SIMULATION ANALYSES OF INTEGRATED TAGGING AND CATCH-AT-AGE ANALYSIS MODELS AND APPLICATION TO LAKE ERIE WALLEYE

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ABSTRACT

SIMULATION ANALYSES OF INTEGRATED TAGGING AND CATCH-AT-AGE ANALYSIS MODELS AND APPLICATION TO LAKE ERIE WALLEYE

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Integrated tagging and catch-at-age analysis (ITCAAN) models incorporate tag-recovery data within statistical catch-at-age models for spatially-explicit assessment of fish stocks. I investigated two tag-recovery frameworks for ITCAAN models that assumed natal homing spawning behavior: release-conditioned and recovery-conditioned. In Chapter 1, I investigated the performance of a release-conditioned ITCAAN model under varying levels of parameter complexity, movement rates, data quality, and misspecification of natural mortality or reporting rates. The release-conditioned ITCAAN model simultaneously estimated movement rates, natural mortality, and tag reporting rates, though accuracy and precision of model estimates decreased with greater model complexity and fewer tags released. In Chapter 2, I investigated a recovery-conditioned ITCAAN model under a range of model complexities, different movement rates, misspecification of natural mortality or reporting rates, and spatially varying reporting rates. The recovery-conditioned ITCAAN model accurately estimated relative reporting rates at low intermixing rates. Biased estimates of individual population abundance resulted when intermixing was high and the reporting rate was assumed to be spatially constant, but the true reporting rates were not. I recommend recovery-conditioned ITCAAN model only be used for assessment of intermixed fish stocks when there is high certainty of spatially constant reporting rates. Both release- and recovery-conditioned ITCAAN models had difficulty estimating individual population abundances and reporting rates under high rates of movement and large differences in population sizes. For both ITCAAN frameworks, estimation of both natural mortality and reporting rates reduced the accuracy and precision of model estimates, but estimates were less biased than misspecifying one of these parameters by 50%. In all investigated simulations, parameter estimates from the release-conditioned ITCAAN model were more accurate and precise compared to the recovery-conditioned ITCAAN model. In Chapter 3, I examined

the ability of a release-conditioned ITCAAN model to estimate time-varying natural mortality and reporting rate parameters and sensitivity to tag-shedding, high-reward tag-recovery data, and seasonal movement dynamics. Natural mortality and reporting rate estimates were most precise and accurate when estimated in 5-year time blocks. Estimation of natural mortality and reporting rates as temporally constant when reporting rates decreased linearly over time caused severe bias in abundance estimates, especially as the frequency of high-reward tag release events decreased. I recommend that high-reward tags be released annually to increase the precision and accuracy of ITCAAN model estimates. The release-conditioned ITCAAN model was sensitive to whether the operating model simulated tag-shedding and seasonal movement dynamics. In Chapter 4, a release-conditioned ITCAAN model was applied to Lakes Erie and Huron walleye (*Sander vitreus*) data and estimates were compared to current assessment models. Reasonable fits to all data sources were obtained for an ITCAAN model that estimated a single reporting rate for all recreational fisheries and assumed the effective sample size of the tag-recovery data was equal to the number of tags released divided by 10. Estimates of population abundance from the ITCAAN model were similar to the model currently used to manage Lake Huron walleye. Conversely, estimates of abundance and natural mortality for the western/central basin of Lake Erie were lower compared to the assessment model currently used to manage the stock. Estimates of natural mortality and abundance for the eastern basin of Lake Erie from the ITCAAN model were larger than estimates for the current assessment model. Based on results from Chapters 1 and 3 the estimates of abundance for the eastern basin of Lake Erie may be overestimated. Given the level of movement within and between Lakes Erie and Huron, ITCAAN models may be a beneficial assessment methodology for management. I recommend future tagging studies of walleye on Lakes Erie and Huron be designed such that high-reward tags and standard-reward tags be released annually so that ITCAAN models can provide accurate abundances, natural mortality, and reporting rates estimates. Additionally, I recommend creel surveys be conducted on the Huron-Erie corridor by the Michigan Department of Natural Resources and Ontario Ministry of Natural Resources and Forestry to measure the currently unaccounted for walleye harvest, which is likely a significant source of mortality.

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PREFACE

The chapters in this dissertation were drafted as standalone papers that will be submitted for publication in peer-reviewed journals. Chapter 1 was submitted and accepted for publication in the *Canadian Journal of Fisheries and Aquatic Sciences*. When submitted, all other chapters will include one or more co-authors. Consequently, all chapters are written with first person, plural narratives, even though I am listed as the sole author of the dissertation. All references are formatted in a style consistent with the *Canadian Journal of Fisheries and Aquatic Sciences*.

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INTRODUCTION

Marine and freshwater organisms are harvested to feed an ever-growing human populous. However, ecosystem capacity to sustain harvest is inherently limited because species have a finite capacity to replace harvested biomass through growth and reproduction. Therefore, fisheries management is often focused on maximizing yield from a population, while simultaneously maintaining a spawning stock abundant enough to successfully reproduce and replace the current stock (i.e., sustainable fishing) (Hilborn and Walters 1992). Management policies designed to keep biomass within sustainable levels are often based on the results of stock assessment methods, which estimate current and historical abundances, mortality components, and recruitment levels (Butterworth and Punt 1999; Punt et al. 2001).

Assessment models have become increasingly complex, but many still make the assumption that harvest and survey data are from one reproductive unit and immigration and emigration rates for the region are negligible (Beverton and Holt 1957; Hilborn and Walters 1992; Goethel et al. 2011). However, there is increasing recognition that this assumption is commonly violated in both freshwater and marine systems (Haist et al. 1999; Punt et al. 2000; Humston et al. 2004; McGarvey et al. 2010; Goethel et al. 2015a; Vandergoot and Brenden 2014). The inclusion of spatial dynamics in stock assessment models are at the forefront of current assessment modeling research (Goethel et al. 2011). Throughout this dissertation, a stock will be defined as an exploited fishery unit defined by the region of harvest, typically a management area (Cadrin et al. 2004). Populations will be defined as interbreeding groups of individuals that are self-sustaining and share similar life history characteristics. In the context of modeling, the boundaries of a population can be delineated based on environmental characteristics of the region or through management boundaries set by jurisdictional authority. Consequently, boundaries used to designate regions for stock assessment may not have any biological significance to the populations they are intended to assess. Incorrect estimation of abundance and productivity by assessment models can easily lead to the overexploitation of populations. When intermixing is high, less productive stocks are

susceptible to overharvest if management actions and assessment methods do not account for spatial dynamics of the species (Ying et al. 2011; Guan et al. 2013; Hulson et al. 2013; Molton et al. 2013; Li et al. 2014). The collapse of some economically important fish stocks has been partly attributed to inadequately accounting for the spatial dynamics that arise from movement, such as Atlantic cod (*Gadus morhua*; Fu and Fanning 2004; Hutchinson 2008) and many Pacific salmon populations (*Oncorhynchus* spp.; Morishima and Henry 1999). Therefore, accounting for the movement of fish when assessing intermixed populations is difficult, but imperative for the sustainable management of all harvested populations.

Incorporation of spatially-explicit stock dynamics in assessment models has long been a subject of interest (Skellam 1951; Beverton and Holt 1957; Jones 1976). However, information regarding movement of individuals between management regions and intermixing of spawning fish populations is often lacking, and inhibits the development of spatially-explicit assessment models (Goethel et al. 2011). Data on the movement rates of fish is obtained primarily from tagging studies using either conventional or electronic tags (Jones 1959; Ishii 1979; Hilborn 1990). Therefore, most models that include spatial dynamics of stocks have incorporated tagging data into the model's framework. Integrated tagging and catch-at-age analysis (ITCAAN) assessment models incorporate 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 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, where they may stay 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 overlapping 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. 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 spatially-explicit assessment models, and incorporating tagging data will likely inform the estimation of these rates. Catch-at-age models typically use 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 and simulations suggest that in the absence of structural model error this parameter may be estimable (Fu and Quinn 2000; Wang and Liu 2006; Lee et al. 2011; Maunder and Wong 2011; Jiao et al. 2012; Johnson et al. 2015; Sippel et al. 2017). Conversely, tag-recovery data are frequently 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 accuracy and bias of some parameters may be affected by the degree of movement among or differences in relative size of the

fish populations.

Tag-recovery data can be fit to different model frameworks depending on the parameters of interest and the validity of assumptions. Tag-recovery data are most commonly modeled as the number of tags recovered within a given time frame and region, divided by the total number of tags released in a given tagging event (Hilborn 1990; Maunder 1998; Punt et al. 2000; Hulson et al. 2011, 2013; Kerr et al. 2013; Goethel et al. 2015a). This framework for tag-recovery will be referred to as the release-conditioned model and the multinomial likelihood distribution with the scaling constants removed used to fit these data is:

$$L = \prod_i \left[\prod_r \prod_y v_{iry}^{R_{iry}} \right] w_i^{NR_i}$$

where

$$v_{iry} = \frac{\hat{R}_{iry}}{T_i} \qquad \text{and} \qquad w_i = \frac{\widehat{NR_i}}{T_i}$$

(0.0.1)

In this formula, the accented variables are those that are predicted by the model from other parameters, for example $\hat{R}_{iry}$ is the predicted recoveries in year y and region r, for the release group i and R is the observed recoveries. In the equations, T_i is the total number of tags released in group i, NR_i is the number of tags that were never recovered, and L is the likelihood. The denominator for the calculation of v and w gives the name for this analysis of tag-recovery data: the release-conditioned framework.

The release-conditioned model requires assumptions regarding the rates of tag induced mortality, tag shedding, and tag reporting to limit the bias in parameter estimates, and allow the separation of mortality into fishing and natural components (Brenden et al. 2010). Some common approaches when analyzing tag-recovery data are to assume that these rates are negligible (Kleiber et al. 1987; Hilborn 1990), make assumptions based on expert knowledge (Hampton 1997; Vandergoot and Brenden 2014), or to conduct specialized experiments that allow these parameters to be estimated internally or externally to the integrated assessment model (Pollock et al. 2001, 2002; Agnew et al. 2006; Vandergoot et al. 2012; Goethel et al. 2015a). Even with these experiments, biased results can

still occur due to small sample sizes or incorrect model-structure assumptions. Estimates of fishing and natural mortality rates in tag-recovery studies have been found to be sensitive to inaccuracies in reporting rates (Brenden et al. 2010). The tag-reporting rate has been considered one of the most difficult variables to estimate in a tagging experiment (Denson et al. 2002; Miranda et al. 2002). Thus, the modeling of tag-recovery data in terms of total number of tags released has the potential of being suboptimal.

An alternative formulation for analyzing tag-recovery uses the number of tags returned within a region and time period, divided by the total number of returns from a given release event (McGarvey and Feenstra 2002). The multinomial likelihood for the recovery-conditioned model differs from the likelihood for the release-conditioned model in two primary ways. First, tags that were never recovered are not predicted by the model and are not included in the likelihood. Secondly, the denominator for the predicted proportion is the total number of tags recovered (summed across time and space) from a release group i:

$$LH = \prod_i \prod_r \prod_y v_{iry}^{R_{iry}}$$

where   (0.0.2)

$$v_{iry} = \frac{\hat{R}_{iry}}{\sum_{ry} \hat{R}_{iry}}.$$

Tagging-induced mortality, tag shedding, and non-reporting rate of tag-recoveries often require additional costly experiments to estimate. With this formulation, tagging-induced mortality, tag shedding, and non-reporting rate of tag recoveries cancel out of the likelihood equations for this framework if they are assumed to be spatially and temporally constant, i.e. they do not need to be estimated (McGarvey and Feenstra 2002; McGarvey et al. 2010). This is considered beneficial as collection of data for estimating these factors can be expensive. There have been limited evaluations of the performance of the recovery-conditioned model (McGarvey et al. 2010), and ITCAAN models using a recovery-conditioned framework have not been fit to many real-world fisheries data. The recovery-conditioned tag-integrated catch-at-age model has the potential to accurately estimate important population dynamics parameters without the possible bias introduced by the nuisance

tagging parameters, if indeed they are spatially and temporally constant. This could result in more accurate and precise tag-integrated models compared to the release-conditioned models, and thus would be a preferable model. However, this model has not been tested under circumstances where these nuisance parameters are not spatially constant; therefore, the robustness of recovery-conditioned ITCAAN models is not presently known.

Lakes Erie and Huron Walleye

Walleye (*Sander vitreus*) is a piscivorous keystone species, which aggregates during the early spring in rivers and shallow rocky reefs for spawning (Busch et al. 1975). Walleye typically exhibit spawning-site fidelity (Crowe 1962; Hayden et al. 2014), but genetic analyses have shown there may be significant straying and interbreeding among spawning populations (Stepien and Faber 1998; Strange and Stepien 2007; Brenden et al. 2015; Hayden et al. 2017). After spawning, walleye often make directed and sometimes long-distance movements towards summer feeding grounds. Feeding grounds are believed to be selected based on thermal conditions and prey availability (Wang et al. 2007; Zhao et al. 2011; Hayden et al. 2014; Vandergoot and Brenden 2014; Herbst et al. 2016). Long distance movement by walleye between interconnected lakes has been shown throughout their range (Smith et al. 1952; Rasmussen et al. 2002; Wang et al. 2007; Zhao et al. 2011; Hayden et al. 2014; Vandergoot and Brenden 2014; Herbst et al. 2017). This dispersal of walleye after spawning is recognized to be potentially problematic for management as fish can cross multiple jurisdictional boundaries when moving between spawning and feeding grounds. Consequently, fisheries for walleye may depend on spawning populations and systems over which managers have no jurisdictional authority (Brenden et al. 2015; Herbst et al. 2017).

Both historical (jaw tag) and contemporary (acoustic telemetry) tagging studies, as well as genetic analysis have found that movement of walleye within and between Lakes Erie and Huron occurs frequently (Vandergoot and Brenden 2014; Brenden et al. 2015; Hayden et al. 2017). For some walleye spawning populations in the western basin of Lake Erie, movement rates to Lake Huron were estimated at around 1–2% (Wang et al. 2007; Vandergoot and Brenden 2014; Hayden

et al. 2017). Movement from the western basin to the eastern basin has been shown to be substantial through jaw tag recoveries (Wang et al. 2007; Vandergoot and Brenden 2014) and telemetry studies (Chris Vandergoot, personal communication). 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). Given the differences in walleye abundance between the Lake Erie basins and Lake Huron, even the low rate of movement means that a considerable amount of the harvest in this region is fish from the western basin population (McParland et al. 1999; Brenden et al. 2015).

Walleye are exploited commercially and recreationally throughout the Great Lakes (Pandit et al. 2013; Fielder and Bence 2014; Wills et al. 2016). The two largest fisheries for walleye in the Great Lakes region occur in Lakes Erie and Huron (Baldwin et al. 2009). In 2000, harvest of walleye in Lake Erie was worth $9.8 million in dock side value from commercial fisheries, which does not account for the economic value of the recreational fishery (Baldwin et al. 2009). The recreational fishery for walleye in Ohio during 2013 was estimated to generate $67 million in total direct expenditures (Sohngen et al. 2015). Management of walleye in Lake Erie is currently facilitated by the Great Lakes Fishery Commission, which was formed by the 1954 Convention on Great Lakes Fisheries between the United States and Canada. Specifically, a walleye management plan was developed by the Lake Erie Percid Management Advisory Group, which is comprised of stakeholders, fisheries managers, agency fishery biologists, and stock assessment scientists. The WTG provides annual harvest recommendations to the Lake Erie Committee (LEC) based on assessment estimates of population status and the harvest control rules set forth by the management plan. The LEC determines the annual total allowable catch (TAC), with harvest quotas then allocated to individual jurisdictions based on water area (Wills et al. 2016). The four U.S. states (Michigan, New York, Ohio, and Pennsylvania) and the Canadian province (Ontario) manage the harvest

of walleye through regulations specific to the jurisdiction. Presently, separate SCAA assessment models are used to estimate walleye population abundances and mortalities in Lakes Erie and Huron to gauge the health of the populations and assist in setting harvest regulations (Fielder and Bence 2014; Wills et al. 2016). Walleye in Lake Erie are currently managed assuming limited movement between management areas (Wills et al. 2016), whereas the assessment in Lake Huron attempts to account for this intermixing (Fielder and Bence 2014). There has been increasing interest in the development and use of spatially-explicit models for assessing the walleye populations in Lakes Erie and Huron due to the economical and ecological importance of the species and the degree of movement that has been estimated to occur both within and between the lakes.

The current assessment model for walleye estimates the abundance of the stock in the western and central basins of Lake Erie (Wills et al. 2016). This assessment does not account for the intermixing of populations from other regions or the emmigration of walleye out of this region. Although the contribution of western basin origin walleye to the harvest in the eastern basin is acknowledged, the assessment of the eastern basin does not explicitly account for immigration from the western basin of Lake Erie. However, previous research has attempted to estimate the population in the eastern basin of Lake Erie and account for intermixing of fish from different populations (Zhao et al. 2011). The assessment model for Lake Huron walleye attempts to account for the immigration of western basin walleye by incorporating abundance estimates from the western basin of Lake Erie assessment and the 3-year average of annual proportion of jaw tags returned from the western basin captured in Lake Huron (Fielder and Bence 2014). However, jaw-tagging of walleye in western basin of Lake Erie has not occurred since 2010 and recent recoveries are infrequent. Previous attempts to integrate tag-recovery data into the assessment model for Lake Huron ultimately resulted in the selection of the model that did not incorporate this data (Fielder and Bence 2014). The three assessment methods used to provide management advice assume natural mortality is known and movement of walleye between management boundaries are not fully accounted for. Therefore, assessments that attempt to estimate natural mortality and intermixing may be useful for management of walleye in Lakes Erie and Huron.

Application of tag-integrated assessment models have become increasingly common in recent years (McGarvey et al. 2010; Hulson et al. 2013; Goethel et al. 2015a). Though it is standard practice in stock assessments to test new modeling techniques through simulations (Bence et al. 2008), evaluation of the performance of ITCAAN models through simulation has not been widely conducted. A comparison of model performance of release-conditioned and recovery-conditioned models would be beneficial to fisheries scientist interested in using a spatially-explicit ITCAAN model. The overall goal of my dissertation is to evaluate performance (i.e., parameter estimability, parameter sensitivity) of release- and recovery-conditioned ITCAAN models and determine appropriateness of the models for application to Lakes Erie and Huron walleye. Specific objectives for each chapter are as follows:

1. Determine precision and accuracy of parameters in release-conditioned ITCAAN models with increasing complexity incorporated into model scenarios.

2. Evaluate precision and accuracy of parameters in recovery-conditioned ITCAAN models with increasing complexity incorporated into model scenarios and sensitivity to the assumption of spatially constant nuisance parameters.

3. Evaluate the sensitivity of release-conditioned ITCAAN models to common assumptions made when evaluating model performance.

4. Apply an ITCAAN model to data from Lakes Huron and Erie walleye and determine suitability of the model to provide management advice.

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CHAPTER 1

SIMULATION TESTING THE ROBUSTNESS OF A MULTI-REGION TAG-INTEGRATED ASSESSMENT MODEL THAT EXHIBITS NATAL HOMING AND ESTIMATES NATURAL MORTALITY AND REPORTING RATE

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) and the migratory behavior exhibited by both freshwater and marine species (Punt et al. 2000; Hayden et al. 2014; Goethel et al.

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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; Molton et al. 2013). 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 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

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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 overlapping 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 (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 (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. Postspawning walleye distribute throughout the lakes (Wang et al. 2007; 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.A.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 mass-at-age or mass-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

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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 1.A.2). Mass 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 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 Supplementary Material 1. Symbols and equations used to model the dynamics for both the operating model and ITCAAN model are presented in Appendix 1.B. Parameter values assumed in the operating model and likelihood equations used within the ITCAAN model are presented in Supplementary Material 1.

Operating Model

Recruitment for the spawning populations assumed Ricker stock-recruitment functions with spawners equal to the spawning biomass 2 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 (1.B.2.1)). 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 1.A.2; Supplementary Material 1 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 (1.B.2.2)). 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 research 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 (Equations (1.B.2.4) and (1.B.2.5)). The apical fishing mortality rates for the harvest regions were randomly generated from first-order autoregressive processes (Equation (1.B.2.9)), where the means of the processes were different for each region and were based on estimates from Lakes Erie and Huron (Supplementary Material 1 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 fishing mortality (Supplementary Material 1 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 section on Simulation Scenarios), but in all cases was assumed to be the same proportion to all non-natal regions for all populations, which was temporally and age-invariant. Fishery effort data were generated assuming a lognormal observation error (Equation (1.B.2.10)). 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 (Equations (1.B.2.13) and (1.B.2.14)).

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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 2000 fish per year and region, but lower tagging levels were considered for some scenarios (Table 1.A.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 1 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 (1.B.2.16)). 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 (1.B.2.17)). The probabilities of a tagged fish being harvested (Equation (1.B.2.18)), surviving (Equation (1.B.2.19)), or dying (Equation (1.B.2.20)) in a harvest region were then calculated based on the fishing, total, and natural mortalities in a region. These probabilities (Equation (1.B.2.21)) were used in a multinomial random number generator to determine the number of fish in each fate category (Equation (1.B.2.22)). 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 (1.B.2.24)). 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 (1.B.2.23)). 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 (1.B.2.25)).

A limitation that we imposed on our simulations was that abundances for any of the four populations could not decrease to less than 40000 fish. If this occurred, that iteration was discarded and another simulation created. An abundance of less than 40000 fish would mean that more than 5% of a population was tagged within a year at the baseline tagging rate of 2000 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 1.A.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 multiplicative random-walk deviations were assumed to be from a lognormal distribution (Equation (1.B.2.3)) with the log-standard deviation fixed at 4. The last 2 years of recruitment in the ITCAAN model were set equal to the mean recruitment for the previous 3 years for each population, which was necessary for the model to converge with a positive-definite Hessian matrix. Abundances in the first modeled year for age-3 and older fish were estimated as the product of a mean abundance and multiplicative age-specific deviations that were assumed to be from a lognormal distribution and constrained to sum to 0 across ages (Equation (1.B.2.28)). Year-specific fishery catchabilities were modeled using a random-walk process (Equation (1.B.2.12)), as advocated by Wilberg and Bence (2006). Age-specific selectivities were estimated for ages 2 to 7 individually for each fishery and were assumed constant through time. Depending on the examined scenario, natural mortality and reporting rate were either estimated or set equal to assumed (sometimes misspecified) values in the ITCAAN model. Region-specific survey catchabilities and age-specific survey selectivities

were assumed constant over time and were estimated parameters in all simulations. Movement rates, including the proportion staying in the natal region, were estimated through a multinomial logit transformation that constrained movement rates to be between 0 and 1 and to sum to 1 (Vandergoot and Brenden 2014). The formulation is similar to that of Goethel et al. (2015a) except the parameter for movement to region 4 for all populations was set equal to 0, instead of the residency parameter. Three parameters for each population were then transformed into movement rates to the four regions so that the model was identifiable (Equation (1.B.2.15)). As with the operating model, movement rates were assumed to be temporally and age-invariant. When estimated, reporting rates were modeled using a logistic function, which constrained the reporting rate to be between 0 and 1.

Numbers of recovered tags were predicted based on the known number of tags released by age each year, estimated population movement rates, survival estimates, and a fishery-specific estimated reporting rate (Equation (1.B.2.26)). Proportion of yearly regional tags recovered and tags never recovered relative to the total number of tags released were assumed to be multinomially distributed and were used in likelihood calculations.

Highest posterior density estimation, which is also referred to as maximum penalized likelihood, was used to estimate the parameters of the ITCAAN model. Diffuse upper and lower bounds were specified for all parameters to keep the optimization algorithm from flat parts of the likelihood surface and to prevent unreasonable parameter estimates. The objective function was the sum of multiple negative log-likelihood and log-penalty components. Age-composition and tag-recovery data were modeled as multinomial distributions, while all other data and parameter penalties were modeled as lognormal distributions (Supplementary Material 1 Table 4).

An ITCAAN model was assumed to have converged if the maximum gradient across all parameters was 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 1000 iterations with a converged ITCAAN model were obtained. The total number of simulations needed to reach a sample size of 1000 for each scenario, percent convergence, and the number of simulations rejected

for the two conditions are presented in Table 1.A.1.

Simulation Scenarios

We evaluated ITCAAN model performance through scenarios grouped into five categories (Table 1.A.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 among simulation scenarios and differences are presented in Table 1.A.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, 2000 fish were tagged from each population every year, unless otherwise specified (Table 1.A.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 1.A.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.A.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.A.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: 1500, 1000, 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 1500 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 2000 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, 2000 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 1.A.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 with 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 1.A.2). Unique auto-regressive parameters (ρ_p) and innovations variance parameters (σ_p^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 with 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 1. Parameters not presented showed either no bias in estimates or

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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 (i.e., estimate minus true) to facilitate comparisons across scenarios, though movement REE are presented in the Supplementary Material 1. Errors in parameters that were age-specific (e.g., selectivity; results shown in Supplementary Material 1) or year-specific (e.g., recruitment) were calculated for each age or year separately for the 1000 simulations and then aggregated by region for summarization and plotting. For example, the boxplots of recruitment show 40000 values (i.e., 40 years of recruitment times 1000 iterations). The median and interquartile ranges (IQR) of the REE and actual error of the 1000 simulated data sets 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 40000 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 1000 simulations in Table 1.A.1 because this was a result of the operating model and not the ITCAAN model. Abundance in the operating model varied widely among 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 1.A.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. Mean 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 1.A.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.A.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.A.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.A.1).

ITCAAN Model Performance

Recruitment Relative Error

Movement rates had a large effect on both the bias and precision of recruitment estimates (Figure 1.A.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 1.A.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 1.A.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 = 37.72%; Figure 1.A.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 = -64.38), which was nearly double the bias observed for the BEst20 scenario (BEst20 population 2: median REE -31.38%). When natural mortality was specified at 1.5 times the true value, the median recruitment was strongly positively biased (RSensO population 2: median REE = 125.24%), and one of the least precise among the evaluated scenarios for all populations (Figure 1.A.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 1.A.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 with the BEst20 scenario (ESS50 population 2: median REE = -34.7%). Compounding a smaller effective sample size with greater levels of measurement error had only a marginal effect on bias (HighVar population 2: median REE = -37.6%). 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 1.A.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 1.A.5). When reporting rates were estimated as spatially constant, median REE in recruitment for population 2 were approximately -14%. 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 1.A.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 = -2.3% to -4.6%). 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 1.A.6). Median actual errors were within -0.26 and 0.08 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 bias in movement rate estimates into each of the

regions was observed when reporting rates were estimated but natural mortality in the ITCAAN model was fixed at its true value for 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 for the high movement rate scenario (BEst20; Figure 1.A.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 regions 1 and 2 when either natural mortality or reporting rates were misspecified (Figure 1.A.7). The precision of movement estimates was relatively consistent among scenarios when the number of tags released in each region was 2000 (BEst20 region 2: IQR actual error = 1.47). 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 = 4.38). Despite this, the movement estimates from the examined scenarios were precise and also remained relatively unbiased (Figure 1.A.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 1.A.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 = 0.85% to 0.90%). 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 1.A.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 ≈ -14%). Conversely, median relative errors in reporting rates for the other

regions were generally within ± 5%.

Estimates of natural mortality were highly affected by incorrectly specifying the reporting rate in the ITCAAN model (Figure 1.A.9). When reporting rate was misspecified at 1.5 times its actual value, natural mortality estimates were positively biased (MSens: median REE = 20.64%). 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 1.A.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 1.A.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 (median REE = -1.40%).

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Total Abundance Relative Error

Bias and precision of total abundance estimates varied by examined scenario (Figure 1.A.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 1.A.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 1.A.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 1.A.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 50.89%) and when natural mortality was fixed at 1.5 times the true value (RSensO median REE 131%; Figure 1.A.10). Conversely, there was negative bias in total abundance when natural mortality was fixed at half the true value (RSensU

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median REE -48%). Simulations that tested different structural assumptions and data quality had similar median REE values compared with 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 = 11%; 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 data sets by simulating stochastic first-order autoregressive annual fishing mortality and recruitment processes and applied observation error for four populations with drastically different magnitudes of spawning population size. These stochastic processes were included to create data sets 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 (Maunder 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 data sets. 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 1.A.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 by both 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 variables (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; 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 that 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 ope-

rating 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; Hutchinson 2008; 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 are 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 and 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

APPENDICES

APPENDIX 1.A

TABLES AND FIGURES

Table 1.A.1: Abbreviations used in figures and text, model characteristics, and convergence rates of the ITCAAN model for investigated scenarios.

Scenario Group	Abbrv.	ITCAAN model		Operating model		# needed for 1000 converged	Percent converged	NPD Hessian	Maximum Gradient > 0.05
		Reporting rate	Natural mortality	Emigration rate	tags per region				
1	MvFix1*	Known	Known	1%	2000	1297	77.1	1	296
1	MRFix1	Known	Known	1%	2000	1250	80.0	5	249
1	MEst1	Known	Est. RC	1%	2000	1266	79.0	4	265
1	REst1	Est. RU	Known	1%	2000	1310	76.3	2	310
1	BEst1	Est. RU	Est. RC	1%	2000	1283	77.9	0	283
1	MvFix5*	Known	Known	5%	2000	1014	98.6	2	13
1	MRFix5	Known	Known	5%	2000	1028	97.3	4	28
1	MEst5	Known	Est. RC	5%	2000	1015	98.5	2	15
1	REst5	Est. RU	Known	5%	2000	1027	97.4	3	26
1	BEst5	Est. RU	Est. RC	5%	2000	1035	96.6	3	35
1	MvFix10*	Known	Known	10%	2000	1007	99.3	6	2
1	MRFix10	Known	Known	10%	2000	1012	98.8	12	4
1	MEst10	Known	Est. RC	10%	2000	1005	99.5	5	0
1	REst10	Est. RU	Known	10%	2000	1006	99.4	6	2
1	BEst10	Est. RU	Est. RC	10%	2000	1005	99.5	4	3
1	MvFix20*	Known	Known	20%	2000	1028	97.3	27	4
1	MRFix20	Known	Known	20%	2000	1024	97.7	24	1
1	MEst20	Known	Est. RC	20%	2000	1023	97.8	23	2
1	REst20	Est. RU	Known	20%	2000	1015	98.5	15	3

Table 1.A.1 (cont'd)

1	BEst20	Est. RU	Est. RC	20%	2000	1024	97.7	23	6
2	MSens	1.5×True	Est. RC	20%	2000	1030	97.1	30	4
2	RSensU	Est. RU	0.5×True	20%	2000	1012	98.8	11	5
2	RSensO	Est. RU	1.5×True	20%	2000	1051	95.1	49	13
3	T1500	Est. RU	Est. RC	20%	1500	1010	99.0	10	1
3	T1000	Est. RU	Est. RC	20%	1000	1010	99.0	10	2
3	T500	Est. RU	Est. RC	20%	500	1018	98.2	18	4
3	T250	Est. RU	Est. RC	20%	250	1017	98.3	16	4
3	ESS50[†]	Est. RU	Est. RC	20%	2000	1022	97.8	22	7
3	HighVar[†‡]	Est. RU	Est. RC	20%	2000	1032	96.9	32	1
4	RC_MC	Est. RC	Est. RC	20%	2000	1017	98.3	17	0
4	RC_MU	Est. RC	Est. RU	20%	2000	1022	97.8	22	3
4	RU_MU	Est. RU	Est. RU	20%	2000	1006	99.4	5	4
5	EqProd[§]	Est. RU	Est. RC	20%	2000	1003	99.7	3	2

[*] **Note:** Est. = Estimated in ITCAAN; RC = Regionally constant; RU = Regionally unique; Known = Fixed at true value; NPD = Not positive-definite

[*] Movement rate fixed at true value; For all other scenarios movement is estimated

[†] 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

Table 1.A.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 Other Scenarios	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 Catch Per Effort	Lognormal CV 20%	Lognormal CV 40%	Lognormal CV 20%	Lognormal CV 20%
Catch Age Composition	Multinomial ESS 100	Multinomial ESS 50	Multinomial ESS 50	Multinomial ESS 100
Survey Age Composition	Multinomial ESS 100	Multinomial ESS 50	Multinomial ESS 50	Multinomial ESS 100
Ricker Stock-Recruitment Parameters (α & β)	Different among populations	Different among populations	Different among populations	Same across populations
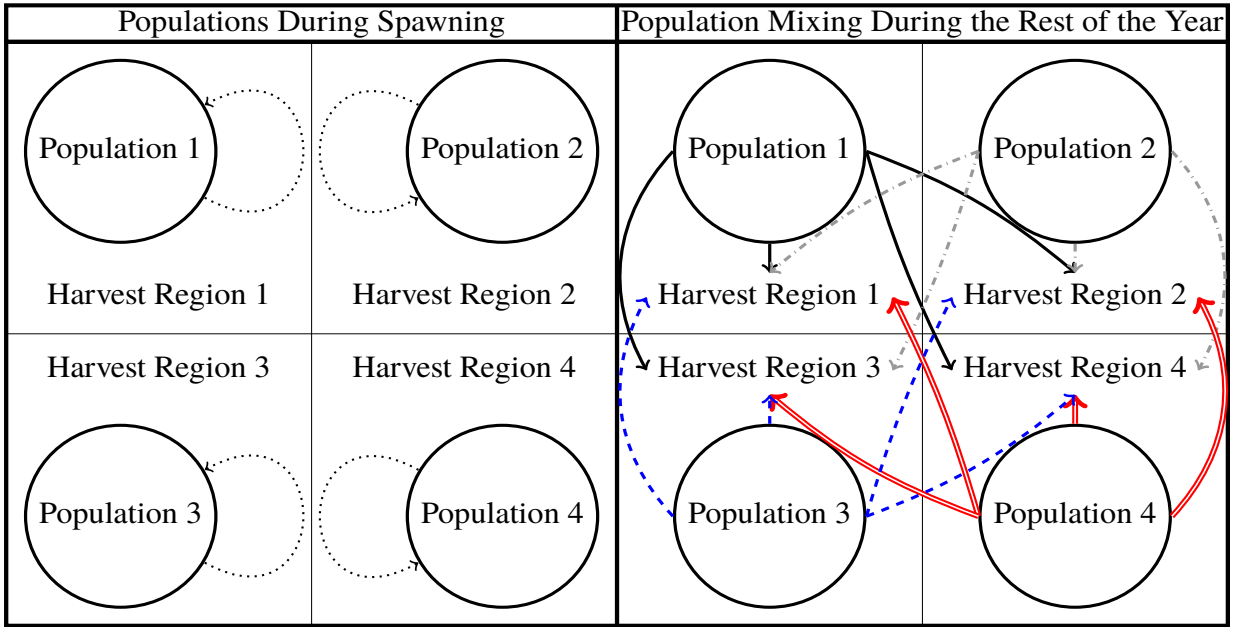
Figure 1.A.1: Movement dynamics simulated by the four-region operating model assuming natal homing. The left half of the figure represents fish during spawning at the beginning of every year, which are assumed to return to their natal population to spawn. The right half of the figure shows the distribution of fish during the remainder of the year that mix to all harvest regions and stay for the rest of the year.
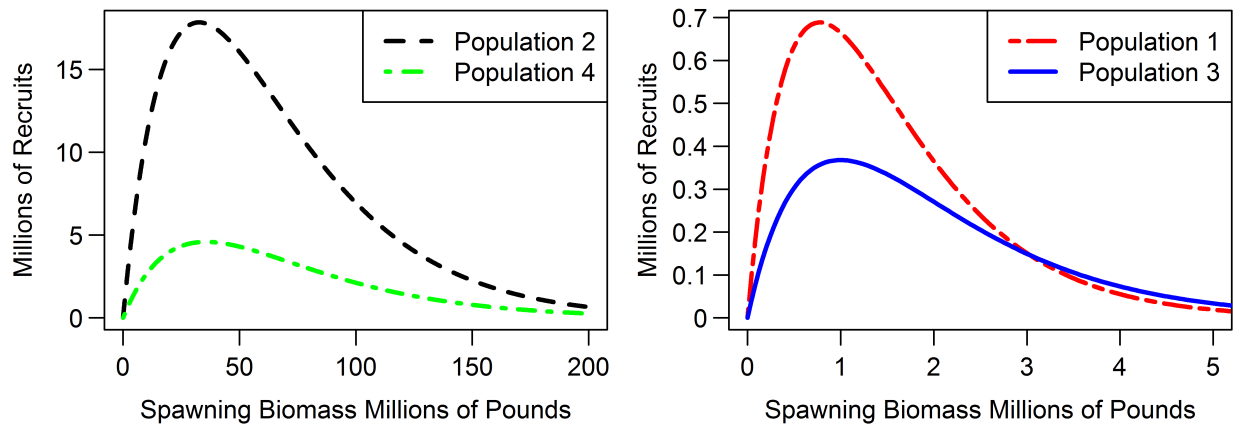
Figure 1.A.2: Ricker stock-recruit relationships used to create the recruitment dynamics of the four populations in the simulation. Note the large difference in axes scale between the two panels.
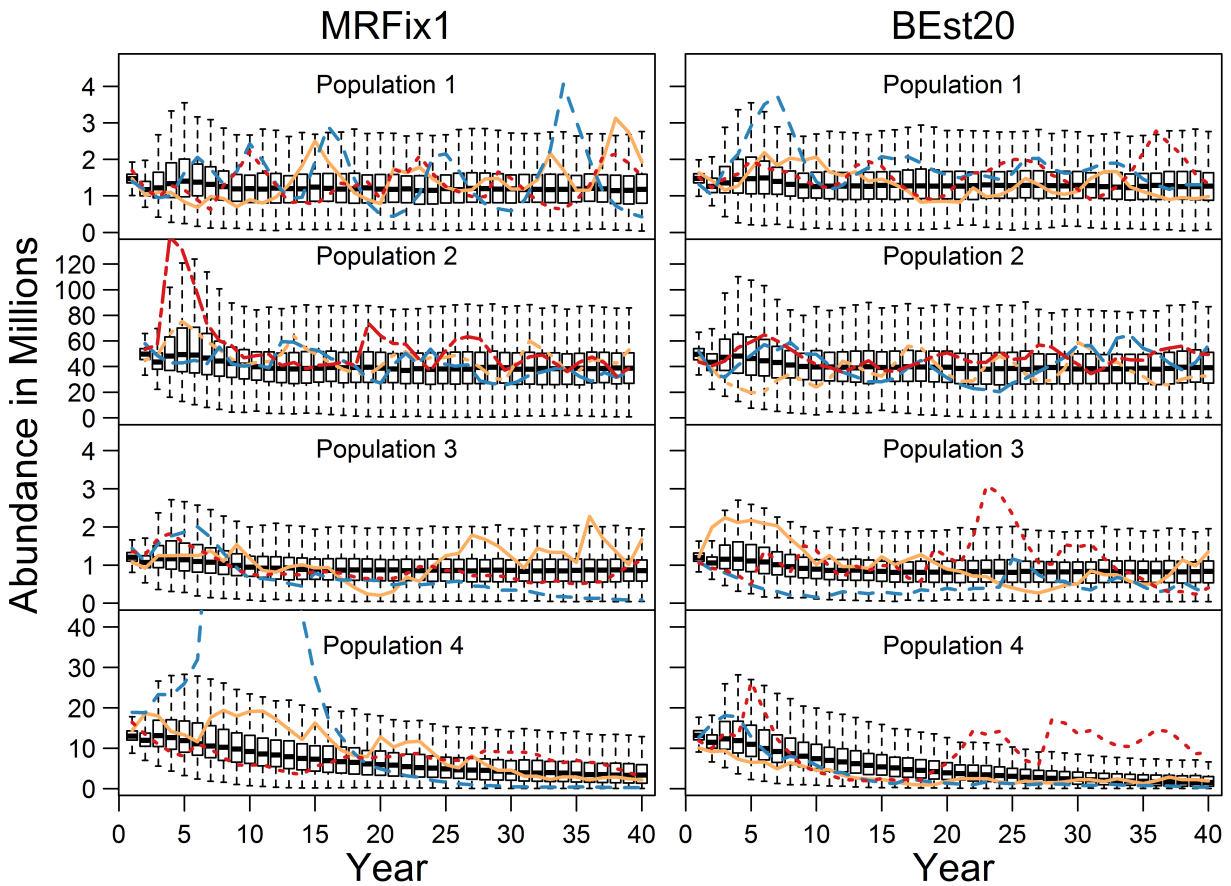
Figure 1.A.3: Total abundance trends of each population for two different scenarios in a spatially-explicit operating model for 1000 simulation iterations. The left column of figures is for populations with 1% movement and the right column is for populations with 20% movement to non-natal regions. The lines show three examples of simulated time series of abundance for each population. Whiskers on the boxplots extend to 1.5 times the interquartile range or the most extreme observed data point, whichever is less extreme. Relative errors outside the whisker range were not plotted.
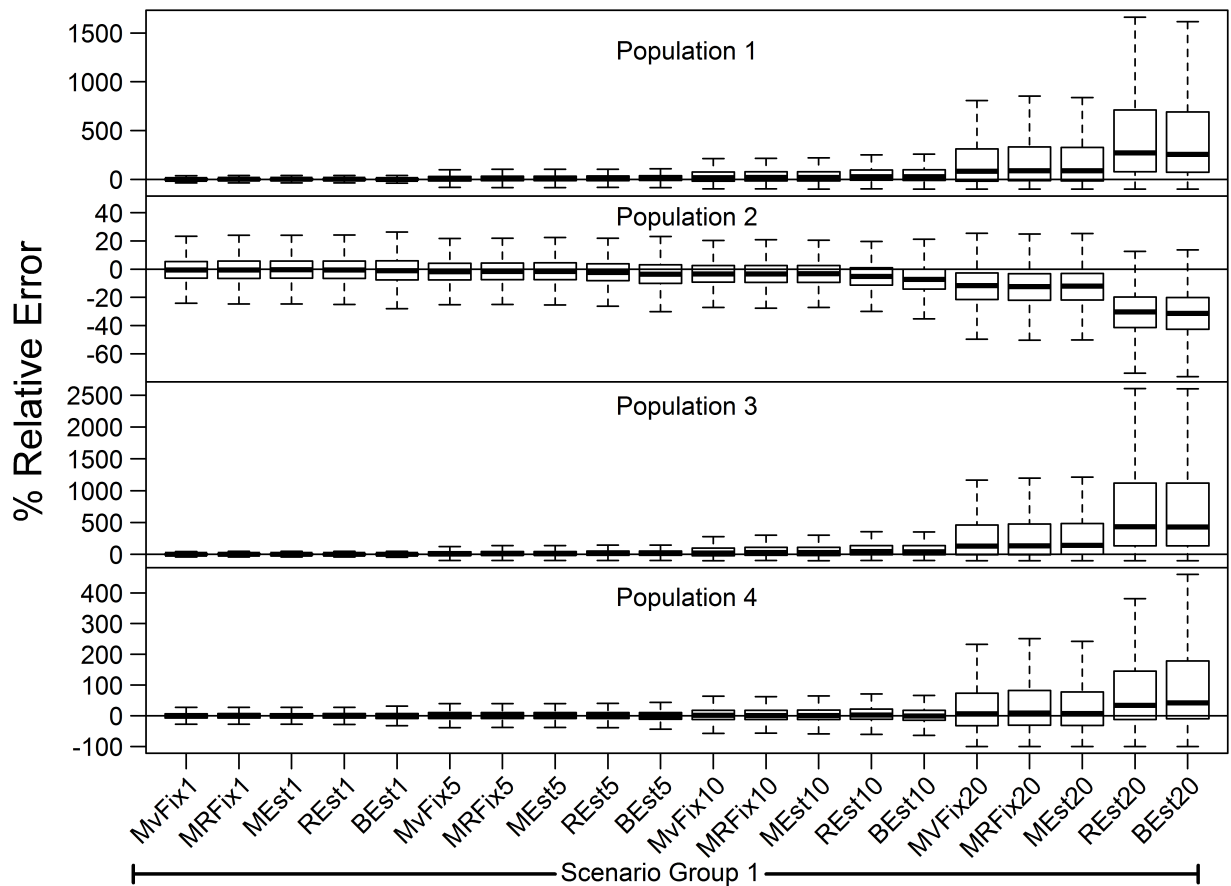
Figure 1.A.4: Relative error (%) of annual recruitment estimates for each population of an ITCAAN model under different movement rates and parameter estimation assumptions (scenario Group 1) for 1000 simulation iterations. Table 1.A.1 lists the model abbreviations and corresponding model components. Whiskers on the boxplots extend to 1.5 times the interquartile 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 among populations.
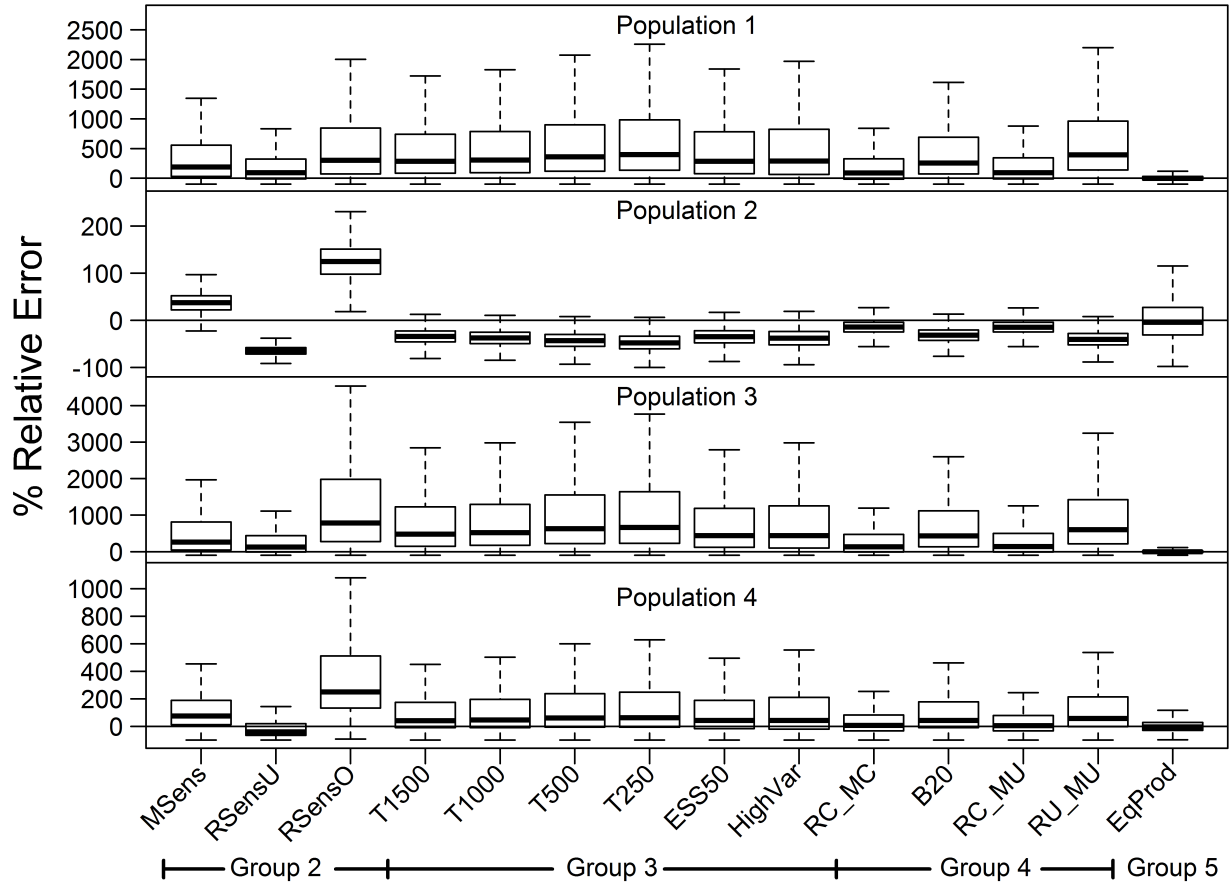
Figure 1.A.5: Relative error (%) of recruitment estimates for each population of an ITCAAN model under scenarios investigating misspecfied natural mortality and reporting rates, data quality, spatial complexities, and equal productivities (scenario Groups 2–5) for 1000 simulation iterations. Table 1.A.1 lists the model abbreviations and corresponding model components. Whiskers on the boxplots extend to 1.5 times the interquartile 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 among populations.

