 2015
Available online 26 September 2015

Keywords:
Age/length based genetic stock identification (GSI)
Mixed stock
Relative year-class strength
Recruitment
Lake sturgeon
Great Lakes
Stock assessment
Bayesian methods

ABSTRACT

We developed an approach for estimating changes in relative year-class strength of source populations contributing to mixtures by incorporating ages or lengths of mixture individuals in genetic stock identification models. The approach is intended for long-lived fishes with high pre-recruitment and low post-recruitment mortality rates for which consistent temporal changes in recruitment can be assumed. Age- and collection-year specific contributions of sources to the mixture are modeled as linear functions of two source-specific parameters: an intercept representing relative recruitment for the first modeled year class and a slope representing how relative recruitment changes annually. Based on simulations, the estimation approach performed reasonably well under diverse conditions, including varying numbers of sources, levels of genetic divergence among sources, degrees of change in year-class strength, durations and frequencies of sampling from mixtures, age ranges of individuals from mixtures, and sample sizes from mixtures. The estimation approach was also robust to aging error and uncertainty in length-age relationships. We applied the approach to genetic and length data for lake sturgeon *Acipenser fulvescens* from Green Bay, Lake Michigan, collected from 2002 to 2008, with sources corresponding to five Lake Michigan tributaries. Two of the Lake Michigan sources showed declining recruitment levels, whereas the other three sources showed increasing recruitment levels. We believe our proposed approach for indexing changes in year-class strength shows promise as a tool for identifying sources potentially at risk due to declining recruitment and for relating changes in recruitment to biotic or abiotic factors.

1. Introduction

Understanding variation in recruitment of fish populations is critical for effective fisheries management (Hilborn and Walters, 1992; Miller, 2007; Ludsin et al., 2014). The ability to accurately assess recruitment provides important information concerning long-term population viability as well as sustainable harvest levels for populations. However, assessing recruitment patterns can be difficult because of typically high inter-annual variability that can result from an array of factors (Ludsin et al., 2014). Assessing recruitment patterns becomes even more difficult when individuals from multiple spawning populations (hereafter referred to as sources) intermix during non-spawning periods (hereafter referred to as mixtures), as it can be difficult to trace individuals back to their sources (Guan et al., 2013; Li et al., 2015). Mixtures commonly occur in both marine and freshwater systems and can arise naturally as a result of a species life history (Morishima and Henry, 1999; Waldman et al., 2014) or as a consequence of natural or anthropogenic disturbances (Ebener et al., 2010). One of the challenges in managing fisheries that exploit mixtures is designing policies that take advantage of abundant sources without jeopardizing those that are less abundant and/or productive (Ricker, 1958, 1973; Hutchings, 1996, 2000; Stephenson, 1999; Frank and Brickman, 2000). Thus, understanding mixture composition and how it changes in space and time is considered critical for successful management of mixtures (Ruzzante et al., 2000; Manel et al., 2005; Beacham et al., 2012). The development of a new method that

---

* Corresponding author. Present Address: Wisconsin Department of Natural Resources, 2801 Progress Road, Madison, WI 53716, USA.
E-mail addresses: tsehaye@msu.edu, iyob.tsehaye@wisconsin.gov (I. Tsehaye).

http://dx.doi.org/10.1016/j.fishres.2015.09.004
0165-7836/Published by Elsevier B.V.

extracts previously unavailable information on year-class recruitment from genetic and length/age data can contribute to a better understanding of recruitment dynamics in mixtures.

Model-based genetic stock identification (GSI) analyses have been used to provide compositional estimates of mixtures to inform fisheries management for numerous species, including Atlantic cod *Gadus morhua* (Ruzzante et al., 2000), chum salmon *Oncorhynchus keta* (Seeb et al., 2004), sockeye salmon *Oncorhynchus nerka* (Beacham and Wood, 1999; Dann et al., 2013), Chinook salmon *Oncorhynchus tshawytscha* (Manel et al., 2005; Hess and Narum, 2011; Rawding et al., 2014), walleye *Sander vitreus* (McParland et al., 1999; Gatt et al., 2003; Brenden et al., 2015a), lake trout *Salvelinus namaycush* (Marsden et al., 1989; Page et al., 2003), lake whitefish *Corgeonus clupeaformis* (Stott et al., 2012), and lake sturgeon *Acipenser fulvescens* (Bott et al., 2009). In some cases, GSI analyses have incorporated genetic markers that can be processed rapidly, providing a means for real-time monitoring of mixture composition so that fisheries can be closed or effort diverted to protect vulnerable sources from overharvest (Manel et al., 2005; Dann et al., 2013).

Model-based GSI analyses are based on finite mixture modeling whereby genotypes of individuals collected from mixtures along with genotype frequencies from sources are used to infer source contributions (Manel et al., 2005). There has been a growing tendency for model-based GSI analyses to incorporate information other than just genetics data to aid in the estimation of source contributions. Initial attempts at this involved incorporating phenotypic measurements of individuals from sources and mixtures and estimating source contributions using genetic and phenotypic measurement data jointly (Fournier et al., 1984). More recently, ecological covariates have been incorporated in model-based GSI analysis through a hierarchical Bayesian framework to inform the estimation of source contributions to mixtures (Okuyama and Bolker, 2005; Bjorndal and Bolten, 2008). A similar approach has also been used to estimate metapopulation contributions to newly formed colonies (Gaggiotti et al., 2004; Guo et al., 2008), which from an analytic standpoint shares much in common with GSI analyses. Moran et al. (2014) proposed blending the two previous methods (i.e., incorporating phenotypic measures and Bayesian hierarchical modeling) to both estimate source contributions to mixtures and make inferences regarding the distribution of phenotypic traits among sources. Methods for model-based GSI analyses have also expanded to account for other complexities, such as modeling source contributions to multiple mixtures (Bolker et al., 2007) and accounting for sampling error in the determination of allele frequencies in sources (Bolker et al., 2003).

Oftentimes, GSI analyses were conducted by pooling individuals across a range of ages and/or sampling years when there is no intention to assess annual changes in stock composition; thus, estimated contributions represent a type of average over ages and sampling years. However, source contributions to mixtures are a reflection of multiple demographic processes, including recruitment, mortality, and movement, and variations in any of these processes can lead to temporal variation in source contributions (Bjorndal and Bolten, 2008). So long as the effects of other confounding processes can be controlled or accounted for, temporal variation in source contributions may then be used to estimate changes in the demographic process or processes giving rise to the variations in source contribution. In this study, we sought to develop a method that could use the temporal variation in source contributions as a means to index changes in recruitment levels (i.e., year-class strengths) of sources contributing to mixtures. We were specifically interested in indexing changes in recruitment given its prominence in the fishery management process, and because recruitment is one of the most difficult demographic processes to measure (Hilborn and Walters, 1992). Information on how year-class strength of sources has changed temporally would aid in assessing source-specific susceptibility to overharvest as well as in identifying environmental or anthropogenic disturbances that may be responsible for the changes in recruitment (Fiksen and Slotte, 2002; Holt and Peterman, 2004).

In this study, we expanded model-based GSI methods to include age or length data of mixture individuals for estimating consistent changes in year-class strength of contributing sources. The specific approach described herein is intended for long-lived species that experience high pre-recruitment but low post-recruitment mortality rates. We explore through stochastic simulations how accuracy of our proposed approach is affected by factors such as mixture sample size and number of sources contributing to mixtures. We also explore sensitivity to factors such as aging uncertainty or uncertainty in age-length relationships when length is used as surrogate for age. We then demonstrate an application using genetic and length data collected from Lake Michigan lake sturgeon, a migratory species of conservation concern in the Laurentian Great Lakes for which lack of information on individual spawning populations has impeded the development of effective restoration programs (Bott et al., 2009).

2. Methods

2.1. Estimation methodology

For a regular model-based GSI analysis that does not account for age or length, the likelihood (ℓ) of observing mixture genotype samples (X) given proportional contributions of sources ($\boldsymbol{p}$) and allele relative frequencies at each locus and source ($\boldsymbol{Q}$) can be specified as

$$\ell\,(\mathrm{X}|\boldsymbol{Q},\boldsymbol{p})=\prod_{m=1}^{M}\sum_{i=1}^{I}p_i f(\mathrm{X}_{\mathrm{m}}|\boldsymbol{Q}_i), \tag{1}$$

where M is the total number of sampled fish from the mixture, I is the number of sources, p_i is an element of $\boldsymbol{p}$, and $f(\mathrm{X}_{\mathrm{m}}|\boldsymbol{Q}_i)$ denotes the expected frequency of individuals from the i-th source with the same genotype as the m-th observed individual from the mixture, which is determined from the allele relative frequencies estimated for the sources and assuming a particular genetic model f for determining genotype frequencies from allele frequencies (Pella and Milner, 1987; Pella and Masuda, 2001). Generally, expected genotype frequencies are calculated assuming Hardy–Weinberg equilibrium applies to each locus.

For inferring changes in year-class strength, we cannot rely on a single proportional contribution estimated for each source. Rather, we need to estimate a proportional contribution of each age class of each source. Thus, Eq. (1) is expanded to

$$\ell(\mathrm{X}|\boldsymbol{Q},\boldsymbol{P}^{\mathrm{ys}})=\prod_{m=1}^{M}\sum_{i=1}^{I}P_{i,a}^{\mathrm{ys}} f(\mathrm{X}_{\mathrm{m}}|\boldsymbol{Q}_i), \tag{2}$$

where X now consists of both the genotype and age of each individual from the mixture and we use $\boldsymbol{P}$ rather than $\boldsymbol{p}$ to indicate contributions to reflect the greater complexity of the contributions we are estimating. The sampling year (ys) superscripting on P and $\boldsymbol{P}$ in Eq. (2) reflects the fact that for each year of sampling from the mixture the source and age contributions are expected to change due to abundance differences caused by variation in recruitment and/or mortality. Thus, there will be a separate likelihood component for mixture sampling year. Despite the greater complexity, $\boldsymbol{P}^{\mathrm{ys}}$ still is defined on the simplex, meaning that the contributions across all sources and ages are greater than or equal to 0, less than or equal to 1, and the sum over all elements is 1.

