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Integrated Spatial and Age Mark Recapture (ISAMR) Model (v2.0) for Lower Fraser River White Sturgeon

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EXECUTIVE SUMMARY

A stock reduction analysis (SRA) for Lower Fraser River White Sturgeon described in Whitlock and McAllister (2012) suggested that the population vulnerable to capture in the lower Fraser recreational fishery was substantially higher than the estimates derived from the Bayesian mark-recapture model. A review of the data and assumptions used in the SRA model revealed substantial concerns regarding the reliability of these population estimates (English and Bychkov 2012). Given these concerns and the known movement of sturgeon into and out of the assessment area, English and Bychkov (2012) recommended the development of a multi-year mark-recapture model that would use all available PIT tag data (since October 1999) in the Fraser River Sturgeon Conservation Society (FRSCS) database.

The first investigation related to a multi-year mark-recapture model identified a single state closed robust design (CRD) as the best available model using the MARK software (White and Burnham 1999). However, several deficiencies were identified with the CRD design (Gazey and English 2014). These and other findings led to the decision to pursue the development of the Integrated Spatial and Age-structured Mark-Recapture (ISAMR) model in 2015.

This report provides a detailed description of the Version 2.0 of ISAMR model and compares the abundance estimates derived from this model with those derived from the Bayesian (24 month) mark-recapture (BMR24) model (Nelson et al. 2017). Both the ISAMR and BMR24 models use Bayesian estimation to provide point estimates and credible intervals, however the two have very different population modelling structure. The ISAMR uses age classes, while the BMR24 model employs size groups. Furthermore, the ISAMR reconstructs and tracks the transition of fish through the available age classes over the course of the assessment period, while for the BMR24 model individuals are fixed within size-class for each 24-month analysis period. The two models also differ in how differences in gear selectivity are handled. The ISAMR model directly includes a selectivity-at-age relationship that is estimated based on the data, while the BMR24 model assumes that size groups of interest are fully recruited into the fishery. The ISAMR model also includes information on sampling effort and considers all captures within the assessment period in a single analysis, while the BMR24 model does not include sampling effort and uses a 24-month rolling window. Despite these differences, estimates of total yearly abundance for each of the three main size/age classes showed good agreement between the two models.

A major advantage of the ISAMR model is that forward population projections can be created under potential recruitment scenarios. In the "*Population Projections*" section, the overall sturgeon abundances were predicted to continue the recent decline if recruitment remains at its current level. This includes large-sized sturgeon age 23-55 (160-279 cm fork length [FL]), which were projected to reach peak abundance in 2022 and then decline steadily thereafter. The model results also project that annual age-1 recruitment would need to increase by a minimum of 1.6 times the recruitment in recent years (2011-2016) to stop the projected decline and rebuild sturgeon abundances to the 2016 level by 2028. Much higher recruitment rates and/or higher survival rates would be required to rebuild abundances to the levels estimated for 2004-06.

These results emphasize the importance of taking immediate actions to improve both recruitment of age-1 fish and survival rates for ages 1-6 fish. Actions should include: the protection of

sturgeon spawning and juvenile rearing habitat; the removal of all fishing gear from known sturgeon spawning areas during the spawning period; and the protection of the spawning and rearing areas of sturgeon prey species (e.g., salmon and eulachon). Recent efforts to improve handling techniques for sturgeon anglers (and for fishers that intercept sturgeon as bycatch while targeting other species) are expected to positively impact both survival and spawning rates for adult sturgeon and should continue to be supported.

The results presented in this report should be used to help set medium- and long-term targets for rebuilding the Lower Fraser River White Sturgeon population. Given that the abundance of age 7-55 sturgeon has approached 60,000 fish as recently as 2005, we believe that this would be a reasonable interim long-term population recovery goal. Similarly, a spawning population (age 22-55 sturgeon) goal of 20,000 fish should also be considered as a reasonable target. Both the ISAMR and BMR24 models should be used to monitor progress toward achieving these goals. However, the mark-recovery program should be augmented by juvenile (age 2-6) sampling programs and consistent efforts to protect sturgeon spawning and rearing habitat. Given the long-lived nature of White Sturgeon, it will take a considerable amount of time to achieve these goals.

The final set of recommendations resulting from this work include:

1. The ISAMR model and BMR24 model should be used in tandem to derive annual abundance estimates and trends from the PIT tag mark-recapture data for Lower Fraser River White Sturgeon.

2. Immediate actions should be implemented to improve age-1 recruitment and survival rates for age 1-6 sturgeon. These measures should include: protection of sturgeon spawning and juvenile rearing habitat, the removal of all fishing activity from known sturgeon spawning areas during the spawning period, a reduction in all known sources of sturgeon mortality, and the protection of spawning and rearing areas for areas of the prey species upon which juvenile and adult sturgeon depend (e.g., salmon and eulachon).

3. Management agencies, recreational anglers, guides and First Nations should continue to support measures to improve survival rates and spawning success for adult sturgeon.

4. An interim medium-term population recovery goal for Lower Fraser White Sturgeon should be set at 60,000 for age 7-55 (60-279 cm FL) sturgeon.

5. An interim spawning population goal for Lower Fraser White Sturgeon should be set at 20,000 for age 22-55 (160-279 cm FL) sturgeon.

6. Indications that progress has been made to achieve these interim goals would be a significant increasing trend in abundance of age 7-12 (60-99 cm FL) sturgeon by 2025.

7. The operation of the ISAMR model program could be improved by removing all computer code that is no longer used and streamlining the data input formats.

8. Further enhancement to the ISAMR model would include the addition of seasonal stratification for both movement pattern and abundance estimation; however, the management benefits from this added complexity are not clearly evident at this time.

9. Any changes in age-1 recruitment starting in 2017 will not affect age 22-55 sturgeon abundance until after 2038.

INTRODUCTION

Passive integrated transponder (PIT) tags have been applied to White Sturgeon (*Acipenser transmontanus*) in the lower Fraser River through a monitoring program run by the Fraser River Sturgeon Conservation Society (FRSCS) since 1999 (Nelson et al. 2013). Estimates of the population size of White Sturgeon in the lower Fraser River during successive 24-month periods have been estimated using a Bayesian mark-recapture model that does not explicitly account for temporary emigration (Gazey and Staley 1986; Nelson et al. 2013). White Sturgeon are known to move out of the lower Fraser River assessment area and into marine (Strait of Georgia) or lacustrine (Pitt and Harrison lakes) areas (e.g., Veinott et al. 1999), at least temporarily (Robichaud et al. 2017). Acoustic tagging studies have provided some information on the timing of movement between these areas but the portion of the lower Fraser River population using these habitats outside our assessment area is unknown. A stock reduction analysis (SRA) for Lower Fraser River White Sturgeon described in Whitlock and McAllister (2012) suggested that the population vulnerable to capture in the lower Fraser recreational fishery was substantially higher than the estimates derived from the Bayesian mark-recapture model. One possible explanation for this difference is that a substantial portion of the Lower Fraser River White Sturgeon population may reside outside the Fraser River for extended periods and are thus not included in the population estimates derived using the Bayesian mark-recapture model. Further review of the data and assumptions used in the SRA model revealed substantial concerns regarding the reliability of its population estimates (English and Bychkov 2012). Given these concerns and the known movement of sturgeon into and out of the assessment area, English and Bychkov (2012) recommended the development of a multi-year mark-recapture model that would use all the available PIT tag data contained in the FRSCS database that commenced in October 1999.

The first investigation related to a multi-year mark-recapture model involved loading all the data into Program MARK (White and Burnham 1999) and conducting the analysis using a multi-state closed robust design (MSCRD) and a single state closed robust design (CRD). The conclusion from these analyses was that the best available model using Program MARK was a yearly CRD design with constant survival and yearly migration and population size parameters. However, several deficiencies were identified with the CRD design, including the tendency for single-region models to underestimate the population size because of heterogeneous catchabilities and the practical problem that even a simple MARK model with two sampling regions took more than nine hours to execute (Gazey and English 2014). These and other findings led to the decision to pursue the development of the integrated spatial and age-structured mark-recapture (ISAMR) model in 2015.

There were a number of challenges associated with the initial development and testing of the ISAMR model, including: ensuring the model was using the correct set of data; incorporating appropriate age selectivity curves; and checking model assumptions, structure, and function. Despite the challenges, we are pleased to confirm that we have been able to transfer the model from the University of British Columbia (UBC) to LGL Limited and confirm that it is fully operational and providing reasonable estimates of age-specific abundance that can be compared with the results from the other mark-recapture analyses.

The primary conservation benefits from this work are: 1) a better understanding of the historical data available for Lower Fraser River White Sturgeon; 2) confirmation of the recent abundance estimates derived from the Bayesian (24 month) mark-recapture (BMR24) model; and 3) the development of an age-structured model that can be used to assess trends in recruitment and forecast future populations, which will be important for management decisions regarding First Nation and recreational sturgeon fisheries.

In this report, we present an overview of the ISAMR model formulation and operation. The model was used to analyze captures and releases from 2000 through to 2016, across four sampling regions (sampling regions A-D; Figure 1) and 58 age classes. Because of the fine structuring of the population model incorporated in the ISAMR model it was possible to generate population estimates and trajectories at a very granular level (i.e., any combination of age class, sampling region, and assessment year). This allowed us to make population estimates that are roughly comparable to the regional estimates generated from the BMR24 model, which use the same sampling regions (see Figure 1), but produces abundance estimates by size group rather than age class. Direct comparison of the ISAMR and BMR24 model results allowed us to look for similarities and differences provided by the two approaches. In addition, we also conducted a sensitivity analysis on the ISAMR model to investigate how assumptions surrounding selectivity impact population estimates.

MODEL OVERVIEW

The original version of the ISAMR Model was developed in 2015 by Dr. Tom Carruthers, in collaboration with Karl English and Bill Gazey (version 1.6). In 2016, as part of the transfer to LGL, the model was modified and extended by Dr. Wendell Challenger and Karl English (currently version 2.0). A summary of changes between versions is outlined in Table A1, with the current version discussed within this report.

The two primary design goals for the ISAMR were to build an age-structured population model and to incorporate all available PIT tag data from White Sturgeon studies in the lower Fraser River since 1999. Age structuring allows for several advantages over the BMR24 model; these include: 1) the ability to make population projections based on the current population age structure; 2) the ability accommodate for reduction in mortality as sturgeon age; and 3) the ability to accommodate for differences in "catchability" by sturgeon age. The latter issue is herein referred to as selectivity. Additional goals for the model included the ability to incorporate all sources of catch data (i.e., releases with and without tags). The inclusion of data from two types of experiments: 1) capture-mark-recapture, where all captured individuals are released with a tag, and 2) catch data regardless of whether an individual is tagged. As such the ISAMR model can be considered an integrated analysis as it combines several data sources into a single analysis (Maunder and Punt 2013).

These design goals were accomplished by separately considering the population dynamics of the un-tagged ($\boldsymbol{U}$) and tagged ($\boldsymbol{T}$) populations simultaneously (Figure 2). Each population ($\boldsymbol{U}$ and $\boldsymbol{T}$) has both spatial and age structuring and both are taken through the same population dynamic processes such as mortality, movement between sampling regions, and aging. Captures from the un-tagged population ($\boldsymbol{U}$) are used to inform the un-tagged catch component of the model, while catch from the tagged population ($\boldsymbol{T}$) informs the mark-recapture component of the model (a

Cormack-Jolly-Seber [CJS] model). Individuals are only recruited into the un-tagged population, while marked individuals are transferred from the un-tagged to the tagged population based on recorded tagging events from the capture and release records (Figure 2).

In this manner, the ISAMR model is similar to other age-structured mark-recapture models which analyze mark-recapture within a virtual population analysis (VPA) framework (Coggins et al. 2006). The ISAMR model can also be viewed as a state-space implementation of a multi-state mark-recapture experiment and a multi-state catch-at-age model. The abundances of the two-population ($\boldsymbol{U}$ and $\boldsymbol{T}$) not directly observable (i.e., the latent state) but are estimated through a sampling process where un-tagged sturgeon that are captured are released either with or without a tag, and recaptures of previously tagged individuals are recorded. Finally, because both populations feature the same spatial and age structuring, a variety of population estimates may be generated for differing combinations of age class and sampling regions (Figure 1), which offers in-depth information about the underlying health of the sturgeon population.

Model Components

The specification of the ISAMR model can be broken down into two major components: 1) the population model (i.e., un-tagged $\boldsymbol{U}$ and tagged $\boldsymbol{T}$ populations – model states) and 2) the observation model (i.e., how observed catch is related to the underlying model states). We include a brief overview of each component in the next two subsections, with the full specification found in Appendix B. Both components include unknown parameters that are estimated by minimizing the discrepancy between the observed and predicted catch generated from the observation model (which is informed by the population model). Finally, while the ISAMR model estimates nearly all unknown parameters, some fixed values are still required (e.g., maximum survival rate; see Table B1). That said, compared to the earlier version (i.e., version 1.6) nearly all unknown parameters are now estimated (see Table B2, Appendix B).

Population Model

The population model functions by creating and maintaining two distinct spatial- and age-structured population arrays for the un-tagged ($\boldsymbol{U}$) and tagged ($\boldsymbol{T}$) populations over the course of the assessment period (Figure 2). These population arrays can be considered to represent all fish at risk of capture and are considered to be states that not directly observed, except through the sampling process. Internally, the model maintains a three-dimensional array to represent the number of un-tagged and tagged fish in the system for any combination of assessment year (y), age class (a), and sampling region (r), however for ease of reference we will refer to two-dimensional slices of the arrays. For example, $\boldsymbol{U}_y$ represents a year-specific un-tagged population matrix (by age class and sampling region) in year y. Similarly, $\boldsymbol{U}_r$ represents the population trajectory (year by age class) for sampling region r.

The easiest way to conceptualize the model is to view population arrays as a succession of yearly population matrices, $\boldsymbol{U}_y$ and $\boldsymbol{T}_y$ (i.e., the un-tagged and tagged populations [age class by sampling region] in assessment year y). For example, $\boldsymbol{U}_{y=1}$ represents the un-tagged population matrix in the first assessment year. The total population on a given year ($\boldsymbol{N}_y$) is therefore derived by adding the un-tagged and tagged matrices together, that is $\boldsymbol{N}_y = \boldsymbol{U}_y + \boldsymbol{T}_y$.

A difficulty with a virtual population analysis is that we must estimate the number of un-tagged and tagged fish in each sampling region and age class at the start of the experiment (i.e., the first assessment year). Abundances are set to zero for all age classes and sampling regions in the tagged population matrix in the first year ($\boldsymbol{T}_{y=1}$) because no marks have been deployed. Analyses interested in a subset of assessment years (i.e., after tagging has commenced) are implemented by ignoring previously deployed tags until they are first encountered. Initializing the un-tagged population is more problematic due to the number of age classes and sampling regions. The un-tagged abundances could all be treated as unknown parameters, but this would require an excessively large number parameters just to initialize the un-tagged population matrix (i.e., $R \times (A-1) = 4 \times 57 = 228$), which is more than double the total number of unknown parameters currently estimated (Table B2).

ISAMR v2.0 reduced the number of unknown parameters by estimating historical recruitment ($\boldsymbol{U}^h$) for the $A-1$ (i.e., 57) years prior to the start of the assessment period and then used the same demographic processes (i.e., mortality, movement, and aging) on each historical cohort as used for cohorts recruited in the current assessment period. This allows a partial reconstruction of historical abundances, which allows for the initialization of the un-tagged population in the first year (i.e., $\boldsymbol{U}_{y=1}$; full details are available in "*Initialization*" in Appendix B). This implementation can be considered a "forward propagation" model with constraints that reduce the number of unknown parameters by a quarter. We further reduced the number of parameters by restricting the first 20 years of historical recruitment to use the same values. This second constraint was implemented after tests showed very little differences in the final population estimates when the first 20 years of recruitment were independently estimated. Finally, this approach also differs from earlier versions of the ISAMR model (i.e., v1.6) which relied on an external analysis that required the population to have a stable age distribution prior to the start of the assessment period (Appendix A). These earlier versions of the model produced large catch discrepancies in early years; this suggested that the age structure was not being initialized correctly.

Once the un-tagged population array ($\boldsymbol{U}_{y=1}$) has been initialized, the first-year recruitment is added to the un-tagged population and the model transfers individuals from the un-tagged to the tagged ($\boldsymbol{T}$) arrays based on recorded year-, age-, and area-specific marking events (Figure 2)[1]. At the end of each year, both yearly population matrices (e.g., $\boldsymbol{U}_{y=1}$ and $\boldsymbol{T}_{y=1}$) are taken through a series of sequential steps to account for age-class-specific mortality rates, movements between sampling regions, and aging to next age class. The full specification for each of these transitions is available in Appendix B (see "*Mortality, Movement, and Aging*"). Transitions are assumed to occur at the end of each yearly time step, however it should be possible to extend the model to introduce a finer temporal scale (e.g., seasonality). This and other future model extensions are summarized in Appendix C.

Once mortality, movement, and aging has been accounted for, the year-end population matrices represent the initial population size in following year's population matrix. This leaves the first

[1] This is the only process in which the tagged population can be incremented, after which mortality will decrement the tagged population and movement and aging will redistribute individuals.

age class unpopulated for both the $\boldsymbol{U}$ and $\boldsymbol{T}$ matrices, where recruitment occurs only into the un-tagged population matrix ($\boldsymbol{U}$) and the first age class in the tagged population matrix ($\boldsymbol{T}$) is set to zero. Un-tagged recruitment is allocated proportionately as the product of total number of recruits estimated each year (R_y) and the regional recruitment allocation proportion (δ_r). The same regional recruitment allocation proportion values are used across all assessment years. Both parameters are freely estimated. This differs from the earlier version of ISAMR model (i.e., v1.6), which based recruitment on a stock-recruitment relationship (see Appendix A). Finally, recruitment into the first age class is assumed to occur before sampling within a given year. While in reality sampling and recruitment may occur concurrently, very little catch occurs for the youngest age classes (due to gear selectivity being virtually zero) so any overlap should not notably affect estimates.

After recruitment, the model continues through the same steps of transferring newly tagged fish from $\boldsymbol{U}$ to $\boldsymbol{T}$ based on recorded tagging events for each age class and sampling region, followed by mortality, movement, and aging steps that occur at the end of each year. This time-stepped process is repeated over the duration of the assessment period and the model predictions are then fit to the observations based on the observation model (see Appendix B for the full specification).

Observation Model

Estimates of free parameters (see Table B2, Appendix B) are based on minimizing the discrepancy between the predicted and observed tagged and un-tagged catches. Un-tagged catch (a portion of which is released with a tag, with the remaining released without a tag) is described by a catch-at-age model, while tagged catch is described in terms of the observed mark-recapture return rates (see "Observation Model" in Appendix B). Both require the ability to predict un-tagged and tagged catch by year, age class, and sampling region. For example, the predicted un-tagged and tagged catch can be determined as:

$$C_{y,a,r}^{U} = U_{y,a,r}\left(1 - \exp\left(-F_{y,a,r}^{*}\right)\right)$$
$$C_{y,a,r}^{T} = T_{y,a,r}\left(1 - \exp\left(-F_{y,a,r}^{*}\right)\right).$$

Where $U_{y,a,r}$ and $T_{y,a,r}$ are the number of un-tagged and tagged fish available and $1 - \exp\left(-F_{y,a,r}^{*}\right)$ is the probability of capture, which is a function of the realized instantaneous fishing rate $\left(F_{y,a,r}^{*}\right)$. The model is then fit using Bayesian estimation techniques based on minimizing discrepancies between observed and predicted catch.

The realized fishing rate is specific to each age class within each sampling region in each given year; and both the un-tagged and tagged components use the same rate. Because the realized sampling rate is expected to be a function of age, with younger individuals being less catchable than older individuals that are fully recruited into the fishery, the realized fishing rate is modelled as a function of two components: 1) the fully gear-recruited fishing rate $\left(F_{y,r}\right)$ and 2) the age-class-dependent gear selectivity $\left(S_{y,a}\right)$, that is

$$F_{y,r,a}^{*} = F_{y,r} \times S_{y,a}.$$

Selectivity is a parameter that ranges from 0 to 1 indicating the degree to which an age class is recruited into the fishery. For fully gear-recruited individuals the age-class selectivity equals one (i.e., $S_{y,a} = 1$) and the realized fishing rate defaults to the yearly regional fishing rate for fully recruited individuals (i.e., $F^*_{y,r,a} = F_{y,r}$). For age classes not fully recruited, selectivity is less than one (i.e., $0 \leq S_{y,a} < 1$) and the realized fishing rate will be less than the fully recruited rate (i.e., $F^*_{y,r,a} < F_{y,r}$). Because the fully gear-recruited fishing rate is indexed by year and sampling region (i.e., a different value for each combination of year and sampling region) and selectivity is indexed by year and age class (i.e., sampling regions share the same age-specific selectivity values), they together provide a unique realized sampling rate for each combination of sampling region, year, and age class. While a unique selectivity value is *possible* for every year and age class, in practice, we used the same age-class-specific values for blocks of sequential years, referred to as "selectivity epochs". Finally, selectivity-at-age was modelled to follow an S-curve shape, where age determines when sturgeon become fully recruited. The parameter space explored by the ISAMR model allows for a diversity of selectivity curve shapes (Figure 3).

Earlier versions of the ISAMR independently estimated the fully recruited fishing rate $\left(F_{y,r}\right)$, requiring a large number of unknown parameters to be estimated ($Y \times R = 17 \times 4 = 68$). However, catch was found to vary linearly as a function of the number of boat trips regardless of the sampling region (Figure 4). Furthermore, freely estimated sampling rates showed a very strong linear relationship with the number of yearly boat trips in each sampling region (Figure B3, Appendix B).

As such, information about effort was included by modelling the fully recruited fishing rate $\left(F_{y,r}\right)$ as simple linear regression against the number of sturgeon fishing boat trips by program volunteers (i.e., effort), that is:

$$F_{y,r} = \beta_{0,r} + \beta_{1,r} \times \mathrm{Trips}_{y,r}.$$

Parameters $\beta_{0,r}$ and $\beta_{1,r}$ represent the region-specific intercept and slope terms estimated within the ISAMR statistical model, and $\mathrm{Trips}_{y,r}$ is the total number of boat trips in a sampling region within a calendar year. This reduced the number of unknown parameters from 68 to 8, while resulting in nearly identical estimates of sampling rates.

MODEL OPERATION

The ISAMR model is implemented in two parts, a statistical model built using AD Model Builder (herein referred to as ADMB), and a codebase developed in the R computing environment (R Core Team 2016) to support the ADMB model (Figure 5).

The ADMB statistical model is compiled from the source authoring file (*ISAMR.tpl*) into an executable file (*ISAMR*, no extension) that is specific to the operating system on which the authoring file is compiled. Once compiled, all that is required to initiate the model's fitting process is a system call to execute the *ISAMR* executable, which in turn looks for, and reads in, the corresponding data input file (*ISAMR.dat*). This single input file contains all the data required by an ADMB model, including observed data (e.g., mark-recapture records, un-tagged catch, boat trips, length-at-age) as well as a variety of model settings. Once the ADMB fitting process has completed (a process than can take upwards of 10 minutes) the ADMB executable binary creates a variety of output files (e.g., *ISAMR.rep*). ADMB's built in Markov Chain Monte Carlo (MCMC) functionality, which uses the Metropolis-Hastings algorithm, is used to estimate the posterior distributions for key derived parameters, from which 95% credible intervals are presented.

While all input and output files are in plain text format and can be read and formatted manually with any program capable of reading plain text files, doing so is a time-consuming process so the R codebase was created to automate this process. The codebase consists of a main R analysis script along with a supporting library of function and scripts used to read in and process various input data and create final output figures and tables (Figure 5). Raw input data (Table 1) along with model attributes (e.g., number of selectivity curves) and any fixed relationships (e.g., length-at-age) are combined and written out as the single plain text input file in the format required by the ADMB model (Appendix D). The R analysis script then makes a system call to the *ISAMR* executable, thereby initiating the fitting process. The system call does not have to come from R, but we use this approach to simplify the analysis process. Once the ADMB fitting process has finished, the R script then proceeds to read in and parses the output files, then passes on the results to a variety of plotting and data summary scripts used to create the final output tables and figures included in the report (Figure 5). Part of the R codebase was transferred to LGL from Dr. Tom Carruthers, and additional code was developed by LGL.

A detail summary of input data and user-specified settings required for the model, along with the estimated and derived population parameters generated by the model, are provided below.

Input Data

A full list of the raw input data is provided in Table 1 (with examples in Appendix F) and can be divided into three broad categories:

1) Sturgeon catch data, which includes:
    a. releases without tags (Table 1, row 1);
    b. tagged releases that resulted in a subsequent recapture (Table 1, row 2); and
    c. individuals tagged and released, but never recaptured (Table 1, row 3).
2) Optional model overrides, that currently includes:
    a. User-specified selectivity-at-age values that can be used in place of estimated values (Table 1, row 4).
3) Covariate data including:
    a. Fishing effort used to model sampling rates (Table 1, row 5); and
    b. Length-at-age values used to model mortality (Table 1, row 6).

4) Fixed values that include:

    a. Basic design characteristics (e.g., assessment years, sampling regions and age classes; see Table B1, rows 1-3); and

    b. Fixed parameter values (currently maximum survival; see Table B1, row 4).

The R codebase then processes and aggregates the data into various summary tables (Table 2) which are eventually included in the ADMB model input file (see Appendix D for the full specification)

Sturgeon Catch Data

The ISAMR is an integrated model as it combines catch data from a catch-and-release program that does not apply tags, with catch data from a mark-recapture style experiment (i.e., captured individuals are released with a tag, recaptured tags are recorded).

The age for the first release was estimated using length measurements and an age-length relationship for Lower Fraser River White Sturgeon (English and Bychkov 2012). The age for each recapture was derived by adding the elapsed time (i.e., days from the first release to the subsequent recapture event) to the age at first release to derive the age at capture. All aggregate summaries were based on rounding the estimated age at release and age at recapture to the nearest whole year. For example, a sturgeon estimated to be 7.3 years old at release would be aggregated into age-7 with all other sturgeon between 6.50 and 7.49 years old at release, and if this sturgeon was recapture 1.5 years later, its recapture age (8.8 years old) would be rounded to age-9 for the recapture event.

Un-tagged Captures

Un-tagged catch is simply individuals captured without a tag. Assuming tag loss has not been an issue, these are individuals that have not entered the mark-recapture experiment. A subset of the un-tagged catch is marked with a tag prior to release, which transfers them into the mark-recapture experiment. The un-tagged catch is used to inform the un-tagged capture component of the observation model (Appendix B) and is derived from three raw input sources:

1. Un-tagged captures released without being marked (i.e., Table 1, row 1);

2. The first occurrence of a marked individual in the tagged release with recapture data (i.e., Table 1, row 2); and

3. All occurrences of newly marked individuals that were never again observed (i.e., Table 1, row 3).

These sources are then aggregated into frequencies by year, age class and sampling region (Table 2, row 1), which is then included in the ADMB data input file (Appendix D).

Tagged Catch

Mark-recapture data consists of sturgeon that were captured, marked with PIT tags, and released, and a subset of the marked releases that were recaptured at a later point in the assessment period. These records were organized in two groups:

1. Marked releases that were recaptured within the assessment period (Table 1, row 2); and

2. Newly marked releases that were never observed again within the assessment period (Table 1, row 3).

Both record types contain information on the date, location, and age of the individual sturgeon at the time of the event. For releases with recaptures, date, location, and age data are needed for both the release and recapture events. These two sources of individual capture records are then aggregated into the frequency of tagged releases with a recapture (i.e., Table 2, row 2) and a summary of final releases (i.e., Table 2, row 3). For the frequency of tagged releases with a recapture, releases are broken down by year, age class, and sampling region, with recaptures by year and sampling region. The initial age of fish is assigned at first capture, after which fish are reassigned to a single age class per year until they reach the oldest age category. Recaptures that would produce an associated age class higher than the oldest age in the model are simply assigned the oldest age category. The final release summaries are the final point at which each individual was observed in the assessment period, with frequencies broken down by year, age class and sampling region (i.e., Table 2, row 3). The final capture record (and release for live sturgeon) from the marked recaptures (i.e., Table 1, row 2) and the newly marked releases without a recapture (i.e., Table 1, row 3) are the data sources. Both components are modeled in the tagged recapture component of the observation model (see "*Tagged Catch*" in Appendix B).

