

# Parameter estimation performance of a recapture-conditioned integrated tagging catch-at-age analysis model

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## Abstract

Recapture-conditioned models are infrequently used to analyze tag-recovery data, but have been proposed as an alternative to release-conditioned models for estimating movement from tagging studies when tag-loss processes (e.g., tag reporting, tag shedding) can be assumed constant and estimates of these processes are not available. Through simulations, we investigated the performance (bias and precision) of a recapture-conditioned integrated tagging catch-at-age analysis (ITCAAN) under varying model complexities and intermixing rates and compared the results to those from a release-conditioned ITCAAN. We also investigated how misspecification of natural mortality, parity in population productivities, tag shedding, and spatially-varying reporting rates affected model estimates. At low intermixing rates, estimates of total abundance and spawning population abundances were accurate and precise, with precision decreasing when natural mortality was estimated for the recapture-conditioned ITCAAN. Accuracy and precision of individual population abundances declined with higher intermixing rates, with the largest bias and lowest precision occurring when estimating relative reporting rates. Assuming reporting rates were spatially constant in the ITCAAN when they varied regionally in the operating model led to biased estimates of movement rates and population abundances for both ITCAANs; attempting to estimate relative reporting when reporting varied spatially greatly improved parameter estimates compared to assuming spatially constant reporting. When tag shedding was simulated to occur, the recapture-conditioned ITCAAN yielded unbiased estimates of total abundance without additional data on the tag-shedding rate, whereas the release-conditioned ITCAAN estimates were dependent on the quality of the tag-shedding estimates. For most scenarios investigated, the release-conditioned ITCAAN estimates were less biased and/or variable compared to the recapture-conditioned models. However, both models performed poorly in estimating population specific abundances for scenarios when intermixing rates were high and that assumed regionally constant reporting rates in the ITCAAN but varying rates in the operating model.

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## 1 Introduction

2 Spatially-explicit population assessment models simultaneously estimate abundances, mortalities, and  
3 movement rates of populations that are exploited as mixed stocks during the fishing season (Goethel et al.,  
4 2011). Herein we define a population as an interbreeding group of fish that are self-sustaining and share  
5 similar life history characteristics. We define a stock as an exploited fishery unit delineated by region  
6 of harvest (Cadrin et al., 2004). Therefore, a mixed stock is comprised of individuals from two or more  
7 populations that are exploited as a single unit. Mixed stocks create overharvest risks for less productive  
8 populations depending on how stocks are managed (Ying et al., 2011; Guan et al., 2013; Hulson et al.,  
9 2013; Molton et al., 2013; Li et al., 2014). Integrated tagging and catch-at-age analysis (ITCAAN) models  
10 (Maunder, 2001; Goethel et al., 2015b; Vincent et al., 2017), which incorporate tag-recovery data within a  
11 statistical catch-at-age assessment model, are spatially-explicit assessments that can assess and help manage  
12 mixed stocks.

13 Two approaches are generally used to analyze tag-recovery data. The most common approach is for  
14 tag recoveries to be conditioned on the number of tags released (release-conditioned framework) (Brownie  
15 et al., 1987; Hoenig et al., 1998; Frusher and Hoenig, 2003; Latour et al., 2003; Jiang et al., 2007). We  
16 refer to this approach as a release-conditioned framework as this accurately describes the denominator of  
17 the recovery probability, but it has also been called the tag-conditioned model (McGarvey and Feenstra,  
18 2002; McGarvey, 2009; McGarvey et al., 2010). The number and probability of tags never recovered are  
19 an important component of a release-conditioned framework. The probability of never recovering a tag is  
20 influenced by several tag-loss processes including tag reporting, tagging mortality, and tag shedding; these  
21 tag-loss processes must be accounted for in a release-conditioned framework to prevent biased parameter  
22 estimates (Hampton, 1997; Denson et al., 2002; Cowen et al., 2009; Brenden et al., 2010; Vandergoot et al.,  
23 2012). The other tagging framework is to condition tag recoveries on the total number of recoveries (McGar-  
24 vey and Feenstra, 2002; McGarvey, 2009). To remain consistent with published literature, we refer to this  
25 method as the recapture-conditioned framework; however, the likelihood formula uses terminal tag recover-  
26 ies (i.e. tags that were caught and returned to the tagging agency). The recapture-conditioned framework  
27 was proposed to eliminate the need to account for tag-loss processes (e.g., tag reporting) when estimating  
28 movement rates from tag-recovery data (McGarvey and Feenstra, 2002). Removing the need to account for  
29 tag-loss processes can be beneficial because studies to accurately estimate parameters associated with these

30 processes can be expensive and difficult to complete. The framework for the recapture-conditioned formu-  
31 lation was derived from the following property: when tag-loss processes such as tag reporting are constant,  
32 they cancel out of likelihood equations and therefore do not need to be estimated (McGarvey and Feen-  
33 stra, 2002). However, the original tagging framework required external estimates of spatially explicit fishing  
34 mortality rates and implicitly assumed that tag-loss processes were constant both temporally and spatially.  
35 Whether the assumption of spatially and temporally constant tag-loss processes could be met empirically is  
36 questionable. If tag-loss processes are not spatially constant, they do not fully cancel out of the likelihood,  
37 and if not accounted for in the model could lead to biased parameter estimates. The recapture-conditioned  
38 framework can be reformulated to include a parameter for any tag-loss processes that is deemed to not be  
39 constant. However, simulation testing of such formulation of a recapture-conditioned tagging framework has  
40 not been conducted and the ability to estimate tag-shedding parameters, such as reporting rate, within a  
41 recapture-conditioned ITCAAN is unknown. The recapture-conditioned framework was intended to nullify  
42 the need to account for tag-loss processes required for a release-conditioned analysis. However, if some tag-  
43 loss estimates are available and are shown to be spatially variable these parameters could be input into a  
44 reformulated recapture-conditioned framework. Additionally, it would be beneficial to know how sensitive  
45 recapture-conditioned models are to tag-loss processes that are not spatially or temporally constant.

46 The recapture-conditioned framework has been infrequently used for analyzing tag-recovery data, al-  
47 though see McGarvey and Feenstra (2002) and McGarvey (2009). There also has been limited application  
48 and simulation evaluation of ITCAANs that incorporate a recapture-conditioned framework, although see  
49 McGarvey et al. (2010). As a result of its limited use, it is not presently known how complex of a parameter-  
50 ization (e.g. natural mortality estimation) can be handled by recapture-conditioned ITCAANs. The model  
51 has also not been tested using an alternative formulation described above whereby a specific tag-loss process  
52 (e.g., reporting rate) is not assumed to be constant.

53 We conducted a simulation study to investigate the performance of a recapture-conditioned ITCAAN  
54 based on walleye (*Sander vitreus*) populations in the Laurentian Great Lakes of North America. Walleye  
55 have been found to be highly migratory both in the Great Lakes (Wang et al., 2007; Zhao et al., 2011;  
56 Vandergoot and Brenden, 2014; Hayden et al., 2014) and in inland systems (Smith et al., 1952; Rasmussen  
57 et al., 2002; Herbst et al., 2016). For both the Great Lakes and inland systems, appropriately addressing  
58 walleye migration has been identified as a management challenge (Brenden et al., 2015; Herbst et al., 2017).  
59 Walleye are economically important in the Great Lakes region and are exploited both commercially and  
60 recreationally (Fielder and Bence, 2014; Wills et al., 2016). Walleye spawn in rivers or on shallow reefs  
61 during early spring. After spawning, walleye disperse throughout the Great Lakes (Wang et al., 2007; Zhao  
62 et al., 2011; Vandergoot and Brenden, 2014; Hayden et al., 2014), but typically return annually to natal

63 regions to spawn (Stepien and Faber, 1998; Haponski and Stepien, 2014; Hayden et al., 2014; Wilson et al.,  
64 2017).

65 The largest walleye fisheries in the Great Lakes are in Lakes Erie and Huron, which are connected via  
66 Lake St. Clair and the Detroit and St. Clair Rivers. Walleye abundance in Lake Huron has been estimated  
67 to be between one and four million fish (Fielder and Bence, 2014). In Lake Erie, abundance of walleye in  
68 the eastern basin of the lake has been estimated on the order of tens of thousands of fish (Zhao et al., 2011),  
69 whereas abundance in Lake Erie’s western basin is believed to be closer to tens of millions of fish (Wills  
70 et al., 2016). Tagging studies have found walleye migrating between Lakes Erie and Huron (Wang et al.,  
71 2007; Hayden et al., 2014; Vandergoot and Brenden, 2014). Intermixing rates of walleye from some spawning  
72 populations in Lake Erie’s western basin to Lake Huron and the eastern basin of Lake Erie have been  
73 estimated at around 1 to 2% (Wang et al., 2007; Fielder and Bence, 2014; Vandergoot and Brenden, 2014).  
74 This rate of intermixing may be low, but a considerable amount of the harvest in all regions may originate  
75 from the western basin population given region-specific differences in population abundances (McParland  
76 et al., 1999; Brenden et al., 2015). Reporting rates of tagged fish have been found to be fishery dependent,  
77 with commercial fishery reporting in Canadian waters being much lower than recreational fishery reporting  
78 in U.S. waters. Factors that can lead to spatially varying reporting rates include how well the tagging  
79 study is advertised, degree of apathy toward the tagging study, differing language between regions, or region  
80 specific relationships with the agency conducting the tagging study (Hoenig et al., 1998; Denson et al., 2002;  
81 Vandergoot et al., 2012), which can be associated with the nature of the fishery (e.g., commercial versus  
82 recreational). Interest in developing spatially-explicit models to assist with the management of Lakes Erie  
83 and Huron walleye has increased in recent years due to recognition of the movement between the lakes and  
84 the value of the respective fisheries (Fielder and Bence, 2014; Wills et al., 2016).

85 The purpose of this research was to evaluate the bias, precision, and robustness of model parameters for  
86 a recapture-conditioned ITCAAN for populations that display natal homing. Specifically, we investigated  
87 how bias and precision of parameter estimates were affected by the following: 1. whether movement, natural  
88 mortality, and/or reporting rates were estimated and how performance was affected by population intermix-  
89 ing levels; 2. spatial variability in reporting rates among regions and whether reporting rates were estimated  
90 in the ITCAAN or presumed to be constant; 3. misspecification of natural mortality when the parameter is  
91 treated as known within the recapture-conditioned ITCAAN; 4. tag shedding; and 5. parity in productivities  
92 of the spawning populations. Vincent et al. (2017) conducted similar evaluations for a release-conditioned  
93 ITCAAN; consequently, we were also able to compare the performance between the two ITCAAN frame-  
94 works. We were motivated to explore the performance of both ITCAAN frameworks to spatially varying  
95 reporting rates because in our case study reporting rates are unlikely to be spatially constant. We were also

106 interested in how tag shedding and potential bias in external estimates of these rates would affect model  
107 estimates. The intention of this research was to provide information to fishery managers and scientist on how  
108 a recapture-conditioned ITCAAN performed when assumptions are violated and provide some guidance as  
109 to situations where a recapture- or release-conditioned ITCAAN may be preferable over the other approach.