Figure 1.A.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 1000 simulation iterations. Table 1.A.1 lists the model abbreviations and differences in operating and ITCAAN models. Whiskers on the boxplots extend to 1.5 times the interquartile range or the most extreme observed data point, whichever is less extreme. Actual errors outside the whisker range were not plotted.

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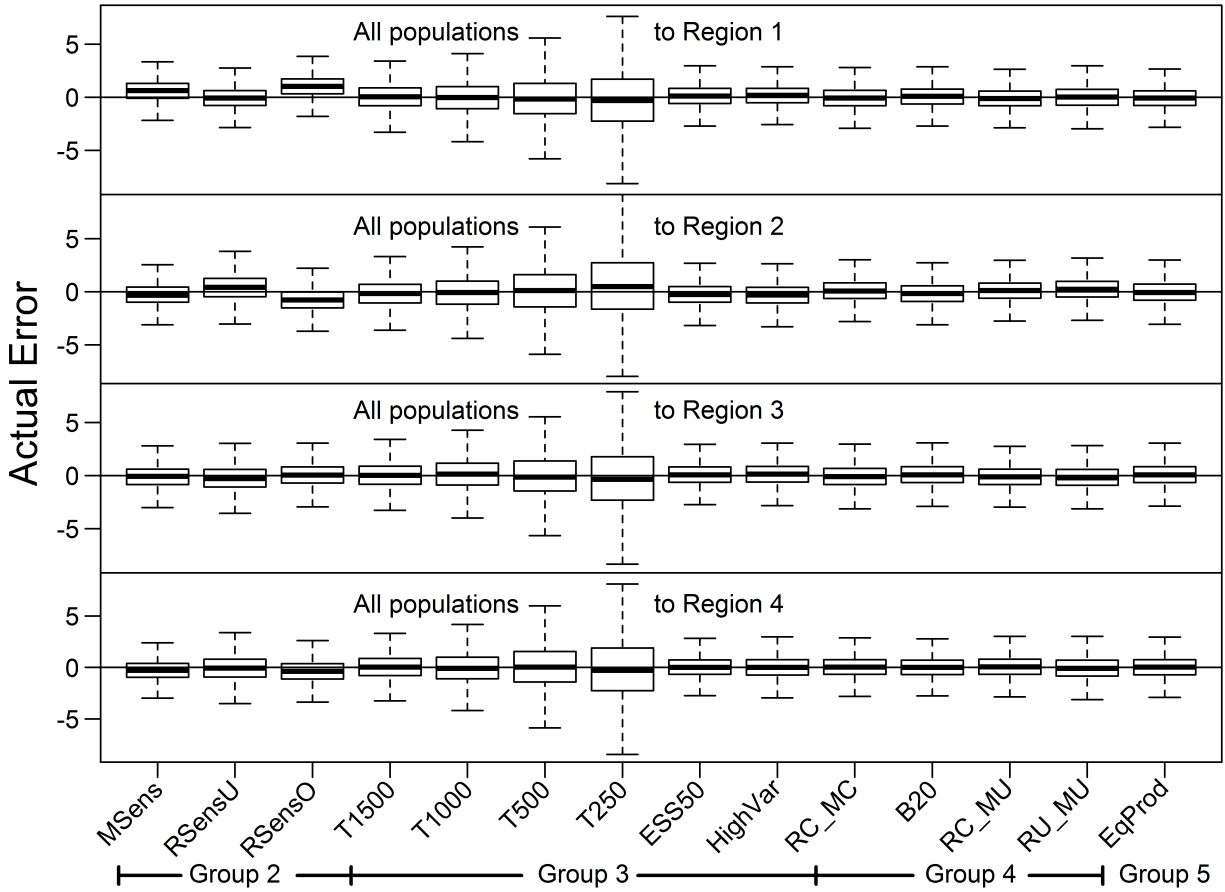
Figure 1.A.7: Actual error of movement rate estimates from all populations to individual harvest regions of an ITCAAN model under scenarios investigating misspecified natural mortality and reporting rates, data quality, spatial complexities, and equal productivities (scenario Groups 2–5) for 1000 simulation iterations. Table 1.A.1 lists the model abbreviations and corresponding model components. Whiskers on the boxplots extend to 1.5 times the interquartile range or the most extreme observed data point, whichever is less extreme. Actual errors outside the whisker range were not plotted.
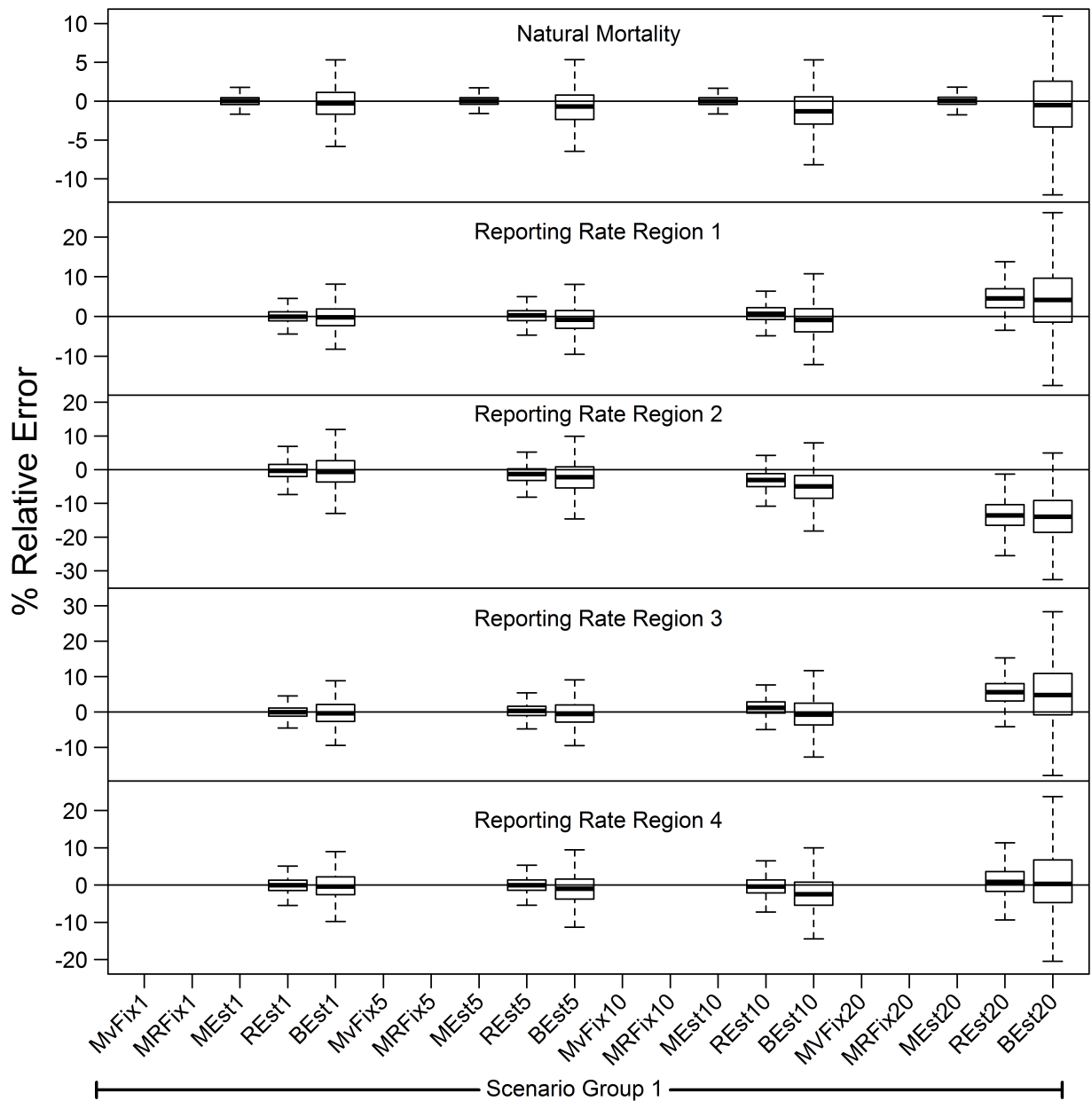
Figure 1.A.8: Relative error (%) of natural mortality and regional reporting rate estimates of an ITCAAN model under different movement rates and parameter estimation assumptions (scenario Group 1) for 1000 simulation iterations. Table 1.A.1 lists the model abbreviations and corresponding model components. Whiskers on the boxplots extend to 1.5 times the interquartile range or the most extreme observed data point, whichever is less extreme. Relative errors outside this range were not plotted.
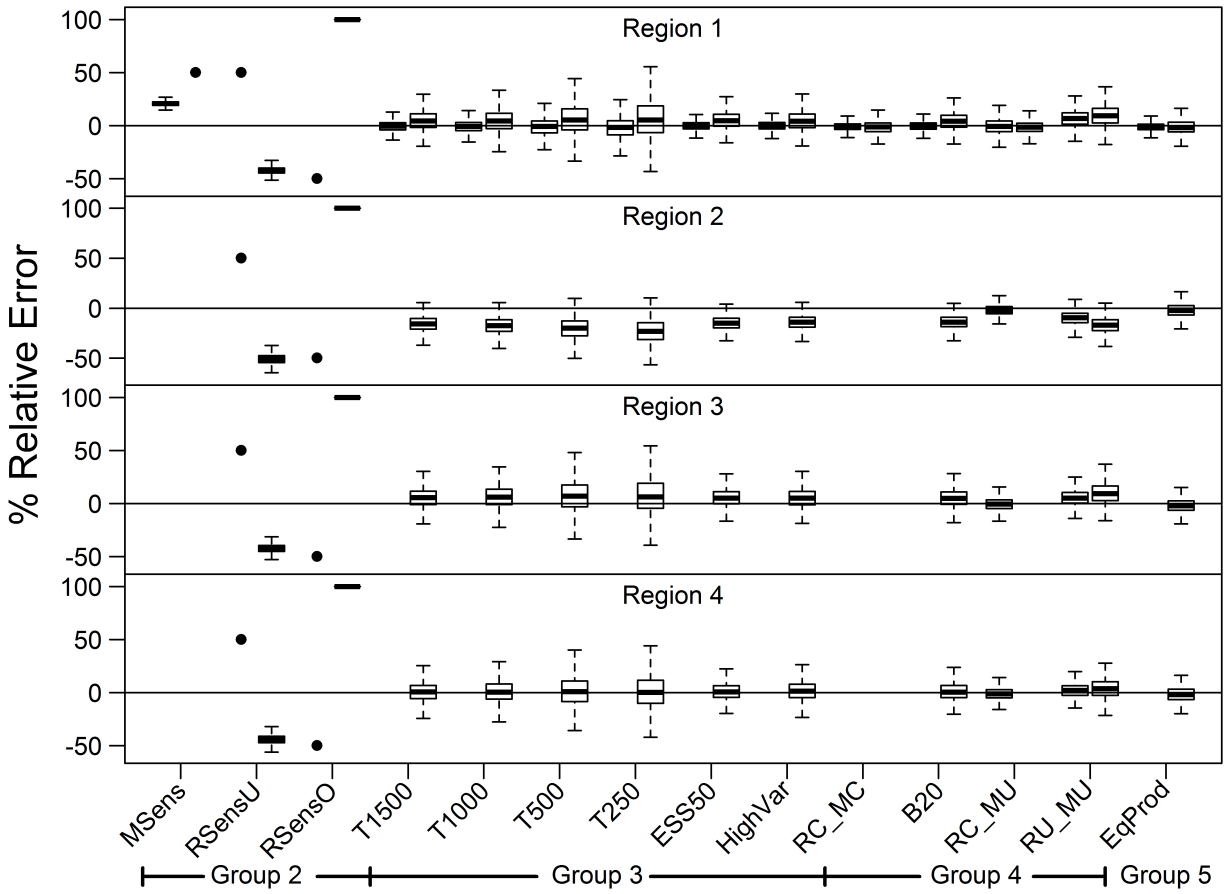
Figure 1.A.9: Relative error (%) of natural mortality (first plot in each pair) and reporting rate (second in pair) estimates for each region of an ITCAAN model under scenarios investigating misspecfied natural mortality and reporting rates, data quality, spatial complexities, and equal productivities (scenario Groups 2–5) with BEst20 plotted as a reference for 1000 simulation iterations. Table 1.A.1 lists the model abbreviations and corresponding model components. Whiskers on the boxplots extend to 1.5 times the interquartile 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.
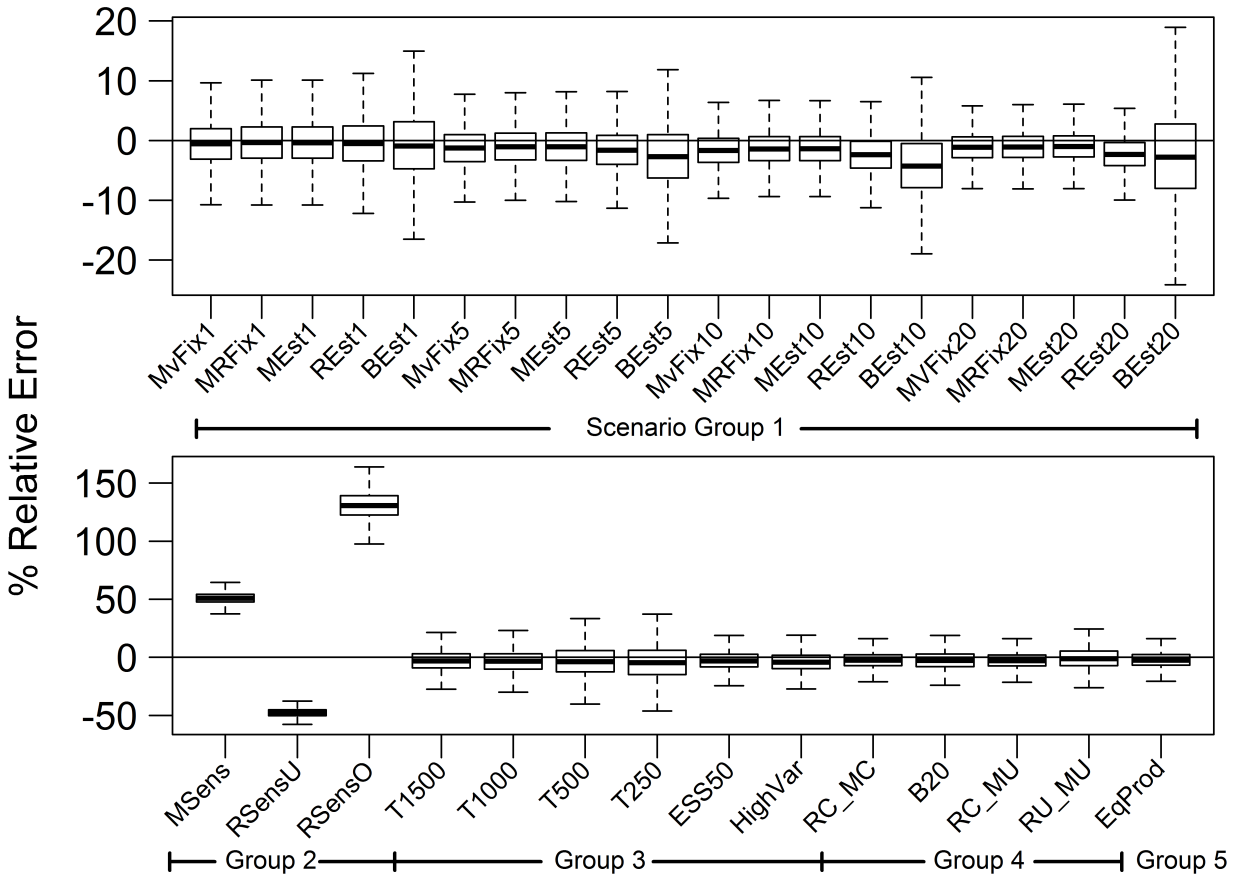
Figure 1.A.10: Relative error (%) of total abundances for all years aggregated from an ITCAAN model for all simulation scenarios described in Table 1.A.1 for 1000 simulation iterations. Whiskers on the boxplots extend to 1.5 times the interquartile range or the most extreme observed data point, whichever is less extreme. Relative errors outside the whisker range were not plotted. Note the difference in scale between the top and bottom panel.
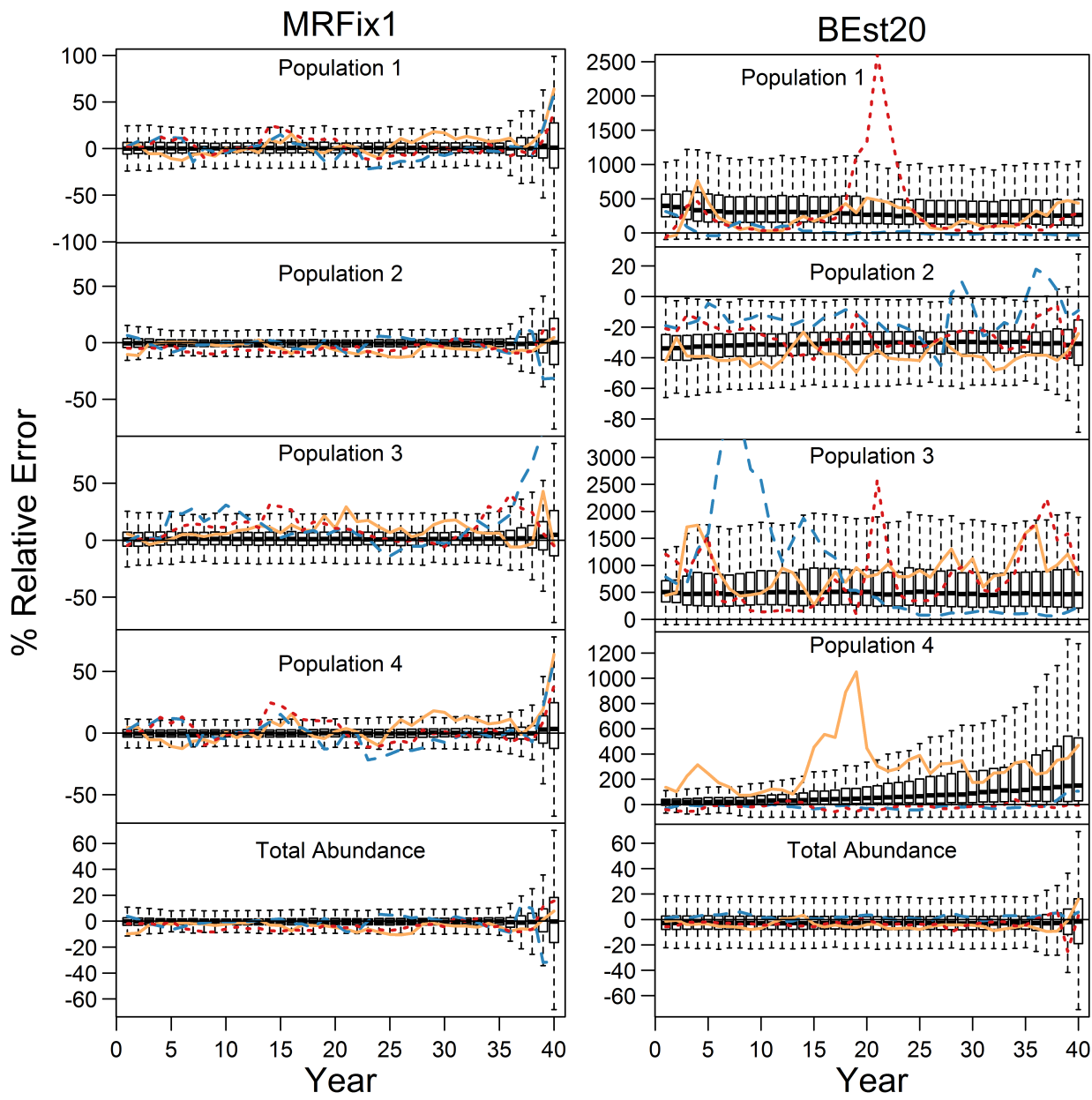
Figure 1.A.11: Relative error (%) of population-specific abundances and total abundances (summed across populations) for 1000 simulation iterations of an ITCAAN model for a 1% movement with natural mortality and reporting rate fixed at true values in the left column and in the right column 20% movement with natural mortality and reporting rate estimated. 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 interquartile 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 among populations.

PARAMETER LIST AND MODEL EQUATIONS

Table 1.B.1: Symbols and descriptions of variables used in Operating and ITCAAN models.

Symbol	Description	Model	Type
y	Subscript for year	Both	Index
Y	Last year in model	Both	Index
a	Subscript for age	Both	Index
A	Subscript for oldest modeled age	Both	Index
p	Subscript for spawning population	Both	Index
r	Subscript for region	Both	Index
l	Subscript for release cohort unique by year and population	Both	Index
N	Population abundance	Both	Derived Variable
α	Parameter of Ricker stock-recruit function	Operating	Fixed values
β	Parameter of Ricker stock-recruit function	Operating	Fixed values
w	Mass at age	Operating	Fixed values
m	Maturity at age	Operating	Fixed values
ϵ	Autoregressive annual deviation in recruitment	Operating	Random variable
ρ_p	Autoregressive coefficient in autoregressive recruitment	Operating	Random variable
δ_p	White noise annual deviation in recruitment	Operating	Random variable
σ_p^2	Recruitment innovation variance	Operating	Random variable
Λ	Recruitment in the first year	ITCAAN	Estimated variable
λ	Annual recruitment deviation	ITCAAN	Estimated variable
$T_{p,r}$	Movement rate from population p to region r	Both	Fixed variable in operating model; Derived variable in ITCAAN*
S	Survival	Both	Derived Variable
Z	Total mortality	Both	Derived Variable
M	Natural mortality	Both	Fixed in Operating Model; Estimated in ITCAAN*
F	Age-specific fishing mortality	Both	Derived Variable
f	Apical fishing mortality	Operating	Random variable
μ	Mean fishing mortality in autoregressive process	Operating	Fixed values

Table 1.B.1 (cont'd)

σ_r^2	Fishing mortality innovation variances	Operating	Fixed values
ρ_r	Autoregressive coefficient in simulated fishing mortality	Operating	Fixed values
δ_r	White noise annual deviation in fishing mortality	Operating	Random variable
v	Age-specific fishery selectivity	Both	Fixed variable in operating model; estimated in ITCAAN
E	Observed fishing effort	Both	Simulated data
q	Fishery catchability coefficient	Both	Fixed variable in operating model; Derived variable in ITCAAN
γ	Observation error in effort	Operating	Random variable
σ_E^2	Variance of effort data observation error	Operating	Fixed value
K	Catchability parameter in the first year	ITCAAN	Estimated variable
κ	Annual catchability deviation	ITCAAN	Estimated variables
I	Survey abundance index	Both	Simulated Data
Q	Survey catchability coefficient	Both	Fixed variable in operating model; Estimated variable in ITCAAN
V	Age-specific survey selectivity	Both	Fixed variable in operating model; Estimated variable in ITCAAN
τ	Observation error in survey index	Operating	Random variable
σ_I^2	Variance of survey index data observation error	Operating	Fixed value
$\omega_{p,r}$	Multinomial logit parameter for estimating movement from population p to region r	ITCAAN	Estimated variable*
n	Number of tagged fish alive	Both	Derived variable
R	Number of tagged fish released	Both	Fixed values
t	Number of tags captured by fishery F, die naturally M, or survive S	Operating	Random variable
ϕ^F	Expected proportion of tagged cohort harvested	Operating	Derived variable
ϕ^S	Expected proportion of tagged chort to survive	Operating	Derived variable
ϕ^M	Expected proportion of tagged cohort to die from natural mortality	Operating	Derived variable
$\mathbf{\Phi}$	Vector of expected proportions of the fates of tagged cohorts	Operating	Derived variables
$t^{F,S,M}$	Vector of tags captured by fishery F, die naturally M, or survive S	Operating	Random variables

Table 1.B.1 (cont'd)

d	Number of tags recovered	Both	Simulated data in operating model; Derived variable in ITCAAN
Υ	Angler reporting rate of tags	Both	Fixed value in operating model; Estimated variable in ITCAAN
$d_{l,NR}$	Number of tags never recovered	Both	Simulated data in operating model; Derived variable in ITCAAN
Γ	Mean abundance for first model year	ITCAAN	Estimated variable
Δ	Age-specific abundance deviations in first year	ITCAAN	Estimated variable
C	Harvest in numbers caught	Both	Simulated data in operating model; Derived variable in ITCAAN
ζ	Observation error in harvest	Operating	Random variable
σ_C^2	Variance of harvest data observation error	Operating	Fixed value
P	Harvest age composition	ITCAAN	Simulated data in operating model; Derived variable in ITCAAN

[*]When not fixed at true value for some scenarios

Table 1.B.2: Equations used to model and estimate population dynamics in Operating and ITCAAN models.

Equation Number	Equation	Model
Recruitment		
(1.B.2.1)	$N_{y+2,a=1,p} = \alpha_p \sum_a (m_a w_a N_{y,a,p}) e^{-\beta_p \sum_a (m_a w_a N_{y,a,p})\epsilon_y}$	Operating
(1.B.2.2)	$\epsilon_y = \begin{cases} \rho_p \epsilon_{y-1} + \sqrt{1 - \rho^2}_p \delta_{p,y} & \text{for } y > 1 \\ \delta_{p,y} & \text{for } y = 1 \end{cases}$ where $\delta_{p,y} \sim N\left(\dfrac{-\sigma_p^2(1-\rho_p)}{2\sqrt{1-\rho_p^2}}, \sigma_p^2\right)$	Operating
(1.B.2.3)	$\begin{aligned} \widehat{N}_{y=1,a=1,p} &= \widehat{\Lambda}_p & \text{for} & \quad y = 1 \\ \widehat{N}_{y,a=1,p} &= \widehat{N}_{y-1,a=1,p} e^{\widehat{\lambda}_{y,p}} & \text{for} & \quad 1 < y \leq Y - 2 \\ \widehat{N}_{y,a=1,p} &= (\widehat{N}_{Y-2,a=1,p} + \widehat{N}_{Y-3,a=1,p} + \widehat{N}_{Y-4,a=1,p})/3 & \text{for} & \quad y = Y - 1 \text{ or } Y \end{aligned}$	ITCAAN
Abundance and Survival		
(1.B.2.4)	$N_{y+1,a+1,p} = \sum_r N_{y,a,p} T_{p,r} S_{y,a,r}$ where $a < A - 1$	Both
(1.B.2.5)	$N_{y+1,A,p} = \sum_r N_{y,A,p} T_{p,r} S_{y,A,r} + N_{y,A-1,p} T_{p,r} S_{y,A-1,r}$	Both
(1.B.2.6)	$Z_{y,a,r} = M + F_{y,a,r}$	Both
(1.B.2.7)	$S_{y,a,r} = e^{-Z_{y,a,r}}$	Both
Fishing Mortality and Effort		
(1.B.2.8)	$F_{y,a,r} = f_{y,r} v_{a,r}$	Operating
(1.B.2.9)	$f_{y=1,r} \sim \text{Trunc. Normal}\left(\mu_r, \sigma_r^2, 0, \infty\right)$ for $y = 1$ $f_{y+1,r} = \left(\mu_r(1 - \rho_r)\right) + \rho_r f_{y,r} + \delta_{r,y}$ for $1 < y \leq Y$ where $\delta_{r,y} \sim \text{Trunc. Normal}\left(0, \sigma_r^2, -(\rho_r f_{y,r} + \mu_r(1 - \rho_r)), \infty\right)$	Operating

Table 1.B.2 (cont'd)

(1.B.2.10)	$E_{y,r} = f_{y,r}\gamma_{y,r}/q_r$ where $\gamma_{y,r} \sim LN\left(-\sigma_E^2/2, \sigma_E^2\right)$	Operating
(1.B.2.11)	$F_{y,a,r} = E_{y,r}\hat{q}_{y,r}\hat{v}_{a,r}$	ITCAAN
(1.B.2.12)	$\hat{q}_{y=1,r} = \hat{K}_r$ for $y = 1$ $\hat{q}_{y,r} = \hat{q}_{y-1,r}e^{\hat{k}_{y,r}}$ for $1 < y \leq Y$	ITCAAN

Survey Calculations

(1.B.2.13)	$I_{y,a,r} = Q_r\, V_{a,r}\, \sum_p N_{y,a,p}\, T_{p,r}\, e^{-Z_{y,a,r}\,10/12}$	Both
(1.B.2.14)	$I_{y,r} = \tau_{y,r} \sum_a I_{y,a,r}$ where $\tau_{y,r} \sim LN\left(-\sigma_I^2/2, \sigma_I^2\right)$	Operating

Movement Estimation

(1.B.2.15)	$\widehat{T}_{r,p} = \dfrac{e^{\omega_{r,p}}}{\sum_{r=1}^{3} e^{\omega_{r,p}}},$ where $\omega_{r=4,p} = 0$	ITCAAN

Tag Dynamics

(1.B.2.16)	$n_{l,y,a} = R_{l,a}$ for $y = l$	Both
(1.B.2.17)	$t_{l,y,a,r} \sim MN\left(n_{l,y,a}, T_{p,r}\right)$	Operating
(1.B.2.18)	$\phi_{y,a,r}^{F} = \frac{F_{y,a,r}}{Z_{y,a,r}}\left(1 - S_{y,a,r}\right)$	Operating
(1.B.2.19)	$\phi_{y,a,r}^{S} = S_{y,a,r}$	Operating
(1.B.2.20)	$\phi_{y,a,r}^{M} = \frac{M}{Z_{y,a,r}}(1 - S_{y,a,r})$	Operating
(1.B.2.21)	$\mathbf{\Phi}_{y,a,r} = \left(\phi_{y,a,r}^{F}, \phi_{y,a,r}^{S}, \phi_{y,a,r}^{M}\right)$	Operating
(1.B.2.22)	$t_{l,y,a,r}^{F,S,M} \sim MN\left(t_{l,y,a,r}, \mathbf{\Phi}_{y,a,r}\right)$	Operating
(1.B.2.23)	$n_{l,y+1,a+1} = \sum_r t_{l,y,a,r}^{S}$	Operating
(1.B.2.24)	$d_{l,y,a,r} \sim BIN\left(t_{l,y,a,r}^{F}, \Upsilon_r\right)$	Operating

Table 1.B.2 (cont'd)

$$(1.B.2.25) \qquad d_{l,NR} = \sum_a R_{l,a} - \sum_y \sum_a \sum_r d_{l,y,a,r} \qquad \text{Both}$$

$$(1.B.2.26) \qquad \widehat{d}_{l,y,r} = \sum_a \widehat{n}_{l,y,a} \, \widehat{T}_{p,r} \frac{\widehat{F}_{y,a,r}}{\widehat{Z}_{y,a,r}} \left(1 - \widehat{S}_{y,a,r}\right) \widehat{\Upsilon}_r \qquad \text{ITCAAN}$$

$$(1.B.2.27) \qquad
\begin{aligned}
\widehat{n}_{l,y,a} &= R_{l,a} & \text{for} \quad y = l \\
\widehat{n}_{l,y+1,a+1} &= \sum_r \widehat{n}_{l,y,a} \widehat{T}_{p,r} \widehat{S}_{y,a,r} & \text{for} \quad a < A-1 \\
\widehat{n}_{l,y+1,A} &= \sum_r \widehat{n}_{l,y,A} \widehat{T}_{p,r} \widehat{S}_{y,A,r} + \widehat{n}_{l,y,A-1} \widehat{T}_{p,r} \widehat{S}_{y,A-1,r} & \text{for} \quad a = A
\end{aligned}
\qquad \text{ITCAAN}$$

Initial Abundance Estimation

$$(1.B.2.28) \qquad \widehat{N}_{y=1,a,p} = exp(\widehat{\Gamma}_p + \widehat{\Delta}_{p,a}) \qquad \text{for} \qquad a > 2 \qquad \text{where} \sum_a \widehat{\Delta}_{p,a} = 0.0 \qquad \text{ITCAAN}$$

Catch Calculations

$$(1.B.2.29) \qquad C_{y,r} = \zeta_{y,r} \sum_a C_{y,a,r} \qquad \text{where} \qquad \zeta_{y,r} \sim LN(-\sigma_C^2/2, \sigma_C^2) \qquad \text{Operating}$$

$$(1.B.2.30) \qquad C_{y,a,r} = \sum_p \frac{F_{y,a,r}}{Z_{y,a,r}} N_{y,a,p} \, T_{p,r} \, (1 - S_{y,a,r}) \qquad \text{Both}$$

$$(1.B.2.31) \qquad C_{y,r} = \sum_a C_{y,a,r} \qquad \text{ITCAAN}$$

$$(1.B.2.32) \qquad P_{y,r} = C_{y,a,r}/C_{y,r} \qquad \text{ITCAAN}$$

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CHAPTER 2

PARAMETER ESTIMATION PERFORMANCE IN A RECOVERY-CONDITIONED INTEGRATED TAGGING CATCH-AT-AGE ANALYSIS MODEL

Abstract

Recovery-conditioned models are infrequently used in fisheries science to analyze recovery data from tagging experiments, but were proposed as an alternative to release-conditioned models when nuisance factors such as tag reporting or shedding rates were spatially constant. Integrated tagging and catch-at-age analysis (ITCAAN) models incorporate tag-recovery information as data components within statistical catch-at-age models for spatially-explicit assessment of fish stocks. Through simulations, we investigated the performance of recovery-conditioned ITCAAN models under a range of model complexities and different intermixing rate scenarios. We also investigated how misspecification of natural mortality, parity in population productivities, and spatially varying reporting rates affected ITCAAN model estimates. An operating model based on Lake Erie walleye (*Sander vitreus*) with four populations that exhibited natal homing and intermixing during harvest periods was used to simulate data. At low intermixing rates, ITCAAN model estimates of total abundance and spawning population abundances were accurate and precise with median relative error within ±10% and inter-quartile ranges of relative errors between 5 and 42%, with precision decreasing when natural mortality was estimated. Accuracy and precision of individual spawning population abundance estimates declined with higher intermixing rates, with the largest bias and imprecision occurring when estimating relative reporting rates. This bias was not evident when simulated populations had similar productivity levels, even at high intermixing rates. The accuracy and precision associated with estimating relative reporting rates depended on intermixing and productivity levels of the associated spawning population. Natural mortality estimates were accurate and precise for most examined scenarios, though precision generally decreased with higher intermixing rates. Estimating relative reporting rates resulted in biased and less precise movement

rate estimates. Assuming reporting rates were spatially constant when they varied regionally caused biased estimation of movement rates and spawning population abundances. Based on our results, we recommend recovery-conditioned ITCAAN models only be used for spatially-explicit assessments of intermixed fish stocks when there is high certainty that tag reporting rates are spatially constant or when spawning populations can be assumed to have similar levels of productivity.

Introduction

Spatially-explicit population assessment models simultaneously estimate abundances, mortalities, and movement rates of populations that are exploited as mixed stocks during the fishing season (Goethel et al. 2011). For our purposes, populations are defined as self-sustaining groups of fish that interbreed and share similar life history characteristics. Stocks are defined as exploited fishery units delineated by region of harvest (Cadrin et al. 2004). Therefore, a mixed stock is comprised of individuals from two or more populations that are exploited as a single unit. Mixed stocks create overharvesting risks for less productive populations depending on how stocks are managed (Ying et al. 2011; Guan et al. 2013; Hulson et al. 2013; Molton et al. 2013; Li et al. 2014). Integrated tagging and catch-at-age analysis (ITCAAN) models (Maunder 2001; Goethel et al. 2015b; Vincent et al. 2017), which incorporate tag-recovery data within a statistical catch-at-age assessment model, is one spatially-explicit assessment approach that has been used to assess and help manage mixed stocks. Performance of ITCAAN models has been explored through simulations under a range of model complexities and different movement dynamics of fish populations (e.g., reproductive mixing, natal homing) (Hulson et al. 2013; Goethel et al. 2015b; Vincent et al. 2017).

Two contrasting approaches are used to analyze tag-recovery data. The most common approach is for tag recoveries at different time periods or by different harvest methods to be conditioned on the number of tags released (release-conditioned framework) (Brownie et al. 1987; Hoenig et al. 1998; Frusher and Hoenig 2003; Latour et al. 2003; Jiang et al. 2007). With a release-conditioned framework, the number of tags that are never recovered and the probability of tags never being recovered are factored into analyses. The probability of never recovering a tag is

influenced by several nuisance factors including tag reporting, tagging mortality, and tag shedding; these nuisance factors must be accounted for in recovery probabilities to prevent biased parameter estimates (Hampton 1997; Denson et al. 2002; Cowen et al. 2009; Brenden et al. 2010; Vandergoot et al. 2012). The other general approach for analyzing tag-recovery data is for tag recoveries at different time periods and by different harvest methods to be conditioned on the total number of recoveries (recovery-conditioned framework, also referred to as recapture-conditioned) (McGarvey and Feenstra 2002; McGarvey 2009). The recovery-conditioned framework was proposed to eliminate the need to account for nuisance factors (e.g., tag reporting) to estimate movement rates. The framework for this formulation was derived from the following property: when nuisance factors such as tag reporting are assumed to be spatially constant, they cancel out in likelihood equations and thus do not influence model fit (McGarvey and Feenstra 2002). The assumption of spatially constant nuisance parameters is commonly made for the recovery-conditioned framework (McGarvey et al. 2010), but whether this assumption will be met with actual fishery data is questionable. If nuisance parameters are not spatially constant they do not cancel out in the likelihood and therefore need to be accounted for in the model, either as parameters to be estimated or as assumed values, or else parameter estimates may be biased.

The recovery-conditioned framework has been infrequently used for analyzing tag-recovery data in fisheries science, although see McGarvey and Feenstra (2002) and McGarvey (2009). There also has been limited application and simulation evaluation of ITCAAN models that incorporate a recovery-conditioned framework, although see McGarvey et al. (2010). As a result of its limited use, it is not presently known how complex of a parameterization (e.g. natural mortality estimation) can be handled by a recovery-conditioned ITCAAN model. Additionally, it is unknown how sensitive parameter estimates are to assuming nuisance parameters, such as reporting rates, are spatially constant when the true dynamics are spatially variable.