Optional Data (Selectivity-at-age)

By default the ISAMR model estimates parameters associated with the selectivity-at-age curves (see "*Selectivity-at-age*" in Appendix B for more details). This produces a unique selectivity-at-age curve for each year, with most years being constrained to use the same curve. When desired, these yearly selectivity-at-age values can be specified by the user rather than estimated (Table 1, row 4). Selectivity values cannot be below 0 or above 1, and must be specified for each age class over each assessment year. These values are then used in place of the estimated selectivity-at-age values.

Covariate Data

The ISAMR includes covariate data from two sources:

1. Regional seasonal boat trips (Table 1, row 5); and

2. Average sturgeon length-at-age (Table 1, row 5).

Regional seasonal boat trips are summarized as yearly boat trips by sampling region (Table 2, row 4) and are used to model sampling rates (see "*Estimating yearly regional sampling rates*" in Appendix B). The average length-at-age values specified directly in the ADMB input file based on the von Bertalanffy growth model determined by Nelson et al. (2007) (i.e., $\mathrm{L_a} = 370.1 \times (1 - \exp(-0.025\mathrm{a}))$). It is possible to specify other length-at-age relationships directly by changing the length-at-age covariate data.

Model Output

The results presented in this report are from the ISAMR model runs using lower Fraser River White Sturgeon data from 2000 through 2016 for four sampling regions (i.e., A, B, C, and D; Figure 1) and 58 age classes. A single selectivity epoch is used for the entire assessment period. Model output includes estimates of all unknown parameters (Table B2, Appendix B) along with estimates of a number of derived parameters (Table B3, Appendix B). An overview of key derived parameters estimated by the ISAMR model is provided (Figure 6). Separate figures provide annual estimates of age-1 recruitment (Figure 7), a regional breakdown of abundances for three age-class bins partially recruited into the fishery (Figure 8), and regional abundance estimates for the two age-class bins (Age 1, Age 2-6 and Age 7-12) fully recruited into the fishery (Figure 9). Detailed accounts of key derived output likely of interest to managers are provided below.

Current and Historical Recruitment

The ISAMR model provides estimates of both historical and current recruitment into age-1 (Figure 6c). Historical recruitment can be estimated for $A - 1$ years prior to the start of the assessment period, however only historical recruitment back to 1980 is displayed. The ISAMR model also provides 95% credible intervals for each recruitment estimate (Figure 7).

Population Size

Abundance estimates provided by un-tagged ($\boldsymbol{U}_y$) and tagged ($\boldsymbol{T}_y$) matrices are combined to provide overall yearly population abundance estimates. Depending on the age class and sampling regions considered, abundance estimates can be derived for a variety age class and regional combinations (e.g., Figure 8 and Figure 9). Estimates for earlier age classes are less precise as those age classes are not fully recruited into the fishery and have been exposed to fewer years of sampling (Figure 8). By contrast, abundance estimates for older age classes are more precise due to these age classes being fully recruited into the fishery and exposure to more years of sampling (Figure 9). These differences are also reflected in the percentage of the population tagged (Figure 10). Younger age classes had a much smaller proportion of the population tagged, which contributes to the higher overall levels of uncertainty. By contrast, older age-class bins have a much higher percentage of the population tagged, resulting in much more precise estimates of abundance. For the oldest age classes (i.e., age 23-55 sturgeon) nearly 90% of the population was estimated to be tagged by the end of the assessment period. This is close to a complete census, resulting in very precise estimates of abundances (i.e., narrow 95% credible intervals; Figure 9).

Finally, the ISAMR output is not restricted to the regional and age class breakdowns provided, the current breakdown is only provided for illustrative purposes. Summaries can be created based on any combination of age class and sampling region.

Instantaneous Sampling Rates

The instantaneous sampling rates ($F_{y,r}$) were estimated as part of the observation model and describes the portion of the estimated abundance in each sampling region that is sampled each year (Figure 6d). Sampling rates were used when predicting catches from both the un-tagged and tagged populations. The current model formulation estimates these rates as a function of yearly regional fishing trips (see "*Estimating yearly regional sampling rates*" in Appendix B).

Mortality Rates

The instantaneous mortality rate for a given age class (M_a) is also estimated (Figure 6b). Estimates are based on a logistic regression against length-at-age (see "*Survival/Mortality and Aging*" in Appendix B). These estimates can be useful when projecting the population matrices forward in time (see "*Population Projections"* below).

Yearly Selectivity-at-Age

Estimates of the selectivity-at-age for each year ($S_{y,a}$) are provided as final output. Figure 6e shows a single curve because the model estimates presented in Figure 6 were derived using the same selectivity-at-age curve across all years. Values for some years may be identical depending on the number of independent selectivity curves selected. When user-defined selectivity curves are used, or the model estimates year- or epoch-specific selectivity curves, Figure 6e will include multiple curves (see "*Selectivity-at-age*" in Appendix B).

Movement Probabilities

A full Markovian movement model was also estimated as a $R \times R$ probability matrix representing the probability of movement from any one sampling region to the next (Figure 6f). Probabilities were directly estimated based on region-specific return rates in the mark-recapture experiment (see "*Movement*" in Appendix B).

Population Projections

The age structuring of the ISAMR model makes forward population projections possible by combining age-specific estimates of natural mortality with abundance estimates for each age and alternative assumptions regarding the abundance of age-1 sturgeon (i.e., recruitment). For example, population projections from 2017-2035 were created based on two recruitment scenarios (Figure 11). The first scenario assumes that age-1 recruitment for 2017-2035 remains at the same level as the average estimated for the 2011-2016 period. The second scenario provides the population projections if age-1 recruitment after 2016 increases to 1.6 times the average recruitment for the 2011-2016 period.

MODEL TRANSFER

Source code (both ADMB and R) was transferred from Dr. Tom Carruthers to LGL in the spring of 2016. In April 2016, Dr. Wendell Challenger successfully compiled ADMB source code into an executable program for the Apple OS X platform. This executable was then used to conduct the presented sensitivity analysis. Because both AMDB and R are available across multiple computer platforms (i.e., Windows, Apple OS X and Linux) with minor modifications the ADMB model can be recompiled and run on Windows or Linux platforms. This allows the model to be deployed across a variety of computer platforms, including web servers.

COMPARING ISAMR AND BMR24 ABUNDANCE ESTIMATES

Both the ISAMR and BMR24 models use Bayesian estimation to provide point estimates and credible intervals, however the two have very different population modelling structure. The ISAMR uses age classes, while the BMR24 model employs size groups. The two models also differ in how differences in gear selectivity are handled. The ISAMR model directly includes a selectivity-at-age relationship that is estimated based on the data, while the BMR24 model assumes that size groups of interest are fully recruited into the fishery. The ISAMR model also includes information on sampling effort and considers all captures within the assessment period in a single analysis, while the BMR24 model does not include sampling effort and uses a 24-month rolling window.

Population estimates from both models were only compared after development of the ISAMR model version 2.0 was complete. Assessment of the ISAMR model fit during development was largely guided by comparisons between observed and predicted catches (Appendix H).

In order to compare the two models considerations were made to account for differences in model structuring (i.e., size groups vs age classes) and differences in the selectivity. Model structuring differences were handled by matching the BMR24 size groups to the corresponding ISAMR age classes, based on the length-at-age growth model proposed by Nelson et al. (2007) (Table 3). Considerations towards the differences in the selectivity assumption were handled by generating adjusted ISAMR abundance estimates as if all age classes under consideration were fully recruited into the fishery. Due to the sensitivity of the ISAMR model to selectivity assumptions (see "*SELECTIVITY SENSITIVITY ANALYSIS*"), we could not simply refit the ISAMR model with a selectivity value of 1 for all age classes. Instead, abundance estimates comparable to those of the BMR24 were generated by adjusting the age-class-specific un-tagged ($\boldsymbol{U}$) population estimates for the corresponding selectivity-at-age values. For example, if an age class in the $\boldsymbol{U}$ array (i.e., all years and sampling regions) had an estimated selectivity-at-age value of 0.5, then corresponding unadjusted abundance estimate was reduced by half; and if the selectivity value was 0.75 for an age class, then the adjusted abundance would be three-quarters unadjusted abundance, (etc.).

Comparing estimates of total yearly abundance for the three main size groups (and corresponding year classes) showed good agreement between the two models, especially when comparing adjusted ISAMR abundance to BMR24 abundance (Figure 12). Each of the three age/size group categories showed a different population trajectory, with each model showing a similar trend for each of the categories, especially when comparing adjusted ISAMR abundances (i.e., assuming equal selectivity). The most notable discrepancy between the two models occurs when comparing unadjusted ISAMR estimates to BMR24 estimates for the smallest size group (60-99 cm FL, which roughly corresponds roughly to age 7-12 sturgeon; Figure 12b, leftmost panel). Here unadjusted ISAMR abundance (i.e., regular estimates) showed a similar trend, but higher overall abundance estimates. This is not unexpected as this age range showed partial recruitment into the fishery, with estimated selectivity ranging from 0.522 (age-7) to 0.996 (age-12; see Figure 6e). Because the BMR24 model does not consider selectivity differences, catch from some of the younger age/size groups will be under represented in the model, resulting in negatively biased population estimate for the 60-99 cm FL size group. Combining the upper two size/age categories, where all individuals are expected to be fully recruited, we can again see how well the two models agree and that there is virtually no difference between unadjusted and adjusted abundance estimates (Figure 13, rightmost graphs). There are some notable differences between the two models estimates for 2005-09 for Age 7-12 sturgeon and 2009-11 for Age 13-55 sturgeon (Figure 13, top graphs). The consistently higher estimates derived from the ISAMR model for these years were probably the result of recent recoveries of sturgeon not seen since their initial release in the early 2000's. These fish were clearly alive in the population and included in the ISAMR analysis but not included in the BMR24 analyses for the years when they were not detected.

Breaking down the estimates further by considering sampling region, the same trends play out for both adjusted (Figure 14) and unadjusted (Figure 15) ISAMR abundances. Both models show similar regional population trends with the ISAMR model showing smoother trajectories, and the unadjusted ISAMR abundances are again higher for the 60-99 cm FL size group (Figure 15, leftmost panels). The only regional abundance estimates that appears to systematically differ between the two models is sampling region A for size group 100-159 cm FL (i.e., age 13-22); here the BMR24 model showed consistently higher estimates in all assessment years. It is not clear why there appears to be a systematic difference between ISAMR and BMR24 estimates for this combination of sampling region and age/size group. That said, sampling region A, which includes the mouth of the Fraser River (Figure 1), has low sampling rates (Figure 6d) and generally low estimated abundances, thus the impact on overall population estimates is small.

It is reassuring that both models are in such close agreement, even when comparing abundance estimates on a regional scale. The complex ISAMR age and spatial structuring, combined with a singular movement matrix used for all assessment years could potentially lead to regional abundance discrepancies relative to the BMR24 model (the latter is much more flexible and better suited to accommodate changes in regional abundances that may result in year-to-year differences in movement rates). The close agreement between the two models, even on the regional scale, suggests that the ISAMR has been appropriately formulated to deal with underlying spatial and age structuring of the population under study.

The smooth population trajectories shown by the ISAMR model, relative to the BMR24 model, are likely the product of the age structuring included in the ISAMR model, which considers all captures across the assessment period simultaneously; this can be expected stabilize estimates relative to the BMR24 model. Age structuring can be expected to smooth estimates because the effects of random catch discrepancies are more likely to be attributed to random sampling error, rather than underlying population structure. If the catch discrepancy represented actual population differences (i.e., a particular age class having more individuals than predicted), then similar discrepancies should be observed in the appropriate age classes in years preceding and succeeding current observation under consideration. As such, observed catch in each unique category (i.e., age class, by sampling region, and year) needs to be supported by observed catch in the associated categories that occurs over the course of the assessment period. Therefore, the ISAMR model can be viewed as integrating a large amount of information when considering observed catch in each category. As such, the spatial and age structuring provides a powerful way to distinguish observational error from true discrepancies in the predicted population structure (this distinction is judged within the model likelihood). By contrast, the BMR24 model can only consider catches within a 24-month period, and therefore cannot integrate information outside that window (e.g., catch observed 10 years later) when considering the most likely estimate for the current period.

There are also potential drawbacks to the deep and complex model structuring contained within the ISAMR model. Complex structuring may limit the model's ability respond to real changes in the underlying population structuring, especially if important population processes are left out of the model structuring. By contrast, the lack of cohort structuring in BMR24 model should result in a more flexible fit to the data and therefore the ability to respond more quickly to underlying population changes. The fact that both models were generally in tight agreement for overall population trajectories suggests that the ISAMR model structuring is adequate to describe the underlying population changes occurring in the Lower Fraser River White Sturgeon population. This is not surprising, given that both the long-lived nature of the sturgeon and the high survival rates of mature animals should lead to a fairly stable population structure without rapid year-to-year changes.

SELECTIVITY SENSITIVITY ANALYSIS

The complexity of the spatial and age structuring used in the ISAMR model can potentially make results sensitive to assumption and structural misspecifications. The interdependence of modelling components such as recruitment, selectivity, and mortality can make population estimates sensitive to assumptions or restrictions for any individual component. For example, if mortality values were fixed, or otherwise restricted to values that are too high, then recruitment estimates will likely be higher to accommodate for differences. Similarly, if selectivity is restricted to be too low for a given age class, then higher recruitment and population estimates in the affected age class are likely to result. The inclusion of selectivity in the ISAMR model is especially of interest, as it represents a major addition to the analysis of these mark-recapture data.

The ISAMR model results presented in this report (section "*Model Output*"), were derived using a single selectivity curve. However, an initial catch curve analysis (William Gazey, pers. comm., see Appendix E) suggested that there were two distinct selectivity epochs (1999-2004, and 2005-2012) which may reflect differences in fishing gear and techniques. To explore the impact of selectivity assumptions on population estimates, a sensitivity analysis was conducted using two model runs. Both were performed using release data from 1999 to 2012 to replicate the Gazey analysis periods. The first run used fixed selectivity-at-age values based on Gazey's estimated values (Table E1). The second run used the same selectivity epoch periods, but the selectivity curves were freely estimated by the ISAMR model.

Freely estimating selectivity curves in the two epochs showed little difference between epoch periods (right panel in Figure 16). Overall, both ISAMR-estimated selectivity curves showed a close similarity to Gazey's 1999-2004 selectivity curve, suggesting that recruitment into the fishery in the 2005-2012 period was earlier than Gazey had estimated (Appendix E). Application of the fixed selectivity-at-age values, rather than the freely estimated values, affected estimated population trends. The population trajectories for sturgeon age-5 and older were broadly similar, but with a large difference in sampling region A (Figure 17), despite total recruitment across all areas combined being similar (Figure 18). The difference in the region A estimates was largely the result of a higher regional recruitment allocation proportion for this sampling region (i.e., parameter δ_r in Table B2), combined with the generally low fishing effort in this region (Figure 19) and lower estimated mortality rates by age (used across all sampling regions), resulted in large un-tagged population estimates for this region. The estimated sampling rates for sampling region A under the fixed selectivity-at-age values were excessively low (Figure 19a) and do not appear to reflect the changes in sampling intensity (i.e., boat trips) for this sampling region during the assessment period (Figure 4a).

The abundance estimates for region A generated under the fixed selectivity scenario also conflict with other information regarding the relative abundance of sturgeon in region A versus other regions, and as such these estimates should not be considered representative. Rather, these estimates demonstrate the sensitivity of the ISAMR model to misspecification. Likely, the generally low effort and low catch in sampling region A provided less information to the model likelihood for this sampling region relative to other sampling regions. For sampling region D, which also had a low level of annual effort (Figure 4a), the smaller regional abundance translated to a sampling rate that was more comparable to sampling regions B and C than to sampling region A. As such, misfit between observed and predicted catch, caused by the use of fixed selectivity-at-age values (especially for the 2005-2012 period), appears to be limited to the region A estimates due to the lower sampling rate for region A. The effect was also noticeable in spite of the only substantive differences in selectivity having occurred in the latter half of the assessment period (i.e., for the 2005-2012 epoch). This was likely the effect of ISAMR age structuring. Catch by age class starts to peak around age-10 (Figure 20). Incorrectly specified selectivity values for this and surrounding age classes could heavily impact estimates of prior recruitment. For example, errors in the age-10 catch caused by incorrect selectivity-at-age values in the 2005-2012 epoch would translate to errors in historical recruitment from 1995 onwards. These errors would then continue to propagate throughout the assessment period because of age and spatial structuring present in the ISAMR model. It is therefore not surprising that the population trajectories estimated under fixed selectivity values strongly deviated from the BMR24 model results (Figure 21). This was not the case however when selectivity values were freely estimated for both epochs (Figure 22).

The results of this sensitivity analysis demonstrate that, while there is great utility in the complex specification of the ISAMR model, population abundance estimates are sensitive to model misspecification and assumptions. Furthermore, model misspecifications at any point in time have the potential to impact estimates throughout the entire assessment period. As an example of this, fixing selectivity rates (which can be considered either a very strong assumption or a misspecification) to values that differ from the freely estimated values appeared to significantly impact the population dynamics portion of the model. In this context, having an independently derived model (i.e., the BMR24 model) that relies on a different set of working assumptions provides an important check for ISAMR model misspecifications. It is therefore advisable that estimates from both the ISAMR and BMR24 models are considered in tandem when assessing population status and management options. Finally, future analyses may also want to consider the impact of other strong modeling assumptions such as the shape of the selectivity curve and the mortality model used (see Appendix C for a full list).

REVISIONS AND EXTENSIONS

During the model ownership transfer from Dr. Tom Carruthers to LGL in the spring of 2016, a comprehensive list of fixes and future extensions were identified along with some additional issues identified during further model development (Appendix C). As of the current version (i.e., v2.0), all major errors have been resolved and many of the identified extensions were implemented. Of the remaining tasks identified the most important identified are:

1. Administrative tasks:
    a. Removal of technical debt;
    b. Improved data simulator; and
2. Addition of seasonality.

Technical debt is a concept in programming that reflects the extra development work that arises when code that is easy to implement in the short run is used instead of applying the best overall solution. Where possible, the best overall solution was attempted when creating the supporting R code base and ADMB model, yet the current version represents the product of a rapid development cycle that took the model from v1.6 to v2.0, which included some major revisions to the population model. As a result, the code contains legacies of this process that should be removed to make future development and application of the ISAMR model as straightforward as possible.

The current data simulator used to test and validate the ISAMR model is based on generating expected aggregate frequencies and only produces the finalized data format inputted into the ADMB model. As such, the simulator does not test the codebase used to convert the records retrieved from the FRSCS database into the final data inputted to the ADMB model (see Figure 5). While these components were informally tested and verified in parts, it will be useful to test the entire analysis workflow to ensure no errors are present. Furthermore, the current simulator does not yet include a variable effort component (initial ISAMR model validations were based on constant sampling effort), so further work on the data simulator is also required regardless of approach. Ideally, a second implementation of the data simulator should be created based on simulating the life histories of individual sturgeon. This would allow records in the FRSCS database to be directly simulated, allowing all components in the analysis chain to be tested. Furthermore, by formulating a data simulator in this manner it would be possible to add additional un-modelled components such as individual variability in mortality, movement, and temporary emigration out of the assessment area. The ability to optionally include un-modelled components would allow for the robustness of the ISAMR model to be tested against different modelling assumptions, providing a more in-depth assessment of the weaknesses and strengths of the current formulation.

Finally, all formulations of the ISAMR model used a yearly time step, and as such quantities such as sampling rates, mortality, and movement rates represent yearly averages. Behaviour of Lower Fraser River White Sturgeon and sampling effort are known to differ throughout the year. Moving to a seasonal time step would allow these differences to be directly modeled. For example, most sampling occurs in the summer and fall; using a two-season time step (i.e., spring/winter and summer/fall) could allow estimated sampling rates to better reflect effort. Similarly, movement, recruitment, and, potentially, mortality are also likely to differ between these two periods making the two-season time step suitable for all model components. That said, it is possible that spring and winter samples are too sparse to generate reliable seasonal model parameter estimates.

DISCUSSION

The ISAMR model represents a novel implementation of an age-structured mark-recapture model that includes both spatial and age structuring. The model integrates data from multiple sources (i.e., tagged and un-tagged releases) into a single analysis. Similar to other age-structured mark-recapture models (e.g., Coggins et al. 2006), the model uses a virtual population analysis to generate estimates of the number of individuals available in each age class (and in each sampling region). These estimates are then used to predict both un-tagged and tagged catch for each age class in each sampling region.

Our implementation differs from other age-structured models in some key areas due to the challenges faced in constructing a spatial and age structured model. Including both regional and age class structuring would typically have resulted in an excessively large number of unknown parameters (particularly associated with unique initialization values for each regional age class, and the requirement for unique yearly regional sampling rates). This hurdle was overcome by intelligently applying modeling constraints. Size- and region-specific initialization abundances were estimated based on a forward propagating virtual population model that relied on age-specific mortality rates, and regional movement rates estimated for the assessment period, thus quartering the number of free parameters required. The strong relationship between the number of regional boat trips and regional catch was also exploited to greatly reduce the number of free parameters associated with estimating yearly regional sampling rates. The considerable reduction in free parameters lent stability and consistency to the model's performance.

Although they were based on nearly the same data set, it was not a given that the ISAMR model results would be in such close agreement with those of the BMR24 model. Their overall agreement was reassuring, yet the ISAMR model *did* feature smoother year-to-year population trajectories and higher abundance estimates in the younger age classes than the BMR24 model. The differences for younger age classes were due to the addition of age-specific sampling selectivity in ISAMR model. While models based on nearly the same data have the potential for good agreement, there was certainly no guarantee of tight agreement between these two models. As was shown in the selectivity sensitivity analysis, ISAMR model misspecification can result in large deviations in population trajectories between these two models. Therefore, we recommend that both models should be used each year to derive abundance estimates from the PIT tag mark-recapture data.

The impetus for the development of the ISAMR model was to overcome several of the shortcomings of its BMR24 counterpart. Yet the advantages of the new formulations do not stop there; a major advantage of the ISAMR model is that it allows us to make forward population projections under various potential recruitment scenarios. In the "*Population Projections*" section, we predicted that overall sturgeon abundances will continue to decline if recruitment remains at its current level; and that even the large-sized sturgeon age 23-55 (160-279 cm FL) are projected to peak in abundance in 2022 and decline steadily thereafter. The model results have also been used to project that annual age-1 recruitment would need to increase by a minimum of 1.6 times the recruitment levels in recent years (2011-2016) to stop the projected population decline and rebuild sturgeon abundances to the 2016 level by 2028 (Figure 11b). With this higher recruitment level, the abundance of age 7-12 sturgeon is projected to improve substantially from 2022-2028, while the abundance of age 13-22 sturgeon is projected to increase after 2028. The abundance projection for age 23-55 sturgeon is the same in both projections (i.e., Figure 11a and b) because abundances in these older age classes has already been determined by the corresponding age classes in the 1980-2013 period. Any changes in age-1 recruitment starting in 2017 will not affect age 22-55 sturgeon abundance until after 2038.

These population projections are dependent on the validity of the underlying assumptions. For example, we are assuming that mortality rates remain constant, but our predicted abundances will be underestimated if survival rates increase, and populations levels will be lower than predicted if survival rates decrease in the future.

It is important to note that recent trends in recruitment cannot be reliably assessed using the PIT tag mark-recapture data. Too few sturgeon age-7 or under (< 60 cm FL) have been tagged, and estimates of their abundance are not reliable. Because of that, levels of recruitment into the population cannot begin to be assessed until seven years afterwards. This was the primary reason why age-1 recruitment from 2011-2016 was fixed at the 2011 level in the ISAMR model (see Figure 7). For example, 2012 recruitment was fixed to be the same value as 2011, because very few age-5 sturgeon were captured in 2016. Age-6 is the first for which capture rates begin to improve. As such, 2012 recruitment can only be reliably estimated starting in 2017, with precision of this estimate improving with each subsequent assessment year, as more observations on the cohort are gained (e.g., age -7 captures in 2018, age-8 captures in 2019, etc.). Therefore, more years of mark-recapture data or additional sampling programs for Age 2-6 sturgeon will be needed to determine if the recruitment trend in 2009-2011 has continued into 2012-2016. While assessing trends in recruitment using mark-recapture is a slow process, it is also subject to substantial uncertainty, as assessments depend on imperfect knowledge about short-term changes in age-specific survival rates.

These results emphasize the importance of taking immediate actions to improve both recruitment of age-1 fish, and survival rates for age 1-6 sturgeon. Actions should include: the protection of sturgeon spawning and juvenile rearing habitat; the removal of all fishing gear from known sturgeon spawning areas during the spawning period; and the protection of the spawning and rearing areas of sturgeon prey species (e.g., salmon and eulachon). Fishery management actions should be implemented to reduce all known sources of sturgeon mortality. Recent efforts to improve handling techniques for sturgeon anglers (and for fishers that intercept sturgeon as bycatch while targeting other species) are expected to positively impact both survival and spawning rates for adult sturgeon and should continue to be supported. Unfortunately, because of the late age at which sturgeon recruit to the fishery, the results of management decisions made today to improve recruitment will not be detected in the PIT tag mark-recapture estimates for many years, making it difficult to judge the efficacy of management actions. Similarly, the full extent of negative impacts (e.g., gravel mining on spawning areas) will not be immediately apparent, and may not even be detectable for decades.

The results presented in this report should be used to help set medium- and long-term targets for rebuilding the Lower Fraser River White Sturgeon population. Given that the abundance of age 7-55 sturgeon has approached 60,000 fish as recently as 2005, we believe that this would be a reasonable interim medium-term population recovery goal. Similarly, a spawning population (age 22-55) goal of 20,000 fish should also be considered as a reasonable target. Both the ISAMR and BMR24 models should be used to monitor progress toward achieving these goals. However, the mark-recovery program should be augmented by juvenile (age 2-3) sampling programs and consistent efforts to protect sturgeon spawning and rearing habitat. Given the long-lived nature of White Sturgeon, it will take a considerable amount of time to achieve these goals.

RECOMMENDATIONS

1. The ISAMR model and BMR24 model should be used in tandem to derive annual abundance estimates and trends from the PIT tag mark-recapture data for Lower Fraser River White Sturgeon.

2. Immediate actions should be implemented to improve age-1 recruitment and survival rates for age 1-6 sturgeon. These measures should include: protection of sturgeon spawning and juvenile rearing habitat, the removal of all fishing activity from known sturgeon spawning areas during the spawning period, a reduction in all known sources of sturgeon mortality, and the protection of spawning and rearing areas for areas of the prey species upon which juvenile and adult sturgeon depend (e.g., salmon and eulachon).

3. Management agencies, recreational anglers, angling guides, and First Nations should continue to support measures to improve survival rates and spawning success for adult sturgeon.

4. An interim medium-term population recovery goal for Lower Fraser White Sturgeon should be set at 60,000 for age 7-55 (60-279 cm FL) sturgeon.

5. An interim spawning population goal for Lower Fraser White Sturgeon should be set at 20,000 for age 22-55 (160-279 cm FL) sturgeon.

6. Indications that progress has been made to achieve these interim goals would be a significant increasing trend in abundance of age 7-12 (60-99 cm FL) sturgeon by 2025.

7. The operation of the ISAMR model program could be improved by removing all computer code that is no longer used and streamlining the data input formats.