## 100 **Methods**

101 An operating model generated the true dynamics of simulated fish populations and tagged cohorts.  
102 From this operating model, 40 year time series of observed data were simulated, which were then fit  
103 to a recapture-conditioned ITCAAN. For scenarios not previously evaluated by Vincent et al. (2017),  
104 we also fit a release-conditioned ITCAAN to the generated data. The operating model used in this re-  
105 search was identical to that presented in Vincent et al. (2017), but will be summarized here; equations  
106 and parameter values for the operating model are provided in the Supplementary Materials (available at:  
107 <https://figshare.com/s/40f510c92539da065558>). The operating model simulated the abundances and dynam-  
108 ics of four populations that intermixed among four regions. Fish were assumed to aggregate in their natal  
109 region at the beginning of each year to spawn (i.e., 100% spawning site fidelity was assumed). Fishing was  
110 assumed to not occur while fish were aggregated for spawning. Recruitment was simulated from population-  
111 specific Ricker stock-recruitment functions with a first-order autoregressive process error. Values for the  
112 first-order autoregressive process for each population were randomly drawn from posterior distributions for  
113 Percidae (Thorson et al., 2014). Equilibrium stock sizes and productivities (i.e., stock-recruit steepnesses)  
114 were assumed to differ among the four populations for most scenarios (Table 1); values for these are reported  
115 in Supplementary Materials Table 2. The stock-recruit parameters for population 1 were based on Lake  
116 Huron walleye, while the stock-recruit parameters for populations 2, 3, and 4 were based on western, central,  
117 and eastern Lake Erie walleye, respectively.

118 After spawning, fish were assumed to instantaneously mix among the four regions using a box-transfer  
119 model (Goethel et al., 2011); after moving to an area, fish were assumed to remain for the rest of the year  
120 and were subject to fishing. The exploitation rates experienced by the mixed stocks were region-specific.  
121 Apical fishing mortality rates for the regions were generated using first-order autoregressive processes with  
122 regionally-unique means based on estimated fishing mortalities for Lakes Erie and Huron (Table 1; see  
123 Supplementary Materials Table 2). Region-specific catchability coefficients and lognormal multiplicative ob-  
124 servation errors with CVs of 10% were used to simulate time series of fishing effort. The instantaneous natural  
125 mortality rate for all ages was assumed to be  $0.32 \text{ year}^{-1}$  in all populations for the entire time series of the  
126 simulations. Age-specific selectivities for the fishery in each region were assumed to be temporally constant  
127 but regionally unique (Supplementary Materials Table 1). Observed region-specific annual harvest data (i.e.,

128 summed across populations) were generated from actual harvest multiplied by lognormal observation errors  
 129 with CVs of 10% for the entire time series. Observed harvest age composition for each region and year was  
 130 simulated from multinomial distributions that used the actual harvested age composition as the underlying  
 131 proportions and assumed a sample size of 100 fish. Fishery-independent surveys were simulated to occur  
 132 in the regions during October (i.e., during the intermixed period each year). Region-specific catchabilities  
 133 and age-specific selectivities were used to simulate a survey catch per effort time series with multiplicative  
 134 lognormal observation errors with CVs of 20%. Age-composition data for all years were also simulated for  
 135 each survey from multinomial distributions based on the intermixed abundance present in October with  
 136 sample sizes of 100.

137 In the simulation, 2000 fish were tagged annually from each population at the beginning of the year  
 138 when fish had returned to their associated spawning grounds. The simulation assumed that all recoveries of  
 139 tagged fish were terminal recoveries and did not account for fishery agency encounters of tagged fish during  
 140 surveys. Consequently, all releases of tagged fish were simulated to be newly tagged fish. Simulations with  
 141 an abundance of less than 40000 fish for any of the four populations were excluded and replaced with a  
 142 new simulation, because we believed it was unlikely that more than 5% of a population would be tagged  
 143 in a particular year. The fate (i.e., survived, harvested, or died due to natural causes) of tagged fish each  
 144 year were generated from multinomial distributions with expected proportions equal to the dynamics of the  
 145 at-large populations (e.g., exploitation rate). Tag reporting was assumed to be imperfect (i.e., < 100%)  
 146 for all simulations, with different assumed regional reporting rates for different scenarios (see Simulation  
 147 Scenarios). The number of tags recovered were simulated using a binomial process based on the number of  
 148 tagged fish harvested by the region specific fisheries and the regional reporting rate. The number of terminal  
 149 recoveries of tagged fish were used in the likelihood function of the ITCAANs.

150 Unless otherwise specified, the operating model assumed no tag shedding occurred. For the three scenarios  
 151 where tag shedding was assumed to occur, tag-retention probability was calculated using the following  
 152 equation:

$$153 \quad \Pi_{y,r} = \chi_r * e^{-\Omega_r * y} \quad (1)$$

154 where  $\Pi$  is the proportion of tags retained,  $\chi_r$  is the region-specific tag-retention rate immediately after  
 155 tagging,  $\Omega_r$  is the region-specific chronic shedding rate, and  $y$  is the number of years after release. The  
 156 proportion of tags retained given the number of years after release was multiplied by the number of tags  
 157 alive at the beginning of the year to simulate tag shedding (See Supplementary Materials for equations).

158 The data sources generated from the operating model were region-specific harvest in numbers, harvest  
 159 age composition, region-specific mixed population survey catch per effort, survey age composition, number

160 of tags released each year, number of tags recovered by each fishery each year, and fishery effort per region.  
 161 Both the operating and ITCAANs tracked the dynamics of walleye between the ages of 2 and 7, with the  
 162 last age group in the model aggregating all fish age 7 and older. The operating model was programmed in  
 163 R version 3.5.1 (R Core Team, 2016), whereas the ITCAAN was programmed in AD Model Builder version  
 164 12.0 (Fournier et al., 2012). A complete description and code for the operating and ITCAANs can be found  
 165 in the Supplementary Materials (available at: <https://figshare.com/s/40f510c92539da065558>).

### 166 *ITCAAN Models*

167 Two ITCAANs were used in this research to evaluate their relative performance, a recapture-conditioned  
 168 and a release-conditioned model. Parameters and equations for the recapture-conditioned ITCAAN are pre-  
 169 sented in the Supplementary Materials. In brief, the ITCAAN was structured to estimate the dynamics of  
 170 four populations that intermix among four regions and display natal homing every year. Recruitment was  
 171 estimated through a random-walk process for each region with the last two years of recruitment set equal to  
 172 the mean for the previous three years. Annual fishery catchabilities were modeled using random-walk pro-  
 173 cesses, but region-specific survey catchabilities were assumed constant through time. Selectivities for surveys  
 174 and fisheries were estimated as age-specific parameters for ages 2 through 7 and assumed constant through  
 175 time. Movement rates, including the proportion remaining in the natal region were estimated through a  
 176 multinomial logit transformation that constrained movement rates to be between 0 and 1 (Vandergoot and  
 177 Brenden, 2014). Catch and effort data were assumed to be lognormally distributed, whereas age compo-  
 178 sition data for the surveys and the fisheries and the tag-recovery data were assumed to be multinomially  
 179 distributed.

180 The negative log likelihood equation for the tagging component of the recapture-conditioned ITCAAN,  
 181 ignoring scaling constants, was:

$$182 \quad L = - \sum_l \sum_r \sum_y \log \left( \frac{\widehat{d}_{l,y,r}}{\sum_y \sum_r \widehat{d}_{l,y,r}} \right) * d_{l,y,r} \quad (2)$$

183 where  $d$  is the observed number of tags recovered and  $\widehat{d}$  is the model predicted number of tags recovered.  
 184 The subscripts for  $d$  are the unique release event for each population and year ( $l$ ), the year of recovery ( $y$ )  
 185 and the region of recovery ( $r$ ). The predicted number of tags recovered from a tagged cohort were calculated  
 186 as:

$$187 \quad \widehat{d}_{l,y,r} = \sum_a \widehat{n}_{l,y,a} \Pi_{y,r} \widehat{T}_{p,r} \frac{\widehat{F}_{y,a,r}}{\widehat{Z}_{y,a,r}} (1 - \widehat{S}_{y,a,r}) \widehat{\Upsilon}_r \quad (3)$$

188 where  $\widehat{n}_{l,y,a}$  is the predicted number of tags alive in year  $y$  of age  $a$  from tag release group  $l$  that is year  
 189 and population specific,  $\Pi_{y,r}$  is the region-specific tag retention probability,  $\widehat{T}_{p,r}$  is the predicted movement

190 rate from population  $p$  to region  $r$ ,  $\hat{F}_{y,a,r}$  is the predicted instantaneous fishing mortality rate,  $\hat{Z}_{y,a,r}$  is the  
 191 predicted instantaneous total mortality rate,  $\hat{S}_{y,a,r}$  is the finite survival rate, and  $\hat{\Upsilon}_r$  are the region-specific  
 192 reporting rates. This formulation of the recapture-conditioned likelihood is different from that originally  
 193 presented by McGarvey and Feenstra (2002) in that it includes specific parameters for the tag-reporting and  
 194 tag-shedding rates. This formulation allows for fishery-specific reporting rates, but if the reporting rates are  
 195 fixed at a spatially constant value they cancel from the likelihood and the model estimates are identical to the  
 196 original formulation. Similarly, the recapture-conditioned ITCAAN assumed that tag-retention probability  
 197 equaled 1 for all scenarios and thus did not affect parameter estimates.

198 In a recapture-conditioned framework, actual reporting rates for the regions are not estimable because  
 199 unique solutions do not exist given Equations (2) and (3). In other words, region-specific reporting rates  
 200 of 10%, 20%, 30%, and 40% would produce the same model fit (i.e., same likelihood) as region-specific  
 201 reporting rates of 20%, 40%, 60%, and 80%. In this research, we explored the estimability of relative  
 202 reporting rates in a recapture-conditioned framework by fixing the reporting rate for region one to a value  
 203 of 1.0 and then estimated the reporting rates for the remaining regions as bounded parameters between 0.01  
 204 and 100. The relative reporting rates formulation produces unique solutions, and in the above examples  
 205 would equal 1.0, 2.0, 3.0, and 4.0 if scaled relative to region 1. For scenarios where reporting rates were not  
 206 estimated but treated as fixed values, region-specific reporting rates were treated as relative values for the  
 207 recapture-conditioned ITCAAN. For the recapture-conditioned ITCAAN, fixing the relative reporting rates  
 208 equal among regions was equivalent to assuming that reporting rates canceled out of the likelihood equation.

209 Although release-conditioned ITCAAN results for many of the simulation scenarios were directly available  
 210 from Vincent et al. (2017), we elected to refit the release-conditioned ITCAAN to the time series generated  
 211 for this research to ensure consistency when comparing with recapture-conditioned ITCAAN results. The  
 212 release-conditioned ITCAAN used for this study was identical to that described in Vincent et al. (2017),  
 213 with two exceptions. First, the tagging shedding formulation in the release-conditioned ITCAAN used in  
 214 this research incorporated an initial tag loss which was not previously included. Secondly, we scaled the  
 215 negative log likelihood for multinomially distributed random variables to equal zero when the data were fit  
 216 perfectly. These changes were made to better represent the tag shedding processes present in the study  
 217 system and to improve model convergence, but were otherwise not expected to affect parameter estimates.  
 218 For the tag shedding scenarios that were not previously conducted by Vincent et al. (2017), the value of the  
 219 tag retention probability input into the ITCAAN ( $\Pi_{y,r}$ ) were calculated using Equation (1) with different  
 220 values of  $\Omega$ . All other scenarios assumed  $\Pi_{y,r}$  equaled 1 for all years after recapture.

221 ITCAANs were fit to data time series from the operating model by highest posterior density estimation,  
 222 also referred to as maximum penalized likelihood estimation (Stewart et al., 2013). We assessed convergence



223 of the ITCAANs by whether the maximum gradient across all parameters was less than 0.05 and the model  
224 produced a positive-definite Hessian matrix. This cutoff for the maximum gradient was determined after  
225 preliminary results for the low-movement scenario showed that gradients smaller than this were infrequent  
226 and estimates were within the range of plausibility. Simulated datasets were fit by the ITCAANs until 1000  
227 datasets had converged on estimates. Table 2 presents the number of simulations that were required to reach  
228 a sample size of 1000 and the number of simulations that failed to converge for either criteria.

