Canadian Journal of Fisheries and Aquatic Sciences
Journal canadien des sciences halieutiques et aquatiques

Simulation testing the robustness of a multi-region tag-integrated assessment model that exhibits natal homing and estimates natural mortality and reporting rate

Journal:	<i>Canadian Journal of Fisheries and Aquatic Sciences</i>
Manuscript ID	cjfas-2016-0297.R3
Manuscript Type:	Article
Date Submitted by the Author:	09-Feb-2017
Complete List of Authors:	Vincent, Matthew; Michigan State University, Department of Fisheries and Wildlife Brenden, Travis; Michigan State University, Department of Fisheries and Wildlife Bence, James; Michigan State University
Keyword:	TAGGING < General, STOCK ASSESSMENT < General, MARK-RECAPTURE < General, POPULATION DYNAMICS < General, POPULATION STRUCTURE < General

SCHOLARONE™
Manuscripts

Simulation testing the robustness of a multi-region tag-integrated
assessment model that exhibits natal homing and estimates natural
mortality and reporting rate

Matthew T. Vincent

vince151@msu.edu Quantitative Fisheries Center, Department of Fisheries and Wildlife,
Michigan State University, 375 Wilson Rd., UPLA Room 101,
East Lansing, Michigan, USA, 48824-1101 ¹

Travis O. Brenden

brenden@anr.msu.edu Quantitative Fisheries Center, Department of Fisheries and
Wildlife, Michigan State University, 375 Wilson Rd., UPLA Room 101,
East Lansing, Michigan, USA, 48824-1101

James R. Bence

bence@msu.edu Quantitative Fisheries Center, Department of Fisheries and Wildlife,
Michigan State University, 375 Wilson Rd., UPLA Room 101,
East Lansing, Michigan, USA, 48824-1101

¹Corresponding author: Matthew T Vincent (email: mtvincen@vt.edu, Telephone: 517-355-0003).

Abstract

The influence of model complexity on Integrated Tagging and Catch-at-Age ANalysis (ITCAAN) parameter estimation is poorly understood for populations exhibiting natal homing. We investigated ITCAAN performance under varying levels of movement, degree of similarity in population productivities, data quality, spatial complexity in parameterization, and whether natural mortality and/or reporting rates were fixed at actual values, estimated, or misspecified. Dynamics of four populations with natal homing that intermixed during periods of harvest were simulated based on Lake Erie walleye (*Sander vitreus*). Our results suggest, when high quality tagging data are available, ITCAAN models are able to simultaneously estimate movement rates, natural mortality and tag reporting rates, though accuracy and precision of model estimates will decrease with greater model complexity and fewer tags released. Additionally, ITCAAN models may have difficulty estimating individual population abundances under certain movement rates when population productivities are vastly different. ITCAAN models that estimate natural mortality and reporting rates may perform best with similar sized populations and when data are available to assist the estimation of reporting rates.

Introduction

Fishery scientists and managers commonly assume fish harvested in a single management unit originate from an isolated spawning population (Beverton and Holt 1957). The validity of this assumption has come under increased scrutiny due to recognition of stock complexity (Cadrin et al. 2004; Goethel et al. 2011; La Valley and Feeney 2013; Haponski and Stepien 2014) and the migratory behavior exhibited by both freshwater and marine species (Haist et al. 1999; Punt et al. 2000; McGarvey et al. 2010; Hayden et al. 2014; Vandergoot and Brenden 2014; Goethel et al. 2015a). Numerous simulation studies have shown that ignoring spatial complexity of intermixed populations can result in overexploitation of less productive populations (Ying et al. 2011; Guan et al. 2013; Hulson et al. 2013; Molton et al. 2013; Li et al. 2014). The collapse of some high profile fish stocks such as Atlantic cod (*Gadus morhua*; Fu and Fanning 2004; Hutchinson 2008) and many Pacific salmon populations (*Oncorhynchus* spp.; Morishima and Henry 1999) are believed to have in part resulted from inadequate accounting of spatial complexity arising from movement. This in turn led to the development and use of assessment methods that account for the spatial complexity of migratory behavior in order to reliably estimate abundances, mortality components, and/or movement rates of multiple populations in mixed stocks (Hampton 1991; Goethel et al. 2011; Maunder and Punt 2013).

Some terms will be explicitly defined for clarity, because many definitions exist. A stock is defined, following that of Cadrin et al. (2004), as an exploited fishery unit defined by the region of harvest. A population is defined as a self-sustaining group of fish that interbreed and share similar life history characteristics. Thus a stock may be composed of individuals from multiple populations. An intermixed fishery is any fishery that harvests individuals from multiple populations while operating within a single management unit.

Integrated tagging and catch-at-age analysis (ITCAAN) assessment models incorporate return/recovery information from tagging studies as data components within statistical catch-at-age (i.e., integrated) assessment models. These models have been used to estimate the abundance and mortality rates of multiple species (Maunder 2001; Fielder and Bence 2014; Goethel et al. 2015a). However, parameter estimability in ITCAAN models has not been rigorously tested, and studies conducted have generally assumed a particular movement dynamic. Previous simulation analyses of ITCAAN models have all assumed reproductive mixing of multiple subpopulations when testing model performance (Maunder 2001; Hulson et al. 2011; 2013; Goethel et al. 2015b). Reproductive mixing of multiple subpopulations occurs when individuals from a spawning populations move to a new region and then spawn in the new region and stay there indefinitely (i.e., individuals become part of the spawning population in the region; Goethel et al. 2011). Alternatively, populations can mix among regions during periods of harvest but return to their natal regions to reproduce each year. This type of movement has been referred to as population overlap (Porch et al. 2001) and overlap-

ping populations with natal homing (Goethel et al. 2011). Spatially explicit models that incorporate natal homing movement characteristics do not always perform the same as models with reproductive mixing of multiple subpopulations (Cope and Punt 2011; Ying et al. 2011; Guan et al. 2013; Li et al. 2014). Testing parameter estimability of ITCAAN models accounting for natal homing and other movement dynamics is needed as differences in model structure may affect model performance.

The inclusion of tagging data in ITCAAN models ostensibly allows the estimation of parameters beyond those generally estimated in traditional assessment models; however, the extent of parameterization that can accurately be estimated by incorporating tagging data is uncertain and requires investigation. Mixing rates, natural mortality, and reporting rates are parameters that potentially can be estimated in ITCAAN models. Estimation of mixing or movement rates of populations is an essential process for a spatially-explicit catch-at-age assessment model, and incorporating tagging data will likely inform the estimation of these rates. Catch-at-age models typically require an *a priori* estimate of natural mortality (Doubleday 1976; Deriso et al. 1985), though attempts have been made to estimate natural mortalities using information inherent in the age composition with varied success (Wang and Liu 2006; Lee et al. 2011). However, tag-recovery data frequently are used to estimate the natural mortality rates of tagged cohorts of fish (Hoenig et al. 1998; Latour et al. 2001; 2003; Frusher and Hoenig 2003; Vandergoot and Brenden 2014). ITCAAN models that use both harvest age composition and tag-recovery data may result in reliable estimates of natural mortality. Fishery reporting rates of recovered tags are additional parameters that are seemingly estimable in ITCAAN models (Goethel et al. 2015b). The extent that parameters such as movement, tag reporting, and natural mortality rates can be reliably estimated in combination with each other or with additional parameters such as abundance and fishing mortality for multiple stocks is not currently understood. It is possible, even likely, that some of these parameters may be confounded and the estimability of some parameters may be affected by the degree of movement among or differences in relative size of the fish populations.

The goal of our research was to evaluate the estimability of model parameters within a release-conditioned ITCAAN model under a range of conditions. We used information from walleye (*Sander vitreus*) populations in the Laurentian Great Lakes of North America as the basis for simulating population dynamics and associated time series of data. However, the operating model was intended to be sufficiently generic with stochasticity in both annual recruitments and fishing mortalities for the results to be applicable elsewhere. Simulations were conducted exploring how bias and precision of parameter estimates were affected by the following: 1. movement rates and whether movement, natural mortality, and/or reporting rates were estimated or treated as known and fixed quantities; 2. misspecification of reporting rate or natural mortality when treated as known and fixed quantities in the ITCAAN model; 3. varying levels of data quality, including tagged cohort size; 4. assumptions as to spatial complexity of reporting rate and natural mortality

parameters estimated in the ITCAAN model; and 5. parity in productivities of the spawning populations (i.e., equal stock-recruitment relationships).

Lakes Erie and Huron Walleye

Walleye is a piscivorous keystone species that is harvested commercially and recreationally throughout the Great Lakes (Pandit et al. 2013). Walleye spawn in early spring either in rivers or on shallow rocky reefs. Post spawning walleye distribute throughout the lakes (Wang et al. 2007; Zhao et al. 2011; Vandergoot and Brenden 2014; Hayden et al. 2014) but display a high degree of natal homing each year while spawning (Stepien and Faber 1998; Haponski and Stepien 2014; Hayden et al. 2014).

Two of the largest and most valuable walleye fisheries in the Great Lakes are in Lakes Erie and Huron. Tagging studies have documented the movement of walleye between Lakes Erie and Huron via the Detroit River, Lake St. Clair, and St. Clair River (Wang et al. 2007; Vandergoot and Brenden 2014; Hayden et al. 2014). Lake Erie is generally regarded as consisting of three basins (western, central, and eastern) that increase in depth moving eastward, but decrease in walleye abundance. The western basin population is estimated to be on the order of tens of millions of fish (Wills et al. 2016), whereas abundance for the eastern basin population of Lake Erie is closer to tens of thousands of fish (Zhao et al. 2011). Abundance of walleye in Lake Huron has been estimated to be approximately one to four million fish (Fielder and Bence 2014). For some walleye spawning populations in the western basin of Lake Erie, movement rates to the eastern basin of Lake Erie and Lake Huron were estimated at around 1–2% (Wang et al. 2007; Vandergoot and Brenden 2014). Given the differences in walleye abundance between the Lake Erie basins and Lake Huron, even this low rate of movement means that a considerable amount of the harvest in these other regions is fish from the western basin population (McParland et al. 1999; Brenden et al. 2015). There is developing interest in using ITCAAN models as the basis for management decisions for Lakes Erie and Huron walleye because of the degree of movement between and within the lakes and the value of the respective fisheries.

Methods

The simulation framework used in this research consisted of an operating model that generated and tracked the true dynamics of fish populations and tagged cohorts. Given the true dynamics from the operating model, observed time series of data (e.g., fishery harvest in numbers caught, fishery harvest age composition, tag-recovery data) were generated. These data were then used in a release-conditioned ITCAAN model to estimate dynamics of the fish populations. The spatial framework of the simulation consisted of four spawning populations that overlapped with four regions of harvest (Figure 1). After spawning at the beginning of

the year, individuals from each of the spawning populations could move to any of the harvest regions. For simplicity, a single fishery was assumed to operate in each region. Catch-at-age models in the Great Lakes region are generally based on abundance. Even species for which observed harvest is biomass based (e.g., yellow perch (*Perca flavescens*)), predicted harvest is calculated based on assumed weight-at-age or weight-at-length values (i.e., growth is not dynamically modeled in the assessment models). Thus, for our research both the operating and ITCAAN models were predominantly abundance based. The four spawning populations differed considerably with regards to productivity (i.e., stock-recruitment steepness) and equilibrium spawning stock biomass, although as part of a sensitivity analysis we explored how results changed when stock-recruitment parameters were identical among spawning populations. Characteristics of the four spawning populations and harvest regions were based on estimated parameters for Lakes Huron and Erie walleye populations and fisheries exploiting these stocks. The first population had characteristics that were similar to the spawning population in Saginaw Bay of Lake Huron. The second population was based on the very productive western basin of Lake Erie, whereas the third and fourth populations were based respectively on the central and eastern basins of Lake Erie (Figure 2). Weights and maturity at age were assumed to be spatially and temporally constant in the operating and ITCAAN models.