8. Further enhancement to the ISAMR model would include the addition of seasonal stratification for both movement pattern and abundance estimation, however, the management benefits from this added complexity are not clearly evident at this time.

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LITERATURE CITED

Coggins, L. G., Jr., W. E. Pine III, C. J. Walters, and S. J. D. Martell, 2006. Age-structured mark–recapture analysis: a virtual-population-analysis-based model for analyzing age-structured capture–recapture data. North American Journal of Fisheries Management 26: 201–205. doi:10.1577/M05-133.1.

English K. K., and Y. Bychkov. 2012. Stock reduction analysis for Lower Fraser White Sturgeon - Progress report for 1st study year. Report prepared for Habitat Conservation Trust Foundation. 29 p.

Gazey, W.J. and K.K. English. 2014. Analysis of 2000-2012 Fraser River White Sturgeon Mark-Recapture Data using MARK – Progress Report for work completed in 2013-14. Prepared by LGL Limited and W.J. Gazey Research for Habitat Conservation Trust Foundation, Victoria, BC. 31 p

Gazey, W. J., and M. J. Staley. 1986. Population estimation from mark-recapture experiments using a sequential Bayes algorithm 67:941–951.

Lorenzen, K. 2000. Allometry of natural mortality as a basis for assessing optimal release size in fish-stocking programmes. Canadian Journal of Fisheries and Aquatic Sciences 57: 2374–2381. doi:10.1139/f00-215.

Maunder, M.N. and A.E. Punt. 2013. A review of integrated analysis in fisheries stock assessment. Fisheries Research 142: 61–74. doi:10.1016/j.fishres.2012.07.025.

Nelson, W. A., C. D. Levings, and A. J. Paul. 2007. Population growth and demography of White Sturgeon in the lower Fraser River. American Fisheries Society Symposium 56: 381–396.

Nelson, T. C., D. Robichaud, T. Mochizuki, J. Rissling, K. K. English, and W. J. Gazey. 2017. Status of White Sturgeon in the lower Fraser River: Report on the Findings of the Lower Fraser River White Sturgeon Monitoring and Assessment Program 2016. Manuscript report prepared by LGL Limited, Sidney, BC.

Nelson, T. C., W. J. Gazey, D. Robichaud, K. K. English, and T. Mochizuki. 2013. Status of White Sturgeon in the lower Fraser River: Report on the findings of the Lower Fraser River White Sturgeon Monitoring and Assessment Program 2012. Summary report prepared by LGL Limited, Sidney, BC.

R Core Team (2016). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Robichaud, D., K. K. English, and T. C. Nelson. 2017. Annual movements of acoustic-tagged White Sturgeon in the lower Fraser River and its tributaries. Transactions of the American Fisheries Society 146: 611-625.

Thompson, G. G. 1994. Confounding of gear selectivity and the natural mortality rate in cases where the former is a nonmonotone function of age. Canadian Journal of Fisheries and Aquatic Sciences 51: 2654–2664. doi:10.1139/f94-265.

Veinott, G., M. Northcote, M. Rosenau, and R. D. Evans. 1999. Concentrations of strontium in the pectoral fin rays of the White Sturgeon (*Acipenser transmontanus*) by laser ablation sampling - inductively coupled plasma - mass spectrometry as an indicator of marine migrations. Canadian Journal of Fisheries and Aquatic Sciences 56: 1981-1990.

White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46 Supplement: 120–139.

Whitlock, R. and M. McAllister. 2012. Incorporating spatial and seasonal dimensions in a stock reduction analysis for Lower Fraser River White Sturgeon (*Acipenser transmontanus*). Canadian Journal of Fisheries and Aquatic Sciences 69: 1674–1697. doi: 10.1139/f2012-079.

TABLES

Table 1. Required and optional raw input data.

Input Data		Type	Region Specific	Age Specific	Description
1)	Releases without tags	Release	Yes	Yes	Records indicating events where an individual was capture without a tag and again released without a tag. Each record consists of a release date, release location and the relative age the time of release (see Table F1 for example records). **File:** *SturgeonAge_NotTangle_NotTagged.csv*
2)	Tagged releases with recapture	Mark-recapture	Yes	Yes	Records indicating individual release with a tag and the next recapture event. Each record consists of a release and recapture date, release and recapture location and the relative age the time of release and recapture, along with the unique individual PIT tag (see Table F2 for example records). All records for a single PIT tag should indicate an unbroken chain of release and recapture events. Final release (i.e., no recapture) is contained in source (3). **File:** *SturgeonAge_NotTangle.csv*
3)	Tagged release without recapture	Mark-recapture	Yes	Yes	Records indicating untagged individuals that were tagged and released, but never observed again within the defined assessment period. Each record consists of a release date, release location and the relative age the time of release, along with the unique individual PIT tag (see Table F3 for example records). **File:** *SturgeonAge_NotTangle_NotRecapped.csv*
4)	Selectivity-at-age by year	Optional	No	Yes	Selectivity-at-age overrides for all age classes and years (see Table F4 for an example). **File:** *selectivities.csv*
5)	Regional boat trips	Sampling Rate Covariate	Yes	No	Records indicating the number of fishing trips to each sampling region on each season and year, used as a measure of fishing effort (see Table F5 for an example). **File:** *BoatTrips_20170424.xlsx*
6)	Length-at-age	Mortality Covariate	Yes	No	Expected average lengths by age class based on the von Bertalanffy growth model determined by Nelson et al. (2007): $L_a = 370.1 \times (1 - \exp(-0.025a))$.

Table 2. Aggregate data used when specifying the ADMB data input file.

Aggregate Data	**Type**	**Details**
1) Un-tagged captures	Catch frequency	Frequency data indicating individuals captured without a tag. This includes all records for individuals released without a tag (Table 1, row 1), select records from recaptures (i.e., first occurrence in release/recapture data; Table 1, rows 2), and all records for individuals released without a tag (i.e., Table 1, rows 3). See Table G1 for example records, this aggregated data was used for the untagged capture component (see Appendix B).
2) Tagged with re-captures	Catch frequency	Frequency data indicating tagged individuals that were latter captured within the assessment period. Includes all records from Table 1, rows 2. See Table G2 for example records. This aggregated data was used in the tagged captures component (see Appendix B).
3) Final releases	Catch frequency	Frequency data indicating a release of a tagged individuals without a recapture within the assessment period. This includes newly tagged individuals that were never again observed (Table 1, rows 3) and the last recapture event for marked releases that were recaptured (Table 1, rows 2). See Table G3 for example records. This aggregated data was used in the tagged captures component (see Appendix B).
4) Yearly regional boat trips	Covariate	Frequency of boat trips broken down by sampling region and year. Source is the seasonal boat trip data (Table 1, rows 5). See Table G4 for example records. This aggregated data was used to model sampling rates (see Appendix B).

Table 3. BMR24 size groups and corresponding ISAMR age class used in the abundance comparison between the two models.

BMR24	**ISAMR**	
Size Group (cm, FL)	**Age Class**	**Fork Lengths (cm)[1]**
60-99	7-12	59-96
100-159	13-22	103-157
160-279	23-55	162-276

[1] ISAMR age class lengths were based on length-at-age based on the von Bertalanffy growth model determined by Nelson et al. (2007): $L_a = 370.1 \times (1 - \exp(-0.025a))$.

FIGURES

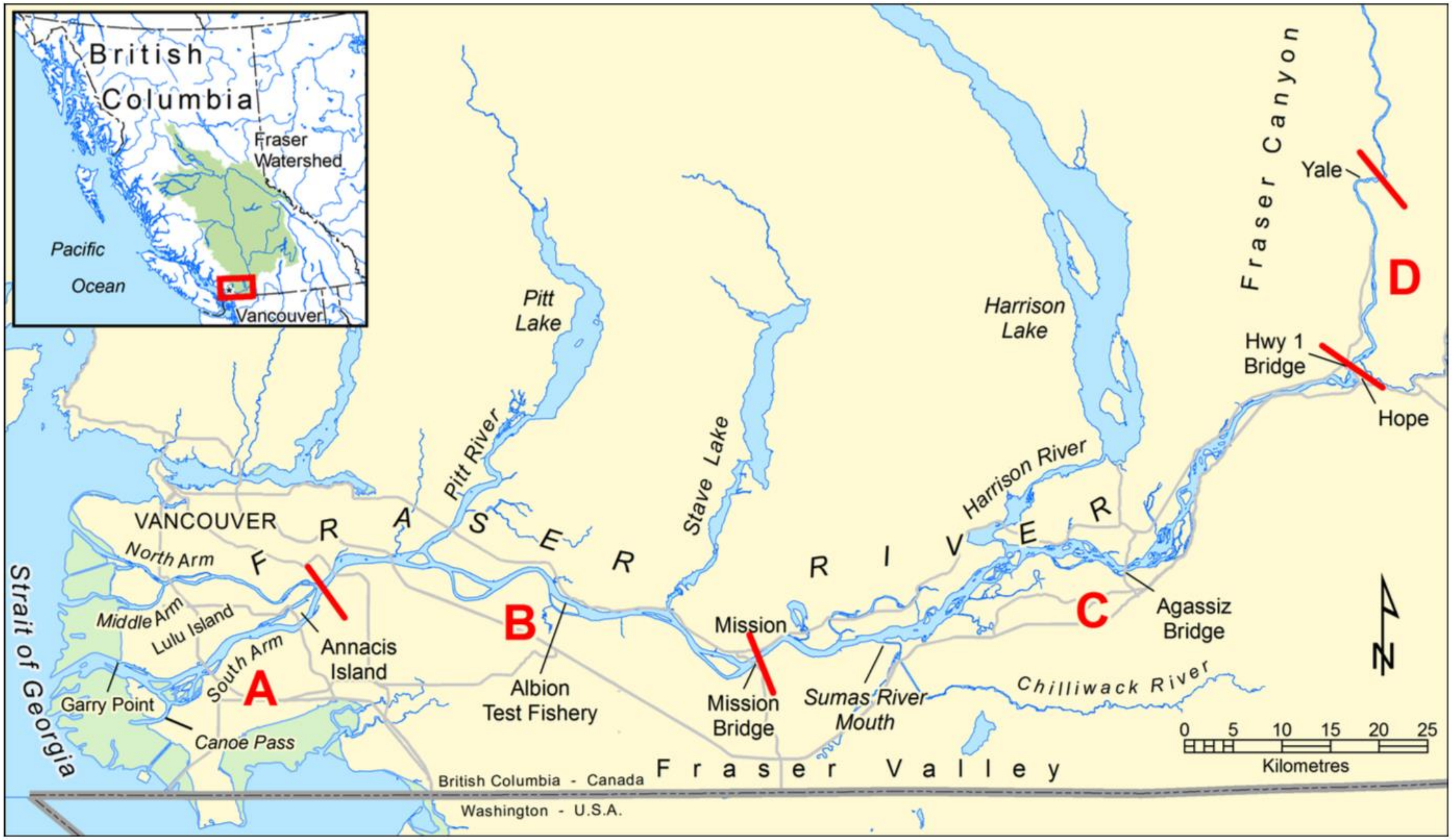

Figure 1. Illustration of the general assessment area and the location of the four sampling regions (A, B, C, and D) used to generate abundance estimates of White Sturgeon presented in this report.

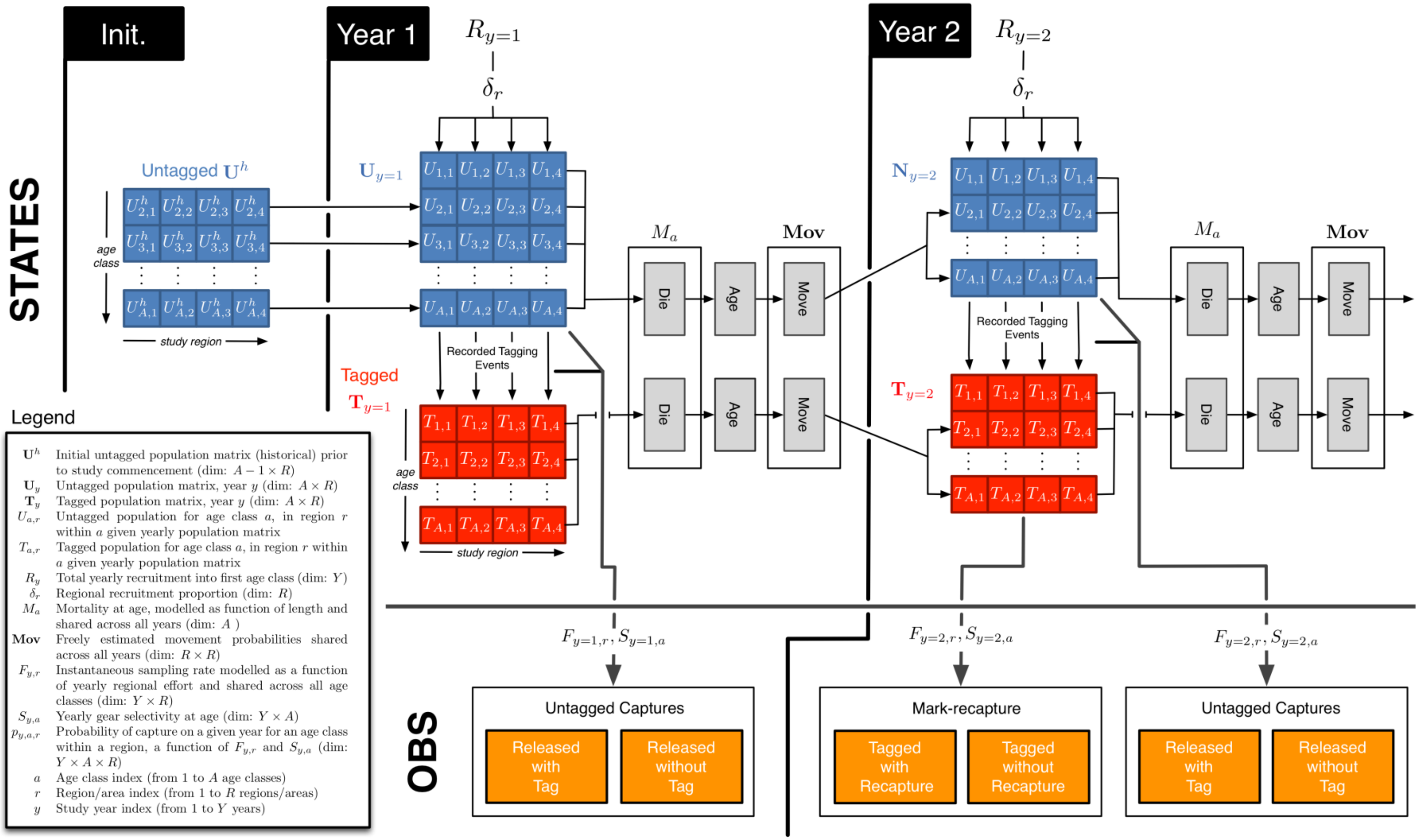

Figure 2. Flow diagram indicating underlying model states, transitions between states, and functional relationships.

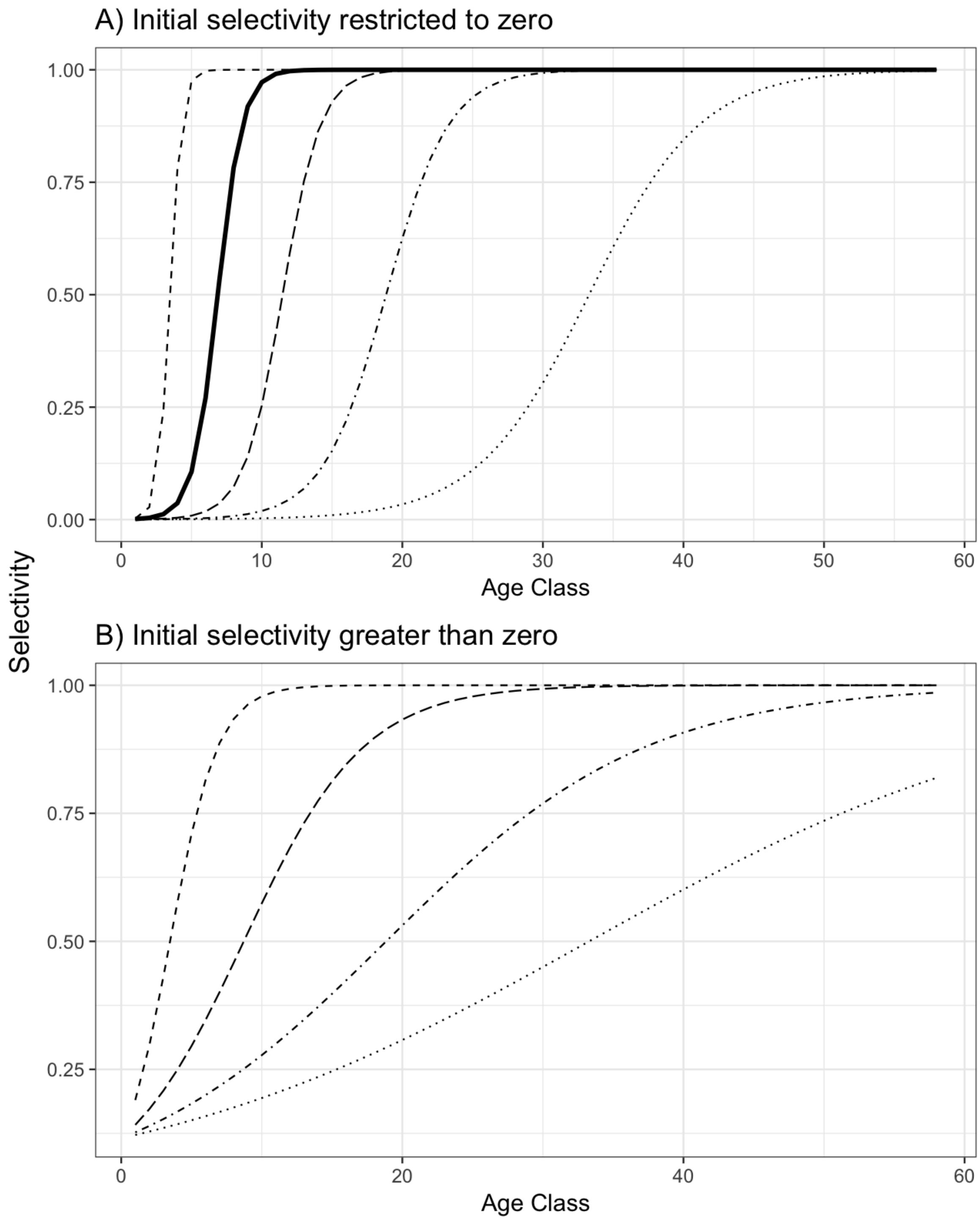

Figure 3. Example of a sub-space of possible selectivity-at-age curves explored by the ISAMR model where A) initial selectivity is restricted to zero for age-1 and B) initial selectivity for age-1 may be greater than zero. Heavy solid line indicates selectivity curve estimated in the example analysis.

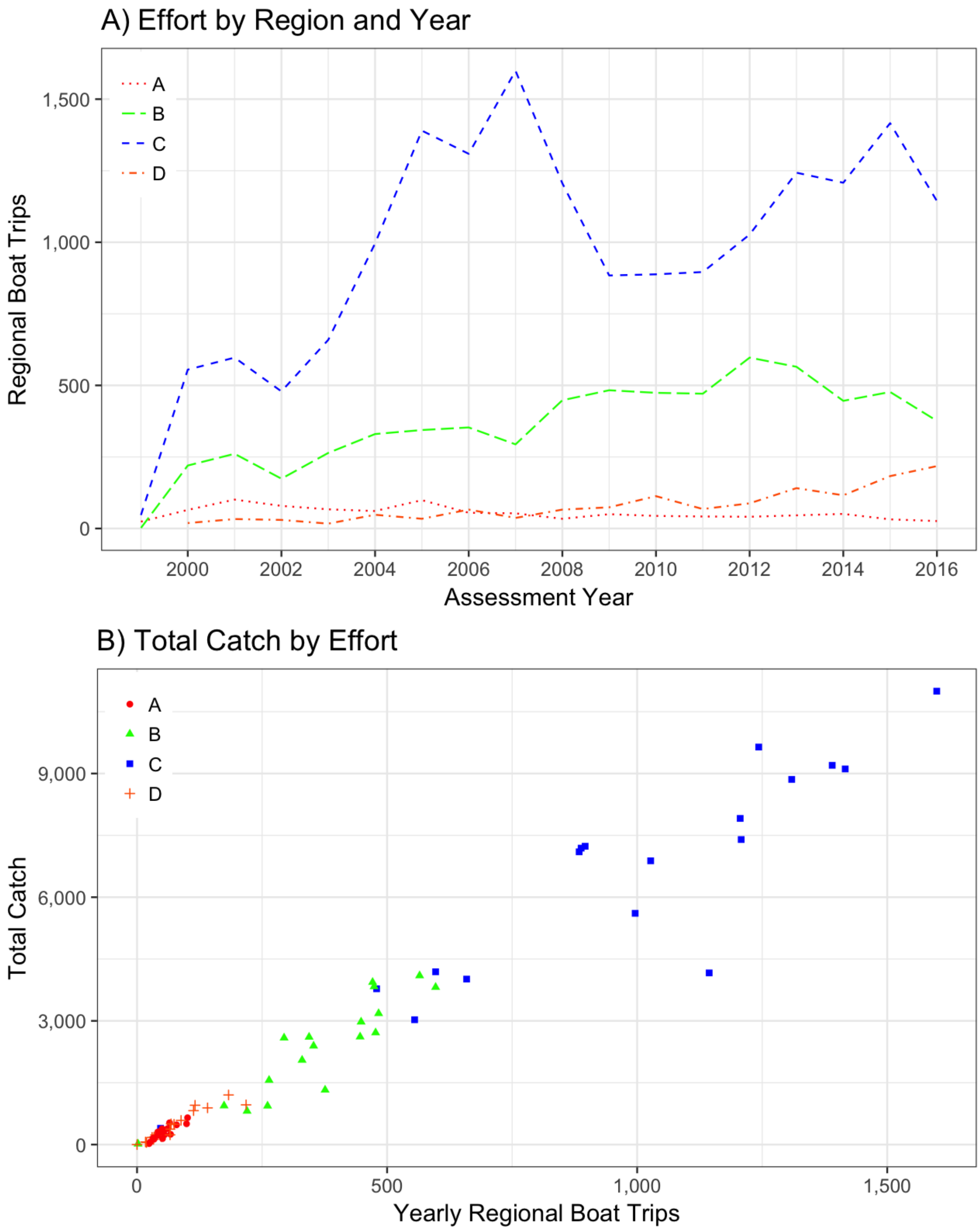

Figure 4. Summary of A) the total number of fishing trips by sampling region and B) the total catch plotted against the number of yearly regional fishing trips.

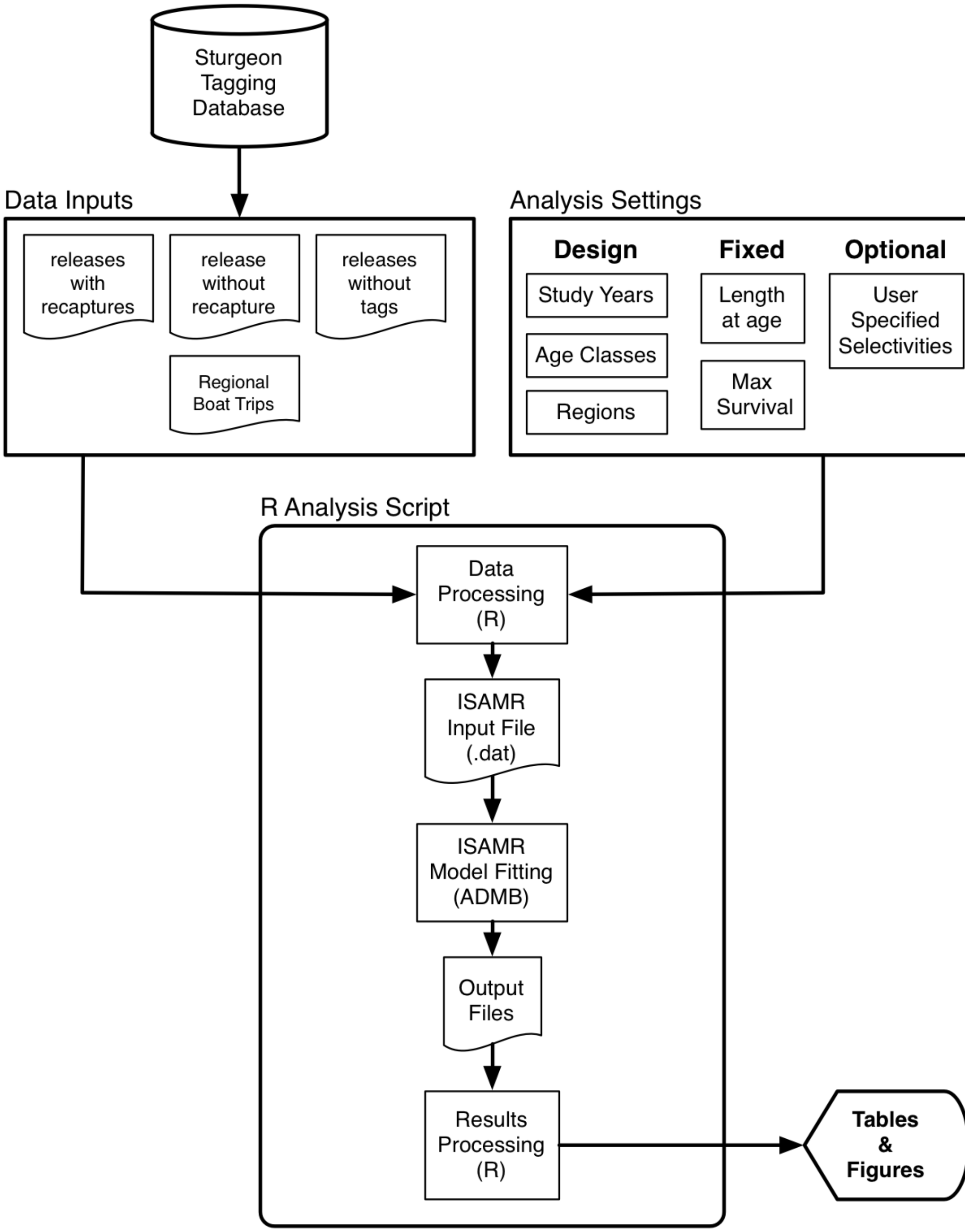

Figure 5. Flow diagram of the ISAMR model operation, which requires the user to provide both data and constant value relationships.

