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The Robustness of Brownie Tag Return Models to Complex Spatiotemporal Dynamics Evaluated through Simulation Analysis

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Title: The Robustness of Brownie Tag Return Models to Complex
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Abstract

The development of a reliable tagging program requires simulation testing the experimental design. However, the potential for model misspecification, particularly in the underlying spatiotemporal dynamics, is often ignored. A continuous time, spatially-explicit, age-structured, capture-recapture operating model was developed to better emulate real-world population dynamics typically overlooked in spatially-aggregated or discrete time tagging models. Various spatiotemporal model parametrizations, including case studies with Atlantic bluefin and yellowfin tunas, were explored to evaluate the bias associated with Brownie tag return estimation models. Simulations demonstrated that accounting for connectivity was essential for obtaining unbiased parameter estimates, and that migration rates could be reliably estimated without the correlation associated with other parameters (e.g., between tag reporting and mortality). Mortality parameter estimates were particularly sensitive to the temporal dynamics of the tagging and fishing seasons, but accounting for the seasonality in tag releases and fishery recaptures allowed for relatively unbiased estimation. Our results indicate that parameter bias and uncertainty can be severely underestimated when discrete time or spatially-aggregated operating models are used to determine optimal experimental design of tagging studies.

Keywords: tagging, spatial dynamics, temporal dynamics, population dynamics, connectivity, bluefin tuna

Introduction

Many marine fish, particularly pelagic tunas, exhibit intricate movement patterns resulting in complex spatial structure. Stock assessments and resulting management actions have been increasingly accounting for spatial dynamics caused by connectivity within and among population units (Goethel et al. 2016). However, development of spatially-explicit stock assessment models often requires auxiliary data sources to estimate migration rates (Goethel et al. 2011). Capture-recapture experiments, including tag return studies, are commonly used to determine fish movement patterns and estimate rates of migration between regions (Hilborn 1990). A carefully designed tagging study allows for estimation of population parameters (i.e. natural mortality and migration), which are difficult to estimate from typical fishery data (e.g., landings and relative abundance). Despite the knowledge that can be gained from tagging studies, many pitfalls exist (e.g., dealing with nuisance parameters such as tag reporting rate and tag loss, which can hinder direct estimation of natural and fishing mortality simultaneously; Brownie et al. 1985; Pollock et al. 2001, 2002; Pine et al. 2003). Accounting for spatial dynamics using multistate capture-recapture models (Schwartz et al. 1993; Kendall et al. 1997; Lebreton et al. 2009) leads to more complex tagging analyses, but can avoid violation of important assumptions of spatially-aggregated models (i.e. that the study area is closed to immigration or emigration or that emigration is permanent in open population models; Ishii 1979; Seber 1986; Hilborn 1990; Sibert et al. 1999).

It is widely recognized that the experimental design of any tagging study should be tested *a priori* to determine if it can be expected to achieve the purported objectives (DeLury 1951). Simulation analysis is the preferred method currently used to optimize the distribution of releases and expected recaptures in a way that minimizes bias and variance of estimated parameters (Xiao

1995). Simulation testing of models is ubiquitous in fisheries science, but often these analyses tend to address robustness to measurement error and only peripherally investigate the impact of model misspecification error (Kerr and Goethel 2014). Deroba et al. (2015) demonstrated through model cross-testing of stock assessments that robustness to model misspecification was often limited. Their research highlighted the need for testing estimation model performance across an array of underlying operating model assumptions. For Brownie tagging models, research on robustness to model misspecification has focused on the impact of estimating (or ignoring) tag mortality and tag shedding (Arnason and Mills 1981; Seber and Felton 1981; McGarvey et al. 2009), incomplete mixing of tagged fish (Waterhouse and Hoenig 2011, Kolody and Hoyle 2015), and tag reporting rates (Pollock et al. 2001, 2002).

Evaluation of the robustness of capture-recapture analyses to model misspecification has been limited (e.g., mortality parameter estimation bias resulting from incorrect assumptions regarding the spatiotemporal population dynamics). It is well understood that violation of the closed population assumption can be detrimental to the performance of tagging models (Pine et al. 2003), which led, in part, to a surge in spatial modeling techniques throughout the last two decades (Hilborn 1990; Sibert et al. 1999). Generalized versions of the Brownie et al. (1985) model have become the most widely applied technique for spatially-explicit tagging analyses, because they allow simultaneous estimation of fishing mortality, natural mortality, and migration across multiple regions and years (Polacheck et al. 2006a, 2010). Simulations of spatial Brownie models have demonstrated that the framework is generally robust for estimating mortality and migration rates, and that estimates can be improved with the inclusion of alternate tagging types (e.g., radiotelemetry, archival or satellite tags; Pollock et al. 2004; Bacheler et al. 2009; Eveson et al. 2012) or information on tag reporting (Pollock et al. 2001, 2002). However, the discrete

time approximation to continuous time dynamics, which is inherent in many modeling applications (Zeigler et al. 2000), remains under-studied for Brownie models. Although population dynamics, fishery dynamics, and tagging are generally continuous processes, most models assume a discrete seasonal or yearly timestep for computational convenience (Miller and Andersen 2008). For instance, ignoring the fishing season length in relation to the timing of tag releases has been shown to result in considerable bias, particularly for parameter estimates in the year of release, because the tagged population no longer undergoes a full year of fishing mortality (Hearn et al. 1998; Hoenig et al. 1998a; Mathur 2007).

Even though electronic tags are quickly gaining popularity for their ability to provide continuous time tracks of individual movement patterns, conventional tagging remains widespread due to the ratio of cost to information content along with there being long-established analytical methods for evaluating mark-recapture information. However, despite Brownie-type tag return models having been explored for measurement error, spatial model misspecification or temporal model misspecification, all three have not been explored simultaneously. Therefore, we developed a spatially-explicit, continuous time tag simulator that is able to simulate tag releases and returns (with stochasticity) across multiple geographic areas, while allowing continuous and finite fishing and tagging seasons (to allow for temporal asynchrony among these processes). We then tested the robustness of various age-structured, discrete time Brownie tag return estimation models, which differed in their assumptions of spatial structure and assumed timing of tagging events, to underlying spatiotemporal model misspecification. We conclude with Atlantic bluefin (*Thunnus thynnus*) and yellowfin (*Thunnus albacares*) tuna case studies, which evaluated the robustness of Brownie estimation models confronted with the more complex dynamics expected in real world applications. Our results provide new insight into how Brownie

models perform when confronted with model misspecification inherent in typical fisheries mark-recapture applications.

Methods

The simulation framework was written as two statistical packages and is available for download from a public Github repository (<https://github.com/dgoethel/Tagging-Simulator>). The spatially-explicit operating model (written in Program R; R Core Team 2012) incorporated complex temporal structure including stochastic age-at-release to calculate individual probabilistic fates for marked animals, which were then summarized to provide simulated observed tag recaptures by release cohort that contained observation error (due to the probabilistic nature of the calculations). The estimation model (written in AD Model Builder; Fournier et al. 2012) was a discrete, age-structured Brownie (Brownie et al. 1985) mark-recapture estimator, and was used to investigate the bias and variance in estimated population parameters due to spatiotemporal model misspecification and observation error. The Brownie model utilized a tag attrition setup with multiple release and recapture events, which allowed prediction of tag returns and estimation of the associated movement and mortality parameters for each year of recapture (Appendix A Equations 3-4; Polacheck et al. 2010). Reporting rates were directly estimated (or fixed) allowing natural and fishing mortality to be independently estimated (as opposed to a composite estimate of total mortality). Parameter estimates were obtained through comparison of predicted (i.e., from the estimator) and observed (i.e., simulated by the operating model) tag returns with maximum likelihood methods (Appendix A, Equation 7). A complete description of the parameter definitions, operating model, and estimation model is provided in Appendix A and summarized below.

The operating model was comprised of three components: the tagging model defining the nature of releases; the population model simulating the dynamics of the marked population; and the fishery model determining the dynamics of recaptures (Appendix A, Table A2). For discrete time models, spawning and tagging were assumed to occur instantaneously at the beginning of the year, while fishing acted continuously over the entire year. In continuous time models, spawning, tag releases, and fishing were defined to occur over subsets of each yearly time interval. Daily frequencies of spawned individuals and tag releases were defined by uniform distribution functions, whereas fishing was either occurring or not based on the start date and length of the fishing season (see Figure 1 and Appendix A, Operating Model for a complete description of temporal dynamics). A marked fish was assigned a random birth date (based on the distribution of spawning) and an associated age (based on the distribution of age compositions; Figure 2). It was then marked and released on a particular day of the year (determined randomly from the distribution of tagging effort). Individual probabilistic fates for each marked fish were then calculated based on the unique mortality regime encountered, which differed due to an individual's stochastic date of birth, tagging date, age, and movement probability (i.e. the mortality probability experienced was an amalgamation of region-, age-, and year-specific mortality rates across a given year of life from birth date to birth date, not January 1 to December 31; see Ageing section in Appendix A).