The operating model generated a 40-year time period of observations, with the ITCAAN model applied once at the end of the time period. Both the operating and ITCAAN models followed the dynamics of age-2 to age-7 fish, with the last age class an aggregate group including age-7 and older fish. The operating model was programmed in R version 2.15.1 (R Development Core Team 2016), whereas the ITCAAN model was programmed in AD Model Builder version 11.5 (Fournier et al. 2012). Code for the operating model and ITCAAN model can be found in the Supplementary Material. Symbols and equations used to model the dynamics for both the operating model and ITCAAN model are presented in Appendix A. Parameter values assumed in the operating model and likelihood equations used within the ITCAAN model are presented in the Supplementary Material.

Operating Model

Recruitment for the spawning populations assumed Ricker stock-recruitment functions with spawners equal to the spawning biomass two years prior to the year of recruitment. An autoregressive recruitment deviation randomly generated for each population independently was also used to calculate annual reproduction (Equation A2.1). Consistent with information for walleye populations within Lakes Erie and Huron, recruitment steepnesses (i.e., productivities) of the individual populations were chosen so there was considerable variation among populations (Figure 2; Supplementary Material Table 2). Spawning site fidelity was assumed to be

100% with instantaneous return annually at the time of spawning. Recruitment deviations on a $\log_e$ scale for the spawning populations were generated from a first-order autoregressive process (Equation A2.2). Thorson et al. (2014) used a hierarchical Bayesian approach to estimate posterior distributions of mean autoregressive coefficients and innovations (uncorrelated errors) variances for a variety of exploited taxonomic orders. Values of the autoregressive coefficient (ρ_p) and innovations variances (σ_p^2) for each spawning population and simulation iteration for this project were randomly generated from the posterior distribution estimated for Percidae (Thorson et al. 2014). The mean of the autoregressive process, δ_y , was calculated such that it would have a mean of 1 when exponentiated to give a mean unbiased process (Thorson et al. 2016) and the variance of the stationary distribution would equal the variance randomly drawn from the posterior distribution estimated for Percidae. Spawning was assumed to occur at the beginning of the year.

Abundances at age for the spawning populations were calculated using standard exponential population models. Underlying equations accounted for movement and harvest of populations in multiple harvest regions with the older ages accumulating in the oldest age group (Equation A2.4 and A2.5). The apical fishing mortality rates for the harvest regions were randomly generated from first-order autoregressive processes (Equation A2.8), where the means of the processes were different for each region and were based on estimates from Lakes Erie and Huron (Supplementary Material Table 2). Assumed selectivities and catchabilities were based on estimated values for walleye in Lakes Erie (Wills et al. 2016) and Huron (Fielder and Bence 2014) and were used to simulate fishery effort data (Supplementary Material Tables 1 and 2). Movement was based on a box-transfer process that assumed instantaneous movement to harvest regions, in which fish remained for the rest of the year (Goethel et al. 2011). The proportion of the population that moved to each harvest region varied depending on the examined scenario (see Simulation Scenarios), but in all cases was assumed to be the same proportion to all non-natal regions for all populations, and was temporally and age invariant. Fishery effort data were generated assuming a lognormal observation error (Equation A2.10). A fishery-independent survey was assumed to be conducted on each harvest region during October when fish were intermixed, which collected a relative abundance time-series and age-composition data (Equation A2.12 and A2.13).

Cohorts of tagged fish from each spawning population were assumed to experience the same dynamics as the at-large populations (i.e., tagged individuals were fully mixed with the at-large populations). All tagging was conducted when fish were located in their spawning regions. Our baseline tagging rate was 2 000 fish per year and region, but lower tagging levels were considered for some scenarios (Table 1). Tags were allocated to different ages based on the real-world average proportion at age observed from tagged fish in Lake Erie (Supplementary Material Table 1). However, all ages were treated as a single release cohort in each year and region when simulating the data for the number of tags recaptured (Equation A2.15).

Tagging-induced mortality and tag shedding were assumed to not occur. Actual numbers of fish from a tagged cohort that moved to each harvest region after spawning were randomly generated from multinomial distributions with the underlying proportions equal to the assumed movement rates for that particular scenario (Equation A2.16). The probabilities of a tagged fish being harvested (Equation A2.17), surviving (Equation A2.18), or dying (Equation A2.19) in a harvest region were then calculated based on the fishing, total, and natural mortalities in a region. These probabilities (Equation A2.20) were used in a multinomial random number generator to determine the number of fish in each fate category (Equation A2.21). A binomial random variable based on an assumed fishery reporting rate with a sample size equal to the number of tags recovered was then used to determine the number of harvested fish that were reported (Equation A2.23). A reporting rate of 50% was assumed in the operating model for all examined scenarios and fisheries. The number of tagged fish that survived were then progressed to the next age and year (Equation A2.22). The number of tags never recovered was calculated as the number of tags released minus the total tags returned summed across year, age and region (Equation A2.24).

A limitation that we imposed on our simulations was that abundances for any of the four populations could not decrease to less than 40 000 fish. If this occurred, that iteration was discarded and another simulation created. An abundance of less than 40 000 fish would mean that more than 5% of a population was tagged within a year at the baseline tagging rate of 2 000 fish per year and region, which seemed an unrealistic tagging rate even for fish that exhibit natal homing.

We simulated data that were subject to observation error and available for all regions every year that were summed across populations (i.e., stock-specific not population specific values). The following data sources were used in the ITCAAN model: total harvest in number of fish, harvest age composition, fishing effort, survey index of abundance, survey age composition, and tag recovery data. The values and distributions assumed for each of the simulated data sources for examined scenarios are summarized in Table 2.

ITCAAN Model

The ITCAAN model used in this research was similar to that of Goethel et al. (2015a), but differed in that we modeled 100% natal homing, included more spawning populations and harvest regions, and in at least some scenarios accounted for a more complex model parameterization (e.g., estimating both natural mortality and reporting rates). The dynamics assumed in the ITCAAN model were similar to assumptions in the operating model (e.g., box-transfer movement, 100% spawning site fidelity, full mixing between tagged cohorts and at-large populations).

Annual recruitment in the ITCAAN model was estimated through a random walk process in which the

220 multiplicative random walk deviations were assumed to be from a lognormal distribution (Equation A2.3)
221 with the log-standard deviation fixed at 4. The last two years of recruitment in the ITCAAN model were set
222 equal to the mean recruitment for the previous three years for each population, which was necessary for the
223 model to converge with a positive-definite Hessian matrix. Abundances in the first modeled year for age-3 and
224 older fish were estimated as the product of a mean abundance and multiplicative age-specific deviations that
225 were assumed to be from a lognormal distribution and constrained to sum to 0 across ages (Equation A2.27).
226 Year-specific fishery catchabilities were modeled using a random-walk process (Equation A2.11), as advocated
227 by Wilberg and Bence (2006). Age-specific selectivities were estimated for ages 2 to 7 individually for each
228 fishery and were assumed constant through time. Depending on the examined scenario, natural mortality and
229 reporting rate were either estimated or set equal to assumed (sometimes misspecified) values in the ITCAAN
230 model. Region-specific survey catchabilities and age-specific survey selectivities were assumed constant over
231 time and were estimated parameters in all simulations. Movement rates, including the proportion staying
232 in the natal region, were estimated through a multinomial logit transformation that constrained movement
233 rates to be between 0 and 1 and to sum to 1 (Vandergoot and Brenden 2014). The formulation is similar
234 to Goethel et al. (2015a) except the parameter for movement to region 4 for all populations was set equal
235 to 0, instead of the residency parameter. Three parameters for each population were then transformed
236 into movement rates to the four regions so that the model was identifiable (Equation A2.14). As with
237 the operating model, movement rates were assumed to be temporally and age invariant. When estimated,
238 reporting rates were modeled using a logistic function, which constrained the reporting rate to be between
239 0 and 1.

240 Numbers of recovered tags were predicted based on the known number of tags released by age each
241 year, estimated population movement rates, survival estimates, and a fishery specific estimated reporting
242 rate (Equation A2.25). Proportion of yearly regional tags recovered and tags never recovered relative to
243 the total number of tags released were assumed to be multinomially distributed and were used in likelihood
244 calculations.

245 Highest posterior density estimation, which is also referred to as maximum penalized likelihood, was
246 used to estimate the parameters of the ITCAAN model. Diffuse upper and lower bounds were specified for
247 all parameters to keep the optimization algorithm from flat parts of the likelihood surface and to prevent
248 unreasonable parameter estimates. The objective function was the sum of multiple negative log-likelihood
249 and log-penalty components. Age compositions were modeled as multinomial distributions, while all other
250 data and parameter penalties were modeled as lognormal distributions (Supplementary Material Table 4).

251 An ITCAAN model was assumed to have converged if the maximum gradient across all parameters was
252 less than 0.05 and the model produced a positive-definite Hessian matrix. If the ITCAAN model for an

individual simulation did not converge based on these criteria, the results from that simulation run were discarded. Additional simulations were conducted until 1 000 iterations with a converged ITCAAN model were obtained. The total number of simulations needed to reach a sample size of 1 000 for each scenario, percent convergence, and the number of simulations rejected for the two conditions are presented in Table 1.

Simulation Scenarios

We evaluated ITCAAN model performance through scenarios grouped into five categories (Table 1). In the first group of scenarios, we explored how parameter estimates were affected by variation in movement rates in combination with whether movement, natural mortality, and/or reporting rates were estimated or treated as known quantities fixed at their correct values in the ITCAAN model. In the second group of scenarios, we explored sensitivity of parameter estimates to misspecification of reporting rates or natural mortalities when these parameters were assumed known in the ITCAAN model. We used a third group of scenarios to examine the influence of data quality on parameter estimates, and a fourth group to explore the ability to estimate spatially varying reporting rates and/or natural mortalities. We simulated a fifth group of just one scenario to examine the influence of assuming the same productivity (i.e. Ricker parameters) for all populations on parameter estimates.

Many parameters were consistent between simulation scenarios and differences are presented in Table 2. All scenarios assumed a natural mortality rate of 0.32 in the operating model and if the parameter was not estimated it was correctly specified in the ITCAAN model, except under scenarios RSensO and RSensU (reporting rate sensitivity to natural mortality over and under the true value, respectively; Group 2). The reporting rate in the operating model was 50% for all regions and years, which was correctly specified when not estimated except for scenario MSens (natural mortality sensitivity; Group 2). While fish were aggregated for spawning each year, 2 000 fish were tagged from each population every year, unless otherwise specified (Table 1; Group 3). The variance of simulated data and the effective sample size was consistent for most simulation scenarios but differed for a few scenarios (Table 2; Group 3). When the reporting rate was estimated in the ITCAAN model it was assumed to be a unique parameter for each region, unless otherwise specified (Table 1; Group 4). When natural mortality was estimated within the ITCAAN model it was assumed to be a single parameter across all regions, unless specified differently below (Table 1; Group 4).

