Integration of Auxiliary Information in Statistical Catch-at-Age (SCA) Analysis of the Saginaw Bay Stock of Walleye in Lake Huron

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Abstract
Estimates of mortality rates and abundance for the Saginaw Bay stock of Walleye Sander vitreus has traditionally been performed with an analysis of tag returns using a Brownie-style analysis. An estimation approach that more fully accounted for sources of exploitation in addition to the recreational fishery in Saginaw Bay and inclusive of the rest of Lake Huron was needed. We developed a statistical catch-at-age model to accomplish this and evaluated four versions including three different treatments of natural mortality ($M$): a constant value, age-based $M$ values, and time-varying $M$ values. Deviance information criterion model selection procedures indicated that an age-based $M$ model version was optimal. We also evaluated an integrated version that incorporated tag returns as auxiliary information for the recreational component. In this case, model selection was based on conformity between observed and predicted data and model convergence. The integrated version was ruled out due to poor agreement of the observed and predicted values and predictions of abundance that were not reflected by the fisheries. We concluded that the component of the population used for tagging may exhibit dynamics that differ from the rest of the stock. Total annual mortality of Walleyes was greatest for older ages in all fisheries and ranged from 32% for age-2 fish to 39% for fish of ages 10 and older. The recreational fishery accounted for the majority of fishing mortality, but the commercial trap-net fishery in the main basin of Lake Huron and bykill from other trap nets in the bay accounted for proportionally greater fishing mortality of younger ages of fish. Abundance peaked in 2007 at 4 million Walleyes age 2 and older, but estimates indicated a previous period of high abundance in the late 1980s, forcing the reconsideration of the past stock as depressed and dependent on stocking.

Statistical catch-at-age (SCA) methods are widely regarded as the state of the art approach to stock assessment (NRC 1998; Quinn and Deriso 1999; Maunder 2003; Hilborn 2012) and are a form of “integrated analysis” (Quinn and Deriso 1999; Punt et al. 2001). Statistical catch-at-age models are age-structured and describe changes in abundance of individual cohorts over time (Megrey 1989). Such models include a population submodel from which estimates of abundance and mortality rates are derived. In addition, observation submodels describe the fisheries and fishery-independent assessment (Fournier and Archibald 1982; Methot 1990, 2000). The modern day approach to model fitting is a likelihood-based approach (Methot 1990, 2000), sometimes in a Bayesian context (Maunder 2003), from which the model parameters are adjusted so that a match to observed

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Walleye *Sander vitreus* from Saginaw Bay in Lake Huron is a stock with complex dynamics that requires a flexible approach to assessment. Walleyes are an important native predator in Lake Huron (Roth et al. 2013) and the Saginaw Bay stock is the largest source of recruits (Schneider and Leach 1979). Saginaw Bay is a relatively shallow, coolwater embayment of about 2,947 km² that lies entirely in the Michigan waters of Lake Huron (Figure 1). The Saginaw Bay Walleye fishery dates to the late 1800s and historically was the second largest in the Great Lakes, behind that of Lake Erie (Baldwin and Saalfeld 1962; Schneider 1977). Fielder and Thomas (2006) characterized the history of the Walleye in Saginaw Bay as having three phases. The first period, characterized by unbridled commercial exploitation, severe habitat degradation, and effects of invasive species, ended with collapse of the fishery in the mid-1940s (Schneider 1977; Schneider and Leach 1977, 1979). After the passage of water quality legislation in the 1970s, closure of the commercial fishery, and the initiation of a fingerling stocking program, a recreational fishery emerged (Fielder et al. 2014), but it was believed to have remained dependent on stocking (Fielder 2002; Fielder and Thomas 2006). Most recently a period of recovery has occurred and is attributed to the disappearance of the invasive Alewife *Alosa pseudoharengus* and substantial decline in Rainbow Smelt *Osmerus mordax* (Riley and Roseman 2013), which were predators on newly hatched percids (Fielder et al. 2007).

Since the early 1970s, the Michigan Department of Natural Resources (DNR) has recognized the importance of stock assessment information for Saginaw Bay Walleye. Investments in assessment included analysis of trends in abundance, recruitment, and growth rates since 1971 (Fielder and Thomas 2014), creel surveys to document extraction since 1986 (Fielder et al. 2014), and an analysis of mortality and exploitation rates based on a tagging program conducted since 1981 (Fielder 2014).

The spatial extent of the Saginaw Bay stock of Walleye, however, reaches beyond the confines of the bay (Hile 1954). Return of jaw tags has been limited to the recreational fishery (Fielder 2014) but has indicated considerable out-migration from Saginaw Bay proper to much of the rest of Lake Huron. Genetic studies have also documented that Tittabawassee River genotypes of Walleye (a spawning tributary within Saginaw Bay) have been found to comprise as much as 9% of the harvest of Walleyes in commercial fisheries operating in the southern Ontario waters of the lake even before the recovery (McParland et al. 1996).

More recently, an acoustic telemetry study has indicated that as many as half of the adult Walleyes are emigrating from Saginaw Bay during the open-water months (T. Hayden, U.S. Geological Survey, personal communication). Other fisheries thought to be likely exploiting Saginaw Bay Walleyes outside the bay includes the recreational fishery in the nearshore waters of Lake Huron and a tribal gill-net fishery in the area of northern Lake Huron defined by the 1836 Treaty (Figure 1) where Walleyes are retained as bycatch. Bykill of Walleyes also occurs in the state-licensed commercial fishery that operates in the bay and constitutes another source of mortality (MacMillan and Roth 2012).

Compounding the challenges of stock assessment for Saginaw Bay Walleye is the effect of immigration of Walleyes from Lake Erie. Some Walleyes from the central and western basins of Lake Erie are documented to inhabit portions of Lake Huron seasonally (Wolfert 1963; Ferguson and Derksen 1971; Thomas and Haas 2005; Wang et al. 2007). A mixed-stock analysis of Walleye from commercial fisheries on the Ontario portion of southern Lake Huron indicated that Walleyes from western Lake Erie contributed as much as 67–72% of the total commercial catch in 1994 and 1995 (McParland et al. 1996). Tag returns from Lake Huron of Walleyes tagged in Lake Erie average about 1% but have been as great as 2.6% in some years (Lake Erie Walleye Task Group, Great Lakes Fishery Commission, unpublished data). These are proportions of the entire exploitable Walleye population in central and western Lake Erie, which regularly number in the tens of millions. This outside source of Walleyes must also be accounted for in a comprehensive stock assessment for Saginaw Bay Walleye.
The objective of this study was to use SCA methods to more fully characterize population dynamics of the Saginaw Bay stock of Walleye. We sought to develop a model that accounted for four fisheries (Michigan recreational fishery, Ontario trap-net fishery, Ontario and tribal gill-net fishery, and the effects of commercial bykill within the bay) and adjusted for immigration of Lake Erie Walleyes and their contribution to each of the fisheries. We also evaluated whether existing tag return data could be incorporated as auxiliary information to yield a superior integrated model.

METHODS

The analytical approach to this analysis was to (1) develop an SCA model for the Saginaw Bay stock of Walleye in Lake Huron, including adjustments for migrants from Lake Erie, (2) evaluate three options of natural mortality and settle on a final "baseline" model version, and lastly (3) develop an integrated model version incorporating tag returns as auxiliary information and determine the optimal model (baseline versus the integrated version).

Statistical catch-at-age model.—The SCA analysis was conducted on annual time steps from 1986 through 2011. The modeling began with 1986 because recreational harvest estimates were not consistently available before that year. Ages of Walleyes modeled were 2 through 13, and age-13 fish included an aggregate of all Walleyes age 13 and over. These ages were selected because younger Walleyes (<age 2) are not typically recruited to most of the fisheries. We chose age 13 to aggregate because the Saginaw Bay stock of Walleye has exhibited considerable longevity at certain points in its history. There was no attempt to quantify aging error from any of the fisheries or survey.

Population submodel.—Predicted Walleye numbers \( N \) at age \( a + 1 \) at the start of year \( y + 1 \) were derived by the population equation:

\[
N_{a+1,y+1} = N_{a,y} e^{-Z_{a,y}} = N_{a,y} e^{-(Ma,y + Fa,y)},
\]

where \( Z \) is the total instantaneous mortality rate for the corresponding age and year; \( Z \) is the sum of instantaneous natural mortality, \( M \), and the total instantaneous fishing mortality, \( F \), for age \( a \) and year \( y \).