For continuous time models, further adjustments to mortality regimes were required to account for the timing of the fishing season and tagging date in relation to the year-round natural mortality (see Hoenig et al. 1998a for a complete discussion and the Temporal Dynamics section of Appendix A for equations). Essentially, the mortality schedule encountered by an individual was broken into three periods during a given year: natural mortality prior to the start of the

fishing season; natural and fishing mortality during the fishing season; and natural mortality after the conclusion of the fishing season. Probability of survival (or, conversely, mortality) during each period was adjusted to account for the proportion of the yearly mortality encountered, and the probability of harvest was likewise adjusted for the proportion of total natural mortality encountered during the fishing season (fishing mortality was not discounted as the full mortality was encountered each year during the fishing season except in the year of tag release; Appendix A, equation 1). Additional adjustments were required in the year of tag release to account for whether the tag event took place before the fishing season (survival probability prior to fishing needed to be adjusted for the amount of natural mortality that took place from the tag event to the commencement of the fishing season) or after (harvest probability, i.e. the total fishing mortality rate, needed to be discounted for the temporal difference between the tag event and the start of the fishing season; see Appendix A, Equation 2).

Both the operating model and estimation model were developed to allow flexibility in the spatiotemporal dynamics. The operating model was designed to allow continuous time or discrete time dynamics, whereas the estimation model only operated on discrete time scales. The latter has been an almost ubiquitous trait of tagging analyses, and, along with migration assumptions, were the key sources of model misspecification investigated. Observation error was included in the tag returns through the use of probabilistic fates (i.e., each event was defined by a probabilistic outcome and was not deterministic; Appendix A, Table A2). The estimation model had inherent bias in the mortality-at-age, because the estimation model did not account for true birth date and assumed all fish were born January 1st and experienced the full mortality for that region, year, and age. The operating model used the true population rates-at-age based on

the actual birth date of the fish (see the section Ageing under Operating Model in Appendix for more details).

Model development and application was divided into three phases: model testing, sensitivity runs, and case studies. In the first stage, a stepwise model building exercise was undertaken in an attempt to separate the impact of each source of model misspecification on the estimation model results. First, a discrete time operating model was implemented to investigate the impact of spatial structure assumptions. Then, the continuous time operating model (utilizing within year temporal dynamics) was implemented and various temporal mortality adjustments were made to the estimation model to attempt to account for these continuous processes. Various sensitivity runs were utilized to explore the ability to estimate natural mortality in addition to the suite of other model parameters, and to explore the impacts of incorrect assumptions regarding natural mortality rate. Finally, case studies with Atlantic bluefin and yellowfin tuna were implemented to demonstrate the performance of the framework with more realistic spatiotemporal parametrizations. For each model implementation, the estimation model was fit to 1,000 simulated datasets from the operating model. The bias and precision of predicted tag returns and estimated parameters were examined.

Stepwise Model Building

The base models were set up to limit the effect of regional-, age- or year-specific variation on estimation model performance. The goal was to loosely mimic a traditional tag release experimental design, while isolating the major sources of bias to either spatial or temporal dynamics caused by the associated model misspecification. The models assumed four regions, four ages, four years of tag releases, and four years of tag recaptures. Releases were

evenly distributed across regions and ages with 10,000 tags released per year; each region received 2,500 tags a year and these were evenly distributed across age classes. When movement was implemented, residency rate was set at 0.6 with symmetric movement to all other regions (Figure 3). No movement occurred in the year of release and movement rates were assumed time- and age-invariant. Reporting rates were set to 0.5 for each region. Fishing mortality parameters varied by region, year, and age (mean of 0.44), but were constant across runs and scenarios. Natural mortality was age-specific, but region and time-invariant, and fixed at the true value ($M_a = 0.274, 0.23, 0.206, 0.191$) for the base models (sensitivity runs investigated natural mortality estimation). All other parameters were freely estimated including region-specific movement and reporting rate along with age-, region-, and year-specific fishing mortality. No handling mortality or tag loss occurred.

Discrete Time Models

The temporal dynamics of the discrete time operating model matched the assumptions of the estimation model by using a discrete yearly timestep with spawning and tag releases both occurring on January 1 and fishing occurring for the duration of the year (Figure 1). The purpose of the discrete operating model was to evaluate the influence of spatial structure on estimation model performance. The first step was to perform a self-consistency run (Scenario 1) where all parameters were fixed at their true value with consistent movement and mortality assumptions between the operating and estimation models. The self-consistency check allowed for determination of the bias and variance in predicted tag returns that resulted from the stochastic processes inherent in the simulation model (i.e. inherent observation error). It also provided a baseline level of bias and variance that could be used to compare each subsequent model. In the

second model (Scenario 2), migration amongst regions was set to zero and parameters were estimated (i.e., fishing mortality, movement, and reporting rate) to determine model performance when no movement occurred (i.e. the bias associated with a spatially-explicit estimation model that estimated movement when no connectivity was occurring). In model Scenario 3, movement was included in the operating model but ignored in the estimation model in order to investigate the impact of ignoring connectivity. The base discrete time model (Scenario 4) included movement in both the operating and estimation models, and kept natural mortality fixed at the true values.

Continuous Time Models

In the next phase, the operating model utilized a continuous time framework and the impact of various temporal adjustments in the estimation model were assessed. In each scenario, different temporal adjustments were made to the estimation model mortality calculations to better account for the underlying continuous time dynamics of the spawning, fishing, and tagging processes. The operating model assumed a uniform distribution for the spawning and tagging seasons where spawning occurred May 1 to July 31 and tagging occurred June 1 to August 31 (see Figure 1). Additionally, fishing was assumed to have a discrete season within the year, which occurred from March 1 to October 31 with no fishing outside of this period (Figure 1). In the estimation models with optimal mortality adjustments, which better accounted for the continuous processes given the discrete yearly time step, mortality was adjusted similarly to the simulated survival and harvest probabilities (described above) based on the length of the fishing season and the average tag date in the year of release (not individual tag date; see Temporal Adjustments under Brownie Tag Return Estimation Model in Appendix A). Available tags in

the estimation model were calculated twice per year (at the start of the year to account for natural mortality after the fishing season in the previous year and prior to the commencement of fishing to account for natural mortality before fishing). Recaptures were adjusted for the amount of natural mortality that occurred during the fishing season along with adjustments in the year of tag release to account for the relationship between average tag date and the commencement of fishing.

A consistency-type run (Scenario 5) was performed with parameters fixed at the true simulation values and optimal mortality adjustments undertaken, which demonstrated the minimum bias that could be expected in a discrete time estimation model when true underlying processes were continuous. Next, the discrete time base estimation model, which did not adjust mortality parameters for tag timing (i.e. tagging was assumed to occur at the start of the year and full mortality was applied in all years), was fit to observed tag returns from the continuous time operating model (Scenario 6) providing a baseline to compare various temporal adjustments to the estimation model. Finally, the base estimation model for the continuous time operating model was applied (Scenario 7), which estimated the same parameters as the discrete time counterpart (Scenario 4), but included the optimal temporal mortality adjustments.

Sensitivity runs

A handful of sensitivity runs were explored to demonstrate model performance when natural mortality was fixed at the wrong value or directly estimated, and when external information on tag reporting rate was available. As natural mortality is assumed known in some modeling applications, a sensitivity run with natural mortality fixed at an incorrect value was carried out (Scenario 8; a fixed natural mortality-at-age was input as $M_a = 0.3$, which was greater

than the simulation values). Next, the estimation model was allowed to directly estimate natural mortality (Scenario 9) along with all other parameters (migration, reporting rates, and fishing mortalities). Then, because reporting rate is typically confounded with mortality and external information on reporting rate levels is sometimes available (e.g., observer documented recaptures or high reward tag returns), an informative, normally-distributed penalty ($\mu = 0.5$, $\sigma = 0.1$) on reporting rate was included and all parameters including natural mortality were estimated (Scenario 10).

Case studies

Large-scale tagging programs for bluefin and yellowfin tuna in the Atlantic Ocean have been ongoing or proposed in order to help estimate movement and mortality parameters (<http://www.iccat.int/GBYP/en/>; <http://www.iccat.int/AOTTP/en/>). However, tagging studies have demonstrated limited success, especially for bluefin tuna (e.g., due to low tag return rates; Di Natale and Tensek 2016). Atlantic tunas provide interesting case studies for our spatiotemporal simulation framework due to their broad-scale distributions, complex migration patterns, and distinct seasonality of fishing and proposed tagging efforts. We constructed simulation scenarios meant to mimic the complex dynamics observed for both species in order to gain understanding of the expected parameter bias and uncertainty from a Brownie estimation model confronted with spatiotemporal dynamics that are more representative of the real-world. In addition, the results of these applications can be used directly to provide advice on best practices for the experimental design of each tagging program.

Gene-tagging Program for Atlantic Bluefin Tuna

Genetic tagging methods have been proposed for bluefin tuna (Davies et al. 2008, Bravington et al. 2016), with ongoing pilot studies aimed at understanding the feasibility of the approach in the Atlantic Ocean. The expected benefits of genetic tagging include negligible tag loss due to high resolution genetic sequencing and near perfect reporting of recaptured fish screened for genetic recapture. By using genetic tagging methods, it is expected that the poor performance of current conventional tagging studies, due to low reporting of tags, can be improved.