Group 1: Varying Movement and Reporting Rate and Natural Mortality Estimation

We simulated a total of 20 scenarios to examine how assumed movement rates, and the estimation of movement, natural mortality, and/or reporting rates affected ITCAAN performance: four movement rates

(the percentage of the populations that moved to each non-natal region, (1%, 5%, 10%, and 20%) were each crossed with five estimation approaches for the ITCAAN model (MvFix: fixed movement, natural mortality, and reporting rate (only scenario with fixed movement); MRFix: fixed natural mortality and reporting rate but movement estimated; MEst: estimated natural mortality and movement but known reporting rate; REst: estimated reporting rates and movement but known natural mortality; BEst: both natural mortality, and reporting rate estimated along with movement). When movement, natural mortality, or reporting rate were treated as known, they were fixed at their correct value (i.e., the value assumed in the operating model) in the ITCAAN model. When presenting the results for these scenarios, we use the abbreviations for each estimation approach followed by the assumed movement rate (e.g., MRFix1 scenario refers to 1% movement rate where movement is estimated but natural mortality and reporting rate are assumed known and fixed in the ITCAAN model).

Group 2: Sensitivity to Misspecified Reporting Rate and Natural Mortality

Our second group of scenarios explored the consequences on parameter estimates of misspecifying reporting or natural mortality rates in the ITCAAN model when these parameters were treated as fixed and known. This group had three scenarios, all with data generated assuming the highest movement rate (20%). In the first scenario, a reporting rate of 75% was assumed in the ITCAAN model when the true reporting rate in the operating model was 50% for all fisheries. We conducted this scenario (referred to as the MSens scenario) to determine the sensitivity of natural mortality estimates and other parameter estimates to reporting rate misspecification. We used the two other scenarios to explore the sensitivity of reporting rate and other parameter estimates when natural mortality in the ITCAAN model was specified too low [RSensU scenario: reporting rate sensitivity to natural mortality specified under the true value (i.e., 0.16 in the ITCAAN model versus 0.32 in the operating model)] or specified too high [RSensO scenario: reporting rate sensitivity to natural mortality specified over the true value (i.e., 0.48 in the ITCAAN model versus 0.32 in the operating model)].

Group 3: Data Quality

The third group of scenarios examined sensitivity of parameter estimates to differing levels of data quality, including fewer tags released per region and year, smaller effective sample size for age composition data, and/or larger measurement error in fishing effort, harvest, and survey indices of abundance data. In these scenarios, reporting rates and natural mortalities were always estimated in the ITCAAN model and assumed a 20% movement rate in the operating model. We conducted four scenarios with smaller annual tagged cohort size per region than in scenario Group 1: 1 500, 1 000, 500 and 250 tags per region and year. These

scenarios were abbreviated by T, for tagging, followed by the number of tags released per year and region (e.g., T1500 scenario refers to 1 500 tags being released per year and region). We conducted a scenario in which the effective sample size of the harvest and survey age compositions was reduced to 50 in the operating and ITCAAN models but 2 000 tags were still released per year and region. We refer to this as the ESS50 scenario. The last scenario in this group was referred to as the high variance scenario (HighVar). For this scenario, 2 000 tags were released per year and region; however, the measurement error associated with the effort and survey index data was double that of all other examined scenarios and the effective sample sizes of the harvest and survey age compositions were set to 50 in the operating and ITCAAN models (Table 2).

Group 4: Spatial Complexity in Reporting Rates and Natural Mortalities

The fourth group of scenarios evaluated the consequences of estimating spatially varying natural mortality and/or reporting rates in the ITCAAN model. Three scenarios were conducted for this group that differed with respect to spatial complexity considered in the ITCAAN model, all with a 20% movement rate. In the first scenario (RC_MC scenario: reporting rate constant and natural mortality constant), a single natural mortality and reporting rate was estimated in the ITCAAN model that was applied to all regions. In the second scenario (RC_MU scenario: reporting rate constant and natural mortality unique), a single reporting rate was estimated that was applied to all regions but unique natural mortality rates were estimated for each region in the ITCAAN model. In the third scenario (RU_MU scenario: reporting rate unique and natural mortality unique), unique natural mortality and reporting rates for each region were estimated in the ITCAAN model. The results from these scenarios were compared to those from the BEst20 scenario because it estimated a single natural mortality but spatially unique reporting rates. The RC_MC, BEst20, RC_MU, and RU_MU scenarios represent a gradient in parameterization complexity to examine ITCAAN model sensitivity to spatial complexity.

Group 5: Equal Productivity

The fifth group of scenarios consisted of just a single scenario (EqProd scenario: Equal productivity) that investigated how parity in productivities among the four populations affected ITCAAN performance. For this scenario, all populations were assigned the same stock-recruitment parameters (i.e., Ricker α and β parameters for population 2 in other scenarios, Figure 2). Unique autoregressive parameters (ρ_p) and innovations variance parameters (σ_r^2) for each of the populations were still generated as previously described.

Performance Metrics

The performance of the ITCAAN model was explored by comparing parameter estimates to the true values assumed in the operating model. For the sake of brevity, we discuss the precision and accuracy in estimates of annual recruitment, movement, natural mortality, reporting rates, and total abundance (i.e., abundances summed over all regions); results for all other parameters are included in the Supplementary Material. Parameters not presented either showed no bias in estimates or biases similar to recruitment, though not always in the same direction. The percent relative error estimate (REE) for all parameters except movement were calculated by subtracting the true value from the estimate and then dividing by the true value and multiplying by 100. Error in movement rate estimates was assessed (and presented) as actual error, estimate minus true, to facilitate comparisons across scenarios, though movement REE are presented in the Supplementary Material. Errors in parameters that were age-specific (e.g., selectivity, results shown in Supplementary Material) or year-specific (e.g., recruitment) were calculated for each age or year separately for the 1 000 simulations and then aggregated by region for summarization and plotting. For example, the boxplots of recruitment show 40 000 values, i.e. 40 years of recruitment times 1 000 iterations. The median and interquartile ranges (IQR) of the REE and actual error of the 1 000 simulated datasets were used to summarize model bias and precision, respectively, for the scenarios.

Results

Operating Model Trends in Abundance

To meet the condition that no more than 5% of a population was tagged (i.e. an abundance greater than 40 000 for all populations and years) approximately 7% of the simulations that were conducted were discarded from the analysis. However, the number rejected are not included in the number of runs required to reach 1 000 simulations in Table 1 because this was a result of the operating model and not the ITCAAN model. Abundance in the operating model varied widely between year, population, operating model scenario, and simulation iteration. As a result, the proportion of the population that was tagged also varied by these conditions. For scenarios that released 2000 tags per population, the median proportion of the population tagged was 0.093%. For the scenario that released 250 tags per population each year (T250), the median proportion of the populations tagged was 0.013%.

Assumed movement level affected annual trends in abundance in the operating model for the four populations (Figure 3). When averaged over all iterations, decreases in abundance were observed for all populations under all movement rates, but the level of depletion varied by movement rate and region. For populations

1, 2 and 3, median abundance generally stabilized after approximately 10 years. However, for the least productive population (population 4), abundance declined throughout the duration of the simulations and the magnitude of depletion was greatest under high movement. Average exploitation rates were different for each region and were higher in regions where the natal population was more productive. Therefore, at higher movement rates a larger proportion of the population would be exposed to higher rates of exploitation, which lead to greater declines in abundance. On a per simulation basis, interannual variability in abundance levels could be quite large due to the autoregressive processes of recruitment and fishing mortality (Figure 3). This variability matches observed walleye population dynamics in Lakes Erie (Zhao et al. 2009; 2013; Wills et al. 2016) and Huron (Fielder and Bence 2014).

ITCAAN Model Convergence

The convergence rate of the ITCAAN model (i.e., proportion of simulations where both the maximum gradient of the parameters was less than 0.05 and a positive-definite Hessian matrix was produced) exceeded 95% for all scenarios except those assuming 1% movement rates, for which the convergence rate was approximately 75% (Table 1). At the 1% movement rate, a maximum gradient larger than 0.05 was the main factor causing non-convergence, though nearly all iterations had a positive-definite Hessian matrix. At movement rates of 10 and 20%, failures of the ITCAAN model to converge generally was a consequence of neither criteria being met. Whether movement, natural mortality, and/or reporting rate were estimated by the ITCAAN model did not appear to have a major influence as to whether ITCAAN models converged (Table 1). Similarly, convergence rates of the ITCAAN model did not appear to be influenced by the conditions assumed in scenario Groups 2 through 5, as failed convergence rates ranged from 1% to 5% across the scenarios (Table 1).

ITCAAN Model Performance

Recruitment Relative Error

Movement rates had a large effect on both the bias and precision of recruitment estimates (Figure 4). Under a 1% movement rate when natural mortality and reporting rate were estimated (BEst1 scenario), recruitment estimates for the four populations were mostly accurate and precise. As movement rate increased, the level of imprecision increased and the magnitude of bias increased, with the direction of bias depending on the size of the population. For population 2 (i.e., the largest and most productive population), recruitment was generally negatively biased, whereas recruitment estimates for the smaller populations were positively biased (Figure 4). The degree of bias and imprecision were generally the greatest when reporting rates were estimated, either alone or in conjunction with natural mortality. The precision of recruitment also decreased

when reporting rate was estimated and became more biased for some regions (Figure 4).

When reporting rates were specified (i.e., not estimated) too high in the ITCAAN model (1.5 times the true value), recruitment for population 2 was positively biased (MSens population 2: median REE = 36.29%; Figure 5), which was the opposite direction of the bias observed in either the MEst20 or BEst20 scenarios. When natural mortality was specified at 0.5 times the true value, recruitment was strongly negatively biased for population 2 (RSensU population 2: median REE = -61.85), which was nearly double the bias observed for the BEst20 scenario (BEst20 population 2: median REE -32.2%). When natural mortality was specified at 1.5 times the true value, the median recruitment was strongly positively biased (RSensO population 2: median REE = 112%), and among the least precise among the evaluated scenarios for all populations (Figure 5).

The effects of data quality on recruitment REE from the ITCAAN model depended on the scenario under consideration. Releasing fewer tags per region and year magnified the bias and decreased the precision in recruitment estimates for all populations (Figure 5). Reducing the age composition effective sample size to 50 resulted in slightly larger negative bias of population 2 recruitment for the ESS50 scenario compared to the BEst20 scenario (ESS50 population 2: median REE = -36%). Compounding a smaller effective sample size with greater levels of measurement error had only a marginal effect on bias (HighVar population 2: median REE = -38%). Reducing the amount of tags released had a much larger impact on recruitment estimates than reducing the effective sample size or increasing the variance of data sources (Figure 5).

The degree of spatial complexity assumed for natural mortality and reporting rates in the ITCAAN model affected bias and precision of recruitment estimates, with results most sensitive to spatial complexity in reporting rates (Figure 5). When reporting rates were estimated as spatially constant, median REE in recruitment for population 2 were approximately -15%. Conversely, the median REE in recruitment for population 2 when reporting rates were estimated as spatially unique was approximately two times greater. Similar patterns were observed for the other populations. The precision of recruitment estimates for population 2 was relatively unaffected by the degree of spatial complexity; however, for the three smallest populations precision decreased as spatial complexity increased (Figure 5).