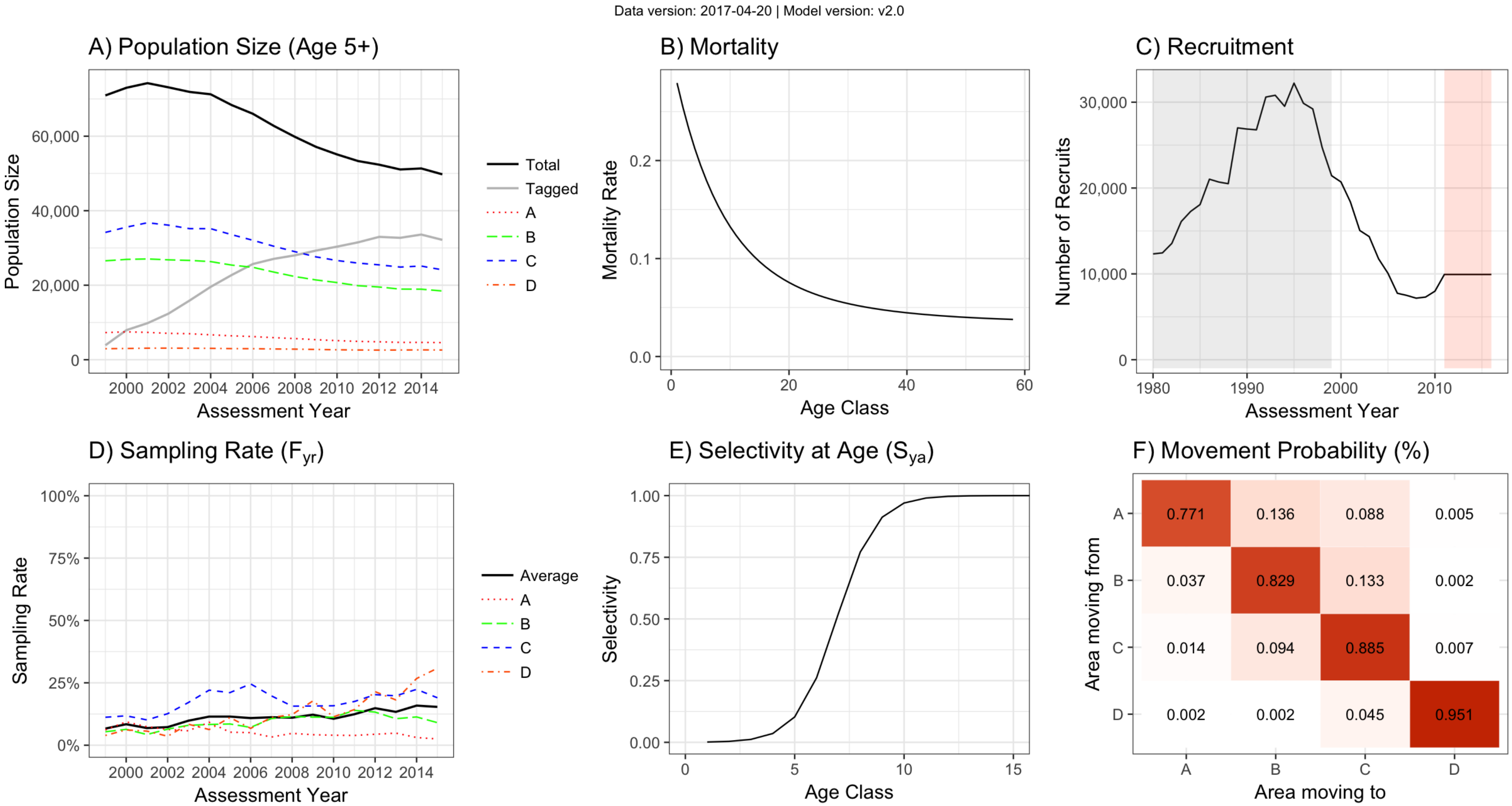

Figure 6. Model output displaying some of the ISAMR estimated quantities. These include: A) population abundances for age-5 and above by sampling region; B) estimated mortality rate; C) historical and current recruitment (grey shading indicates historical recruitment, orange shading indicates terminal years that are constrained to be equal); D) regional sampling rates; E) selectivity-at-age; and F) regional movement probabilities.

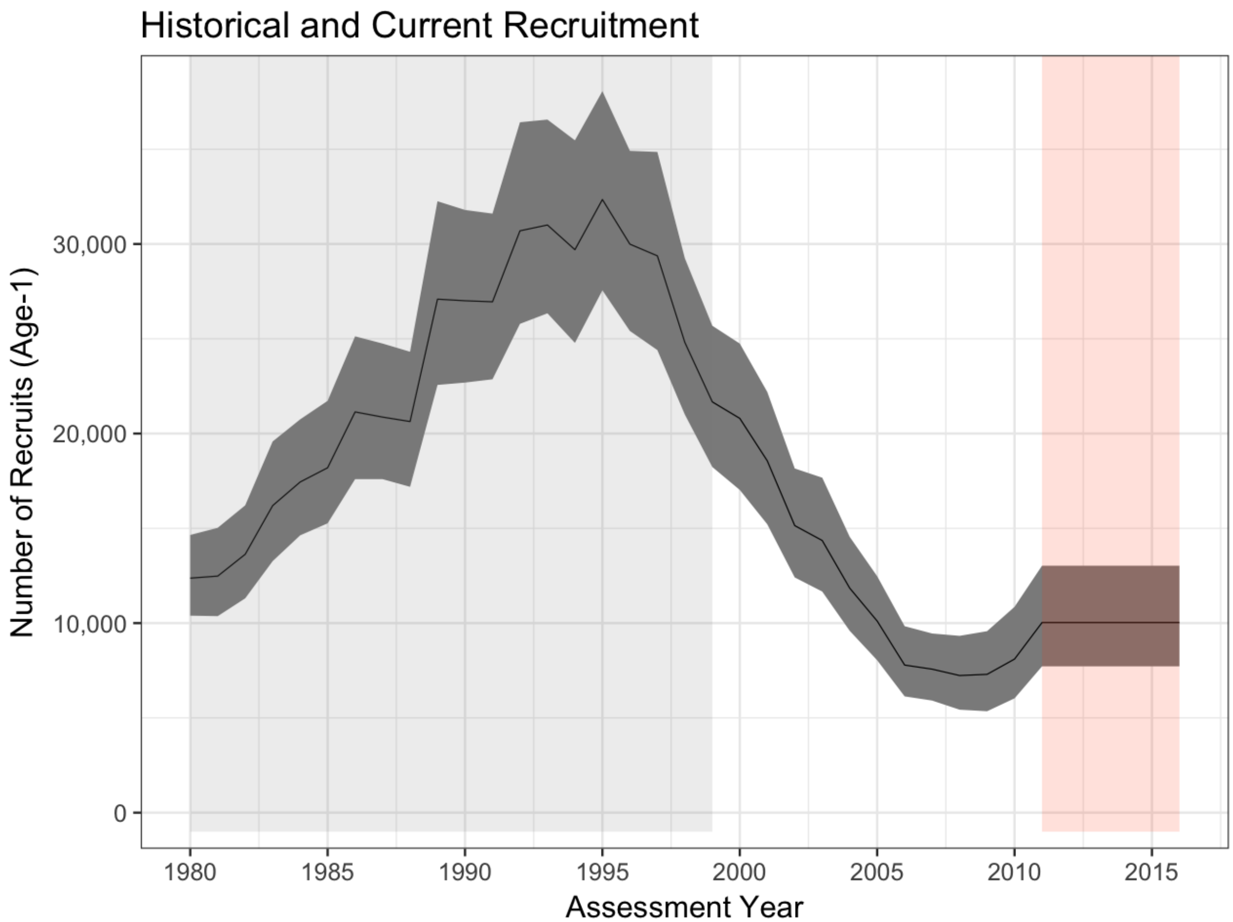

Figure 7. Estimated recruitment into age-1 prior to and during the assessment period, with 95% credible intervals (dark grey shading). Light grey shaded region indicates historical period and light orange shading indicates years constrained to have equal recruitment into age-1.

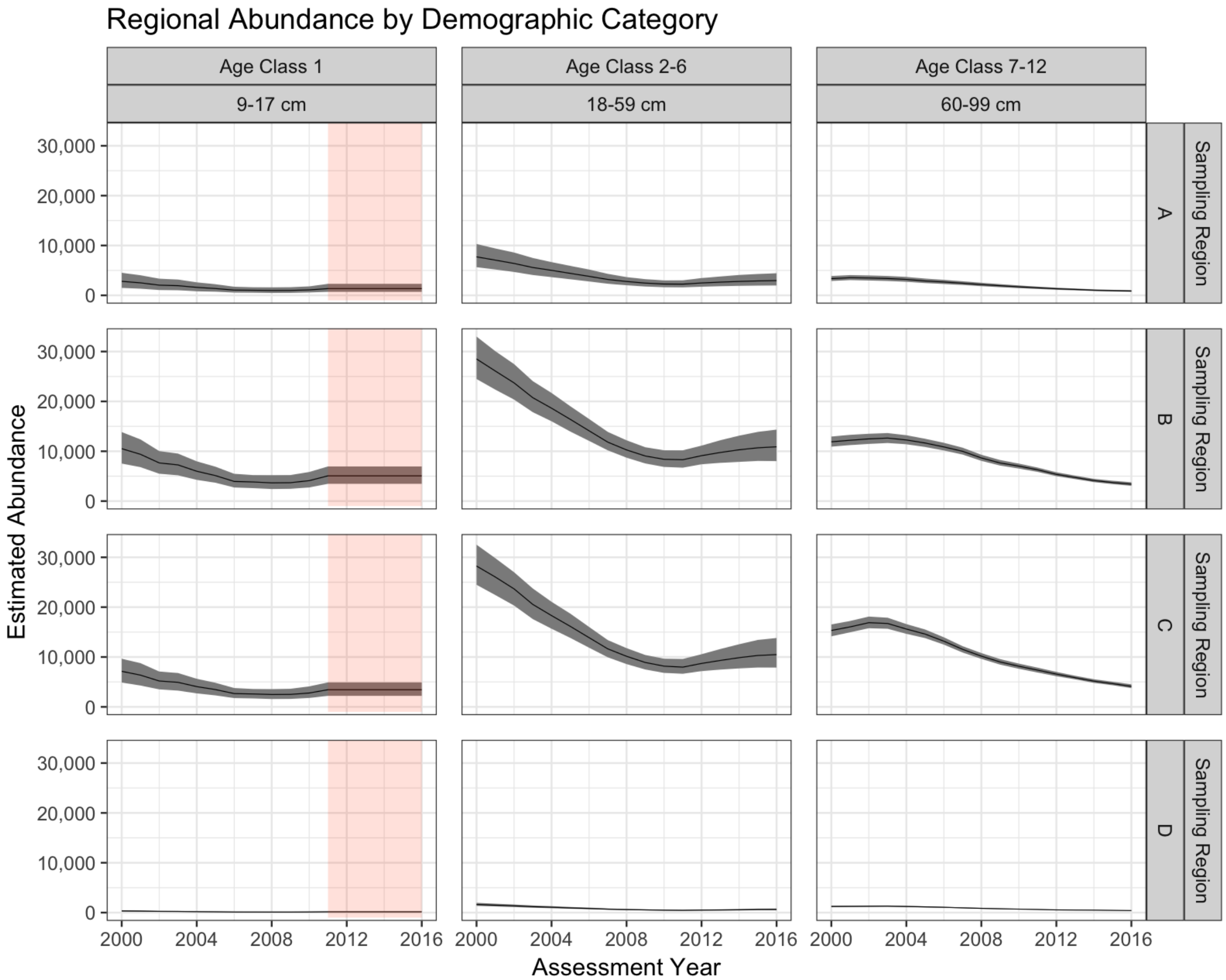

Figure 8. Estimates of region-specific abundances (sampling regions A, B, C, and D), broken down by age class for ages that are not fully recruited into the fishery (i.e., estimated age class selectivity is less than one). Age-1 represents recruitment with the corresponding size groups based on the Nelson et al. (2007) growth model. Dark shaded region indicates 95% credible intervals, while light orange shading indicates years constrained to have equal recruitment into age-1.

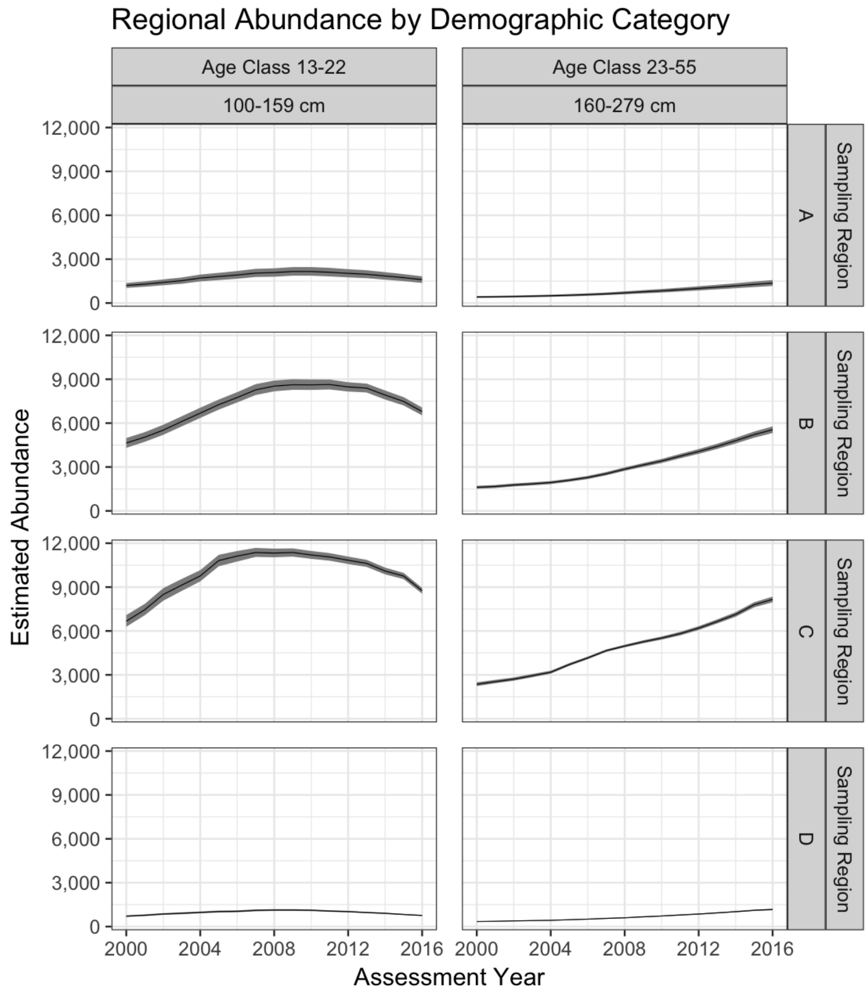

Figure 9. Estimates of region-specific abundances (sampling regions A, B, C, and D), broken down by age class for ages that are fully recruited into the fishery. Indicated size groups are based on the Nelson et al. (2007) growth model. Shaded region indicates 95% credible intervals.

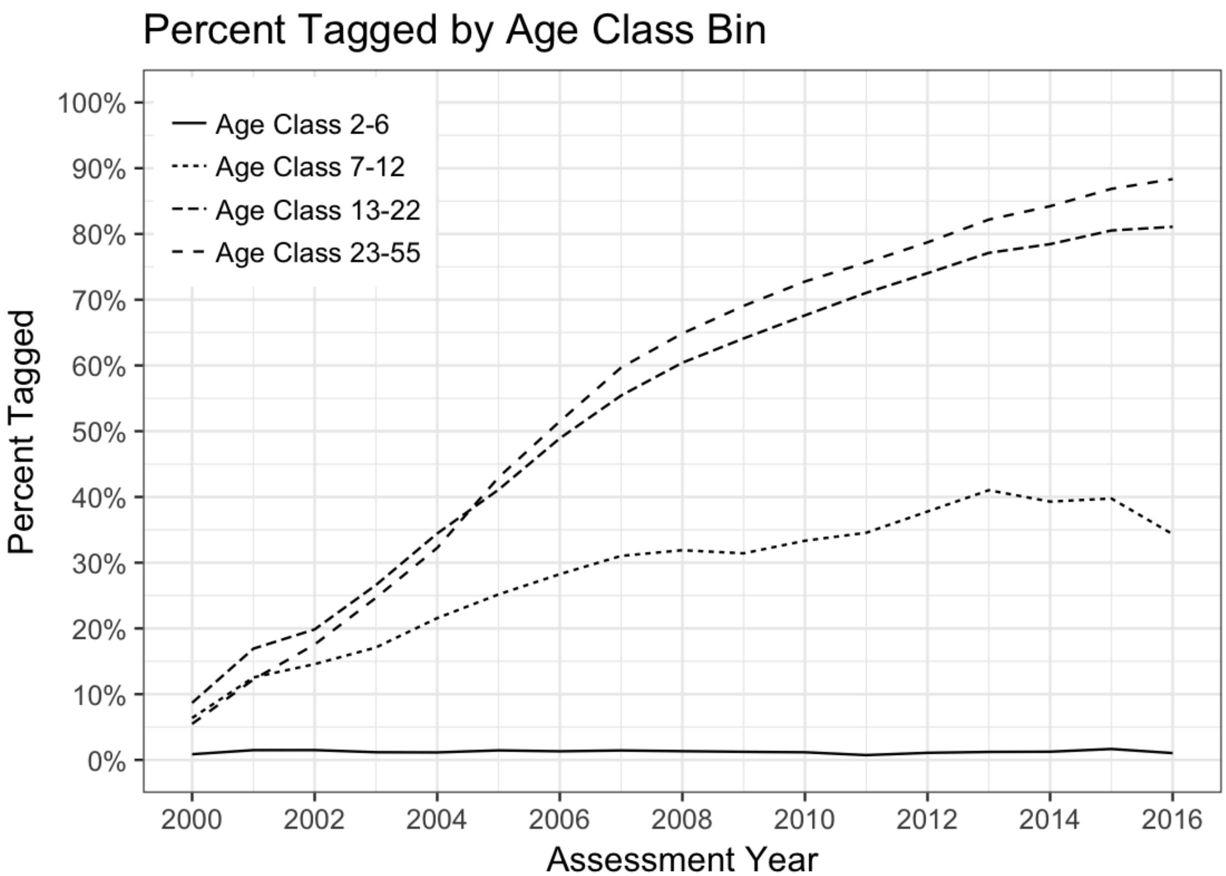

Figure 10. Estimated percent of the population tagged, by age class bin and assessment year.

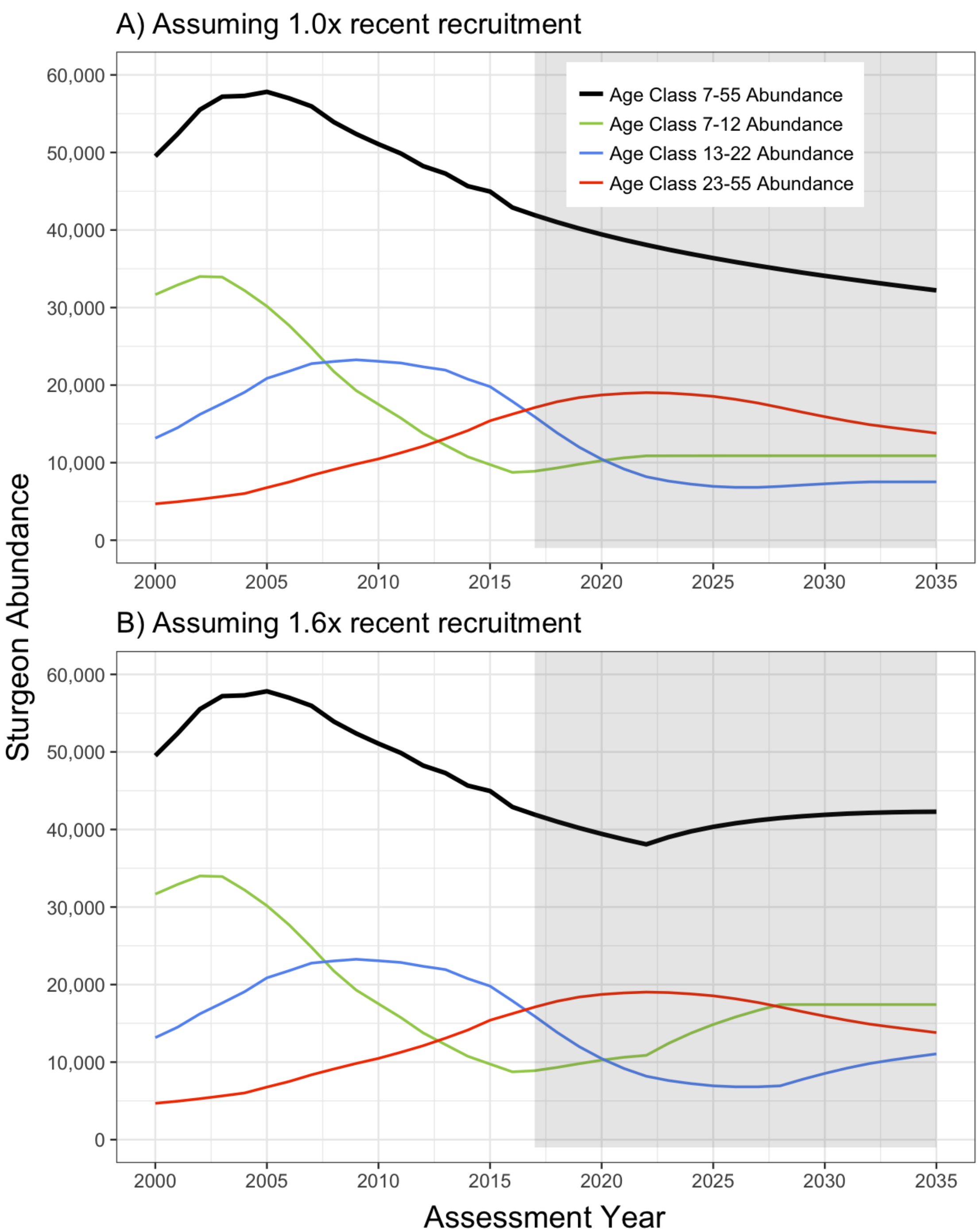

Figure 11. Abundance projections for Lower Fraser River White Sturgeon for 2017-2035 assuming A) that annual age-1 recruitment remains the same as recent estimates (i.e., 2011-2016 recruitment), and B) recruitment that is 1.6 times recent recruitment. Grey shading indicates projected years.

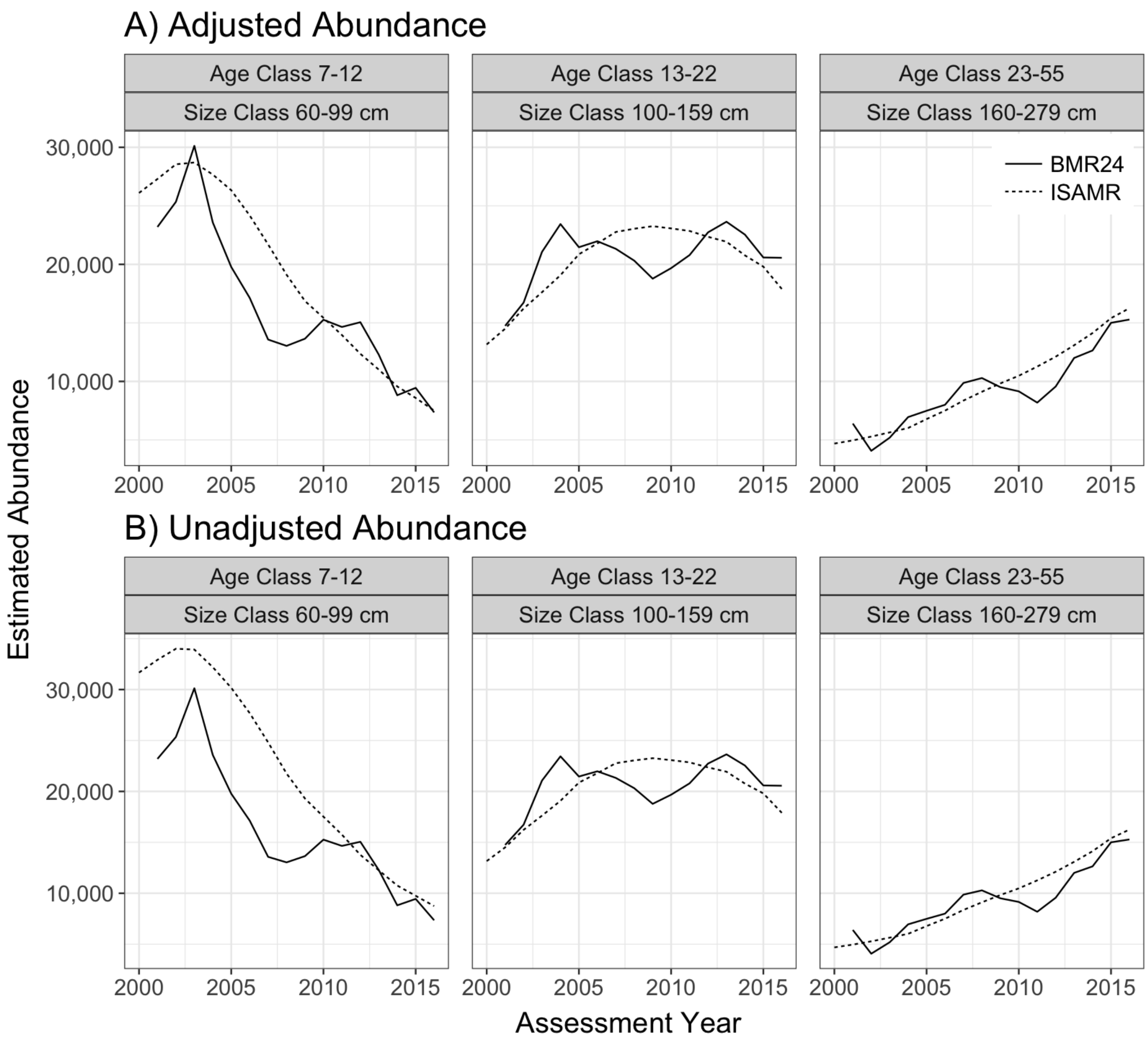

Figure 12. Comparison of assessment area BMR24 and ISAMR abundances by size groups (see Nelson et al. 2007) for A) adjusted ISAMR abundances and B) unadjusted ISAMR abundances. Adjusted ISAMR abundance modeling removes the effect of age-specific selectivity for comparison with the BMR24 estimates. Unadjusted ISAMR abundance modeling includes gear selectivity differences, and thus abundance results are larger than the adjusted ISAMR estimates for age 7-12 sturgeon which are not fully recruited into the fishery.

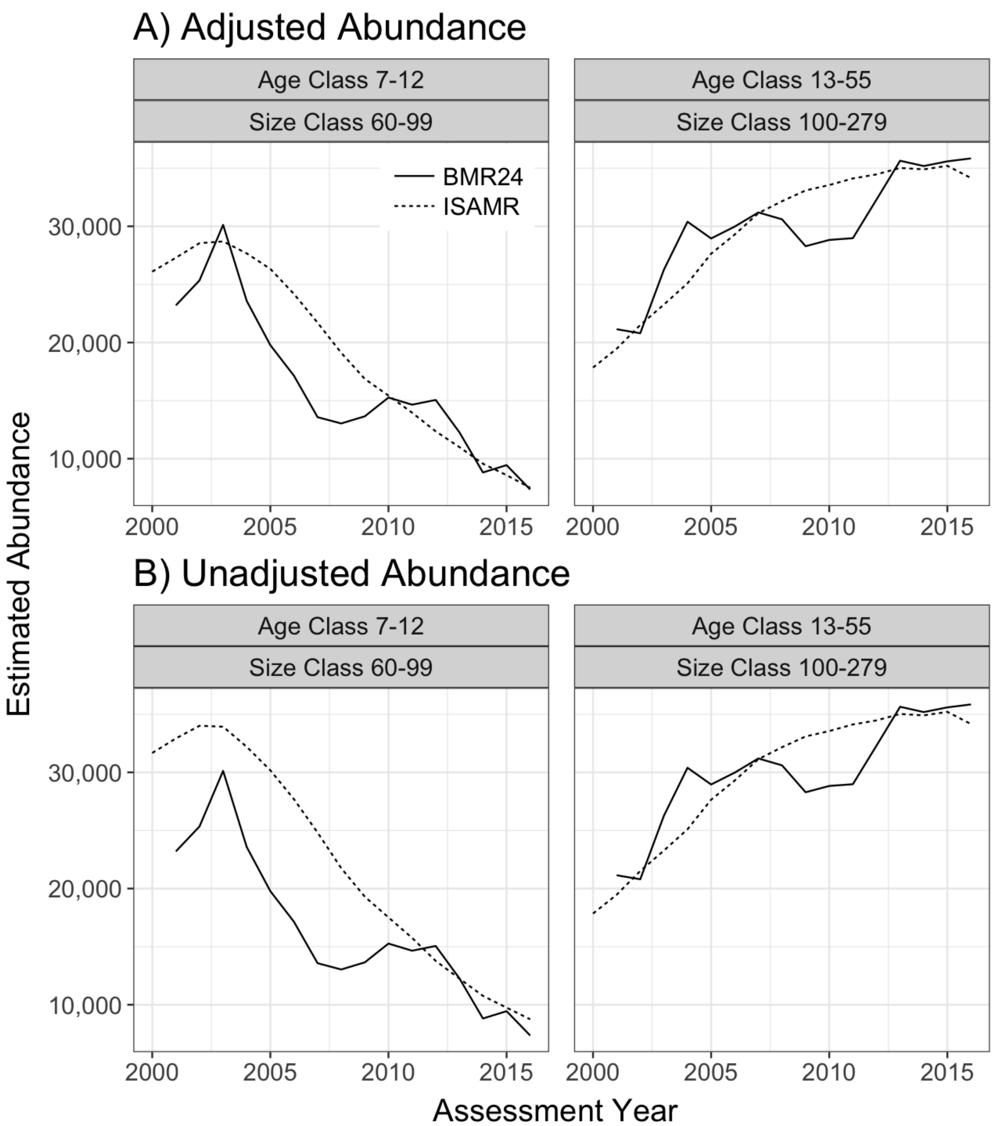

Figure 13. Comparison of assessment area BMR24 and ISAMR abundances for size groups with gear selectivity differences for A) adjusted ISAMR abundances and B) unadjusted ISAMR abundances. Size groups (see Nelson et al. 2007) affected by gear selectivity differences are located in the left-side panels, while groups largely unaffected by gear selectivity differences are located in the right-side panels. Adjusted ISAMR abundance modeling removes the effect of age-specific selectivity for comparison with the BMR24 estimates. Unadjusted ISAMR abundance modeling includes gear selectivity differences, and thus results are larger than the adjusted ISAMR estimates for age 7-12 sturgeon which are not fully recruited into the fishery.