The purpose of this research was to evaluate the accuracy, precision, and robustness of model parameters for a recovery-conditioned ITCAAN model through simulations. Specifically, we investigated how accuracy and precision of parameter estimates were affected by the following:

1. whether movement, natural mortality, and/or reporting rates were estimated or treated as known and fixed quantities and how this was affected by the degree of intermixing of the populations; 2. spatial variability in reporting rates among regions and whether reporting rates were estimated in the recovery-conditioned ITCAAN model or presumed to be constant; and 3. misspecification of natural mortality when these parameters were treated as known within the recovery-conditioned ITCAAN model and parity in productivities of the spawning populations. We were motivated to explore the performance of recovery-conditioned ITCAAN models to spatially varying reporting rates because reporting rates in actual systems are unlikely to be constant across space. Factors that can lead to spatially varying reporting rates include differences in types of fisheries (e.g., commercial versus recreational fisheries) operating in different regions of the system, how well the tagging study is advertised, degree of apathy toward the tagging study, or relationship with the agency conducting the tagging study (Hoenig et al. 1998; Denson et al. 2002; Vandergoot et al. 2012). As a result, fishery managers and biologist choosing which tagging framework to use in an ITCAAN model would benefit from knowing how recovery-conditioned ITCAAN models perform when confronted with spatially-varying reporting rates.

Simulations were based on walleye (*Sander vitreus*) populations in the Laurentian Great Lakes of North America. Walleye have been found to be highly migratory both in the Great Lakes (Wang et al. 2007; Zhao et al. 2011; Vandergoot and Brenden 2014; Hayden et al. 2014) and in inland systems (Smith et al. 1952; Rasmussen et al. 2002; Herbst et al. 2016). For both the Great Lakes and inland systems, walleye migration has been identified as potentially problematic for management (Brenden et al. 2015; Herbst et al. 2017).

Lakes Erie and Huron Walleye

Walleye are economically important in the Great Lakes region and are subject to both commercial and recreational exploitation (Fielder and Bence 2014; Wills et al. 2016). Walleye spawn in rivers or on shallow reefs during the early spring. After spawning, walleye disperse throughout the Great Lakes (Wang et al. 2007; Zhao et al. 2011; Vandergoot and Brenden 2014; Hayden et al. 2014),

but typically return to their natal region to spawn each year (Stepien and Faber 1998; Haponski and Stepien 2014; Hayden et al. 2014; Wilson et al. 2017).

The largest walleye fisheries in the Great Lakes region are in Lakes Erie and Huron, which are connected via Lake St. Clair and the Detroit and St. Clair Rivers. Walleye abundance in Lake Huron has been estimated to be between one and four million fish (Fielder and Bence 2014). In Lake Erie, abundance of walleye in the eastern basin of the lake has been estimated on the order of tens of thousands for fish (Zhao et al. 2011), whereas abundance in Lake Erie's western basin is closer to tens of millions of fish (Wills et al. 2016). Tagging studies have documented walleye migrating between Lakes Erie and Huron (Wang et al. 2007; Hayden et al. 2014; Vandergoot and Brenden 2014). Estimated intermixing rates of walleye from some spawning populations in Lake Erie's western basin to Lake Huron and the eastern basin of Lake Erie have been around 1 to 2% (Wang et al. 2007; Fielder and Bence 2014; Vandergoot and Brenden 2014). This rate of intermixing may be low, but a considerable amount of the harvest in all regions may originate from the western basin population given the large differences in population abundances between the areas (McParland et al. 1999; Brenden et al. 2015). Interest in developing spatially-explicit models to assist with the management of Lakes Erie and Huron walleye has increased in recent years due to the recognition of the movement between the lakes and the value of the respective fisheries (Fielder and Bence 2014; Wills et al. 2016).

Methods

An operating model was used to generate and track the true dynamics of simulated fish populations and tagged cohorts. From this operating model, observed time-series data were generated, which were then fit in a recovery-conditioned ITCAAN model. The operating model used in this research was identical to that presented in Vincent et al. (2017), but will be summarized here. The operating model simulated the abundances and dynamics of four populations that intermixed among four regions. Fish were assumed to aggregate in their natal region at the beginning of each year to spawn (i.e., 100% spawning site fidelity was assumed). Recruitment was simulated

from population-specific Ricker stock-recruitment functions with a first-order autoregressive process error. Values for the first-order autoregressive process were randomly drawn from posterior distributions for Percidae for each population (Thorson et al. 2014). The equilibrium stock size and productivity (i.e., stock-recruit steepness) were assumed to differ among the four populations for most scenarios (Table 2.A.1). The stock-recruit parameters for population 1 were based on Lake Huron walleye, while the stock-recruit parameters for populations 2, 3, and 4 were based on western, central, and eastern Lake Erie walleye, respectively.

After spawning, fish were assumed to instantaneously mix among the four regions using a box-transfer model (Goethel et al. 2011), where they were assumed to remain for the rest of the year and were subject to fishing. The exploitation rates experienced by the mixed stocks were region-specific. Apical fishing mortality rates for the regions were generated using first-order autoregressive processes with regionally unique means based on estimated fishing mortalities for Lakes Erie and Huron (Table 2.A.1). Region-specific catchability coefficients and lognormal multiplicative observation errors with a CV of 10% were used to simulate fishery-specific time series of fishing effort. The natural mortality rate was assumed to be 0.32 year^{-1} in all populations for the entire time series of the simulations. Age-specific selectivities for each fishery were assumed to be temporally constant but regionally varying. Region-specific harvest data (i.e., summed across populations) were generated from actual harvest multiplied by lognormal observation errors with a CV of 10% for all 40-years. Observed harvest age composition for each fishery was simulated from multinomial distributions that used the actual harvest age composition as the underlying proportions and assumed a sample size of 100 fish. A fishery-independent survey was simulated to occur in each region during October (i.e., during the intermixed period). Region-specific catchabilities and age-specific selectivities were used to simulate a survey catch per effort time series with multiplicative lognormal observation errors with a CV of 20%. Age-composition data for all years were also simulated for each survey from multinomial distributions based on the intermixed age distribution present in October with a sample size of 100.

Two thousand fish were simulated to be tagged annually from each population at the beginning

of the year when fish were aggregated for spawning. The fate (i.e., survived, harvested, or died due to natural causes) of tagged fish each year were generated from multinomial distributions with expected proportions equal to the dynamics of the at-large populations (e.g., exploitation rate). Tag reporting was assumed to be imperfect for all simulations, but the assumed regional reporting rates varied among the different scenarios (see Simulation Scenarios). The number of tags recovered were simulated using a binomial process based on the number of harvested tagged fish and the regional reporting rate. Simulations that had an abundance for any of the four populations less than 40000 fish were automatically excluded and replaced with a new simulation, because we believed that it was unlikely that more than 5% of a population would be tagged within a year.

Forty years of data were generated by the operating model; the full time series of observations were then fit using the ITCAAN model. The data sources generated by the operating model were region-specific fishery harvest in numbers, fishery harvest age composition, region-specific mixed population survey catch per effort, survey age composition, tag-recovery data, and fishery effort per region. Both the operating model and the ITCAAN model tracked the dynamics of walleye between the ages of 2 and 7, with the last age group in the model aggregating all fish age 7 and older. The operating model was programmed in R version 2.15.1 (R 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 2.

ITCAAN Model

The ITCAAN model used in this research was nearly identical to that used in Vincent et al. (2017). The primary difference between these models was this study used a recovery-conditioned framework to analyze the tag-recovery data. Therefore, the negative log likelihood equation for the tagging component of the ITCAAN model in this research, ignoring scaling constants, was as follows:

$$L = -\sum_l \sum_y \sum_r log\left(\frac{\widehat{d_{l,y,r}}}{\sum_y \sum_r \widehat{d_{l,y,r}}}\right) * d_{l,y,r} \qquad (2.0.1)$$

where d is the observed number of tags recovered and $\hat{d}$ is the model predicted number of tags

recovered. The subscripts for d are the unique release event for each population and year (l), the year of recovery (y) and the region of recovery (r). The predicted number of tags recovered from a tagged cohort were calculated as

$$\widehat{d_{l,y,r}} = \sum_a \hat{n}_{l,y,a} \, \widehat{T}_{p,r} \, \frac{\hat{F}_{y,a,r}}{\hat{Z}_{y,a,r}} \left(1 - \widehat{S}_{y,a,r}\right) \widehat{\Upsilon_r} \qquad (2.0.2)$$

where $\hat{n}_{l,y,a}$ is the predicted number of tags alive in year y of age a from tag release year and population l, $\widehat{T}_{p,r}$ is the predicted movement rate from population p to region r, $\hat{F}$ is the predicted instantaneous fishing mortality rate, $\hat{Z}$ is the predicted instantaneous total mortality rate, $\hat{S}$ is the survival rate, and $\widehat{\Upsilon_r}$ are the region-specific reporting rates. With a recovery-conditioned framework, actual reporting rates for the regions are not estimable because unique solutions do not exist given Equations (2.0.1) and (2.0.2). In other words, region-specific reporting rates of 10%, 20%, 30% and 40% would be expected to produce the same model fit as region-specific reporting rates of 20%, 40%, 60%, and 80%. In this research, we explored the estimability of relative reporting rates in a recovery-conditioned framework by fixing the reporting rate for one region to a particular value and then estimating the reporting rates for the remaining regions. A relative reporting rates formulation produces unique solutions, and in the above examples would equal 1.0, 2.0, 3.0, and 4.0 if scaled relative to region 1. However, the existence of unique solutions for relative reporting rates does not guarantee that accurate and precise parameter estimates can be obtained from a recovery-conditioned ITCAAN model, due to possible confounding with other parameter estimates. For this research, we fixed the reporting rate for region 1 at a value of 1.0 and then estimated the relative reporting rates for the other three regions as bounded parameters between 0.01 and 100. For scenarios where reporting rates were not estimated but were treated as fixed values, region-specific reporting rates were still treated as relative values. Thus, if the operating model assumed a reporting rate of 0.5 for all regions and the reporting rates were assumed known in the ITCAAN model, the relative reporting rates were specified at 1.0 for all regions. Fixing the relative reporting rates equal among regions was equivalent to assuming that reporting rates canceled out of the likelihood equations.

ITCAAN models were fit to generated data from the operating model using highest posterior

density estimation, also referred to as maximum penalized likelihood estimation (Stewart et al. 2013). We assessed convergence of the ITCAAN model by whether the maximum gradient across all parameters was less than 0.05 and the model produced a positive-definite Hessian matrix. This cutoff for the maximum gradient was determined after preliminary results for the low movement scenario showed that gradients much smaller than this were infrequent and estimates were within the range of plausibility. Simulated datasets were fit by the ITCAAN model until 1000 datasets had converged. Table 2.A.2 presents the number of simulations that were required to reach a sample size of 1000, as well as the number of simulations that failed to converge for either criteria.

Simulation Scenarios

Three groups of scenarios were investigated to examine recovery-conditioned ITCAAN model performance. The first group of scenarios evaluated the estimability of movement, natural mortality, and/or relative reporting rates under different rates of population intermixing. The second group of scenarios analyzed the influence of spatially varying reporting rates on parameter estimates when either estimating relative reporting rates or assuming the reporting rates were regionally constant (i.e., canceled out of likelihood). The third group of scenarios evaluated the influence of misspecifying natural mortality in an ITCAAN model and the effect of equal productivities among populations.

Group 1: Estimation of Movement, Relative Reporting Rates, and Natural Mortality Under Varying Intermixing Rates

Simulations were conducted for a total of 20 scenarios to examine how the estimation of movement, natural mortality, and/or relative reporting rates in the ITCAAN model and the intermixing rate of the simulated populations influenced ITCAAN model performance. Four assumed intermixing scenarios were crossed with five ITCAAN model parameterizations. The four intermixing scenarios consisted of different rates of movement from natal region to each non-natal region. The examined rates were 1%, 5%, 10%, and 20% of the population. For example, under a 20% intermixing

rate 40% of the populations would remain in their natal region and 20% of the populations would move to each of the other three regions. The five ITCAAN parameterizations varied with regards to whether movements, natural mortality, and/or relative reporting rates were estimated as part of the model fitting process or fixed at the true values assumed in the operating model. The first parameterization assumed that movements, natural mortality, and relative reporting rates were fixed at their true values and this was the only parameterization where movement rates were not estimated (MvFix). The second parameterization estimated movement rates, but assumed natural mortality and relative reporting rates were fixed at their true values (MRFix). The third parameterization estimated movement rates and natural mortality, but assumed relative reporting rates were fixed at their true values (RFix). The fourth parameterization estimated movement rates and relative reporting rates but fixed natural mortality at the true value (MFix). The final parameterization estimated movement, natural mortality, and relative reporting rates (NoFix). The results are presented using the estimation approach of the ITCAAN model followed by the intermixing rate in the operating model. For example, MFix20 refers to the ITCAAN parameterization where relative reporting rates and movement rates were estimated, but natural mortality was fixed in the ITCAAN model and the operating model assumed a 20% intermixing rate.

Group 2: Regionally Varying Reporting Rates

The second group of scenarios investigated the influence of regionally varying reporting rates in the operating model on different treatments of reporting rates in the ITCAAN model. All scenarios in this group assumed a 20% intermixing rate for the simulated populations. We investigated two scenarios of spatially varying reporting rates in the operating model. The first scenario with reporting rates varying spatially (RV1) assumed that the reporting rates were the highest for regions where the natal populations were the least productive (Table 2.A.1). The second scenario with reporting rates varying (RV2) assumed that the reporting rate was the highest in regions where the natal populations were the most productive and decreased with decreasing productivity. For both of these reporting rate scenarios, we attempted to estimate the relative reporting rates for the regions

using the method described in the ITCAAN model section. We also explored the consequence of assuming the reporting rates were constant in the ITCAAN model under these two scenarios by fixing the relative reporting rates for all regions to 1.0. Scenarios in this group that estimated relative reporting rates were referred to as Est scenarios (e.g., RV1Est); when relative reporting rates were assumed to be spatially constant, we refer to these simulations as Canc scenarios (e.g., RV1Canc).

Group 3: Sensitivity to Misspecified Natural Mortality and Equal Productivity

The third group of simulations investigated the consequences of misspecifying natural mortality in a recovery-conditioned ITCAAN model and the effect of assuming equal productivities among spawning populations in the operating model. All scenarios in this group assumed a 20% inter-mixing rate in the operating model. The first scenario examined the influence of misspecifying the natural mortality in the ITCAAN model at 0.5 times the true value (i.e., 0.16). This scenario was referred to as SensU because it evaluated sensitivity to natural mortality that was specified to be less than (under) the true value. The second scenario in this group examined the effect of specifying the natural mortality in the ITCAAN model at 1.5 times the true value (i.e., 0.48). This scenario was referred to as SensO because it evaluated the sensitivity of parameter estimates to specifying natural mortality to be greater than (over) the true value. The third scenario in this group evaluated how parity in productivities among the four populations affected ITCAAN parameter estimation. This scenario was referred to as EqProd to stand for equal productivities among populations. For this scenario, all populations were assumed to have the same stock-recruitment parameters in the operating model (i.e., Ricker parameters for population 2 in other scenarios), and natural mortality and relative reporting rates were estimated in the ITCAAN model.

Performance Metrics

ITCAAN model performance was evaluated by comparing parameter estimates to the true population dynamics in the operating model and the number of simulations that converged for each

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scenario (Table 2.A.2). Model performance was assessed through percent relative error, which was calculated by subtracting the true value from the estimate and then dividing by the true value and multiplying by 100. For the sake of brevity, we discuss the precision and accuracy of model estimates of total abundance (i.e., abundance summed over all populations), spawning population abundance, relative reporting rate, natural mortality, and movement rates. Performance of all other parameter estimates are presented in the Supplementary Material 2. Parameters not presented either showed no bias in estimates or were biased similar to population abundances, though not always in the same direction. Relative error was calculated for all parameters including those that are age specific (e.g, selectivity, results shown in Supplementary Material 2) and year specific (e.g., abundance) for all converged simulations and then aggregated by region for plotting. For example, the boxplots of population abundance summarizes 40 years of error in abundance estimates times 1000 simulations. The median of the relative errors was used as a metric of model accuracy and the interquartile range (IQR) was used as a metric of estimate precision. Accuracy and precision of parameter estimates were compared across scenarios to give a holistic view of recovery-conditioned ITCAAN model performance.

Results

ITCAAN Model Convergence

Convergence of the recovery-conditioned ITCAAN model varied depending on the intermixing rate of the operating model (Table 2.A.2). A convergence rate greater than 95% occurred for simulation scenarios where the assumed intermixing rates were 5% or greater. Simulation scenarios at the 1% intermixing rate had approximately 80% of simulations converged. Simulations at the 1% intermixing rate typically failed to converge due to a maximum gradient greater than 0.05. A decrease in convergence as a result of failing both criteria was observed for one of the scenarios where reporting rates were spatially varying but assumed constant in the ITCAAN model (RV2Canc).

Model Performance

Total Abundance Relative Error

Accuracy and precision of total abundance summed across all populations, as measured by median and IQR relative error, varied among the simulation scenarios. Median relative errors in total abundance for Group 1 scenarios were between -0.13% and -7.99% suggesting a consistent negative bias in total abundance estimates from a recovery-conditioned ITCAAN model. However, in all cases the relative error IQR encompassed 0% (Figure 2.A.1). In scenarios where natural mortality was estimated (i.e., RFix and NoFix scenarios), total abundance estimates had greater bias and imprecision compared to scenarios where natural mortality was fixed at the true value (i.e., MvFix, MRFix, and MFix) (Figure 2.A.1). Scenarios in which relative reporting rates were estimated, but natural mortality was fixed (i.e., MFix) had levels of bias and imprecision similar to scenarios where both natural mortality and reporting rates were fixed(i.e., MRFix) (Figure 2.A.1). Across all scenarios in which natural mortalities were fixed at their true values, accuracy and precision of total abundance estimates were fairly consistent across the evaluated intermixing levels. For scenarios in which natural mortality was estimated, the highest (i.e., 20%) intermixing rates resulted in the largest imprecision of total abundance estimates.

The influence of spatially varying reporting rates on total abundance depended on how reporting rates were parameterized in the ITCAAN model. Median and IQR relative error for total abundance estimates in the ITCAAN models with relative reporting rates and natural mortality estimated (RV1Est and RV2Est scenarios) were similar to the RFix20 and NoFix20 scenarios. Conversely, when reporting rates were assumed to be spatially constant in the ITCAAN model (RV1Canc and RV2Canc scenarios), accuracy and precision of total abundance estimates worsened. Under conditions where the reporting rates were the largest in the most productive natal region (RV1Canc), the total abundance estimates were slightly positively biased, but imprecision was approximately 2 times greater than the RFix20 or NoFix20 scenarios. Total abundance was very negatively biased for the scenario with reporting rate smallest in the most productive natal region (RV2Canc).

The misspecification of natural mortality at 0.5 times the true value resulted in an underestimation of the total abundance with a median relative error of approximately -50%. Conversely, setting natural mortality at 1.5 times the true value in the ITCAAN model resulted in a positive bias in total abundance with a median relative error equal to 385%. Specifying natural mortality above the true value also resulted in the largest imprecision in total abundance observed among the examined scenarios (Figure 2.A.1). When all populations were assumed to have equal productivity levels, total abundance estimates from the ITCAAN model had bias similar to the NoFix20 scenario, but were slightly more precise (Figure 2.A.1).

Population Abundances Relative Error

Estimates of individual population abundances were generally more imprecise and biased than estimates of total abundance. Abundance estimates of population 2, the most productive population, for Group 1 scenarios were generally negatively biased, while biases for all other populations were positive (Figure 2.A.2). As intermixing rate increased, the bias and imprecision in population abundance estimates generally increased. Among scenarios with low intermixing rates, the largest bias and imprecision in population abundance for populations 2 and 4 occurred in when natural mortality was estimated (RFix and NoFix) (Figure 2.A.2). For populations 1 and 3, the largest amount of bias and imprecision occurred in scenarios where reporting rates were estimated (MFix and NoFix) (Figure 2.A.2). Estimates for all populations were the most biased and imprecise for high intermixing rate scenarios when reporting rates were estimated (MFix20 and NoFix20) (Figure 2.A.2).

Individual population abundances were most biased for Group 2 scenarios when reporting rates were assumed to be spatially constant (i.e., were not estimated). Bias and precision of individual population abundance estimates for models that estimated relative reporting rates under both spatially varying reporting rates scenarios (RV1Est and RV2Est) were similar to the NoFix20 scenario. The bias in individual population abundance estimates, for ITCAAN models that assumed a spatially constant reporting rate, were greatly influenced by which region had the highest assumed

reporting rate. When the highest reporting rates occurred in regions associated with the most productive populations (RV1Canc), abundance estimates for populations 2 and 4 were severely underestimated, whereas abundance of population 3 was severely overestimated (median relative error approximately 5000%) (Figure 2.A.3). When the highest reporting rates occurred in regions associated with the least productive populations (RV2Canc) the abundance of populations 2 and 3 were underestimated, the abundance of population 4 was greatly overestimated, and the abundance for population 1 was slightly overestimated (Figure 2.A.3).

Incorrect specification of natural mortality had large consequences on population estimates (Figure 2.A.3). When natural mortality was specified at 0.5 times the true value in the ITCAAN model (SensU), abundance estimates for population 1 and 3 were positively biases, whereas abundance estimates for population 2 were negatively biased (Figure 2.A.3). The absolute magnitude of bias for populations 1, 3 and 4 was between that observed for the RFix20 and MFix20 scenarios. However, for population 2 the absolute magnitude of bias was considerably greater than what was observed from the RFix20 or MFix20 scenarios. When natural mortality was set at 1.5 times the true value in the ITCAAN model, all population abundances were significantly overestimated (Figure 2.A.3). When the productivities among the populations were equal, individual population abundance estimates were accurate and precise, with precision consistent across populations.

Natural Mortality and Relative Reporting Rates Relative Error

Natural mortality estimates for Group 1 scenarios were accurate (within ±5%), but precision varied between scenarios (Figure 2.A.4). The IQR of the relative error for natural mortality was relatively consistent for the 1%, 5% and 10% intermixing scenarios, but doubled for the 20% intermixing scenario. Additionally, a slight negative bias in natural mortality estimates occurred when the intermixing rates were 20%. Estimation of relative reporting rates concurrently with natural mortality did not affect accuracy or precision of the natural mortality estimates (Figure 2.A.4). For Group 2 scenarios, natural mortality estimates were also fairly accurate when the relative reporting rates were estimated (RV1Est and RV2Est). When reporting rates were assumed constant in the

ITCAAN model, a positive bias in natural mortality estimates occurred in the scenario where reporting rates were the greatest in the region associated with the most productive population (RV1Canc). This bias was not observed under the scenario where reporting rates were the lowest in the region associated with the most productive population (RV2Canc) (Figure 2.A.4). For both the RV1Canc and the RV2Canc scenarios, precision of natural mortality estimates was poor compared to Group 1 scenarios (Figure 2.A.4). For the Group 3 scenario in which spawning populations had equal productivities, accuracy and precision of natural mortality estimates were similar to Group 1 scenarios under a 20% intermixing rate.

Accuracy and precision of relative reporting rates varied by intermixing rate scenario and region (Figure 2.A.4). For Group 1 scenarios, relative reporting rates were fairly accurate for regions 3 and 4 across the evaluated intermixing levels; conversely, relative reporting rates for region 2 were negatively biased with the degree of bias increasing as the intermixing rate increased (Figure 2.A.4). For all regions, precision of the relative reporting rates improved with higher intermixing. For Group 2 scenarios, accuracy and precision of relative reporting rates varied depending on the spatial pattern of reporting rates. When reporting rates were the highest in the natal region for the largest population (RV1Est), the relative reporting rate parameter for this region was negatively biased and was the least precise estimate for this region among scenarios investigated. Conversely, when reporting rate was the lowest for the largest population (RV2Est), the relative reporting rates for all regions were generally unbiased and precise. Misspecification of natural mortality within the ITCAAN model had comparatively little influence on estimates of relative reporting rates. Estimates of relative reporting rates were unbiased and accurate for the scenario that assumed 20% intermixing and equal productivities among populations.

Movement Rate Relative Error

For Group 1 scenarios where reporting rates were assumed spatially constant, estimated movement rates were accurate and precise when reporting rates were fixed at the true values, with the most precise estimates at 5 and 10% intermixing rates (Figure 2.A.5). For scenarios where relative

reporting rates were estimated, imprecision in movement rates was generally greater than when relative reporting rates were not estimated at the same level of intermixing. For all regions, accuracy and precision declined as intermixing rates increased (Figure 2.A.5). For Group 2 scenarios, spatially varying reporting rates had little influence on accuracy and precision of movement rates when relative reporting rates were estimated, but had large influences when reporting rates were assumed spatially constant. Scenarios with spatially varying reporting rates but assumed spatially constant reporting rates resulted in larger biases and greater imprecision in movement estimates compared to the NoFix20 scenario (Figure 2.A.5). As with other parameters, misspecification of natural mortality at 0.5 times the true value did not have a large effect on accuracy or precision of movement rates; however, misspecifying natural mortality at 1.5 times the true value had a large effect on accuracy and precision of the movement rate estimates (Figure 2.A.5). Movement rates for all regions were accurate and precise when spawning populations were assumed to have similar productivity levels (Figure 2.A.5).

Discussion

Simulation studies are an essential tool for determining the effectiveness of a model to estimate parameters and capture the population dynamics of a system. Simulations analyses have been conducted for various ITCAAN models, but previous analyses have mostly been conducted assuming a release-conditioned framework for tag-recovery data (Hulson et al. 2011, 2013; Goethel et al. 2015b; Vincent et al. 2017). This study analyzed the performance of a recovery-conditioned ITCAAN model under an assumption of natal homing of the spawning populations and explored different model complexities of parameter estimation. Our main purpose was to determine the utility of recovery-conditioned ITCAAN models and the feasibility of accounting for spatially-varying reporting rates with this framework.

The data used in these simulation scenarios would be considered very high quality. The operating model simulated 8000 tags released annually for 40 years, which may be an unrealistic number of tags released for a prolonged period of time even for high-valued fisheries. Vandergoot

and Brenden (2014) reported that on average 6100 walleye were tagged annually in Lake Erie between 1990 and 2017, with the number of tags released in some years exceeding 10000 (C.S. Vandergoot, USGS, *personal communication*) so the tagging level assumed in our research was not outside the realm of possibility. The dynamics of tagged fish in the operating model were a simplistic representation of the processes that could happen in the real world and were constrained by numerous assumptions. First, tagging induced mortality was not simulated and tagged fish never lost or shed their tags. These two processes would reduce the amount of tagged fish alive and thus the number of tags recovered would be less, which would decrease model precision (Dorazio and Rago 1991). Additionally, if tag shedding is not accounted for by the model, then estimates will be biased (Brenden et al. 2010). The operating model simulated the fates of tagged fish through a multinomial process, yet overdispersion relative to a multinomial distribution in tag-recovery data is often observed (Bacheler et al. 2008; Vandergoot and Brenden 2014; Hanselman et al. 2015; Mayakoshi and Kitada 2016). This perfect match between the operating model and the estimation likelihood in the ITCAAN model would lead to more precise estimates than if a mismatch occurred between the processes. The operating model also assumed that tagged fish experienced the same dynamics as the rest of the population. If a mismatch existed between the dynamics the tagged cohorts experienced and the rest of the population, due to factors such as delayed mixing or altered behavior as a consequence of tagging, then parameter estimation would undoubtedly have been affected. Finally, tagged fish were simulated to move instantaneously and then remain sedentary for the remainder of the year. This is a common assumption when simulation testing ITCAAN models (Hulson et al. 2013; Goethel et al. 2015b; Vincent et al. 2017), but is unlikely to reflect actual fish movement. Additional evaluations of ITCAAN models would benefit from loosening some of the restrictions above to see how models performed with poorer-quality data, in addition to accounting for alternative ecological dynamics in simulated populations.

The estimation of movement rates by the recovery-conditioned tag-recovery framework was tested through simulations by McGarvey et al. (2010). Their simulation framework replicated the dynamics of southern rock lobster (*Jasus edwardsii*) in south Australia and consisted of 2 regions in

which tagged lobsters were harvested. McGarvey et al. (2010) simulated tag-recovery data through an individual-based model using a daily time step with simulated releases occurring at dates of actual releases from empirical studies. Simulation of movement dynamics in the individual-based model was not clear, but we assume was based on an instantaneous movement assumption once during the year based on the estimation model. Likewise, McGarvey et al. (2010) did not indicate what reporting rate was assumed to generate tag recovery data. Their simulation study found that the recovery-conditioned tag-recovery framework produced unbiased estimates of movement when mortality rates (both fishing and natural) were assumed at correct values. Conversely, they found estimating movement rates as simple proportions of recoveries of tagged fish in a new region divided by the total number of recoveries resulted in over-estimation of movement rates. However, McGarvey et al. (2010) did not test the estimation of other ITCAAN model parameters, or the estimation of movement rates when mortalities were not known precisely.

McGarvey et al. (2010) used a recovery-conditioned ITCAAN model to analyze empirical southern rock lobster harvest and tag recovery data. The underlying population model was length structured and sex dependent for two regions and estimated the mortality components. Estimates of movement and mortality were obtained from the recovery-conditioned ITCAAN model. However, the authors noted that movement rate estimates from the recovery-conditioned ITCAAN model differed from estimates obtained from a recovery-conditioned tagging framework that was provided mortality estimates from a catch-at-length model that did not incorporate movement. In other words, the mortality and movement rate estimates changed when both processes were estimated simultaneously as opposed to independently. Additionally, different weightings of the tag-recovery data within the ITCAAN model resulted in noticeably different fits to the harvest and catch per unit effort data. This research assumed the effective sample size of the multinomial distribution to model the tag-recovery data was equal to the number of tags recovered. Other simulation analysis have assumed different effective sample sizes of the tag-recovery data, such as equal to the effective sample size of the age composition (Goethel et al. 2015a) or equal to the number of tags released (Vincent et al. 2017). The weighting of tag-recovery data in an ITCAAN model influences

parameter estimates regardless of the tagging framework used, but guidelines for weighting of tagging data in an ITCAAN model requires additional research.

The simulation framework used in this study was quite different from that of McGarvey et al. (2010). Our simulations consisted of four populations that intermixed between four regions and tested the accuracy and precision of movement rate estimates as well as other ITCAAN model parameters that are important for management of intermixed fish stocks (e.g., abundances, mortalities). Tag recoveries were simulated using yearly time steps and movement was assumed to occur at the beginning of the year. We also tested the effect that non-spatially constant reporting rates had on model performance and whether relative reporting rates could be estimated by the model.

We found that a recovery-conditioned ITCAAN model performed adequately for some parameters under certain conditions, but poorly under others. Model parameter estimates were generally unbiased and accurate when intermixing rates were low and the relative reporting rates and natural mortality were correctly specified. Bias in individual population estimates at high intermixing rates was due to the large difference in abundances between the populations, which were not present when populations were assumed to have the same productivities. Accurate and precise estimation of individual population abundances became more problematic as movement rates increased and as the estimation models became more complex. A similar performance issue was observed for a release-conditioned ITCAAN model (Vincent et al. 2017).

The recovery-conditioned ITCAAN model investigated in this simulation study was very sensitive to assumptions regarding the reporting rates. As previously indicated, actual reporting rates cannot be estimated in a recovery-conditioned ITCAAN model. We attempted to estimate relative reporting rates for regions under the belief that reporting rates are unlikely to be constant across space. We found that a recovery-conditioned ITCAAN model had difficulty estimating relative reporting rates particularly for the region that corresponded to the natal region where the largest population spawned. Higher intermixing rates only exacerbated the difficulty in estimating relative reporting rates for the regions. Estimation of relative reporting rates also resulted in biases in other model parameters such as movement rates. Alternatively, assuming that the reporting rates were

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spatially constant in the ITCAAN model when the reporting rates were spatially variable resulted in large biases in individual population abundance estimates. When high reporting rates occurred in the natal region corresponding to the least productive population the estimates of relative reporting rates were generally unbiased and had slightly more precise estimates of relative reporting rates than scenarios where reporting rates were spatially constant. These results suggest that recovery-conditioned ITCAAN models are somewhat able to estimate relative differences in reporting rates between regions; however, when there are large differences among stock sizes some estimation problems may arise. As with population abundances, when populations were simulated under an assumption of equal productivity levels, precise and accurate relative reporting rates were estimated from a recovery-conditioned ITCAAN model.

The recovery-conditioned ITCAAN model generally provided unbiased estimates of natural mortality. However, when the natural mortality parameter was estimated in the ITCAAN model the precision of total abundance estimates decreased severely. Additionally, the estimates of natural mortality became less precise as movement levels increased. Misspecification of natural mortality caused severe biases in abundance estimates, which were worse when specified above the true value. The recovery-conditioned likelihood has some information that contributes to the estimation of natural mortality, but a release-conditioned ITCAAN framework performed better (Vincent et al. 2017). Across Group 1 simulation scenarios, IQRs in total abundance estimates for the recapture-conditioned were 1.11 to 5.98 times larger than release-conditioned IQRs. The largest difference in precision occurred when natural mortality was estimated by the ITCAAN models under high intermixing. Additionally, median estimates of total abundance and population abundance were more biased by up to 7%. In general, the release-conditioned ITCAAN model performed superior to the recovery-conditioned ITCAAN model.

In conclusion, the recovery-conditioned ITCAAN model was able to estimate natural mortality reasonably well but had biased estimates of relative reporting rates at high mixing rates. A recovery-conditioned ITCAAN model may be appropriate if there is high certainty that reporting rates are spatially constant and intermixing rates are low or stocks are of similar size and productivity.

However, when different fisheries occur in different spatial regions it may not be reasonable to assume that reporting rates are spatially constant and could result in biased estimates within an ITCAAN model. The consequence of assuming spatially constant reporting rates when they are not and the bias in reporting rate estimates at high intermixing rates, pose a quandary for stock assessment scientists attempting to fit a recovery-conditioned ITCAAN model. We recommend release-conditioned ITCAN models be preferred to recovery-conditioned models based on the problems with treating reporting rates in the recovery-conditioned ITCAAN model, imprecision in natural mortality estimates, and release-conditioned ITCAAN models providing more precise and accurate model estimates.

Acknowledgments

APPENDIX

Table 2.A.1: Regional reporting rates, average fishing mortality, unfished spawning stock biomass, and recruitment steepness specified in the operating model for investigated scenarios, where SSB is spawning stock biomass.

Parameter	Scenario	Region 1	Region 2	Region 3	Region 4
Steepness	EqProd	0.849	0.849	0.849	0.849
Steepness	All Other Scenarios	1.255	0.849	0.619	0.267
Unfished SSB	EqProd	5.903E7	5.903E7	5.903E7	5.903E7
Unfished SSB	All Other Scenarios	1.778E6	5.903E7	1.412E6	1.285E7
Average Apical F	All Scenarios	0.438	0.194	0.232	0.194
Reporting Rate	RV1	0.3	0.7	0.1	0.5
Reporting Rate	RV2	0.5	0.1	0.7	0.3
Reporting Rate	All Others	0.5	0.5	0.5	0.5

Table 2.A.2: Abbreviations, model characteristics, and convergence rates of simulation scenarios to investigate the influence of parameterization and movement (Group 1), spatially varying reporting rate (Group 2), and misspecification of natural mortality or reporting rate (Group 3), where movement is estimated unless noted.

| Scenario Group | Abbrv. | ITCAAN model | | Operating model | # needed | NPD | Maximum |
		Relative reporting	Natural mortality	Intermixing	for 1000 converged	Hessian	Gradient > 0.05
1	MvFix1*	Known	Known	1%	1149	3	147
1	MRFix1	Known	Known	1%	1155	3	155
1	RFix1	Known	Est. RC	1%	1165	5	164
1	MFix1	Est. Rel	Known	1%	1141	2	141
1	NoFix1	Est. Rel	Est. RC	1%	1176	2	175
1	MvFix5*	Known	Known	5%	1011	2	10
1	MRFix5	Known	Known	5%	1019	4	19
1	RFix5	Known	Est. RC	5%	1021	10	19
1	MFix5	Est. Rel	Known	5%	1072	2	71
1	NoFix5	Est. Rel	Est. RC	5%	1084	6	82
1	MvFix10*	Known	Known	10%	1017	17	4
1	MRFix10	Known	Known	10%	1014	14	4
1	RFix10	Known	Est. RC	10%	1010	10	5
1	MFix10	Est. Rel	Known	10%	1031	8	27
1	NoFix10	Est. Rel	Est. RC	10%	1031	12	23
1	MvFix20*	Known	Known	20%	1022	22	4
1	MRFix20	Known	Known	20%	1036	36	3
1	RFix20	Known	Est. RC	20%	1029	29	10
1	MFix20	Est. Rel	Known	20%	1010	10	3
1	NoFix20	Est. Rel	Est. RC	20%	1008	7	2
2	RV1Canc	Canc	Est. RC	20%	1128	109	94
2	RV1Est	Est. Rel	Est. RC	20%	1011	11	3
2	RV2Canc	Canc	Est. RC	20%	1025	25	12
2	RV2Est	Est Rel	Est. RC	20%	1015	11	7
3	SensU	Est. Rel	0.5×True	20%	1026	26	5
3	SensO	Est. Rel	1.5×True	20%	1012	12	3
3	EqProd	Est. Rel	Est. RC	20%	1018	18	8

* **Note:** NPD = Not Positive-Definite; Known = Fixed at true value; Est. = Estimated in ITCAAN; Rel = Reporting rates relative to region 1; RC = regionally constant; Canc = Reporting rates assumed regionally constant