Natural mortality options.—Instantaneous natural mortality is not typically estimable from within a SCA model and instead is supplied (Quinn and Deriso 1999). Three alternative assumptions regarding natural mortality were used in alternative assessment models compared in this analysis, and in each case treating values for \( M \) as known. First, we used time-varying (annual) estimates \( (M_a) \) derived from the analysis of the tagging operation conducted annually by the Michigan DNR (Fielder and Thomas 2014). Second, we used age-based estimates of \( M_a \) borrowed from the Walleye tagging assessment in the neighboring western basin Lake Erie (Vandergoot and Brenden 2014). Those values were 0.335 for ages 2–4 and 0.152 for ages 5+.

Lastly we used a variable for \( M = 0.23 \) that was constant over years and ages derived from the Pauly (1980) equation, taking into account von Bertalanffy growth parameters and temperature data. Growth parameters of \( L_\infty \) and \( K \) were obtained from survey data for Saginaw Bay Walleye (Fielder et al. 2000; Fielder and Thomas 2006, 2014) based on all available data from the initiation of the survey in 1989 through 2011, and temperature was derived from mean annual air temperature data obtained from Midland–Bay City–Saginaw (MBS) airport.

Fishing mortality.—All model variations evaluated included the same treatment of fishing mortality. For the recreational, commercial trap-net, and commercial gill-net fisheries, instantaneous fishing mortality was treated as separable by age and year such that

\[
F_{a,y} = s_a q E_y \epsilon_y,
\]

where \( s_a \) is the age-specific selectivity of the fishery, \( q \) is the catchability of the fishery, \( E_y \) is the year-specific fishing effort, and \( \epsilon_y \) represents the catchability deviations (process error). These elements, aside from the effort, are estimated as parameters (or calculated from estimated parameters) in the model. Selectivity for each fishery was freely estimated out to age 10, and fish older than age 10 were assumed to have the same selectivity as age-10 fish. Depending on the fishery, the catchability deviations were either based on a white-noise (trap-net and gill-net commercial fisheries) or a random-walk (recreational fishery) model. In the case of white noise, \( \epsilon_y \) are assumed to come from a lognormal distribution. For the random walk, \( \epsilon_y \) are modeled as

\[
\epsilon_y = \epsilon_{y-1} \delta_y, \quad y > 1986
\]

\[
\epsilon_y = 1, \quad y = 1986,
\]

and \( \delta_y \) (random walk deviations) are lognormal. In the case of white noise, the catchability deviations allow for variation around a mean catchability, but the model fit is penalized when \( \epsilon_y \) deviates from that mean. In this case the \( \epsilon_y \) are estimated parameters. In the case of the random walk, the random walk deviations, \( \delta_y \), are what is penalized in the model fit for changes in catchability from one year to the next, and these rather than the \( \epsilon_y \) are the estimated parameters.

We used a random walk to model \( \epsilon_y \) for the recreational fishery because of the colonization of Saginaw Bay by dreissenid mussels in 1992–1993 midway through the time series (Nalepa et al. 1995). Dreissenid mussels were documented to increase water clarity and are theorized to have affected catchability in some fisheries including that in Saginaw Bay (Fielder et al. 2000). The use of random walks is an omnibus approach to estimating time-varying parameters when they may not come from a distribution with a consistent mean (Wilberg and Bence 2006; Wilberg et al. 2010). We presumed that catchability would
be more stable for the commercial trap-net and gill-net fisheries, which are prosecuted outside Saginaw Bay, and hence used the white-noise model in those cases.

Instantaneous fishing mortality stemming from the commercial bycatch (constituting bykill) in Saginaw Bay could not be derived as it was for the other fisheries because only one estimate of bykill was available (for 2010). However, this source of extraction is believed to be large (MacMillan and Roth 2012) and could not be ignored. To calculate \( F \) for this source of extraction, the Newton–Raphson method (Quinn and Deriso 1999; Haddon 2001) was employed to find a catchability value so that the 2010 bykill was matched. Year-specific \( F \) values were determined as the product of catchability and annual commercial effort in the bay (Michigan DNR, unpublished data), which is functionally equivalent to equation (2) with an assumption of constant selectivity (1.0) across ages. The resulting annual values for \( F \) derived for the commercial bykill in Saginaw Bay were then included in population calculations (as a component of the total instantaneous \( F \) value). While the inclusion of bykill influences fit to the data, it is not directly part of the objective function given that there was only one bykill observation that was exactly matched. MacMillan and Roth (2012) offered two estimates of bykill for Saginaw Bay commercial fisheries: a lesser value of 23,500 Walleyes represented their observed period of May–August and an extrapolated larger value of 102,000 Walleyes was given the entire year. The larger expanded value represented a set of assumptions that were regarded as tenous so we used the lower value from the observed period in our model fitting. Using our final model (after model selection), we evaluated sensitivity to the bykill by refitting the model with the larger expanded value. We did not directly incorporate other sources of discard mortality. However, as part of our sensitivity analysis we did evaluate how estimates were influenced when a higher-than-reported recreational harvest occurred.

**Observation submodels.**—Predicted catch from each of the four fishery components was treated the same across the model variations and was derived from the Baranov catch equation (Quinn and Deriso 1999):

\[
\hat{C}_{a,y} = \frac{F_{a,y} N_{a,y}}{Z_{a,y}} (1 - e^{-Z_{a,y}}), \tag{4}
\]

where the predicted catch at age \( a \) in year \( y \) is the product of the ratio of fishing mortality to total mortality and the numbers of fish dying each year.

The predicted survey CPUE \( \hat{I} \) was derived as

\[
\hat{I}_{a,y} = q_{a}^{surv} s_{a}^{surv} N_{a,y} e^{-\frac{k_1}{\sigma} Z_{a,y}}, \tag{5}
\]

where \( q_{a}^{surv} \) is survey catchability and \( s_{a}^{surv} \) is age-specific survey selectivity. The term \( e^{-\frac{k_1}{\sigma} Z_{a,y}} \) sets the corresponding population size for that age and year to the time of year the survey is conducted. As with the fisheries, the survey selectivity was fixed for ages 11–13 to that estimated for age 10. The \( q_{a}^{surv} \) was modeled as a random walk, similarly to the catchability deviations for the recreational fishery (equation 3), for the same reasons (as this survey is conducted in Saginaw Bay) but starting in 1989 rather than 1986 when this survey was initiated. The treatment of survey CPUE was the same across the model variations.

Other parameters include initial abundance at age of Walleyes \( (N_{age \ 2} \ to \ N_{age \ 13}) \) in 1986 (first year of modeling) and initial numbers at age 2 for each year of the model (recruitment) (Table 1). Because of the use of random-walk and white-noise penalties in the objective function, however, fewer than the total 181 parameters represented in Table 1 were freely estimated.

**Auxiliary information.**—Each year during the time series, about 3,000 Walleyes were jaw-tagged and released during the annual spawning run (late March or early April) at Dow Dam on the Tittabawassee River (Figure 1). Tag returns came from the recreational fishery, and tags were rarely or never reported from the other fisheries even when encountered. We developed a version of SCA that included the fit to the recreational tag return data as a component in the objective function, and we evaluated this integrated model version. The number reported by anglers in any given year \( j \) after initial release year \( r \) is a function of annual survivals \( S_i \), for \( i \) in years \( r \) to \( j - 1 \), and the recovery rate in the recreational fishery \( f_j \). Thus, the probability of a tag return being observed in year \( j \) in the recreational fishery given the fish was tagged in year \( r \) is

\[
p_{r,j} = \left( \prod_{i=r}^{j-1} S_i \right) f_j, \tag{6}
\]
where $\theta$ is a tag retention rate described by Fielder (2014) and originally obtained from VanderGoot et al. (2012). In conventional Brownie et al. (1985) tag-return analysis, the values of $S_i$ and $f_j$ are parameters estimated solely based on the tagging data, but in our integrated model their values are obtained as functions of parameters that are already estimated as part of the population model. We assumed that equation (6) applied only to Walleye ages 4 and above, given that fish younger than that age are not typically tagged as part of that survey (Fielder 2014). During model fitting, estimates of $S_i$ were calculated as the ratio of modeled numbers of age-5+ fish alive in year $i + 1$ to the number of age-4+ fish that were alive in year $i$. The $f_j$ values were calculated as the exploitation rate for year $j$ (estimate of harvest of fish age 4 and older based on equation 4 divided by estimate of $N$ for fish age 4 and older at start of year $j$). Equation (6) is not age structured. While methods exist for age structuring Brownie style analyses, that approach has not been taken by Michigan DNR, as often the number of aged specimens was insufficient to organize an age-based tag-return analysis.