For the purpose of indexing year-class strength changes of sources, we propose modeling the elements of $\boldsymbol{P}^{\text{ys}}$ via a population-specific process. To do this, we first express recruitment through a standard population growth function

$$N_{i,0}^{\text{yc}} = \alpha_i \exp(\beta_i \text{yc}), \tag{3}$$

where $N_{i,0}^{\text{yc}}$ is abundance at age 0 (or some other specified age of recruitment) for the i-th source and the yc-th year class, α_i is recruitment level for the i-th source for the first assessed year class (for which yc = 0), which is a function of the years that samples are collected and the age range of collected individuals from the mixtures, β_i represents the instantaneous rate of change in recruitment levels for the i-th source. After $\log_e$ transformation, this function is linearized to

$$\log_e(N_{i,0}^{\text{yc}}) = \log_e(\alpha_i) + \beta_i \text{yc}. \tag{4}$$

The determination of absolute source-specific recruitment is not possible based simply on composition of mixtures. As a result, it is necessary to impose a constraint on the $\log_e(\alpha_i)$ such that

$$\sum_i \log_e(\alpha_i) = 0, \tag{5}$$

This effectively redefines all recruitment levels in Eq. (4) as relative recruitments. Additionally, to reduce correlations among parameters, the average slope and deviations from that average are estimated, rather than the slope directly. Thus

$$\begin{aligned} &\beta_i = \bar{\beta} + \delta_i, \\ &\sum_i \delta_i = 0 \end{aligned} \tag{6}$$

where $\bar{\beta}$ is the overall mean instantaneous rate of change in year-class strength of the sources and δ_i are the source-specific deviations from the overall mean value, both of which are estimated quantities. Relative abundances at age of the sources can be projected assuming an exponential population model

$$N_{i,a}^{\text{yc}} = N_{i,0}^{\text{yc}} \exp\left(-\sum_{j=0}^{a-1} Z_{i,j}\right), \tag{7}$$

where $N_{i,a}^{\text{yc}}$ is the relative abundance at age a of the i-th source from the yc-th year-class, and $Z_{i,a}$ is the instantaneous total mortality for the i-th source at age a. Combining Eqs. (3) and (7) and taking the $\log_e$ transformation results in

$$\log_e(N_{i,a}^{\text{yc}}) = \log_e(\alpha_i) + \beta_i \text{yc} - \sum_{j=0}^{a-1} Z_{i,j}. \tag{8}$$

There is an inherent confounding between the β_i and the $Z_{i,a}$ so that these parameters cannot be simultaneously estimated without additional information. Our approach was to assume that external estimates of $Z_{i,a}$ were available, which could arise from an appropriately designed tagging study or some other assessment approaches.

When collections are made from a mixture in a particular sampling year, collected individuals represent a range of year classes with the range depending on the sampling year and ages of collected individuals. Consequently, the expected proportional contributions to the mixture from the i-th source for the a-th age class can be calculated

$$P_{i,a}^{\text{ys}} = \frac{N_{i,a}^{\text{ys}-a}}{\sum_{i=1}^{I} \sum_{a=\min(\text{age})}^{\max(\text{age})} N_{i,a}^{\text{ys}-a}}, \tag{9}$$

where min (age) and max (age) indicate the minimum and maximum age, respectively, in the mixture for which source contributions will be assessed and ys – a indexes the correct year class for the contributions. Under this formulation, the likelihood in Eq. (2) can be re-expressed as

$$\ell(\text{X}|\mathbf{Q}, \boldsymbol{\alpha}, \bar{\beta}, \boldsymbol{\delta}) = \prod_{m=1}^{M} \sum_{i=1}^{I} (P_{i,a}^{\text{ys}}|\boldsymbol{\alpha}, \bar{\beta}, \boldsymbol{\delta}) f(\text{X}_\text{m}|\mathbf{Q}_i). \tag{10}$$

Movement rates of sources to the mixture were not incorporated in any of the above descriptions as it is not necessary to know movement in order to estimate parameters. Rather, it is only necessary for movement to be constant both in time and across ages for the purpose of assessing year-class strength changes within sources. If movement rate estimates were available, they could be incorporated in Eq. (9) in a straightforward manner. One clear benefit of incorporating movement rates is that it would permit inter-source comparison of recruitment levels.

2.1.1. Incorporation of aging error

When fish are aged using bony structures (e.g., scales, otoliths, cleithra), there generally is uncertainty associated with assigned ages, with the potential for greater error for older ages of fish. Our formulation prior to this point has not addressed aging uncertainty. Here we expand the approach to account for such error. We assume there is an appropriately constructed aging error matrix for the aging structure and the populations under study

$$T_{a',a} = \frac{P(a'|a)}{\sum_{a'=\min(\text{age})}^{\max(\text{age})} P(a'|a)}, \tag{11}$$

where $P(a'|a)$ is the probability that an individual identified as being age a' is actually a. For additional discussion on construction of aging error matrices, see Richards et al. (1992). With aging error, the likelihood in Eq. (10) can be expressed as

$$\ell(\text{X}|\mathbf{Q}, \boldsymbol{\alpha}, \bar{\beta}, \boldsymbol{\delta}) = \prod_{m=1}^{M} \sum_{i=1}^{I} \sum_{j=\min(\text{age})}^{\max(\text{age})} T_{a',j} (P_{i,j}^{\text{ys}}|\boldsymbol{\alpha}, \bar{\beta}, \boldsymbol{\delta}) f(\text{X}_\text{m}|\mathbf{Q}_i). \tag{12}$$

Eq. (12) does not include parameters associated with the aging error matrix because we are treating these as fixed values for simplicity. In principle, we could include the aging error data and estimate parameters needed to construct the matrix along with the other parameters, which would require an extension to Eq. (12). Such an extension would be relatively straightforward, although this could lead to estimation difficulties.

2.1.2. Using length as a surrogate for age

For situations in which ages of fish from the mixture are not available, analyses can still be conducted based on lengths of individuals from the mixture if von Bertalanffy growth models, or some other growth functions, are available for each of the sources. The von Bertalanffy growth model with a multiplicative error structure can be expressed as

$$\begin{aligned} &L_a = L_\infty(1 - \exp(-\kappa(a - t_0)))\exp(\epsilon_{L_a}), \\ &\epsilon_{L_a} \sim N(0, \sigma_L^2) \end{aligned} \tag{13}$$

where L_a is length at age a, L_∞ is the asymptotic length, κ is the Brody growth coefficient, t_0 is the theoretical age at which length would be 0, and ϵ_{L_a} is a normally distributed error term. Under this specification, the likelihood of an individual of length L_m being age a can be expressed as

$$\ell(L_m) = N(\log_e(L_m)|\log_e(E(L_a)), \sigma_L^2), \tag{14}$$

where $E(L_a)$ is the expected length at a given age from Eq. (13). Therefore, the likelihood of the observations from the mixture given the unknown parameters can be expressed as

$$\ell(\mathrm{X}|\mathbf{Q},\boldsymbol{\alpha},\bar{\beta},\boldsymbol{\delta})=\prod_{m=1}^{M}\sum_{i=1}^{I}\sum_{j=\min(\mathrm{age})}^{\max(\mathrm{age})}T_{i,L_m,j}(P_{i,j}^{\mathrm{ys}}|\boldsymbol{\alpha},\bar{\beta},\boldsymbol{\delta})f(\mathrm{X}_\mathrm{m}|\mathbf{Q}_i)\quad(15)$$

where $T_{i,L_m,a}$ is the likelihood that the m-th individual of length L_m from the mixture is age a given that it is from the i-th source, which is calculated using Eq. (14).

2.2. *Model fitting approach*

We programmed an estimation procedure capable of fitting each of the models described above in AD Model Builder (Fournier et al., 2012). We elected to use a Bayesian approach for model fitting as it would better allow characterization of uncertainty of the parameter estimates describing the changes in recruitment of the sources contributing to the mixture. Under a Bayesian approach, the posterior probability distribution for the unknown parameters for the model can be specified as

$$\pi(\mathbf{Q},\boldsymbol{\alpha},\bar{\beta},\boldsymbol{\delta}|\mathrm{X},\mathrm{Y})\propto\ell(\mathrm{X}|\mathbf{Q},\boldsymbol{\alpha},\bar{\beta},\boldsymbol{\delta})\pi(\mathbf{Q}|\mathrm{Y})\pi(\log_e(\boldsymbol{\alpha}))\pi(\bar{\beta})\pi(\boldsymbol{\delta}),\quad(16)$$

where $\pi(\log_e(\boldsymbol{\alpha}))$, $\pi(\bar{\beta})$, and$\pi(\boldsymbol{\delta})$ are the prior probability distributions assigned to the parameters for assessing changes in relative recruitment strength of the sources, $\pi(\mathbf{Q}|\mathrm{Y})$ is the prior probability distribution for allele relative frequencies of the sources ($\mathbf{Q}$) given the collection and genotyping of individuals from the sources (Y), and $\ell(\mathrm{X}|\mathbf{Q},\boldsymbol{\alpha},\bar{\beta},\boldsymbol{\delta})$ is as defined in Eqs. (10), (12), or (15) depending on whether ages or lengths of individuals from the mixture is observed and whether aging error occurs.

Our specification of $\pi(\mathbf{Q}|\mathrm{Y})$ followed that of Rannala and Mountain (1997), although other specifications could also have been used. Thus, even though $\pi(\mathbf{Q}|\mathrm{Y})$ in Eq. (16) is presented as prior probability distributions, it is obtained as a posterior probability distribution from a separate analysis so that the distribution of $\mathbf{Q}$ was not updated as part of our GSI estimation model. As in Rannala and Mountain (1997), a Dirichlet probability density function was assumed for $\pi(\mathbf{Q}|\mathrm{Y})$. For the other prior probability distributions, $\log_e(\alpha_i)$ were assigned normal densities with means and standard deviations of 0 and 15, respectively, $\bar{\beta}$ were assigned normal densities with means standard deviations of 0 and 2, respectively, and δ_i were assigned uniform densities with lower and upper limits of −2.0 and +2.0, respectively. The intent here was for these priors to be weakly informative, so that when informative data were available the data would dominate the results.

2.3. *Evaluation of model performance and sensitivity*

Stochastic simulations were used to investigate the performance of our proposed estimation approach under a range of conditions. These simulations were used to generate source and mixture genotype data. Details of how we simulated source and mixture data are provided in Supplementary material 1. Briefly, all simulations assumed the same number of loci (15 loci), number of alleles per locus (10 alleles per locus), source sample size (100 fish), and total annual mortality rates for the sources ($Z_{i,a}=0.05$). The 0.05 total annual mortality rates assumed for all ages is close to what has been estimated for actual lake sturgeon populations in the Laurentian Great Lakes region (Baker, 1980; Nowak and Jessop, 1987; Bruch, 2008) and has been used in other simulation studies designed around lake sturgeon populations (Schueller and Hayes, 2010, 2011a,b). The age range of individuals from the mixed stock was assumed to be 0–37 based on lake sturgeon age composition data from Lake Michigan.

Table 1
Assumed $\log_e(\alpha_i)$ values for simulations involving 6, 12, or 24 sources for evaluating the accuracy/sensitivity of the proposed approach for indexing changes in recruitment levels of sources contributing to a mixture.

6 Sources	12 Sources	24 Sources	
0.83	0.78	0.88	−0.01
0.63	0.70	0.71	−0.04
0.39	0.60	0.70	−0.05
0.06	0.50	0.63	−0.13
−0.44	0.39	0.53	−0.25
−1.47	0.26	0.51	−0.33
	0.11	0.49	−0.41
	−0.07	0.35	−0.44
	−0.28	0.23	−0.54
	−0.55	0.09	−0.60
	−0.92	0.02	−0.96
	−1.52	0.01	−1.37

Model performance was evaluated under varying numbers of sources (2 levels: 6 or 12 sources), genetic differences among sources (3 levels: low, high, or varied [see Supplementary material 1]), degrees of change in year class strength (β) for the sources (3 levels: low, high, or varied [see Supplementary material 1]), mixture sampling durations (2 levels: 6 or 12 years), mixture sampling frequencies (3 levels: annual, every 2 years, or every 3 years), age ranges of mixture individuals (2 levels: 1–6 or 10–35), and mixture sample sizes (2 levels: 100 or 300 fish). The $\log_e(\alpha_i)$ values used to simulate data depended on the number of sources and were assumed constant across simulations (Table 1). Based on a full factorial design ($2\times3\times3\times2\times3\times2\times2$), we evaluated a total of 432 scenarios of factor-level combinations, using1000 simulations for each combination.