When all populations were assumed to have equal parameters in the Ricker stock-recruitment functions, recruitment estimates were unbiased across all populations under a 20% movement rate (EqProd populations 1–4: median REE = -2% to -3%). For population 2, the imprecision in recruitment estimates was the second largest of the evaluated scenarios. However, for all other populations, the recruitment estimates were the most precise among the evaluated scenarios (EqProd populations 1–4: IQR REE ~ 60%).

Movement Rate Actual Error

Estimates of the movement rate to regions were largely accurate regardless of the assumed movement rate and whether reporting rates and/or natural mortality were estimated or treated as known (Figure 6). Median actual errors were within -0.30 and 0.13 for all examined scenarios and regions examined in Group 1 scenarios. Precision in the movement rate estimates decreased as the level of assumed movement increased. A small level of bias in the movement rates into each of the regions was observed when reporting rates were estimated but natural mortality in the ITCAAN model was fixed at its known value at the highest movement rate (REst20). The direction of bias in movement to each region was in the same direction as the bias in recruitment for natal populations in that region. These biases were not observed when both natural mortality and reporting rates were estimated (BEst20; Figure 6).

Estimates of movement to regions were also accurate and precise for simulations conducted as part of scenario Groups 2 through 5. Some biases resulted in movement to region 1 and 2 when either natural mortality or reporting rates were misspecified (Figure 7). The precision of movement estimates was relatively consistent among scenarios when the number of tags released in each region was 2 000 (BEst20 region 2: IQR actual error = 1.44). However, when the number of tags released was reduced to 250 in each region the IQR of movement actual error nearly tripled (T250 region 2: IQR actual error = 3.93). Despite this, the movement estimates from the examined scenarios were precise and also remained relatively unbiased (Figure 7).

Natural Mortality and Reporting Rate Relative Error

When estimated in the ITCAAN model, natural mortality was generally accurate and precise across each of the Group 1 scenarios (Figure 8). When natural mortality was estimated and reporting rate was fixed at its true value, the estimates of natural mortality were very precise (MEst1, MEst5, MEst10 and MEst20: IQR REE = 0.92% to 0.96%). However, estimating both reporting rates and natural mortality decreased the precision of natural mortality estimates, with the degree of imprecision increasing as movement rates increased. Similar results with respect to precision were observed for reporting rate, i.e. precision decreased when both natural mortality and reporting rate were estimated and movement rate increased (Figure 8). Unlike natural mortality estimates, some bias in reporting rates occurred with bias generally increasing as movement rates increased. The bias in reporting rate was most noticeable for region 2 under a 20% movement rate when reporting rate was estimated alone or in conjunction with natural mortality (REst20 and BEst20 region 2: median REE $\approx$ -14%). Conversely, median relative errors in reporting rates for the other regions were generally within $\pm$ 5%.

Estimates of natural mortality were highly affected by incorrectly specifying the reporting rate in the ITCAAN model (Figure 9). When reporting rate was misspecified at 1.5 times its actual value, natural mortality estimates were positively biased (MSens: median REE = 20.85%). Similarly, reporting rate estimates were affected when natural mortality was fixed at an incorrect value in the ITCAAN model. When natural mortality was fixed at half of its true value (RSensU), reporting rates were negatively biased. Conversely when the natural mortality value in the ITCAAN model was fixed at 1.5 times the true value (RSensO), the estimated reporting rates for all regions had median REEs near 100%. This would imply that the model was estimating that all tags recaptured were reported (i.e., 100% reporting rate) for all regions.

The number of tags released per region and year affected the precision of the natural mortality and reporting rate estimates and had a slight influence on bias of reporting rate estimates (Figure 9). Decreasing the number of tags released resulted in less precise estimates of natural mortality and reporting rate. A slight negative bias was also observed for region 2 as fewer tags were released. Reducing the effective sample size of the age compositions or doubling the error in the other data sources had little influence on estimates of natural mortality and reporting rate.

Among the Group 4 scenarios, the largest biases in natural mortality and reporting rate were observed for the scenario where both natural mortality and reporting rate were estimated as spatially unique parameters (RU_MU). Natural mortalities and reporting rates were both negatively biased in region 2 but positively biased in all other regions for scenario RU_MU (Figure 9). The least amount of bias in reporting rate was observed among the Group 4 scenarios when the parameter was assumed to be spatially constant in the ITCAAN model (RC_MC and RC_MU). IQR REE for both natural mortality and reporting rate increased as the complexity (i.e., number of parameters) of the estimation model increased for the respective parameters.

Reporting rate estimates were unbiased for the scenario with equal Ricker stock-recruitment parameters (EqProd). The IQR REE of reporting rate were consistent across the four regions. Estimation of natural mortality for the EqProd scenario was unbiased (EqProd: median REE = -0.40%).

Total Abundance Relative Error

Bias and precision of total abundance estimates varied by examined scenario (Figure 10). For all movement rates examined in the Group 1 scenarios, there was a slight negative bias in total abundance estimates. The degree of bias increased with higher movement and when reporting rates were estimated regardless of whether natural mortality was estimated or fixed in the ITCAAN model at its true value. The precision in total abundance was relatively similar when reporting rate was not estimated (MvFix, MRFix, and MEst scenarios) and was largest when both natural mortality and reporting rate were estimated (BEst).

Examination of relative errors in annual abundances for some of the Group 1 scenarios identified the

source of the biases observed in total abundances. For the MRFix1 scenario, annual abundance estimates for all populations and combined across populations were accurate and relatively precise, except for the last few years of the simulations (Figure 11). However for the BEst20 scenario, annual abundances were consistently biased for all populations; estimates for population 2 were consistently negatively biased and estimates for the other populations were positively biased. The biases were consistent for the duration of the simulations for all populations except population 4, in which bias increased throughout the time series. The strength of the bias varied by population size (Figure 11); for population 2 (i.e., the largest population), the median REE in annual abundance was consistently around -35%, whereas for some of the other populations median REE approached 500%. With respect to total annual abundance, these population-specific biases largely canceled each other out (Figure 11). For population 2, precision of abundance decreased in the last few years of the simulations. Conversely, for populations 1 and 3, the precision in annual abundances were fairly consistent throughout the duration of the simulations, whereas for population 4 the precision decreased annually throughout the simulations.

Large positive biases in total abundance estimates were observed when reporting rate was fixed at 1.5 times the true value (MSens median REE 50%) and when natural mortality was fixed at 1.5 times the true value (RSensO median REE 116%; Figure 10). Conversely, there was negative bias in total abundance when natural mortality was fixed at half the true value (RSensU median REE -46%). Simulations that tested different structural assumptions and data quality had similar median REE values compared to the BEst20 scenario. However, when the number of tags released was reduced to 250 per region the IQR REE of total abundance doubled (BEst20 total: IQR REE = 10%; T250 total: IQR REE = 21%).

Discussion

Simulation analysis is an important tool in fishery science for determining how well models can accurately and precisely estimate parameters and the robustness/sensitivity to violations in model assumptions, data quality, and/or structural uncertainties. Previous simulation analyses of ITCAAN models had investigated reproductive mixing movement dynamics with natural mortality fixed at the true value (Hulson et al. 2011; 2013; Goethel et al. 2015b). This study analyzed the performance of an ITCAAN model with natal homing movement dynamics and more harvest regions and populations than had previously been simulated, while testing the estimability of natural mortality, movement rates and tag reporting rates. Additionally, our operating model created datasets by simulating stochastic first-order autoregressive annual fishing mortality and recruitment processes and applied observation error for four population with drastically different magnitudes of spawning population size. These stochastic processes were included to create datasets that were generic

such that the results would be broadly applicable. Our study allowed for the estimation of natural mortality and tag reporting rate simultaneously with other population dynamics parameters internal to the ITCAAN model. The intent of this study was to establish a baseline of parameter estimability performance for a four region ITCAAN model with the movement dynamics modeled as intermixed populations with natal homing, which expands on previous simulation analyses (Hulson et al. 2011; 2013; Goethel et al. 2015b).

An issue we encountered when fitting the ITCAAN model was that different parameterizations could have large consequences on model fit. For example, initial configurations of our ITCAAN model estimated recruitment as a white-noise process that resulted in large systematic biases in recruitment estimates. Specifically, the ITCAAN model underestimated recruitment early in the time series and overestimated recruitment later in the time series. Conversely, estimating recruitment through a random walk process with a large assumed variance term removed these systematic biases and greatly improved precision of the recruitment estimates. We suspect that the key feature here is that we allowed for the mean recruitment to be non-stationary (Maun-der and Deriso 2003; Li et al. 2014). Similarly, issues were encountered in estimating initial abundances and the last few years of recruitment, which affected whether the model could reliably produce a positive-definite Hessian matrix for many simulated datasets. Ultimately, the ITCAAN model parameterization that we used in our study was the best approach we could find to correct the estimation complications we encountered. Such estimation issues could easily remain undiscovered in empirical applications of ITCAAN models. We thus recommend that the sensitivity of alternative parameterizations be routinely evaluated in real-world applications, and in agreement with Goethel et al. (2015b) that simulations be used to evaluate the most appropriate approach when such sensitivity exists.

Part of our motivation for this research was that we envisioned there could be confounding among parameters that fishery scientists might be interested in estimating with an ITCAAN model. Additionally, the estimation of reporting rates within an ITCAAN model is a recent proposal (Goethel et al. 2015a;b). We found that natural mortality, tag reporting rates and movement rates can all be accurately and precisely estimated simultaneously in an ITCAAN model assuming natal homing. Across the range of scenarios considered in this research, movement rates were accurately and precisely estimated even at the lowest tagging level. Accuracy and precision of natural mortality and reporting rates were largely unaffected by the degree of measurement error assumed in the statistical catch-at-age data (Table 2). However, precision and bias of natural mortality, movement rates and reporting rates were appreciably affected by reductions in tagged cohort sample size. This suggests that tag-recovery data are the primary source of information that allows estimation of these parameters in ITCAAN models, and such data will typically be necessary in order to estimate movement rates in spatial assessment models (Goethel et al. 2015b). The ability to estimate these parameters is important because fixing them at incorrect values can cause severe biases in all other

model parameters.

Given the consequences on ITCAAN model parameter estimates from misspecifying reporting rates and natural mortalities, we advocate initially attempting to estimate these parameters simultaneously rather than fixing them at assumed values. Admittedly, the ability to estimate reporting rates and natural mortalities simultaneously might be more challenging than what we encountered because actual data will likely have greater uncertainty than generated data. Our simulation scenarios that explored the consequences of data quality showed that greater levels of bias and imprecision in parameter estimates resulted with lower quality data; however, the amount of bias in parameter estimates were generally greater when reporting rates or natural mortalities were misspecified. The natal homing assumed for this study may influence the extrapolation of these results to other movement types; nevertheless, we speculate that the specification of the natural mortality rate may have been incorrect in the reproductive mixing movement ITCAAN model of Goethel et al. (2015a), and likely led to biases in reporting rates and other parameters. Supporting this speculation, Goethel et al. (2015a) noted that the region-specific reporting rates estimated by the ITCAAN model were all lower than an estimate for all areas combined from a high reward tagging study (Cadrin 2006). In general this issue can be addressed both by evaluating sensitivity of results to specified natural mortality rates and evaluating whether the natural mortality parameter can be estimated. If difficulty in estimating natural mortality and reporting rate concurrently exists, model convergence may be improved by incorporating methods that normally are factored into tagging studies. For example, the release of high-reward tags, using observers, or planted tags (Polacheck et al. 2006; Eveson et al. 2007) could be incorporated in the likelihood of the ITCAAN model.