### 229 *Simulation Scenarios*

230 Three groups of scenarios were investigated to examine performance of the recapture-conditioned IT-  
231 CAAN and to compare its performance with a release-conditioned ITCAAN. The first group of scenarios  
232 evaluated the estimability of movement, natural mortality, and/or relative tag reporting rates under different  
233 levels of population intermixing. The second group of scenarios analyzed the influence of spatially varying  
234 reporting rates on parameter estimates when either estimating relative reporting rates or assuming the re-  
235 porting rates were regionally constant (i.e., canceled out of likelihood for the recapture-conditioned model).  
236 The third group of scenarios evaluated the influence of misspecifying natural mortality in an ITCAAN, tag  
237 shedding, and the effect of equal productivities among populations. Model assumptions for each simulation  
238 scenario described below were identical for both the recapture- and release-conditioned ITCAANs unless  
239 otherwise stated and both models were fit to the same simulated data. The recapture-conditioned ITCAAN  
240 was formulated as reporting rates relative to region 1, whereas the release-conditioned ITCAAN estimated  
241 reporting rates for all regions. Therefore, we denote this difference throughout the paper with the notation  
242 “(relative) reporting rates”.

### 243 *Group 1: Estimation of Movement, Relative Reporting Rates, and Natural Mortality Under Varying Inter-* 244 *mixing Rates*

245 Simulations were conducted for a total of 20 scenarios to examine how ITCAAN performance was influ-  
246 enced by the intermixing rate of the simulated populations and the estimation of rates of movement, natural  
247 mortality, and/or tag reporting. Four assumed intermixing scenarios were crossed with five ITCAAN pa-  
248 rameterizations. The four intermixing scenarios consisted of different rates of movement from natal region  
249 to each non-natal region. The examined rates were 1, 5, 10, and 20% of the population. For example, under  
250 a 20% intermixing rate 40% of the populations remained in their natal region and 20% of the populations  
251 moved to each of the other three regions. The five ITCAAN parameterizations varied with regards to whether  
252 movements, natural mortality, and/or (relative) reporting rates were estimated as part of the model fitting  
253 process or fixed at the true values assumed in the operating model. The first parameterization assumed  
254 that movement, natural mortality, and (relative) reporting rates were fixed at their true values and this was

255 the only parameterization where movement rates were not estimated (MvFix). The second parameteriza-  
256 tion estimated movement rates, but assumed natural mortality and (relative) reporting rates were fixed at  
257 their true values (MRFix). The third parameterization estimated movement and natural mortality rates,  
258 but assumed (relative) reporting rates were fixed at their true values (RFix). The fourth parameterization  
259 estimated movement and (relative) reporting rates but fixed natural mortality at the true value (MFix). The  
260 final parameterization estimated movement, natural mortality, and (relative) reporting rates (NoFix). The  
261 results are labeled using the parameterization label of the ITCAAN followed by the intermixing rate in the  
262 operating model. For example, MFix20 refers to the ITCAAN parameterization where (relative) reporting  
263 rates and movement rates were estimated, but natural mortality was fixed in the ITCAAN and the operating  
264 model assumed a 20% intermixing rate.

### 265 *Group 2: Regionally Varying Reporting Rates*

266 The second group of scenarios investigated the influence of regionally varying reporting rates in the  
267 operating model on different treatments of reporting rates in the ITCAANs. All scenarios in this group  
268 assumed a 20% intermixing rate for the simulated populations and estimated natural mortality as part of the  
269 ITCAAN fitting process. We investigated two scenarios of spatially varying reporting rates in the operating  
270 model. The first scenario with reporting rates varying spatially (RV1) assumed that the reporting rates were  
271 the highest for regions where the natal populations were the least productive (Table 1). The second scenario  
272 with reporting rates varying (RV2) assumed that the reporting rate was the highest in regions where the natal  
273 populations were the most productive and decreased with decreasing productivity. For these two spatially  
274 varying reporting rate scenarios, we attempted to estimate relative reporting rates with the recapture-  
275 conditioned ITCAAN and reporting rates for each region with the release-conditioned ITCAAN (ITCAAN  
276 section). We also explored the consequence of assuming the reporting rates were constant in the ITCAANs  
277 under these two spatially varying reporting rate scenarios. For the recapture-conditioned ITCAAN we fixed  
278 the relative reporting rates for all regions to 1.0, which is analogous to the original formulation employed by  
279 McGarvey and Feenstra (2002). For the release-conditioned ITCAAN we estimated a single reporting rate  
280 parameter that was shared among the four model regions. Scenarios in this group that estimated (relative)  
281 reporting rates were referred to as Est scenarios (e.g., RV1Est); we refer to simulations when (relative)  
282 reporting rates were assumed to be spatially constant as Const scenarios (e.g., RV1Const). Scenarios with  
283 spatially varying reporting rates were not included in the simulations conducted by Vincent et al. (2017) for  
284 a released-conditioned ITCAAN, therefore results from the simulations are described in greater detail than  
285 the other scenarios and without citation to Vincent et al. (2017).

286 *Group 3: Sensitivity to Misspecified Natural Mortality, Equal Productivity, and Tag Shedding*

287 The third group of simulations investigated the consequences of misspecifying natural mortality in the  
288 ITCAAN, the effect of assuming equal productivities among spawning populations in the operating model,  
289 and a simulated tag-shedding process. The tag-shedding scenario assumed an intermixing rate of 10%, while  
290 all other scenarios in this group assumed a 20% intermixing rate in the operating model. The first scenario  
291 examined the influence of misspecifying the natural mortality in the ITCAAN at 0.5 times the true value  
292 (i.e., 0.16). This scenario was referred to as SensU because it evaluated sensitivity to natural mortality that  
293 was specified to be less than (under) the true value. The second scenario in this group examined the effect  
294 of specifying the natural mortality in the ITCAAN at 1.5 times the true value (i.e., 0.48). This scenario  
295 was referred to as SensO because it evaluated the sensitivity of parameter estimates to specifying natural  
296 mortality to be greater than (over) the true value. For both the SensU and SensO scenarios, movement  
297 and (relative) reporting rates were estimated as part of the ITCAAN fitting process. The third scenario in  
298 this group evaluated how parity in productivities among the four populations affected ITCAAN parameter  
299 estimation. This scenario was referred to as EqProd to stand for equal productivities among populations. For  
300 this scenario, all populations were assumed to have the same stock-recruitment parameters in the operating  
301 model (i.e., Ricker parameters for population 2 in other scenarios), and movement, natural mortality, and  
302 (relative) reporting rates were estimated in the ITCAAN. The fourth through sixth scenarios in this group  
303 simulated the shedding of tags at rates that were specific to each region of release (Vandergoot et al., 2012;  
304 Supplementary Materials Table 2). These three scenarios assumed that natural mortality and reporting rates  
305 were known and fixed in the ITCAANs. The recapture-conditioned ITCAAN was not provided information  
306 regarding tag shedding within the model (i.e., assuming that a shedding experiment was not conducted)  
307 and is only presented under the ShedExact scenario. Three assumptions regarding the estimated accuracy  
308 of the tag-loss process parameters input into the release-conditioned ITCAAN were tested: exact knowledge  
309 of the parameters (ShedExact), chronic tag-shedding rates ( $\Omega$ ) were 20% overestimated (ShedOver), and  
310 chronic tag-shedding rates ( $\Omega$ ) were 20% underestimated (ShedUnder). The ShedExact scenario for the  
311 release-conditioned ITCAAN provided the true proportion of tags that retained their tags. The resulting  
312 proportion of tags retained calculated using Equation (1) was then used in the release-conditioned ITCAAN  
313 during estimation of parameters. The tag-shedding scenarios were not included in the simulations conducted  
314 by Vincent et al. (2017) for a released-conditioned ITCAAN, therefore results from the simulations are  
315 described in greater detail than the other scenarios and without citation to Vincent et al. (2017).

## 316 *Performance Metrics*

317 ITCAAN performance was evaluated by comparing parameter estimates to the true values generated by  
318 the operating model. Percent relative error  $((\text{estimate} - \text{true})/\text{true} \times 100\%)$  was calculated for all parameters,  
319 except movement which was calculated as actual error. Parameters that were age specific (e.g, selectivity,  
320 results shown in the Supplementary Materials) and year specific (e.g., abundance) calculated the relative  
321 error for all parameters in a converged simulation and then aggregated by region or population for plotting.  
322 For example, the boxplots of population abundance summarizes 40 years of error in abundance estimates  
323 times 1000 simulations. Error in movement rate estimates was assessed as actual error (estimate - true)  
324 to facilitate comparisons across scenarios, though relative errors of movement rates are presented in the  
325 Supplementary Materials. For the sake of brevity, we discuss the bias and precision of model estimates of  
326 total abundance (i.e., abundance summed over all populations), spawning population abundance, (relative)  
327 reporting rate, natural mortality, and movement rates. Performance of all other parameter estimates are  
328 presented in the Supplementary Materials. Parameters not presented in the manuscript either showed no  
329 bias in estimates or were biased similar to population abundances, though not always in the same direction.  
330 Medians of relative or actual errors were used to evaluate model bias and the interquartile ranges (IQRs)  
331 were used to evaluate precision. Bias and precision of parameter estimates were compared across scenarios  
332 to give a relative view of ITCAAN performance between the recapture- and release-conditioned frameworks.  
333 Only the results for the release-conditioned ITCAAN for the Group 2 and Group 3 tag-shedding scenarios  
334 are presented in detail because results of all other scenarios are described in Vincent et al. (2017); the  
335 presentation of results for all other scenarios is solely for comparing with results for a recapture-conditioned  
336 model. In addition to using estimation errors as a means to evaluate model performance, we also considered  
337 the number of simulations that failed to converge by the two selection criteria for each scenario as an indicator  
338 of model performance (Table 2).

## 339 **Results**

### 340 *Model Performance*

#### 341 *ITCAAN Model Convergence*

342 Convergence of the ITCAANs varied depending on the intermixing level assumed in the operating model  
343 and the tagging framework (Table 2). A convergence rate greater than 90% was observed for simulation  
344 scenarios where the assumed intermixing rates were 5% or greater. For scenarios with intermixing greater  
345 than 5% and (relative) reporting rates fixed, the recapture-conditioned ITCAAN exhibited marginally better  
346 convergence properties because it was less likely to have a non-positive definite Hessian than the release-  
347 conditioned ITCAAN (Vincent et al., 2017). For scenarios with intermixing greater than 5% and (relative)

348 reporting rates estimated, the recapture-conditioned ITCAAN exhibited worth convergence properties be-  
349 cause it had more large maximum gradients compared to the release-conditioned ITCAAN (Vincent et al.,  
350 2017). Simulation scenarios with a 1% intermixing rate had between 74 and 86% of simulations converged  
351 for the recapture-conditioned ITCAANs, which was less than the convergence rate for a release-conditioned  
352 ITCAAN with similar scenarios (Vincent et al., 2017). Simulations at the 1% intermixing rate for the  
353 recapture-conditioned ITCAANs typically failed to converge due to a maximum gradient greater than 0.05.  
354 The convergence rate of models decreased to approximately 80% for the recapture- and release-conditioned  
355 ITCAANs that assumed a spatially constant reporting rate when the operating model assumed the reporting  
356 rate was highest in the least productive natal regions (RV1Const; Table 2). However, convergence for the  
357 other configuration of spatially varying reporting rates (RV2Const) did not display such lack of convergence.  
358 A 100% convergence rate occurred for the equal productivity scenario for both ITCAANs.