For the bluefin case study, the dynamics of adult tuna (ages 9 to 16) within the eastern and western Atlantic Ocean were simulated. The migration dynamics included natal homing (i.e. life history parameters and movement rates were based on natal region) with a regional transition from west to east of 10% and east to west of 30% (Figure 3). Input movement parameters are hypothetical rates generalized across ages based on expert opinion informed by satellite and conventional tagging data and roughly corresponding to those used by Kerr et al. (2017, this issue) to simulate bluefin dynamics for all ages and across seven modeled regions (the rates were based on the model estimates of Taylor et al. 2011). Fish were assumed to migrate in the year of release, as mature individuals are known to leave the spawning grounds and migrate to foraging areas in both regions of the Atlantic Ocean soon after spawning (Block et al. 2005).

The spawning season was assumed to be uniform from April 1 to June 15 (Teo et al. 2007, Figure 1). Tagging was assumed to occur over a two-week period directly after the spawning season by sampling of adult fish (e.g., through passive DNA sampling gears) prior to exiting the spawning grounds or from parentage identification from the sampling of larvae or recently spawned juveniles. We assumed 2,500 tagged individual released per region per year for a period of five years and, because fish were tagged within a spawning area, natal population

was assumed to be known exactly (i.e. because Atlantic bluefin tuna populations are thought to have distinct natal spawning site fidelity; Block et al. 2005). The recapture of individuals was assumed to occur from the fisheries operating in the Atlantic Ocean from July 1 to October 31 (Figure 1) based on the temporal distribution of observed catches from the major fisheries in that region.

Key assumptions of the genetic tagging program were that handling mortality and tag loss were negligible (assumed 0%). Furthermore, it was assumed that 20% of the catch of adult bluefin tuna would be screened for genetic recapture. This value was input as a fixed reporting rate in the simulation and estimation models, because perfect reporting of sampled landings would be expected given that fisherman cannot distinguish between marked and unmarked fish. In the operating model, the values of natural and fishing mortality-at-age for both regions (i.e. fishing mortality-at-age varied across regions and years) were taken from the most recent stock assessments (ICCAT 2014). The age composition of releases was calculated as the average relative proportion of fish aged 9 to 16 based on abundance-at-age estimates from the recent stock assessment for the period 2008 to 2012.

Two alternative scenarios were modeled. The first estimated migration rates in addition to fishing mortality-at-age (Scenario 11). For the second, it was assumed that alternate tagging data (e.g., satellite tags) were able to provide accurate estimates of stock mixing and migration. The goal was then to estimate fishing mortality-at-age and natural mortality-at-age assuming movement was correctly specified and fixed (Scenario 12), which would potentially eliminate any confounding that could be caused by estimating movement and mortality parameters simultaneously.

Atlantic Ocean Tuna Tagging Program for Yellowfin Tuna

The conventional tagging program for Atlantic tropical tunas has been designed and funded, and program implementation began in 2016 (<http://www.iccat.int/AOTTP/en/>). The program objectives were numerous and included estimation of natural mortality, fishing mortality, migration, and growth. To understand the ability to meet the first three objectives, we parameterized the simulation based on current information and the proposed study design for yellowfin tuna.

The spatial study design calls for tagging in seven major regions including: 1) Mauritania/Guinea, 2) the Gulf of Guinea, 3) the Canary Islands, 4) the Azores/Madeira, 5) Venezuela and the Caribbean, 6) Brazil, and 7) South Africa/Namibia/St. Helena (Figure 3). No information exists on the migration rates of yellowfin tuna between these regions, so we parameterized a generalized mixing matrix that assumed Markovian movement (i.e., migration rates depended on current region and not natal region), and 40% percent residency within a region, 20% migration to two directly adjacent regions, and 5% migration to each of the other four regions. An example of the migration assumptions is shown in Figure 3 for region 1.

The spawning season for yellowfin is unknown, but the species is assumed to have protracted spawning. For the simulation, we assumed a uniform spawning season from March 1 to September 31. The tagging program has a target number of marks to be released in each region that are to be equally distributed among three main target species, bigeye (*Thunnus obesus*), yellowfin, and skipjack (*Katsuwonus pelamis*) tunas. The proposed tagging and fishing seasons vary by region and estimates of temporal timing were provided by the tagging program coordinators (P. Guemes, International Commission for the Conservation of Atlantic Tunas, Madrid, Spain, personal communication, 2016); Figure 1 shows the seasonal distribution

assumptions. Several regions show a bimodal seasonality in the fishing seasons, which was accounted for in the operating model but not the estimation model (see Temporal Mortality Adjustments section under Brownie Tag Recapture Estimation Model in Appendix A).

The values of natural and fishing mortality in the operating model were adopted from the recent stock-wide assessment (ICCAT 2011). Tag loss and handling mortality were assumed negligible. Fleet-specific reporting rates were borrowed from the Indian Ocean tagging program (Carruthers et al. 2015) and proportionately scaled by Atlantic Ocean observed catch by fleet (taken from the ICCAT database; <https://www.iccat.int/en/accesingdb.htm>) in order to linearly extrapolate an average reporting rate by region (region-specific reporting rates were 0.74, 0.82, 0.25, 0.19, 0.30, 0.25, 0.37, respectively, by region according to the region numbers in Figure 3). Because no reporting rate values existed for the Atlantic Ocean, these calculations were used to provide a rough approximation of what potential regional reporting rates might be given the fleet composition in each region. Given that tagging will be conducted using bait boats, the expected age composition proportions (ages 1 to 4) of tag releases were based on the average (from 2006 to 2010) numbers-at-age from the 2011 stock assessment multiplied by the (domed) selectivity of bait boats.

Three scenarios were simulated for Atlantic yellowfin tuna. The first attempted to estimate migration rates among regions, regional reporting rates, natural mortality-at-age, and regional fishing mortalities-at-age (Scenario 13). This setup mimicked the proposed experimental design for the Atlantic Ocean tuna tagging program (i.e. to estimate all movement and mortality parameters simultaneously). The second assumed that reporting rate was fixed at a known rate from an accurate high-reward program, observer reported recaptures, or tag seeding experiments (Scenario 14). The final scenario assumed that reporting levels were known and

that electronic tagging data was available to inform migration rates, which allowed exploration of the ability to estimate independent mortality parameters assuming that auxiliary information was available (Scenario 15).

Performance Metrics

Estimation model performance was assessed based on a variety of diagnostics. For each model implementation, the estimation model was fit to 1,000 simulated datasets from the operating model. Convergence was signified by the ability to invert the Hessian matrix, there being a nonsingular covariance matrix, and a maximum gradient from the minimization of the objective function less than 0.001 (Goethel et al. 2015a). Scenario runs that did not converge were removed from the analysis. Convergence rates for each model application were provided, which gave an indication of model stability (an indicator of overparameterization and robustness). Convergence rates greater than 95% were considered to indicate relatively stable estimation. Results were graphically summarized by percent relative error distributions for critical parameters (fishing mortality, reporting rate, migration rates, and natural mortality, where applicable). The percent median relative error (MRE) and range in percent relative error, expressed as the interdecile range (IDR; i.e. between the 10th and 90th percentiles), were determined across the 1,000 trials and calculated for each parameter group, including predicted tag returns. In addition to the range in MRE, the 95% confidence intervals (CI) of MRE were calculated (using the MedianCI function in the DescTools package in R) to determine significance of parameter bias.

Results

Discrete Time Models

The operating and estimation models showed a high level of consistency under the discrete time scenarios. When the parameter inputs were fixed at the simulation values (Scenario 1), predicted tag returns from the estimation model were unbiased (MRE = 0.1 %, Table 1). The relative error around predicted tag returns (IDR of -8 to 10%) exemplified the variation from the combined random processes in the operating model when the spatiotemporal assumptions of the estimation model were correct and parameter estimates were exact. Estimates of reporting rates (MRE = 0.1%, CI = -0.05 to 0.3%, IDR of -5 to 7%) and fishing mortality-at-age (MRE = -0.3%, CI = -0.4 to -0.2%, IDR of -15 to 16%) were minimally biased when the population was closed to migration (Scenario 2). However, when movement occurred but was not accounted for (Scenario 3) significant negative bias in reporting rate estimates was observed (MRE = -28.7%, CI = -28.8 to -28.6%, IDR of -32 to -25%) along with strong positive bias in fishing mortality estimates (MRE = 58%, CI = 57.9 to 58.3%, IDR of 32 to 89%); Tables 1-2, Figure 4).