Bias and precision in reporting rates and natural mortality were affected by the degree of spatial complexity assumed for reporting rate and natural mortality parameters in the ITCAAN model. Our findings illustrate that caution should be used when considering the complexity of parameterization within ITCAAN models, as greater model complexity may lead to greater variability in parameter estimates. Model selection criteria, such as deviance information criteria, may be useful to determine the spatial complexity that can be supported by observed data (Wilberg and Bence 2008; Linton and Bence 2011). In some cases, it might be possible to estimate spatially-varying parameters by modeling rates as a function of some measured quantity, such as modeling natural mortality as a function of temperature. However, fisheries scientists will need to consider whether parameters should be modeled as an environmental characteristic of the region occupied or a genetic feature of the originating population.

One of the main parameters of interest in an ITCAAN model is the estimation of movement rates among the populations. Previous simulations of ITCAAN models under different movement dynamics found that movement rate estimates were accurate even when movement varied as a function of environmental vari-

ables (Hulson et al. 2013) or as a function of regional stock density (Goethel et al. 2015b). Our findings in combination with these other studies suggest that unbiased and precise estimation of movement is a robust feature of ITCAAN models. However, this conclusion may depend on the simplistic movement dynamics in the operating models used to generate the tagging data. Our study, as well as those of Hulson et al. (2013) and Goethel et al. (2015b), assumed movement occurred instantaneously and that after movement fish became sedentary. In actuality, movement will not be instantaneous and may vary seasonally or across even shorter time periods. Additionally, our estimates of precision may be conservative because we generated tag recoveries assuming a multinomial process, but overdispersion relative to this distribution in tagging data is often observed (Bacheler et al. 2008; Vandergoot and Brenden 2014; Hanselman et al. 2015; Mayakoshi and Kitada 2016). We assumed tagged cohorts were fully mixed with the at-large population (i.e., both at-large populations and tagged cohorts experienced the exact same dynamics). If the dynamics which the tagged cohorts experience are different than the at-large populations, then parameter estimation undoubtedly would have been affected. Future evaluations of ITCAAN models would benefit from including more complex movement scenarios to determine whether the apparent robustness of ITCAAN models for estimating movement is a general feature of the models or an artifact of the simplified movement characteristics assumed in the operating model.

Although we attempted to incorporate a range of scenarios in this study, it is important to acknowledge that our results are nevertheless influenced by assumed conditions, both in the operating and ITCAAN models. Our assumed 40 year time series of tagging and fishery harvest data is perhaps an unlikely scenario of data availability and a shorter time series of data may encounter different estimation issues. Our study did not include chronic tag loss and tag-induced mortality. These processes would effectively reduce the sample size of tags released and could affect bias and precision of parameter estimates if not accounted for in the ITCAAN model. We did not consider the weighting of tagging data versus harvest and survey data in the ITCAAN model and there may be situations where down-weighting of tagging data may be beneficial or necessary due to some of the issues mentioned above (non-mixing, more complex movements, etc.) (Fielder and Bence 2014; Francis and McKenzie 2015; Goethel et al. 2015a). We did not investigate the model misspecification of incorrectly identifying spawning populations. Spawning population identification is difficult (Cadrin et al. 2004), and could easily result in identifying a separate spawning population that does not exist or combining multiple spawning populations into one. How the estimates obtained from a spatially explicit ITCAAN model are influenced by model misspecification of the spatial structure has yet to be evaluated for both natal homing and reproductive mixing ITCAAN models. Similarly, simulations that incorporate harvest by multiple fisheries within a single region may be useful to expand our understanding of ITCAAN models. Additional sources of uncertainty that may be present in real data that were not explored

include: time varying selectivity, selectivity that is size based with annually varying growth, fishing mortality that is not linearly related to fishing effort or changes over time, contradicting trends in multiple surveys, and time-varying natural mortality and/or reporting rates. These types of model misspecification would likely make the estimates of parameters more uncertain and their influence could be evaluated through additional simulation experiments.

One of the major motivators for incorporating spatially-explicit dynamics in assessment models is the concern that less productive populations may be overexploited or even extirpated if spatially-varying dynamics are not incorporated in the management process (Stephenson 1999; Hutchings 2000; Hutchinson 2008; Ying et al. 2011; Molton et al. 2013; Li et al. 2014). For fishery scientists and managers responsible for assessing and/or managing fish populations exhibiting complex spatial structuring, ITCAAN models are likely an attractive assessment approach. One of the key findings from our study was that under conditions of high movement and large differences in spawning population size, ITCAAN models were biased and imprecise estimators of individual population annual recruitment. Additionally, biases in recruitment estimates become more pronounced when reporting rates were estimated, which may indicate that the estimation of reporting rates within an ITCAAN model could lead to biased estimates if large differences in population size are present. Likewise, the abundance in population 4 in the BEst20 scenario was increasingly overestimated as the population size declined, but this was not observed for the EqProd scenario. This suggests that even a spatially explicit ITCAAN model may have difficulty estimating abundance for a population that is close to collapse, if a large portion of the catch comes from other populations. An assumption of large differences in population size and depletion level among the spawning populations, used in our simulations, may be more reflective of actual conditions for many species than an assumption of equality in stock-recruitment relationships. Consequently, the potential for overestimating recruitment of smaller populations and underestimating recruitment of larger populations under conditions of high movement and large differences in relative size of spawning populations is an important issue to consider for fishery scientists looking to implement ITCAAN models. However, this overestimation of recruitment was only severe when movement was at the 20% mixing rate. Real world scenarios where more than half of the population leave the natal region (i.e., for the 20% movement scenarios 60% of populations leave natal region), may be rare occurrences. Thus, a more thorough investigation is required into what proportion or relative quantity of regional catch non-natal stocks must contribute such that the natal population is overestimated. If movement rates among the populations is anticipated to be high, the implementation of standardized surveys when populations are unmixed may be beneficial for improving accuracy and precision of recruitment estimates from ITCAAN models. Alternatively, the incorporation of genetic data to determine the population source of fish caught in a mixed survey and/or fishery could improve the ability of ITCAAN models to accurately estimate individual

population abundance, but requires additional investigation.

In conclusion, we found that release-conditioned ITCAAN models yielded accurate and precise parameter estimates under moderate to low movement rates. However, biases in some parameters could result under conditions of high movement and large differences in stock-recruitment relationships among spawning populations. Misspecification of certain parameters, such as natural mortalities and reporting rates, induced larger biases, for tested misspecification levels, than when parameters were estimated; thus, we urge caution in fixing parameters at assumed values when utilizing ITCAAN models. We recommend additional investigation of factors such as the inclusion of additional data sources, greater levels of uncertainty in data sources, greater spatial complexity, weighting of tagging data relative to fishery harvest/survey data, temporal complexity of parameters (e.g., natural mortality and reporting rate), alternative parameterizations (e.g., recruitment estimation as random walk or white noise), and model misspecification to gain additional perspectives on the performance of ITCAAN models. Finally we recommend the use of management strategy evaluations for specific situations to determine whether some combination of using ITCAAN models and appropriate harvest policies can maintain desirable levels of biomass for all spawning populations.

Acknowledgments

The authors would like to thank three anonymous reviewers and Mark Maunder for comments that helped improve the manuscript. This work was partially funded by grant 2012.1250 from the Great Lakes Fishery Trust and 2013.BRE.44025 from the Great Lakes Fishery Commission. Additional funding support was provided by Supporting Partners of the Michigan State University Quantitative Fisheries Center. The authors acknowledge the support of Michigan State University High Performance Computing Center and the Institute for Cyber-Enabled Research. This is publication number 20XX-XX of the Quantitative Fisheries Center at Michigan State University.

References

- Bacheler, N.M., Hightower, J.E., Paramore, L.M., Buckel, J.A., and Pollock, K.H. 2008. An age-dependent tag return model for estimating mortality and selectivity of an estuarine-dependent fish with high rates of catch and release. *Trans. Am. Fish. Soc.* **137**(5): 1422–1432. doi:10.1577/T07-254.1.
- Beverton, R.J.H. and Holt, S.J. 1957. On the dynamics of exploited fish populations. *Fishery Investigations Series II Volume XIX*. Her Majesty's Stationary Office.

- Brenden, T.O., Scribner, K.T., Bence, J.R., Tsehay, I., Kanefsky, J., Vandergoot, C.S., and Fielder, D.G. 2015. Contributions of Lake Erie and Lake St. Clair walleye populations to the Saginaw Bay, Lake Huron recreational fishery: evidence from genetic stock identification. *N. Am. J. Fish. Manage.* **35**(3): 567–577. doi:10.1080/02755947.2015.1020079.
- Cadrin, S.X. 2006. Yellowtail flounder tagging study. Technical report, Northeast Consortium Interim Final Report.
- Cadrin, S.X., Friedland, K.D., and Waldman, J.R., editors 2004. Stock Identification Methods: Applications in Fishery Science. Elsevier Academic Press, Burlington, MA.
- Cope, J.M. and Punt, A.E. 2011. Reconciling stock assessment and management scales under conditions of spatially varying catch histories. *Fish. Res.* **107**(1–3): 22–38. doi:10.1016/j.fishres.2010.10.002.
- Deriso, R.B., Quinn, II, T., and Neal, P.R. 1985. Catch-age analysis with auxiliary information. *Can. J. Fish. Aquat. Sci.* **42**(4): 815–824. doi:10.1139/f85-104.
- Doubleday, W.G. 1976. Least squares approach to analyzing catch-at-age data. *Int. Comm. Northwest Atl. Fish. Res. Bull.* **12**(1): 69–81. Available from <https://www.nafo.int/ICNAF/library/res-bull/res-bull-12.PDF> [accessed 25 May 2016].
- Eveson, J.P., Polacheck, T., and Laslett, G.M. 2007. Incorporating fishery observer data into an integrated catch-at-age and multiyear tagging model for estimating mortality rates and abundance. *Fish. Bull.* **105**(4): 493–508. Available from <http://fishbull.noaa.gov/1054/eveson.pdf> [accessed 25 May 2016].
- Fielder, D.G. and Bence, J.R. 2014. Integration of auxiliary information in statistical catch-at-age (SCA) analysis of the Saginaw Bay stock of walleye in Lake Huron. *N. Am. J. Fish. Manage.* **34**(5): 970–987. doi:10.1080/02755947.2014.938141.
- Fournier, D.A., Skaug, H.J., Ancheta, J., Ianelli, J., Magnusson, A., Maunder, M.N., Nielsen, A., and Sibert, J. 2012. AD Model Builder: using automatic differentiation for statistical inference of highly parameterized complex nonlinear models. *Optim. Method. Softw.* **27**(2): 233–249. doi:10.1080/10556788.2011.597854.
- Francis, R. and McKenzie, J. 2015. Assessment of the SNA 1 stocks in 2013. Technical report, New Zealand Fisheries Assessment Report 2015/76. Available from <https://www.mpi.govt.nz/document-vault/10580> [accessed 19 January 2017].
- Frusher, S.D. and Hoenig, J.M. 2003. Recent developments in estimating fishing and natural mortality and tag reporting rate of lobsters using multi-year tagging models. *Fish. Res.* **65**(1–3): 379–390. doi:10.1016/j.fishres.2003.09.027.