### 359 *Total Abundance Relative Error*

360 Bias and precision of total abundance summed across all populations, as measured by median and IQR  
361 relative error respectively, varied among the simulation scenarios. Median relative errors in total abundance  
362 for the recapture-conditioned ITCAANs in Group 1 scenarios were between -0.17% and -8.33% suggesting  
363 a small but consistent negative bias in total abundance estimates, which was consistent with the release-  
364 conditioned ITCAAN (Vincent et al., 2017). For the recapture-conditioned ITCAAN model in scenarios  
365 where natural mortality was estimated (i.e., RFix and NoFix scenarios), total abundance estimates had  
366 greater bias and variability (i.e., lower precision) compared to scenarios where natural mortality was fixed  
367 at the true value (i.e., MvFix, MRFix, and MFix; Figure 1). Scenarios in which relative reporting rates  
368 were estimated, but natural mortality was fixed for the recapture-conditioned ITCAAN (i.e., MFix) had  
369 levels of bias and precision similar to scenarios where both natural mortality and reporting rates were fixed  
370 (i.e., MRFix; Figure 1). For the recapture-conditioned ITCAAN scenarios in which natural mortality was  
371 estimated, the highest intermixing rates (i.e., 20%) resulted in the lowest precision in total abundance  
372 estimates. Scenarios for the release-conditioned ITCAAN where reporting rates were estimated (i.e., MFix  
373 and NoFix) had greater bias and variability compared to scenarios where the reporting rate was fixed at the  
374 true value (Vincent et al., 2017). Total abundance estimates were most biased and variable for the release-  
375 conditioned ITCAAN when both reporting rates and natural mortality were estimated (Vincent et al., 2017).  
376 For all Group 1 scenarios, the recapture-conditioned model performed worse in estimating overall abundance  
377 (i.e. higher bias and variability) compared to the release-conditioned model.

378 The influence of spatially varying reporting rates in the operating model on total abundance estimates de-  
379 pended on whether reporting rates were estimated as spatially variable or constant and whether a recapture-

380 or release-conditioned framework was assumed in the ITCAAN. When reporting rates varied spatially and  
381 were estimated (RV1Est and RV2Est), bias and precision of total abundance estimates in the recapture- and  
382 release-conditioned ITCAANs were similar to the RFix20 and NoFix20 scenarios. When reporting rates were  
383 assumed to be spatially constant in the recapture-conditioned ITCAAN median estimates were marginally  
384 above zero for the RV1Const scenario, but were more negatively biased for the RV2Const scenario; variability  
385 of total abundance estimates by the recapture-conditioned ITCAAN increased (i.e, precision decreased) for  
386 both these scenarios (Figure 1). The release-conditioned ITCAAN had a large positive bias and variability in  
387 total abundance estimates when a spatially constant reporting rate was estimated for both spatially varying  
388 scenarios (RV1Const and RV2Const; Figure 1). For scenarios that assumed spatially constant reporting  
389 rates, the IQRs of estimates from the recapture-conditioned ITCAAN were approximately two times larger  
390 than the RFix20 or NoFix20 scenarios, whereas the release-conditioned ITCAAN estimates were approx-  
391 imately five times larger than the NoFix20 scenario. Both ITCAAN frameworks performed better when  
392 estimating spatially variable reporting rates compared to estimating a spatially constant reporting rate for  
393 scenarios where the operating model simulated spatially varying reporting rates.

394 The misspecification of natural mortality at 0.5 times the true value resulted in an underestimation of  
395 the total abundance with a median relative error of approximately -50% for ITCAANs with either tagging  
396 framework. Conversely, setting natural mortality at 1.5 times the true value in the ITCAAN resulted in a  
397 positive bias in total abundance with a median relative error equal to 374% and 131% for the recapture- and  
398 release-conditioned ITCAANs, respectively (Vincent et al., 2017). Specifying natural mortality above the  
399 true value also resulted in the largest IQR in total abundance among the examined scenarios for the recapture-  
400 conditioned ITCAAN (Figure 1). When all populations were assumed to have equal productivity levels, total  
401 abundance estimates from the ITCAAN had bias similar to the NoFix20 scenario, but marginally better  
402 precision (Figure 1). Total abundance estimates were unbiased and precise for the recapture-conditioned  
403 ITCAAN in the scenario with tag shedding simulated to occur with both natural mortality and reporting  
404 rates fixed at the true value (ShedExact). The estimates for the release-conditioned ITCAAN in the tag-  
405 shedding scenario was unbiased when provided the exact shedding rates, but were biased by 5% in the  
406 opposite direction of the 20% bias in the chronic tag-shedding rate.

#### 407 *Population Abundances Relative Error*

408 Estimates of individual population abundances had larger median relative error bias and variability (rela-  
409 tive error IQR) than estimates of total abundance. Abundance estimates of population 2, the most productive  
410 population, for Group 1 scenarios were generally negatively biased, while biases for all other populations were  
411 positive (Figure 2). As intermixing rates increased, the bias and variability of population abundance esti-

412 mates generally increased for recapture-conditioned ITCAANs. Among scenarios with low intermixing rates  
413 for the recapture-conditioned ITCAAN, the largest bias and variability in population abundance for popula-  
414 tions 2 and 4 occurred when natural mortality was estimated (RFix and NoFix; Figure 2); for populations 1  
415 and 3, the largest bias and variability occurred in scenarios where reporting rates were estimated (MFix and  
416 NoFix; Figure 2). Scenarios of high intermixing, 10% and larger, for the recapture-conditioned ITCAANs  
417 were more biased and variable than the low intermixing scenarios and performed worst when reporting rates  
418 were estimated (MFix20 and NoFix2; Figure 2). For all scenarios in Group 1 the recapture-conditioned  
419 ITCAAN performed worse (less accurate and precise) than the release-conditioned ITCAAN.

420 Individual population abundances typically were most biased for Group 2 scenarios when reporting rates  
421 were assumed to be spatially constant (RV1Const and RV2Const). Bias and precision of individual popula-  
422 tion abundance estimates for models that estimated (relative) reporting rates under both spatially varying  
423 reporting rates scenarios (RV1Est and RV2Est) were similar to the NoFix20 scenario for both the recapture-  
424 and release-conditioned ITCAANs. The estimates of population abundance from the recapture-conditioned  
425 ITCAAN were more biased and variable compared to the release-conditioned ITCAAN when spatially vary-  
426 ing reporting rates were estimated. However, the recapture-conditioned ITCAAN estimates were less biased  
427 and variable when a spatially constant reporting rate was assumed. For ITCAANs that assumed a spatially  
428 constant reporting rate (RV1Const and RV2Const), bias in individual population abundance estimates were  
429 greatly influenced by which region had the highest assumed reporting rate. When the highest reporting rates  
430 occurred in regions associated with the most productive populations (RV1Const), abundance estimates for  
431 populations 2 and 4 were severely underestimated, whereas abundance of population 3 was severely overes-  
432 timated, median relative error approximately 5000% and 10000% for the recapture- and release-conditioned  
433 ITCAANs (Figure 3). Estimates of population 1 in the RV1Const scenario by the recapture- and release-  
434 conditioned ITCAAN were both positively biased, but were less variable for the recapture-conditioned IT-  
435 CAAN. When the highest reporting rates occurred in regions associated with the least productive populations  
436 (RV2Const) the recapture- and release-conditioned ITCAANs underestimated abundance of populations 2  
437 and 3, but greatly overestimated the abundance of populations 1 and 4 (Figure 3).

438 Incorrect specification of natural mortality had large consequences on population estimates for both  
439 tagging frameworks (Figure 3; Vincent et al., 2017). When natural mortality was specified at 0.5 times  
440 the true value in the ITCAAN (SensU), abundance estimates for population 1 and 3 were positively biased,  
441 whereas abundance estimates for population 2 were negatively biased for both tagging frameworks (Figure 3).  
442 Estimates of population 4 abundance for the SensU scenario were unbiased for the recapture-conditioned  
443 ITCAAN, but greatly positively biased for the release-conditioned ITCAAN. When natural mortality was  
444 set at 1.5 times the true value in the ITCAAN, the recapture-conditioned ITCAAN significantly overesti-

445 mated all population abundances (Figure 3). Population abundance estimated under this scenario for the  
446 release-conditioned ITCAAN were overestimated for all populations except population 4, but were a much  
447 lower magnitude compared to the recapture-conditioned ITCAAN (Vincent et al., 2017). When the produc-  
448 tivities among the populations were equal, individual population abundance estimates were accurate and  
449 precise where precision was equal between populations for both tagging frameworks. Population abundance  
450 estimates for the equal productivities scenario were most variable for the recapture-conditioned ICTAAN  
451 model compared to the release-conditioned ITCAAN (Vincent et al., 2017). Bias and precision of estimates  
452 from the release-conditioned ITCAAN under tag-shedding scenarios were positive and similar among the  
453 scenarios for all populations except population 2. Estimates of population 2 were least biased when the  
454 release-conditioned ITCAAN was given tag-shedding rates under the true rates and most biased when given  
455 tag-shedding rates over the true value.

#### 456 *Natural Mortality and (Relative) Reporting Rates Relative Error*

457 Natural mortality estimates for Group 1 scenarios were accurate (median generally within  $\pm 5\%$ ), but  
458 precision (relative error IQR) varied across scenarios (Figure 4). For the recapture-conditioned ITCAAN,  
459 the variability of relative error for natural mortality was relatively consistent for the 1%, 5%, and 10%  
460 intermixing scenarios, but doubled for the 20% intermixing scenario. A negative bias in natural mortality  
461 estimates occurred when the intermixing rates were 20% for the recapture-conditioned ITCAAN. Estimation  
462 of relative reporting rates for the recapture-conditioned ITCAAN concurrently with natural mortality did not  
463 affect bias or precision of the natural mortality estimates, unlike the release-conditioned ITCAAN (Figure 4;  
464 Vincent et al., 2017). Estimates of natural mortality were much less precise and accurate for the recapture-  
465 conditioned ITCAAN than the release-conditioned ITCAAN (Vincent et al., 2017). For Group 2 scenarios,  
466 natural mortality estimates were comparably accurate when the (relative) reporting rates were estimated as  
467 spatially unique parameters (RV1Est and RV2Est) for both the recapture- and release-conditioned ITCAANs.  
468 When reporting rates were assumed spatially constant in the ITCAAN, a positive bias in natural mortality  
469 estimates occurred for both tagging frameworks in the scenario where reporting rates were the greatest in  
470 the region associated with the most productive population (RV1Const). Estimates of natural mortality  
471 from the recapture-conditioned ITCAAN in the scenario where reporting rates were the lowest in the region  
472 associated with the most productive population (RV2Const) were unbiased but the most variable among  
473 the investigated scenarios (Figure 4). Natural mortality estimates from the release-conditioned ITCAAN  
474 for the RV2Const scenario were very positively biased similar to the RV1Const scenario. For RV1Const  
475 and RV2Const scenarios, precision of natural mortality estimates was low compared to Group 1 scenarios  
476 for both tagging frameworks (Figure 4). Natural mortality estimates from the Group 3 scenario in which



477 spawning populations had equal productivities were similar in bias and precision to the NoFix20 scenario.