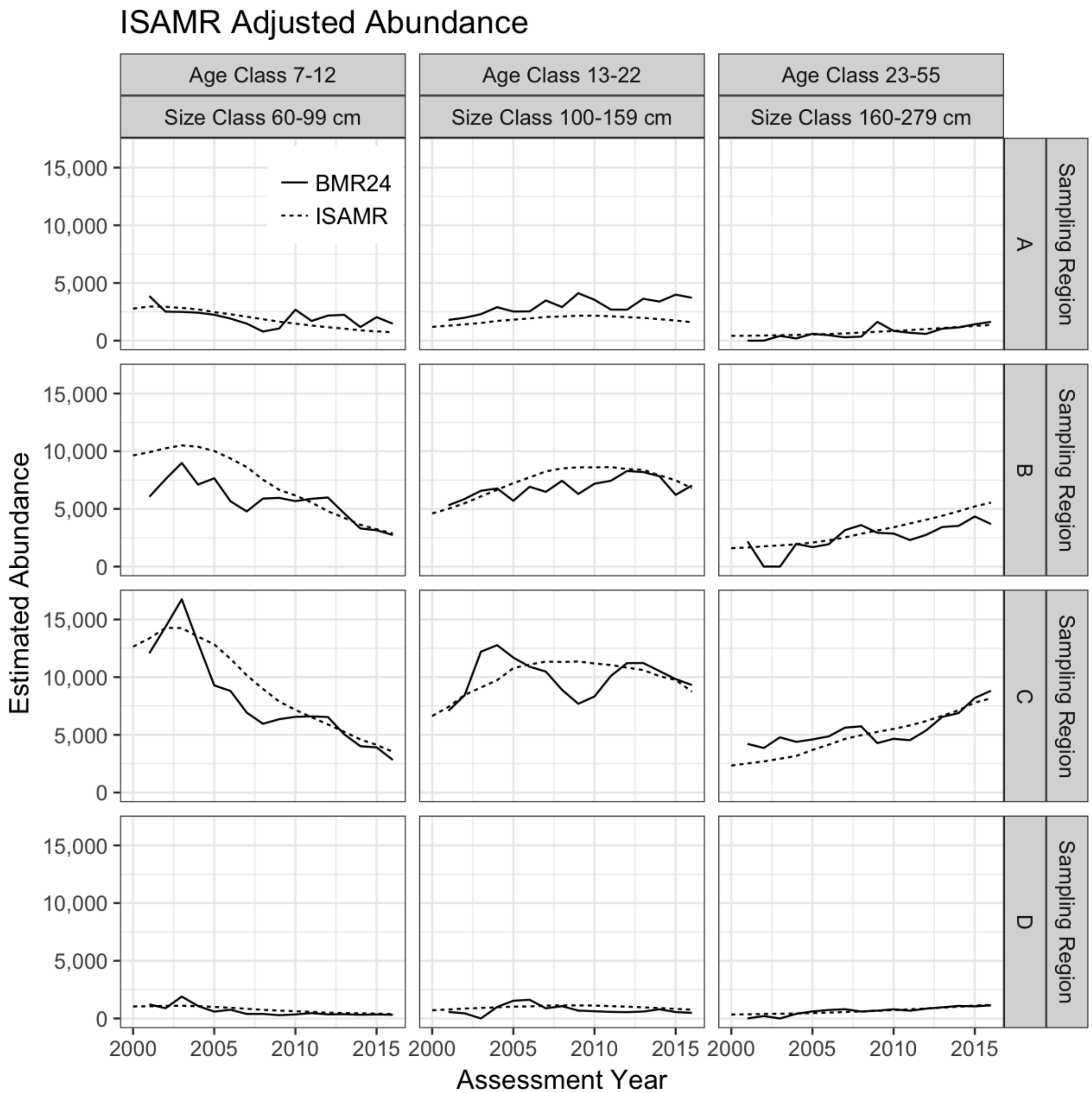

Figure 14. Comparison of region-specific BMR24 abundances and ISAMR adjusted abundances. ISAMR age classes where matched to corresponding size groups. Because the ISAMR estimates considered gear selectivity, abundances were adjusted to assume that all age classes had the same selectivity.

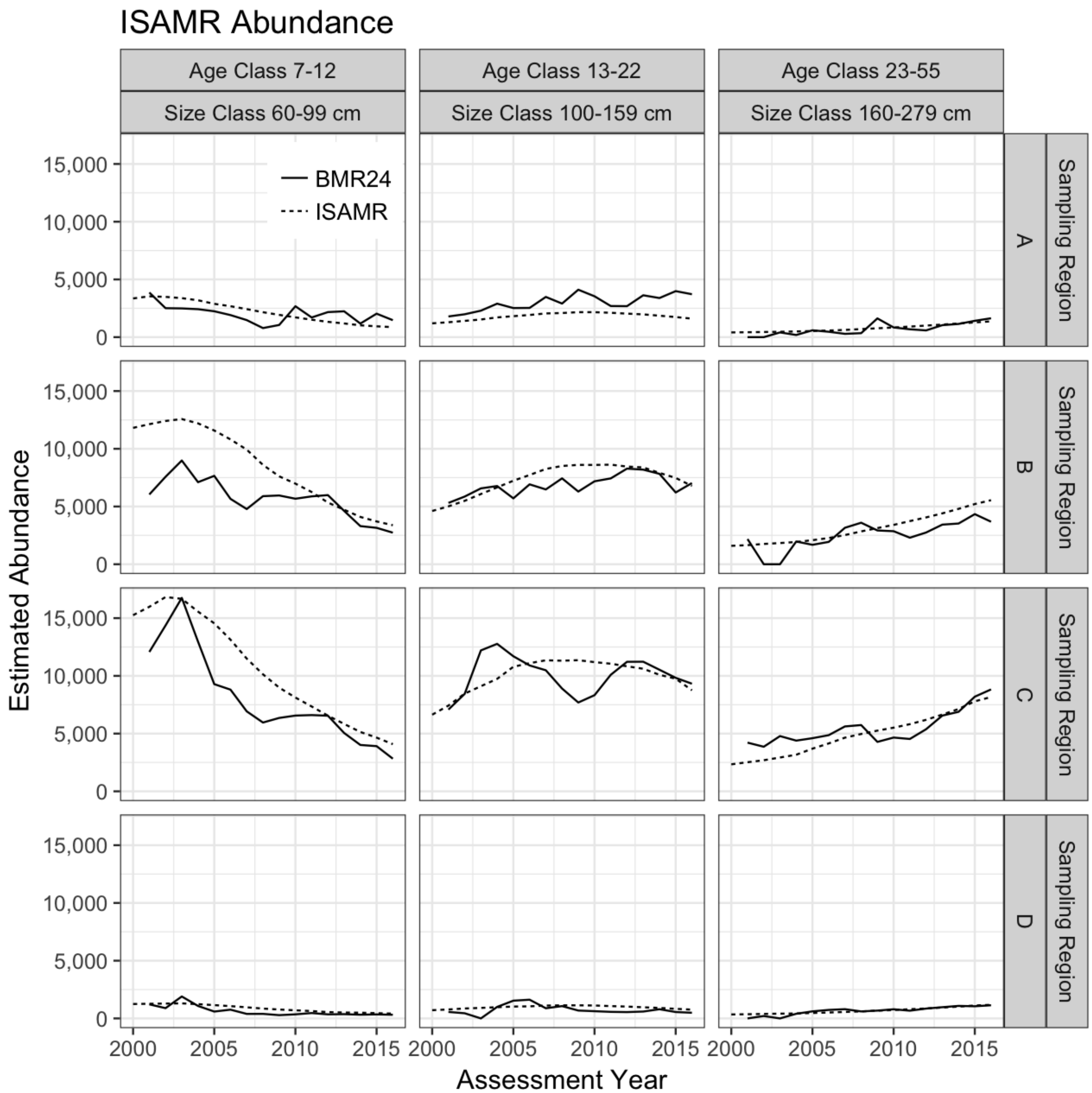

Figure 15. Comparison of region-specific BMR24 abundances and ISAMR unadjusted abundances. ISAMR age classes where matched to corresponding size groups. ISAMR unadjusted abundances considered gear selectivity differences, while BMR24 assumed a constant selectivity.

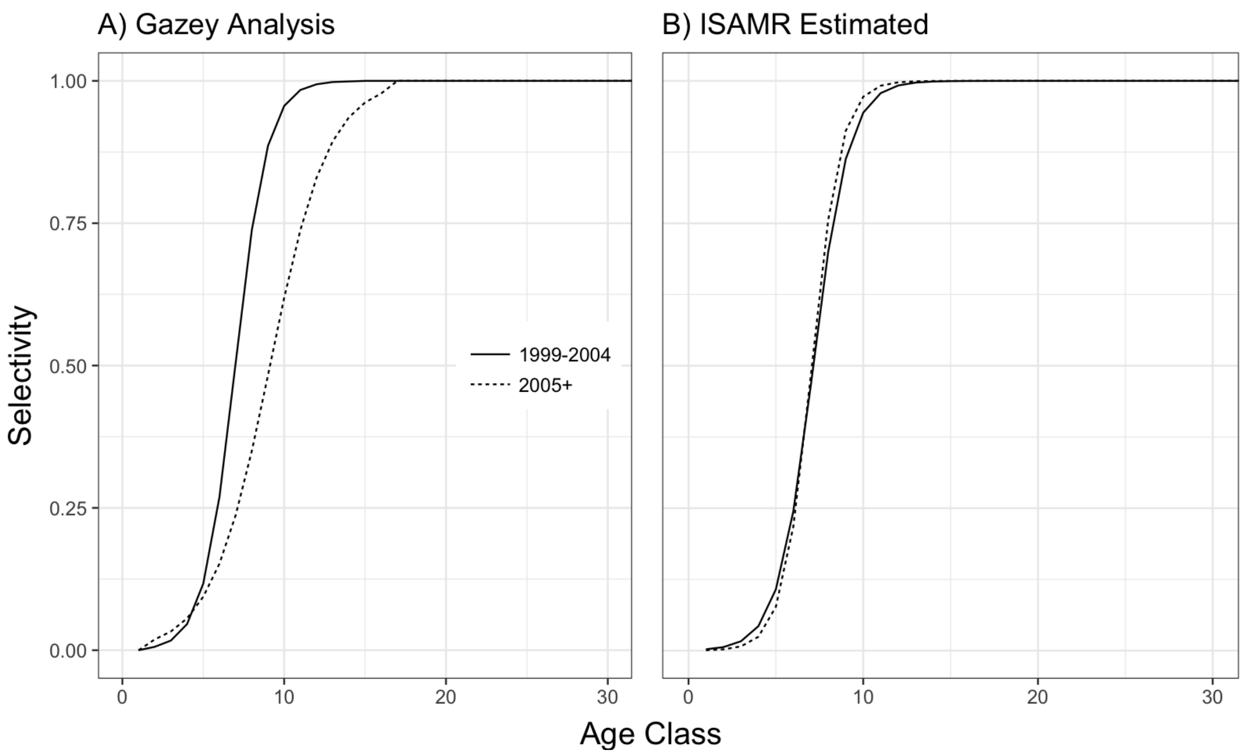

Figure 16. Comparison of selectivity values for A) the two selectivity epochs used in the Gazey Analysis (see Appendix E), and B) ISAMR estimated selectivity values for the same epochs.

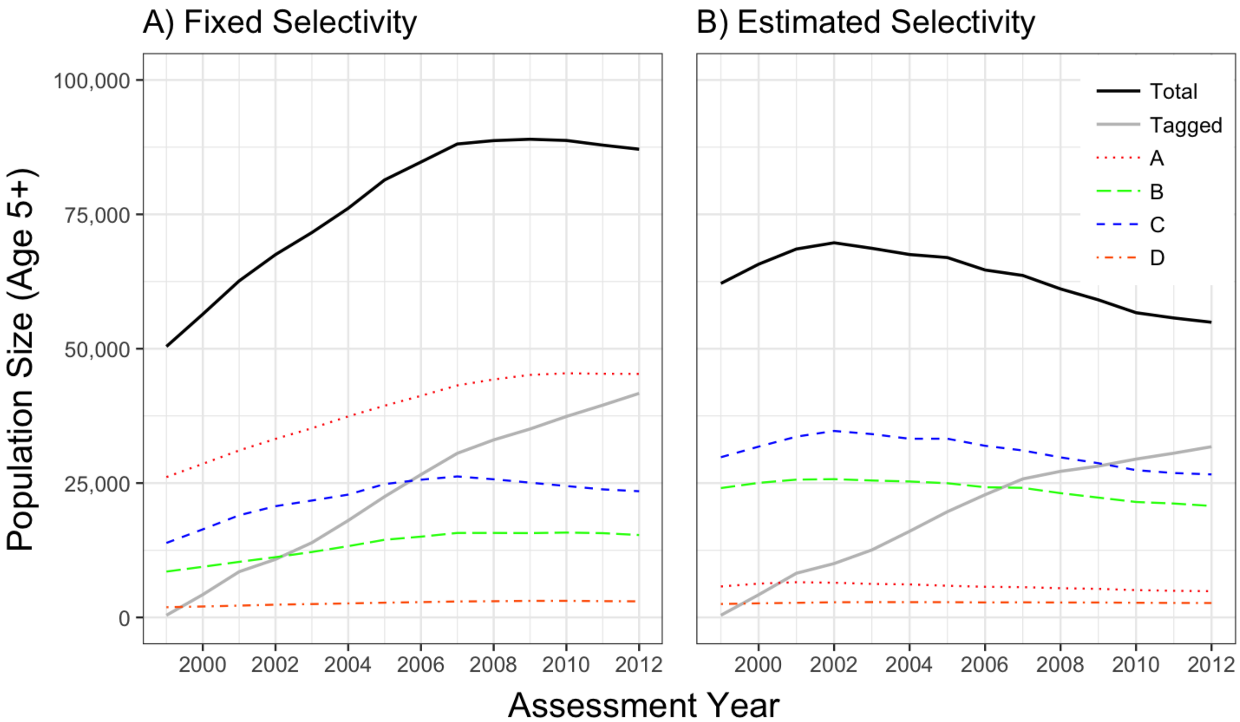

Figure 17. Population estimates for age-5+ sturgeon for ISAMR model runs using A) two epoch fixed selectivity values (see Appendix E), and B) freely estimated selectivity values for the same epochs.

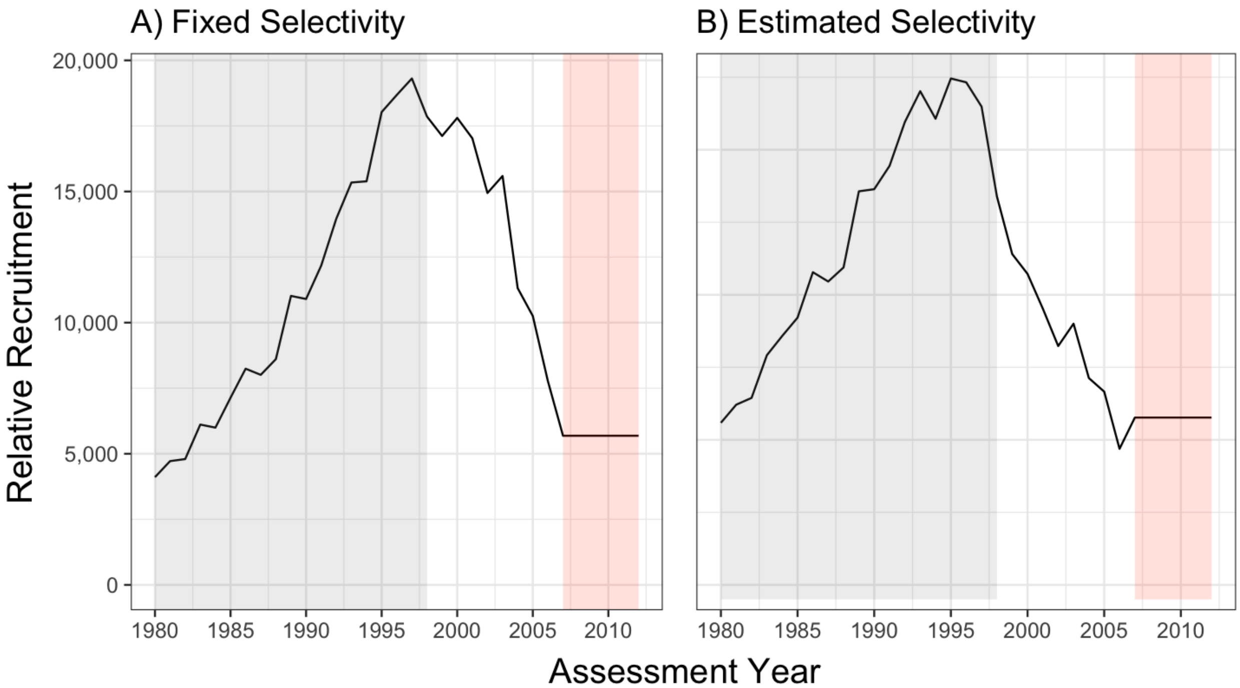

Figure 18. Estimated recruitment for ISAMR model runs using A) two epoch fixed selectivity values (see Appendix E), and B) freely estimated selectivity values for the same epochs.

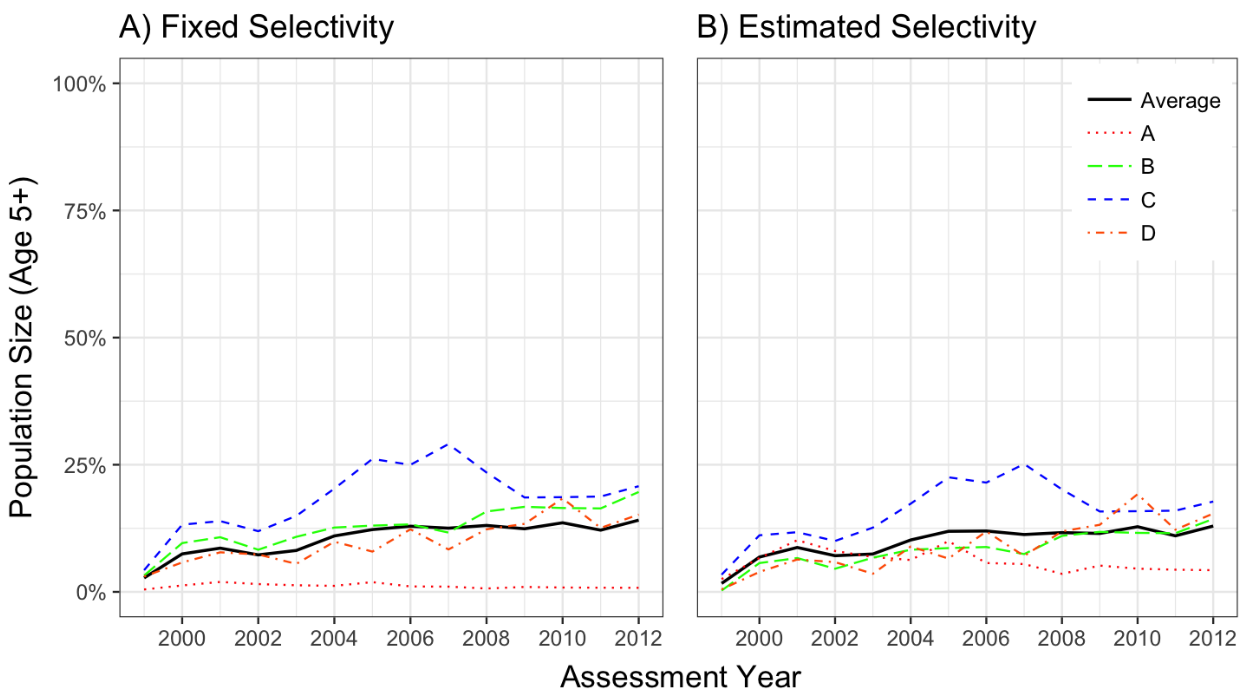

Figure 19. Estimated sampling rates for ISAMR model runs using A) two epoch fixed selectivity values (see Appendix E), and B) freely estimated selectivity values for the same epochs.

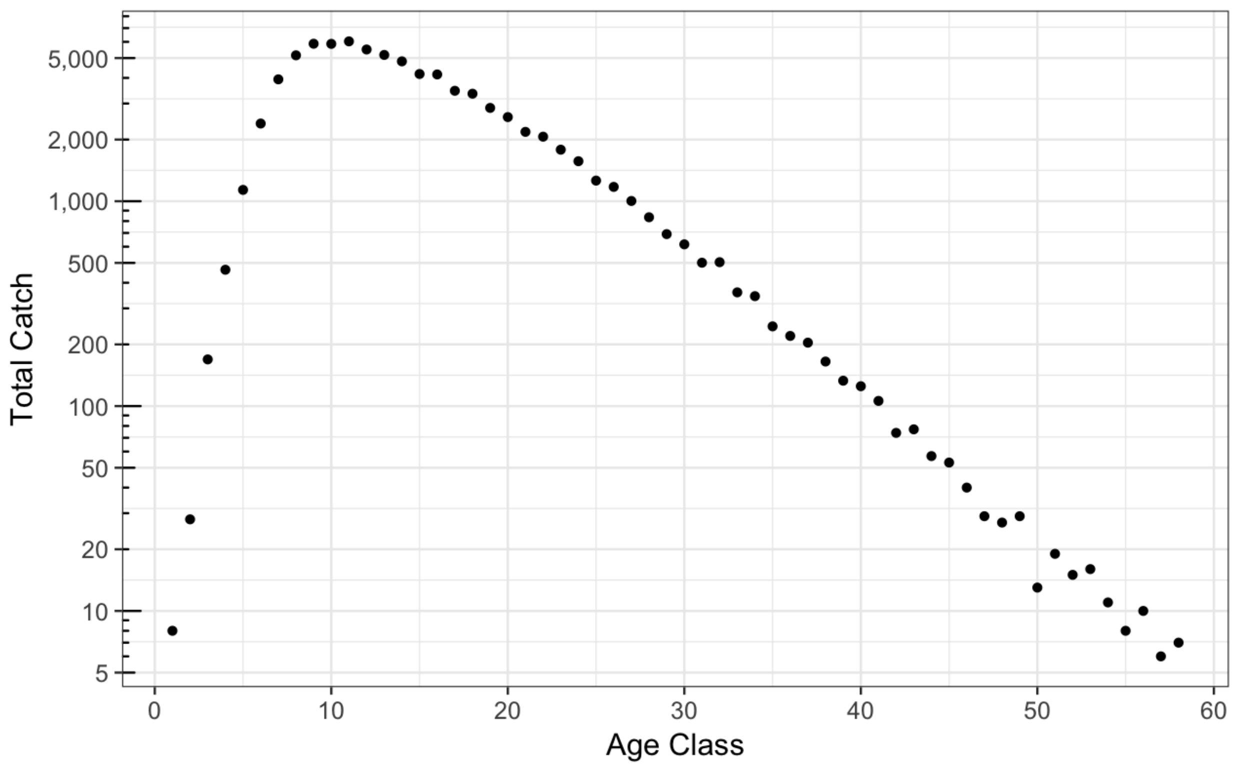

Figure 20. Total catch by age class for all sturgeon caught between 1999 and 2012 of age-58 or lower. Catch-curve has been linearized by displaying total catch on the $\log_{10}$ scale.

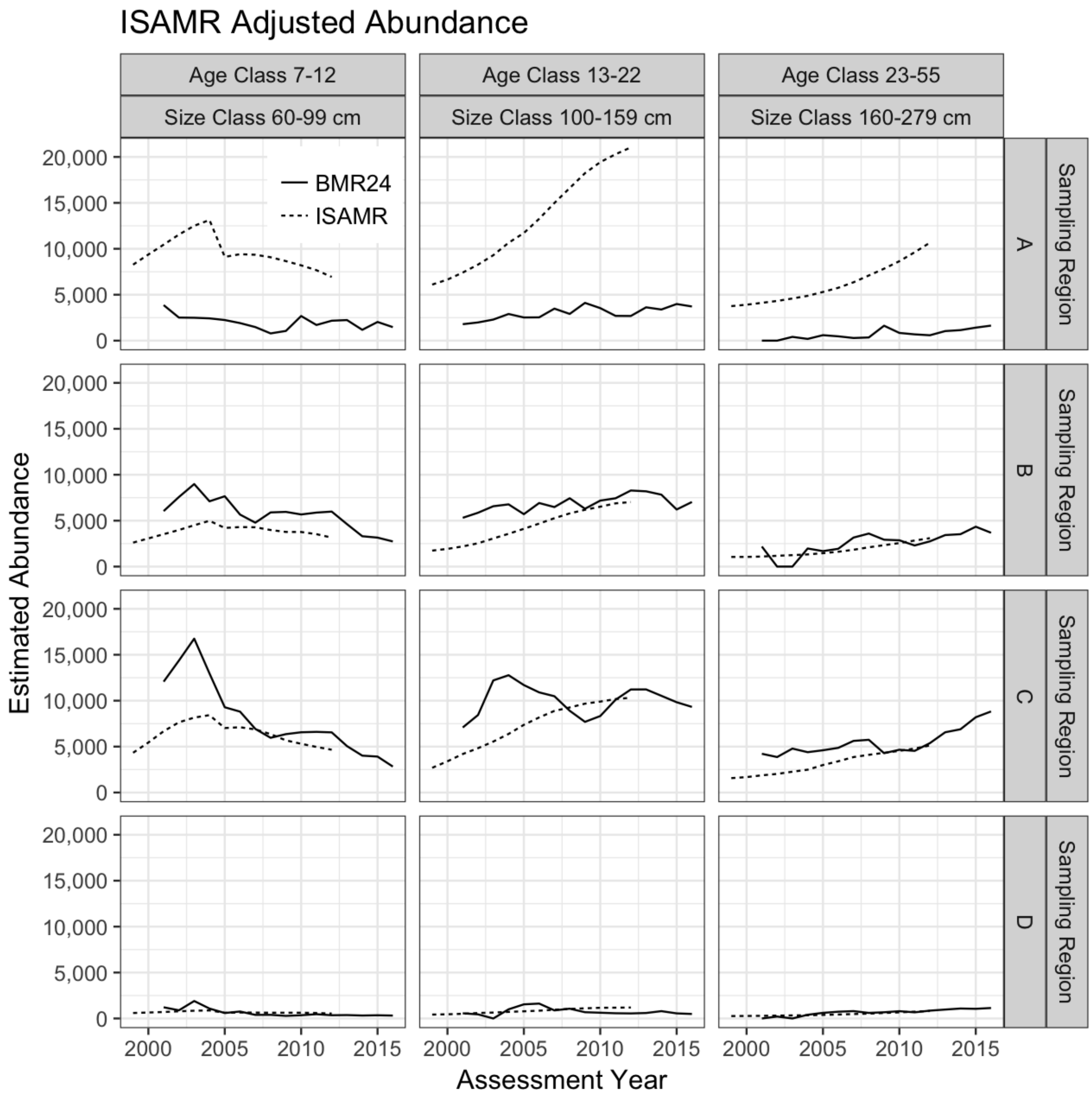

Figure 21. Comparison of region-specific ISAMR adjusted abundances relative to the BMR24 model when the Gazey selectivity curves (see Appendix E) were used for each epoch.