The Brownie tag return model demonstrated stable model performance (100% convergence for all discrete model scenarios), and provided unbiased estimates for all parameters (migration, reporting, and fishing-mortality rates) under the discrete time, open migration model with natural mortality fixed at the true value (Scenario 4). The median bias in estimates of migration rates (MRE = 0.1%, CI = -0.2 to 0.1%, IDR of -10 to 10%), regional reporting rates (MRE = 0.04%, CI = -0.2 to 0.1%, IDR of -6 to 6%), and regional fishing mortality-at-age (MRE = -0.1, CI = -0.2 to 0.1, IDR of -14 to 16%) was relatively negligible, especially compared to Scenario 3 (i.e. when movement was ignored; Tables 1-2, Figure 4). These results validated the accuracy of the estimation model under the simplified spatiotemporal population dynamics,

including discrete spawning, tagging, and fishing seasons (Figure 1), and stable age structure of tagged individuals (Figure 2).

Continuous Time Models

For the continuous time operating model and a discrete time estimation model with optimal mortality adjustments and parameters fixed at the true values (Scenario 5), there was still high accuracy in predicted tag returns (MRE = 1%, Table 1). However, we observed a higher median bias and lower precision in predicted tag returns with the continuous time operating model (IDR = -9 to 13 % bias) compared to the discrete time self-consistency model. The bias and precision in predicted tag returns from Scenario 5 demonstrated the base level of error associated with the combination of operating model random processes and continuous time dynamics (e.g., finite but continuous spawning, tagging season, and fishery dynamics within a given year).

Failing to account for the temporal dynamics (i.e. using a discrete time assumption with no mortality adjustments, Scenario 6) resulted in significant bias in fishing mortality parameter estimates (Tables 1-2, Figure 4). In this scenario, regional reporting rates were positively biased (bias = 100%) and at the upper bounds (i.e. reporting rate was estimated to be 100% for all regions), which resulted in a consistent, strong negative bias in fishing mortalities (MRE= -70.5, CI = -70.6 to -70.4, IDR = -80 to -65). However, estimates of migration rates were unbiased (MRE = -0.1%, CI = -0.15 to 0.02%, IDR = -8 to 8%). Therefore, movement was accurately estimated despite misspecification of temporal dynamics (Table 1, Figure 4), and, unlike reporting rate, confounding of mortality parameters with migration rate estimates was not observed.

Adjustment of mortality rates (Scenario 7; continuous time base model) based on the temporal dynamics of tagging and fishing seasons significantly reduced the bias in parameter estimates. Estimates of reporting rates (MRE = 0.2%, CI = -0.1 to 0.5%, IDR of -8 to 10%) and fishing mortalities (MRE = -1.8%, CI = -2 to -1.7%, IDR of -19 to 19%) showed a minor bias in central tendency, but with reduced precision compared to the discrete base model (Scenario 4; Figure 4). The estimates of migration rates remained unbiased (MRE = -0.1, CI = -0.2 to 0.03, IDR = -9 to 9%; Figure 4, Table 1).

Sensitivity Runs

Sensitivity runs examining treatment of natural mortality demonstrated that fixing natural mortality at the incorrect value (Scenario 8) greatly biased reporting rate (MRE = 25%, CI = 25 to 26%, IDR of 13 to 41%) and fishing mortality estimates (MRE = -22.1%, CI = -22.2 to -21.9%, IDR of -37 to -4). When we estimated natural mortality in concert with other population parameters (migration rates, reporting rates, and fishing mortalities; Scenario 9), considerable bias in natural mortality estimates occurred in both positive and negative directions (demonstrating a bimodal distribution but with an MRE = -10%, CI = -13 to -6%; Figure 4) with high uncertainty around estimates (IDR of -100 to 92%). However, incorporating an informative penalty on reporting rate greatly improved the precision of parameter estimates (Scenario 10), particularly natural mortality (MRE = -6%, CI = -7 to -5%, IDR of -48 to 50; Figure 4, Table 1), which no longer maintained a bimodal distribution.

Overall, Brownie model stability was high (98 to 100% convergence across discrete, continuous time, and sensitivity scenarios). The model demonstrated robustness in estimating migration rates from tag return data, with little confounding or correlation of migration rate

estimates with mortality (natural or fishing) or reporting rates. Mortality parameter bias was minimized when informative penalties were placed on tag reporting (e.g., from return information on high reward tags or scientific observer reporting of recaptured individuals). Although the continuous time operating model dynamics led to severe bias in mortality and reporting rate parameters, relatively simple adjustments for the length of the fishing season in relation to year-round natural mortality and the average time of tag releases greatly reduced bias in most parameters.

Case Studies

The simulated genetic tagging program for Atlantic bluefin tuna demonstrated stable convergence (99.3%) and produced relatively unbiased estimates of migration rates and fishing mortality-at-age when the natural mortality was assumed to be known without error (Scenario 11; Tables 1-2, Figure 4). Estimates of migration were unbiased (MRE = 0.0%, CI = -0.3 to 0.3%) and relatively precise (IDR of -17 to 20%), while estimates of fishing mortalities were minimally biased (MRE = -3.7%, CI = -4.1 to -3.3%) but more variable (IDR of -66 to 70%). Natural mortality estimates were negatively biased despite known reporting rates (Scenario 12, MRE = -59, CI = -66 to -51%) with high variation observed across trials (IDR of -100 to 262%). One explanation for the high imprecision in both tag returns and mortality parameters for the bluefin tuna case study was the low number of tag returns. Because simulated fishing mortalities were small (average F of 0.04) and reporting rates were fixed at relatively low values (i.e. 20%), total tag returns were much lower than in other model scenarios (e.g., in Scenario 11, less than 10 tag returns were observed across trials for each cohort-region-year estimation block). With

the limited number of data points for each release cohort and recapture year, the imprecision of natural and fishing mortality estimates was, not surprisingly, high.

For the yellowfin tuna simulations, the seasonality of spawning (protracted spawning season) and tagging (regionally variable seasons) resulted in a more dynamic age structure of the tagged population compared to all other scenarios (Figure 2). When all parameters were estimated (Scenario 13), large bias in mortality estimates and high variance in all parameters resulted (Figure 4, Tables 1-2). However, estimates of migration amongst the seven regions were minimally biased (MRE = -6%, CI = -6.5 to -5.5%) and more precise (IDR = -63 to 60) than reporting rate or mortality estimates. Regional reporting rate (MRE = -3%, CI = -6.5 to -0.5%, IDR = -56 to 237%), fishing mortality (MRE = -12%, CI = -13 to -11%, IDR = -75 to 139%) and natural mortality (MRE = -16%, CI = -18 to -15%, IDR = -65 to 28%) estimates were all negatively biased. The assumption of known reporting rate had no effect on estimates of migration rates (Scenario 14), but reduced the bias in estimates of fishing mortality-at-age (MRE = -9%, CI = -9.2 to -8.8%, IDR = -44 to 47%) and natural mortality-at-age (MRE = -10%, CI = -11 to -9%, IDR = -50 to 29%). Fixing migration rates at the true value did not improve estimation of mortality rates (Scenario 15). These results indicated that accurate migration rates might be achieved from the Atlantic Ocean Tuna Tagging Program using conventional tags if the movement of the population occurs during discrete periods (e.g., spawning migrations), but that estimates of natural and fishing mortality could be considerably biased, especially if no auxiliary information exists (e.g., to inform tag reporting rates).

Discussion

Brownie-type tag return models are widely used in tagging analyses based on fishery recaptures because of their ability to estimate both fishing and natural mortality on a yearly basis when multiple release and recapture events occur (Polacheck et al. 2010). Spatially-explicit varieties have been widely applied to account for connectivity among regions with spatially-varying fishing mortality and population dynamics (Hilborn 1990). The general conclusion from these studies is that the Brownie model is a robust estimator for many parameters (e.g., migration and fishing mortality), particularly when reporting rate can be externally estimated (allowing natural mortality to be estimated directly; Xiao 1995; Pollock et al. 2001, 2002), which is further supported by our results. Although the implications of ignoring spatial structure are well-documented (e.g., Goethel et al. 2015b) and clearly demonstrated in our work, the importance of correctly accounting for fishery and tagging temporal dynamics is less acknowledged (Hearn et al. 1998; Mathur 2007). Prorating mortality estimates for tag timing has been common in many tagging studies, but our results indicated that accounting for the seasonality and duration of fishing operations is equally important. Given the lower computational demand and ease of implementation of discrete time models, it is unlikely that application of continuous time models (e.g., Miller and Andersen 2008) will become standard practice in the near future (Eveson et al. 2012). Therefore, closer examination of model misspecification resulting from spatiotemporal dynamics in real world populations is warranted when applying discrete time tagging models. In most instances, limited model misspecification has been accounted for when developing tagging simulators (e.g., Xiao 1995), which, based on our findings, results in considerable underestimation of parameter bias and variance. Additionally, we demonstrated that reliable parameter estimates may be obtainable from discrete-time tagging estimation models, but only

544 when spatial dynamics are accounted for and temporal adjustments are made for mortality
545 parameters.