478 Bias and precision of relative reporting rates varied by intermixing rate scenario, region and tagging  
479 framework (Figure 4). For Group 1 scenarios, relative reporting rate estimates from the recapture-conditioned  
480 ITCAAN were mostly accurate for regions 2 and 4 across the evaluated intermixing levels; conversely, relative  
481 reporting rates for region 3 were negatively biased with the degree of bias increasing as the intermixing rate  
482 increased (Figure 4). For all regions, precision of the relative reporting rates improved with higher intermixing  
483 for the recapture-conditioned ITCAAN. Reporting rate estimates from the recapture-conditioned ITCAAN  
484 were more biased and variable compared to the release-conditioned estimates for regions 3 and 4 in except  
485 when intermixing rates were 20%. Conversely, reporting rate estimates for region 2 were less variable and  
486 biased for the recapture-conditioned model (Vincent et al., 2017).

487 For Group 2 scenarios, bias and precision of relative reporting rates varied depending on the spatial pat-  
488 tern of the reporting rates assumed in the operating and ITCAANs. When reporting rates varied spatially  
489 and were estimated as spatially independent parameters (R1Est and RV2Est), bias and precision of report-  
490 ing rate estimates were consistent with the NoFix20 scenario for both ITCAAN frameworks. Estimates of  
491 reporting rates from the release-conditioned ITCAAN were unbiased for the region with the highest report-  
492 ing rate but positively biased for all other regions, where estimates from all regions were highly variable.  
493 Misspecification of natural mortality both above and below the true value within the recapture-conditioned  
494 ITCAAN had comparatively little influence on estimates of relative reporting rates. Misspecification of nat-  
495 ural mortality above or below the true value in the release-conditioned ITCAAN resulted in large bias in  
496 reporting rate estimates in the same direction (Vincent et al., 2017). Estimates of relative reporting rates  
497 were unbiased and accurate for the scenario that assumed 20% intermixing and equal productivities among  
498 populations.

#### 499 *Movement Rate Actual Error*

500 For Group 1 scenarios, estimated movement rates from the recapture-conditioned ITCAAN were accurate  
501 and precise when reporting rates were fixed at the true values, with the most precise estimates at low  
502 intermixing rates (Figure 5). Movement rate estimates from the recapture-conditioned ITCAAN in scenarios  
503 where relative reporting rates were estimated were more variable and biased than when relative reporting  
504 rates were not estimated. Estimates of movement from both tagging frameworks for all regions were more  
505 variable as intermixing rates increased, but only estimates from the recapture-conditioned ITCAAN were  
506 more biased with increasing intermixing (Figure 5). Movement rate estimates from the recapture-conditioned  
507 ITCAAN were generally more biased and variable compared to the release-conditioned ITCAAN (Vincent  
508 et al., 2017).

509 Compared to the NoFix20 scenario, Group 2 scenarios with spatially varying reporting rates in the  
510 operating model and relative reporting rates estimated regionally in the recapture-conditioned ITCAAN  
511 (RV1Est and RV2Est) had similar bias and precision in movement rate estimates (Figure 6). Scenarios  
512 with spatially varying reporting rates in the operating model but assumed spatially constant reporting rates  
513 in the recapture-conditioned ITCAAN (RV1Const and RV2Const) resulted in large biases and variability  
514 in movement rate estimates. Movement rate estimates from the recapture-conditioned ITCAAN were less  
515 precise and accurate compared to the release-conditioned ITCAAN for most Group 2 scenarios (Figure 6).

516 Misspecification of natural mortality at 0.5 times the true value did not have a large effect on bias  
517 or precision of movement rates for either tagging frameworks. However, misspecifying natural mortality  
518 at 1.5 times the true value had a large effect on bias and precision of the movement rate estimates for  
519 the recapture-conditioned ITCAAN (Figure 6). Movement rates for all regions were accurate and precise  
520 when spawning populations were assumed to have similar productivity levels, where estimates from the  
521 recapture-conditioned ITCAAN were less precise (Figure 6; Vincent et al., 2017). Estimates of movement  
522 rates from the recapture-conditioned ITCAAN with tag shedding simulated were unbiased, but less precise  
523 than most other scenarios in the group due to the lower number of tag returns. Movement rate estimates  
524 for the release-conditioned ITCAAN were unbiased and very precise when provided the exact tag-shedding  
525 rate. However, movement estimates were biased when the release-conditioned ITCAAN was provided with  
526 incorrect tag-shedding rate with the direction of bias depending on the population and the direction of bias  
527 in the tag-shedding rates (Figure 6).

## 528 **Discussion**

529 Simulation studies are an essential tool for determining the effectiveness of models at estimating param-  
530 eters and their ability to describe the dynamics of a system. Simulations analyses have been conducted for  
531 various ITCAANs, but previous analyses have mostly been conducted assuming a release-conditioned frame-  
532 work for tag-recovery data (Hulson et al., 2011, 2013; Goethel et al., 2015b; Vincent et al., 2017). This study  
533 analyzed the performance of a recapture-conditioned ITCAAN under an assumption of natal homing of the  
534 spawning populations and explored different model complexities of parameter estimation. Because similar  
535 simulation scenarios were conducted for a release conditioned ITCAAN (Vincent et al., 2017), we were also  
536 able to compare the performance between recapture- and release-conditioned ITCAANs. Our main purpose  
537 was to compare the performance of recapture- and release-conditioned ITCAANs under a range of inter-  
538 mixing scenarios and to investigate how well either tagging framework could account for spatially-varying  
539 reporting rates and tag shedding.

540 The quality of the data assumed in these simulation scenarios was high. The operating model simulated

541 8000 tags released annually for 40 years, which may be at the upper end of plausibility for the number of  
542 tags released for a prolonged period of time even for high-valued fisheries. Vandergoot and Brenden (2014)  
543 reported that on average 6100 walleye were tagged annually in Lake Erie between 1990 and 2017, with the  
544 number of tags released in some years exceeding 10000 (C.S. Vandergoot, USGS, *personal communication*);  
545 therefore, the tagging level assumed in our research was not outside the realm of possibility and is based on  
546 the study system our simulations were modeled after. The dynamics of tagged fish in the operating model  
547 were a simplistic representation of the processes that could happen in the real world and were constrained by  
548 numerous assumptions. First, the operating model simulated the fates of tagged fish through a multinomial  
549 process, yet overdispersion relative to a multinomial distribution in tag-recovery data is often observed  
550 (Bacheler et al., 2008; Vandergoot and Brenden, 2014; Hanselman et al., 2015; Mayakoshi and Kitada,  
551 2016). This perfect match between the operating model and the estimation likelihood in the ITCAAN would  
552 lead to more precise estimates than is to be expected from real data. The operating model also assumed  
553 that tagged fish experienced the same dynamics as the rest of the population. If the dynamics the tagged  
554 cohorts experienced did not match the rest of the population, due to factors such as delayed mixing or altered  
555 behavior as a consequence of tagging, then parameter estimation would have been affected. Finally, tagged  
556 fish were simulated to move instantaneously and then remain sedentary for the remainder of the year. This is  
557 a common assumption when simulation testing ITCAANs (Hulson et al., 2013; Goethel et al., 2015b; Vincent  
558 et al., 2017), but it unlikely reflects actual fish movement. Additional evaluations of ITCAANs would benefit  
559 from loosening some of the restrictions above to determine how models perform with poorer-quality data  
560 and alternative ecological dynamics.

561 The estimation of movement rates by the recapture-conditioned framework was tested through simu-  
562 lations by McGarvey et al. (2010). Their simulation framework replicated the dynamics of southern rock  
563 lobster (*Jasus edwardsii*) in south Australia and consisted of two regions in which tagged lobsters were  
564 harvested. McGarvey et al. (2010) simulated tag-recovery data through an individual-based model using a  
565 daily time step with simulated releases occurring at dates of actual releases from empirical studies. Simu-  
566 lation of movement dynamics in the individual-based model was not clear, but we assume was based on an  
567 instantaneous movement assumption once during the year based on the estimation model. Likewise, Mc-  
568 Garvey et al. (2010) did not indicate what reporting rate was assumed to generate tag-recovery data. Their  
569 simulation study found that the recapture-conditioned tag-recovery framework produced unbiased estimates  
570 of movement when mortality rates (both fishing and natural) were assumed at correct values. Conversely,  
571 they found estimating movement rates as simple proportions of recoveries of tagged fish in a new region  
572 divided by the total number of recoveries resulted in over-estimation of movement rates. McGarvey et al.  
573 (2010) did not test the estimation of other ITCAAN parameters, or the estimation of movement rates when

574 mortalities were not known precisely. The simulation framework used in this study was quite different from  
575 that of McGarvey et al. (2010). Our simulations consisted of four populations that intermixed between four  
576 regions and we fit an ITCAAN with estimated movement rates along with other model parameters that  
577 are important for management of intermixed fish stocks (e.g., abundances, mortalities). Tag recoveries were  
578 simulated using yearly time steps and movement was assumed to occur once at the beginning of the year.  
579 We also tested the effect that non-spatially constant reporting rates had on model performance and whether  
580 relative reporting rates could be estimated by the model and the influence of tag shedding on parameter  
581 estimates. Therefore, our study provides a broader overview of the bias and precision of movement rate  
582 estimates for a more complex population structure within a recapture-conditioned ITCAAN than has been  
583 previously tested.

584 McGarvey et al. (2010) used a recapture-conditioned ITCAAN to analyze empirical southern rock lobster  
585 harvest and tag-recovery data. The underlying population model was length structured and sex dependent  
586 for two regions. Estimates of movement and mortality rates were obtained from the recapture-conditioned  
587 ITCAAN. However, the authors noted that movement rate estimates from the recapture-conditioned IT-  
588 CAAN differed from estimates obtained from a recapture-conditioned tagging framework that treated prior  
589 mortality estimates (from a catch-at-length model that did not incorporate movement) as known. In other  
590 words, the mortality and movement rate estimates changed when both processes were estimated simultane-  
591 ously as opposed to independently, which is a predictable result. Additionally, different weightings of the  
592 tag-recovery data within the ITCAAN resulted in noticeably different fits to the harvest and catch per unit  
593 effort data. This research assumed the effective sample size of the multinomial distribution to model the tag-  
594 recovery data was equal to the number of tags recovered. Other simulation analyses have assumed different  
595 effective sample sizes of the tag-recovery data, such as equal to the effective sample size of the age composi-  
596 tion (Goethel et al., 2015a) or equal to the number of tags released (Vincent et al., 2017). The weighting of  
597 tag-recovery data in an ITCAAN influences parameter estimates regardless of the tagging framework used,  
598 but guidelines for weighting of tagging data in an ITCAAN requires additional research. Techniques used  
599 for weighting effective sample size such as iterative weighting methods of age composition data (Truesdell  
600 et al., 2017) and size-structured models that integrate tagging information to estimate growth (Punt et al.,  
601 2017) may be a starting point for such future research.