Model fitting.—We used highest posterior density (HPD) estimation to obtain point estimates of parameters and quantities estimated from parameters. This Bayesian approach and its application in fisheries have evolved from a maximum likelihood approach (Fournier and Archibald 1982; Methot 1990; Aldrich 1997) to account for process errors (Schnute 1994; Linton and Bence 2008). Using this approach, parameters are estimated based on the minimization of an optimization function, which is the sum of the negative log likelihood for the data and the negative log prior densities for the parameters. The separate negative log-likelihood components for each type of data predicted by each of the submodels were summed, yielding the joint negative log-likelihood term. In addition, for parameters allowing for catchability variations, there was a negative log prior term associated with each fishery or the survey based on the assumed prior distribution for either the $\varepsilon_i$ (white noise) or $\delta_i$ (random walk) deviation for that fishery or survey. These prior terms were summed to obtain the joint negative log prior density. We assumed bounded uniform priors for other parameters, and thus prior densities were constant within the bounds so were not included in the objective function. The objective function was minimized using AD Model Builder version 10.0 (AD Model Builder Project 2011; Fournier et al. 2012). The prior components can be viewed as penalties for deviations from the values deemed most likely to be a priori, and HPD estimation is also referred to as penalized likelihood estimation.

For each of the observed fishery catches (recreational, Ontario trap net, lake wide gill net), each of the four sets of fishery or survey catchability deviations ($\varepsilon_i$ for white noise or $\delta_i$ for random walks) and for the survey CPUE, a lognormal distribution was assumed

$$L_i = IC + n \ln \hat{\sigma}_i + \frac{1}{2} \sum_y \left( \frac{\ln X_{i,y} - \ln \hat{X}_{i,y}}{\hat{\sigma}_i} \right)^2,$$

(7)

where $IC$ is an ignorable constant that was not included in our calculations. Each data source is designated by $i$, sample size is denoted by $n$, and $\hat{\sigma}_i$ is the SD that applies to each quantity $X_{i,y}$. In the case of fishery catch and survey CPUE, $\hat{X}_{i,y}$ represents a model prediction of observed catch or CPUE and $X_{i,y}$ represents the observed number of fish caught. In the cases of the components for white noise catchability, $\hat{X}_{i,y}$ represents the catchability deviations ($\varepsilon_i$), and for the random walk component, $\hat{X}_{i,y}$ represents random-walk deviations ($\delta_i$). In both of these cases $\hat{X}_{i,y}$ has an assumed value of 1. Thus there are eight lognormal components ($L_i$): three for the different fitted fishery catches (all fisheries except the bykill from state-licensed trap-nets), one for the CPUE from the survey, two for random-walk deviations (for the survey and recreational fishery), and two for white-noise catchability deviations (Ontario trap-net fishery and lake-wide gill-net fishery).

The values of $\hat{\sigma}_i$ play a role in all eight lognormal components. Unfortunately, we know from the theory of penalized likelihood that not all of these $\hat{\sigma}_i$ values can be estimated during model fitting (Linton and Bence 2008). Our approach was to estimate the $\hat{\sigma}_i$ associated with the observed data (fishery catch or CPUE), so four of these were estimated. The $\hat{\sigma}_i$ for the white-noise or random-walk deviations were then calculated based on an assumed ratio of their variance ($\hat{\sigma}_i^2$) relative to the variance for catch or CPUE from the same fishery or survey.

We set the ratios for both the survey and recreational fishery catchability random-walk variance to 0.85, hypothesizing that the interannual changes in catchability, as a proportion of the current value, would be of lesser magnitude than the observation error associated with catch (as a proportion of the true or expected value), but nearly as large. We set the ratios for the commercial fishery effort deviation variances to 1.0 for the lake-wide gill-net fishery and to 0.25 for the Ontario trap-net fishery. For the gill-net fishery we had no specific reason to expect actual changes in catchability, but we assumed that estimation error variance for effort would be at least as large as for the actual landings, as effort reporting is not a focus. For the Ontario trap-net fishery we hypothesized that variance in effort estimates would be substantially less than those of harvest, as they are not subject to all of the errors that beset harvest (e.g., weighing, converting from weight to numbers), and the Ontario effort reporting system is well developed. We acknowledge that these ratios, while based on our best judgment, are somewhat arbitrary. Consequently we explored the influence of the ratios in our sensitivity analysis.

The age-composition data (proportions at age) from each fishery and the survey were based on age samples assumed to arise from a multinomial distribution, leading to the likelihood equation:

$$L_i = - \sum_y N_{i,y} \sum_a p_{i,y,a} \ln p_{i,y,a},$$

(8)
where $N_{r,y}$ is the sample size for the number of specimens aged but was capped at an effective sample size of 200. This cap limited the influence of the component in the objective function and prevented this likelihood component from being overweighted for a specific year and data source (Fournier and Archibald 1982). The cap of 200 is consistent with the examination of residuals, which suggested markedly better fits were not obtained for year and data sources when age composition sample size exceeded the cap. The observed proportion of age $a$ in year $y$ for each source of age-composition data were denoted as $p_{r,y,a}$, and the corresponding predicted value as $\hat{p}_{r,y,a}$ is the predicted proportion.

The likelihood component for the auxiliary information (tag return comparison) was based on the multinomial distribution as

$$L_{13} = -\sum R_{r,j} \ln p_{r,j} + UR_{r} \ln \left(1 - \sum R_{r,j} \right),$$

where $p_{r,j}$ is the probability of the tag recovery from the $r$th tagging year in the $j$th recovery year, $UR_{r}$ is the number of tags not recovered from the original lot tagged in year $r$, and $R_{r,j}$ is the number of tags recovered from tagging year $r$ in recovery year $j$; $R_{r,j}$ was the adjusted value of the actual number of tags reported expanded by the year-specific correction factor for nonreporting (Fielder 2014).

Two model versions were developed. The baseline version omitted the tag return component from the objective function, and the integrated version included the tag return evaluation in the objective function. The baseline version was the SCA model chosen from the three candidate models (based on the natural mortality options) as a result of the model selection criteria. Because the predicted tag returns were generated with existing parameters, the total parameter set (181 parameters) was the same for the baseline and integrated model versions. Comparison of the two versions is addressed in following sections on sensitivity analysis and model selection.

_Fisheries and fishery-independent data._—Estimates of recreational harvest and effort were available for most of the Michigan waters of Lake Huron since 1986. In this context, harvest refers to actual number retained and does not account for any discarded fish that die due to hooking mortality. While we do not adjust for such mortality, we do evaluate the consequences of underreported recreational harvest in our sensitivity analyses. Because the Saginaw Bay stock of Walleye is the subject population, decisions had to be made as to what estimates of harvest to include. Although there is undoubtedly some local natural reproduction outside the bay, the decision was made to assume that it was negligible and the majority of Michigan’s main-basin Walleye harvest could be credited to the Saginaw Bay stock because of the seasonal movement from the bay.

While Walleyes are sought by recreational anglers in Ontario, recreational harvest is not regularly estimated there. Based on the bathymetry of Lake Huron, we rationalized that Saginaw Bay Walleyes would not likely reach Ontario waters past the abyssal area of Lake Huron north of the Sixth Fathom Scarp, effectively limiting them to the Ontario waters in the southernmost portion of the main basin from Point Clark to Sarnia, Ontario. For the purpose of this SCA analysis, the recreational fishery was regarded as negligible, but as indicated above the influence of higher-than-reported recreational harvest was evaluated as an assumption in the sensitivity analysis.

Recreational Walleye fishery harvest estimates were obtained from the Michigan DNR’s statewide annual creel survey study and direct reporting for charter boat operations. The creel survey follows the methods of Schneider (2000). Michigan DNR creel survey estimates were obtained from Fielder et al. (2014) and as unpublished data. Ages of Walleyes were obtained from annual biological samples of the recreational fishery throughout the survey season. Ages were estimated from hard structures: scales for early years and spines since 2009. Numbers of fish aged each year averaged 521. Proportions at age for the recreational fishery were derived from those annual biological samples.

Commercial harvest numbers are calculated based on yield-reporting programs and the average weight of harvested fish each year for each fishery, based on biological sampling. Walleye is a highly valued species and we assumed that commercial discard was negligible. The provincially licensed commercial trap-net fishery occurs in the Ontario southern basin waters of Lake Huron from Point Clark to Sarnia. Most of the effort is reported to occur in the most south-westerly area around Sarnia. While all reported harvest was included as the observed harvest for this fishery, we only used effort targeted on Walleyes (number of trap-net lifts). Ages of Walleyes were obtained from samples of the trap-net harvest and estimated from hard structures (scales or spines), and numbers averaged 527 per year. Proportions at age for the trap-net fishery were derived from the sample.