* Movement Rate Fixed at True Value
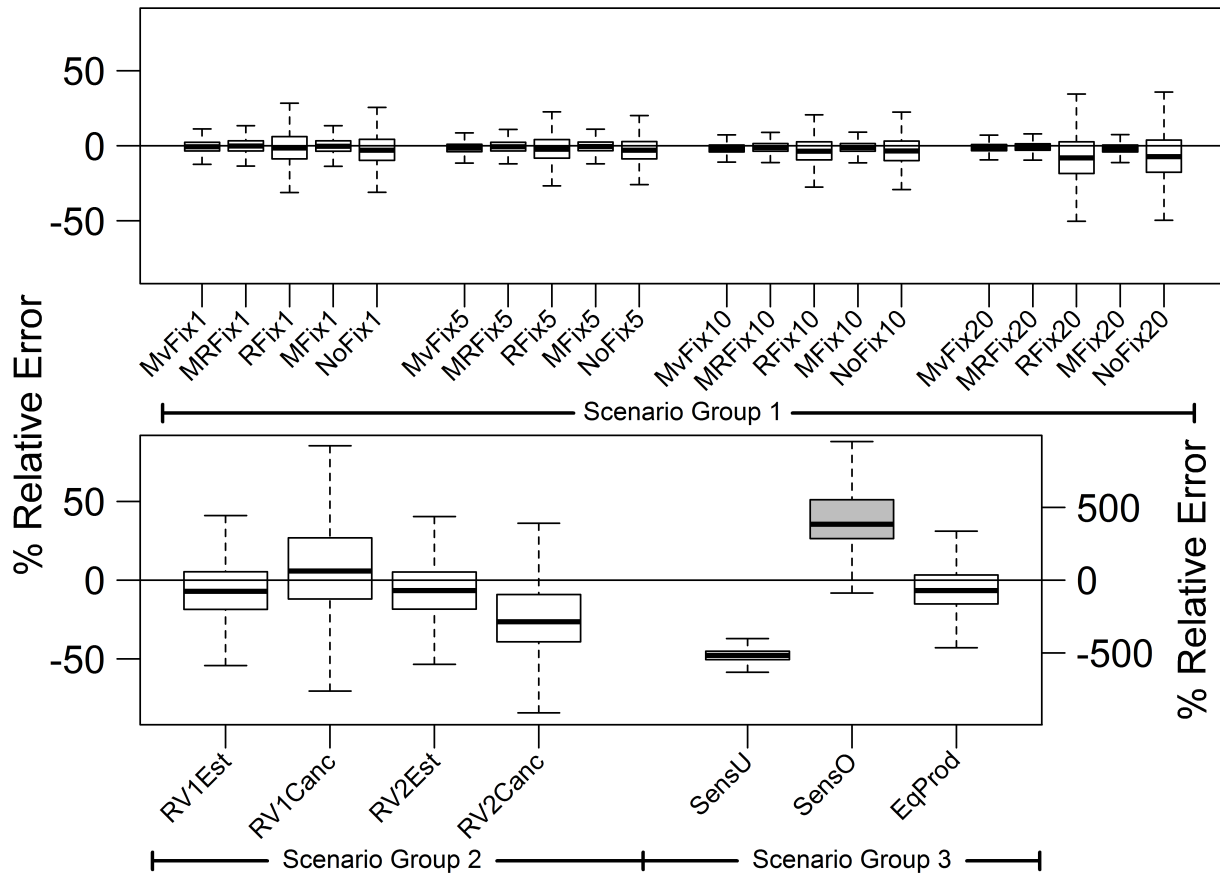
Figure 2.A.1: Relative error (%) of abundance summed across populations for a four region ITCAAN model under different intermixing rates and parameter estimation assumptions (Group 1), spatially varying reporting rates (Group 2), and misspecification of natural mortality and equal productivities (Group 3) for 1000 simulation iterations. The grey colored boxplot corresponds to the y-axis on the right side of the bottom plot. Table 2.A.2 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 relative error, whichever is less extreme. Relative errors outside the whisker range were not plotted.
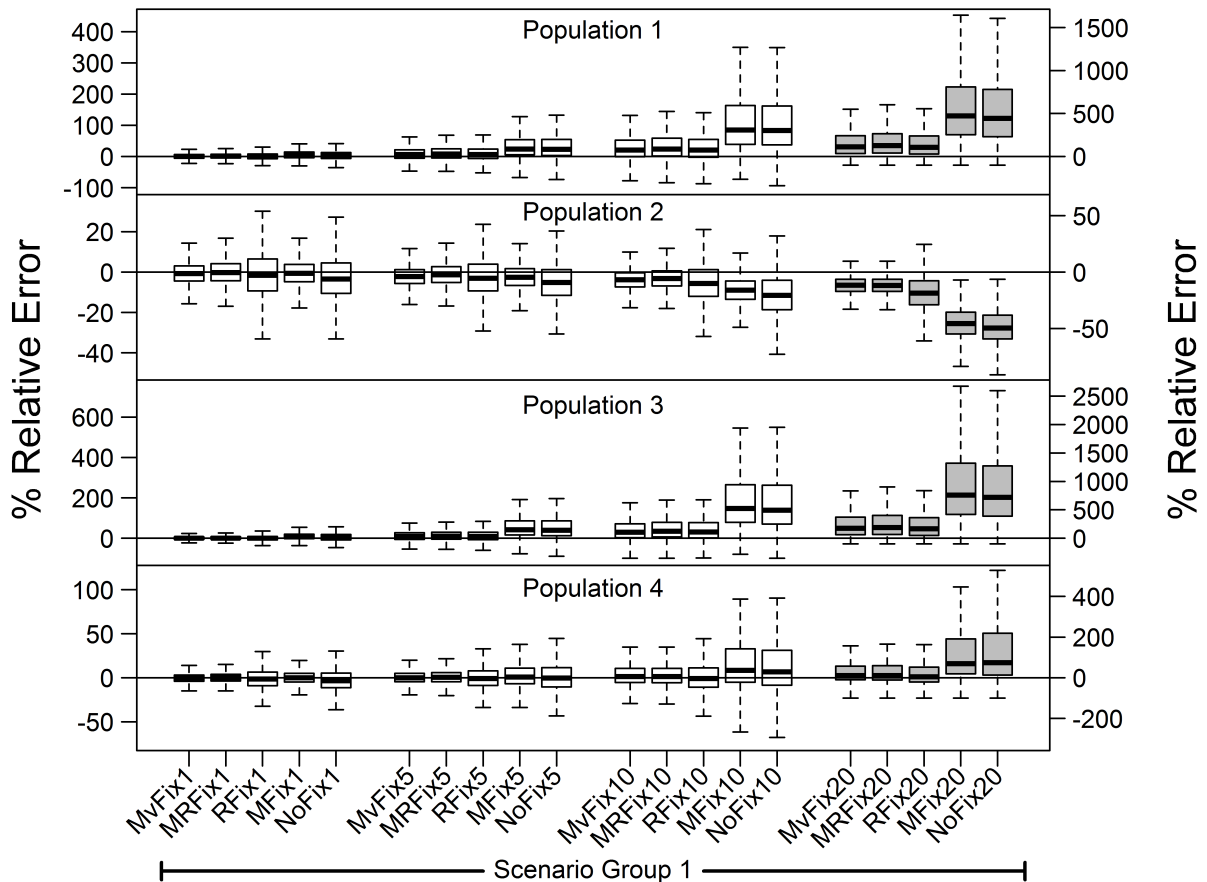
Figure 2.A.2: Relative error (%) of population abundance for a four region ITCAAN model under different intermixing rates and parameter estimation assumptions. The grey colored boxplots corresponds to the y-axis on the right side of the figure. Table 2.A.2 lists the model abbreviations and corresponding model components. Whiskers on the boxplots extend to 1.5 times the interquatile range or the most extreme relative error, which ever is less extreme. Relative errors outside the whisker range were not plotted.
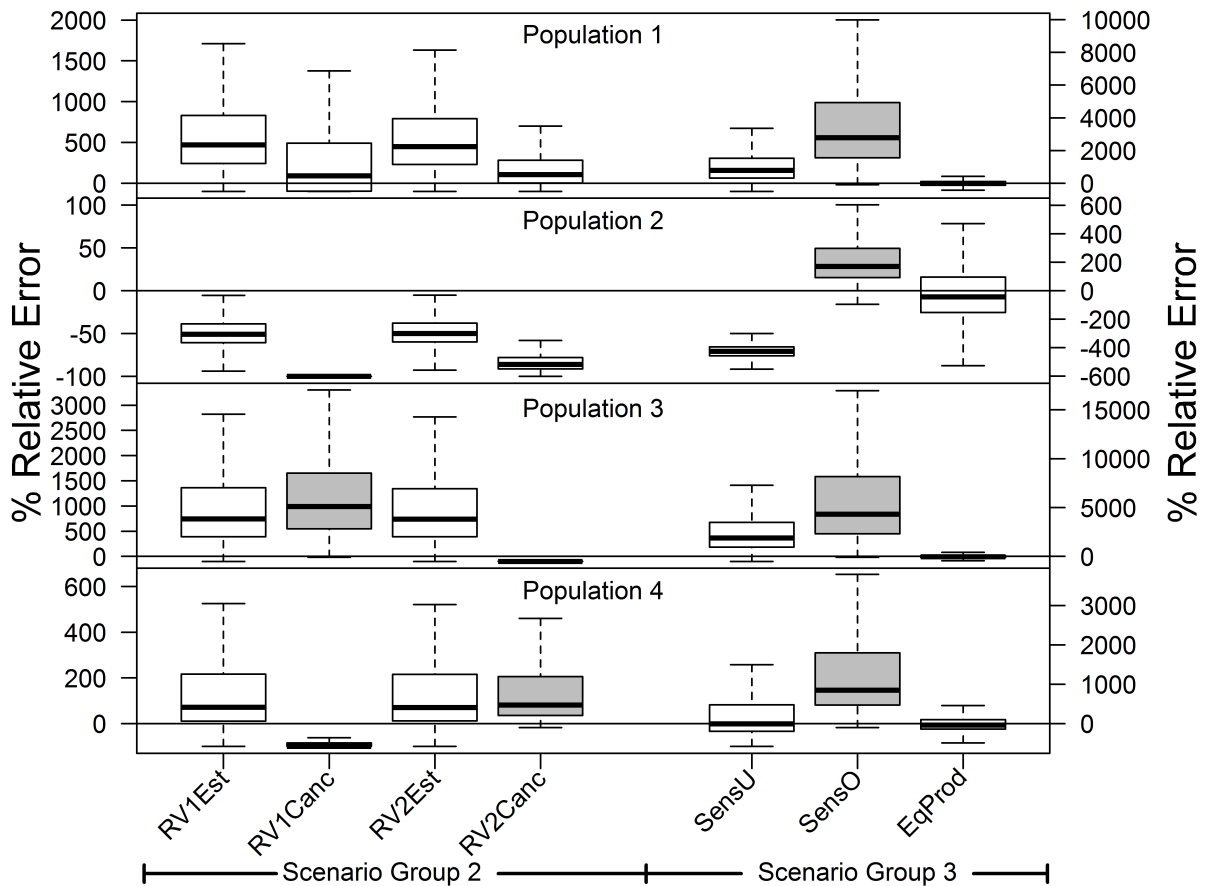
Figure 2.A.3: Relative error (%) of population abundance for a four region ITCAAN model under spatially varying reporting rates (Group2) and misspecification of natural mortality and equal productivities (Group 3) for 1000 simulation iterations. The grey colored boxplots corresponds to the y-axis on the right side of the figure, note that only population 3 of scenario RV1Canc and population 4 of scenario RV2Canc corresponds to the axis on the right. Table 2.A.2 lists the model abbreviations and corresponding model components. Whiskers on the boxplots extend to 1.5 times the interquatile range or the most extreme relative error, which ever is less extreme. Relative errors outside the whisker range were not plotted.
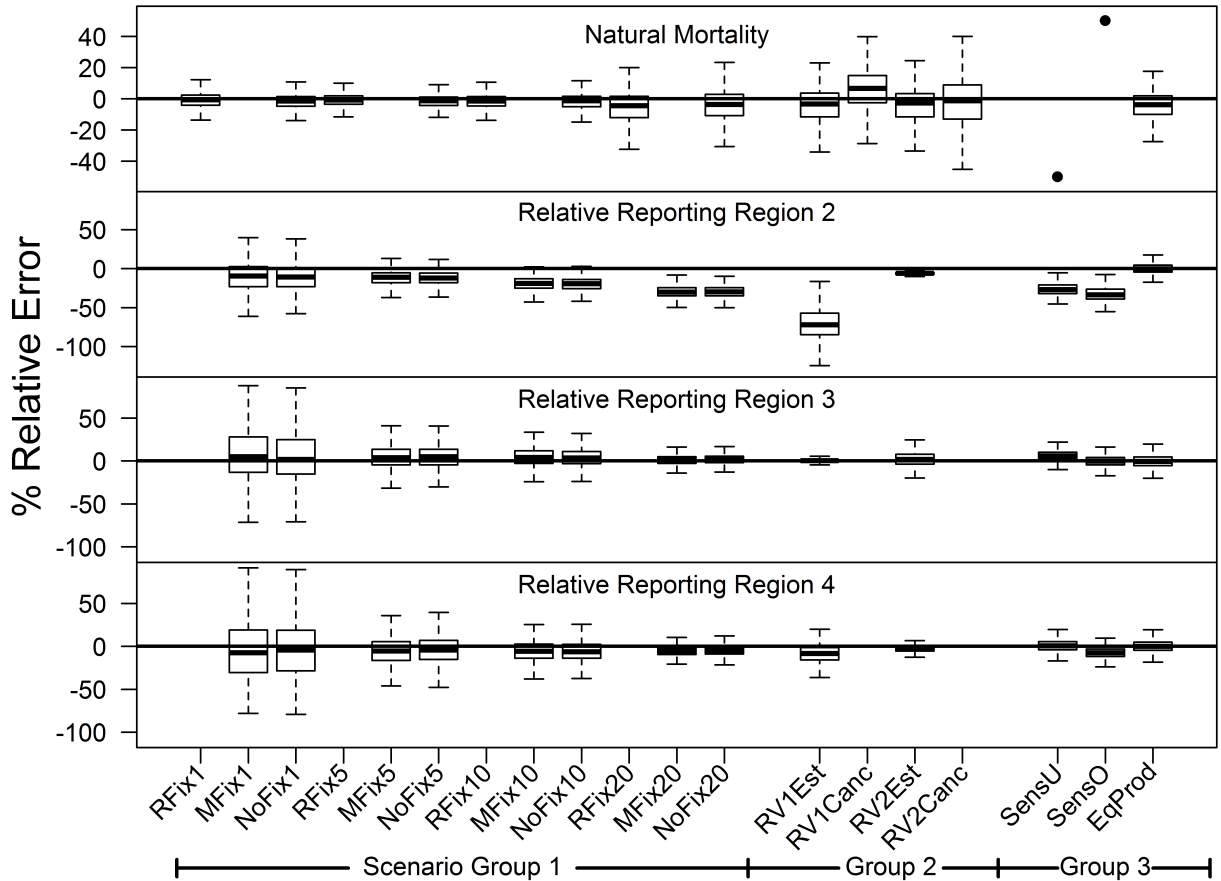
Figure 2.A.4: Relative Error (%) of relative reporting rates and natural mortality for a four region ITCAAN model under different intermixing rates and parameter estimation assumptions (Group 1), spatially varying reporting rates (Group2) and misspecification of natural mortality and equal productivities (Group 3) for 1000 simulation iterations. Table 2.A.2 lists the model abbreviations and corresponding model components. Dots indicate parameters that are fixed within the ITCAAN model at incorrect values. Whiskers on the boxplots extend to 1.5 times the interquatile range or the most extreme relative error, which ever is less extreme. Relative errors outside the whisker range were not plotted.
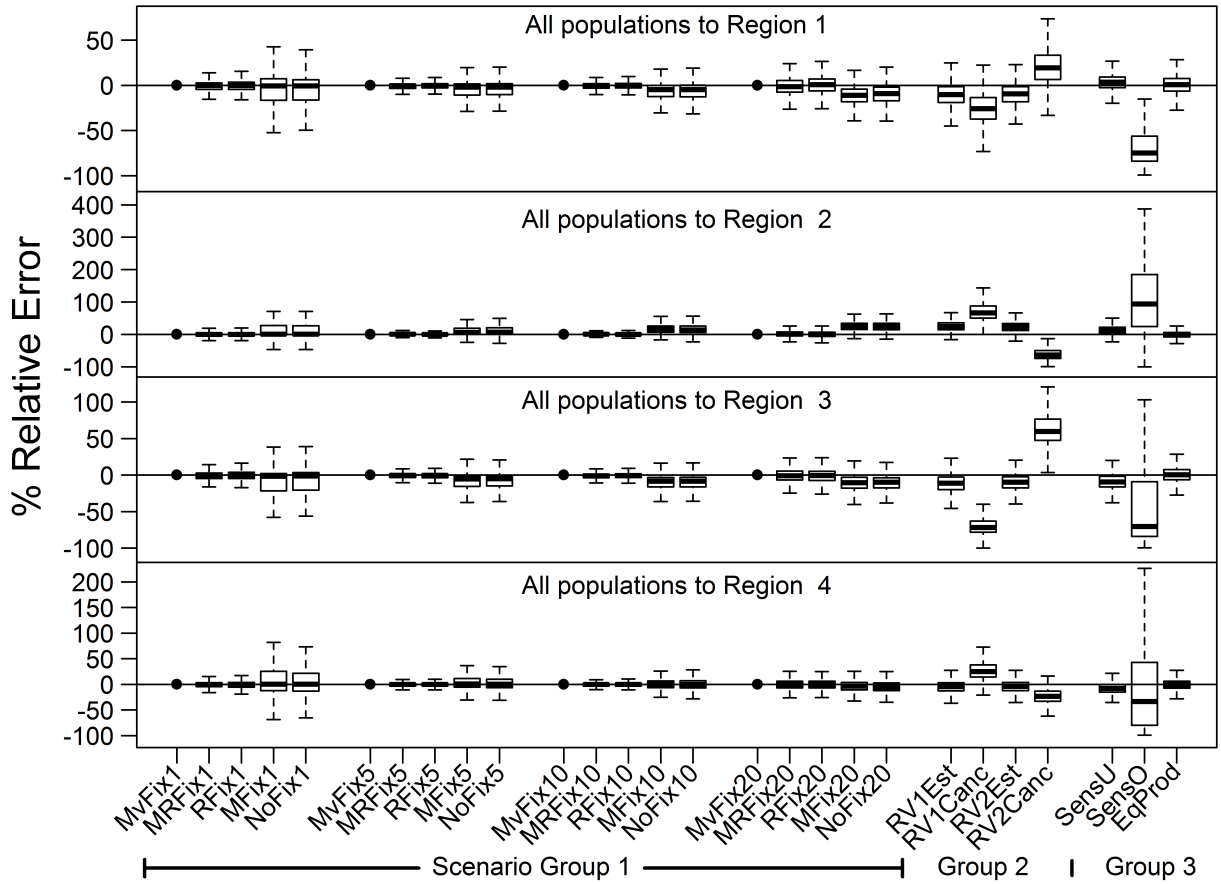
Figure 2.A.5: Relative Error (%) of movement rates of all populations to a harvest region for a four region ITCAAN model under different intermixing rates and parameter estimation assumptions (Group 1), spatially varying reporting rates (Group2) and misspecification of natural mortality and equal productivities (Group 3) for 1000 simulation iterations. Table 2.A.2 lists the model abbreviations and corresponding model components. Dots indicate parameters that are fixed within the ITCAAN model at the true value. Whiskers on the boxplots extend to 1.5 times the interquatile range or the most extreme relative error, which ever is less extreme. Relative errors outside the whisker range were not plotted.

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CHAPTER 3

TESTING COMMON ASSUMPTIONS USED IN SIMULATIONS OF MULTI-REGION INTEGRATED TAGGING AND CATCH-AT-AGE ANALYSIS MODEL PERFORMANCE

Abstract

Integrated tagging and catch-at-age analysis (ITCAAN) models provide a means for estimating spatially-varying population abundances, mortality rates, intermixing rates, and other important parameters associated with fisheries that exploit mixed stocks and the populations that contribute to these mixtures. Several simulation studies have been conducted investigating ITCAAN model performance under various conditions; however, previous studies have made simple assumptions about movement dynamics and the degree of temporal variation in important population and/or fishery dynamics rates. Additionally, previous studies have not incorporated important features of tagging studies, such as releases of high-reward tags or the possibility of tag shedding. The goal of our research was to advance the understanding of ITCAAN model performance and sensitivity to assumptions by conducting simulations incorporating more complicated (i.e., seasonal) movement dynamics, temporally varying natural mortality and reporting rates, release of high-reward tags, and imperfect tag retention. The simulations assumed four spatial regions and four spawning populations with fishery characteristics and dynamics based on Lakes Erie and Huron walleye (*Sander vitreus*) populations. We found that annual releases of high-reward tags increased the precision of model estimates and reduced some, but not all, bias in individual population abundance estimates. ITCAAN models performed best with estimation of natural mortality and reporting rates in 5-year blocks and performed worst when estimating both parameters as temporally constant. Temporal trends in reporting rate biases were evident when true reporting rates decreased linearly but were estimated in 5-year blocks; estimating temporally constant reporting rates resulted in the largest regional biases and imprecision when high-reward tagging was infrequent. Seasonal movements resulted in more accurate population abundance estimates due to an overall average

lower movement rate, but movement rates tended to be biased when compared to the average movement rate across seasons. We caution that ITCAAN models may produce biased estimates of population abundances when mixing rates are high and there are very large differences in the size of the populations. Additionally, tagging studies intended for use in ITCAAN models should be designed to estimate annual reporting rates and tag retention rates. We propose that reporting rates and natural mortality parameters be estimated in ITCAAN models using multi-year time blocks or whenever high-reward tags are released to reduce bias in population abundance estimates.

Introduction

Integrated tagging and catch-at-age analysis (ITCAAN) models (Maunder 2001; Hulson et al. 2011; Goethel et al. 2015a) incorporate tag-recovery data within a statistical catch-at-age (SCAA) framework; these models are a spatially-explicit assessment approach used to estimate abundances, mortalities, and intermixing rates of populations that are exploited as mixed stocks during the fishing season (Hulson et al. 2013; Goethel et al. 2015b; Vincent et al. 2017). Herein, populations are groups of fish that interbreed and share similar life-history characteristics. Stocks are fishery units that are characterized by the region in which they are harvested (Cadrin et al. 2004). Therefore, a mixed stock consists of fish from multiple populations that are harvested within a defined region, such as a management unit. Several simulation studies have been conducted investigating ITCAAN model performance under varying model complexities, movement strategies, and tag-recovery likelihood frameworks (Hulson et al. 2011, 2013; Goethel et al. 2015b; Vincent et al. 2017, in preparation). Such simulation studies have yielded valuable information concerning ITCAAN model performance under various conditions. However, these simulations have made simple assumptions with regards to fish movement, the degree of temporal variation in important population (e.g., natural mortality) and fishery (e.g., tag reporting) dynamic rates, and have not considered important features of tagging studies (e.g., release of high-reward tags, tag shedding). Consequently, there remains much to learn about the performance and sensitivities of ITCAAN models.

ITCAAN model performance has been explored under both reproductive mixing (Goethel et al.

2011; Hulson et al. 2013; Goethel et al. 2015a) and natal homing (Vincent et al. 2017) movement strategies. Reproductive mixing occurs when individuals of a population move to a different region and contribute to the spawning stock in the new region. Natal homing occurs when individuals from multiple populations intermix at particular time periods, but return to separate areas to spawn. Simulations indicated that movement rate estimates from ITCAAN models were highly precise and accurate for both movement strategies (Hulson et al. 2011, 2013; Goethel et al. 2015a; Vincent et al. 2017). However, previous simulation studies assumed that movement occurred instantaneously at a single point in time during the year and that fish then remained sedentary and were subject to regional exploitation. Such movement dynamics are not realistic for actual fish populations. Although it might be desirable to estimate movement rates at finer temporal scales, this has the potential to greatly increase model complexity and could result in model estimation problems. Consequently, it would be beneficial to understand the sensitivity to finer temporal scale movements for ITCAAN models that assume annual movement dynamics.

Fishery managers and biologists are often interested in incorporating estimation of natural mortalities into assessment methods, such as SCAA models, given that natural mortality can be an important determinant of sustainable harvest policies. In actual systems, natural mortality rates are unlikely to be temporally constant as factors such as predation, disease, starvation, and environmental conditions are likely to change over time (Jiao et al. 2012; Johnson et al. 2015). Ultimately, the ability to estimate time-varying natural mortalities within assessment models would be highly desirable. For SCAA models, the estimation of natural mortality rates is highly dependent on the quality of length- or age-composition data (Beverton and Holt 1957; Maunder and Wong 2011). According to Jiao et al. (2012), estimating time-varying natural mortalities within a SCAA model may be possible, although based on the results of Fu and Quinn (2000) this has the potential to result in biased estimates of other parameters. Currently, the benefit of estimating time-varying natural mortality within an SCAA model is uncertain when weighed against the possibility of the biases it may induce (Fu and Quinn 2000; Johnson et al. 2015). For ITCAAN models, the inclusion of tag-recovery data within a SCAA framework provides additional information that

can be used for estimating natural mortalities. Vincent et al. (2017) conducted simulations and found that temporally constant natural mortalities could be estimated within an ITCAAN model, although estimates were affected by the number of tags released and model complexity. Whether time-varying natural mortalities can be estimated under any circumstances within an ITCAAN model is presently unknown, but this information would be of immense value given the importance of natural mortality estimates for management.

For tag-recovery studies, two important design features to consider are the rates that tags are reported by anglers and the possibility that some tags may be shed while recoveries are still being collected. Both tag non-reporting and shedding can result in positively biased natural mortality estimates and negatively biased fishing mortality estimates if unaccounted for in analysis of recovery data (Hearn et al. 1987; Dorazio and Rago 1991; Fabrizio et al. 1996; Hampton 1997; Brenden et al. 2010). Within an ITCAAN model, tag non-reporting and shedding would ostensibly lead to incongruences between estimated dynamics for tagged cohorts and at-large populations if these factors were not incorporated into the model. In traditional tag-recovery studies, multiple approaches have been used to estimate tag non-reporting rates, such as releasing high-reward tags, placing observers on fishing vessels or cleaning stations, or conducting mail surveys (Pollock et al. 1991; Denson et al. 2002; Taylor et al. 2006; Konrad et al. 2016). Goethel et al. (2015b) found that estimation of tag-reporting rates may be possible within an ITCAAN model without additional sources of data; however, Vincent et al. (2017) found that reporting rate estimates could be biased in cases of large differences in population productivities and high movement rates. Simultaneous estimation of reporting rates and natural mortalities led to reduced accuracy and precision, but were superior to estimates when one of the parameters was incorrectly assumed. Vincent et al. (2017) suggested that inclusion of an additional data source, such as recoveries from high-reward tagging release, might improve ITCAAN model estimation of tag reporting rates and perhaps improve the accuracy and precision of other parameter estimates. Given that tag reporting rates can vary temporally due to factors such as apathy towards the tagging study, how well a tagging study is advertised, relationship with or trust in the tagging agency, and the relative harvest of

different fisheries (e.g., commercial versus recreational fisheries) (Hoenig et al. 1998; Denson et al. 2002; Vandergoot et al. 2012), the ability to estimate temporally-varying reporting rates would be an attractive feature of ITCAAN models. To our knowledge, evaluations of ITCAAN model performance have not considered the ability to estimate temporally-varying tag reporting rates or natural mortalities. Furthermore, how accuracy and precision of parameter estimates may be affected by tag shedding or the release and recovery of high-reward tags requires additional investigation.

The goal of this research was to build upon previous studies of ITCAAN model performance by conducting simulations incorporating more complicated movement dynamics, temporally-varying natural mortality and reporting rates, release of high-reward tags, and imperfect tag retention for the purpose of evaluating parameter estimability and robustness of release-conditioned ITCAAN models. Simulations were based on walleye (*Sander vitreus*) populations in the Laurentian Great Lakes (Zhao et al. 2009, 2011; Fielder and Bence 2014; Wills et al. 2016), which exhibit complex movement patterns and large differences in population abundances (Wang et al. 2007; Vandergoot and Brenden 2014; Hayden et al. 2014; Herbst et al. 2016). Specifically, we investigated how accuracy and precision of ITCAAN model estimates were affected by the following: 1. whether the operating and ITCAAN models incorporated tag loss and/or the release of high-reward tags; 2. simulation of time-varying natural mortality and/or reporting rates and estimation of these parameters annually, in 5-year time blocks or temporally constant; 3. the frequency of high-reward tag release; and 4. movement dynamics simulated as seasonally varying (4 seasons per year), but estimated as an annual rate.

Lakes Erie and Huron Walleye

Walleye is a piscivorous species that is exploited by both recreational and commercial fishers in the Great Lakes (Fielder and Bence 2014; Wills et al. 2016). Walleye aggregate during the early spring in rivers and shallow rocky reefs for spawning (Busch et al. 1975). After spawning, walleye often make directed and sometimes long-distance movements towards summer feeding grounds

that are selected based on thermal conditions and prey availability (Wang et al. 2007; Zhao et al. 2011; Hayden et al. 2014; Vandergoot and Brenden 2014; Herbst et al. 2016). This dispersal of walleye after spawning is recognized to be potentially problematic for management as fish can cross multiple jurisdictional boundaries when moving between spawning and feeding grounds. Consequently, fisheries may depend on spawning populations and systems over which managers have no jurisdictional authority (Brenden et al. 2015; Herbst et al. 2017).

Lakes Huron and Erie contain two of the largest and most valuable fisheries in the Great Lakes region (Baldwin et al. 2009). Presently, separate SCAA assessment models are used to estimate walleye population abundances and mortalities in Lakes Erie and Huron to gauge the health of the populations and assist in setting harvest regulations (Fielder and Bence 2014; Wills et al. 2016). The abundance of walleye in Lake Huron has been estimated to be between one and four million fish (Fielder and Bence 2014). Lake Erie is generally regarded to consist of three basins (western, central, and eastern) that decrease in walleye abundance moving eastward. The abundance of walleye in the western and central basin of Lake Erie has been estimated to be upwards of tens of millions of fish (Wills et al. 2016), whereas walleye abundance in the eastern basin has been estimated to be closer to tens of thousands of fish (Zhao et al. 2011). Estimates of intermixing rates between Lake Huron and the western basin of Lake Erie have been around 1 to 2% (Hayden et al. 2014; Fielder and Bence 2014; Vandergoot and Brenden 2014). Although this degree of movement may seem inconsequential, given the difference in population abundances it may mean a considerable number of walleye are migrating from Lake Erie to Lake Huron (Fielder and Bence 2014). A larger movement rate ($\sim$ 10%) has been estimated for fish moving from the western basin of Lake Erie into the Huron Erie Corridor (Wang et al. 2007; Vandergoot and Brenden 2014). Movement from the western basin to the eastern basin has been shown to be substantial through jaw tag recoveries (Wang et al. 2007; Vandergoot and Brenden 2014) and telemetry studies (Chris Vandergoot, USGS, *personal communication*). There has been increasing interest in the development and use of spatially-explicit models for assessing the walleye populations in Lakes Erie and Huron due to the species' economic and ecological importance and the estimated degree

of movement both within and between the lakes.

Methods

Fish populations and tagged cohorts were simulated through an operating model with specified recruitment functions, population dynamic rates, and intermixing rates. A 40-year time-series of data were generated from the operating model, which were then fit by a release-conditioned ITCAAN model. The operating and ITCAAN model used in this research were similar to those described in Vincent et al. (2017, in preparation). Summaries and alteration from previous analyses (Vincent et al. 2017, in preparation), are provided below for the operating and ITCAAN models used in this research. Both the operating and ITCAAN models tracked the dynamics of age-2 through age-7 fish, with the last age class an aggregate group of age-7 and older fish. Code for the operating and ITCAAN models can be found in the Supplementary Material 3. The ITCAAN model was programed in ADMB version 11.5 (Fournier et al. 2012), while the operating model was programmed in R version 2.15.1 (R Core Team 2016). Parameter values assumed in the operating model can be found in the Supplementary Material 3.

Operating Model

The operating model simulated the dynamics of four independent spawning populations that intermixed among four harvest regions. Recruitments were simulated using population-specific Ricker stock-recruitment curves with annual error simulated from a first-order autoregressive (AR1) process. Parameters of the AR1 process for each population and investigated scenario were generated from the posterior distribution for Percidae from Thorson et al. (2014). The Ricker stock-recruitment functions were based on perceived conditions of walleye populations in Lakes Huron and Erie and had very different unfished spawning stock biomasses and productivities. Stock-recruit parameters for population 1 were chosen to mimic Lake Huron walleye, while the stock-recruit parameters for populations 2, 3, and 4 were based on estimates from the western, central, and eastern Lake Erie walleye populations, respectively (Supplementary Material 3 Table 3). After spawning, a box-

transfer model (Goethel et al. 2011) was used to simulate movement of the spawning populations to different regions. For most scenarios, intermixing was simulated where 20% of the population moved to each non-natal region for all scenarios (i.e., 40% of each spawning population was assumed to remain in their natal region). In previous analyses, this rate of intermixing resulted in biased reporting rates and population abundances for ITCAAN models Vincent et al. (2017, in preparation). Part of the impetus for this study was to determine whether recoveries from high-reward tagging would rectify these regional biases. For a few scenarios (see Simulation Scenarios section) movement was simulated to occur immediately after spawning and at three other evenly spaced time periods within a year (i.e., seasonally) to test the impact such dynamics had on parameter estimation.

One difference in the operating model used in this research from that described in Vincent et al. (2017) was that two fisheries were assumed to operate in each harvest region, similar to what occurs in Lakes Huron and Erie. Annual apical fishing mortality rates for each region-specific fishery were simulated using a truncated AR1 process, which constrained values to be greater than zero. The average fishing mortality and selectivity-at-age parameters for each fishery and region are presented in the Supplementary Material 3 and are based on commercial and recreational fishery estimates from Lakes Erie and Huron. The instantaneous natural mortality rates assumed in the operating model varied by scenario (see Simulation Scenario section) but in all cases had a mean value of 0.32 year^{-1} and were invariant over ages and regions.

The operating model also tracked the fates of tagged cohorts of fish and included some processes that were not included in the simulations of Vincent et al. (2017, in preparation). Annually 2000 fish were assumed to be tagged with standard-reward tags and released from each population at the beginning of the year when fish were aggregated for spawning. The age of tagged fish at the time of release were assumed known in the operating model based on a temporally constant set of proportions at age (Supplementary Material 3 Table 2). The fate of tagged fish were simulated from age-specific mortality rates, but simulated tag-recovery data were pooled across ages. If the simulated abundance for any of the four populations was less than 40000 fish at any point in time,

the simulation was discarded from further analysis and replaced with a new simulation because we believed it was unlikely that more than 5% of a population would be tagged within a year. For some investigated scenarios, the fates of 200 fish tagged with high-reward tags from each population were also tracked in the operating model; the frequency of releases of high-reward tagged fish was one of the factors evaluated as part of this research. Tagged fish were assumed to intermix immediately with the at-large populations, meaning that both standard and high-reward tagged fish experienced the same dynamics (e.g., mortalities and movements) as the at-large populations. However, 100% of recaptures of fish tagged with a high-reward tag were reported, but reporting rates of standard tags varied by simulation scenario (see Simulation Scenarios and Supplementary Material 3 Table 1).

Most investigated scenarios assumed some level of tag shedding. The probability of tag retention given the number of years after release were calculated from parameters estimated by Vandergoot et al. (2012) for Lake Erie walleye and are presented in Table 4 of the Supplementary Material 3. The numbers of fish that retained their tags from each tagging cohort were generated by multiplying the number of tags alive at the beginning of the year by the tag retention probability given the number of years after release and rounding to the nearest number. In essence, tag shedding was assumed to occur instantaneously at the beginning of the year, when simulated. For scenarios with annual movement rates, movement of tagged fish to different regions were generated from multinomial distributions with 20% of the tags moving to each non-natal region. Whether standard- or high-reward tagged fish survived, were harvested, or died due to natural causes in each region were simulated from multinomial distributions with expected proportions equal to the dynamics of the stock within the region (e.g., exploitation rate). For scenarios with seasonal movement, each year was evenly divided into four time periods or seasons. At the beginning of each season, tagged fish were simulated to move based on seasonal movement parameters and then exploited at region specific mortalities. Seasonal instantaneous mortality rates were assumed to be one quarter of the annual instantaneous mortality rate for all seasons (i.e., equal mortality rate throughout the year). The number of recovered tags were generated from multinomial distributions in each season; these

recoveries were summed across age and season to determine annual recovery counts. The at-large populations for these seasonal scenarios experienced the same movement and regional mortalities as tagged fish.

Data used by the ITCAAN model were generated from the operating model with assumed levels of observation error. Fishery-specific time-series of fishing effort were generated from the apical fishing mortalities using fishery-specific catchability coefficients (Supplementary Material 3 Table 1) and lognormal multiplicative observation errors with a CV of 10%. Observed region-specific harvest data were created from actual harvests summed across populations within a region multiplied by annual random errors with a CV of 10%. During October (i.e., during intermixing), a fishery-independent survey was simulated to occur within each region. A survey catch per effort time-series for each region was simulated using intermixed stock abundance multiplied by region-specific catchability coefficients, age-specific selectivity parameters, and lognormal observation error with a CV of 20%. Annual age-composition data of fish captured by fisheries and surveys were simulated independently using multinomial distributions based on the true age compositions and a sample size of 100. The number of reported tags by fishery and year of recapture for each release event (i.e., by region and year of release) were simulated using a binomial process. Reporting of harvested fish equipped with standard tags by commercial and recreational fisheries was assumed to be imperfect for all investigated scenarios. The numbers of tags reported by each fishery were generated from binomial distributions based on the number of tags harvested by fishery and fishery-specific reporting rates, the values of which depended on the scenario of investigation (see Simulation Scenarios and Supplementary Material 3 Table 1).

ITCAAN Model

The release-conditioned ITCAAN model used in this research was nearly identical to that used in Vincent et al. (2017). The primary modifications in the ITCAAN model from previous work were that 1. release and recovery of high-reward tags were included as data components in the model for scenarios that assumed high-reward tagging; 2. the predicted number of tags reported incorporated

tag shedding rates for scenarios that evaluated tag shedding; and 3. fishing mortality was expanded to estimate dynamics for both recreational and commercial fisheries. The recovery-probability equations for high-reward tags were the same as those for standard tags with the exception that tag reporting was assumed to be 100% for high-reward tags. For the purpose of this research, we assumed that tag-shedding rates were precisely known and therefore tag shedding rates were fixed at known values in calculations of the predicted number of tags recovered.

The ITCAAN model was fit to generated data and estimated parameters using maximum penalized likelihood in ADMB (Stewart et al. 2013). Lognormal likelihoods were assumed for the harvest, effort, and survey catch per effort data, whereas multinomial distributions were assumed for tag-recovery data and age compositions of each fishery and survey. Regional variances of the harvest data were estimated. Variance for effort and survey catch per effort data sources were calculated based on assumed ratios of their variances relative to the estimated variances of the harvest data. The assumed ratios were equal to the actual ratios in variances from the operating model. Effective sample sizes for age compositions were assumed equal to 100 for both the fisheries and surveys, whereas for the tag-recovery data the effective sample size was the number of tags released each year. ITCAAN model convergence criteria was based on whether the model produced a positive-definite Hessian matrix and the maximum gradient for all parameters was less than 0.05, as in (Vincent et al. 2017, in preparation). Simulations were conducted until 1000 ITCAAN estimates had converged. Table 3.A.1 reports the number of simulations required to reach a sample size of 1000, the percent convergence, and the number of simulations that failed based on the different criteria.

Simulation Scenarios

Seven groups of simulation scenarios were conducted exploring ITCAAN model estimation performance. The first group of scenarios explored the influence of incorporating tag shedding and high-reward tagging on ITCAAN model performance. Four groups of scenarios simulated different combinations of time-varying natural mortalities and reporting rates crossed with three approaches

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for estimating these time varying rates. One group of scenarios investigated the influence of releasing high-reward tags at frequencies of 5 or 10 years. The final group of scenarios explored the sensitivity of ITCAAN models to seasonal movement dynamics.

Tag Shedding and Release of High-Reward Tags

The first group of scenarios investigated the consequences of tag shedding and release of high-reward tags on ITCAAN model performance. These scenarios assumed that natural mortality and reporting rates were temporally constant in the operating model and estimated with the same assumption in the ITCAAN model. Reporting rates were unique for each fishery, but in all regions the reporting rates for commercial fisheries were lower than recreational fisheries (Supplementary Material 3 Table 1). These scenarios assumed that movement occurred once during the year after returning to the natal region to spawn. The first scenario in this group assumed that no high-reward tags were released and no tag shedding occurred (NoRwrdNoLoss). The second scenario assumed that no high-reward tags were released, but tag shedding was included in the operating and ITCAAN models (NoRwrdLoss). The final scenario assumed that 200 high-reward tags were released annually in each region and both the operating and ITCAAN models incorporated tag shedding (RwrdLoss).

Time-Varying Natural Mortality

The second group of scenarios investigated how well an ITCAAN model could estimate time-varying natural mortalities. Annual natural mortalities in the operating model were simulated using a AR1 process that was truncated such that natural mortalities could not be less than or equal to zero. The AR1 process assumed a mean of 0.32, a standard deviation of 0.05, and an autocorrelation coefficient of 0.8 (Figure 3.A.1). Natural mortalities were estimated using three different methods: annually, in 5-year time blocks (i.e., one parameter for 5 years), and temporally constant. The annual natural mortality model estimated a free parameter for each model year and was referred to in the scenario names as Ann. The block estimation of natural mortality

also estimated each parameter freely for eight 5-year segments and was referred to as Block in the scenario abbreviations. Natural mortality was also estimated as temporally constant and these scenarios were referred to as Const. Given this group of scenarios investigated time-varying natural mortality, the three scenarios in this group were referred to as TVMAnn, TVMBlock, and TVMConst. Both the operating and ITCAAN models assumed that reporting rates were temporally constant but varied by fishery for these scenarios (Supplementary Material 3 Table 1). Tag shedding was incorporated in both the operating and ITCAAN models. Additionally, all simulations in this group incorporated annual releases of high-reward tags and assumed annual movement dynamics similar to Vincent et al. (2017).

Time-Varying Reporting Rates

The third group of scenarios investigated how well an ITCAAN model could estimate time-varying reporting rates. Annual reporting rates for each fishery in the operating model were generated using an AR1 process that was constrained between 0 and 1 with fishery-specific means (43% for recreational fisheries; 15% for commercial fisheries), a standard deviation of 0.05, and an autocorrelation coefficient of 0.7 (Figure 3.A.1). As with the time-varying natural mortality group of scenarios, three different approaches for estimating reporting rates were considered: 1. estimating annually varying reporting rates (TVRRAnn), 2. estimating reporting rates in 5-year time blocks (TVRRBlock), and 3. estimating a constant reporting rate for each fishery (TVRRConst). Annual estimates of reporting rates were estimated through a logit-transformed random walk (i.e., constrained to be between 0 and 1). The reporting rates in the first year were estimated as logit transformed parameters, while subsequent years were estimated using the equations:

$$\text{Reporting Rate}_y = \frac{1}{1 + exp(-(RR_y))}$$

(3.0.1)

$$\text{where} \quad RR_y = RR_{y-1} + \epsilon_y.$$

In the equation above, the estimated parameters are the deviations from the previous year's reporting rate, ϵ_y, which were constrained by a normal penalty with an assumed standard deviation

of 2. The block parameterization ITCAAN model estimated eight 5-year blocks of reporting rates for each fishery, while the constant parameterization estimated a single temporally constant parameter for each fishery. In the simulations for this group of scenarios, natural mortality was assumed to be temporally constant with a value of 0.32 year^{-1} in the operating model and was estimated as a temporally constant parameter in the ITCAAN model. Simulations in this group integrated tag shedding and annual release of high-reward tags in both the operating and ITCAAN models, which assumed annual movement dynamics similar to Vincent et al. (2017).

Time-Varying Natural Mortality and Reporting Rates

The fourth group of scenarios investigated how well ITCAAN models could simultaneously estimate time-varying natural mortalities and reporting rates. Annual natural mortalities and reporting rates were generated using the AR1 processes previously described (Figure 3.A.1). All simulations in this group assumed annual releases of high-reward tags and tag shedding in the operating and ITCAAN model while assuming a single annual movement. As with the previous two groups of scenarios, three different approaches for estimating natural mortalities and reporting rates were considered: 1. estimating natural mortalities and reporting rates as both annually varying (BothTVAnn), 2. estimating natural mortalities and reporting rates in 5-year time blocks (BothTVBlock), and 3. estimating constant parameters for both natural mortalities and reporting rates (BothTVConst).

Decreasing Reporting Rates

The fifth group of scenarios investigated how well an ITCAAN model could estimate reporting rates that declined over time. In the operating model, natural mortality was simulated using the AR1 process previously described. Reporting rates were generated assuming a constant linear decline; the values at the start and end of the time series for the reporting rates are presented in Table 1 of the Supplementary Material 3. Similar to the other scenarios, commercial reporting rates were assumed to be lower than the recreational fisheries and were region-specific. The ITCAAN model was parameterized to estimate natural mortalities and reporting rates as either

annual (DecrRRAnn), in 5-year time blocks (DecrRRBlock), or constant values (DecrRRConst).

These simulations assumed a single annual movement and incorporated tag shedding and annual

releases of high-reward tags in both the operating and ITCAAN model.

High-Reward Releases Every 5 or 10 Years

The sixth group of scenarios evaluated the effects of less frequent (every 5 years or every 10 years)

releases of fish tagged with high-reward tags. We assumed that 200 fish were tagged with high-

reward tags when releases occurred. For both groups of scenarios, time-varying natural mortalities

in the operating model were generated using the AR1 process previously described. Time-varying

reporting rates for these scenarios were generated assuming a linear decrease identical to that

described in the Decreasing Reporting Rates group of scenarios. We again tried estimating natural

mortalities and reporting rates as either annual (Rwrd5Ann and Rwrd10Ann), 5-year time blocks

(Rwrd5Block and Rwrd10Block), or constant values (Rwrd5Const and Rwrd10Const). Both the

operating and ITCAAN models assumed annual movement dynamics similar to Vincent et al.

(2017) and tag shedding for all scenarios in this group.

Seasonal Movement

The final group of scenarios investigated the influence of seasonal movement on the performance of

ITCAAN model estimation. Natural mortality was simulated through an AR1 process and reporting

rates were assumed to decrease linearly throughout the time-series. For the operating model, each

year was separated into four seasons that had unique movement matrices (Figure 3.A.2). Movement

rates were chosen to simulate all fish returning to their natal regions at the beginning of the year,

followed by population intermixing increasing throughout the year to a maximum during the third

season, with fish beginning to return to their natal regions to spawn in the fourth season.

Movement was simulated to occur at the beginning of the season after which the fish experienced

region-specific mortality rates. In the operating model, the annual instantaneous mortality rates

were evenly divided between the four seasons and were simulated to occur after movement for each

season. The mixing rate averaged over the year for this scenario was less than the movement rate investigated for all other simulation scenarios (Figure 3.A.2). We again tried estimating natural mortalities and reporting rates either as annual (SeasonAnn), in 5-year time blocks (SeasonBlock), or as constant values (SeasonConst), where mortalities and movement rates were assumed constant within a year. The ITCAAN and operating models incorporated tag shedding and high-reward tags were released every 10 years.

Performance Metrics

The performance of the ITCAAN model was evaluated using percent relative error of estimated model parameters. Percent relative error compares parameter estimates to true values in the operating model by subtracting true values from their estimates, then dividing by the true values and multiplying by 100. The precision and accuracy of total abundance (i.e., abundances summed over all populations), population abundances, movement, natural mortality, and reporting rates are presented here for the sake of brevity; precision and accuracy of other model parameters are presented in the Supplementary Material 3. Parameters not presented either showed no bias in estimates or biases similar to other model parameters, though not always in the same direction. Errors in parameters that were year-specific (i.e. abundance) or age-specific (e.g. selectivity, results in Supplementary Material 3) were calculated for each age or year for each of the 1000 simulations and then aggregated by region or population for summarization and plotting. For example, the boxplots of total abundance show 40000 values (i.e., 40 years of total abundance times 1000 iterations). The interquartile ranges (IQR) and medians of the relative error of the 1000 iterations were used to summarize precision and bias of parameter estimates for the scenarios, respectively.