602 We found that a recapture-conditioned ITCAAN performed adequately for some parameters under certain  
603 conditions, but poorly for other parameters under other conditions. Consistent with results from McGarvey  
604 et al. (2010), recapture-conditioned ITCAAN estimates were generally unbiased and precise when intermixing  
605 rates were low and relative reporting and natural mortality rates were correctly specified. Bias in individual  
606 population estimates at high intermixing rates was due to the large difference in abundances between the

607 populations; this bias was not present when populations were assumed to have the same productivities. A  
608 release-conditioned ITCAAN also had difficulties in estimating individual population abundances at high  
609 intermixing rates when there were large differences in abundances (Vincent et al., 2017). It became more  
610 difficult to obtain unbiased and precise estimates of individual population abundances for the recapture-  
611 conditioned ITCAAN as movement rates increased and as the estimation models became more complex.  
612 When tag shedding occurred, the recapture-conditioned model was able to provide unbiased estimates of  
613 movement and total population abundance without requiring external estimates of tag shedding. Conversely,  
614 the release-conditioned ITCAAN required an external estimate of tag shedding, which would necessitate  
615 additional experimentation, which could be costly. Additionally, if external estimates of tag-shedding rates  
616 were biased this could impose biases on other parameter estimates. The recapture-conditioned ITCAAN  
617 would be useful in situations where tag-loss processes such as tag shedding and tagging-induced mortality  
618 are not estimated and reporting rates can be assumed to be spatially constant. Abundance estimates will be  
619 biased if these tag-loss processes are not accounted for in release-conditioned ITCAANs. However, if these  
620 tag-loss processes are accurately estimated and natural mortality is estimated within the ITCAAN, then  
621 the release-conditioned ITCAAN will generally give more accurate and precise estimates than the recapture-  
622 conditioned ITCAAN. Additionally, if a reasonable value for natural mortality cannot be estimated by an  
623 ITCAAN then the release-conditioned ITCAAN would be preferred due to less sensitivity to misspecifying  
624 this parameter.

625 The recapture-conditioned ITCAAN investigated in this simulation study was very sensitive to assump-  
626 tions regarding reporting rates. Actual reporting rates cannot be estimated in a recapture-conditioned  
627 ITCAAN, and we encountered difficulties in estimating relative reporting rates for different regions. In par-  
628 ticular, the recapture-conditioned ITCAAN had difficulty estimating relative reporting rates particularly for  
629 the region that corresponded to the natal region where the smallest population spawned. Higher intermixing  
630 rates only exacerbated the difficulty in estimating relative reporting rates for this region and also resulted  
631 in biases in other model parameters such as movement rates. Estimation of relative reporting rates were  
632 not influenced by misspecification of natural mortality values in the ITCAAN and were most precise and  
633 accurate when populations were simulated under an assumption of equal productivity levels. The results  
634 of this simulation study suggest that recapture-conditioned ITCAANs are able to estimate relative differ-  
635 ences in reporting rates between regions under certain conditions; however, estimation problems may arise  
636 when there are large differences among stock sizes and high intermixing rates. Estimates of population  
637 abundance from the recapture-conditioned ITCAAN were generally less accurate and precise compared to  
638 estimates from the release-conditioned ITCAAN. However, if it is necessary to assume for modeling pur-  
639 poses that reporting rates are spatially constant due to model convergence problems, it may be preferable

640 to use a recapture-conditioned ITCAAN as abundance estimates were less sensitive compared to the release-  
641 conditioned ITCAAN. The challenges in estimating relative reporting rates is important given large biases  
642 resulted when reporting rates were assumed to be constant when they were not. The canceling of the re-  
643 porting rates from the likelihood equations does not occur for the recapture-conditioned ITCAAN when  
644 tagged fish are captured by multiple fisheries with known differences in reporting rates (e.g., recreation  
645 and commercial fisheries). Therefore, a recapture-conditioned ITCAAN may not be the optimal assessment  
646 method for estimation of reporting rates when these parameters are spatially complex or are required for  
647 multiple fisheries. Additionally, the recapture-conditioned model was formulated for a single fishery scenario  
648 and cannot account for scenarios where reporting rates differ between fisheries because they do not cancel  
649 from the likelihood. We advise caution in using of the recapture-conditioned framework for scenarios with  
650 multiple fisheries until additional simulation testing is conducted to determine if this tagging framework can  
651 provide accurate estimates for multiple fisheries with disparate reporting rates.

652 The recapture-conditioned ITCAAN generally provided unbiased estimates of natural mortality, but when  
653 this parameter was estimated in the ITCAAN the precision of total abundance estimates decreased substan-  
654 tially. Additionally, the estimates of natural mortality became less precise as movement levels increased.  
655 Misspecification of natural mortality caused severe biases in abundance estimates, which were worse when  
656 specified above the true value. The recapture-conditioned likelihood has some information that contributes  
657 to the estimation of natural mortality, but the release-conditioned ITCAAN framework estimates were more  
658 accurate and precise (Vincent et al., 2017). Across Group 1 simulation scenarios, IQRs in total abundance  
659 estimates for the recapture-conditioned were larger than the IQRs observed in the release-conditioned IT-  
660 CAAN.

661 In conclusion, a recapture-conditioned ITCAAN can produce accurate and precise parameter estimates  
662 under conditions of low movement, equal population productivities, and when tag-loss processes (e.g., re-  
663 porting rates) are spatially constant as it was originally intended. The recapture-conditioned ITCAAN  
664 performed worse when attempting to estimate natural mortality and was generally outperformed by the  
665 release-conditioned ITCAAN. Furthermore, in situations where tag-loss processes are not spatially constant  
666 and when populations have highly varying productivity levels and high levels of intermixing, ITCAANs  
667 can produce highly biased and variable estimates of individual population abundance. This bias can be  
668 problematic given that some populations may be at risk of overharvest in mixed stock fisheries. Recapture-  
669 conditioned ITCAANs have some capacity to estimate relative reporting rates in situations where reporting  
670 rates vary spatially when movement rates are low. Attempting to estimate relative reporting rates within the  
671 ITCAAN may be the preferred approach to assuming reporting rates are spatially constant given the degree of  
672 bias and variability that was observed when this assumption was violated. However, the release-conditioned

673 ITCAAN generally provided less biased and more precise estimates of abundance when estimating reporting  
674 rates and natural mortality.

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Table 1: Regional reporting rates, average fishing mortality, unfished SSB (spawning stock biomass), and recruitment steepness specified in the operating model for investigated scenarios. EqProd stands for equal productivity scenario and RV1 and RV2 are scenarios with reporting rates spatially varying as shown below and see Table 2.

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	30%	70%	10%	50%
Reporting Rate	RV2	50%	10%	70%	30%
Reporting Rate	All Others	50%	50%	50%	50%

Table 2: Model name abbreviations, operating and ITCAAN 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, tag shedding, or equal productivity (Group 3), where movement is estimated unless noted. Converge rates are provided for release-conditioned ITCAANs rather than referencing results from Vincent et al. (2017) because the scaling of the negative log likelihoods for multinomially distributed random variables was expected to improve convergence performance.

Scenario Group	Abbrev.	ITCAAN			Operating model	# needed for 1000 con- verged	NPD Hessian	Maximum Gradient > 0.05
		Relative reporting	Natural mortality	Release or recapture	Intermixing			
1	MvFix1*	Known	Known	recapture	1%	1343	0	343
1	MvFix1*	Known	Known	release	1%	1214	42	180
1	MRFix1	Known	Known	recapture	1%	1268	0	268
1	MRFix1	Known	Known	release	1%	1179	36	147
1	RFix1	Known	Est. RC	recapture	1%	1300	0	300
1	RFix1	Known	Est. RC	release	1%	1221	44	173
1	MFix1	Est. Rel	Known	recapture	1%	1161	0	161
1	MFix1	Est. Rel	Known	release	1%	1246	59	199
1	NoFix1	Est. Rel	Est. RC	recapture	1%	1211	0	211
1	NoFix1	Est. Rel	Est. RC	release	1%	1194	55	143
1	MvFix5*	Known	Known	recapture	5%	1010	0	10
1	MvFix5*	Known	Known	release	5%	1062	48	15
1	MRFix5	Known	Known	recapture	5%	1017	0	17

Table 2 (cont'd)

1	MRFix5	Known	Known	release	5%	1053	35	18
1	RFix5	Known	Est. RC	recapture	5%	1010	0	10
1	RFix5	Known	Est. RC	release	5%	1075	52	23
1	MFix5	Est. Rel	Known	recapture	5%	1095	36	95
1	MFix5	Est. Rel	Known	release	5%	1046	24	23
1	NoFix5	Est. Rel	Est. RC	recapture	5%	1104	21	104
1	NoFix5	Est. Rel	Est. RC	release	5%	1054	16	38
1	MvFix10*	Known	Known	recapture	10%	1004	3	4
1	MvFix10*	Known	Known	release	10%	1030	28	4
1	MRFix10	Known	Known	recapture	10%	1002	2	2
1	MRFix10	Known	Known	release	10%	1069	68	3
1	RFix10	Known	Est. RC	recapture	10%	1002	2	2
1	RFix10	Known	Est. RC	release	10%	1059	57	5
1	MFix10	Est. Rel	Known	recapture	10%	1061	42	60
1	MFix10	Est. Rel	Known	release	10%	1040	40	0
1	NoFix10	Est. Rel	Est. RC	recapture	10%	1057	37	55
1	NoFix10	Est. Rel	Est. RC	release	10%	1038	38	2
1	MvFix20*	Known	Known	recapture	20%	1010	10	8
1	MvFix20*	Known	Known	release	20%	1080	80	11
1	MRFix20	Known	Known	recapture	20%	1008	8	5
1	MRFix20	Known	Known	release	20%	1087	87	6
1	RFix20	Known	Est. RC	recapture	20%	1008	8	7

Table 2 (cont'd)

1	RFix20	Known	Est. RC	release	20%	1107	107	8
1	MFix20	Est. Rel	Known	recapture	20%	1066	63	56
1	MFix20	Est. Rel	Known	release	20%	1052	52	2
1	NoFix20	Est. Rel	Est. RC	recapture	20%	1008	7	2
1	NoFix20	Est. Rel	Est. RC	release	20%	1065	62	51
2	RV1Const	Const	Est. RC	recapture	20%	1154	123	144
2	RV1Const	Const	Est. RC	release	20%	1306	242	237
2	RV1Est	Est. Rel	Est. RC	recapture	20%	1006	6	6
2	RV1Est	Est. Rel	Est. RC	release	20%	1083	83	4
2	RV2Const	Const	Est. RC	recapture	20%	1014	13	11
2	RV2Const	Const	Est. RC	release	20%	1094	94	29
2	RV2Est	Est. Rel	Est. RC	recapture	20%	1001	1	1
2	RV2Est	Est. Rel	Est. RC	release	20%	1070	68	9
3	SensU	Est. Rel	$0.5 \times \text{True}$	recapture	20%	1003	3	2
3	SensU	Est. Rel	$0.5 \times \text{True}$	release	20%	1091	91	3
3	SensO	Est. Rel	$1.5 \times \text{True}$	recapture	20%	1007	7	4
3	SensO	Est. Rel	$1.5 \times \text{True}$	release	20%	1125	125	26
3	EqProd	Est. Rel	Est. RC	recapture	20%	1000	0	0
3	EqProd	Est. Rel	Est. RC	release	20%	1000	0	0
3	TagExact	Known	Known	recapture	20%	1008	8	7
3	TagExact	Known	Known	release	20%	1025	25	5
3	TagOver	Known	Known	release	20%	1023	23	4



Table 2 (cont'd)

3	TagUnder	Known	Known	release	20%	1008	3	6
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**Note:** NPD = Not Positive-Definite; Known = Fixed at true value; Est. = Estimated in ITCAAN; Rel = Reporting rates relative to region 1; RC = regionally constant; Const = Reporting rates assumed regionally constant