Given the total number of simulations conducted, it was not feasible time-wise to use Bayesian-based estimation routines that relied on Markov Chain Monte Carlo (MCMC) methods to characterize posterior probability distributions of estimated parameters. Therefore, for our analysis using simulated data, models were fit by highest posterior density estimation. Models were fit in AD Model Builder and were considered to have converged on a solution when the maximum gradient of the parameters with respect to the objective function was less than 1.0E-4.

Performance of the estimation approach for each of the 432 simulation scenarios was evaluated based on accuracy and precision when estimating $\log_e(\alpha_i)$, β_i, and the $\log_e$ relative recruitment for the last modeled year class of the sources, which we denote as $\log_e(N_{i,0}^{\mathrm{last}})$. For the $\log_e(\alpha_i)$ and $\log_e(N_{i,0}^{\mathrm{last}})$, relative errors [(estimate − true)/true)] were calculated for each iteration. For the β_i, we calculated absolute error (estimate − true) because these parameters were defined on a $\log_e$scale. The median and interquartile range (IQR) of the relative and absolute errors calculated across all iterations for a particular scenario were used as measures of accuracy and precision, respectively.

Sensitivity of the estimation program to aging error, uncertainty in age-length relationships when length is used as a surrogate for age, errors in estimates of Z, and an increase to higher number of sources was conducted to assess robustness of our proposed method. Sensitivity analyses were conducted assuming a mixture sampling duration of 6 years with annual collections. Specific details on how the sensitivity analyses were performed are provided in Supplementary material 1. Briefly, aging error matrices were constructed using the normal model approach of Richards et al. (1992); estimated ages were assumed to be unbiased but there were low to moderate levels of ageing noise corresponding to standard deviations in estimated ages of 0.10 and 0.20, respectively. For sensitivity scenarios using length as a surrogate for age, lengths of individuals in the admixture were randomly generated from a normal distribution with a CV = 10% and von Bertalanffy growth parameters of $L_\infty = 184.1$ cm, $k = 0.0755$, and $t_{0=} -2.365$ yrs. For sensitivity to total mortality, we considered two scenarios: random noise and source-specific bias (see Supplementary material 1 for details). For the high number of sources, we increased the number of sources to 24 (see Table 1 for the $\log_e(\alpha_i)$ values assumed for each source). Sensitivity was evaluated based on relative error in $\log_e(\alpha_i)$ and $\log_e(N_{i,0}^{\text{last}})$ estimates and absolute error in the β_i estimates.

2.4. Application to Lake Michigan lake sturgeon

The Lake Michigan lake sturgeon mixture data consisted of genetic information from a total of 720 lake sturgeon collected from Green Bay by U.S. Fish and Wildlife Service and Wisconsin Department of Natural Resources researchers and commercial fishers using trap nets and gill nets from 2002 to 2007. Commercial fishers were generally targeting either lake whitefish (*C. clupeaformis*) or yellow perch (*Perca flavescens*), so captured lake sturgeon were by-catch and fishers were required to release the fish. Trap nets varied in dimensions but all had leads of approximately 300 m and pot mesh sizes of 11.43 cm. Commercial gill net mesh size ranged from 6.35 to 11.43 cm. Graded mesh research gill nets targeting lake sturgeon were 20.23–35.56-cm stretch mesh. Nets were deployed throughout the calendar year, although the majority of samples came from collections in the spring and early summer. A total mixture sample size of 754 was available (2002: $n = 53$, 2003: $n = 197$, 2004: $n = 74$; 2005: $n = 303$; 2006: $n = 93$; 2007: $n = 27$). The source data came from fish collected from five Lake Michigan tributaries: Fox ($n = 65$), Peshtigo ($n = 115$), Menominee ($n = 64$), Muskegon ($n = 53$), and Manistee ($n = 97$) Rivers (Fig. 1).

Fin clip tissue samples were obtained from all mixture and source lake sturgeon. Detailed descriptions of the locus-specific PCR amplification and genotyping of tissue samples from the mixture and sources are provided in DeHaan et al. (2006), Bott et al. (2009), and Scribner et al. (2010). Briefly, tissue samples were genotyped at 12 microsatellite loci: *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, 2004). The number of alleles per locus ranged from 2 to 12. Potential strays (i.e., individuals that strayed from a presumed natal stream to a different stream at the time of spawning) were identified as described in Homola et al. (2012) and removed from the source datasets. Mean pairwise F_{ST} values between sources ranged from 0.03 to 0.07 (Supplementary material 2). Mixture simulations of the genotype data for the Lake Michigan sources indicated that there was a high degree of confidence (>90%) in differentiating among the sources based on existing genetics data (Supplementary material 2).

Ages of lake sturgeon from Green Bay, Lake Michigan were not available, so we used the length-based model to analyze changes in year-class strengths of the five Lake Michigan tributaries. 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 $L_\infty = 181.46$ cm, $k = 0.079$, $t_0 = -2.023$ yrs, and $\sigma_{\epsilon_L} = 0.109$ was used to convert lengths of fish in mixture samples to ages. Based on the resulting ages, we used an age range of 0–37 years for assessing recruitment changes. Given this age range and that the first year of collection from the mixture was 2002, the first modeled year class corresponded to 1965 whereas the last modeled year class corresponded to 2007.

The Lake Michigan lake sturgeon model was fit using a Bayesian approach. To assess uncertainty in parameter estimates, posterior distributions for parameters and derived variables were obtained by MCMC simulations with a Metropolis Hastings algorithm (Fournier et al., 2012). The MCMC simulations were run for 1.1 million samples saving every 100th sample to produce a total saved sample size of 10,000 after 1000 samples were discarded as burn-in. MCMC chains were evaluated for adequacy (convergence and sufficient information) using trace plots for each estimated parameter and derived variable as a visual check to ensure the chain was well-mixed and did not show “stickiness”, the effective sample size of the saved MCMC chains, and the similarity between the first 10% and last 50% of the saved chains using a standard *Z*-score test (Geweke, 1992). MCMC chain diagnostics were conducted in R (R Core Team, 2014) using the CODA package (Plummer et al., 2006). Here we used parameters (or quantities calculated from them) that produced the highest posterior density as point estimates (HPD) and summarized uncertainty via 95% credible intervals.

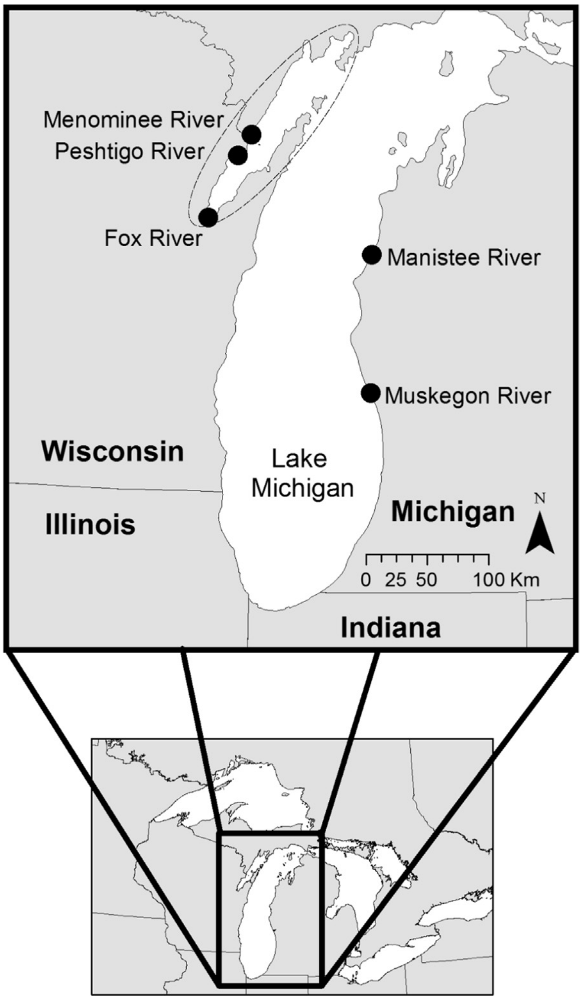

Fig. 1. Map of Lake Michigan showing the location of rivers associated with the lake sturgeon sources contributing to the open-water Green Bay (circled) mixture that served as an empirical application of the proposed approach for indexing changes in recruitment levels of sources contributing to a mixture. Inset shows Lake Michigan in relation to the other Great Lakes.

3. Results

3.1. Performance of estimation model under simulated scenarios

For most simulation scenarios, results were consistent across individual sources; consequently, we averaged the median and IQR of relative errors of $\log_e(\alpha_i)$ and $\log_e(N_{i,0}^{\text{last}})$ and of absolute errors of β_i across sources to simplify the presentation of results (Figs. 2–4). The only exception to this was for scenarios where genetic differences between sources and levels of change in year-class strength of the sources were varied; we present results for individual sources