The commercial gill-net fishery exists in two regions of Lake Huron thought to include the Saginaw Bay stock of Walleye. There is a provincially licensed gill-net fishery targeting Walleye and other species in the southern main basin of the Ontario waters of the lake from Point Clark to Sarnia concurrent with the trap-net fishery. The second portion of the gill-net fishery is a tribal fishery authorized under the 1836 Treaty and 2000 Consent Decree (USA v. State of Michigan 2000). That fishery exists from the Straits of Mackinaw east to De Tour Passage, Michigan, (Figure 1) excluding the embayments of the Les Cheneaux Islands. That fishery is similar to the Ontario gill-net fishery and nets comprise mesh sizes from 114 to 140 mm stretch measure. Tribal harvest is permitted as a retention of the Walleye bycatch. Annual effort was recorded as the cumulative kilometers of nets fished. These data were obtained from the Chippewa–Ottawa Resource Authority and Ontario Ministry of Natural Resources. Age distributions were also similar allowing them to be combined with sample sizes of around 100 per year. All SCA model
variations combined the two gill-net fisheries as a single fishery in the estimation.

The fishery-independent survey is a gill-net-based assessment operation, using variable-mesh gear, conducted annually each September by the Michigan DNR since 1989 (Fielder et al. 2000; Fielder and Thomas 2006, 2014). Walleyes as young as age 1 were vulnerable to this gear in all years (Fielder and Thomas 2006). Age distributions were obtained from ages of hard structures (scales in early years, spines since about 1997) numbering about 500 each year. Walleyes in all the catches were aged.

**Immigrants from Lake Erie.**—Each fishery and survey component had the potential for augmentation by migratory Lake Erie Walleyes and needed some level of adjustment. In each case, the predicted fishery catch or survey CPUE compared with the observed value in our objective function was the sum of Saginaw Bay stock of Walleye and Lake Erie Walleye. Immigrant Walleyes from Lake Erie were given by

\[ n^E_y = N^E_y P_{y,a} T_y \omega_y C_a, \tag{10} \]

where \( n^E_y \) is the number of Walleyes at age \( a \) in year \( y \) in Lake Huron that resulted from Lake Erie migrants, \( N^E_y \) is the total Walleye population in the central and western basins of Lake Erie in a given year, \( P_{y,a} \) is the year-specific age distribution of the Lake Erie Walleye population, and \( T_y \) is the year-specific proportion of Walleyes migrating to Lake Huron based on the jaw-tag returns. Those values are reported by the Lake Erie Walleye Task Group (LEWTG) of the Great Lakes Fishery Commission (Thomas et al. 2011). The proportion of Lake Erie Walleyes migrating to Lake Huron based on jaw tags reported from Lake Erie fish \( (T_y) \) was further adjusted based on a running 3-year average (the average of the previous 2 years plus the reported value for the current year became the new value for the “current” year).

A year-specific correction factor for the nonreporting of tags from the recreational fishery in Lake Huron was incorporated as \( \omega_y \) (Fielder 2014). The contribution (expressed as a proportion) of each age that is thought to make the migration from Lake Erie is denoted as \( C_a \). This value is 1.0 for Walleyes of ages 5 and up but is reduced to 0.5 for age-4 fish and 0.0 for fish of ages 2–3. The reduction for younger fish is based on information reported by Wolfert (1963), Ferguson and Derksen (1971), and Wang et al. (2007), who observed that younger Lake Erie Walleyes were less prone to large migrations.

The estimates generated by the Lake Erie SCA model are specific to the western- and central-basin stocks in that lake (Thomas et al. 2011). The same model also estimates proportions at age; however, those are aggregated at age 7+. To adjust the Lake Erie estimated age distribution out to age 13 to conform with that used in this (Saginaw Bay) model, the aggregated age-7+ fraction was distributed across ages out to age 13 based on assuming a 50% survival rate of Walleyes for each subsequent age beginning with age 6.

Unlike the estimation process for the catch of the Saginaw Bay stock of Walleye, fishing mortality \( F \) was not estimated directly for Lake Erie Walleye but rather as a fraction of the \( F \) for Saginaw Bay fish for each of the fisheries. The Lake Erie \( F \) within Lake Huron was set at half (0.5) of the corresponding fishery \( F \) for each of the fisheries operating in Lake Huron including the bykill in the Saginaw Bay commercial fishery. This was based on the belief that once in Lake Huron, Walleyes from Lake Erie would be subject to the same fishing mortality rate as the Saginaw Bay stock but for approximately half the year. The one exception is for the gill-net fishery, which was spatially split between southern Lake Huron and northern Lake Huron. Rationalizing that Lake Erie Walleyes will not substantially migrate as far north as northern Lake Huron, only half of the gill-net fishery was set to exploit fish from Lake Erie, and thus the multiplier for the gill-net \( F \) was 0.25. Values for natural mortality of Lake Erie immigrants were similarly adjusted by these fractions. The catch attributable to Lake Erie fish was derived from the Baranov catch equation (equation 4) applying the fishing mortality rates described above, and \( n^E_y \).

The survey CPUE was adjusted for Lake Erie contributions by using equation (5) (for the predicted survey CPUE) but applying the formulation to numbers and total mortality rate specific to Lake Erie fish. This approach used the same estimated survey selectivity and catchability as estimated by the model for Saginaw Bay fish. As with the fisheries, the predicted values used in the calculation of the likelihood component was the sum of the two predicted CPUE values.

**Spawning-stock biomass.**—The mean weight at age and by sex was available for the time series from the Walleyes caught in the Michigan DNR survey (Fielder and Thomas 2014). Similarly the survey provided a matrix of maturity (expressed as proportions) of females by year and age. Spawning-stock biomass at age and year was derived as half the total biomass (to reflect females only) and the product of the maturity matrix.

**Model selection.**—Deviance information criterion (DIC) was used to select among the models of the three candidate treatments of natural mortality \( M \). Deviance information criterion is a Bayesian approach to selecting among models, analogous to Akaike’s information criterion used when fitting models by maximum likelihood (Spiegelhalter et al. 2002). Because DIC is limited to models involving the same data, this technique could not be used to select between models including or excluding the tag return data. The “best” model is the one with the lowest DIC value. Wilberg and Bence (2008) found DIC to work well as a model selection technique for SCA analysis.

Deviance information criterion model selection is based on Markov Chain Monte Carlo (MCMC) analysis, which is implemented in AD Model Builder based on the Metropolis–Hastings algorithm and begins by first obtaining the parameter values based on the HPD and the associated asymptotic variance–covariance matrix (Wilberg and Bence 2008; AD Model Builder Project 2011).
When calculating DIC, we used the half of the variance of the individual deviance values method for estimating the effective number of parameters (Spiegelhalter et al. 1998; Gelman et al. 2004) and HPD point estimates.

In our MCMC chain, we implemented 1,000,000 steps and saved every 200th step to thin the chain and save on computing time, which resulted in 5,000 values. The first 1,000 were discarded as a burn-in period and DIC analysis was based on the remaining 4,000 values. To determine whether the length of our burn-in period was long enough to ensure convergence, we visually inspected trace plots of the MCMC chains (of the objective function) and evaluated our burn-in point with stabilization in the plot (Gelman et al. 2004).

The model that we selected using DIC was then deemed the “baseline” model and contrasted with the model integrated with tag returns as auxiliary information. The question was whether the added influence of tag returns in the evaluation of the model objective function would result in an overall improved estimation. Selection between these two candidate models (with and without tag returns) was based on model fit between observed and predicted values, and particularly evaluation of whether there were systematic patterns to residuals.

**Uncertainty and sensitivity analysis.**—Sensitivity analysis was only applied to the baseline model selected by DIC. Analysis of the sensitivity of the model to the various likelihood components was based on performance metrics of management interest. Performance metrics included spawning-stock biomass of females (SSB) and total annual mortality (A). Further performance metrics included the exploitation rates of each of the four fisheries modeled but was limited to age-4 and older Walleyes to limit comparison with age-groups fully selected in each fishery type. Lastly, the annual population sizes were compared as a measure of sensitivity to each model component. All metrics were evaluated on time series means as percent of the optimal model. Minimum estimates of 95% confidence intervals were based on 1.96 of the asymptotic posterior SD.

Analysis of sensitivity was conducted by applying a weighting factor lambda (λ) of either 0.5 or 2.0 to each of the likelihood and prior components. This served to either deemphasize or overemphasize the effect of that component in order to examine the effect on the aforementioned performance metrics. Lambda was left at 1.0 for all other likelihood components to evaluate each component’s sensitivity singularly. In some cases, the model would then not converge.