- 717 Fu, C. and Fanning, L.P. 2004. Spatial considerations in the management of Atlantic Cod off Nova Scotia,
718 Canada. N. Am. J. Fish. Manage. **24**(3): 775–784. doi:10.1577/M03-134.1.
- 719 Goethel, D.R., Legault, C.M., and Cadrin, S.X. 2015a. Demonstration of a spatially explicit, tag-integrated
720 stock assessment model with application to three interconnected stocks of yellow tail flounder off of New
721 England. ICES J. Mar. Sci. **72**(1): 164–177. doi:10.1093/icesjms/fsu014.
- 722 Goethel, D.R., Legault, C.M., and Cardin, S.X. 2015b. Testing the performance of a spatially explicit
723 tag-integrated stock assessment model of yellowtail flounder (*Limanda ferruginea*) through simulation
724 analysis. Can. J. Fish. Aquat. Sci. **72**(4): 582–601. doi:10.1139/cjfas-2014-0244.
- 725 Goethel, D.R., Quinn, II, T.J., and Cadrin, S.X. 2011. Incorporating spatial structure in stock assessment:
726 Movement modeling in marine fish population dynamics. Rev. Fish. Sci. **19**(2): 119–136. doi:10.1080/
727 10641262.2011.557451.
- 728 Guan, W., Cao, J., Chen, Y., and Cieri, M. 2013. Impacts of population and fishery spatial structures on
729 fishery stock assessment. Can. J. Fish. Aquat. Sci. **70**(8): 1178–1189. doi:10.1139/cjfas-2012-0364.
- 730 Haist, V., Fournier, D., and Saunders, M.W. 1999. Reconstruction of B.C. sablefish stocks, 1966–198, and
731 catch projections for 1999, using an integrated catch-age mark-recapture model with area and depth
732 movement. Technical Report Research Document 99/79, Canadian Stock Assessment Secretariat, Ottawa,
733 Canada.
- 734 Hampton, J. 1991. Estimation of southern bluefin tuna *Thunnus maccoyii* natural mortality
735 and movement rates from tagging experiments. Fish. Bull. **89**(4): 591–610. Available from
736 <http://fishbull.noaa.gov/894/hampton2.pdf>.
- 737 Hanselman, D.H., Heifetz, J., Echave, K.B., and Dressel, S.C. 2015. More it or lost it: movement and mor-
738 tality of sablefish tagged in Alaska. Can. J. Fish. Aquat. Sci. **72**(2): 238–251. doi:10.1139/cjfas-2014-0251.
- 739 Haponski, A.E. and Stepien, C.A. 2014. Genetic connectivity and diversity of walleye (*Sander vitreus*)
740 spawning groups in the Huron-Erie corridor. J. Great Lakes Res. **40**(2): 89–100. doi:10.1016/j.jglr.2012.
741 12.006.
- 742 Hayden, T.A., Holbrook, C.M., Fielder, D.G., Vandergoot, C.S., Bergstedt, R.A., Dettmers, J.M., Krueger,
743 C.C., and Cooke, S.J. 2014. Acoustic telemetry reveals large-scale migration patterns of walleye in Lake
744 Huron. PLoS ONE **9**(12): e114833. doi:10.1371/journal.pone.0114833.

- Hoenig, J.M., Barrowman, N.J., Hearn, W.S., and Pollock, K.H. 1998. Multiyear tagging studies incorporating fishing effort data. *Can. J. Fish. Aquat. Sci.* **55**(6): 1466–1476. doi:10.1139/f97-256.
- Hulson, P.J.F., Miller, S.E., Ianelli, J.N., and Quinn, II, T.J. 2011. Including mark-recapture data into a spatial age-structured model: Walleye pollock (*Theragra chalcogramma*) in the eastern Bering Sea. *Can. J. Fish. Aquat. Sci.* **68**(9): 1625–1634. doi:10.1139/F2011-060.
- Hulson, P.J.F., Quinn II, T.J., Hanselman, D.H., and Ianelli, J.N. 2013. Spatial modeling of Bering Sea walleye pollock with integrated age-structured assessment models in a changing environment. *Can. J. Fish. Aquat. Sci.* **70**(9): 1402–1416. doi:10.1139/cjfas-2013-0020.
- Hutchings, J.A. 2000. Collapse and recovery of marine fishes. *Nature* **406**(6798): 882–885. doi:10.1038/35022565.
- Hutchinson, W.F. 2008. The dangers of ignoring stock complexity in fisheries management: The case of the North Sea cod. *Biol. Lett.* **4**(6): 693–695. doi:10.1098/rsbl.2008.0443.
- La Valley, K.J. and Feeney, R.G. 2013. Reconciling spatial scales and stock structure for fisheries science and management. *Fish. Res.* **141**(1): 1–2. doi:10.1016/j.fishres.2013.02.014.
- Latour, R.J., Hoenig, J.M., Hepworth, D.A., and Frusher, S.D. 2003. A novel tag-recovery model with two size classes for estimating fishing and natural mortality, with implications for the southern rock lobster (*Jasus edwardsii*) in Tasmania, Australia. *ICES J. Mar. Sci.* **60**(5): 1075–1085. doi:10.1016/S10543139(03)00093-6.
- Latour, R.J., Hoenig, J.M., Olney, J.E., and Pollock, K.H. 2001. Diagnostics for multiyear tagging models with application to Atlantic striped bass (*Morone saxatilis*). *Can. J. Fish. Aquat. Sci.* **58**(9): 1716–1726. doi:10.1139/cjfas-58-9-1716.
- Lee, H.H., Maunder, M.N., Piner, K.R., and Methot, R.D. 2011. Estimating natural mortality within a fisheries stock assessment model: An evaluation using simulation analysis based on twelve stock assessments. *Fish. Res.* **109**(1): 89–94. doi:10.1016/j.fishres.2011.01.021.
- Li, Y., Bence, J.R., and Brenden, T.O. 2014. An evaluation of alternative assessment approaches for intermixing fish populations: a case study with Great Lakes lake whitefish. *ICES J. Mar. Sci.* **72**(1): 70–81. doi:10.1093/icesjms/fsu057.
- Linton, B.C. and Bence, J.R. 2011. Catch-at-age assessment in the face of time-varying selectivity. *ICES J. Mar. Sci.* **68**(3): 611–625. doi:10.1093/icesjms/fsq173.

- 774 Maunder, M.N. 2001. Integrated tagging and catch-at-age analysis (ITCAAN): Model development and
775 simulation testing. In *Spatial Processes and Management of Marine Populations*, edited by G.H. Kruse,
776 N. Bez, A. Booth, M.W. Dorn, S. Hills, R.N. Lipcius, D. Pelletier, C. Roy, S.J. Smith, and D. Witherell.
777 University of Alaska Sea Grant, Fairbanks, Alaska, USA, number AK-SG-01-02 in Alaska Sea Grant
778 College Program Report, pp. 123–142.
- 779 Maunder, M.N. and Deriso, R.B. 2003. Estimation of recruitment in catch-at-age model. *Can. J. Fish.*
780 *Aquat. Res.* **60**(10): 1204–1216. doi:10.1139/F03-104.
- 781 Maunder, M.N. and Punt, A.E. 2013. A review of integrated analysis in fisheries stock assessment. *Fish.*
782 *Res.* **142**(1): 61–74. doi:10.1016/j.fishres.2012.07.025.
- 783 Mayakoshi, Y. and Kitada, S. 2016. Overdispersion in the estimation of salmon escapement by mark-
784 recapture surveys and its related factors. *Trans. Am. Fish. Soc.* **145**(2): 269–276. doi:10.1080/00028487.
785 2015.1121922.
- 786 McGarvey, R., Linnane, A.J., Feenstra, J.E., Punt, A.E., and Matthews, J.M. 2010. Integrated recapture-
787 conditioned movement estimation into spatial stock assessment: A South Australian lobster fishery appli-
788 cation. *Fish. Res.* **105**(2): 80–90. doi:10.1016/j.fishres.2010.03.006.
- 789 McParland, T.L., Ferguson, M.M., and Liskauskas, A.P. 1999. Genetic population structure and mixed-stock
790 analysis of walleyes in the Lake Erie–Lake Huron corridor using allozyme and mitochondrial DNA markers.
791 *Trans. Am. Fish. Soc.* **128**(6): 1055–1067. doi:10.1577/1548-8659(1999)128<1055:GPSAMS>2.0.CO;2.
- 792 Molton, K.J., Brenden, T.O., and Bence, J.R. 2013. Harvest levels that conserve spawning biomass can
793 provide larger and more stable and sustainable yields in intermixed fisheries. *Fish. Res.* **147**(1): 264–283.
794 doi:10.1016/j.fishres.2013.07.004.
- 795 Morishima, G.S. and Henry, K.A. 1999. The history and status of Pacific Northwest Chinook and Coho
796 Salmon ocean fisheries and prospects for sustainability. In *Sustainable Fisheries Management: Pacific*
797 *Salmon*, edited by E.E. Knudsen, C.R. Steward, D.D. MacDonald, J.E. Williams, and D.W. Reiser, CRC
798 Press, pp. 219–236. doi:10.1201/9781439822678.ch16.
- 799 Pandit, S.N., Zhaoa, Y., Ciborowski, J.J., Gorman, M., and Knight, C.T. 2013. Suitable habitat model for
800 walleye (*Sander vitreus*) in Lake Erie: Implications for inter-jurisdictional harvest quota allocations. *J.*
801 *Great Lakes Res.* **39**(4): 591–601. doi:10.1016/j.jglr.2013.09.011.

- Polacheck, T., Eveson, J.P., Laslett, G.M., Pollock, K.H., and Hearn, W.S. 2006. Integrating catch-at-age and multiyear tagging data: a combined Brownie and Petersen estimation approach in a fishery context. *Can. J. Fish. Aquat. Sci.* **63**(3): 534–548. doi:10.1139/f05-232.
- Porch, C.E., Turner, S.C., and Powers, J.E. 2001. Virtual population analyses of atlantic bluefin tun with alternative models for transatlantic migration: 1970-1997. *Collect. Vol. Sci. Pap. ICCAT* **52**(3): 1022–1045. Available from https://www.iccat.int/Documents/CVSP/CV052_2001/no_3/CV052031022.pdf [accessed 25 May 2016].
- Punt, A.E., Pribac, F., Walker, T.I., Taylor, B.L., and Prince, J.D. 2000. Stock assessment of school shark, *Galeorhinus galeus*, based on a spatially explicit population dynamics model. *Mar. Freshwater Res.* **51**(3): 205–220. doi:10.1071/MF99124.
- R Development Core Team 2016. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0.
- Stephenson, R.L. 1999. Stock complexity in fisheries management: A perspective of emerging issues related to population sub-units. *Fish. Res.* **43**(1–3): 247–249. doi:10.1016/S0165-7836(99)00076-4.
- Stepien, C.A. and Faber, J.E. 1998. Population genetic structure, phylogeography and spawning philopatry in walleye (*Stizostedion vitreum*) from mitochondrial dna control region sequences. *Mol. Ecol.* **7**(12): 1757–1769. doi:10.1046/j.1365-294x.1998.00512.x.
- Thorson, J.T., Jensen, O.P., and Zipkin, E.F. 2014. How variable is recruitment for exploited marine fishes? A hierarchical model for testing life history theory. *Can. J. Fish. Aquat. Sci.* **71**(7): 973–983. doi:10.1139/cjfas-2013-0645.
- Thorson, J.T., Jensen, O.P., and Zipkin, E.F. 2016. Corrigendum: How variable is recruitment for exploited marine fishes? A hierarchical model for testing life history theory. *Can. J. Fish. Aquat. Sci.* doi:10.1139/cjfas-2013-0645.
- Vandergoot, C.S. and Brenden, T.O. 2014. Spatially varying population demographics and fishery characteristics of Lake Erie walleyes inferred from a long-term tag recovery study. *Trans. Am. Fish. Soc* **143**(1): 188–204. doi:10.1080/00028487.2013.837095.
- Wang, H.Y., Rutherford, E.S., Cook, H.A., Einhouse, D.W., Haas, R.C., Johnson, T.B., Kenyon, R., Locke, B., and Turner, M.W. 2007. Movement of walleyes in Lakes Erie and St. Clair inferred from tag return and fisheries data. *Trans. Am. Fish. Soc* **136**(2): 539–551. doi:10.1577/T06-012.1.