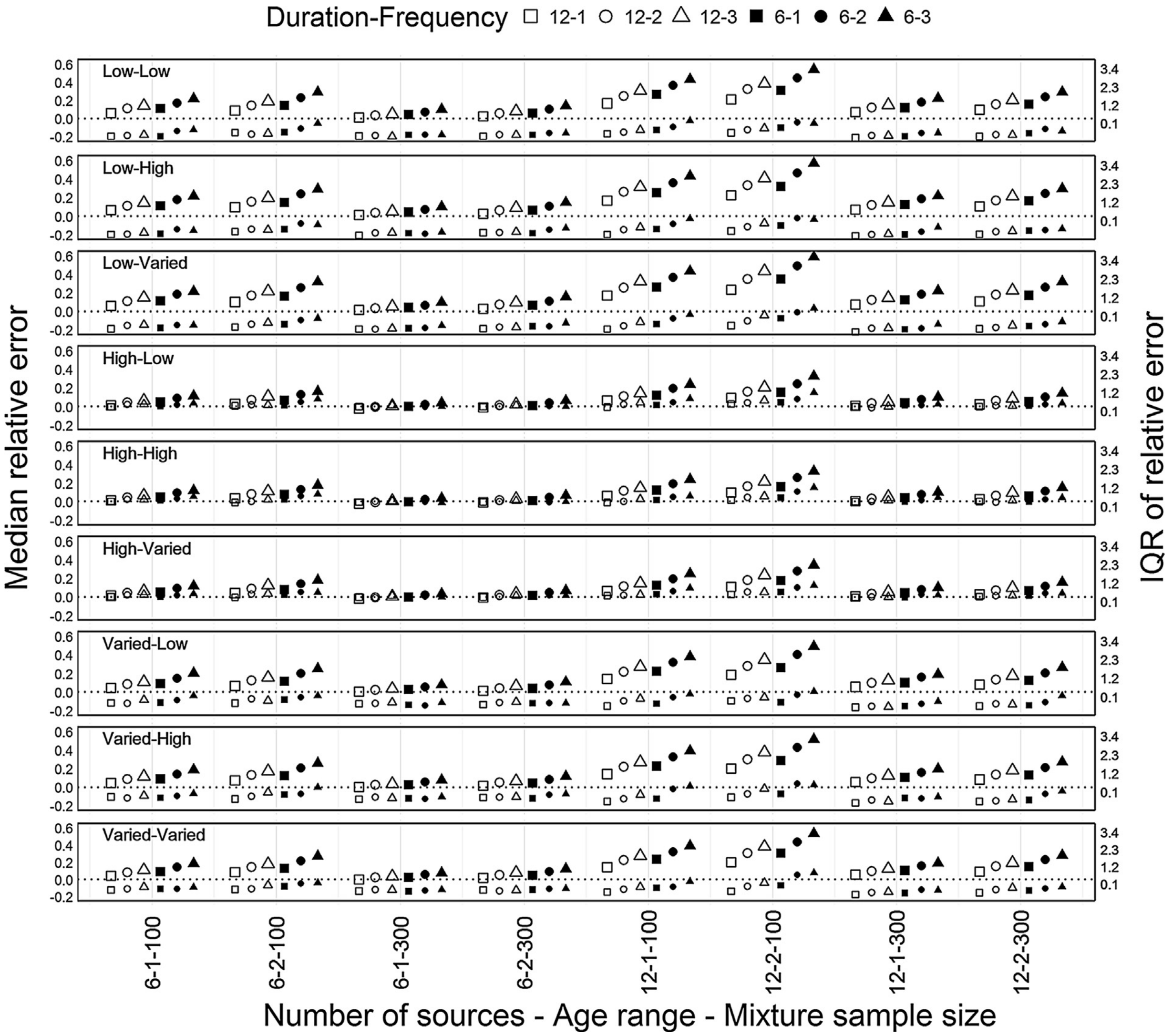

Fig. 2. Median (smaller symbols) and interquartile range (larger symbols) of relative error of $\log_e(\alpha_i)$, averaged across sources, from the simulations conducted to evaluate performance the proposed approach for indexing changes in recruitment levels of sources contributing to a mixture. The panel labels indicate particular combinations of level of genetic difference between sources and degree of change in year-class strength (e.g., Low–High = low genetic difference and high change in year-class strength). The groups of symbols within a panel correspond to different combinations of number of sources (6 or 12), age range of individuals (1 = 1–6; 2 = 10–35), and mixture sample size (e.g., 6–2–100 = 6 sources, large age range, and mixture sample size of 100). Different shapes and colors of symbols identify different combinations of mixture sampling durations (6 = 6 years; 12 = 12 years) and mixture sampling frequencies (1 = annual, 2 = every 2 years; 3 = every 3years) (e.g., 12–3 = sampling duration of 12 years with sampling every 3 years). The dashed horizontal line is a reference line corresponding to a median relative error of 0.

for these scenarios (Figs. 5–7). We present additional results for individual sources (for a subset of simulation scenarios; 6 years of annual sampling from the mixture) in Supplementary material 3 (Fig. S1) for those that are interested in individual source results.

Median relative errors of $\log_e(\alpha_i)$ (Fig. 2) and $\log_e(N_{i,0}^{\text{last}})$ (Fig. 3), averaged across sources, ranged from −0.2 to 0.2 across the simulation scenarios, whereas the median absolute error of β ranged from −0.01 to 0.01 (Fig. 4). Combined, these finding suggests that the estimation approach on average provided accurate parameter estimates across the range of examined scenarios. The IQRs of the relative and absolute errors of the parameters were more variable (Figs. 2–4), suggesting that precision of the estimates varied among the combinations of factor levels under evaluation. Based on both the median and IQR of the relative and absolute errors of the parameters, performance of the estimation approach improved with fewer sources, larger mixture sample sizes, higher genetic divergence among sources, and higher sampling duration and frequency. In some cases, the effects of a given factor on the accuracy and precision of parameter estimates varied depending on the levels of other factors. For example, the effects of duration and frequency of sampling from the mixture were more pronounced when the number of sources was larger and/or mixture sample size was smaller.

The effect of age range of individuals from the mixture on accuracy and precision of estimates varied by parameter. Accuracy of parameter estimates generally improved with a larger age range of individuals; this was most noticeable for β for simulations involving 12 sources and mixture sampling duration of 6 years where at a low age range estimates were often negatively biased with the bias decreasing for a larger age range (Fig. 4). For $\log_e(\alpha_i)$, the IQR of the relative error slightly increased with a larger age range. Conversely, for β and $\log_e(N_{i,0}^{\text{last}})$ precision improved with a larger age range (Figs. 3 and 4), and was most noticeable for β at low mixture sample sizes (Fig. 4).

For scenarios with varying levels of genetic difference among sources and varying β_i, the sources that were assigned large changes in year-class strengths (i.e., β_i values ranging from +0.02 to +0.03) experienced less variability in relative errors of$\log_e(\alpha_i)$ and

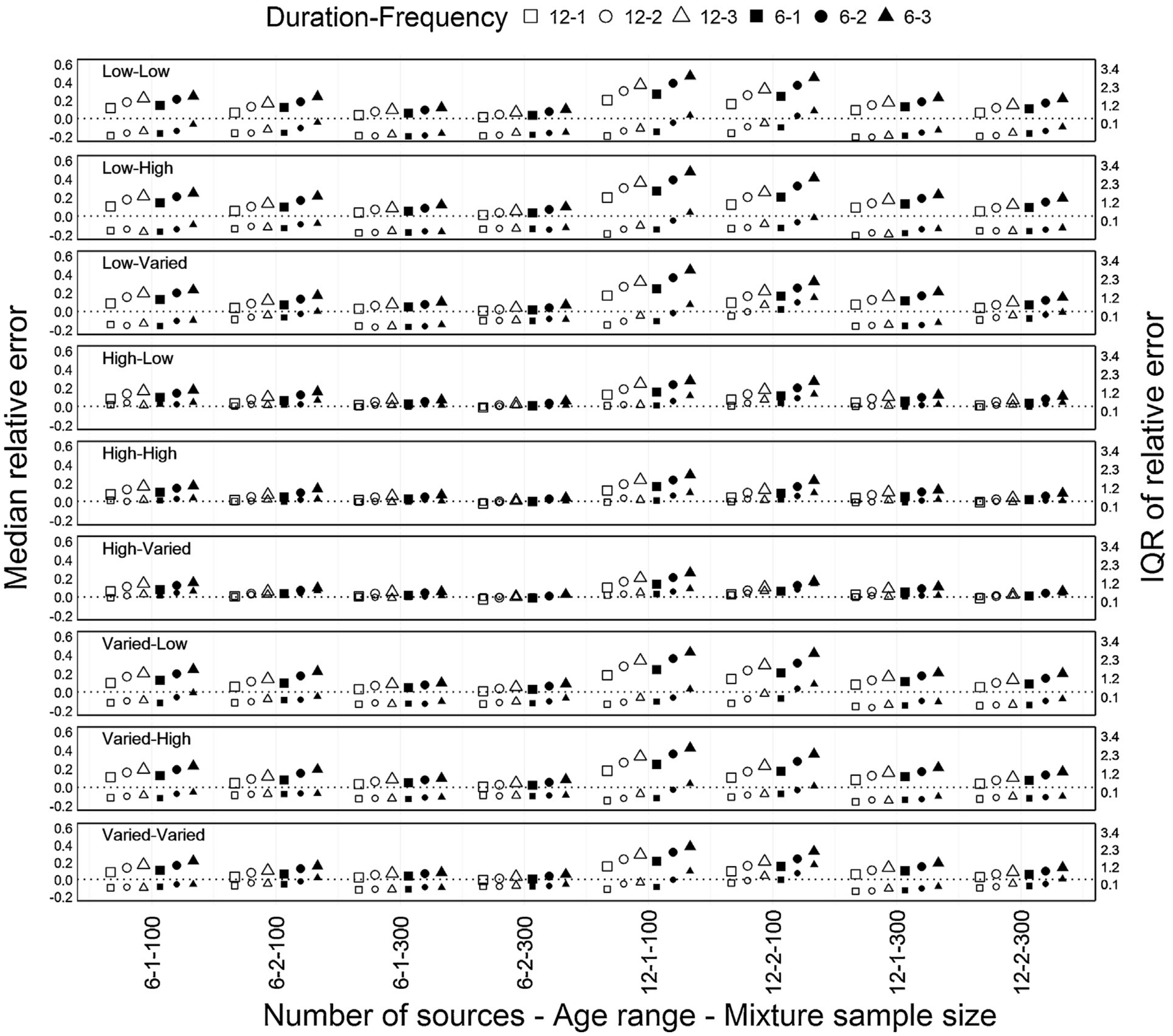

Fig. 3. Key same as in Fig. 2 except for relative error of $\log_e(N_{i,0}^{\text{last}})$.

$\log_e(N_{i,0}^{\text{last}})$ than populations that were assigned small changes in year class strength (Figs. 5 a–7 a). This was particularly noticeable for $\log_e(\alpha_i)$ and β_i for mixture sample sizes of 300 fish (Figs. 6 a–7 a). Despite this greater variability, accuracy in the parameter estimates was not affected, as evidenced by the median relative errors in $\log_e(\alpha_i)$ and $\log_e(N_{i,0}^{\text{last}})$ and absolute errors in β_i being close to 0 (Figs. 5 a–7 a).

3.2. Model sensitivity

Sensitivity results were consistent across the range of scenarios examined. Consequently, for brevity, we report on scenarios involving varied levels of genetic difference among sources and varying β_i. The results for other combinations of genetic differences among sources and levels of change in year-class strengths of sources are shown in Supplementary material 3 (Figs. S2–S5).