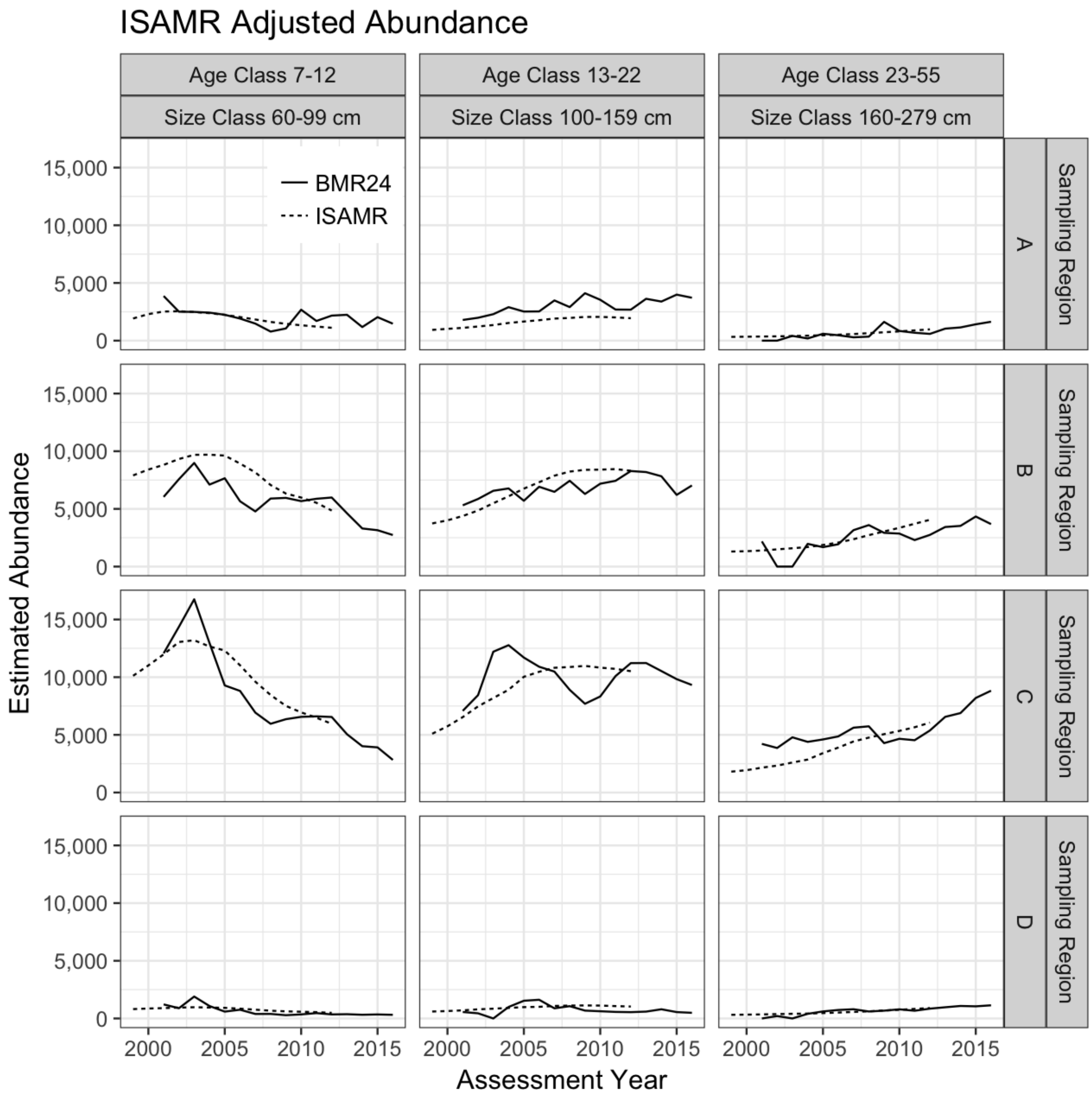

Figure 22. Comparison of region-specific ISAMR adjusted abundance relative to the BMR24 model when the Gazey selectivity epochs (see Appendix E) were freely estimated.

APPENDIX A

COMPARISON OF ISAMR VERSIONS

The original version of the Integrated Spatial and Age Mark Recapture (ISAMR) Model was developed in 2015 by Dr. Tom Carruthers, in collaboration with Karl English and Bill Gazey (version 1.6). The model has since been modified and extended in 2016 by Wendell Challenger and Karl English (v2.0). A summary of changes are outlined below in Table A1.

Table A1. Changelog of ISAMR features since the ISAMR model transfer to LGL.

Feature	**ISAMR v1.6**	**ISAMR v2.0**	**Notes/Details**
Historical abundance initialization	No	Yes	All models require that the population matrix is initialized for the start of the experiment. This requires values in 57 age classes across four sampling regions in order to initialize the population matrix. By contrast v1.6 initializes the matrix based on the population being in a stable age distribution just prior to the start of the experiment and initial abundance and regional distribution was estimated by the model. In contrast, v2.0 does not assume a stable age distribution, but instead initializes the abundance by age class for each sampling region using a forward propagation approach which combines annual estimates of historical age-1 recruitment with age-specific mortality rates and regional movements estimated by the model.
Regional distribution of age-1 recruitment	Fixed	Estimated	The original formulation (v1.6) uses the estimated movement matrix for all tagged age classes to derive a stationary regional distribution for age-1 recruitment. By contrast, v2.0 estimates the distribution of age-1 recruitment independent of the movement matrix used for all tagged age classes. Estimates likely reflects the relative distribution derived from the abundance estimates for each sampling region combined with differences in movement rates for these earlier age classes.
Movement probabilities	Estimated	Estimated	Both models use the same Markovian movement model that is used across all years.
Gear Selectivity	Estimated or Fixed	Estimated or Fixed	Both use one or more flat top selectivity curves that can be freely estimated or fixed to user values.

Feature	ISAMR v1.6	ISAMR v2.0	Notes/Details
Sampling rate as a function of effort	No	Yes	The original formulation (v1.6) estimated regional sampling rates independently for each year without effort data. By contrast, v2.0 models the sampling rate as function of the number of boat trips in a specific sampling region on a given year
Mortality curve	Fixed	Estimated	The original formulation (v1.6) used a fixed mortality-at- age relationship. By contrast, v2.0 estimates the mortality-at-age based on a regression relationship using the average length-at-age as an explanatory variable.
Tagged /untagged population matrices	Yes	Yes	Both versions contain this formulation.
Untagged Population Amendments	Predicted	Predicted	The untagged population matrix is decremented by the predicted age- and region-specific catch for both model versions
Tagged Population Amendments	Predicted	Actual	The original formulation (v1.6) estimated the number of fish tagged in each year, age and sampling region. By contrast, v2.0 uses the actual number of fish tagged by year, age and sampling region.

APPENDIX B

FULL MODEL SPECIFICATION

Background

The ISAMR model represents a novel implementation of an age-structure mark-recapture model that includes both spatial and age structuring. The model integrates data from multiple data sources into (i.e., tagged and un-tagged releases) into a single analysis. Similar to other age-structured mark-recapture models (e.g., Coggins et al. (2006)), the model uses a virtual population analysis generate estimates of the number of individuals available in each age class (and each sampling region). These estimates are then used to predict both un-tagged and tagged catch for each sub population (i.e., an age class at a given sampling region).

While there are similarities to other age-structured mark-recapture models, our implementation differs in some key areas from Coggins et al. (2006). For example, components for the un-tagged and tagged likelihood components differ with a more flexible un-tagged catch model (lognormal) and a more constrained tagging component (multinomial) is used due large number of tags deployed in the system and the wealth of available information. The ISAMR implementation also includes a number of intelligent modeling constraints in order to deal with the large number of unknown parameters introduced by the regional and age class structuring.

The specification of the ISAMR model can be broken down into two major components the population model (i.e., un-tagged $\boldsymbol{U}$ and tagged $\boldsymbol{T}$ populations – model states) and the observation model (i.e., how observed catch from is related to the underlying model states). The ISAMR makes use of some fixed parameters and setting (Table B1), but estimates most unknown parameters (Table B2). A number of derived parameters useful for population assessments, management decisions and model fit diagnostics are also considered (Table B3).

The next three sections provide a more in-depth overview of the underlying population model, the observation model used to relate the underlying population states to observed catch records and finally the model likelihood and posterior distribution. The model was developed and fit using the AD Model Builder (ADMB) framework.

Table B1. Summary of fixed model parameters in the ISAMR model.

Parameter	npar	Description
Y	1	Number of assessment years, $Y = 17$ for the current population assessment (i.e., 2000 -2016).
A	1	Number of age classes, $A = 58$ for the current population assessment.
R	1	Number of sampling regions, $R = 4$ for the current population assessment (see Figure 1).
$\phi^{\max}$	1	Maximum survival (0.97) in the length-at-age regression.
L_a	A	Length-at-age based on the von Bertalanffy growth model determined by Nelson et al. (2007): $L_a = 370.1 \times \left(1 - \exp(-0.025a)\right)$. Other length-at-age relationships can be specified at model run time.

Table B2. Summary of fundamental model parameters estimated in the ISAMR model.

Parameter	npar	Description
R_a^h	38	Historical recruitment that corresponds to the abundance in age class a. A total of $A-1$ values, the twenty oldest age classes were constrained to be equal resulting in 38 free parameters.
R_y	12	Total number of sturgeon recruited into age-1 in assessment year y. Recruitment in the final 6 assessment years is constrained to be equal little corresponding catch, resulting in 12 free parameters
δ_r	3	Proportion of yearly recruitment allocated sampling region r, three free parameters.
ϕ_a	$A-1$	Survival from age class a to age class $a+1$. For the final age class A, ϕ_{A-1} is the probability of surviving and remaining in age class A. Survival-at-age is based on a length-at-age regression, where length-at-age based on the von Bertalanffy growth model determined by Nelson et al. (2007): $L_a = 370.1 \times (1-\exp(-0.025a))$.
α_0, α_1	2	The slope and intercept parameters for the survival by length-at-age regression relationship.
$\beta_{0,r}, \beta_{1,r}$	8	The slope and intercept parameters for the region-specific sampling rate to effort regression relationships.
$a_{50,y}, a_{sl,y}$	2 or 4	Selectivity parameters used to determine the selectivity-at-age in a given year ($S_{y,a}$). Currently, selectivity is constrained to be the same for a series of years (two free parameters) within two curves are used for different epochs (four free parameters).
$Mov_{r,r}$	12	Steady-state Markovian movement parameters indicating the probability of moving from one sampling region to the next. $(R-1)^2$ parameters are required (nine currently). A total of 16 possible transitions and 12 free parameters
σ_C	1	Variability in the log catch model for untagged captures.
Total:	78 to 80	

Table B3. Summary of derived model parameters.

Parameter	npar	Description
$\boldsymbol{U}_r^h$	228	Initial untagged population matrix (age class by sampling region), derived from a forward propagation approach that uses historical recruitment and demographic processes such as survival, movement and aging.
$\boldsymbol{U}$	3,944	Three-dimensional array $(Y \times A \times R)$ containing the un-tagged population abundances broken down by year, age class, and sampling region.
$\boldsymbol{U}_y$	232	A slice of the un-tagged population array giving a yearly population matrix (age class by sampling region) in assessment year y.
$\boldsymbol{U}_r$	986	A slice of the un-tagged population array giving the population trajectory matrix (year by age class) in sampling region r.
$\boldsymbol{T}$	3,944	Three-dimensional array $(Y \times A \times R)$ containing the tagged population abundances broken down by year, age class, and sampling region.
$\boldsymbol{T}_y$	232	A slice of the tagged population array giving a yearly population matrix (age class by sampling region) in assessment year y.
$\boldsymbol{T}_r$	986	A slice of the tagged population array giving the population trajectory matrix (year by age class) in sampling region r.
M_a	57	Mortality-at-age for surviving from age class a to age class $a + 1$, derived from the mortality vs length of age regression. A total of $A - 1$ (i.e., 57) values are derived.
$F_{y,r}$	68	Year- and region-specific sampling rates based on the boat trip regression. A total of $Y \times R = 17 \times 4 = 68$ parameters, where Y is the number of years (i.e., 17) and R is the number of sampling regions (i.e., 4).
$S_{y,a}$	986	Selectivity-at-age values for age class a in assessment year y, based on the estimated selectivity relationship.
$p_{y,a,r}$	3,944	Probability of capturing an individual of age class a in sampling region r in assessment year y and is a function of sampling rates ($F_{y,r}$) and selectivities ($S_{y,a}$).
$C_{y,a,r}^U$	3,944	Predicted un-tagged catch, which is a function of the available untagged catch $\left(\boldsymbol{U}_y\right)$ and capture probabilities $\left(p_{y,a,r}\right)$.
$C_{y,a,r}^T$	3,944	Predicted tagged catch, which is a function of the available un-tagged catch $\left(\boldsymbol{T}_y\right)$ and capture probabilities $\left(p_{y,a,r}\right)$.

State Model (Population Model)

The state model deals with changes to the un-tagged ($\boldsymbol{U}$) and tagged ($\boldsymbol{T}$) population arrays over time (Figure 2). This can include recruitment into the population (i.e., the un-tagged population only), transfer of individuals from the un-tagged to tagged populations as the result of tagging events, and finally, movement, aging, and mortality that occurs in both populations.

Initialization

The fact that the Lower Fraser River White Sturgeon population existed prior to the start of the observation period necessitates that the un-tagged population matrix be initialized for all sampling regions and age classes at the start of the assessment period. Because the current model is implemented with $R = 4$ sampling regions and $A = 58$ age classes, this required $R \times (A - 1) = 228$ population abundances. Estimating each sampling region by age class abundance independently from catch data is problematic as corresponding catch values may be missing due to either a lack of individuals and/or sampling error.

This necessitates formulating a model to predict these initial values. Earlier versions of the ISAMR (i.e., ISAMR v1.6, Appendix A) initialized the population structure based on a stock-recruitment relationship that required the population to be in a stable age distribution prior to the start of the experiment; however, this assumption was problematic for Lower Fraser River White Sturgeon. Commercial fishing from 1880-1980 left the population at its lowest levels in the mid-twentieth century (English and Bychkov, 2012; Whitlock and McAllister, 2012,). Furthermore, habitat loss due to development and industrialization have further impacted the population. As such, it is unlikely that this requirement is true, which will likely result in model misfit at the start of the experiment.

To accommodate for this limitation ISAMR v2.0 directly estimates the number of recruits into age class one for the years leading up to the start of the assessment period $\left(R_y^h\right)$, herein referred to as historical recruitment. Because a stable equilibrium of age and regional structure of the population is unlikely, each yearly cohort of historical recruits are taken through the same demographic processes as cohorts recruited in the assessment period (see "*Recruitment*" and "*Mortality, Movement, and Aging*"). Total recruitment is first apportioned regionally (δ_r) and then iteratively taken through the same yearly mortality, movement and aging steps as recruits in the current assessment period. This process continues to the start of the assessment period, creating an upper triangle matrix historical un-tagged population matrix for each regional slice (Figure B1). This process can be considered as a forward propagating virtual population analysis. The resulting partial reconstruction is then used to initialize the un-tagged population array in the first assessment year with abundances of all age classes, except the first age class which is populated with the estimated recruitment abundance for that year.

Estimates of historical recruitment are informed by minimizing the discrepancy between observed and predicted catch in the corresponding age classes (e.g., catch of age-50 sturgeon observed in the year 2000 were originally recruited in 1951). Because the relatively high sampling rates in the lower Fraser River White Sturgeon fishery there is ubiquity of information available for most age classes. That said, if breaking age-specific catch further to each sampling region, the catch data becomes more sparse especially for sampling regions with lower overall catch (e.g., sampling region A and D). As such, independently estimating each age class within each sampling region separately was not feasibly. As such, this approach focuses on estimate the total cohort recruitment, then makes use of other processes (regional apportionment and movement) to distribute each cohort spatially over time. This requires few free parameters, does not require stable age distributions, but does require the regional apportionment and movement rates to reasonably represent the average population behaviour. Furthermore, estimates of regional apportionment should reflect the relative abundance distribution of age class one recruits, but may also reflect differences in movement rates for these earlier age classes. Estimates of recruitment also rely on the same mortality, rates used in the current period, which may not be accurate. As such, historical recruitment should be viewed with some caution. The primary goal was to allow for a flexible approach for initializing the population structure, rather than an accurate account of historical population dynamics. Likely, estimated recruitment represents a running average of actual cohort strengths and should be viewed with some caution. For this reason, we only provide historical recruitment strengths back to 1980, although the model estimates as far back as 1943 for a assessment period starting in 2000.

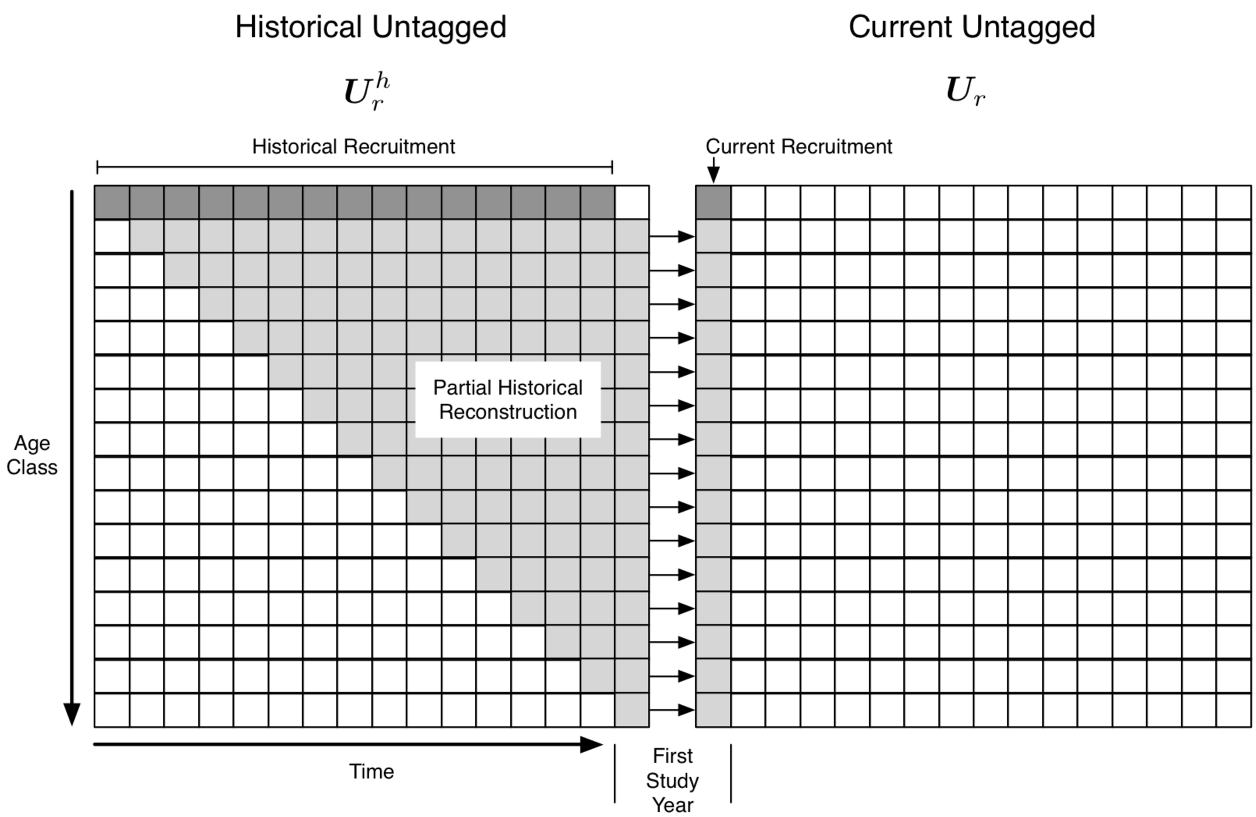

Figure B1. Example of a partial historical reconstruction is used to initialize all age categories, except the first age class, of the un-tagged population matrix. Illustration is for a single sampling region.

Recruitment

The ISAMR model considers recruitment into the first age class for both the current assessment years (R_y) and for years leading up to the start of the population assessment (R_y^h), herein referred to as historical recruitment. Estimates of historical recruitment are estimated to minimize the discrepancy between observed and predicted catch in the corresponding age classes (e.g., catch in age class 50 observed in the year 2000 were originally recruited in 1951). The first 20 years of historical recruitment were constrained to be equal as the catch in corresponding age classes was low and initial model runs indicated only small differences in estimated recruitment for these years. The final 6 years of recruitment in the assessment period were also constrained to be equal, due to very little catch in the first six age classes (i.e., see “Selectivity-at-age”).

The ISAMR model estimates recruitment as log recruitment with a normal prior for both the historical log recruitment,

$$\log(R_y^h) \sim \text{Normal}(9, 0.9) \quad y = 20, 21, \ldots, A - 1,$$

and the current log recruitment,

$$\log(R_y) \sim \text{Normal}(9, 0.9) \quad y = 1, 2, \ldots, Y - 5.$$

Informative priors were chosen to help bound the recruitment estimates to something biological realistic, with an expected recruitment of around 8,000 individuals.

Total recruitment is then apportioned by sampling region by the regional apportionment parameter (δ_r), as such historical recruitment into the first age class by sampling region is determined as

$$U_{y,a=1,r}^h = R_y^h \cdot \delta_r,$$

and recruitment into the current assessment period by region is determined as

$$U_{y,a=1,r} = R_y \cdot \delta_r.$$

Finally, the regional apportionment parameter (δ_r) is given a uniform prior,

$$\delta_r \sim \text{Uniform}(0,1).$$

Note that only three free parameters are estimated as the fourth is the mathematical complement.

Mortality, Movement, and Aging

At the end of each time step the yearly population matrices (i.e., $\boldsymbol{U}_y$ and $\boldsymbol{T}_y$) are is taken through steps to account for mortality, movement, and survival (Figure 2).

Survival/Mortality and Aging

The survival between age classes was modeled as a logistic regression against the expected length-at-age (see Figure B2a). A generalized logistic function was used in place of logit function for the link function so that order bound the upper estimate of survival could be restricted to be than one, in this case the upper asymptote was fixed to 0.97. The generalized logistic function allows for a more flexible S-shaped curve relative to a regular logistic function, such as allowing for the lower and upper asymptotes to differ from 0 and 1 respectively.

Let ϕ_a be apparent probability of surviving (emigration and/or death cannot be distinguished) from age class a to age class $a + 1$, then the generalized logistic regression function used was

$$g(\phi_a) = \log\left(\frac{\phi_a}{0.97 - \phi_a}\right) = \alpha_0 + \alpha_1 \cdot L_a.$$

The parameters α_0 and α_1 are freely estimated and L_a is the average length for a given age class (Figure B2a), and follows the von Bertalanffy growth model determined by Nelson et al. (2007):

$$L_a = 370.1 \times (1 - \exp(-0.025a)).$$

The regression can be rewritten solving for ϕ_a, which gives:

$$\phi_a = \frac{0.97}{\frac{1}{e^{(\alpha_0 + \alpha_1 \cdot L_a)}} + 1}.$$

The only difference between this formulation and typical logistic regression is that the numerator is 0.97 instead of one. This nonstandard formulation was chosen because mature sturgeon are known to have high survival rates in the wild, with a number of age classes having a similar high survival rate. As such, natural survival can be expected to asymptote relatively quickly once sturgeon reach maturity. Because these individuals are also fully recruited into the fishery a regular a model employing the common logit link function would likely force estimated survival rates to approach one (i.e., perfect survival) for many age classes under assessment. While survival rates for mature sturgeon are high, and indeed close to one, perfect survival is clearly not realistic and could bias population estimates. The use of the generalized logit formulation allows survival to approach the asymptote early (i.e., for mature age classes) without survival being force to be an unrealistically high value (e.g., Figure B2b shows that estimated age-class-specific survival rates were close to the asymptote for many age classes). Finally, some development models were attempted to estimate the upper asymptote, but initial models did not appear to produce stable estimates.

Often age-class specific, the instantaneous mortality rates (M_a) are also of interest. Here the apparent probability of survival relates to the instantaneous mortality rate as:

$$P(\text{survival}) = \exp(-M_a).$$

Therefore, mortality-at-age (M_a) can be estimated as:

$$M_a = -\log(\phi_a).$$

The final numbers at year end after aging is accounted for are then determined as:

$$U^*_{y,a,r} = U_{y,a,r} \times \phi_a \quad \text{for } a = 1,2,\dots,A \text{ and } r = 1,2,\dots,R$$
$$T^*_{y,a,r} = T_{y,a,r} \times \phi_a \quad \text{for } a = 1,2,\dots,A \text{ and } r = 1,2,\dots,R.$$

Note that for the final age class this is the probability of surviving in the final age class bin. For all other age classes this is the probability of surviving to the next age class when we account for aging.