Results

ITCAAN Model Convergence

Across all simulation scenarios, the average convergence rate of the ITCAAN models was 80%. Among scenarios where natural mortality and reporting rates were estimated annually, the conver-

gence rates were generally greater than 90%, whereas when these parameters were estimated in 5-year blocks the convergence rate was around 70%. The 5-year time block and constant ITCAAN models failed to converge primarily as a result of a maximum gradient larger than 0.05. About two-thirds of the iterations that failed to converge due to a large maximum gradient for the 5-year time block and constant ITCAAN models had maximum gradients that were between 0.05 and 0.1. The inclusion of annual high-reward tag releases increased the convergence rate by approximately 10% (i.e., from 70% to 80%; Table 3.A.1).

ITCAAN Model Performance

Total Abundance

The accuracy and precision of total abundance estimates were affected by the inclusion of high-reward tag releases, the true dynamics of natural mortality and reporting rates, and the parameterization of the ITCAAN model. Across all examined scenarios, median relative errors of total population abundance were between ± 5%, except for the Rwrd5Const, Rwrd10Const, and SeasonConst scenarios (Figure 3.A.3). Tag shedding without the release of high-reward tags (NoRwrdLoss) decreased precision in total population abundance by 1.4 times when compared to the scenario where no tag shedding occurred (NoRwrdNoLoss; Figure 3.A.3). Scenarios that did not simulate high-reward tag releases (NoRwrd Scenarios) resulted in median estimates of total abundance that were negatively biased by 4% and were less precise than scenarios that simulated annual high-reward tag releases. However, the combination of tag shedding and high-reward tag releases (RwdLoss) improved both the accuracy and precision of total population abundances (Figure 3.A.3). Among the scenarios where natural mortalities and/or reporting rates were time-varying in the operating model, the estimation of these parameters as temporally constant (Const) resulted in the most imprecise total abundance estimates compared to when these parameters were estimated annually or in 5-year time blocks (Figure 3.A.3). For the scenario where natural mortality was simulated as time-varying and reporting rate was constant, the estimation of natural mortality

in 5-year time blocks (TVMBlock) resulted in marginally more precise estimates of total abundance compared to annual estimation, though accuracies of the estimation approaches were equivalent. For scenarios where only reporting rates were time-varying, the estimation of annual reporting rates (TVRRAnn) had similar precision compared to 5-year time block estimation, but was slightly more negatively biased (TVRRAnn: median relative error = -1.4%; TVRRBlock: median relative error = -0.88%). Relative errors of total abundance estimates for scenarios where both natural mortalities and reporting rates were simulated by AR1 processes (BothTV) were more similar to the Time-Varying Natural Mortality group of scenarios than to the Time-Varying Reporting Rate group of scenarios. Scenarios that simulated the release of high-reward tags at a frequency of either 5 years or 10 years and estimated reporting rates and natural mortalities as temporally constant in the ITCAAN model had large imprecision and positive median bias in total abundance estimates greater than 10% (Figure 3.A.3). Simulating the movement as a seasonal process resulted in relative error in total abundance estimates similar to Rwrd10 scenarios (Figure 3.A.3).

Population Abundance

Estimates of population abundances were more biased and imprecise compared to estimates of total abundance. Median estimates of abundance for the largest population (i.e., population 2) were negatively biased across all scenarios, except for the SeasonConst scenario, while estimates of abundance for all other populations were positively biased (Figure 3.A.4). The largest bias and imprecision in abundance estimates for populations 2 and 3 manifested when tag shedding occurred and no high-reward tags were released (NoRwrdLoss) and was similar to the scenario where high-reward tags were released every 10 years and natural mortality and reporting rate parameters were estimated as temporally constant (Rwrd10Const). Bias and imprecision in all populations were halved when high-reward tags were released annually (RwrdLoss) compared to when no tags were released and tag loss was present (NoRwrdLoss). Simulation of time-varying natural mortality and/or reporting rates resulted in marginally less precise estimates compared to the tag shedding and high-reward tagging scenario for all populations. Within the same simulation type

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when high-reward tags were released annually, the median relative error of estimates were similar between the three ITCAAN parameterizations, though constant estimation of natural mortality and reporting rate was less precise (Figure 3.A.4). Estimation of reporting rates and natural mortalities as temporally constant generally resulted in increased bias and imprecision of population abundance estimates, especially for populations 2 and 4 when high-reward tag releases were less frequent than annual (Rwrd5Const and Rwrd10Const scenarios). However, median relative error in abundance estimates for population 2 when estimating constant reporting rates and natural mortalities with high-reward tags released less frequently than annual (Rwrd5Const and Rwrd10Const) were less biased compared to annual and block estimation, though estimates were two times as imprecise. As the frequency of high-reward tag releases decreased, the bias and imprecision for all population abundance estimates increased for annual and block parameterizations of reporting rates and natural mortalities. Population abundance estimates were the most precise and accurate when movement and other dynamics were simulated in four seasons, except for population 2 when natural mortality and reporting rates were estimated as temporally constant (Figure 3.A.4).

Movement Rate

Movement estimates were precise and accurate for most scenarios investigated. A marginal decrease in precision in movement estimates was observed for all regions when tag shedding occurred and no high-reward tags were released (NoRwrdLoss) compared to the scenario without tag shedding and no release of high-reward tags (NoRwrdNoLoss). Conversely, the scenario that incorporated tag shedding and annual releases of high-reward tags (RwdLoss) had precision similar to the scenario where no reward tags were released and no tag loss (NoRwrdNoLoss; Figure 3.A.5). Simulation of natural mortality or reporting rates through AR1 processes had little influence on movement estimates, though these parameters were estimated as constant in the ITCAAN model, movement rate estimates were marginally less precise (TVMConst, TVRRConst, and BothTVConst) compared to scenarios when natural mortality and reporting rate parameters were estimated annually or in 5-year time blocks. Movement rate estimates with linearly decreasing reporting rates and natural

mortalities and reporting rates estimated annually or in 5-year time blocks (DecrRRAnn and DecrRRBlock) were similar in precision and bias compared to estimates when natural mortality and reporting rates were simulated by AR1 processes. Median absolute relative errors between 1.7 and 6.1% were observed in scenarios with linearly decreasing reporting rates and constant estimation of natural mortality and reporting rates (DecrRRConst, Rwrd5Const, Rwrd10Const), where bias was positive in regions 2 and 4 and negative in regions 1 and 3. Precision in movement rate estimates decreased when the frequency of high-reward tag releases decreased to 5 and 10 years for all three ITCAAN parameterizations (Figure 3.A.5). When movement was simulated to occur seasonally in the operating model, movement rate estimates were negatively biased for all populations; median relative errors in movement rates ranged from -0.6 to -8.6% using the seasonal-average movement rate as the true value for calculations. The largest biases under seasonal movement were for movement rates of all populations into regions 2 and 3.

Natural Mortality

Natural mortality estimates were generally accurate, but precision varied by simulation scenario and ITCAAN model parameterization. Median relative error of natural mortality estimates were within ± 1.5% of zero, with the exception of the DecrRRConst, Rwrd5Const and Rwrd10Const scenarios (Figure 3.A.6). Imprecision in natural mortality estimates was 1.6 times larger for the models that incorporated tag shedding (NoRwrdLoss) versus those that did not (NoRwrdNoLoss). Precision of natural mortality estimates was considerably better when high-reward tags were released annually (RwrdLoss) compared to the scenario without high-reward tags (NoRwrdLoss; Figure 3.A.6). The simulation of natural mortality through an AR1 process greatly decreased precision in natural mortality estimates compared to scenarios where natural mortality was simulated and estimated as temporally invariant, although estimates remained relatively unbiased. Estimation of annual natural mortality parameters resulted in imprecision of estimates 1.7 times greater than when natural mortality was estimated in 5-year time blocks (Figure 3.A.6). Simulation of both natural mortality and reporting rates as AR1 processes (BothTV scenarios) resulted in precision and bias

of natural mortality estimates similar to when only natural mortality was simulated as an AR1 process (TVM scenarios). When reporting rates decreased linearly over time, a small negative bias (median relative error = -7.0%) resulted when natural mortalities were estimated as temporally constant (DecrRRConst). A decrease in the frequency of high-reward tag releases caused an increase in imprecision of natural mortality estimates among all ITCAAN parameterizations, and slight changes to accuracy of estimates when natural mortality and reporting rates were estimated as temporally constant (Rwrd5Const and Rwrd10Const; Figure 3.A.6). Seasonal movement dynamics had little influence on the accuracy and precision of natural mortality parameters for the annual and block estimations.

For scenarios where high-reward tags were released less frequently than annually, natural mortality estimates were most precise in years when high-reward tags were released (Figure 3.A.7, Rwrd10Ann scenarios). Additionally, the precision in natural mortalities greatly decreased in the last few years of the time-series when estimated annually. Similarly, precision in natural mortality estimates was worst in the last 5-year time block (Block scenarios). Within a 5-year time block natural mortality estimates in the second, third, and fourth years were generally more precise than the first and last year (Figure 3.A.7). Imprecision and bias in natural mortality was fairly consistent across the time series when this parameter was estimated as temporally constant.

Reporting Rate

Accuracy and precision in reporting rate estimates varied greatly between fisheries, ITCAAN parameterizations, and scenarios. The most precise estimates of reporting rates occurred when high-reward tags were released annually and reporting rates were simulated as temporally constant (RwrdLoss and TVM scenarios; Figure 3.A.6). The largest imprecision and bias in reporting rate estimates occurred when high-reward tags were released every 10 years, reporting rates decreased linearly throughout the time-series, and the ITCAAN estimated reporting rates as temporally constant (Rwrd10Const and SeasonConst). When reporting rates were temporally constant, no high-reward tags were released, and the model did not include tag loss (NoRwrdNoLoss), reporting

rate estimates were biased with the direction of bias inversely related to population size (i.e., negatively biased in region 2, but positiviely biased in other regions). The occurrence of tag shedding amplified the bias and imprecision in reporting rates.

When reporting rates were simulated by an AR1 process, the reporting rate estimates were four times less precise compared to scenarios where reporting rates were temporally constant, though estimates generally remained unbiased (Figure 3.A.6, TVRR and BothTV scenarios). Estimates of reporting rates for commercial fisheries, which were assumed to have lower reporting rates than recreational fisheries in the operating model for each region, were less precise compared to recreational fisheries in the same region for most scenarios and regions. Estimation of annual reporting rates resulted in the most precise estimates of reporting rates when this parameter was simulated by an AR1 process (TVRRAnn and BothTVAnn), whereas estimation of reporting rates as temporally constant were the least precise and most biased (TVRRConst and BothTVConst). When reporting rates were simulated to decrease linearly throughout the time-series, estimation of reporting rates in 5-year time blocks resulted in the most precise estimates (DecrRRBlock, Rwrd5Block, and SeasonBlock); alternatively, estimating reporting rates as temporally constant resulted in the least precise estimates (Figure 3.A.6). However, systematic trends of underestimating the first two years and over estimating the last two years in the 5-year time block were observed for scenarios with linearly decreasing reporting rates (Figure 3.A.8). Temporal trends were consistent between recreational and commercial fisheries, but the level of bias and imprecision varied by fishery (Figures 3.A.6, 3.A.8 and 3.A.9). Region-specific biases in reporting rates when high-reward tags were released less frequently than annually and reporting rates were estimated annually or in 5-year time blocks were similar to estimates for the scenario with tag shedding and no high-reward tags released (NoRwrdLoss). Positive bias in all estimates occurred when reporting rates were estimated as temporally constant and high-reward tags were released less frequently than annually (Figure 3.A.6). Precision and bias of reporting rate estimates did not appear to be influenced by seasonal movements.

Discussion

Simulation studies are beneficial for testing how well assessment models can estimate parameters of interest. Additionally, simulations can test how sensitive models are to violations of assumptions, including mismatches between assumed and actual underlying dynamics. While ITCAAN models have been in use since the late 1990s (Maunder 1998, 2001), to date there have been relatively few simulation studies conducted that have explored ITCAAN model performance (Hulson et al. 2011, 2013; Goethel et al. 2015b; Vincent et al. 2017, in preparation). Studies that have been conducted assumed the population and fishery dynamics were relatively simple. Our goal for this research was to improve understanding of ITCAAN model performance by incorporating additional complexities in the simulation analyses and including some mismatches between operating and estimation model processes. We found that inclusion of tag shedding processes in the operating and ITCAAN models decreased accuracy and precision of parameter estimates. Conversely, accuracy and precision of parameter estimates improved with high-reward tag releases, although the frequency that high-reward tags were released did affect ITCAAN model performance. Large biases in abundance estimates were present when the operating model simulated reporting rates as linearly decreasing and natural mortality through an AR1 process, but the ITCAAN model estimated natural mortality and reporting rates as constant. The estimation of an annual movement rate when the underlying movements were seasonal resulted in biased estimates of movement rates, whereas all other scenarios showed unbiased movement estimates. Comparison of the results from our no tag shedding and no high-reward tag releases with results from Vincent et al. (2017) showed similar precision and bias of total abundance estimates, but this study had lower convergence rates compared to when only a single fishery was assumed to operate in each region. Although all simulation models are simplifications of the actual system they are attempting to replicate, previous simulation studies of ITCAAN models may have been oversimplifications. By assuming instantaneous movement occurs once at the beginning of the year, temporally constant natural mortality and reporting rates, and no tag shedding previous simulation analyses of ITCAAN performance likely overestimated the precision and accuracy of parameter estimates.

In our non-seasonal simulations, we assumed that 20% of the population moved to each non-natal region for all scenarios (i.e., 40% of each spawning population was assumed to remain in their natal region). This was the highest movement rate evaluated in the simulations conducted by Vincent et al. (2017) and resulted in the largest bias and imprecision in abundance estimates from the ITCAAN model. We chose this high movement rate partly to determine whether the incorporation of high-reward tags could remove bias observed in population estimates and reporting rates. Similar to the results from Vincent et al. (2017), the ITCAAN model generally overestimated population abundances for the less productive population and underestimated the population abundance for the most productive population (i.e., region 2). Accuracy was improved with annual releases of high-reward tags, but some bias was still evident. Therefore, fisheries scientists should keep in mind that even when attempting to account for the intermixing of stocks in an ITCAAN model, small populations may be overestimated and at risk of overharvest if populations are of very different size and intermixing rates are high. Accuracy in estimates for smaller populations may be improved by including fishery independent survey data that capture juvenile fish as a metric of recruitment in each region. Similarly, fishery-independent surveys that measure catch per effort while the fish are separated by population during spawning could improve estimation. Non-extractive sampling methods, such as cameras or hydroaccoustic methods may be ideal methods to provide such data to limit interference with reproduction. Whether an ITCAAN model, a spatially aggregated catch-at-age model, or independent catch-at-age models provide better management advice will ultimately depend on the specific scenario and we recommend conducting a management strategy evaluation (Butterworth and Punt 1999; Punt et al. 2001).

Simulating movement in four seasons affected the estimation of movement and individual population abundance, but did not have a large influence on total abundance estimates. The bias in individual population abundance estimates was reduced likely due to the lower average emigration rate (Vincent et al. 2017). The movement rates were generally underestimated compared to the annual average and were much lower compared to peak mixing rates. In general, this seasonal movement scenario showed that the ITCAAN model is sensitive to how movement is simulated in the

operating model. This also suggests that previous analyses of ITCAAN models may overestimate the precision and accuracy of movement rate estimates in ITCAAN models (Hulson et al. 2011, 2013; Goethel et al. 2015b; Vincent et al. 2017). Given that the magnitude of movement rates assumed in the operating model can influence ITCAAN model performance, it is difficult to determine whether seasonal movement would ultimately result in greater imprecision or bias in parameter estimates of interest to managers such as abundance and mortality rates. Further investigation of ITCAAN model sensitivity to the assumed movement dynamics is required. Additionally, how ITCAAN model performance changes as a result of seasonal movement paired with fishing mortalities that are not evenly divided between seasons is an area of needed research. Investigation of ITCAAN sensitivity to other methods that simulate the intermixing of fish beyond multiple box-transfer processes are recommended, such as individual (or agent) based models (Railsback et al. 1999; Scheibe and Richmond 2002).

When high-reward tags were released annually, estimates of total abundance were generally unbiased and much more precise compared to estimates without this data when simulated as temporally constant. Similarly, bias in total abundance and population abundances increased as the frequency of high-reward tag releases decreased. Therefore, we recommend that high-reward tags be released annually to provide accurate estimates of reporting rates thereby providing more accurate and precise estimates of population abundance. Imprecision and bias in total abundance estimates were largest under scenarios where linear trends in reporting rates were not accounted for. We recommend that applications of ITCAAN models attempt to estimate reporting rates as either annual parameters or in time blocks and estimate natural mortality in time blocks. The size of these time blocks should coincide with the release of high-reward tags throughout the time-series, when releases occur less frequently than every 5-years. Additionally, a larger time-block for the terminal years of the model for natural mortality is recommended because parameter estimates were highly uncertain at the end of the time-series. We recommend avoiding the estimation of reporting rates and natural mortality as temporally constant, when possible, as large biases in abundance estimates are likely to occur in the presence of temporal trends.

Estimation of natural mortality within a statistical catch at age model has been shown to be possible through simulations (Wang 1999; Wang and Liu 2006; Lee et al. 2011; Johnson et al. 2015; Vincent et al. 2017); however, the estimation of this parameter in assessment models remains a controversial topic (Francis 2012). The estimation of natural mortality in catch-at-age models may be affected by recruitment variability, the selectivity pattern, and the fishing mortality history (Fu and Quinn 2000; Wang and Liu 2006; He et al. 2011; Lee et al. 2011). When estimated, natural mortality is commonly assumed to be temporally constant within the model (Wang 1999; Wang and Liu 2006; Lee et al. 2011; Johnson et al. 2015), except see Jiao et al. (2012). The results of this simulation analysis showed that the incorporation of tag-recovery data could assist the estimation of time-varying natural mortality, where a 5-year time block provided the most precise estimates. The results of this simulation also suggest that the variability of natural mortality has a larger influence on the accuracy and precision of ITCAAN model abundance estimates compared to the variability of the reporting rates. This simulation study did not evaluate the impact or estimation of age- or region/population- specific natural mortalities within the ITCAAN model and additional evaluation of the estimability and importance of such rates relative to temporal variability are required. Estimation of natural mortality as temporally constant or as non-stationary in catch-at-age and ITCAAN models will likely remain a debated topic as uncertainty in real data are likely greater than simulation analyses depict, which can make the estimation of reporting rates and natural mortalities in an ITCAAN model difficult to estimate regardless of the parameterization. Therefore, simulation analyses should attempt to investigate a wide range of assumptions and uncertainties to provide a holistic understanding of accuracy and precision in assessment methods.

A variety of assumptions were made when conducting this research and it is important to consider our results in the context of these assumptions. In our simulations, we did not account for tagging-induced mortality, although it is reasonable to expect that its consequences would be similar to that of tag shedding. We also assumed that the rates of tag shedding in the operating model were precisely known and the exact values could be incorporated in the ITCAAN model. In actuality, tag shedding rates will never be known precisely and errors in tag shedding rates would

be anticipated to affect accuracy and precision of ITCAAN model estimates. We additionally assumed that dynamics of the tagged cohorts matched the at-large population. Future research examining the consequences of a mismatch between the dynamics of the tagged cohorts and the at-large populations would be beneficial for diagnosing whether such a mismatch occured with real data. The variance ratios of catch data relative to the survey data were assumed known. The results of this study may be subject to change if the models were tuned to the data and the weightings of the data sources differed from the simulated true dynamics (Maunder and Wong 2011; Johnson et al. 2015). Previous simulation analyses have assumed the effective sample size of tag recovery data was equal to the age composition with a value of 100 (Goethel et al. 2015b) or equal to the number of tags released (Vincent et al. 2017, in preparation). The weighting of tagging data, presumed either implicitly or explicitly, relative to other data sources and the assumed distribution of tag-recovery data (Maunder 2001; Hulson et al. 2011, 2013; Goethel et al. 2015b; Vincent et al. 2017) in ITCAAN models is an area of research that should be conducted. Finally, the operating model and ITCAAN model were created with the same number of populations and harvest regions, which may not be a realistic assumption for real fish populations. Therefore, we recommend additional investigations into the influence of incorrectly identifying the number of populations within an ITCAAN model.

In conclusion, tag-shedding will reduce the precision of parameter estimates even when this process is correctly accounted for in the ITCAAN model. The inclusion of high-reward tag releases in an ITCAAN model will increase the precision and accuracy in parameter estimates, especially if released annually. Population abundance estimates were less biased when high-reward tag-recovery data were incorporated into the ITCAAN model, but bias was still present under the high intermixing rates simulated. Imprecision and bias in natural mortality and reporting rate parameters increased with lower frequency of high-reward tag releases, especially when estimated as temporally constant. Therefore, we recommend that high-reward tags be released as frequently as possible to increase the precision of model estimates. The estimation of natural mortality performed best when estimated in 5-year time blocks, whereas reporting rates estimated through a logit transformed random-walk

process and as 5-year time blocks performed best under different assumption of the true reporting rate. We suggest estimation of time-varying natural mortality and/or reporting rate parameters be attempted in ITCAAN models. The ITCAAN model underestimated the annual average movement rate when movement was simulated to occur through box-transfer movement over 4 seasons within a year. Other simulation frameworks, such as individual based models, should be evaluated to determine how sensitive the ITCAAN model is to the assumption of movement occuring as a box-transfer process in the operating model. We reiterate the conclusion of Vincent et al. (2017) that ITCAAN models should only be used where spawning stock sizes are similar between populations or intermixing rates in stocks are low to prevent biased population estimates.

Acknowledgments

APPENDIX

Table 3.A.1: Abbreviations used in figures and text, operating and ITCAAN model characteristics, number of iterations need to reach 1000 converged estimates, and convergence rates of the ITCAAN model for investigated scenarios.

Scenario name	ITCAAN model		Operating model				# needed for 1000 converged	Percent conver-gence	NPD Hessian	Maximum Gradient > 0.05
	Reporting rates	M	High-Reward	Tag Loss	Reporting rates	M				
NoRwrdNoLoss	Const	Const	Never	No	Const	Const	1373	72.8	16	364
NoRwrdLoss	Const	Const	Never	Yes	Const	Const	1362	73.4	12	356
RwrdLoss	Const	Const	Annual	Yes	Const	Const	1216	82.2	28	200
TVMAnn	Const	Annual	Annual	Yes	Const	AR1	1128	88.7	23	115
TVMBlock	Const	Block	Annual	Yes	Const	AR1	1229	81.4	24	210
TVMConst	Const	Const	Annual	Yes	Const	AR1	1261	79.3	26	244
TVRRAnn	Annual	Const	Annual	Yes	AR1	Const	1077	92.9	67	76
TVRRBlock	Block	Const	Annual	Yes	AR1	Const	1399	71.5	21	385
TVRRConst	Const	Const	Annual	Yes	AR1	Const	1209	82.7	18	198
BothTVAnn	Annual	Annual	Annual	Yes	AR1	AR1	1086	92.1	70	83
BothTVBlock	Block	Block	Annual	Yes	AR1	AR1	1375	72.7	25	363
BothTVConst	Const	Const	Annual	Yes	AR1	AR1	1236	80.9	29	214
DecrRRAnn	Annual	Annual	Annual	Yes	Decr	AR1	1057	94.6	56	55
DecrRRBlock	Block	Block	Annual	Yes	Decr	AR1	1311	76.3	19	299
DecrRRConst	Const	Const	Annual	Yes	Decr	AR1	1201	83.3	18	188
Rwrd5Ann	Annual	Annual	5 Year	Yes	Decr	AR1	1044	95.8	40	43
Rwrd5Block	Block	Block	5 Year	Yes	Decr	AR1	1320	75.8	24	305
Rwrd5Const	Const	Const	5 Year	Yes	Decr	AR1	1200	83.3	14	190
Rwrd10Ann	Annual	Annual	10 Year	Yes	Decr	AR1	1027	97.4	23	21

Table 3.A.1 (cont'd)

Rwrd10Block	Block	Block	10 Year	Yes	Decr	AR1	1396	71.6	21	381
Rwrd10Const	Const	Const	10 Year	Yes	Decr	AR1	1211	82.6	22	198
SeasonAnn	Annual	Annual	10 Year	Yes	Decr	AR1	1162	86.1	12	158
SeasonBlock	Block	Block	10 Year	Yes	Decr	AR1	1469	68.1	6	466
SeasonConst	Const	Const	10 Year	Yes	Decr	AR1	1420	70.4	4	418

[*] **Note:** M = Natural Mortality; NPD = Not Positive-Definite; Const = temporally constant; AR1 = simulated as a first order autoregressive process; Decr= reporting rates decreased linearly over the time-series; and Block = estimation in 5-year time blocks
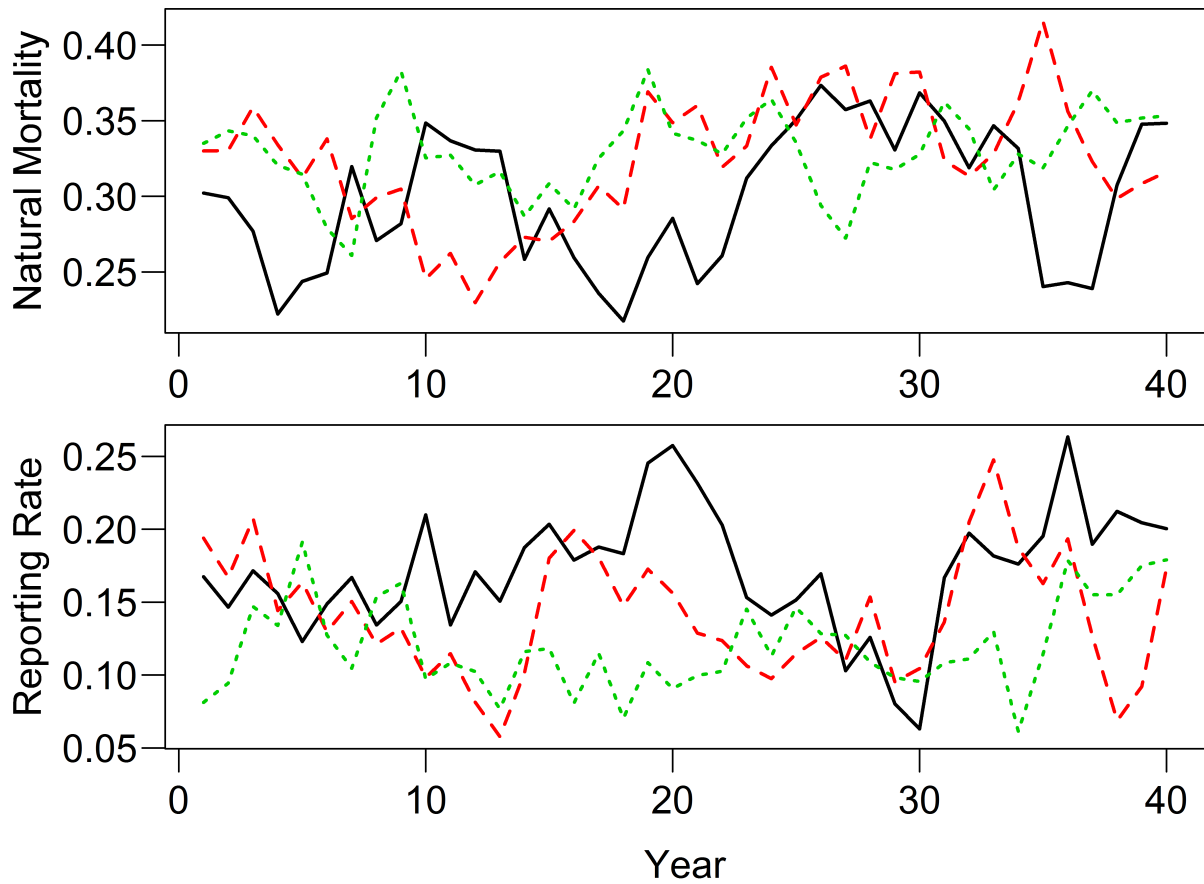
Figure 3.A.1: Examples of annual natural mortalities and reporting rates for the commercial fishery in region 1 simulated by a truncated first-order autoregressive process.

From \To	Reg 1	Reg 2	Reg 3	Reg 4	Reg 1	Reg 2	Reg 3	Reg 4
	Season 1: Spawning				Season 2: Dispersal			
Pop 1	1	0	0	0	0.60	0.25	0.10	0.05
Pop 2	0	1	0	0	0.15	0.60	0.15	0.10
Pop 3	0	0	1	0	0.10	0.15	0.60	0.15
Pop 4	0	0	0	1	0.05	0.10	0.25	0.60
	Season 3: Fully Mixed				Season 4: Return to Spawn			
Pop 1	0.4	0.2	0.2	0.2	0.60	0.25	0.10	0.05
Pop 2	0.2	0.4	0.2	0.2	0.15	0.60	0.15	0.10
Pop 3	0.2	0.2	0.4	0.2	0.10	0.15	0.60	0.15
Pop 4	0.2	0.2	0.2	0.4	0.05	0.10	0.25	0.60
	Annual Average							
Pop 1	0.650	0.175	0.100	0.075				
Pop 2	0.125	0.650	0.125	0.100				
Pop 3	0.100	0.125	0.650	0.125				
Pop 4	0.075	0.100	0.175	0.650				

Figure 3.A.2: Matrices used to simulate seasonal movement and the average annual movement rates for the Season scenario, where the rows are the natal population the fish come from and the columns are the region to which the fish move.
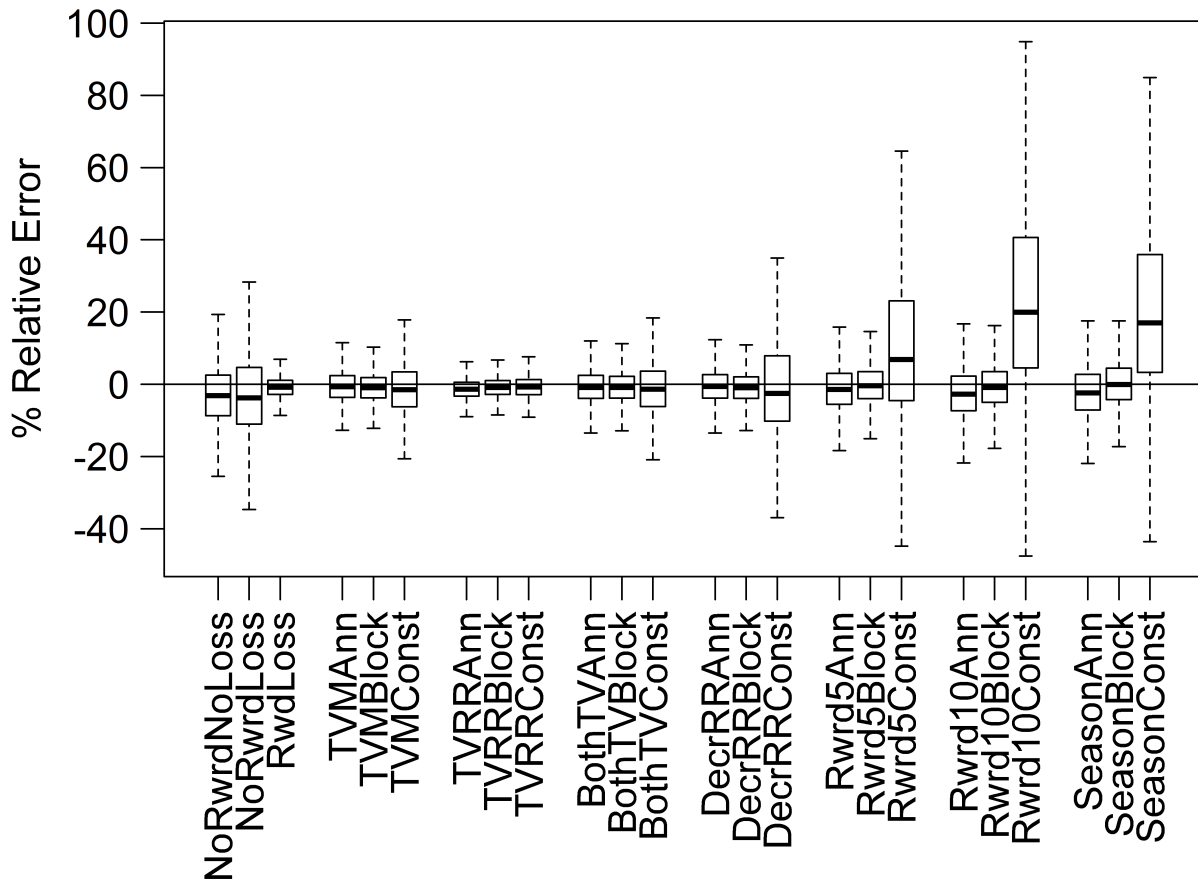
Figure 3.A.3: Relative error (%) of abundance summed across populations for a four region ITCAAN model under differing assumptions of tag loss, frequency of high-reward tag releases, whether movement was simulated annually or seasonally, the true dynamics of natural mortality and reporting rates, and parameterization in the ITCAAN model. Table 3.A.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 relative error, whichever is less extreme. Relative errors outside the whisker range were not plotted.
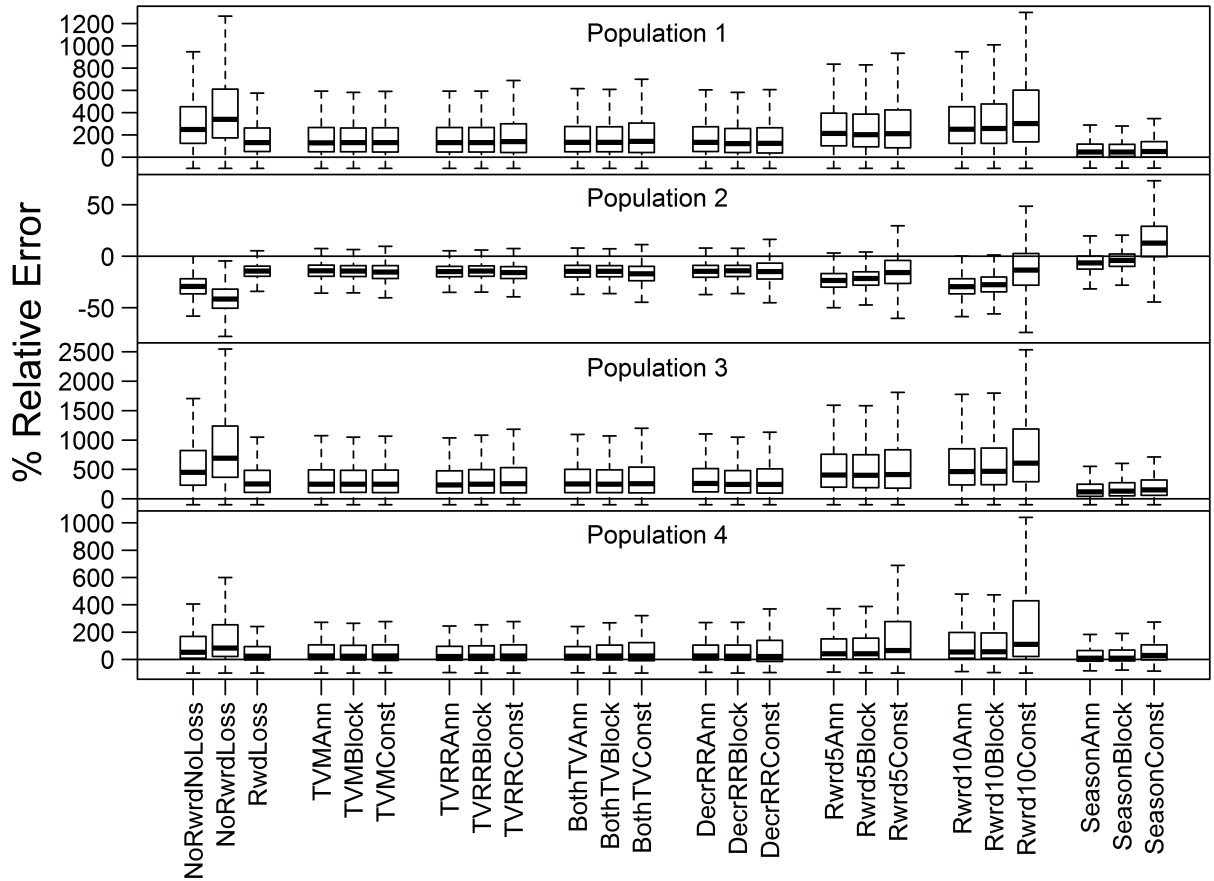
Figure 3.A.4: Relative error (%) of population abundance for a four region ITCAAN model under differing assumptions of tag loss, frequency of high-reward tag releases, whether movement was simulated annually or seasonally, the true dynamics of natural mortality and reporting rates, and parameterization in the ITCAAN model. Table 3.A.1 lists the model abbreviations and corresponding model components. Whiskers on the boxplots extend to 1.5 times the interquartile range or the most extreme relative error, which ever is less extreme. Relative errors outside the whisker range were not plotted.
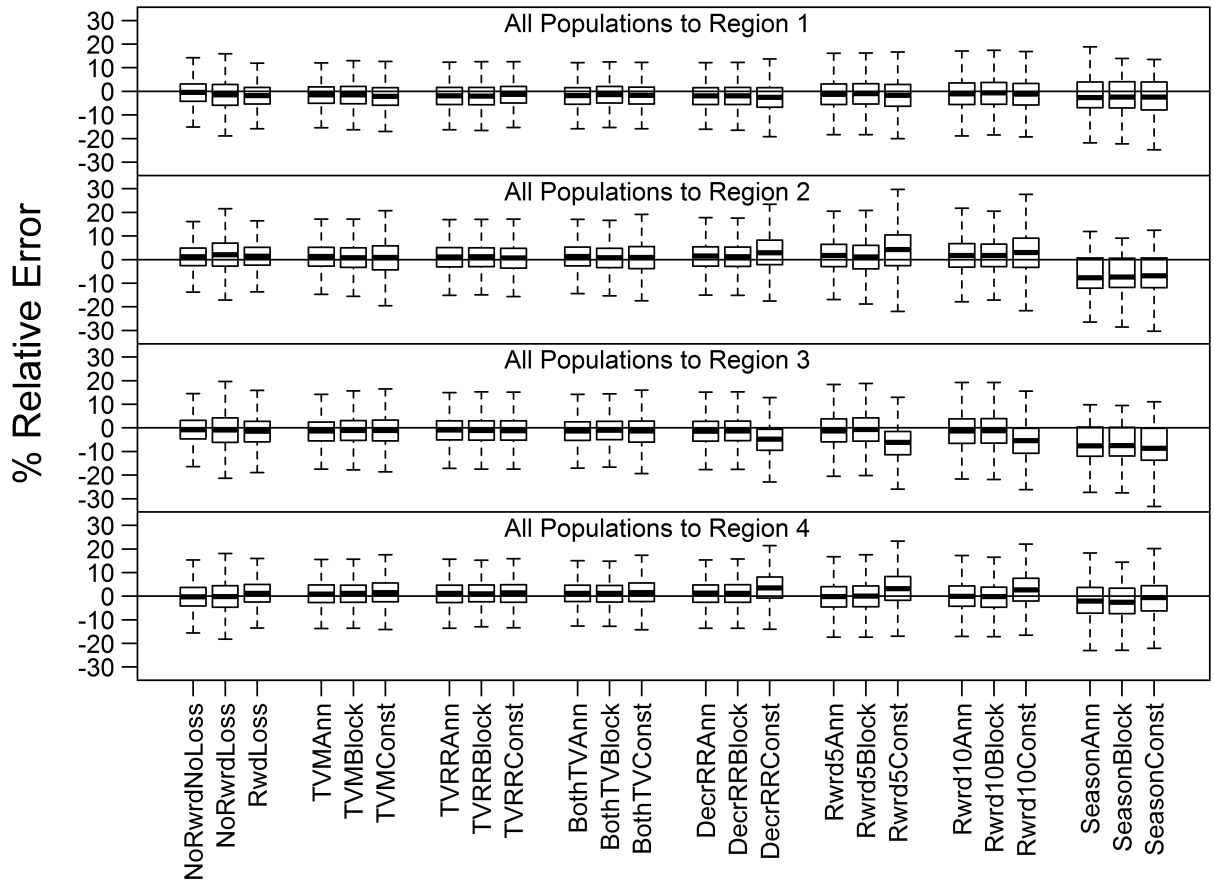
Figure 3.A.5: Same as Figure 3.A.4 but for the movement rate for all populations into the region.
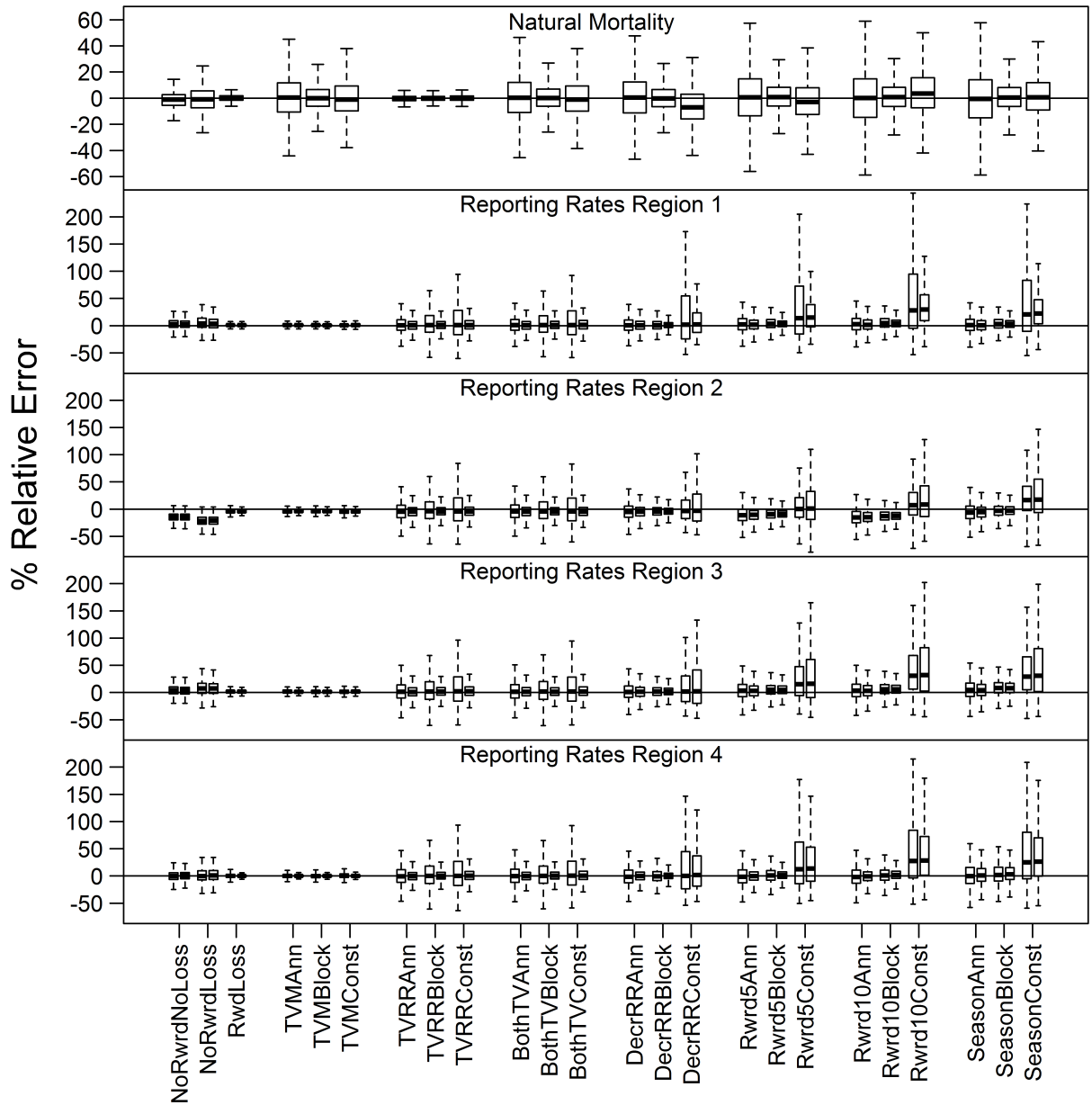
Figure 3.A.6: Same as Figure 3.A.4 but for natural mortality (top plot) and reporting rate parameters (bottom 4 plots), where the boxplot on the left of each pair for the bottom 4 plots is the relative error for the commercial fishery and the boxplot on the right is for the recreational fishery.
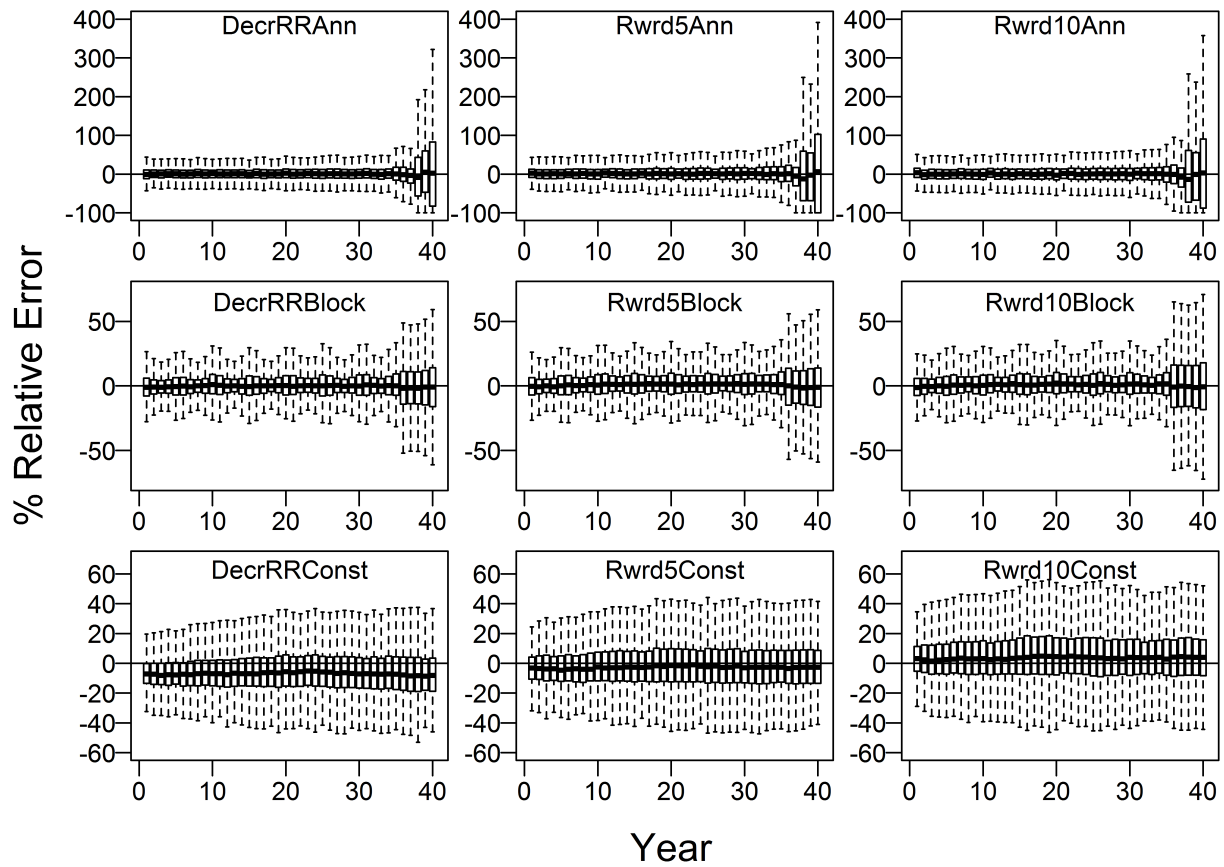
Figure 3.A.7: Relative Error (%) of annual natural mortality for varying frequencies of high-reward tag releases and when natural mortality was estimated annually, in 5-year time blocks, or as temporally constant. Scenario abbreviations and model components are presented in Table 3.A.1. Whiskers on the boxplots extend to 1.5 times the interquartile range or the most extreme relative error, which ever is less extreme. Relative errors outside the whisker range were not plotted.
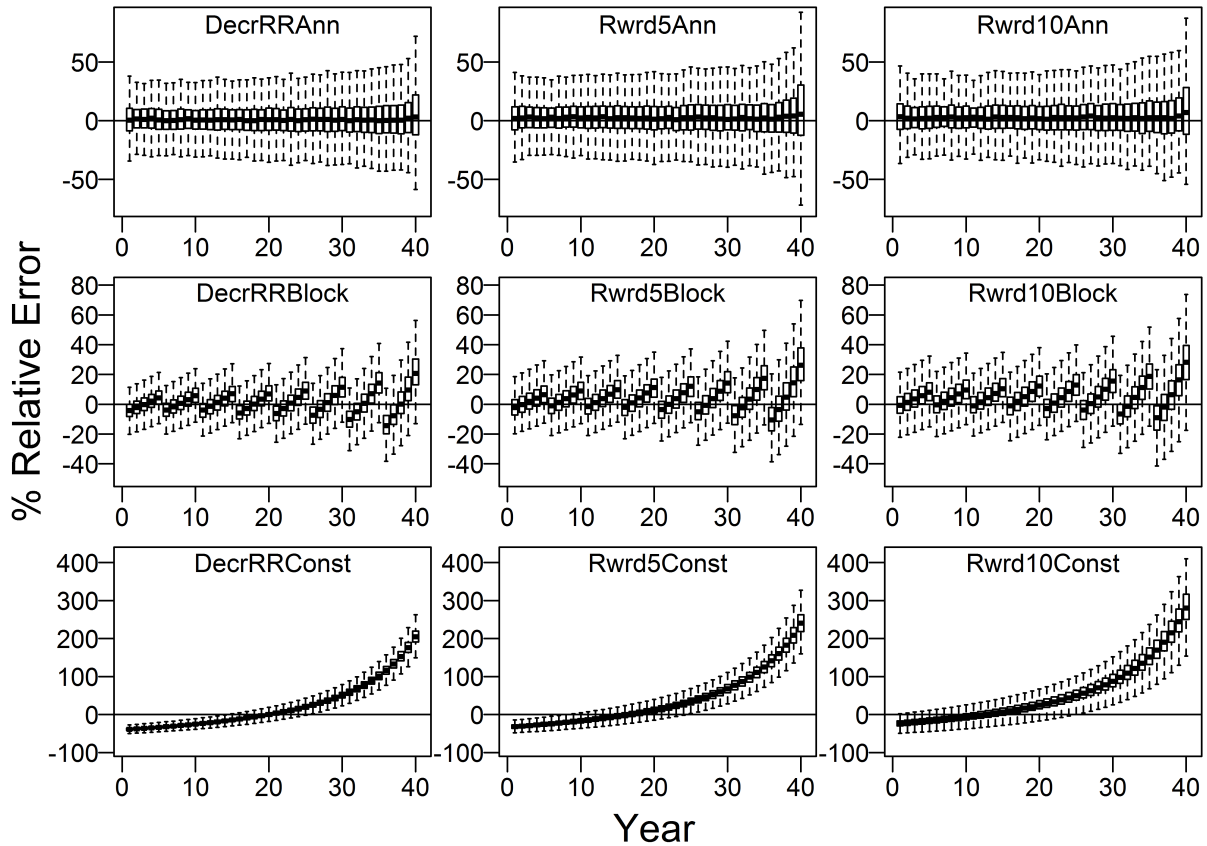
Figure 3.A.8: Relative Error (%) of annual reporting rates of the commercial fishery in region 1 for scenarios where reporting rates were simulated as linearly decreasing and high-reward tags were released annually or every 5 or 10 years, crossed with reporting rates estimated annually, in 5-year time blocks, or as temporally constant. Scenario abbreviations and model components are presented in Table 3.A.1. Whiskers on the boxplots extend to 1.5 times the interquartile range or the most extreme relative error, which ever is less extreme. Relative errors outside the whisker range were not plotted.
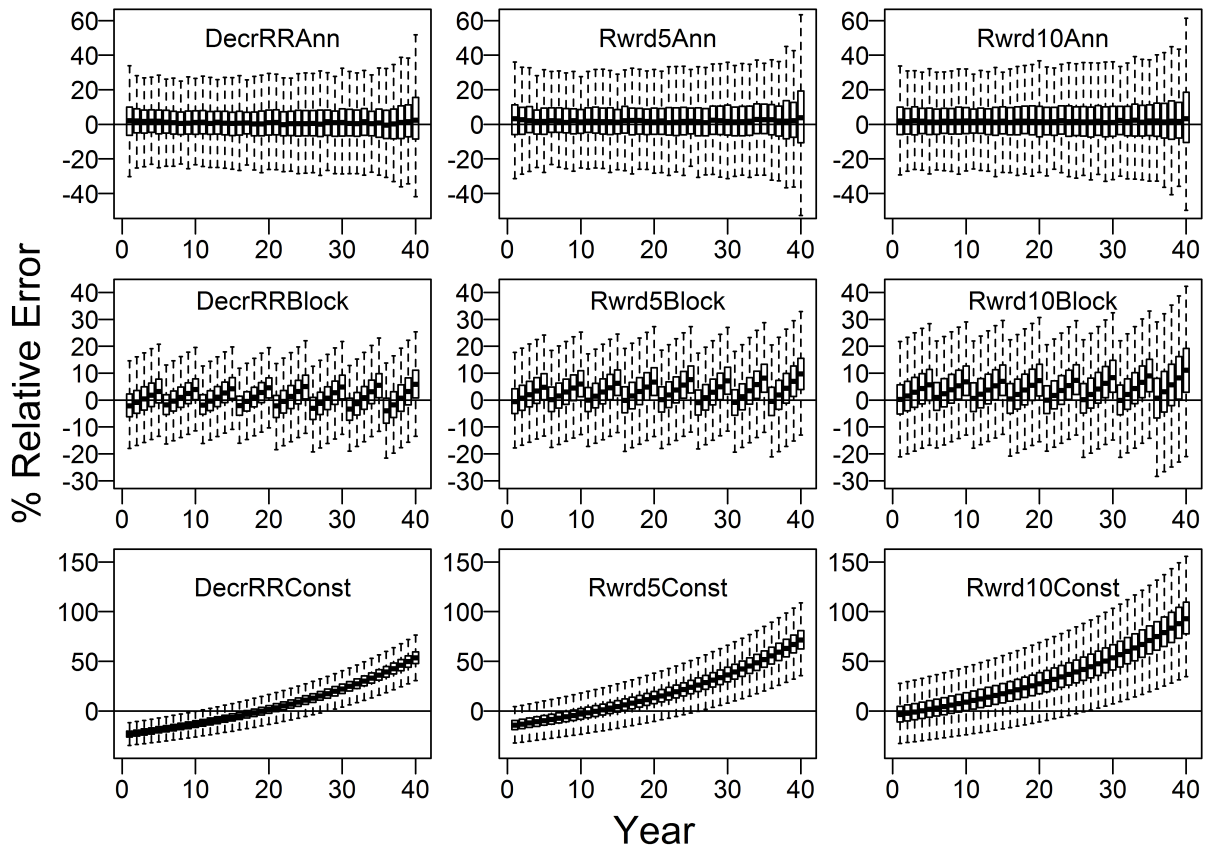
Figure 3.A.9: Same as Figure 3.A.8, but for the recreational fishery in region 1.