Based on the relative errors in $\log_e(\alpha_i)$ and $\log_e(N_{i,0}^{\text{last}})$ and absolute error in β_i for individual sources, the estimation approach appeared fairly robust to the incorporation of aging error in the analyses. With moderate aging error, the distributions in relative and absolute errors for individual sources appeared to match those from analyses without aging error (compare Fig. 5 b with 5 a, 6 b with 6 a, and 7 b with 7 a), with the exception that for some scenarios the precision of the parameter estimates became slightly poorer (e.g., 6 source populations with a large age range of mixture individuals and mixture sample size of 300 fish). The same was obviously true with low aging error with the change in precision being even less noticeable for most scenarios (results not shown). The use of length as a surrogate for age did not affect the accuracy of the estimation approach as the medians of the relative errors in $\log_e(\alpha_i)$ and $\log_e(N_{i,0}^{\text{last}})$ and absolute errors in β_i continued to be centered close to 0.0; however, the precision of the estimates became noticeably poorer when length was used as a surrogate for age compared to an age-based model without aging error (compare Fig. 5 c with 5 a, 6 c with 6 a, and 7 c with 7 a). The estimation approach was robust to random noise in total mortality with regards to accuracy and precision (results not shown). However, the model was sensitive to source-specific bias in total mortalities. When the same mortality (0.05) was assumed for all sources, the estimation model overestimated $\log_e(\alpha_i)$ and underestimated β_i, for the sources for which total mortalities were generated from a $N(0.04, 0.008)$ distribution. Conversely, the estimation approach underestimated $\log_e(\alpha_i)$ and overestimated β_i for the sources with for which total mortalities were generated from a $N(0.06, 0.0012)$ distribution (compare Fig. 5 d with 5 a, and 7 d with 7 a). Source-specific biases in mortality had little effect on $\log_e(N_{i,0}^{\text{last}})$ (compare

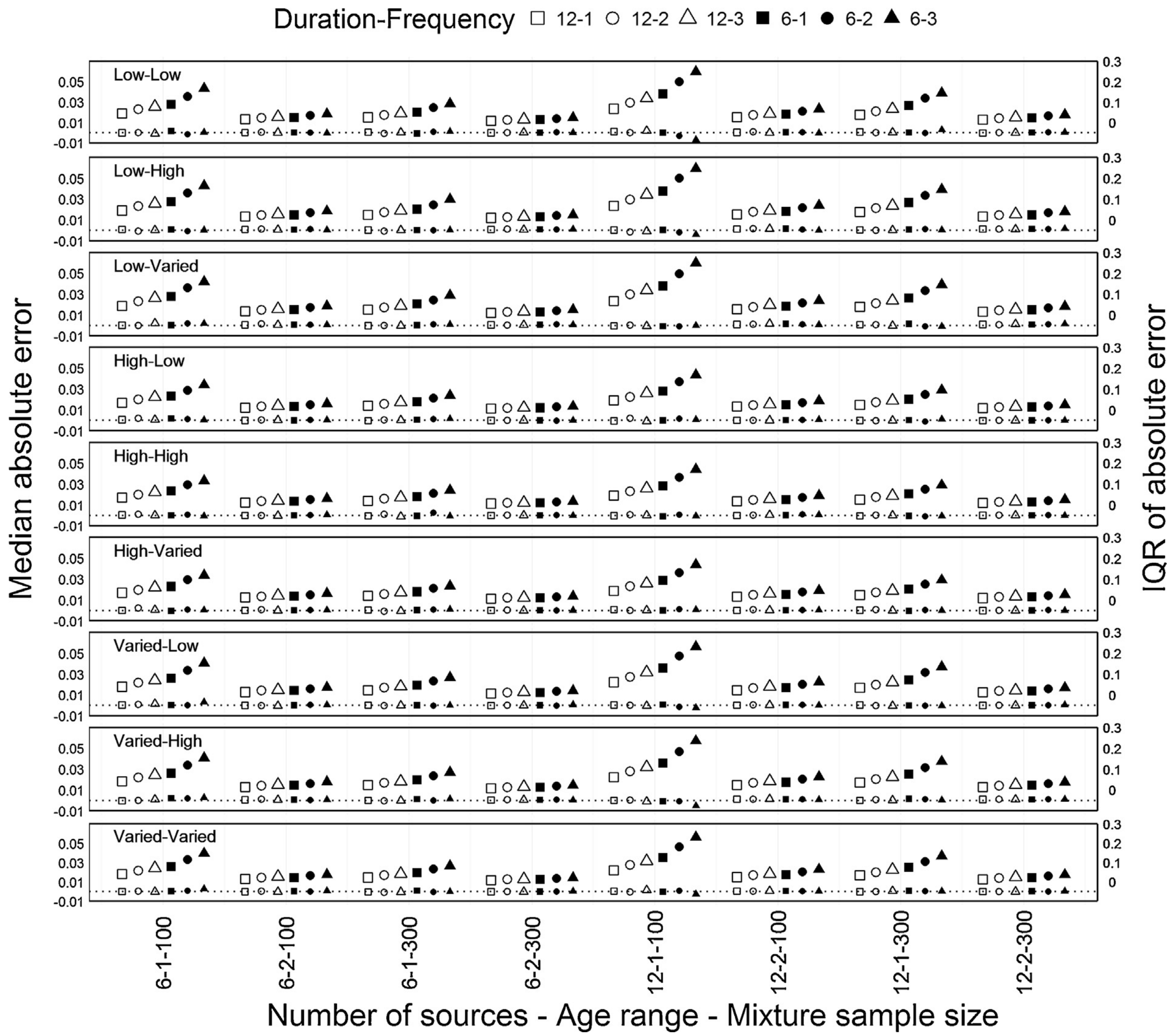

Fig. 4. Key same as in Fig. 2 except for absolute error of β_i.

Fig. 6 d with 6 a). Lastly, an increase in the number of sources to 24 primarily resulted in greater imprecision in the estimated parameters as evidenced by the larger IQRs of the relative errors for $\log_e(\alpha_i)$, $\log_e(N_{i,0}^{\text{last}})$ and β_i compared to an age-based analysis without aging uncertainty (compare Fig. 5 e with 5 a, 6 e with 6 a, and 7 e with 7 a).

3.3. Stock contributions to Lake Michigan lake sturgeon

The $\log_e(\alpha_i)$, β_i, and $\log_e(N_{i,0}^{\text{last}})$ for the lake sturgeon sources contributing to the Green Bay, Lake Michigan mixture were estimated with a relatively high degree of certainty, with the posterior distributions for the parameters having relatively narrow 95% Bayesian credible intervals (Table 2). Based on all criteria used to evaluate convergence, the MCMC chain for each of the parameter estimates was judged to have converged to the underlying posterior probability distribution and to contain enough information to characterize the distribution. Trace plots showed no “stickiness,” and the means of the first 10% and last 50% of the saved samples were similar based on Geweke’s (1992) *Z*-score, with the absolute value of the *Z*-score of the difference between the means of the first 10% and last 50% being less than two for all parameters.

The $\log_e(\alpha_i)$ estimates were the largest for the Fox and Peshtigo River sources, whereas the Manistee and Muskegon River sources had the lowest estimates (Table 2). As indicated in the methods, using these estimates to make inter-source comparisons of recruitment levels is complicated due to confounding with movement, so we cannot be sure to what extent the high $\log_e(\alpha_i)$ estimates for

Table 2
Highest posterior density estimates (HPD) and lower and upper 95% Bayesian credible limits (CLs) of $\log_e(\alpha_i)$, β, and $\log_e(N_{i,0}^{\text{last}})$ estimated for the Green Bay lake sturgeon mixture.

Parameter/variable	Source	HPD	Lower CL	Upper CL
$\log_e(\alpha_i)$	Fox	1.501	0.802	2.932
	Peshtigo	1.621	1.018	3.040
	Menominee	1.022	0.335	2.470
	Muskegon	−2.173	−5.832	0.181
	Manistee	−1.970	−6.528	0.430
β_i	Fox	−0.034	−0.058	−0.008
	Peshtigo	0.007	−0.010	0.026
	Menominee	−0.014	−0.036	0.010
	Muskegon	0.036	−0.035	0.167
	Manistee	0.008	−0.117	0.183
$\log_e(N_{i,0}^{\text{last}})$	Fox	0.056	−0.825	1.655
	Peshtigo	1.936	1.203	3.472
	Menominee	0.433	−0.383	1.977
	Muskegon	−0.644	−2.089	1.740
	Manistee	−1.611	−5.342	1.729

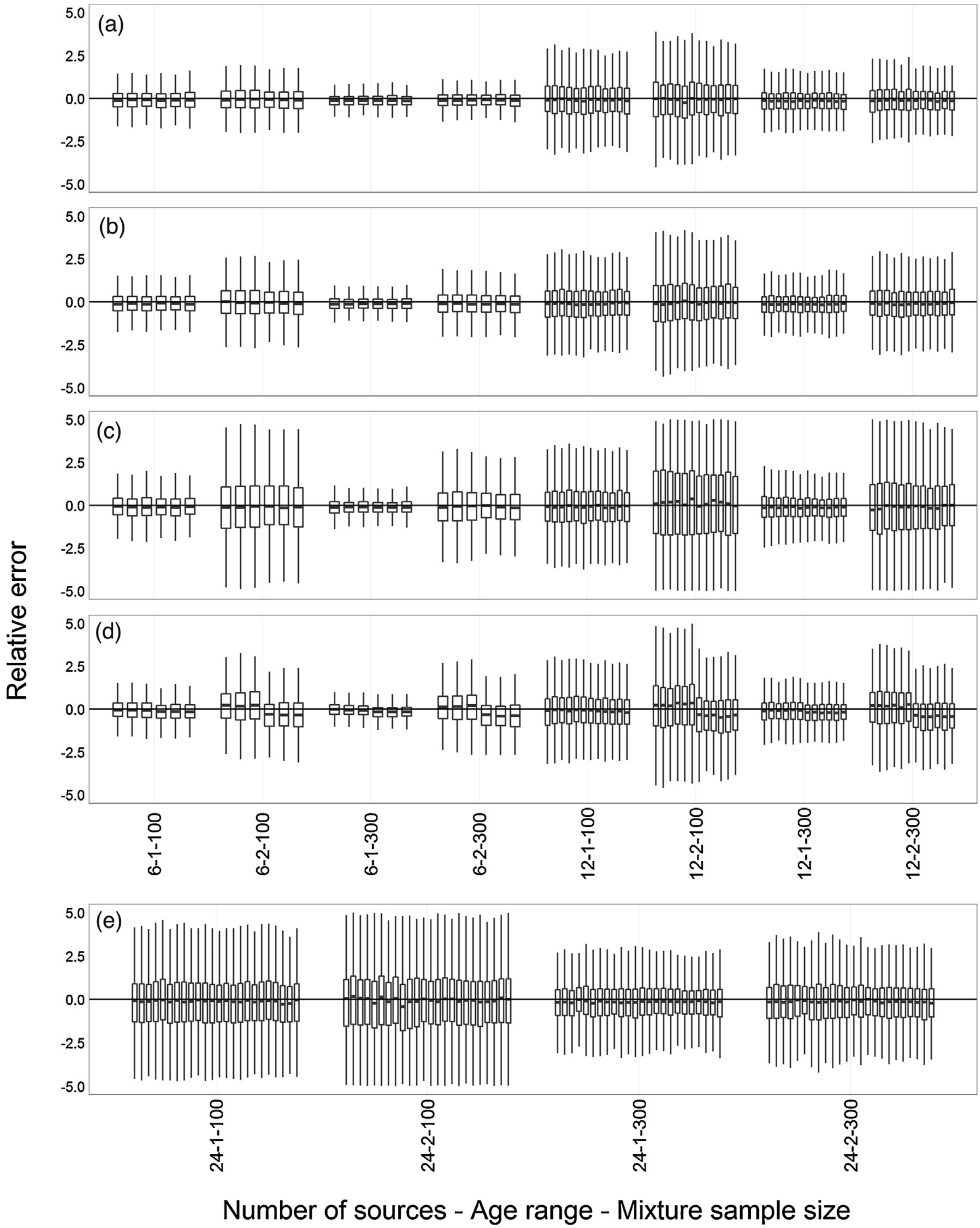

Fig. 5. Boxplots of relative error of $\log_e(\alpha_i)$ under selected factor-level combinations (6 years of sampling; annual sampling, varied population divergences and varied changes in year class strength) from (a) an age-based analysis with no aging error, (b) an age-based analysis with σ_a assumed to be 20% of expected true age, (c) a length-based analysis with σ_{ϵ_L} assumed to be 10% of $\log_e(E(L_a))$, (d) an age-based analysis with no aging error with mixture data generated assuming $Z \sim N(0.04, 0.008)$ for one half of the sources and $Z \sim N(0.06, 0.0012)$ for the other half, but the estimation program assumed Z= 0.05, and (e) from an age-based analysis without aging error assuming 24 sources. The first half of displayed sources for the different boxplot grouping were assigned low changes in year class strengths (i.e., β_i ranging from −0.005 and +0.005), whereas the second half of displayed sources were assigned high changes in year-class strengths (i.e., β_i ranging from +0.02 to +0.03).