546 Brownie tagging models have a number of alternate assumptions that can lead to severe
547 bias if not adhered to or accounted for in the modeling framework (e.g., incomplete mixing;
548 Hoenig et al. 1998b, Waterhouse and Hoenig 2011). Typically it is assumed that tag shedding
549 and tag mortality are both negligible, but if they do occur it can lead to large negative biases in
550 fishing mortality and positive bias in natural mortality estimates, because fewer returns are seen
551 than would be predicted. Therefore, our results are likely to underestimate potential bias,
552 because we did not assess tag loss or handling mortality, which warrants further future
553 investigations. Additionally, it is often assumed that the age of fish is known exactly (i.e. there
554 is no ageing error). We implicitly incorporated ageing error by allowing fish to have stochastic
555 birth and tagging dates. Therefore, a fish actually underwent aggregate mortality rates (i.e.
556 averaged across multiple year-, age-, and region-specific values) during a given year of life (i.e.
557 from birth date to birth date). Because the discrete estimation model assumes that age and year
558 overlap (i.e. all fish are born on January 1st), it does not account for differential mortality within
559 a given age. The resulting bias can be interpreted analogously to ageing error in terms of
560 estimating mortality-at-age. Our findings indicated that this type of ageing error was not highly
561 influential; supporting the findings of Polacheck et al. (2006b) that ageing error does not appear
562 to be a strong detrimental factor in Brownie models. However, some of the observed bias in
563 mortality estimates from the yellowfin tuna case studies may be attributed to error in age
564 assignment resulting from a protracted spawning period and high stochasticity in the age
565 structure of tagged individuals.

Model cross testing, in which an estimation model is fit to simulated data from an operating model with differing underlying assumptions, can be a valuable tool for determining model robustness to model misspecification (Deroba et al. 2015). The current study was designed to demonstrate how spatiotemporal model misspecification error can be implemented in a simulation framework and to illustrate the potential pitfalls of ignoring it. The comparison of results across simulated scenarios (i.e. the general application along with the two case studies) provided a suite of informative patterns that may hold for many real-world applications. For instance, it appears that movement parameters tend to be well estimated and independent of the correlation issues inherent in mortality parameters. These results support Hilborn (1990), Xiao (1995), and Eveson et al. (2012), who also indicated that conventional tag returns can be sufficient for estimating discrete migration rates among populations. Our results indicated that electronic tags were not necessary to estimate migration rates, but there remains a clear benefit for using archival and telemetry tags for identifying movement pathways and defining connectivity structure (Eveson et al. 2012; Sippel et al. 2015).

The relatively accurate estimation of movement in our models is clearly a factor of the simplified movement dynamics simulated and the assumption that the estimation model is correctly specified in regards to the underlying movement parametrization. Misidentification of migration parameters (e.g., not accounting for within year migrations, ignoring age- or year-dependent movement or simply mis-specifying the functional form of movement processes) may lead to bias equivalent to ignoring movement completely (Hestbeck 1995; Goethel et al. 2015b). However, the increased number of parameters associated with more complex (e.g., age-specific) spatial estimation models has been shown to cause decline in model performance (Hanselman et al. 2015). Additionally, migration rate parameter estimation degrades rapidly with increasing

number of spatial areas (Polacheck et al. 2006b), which was illustrated by the high variance in migration, fishing, and natural mortality rates seen with the seven area model for yellowfin tuna. Although it is important that the model accurately reflect the observed connectivity dynamics, there is a clear tradeoff between parameter variance and model realism that must be considered in real world applications (Eveson et al. 2012).

The box-transfer approach can be a useful approximation to underlying movement dynamics of populations. However, when movement is assumed to occur instantly (i.e. as is done with box-transfer models), mortality processes only occur within a single region during a time period (Hestbeck 1995). In reality, the mortality regime encountered by a fish is amalgamated across regions due to movement among them throughout the time step (Miller and Andersen 2008). Including continuous movement rates (analogous to continuous fishing mortality parametrizations; e.g., Miller and Andersen 2008) in the operating model would account for within year movement among regions, which may lead to more realistic assessment of migration rate bias and uncertainty (Hestbeck 1995).

Although we attempted to increase the complexity of our operating model compared to previous tagging simulators, many aspects were still simplified representations of real-world processes. Many parameters were assumed to be time-invariant (e.g., movement, reporting rate, and natural mortality), which greatly improved the performance of the estimation model. Including more complex parametrization often degrades estimation model performance due to increased parameter confounding resulting in increased parameter variance (e.g., when attempting to estimate time-varying reporting rate; Mathur 2007). Time-varying parameters can be expected, but may not be of concern over relatively short (e.g., 1-5 year) timescales, which highlights the cost-benefit of performing long-term versus short-term tagging analyses

(Hanselman et al. 2015; Cadigan and Bratney 2006). Short-term studies can potentially ignore parameter non-stationarity, but lack the ability to provide a consistent time-series of movement and natural mortality parameters that could be useful when incorporating tagging information directly into, or verifying the results of, stock assessments and management procedure evaluations (Goethel et al. 2015b).

Similarly, our model scenarios greatly simplified the parametrization of fishery dynamics by simulating a regional fishing mortality-at-age and not accounting for fleet specific (or country-specific, particularly for the tuna case studies) dynamics, which greatly reduced the number of estimated parameters. For many integrated analyses used as the basis of stock assessment, fleets within a region are modeled directly; each with unique mortality, selectivity patterns, and reporting rates (Maunder and Punt, 2013). The ability to verify or inform fleet-specific mortality estimates from tagging models would be useful. Once again, though, the balance between complexity and parsimony will depend on the quantity and quality of data available, and can be informed using model information metrics. Attempting to estimate time-varying model parameters in concert with fleet-specific mortality and reporting rate is unlikely to yield accurate or precise results. Although our results almost certainly underestimate the bias and uncertainty that might be expected from real-world applications, they provide more realistic expectations compared to tagging simulations that ignore many aspects of spatiotemporal complexity. In the future, incorporation of fleet-specific dynamics including reporting, selectivity, mortality, and fishing season length may better elucidate biases associated with estimating cumulative fishing mortality rates across regions. However, generalizing to fleet-specific continuous time dynamics may not be straightforward and is not, necessarily, essential in the estimation of population abundance.

Incorporating auxiliary information on tag reporting, tag loss, handling mortality, or natural mortality can greatly improve parameter estimation and may simplify model parametrization (e.g., if a given set of parameters can be fixed; Pollock et al. 2001, 2002, 2004; Pine et al. 2003; Polacheck et al. 2006a,b; Eveson et al. 2012). We implicitly accounted for auxiliary information on reporting rates (e.g., from high reward tag returns or scientific observer reported recaptures), migration rates (e.g., from electronic tagging), and natural mortality (e.g., from telemetry studies) by performing simulations with informative penalties on reporting rate or fixing migration or natural mortality. Not surprisingly, model performance increased significantly (i.e. there was reduced bias and variance in most parameters) when an informative penalty was included for tag reporting rate, which allowed natural mortality to also be accurately estimated. Polacheck et al. (2006a) suggest an alternate approach when high reward tagging is included in the study design where the high reward tag returns are fit directly (i.e. in the same way conventional tags are fit) by including an additional likelihood component in the objective function. The method provides a statistically integrated approach to incorporate tag reporting information into Brownie tag return models. Similarly, tagging analyses that simultaneously model conventional and electronic tags, particularly archival telemetry tags, have been shown to greatly improve estimation of natural mortality (Pollock et al. 2004; Bacheler et al. 2009; Eveson et al. 2012).

The two case studies illustrated that when simulated dynamics which are more representative of the real-world are incorporated, the ability to accurately and precisely estimate parameters decreases substantially compared to our idealized base models. Even though the bluefin example fixed reporting rate (a common nuisance parameter that is confounded with mortality), estimates of mortality parameters were not well informed due to the low number of

tag returns. The ability to maintain relatively high return rates (i.e. the combination of recapture and reporting probabilities) is essential for a successful Brownie tagging experiment. This is amplified when tags are released over a large spatial domain and spatially-explicit parameter estimation is warranted. All of these factors emphasize that the release design needs to be carefully planned to ensure representative returns across all regions of the domain are obtained (Goethel et al. 2015a).

Given the reliance of Brownie model performance on the ability to accurately determine reporting rates (when independent estimates of natural mortality are desired), the development of genetic markers for individual identification offers an interesting potential solution. When genetic tagging methods are implemented, reporting rate can be defined as the proportion of the catch-at-age screened for genetic recapture times the estimated error rate associated with genotyping (i.e. false negatives on recaptures). Similarly, the tag loss rate can be directly determined by running duplicate samples to determine the rate of genetic misidentification. A side benefit of genetic sampling is that it is a noninvasive tagging method where either passive sampling gears are utilized, or identification of spawning individuals is obtained from their offspring (i.e. larval genotyping; Bravington et al. 2016). While offspring parentage assignment models were not explicitly simulated here, the simulation framework could be adapted to model the close-kin mark-recapture approach. Although genetic tagging may improve tag experiments by providing an accurate value of tag reporting rate, further research is needed into ways to reduce costs so that sampling rates (i.e. genotyping) can be improved and realized reporting rates (i.e. proportion of catch screened) can be increased.