Starting values for parameters were varied typically as half and twice the selected values to test for robustness of model convergence. Failure to converge or large departures of model predictions from observed values would increase concerns that the final “converged” estimates obtained from the starting values might not be at the global minimum for the objective function. Starting values were adjusted until values that met this criterion were identified.

The SCA model was structured by having to make certain assumptions about Walleye stock structure and fishery dynamics. These assumptions constitute a source of uncertainty. To evaluate the significance of these assumptions, performance metrics were also examined by increasing and decreasing assumed values. These assumptions included the following: (1) The duration of time Lake Erie Walleyes inhabited Lake Huron. This was set in the model by assigning mortality rates that were one-half of those of the Saginaw Bay fish, but was trialed here at ±20%, implying 7.2-month and 4.8-month durations as opposed to a 6-month duration. (2) The proportion of fish of each age of Lake Erie Walleyes migrating to Lake Huron. Fish of ages 2, 3, and 4 were trialed at 50, 100, and 100%, respectively, in their propensity to migrate to Lake Huron instead of none for ages 2 and 3 and 50% for age 4. (3) The assumption of Ontario’s recreational fishery harvest being nil is improbable as is the assumption of no catch-and-release mortality, so elevating the recreational catch by an additional 10% of the present observed values was evaluated for effect on the performance metrics. (4) The larger expanded value of bykill reported by MacMillan and Roth (2012) was evaluated. (5) We evaluated the sensitivity to variance ratios by choosing alternative values. Recognizing that a variance ratio of 1.0 implied the same variance for the effort deviations or catchability random walk as the catch or CPUE, we chose alternative values to test for sensitivity by selecting values of similar proportions above or below 1.0. (6) We evaluated the sensitivity of model predictions to the assumption of time-varying catchability for the recreational fishery. Preliminary analysis suggested that catchability did vary but not in anticipated patterns. To explore the influence of allowing expected catchability to drift over time for the recreational fishery, we refit the model with a white-noise treatment of the variability of recreational catchability, which assumes catchability varies about a constant mean. (7) Lastly, we evaluated our treatment of the age-based M as fully known. This was done in two ways: first we treated M_{age} as a prior of its own and incorporated it in the objective function based on a lognormal distribution using equation (7). For that purpose σ was approximated at one-quarter of the maximum range of the confidence intervals for the age-based M values from VanderGoot and Brenden (2014). Secondly, we evaluated model sensitivity to alternative set values of M_{age} using the upper and lower 95% confidence limits.

Standardized residual values between observed and predicted for the baseline model were examined. Residuals were based on the proportions at age for the survey CPUE and each fishery catch with the residuals computed as the observed minus predicted and standardized as the quotient of the difference and the predicted SD. A uniform scatter for each about zero was interpreted to mean that no systematic pattern existed.

**RESULTS**

**Model Selection**

Application of the DIC model selection procedures indicated that the age-varying natural mortality best reflected the observed data. In spite of this candidate model having the greatest...
TABLE 2. Deviance information criterion (DIC) model selection of three candidate SCA models for the Saginaw Bay stock of Walleye in Lake Huron based on different treatment of natural mortality (M): constant, age varying, and time varying. Included is the effective number of parameters (pD).

<table>
<thead>
<tr>
<th>Model</th>
<th>DIC value</th>
<th>Delta from minimum</th>
<th>“Best” model</th>
<th>pD</th>
</tr>
</thead>
<tbody>
<tr>
<td>Constant M</td>
<td>60208.4</td>
<td>66.2</td>
<td>No</td>
<td>160</td>
</tr>
<tr>
<td>Age-varying M</td>
<td>60142.2</td>
<td>0.0</td>
<td>Yes</td>
<td>180</td>
</tr>
<tr>
<td>Time-varying M</td>
<td>60340.8</td>
<td>198.7</td>
<td>No</td>
<td>149</td>
</tr>
</tbody>
</table>

effective number of parameters, analysis indicated it had the lowest overall DIC value (Table 2). Consequently, it was the age-varying natural mortality model version that then constituted the baseline model version for integration with tag returns as an alternative model version for further evaluation. The integrated model resulted in a fit of predicted and observed values that compared favorably with the baseline model except that the predicted recreational catch was overestimated relative to the observed (Figure 2A). The mean (over years) recreational catch predicted by the integrated model was more than twice the mean catch predicted by the baseline model. In contrast, the baseline model predictions of recreational catch were within 1% of the observed values.

The integrated version of the model generated predicted tag returns by utilizing the annual recreational exploitation and survival rates to generate the tag-return probabilities. Exploitation rates differed between the Brownie model and the baseline model since 2004 (Figure 2B). The elevated exploitation rate depicted by the observed tag returns probably resulted in an inflation of the recreational catch causing the departure from the observed. The result was an elevated (72% greater) population estimate. The integrated version also estimated that the population had declined in the last 2 years of the time series (2010 and 2011) to record lows, which were not consistent with the observed fishery trends. From this, and the systematic overestimation of observed recreational harvest by the integrated model, we concluded that the inclusion of the tag return auxiliary information did not result in a superior model and we retained the baseline version as our selected model.

Baseline Model

The baseline model achieved an overall good fit of the observed data sets (fishery extractions and fishery independent survey; Figure 3). An examination of standardized residual proportions at age for the survey and each fishery generally revealed no consistent pattern. There was a slight preponderance of positive residuals over negative values, especially for older ages across fisheries. This may have been a result of aging error or overestimation of certain terminal age-groups.

Abundance of the Walleye stock was estimated by the baseline SCA model to have declined steadily since 1988 and then increased beginning in 2005. The stock peaked at about 4 million Walleyes (age 2 and older) in 2007 before declining again and leveling off at about 2.4 million by the end of the time series (Figure 4). Uncertainty in the abundance was greatest in recent years likely reflecting the model’s estimation uncertainty over year-classes not yet depleted, a characteristic common to SCA fits (Figure 4).

Selectivities steadily increased for older ages of Walleyes through age 10 in the lake-wide gill-net and recreational fisheries (at which point selectivities were assumed to remain at the age-10 value and were not estimated; Figure 5). In contrast, the highest selectivity for the trap-net fishery was at ages 3 and 4. Minimum mesh sizes in the gill-net fishery and minimum length limits in the recreational fishery may have contributed to the low selectivity of age-2 and age-3 fish in those fisheries.

Estimated catchability of the recreational fishery and survey varied considerably over the series (Figure 6). The survey catchability reflected a greater catchability before dreissenid mussel colonization (about 1993), as we had hypothesized to occur due to changes in water clarity. However, catchability of Walleyes in the recreational fishery reflected a pattern that was more characteristic of recent population trends or perhaps the disappearance of Alewives.
Total annual mortality ranged from a low of 32% in 1991 to a high of 53% in 1986 (Figure 7). Uncertainty about total mortality was greatest for 1986 and was likely associated with the need to estimate an initial population consisting of some cohorts that were reflected in only a few years of data. Uncertainty in estimates of total mortality increased slightly beginning in 2001. Total annual mortality rates generally followed a pattern that suggested, to some degree, mortality was an inverse function of abundance of fish (Figures 4, 7).

Estimated age-specific total annual mortality of Walleyes showed a consistent qualitative pattern over time, in which a peak occurred at age 4 and a decline to a substantially lower value occurred at age 5, followed by a gradual increase to the levels experienced by age-10 and older fish (Figure 8). The total annual mortality reached for fish of ages 10 and older, however, decreased over the time series. The age-specific patterns reflect selectivity and natural mortality rates, and the sharp decrease from age 4 to age 5 corresponds to the lower $M$ for age-5 and older Walleyes and a decrease in selectivity for the trap-net fishery.
FIGURE 6. Time-varying catchability ($q$) and the $\pm 1.96$ SE (dashed lines) confidence interval of the (A) recreational fishery and (B) survey of the Saginaw Bay stock of Walleye in Lake Huron from the age-based natural mortality (baseline) version of the SCA model, 1986–2011.

Recreational fishing mortality ($F_{\text{mrc}}$) of Walleyes was greatest in the proportion of all sources of combined fishing mortality for all ages and was nearly 80% of the total by age 7 and older (Figure 9). Fishing mortality increased with Walleye age for the recreational and gill-net fisheries, likely reflecting increasing selectivity as a function of length limits and mesh sizes. This was in contrast with the Ontario trap-net fishery, where fishing mortality was highest in the younger age-groups and then declined with age. Recreational fishing mortality increased over the time series, especially after 2000, when age 5 was used as an indicator (Figure 10). Fishing mortality declined or was steady for the other fisheries over the same time series.