\* Movement Rate Fixed at True Value

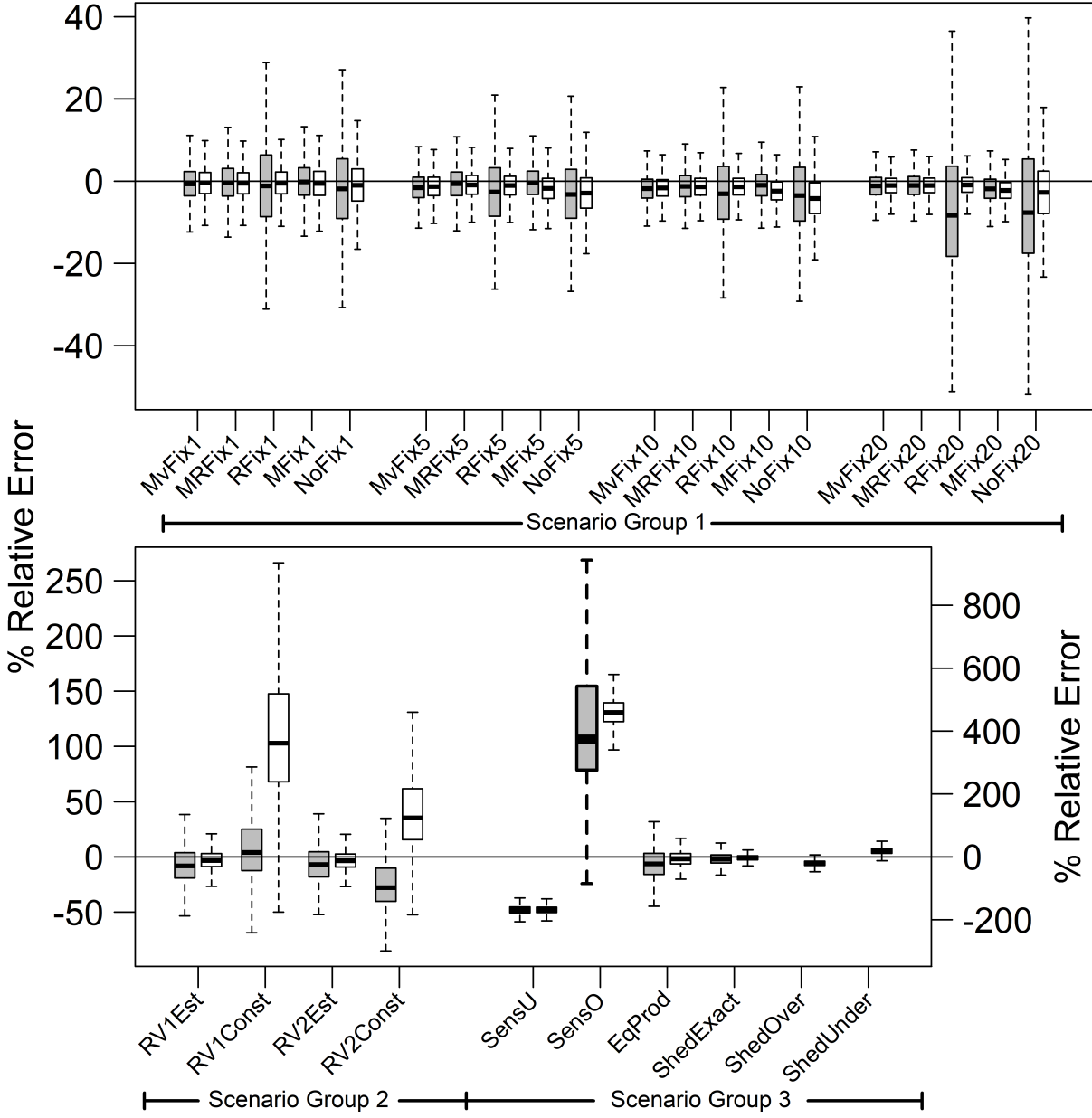


Figure 1: Relative error (%) of abundance summed across populations for a four region ITCAAN under different intermixing rates and parameter estimation assumptions (Group 1), spatially varying reporting rates (Group 2), and misspecification of natural mortality, tag shedding, and equal productivities (Group 3) for 1000 simulations. The grey colored boxplots on the left are for the recapture-conditioned ITCAAN and the white boxplots on the right are for the release-conditioned ITCCAN. The boxplot outlined in a thick line correspond to the y-axis on the right side of the bottom plot. Table 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.

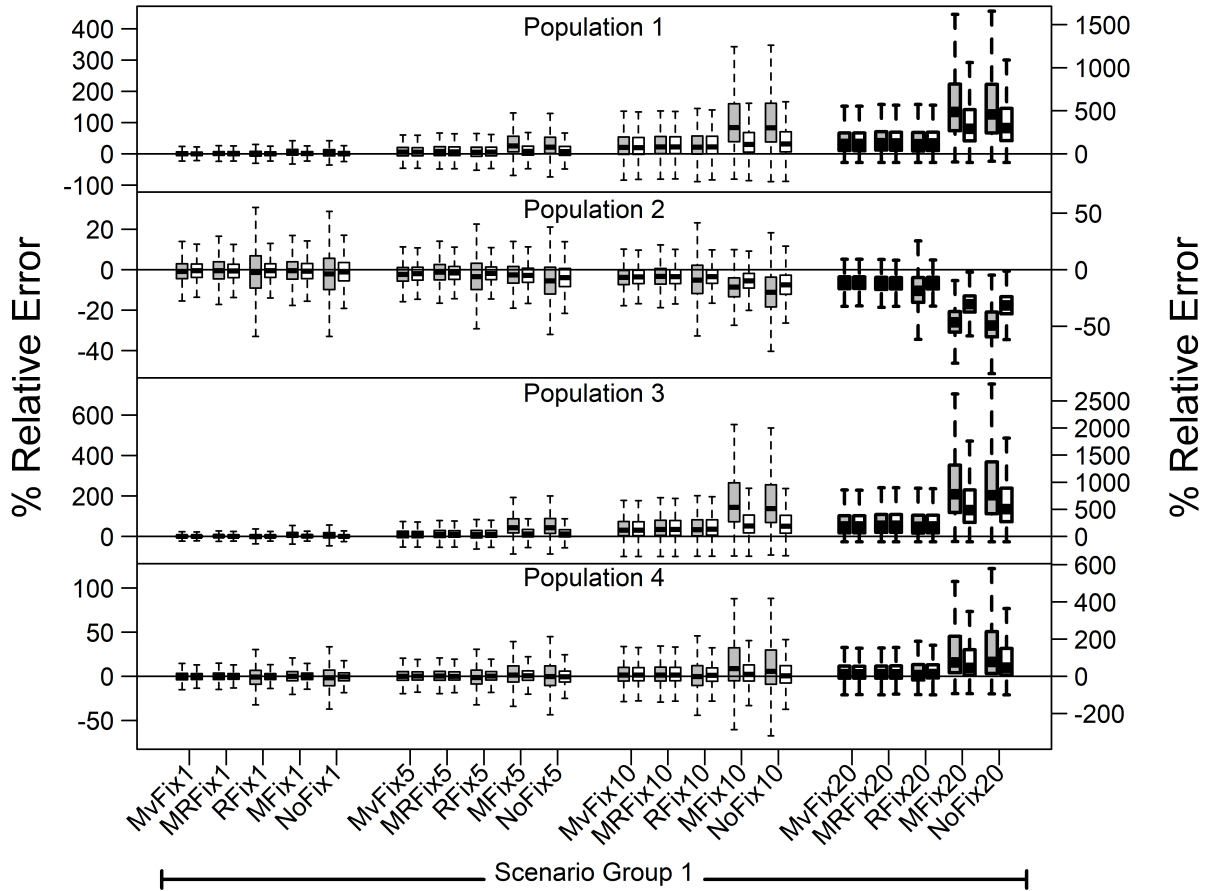


Figure 2: Relative error (%) of population abundance for a four region ITCAAN under different intermixing rates and parameter estimation assumptions for 1000 simulations. The grey colored boxplots on the left are for the recapture-conditioned ITCAAN and the white colored boxplots on the right are for the release-conditioned ITCAAN. Boxplots outlined in thick lines corresponds to the y-axis on the right side of the figure. Table 2 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.

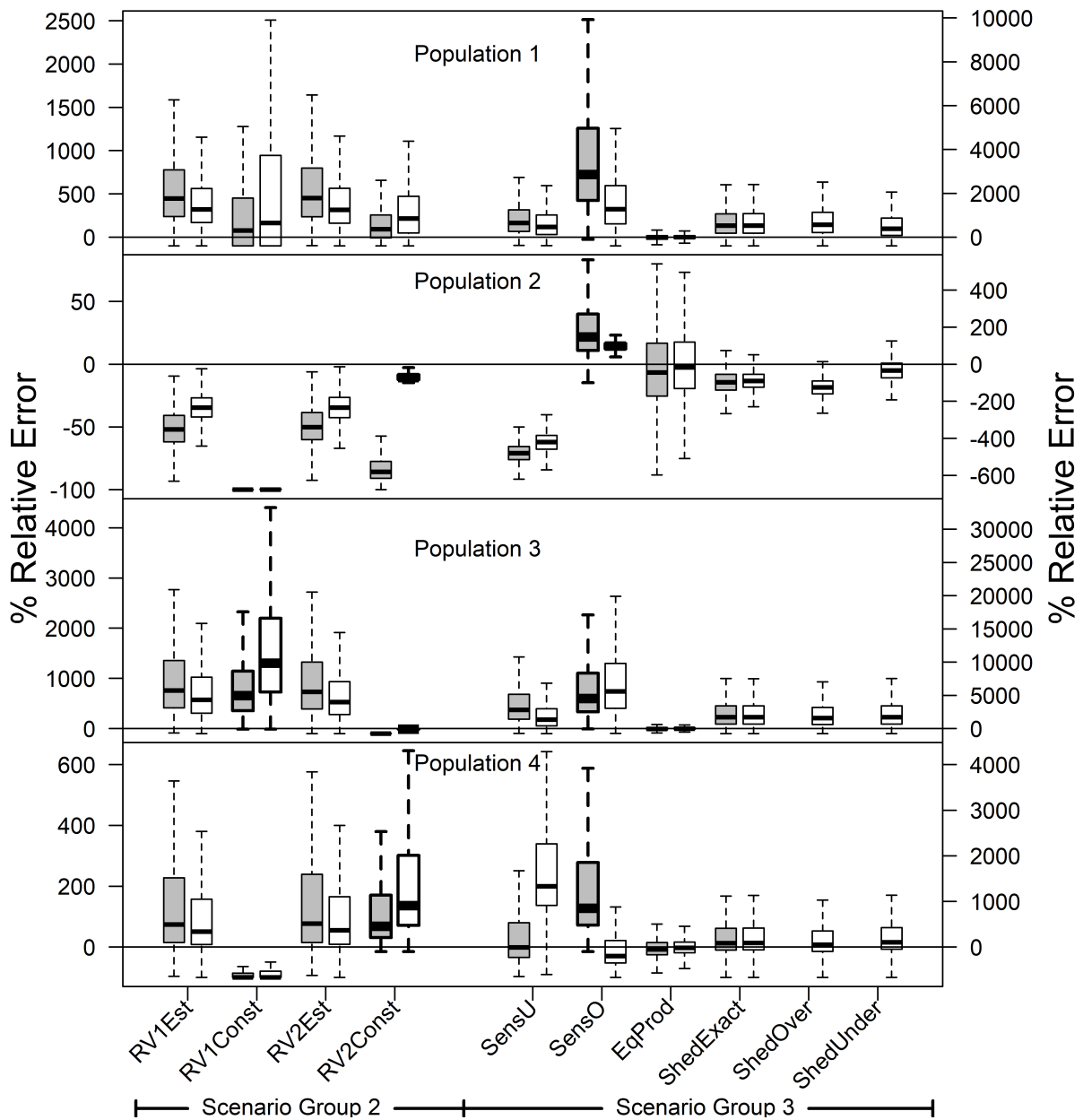


Figure 3: Same as Figure 2 but population abundance relative error (%) for models under spatially varying reporting rates (Group2) and misspecification of natural mortality, tag shedding, or equal productivities (Group 3).