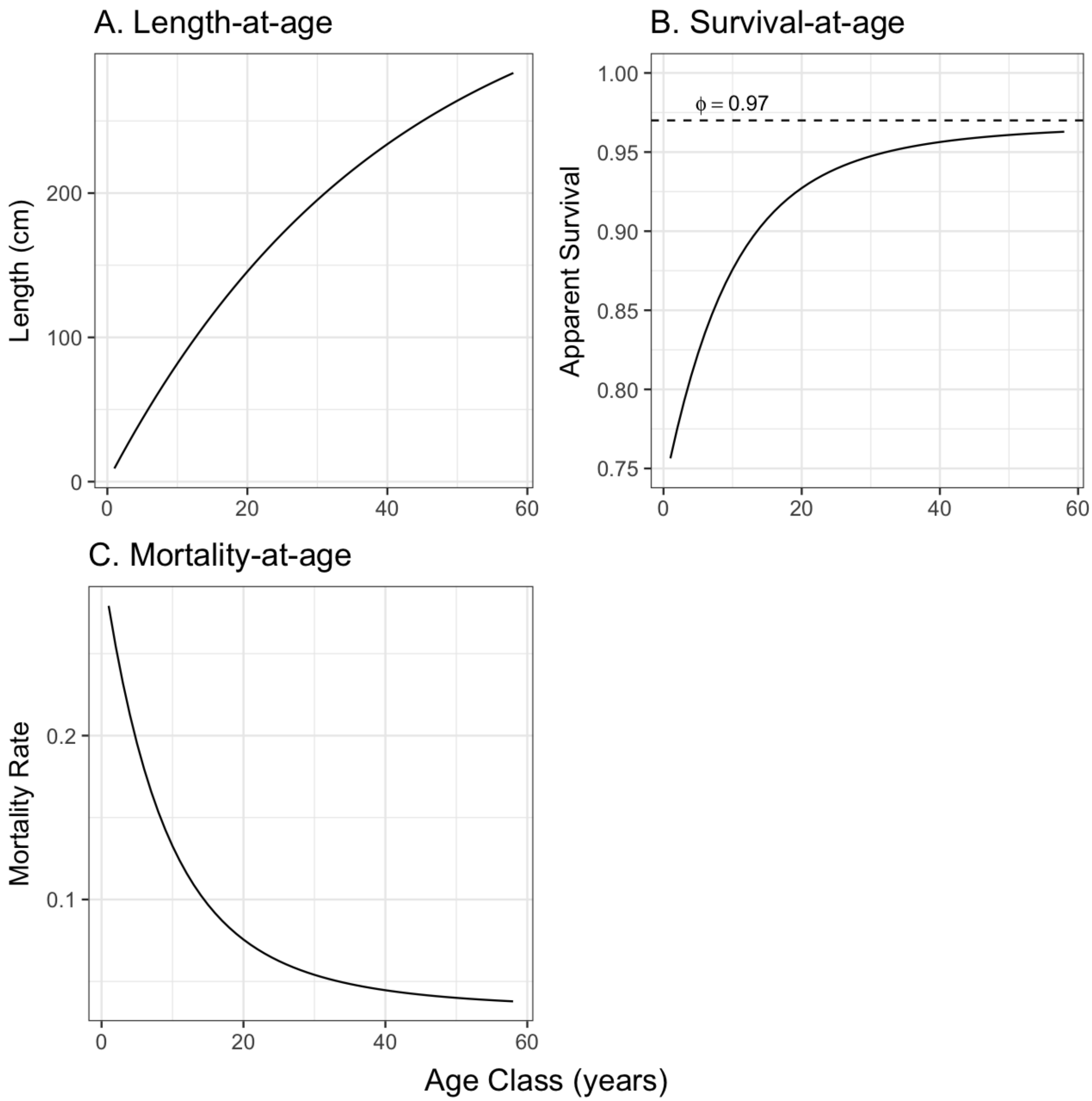

Figure B2. The sturgeon length-at-age relationship (A) proposed by Nelson et al. (2007) was used to model the apparent probability of survival (B), and by extension mortality rates (C).

Movement

Movements are applied after mortality, and can be summarized as a matrix multiplication between the yearly population matrix after mortality with the matrix of movement probabilities.

$$\boldsymbol{U}_y^{**} = \boldsymbol{U}_y^{*} \times \mathbf{Mov}$$
$$\boldsymbol{T}_y^{**} = \boldsymbol{T}_y^{*} \times \mathbf{Mov}$$

Aging

The last transition involves moving individuals to the next age class to finalize the regional age class abundance in the next year (i.e., $y + 1$). For all age classes except the terminal age class this is done by simply assigning abundances in each age class to the subsequent age class, that is

$$U_{y+1,a+1,r} = U_{y,a,r}^{**} \quad \text{for } a = 1,2, \dots, A-1$$
$$T_{y+1,a+1,r} = T_{y,a,r}^{**} \quad \text{for } a = 1,2, \dots, A-1.$$

The final age class is treated differently as it is bin for all age classes of age A and older, that is

$$U_{y+1,A,r} = U_{y,A,r}^{**}$$
$$T_{y+1,A,r} = T_{y,A,r.}^{**}$$

Observation Model

On any given year the number sturgeon caught (tagged and/or untagged) can be predicted on a year, age-class, and sampling region level based the tagged and untagged population matrices (i.e., $\boldsymbol{N}_y$ to $\boldsymbol{T}_y$; Figure 2), the estimated instantaneous sampling rates ($F_{y,r}$), estimated or fixed selectivity-at-age rates ($S_{y,a}$), and the non-detection rate (NDR), which is currently fixed to zero. As such, the observation component of the models objective function compares three types of observed frequencies to their predicted values:

1. Untagged catch:
    a. sturgeon releases without tags, and;
    b. sturgeon releases with tags.
2. Tagged catch:
    a. sturgeon tagged releases that were recaptured within the assessment period; and
    b. sturgeon tagged releases that were not observed within the assessment period.

The model describes each of these observation types as independent processes. The model also describes these in terms of aggregated totals so the current formulation will not support the use of individual covariates to model the probability of capture or survival.

Untagged Catch Model

Untagged catch was summarized as the total number of captures by assessment year, age class, and sampling region (see Appendix D). This included captures that were released with a tag as well as captures released without a tag. The predicted number of untagged captures in a given year, sampling region, age class ($C^U_{y,a,r}$) will be a function of the population of untagged individuals ($N_{y,a,r}$), the instantaneous sampling rate rates ($F_{y,r}$), and the selectivity-at-age ($S_{y,a}$), that is:

$$C^U_{y,a,r} = U_{y,a,r}\left(1 - \exp\left(-F_{y,r} \cdot S_{y,a}\right)\right).$$

Note that $\left(1 - \exp\left(-F_{y,r} \cdot S_{y,a}\right)\right)$ is the probability of capture for a given a given age class, sampling region, and assessment year $p_{y,a,r}$.

The frequency of observed untagged catches by year, age class, and sampling region were compared to the predicted catches based on a log normal catch formulation in the model likelihood function (see "*Model Likelihood* and Posterior Distribution").

Tagged Catch

Tagged releases can be broken down into two main categories: 1) tagged releases that were recaptured again at some point in the assessment period and 2) tagged releases that were never observed again within the assessment period.

Probability of an observing a tagged return

For a sturgeon release of age $a1$, in year $y1$ and sampling region $r1$, the probability of recapturing the individual at a later point in time ($y2$) and space ($r2$) is determined by the probability the individual survived to year $y2$, moved to sampling region $r2$, is the probability of capture given the sturgeon is available for capture (i.e., non-detection rates). This can be summarized as the following probability statement:

$$\begin{aligned} &P\left(\text{return}(y2, y2)|\text{release}(y1, a1, r1)\right) \\ &\qquad = P(\text{survived w/ no prior captures}) \cdot P(\text{moved to } r2) \\ &\qquad \cdot P(\text{capture}(y2, a2, r2)\ |\text{available}) \cdot P(\text{available}) \end{aligned}$$

The probability of survival is determined by the ages of the animal over the period in question and the fixed mortality relationship (see "*Survival/Mortality*"). The probability of being found in r_2 is based on the estimated parameters in the Markov transition matrix, which represents steady-state movements between sampling regions that are assumed to occur at the end of each year. Finally, whether the animal is observed at a given point in space and time depends on the associated capture probability and availability of that animal to sampling. The probability of availability is dependent on the non-detection rate (NDR), and can be viewed as accounting for temporary emigration. If available for capture, then the probability of being re-captured at that place and time is determined as:

$$P(\text{capture}(y2, a2, r2)\ |\text{available}) = p_{y2,a2,r2} = 1 - \exp\left(-F_{y2,r2} \cdot S_{y2,a2}\right),$$

where F_{y^c,r^c} is the instantaneous sampling rate in the recapture year and sampling region of interest and S_{y^c,a^c} represents the age vulnerability in that year.

The component $P(\text{survived w/ no prior captures})$ is the probability of surviving and not being captured in intervening years between release and before the capture year is a bit more complicated to compute and depends on the number of intervening years. Here we must consider the possible movements and the corresponding capture probabilities. We will also consider $P(\text{moved to } r2)$ at the same time as it also depends on the number of intervening years.

For captures occurring the year after release (i.e., $y2 - y1 = 1$), there was no opportunity to capture the animal prior to the current recapture occasion and

$$P(\text{survived w/ no prior captures}) = 1,$$

and the animal had to directly move to the sampling region of capture, therefore $P(\text{moved to } r2) = \text{Mov}_{r1,r2}$ (see "*Movement*" for more details on how movements were estimated).

For recaptures occurring two years after release (i.e., $y2 - y1 = 2$), then there was one opportunity to capture the animal. The probability of surviving without being captured in the intervening year is becomes:

$$P(\text{survived w/ no prior captures}) = \sum_{r}^{R} (\phi_{a1})\text{Mov}_{r1,r} \cdot \left(1 - p_{y1+1,a1+1,r}\right),$$

and $P(\text{moved to } r2) = \sum_{r=1}^{R} \text{Mov}_{r,r2}$ because the animal could have been in any of the R sampling regions before moving into the sampling region of capture ($r2$). The parameter ϕ_{a1} represents the probability of surviving from age class $a1$ to $a1 + 1$ (see "*Survival/Mortality*"). In the case of the terminal age class (A) ϕ_A is the probability of surviving and remaining in the terminal age class. Sturgeon first captured that belonged to an age class older than A were not included in the model, but sturgeon that age into the final age class are retained. The parameter Mov is the probability of moving from one sampling region to the next in the intervening year. Finally, $1 - p_{y1+1,a1+1,r}$ is the probability of not being captured in a respective sampling region.

For recaptures occurring more than two years after release (i.e., $y2 - y1 > 2$) there are more possibilities, which necessitate a more complicated expression. In this case, the probability of not capturing the individual in the intervening years becomes:

$$P(\text{survived w/ no prior captures}) = \sum_{r}^{R} (\phi_{a1}) Mov_{r1,r} \cdot \left(1 - p_{y1+1,a2+1,r}\right) \cdot \prod_{y=y1+2}^{y2-1} \left(\sum_{r=1}^{R} \sum_{s=1}^{R} \phi_{\text{a2}-1} \cdot \text{Mov}_{r,s} \cdot \left(1 - p_{y,\text{a2},\text{s}}\right) \right).$$

Note that the index $a2 = \min(A, a1 + y - y1)$ to accommodate for the fact the final age class encompasses tagged sturgeon of age class A or older. Finally, similar to the case for two years between capture $P(\text{moved to } r2) = \sum_{r=1}^{R} \text{Mov}_{r,r2}$.

The likelihood then includes all of the observed recapture frequencies based on a multinomial likelihood function (see "*Model Likelihood and Posterior Distribution*")

Probability of not observing a tagged release

The second set of mark recapture data described by the model are releases that were never observed again within the assessment period. This could have been the final release of an animal in the assessment period (e.g., the analysis/assessment period ends in 2016, but we are not considering the capture that occurred in 2017) or animals never observed again after the first tagging event. The model does not distinguish between the two events as we are only concerned with release and recapture events.

In general, the probability statements for these histories can involve quite complicated expressions as all possible fates must be considered simultaneously because it is unknown whether the individual survived and was not observed or perished at any point in time. While complicated, the probability statement specified by taking the mathematical complement of the probability of observing the release again at all possible spatial-temporal points in the future, that is:

$$P\left(\text{no return}\middle|\text{release}(y1, a1, r1)\right) = 1 - \sum_{y=y1+1}^{Y} \sum_{r=1}^{R} P\left(\text{return}(y, r)|\text{release}(y1, a1, r1)\right).$$

The frequency releases without a return are included as part of the mark-recapture likelihood component (see "*Model Likelihood and Posterior Distribution*").

Sampling Rate, Selectivity, Capture Probability

The observed un-tagged and tagged catch across sampling region and age classes is modelled as a function of the yearly regional fishing rate $\left(F_{y,r}\right)$ and the age-dependent gear selectivity (S_a). The yearly regional fishing rate $F_{y,r}$ represents the fishing rate for a given sampling region on a given year for individuals that are fully recruited into the fishery. Individuals that are not fully recruited can be expected to exhibit a lower sampling rate with younger sturgeon being recruited less than older, larger individuals. These differences in sampling rates are represented by S_a which takes a value between 0 (i.e., not catchable) to 1 (full recruited into the fishery). These two components are assumed to function independently and therefore the realized fishing rate for a given age class $\left(F^*_{y,r,a}\right)$ is becomes the product, that is:

$$F^*_{y,r,a} = F_{y,r} \times S_a$$

For age classes that are fully recruited into the fishery selectivity equals one (i.e., $S_a = 1$) and the realized fishing rate defaults to the yearly regional fishing rate (i.e., $F^*_{y,r,a} = F_{y,r}$). For age classes that are not fully recruited (i.e., $S_a < 1$) the realized fishing rate will be less than the yearly regional rate (i.e., $F^*_{y,r,a} < F_{y,r}$).

Estimating yearly regional sampling rates

Early versions of the ISAMR were constructed by freely estimating the yearly regional fishing rates, however this required the estimation of many free parameters which in turned required various modelling constraints (e.g.., strong priors or likelihood penalties). Detailed information on the number of yearly regional fishing effort (i.e., boat trips) was available and investigated to see the feasibility of modeling sampling rates as a function of fishing effort.

While regional fishing effort (measure as the number of boat trips to a sampling region) varied greatly by year and sampling region (Figure 4a), the observed regional catch was strongly correlated with the number of fishing trips (Figure 4b). If fishers consistently fish in the best sturgeon capture locations within a sampling region, and these locations all have a similar density of sturgeon (and therefore a similar probability of capture), we would expect the catch-per-trip relationship to hold constant across a given sampling region, as was observed. That said, the underling probability of capturing a particular individual (out of all available individuals, not the probability of a catching any individual on a fishing trip) could differ greatly due to differences in the underlying population sizes. These assumptions were tested by comparing freely estimated yearly regional sampling rate estimates from earlier development version of the ISAMR model (i.e., without information about the number of boat trips) against the number of regional boat trips (Figure B3). This shows that: 1) the when the ISAMR model is fit without information about the number of regional trips the freely estimated yearly regional sampling rates are strongly predicted by the number of boat trips (i.e., effort); 2) the strong linear relationship was consistent across all sampling regions; and 3) the slope and intercept terms of the linear relationship differ by sampling region. This would be expected if there is no correlation between the underlying population size and the number of good capture locations.

As such the sampling rate was modeled as simple linear regression against boat trips, with a separate intercept and slope for each sampling region, that is:

$$F_{y,r} = \beta_{0,r} + \beta_{1,r} \cdot \text{Trips}_{y,r}.$$

Parameters $\beta_{0,r}$ and $\beta_{1,r}$ represent the region-specific regression intercept and slope terms, which are estimated within the ISAMR model and $\text{Trips}_{y,r}$ is the number of reported boat trips to sampling region r in year y. This provides the year- and region-specific sampling rate for individuals fully recruited into the fishery. All regression parameters were given normal priors, see "*Model Likelihood and Posterior Distribution*."

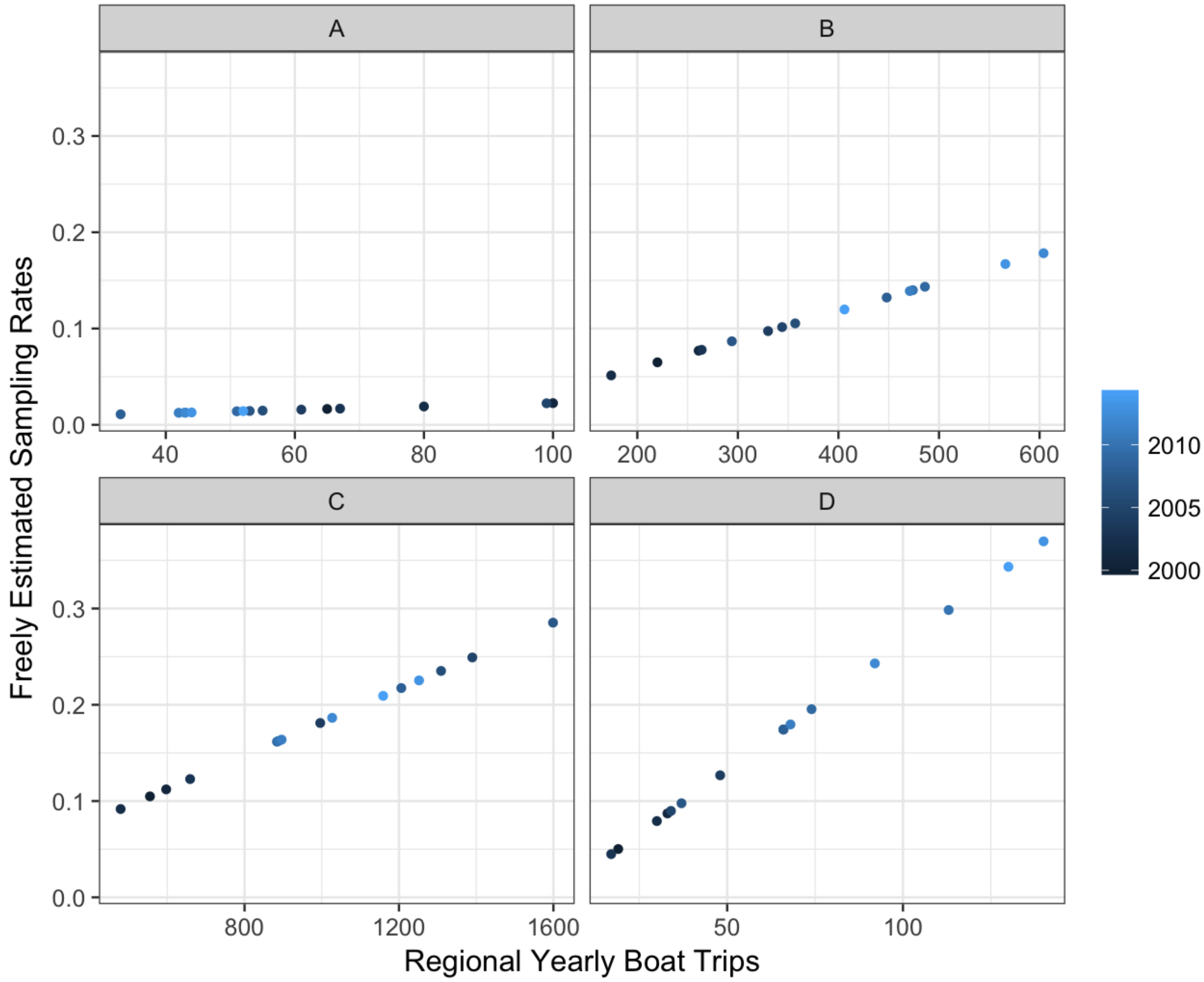

Figure B3. Comparison of freely estimated yearly regional sampling rates (estimated without information about the number of yearly regional boat trips) plotted against the number of yearly regional boat trips.

Selectivity-at-age

Individuals that are not fully recruited into the fishery can be expected to exhibit a lower sampling rate than fully recruited individuals and is herein referred to as "selectivity." Selectivity can be expected to be related to the size (i.e., length) or age of an individual sturgeon with younger sturgeon being recruited less than older, larger individuals. These differences are represented by S_a, the age-class-specific gear selectivity, which takes a value between 0 (not recruited) to 1 (full recruited). Therefore, the age-class-specific sampling rate is determined by taking the product of the regional sampling rate $\left(F_{y,r}\right)$ with the selectivity-at-age (S_a), that is:

$$F^*_{y,r,a} = F_{y,r} \times S_a.$$

This provides a unique sampling rate for each age-class, within each sampling region on each assessment year. Selectivity-at-ag (S_a) was modelled as a smooth flat-top curve (logistic curve) of the following form:

$$s_{y,a} = \frac{1}{1 + \exp\left(\frac{a_{50,y} - a}{a_{sl,y}}\right)},$$

where $s_{y,a}$ is the selectivity-at-age a in a given year, $a_{50,y}$ is the age when selectivity equals 0.5 for a given year y and $a_{sl,y}$ is the reciprocal of logistic slope in the given year.

This selectivity curve formulation was proposed by Bill Gazey after conducting an analysis in 2014 and 2015 to estimate selectivity-at-age from the sturgeon sampling data collected from 1999-2012 under the FRSCS' annual Lower Fraser River White Sturgeon Monitoring and Assessment Program (see Appendix E)

Model Likelihood and Posterior Distribution

Model Likelihood

The ISAMR joint likelihood is a composite likelihood composed of the untagged catch component (L_1) and the tagged catch likelihood component (L_2). Both components are assumed to be independent of one another and as such the full likelihood is written as:

$$L = L_1 \cdot L_2.$$

The un-tagged catch probably represents the data with the most uncertainty and as such we have opted for a flexible log catch model model to describe this component:

$$L_1 = \prod_{y=1}^{Y}\prod_{a=1}^{A}\prod_{r=1}^{R} \text{Normal}\left(\log\left(C_{y,r,a}^{\text{obs}}\right) - \log\left(C_{y,r,a}^{\text{pred}}\right), \sigma_c\right),$$

with the prior distribution on $\sigma_c \sim \text{Uniform}(0.01{,}5)$. The strong prior on the variability in log un-tagged catch was chosen to assist ADMB optimization by restricting to a more likely search space.

The Lower Fraser River White Sturgeon fishery currently has a large number of tags deployed, with currently more than 80% of the adult population tagged. Therefore, the tagged data represents a much richer data set, where a stricter model can be applied. As such, the multinomial likelihood function was chosen, where each categorical outcome is a unique age-, region-, and year-specific release and recapture event. If we let m represent all the possible unique outcomes in an experiment:

$$L_2 = \frac{C_{\text{tot}}^{T}!}{\prod c_{i!}} \prod_{i}^{m} p_i^{*C_i^T}$$

where p_i^* represents the $P(\text{return}|\text{release})$ for a given unique release and recapture event and C_i^T is the observed number of catches unique release and recapture combination and C_{tot}^T is the total tagged catch.

Posterior Distribution

The posterior distribution was implemented in ADMB by creating an objective function that combined the likelihood components with the specified priors. The posterior density is proportional to the product of the likelihood and prior components. ADMB then uses the Markov Chain Monte Carlo (MCMC) to sample from the posterior distribution using the Metropolis-Hastings algorithm to generate and accept parameter proposals. Because of the complexity of the model, MCMC chain was thinned keeping only every 900$^{\text{th}}$ proposal to remove autocorrelation in the derived abundance metric. Trace plots were used to assess convergence of MCMC chain.

APPENDIX C

DEVELOPMENT ROADMAP

During the process of transferring the ISAMR model (version 1.6) from Dr. Tom Carruthers to LGL the spring of 2016, a list of possible of short-term and long-term model fixes and extensions were identified. Short-term fixes and extensions represent relatively minor model modifications that could be carried out within a few hours to a few days. Long-term extensions represent a more substantial investment of time and effort. The current version (v2.0) addresses many of these concerns. The full list and status of each item is provided below and divided into five main section:

1. Short-term Fixes;
2. Short-term Extensions;
3. Long-term Extensions;
4. Sensitivity Analyses; and
5. Administrative.

Short-term Fixes

Final Release Events for Previously Captured Individuals

Due to a data oversight the probability of never observing a released tag was only considered for newly-tagged individuals that were never observed again. The final fate of previously-tagged individuals (i.e., after their final release, of close to 25,000 releases in total) was never considered in the model's likelihood. This oversight can be corrected with a minor revision to the code. Including these data will affect estimates of sampling rate, selectivity-at-age curves, and population estimates.

Fixed: *version 2.0*

Tagged population matrix is incremented by predicted rather than actual tagged releases

Early versions of the ISAMR model (i.e., v1.6) showed a large discrepancy in the abundance of the marked population. It was determined that this was likely the result of incrementing the tagged population matrix based on an estimated marking rate, rather than the actual number of marks deployed.

Fixed*: Version 2.0 now increments the tagged population matrix based on actual number of marks deployed. While the tagged population matrix is incremented by the actual number of marks deployed the un-tagged population matrix is decremented based on predicted marking rates rather than actual marking rates.*

Predictions of Untagged Catch do not Include the Non-Detection Rate

The non-detection rate is a user-defined parameter used to represent the probability that a PIT tag is missed during a capture event. It is currently only used in the tagging portion of the observation model, but should also be used in the untagged catch component of the model as some portion of the observed untagged catch will have been tagged and missed. Because this component is not estimated, but is user-defined, it should also be subject to a sensitivity analysis or considered for removal.

Resolved: *Version 2.0 currently forgoes use of the non-detection rate*

Standardize Aging

Currently, different implementations of the length-at-age equations are used when aging sturgeon within the ADMB model code (i.e., parameters values from Nelson et al. (2007) were used; see Appendix B2) and when aging sturgeon as part of preparing tagged and untagged data sources (i.e., parameter values from English and Bychkov (2012) were used; see ***Tagged Catch***). A single implementation should be decided on and deployed in all components.

Status: *Beyond the initial aging of sturgeon, version 2.0 only uses lengths to model survival rates using a generalized logistic regression. Small changes in the length-at-age formulae will have a small effect, this however can be updated by changing the input covariates.*

Short-term Extensions

Recruitment Deviations

Recruitment deviations in the last two years are constrained to the average recruitment deviation estimated in the preceding years. This constraint was included due to the limited recruitment information available near the end of the assessment period. The two-year window represents an arbitrary time period that could be extended further (e.g., the final 5 years). Furthermore, the fixed recruitment deviations could be set to a different average value, such as the average recruitment strength in the preceding 5 years, rather than all assessment years combined.

Completed: *Version 2.0 restricts the last 6 years of recruitment to be equal.*

Final Age Class

When an individual's age surpasses the maximum age class specified as part of the model setup, they are effectively recruited out of the fishery and are no longer tracked in the model's population matrices. The handling of the final age class should be revised to represent individuals of that age or older. This would require minor changes to the model code base. Input data would also need to be modified to reflect this change.

Completed: *Version 2.0 allows fish in the final age class to be retained replacing them in the same category at the end of each (annual) model step.*

Long-term Extensions

Estimates of Uncertainty

Model output currently does not provide estimates of uncertainty for parameter estimates. Uncertainty estimates will be necessary for model output to be used for management decisions. This may be rectified by computing standard error estimates based on the Hessian matrix provided with the ADMB model output or continuing development in order to produce Bayesian estimates.

Completed: *Version 2.0*

Model Sampling Rates as a Function of Effort

Instantaneous sampling rates can be expected to be a function of effort, however rates are currently estimated independently for each year/sampling region without consideration of effort. This represents a large number of free parameters, that could be reduced (and potential model precision improved) by modeling as a function of known sampling effort.

Completed: *Version 2.0*

Backwards Calculation of Stock Trajectory Using a Stock Reduction Analysis

The untagged population matrix was initialized based on the results of an external analysis that provides the fraction of unfished steady state recruitment represented by each age class at the start of the analysis. Ideally, this analysis should be part of the general model fitting process so that parameter estimates may inform fit. One potential avenue may be to include a stock reduction analysis as part of the analysis so that population levels prior to the commencement of the experiment are predicted and fit to the observed data.

Resolved: *Version 2.0 partially reconstructs historical population, enough to provide initialization of the assessment period population matrix.*

Directly Estimating Mortality Rate

Mark-recapture data often provides rich information on individual survival, that may be used to directly estimate mortality rates, rather than relying on a constant user specified value. The recent shift to a simpler selectivity function in the most recent iteration of the ISAMR model should also make it easier to estimate survival from the mark-recapture data.

Completed: *Version 2.0 uses a generalized logistic regression against length-at-age to model survival.*

Un-tagged population matrix is decremented by predicted mark rate

Due to the fine age and spatial structuring the number of deployed marks may exceed the estimated un-tagged subpopulation size. This will result in an error if there is even a single discrepancy in any sampling region by year-class combination. As a result, the un-tagged population matrix decremented based on predicted marking rates rather than actual marking rates. This did not appear to introduce any significant bias in simulation testing. Future implementation should consider alternative formations to avoid this problem.

***Open**: This issue has not been resolved.*

Error in Assigning Age

Currently, individuals are "aged" at the time of first capture based on the measured length at capture. This can result in aging discrepancies such as differences in known elapsed time and age based on changes in length (see Figure C1). That assigned age may be predictive of subsequent size-dependent survival, but in all likelihood it is not the correct age for assigning fish to a cohort. This means that year-class recruitment and apparent cohort sizes estimated by the ISAMR model are not number of fish recruited by cohort, but rather a smoothed or running average. Options for handling this issue could be investigated and tested. Some potential options include using broader observational categories when describing observations from younger age categories (e.g., see "*Binning of Age Classes*") or extending the likelihood to include information about ages at subsequent captures based on the elapsed time from the initial capture. It is unclear whether the second approach would add bias, as individuals only observed a few times would have less-precise aging than individuals repeatedly observed.