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CHAPTER 4

A MULTI-REGION INTEGRATED TAGGING CATCH-AT-AGE ANALYSIS OF LAKE ERIE AND HURON WALLEYE

Abstract

Walleye (*Sander vitreus*) are economically important piscivores in the Laurentian Great Lakes. This species exhibits long distance migrations between spawning sites and feeding grounds and intermixing among spawning populations occurs frequently. Movement of walleye from the western basin of Lake Erie into Lake Huron and the eastern basin of Lake Erie has been shown through tagging, telemetry, and genetic studies. The contribution of walleye from the western basin of Lake Erie to harvest in these other regions has been identified as potentially problematic for management; consequently, assessment methods that can account for the intermixing of walleye to provide management advice are sought. Integrated tagging and catch-at-age analyses (ITCAAN) models are an assessment approach intended for estimating the dynamics of intermixing populations, including the natural mortality of populations and reporting rates of fisheries. We applied a three-region ITCAAN model to walleye in Lake Huron, the western and central basins of Lake Erie, and the eastern basin of Lake Erie for the time period 1993 to 2015. The ITCAAN tag-recovery data were from a jaw-tagging study conducted on Lakes Erie and Huron starting in 1993 and lasting through 2007 in the eastern basin of Lake Erie (ELE), 2010 in the western basin of Lake Erie (WLE), and 2015 in Lake Huron (HUR). The ITCAAN model incorporated harvest, effort and age-compositions from the fisheries, fishery-independent survey catch per effort and age compositions, tag recoveries by fisheries, and age-0 trawl catch in WLE to estimate movement, abundance, reporting rates, fishing mortalities and regional natural mortalities. To produce a fit to the data with no apparent biases in residuals and reasonable parameter estimates, we assumed a temporally constant reporting rate across all recreational fisheries and reduced the weighting of tag-recovery data. Estimates of natural mortality were within reasonable ranges, though the reporting rate for the

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recreational fisheries was higher than estimates from previous studies. For Lake Huron, estimates of natural mortality (0.24) and abundances from the ITCAAN model closely matched estimates from assessment models used to provide management advice. For WLE, the estimates of natural mortality (0.15) and abundance were lower compared to the current assessment. ITCAAN model abundance and natural mortality estimates for ELE were higher than the current assessment model that did not account for movement. Additionally, the ITCAAN model estimated abundance in ELE to increase following a high recruitment in 2005, where as the current assessment estimated abundance to return to abundance prior to the large recruitment. We recommend that future tagging studies involving walleye in Lakes Huron and Erie include high-reward and double-tagged fish to provide accurate estimation of both reporting rates and tag shedding, which ultimately should improve estimates of natural mortality and population abundance.

Introduction

An integral component of sustainable management of harvested fish species is accurate estimation of current and historic population abundance and exploitation (Quinn and Deriso 1999). Abundance estimates allow for estimation of the productivity (i.e. stock-recruitment relationship) of fishery stock, which in turn can be used to determine harvest regulations. The estimation of population size and productivity is difficult when multiple populations intermix during periods of harvest (Goethel et al. 2011). Throughout this paper we will refer to a population as an interbreeding group of fish that reproduce in a self-sustaining manner with similar life history characteristics. A stock will be referred to as fish within a defined harvest area (Cadrin et al. 2004), such as a management unit. Therefore, an intermixed stock is composed of multiple populations that are harvested in the same region. Incorrect estimation of abundance and productivity can easily lead to populations being overexploited. When intermixing rates are high, less productive stocks are susceptible to overharvest if management actions and assessment methods do not account for the spatial dynamics of the species (Ying et al. 2011; Guan et al. 2013; Hulson et al. 2013; Molton et al. 2013; Li et al. 2014). The collapse of some economically important fish stocks has been partly

attributed to inadequately accounting for the spatial dynamics that arise from movement, such as Atlantic cod (*Gadus morhua*; Fu and Fanning 2004; Hutchinson 2008) and many Pacific salmon populations (*Oncorhynchus* spp.; Morishima and Henry 1999). Therefore, the incorporation of spatial dynamics into population assessment models may be a critical component of sustainable management when populations intermix.

Walleye (*Sander vitreus*) are economically important native piscivores in the Laurentian Great Lakes that spawn in rivers and shallow reef complexes. Walleye are typically considered to exhibit spawning-site fidelity (Crowe 1962; Hayden et al. 2014), although genetic and telemetry studies have shown some straying and interbreeding can occur (Stepien and Faber 1998; Strange and Stepien 2007; Brenden et al. 2015; Hayden et al. 2017). In Lake Erie, the majority of recruits to the western and central basin are believed to come from the Maumee and Sandusky Rivers and the mid-lake reef complex (Busch et al. 1975). Spawning populations of walleye in the Thames River, Ontario and Tittabawassee River, Michigan contribute large amounts of individuals to the populations in Lake St. Clair and Lake Huron, respectively (McParland et al. 1999; Fielder and Bence 2014). Van Buren Bay and Grand River, Ontario are major spawning locations in the eastern basin of Lake Erie (Stepien and Faber 1998; Strange and Stepien 2007). Despite these local spawning populations, individuals from the western basin of Lake Erie are believed to compose a significant proportion of the harvested stock in both Lake Huron and the eastern basin of Lake Erie (McParland et al. 1999; Haponski and Stepien 2014; Brenden et al. 2015). Long distance movement by walleye between interconnected lakes has been shown in Lakes Erie and Huron (Wang et al. 2007; Zhao et al. 2011; Hayden et al. 2014; Vandergoot and Brenden 2014) and elsewhere (Smith et al. 1952; Rasmussen et al. 2002; Herbst et al. 2017). The dispersal characteristics of walleye has been identified as a potentially vexing problem for the management of this species, as fisheries may be dependent on spawning populations that are not under the jurisdictional authority of managers (Brenden et al. 2015; Herbst et al. 2016).

The two largest fisheries for walleye in the Great Lakes are in Lakes Erie and Huron (Baldwin et al. 2009). In 2000, harvest of walleye in Lake Erie was worth $9.8 million in dock-side value from

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commercial fisheries, which does not account for the economic value of the recreational fishery (Baldwin et al. 2009). The recreational fishery for walleye in Ohio during 2013 was estimated to generate $67 million in total direct expenditures (Sohngen et al. 2015). Management of walleye in Lake Erie is currently facilitated by the Great Lakes Fishery Commission, which was formed by the 1954 Convention on Great Lakes Fisheries between the United States and Canada. Specifically, a walleye management plan was developed by the Lake Erie Percid Management Advisory Group, which integrated stakeholders, fisheries managers, agency fishery biologist and stock assessment scientists. The Walleye Task Group (WTG) is a sub-committee of the Lake Erie Committee (LEC), which consists of fisheries scientist from state, provincial and federal agencies responsible for the management of walleye in Lakes Erie and St. Clair and connecting waters. The WTG provides annual harvest recommendations to the LEC based on assessment estimates of population status and the harvest control rules set forth by the management plan. The LEC determines the annual total allowable catch (TAC), with harvest quotas then allocated to individual jurisdictions based on surface area (Wills et al. 2016). The four U.S. states (Michigan, New York, Ohio, and Pennsylvania) and the Canadian province (Ontario) manage the harvest of walleye through regulations specific to their jurisdiction. The current assessment model (Wills et al. 2016) estimates the abundance of the stock in the western and central basins of Lake Erie, hereafter WLE (Figure 4.A.1). This assessment does not account for the intermixing of populations from other regions or the emmigration of walleye out of this region. Although the contribution of WLE walleye to the harvest in the eastern basin of Lake Erie (hereafter ELE) is acknowledged, the assessment model of ELE walleye does not explicitly account for immigration of WLE walleye and is not formally used to set harvest policies in this region. Previous research has attempted to estimate the population in ELE and account for intermixing of fish from different populations (Zhao et al. 2011). The assessment model for Lake Huron walleye attempts to account for the immigration of western basin walleye by incorporating abundance estimates from the WLE walleye assessment and the 3-year average of annual proportion of jaw tags recovered in Lake Huron from the western basin of Lake Erie (Fielder and Bence 2014). However, jaw-tagging of walleye in WLE has not occurred since 2010 and recent recoveries are

infrequent. Previous attempts to integrate tag-recovery data into the assessment model for Lake Huron ultimately resulted in the selection of the model that did not incorporate this data (Fielder and Bence 2014). The three assessment methods currently used to provide management advice do not fully account for movement of walleye between management boundaries and assume natural mortality is known. Therefore, assessment models that attempt to estimate natural mortality and intermixing of populations may be useful for management of walleye in Lakes Erie and Huron.

Integrated tagging and catch at age analysis (ITCAAN) assessment models were developed to account for the spatial dynamics of intermixing populations that result from fish movement (Maunder 2001; Goethel et al. 2011, 2015a; Fielder and Bence 2014; Vincent et al. 2017). IT-CAAN models combine the information from tag-recovery studies, fishery-independent surveys, creel surveys, and commercial harvest monitoring to estimate the movement, mortality rates, and abundance of multiple populations. A traditional stock assessment model estimates the size of the stock within management boundaries defined by the data collected. By accounting for the movement dynamics and intermixing of populations, ITCAAN models attempt to estimate population abundances rather than the abundances in a region of harvest. Simulation analyses have evaluated the precision and accuracy of ITCAAN model estimates for populations that experience movement dynamics characterized as reproductive mixing (Hulson et al. 2011, 2013; Goethel et al. 2015a) and overlapping populations with natal homing (Vincent et al. 2017). Reproductive mixing occurs when individuals move to a new region and contribute to the reproduction in the new region. Alternatively, overlapping populations with natal homing occurs when populations intermix for portions of the year but return to natal regions to spawn. ITCAAN models were shown to reliably estimate the movement rates, natural mortalities and fishing dynamics under low mixing rates or similar population abundances (Hulson et al. 2011, 2013; Goethel et al. 2015a; Vincent et al. 2017). However, estimates of population abundance and reporting rates were biased when there were large differences in stock size and intermixing rates were high (i.e. the majority of each population left the natal region) (Vincent et al. 2017, in preparation). The ITCAAN model generally overestimated the smaller and less productive populations under conditions of high intermixing, even though the

model accurately estimated the intermixing of populations. An ITCAAN model may be appropriate to use for Walleye in Lakes Erie and Huron because movement between and within Lake Erie and Huron has been shown to be considerable, but the majority of the populations remain in the natal region (Wang et al. 2007; Vandergoot and Brenden 2014). Additionally, there is a trawl survey conducted in WLE targeted at age-0 fish, which may aid in the estimation of recruitment although this is not guaranteed since it is only conducted in one region. Although ITCAAN models may not be a panacea for assessing intermixing populations with spatially complex dynamics, this assessment method can provide alternative estimates to compare against assessments that do not account for movement dynamics of the populations (Goethel et al. 2011; Hulson et al. 2011, 2013; Goethel et al. 2015a). Therefore, accounting for the movement of fish when assessing intermixed populations is difficult, but imperative for the sustainable management of all populations.

The goal of this research was to fit a spatially-explicit ITCAAN model to harvest, survey, age-composition and tag-recovery data from Lakes Erie and Huron. Our intent was to evaluate the utility of estimating population abundances through an ITCAAN model to assist the management of walleye in Lakes Huron and Erie. The population assessment component of the ITCAAN model was largely based on the catch-at-age models used to assess the stocks in Lake Huron, western/central Lake Erie and the eastern basin of Lake Erie. Tag recovery data from jaw-tagged walleye released in Lakes Huron, Erie, and St. Clair and various connected rivers were incorporated assuming the mortality components were identical to the rest of the population.

Methods

Data

Data from fisheries, surveys, and tag-recoveries were separated into three regions: Lake Huron and the Huron-Erie Corridor (HUR), WLE, and ELE. (Figure 4.A.1). The HUR region incorporated the Lake Huron basin and the Huron-Erie Corridor (HEC) north of 42.074 °N (Figure 4.A.1). This boundary was chosen because it is the boundary for the Michigan recreational fishery between the Detroit River and Lake Erie. The WLE region encompassed the western and central basins of Lake

Erie and also included harvest and tag recoveries in the Huron, Sandusky, and Maumee Rivers. The ELE region incorporated harvest data and tag recoveries in the eastern basin of Lake Erie and the Niagara and Grand Rivers (Figure 4.A.1). Walleye harvest, fishing effort, and tag-recovery data between 1993 and 2015 were obtained from Ohio Department of Natural Resources (ODNR), Ontario Ministry of Natural Resources and Forestry (OMNRF), Michigan Department of Natural Resources (MDNR), New York State Department of Environmental Conservation (NYSDEC), and Pennsylvania Fish and Boat Commission (PFBC). A summary of the data availability for each region is provided in Table 4.A.3 and a detailed description of all data sources used in the analysis is provided in Appendix 4.B.

ITCAAN Model

The ITCAAN model assumed there were three harvest regions and three spawning populations (Figure 4.A.1). Though there are multiple spawning locations within each region, we assumed that walleye within a region were sufficiently mixed to be considered a single population. The model assumed that walleye returned to their natal region each year to spawn with 100% fidelity. Abundances of the three populations were estimated by the number of individuals recruiting to the population at age two and the abundance at age in 1993 and projected forward based on estimated mortalities by fitting predicted catch to observed catch data. The model used the general approach for statistical catch-at-age models with auxiliary information outlined by (Deriso et al. 1985) with the inclusion of a box-transfer intermixing process (Goethel et al. 2011). The recruitment for each population was estimated by a random-walk process from the previous year (Equation (4.C.2.1)) and an assumed lognormal penalty on recruitment deviates with a standard deviation of 4 (Equation (4.C.3.1)). The initial abundance for ages 3 through 7 were estimated as an average value with age-specific deviations that summed to zero (Equation (4.C.2.2)), which were assumed to be lognormally distributed with a standard deviation of 4 (Equation (4.C.3.2)). Intermixing of the populations was modeled through a box-transfer process (Goethel et al. 2011), which estimated the proportion of the population that moved to each region (Equation (4.C.2.3)).

Movement was assumed to occur instantaneously after spawning at the beginning of the year and was temporally constant. Walleye were modeled to remain in the region for the entire year and were subject to region specific survival (Equations (4.C.2.4) and (4.C.2.5)). Regional survival was modeled by the sum of region-specific natural mortality and total fishing mortality (i.e., summed across fisheries; Equations (4.C.2.6) and (4.C.2.7)).

Fishing mortalities for most fisheries were modeled by estimating annual catchabilities and age-specific selectivity components multiplied by observed fishing effort and an indicator variable, which equaled one if a fishery was active in a region or zero otherwise (Equation (4.C.2.8)).The fisheries modeled by catchability and age-specific selectivity parameters were: the Michigan recreational fisheries in HUR and WLE, HUR trapnet, HUR gillnet, WLE gillnet, Ohio Recreational, ELE gillnet, and the combined NY/PA recreational fishery (Table 4.A.2). For these fisheries, annual catchability coefficients were modeled using a random-walk process (Equation (4.C.2.9)) and selectivity-at-age parameters were estimated relative to an age that was assumed to be fully selected. To adjust for an increase in the minimum legal size in 2004 in the Ohio and WLE Michigan recreational fisheries, selectivity at age two prior to 2004 were estimated as additional parameters. Annual fishing mortalities for the bycatch fishery in Lake Huron were calculated by multiplying the observed fishing effort by an estimated catchability coefficient. The catchability coefficient for the bycatch fishery was assumed to be temporally constant and all ages were assumed to be fully selected to the fishery. Annual fishing mortalities were estimated for the three recreational fisheries in Ontario waters of the three regions and the HEC and all ages were assumed to be fully selected by the fisheries (Table 4.A.2). Catch at age was predicted for each fishery in a region using the Baranov catch equation for the fraction of each population present in the region (Equation (4.C.2.10)). Predicted annual total catch for each fishery was obtained by summing across ages, while the proportion at age were obtained by dividing the catch at age by total catch (Equation (4.C.2.11)).

Fishery-independent surveys were modeled to occur on the mixed stocks within each region at specific times during the year. The surveys for HUR MDNR, WLE OMNRF, WLE ODNR/MDNR, ELE NYSDEC, and ELE OMNRF were assumed to sample the population after it had experienced

8.5/12, 9.5/12, 10/12, 9/12 and 9/12 of the mortality in that year, respectively. Predicted CPE by age were calculated by survey-specific estimated catchability and selectivity-at-age parameters multiplied by the abundance alive for the specific region (Equation (4.C.2.12)). Annual survey catchability coefficients were modeled through a random-walk process (Equation (4.C.2.13)). Total predicted CPE was calculated by summing over ages and proportions at age were obtained by dividing predicted age-specific CPE by total CPE (Equation (4.C.2.14)). The predicted CPE of age-0 walleye by the interagency trawl was calculated by multiplying an estimated annual catchability coefficient by the number of recruits to the fishery at age-2 raised to the power of a scaling factor parameter (Equation (4.C.2.15)). Therefore, the first year of data used by the model for the age-0 trawl was collected in 1991 and compared against estimated recruitment to the fishery at age-2 in 1993. The catchability coefficients of the age-0 trawl survey were estimated using a random-walk process (Equation (4.C.2.15)).

Predicted tag recoveries were calculated using the known number of tags released at age and estimated total fishing and natural mortality parameters that also were used in the catch-at-age components of the model (Equation (4.C.2.16)). In total, there were ten fisheries tracked by the ITCAAN model that recovered tags. The three fisheries in HUR were the Michigan recreational fishery, a combined commercial fishery, and a recreational fishery for tags recovered in Ontario and the HEC. The combined commercial fishery in HUR was modeled as the sum of the mortalities for the Saginaw Bay bycatch, trapnet and gillnet fisheries with a single estimated reporting rate. Tag recoveries in the WLE were assigned to one of four fisheries based on the reported gear of recovery and location of recovery; recoveries in the region by commercial gear were assigned to the WLE gillnet, whereas recreational recoveries were separated between the Ohio recreational, Michigan recreational and Ontario recreational fisheries based on the reported location of recovery and state and international boundaries. In ELE, recovered tagged walleye were caught either by the ELE gillnet fishery, the recreational fishery in Ontario, or the combined recreational fishery for NY/PA. All recreational fisheries in all regions were assumed to share an estimated reporting rate that was temporally constant. Temporally constant reporting rates for the HUR commercial combined, WLE

gillnet, and ELE gillnet fisheries were also estimated. Tag loss was accounted for using parameters estimated by Vandergoot et al. (2012), where each tagging agency had different shedding rates (Table 4.A.1). The formulation of tag retention used in this model was slightly different from that of Vandergoot et al. (2012) because this model predicted number of tags recovered through calculating the number of tags alive each year instead of calculating the recovery probabilities times the number of tags released. Tag retention during the first year of release was calculated by the initial probability the jaw tag was retained multiplied by a half year of chronic tag shedding. Tag retention in all subsequent years after release were assumed to be a full year of chronic tag loss specific to the agency of release (Equation (4.C.2.17)). Tag shedding rates for OMNRF were not estimated by Vandergoot et al. (2012), but this agency used the same tagging technique as ODNR and thus were assumed to have the same shedding rates.

The ITCAAN model was fit by penalized maximum likelihood using ADMB version 11.5 (Fournier et al. 2012). The error structure of observed harvest, survey, and penalties on random-walk parameters were assumed to be lognormally distributed (Equations (4.C.3.1) to (4.C.3.7)). A standard deviation parameter for one data source from each region was estimated as a free parameter (HUR trapnet fishery harvest, WLE OMNFR survey CPE, and ELE OMNRF survey CPE); standard deviations for all other data sources in a region were calculated using assumed variance ratios. Variance ratios for each data source or parameter penalty are presented in Table 4.A.2, which were used to calculate the standard deviation of the likelihood component by Equation (4.C.2.18). We attempted to fit the model based on the ratios of variances estimated by Fielder and Bence (2014), but the resulting model poorly fit the HUR MI recreational harvest data. Therefore, we assigned variance ratios that were on a similar scale as the eastern and western basins of Lake Erie. These ratios were somewhat arbitrary but were assigned based on the confidence in the data source. For WLE, variance ratios were the values used by the WTG as determined from expert opinion by Berger et al. (2012). Variance ratios for data sources in ELE were obtained from the assessment model used by the WTG (Wills et al. 2016). Age compositions for surveys and fisheries in all years were assumed to be multinomially distributed with an effective sample size of 100

(Equations (4.C.3.8) and (4.C.3.9)). This effective sample size was chosen because it was less than the effective sample size predicted by the western basin assessment through iterative reweighting (McAllister and Ianelli 1997) and the sample size of fish aged was greater than this for all years, fisheries, and surveys. The standard and reward tag recoveries by year of release, agency of release, fishery of recovery and year of recovery and tags that were never recovered were assumed to be multinomially distributed (Equation (4.C.3.10)).

We attempted to estimate reporting rates for each fishery, but estimates for the recreational fisheries in New York and Michigan (both Huron and WLE) were consistently estimated to be 100%, which was deemed to be highly unlikley. Therefore, we estimated a single reporting rate parameter for all recreational fisheries that was temporally constant. However, we found that when the effective sample size for the tag-recovery data equaled the number of tags released major discrepancies occurred between observed and predicted values for some data sources (results below). Consequently, we tested multiple weightings of the tag-recovery data by dividing the number of tags released by a weighting factor of 5, 10, 20, or 50. Sensitivity of some parameter estimates to the weighting factor are presented below. Parameter estimates, fits to data, and comparison of abundance estimates to assessment models currently used for WLE and ELE walleye assessments are presented for the ITCAAN model that assumed a tag-recovery weighting factor of 10 because this model resulted in no noticeable bias in all data sources.

Results

The scale of the population abundance estimates were very sensitive to the assumed structure of the reporting rates and the weighting of the tag-recovery data. Reporting rate estimates of 100% for multiple recreational fisheries were determined to be a result of a large number of standard tags recovered in 2003 by these fisheries, but few or no reward tags were recovered from the year 2000 high-reward tag release. Estimates of reporting rates for the WLE and ELE recreational fisheries in 2003 using the method described by Pollock et al. (1991) exceeded 100% (Vandergoot et al. 2012). The ITCAAN model thus fit these data and estimated the reporting for these fisheries near 100%

due to the lack of other high-reward tag releases. By assuming all recreational fisheries shared a common reporting rate the estimated parameter was less than 100%; however, this subsequently resulted in the Ohio recreational harvest being severely underestimated.

The estimated reporting rate for recreational fisheries in all regions was sensitive to the tag-recovery weighting factor, with reporting rates exponentially decreasing as the weighting factor increased in size (Figure 4.A.2). Natural mortalities were also influenced by the tag-recovery weighting factor with estimates for HUR and WLE decreasing as the weighting factor increased. Conversely, natural mortalities for ELE increased as the weighting factor increased. Across the evaluated weighting factors, movement rate estimates from the WLE population to HUR were generally low and inversely related to the tag-recovery weighting factor. Population abundance estimates were also influenced by the tag-recovery weighting factor (Figure 4.A.3). Abundance estimates for the HUR and ELE populations generally decreased as the tag-recovery weighting factor decreased, with the exception of a weighting factor of 50 for the ELE population. Conversely, the estimates of abundance for the WLE population were the lowest for the unweighted tag-recovery data and the highest with a tag-recovery weighting factor of 5. Abundance estimates for the WLE population decreased as the weighting factor increased for factors of 10, 20, and 50 (Figure 4.A.3). Based on the quality of fit to input data sources we chose to use a tag-recovery weighting factor of 10 and all subsequent reported results are based on this weighting factor.

Harvest and survey data were fit well by the ITCAAN model. Observed and predicted fishery-independent survey CPE matched closely, although there was less agreement between observed and predicted values for the western basin age-0 trawl (Figure 4.A.4). Harvest data were not as well predicted as survey data (Figure 4.A.5), but there did not appear to be systematic bias in the residuals for any of the harvest data. Harvest estimates for the HUR bycatch fishery generally decreased throughout the time-series, with the exception of an increase in harvest between 2004 and 2006. Walleye harvest, estimated by tag recoveries only, from the recreational fisheries in Ontario varied greatly between years and ranged between 0 and 155 thousand walleye captured, with an average of 44 thousand walleye per year (Figure 4.A.5). There was little difference in average

number of walleye captured between the Ontario recreational fisheries in HUR, WLE and ELE, but fishing mortality rates varied between the regions. The average apical fishing mortality estimated from tag returns between 1993 and 2015 for the recreational fishery in Ontario waters of HUR and the HEC was 0.0130; average apical fishing mortalities for the Ontario recreational fisheries in WLE and ELE were 0.0023 and 0.0080, respectively. Average apical fishing mortality in HUR was highest for the gillnet fishery (0.02408) followed by the recreational fishery in Michigan (0.08961). The average apical fishing mortality for the trapnet fishery in HUR (0.05057) was more than four times the rate of the bycatch fishery (0.011624). In WLE, the average apical fishing mortality for the gillnet fishery (0.16882) was approximately double that of the Ohio recreational fishery (0.07986) and almost seventeen times larger than the Michigan recreational fishery (0.010252). For ELE, the recreational fishery in New York and Pennsylvania had an average apical fishing mortality (0.05978) more than double that of the gillnet fishery (0.022095).

Selectivity at age for the fisheries varied considerably among the regions (Figure 4.A.6). In HUR, the trapnet fishery was fully selective for age-2 fish and then decreased at older ages, whereas the selectivity of the gillnet and recreational fisheries generally increased with age (Figure 4.A.6). The HUR MDNR survey was nearly fully selective for ages less than 5 but decreased for the oldest ages. For WLE, the fisheries were fully selective for ages 3 and 4, but selectivity declined for older ages. Fishery-independent surveys in WLE were fully selective for age-2 and selectivity decreased as walleye got older. Both commercial and recreational fisheries in ELE had the lowest selectivity for age-2 walleye, with selectivity increasing nearly linearly with age until fully selective for the age 7 and older walleye. The fishery-independent survey by NYSDEC was fully selective for age-2 fish, but ages-4 and older walleye were much less selected by the survey. The OMNRF survey in the ELE region was highly selective for at age 7 and older walleye (Figure 4.A.6).

Natural mortality was estimated to be 0.23 (SE=0.018), 0.15 (SE=0.019), and 0.31 (SE=0.032) in the HUR, WLE, and ELE regions respectively. The reporting rate for the recreational fisheries was estimated to be 58.8% (SE=6.5%). Reporting rates for all commercial fisheries in HUR (0.6%, SE=0.30%), and the commercial gillnet fisheries in WLE (6.4%, SE=0.99%) and ELE (15.4%,

SE=4.63%) were much lower than the estimate for the recreational fisheries. Movement from the HUR population to WLE and ELE was estimated to be 0.25% (SE= 0.20%) and 0.016% (SE = 0.050%) of the population. Movement of walleye from the WLE population to HUR was 3.6% (SE=0.32%) and to ELE was 6.2% (SE=0.89%). Estimates of movement for walleye from the ELE population to WLE was 3.5% (SE =1.5%) and to HUR was 0.12% (SE=0.23%).

Instantaneous total mortality estimates in HUR between 1993 and 2005 were relatively stable between 0.35 and 0.42 year^{-1} for ages 4 and older (Figure 4.A.7). After 2005 the rate of total mortality increased for age 4 and older fish but decreased for walleye ages 2 and 3. The decrease in total mortality on ages 2 and 3 walleye occurred as a result of decreasing fishing mortality by the trapnet fishery from 2005 to 2015. In WLE, mortality varied among ages with the highest mortality on ages 3 and 4. Total mortality estimates in the WLE were highest between 1995 and 2000, relatively low and stable between 2001 and 2011, and increased between 2012 and 2015. Total mortality in ELE was the lowest among the three regions and was greatest on walleye age 7 and older (Figure 4.A.7). Total mortality in the ELE region on the oldest fish generally decreased throughout the time series with a sudden increase during 2006 and 2007 (Figure 4.A.7).

Abundance estimates for the WLE population were nearly an order of magnitude larger than abundance for the HUR and ELE populations (Figure 4.A.8). WLE abundance estimates between 1993 and 2004 were relatively stable around 25 to 30 million walleye followed by a peak abundance in 2005 of 62.6 million walleye (SE = 7.6 million walleye). After the peak in 2005, abundance of the WLE population was estimated to decrease until reaching the lowest abundance at the end of the time series of 15.2 million walleye (SE = 2.2 million walleye). Abundance estimates for HUR and ELE populations were approximately 3 million walleye in 1993 and abundance decreased slightly until 2004. Walleye abundance increased in the HUR and ELE populations between 2005 and 2007, where the abundance for the HUR population peaked at 3.5 million walleye (SE = 0.47 million walleye) and the ELE population peaked at 8.7 million walleye (SE = 1.8 million walleye). Following this increase, abundance of the ELE population was relatively stable, whereas abundance of the HUR population decreased to 2.2 million walleye in 2015 (SE = 0.39 million

walleye) (Figure 4.A.8). Increases in population abundance in 2005 were due to abnormally large recruitment events for both Lake Erie populations, whereas the HUR population experienced multiple years of high recruitment between 2005 and 2007 (Figure 4.A.9).

Agreement in abundance estimates from the ITCAAN model and the assessment models currently used to provide management advice for Lakes Huron and Erie varied depending on the population (Figure 4.A.8). Estimates of walleye abundance age-2 and older for the HUR population were very similar to estimates of abundance from Fielder and Bence (2014). Total abundance estimates by the ITCAAN model for WLE were approximately 20 million walleye less than estimates from the currently used assessment model. The largest difference in the abundance estimates between the two WLE models of nearly 73 million walleye occurred in 2005 at the highest estimated abundance in the time series (Figure 4.A.8). Estimates of total abundance for the ELE population from the ITCAAN model were higher in all years by an average of 600000 walleye compared to the assessment model currently used in that region. Additionally, after the large recruitment in 2005 the general trend estimated by the two models diverged (Figure 4.A.8). The assessment model currently used in ELE estimated an abundance in 2015 of approximately 1.3 million walleye (SE = 0.38 million walleye). Conversely, the ITCAAN model estimated the abundance in the eastern basin in 2015 to remain at abundance consistent with the high recruitment year at nearly 5.2 million walleye (SE = 1.4 million walleye) (Figure 4.A.8). The largest difference in estimated abundance between the two models for ELE of 5.5 million walleye occurred in 2014.