the Fox and Peshtigo Rivers reflects high recruitment or just higher movement rates to the mixture. Given that the Fox and Peshtigo Rivers outlet into Green Bay (Fig. 1), it seems likely this result is due at least partly to higher movement rates compared to some of the other sources. Based on estimates of β_i, the Fox and Menominee River sources were found to have declining year-class strength levels, whereas the Muskegon, Manistee, and Peshtigo River were found to have increasing year-class strength levels. 95% Bayesian credible intervals for β_i for all sources except the Fox River encompassed zero suggesting some uncertainty as to the actual trajectory of the recruitment levels for the sources (Table 2). As a consequence of the estimated changes in year-class strength, by the last

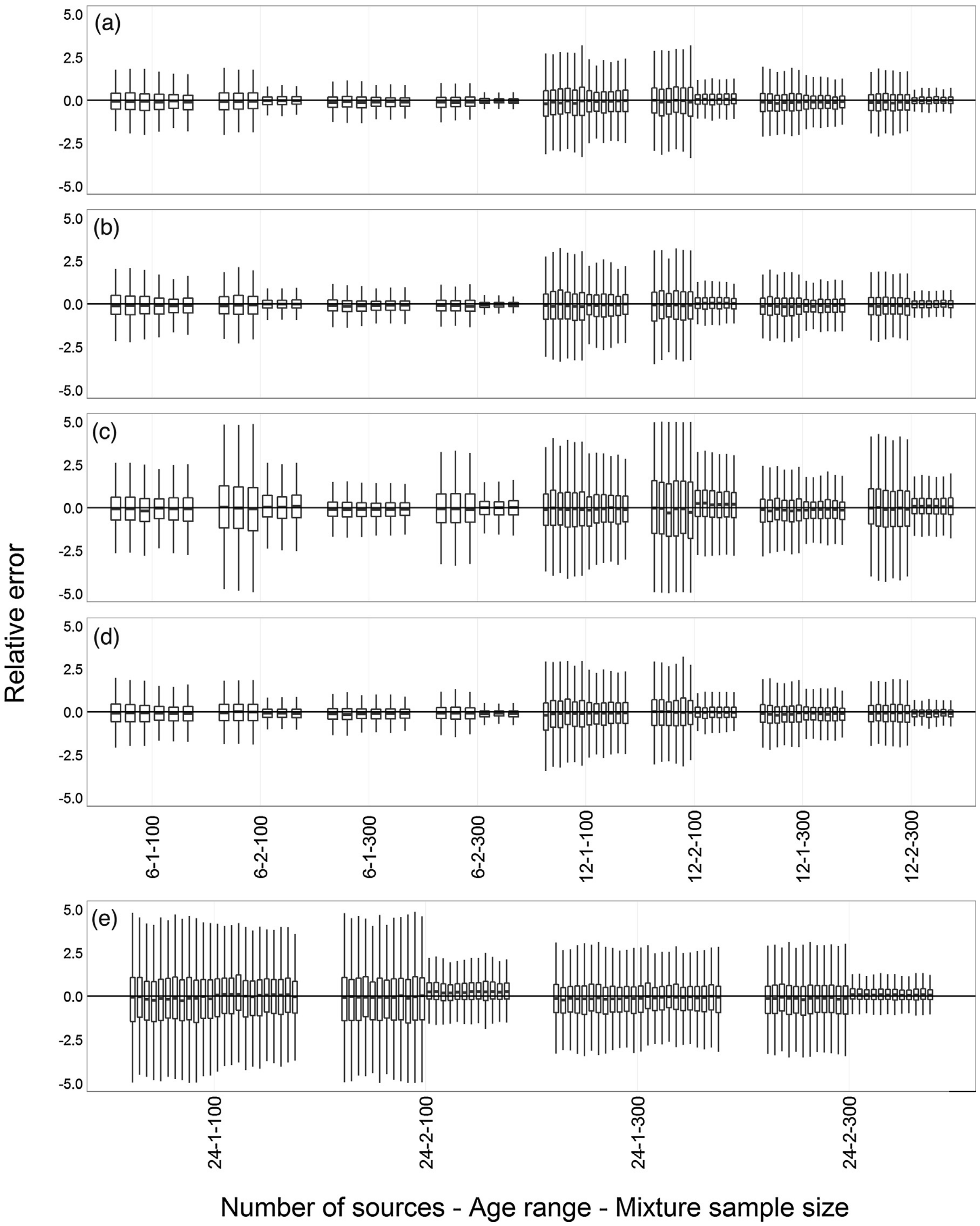

Fig. 6. Key same as in Fig. 5 except for relative error of $\log_e(N_{i,0}^{\text{last}})$.

modeled year class the Peshtigo and Menominee River sources had the largest $\log_e(N_{i,0}^{\text{last}})$ values whereas the Manistee and Muskegon River sources continued to have the lowest values (Table 2).

4. Discussion

By expanding existing model-based methods for genetic stock identification to accommodate age or length data, we developed an approach for estimating changes in relative year-class strength of source populations contributing to mixtures. The approach is intended for long-lived fishes with high pre-recruitment and low post-recruitment mortality rates for which consistent temporal changes in recruitment can be assumed, and it can effectively be used to index recruitment levels of sources and help identify populations of greatest concern where more intensive monitoring is needed. Instead of directly estimating age-specific annual contributions of sources to mixtures, which would require relatively larger amounts of data, the proposed approach estimates age- and collection-year specific contributions of sources to the mixture as linear functions of two source-specific parameters: an intercept

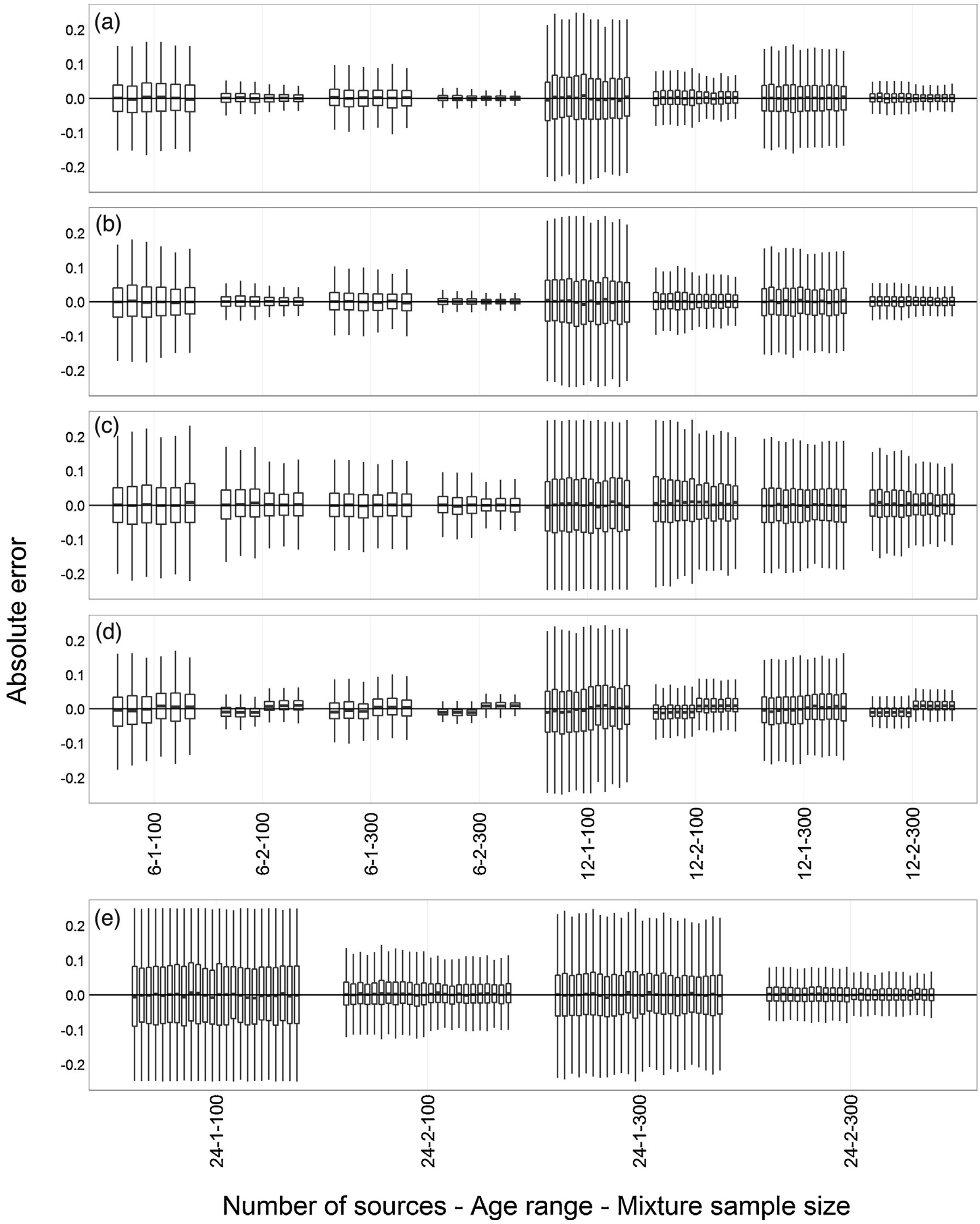

Fig. 7. Key same as in Fig. 5 except for absolute error of β_i.

representing relative recruitment for the first modeled year class and a slope representing how relative recruitment changes annually. By evaluating scenarios with mixture genotype data generated based on initial recruitment values that varied by orders of magnitude and changes in year-class strength that varied over a wide range, the proposed approach was shown to be able to estimate fairly accurately the contributions of even the least productive populations and detect slight annual changes in their recruitment levels.

For long-lived aquatic organisms, it has been argued that management assessments and decisions are best made by incorporating data across different temporal scales (Orensanz et al., 2004). Doing so, however, can be difficult unless standardized sampling programs have been in place for a long time. Our proposed approach demonstrates that compositions of mixtures involving a long-lived species such as lake sturgeon can be used to asses long-term recruitment changes in contributing source populations. The approach can work without a long time-series of collections because a mixture collection reflects demographic processes of source populations over long time frames. The time frame over which year-class strength changes can be assessed through this method depends on how long the mixture has been sampled and the age of individuals collected from mixtures. For a species such as lake sturgeon, which has a longevity of upwards of 150 years, there is the potential to gain information on source-specific recruitment levels over a potentially long time frame, which clearly would be of benefit for management decisions.