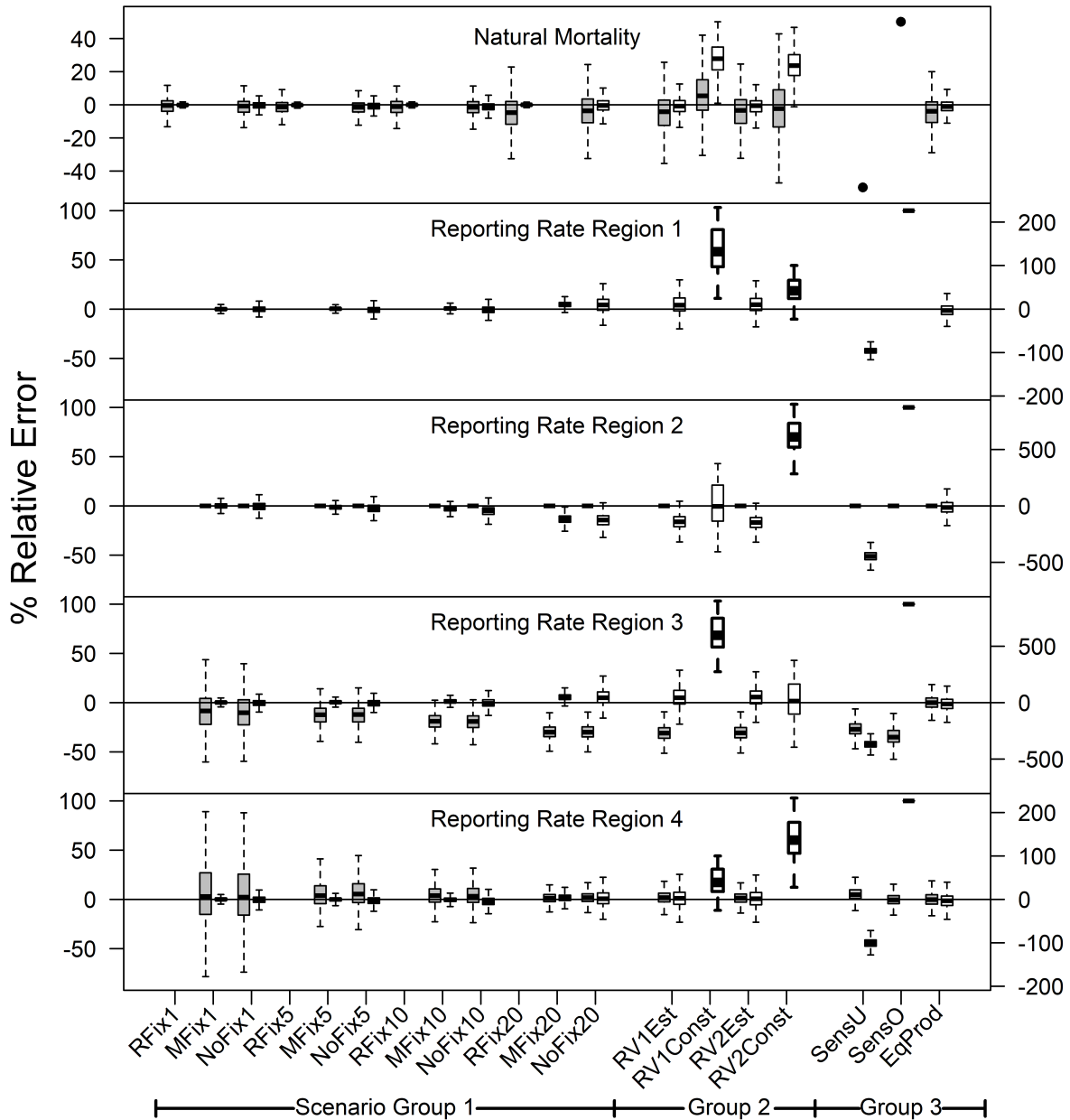


Figure 4: Same as Figure 2 but for relative error (%) of (relative) reporting rates and natural mortality. Scenarios with a dot for natural mortality fixed the parameter at this value and scenarios without boxplots did not estimate that parameter. Reporting rates in region 1 for the recapture-conditioned model were fixed at a value of 1.

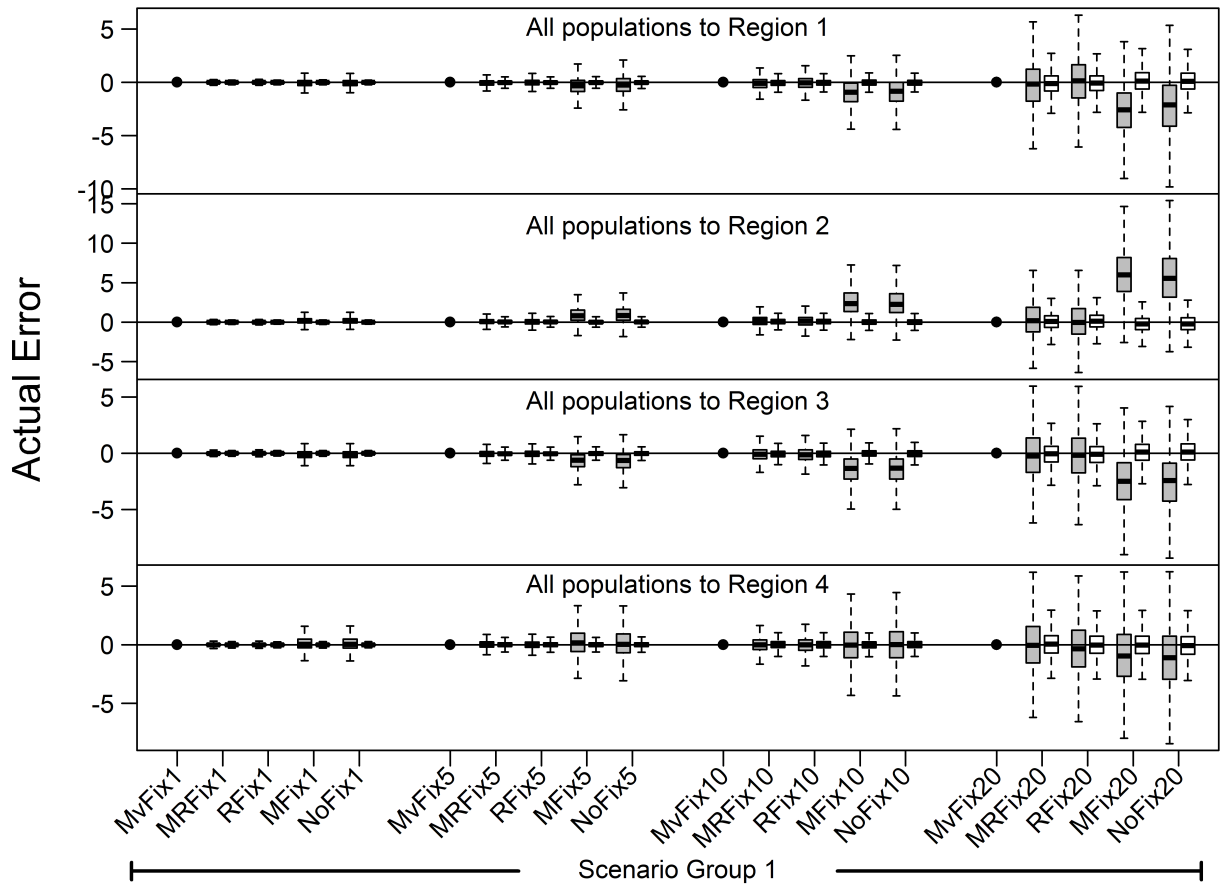


Figure 5: Same as Figure 2 but actual error of movement rates of all populations to a harvest region.

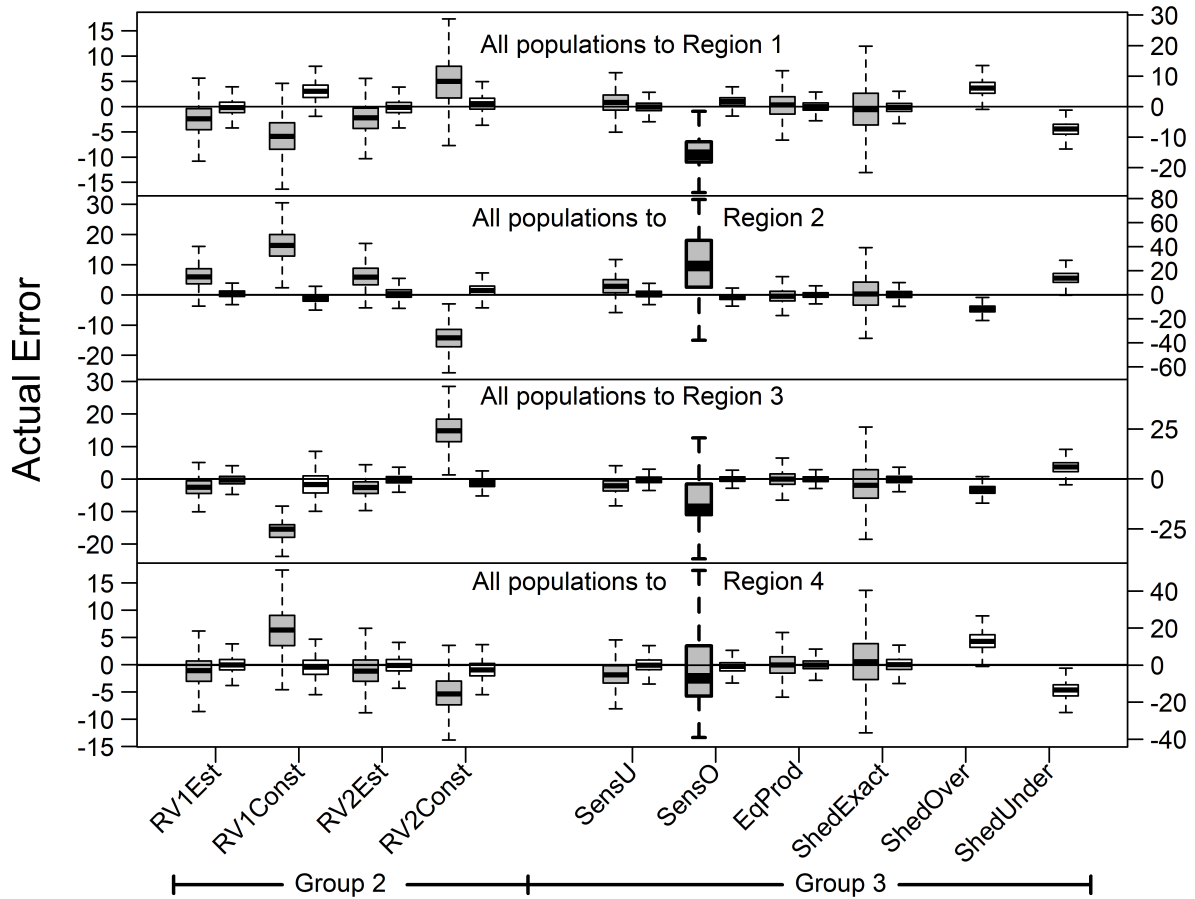


Figure 6: Same as Figure 3 but actual error of movement rates of all populations to a harvest region.