Estimated recruitment of Walleyes at age 2 clearly indicated the resurgence in reproductive success beginning with the 2003 year-class (Figure 11). Total biomass and spawning-stock biomass of the Saginaw Bay stock followed a similar trajectory (Figure 12). Biomass metrics were much higher earlier in the time series, peaking in 1989, and then exhibited a decline until the recent resurgence beginning in 2006. Uncertainty for the estimates was generally less for this time series relative to other
Figure 10. Fishing mortality ($F$) of age-5 Walleyes over time from the four fisheries represented by the age-based natural mortality (baseline) version of the Saginaw Bay stock of Walleye SCA model: Michigan recreational fishery ($F_{mrc}$), Ontario trap-net fishery ($F_{otn}$), the lake-wide (combined Ontario and tribal) gill-net fishery ($F_{gln}$), and the bykill stemming from the state-licensed trap-net fishery in Saginaw Bay ($F_{bkl}$).

Estimated metrics but also increased for the three most recent years.

The baseline SCA model exhibited high sensitivity to weighting for the CPUE of the survey and gill-net harvest, but not the recreational fishery harvest (Table 3). The baseline model was somewhat sensitive to weighting of the age structure of the trap-net and gill-net fisheries. Aside from those cases, there was generally little departure on a percentage basis from the baseline version for most metrics as component weightings were changed. Collectively, altering weighting factors resulted in the model failing to converge just three times.

Although bykill estimation was not directly part of the objective function, the value used to derive the catchability for application to commercial effort of past years did result in estimation differences from the baseline model (Table 4). The higher extrapolated (year-round) estimate of bykill in 2010 (102,000 Walleyes) increased the population estimate by 36% and SSB by 26% (Table 4). Total annual mortality was not affected on average, but corresponding exploitation rates in the fisheries were reduced by about 20% each except for the bykill exploitation rate, which increased 202%. Increasing recreational fishery harvest from the baseline model by 10% resulted in a 5–6% increase in population and SSB estimates and a similar magnitude decline in exploitation rates except for the recreational fishery (Table 4).

The influence of the duration of Lake Erie Walleye habitation in Lake Huron had only minor effects on model estimates when increased from 6 months to 7.2 months (Table 4). A lack of convergence prevented evaluation of a shorter duration. Similarly, the full inclusion of age-3 and one-half of the age-2 Walleyes in the immigration had only a minor effect on the estimates of the baseline model (Table 4).

The baseline (age-based $M$) model proved reasonably robust to the assumptions of variance ratios as shifting the weight of the variance had only minor effects on the metrics of management interest (Table 4). This suggests that, while somewhat arbitrary, the choice of variance ratios did not have a profound effect on the overall estimation.

Model estimates were sensitive to the assumption of time-varying catchability in the recreational fishery (Table 4). Application of an alternative white-noise treatment of $q$ resulted in a 22% increase in total population size on average with most of the departure occurring in the last 7 years of the time series. In order to fit the model with a white-noise treatment of $q$ deviations, the recreational fishery variance ratio had to be increased to 1.10.

Treating the age-based $M$ value as a prior in the estimation process had little effect on model performance in which there...
TABLE 3. Sensitivity of penalized likelihood component analysis of the Saginaw Bay stock of Walleye in Lake Huron SCA model as percent change from the aged-based natural mortality model (baseline) version. Sensitivity was tested by applying a weighting factor lambda (λ) of either 0.5 or 2.0 to each of the 12 likelihood components in the baseline version of the model and assessing the percent change from the time series mean for four metrics of management interest: population size (N), total annual mortality (A), spawning-stock biomass of females (SSB), and the exploitation rate (µ) of the four fisheries. Weighting factors that resulted in a lack of convergence are denoted by DNC (did not converge).

<table>
<thead>
<tr>
<th>Weighting factor</th>
<th>N</th>
<th>A</th>
<th>SSB</th>
<th>Recreational µ</th>
<th>Trap-net µ</th>
<th>Gill-net µ</th>
<th>Bykill µ</th>
</tr>
</thead>
<tbody>
<tr>
<td>Recreational harvest</td>
<td></td>
<td></td>
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</tr>
<tr>
<td>(\lambda_1=0.5)</td>
<td>0.02</td>
<td>0.42</td>
<td>−0.50</td>
<td>2.66</td>
<td>0.63</td>
<td>0.23</td>
<td>1.99</td>
</tr>
<tr>
<td>(\lambda_1=2.0)</td>
<td>0.51</td>
<td>−0.32</td>
<td>0.75</td>
<td>−1.77</td>
<td>−0.94</td>
<td>−0.73</td>
<td>−1.34</td>
</tr>
<tr>
<td>Recreational random walk</td>
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</tr>
<tr>
<td>(\lambda_2=0.5)</td>
<td>0.12</td>
<td>0.28</td>
<td>0.22</td>
<td>0.29</td>
<td>−0.16</td>
<td>−0.22</td>
<td>1.84</td>
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<tr>
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<td>(\lambda_3=0.5)</td>
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<td>−0.06</td>
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<td>2.63</td>
<td>1.43</td>
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<td>(\lambda_3=2.0)</td>
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<td>1.93</td>
<td>0.34</td>
<td>2.22</td>
<td>−1.00</td>
<td>1.36</td>
<td>14.23</td>
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</tr>
<tr>
<td>(\lambda_4=0.5)</td>
<td>289.27</td>
<td>39.29</td>
<td>251.98</td>
<td>−57.56</td>
<td>240.57</td>
<td>128.19</td>
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<td>−0.04</td>
<td>0.09</td>
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<td>−0.13</td>
<td>−0.14</td>
<td>−0.19</td>
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<tr>
<td>Survey random walk</td>
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<tr>
<td>(\lambda_5=0.5)</td>
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<td>0.17</td>
<td>−0.09</td>
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<td>0.15</td>
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<td>DNC</td>
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<td>Survey age structure</td>
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<td>(\lambda_6=0.5)</td>
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<td>−1.01</td>
<td>2.26</td>
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<td>4.79</td>
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<td>(\lambda_7=0.5)</td>
<td>−0.23</td>
<td>0.33</td>
<td>−0.01</td>
<td>0.23</td>
<td>−0.05</td>
<td>0.54</td>
<td>1.39</td>
</tr>
<tr>
<td>(\lambda_7=2.0)</td>
<td>11.80</td>
<td>5.63</td>
<td>8.54</td>
<td>−9.97</td>
<td>−5.68</td>
<td>95.48</td>
<td>11.29</td>
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<td>Trap-net effort</td>
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<td></td>
<td></td>
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</tr>
<tr>
<td>(\lambda_8=0.5)</td>
<td>DNC</td>
<td>DNC</td>
<td>DNC</td>
<td>DNC</td>
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<td>DNC</td>
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<td>−0.13</td>
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<td>Trap-net age structure</td>
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<td>(\lambda_9=0.5)</td>
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<td>−1.15</td>
<td>−0.53</td>
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<td>−85.23</td>
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<tr>
<td>(\lambda_{10}=0.5)</td>
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<td>361.30</td>
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<td>234.87</td>
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<td>DNC</td>
<td>DNC</td>
<td>DNC</td>
<td>DNC</td>
<td>DNC</td>
<td>DNC</td>
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<tr>
<td>Gill-net effort</td>
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<tr>
<td>(\lambda_{11}=0.5)</td>
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<td>1.03</td>
<td>−0.12</td>
<td>0.81</td>
<td>0.50</td>
<td>3.27</td>
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</tr>
<tr>
<td>(\lambda_{11}=2.0)</td>
<td>1.50</td>
<td>−1.42</td>
<td>0.40</td>
<td>−1.38</td>
<td>−0.99</td>
<td>−3.29</td>
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<tr>
<td>Gill-net age structure</td>
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<td></td>
</tr>
<tr>
<td>(\lambda_{12}=0.5)</td>
<td>−0.02</td>
<td>−0.01</td>
<td>−0.19</td>
<td>0.01</td>
<td>−0.11</td>
<td>0.05</td>
<td>−2.46</td>
</tr>
<tr>
<td>(\lambda_{12}=2.0)</td>
<td>411.51</td>
<td>628.02</td>
<td>375.61</td>
<td>−12.94</td>
<td>283.44</td>
<td>−50.40</td>
<td>411.51</td>
</tr>
</tbody>
</table>

was a <1% departure from the baseline for all metrics and an increase in the SD by just 0.1% over the baseline. It did increase uncertainty slightly for some other metrics and added to the parameter load. Trialing age-based \(M\) at the upper and lower 95% confidence limits did result in a modest effect on model metrics (Table 4): generally a 10–20% effect with greater population estimate resulting from the upper limit value, and a lower population from the lower limit value.