For the proposed yellowfin tuna tagging program, in the absence of auxiliary information (e.g., from high reward tagging, observer reported returns, or tag seeding experiments), our

681 results indicate that mortality parameter estimates are likely to be significantly biased.
682 However, reducing the number of regions by combining nearby areas with high mixing rates
683 could potentially improve estimates and reduce bias, particularly for natural mortality. In this
684 regard, electronic tagging data could be useful for defining regional connectivity. Our analyses
685 suggest that, given the large spatial domain and potential temporal dynamics for the species,
686 estimating all parameters simultaneously will not be feasible. By more carefully exploring the
687 interaction among experimental design, population and fishery dynamics, program goals, and
688 potential auxiliary information, it is expected that application and refinement of our simulation
689 framework with yellowfin tuna can help improve the design and implementation of the Atlantic
690 Ocean Tuna Tagging Program.

691 Information gained from the analysis of tagging data is important for verifying stock
692 assessment estimates of mortality, elucidating migration rates, and informing management
693 decisions (e.g., on spatial allocation of quotas; Hanselman et al. 2015). Proper experimental
694 design of tagging studies is critical for obtaining reliable parameter estimates with appropriate
695 levels of uncertainty (Xiao 1995). A primary concern of funding agencies when implementing
696 tagging studies is the number (and distribution) of tags to release per tagging event, because this
697 typically drives the associated costs. By simulation testing the experimental design prior to the
698 implementation of the tagging study, it is possible to determine more cost effective release
699 programs (i.e. timing, spatial extent, and number of tag releases). Concomitantly, it can indicate
700 whether the applied estimation framework or an alternate approach (e.g., Bayesian or state-
701 space) is more appropriate given the characteristics of the species, fisheries, and type of tags
702 being deployed. However, our results suggest that funding agencies could be misled about the
703 potential efficacy of a given tagging program, because the operating models used to simulation

test the tagging design often do not account for complex spatiotemporal dynamics and their impact on resulting parameter estimates. By continually refining and applying our spatiotemporal tagging simulator, a better accounting of the potential limitations and sensitivities of tagging models can be explored, and more robust advice on study design can be provided to the funding agencies that implement tagging programs.

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879 **Tables**

880 **Table 1.** Parameter bias (percent median relative error) and interdecile range (inner 90th percentile; in parentheses) for each
881 simulation scenario.

Scenario	Model type	Convergence	Tag returns	Migration (T_i)	Reporting (β_j)	Fishing mortality (F_a)	Natural mortality (M_a)
1. Discrete consistency	Discrete	100%	0.1 (-8 to 10)	fixed	fixed	fixed	fixed
2. No movement	Discrete	100%	0.0 (-6 to 7)	fixed	-0.1 (-5 to 7)	-0.3 (-15 to 16)	fixed
3. Ignore movement	Discrete	100%	-10 (-19 to 0)	fixed	-29 (-32 to -25)	58 (32 to 89)	fixed
4. Discrete base model	Discrete	100%	0.0 (-6 to 7)	0.1 (-10 to 10)	-0.04 (-6 to 6)	-0.1 (-14 to 16)	fixed
5. Continuous consistency check	Continuous	100%	1 (-9 to 13)	fixed	fixed	fixed	fixed
6. Continuous with discrete estimation	Continuous	100%	-0.2 (-15 to 41)	-0.1 (-8 to 8)	100 (NA)	-71 (-80 to -65)	fixed
7. Continuous base model	Continuous	100%	0.0 (-8 to 9)	-0.1 (-9 to 9)	0.2 (-8 to 10)	-2 (-19 to 19)	fixed
8. Error in M assumption	Sensitivity	100%	0.0 (-8 to 10)	-0.05 (-9 to 9)	25 (13 to 41)	-22 (-37 to -4)	fixed
9. Estimate M	Sensitivity	98.0%	0.0 (-8 to 9)	-0.04 (-9 to 9)	-13 (-27 to 71)	9 (-43 to 46)	-10 (-100 to 92)
10. Estimate M with reporting prior	Sensitivity	100%	0.0 (-8 to 9)	-0.1 (-9 to 9)	-2 (-12 to 7)	2 (-16 to 25)	-6 (-48 to 50)
11. Bluefin gene tagging	Case Study	99.3%	0 (-36 to 77)	-0.01(-17 to 20)	fixed	-4 (-66 to 70)	fixed
12. Bluefin known migration	Case Study	96.9%	-5 (-44 to 85)	fixed	fixed	-2 (-66 to 74)	-59 (-100 to 262)
13. Yellowfin conventional tagging	Case Study	85.1%	0.0 (-21 to 32)	-6 (-63to 60)	-3 (-56 to 237)	-12 (-75 to 139)	-16 (-65 to 28)
14. Yellowfin known reporting	Case Study	95.7%	0.0 (-22 to 33)	-6 (-58 to 55)	fixed	-9 (-44 to 47)	-10 (-50 to 29)
15. Yellowfin known report and migration	Case Study	93.4%	0.0 (-23 to 33)	fixed	fixed	-11(-43 to 31)	-9 (-53 to 34)

882

883

Table 2. Parameter bias (percent median relative error) and associated 95% confidence interval (parentheses; in percent) for each estimated parameter and simulation scenario.

Scenario	Model type	Migration (T_j)	Reporting (β_j)	Fishing mortality (F_a)	Natural mortality (M_a)
1. Discrete consistency	Discrete	fixed	fixed	fixed	fixed
2. No movement	Discrete	fixed	0.1 (-0.05 to 0.3)	-0.3 (-0.4 to -0.2)	fixed
3. Ignore movement	Discrete	fixed	-29 (-29 to -29)	58 (57.9 to 58.3)	fixed
4. Discrete base model	Discrete	-0.1 (-0.2 to 0.1)	0.04 (-0.2 to 0.1)	-0.1 (-0.2 to 0.1)	fixed
5. Continuous consistency check	Continuous	fixed	fixed	fixed	fixed
6. Continuous with discrete estimation	Continuous	-0.06 (-0.15 to 0.02)	100 (NA)	-71 (-71 to -71)	fixed
7. Continuous base model	Continuous	-0.1 (-0.2 to 0.03)	0.2 (-0.1 to 0.5)	-2 (-2 to -1.6)	fixed
8. Error in M assumption	Sensitivity	-0.05 (-0.2 to 0.1)	25 (25 to 26)	-22 (-22 to -22)	fixed
9. Estimate M	Sensitivity	-0.04 (-0.1 to 0.1)	-13 (-14 to -12)	9 (-9 to -10)	-10 (-13 to -6)
10. Estimate M with reporting prior	Sensitivity	-0.1 (-0.2 to 0.01)	-2 (-3 to -2)	1.8 (1.6 to 1.9)	-6 (-7 to -5)
11. Bluefin gene tagging	Case Study	-0.01 (-0.3 to 0.3)	fixed	-3.7 (-4.1 to -3.3)	fixed
12. Bluefin known migration	Case Study	fixed	fixed	-2 (-2.4 to -1.6)	-59 (-66 to -51)
13. Yellowfin conventional tagging	Case Study	-6 (-6.5 to -5.5)	-3 (-6.5 to -0.5)	-12 (-13 to -11)	-16 (-18 to -15)
14. Yellowfin known reporting	Case Study	-5.7 (-6.1 to -5.2)	fixed	-9.0 (-9.2 to -8.8)	-10 (-11 to -9)
15. Yellowfin known report and migration	Case Study	fixed	fixed	-11.1 (-11.3 to -10.9)	-9 (-10 to -8)

887 **Figures**

888

889 **Figure 1.** Temporal dynamics of the simulation model scenarios and case studies. The dark bars

890 represent the spawning season, medium gray bars represent the tagging season, and light gray

891 bars represent the fishing season. For the discrete model, all tagging and spawning occurs

instantly on January 1st. The individual bars in the yellowfin tuna model represent the dynamics of each of the seven regions and fishing seasons.

Figure 2. Simulated age structure of tagged individuals in each model scenario summed across regions.

Figure 3. Spatial dynamics of the simulation model scenarios and case studies. The emigration rates of yellowfin tuna are shown for Region 1 (assumed 20% emigration to directly adjacent regions and 5% emigration to all other regions). Emigration rates for all other regions followed the same generalized assumption.

Figure 4. Percent relative error in discrete Brownie model parameter estimates. The shaded coloring represents a distribution for each time-, space- or age-varying parameter. The numbering on the x-axis corresponds to each model scenario defined in the text and listed in Table 1 (note that no shading indicates that parameters were fixed at the true value).

Appendix A

Model Population Dynamics

Operating Model

A traditional approach for tagging simulation studies has been to define the capture history probability statements over discrete time intervals (Williams et al. 2002), and generate the expected number of observations per outcome assuming a multinomial distribution. However, when the number of states (e.g., age and spatial transitions) or sampling events is large, the ability to define each capture history becomes difficult, particularly for a generalized model. The spatially-explicit operating model developed here treats the fate of each tagged individual stochastically with a series of conditional probability models (Figure A1, Tables A1-A2), which allows generating capture-recapture data with unlimited spatial (i.e. movement) and age-class state transitions, tag cohorts, and recapture events. Continuous time dynamics were utilized to generate individual capture histories for the operating model, but it was generalized to allow a continuum from continuous to discrete seasonal or yearly timesteps. The operating model provided fates for each marked and released individual, while summary matrices were generated to provide the number of tag releases by tag cohort (i.e. release year, region, and age-class) and tag recoveries by release cohort, recapture year, and recapture region in order to emulate the type of data typical gathered from a tag return study.