The performance of the proposed estimation approach varied among the factor-level combinations evaluated, but simulations generally showed that the developed estimation program was accurate under a variety of conditions, including varying numbers of sources, levels of genetic difference among sources, levels of change in year class strength, durations and frequencies of sampling from the mixture, age ranges of individuals from the mixture, and sample sizes from the mixture. Furthermore, our analysis indicated that accurate estimates could be obtained from realistic sampling protocols (i.e., 100–300 samples per year, collected annually or every two or 3 years for a duration of 6–12 years). Performance of the estimation approach improved with larger genetic difference among sources, larger mixture sample sizes, and lower number of sources, which is consistent with previous evaluations of accuracy and precision estimates for regular GSI analyses (Brenden et al., 2015b). Performance also improved with a longer mixture sampling duration, more frequent sampling, and in the case of β, collecting a larger age range of individuals from the mixture. Intuitively these results make sense as such sampling schemes provide more observations for the estimation process.

With respect to robustness of the estimation approach, aging uncertainty was found to have little influence on parameter estimates when an appropriate aging error correction matrix was applied. Therefore, it is likely that bias in parameter estimates would occur if the aging error matrix incorporated in the analyses did not reflect true uncertainty. Although accuracy of parameter estimates was not affected when length was used as a surrogate for age in the estimation process, precision of parameter estimates was affected particularly for those scenarios involving a large age range of individuals from the mixture. We attribute this result to the asymptotic nature of fish growth, which makes it difficult to determine the precise age of larger individuals (Bruch, 2008; Bruch et al., 2009). A potential solution to this problem when using length as a surrogate for age would be to restrict analyses to smaller individuals for which there is better demarcation of ages given fish length. Whereas the estimation approach was largely unaffected by random noise in mortalities for source populations, some bias in parameter estimates could occur if assumed total mortalities for some sources were consistently biased in either positive or negative directions. As we indicated in the methods, there is confounding between mortality and recruitment parameters so this bias is not surprising. For a long-lived species such as lake sturgeon, the highest and most variable mortality often occurs prior to recruitment (Caroffino et al., 2010), and given that individuals from different sources co-occur in mixtures, it should be possible to obtain fairly accurate estimates of post-recruitment total mortalities for the sources. We believe it is important to point out that other methods for indexing recruitment levels of populations based on collections of adult fish also make limiting assumptions regarding mortalities (Isermann et al., 2002), so this sensitivity in model performance to mortalities is not unique to our approach.

An implicit assumption of our proposed estimation approach is that the degree of movement from sources to the mixture is constant both in time and across the assessed ages. Although we did not explore sensitivity of our estimation approach to cases where movement rates were not constant, our expectation is that model performance would be similar to cases where mortality rates were not constant. That is, if year-to-year movement rates randomly varied around a stationary mean, then the results should be fairly robust to such deviations. Conversely, if there is more systematic departure from a constant movement assumption, then some biases in estimation accuracy likely can be expected. For example, when mixtures occur in close proximity to some sources but further away from others, younger individuals from more distant sources may not migrate at an equal rate to older individuals from more distant sources. This would result in estimates of year-class strength changes being negatively biased as the contribution of younger ages in the mixture would be lower than expected relative to older ages. As indicated previously, if estimates of movement were available they could be incorporated in the population-specific processes used to derive contributions by source, age, and mixture sampling year. In cases where movement rates differ by fish age, an alternative solution would be to restrict the ages or lengths of individuals incorporated in analyses.

We envision several avenues for expansion of the estimation approach that we have proposed. As indicated previously, there has been a growing tendency for model-based GSI analyses to incorporate information other than just genetics data to aid in the estimation of source contributions. In particular, it is becoming more commonplace for ecological covariates to be used to inform the estimation of source contributions through a Bayesian hierarchical modeling framework (Gaggiotti et al., 2004; Okuyama and Bolker, 2005; Guo et al., 2008; Bjorndal and Bolten, 2008). Depending on data availability, our approach could be expanded to include a hierarchical framework whereby the source-specific recruitment parameters were informed by ecological covariates similar to what is described in Okuyama and Bolker (2005). There also is the potential for using a hierarchical framework that allowed for deviations in contributions from those expected from the population-specific processes due to variations in movement, mortality rates, or other factors. The estimation approach could also be adapted to situations where sources exhibit inter-annual fluctuations in recruitment levels; such a change could be accommodated by modifying the underlying population-specific process or by adopting a hierarchical framework.

Low recruitment levels have been suggested as factors restricting population recovery in a variety of sturgeon species, including white sturgeon (*Acipenser transmontanus*; Paragamian et al., 1996), pallid sturgeon (*Scaphiryhchus albus*; Webb et al., 2005), and Atlantic sturgeon (*Acipenser oxyrhinchus*; Peterson et al., 2000). Presently within the Laurentian Great Lakes, lake sturgeon abundances are estimated to be less than 1% of historic levels (Hay-Chmielewski and Whelan, 1997). Given these low abundance levels, the ability to monitor recruitment levels of individual sources would be beneficial as major gains in rehabilitation would seemingly be contingent on expanded recruitment levels. The analyses that we conducted on Lake Michigan lake sturgeon primarily were for demonstration purposes and thus we caution about too strict of an interpretation of our results as to potential recruitment problems with the five sources considered in the analyses. In particular, it is believed that one of the reasons why the Fox River source was estimated to have experienced a decline in year-class strength is due to younger fish from this system migrating at a lower rate than older individuals (Elliott and Gunderman, 2008). Future analyses will likely involve limiting the sizes of fish included in the mixture to prevent complications arising from delayed mixing of younger fish. Additionally, we anticipate including more sources in analyses and additional mixtures to determine how consistent results are when considering different parts of Lake Michigan.

Acknowledgments

This research was partially funded by Great Lakes Fishery Trust project 2009.1080. Additional funding was provided by the Michigan Department of Natural Resources, and other contributing partners of the Michigan State University Quantitative Fisheries

Center. The authors wish to thank the commercial fishers and fishery agency personnel that collected the Lake Michigan lake sturgeon tissue samples used in this research. Computational work in support of this research was performed at Michigan State University's High Performance Computing Facility. This is publication 2015–18 of the Quantitative Fisheries Center at Michigan State University.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.fishres.2015.09.004.

References

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 1883, Ann Arbor, Michigan.

Beacham, T.D., Wood, C.C., 1999. Application of microsatellite DNA variation to estimation of stock composition and escapement of Nass River sockeye salmon (*Oncorhynchus nerka*). Can. J. Fish. Aquat. Sci 56, 297–310.

Beacham, T.D., Candy, J.R., Wallace, C., Wetklo, M., Deng, L., MacConnachie, C., 2012. Microsatellite mixed-stock identification of coho salmon in British Columbia. Mar. Coast. Fish. 4, 85–100.

Bjorndal, K.A., Bolten, A.B., 2008. Annual variation in source contributions to a mixed stock: implications for quantifying connectivity. Mol. Ecol. 17, 2185–2193.

Bolker, B.M., Okuyama, T., Bjorndal, K.A., Bolten, A.B., 2003. Sea turtle stock estimation using genetic markers: accounting for sampling error of rate genotypes. Ecol. Appl. 13, 763–775.

Bolker, B.M., Okuyama, T., Bjorndal, K.A., Bolten, A.B., 2007. Incorporating multiple mixtures in mixture analysis: many-to-many analyses. Mol. Ecol. 16, 685–695.

Bott, K., Kornely, G.W., Donofrio, M.C., Elliott, R.F., Scribner, K.T., 2009. Mixed-stock analysis of lake sturgeon in the Menominee River sport harvest and adjoining waters of Lake Michigan. N. Am. J. Fish. Manag. 29, 1636–1643.

Brenden, T.O., Scribner, K.T., Bence, J.R., Tsehaye, I., Kanefsky, J., Vandergoot, C.S., Fielder, D.G., 2015a. Contributions of Lake Erie and Lake St. Clair walleye populations to the Saginaw Bay, Lake Huron recreational fishery: evidence from genetic stock identification. North Am. J. Fish. Manag. 35, 567–577.

Brenden, T.O., Bence, J.R., Liu, W., Tsehaye, I., Scribner, K.T., 2015b. Comparison of the accuracy and consistency of likelihood-based estimation routines for genetic stock identification. Methods Ecol. Evol. 6, 817–827.

Bruch, R.M., 2008. Modeling the Population Dynamics and Sustainability of Lake Sturgeon in the Winnebago System, PhD Dissertation. University of Wisconsin–Milwaukee.

Bruch, R.M., Campana, S.E., Davis-Fouse, S.L., Hansen, M.J., Janssen, J., 2009. Lake sturgeon age validation using bomb radiocarbon and known-age fish. Trans. Am. Fish. Soc. 138, 361–372.

Caroffino, D.C., Sutton, T.M., Elliott, R.F., Donofrio, M.C., 2010. Early life stage mortality rates of lake sturgeon in the Peshtigo River, Wisconsin. North Am. J. Fish. Manag. 30, 295–304.

Dann, T.H., Habicht, C., Baker, T.T., Seeb, J.E., Fraser, D., 2013. Exploiting genetic diversity to balance conservation and harvest of migratory salmon. Can. J. Fish. Aquat. Sci. 70, 785–793.

DeHaan, P.W., Libants, S.V., Elliott, R.F., Scribner, K.T., 2006. Genetic population structure of remnant lake sturgeon populations in the Upper Great Lakes basin. Trans. Am. Fish. Soc. 135, 1478–1492.

Ebener, M.P., Brenden, T.O., Wright, G.M., Jones, M.L., Faisal, M., 2010. Spatial and temporal distributions of lake whitefish spawning stocks in Northern lakes Michigan and Huron, 2003–2008. J. Great Lakes Res. 36 (Suppl. 1), 38–51.

Elliott, R.F., Gunderman, B.J., 2008. Assessment of Remnant Lake Sturgeon Populations in the Green Bay Basin, 2002–2006. Great Lakes Fishery Trust Completion Report. Great Lakes Fishery Trust, Lansing, Michigan.

Fiksen, O., Slotte, M.L., 2002. Stock-recruitment models for Norwegian spring spawning herring (*Clupea harengus*). Can. J. Fish. Aquat. Sci. 59, 211–217.

Fournier, D.A., Beacham, T.D., Riddell, B.E., Busack, C.A., 1984. Estimating stock composition in mixed stock fisheries using morphometric, meristic, and electrophoretic characteristics. Can. J. Fish. Aquat. Sci. 41, 400–408.

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

Frank, K.T., Brickman, D., 2000. Allee effects and compensatory population dynamics within a stock complex. Can. J. Fish. Aquat. Sci. 57, 513–517.

Gaggiotti, O.E., Brooks, S.P., Amos, W., Harwood, J., 2004. Combining demographic, environmental and genetic data to test hypotheses about colonization events in metapopulations. Mol. Ecol. 13, 811–825.