- 831 Wang, Y. and Liu, Q. 2006. Estimation of natural mortality using statistical analysis of fisheries catch-at-age
832 data. *Fish. Res.* **78**(2–3): 342–351. doi:10.1016/j.fishres.2005.11.020.
- 833 Wilberg, M.J. and Bence, J.R. 2006. Performance of time-varying catchability estimators in statistical
834 catch-at-age analysis. *Can. J. Fish. Aquat. Sci.* **63**(10): 2275–2285. doi:10.1139/f06-111.
- 835 Wilberg, M.J. and Bence, J.R. 2008. Performance of deviance information criterion model selection in
836 statistical catch-at-age analysis. *Fish. Res.* **93**(1–2): 212–221. doi:10.1016/j.fishres.2008.04.010.
- 837 Wills, T., Robinson, J., Faust, M., Gorman, A.M., Belore, M., Cook, A., Drouin, R., MacDougall,
838 T., Zhao, Y., Murray, C., and Hosack, M. 2016. Report for 2015 by the Lake Erie walleye
839 task group. Technical report, Lake Erie Committee Great Lakes Fishery Commission. Avail-
840 able from http://www.glfc.org/lakecom/lec/WTG_docs/annual_reports/WTG_report_2016.pdf [accessed
841 25 May 2016].
- 842 Ying, Y., Chen, Y., Lin, L., and Gao, T. 2011. Risks of ignoring fish population spatial structure in fisheries
843 management. *Can. J. Fish. Aquat. Sci.* **68**(12): 2101–2120. doi:10.1139/f2011-116.
- 844 Zhao, Y., Einhouse, D.W., and MacDougall, T.M. 2011. Resolving some of the complexity of a mixed-origin
845 walleye population in the east basin of Lake Erie using a mark-recapture study. *N. Am. J. Fish. Manage.*
846 **32**(2): 379–389. doi:10.1080/02755947.2011.571516.
- 847 Zhao, Y., Jones, M.L., Shuter, B.J., and Roseman, E.F. 2009. A biophysical model of Lake Erie walleye
848 (*Sander vitreus*) explains interannual variations in recruitment. *Can. J. Fish. Aquat. Sci.* **66**(1): 114–125.
849 doi:10.1139/F08-188.
- 850 Zhao, Y., Kocovsky, P.M., and Madenjian, C.P. 2013. Development of a stock-recruitment model and
851 assessment of biological reference points for the Lake Erie walleye fishery. *N. Am. J. Fish. Manage.* **33**(5):
852 956–964. doi:10.1080/02755947.2013.822442.

Table 1: Abbreviations used in figures and text, model characteristics and convergence rate of the ITCAAN model for investigated scenarios, where movement is estimated unless denoted by * (NPD = Not Positive-Definite; RC = regionally constant; RU = regionally unique; Known = Fixed at true value; Est. = Estimated in ITCAAN).

Scenario Group	Abbrev.	ITCAAN model		Operating model		# needed for 1 000 converged	Percent converged	NPD Hess-ian	Maximum Gradient > 0.05
		Reporting rate	Natural mortality	Emigration rate	tags per region				
1	MvFix1*	Known	Known	1%	2 000	1 359	73.6	0	359
1	MRFix1	Known	Known	1%	2 000	1 373	72.8	1	373
1	MEst1	Known	Est. RC	1%	2 000	1 379	72.5	4	379
1	REst1	Est. RU	Known	1%	2 000	1 379	72.5	4	379
1	BEst1	Est. RU	Est. RC	1%	2 000	1 356	73.7	5	356
1	MvFix5*	Known	Known	5%	2 000	1 022	97.8	1	22
1	MRFix5	Known	Known	5%	2 000	1 032	96.9	5	32
1	MEst5	Known	Est. RC	5%	2 000	1 032	96.9	3	32
1	REst5	Est. RU	Known	5%	2 000	1 045	95.7	1	45
1	BEst5	Est. RU	Est. RC	5%	2 000	1 043	95.9	6	43
1	MvFix10*	Known	Known	10%	2 000	1 010	99.0	10	10
1	MRFix10	Known	Known	10%	2 000	1 017	98.3	16	17
1	MEst10	Known	Est. RC	10%	2 000	1 010	99.0	10	10
1	REst10	Est. RU	Known	10%	2 000	1 006	99.4	5	6
1	BEst10	Est. RU	Est. RC	10%	2 000	1 005	99.5	5	5
1	MvFix20*	Known	Known	20%	2 000	1 035	96.6	33	35
1	MRFix20	Known	Known	20%	2 000	1 018	98.2	18	18
1	MEst20	Known	Est. RC	20%	2 000	1 022	97.8	21	22
1	REst20	Est. RU	Known	20%	2 000	1 010	99.0	10	10
1	BEst20	Est. RU	Est. RC	20%	2 000	1 015	98.5	15	15
2	MSens	1.5×True	Est. RC	20%	2 000	1 043	95.9	41	43
2	RSensU	Est. RU	0.5×True	20%	2 000	1 009	99.1	8	9
2	RSensO	Est. RU	1.5×True	20%	2 000	1 048	95.4	47	48
3	T1500	Est. RU	Est. RC	20%	1 500	1 020	98.0	20	20
3	T1000	Est. RU	Est. RC	20%	1 000	1 034	96.7	34	34
3	T500	Est. RU	Est. RC	20%	500	1 015	98.5	13	15
3	T250	Est. RU	Est. RC	20%	250	1 022	97.8	21	22
3	ESS50 [†]	Est. RU	Est. RC	20%	2 000	1 024	97.7	24	24
3	HighVar ^{†‡}	Est. RU	Est. RC	20%	2 000	1 027	97.4	27	27
4	RC_MC	Est. RC	Est. RC	20%	2 000	1 008	99.2	0	8
4	RC_MU	Est. RC	Est. RU	20%	2 000	1 020	98.0	20	19
4	RU_MU	Est. RU	Est. RU	20%	2 000	1 011	98.9	1	11
5	EqProd [§]	Est. RU	Est. RC	20%	2 000	1 008	99.2	8	8

* Movement Rate Fixed at True Value

[†] Effective Sample Size of age composition set at 50

[‡] CV of observation error of harvest=20%, effort=20% and survey=40%, double other scenarios

[§] Ricker parameters for all populations set equal to population 2 in other scenarios

Table 2: Distributions and variance or effective sample size (ESS) assumed to simulate different data sources and stock-recruitment productivity assumptions for scenarios investigated.

Data Source	All Others	HighVar	ESS50	EqProd
Total Catch	Lognormal CV 10%	Lognormal CV 20%	Lognormal CV 10%	Lognormal CV 10%
Fishing Effort	Lognormal CV 10%	Lognormal CV 20%	Lognormal CV 10%	Lognormal CV 10%
Survey CPUE	Lognormal CV 20%	Lognormal CV 40%	Lognormal CV 20%	Lognormal CV 20%
Catch Age Comp	Multinomial ESS 100	Multinomial ESS 50	Multinomial ESS 50	Multinomial ESS 100
Survey Age Comp	Multinomial ESS 100	Multinomial ESS 50	Multinomial ESS 50	Multinomial ESS 100
Ricker Recruitment Parameters (α & β)	Different between populations	Different between populations	Different between populations	Same across populations

Figure 1: Movement dynamics simulated by the four-region operating model assuming natal homing. The left half of the figure represents fish during spawning at the beginning of every year, which are assumed to return to their natal population to spawn. The right half of this figure shows the distribution of fish during the remainder of the year that mix to all harvest regions and stay for the rest of the year.

Figure 2: Ricker stock-recruit relationships used to create the recruitment dynamics of the four populations in the simulation. Note the large difference in axes scale between the two graphs.

Figure 3: Total abundance trends of each population for two different scenarios in a spatially explicit operating model for 1 000 simulation iterations. The left column of figures is for populations with 1% movement and the right column is for populations with 20% movement to non-natal regions. The lines show three examples of simulated time series of abundance for each population. Whiskers on the boxplots extend to 1.5 times the inter-quartile range or the most extreme observed data point, whichever is less extreme. Relative errors outside the whisker range were not plotted.

Figure 4: Relative error (%) of annual recruitment estimates for each population of an ITCAAN model under different movement rates and parameter estimation assumptions (scenario Group 1) for 1 000 simulation iterations. Table 1 lists the model abbreviations and corresponding model components. Whiskers on the boxplots extend to 1.5 times the inter-quartile range or the most extreme observed data point, whichever is less extreme. Relative errors outside the whisker range were not plotted. Note the difference in y-axis scale between populations.

Figure 5: Relative error (%) of recruitment estimates for each population of an ITCAAN model under scenarios investigating misspecified natural mortality and reporting rates, data quality, spatial complexities, and equal productivities (scenario Groups 2–5) for 1 000 simulation iterations. Table 1 lists the model abbreviations and corresponding model components. Whiskers on the boxplots extend to 1.5 times the inter-quartile range or the most extreme observed data point, whichever is less extreme. Relative errors outside the whisker range were not plotted. Note the difference in y-axis scale between populations.

Figure 6: Actual error of movement rates from all populations to individual harvest regions of an ITCAAN model under different movement rates and parameter estimation assumptions (scenario Group 1) for 1 000 simulation iterations. Table 1 lists the model abbreviations and differences in operating and ITCAAN models. Whiskers on the boxplots extend to 1.5 times the inter-quartile range or the most extreme observed data point, whichever is less extreme. Actual errors outside the whisker range were not plotted.

Figure 7: Actual error of movement rate estimates from all populations to individual harvest regions of an ITCAAN model under scenarios investigating misspecified natural mortality and reporting rates, data quality, spatial complexities, and equal productivities (scenario Groups 2–5) for 1 000 simulation iterations. Table 1 lists the model abbreviations and corresponding model components. Whiskers on the boxplots extend to 1.5 times the inter-quartile range or the most extreme observed data point, whichever is less extreme. Actual errors outside the whisker range were not plotted.

Figure 8: Relative error (%) of natural mortality and regional reporting rate estimates of an ITCAAN model under different movement rates and parameter estimation assumptions (scenario Group 1) for 1 000 simulation iterations. Table 1 lists the model abbreviations and corresponding model components. Whiskers on the boxplots extend to 1.5 times the inter-quartile range or the most extreme observed data point, whichever is less extreme. Relative errors outside this range were not plotted.