**DISCUSSION**

The SCA model presented in this study allows the explicit incorporation of multiple fisheries in the stock assessment and overcomes a weakness of the tag-recapture assessment methods that have been used in the past. By incorporating all the fisheries exploiting this stock, more plausible estimates of overall mortality, and consequently fishing mortality, were obtained. Although the recreational fishery accounted for the majority of
TABLE 4. Sensitivity of assumptions analysis of the Saginaw Bay stock of Walleye in Lake Huron SCA model from the age-based natural mortality model (baseline) version for seven key assumptions: (1) An expanded (extrapolated) estimate of the magnitude of commercial bykill in the bay from MacMillan and Roth (2012). (2) An expanded recreational observed catch to simulate an Ontario component. (3) Two alternative durations of residency time for the habitation of Lake Erie (LE) Walleyes in Lake Huron. (4) The ages at which Lake Erie Walleyes are hypothesized to immigrate was adjusted to fully include age-3 and one-half of age-2 fish. (5) Alternative variance ratios used in the likelihood functions for relating white-noise or random-walk deviations of catchability to catch. (6) Treatment of recreational catchability as a white-noise process instead of random walk. (7) Treatment of age-based natural mortality $M$ as a prior in the model estimation and then alternative values based on 95% CIs. Sensitivity was assessed as percent change from the time series mean for four metrics of management interest: population size ($N$), total annual mortality ($A$), spawning-stock biomass of females (SSB), and the exploitation rate ($\mu$) of the four fisheries. A lack of model convergence is denoted by DNC (did not converge).

<table>
<thead>
<tr>
<th>Model version</th>
<th>$N$</th>
<th>$A$</th>
<th>SSB</th>
<th>Recreational $\mu$</th>
<th>Trap-net $\mu$</th>
<th>Gill-net $\mu$</th>
<th>Bykill $\mu$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bykill magnitude</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Extrapolated value</td>
<td>36.18</td>
<td>-0.03</td>
<td>26.34</td>
<td>-19.36</td>
<td>-20.14</td>
<td>-19.68</td>
<td>201.83</td>
</tr>
<tr>
<td>Expanded recreational fishery</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>10% increase</td>
<td>5.75</td>
<td>-0.05</td>
<td>5.15</td>
<td>3.63</td>
<td>-5.63</td>
<td>-5.86</td>
<td>-4.27</td>
</tr>
<tr>
<td>Duration of LE habitation</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0.60 year</td>
<td>-0.75</td>
<td>-0.19</td>
<td>-0.80</td>
<td>-0.34</td>
<td>0.01</td>
<td>0.02</td>
<td>0.11</td>
</tr>
<tr>
<td>0.40 year</td>
<td>DNC</td>
<td>DNC</td>
<td>DNC</td>
<td>DNC</td>
<td>DNC</td>
<td>DNC</td>
<td>DNC</td>
</tr>
<tr>
<td>LE immigration</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Includes ages 2 and 3</td>
<td>-2.89</td>
<td>-1.68</td>
<td>6.10</td>
<td>-1.90</td>
<td>-4.50</td>
<td>1.26</td>
<td>-3.15</td>
</tr>
<tr>
<td>Variance ratios</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Recreational</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1.15</td>
<td>-0.08</td>
<td>-0.02</td>
<td>-0.18</td>
<td>0.31</td>
<td>0.19</td>
<td>0.15</td>
<td>-0.24</td>
</tr>
<tr>
<td>Trap net</td>
<td>0.16</td>
<td>0.15</td>
<td>0.19</td>
<td>0.10</td>
<td>-1.23</td>
<td>0.03</td>
<td>0.72</td>
</tr>
<tr>
<td>Gill net</td>
<td>1.25</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1.25</td>
<td>0.04</td>
<td>-0.06</td>
<td>0.00</td>
<td>-0.01</td>
<td>0.00</td>
<td>-0.69</td>
<td>-0.36</td>
</tr>
<tr>
<td>0.75</td>
<td>-0.06</td>
<td>0.08</td>
<td>-0.02</td>
<td>0.03</td>
<td>0.02</td>
<td>0.84</td>
<td>0.56</td>
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<tr>
<td>Survey</td>
<td>1.15</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1.15</td>
<td>0.04</td>
<td>-0.05</td>
<td>0.01</td>
<td>-0.09</td>
<td>-0.02</td>
<td>-0.02</td>
<td>-0.28</td>
</tr>
<tr>
<td>Catchability deviations</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Recreational white noise</td>
<td>22.22</td>
<td>-10.07</td>
<td>12.21</td>
<td>-19.34</td>
<td>-15.91</td>
<td>-17.95</td>
<td>-47.00</td>
</tr>
<tr>
<td>Age-based $M$ values</td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$M_{\text{age}}$ as a prior</td>
<td>0.45</td>
<td>-0.03</td>
<td>0.01</td>
<td>-0.16</td>
<td>-0.40</td>
<td>-0.04</td>
<td>0.05</td>
</tr>
<tr>
<td>$M_{\text{age}}$ 95% lower limit</td>
<td>-15.51</td>
<td>-3.17</td>
<td>-9.94</td>
<td>7.93</td>
<td>8.77</td>
<td>8.01</td>
<td>15.99</td>
</tr>
</tbody>
</table>

The total fishing mortality (Figure 9), the omission of the other fisheries clearly underestimated overall fishing mortality, especially for younger ages of Walleye. This was most apparent in the annual estimates of natural mortality derived from the Brownie data (as the difference between $Z$ and $F$). This method of $M$ estimation passes any bias in $F$ to $M$ and in the instance of the Brownie model resulted in an overestimation of $M$. That greater value almost certainly reflected the fishing mortality of the trap-net, lake-wide gill-net, and commercial bykill fisheries. The difficulty in obtaining tag returns from commercial fisheries is widespread and methodologies for addressing this have had only limited success, especially in improved estimates of $M$ (Eveson et al. 2007). The elevated $M$ values of the time-varying $M$ model version resulted in the overestimation of the population. That version of the SCA model likely estimated the greater abundance to fulfill the observed fisheries and the supplied high annual $M$ values. While an annual estimate of $M$ might be desirable for use in a SCA model, in our case model selection procedures favored the age-based natural mortality expression.

Natural mortality rates are generally difficult to assess in a fish population and are often assigned an assumed set value for population modeling (Quinn and Deriso 1999; Nait et al. 2011). While we treated $M$ as known, we assumed age-specific natural mortality borrowed from Lake Erie because this proved to fit our data better than other expressions of $M$ (constant and time varying), but we were unable to fully evaluate the accuracy of these values. The DIC selection of the age-varying natural mortality model version may be a reflection that natural mortality of the Saginaw Bay stock does vary by age. It does not necessarily mean that those are the most correct values. Misspecification of $M$ can have considerable influence over model estimates (Clark 1999; Deroba and Schuegger 2013). Deroba and Schuegger (2013) evaluated reliance of a constant $M$ value on stock assessments.
through simulations and found it to bias estimates of SSB and F by as much as ±100% of the estimate for both long- and short-lived species. The degree of bias of a misspecified natural mortality may depend on how M was treated in the model and what the true values were. Deroba and Schueller (2013) reported that parameter bias was generally less when time-varying M values are misapplied than when misspecified as age varying or as a constant, and as such, bias affected estimates of SSB and recruitment.

The difficulty remains in obtaining reliable estimates of time- or age-varying M. Quinn and Deriso (1999) favored using tag-based studies to derive M, but in our instance, this failed to result in an accurate estimate of M because of the lack of representation of the competing fisheries. More stock assessment efforts are turning to estimating M within a SCA analysis, although typically this requires an informative prior value (Wang and Liu 2006; Lee et al. 2011; Maunder and Wong 2011; Vincent 2013). We evaluated this in our sensitivity analysis and found that when our specified values for M were treated as medians of a prior lognormal distribution, this did not materially affect our model point estimates. There was some increase in uncertainty but this was modest. In our instance, we concluded that this did not strengthen our model. We believe that there is more uncertainty associated with transferring estimates of M from Lake Erie to Lake Huron than was captured as estimation error for the Lake Erie estimates. We tested the impact of specifying M at the upper and lower bounds of the Lake Erie estimates and this did have a moderate effect on the abundance and exploitation estimates, suggesting that this is a consequential model term, especially if it were to turn out that natural mortality of Walleyes in Lake Huron was substantially different than in Lake Erie. Future improvements to the model may be better realized by development of stock-specific, age-based M values for Saginaw Bay Walleyes based on a tagging study following the methods of Vandergoot and Brenden (2014).