Discussion

The ITCAAN model produced reasonable estimates of natural mortality and reporting rates and no systematic biases in fits to observed data when a single reporting rate was assumed for all recreational fisheries and weighting of the tag-recovery data was reduced by a factor of 10. Estimates of reporting rates from the ITCAAN model differed from a previous analysis (Vandergoot et al. 2012), even though both studies used portions of the same database of tagged walleye for the eastern and western basins of Lake Erie. Vandergoot et al. (2012) estimated reporting rates of 10% for

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the commercial fishery in the western basin, 33% for the recreational fisheries in WLE, and 39% for recreational fisheries in ELE based on model averaging of fits to standard and high-reward tag recoveries tagged in the year 2000. High-reward tag-recovery data that were tagged in 1990 were also used to estimate reporting rates for WLE recreational fishery of 55% and for WLE commercial fishery of 17% (Vandergoot et al. 2012). Though our analysis did not include the high-reward tag release in 1990, the estimate of recreational reporting rate from the ITCAAN model (58%) was closest to estimates for the recreational fishery during this time period. On average, 1650 more tags were released each year in WLE between 1993 and 1999 compared to between 2000 and 2010. Therefore, it is reasonable that the reporting rate is closer to the 1990 estimates than the 2000 estimates. Estimates of reporting rate for the recreational fisheries were more than double the estimate of 24.8% obtained from returns of reward tags by all fisheries from a telemetry study on the Tittabawassee River (Fielder 2014a), but this data were not included in the ITCAAN model. The estimate of reporting rate for the recreational fishery from the ITCAAN model was within the realm of possibility, but was larger than previous estimates for the region (Vandergoot et al. 2012; Fielder and Bence 2014; Fielder 2014a). Reporting rate estimates from the ITCAAN model for the commercial fishery in the western basin (6.4%) were marginally lower compared to estimates by (Vandergoot et al. 2012). The estimate of reporting rate by the ITCCAN model for the combined commercial fisheries in HUR was very low. This low reporting rate was expected given the very low number of returns from commercial fisheries in this region compared to returns by the recreational fishery. Similarly low estimates of reporting rates were obtained from another ITCAAN model for commercial fisheries on yellowtail flounder in the Atlantic Ocean (Goethel et al. 2015a). The reporting rates estimated by the ITCAAN model for the commercial fisheries were relatively stable across the different modeling assumptions explored. The estimation of reporting rates in this model, especially for the recreational fisheries, would greatly benefit from additional years of high-reward tag releases (Vincent et al. in preparation).

Vandergoot and Brenden (2014) analyzed the Lake Erie jaw tag database and estimated age-specific natural mortality and movement rates in Lake Erie for ages 2, 3, 4, and 5 and older. That

analysis used the reporting rates and tag shedding rates estimated in Vandergoot et al. (2012) and assumed that ages 3 and older were fully selected. Estimates of natural mortality for the western basin of Lake Erie ranged between 0.13 and 0.40 and were lowest for the age-5 and older group. Our estimate of natural mortality for the WLE, which was assumed constant over all ages, of 0.15 was most similar to the estimate for ages 5 and older from Vandergoot and Brenden (2014). More than half of the tagged walleye used in the ITCAAN model were age 5 or older, which likely influenced these estimates. The natural mortality estimate from the ITCAAN model in the western and central basin of Lake Erie was less than half of the value used by the current assessment for walleye of 0.32 (Wills et al. 2016). An analysis of tag recoveries in the eastern basin of Lake Erie estimated natural morality for this region to be 0.22 (Zhao et al. 2011). Zhao et al. (2011) used a similar database as what was used in this analysis, but included the recoveries of tagged walleye by NYSDEC during the tagging process every year. Future analysis of Lake Erie walleye ITCAAN models could attempt to incorporate such data. The natural mortality estimate for the ELE region from the ITCAAN of 0.31 was larger than the estimate by Zhao et al. (2011) or the value used in the current assessment of 0.19. There is much uncertainty in the estimate of natural mortality for the eastern basin given that the New York/PA recreational fishery had great difficulty estimating reporting rates below 100% and the large influence of the tag-recovery weighting factor. The estimate of natural mortality from the ITCAAN model for HUR of 0.23 was nearly identical to a constant value of 0.24 used in a sensitivity analysis for Lake Huron (Fielder and Bence 2014). Estimates of natural mortality from the ITCAAN model for all regions were within the realm of plausibility, but varied in terms of agreement with values used in current assessments.

To our knowledge, this is the first ITCAAN model using empirical harvest, survey, and tag-recovery data to estimate both reporting rates and natural mortality parameters within the assessment model. Previous ITCAAN models have assumed natural mortality was known and estimated reporting rates (Goethel et al. 2015b; Punt et al. 2000), assumed reporting rate was known and estimated natural mortality (Eveson et al. 2012b; Siddeek et al. 2016), or pre-specified both natural mortality and reporting rates (McGarvey et al. 2010). The model was sensitive to the

parameterization of the reporting rate and the weighting of the tag-recovery data. Difficulty in estimating reporting rates that were not 100% was due to the small sample size of reward tags, which were only released in 2000. The results of this study show that estimation of reporting rates likely require large sample sizes of high-reward tags released more frequently than once during the time series. Selection of appropriate weighting of the tag-recovery data in a multi-region ITCAAN model is an area of needed research and beyond the scope of this manuscript. However, estimation of weighting of data with conflicting information has been an area of recent research and has been used for size-structured models that integrate tagging information to estimate growth (Punt et al. 2017). Additionally, determination of the effective sample size through various iterative weighting methods for age composition data relative to other data sources has been explored (Truesdell et al. 2017). Such methods could ostensibly be applied to weighting both the tag-recovery and age-composition data simultaneously.

Model Assumptions and Limitations

The ITCAAN model used in this analysis made numerous assumptions and it is important to consider our results in the context of these assumptions. Data for ELE were the limiting factor for this analysis, specifically data from the commercial gillnet fishery in Ontario and the recreational fishery in Pennsylvania. Tag-recovery data in Lake Erie were available starting in 1990 and include high-reward tag releases in 1990. The model may be expanded to include this data, but would require an assumption and extrapolation regarding the harvest of these two fisheries for the period of 1990-1992. No high-reward tags were released in the eastern basin and thus would likely not influence the estimation of reporting rate for this fishery, but releases in other regions may influence the estimation for other recreational fisheries. Creel surveys to measure the recreational effort and age composition of harvest in the Huron-Erie corridor were sporadically available for the time series and thus were not feasible for the model. For this study, the HEC was combined with Lake Huron to match the current Lake Erie assessment and management boundaries. However, a boundary that incorporates walleye in Lake St. Clair with the population in the western basin of Lake Erie is both

possible and plausible (Strange and Stepien 2007). Though a spawning population exists in the HEC (McParland et al. 1999), we did not attempt to estimate this region as a separate population given the lack of available data. Similarly, the central basin of Lake Erie may contain a separate spawning population from the western basin populations, but we did not attempt to estimate its size given infrequent and small quantities of walleye tags released. Therefore, the model structure of the ITCAAN model used in this analysis are reflective of available data and various simplifying assumptions.

The ITCAAN model assumed that movement of walleye was constant across ages and over time. Additionally, the model assumed that movement occurred once during the year instantaneously after spawning. Therefore, estimated movement proportions between the regions are in terms of the proportion of the population that would reside in that region for the entire year. Though the regions of analysis between this study and Vandergoot and Brenden (2014) are not identical, movement estimates from WLE to the other two regions from the ITCAAN with a weighting factor of 10 appear to be lower. This difference in movement rate estimates is in part due to the tag-recovery weighting-factor assumed, given that movement estimates decreased with lower tag-recovery weighting. Simulation analysis showed that when movement occurs as a seasonal process the ITCAAN model generally underestimates the movement rate (Vincent et al. in preparation). Wang et al. (2007) found that mean length at tagging of walleye of western basin Lake Erie origin recovered in the eastern basin of Lake Erie were larger than those recovered in the western basin or Lake St. Clair. They inferred that walleye moving eastward from the western basin were generally older or larger in length at age. However, movement rate estimates for age-2 through 4 were found by Vandergoot and Brenden (2014) to be similar to movements for age-5 and older walleye. Estimates of selectivity at age from the ITCAAN model for the eastern basin suggest that older fish were more vulnerable to fishing in this region, whereas the western basin walleye were fully selected at ages-3 and 4. Such a difference in selectivity could explain the difference in mean size between the regions in the absence of age- or size- based movement. Yet genetic analysis of contributions of Lake St. Clair and western Lake Erie origin walleye to the Saginaw

Bay stock showed that older walleye were found more frequently during the summer than during the late winter and spring (Brenden et al. 2015). Contributions of age-3 and age-4 walleye from the Lake Erie and Lake St. Clair populations were fairly similar among seasons, suggesting that movement may vary seasonally among ages (Brenden et al. 2015). In our preliminary analyses, we attempted to estimate biennial movement when tagging data were available, but estimates became unreasonably high for the eastern basin in some years when the weighting of the tag-recovery data was reduced. These preliminary model fits suggest that movement may vary over time, especially for the western basin. Similarly, Zhao et al. (2011) showed that the movement of walleye from the western basin to the eastern basin was correlated with the total abundance of walleye in the western basin population, suggesting density-dependent movement. Therefore, the assumption that movement is constant over ages, within a year, and among years is a simplification of reality.

There were many assumptions made with regards to the dynamics of tagged walleye. First, we assumed no tagging-induced mortality, which is a common assumption for jaw tagged walleye (Wang et al. 2007; Zhao et al. 2011; Vandergoot et al. 2012; Vandergoot and Brenden 2014). We also assumed that the parameters for the tag shedding process estimated by Vandergoot et al. (2012) were correct. We were required to extrapolate the estimates beyond the time period analyzed by Vandergoot et al. (2012) to account for tag shedding for the entire time series. If the tag shedding rate estimates were higher than the true value then natural mortality rates would be underestimated. We also assumed that the reporting rate was temporally constant across all fisheries and all recreational fisheries shared a single reporting rate. Estimates of reporting rates from a high-reward tag study in 1990 and 2000 in the western basin of Lake Erie showed that reporting rates for the recreational fishery decreased between these two time periods and were different between the western and eastern basin (Vandergoot et al. 2012). An implicit assumption made by this tagging model was that the reporting rate for a fishery was the same for all recovered walleye. It is possible that recovered walleye have a higher reporting for fish that are tagged in a state different from the state in which they are recaptured. For example, recreational fishers in New York may be more inclined to report a tagged walleye from Michigan or Canada because it is a more memorable experience

compared to catching a tagged walleye from New York. We did not attempt to estimate such a formulation of reporting rate as this would increase the number of this type of parameter estimated, which were already poorly estimated. However, if such characteristics of reporting rates do occur it would cause a mismatch between the true dynamics and the estimation model, which could cause estimation problems.

The ITCAAN model assumes that the dynamics experienced by tagged fish and the population at large were the same (Maunder 1998; Goethel et al. 2011). However, the large population of walleye that spawn on WLE shallow water reef complex may not have been adequately represented in the tagging studies. The population of fish tagged in the rivers of Lakes Erie and Huron may have experienced a higher recreational fishing mortality compared to the rest of the population due to easier access to rivers compared to the lake, and potentially lower exploitation by commercial fisheries as they may not be in areas fished commercially as frequently as walleye from the shallow reefs. Additionally, the tagging in these regions occurred mostly on the U.S. side of Lake Erie and tag-recovery data were not available for the Ontario side of the ELE region. Likewise, a catch at-age model for the western and central basin of Lake Erie provided a superior fit to data when the catch-at-age data were modeled with basin specific catchability and selectivity parameters (Berger et al. 2012). However, the ITCAAN model assumed the central and western basin of Lake Erie were a single uniform area. It is possible that the assumption of identical dynamics between the catch-at-age data and the tag-recovery data was violated. We recommend future tagging studies in Lake Erie and Lake Huron be designed to tag walleye that come from a wide variety of spawning locations including the mid-lake reef complexes.

The ITCAAN model assumed a single spawning population occured within each region. Within each of the three model regions there are multiple known spawning locations (McParland et al. 1999; Stepien and Faber 1998; Strange and Stepien 2007), especially within the western basin of Lake Erie such as the Huron, Maumee and Sandusky Rivers, and numerous shallow water reef complexes. There is genetic evidence to suggest that populations intermix to a large degree in the western basin of Lake Erie (Stepien and Faber 1998; Strange and Stepien 2007) and may be a single

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metapopulation, which is often assumed (Berger et al. 2012; Wills et al. 2016). The model assumed that within a region, walleye returned to their natal population with 100% fidelity. This assumption may be realistic for some populations, such as the Tittabawassee River where returns to spawning site of tagging were 95%; however, this assumption may be more tenuous for other populations, such as the Mauamee River where spawning site fidelity was estimated to be 70% (Hayden et al. 2017). The influence of incorrectly identifying the number of spawning stocks within a region or individuals not returning to their natal population with 100% fidelity has not been evaluated within an ITCAAN model and is an area of needed research.

Natural mortalities were estimated as independent parameters for the three regions of the ITCAAN model. This formulation implicitly assumes that the rate of natural mortality is based on the environmental conditions in which the walleye resides. We assumed that natural mortality would be most strongly influenced by the temperature, availability of prey and other characteristics of the region the walleye inhabits. Thus we assumed that natural mortality was not a genetic factor, which would be different between the different populations. The validity of this assumption is uncertain.

The ITCAAN model assumed 100% reporting rate for walleye tagged with high-reward tags. A $100 (USD) reward was offered for the recovery and reporting of high-reward tags, but no analysis has been conducted to determine if this amount is sufficient to elicit a 100% reporting rate. If a reward tagging study, such as described by Taylor et al. (2006), elucidates that the $100 value was insufficient to garner a 100% reporting rate, then estimates of mortality using these data would be biased (Pollock et al. 1991). Tags were occasionally reported by fish processors, implying that the commercial fisher that caught the fish either failed to see the tag or recognized the tag but did not remove it (Vandergoot et al. 2012). Estimates of jaw tag reporting rates have also been obtained by comparing proportion of standard jaw tags returned to proportion of walleye implanted with telemetry tags returned, which had a $100 reward. These walleye are also tagged with an external t-bar anchor or external loop tags that are highly visible (Hayden et al. 2014). Estimates of reporting rates from the acoustic tag studies have been lower for Tittabawasee River (Fielder and Bence 2014)

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and Van Buren Bay (Jason Robinson, NYSDEC pers. comm.) than estimates from the high-reward study in 2000. This difference in reporting rate estimates of jaw-tagged walleye between these studies could be a result of temporal changes in reporting rates or differences in visibility between jaw and other external tags. However, preliminary returns for a 2016 study conducted in the Thames River Ontario of walleye tagged with anchor tags and jaw tags had a higher return rate compared to walleye tagged with only jaw tags (Andy Cook, OMNRF pers. comm.). If the jaw reward tags are reported at less than 100%, this would be violation of a key modeling assumption.

In this analysis we assumed that the incidental catch from the Pennsylvania commercial fishery was a negligible source of mortality for walleye in ELE. Prior to 1996 the commercial fishery in PA was a gillnet operation and the bycatch of walleye was much greater than the current trapnet fishery. Therefore, the estimates of fishing mortality in ELE are an underestimate of the true fishing mortality, especially during the first 3 years of the model. Yet the average harvest from the commercial bycatch by PA between 2010 and 2015 was 770 pounds, which is small compared to other harvests in the region. Additionally, no tags were reported for this fishery indicating that either the fishing mortality was very low or the reporting rate was very low. Therefore, this assumption perhaps was reasonable, but future analyses should attempt to incorporate this source of mortality.

Comparison to Existing Models

The estimates of abundance in HUR of the ITCAAN model matched almost exactly with estimates from the model described by Fielder and Bence (2014). This was a surprising result as the ITCAAN model incorporated the walleye population in the Huron-Erie corridor into the estimates for the rest of Lake Huron. Estimates of abundance from an ITCAAN model that assumed the effective sample size of the tag-recovery likelihood equal to the number of tags released were nearly double the estimates from the currently used assessment. Therefore, there is a large degree of uncertainty surrounding the estimates of population abundance in the Lake Huron and HEC region. Abundance of the ELE population could potentially be overestimated because simulation studies showed that populations that are much smaller than a large population will generally be overestimated by the

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ITCAAN model under high movement rates (Vincent et al. 2017, in preparation). Bias in population abundance estimates increased with an increase in intermixing and at a rate of 10% of the population median relative error in abundance estimates could be as large as 50% for some small populations. Though the model that assumed a weighting factor of 10 for the tag-recovery data estimated movement to be less than 10% from WLE to ELE, the movement rate was highly sensitive to the assumed weighting of the tag-recovery data and previous estimates of movement between these regions were as high as 12% (Vandergoot and Brenden 2014). Additionally, estimates of abundance in the ELE region were larger than estimates from the current assessment. Therefore, we caution against using estimates of abundance in the eastern basin of Lake Erie for management purposes without further exploration of appropriate weighting of the tag-recovery data and parameterizations of the tag reporting rate. Additionally, analyses that incorporate tags recaptured during the tagging process could provide additional information to estimate spawning population sizes (Zhao et al. 2011). Estimates of population abundance for the western basin were much lower compared to estimates from the assessment model used by the WTG (Wills et al. 2016). This difference is attributed to a large difference in the natural morality assumed in the WTG model and that estimated by the ITCAAN model. Estimates of natural mortality in WLE for all weighting factors of tag-recovery data were much lower than the value assumed in the current model used to provide management advice. Therefore, it is highly possible that natural mortality in the western basin of Lake Erie is lower than 0.32.

Management Recommendations

Although the ITCAAN model described in this paper has many assumptions and limitations, insights to the dynamics of walleye in Lakes Erie and Huron can be gained from this analysis. First, in gathering data for this model we identified a general lack of available data from the Huron-Erie corridor region. However, estimated recreational fishery harvest from the HEC was on the same scale as exploitations from the trapnet fishery in HUR. Harvest in this region is not accounted for in assessment models for neither Lake Huron nor western Lake Erie. As a quarter of walleye

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harvested in Saginaw Bay are from populations in Lake St. Clair and western Lake Erie (Brenden et al. 2015) the HEC is an important connection between Lakes Huron and Erie. Management of walleye populations in the region will require additional data in the HEC region to provide accurate estimates of all sources of exploitation. Therefore, we recommend that annual creel surveys be conducted in the Huron-Erie corridor to quantify the recreational fishing harvest and effort by both MDNR and OMNRF.

The reporting and tag shedding rates are necessary components of tag-recovery data to accurately estimate the exploitation and natural mortality rates (Brenden et al. 2010), which in turn will influence abundance estimates (Schnute and Richards 1995; Johnson et al. 2015). Therefore, the design of tag studies to be used in ITCAAN models should include ways to estimate both tag shedding rates and reporting rates. Tag shedding can be estimated through double tagging individuals with the same or different tag types (Fabrizio et al. 1996; Hampton 1997; Vandergoot and Brenden 2014). Reporting rates can be estimated through various methods, including high-reward tags (Pollock et al. 1991, 2001, 2002; Denson et al. 2002; Frusher and Hoenig 2003). Designing tag-recovery studies to allow for estimation of both the reporting rates and tag shedding may be more costly and complex, but is necessary to provide accurate and precise estimates of the mortality rates of the population. As both reporting rates and tag shedding have the potential to change over time, design components of tagging studies to estimate both rates should be included every year that tags are released. We also recommend conducting a study to determine the necessary level of tagging required to illicit a 100% tag reporting rate (Taylor et al. 2006). Similarly, a comparison study of the reporting rates between jaw tags and Floy tags would be beneficial for choosing the higher reported tag. A higher tag reporting would yield a more accurate estimate of exploitation, natural mortality, and ultimately population abundances. However, given that tagging in the western basin has not been conducted since 2010, the resumption of any tagging would be beneficial for providing more accurate model estimates in the future.

Additional tag-recovery data are available for the region, which could be integrated in the ITCAAN model to provide more accurate estimates. For example, walleye were tagged with PIT

tags and portions of the commercial harvest were scanned for the presence of these tags. It is uncertain whether this tag-recovery dataset would aid the estimation of commercial mortality or complicate the model due to changes in the amount of the harvest scanned for PIT tags each year and/or faulty scanners which would influence reporting rates. Walleye tagged with telemetry tags as a part of the Great Lakes Acoustic Telemetry Observation System could be incorporated into the ITCAAN models in two ways (Hayden et al. 2014, 2017). First, tag recoveries of walleye implanted with telemetry tags could be used as an additional high-reward tag release in the model to aid in the estimation of tag reporting rates. Second, the data from the telemetry receivers could be used to aid the estimation of movement rates and more realistic movement models could be estimated (e.g. seasonal movement) (Eveson et al. 2012a). Finally, future analyses of ITCAAN models for Lake Erie walleye could attempt to incorporate observations of tagged fish that are recovered and released during the tagging processes in each region (Zhao et al. 2011).

Estimation of natural mortality is difficult in catch-at-age models (Wang and Liu 2006; Lee et al. 2011) . However, this parameter is essential for accurately estimating the abundance of a population. The ITCAAN model presented in this work estimated natural mortality rates for the three regions modeled by accounting for tag shedding and tag non-reporting. The estimate of natural mortality for the western basin of Lake Erie was less than half the value currently used in the assessment model of 0.32. Our estimate of natural mortality aligns with the estimates of ages 5 and older by Vandergoot and Brenden (2014). Therefore, it is probable that the value of natural mortality currently used in the assessment model is too high. We recommend using a lower value within the assessment model as an overestimate of natural mortality will generally lead to the overestimation of abundance (Schnute and Richards 1995; Vincent et al. 2017). Future investigations could attempt to estimate age-specific natural mortality parameters.

In conclusion, we were able to use an ITCAAN model to estimate natural mortality, reporting rates, abundance and mortalities for walleye in Lake Huron, the Huron-Erie Corridor and Lake Erie. Estimates of natural morality were reasonable, though estimates of recreational reporting rates were higher than previous estimates. Walleye abundance estimates in the western basin from the ITCAAN

model were much lower compared to the models currently used to provide management advice; this difference was attributed partly to the large difference in natural mortality estimates. The estimates of abundance in the eastern basin of Lake Erie should be used with caution as results of simulations showed that estimates of smaller populations could be positively biased when intermixing rates were 10% or higher and there were large differences in population abundances. We recommend that future tagging studies release high-reward tags and double tag individuals annually to provide more precise estimates of tag shedding and reporting rates. Additional studies to determine if Floy tags provide a higher reporting rate would be beneficial. The estimates of abundance for walleye in Lake Erie and Huron from this study are not intended as a replacement to current assessments used for management decisions. We recommend conducting a management strategy evaluation to determine the performance of this model compared to currently used assessment models and appropriate harvest policies to account for the intermixing of walleye populations (Butterworth and Punt 1999; Punt et al. 2001).

Acknowledgments

APPENDICES

Table 4.A.1: Number of standard (S) and reward (R) tags released from 1993 to 2015 and tag retention parameters for Ontario Ministry of Natural Resources (OMNRF) in the Lake Huron region and in western basin of Lake Erie, Michigan Department of Natural Resources (MDNR) in the Lake Huron region and in the western basin of Lake Erie, Ohio in the western basin of Lake Erie, New York State Department of Environmental Conservation (NYSDEC) and Pennsylvania Fish and Boat Commission combined in the eastern basin of Lake Erie and the instantaneous retention (α) and chronic shedding (β) parameters for each agency.

Year	HUR OMNRF		HUR MDNR		WLE OMNRF		WLE MDNR		WLE ODNR		ELE NYSDEC	
	S	R	S	R	S	R	S	R	S	R	S	R
1993	0	0	2991	0	1647	0	1958	0	4149	0	1906	0
1994	0	0	3429	0	454	0	2544	0	2723	0	1475	0
1995	0	0	3165	0	835	0	965	0	4021	0	1312	0
1996	0	0	2992	0	0	0	2268	0	3494	0	892	0
1997	0	0	2993	0	2784	0	1740	0	1735	0	1144	0
1998	0	0	5484	0	378	0	1290	0	0	0	459	0
1999	0	0	5997	0	0	0	1630	0	0	0	1084	0
2000	0	0	5986	300	1091	115	1874	208	1656	166	999	121
2001	0	0	3042	0	765	0	94	0	2318	0	1061	0
2002	40	3	3234	0	0	0	2822	0	2703	0	1136	0
2003	89	9	3171	0	0	0	1511	0	2132	0	630	0
2004	139	12	3143	0	0	0	2849	0	1005	0	268	0
2005	0	0	3262	0	1520	0	1926	0	2330	0	1630	0
2006	0	0	3107	0	0	0	2388	0	2030	0	1497	0
2007	0	0	2966	0	0	0	396	0	1711	0	1327	0
2008	0	0	3031	0	0	0	1292	0	0	0	0	0
2009	0	0	3094	0	0	0	818	0	0	0	0	0

Table 4.A.1 (cont'd)

Year												
2010	0	0	3063	0	0	0	1008	0	0	0	0	0
2011	0	0	2988	0	0	0	0	0	0	0	0	0
2012	0	0	2994	0	0	0	0	0	0	0	0	0
2013	261	138	2993	0	0	0	0	0	0	0	0	0
2014	204	49	2700	300	0	0	0	0	0	0	0	0
2015	271	69	2699	300	0	0	0	0	0	0	785	0
α_t	0.95		0.99		0.95		0.99		0.95		0.99	
β_t	0.28		0.08		0.28		0.08		0.28		0.07	

Table 4.A.2: Region of activity, variance ratios for observed values and processes error of catchability coefficients for fisheries and surveys modeled. An X in the selectivity, catchability, reporting rate or annual F column indicates these parameters were estimated for this fishery/survey. Reporting rates with the same superscript were assumed to have the same values.

Fishery / Survey	Region	Data Var. Ratio	Penalty Var. Ratio	Select-ivity	Catch-ability	Reporting Rate	Annual F
HUR Comm Bycatch	HUR	2.0			Constant	X [*]	
HUR Comm Trapnet	HUR	1.0	1.0	X	X	X [*]	
HUR Comm Gillnet	HUR	0.9	0.9	X	X	X [*]	
HUR MI Rec	HUR	0.85	0.85	X	X	X [†]	
HUR ON and HEC Rec	HUR					X [†]	X
HUR MDNR Survey	HUR	0.91	1.07	X	X		
WLE Comm Gillnet	WLE	0.91	0.89	X	X	X	
WLE Ohio Rec	WLE	0.85	0.86	X	X	X [†]	
WLE MI Rec	WLE	0.76	0.8	X	X	X	
WLE ON Rec	WLE					X [†]	X
WLE OMNRF Survey	WLE	1.0	2.0	X	X		
WLE ODNR/MDNR Survey	WLE	0.86	2.0	X	X		
WLE Age-0 Trawl	WLE	1.0	2.0	X	X		
ELE NY/PA Rec	ELE	0.9	1.0	X	X	X [†]	
ELE Comm Gillnet	ELE	1.0	0.4	X	X	X	
ELE ON Rec	ELE					X [†]	X
ELE NYSDEC Survey	ELE	0.4	2.0	X	X		
ELE OMNRF Survey	ELE	1.0	2.0	X	X		

Table 4.A.3: Data availability for fisheries and surveys modeled in a three region ITCAAN model for Lakes Erie and Huron Walleye, where § indicates tag recoveries were combined and modeled as a single fishery.