Ageing

The temporal dynamics of the model represented a novel addition for tag-recapture experimental design simulators by allowing for continuous spawning and tagging seasons over discrete periods

within a given year. Stochasticity in birth date, time of tag release, and age-at-tagging was incorporated using defined seasonal distributions (i.e. uniform in the current applications). The distribution defined the shape of spawning and tagging effort over the course of the year, with normalized probabilities of an individual being born or tagged on a particular day.

An individual was assigned to an age-class, a , based on a random multinomial draw with probability equivalent to the input age-composition proportions, $P_{j,a}$, of releases by region, j (see Table A1 for a complete list of model parameters). A random birth date (defined by Julian day of the year) was then assigned to the individual based on a uniform spawning season distribution (defined by the length of the spawning season, s). Finally, a uniform distribution of effort for the tagging season was defined (based on the tag season length, t) and a random day (Julian day of the year) of tag and release was assigned. The age-at-release was then calculated for each marked individual based on the assigned age class, birth date, and tag date following model statement 1 (Table A2).

Temporal dynamics

After assignment of age upon release, instantaneous tag shedding and tag mortality could occur. Tag-induced mortality (model statement 2; Table A2) represented the probability of a fish dying due to the tagging process, while tag shedding (model statement 3; Table A2) was the probability of discrete tag loss immediately upon release. Note that neither tag loss nor handling mortality was included in the model applications of the current study. The assignment of age, probability of tag loss, and handling mortality (model statements 1-3) occurred only once at the time of release, whereas the remaining probability statements occurred repeatedly until a fish died (either

from natural or fishing mortality) or until the end the terminal year (i.e. the fish survived to the end of the study period).

Due to the fact that each individual was given a different birth and tag date, mortality needed to be adjusted to account for both factors (in addition to fishing season length, see below). When an individual's birth date was not at the beginning of the timestep (i.e. it was not born on January 1st), the mortality schedule encountered over a year of life at a given age was actually an amalgamated parameter representing mortality regimes of multiple years and, possibly, regions (if a fish moved during the period). For example, if a fish was born mid-year, the simulation model would allow for a half-year mortality at the current year's mortality schedule for the new age (after the fish reached its birth date in the current year). Then, at the beginning of the next year, the fish could move and the remaining half year mortality for the given age would be the mortality for that age in the new year and the new region (if it moved). Therefore, the mortality for that age would be 'averaged' over the mortality regimes of the two Julian years. Because all fish were assigned a birth date that was maintained for the entire simulation, these calculations applied to fish of all ages regardless of age at tagging. Additionally, the stochastic birth date led to inherent bias in the estimation model, because the Brownie estimator assumed all fish were born on January 1st, and, therefore, encountered the mortality regime from only one year and region at a given age.

Additionally, a discrete fishing season, f , was assumed where fishing occurred continuously across the defined season with no fishing outside of that season, and multiple, discrete fishing seasons could occur within a given year. However, seasons could not extend past the end of the

year (December 31st), because, by definition, the change of year represented the start of a new season (i.e. for spawning output, tagging effort, or fishing mortality). For a year-round fishing season and discrete tagging at the beginning of the year (i.e. a discrete time model), survival and harvest probabilities were defined by F and M and the binomial distribution (provided in model statements 5-6; Table A2), while the probability of a recapture being reported (given that an individual was harvested) was also defined by a binomial distribution determined by the region-specific tag reporting rate, β (proportion of recaptured tags that are reported; model statement 7, Table A2).

Given that natural mortality, M , acted continuously across a given year, mortality adjustments were also needed to account for the temporal relationship between continuous year-round natural mortality, continuous fishing mortality, F , occurring for a defined season (either discrete or year-round), and the date of tagging [see Hearn et al. (1998) and Hoenig et al. (1998) for a complete description of the associated adjustments required]. Therefore, mortality in each year, y , was broken down into three distinct periods: natural mortality prior to fishing (model statement 4; Table A2), total mortality during the fishing season (natural plus fishing mortality, model statement 5; Table A2), and natural mortality post-fishing (model statement 8; Table A2). The total mortality for the year was thus the summation of total mortality within each of the three periods:

$$Z_{Pre-F} = 1 - e^{-M_{j,a} * \left(\frac{f_{start}-1}{365}\right)}$$

$$Z_{During-F} = 1 - e^{-\left(M_{j,a} * \left(\frac{f_{end}-f_{start}+1}{365}\right) + F_{j,y,a}\right)}$$

$$Z_{Post-F} = 1 - e^{-M_{j,a} * \left(1 - \frac{f_{end}}{365}\right)}$$

$$(1) \quad Z_{Total_{j,y,a}} = Z_{Pre-F} + Z_{During-F} + Z_{Post-F}$$

Note that Equation 1 collapsed to the discrete time equivalent of total mortality or, conversely, survival if the fishing season lasted for the entire year (i.e. from day 1 to day 365). When multiple fishing seasons existed within a year (e.g., the yellowfin tuna case studies), further mortality adjustments were incorporated by implementing additional mortality periods between fishing seasons (when only natural mortality acted).

In the year an individual was tagged, the temporal relationship between tagging date and fishing season also influenced the mortality schedule encountered. When tagging occurred before the fishing season commenced, natural mortality prior to fishing was discounted for the tagging date, whereas if tagging occurred after the start of the fishing season, both fishing and natural mortality (during the fishing season period) were discounted for the difference between the tag date, t_{date} , and the start of the fishing season:

$$\begin{aligned} & \text{if } f_{start} > t_{date} \begin{cases} Z_{Pre-F} = 1 - e^{-M_{j,a} * \left(\frac{f_{start} - t_{date}}{365}\right)} \\ Z_{During-F} = 1 - e^{-\left(M_{j,a} * \left(\frac{f_{end} - f_{start} + 1}{365}\right) + F_{j,y,a}\right)} \end{cases} \\ & \text{if } f_{start} \leq t_{date} \begin{cases} Z_{Pre-F} = 0 \\ Z_{During-F} = 1 - e^{-\left(M_{j,a} * \left(\frac{f_{end} - t_{date} + 1}{365}\right) + F_{j,y,a} * \left(1 - \frac{t_{date} - f_{start}}{f_{end} - f_{start} + 1}\right)\right)} \end{cases} \\ & Z_{Post-F} = 1 - e^{-M_{y,a} * \left(1 - \frac{f_{end}}{365}\right)} \end{aligned}$$

$$(2) \quad Z_{Total_{j,y,a}} = Z_{Pre-F} + Z_{During-F} + Z_{Post-F}$$

In the year of release, survival and harvest probability statements (model statements 4-6 and 8 in Table A2) were adjusted appropriately to account for the tagging and fishing season temporal interactions. Additionally, when the discrete time model was implemented (i.e. no seasonality in

tagging or fishing occurred) in the operating model, the survival probabilities (model statements 4-5 and 8 in Table A2) collapsed to a single survival statement and no mortality adjustments were needed.

Spatial Dynamics

The operating model was spatially-explicit allowing for multiple regions with or without movement among them. Movement was implemented with the box-transfer approach where the proportion of the population that instantaneously migrated from region k to region j at the beginning of the year was given by T_k^j , which resulted in a probability of movement among regions that was defined by the multinomial distribution (model statement 9; Table A2). Movement was parameterized to allow for movement in the year that an individual was tagged and released. However, movement did not occur during the release year for most scenarios (i.e. the first movement was in the year following release year), except for the bluefin tuna case studies where movement could occur during the release event. Also, an individual was assumed to remain in a given region for the remainder of the year after movement. Upon migration, an individual was assumed to be well-mixed with all fish in the region.

Various population structures were assumed (i.e. multiple populations with no mixing, metapopulation structure, and natal homing; Goethel et al. 2011), which differed in their assumptions regarding how movement was parametrized. When natal homing was implemented (i.e. all scenarios except the yellowfin tuna case studies), life history parameters were assumed to be genetically defined (Goethel and Berger 2017, This Issue). Therefore, the movement probabilities were defined by the natal population (i.e. the region in which the individual was

tagged and released was assumed to represent the spatial extent of the natal population) and did not change as the fish moved into other regions. A probability of transient movement ($T_{s,k}^j$; model statement 10; Table A2) allowed individuals to ‘stray’ to a new natal population and adopt the movement probability matrix of that population. Straying rates were meant to represent both natal straying and incorrect identification of natal region at the time of tagging (i.e. it essentially implied that a certain fraction of fish did not follow the dynamics of the assumed natal population in which they were tagged and allowed testing the estimation bias that resulted). When transience was implemented, an additional binomial probability statement was incorporated after each movement in order to determine whether the individual retained its natal movement probabilities or adopted the connectivity dynamics of the new region (note that straying was not implemented in any of the model applications of the current study). Conversely, when life history parameters were assumed dependent on the environment (i.e. metapopulation dynamics; yellowfin tuna case studies), movement was modeled as a Markovian process where an individual’s migration probabilities were dependent on the region in which it currently resided (and was independent of natal region).