The time series mean estimate of total annual mortality for Saginaw Bay walleye was 37%, which was same as that from the Brownie model (Fielder 2014) for the same years suggesting that both models are in agreement for total mortality. Brownie model-based estimates of total annual mortality ranged more over time than those generated by SCA, but on average both estimates agreed suggesting Brownie estimation (from tagging analysis) could accurately estimate total mortality, but it overestimated M because of the lack of representation from fisheries other than the recreational.

The trap-net bykill decrease over time resulted from the large decreases in inner Saginaw Bay trap-net fishing effort (Fielder et al. 2014) and our assumption that this source of mortality was directly proportional to the inner Saginaw Bay trap-net fishing effort. Only the recreational fishing mortality increased substantially in recent years, a response to the stock recovery and increases in vulnerability as confirmed by trends in catchability (Figure 6). Generally recreational fishing effort has declined or been stable in recent years (Fielder et al. 2014) so the increasing recreational F must be a function of the time-varying catchability.

The initial peak abundance of Saginaw Bay Walleyes in 1988 is evident in the population estimate (Figure 4) as well as the biomass trends (Figure 12). Previously, when indices of abundance were noted to be high for those early years they were was dismissed as an artifact of Lake Erie immigration and/or increased catchability due to changes in water clarity stemming from dreissenid mussel colonization in 1993 (Fielder et al. 2000; Fielder and Thomas 2006). Our version of the SCA model generated these estimates of abundance and biomass specific to the Saginaw Bay stock, effectively factoring out any effect of Lake Erie fish. Similarly, the utilization of a random-walk procedure for application of changing catchability was intended to allow for any change in catchability stemming from dreissenid colonization and appears to have achieved that for the survey CPUE (Figure 6). In spite of these efforts, the model is still projecting high abundance at a time when generally the Walleye population was still regarded as unrecovered. Alternatively, if our assumption of time-varying catchability in the recreational fishery is mistaken and the white-noise depiction is more accurate, then the abundance in recent years is greater, suggesting that abundance in the early years was not similar to the more recent recovery.

Operating on the premise that recreational fishery catchability was in fact time varying, then this analysis forces us to consider that abundance of the Saginaw Bay Walleye stock most likely was genuinely substantial in those early years of our time series. While it was believed that the fishery was dependent on stocking until 2003 (Fielder 2002; Fielder and Thomas 2014), the use of oxytetracycline marking to identify hatchery fish in stocking evaluations was not available until 1997 (Fielder 2002). Consequently it is difficult to rule out a surge in reproductive success early in the time series. While the abundance estimate in 1988 rivaled the peak of the more recent recovery in 2007, earlier biomass was much greater in both total and spawning stock than during the more recent resurgence (Figure 12). This suggests that the high abundance in 1988 was not merely due to large numbers of young fish but was comprised of mature fish and older or fast-growing fish. Recruitment estimated by the SCA model at age 2 indicated year-class strength in 1984–1986 that was on the same magnitude of some recent years (Figure 11). The downward decline of abundance in the preceding years is consistent with the lower recruitment in the same years. Overall, the phenomenon illustrates that gains in abundance can be lost if recruitment fails to remain strong, at least periodically. The more recent decline in recruitment does not bode well for the on-going recovery of the Saginaw Bay Walleye stock. Fielder et al. (2007) forecasted that recruitment should remain strong as long as Alewives remain scarce, but Fielder and Thomas (2014) suggested that recent lower recruitment may be reflecting density dependence in the stock-recruitment relationship.
Failure of the attempt to strengthen the baseline SCA model by integrating auxiliary information in the form of tag returns raises the question of why these data did not have the intended benefit. We followed the recommendations of Maunder (1998) and Maunder and Punt (2013) for the optimal methods of incorporating tag returns as estimating the probabilities within an SCA model for the corresponding likelihood component, but this still resulted in a poor fit. Customarily if the addition of information reduces the fit of the model, it suggests conflicting or contradictory dynamics (Richards 1991; Schnute and Hilborn 1993; Haddon 2001). Homogeneity of capture probability is a fundamental assumption in tag-return analysis (Brownie et al. 1985) and the tag-based method equivalent to the assumption of single-stock estimation within SCA. This raises the question of how representative the Tittabawassee River spawning run of Walleyes (used as the tagging source) is of the rest of the bay’s population. There are other reproductive sources of Walleye within the bay (Fielder 2002). The operational premise in the management of the bay’s Walleye fishery to date is (1) that the combined reproductive sources operate with a single dynamic (i.e., as a single population), and (2) that the Tittabawassee River is the single largest source and would be most reflective of the bay’s Walleye population. Recent attempts to better understand the mix of reproductive sources within Saginaw Bay, based on otolith microchemistry methods, have suggested that the Tittabawassee River may not be the single greatest reproductive source. (B. Murry, Central Michigan University, personal communication).

New information on movement dynamics of Tittabawassee River Walleyes from a telemetry study suggested that fish are exposing themselves to certain fisheries and not others, by virtue of movement choices each year (Hayden, personal communication). Variable spatial structure of fish stocks complicates stock assessment and can be difficult to account for (Goethel et al. 2011). Accounting for movement of fish, usually from source locations to harvest or “sink” localities in stock assessment typically involves the incorporation of a movement matrix (Quinn et al. 1990; Quinn and Deriso 1999; Bence et al. 2011) and is regarded to be among some of the challenges of the future of stock-assessment modeling in fisheries (Quinn 2003). Such movement can have implications for management of the stocks (Wilberg et al. 2008), and is a challenge to the assessment of other species in the Great Lakes as well (Nalepa et al. 2005) and for Walleye in other locations (Thomas et al. 2011). Some investigators have resorted to entirely different modeling approaches to compensate for the mixing of stocks (Michielsens et al. 2006; Molton et al. 2012). In our instance, we concluded that attempting to use auxiliary information from one specific breeding source in our SCA objective function exposed the differences in dynamics and confounded the model’s estimation. Fielder (2014) has recognized this limitation and has recommended a diversification of source spawning runs for the future continuation of that tagging study. Better stock definition for Walleye is needed in Lake Huron, with the definition not only determined by genetic or microchemistry analyses but by differences in population metrics such as mortality, exploitation patterns, and movement.

Structure of the Saginaw Bay baseline SCA model exhibited sensitivity to only certain components of the joint likelihood function (among data sources). The failure to result in an iterative convergence in just three sensitivity trials suggests that the model structure is reasonably robust. The baseline SCA model is complex, however, given the four fisheries. It is difficult to say how the 181 parameters are interrelated during the model-fitting process. Detailed analysis of parameter correlation may disentangle those relationships, but it is apparent from the sensitivity analysis that the model is generally consistent with its convergence. Future work on this model might explore whether similar estimates and confidence could be obtained with a simpler model or achieve greater resiliency. Key assumptions in this baseline model appear to include the bykill values used with the larger extrapolated year-round values that resulted in a larger Saginaw Bay Walleye population estimate. From this, it might be concluded that the estimates of the baseline are conservative in that relaxed assumptions would tend to lead to a larger estimated population.

The development of an SCA model to describe the Saginaw Bay stock of Walleye in Lake Huron is a significant advancement in the assessment of this population. Not only has it offered age-based estimates of mortality rates and abundance, but it has also helped shed light on deficiencies of the Brownie model and biases that affect those estimates. The integrated version did not result in an improved model in this instance, but if the improvements in the Brownie model suggested by Fielder (2014) are achieved, future integration may still be possible. The SCA models are often used as the basis for forecasting models that allow evaluation of alternative fishery management strategies. Estimates like those generated from our SCA analysis would be essential in developing such a model. Management choices for Walleye in most of the Michigan waters of Lake Huron have been, to date, primarily made using a fixed rule (e.g., length limit, bag limit, and season closure in the spawning rivers) for the recreational fishery, and a yield allowance for bycatch in the tribal gill-net fishery in the northern portion of the lake. A simulation model based on the availability of estimated dynamics including recruitment, abundance, and mortality rates would assist managers to design harvest regulations that are more state based, and even address allocation if different jurisdictions ever feel that is necessary. Ultimately, the utility of this assessment model and its estimates will depend on fishery managers’ willingness to advance management to keep pace with the information stemming from the assessment of this stock.

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REFERENCES