Fishery / Survey	Age Composition	Total Harvest	Effort	Tag Recoveries	CPE
HUR Comm Bycatch			X	§	
HUR Comm Trapnet	X	X	X	§	
HUR Comm Gillnet	X	X	X	§	
HUR MI Rec	X	X	X	X	
HUR ON and HEC Rec				X	
HUR MDNR Survey	X				X
WLE Comm Gillnet	X	X	X	X	
WLE Ohio Rec	X	X	X	X	
WLE MI Rec	X	X	X	X	
WLE ON Rec				X	
WLE OMNRF Survey	X				X
WLE ODNR/MDNR Survey	X				X
WLE Age-0 Trawl					X
ELE NY/PA Rec	X	X	X	X	
ELE Comm Gillnet	X	X	X	X	
ELE ON Rec				X	
ELE NYSDEC Survey	X				X
ELE OMNRF Survey	X				X
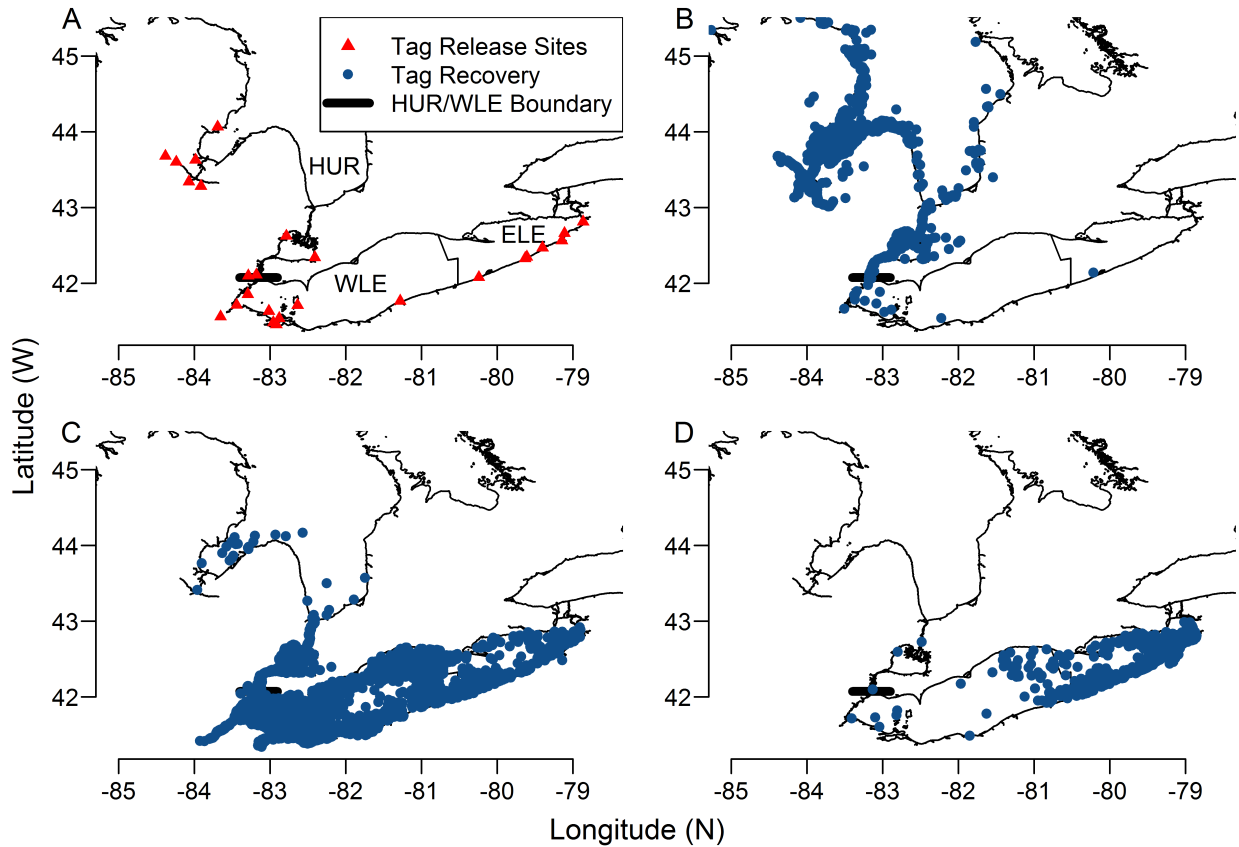
Figure 4.A.1: Boundary lines of the three regions modeled by the ITCAAN Model and location of tag releases indicated by triangles (A). Tag recovery locations for tags that were released in HUR (B), the WLE (C), and the ELE region (D) between 1993 and 2015 indicated by circles.
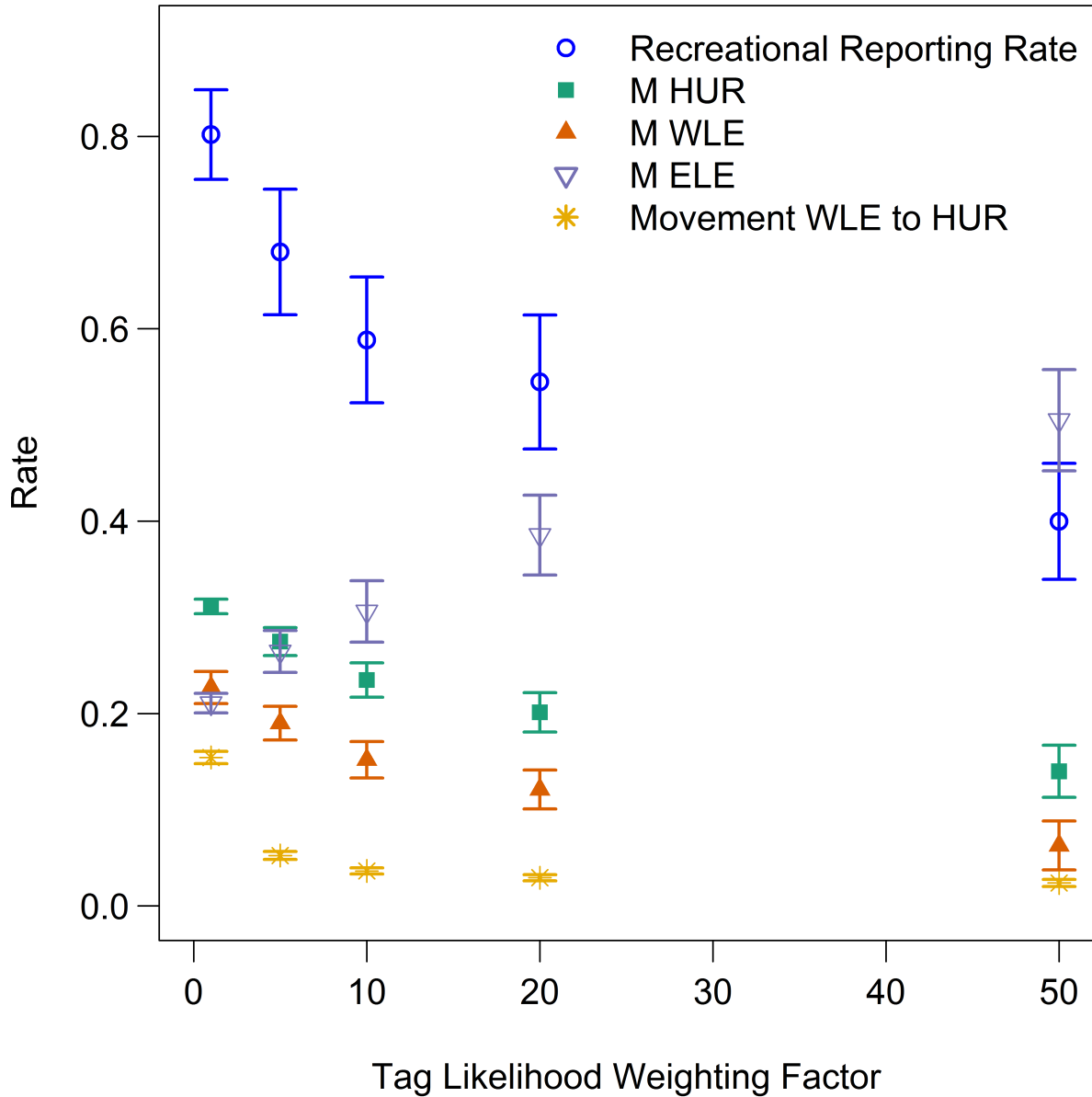
Figure 4.A.2: Estimates and 95% confidence interval of reporting rate for the recreational fisheries across all regions, natural mortality for the Huron, WLE, and ELE regions and movement rates from WLE population to HUR, where the x-axis is the value the weighting factor for the tag-recovery data.
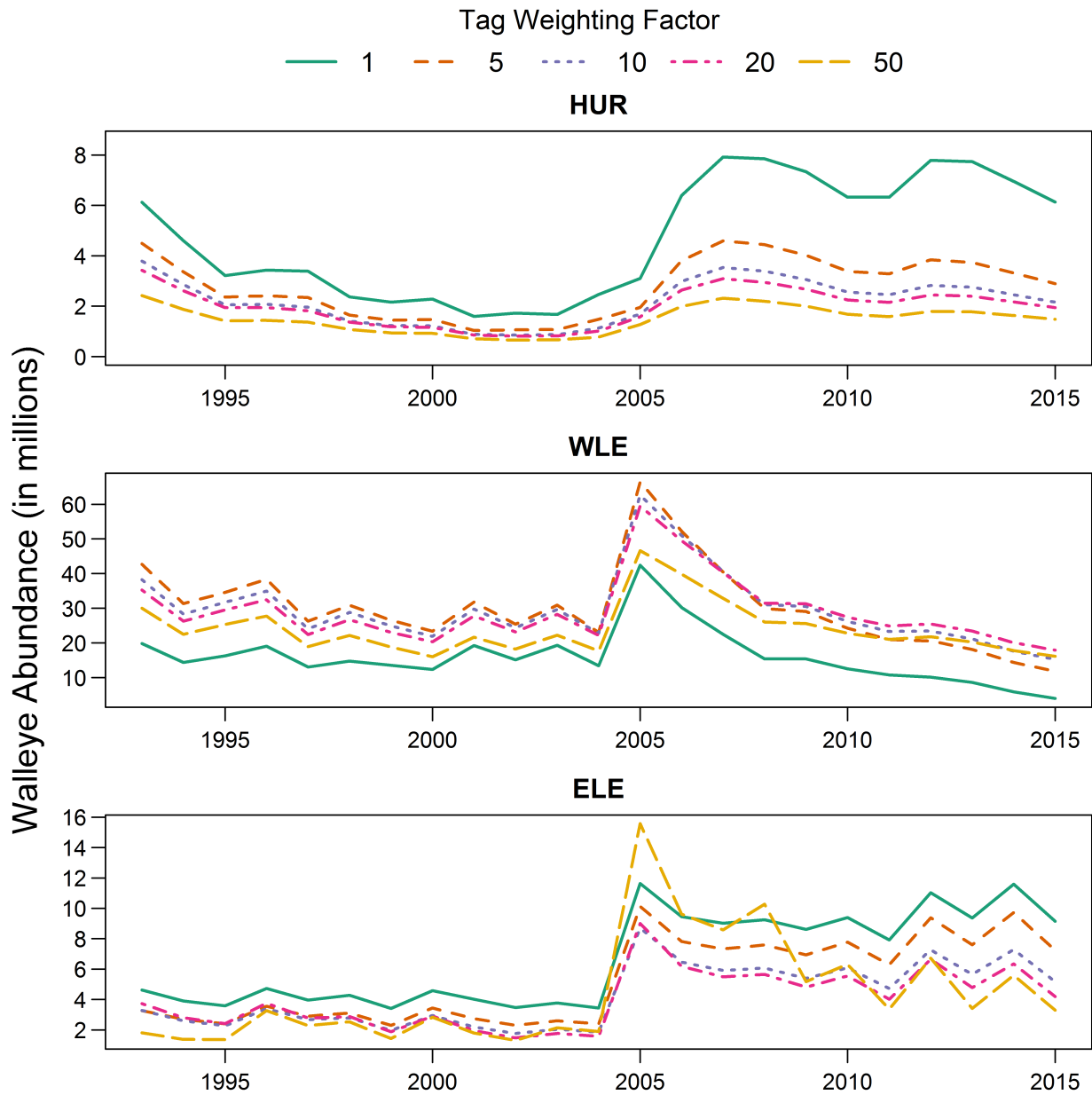
Figure 4.A.3: Estimated total walleye abundance in the three regions of the ITCAAN model for the time period 1993 through 2015 for five weighting factors of the tag-recovery data, where the tag weighting factor is the value that the multinomial likelihood was divided by.
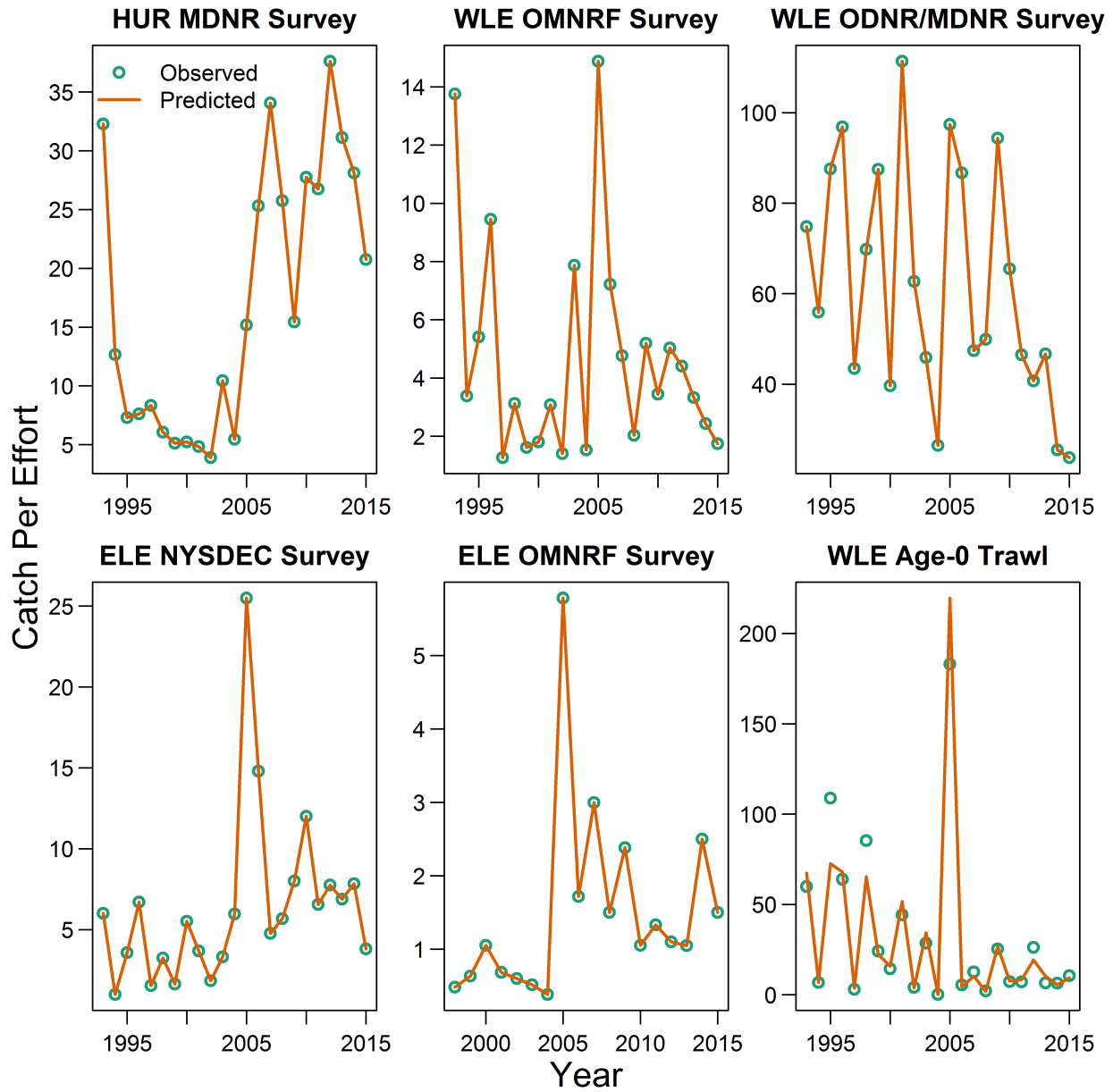
Figure 4.A.4: Observed (open circles) and predicted (solid line) catch per effort of walleye of the six fishery-independent surveys used in a three region ITCAAN model for Lake Huron and Lake Erie.
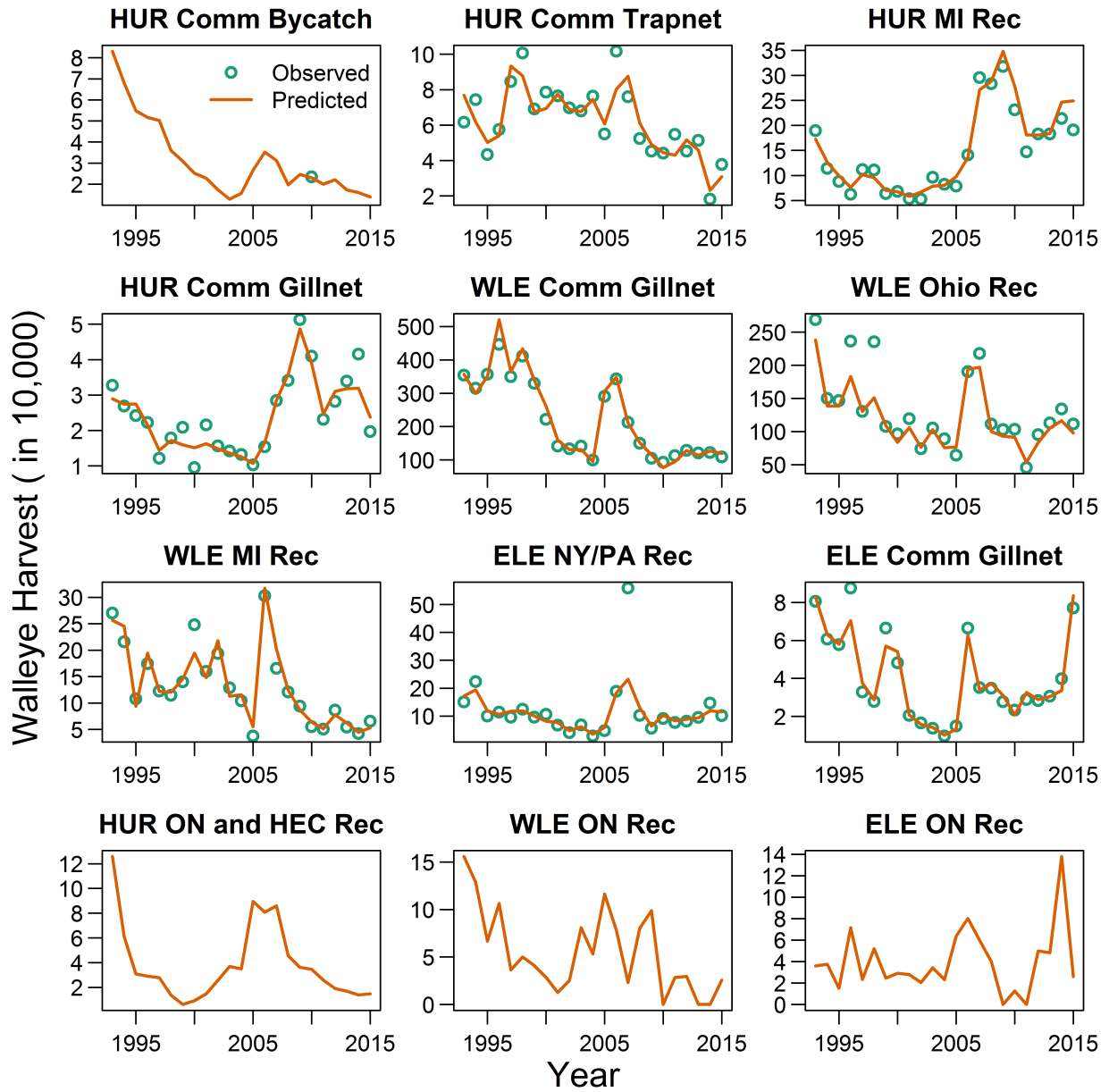
Figure 4.A.5: Observed (open circles) and predicted (solid line) number of walleye harvested by fishery from a three region ITCAAN model for Lake Huron and Lake Erie.
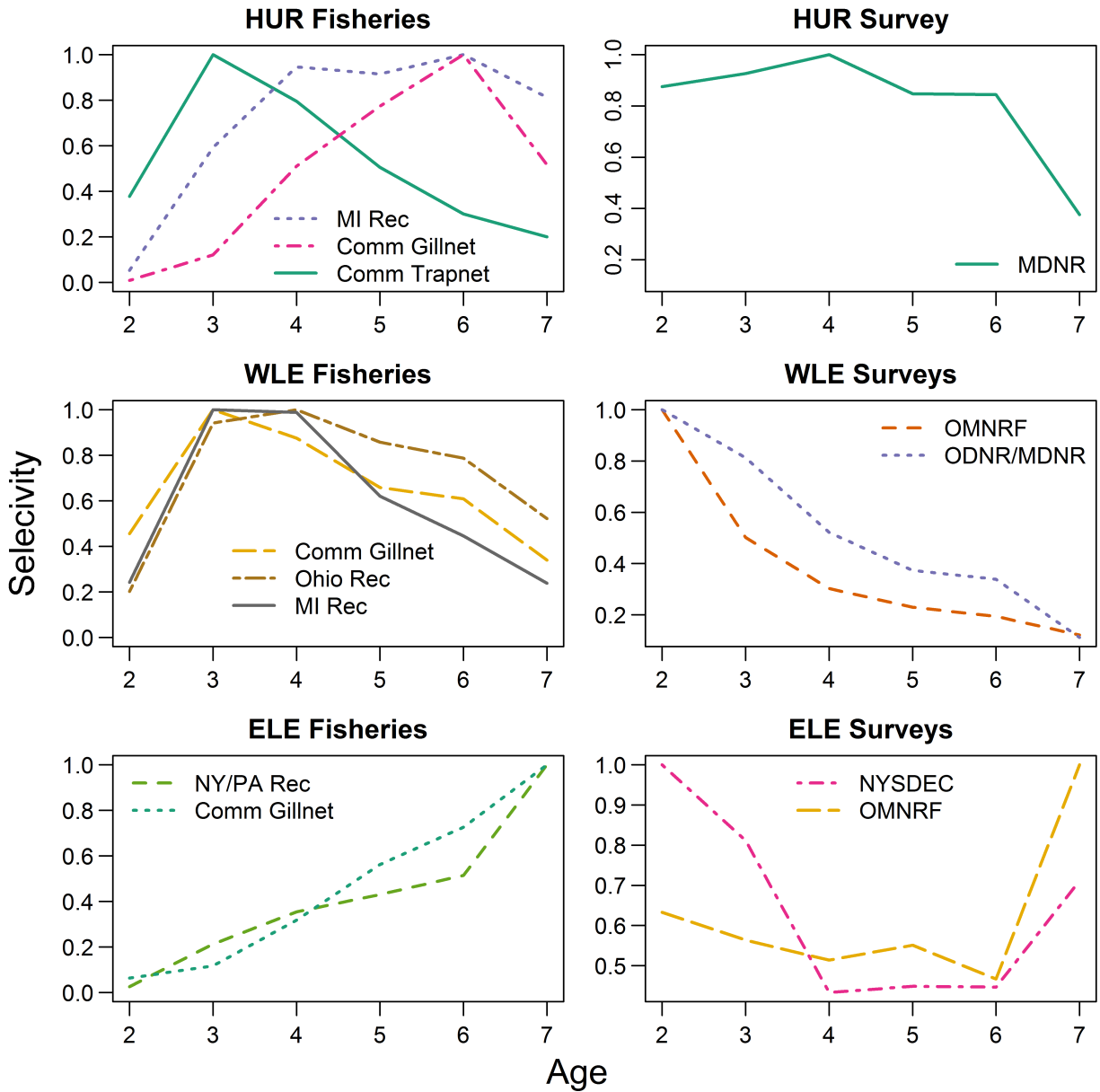
Figure 4.A.6: Selectivity at age for fisheries and surveys operating in the three regions of a tag integrated catch-at-age model for walleye in Lake Huron and Lake Erie.
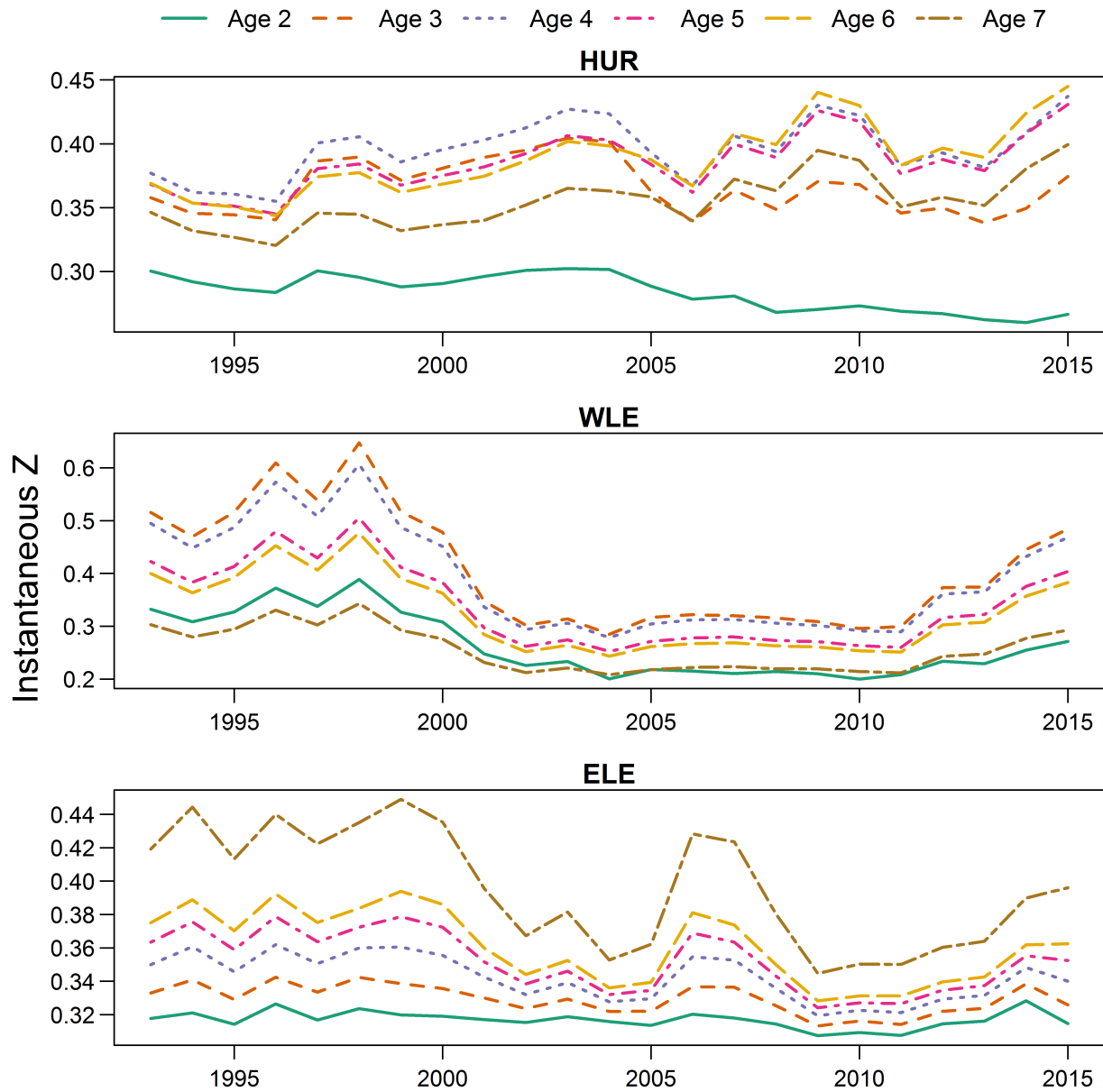
Figure 4.A.7: Total instantaneous regional mortality at age experienced in the three regions estimated by a tag integrated catch-at-age model for Lake Erie and Huron walleye.
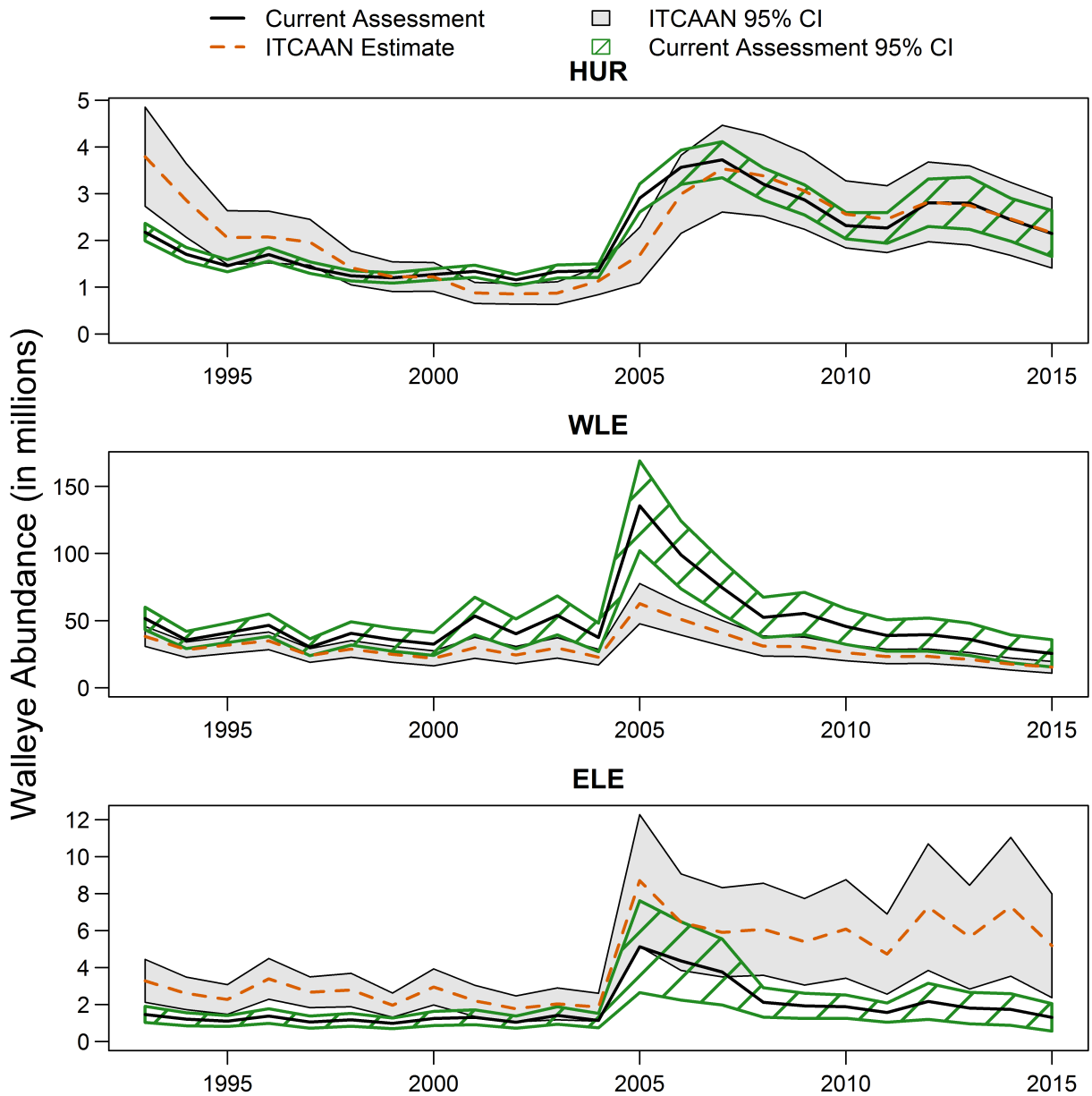
Figure 4.A.8: Estimated population abundance from assessment models currently used to manage the walleye fisheries in Lakes Huron and Erie (solid line) with 95% confidence interval (green hashed region) and from a three region tag integrated catch-at-age model that estimates intermixing of the populations (dashed line) with the 95% confidence interval (shaded region).
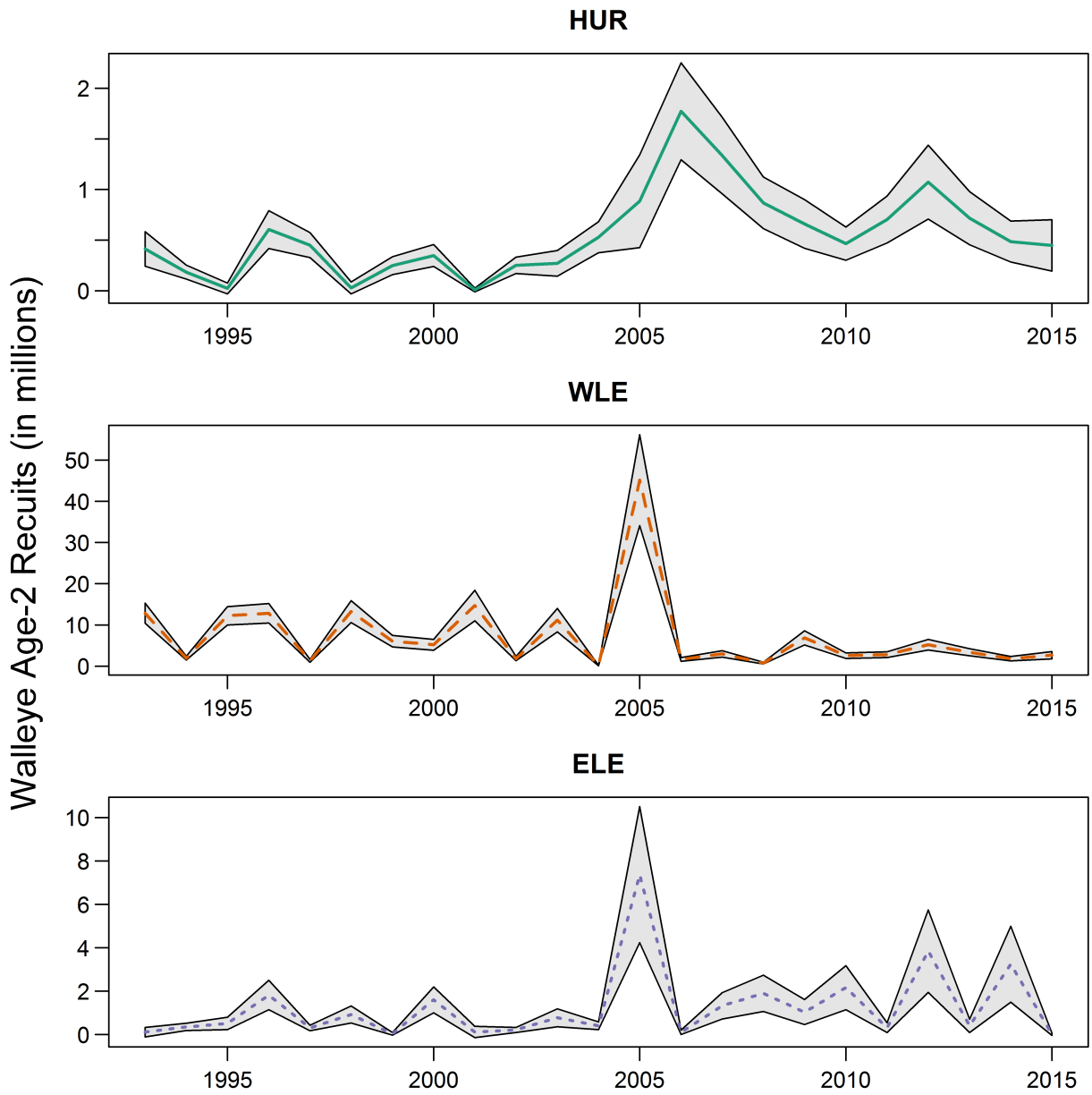
Figure 4.A.9: Recruitment of age-2 walleye to the Lake Huron, western and eastern basin Lake Erie populations as estimated by a three region tag-integrated catch-at-age assessment model and the 95% confidence interval shown by the shaded region.

APPENDIX 4.B

DATA SOURCES

Many datasets were available extending as far back as 1978, but data for the commercial fishery in ELE and the Pennsylvania recreational fishery were available starting in 1993, which is why we excluded earlier data. Total harvest of walleye in number of fish were available for the Ontario trapnet fishery in Lake Huron, the Michigan recreational fishery in Lake Huron, the Ontario gillnet fishery in Lake Huron, the tribal gillnet fishery in Lake Huron, Ontario gillnet fishery in WLE and ELE, Ohio recreational fishery in WLE, Michigan recreational fishery in WLE, New York recreational fishery in ELE and Pennsylvania recreational fishery in ELE. In Lake Huron, harvest and age composition for the Ontario commercial gillnet and the Michigan tribal gillnet fisheries were combined and modeled as a single fishery. Data for the commercial gillnet fisheries in Ontario waters of WLE and ELE were modeled as two separate fisheries (Figure 4.A.1). Consistent with the current assessment in the eastern basin of Lake Erie, the New York and Pennsylvania (NY/PA) recreational fisheries were combined and treated as a single fishery in the model.

Commercial harvest for each fishery was reported in biomass. Following methods used to assess Lake Huron, WLE, and ELE walleye, harvested biomass for each fishery was converted into number of walleye based on weighed and aged fish from subsamples of harvested fish every year. Fishing effort for the Lakes Huron and Erie commercial gillnet fisheries in km of gillnet set and for the Lake Huron trapnet fishery in number of lifts were used as a component of the fishing mortality sub-model. Fishing effort of an additional commercial trapnet fishery that operates in Saginaw Bay of Lake Huron and captures walleye as bycatch was also incorporated into the model. An estimate of 23500 walleye killed by the HUR bycatch fishery in 2010 (MacMillan and Roth 2012) was used to scale the trapnet effort and provide an estimate of bycatch for the entire time series. We were unable to reliably convert the incidental harvest of walleye reported in weight captured by the Pennsylvania commercial yellow perch fishery into number of walleye because age composition and average weight data of the catch were unavailable. Therefore, the harvest by this fishery was

not included in the model, which is consistent with the current assessment of the ELE; additionally, the harvest by the PA commercial fishery was relatively small.

Recreational harvest and fishing effort in angler hours from New York, Pennsylvania, Ohio, and Michigan (in HUR and WLE separately) were obtained from annual creel surveys and charter boat reporting. Recreational catch-at-length data were converted into catch-at-age using annual age-length keys (Wills et al. 2016). Harvest and effort data for the Ohio recreational fishery were the sum of estimates obtained from creel surveys for Lake Erie and the Sandusky and Maumee rivers. Missing years of harvest and effort data for the Sandusky River (1994-1996, 1999, and 2000) and the Maumee River (1994-1996 and 1998-2000) were estimated through linear interpolation. Recreational fishing data for Michigan in Lake Huron included harvest from Lake Huron open water and in the Saginaw and Tittabawassee Rivers. Harvest and effort for the recreational fishery differed from data described by Fielder and Bence (2014) in that we used harvest within a calender year, whereas they assumed a fishing year (i.e., April 1st to March 31). Creel surveys of recreational fishing in all three regions of Ontario and the HEC (both Ontario and Michigan) were infrequently conducted between 1993 and 2015 and were not included in the ITCAAN model. However, recreational fisheries in Ontario and the HEC did recover and report jaw-tagged walleye and we used these recoveries to estimate fishing mortalities associated with these fisheries. The model estimated separate annual fishing mortalities for recreational fisheries in the HEC and Ontario waters of Lake Huron, WLE and ELE.

Multiple fishery-independent catch-per-effort time series were incorporated in the ITCAAN model. A gillnet survey in Saginaw Bay was conducted each September by MDNR. In Canadian waters of WLE, a depth-stratified random-site gillnet survey was conducted jointly by the OMNRF and the Ontario Commercial Fisher's Association during September through mid-October. A depth stratified fixed-site gillnet survey was conducted in the western basin of Lake Erie jointly by ODNR and MDNR in late September through November. An interagency age-0 trawl in WLE was used as an index of recruitment to the population. A gillnet survey conducted by NYSDEC during September in U.S. waters of ELE was also included in the ITCAAN model. The gillnet survey in

Ontario waters of ELE was conducted in late August to early September and data were available starting in 1998. Fishery-independent surveys, with the exception of the age-0 trawl, captured walleye while they were assumed to be intermixed. All walleye captured by the Canadian surveys were weighed, measured for length and aged. Weight and length were measured for all walleye captured by U.S. surveys, but only a subsample were aged and age-compositions for these surveys were calculated using age-length keys. The age composition data for the surveys and the fisheries include walleye age-2 through 7 and all fish older than age-7 were aggregated into an age-7 and older age group.

Tag release and recovery databases were obtained for Lake Erie from the WTG and for Lake Huron from MDNR and OMNRF. Mature walleye were collected and tagged from tributaries and open-water reef spawning locations during the spring by MDNR and OMNRF in HUR from 1993 to 2015, by ODNR, OMNRF, and MDNR in WLE from 1993 through 2010 and by NYSDEC in ELE from 1993 to 2007 and in 2015 (Table 4.A.1). Walleye that were tagged during March through May at tagging sites throughout Lakes Huron and Erie were used in the analysis (i.e., walleye tagging after May were not included in this study; Figure 4.A.1). Walleye were tagged by affixing a hard metal Monel butt-end band to the mandible or maxillary that was inscribed with agency-specific fish identification numbers and tag reporting information and then released (Wang et al. 2007; Fielder 2014b; Vandergoot et al. 2012; Vandergoot and Brenden 2014). Some walleye were also implanted with Passive Integrated Transponder (PIT) tags, but our analysis did not include walleye tagged with only a PIT tag. High-reward tags inscripted with "Reward $100" were released by agencies in both regions of Lake Erie in 2000, by MDNR in HUR in 2000, 2014, and 2015, and by OMNRF in HUR in all years walleye were tagged (Table 4.A.1). The release of tagged walleye were modeled separately by agency as past research indicated that tag shedding rates differed among agencies (Vandergoot and Brenden 2014). Walleye tagged and released by OMNRF and MDNR in HUR and WLE were modeled separately. The PFBC released 72 tags in 2001, which were modeled as tags from NYSDEC. The age of tagged walleye at the time of release were determined differently depending on the database. For tags released by MDNR in HUR,

the number of tags released at age were determined by the total number of tags released and the proportion at age obtained from a subsample of tags aged each year during peak spawning (David Fielder, MDNR pers. comm.). Age at release of tagged walleye in Lake Erie were estimated using year-, sex-, and tagging-basin specific age-length keys applied to the observed length and sex of the tagged fish (Vandergoot and Brenden 2014). Age-length keys were derived from aged walleye samples collected from fishery-independent surveys conducted the fall prior to tagging based on the assumption that growth during the winter was limited (Vandergoot and Brenden 2014). Age at release of tagged walleye from Ontario in 2013 to 2015 were determined by a combination of dorsal fin spines and age-length keys. The age of tagged walleye at release were incorporated into the model and the predicted number of tags recovered were calculated from age-specific fishing mortalities. However, we did not explicitly separate the recoveries by cohorts of age at release, but instead modeled the recoveries summed across ages for each fishery.

We restricted our analysis of tag recoveries to those released and recovered between 1993 and 2015. More than half of the tag recoveries in the database from MDNR for Lake Huron did not have gear information. Of the 6643 tags for which recovery gear was indicated in the recovery database only 27 (0.4%) were reported as recovered from commercial fisheries. Therefore, the tag recoveries for this database that did not have a recovery gear were randomly assigned to either the recreational fishery (with a probability of 99.6%) or commercial fishery. Ten of the 6643 tags were randomly assigned to be recovered by the commercial fishery from the Lake Huron database and the rest were assumed to be recreational recoveries. With the exception of the Lake Huron recovery gear, tags were considered not reported if they did not have a recovery location sufficient to assign to one of the three model regions, a recovery gear, or were missing the year of release or recovery. Tags that were recovered by assessment gear were removed from the number of tags that were released. Tagged fish that were found dead were not explicitly incorporated into the analysis. A total of 15600 standard tag recoveries and 318 high-reward tag recoveries were used in the ITCAAN model. These recovered tags were distinguishable based on the year and agency of release, and the year, region, and fishery of recovery. The total number of tags returned separated

by these five factors were incorporated in the ITCAAN model. Recovered tags were assigned to one of the harvest regions (Huron, WLE, or ELE) based on the reported location of recovery.

APPENDIX 4.C

PARAMETER LIST AND MODEL EQUATIONS

Table 4.C.1: Symbols and descriptions of variables used in Operating and ITCAAN model.

Symbol	Description
Index	
y	Year
Y	Last year modeled
a	Age
A	Oldest modeled age
t	Tagging agency
p	Spawning population
r	Harvest region
ty	Year of tag release
ry	Year of tag recapture
g	Fishing or survey gear
Diacritic	
$\sim$	Variable derived from estimated parameters
$\wedge$	Estimated Parameter
none	Observed Data or assumed value
Parameters	
$\tilde{N}$	Population abundance
$\hat{\Lambda}$	Recruitment in the first year 1993
$\hat{\lambda}$	Annual recruitment deviation
$\hat{\Gamma}$	Mean abundance for 1993
$\hat{\Delta}$	Abundance at age deviations in 1993
$\tilde{T}_{p,r}$	Percent of population p moving to region r
$\hat{\omega}_{p,r}$	Estimated movement parameter from population p to region r
$\tilde{S}$	Survival
$\tilde{Z}$	Total mortality
$\tilde{F}$	Age-specific fishing mortality
$\hat{M}$	Natural mortality
$\hat{v}$	Age-specific fishery selectivity
$\tilde{q}$	Fishery catchability coefficient
E	Observed fishing effort
$\mathbb{1}$	Indicator if fishery is active in region

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Table 4.C.1 (cont'd)

$\hat{K}$	Fishery catchability parameter in 1993
$\hat{\kappa}$	Annual fishery catchability deviation
C	Harvest in numbers caught
PC	Fishery proportion at age
I	Survey abundance index
Υ	Survey specific mortality fraction
$\hat{V}$	Age-specific survey selectivity
$\tilde{Q}$	Survey catchability coefficient
$\hat{\Phi}$	Survey catchability parameter in 1993
$\hat{\phi}$	Annual survey catchability deviation
PI	Survey proportion at age
R	Number of tagged fish released
$\tilde{n}$	Number of tagged fish alive
L	Tag retention probability
α	Immediate tag retention probability
β	Instantaneous rate of chronic shedding
d	Number of tags recovered
$\hat{\rho}$	Fishery reporting rate
$\tilde{\theta}$	Tag recovery proportions
$\tilde{\theta}_{NR}$	Proportion of tags never recovered
$\tilde{\iota}$	Age 0 trawl annual catchability
$\hat{\varepsilon}$	Age 0 trawl catchability in 1993
$\hat{\xi}$	Annual deviation of Age 0 trawl catchability
$\tilde{\eta}$	CPE from Age 0 trawl
$\hat{\zeta}$	Exponent of age 0 trawl W Erie
ψ_g	Standard deviation of specific data source
$\hat{\sigma}_r$	estimated standard deviation specific to each region
VR	Data source specific variance ratio
ψ_N	Standard deviation for abundance deviations in 1993 = 4
ψ_R	Standard deviation for recruitment deviations random walk =4
NLL	Negative Log Likelihood
W	Tag-recovery data weighting factor

Table 4.C.2: Equations used to model and estimate population dynamics in ITCAAN models.

Eq. Number	Equation

(4.C.2.1)

$$\tilde{N}_{y,a=1,p} = \hat{\Lambda}_p \qquad\qquad \text{for} \quad y = 1993$$
$$\tilde{N}_{y,a=1,p} = \tilde{N}_{y-1,a=1,p} \; e^{\hat{\lambda}_{y,p}} \quad \text{for} \quad y > 1993$$

(4.C.2.2)

$$\tilde{N}_{y=1993,a,p} = e^{\hat{\Gamma}_p + \hat{\Delta}_{p,a}} \qquad \text{for} \qquad a > 2 \qquad \text{where} \sum_a \hat{\Delta}_{p,a} = 0.0$$

(4.C.2.3)

$$\tilde{T}_{r,p} = \frac{e^{\hat{\omega}_{r,p}}}{\sum\limits_{r=1}^{2} e^{\tilde{\omega}_{r,p}}}, \qquad \text{where} \;\; \omega_{r=3,p} = 0$$

(4.C.2.4)

$$\tilde{N}_{y+1,a+1,p} = \sum_r \tilde{N}_{y,a,p} \; \tilde{T}_{p,r} \; \tilde{S}_{y,a,r} \qquad \text{where} \qquad a < A - 1$$

(4.C.2.5)

$$\tilde{N}_{y+1,A,p} = \sum_r \tilde{N}_{y,A,p} \; \tilde{T}_{p,r} \; \tilde{S}_{y,A,r} + \tilde{N}_{y,A-1,p} \; \tilde{T}_{p,r} \; \tilde{S}_{y,A-1,r}$$

(4.C.2.6)

$$\tilde{S}_{y,a,r} = e^{-\tilde{Z}_{y,a,r}}$$

(4.C.2.7)

$$\tilde{Z}_{y,a,r} = \hat{M}_r + \sum_g \tilde{F}_{y,a,r,g}$$

(4.C.2.8)

$$\tilde{F}_{y,a,r,g} = \tilde{q}_{y,g} \; E_{y,g} \; \hat{v}_{a,g} \; \mathbb{1}_{r,g}$$

(4.C.2.9)

$$\tilde{q}_{y,g} = \hat{K}_g \qquad\qquad \text{for} \quad y = 1993$$
$$\tilde{q}_{y,g} = \tilde{q}_{y-1,g} \; e^{\kappa_{y,g}} \quad \text{for} \quad y > 1993$$

(4.C.2.10)

$$\tilde{C}_{y,a,g} = \sum_p \frac{\tilde{F}_{y,a,r,g}}{\tilde{Z}_{y,a,r}} \tilde{N}_{y,a,p} \; \tilde{T}_{p,r} \; (1 - \tilde{S}_{y,a,r})$$

(4.C.2.11)

$$\widetilde{PC}_{y,a,g} = \frac{\tilde{C}_{y,a,g}}{\sum\limits_a \tilde{C}_{y,a,g}}$$

(4.C.2.12)

$$\tilde{I}_{y,a,g} = \sum_p \tilde{N}_{y,a,p} \; \tilde{T}_{p,r} \; e^{-\tilde{Z}_{y,a,r}} \; \hat{\Upsilon}_g \; \tilde{Q}_{y,g} \; \hat{V}_{a,g}$$

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Table 4.C.2 (cont'd)

$$\tilde{Q}_{y,g} = \hat{\Phi}_g \qquad \text{for} \quad y = 1993$$
$$\tilde{Q}_{y,g} = \tilde{Q}_{y-1,g}\ e^{\hat{\phi}_{y,g}} \qquad \text{for} \quad y > 1993$$

(4.C.2.13)

$$\widetilde{PI}_{y,a,g} = \frac{\tilde{I}_{y,a,g}}{\sum\limits_a \tilde{I}_{y,a,g}}$$

(4.C.2.14)

$$\tilde{\iota}_y = \hat{\varepsilon} \qquad \text{for} \quad y = 1993$$
$$\tilde{\iota}_y = \tilde{\iota}_{y-1}\ e^{\hat{\xi}_y} \qquad \text{for} \quad y > 1993$$
$$\tilde{\eta}_y = \tilde{\iota}_y\ \tilde{N}^{\hat{\zeta}}_{y,a=1,r=2}$$

(4.C.2.15)

$$\hat{d}_{ty,t,ry,r,g} = \sum_a \tilde{n}_{ty,t,ry,a}\ \tilde{T}_{p,r}\ \frac{\tilde{F}_{ry,a,r,g}}{\tilde{Z}_{ry,a,r}}\left(1 - \tilde{S}_{ry,a,r}\right)\hat{\rho}_g$$

(4.C.2.16)

$$L_{t,ry} = \alpha_t\ e^{-\beta_t*0.5} \qquad \text{for} \quad ry = ty$$
$$L_{t,ry} = e^{-\beta_t} \qquad \text{for} \quad ry > ty$$

(4.C.2.17)

$$\psi_g = \hat{\sigma}_r \div \sqrt{VR_g}$$

(4.C.2.18)

$$\tilde{n}_{ty,t,ry,a} = R_{ty,t,a} \qquad\qquad\qquad\qquad\qquad\qquad \text{for} \quad y = ty$$
$$\tilde{n}_{ty,t,ry+1,a+1} = \sum_r \tilde{n}_{ty,t,ry,a}\ \tilde{T}_{p,r}\ \tilde{S}_{ry,a,r}\ \tilde{L}_{t,ry} \qquad\qquad \text{for} \quad a < A-1$$
$$\tilde{n}_{ty,t,ry+1,A} = \sum_r \tilde{n}_{ty,t,ry,A}\ \tilde{T}_{p,r}\ \tilde{S}_{ry,A,r} + \tilde{n}_{ty,t,ry,A-1}\ \tilde{T}_{p,r}\ \tilde{S}_{ry,A-1,r}\ \tilde{L}_{t,ry} \quad \text{for} \quad a = A$$

(4.C.2.19)

$$\tilde{d}_{ty,t,NR} = \sum_a R_{ty,t,a} - \sum_{ry}\sum_r\sum_g \tilde{d}_{ty,t,ry,r,g}$$

(4.C.2.20)

$$\tilde{\theta}_{ty,t,y,g} = \frac{\tilde{d}_{ty,t,ry,r,g}}{\sum\limits_a R_{ty,t,a}}$$

(4.C.2.21)

$$\tilde{\theta}_{ty,t,NR} = \frac{\tilde{d}_{ty,t,NR}}{\sum\limits_a R_{ty,t,a}}$$

(4.C.2.22)

Table 4.C.3: Likelihood Equations and penalties used in the ITCAAN model.

Equation Number	Likelihood Equation and Penalty
(4.C.3.1)	$NLL_{\text{Rec}} = \sum_y \sum_p \ln\left(\psi_R \sqrt{2\pi}\right) + 0.5\left(\dfrac{\hat{\lambda}_{y,p}}{\psi_R}\right)^2$
(4.C.3.2)	$NLL_{\text{N0}} = \sum_a \sum_p \ln\left(\psi_N \sqrt{2\pi}\right) + 0.5\left(\dfrac{\hat{\Delta}_{p,a}}{\psi_N}\right)^2$
(4.C.3.3)	$NLL_{\text{q}} = \sum_y \sum_g \ln\left(\psi_g \sqrt{2\pi}\right) + 0.5\left(\dfrac{\kappa_{y,g}}{\psi_g}\right)^2$
(4.C.3.4)	$NLL_{\text{Q}} = \sum_y \sum_g \ln\left(\psi_g \sqrt{2\pi}\right) + 0.5\left(\dfrac{(-\phi_{y,g})}{\psi_g}\right)^2$
(4.C.3.5)	$NLL_{\text{Harvest}} = \sum_y \sum_g \ln\left(\psi_g \sqrt{2\pi}\right) + 0.5\left(\dfrac{\left(\ln(C_{y,g}) - \ln(\hat{C}_{y,g})\right)}{\psi_g}\right)^2$
(4.C.3.6)	$NLL_{\text{Survey}} = \sum_y \sum_g \ln\left(\psi_g \sqrt{2\pi}\right) + 0.5\left(\dfrac{\left(\ln(I_{y,g}) - \ln(\hat{I}_{y,g})\right)}{\psi_g}\right)^2$
(4.C.3.7)	$NLL_{\text{Trawl}} = \sum_y \ln\left(\psi_g \sqrt{2\pi}\right) + 0.5\left(\dfrac{\left(\ln(\eta_y) - \ln(\hat{\eta}_y)\right)}{\psi_g}\right)^2$
(4.C.3.8)	$NLL_{\text{CP}} = -100 \sum_y \sum_g \sum_a PC_{y,a,g} \ln\left(\widehat{PC}_{y,a,g}\right)$
(4.C.3.9)	$NLL_{\text{SP}} = -100 \sum_y \sum_a \sum_r IC_{y,a,g} \ln\left(\widehat{IC}_{y,a,g}\right)$
(4.C.3.10)	$NLL_{\text{Tag}} =$ $-\sum_{ty} \sum_t \left[\sum_{ry} \left(\sum_g \left(\sum_r d_{ty,t,ry,r,g} \right) \ln\left(\widehat{\theta}_{ty,t,ry,g}\right) \right) + d_{ty,t,NR} \ln\left(\widehat{\theta}_{ty,t,NR}\right) \right] / W$

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CONCLUSIONS

1. Both release- and recovery-conditioned ITCAAN models yielded accurate and precise parameter estimates under low to moderate movement rates.

2. Abundance and reporting rate parameters were largely biased for both the release- and recovery-conditioned ITCAAN frameworks under conditions of high movement and large differences in stock-recruitment relationships among spawning populations.

3. For the release-conditioned ITCAAN framework under high movement rates and similar stock-recruitment functions, population abundances and reporting rate estimates were unbiased.

4. Misspecification of natural mortality or reporting rate for both the release- and recovery-conditioned ITCAAN frameworks induced larger biases, for tested misspecification levels, than when both parameters were estimated. Therefore, I recommend that both natural mortality and reporting rates be estimated within an ITCAAN model, when possible.

5. Precision of natural mortality and abundance estimates in a release-conditioned ITCAAN model were sensitive to the number of tags released annually.

6. For recovery-conditioned ITCAAN models, estimates of population abundance were extremely biased when the reporting rate was assumed to be spatially-constant in the ITCAAN model but varied in the operating model.

7. Model performance for the release-conditioned ITCAAN model was superior to the recovery-conditioned ITCAAN model for similar scenarios, especially for the natural mortality parameter. Therefore, I recommend that fisheries scientists use the release-conditioned ITCAAN model and attempt to estimate both natural mortality and reporting rates within the model.

8. Bias and imprecision of model estimates were greater when tag-shedding was incorporated into the operating model and ITCAAN models compared to ignoring this process. Inclusion of tag shedding in operating models of future analyses of ITCAAN models is recommended.

9. Performance of release-conditioned ITCAAN models improved greatly when high-reward tags were released annually. However, some biases in population abundance estimates remained under simulation conditions of high movement and large differences in population abundances.

10. Estimation of natural mortality and reporting rates in 5-year blocks performed the best when these parameters varied over the time series. Conversely, estimation of reporting rate and natural mortality as temporally constant in the ITCAAN model resulted in large biases in model parameters, and bias increased as the frequency of high-reward tag releases decreased, when the operating model simulated natural mortality as an AR1 process and reporting rate as linearly decreasing.

11. Movement rates were underestimated compared to the annual average when movement was simulated to occur seasonally. I recommend that additional simulation frameworks, such as individual based models, be conducted to determine how sensitive the ITCAAN model is to the assumption of a box-transfer process.

12. I recommend that tag-recovery studies release high-reward tags annually to increase the precision and accuracy of reporting rate, natural mortality, and abundance estimates.

13. ITCAAN abundance estimates of walleye from the eastern basin of Lake Erie should be used with caution as simulations suggests that small populations can be overestimated under moderate to high movement rates.

14. Estimates of natural mortality and abundance for the western/central basin of Lake Erie from the ITCAAN model suggest that the value of natural mortality, 0.32, used in the current assessment model to provide management advice may be too high.

15. I recommend that future tagging studies of Lake Erie and Lake Huron walleye be designed such that they can estimate reporting and tag shedding rates annually. Additionally, experiments to determine the value of high-reward tags necessary to elicit a perfect (100%) reporting rate should be conducted.

16. Walleye harvest data from the Huron-Erie corridor are generally lacking, but harvest in this region by recreational fishers is substantial; thus annual creel surveys should be conducted to better quantify the amount of harvest and fishing effort on this system.

17. I recommend additional simulation analyses be conducted to investigate how ITCAAN model performance changes as a result of including additional fishery independent surveys that occur when walleye are aggregated during spawning or including region specific indices of recruitment.

18. I recommend conducting a management strategy evaluation to determine the performance of the ITCAAN model compared to the independent assessment models currently used for the management of walleye in Lakes Erie and Huron.