Gatt, M.H., McParland, T.L., Halyk, L.C., Ferguson, M.M., 2003. Mitochondrial DNA variation and mixed-stock analysis of recreational and commercial walleye fisheries in eastern Lake Erie. North Am. J. Fish. Manag. 23, 431–440.

Geweke, J., 1992. Evaluating the accuracy of sampling-based approaches to the calculation of posterior moments. In: Bernardo, J.M., Berger, J.O., Dawid, A.P., Smith, A.F.M. (Eds.), Bayesian Statistics. Oxford University Press, Oxford, UK, pp. 169–193.

Guan, W., Cao, J., Chen, Y., Cieri, M., 2013. Impacts of population and fishery spatial structures on fishery stock assessment. Can. J. Fish. Aquat. Sci. 70, 1178–1189.

Guo, F., Dey, D.K., Holsinger, K.E., 2008. A hierarchical Bayesian approach for estimating the origin of a mixed population. In: Clarke, B., Ghosal, J.K. (Eds.), Pushing the Limits of Contemporary Statistics: Contributions in Honor of Jayanta K. Ghosh. Institute of Mathematical Statistics, Beachwood, Ohio, pp. 237–250.

Hay-Chmielewski, E.M., Whelan, G.E., 1997. Lake Sturgeon Rehabilitation Strategy (Special Report No. 18). Michigan Department of Natural Resources, Fisheries Division, Lansing, Michigan.

Hess, J.E., Narum, S.R., 2011. Single-nucleotide polymorphism (SNP) loci correlated with run timing in adult Chinook salmon from the Columbia River basin. Trans. Am. Fish. Soc. 140, 855–864.

Hilborn, R., Walters, C.J., 1992. Quantitative Fisheries Stock Assessment: Choice, Dynamics & Uncertainty. Chapman and Hall, New York.

Holt, C., Peterman, R., 2004. Long-term trends in age-specific recruitment of sockeye salmon (*Oncorhynchus nerka*) in a changing environment. Can. J. Fish. Aquat. Sci. 61, 2455–2470.

Homola, J.J., Scribner, K.T., Elliott, R.F., Donofrio, M.C., Kanefsky, J., Smith, K.M., McNair, J.N., 2012. Genetically derived estimates of contemporary natural straying rates and historical gene flow among Lake Michigan lake sturgeon populations. Trans. Am. Fish. Soc. 141, 1374–1388.

Hutchings, J., 1996. Spatial and temporal variation in the density of northern cod and a review of hypotheses for the stock's collapse. Can. J. Fish. Aquat. Sci. 53, 943–962.

Hutchings, J.A., 2000. Collapse and recovery of marine fishes. Nature 406, 882–885.

Isermann, D.A., McKibbin, W.L., Willis, D.W., 2002. An analysis of methods for quantifying crappie recruitment variability. North Am. J. Fish. Manag. 22, 1124–1135.

King, T.L., Lubinski, B.A., Spidle, A.P., 2001. Microsatellite DNR variation in Atlantic sturgeon (*Acipenser oxyrinchus oxyrinchus*) and cross-species amplification in the Acipenseridae. Conserv. Genet. 2, 103–119.

Li, Y., Bence, J.R., 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.

Ludsin, S.A., DeVanna, K.M., 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.

Manel, S., Gaggiotti, O.E., Waples, R.S., 2005. Assignment methods: matching biological questions with appropriate techniques. Trends Ecol. Evol. 20, 136–142.

Marsden, J.E., Krueger, C.C., May, B., 1989. Identification of parental origins of naturally produced lake trout fry in Lake Ontario: application of mixed stock analysis to a second generation. North Am. J. Fish. Manag. 9, 257–268.

McParland, T.L., Ferguson, M.M., Liskauskas, A.P., 1999. Genetic population structure and mixed-stock analysis of Walleyes in the Lake Erie-Lake Huron corridor using allozyme and mitochondrial DNR markers. Trans. Am. Fish. Soc. 128, 1055–1067.

McQuown, E.C., Sloss, B.L., Sheehan, R.J., Rodzen, J., Tranah, G.J., May, B., 2000. Microsatellite analysis of genetic variation in sturgeon (Acipenseridae): new primer sequences for *Scaphirhynchus* and *Acipenser*. Trans. Am. Fish. Soc. 129, 1380–1388.

McQuown, E.C., Gall, G.A.E., May, B., 2002. Characterization and inheritance of six microsatellite loci in lake sturgeon. Trans. Am. Fish. Soc. 131, 299–307.

Miller, T.J., 2007. Contribution of individual-based coupled physical–biological models to understanding recruitment in marine fish populations. Mar. Ecol. Prog. Ser. 347, 127–138.

Moran, P., Bromaghin, J.F., Masuda, M., 2014. Use of genetic data to infer population-specific ecological and phenotypic traits from mixed aggregations. PLoS One 9, e98470.

Morishima, G.S., Henry, K.A., 1999. The history and status of Pacific Northwest Chinook and coho salmon ocean fisheries and prospects for sustainability. In: Knudsen, E.E., Steward, C.R., MacDonald, D.R., Williams, J.E., Reiser, D.W. (Eds.), Sustainable Fisheries Management: Pacific Salmon. CRC Press, Boca Raton, Florida, pp. 219–236.

Nowak, A.M., Jessop, C.S., 1987. Biology and management of the lake sturgeon (*Acipenser fulvescens*) in the Groundhog and Mattagami Rivers, Ontario. In: Oliver, C.H. (Ed.), Proceedings of a Workshop on the Lake Sturgeon (*Acipenser Fulvescens*), Fisheries Technical Report Series No 23. Ontario Ministry of Natural Resources, Ontario, Canada, pp. 20–32.

Okuyama, T., Bolker, B.M., 2005. Combining genetic and ecological data to estimate sea turtle origins. Ecol. Appl. 15, 315–325.

Orensanz, J.M., Hand, C.M., Parma, A.M., Valero, J., Hilborn, R., 2004. Precaution in the harvest of Methuselah's clams — the difficulty of getting timely feedback from slow paced dynamics. Can. J. Fish. Aquat. Sci. 61, 1355–1372.

Page, K.S., Scribner, K.T., Bennettm, K.R., Garzel, L.M., Burnham-Curtis, M.K., 2003. Genetic assessment of strain-specific sources of lake trout recruitment in the Great Lakes. Trans. Am. Fish. Soc. 132, 877–894.

Paragamian, V.L., Kruse, G., Wakkinen, V.D., 1996. Kootenai River White Sturgeon Investigations (Annual Progress Report FY 1995. Prepared for US Department of Energy, Bonneville Power Administration), Prepared for US Department of

Energy, Bonneville Power Administration. Idaho Department of Fish and Game, Boise, Idaho.

Pella, J.J., Milner, G.B., 1987. Population genetics and fisheries management. In: Ryman, N., Utter, F. (Eds.), Use of Genetic Marks in Stock Composition Analysis. University of Washington Press, Seattle, Washington, pp. 247–276.

Pella, J., Masuda, M., 2001. Bayesian methods for analysis of stock mixtures from genetic characters. Fish. Bull. 99, 151–167.

Peterson, D.L., Bain, M.B., Haley, N., 2000. Evidence of declining recruitment of Atlantic sturgeon in the Hudson River. North Am. J. Fish. Manag. 20, 231–238.

Plummer, M., Best, N., Cowles, K., Vines, K., 2006. CODA: convergence diagnosis and output analysis for MCMC. R News 6, 7–11.

Rannala, B., Mountain, J.L., 1997. Detecting immigration by using multilocus genotypes. Proc. Natl. Acad. Sci. 94, 9197–9201.

Rawding, D.J., Sharpe, C.S., Blankenship, S.M., 2014. Genetic-based estimates of adult Chinook salmon spawner abundance from carcass surveys and juvenile out-migrant traps. Trans. Am. Fish. Soc. 143, 55–67.

Richards, L.J., Schnute, J.T., Kronlund, A.R., Beamish, R.J., 1992. Statistical models for the analysis of ageing error. Can. J. Fish. Aquat. Sci. 49, 1801–1815.

Ricker, W.E., 1958. Maximum sustainable yields from fluctuating environments and mixtures. Fish. Res. Board Can. 15, 991–1006.

Ricker, W.E., 1973. Two mechanisms that make it impossible to maintain peak-period yields form stocks of Pacific salmon and other fishes. Fish. Res. Board Can. 30, 1275–1286.

Ruzzante, D.E., Taggart, C.T., Lang, S., Cook, D., 2000. Mixed-stock analysis of Atlantic cod near the Gulf of St. Lawrence based on microsatellite DNA data. Ecol. Appl. 10, 1090–1109.

Schueller, A.M., Hayes, D.B., 2010. Sensitivity of lake sturgeon population dynamics and genetics to demographic parameters. Trans. Am. Fish. Soc. 139, 521–534.

Schueller, A.M., Hayes, D.B., 2011a. Minimum viable population size for lake sturgeon (*Acipenser fulvescens*) using an individual-based model of demographics and genetics. Can. J. Fish. Aquat. Sci. 68, 62–73.

Schueller, A.M., Hayes, D.B., 2011b. Inbreeding and allele retention for lake sturgeon populations under different supplementation strategies. North Am. J. Fish. Manag. 31, 1133–1145.

Scribner, K.T., Bott, K., Kanefsky, J., Elliott, R.F., Donofrio, M.C., 2010. Compositional Estimates of Lake Sturgeon, *Acipenser fulvescens*, Populations to Mixtures from Open-water and River Mouth Habitats in Lake Michigan. Great Lakes Fishery Trust Completion Report. Great Lakes Fishery Trust, Lansing, Michigan.

Seeb, L.W., Crane, P.A., Kondzela, C.M., Wilmot, R.L., Urawa, S., Varnavskaya, N.V., Seeb, J.E., 2004. Migration of Pacific Rim chum salmon on the high seas: insights from genetic data. Environ. Biol. Fishes 69, 21–36.

Stephenson, R.L., 1999. Stock complexity in fisheries management: a perspective of emerging issue related to population sub-units. Fish. Res. 43, 247–249.

Stott, W., Ebener, M.P., Mohr, L., Schaeffer, J., Roseman, E.F., Harford, W.J., Johnson, J.E., Fietsch, C.-L., 2012. Genetic structure of lake whitefish, *Coregonus clupeaformis*, populations in the northern main basin of Lake Huron. Adv. Limnol. 63, 241–260.

Waldman, J., Hasselman, D., Bentzen, P., Dadswell, M., Maceda, L., Wirgin, I., 2014. Genetic mixed-stock analysis of American shad in two Atlantic coast fisheries: Delaware Bay, USA, and Inner Bay of Fundy, Canada. North Am. J. Fish. Manag. 34, 1190–1198.

Webb, M.A.H., Williams, J.E., Hildebrand, L.R., 2005. Recovery program review for endangered pallid sturgeon in the upper Missouri River basin. Rev. Fish. Sci. 13, 165–176.

Welsh, A.B., 2004. Factors influencing the effectiveness of local versus national protection of migratory species: a case study of lake sturgeon in the Great Lakes, North America. Environ. Sci. Policy 7, 315–328.