Tag Loss and Handling Mortality

Handling mortality (model statement 2; Table A2) and discrete tag loss (model statement 3; Table A2) were input as age-dependent parameters assumed to occur at the time of release. To allow for estimation of tag loss, a proportion of individuals could be double-tagged (d_a). When double tagging was implemented, an additional binomial probability statement (model statement 11; Table A2) was added to the capture history, prior to model statement 3, to determine if a released individual received two tags. The probability that a double-tagged individual retained at

least one tag was modeled as the complement of the joint probability of losing tags from discrete tag loss. The empirical estimate of tag loss-at-age was calculated from the tag returns of double-tagged individuals based on the number that retained both or just one of the tags (Polacheck et al. 2006; Pine et al. 2012). Note that tag loss, handling mortality, and double tagging were not implemented in any of the model applications of the current study.

Brownie Tag Return Estimation Model

The spatially-explicit Brownie estimation model utilized discrete, age-based population dynamics to calculate the number of tagged individuals at large, n , and predict tag returns, r , by release cohort, c (i.e. defined by release region, release age, and release year), recapture region, and recapture year. The estimation model only operated on discrete time scales, which has been an almost ubiquitous trait of tagging analyses, and, along with migration assumptions, were the key sources of model misspecification investigated. All parameters (i.e. fishing mortality, natural mortality, tag reporting, and migration rates) could be estimated as age-, year-, and region-specific, but with complete flexibility to fix values across a given dimension based on user input values (i.e. parameters could be fixed at true or incorrectly specified values). In order to match the operating model, tag-induced mortality and tag shedding were assumed to be negligible in the model scenarios investigated here.

Because reporting rate was an explicitly defined parameter (either estimated or fixed), it allowed the separation of fishing and natural mortality in the estimation model (instead of estimating a conglomerated mortality parameter). The general tagging dynamics (assuming a yearly timestep) were:

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$$(3) \quad n_{j,y}^c = \sum_k [T_k^j n_{k,y-1}^c e^{-(F_{k,y-1,a-1} + M_{k,a-1})}]$$

176
$$(4) \quad \widehat{r_{j,y}^c} = n_{j,y}^c \beta_j \left(1 - e^{-(F_{j,y,a} + M_{j,a})} \right) \frac{F_{j,y,a}}{F_{j,y,a} + M_{j,a}}$$

177 Because available tags and predicted returns were defined for a cohort, the age subscript was no
178 longer needed for these quantities (i.e. all fish were assumed to be of the same age in a given
179 cohort even though the operating model maintained unique birth dates for each individual).
180 Movement and mortality parameters, however, maintained age subscripts as these values were
181 age-dependent and differed as the cohort aged.

182

183 *Temporal Mortality Adjustments*

184 For estimation models that used mortality adjustments (to account for discrete fishing seasons
185 and the time of tagging), Equations 1-2 were incorporated into Equations 3-4 to adjust total
186 mortality. The temporal mortality adjustments allowed the best possible (i.e. least biased)
187 parameter estimates when the underlying operating model assumed continuous time dynamics
188 (note that the estimation model assumed a January 1st birth date for all fish resulting in inherent
189 bias due to stochastic birth dates in the simulation model; see the Ageing section under
190 Operating Model above). However, instead of using exact dates of tagging, the average tag date
191 (based on the tag season length) was utilized (in Equation 2). Additionally, when multiple
192 fishing seasons existed, the estimation model assumed only a single fishing season, which started
193 on the first day that fishing commenced and ended on the end date of the last season (it was
194 assumed that the fine-scale temporal dynamics of fishing seasons may not be well known for
195 most tagging experiments). In order to appropriately account for the various mortality periods
196 (see the Temporal Dynamics section under Operating Model above), the number of tags
197 available was calculated at both the beginning of the year (accounting for natural mortality after

the end of the fishing season in the previous year) and again at the beginning of fishing season (to properly discount the available tags for natural mortality prior to fishing). Similarly, the number of tags recaptured was adjusted to account for the timing of the fishing season in relation to the assumed tag date and year-round natural mortality (see Equations 1-2).

Maximum Likelihood Estimation

Estimation within AD Model Builder occurred in phases to improve convergence, where each parameter group was estimated in a different phase. Maximum likelihood estimation was used with an assumed multinomial likelihood distribution of tag recaptures. Observed and predicted recapture proportions, P , were fit by recapture state (i.e. release cohort, recapture region, and recapture year along with a not recaptured, NR , state) with proportions calculated by:

$$(5) \quad P_{j,y}^c = \frac{r_{j,y}^c}{n_{j,y,rel}^c}$$

$$(6) \quad P^{c,NR} = \frac{n_{j,y,rel}^c - \sum_j \sum_y r_{j,y}^c}{n_{j,y,rel}^c}$$

An adjusted likelihood was used, which gave a likelihood, L , value of zero for perfect fit [i.e. subtraction of the $\log(\text{observed})$ component in each statement; Legault and Restrepo 1999], and the associated variance was defined by the effective sample size, ESS , for each tagging cohort:

$$(7) \quad -\ln(L) = -ESS_c \sum_c [\sum_j \sum_y (P_{j,y}^c \ln(\widehat{P}_{j,y}^c) - P_{j,y}^c \ln(P_{j,y}^c +)) + (P^{c,NR} \ln(\widehat{P}^{c,NR}) - P^{c,NR} \ln(P^{c,NR}))]$$

Finally, penalties could be enacted for any of the parameters. A penalty could be utilized as a simple bound, which if the parameter exceeded then the difference between the estimated parameter and the bound was added to the objective function. More explicit penalties utilizing a normal distribution worked in a similar manner, but penalized the difference between the

220 estimated parameter and the user defined mean of the normal distribution based on a user input
221 variance. The latter penalty type was essentially equivalent to an informative prior in a Bayesian
222 context, and was utilized to emulate a situation in which external information might be available
223 to help inform a given parameter estimate.

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244   **Table A1.** Definition of parameters used in the operating and estimation models.

Parameter	Description
a	Age
y	Year
j	Region
c	Tag cohort
t	Tag season length
s	Spawning season length
f	Fishing season length
h_a	Handling mortality-at-age
l_a	Discrete tag loss-at-age
$F_{j,y,a}$	Fishing mortality-at-age in region j in year y
$M_{j,a}$	Natural mortality-at-age in region j
$Z_{j,y,a}$	Total mortality-at-age in region j in year y
β_j	Tag reporting rate in region j
T_k^j	Proportional migration rate from region k to region j
$T_{s,k}^j$	Proportional straying rate from region k to region j
n	Number of tag releases
r	Number of tag returns
P	Proportion in a given state
L	Likelihood component value
ESS	Effective sample size

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Table A2. Probability statements defined in the operating model. Probability model statements 1 to 3 and 11 were unique to the tag and release event, while statements 4 to 10 were repeated until the individual experienced a mortality event. The *time_before*, *time_during*, and *time_after* parameters represented the fraction of the year that occurred before, during, and after the fishing season and were used to adjust mortality schedules for survival and harvest probability statements in order to account for the discrete fishing season (see Appendix A, Equation 1 for a full description). Note that in the year of release the survival and harvest probability statements were adjusted to account for the overlap, or lack thereof, of the tagging and fishing seasons (see Appendix A, Equation 2 for a full description of these adjustments).

Model Statement	Process	Probability Model
1*	Age-at-release	$Multinomial(Pr = P_{a,j}) + \frac{[Uniform(d_{t1}, d_{t2}) - Uniform(d_{s1}, d_{s2})]}{365}$
2	Handling mortality	$Binomial(Pr = h_a)$
3	Discrete tag loss	$Binomial(Pr = l_a)$
4	Survival before fishing	$Binomial(Pr = e^{-M_{j,a} \cdot time\_before})$
5	Survival during fishing	$Binomial(Pr = e^{-(F_{j,y,a} + M_{j,a} \cdot time\_during)})$
6	Harvest	$Binomial\left(Pr = \frac{F_{j,y,a}}{F_{j,y,a} + M_{j,a} \cdot time\_during}\right)$
7	Tag reported	$Binomial(Pr = \beta_j)$
8	Survival after fishing	$Binomial(Pr = e^{-M_{j,a} \cdot time\_after})$
9	Movement	$Multinomial(Pr = T_k^j)$
10	Transient	$Binomial(Pr = T_{s,k}^j)$
11	Double-tagged	$Binomial(Pr = d_a)$

* d_{t1} = Julian day of the year that tagging season commences

d_{t2} = Julian day of the year that tagging season concludes

d_I = Julian day of the year spawning season commences

d_{I1} = Julian day of the year spawning season is concludes

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267 **Figure A1.** Sequence of probability statements in the tagging simulation operating model.

268 Numbers represent model probability statements matching those in Table A2.