Figure 9: Relative error (%) of natural mortality (first plot in each pair) and reporting rate (second in pair) estimates for each region of an ITCAAN model under scenarios investigating misspecified natural mortality and reporting rates, data quality, spatial complexities, and equal productivities (scenario Groups 2–5) with BEst20 plotted as a reference for 1 000 simulation iterations. Table 1 lists the model abbreviations and corresponding model components. Whiskers on the boxplots extend to 1.5 times the inter-quartile range or the most extreme observed data point, whichever is less extreme. Relative errors outside this range were not plotted. Circles indicate a parameter specified in the ITCAAN model and boxplots only presented in region 1 were estimated as spatially constant.

Figure 10: Relative error (%) of total abundances for all years aggregated from an ITCAAN model for all simulation scenarios described in Table 1 for 1 000 simulation iterations. Whiskers on the boxplots extend to 1.5 times the inter-quartile range or the most extreme observed data point, whichever is less extreme. Relative errors outside the whisker range were not plotted. Note the difference in scale between the top and bottom plots.

Figure 11: Relative error (%) of population-specific abundances and total abundances (summed across populations) of an ITCAAN model for a 1% movement with natural mortality and reporting rate fixed at true values in the left column and 20% movement with natural mortality and reporting rate estimated for 1 000 simulation iterations. The lines show three examples of time series of relative error in abundance estimates for a single simulation in each population. Whiskers on the boxplots extend to 1.5 times the inter-quartile range or the most extreme observed data point, whichever is less extreme. Estimates outside the whisker range were not plotted. Note the difference in y-axis scale between populations.

Appendix A: Parameter List and Model Equations

Table A1: Symbols and descriptions of variables used in Operating and ITCAAN models.

Symbol	Description	Model	Symbol	Description	Model
y	Subscript for year	Both	a	Subscript for age	Both
A	Subscript for oldest modeled age	Both	l	Subscript for release cohort unique by year and region	Both
p	Subscript for spawning population	Both	r	Subscript for region	Both
F	Age-specific fishing mortality	Both	f	Apical fishing mortality	Both
v	Age-specific fishery selectivity	Both	V	Age-specific survey selectivity	Both
ρ_r	Autoregressive coefficient in autoregressive fishing mortality	Operating	μ	Mean fishing mortality in autoregressive process	Operating
σ_r	Variance of fishing mortality in autoregressive process	Operating	σ_C^2	Variance of harvest data observation error	Operating
σ_I^2	Variance of index data observation error	Operating	σ_E^2	Variance of effort data observation error	Operating
τ	Observation error in survey index	Operating	Z	Total mortality	Both
M	Natural mortality	Both	δ	Random annual deviation in recruitment	Both
ϵ	Autoregressive recruitment variation	Operating	ρ_r	Autoregressive coefficient in autoregressive recruitment	Operating
σ_p^2	Recruitment innovation variance	Operating	β	Parameter of Ricker stock-recruit function	Operating
α	Parameter of Ricker stock-recruit function	Operating	m	Maturity at age	Operating
w	Weight at age	Operating	S	Survival	Both
N	Population abundance	Both	R	Number of tagged fish released	Both
$T_{p,r}$	Movement rate from population p to region r	Both	d	Number of tags recovered	Both
n	Number of tagged fish alive	Both	ϕ^S	Expected proportion of tagged cohort to survive	Operating
ϕ^F	Expected proportion of tagged cohort harvested	Operating	Φ	Vector of expected proportions of the fates of tagged cohorts	Operating
ϕ^M	Expected proportion of tagged cohort to die from natural mortality	Operating	$\omega_{p,r}$	Multinomial logit parameter for estimating movement from population p to region r	ITCAAN
t	Number of tags captured by fishery F, die naturally M, or survive S	Operating	q	Catchability coefficient	Both
I	Survey abundance index	Both	E	Observed fishing effort	Both
C	Harvest in numbers caught	Both	γ	Observation error in effort	Operating
ζ	Observation error in harvest	Operating	Δ	Age-specific abundance deviations in first year	ITCAAN
Γ	Mean abundance for first model year	ITCAAN	λ	Annual recruitment deviation	ITCAAN
Λ	Recruitment in the first year	ITCAAN	κ	Annual catchability deviation	ITCAAN
K	Catchability parameter in the first year	ITCAAN	Υ	Angler reporting rate of tags	ITCAAN
P	Harvest age composition	ITCAAN			

Table A2: Equations used to model and estimate population dynamics in Operating and ITCAAN models.

Equation Number	Equation	Model
Recruitment		
(A2.1)	$N_{y+2,a=1,p} = \alpha_p \sum_a (m_a w_a N_{y,a,p}) e^{-\beta_p \sum_a (m_a w_a N_{y,a,p}) \epsilon_y}$	Operating
(A2.2)	$\epsilon_y = \begin{cases} \rho_p \epsilon_{y-1} + \sqrt{1 - \rho_p^2} \delta_y & \text{for } y > 1 \\ \delta_y & \text{for } y = 1 \end{cases} \quad \text{where} \quad \delta_y \sim N\left(\frac{-\sigma_p^2(1-\rho_p)}{2\sqrt{1-\rho_p^2}}, \sigma_p^2\right)$	Operating
(A2.3)	$\begin{aligned} \hat{N}_{y=1,a=1,p} &= \hat{\Lambda}_p & \text{for } y = 1 \\ \hat{N}_{y,a=1,p} &= \hat{N}_{y-1,a=1,p} e^{\hat{\lambda}_{y,p}} & \text{for } 1 > y \leq Y-2 \\ \hat{N}_{y,a=1,p} &= (\hat{N}_{Y-2,a=1,p} + \hat{N}_{Y-3,a=1,p} + \hat{N}_{Y-4,a=1,p})/3 & \text{for } y = Y-1 \text{ or } Y \end{aligned}$	ITCAAN
Abundance and Survival		
(A2.4)	$N_{y+1,a+1,p} = \sum_r N_{y,a,p} T_{p,r} S_{y,a,r} \quad \text{where} \quad a < A-1$	Both
(A2.5)	$N_{y+1,A,p} = \sum_r r N_{y,A,p} T_{p,r} S_{y,A,r} + N_{y,A-1,p} T_{p,r} S_{y,A-1,r}$	Both
(A2.6)	$Z_{y,a,r} = M + F_{y,a,r}$	Both
(A2.7)	$S_{y,a,r} = e^{-Z_{y,a,r}}$	Both
Fishing Mortality and Effort		
(A2.8)	$\begin{aligned} f_{1,r} &\sim \text{Trunc. Normal}(\mu_r, \sigma_r, 0, \infty) \\ f_{y+1,r} &= (\mu_r(1 - \rho_r)) + \rho_r f_{y,r} + \delta_y \\ \text{where } \delta_y &\sim \text{Trunc. Normal}(0, \sigma_r, -(\rho_r f_{y,r} + \mu_r(1 - \rho_r)), \infty) \end{aligned}$	Operating
(A2.9)	$F_{y,a,r} = f_{y,r} v_{a,r}$	Operating
(A2.10)	$E_{y,r} = f_{y,r} / q_r \gamma_{y,r} \quad \text{where} \quad \gamma_{y,r} \sim LN(-\sigma_E^2/2, \sigma_E^2)$	Operating
(A2.11)	$\begin{aligned} \hat{q}_{y=1,r} &= \hat{K} & \text{for } y = 1 \\ \hat{q}_{y,r} &= \hat{q}_{y-1,r} e^{\hat{\kappa}_{y,r}} & \text{for } 1 > y \leq Y-2 \end{aligned}$	ITCAAN
Survey Calculations		
(A2.12)	$I_{y,a,r} = \sum_p N_{y,a,p} T_{p,r} e^{-Z_{y,a,r} * 10/12} q_r V_{a,r}$	Both
(A2.13)	$I_{y,r} = \tau_{y,r} \sum_a I_{y,a,r} \quad \text{where} \quad \tau_{y,r} \sim LN(-\sigma_I^2/2, \sigma_I^2)$	Operating
Movement Estimation		
(A2.14)	$\hat{T}_{r,p} = \frac{e^{\omega_{r,p}}}{\sum_{r=1}^3 e^{\omega_{r,p}}}, \quad \text{where } \omega_{r=4,p} = 0$	ITCAAN
Tag Dynamics		
(A2.15)	$n_{l,p,y,a} = R_{l,p,a} \quad \text{for } y = l$	Both
(A2.16)	$t_{l,p,y,a,r} \sim MN(n_{l,p,y,a}, T_{p,r})$	Operating
(A2.17)	$\phi_{y,a,r}^F = \frac{F_{y,a,r}}{Z_{y,a,r}} (1 - S_{y,a,r})$	Operating
(A2.18)	$\phi_{y,a,r}^S = S_{y,a,r}$	Operating
(A2.19)	$\phi_{y,a,r}^M = \frac{M}{Z_{y,a,r}} (1 - S_{y,a,r})$	Operating
(A2.20)	$\Phi_{y,a,r} = (\phi_{y,a,r}^F, \phi_{y,a,r}^S, \phi_{y,a,r}^M)$	Operating

(A2.21)	$t_{l,p,y,a,r}^{F,S,M} \sim MN\left(t_{l,p,y,a,r}, \Phi_{y,a,r}\right)$	Operating	
(A2.22)	$n_{l,p,y+1,a+1} = \sum_r t_{l,p,y,a,r}^S$	Operating	
(A2.23)	$d_{l,p,y,a,r} \sim BIN\left(t_{l,p,y,a,r}^F, \Upsilon\right)$	Operating	
(A2.24)	$d_{l,p,NR} = \sum_a R_{l,p,a} - \sum_y \sum_a \sum_r d_{l,p,y,a,r}$	Both	
(A2.25)	$\widehat{d_{l,p,y,r}} = \sum_a \hat{n}_{l,p,y,a} \hat{T}_{p,r} \frac{\hat{F}_{y,a,r}}{\hat{Z}_{y,a,r}} \left(1 - \hat{S}_{y,a,r}\right) \hat{\Upsilon}_r$	ITCAAN	
(A2.26)	$\hat{n}_{l,p,y,a} = R_{l,p,a}$	for $y = l$	ITCAAN
	$\hat{n}_{l,p,y+1,a+1} = \sum_r \hat{n}_{l,p,y,a} \hat{T}_{p,r} \hat{S}_{y,a,r}$	for $a < A - 1$	
	$\hat{n}_{l,p,y+1,A} = \sum_r \hat{n}_{l,p,y,A} \hat{T}_{p,r} \hat{S}_{y,A,r} + \hat{n}_{l,p,y,A-1} \hat{T}_{p,r} \hat{S}_{y,A-1,r}$	for $a = A$	
Initial Abundance Estimation			
(A2.27)	$\hat{N}_{y=1,a,p} = \exp(\hat{\Gamma}_p + \hat{\Delta}_{p,a})$	for $a > 2$ where $\sum_a \hat{\Delta}_{p,a} = 0.0$	ITCAAN
Catch Calculations			
(A2.28)	$C_{y,r} = \zeta_{y,r} \sum_a C_{y,a,r}$	where $\zeta_{y,r} \sim LN(-\sigma_C^2/2, \sigma_C^2)$	Operating
(A2.29)	$C_{y,a,r} = \sum_p \frac{F_{y,a,r}}{\hat{Z}_{y,a,r}} N_{y,a,p} T_{p,r} (1 - S_{y,a,r})$		Both
(A2.30)	$C_{y,r} = \sum_a C_{y,a,r}$		Both