***Open**: This issue has not been resolved*

Temporary Emigration

A portion of Lower Fraser River White Sturgeon are suspected to leave the assessment area for extended period of time, making individuals unavailable for capture. The current model assumes live individuals are available for capture, which could result in heterogeneity in the estimates of sampling rates and selectivity-at-age. Future models could make allowances for temporary emigration by considering an additional unobservable sampling region. Movement parameters could be structured to represent a Markovian temporary migration, with probabilities for leaving the assessment area and returning to the assessment area once away.

***Open:** no work has been conducted on this topic*

Seasonality

The current formulation uses a yearly time step, and as such quantities such as sampling rates, mortality and movement represent a yearly average. Behaviour of Lower Fraser River White Sturgeon are known to differ throughout the year, similarly sampling effort is not consistent though the year as well. Moving to a seasonal time step would allow these differences to be directly modeled. For example, most sampling occurs in the summer and fall, using a two-season step (i.e., spring/winter and summer/fall) could be allow estimated sampling rates to better reflect effort. Similarly, movement, recruitment and potentially mortality could differ between these two periods.

***Open:** no work has been conducted on this topic. Very limited numbers of samples for spring/winter will make resolution of some seasonal parameters difficult.*

Traditional Jolly-Seber Recruitment

The current formulation uses a stock-recruitment relationship and recruitment deviations to estimate recruitment. If a stock-recruitment relationship is not required, the recruitment component of the model could be reformulated using a standard mark-recapture approach, such as the Jolly-Seber formulation which has been used in other age-structured mark-recapture models (e.g., Coggins et al. 2006). The advantages of this formulation are fewer underlying assumptions and a structurally simpler model, which may help in model development and when preparing peer-reviewed publications (i.e., no discussions of appropriate stock-recruitment relationships). This formulation can also be used to validate the more complicated stock recruitment version of the model and demonstrates the general modularity of the ADMB model as developed by Dr. Tom Carruthers.

Implemented: *Version 2.0 directly estimates recruitment (historical and current) in a manner that is similar in concept to the Jolly-Seber approach.*

Forecasting

The ability to forecast population trajectories beyond the assessment period would likely also be of use to managers. Currently, this can be done informally based on model output, but could also be formalized as part of the model output and processing steps.

No change: *Currently, forecasting is done manually by using the current population structure to investigate future population trajectories based on different recruitment scenarios and/or estimates of demographic processes (e.g., mortality-at-age).*

Sensitivity Analyses & Alternate Formulations

Sensitivity analyses can be used to explore how sensitive ISAMR model results are to model assumptions and specifications. The current report looked at the impact of fixing selectivity-at-age values rather than freely estimating values. Similarity other modeling components can be tested in the same manner.

Selectivity-at-age

While selectivity-at-age is estimated, the shape of the curve is fixed to be an S-shaped curve with selectivity maxing out at 1 for older age classes. This assumes that individuals are only recruited into the fishery and never out of it. Excessively large sturgeon may be less catchable by fishing gear, and as such a dome shaped selectivity curve may be more appropriate (e.g., see Thompson 1994). Data could be simulated under different selectivity curve shapes to observe the impact on ISAMR estimates.

Mortality model

The current mortality model is based on modeling survival as a generalized logistic regression against the average length-at-age. The use of two free regression parameters allowed for more flexibility in the curvature of the resulting mortality curve. A more standard fisheries implementation uses the “Lorenzen Model” (Lorenzen 2000), where the asymptotic mortality rate is estimated, but slope of curvature depends on the asymptotic mortality rate. This differs from ISAMR version 2.0 which estimates the curvature, but fixes the asymptotic mortality rate to a known value. The performance of both implementations could be tested.

The current mortality model also assumes a constant mortality-at-age across all years of interest. In addition to varying by age, mortality may also vary by year, especially for younger age classes. As such, year-to-year variation in mortality could be considered using approaches such as yearly random effects.

Tagged and un-tagged catch likelihood components

The likelihood component describing untagged catch uses a different formulation (log normal) than the tagged component (multinomial). This allows for more flexibility in the un-tagged capture component as the variance is no longer tied to the mean value as with a binomial distribution. This differs from other age-structured mark-recapture models which use independent Poisson or binomial distributions to model catch from each age class subpopulation (e.g., Coggins et al. 2006). The impact these versus more standardized formulations could be compared.

Binning of Age Classes

The observation model in the current formulation describes yearly catch from each regional subpopulation (i.e., age class), however larger observational bins (e.g., age classes: 1-5, 6-8, 9-10, 11, 12, 13, etc.) could also be considered an approach to reduce the potential effects of aging errors (see "*Error in Assigning Age*").

Administrative

Technical Debt

Technical debt is a concept in programming that reflects the extra development work that arises when code that is easy to implement in the short run is used instead of applying the best overall solution. Where possible the best overall solution was attempted when creating the supporting R code base and ADMB model, however the current version represents the product of a rapid development cycle that took the model from v1.6 to v2.0, which included some major revisions to the population model. As a result, the code contains legacies of this process that should be removed to make future development and application of the ISAMR model as straightforward as possible.

Data Simulator

The current data simulator used to test and validate the ISAMR model is based on expected values and only produces the finalized aggregate statistics that are included in the final data format inputted into the ADMB model. As such the simulator does not test the codebase used to convert the records retrieved from the FRSCS database to the final data inputted into the ADMB model (see Figure 5). While, these components were informally tested and verified in parts, it could be useful to test the entire analysis workflow to ensure no errors are present. Furthermore, the current simulator does not yet include a variable effort component (ISMAR model validations were based on constant sampling effort), so further work on the data simulator is required. Ideally, a second implementation should be created based on simulating the life histories of individual sturgeon. This would allow records in the FRSCS database to be directly simulated, allowing all components in the analysis chain to be tested. Furthermore, by formulating a data simulator in this manner the robustness of the ISAMR model can be tested against un-modeled components, such as individual variability in mortality, movement, selectivity, and impacts of temporary emigration out of the assessment area. This would allow for a more in-depth assessment of the weaknesses and strengths of the ISAMR model.

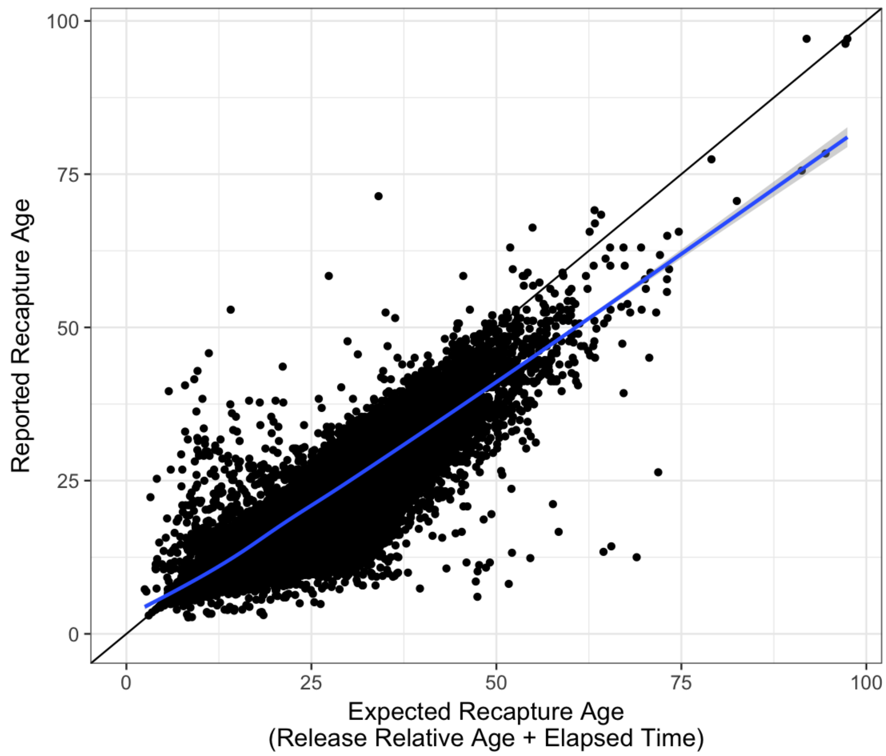

Figure C1. Reported recapture age based on relative length aging and expected age based on elapsed time since release. Solid black diagonal line indicates a 1:1 relationship, blue line indicates regression estimate with 95% confidence bounds.

APPENDIX D
ADMB DATA INPUT FILE SPECIFICATION

The data input file for the ISAMR ADMB model in plain text where model input data are specified in serial ordering (Table D1). Note that several input data items can be considered optional, devalued, or in some instances obsolete. Because the ADMB has strong restrictions on input data, the model needs to be modified and recompiled to change any of the data input specifications. Removal of devalued and obsolete input data falls under technical debt in the development roadmap (see Appendix C).

Table D1. ISAMR v2.0 specification for input data file.

Input	**Type**	**Dimensions**	**Description**
ny	integer	1 x 1	Number of assessment years
na	integer	1 x 1	Number of age classes
nr	integer	1 x 1	Number of sampling regions
nMP	integer	1 x 1	Number of movement parameters to estimates
fullmov	logical	1 x 1	Indicates wither to use full Markov movements (1) or gravity model (0).
Mcv	real	1 x 1	No longer used - standard deviation of the lognormal prior for M
Ccv	real	1 x 1	No longer used - standard deviation of the lognormal catch observation
PRM	real	1 x 1	Not implemented - Post Release Mortality
NDR	real	1 x 1	Not implemented - Non-Detection Rate
L_age	vector	1 x na	fixed length-at-age relationship
W_age	vector	1 x na	No longer used - fixed weight-at-age relationship
mat_age	vector	1 x na	No longer used - fixed maturity-at-age relationship
sel_age	matrix	ny x na	fixed selectivity-at-age values. Specification is required but values are only used if fixed selectivity values are specified.
steep	real	1 x 1	No longer used - steepness of the stock-recruit relationship
initdep	real	1 x 1	No longer used - initial level of stock depletion
nrel	integer	1 x 1	Number of aggregated untagged capture records.
ncap	integer	1 x 1	Number of records of aggregated tagged captures.
nnocap	integer	1 x 1	Number of records of aggregated tagged releases without recapture.
rel	matrix	nrel x 4	Aggregate summary of un-tagged captures (Rel_Y, Rel_A, Rel_R, N).
cap	matrix	ncap x 6	Aggregated summary of tagged release and recapture events in the assessment period (Rel_Y, Rel_A, Rel_R, Cap_Y, Cap_R, N).
nocap	matrix	nnocap x 4	Aggregated summary of final release of tagged fish within the assessment period (Rel_Y, Rel_A, Rel_R, N).
movini	matrix	nr x nr	Debugging mode – fixed movement probabilities to use in debugging.
SMini	matrix	ny x nr	Debugging mode – fixed movement probabilities to use in debugging.
recdevsini	vector	1 x ny	No longer used – fixed recruitment deviation values to use

Input	Type	Dimensions	Description
			in debugging.
R0ini	real	1 x 1	No longer used - fixed unfished recruitment value to use in debugging.
selpars	vector	1 x 2	Not implemented - fixed selectivity parameters to use for model initialization.
SMcv	real	1 x 1	No longer used - sampling rate prior standard deviation
SMmu	real	1 x 1	No longer used - sampling rate prior mean value.
Movcv	real	1 x 1	Prior on S.D. of log movement parameters.
Tagged	3d array	ny x na x nr	Aggregate summary of tagging events.
notagrate	3d array	ny x na x nr	No longer used – proportion of un-tagged captures released without a tag.
verbose	integer	1 x 1	0-2 indicating amount of information to display during fitting.
nselpars	integer	1 x 1	Number of selectivity parameters to estimate.
selblocks	vector	1 x 1	Indicates which years share the same selectivity values (i.e., selectivity epochs).
eff	matrix	ny x nr	Number of boat trips by year and sampling region.
year_start	integer	1 x 1	Calendar year of the first year in the assessment period.
data_ver	integer	1 x 1	Date stamp indicating the version of the analysis data.
datacheck	integer	1 x 1	Known value used to confirm that data was read in correctly.

APPENDIX E

SELECTIVITY CURVE ESTIMATION (GAZEY 2014/2015)

This appendix provides a summary of analyses conducted by William Gazey in 2014 and 2015 to estimate selectivity-at-age from the sturgeon sampling data collected from 1999-2012 as part of the PIT tag mark-recapture program.

Inspection of Catch Data

Length frequencies from Lower Fraser River White Sturgeon caught from 1999 through to 25 Feb 2013 were determined using the von Bertalanffy growth equation,

$$a = \frac{-1}{K} \cdot \log\left(1 - \frac{L}{L_\infty}\right)$$

where a is the age at capture, L is the length at capture, K is the von Bertalanffy coefficient and L_∞ is the asymptotic length. The least squares estimates ($\widehat{K} = 0.0288$, $\widehat{L_\infty}$=344) from English and Bychkov (2012) were used to generate catch frequencies by age class (see Figure E1).

Fitting Catch Curves

A linearized catch curve was created by log transforming catch frequencies (Figure E2) was done using all available years, and by epochs, where mortality or gear selectivity was thought to have changed. The linearized portion of the curve results from constant mortality rates combined with constant gear selectivity. Deviations from a straight line may be the result in differences in gear selectivity or mortality rates.

By inspection it was assumed individuals age-16 and older were fully recruited to the fishing gear and showed constant mortality until at least the mid-fifties age class (Figure E2). In older age classes, the linear relationship showed some signs of breaking down potentially due to lack of data, or due to lengths approaching L_∞. As such, analyses only considered portions of the curve that were clearly linear. Catch curves were also created under two potential epochs (1999-2004 and 2005-2012). A straight line regression curve was fitted to the linear portion of all three catch curves (Figure E3) in order to determine linear regression parameter estimates (Table E1) required to predict theoretical catches frequencies for earlier age classes.

Fitting Selectivity Curves

Assuming constant mortality rate in earlier age classes, the estimated catch curves were used to predict the catch frequencies for earlier age classes (Table E2 and Table E3). Differences between the observed and predicted catch frequencies for earlier age classes (i.e., age 2-16) were interpreted as resulting from younger age classes being less “catchable” by fishing gear than older age classes and is herein refered to as “selectivity.” When individuals become fully recruited by fishing gear, selectivity will equal unity.

Observed selectivity for age 2-16 sturgeon was determined as the ratio of the observed catch frequency to the predicted catch frequency (i.e., exponentiation the difference in observed and predicted log catch frequencies; Table E2 and Table E3). Plotting the observed selectivity values against the age class (Figure E4) indicated selectivity followed a logistic curve of the form:

$$s_{a,y} = \frac{1}{1 + \exp\left(\frac{a_{50,y} - a}{a_{sl,y}}\right)},$$

where where $s_{y,a}$ is the selectivity-at-age a in a given year, $a_{50,y}$ is the age when selectivity equals 0.5 for a given year y and $a_{sl,y}$ is the reciprocal of logistic slope in the given year.

The observed selectivity values were fit to the logistic selectivity curve using non-linear least squares, using the `nls` function in R (R Core Team 2016). Estimated selectivity parameters (Table E1) resulted in a noticeably different selectivity curve for the 1999-2004 epoch (Figure E4).

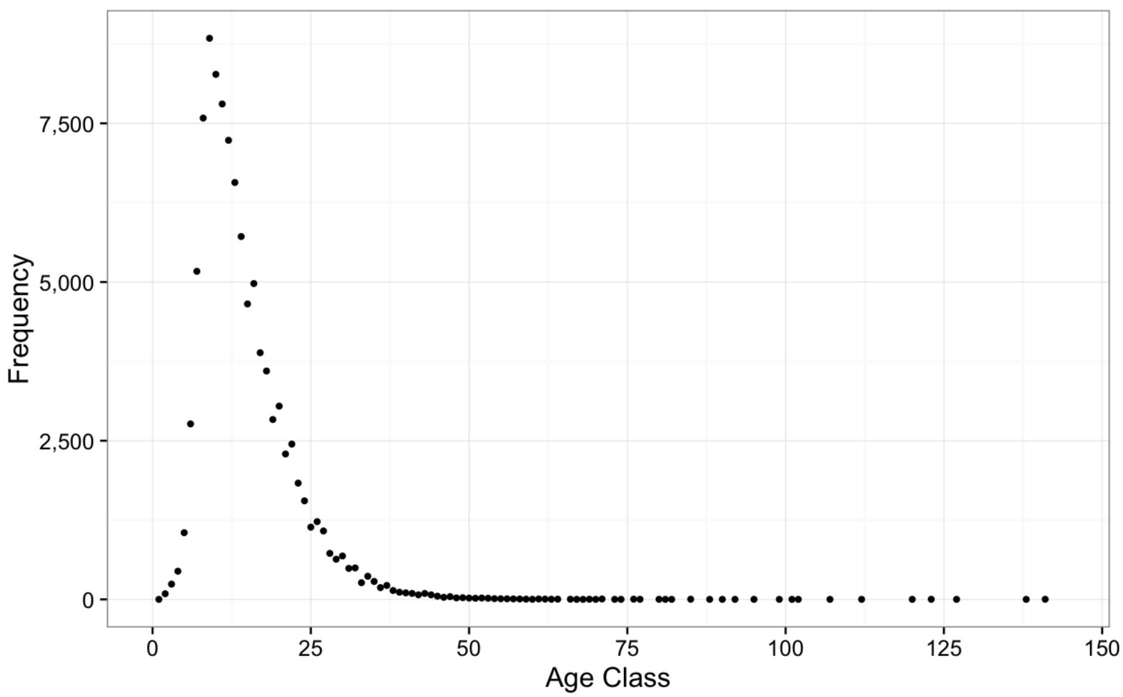

Figure E1. Catch frequency by age class for all sturgeon caught between 1999 and 2012.

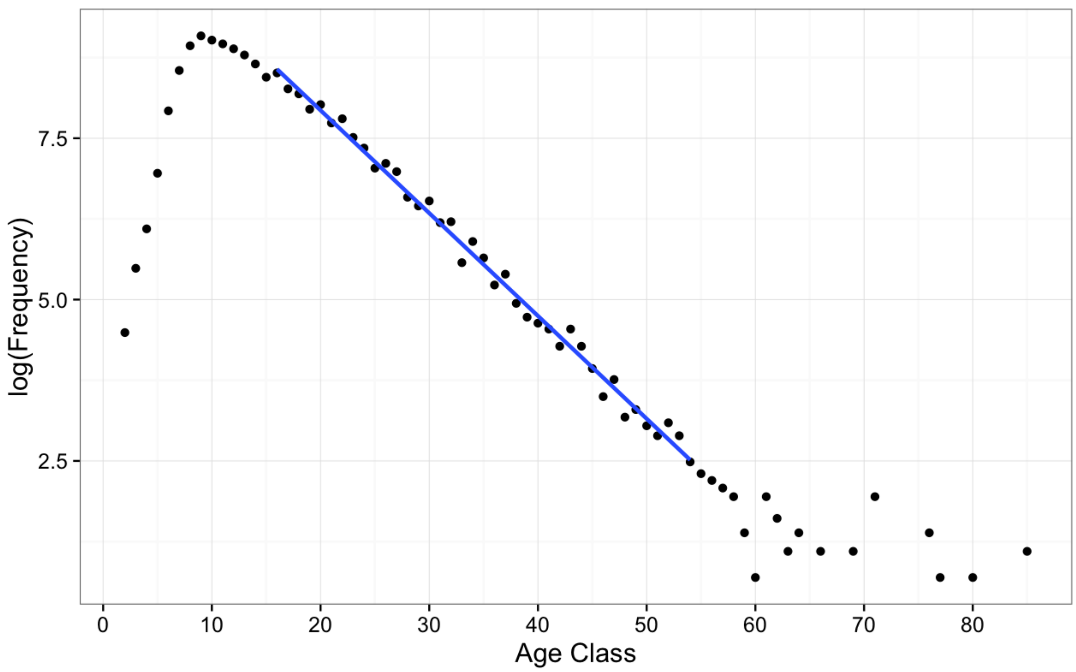

Figure E2. Linearized catch curve using log transformed catch frequencies of all captures from 1999 through to 2012.

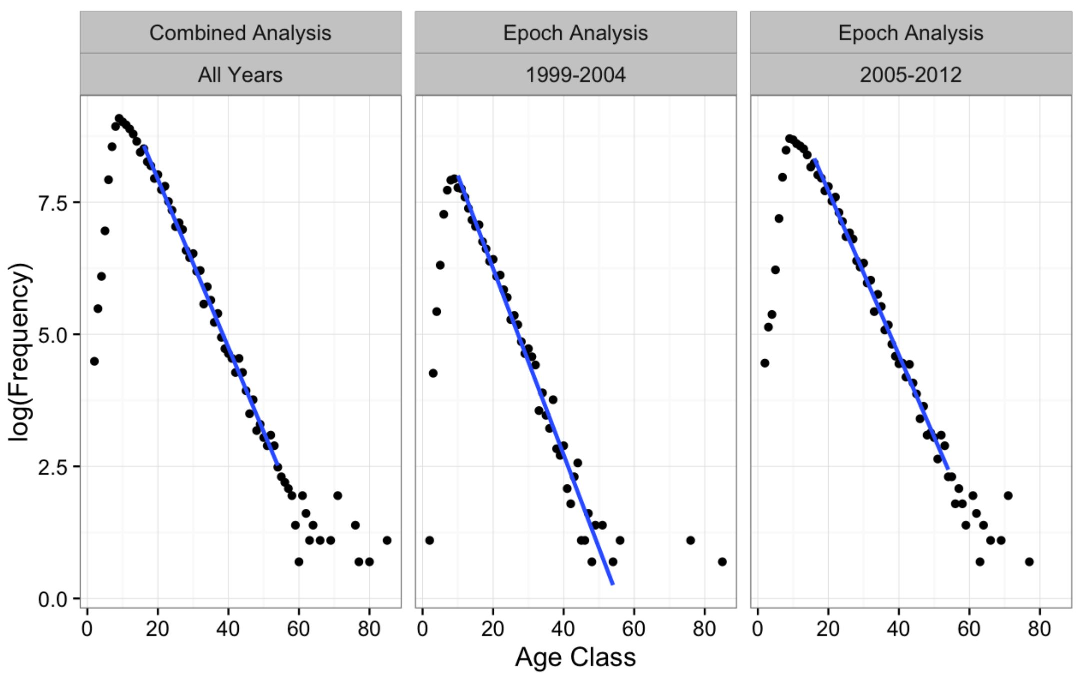

Figure E3. Linearized catch curve analyses based on all available years, or by epoch (1999-2004 and 2005-2012).

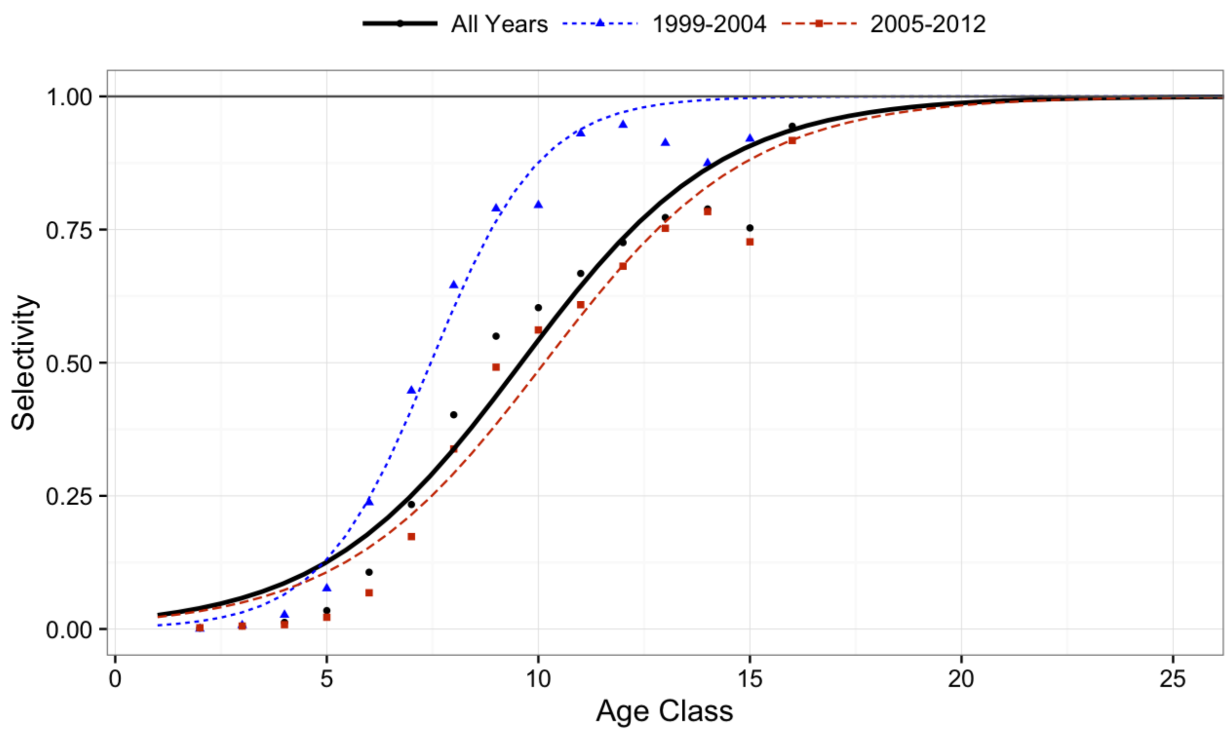

Figure E4. Estimated selectivity curves based on all available data (1999-2012) or by epoch (1999-2004 and 2005-2012).

Table E1. Summary of analysis data and results from the catch curve and selectivity curve analyses

		Catch Curve Analysis				**Selectivity Curve Analysis**			
Analysis	**Years**	**Age Class**	**Parm.**	**Estimate**	**SE**	**Age Class**	**Parm.**	**Estimate**	**SE**
All Years	1999 - 2012	16-54	Intercept	11.12	0.08	2-16	a_{50}	9.60	0.29
			Slope	-0.16	0.002		a_{sl}	2.37	0.27
Epoch	1999 - 2004	10-54	Intercept	9.76	0.129	2-16	a_{50}	7.46	0.29
			Slope	-0.18	0.004		a_{sl}	1.30	0.17
	2005 - 2012	16-54	Intercept	10.81	0.088	2-16	a_{50}	10.14	0.28
			Slope	-0.16	0.002		a_{sl}	2.42	0.26

Table E2. Observed and fitted values from the catch and selectivity curves for analyses using all years of data (1999-2012).

Age Class	Catch Curve[1]		Selectivity Curve	
	Observed	**Predicted**	**Observed**	**Fitted**
2	4.49	10.80	0.002	0.039
3	5.48	10.64	0.006	0.058
4	6.10	10.48	0.012	0.086
5	6.96	10.32	0.035	0.126
6	7.92	10.16	0.107	0.180
7	8.55	10.00	0.234	0.251
8	8.93	9.84	0.402	0.338
9	9.09	9.69	0.550	0.437
10	9.02	9.53	0.603	0.542
11	8.96	9.37	0.668	0.644
12	8.89	9.21	0.726	0.734
13	8.79	9.05	0.773	0.808
14	8.65	8.89	0.789	0.865
15	8.45	8.73	0.753	0.907
16	8.51	8.57	0.944	0.937

[1] Catch curve results are presented as log(frequency).

Table E3. Observed and fitted values from the catch and selectivity curves for analyses fit separately to the 1999-2004 and 2005-2012 epochs.

	Epoch: 1999-2004				**Epoch: 2005-2012**			
	Catch Curve[1]		**Selectivity Curve**		**Catch Curve[1]**		**Selectivity Curve**	
Age Class	**Obs.**	**Fitted**	**Obs.**	**Fitted**	**Obs.**	**Fitted**	**Obs.**	**Fitted**
2	1.10	9.41	0.000	0.015	4.45	10.50	0.002	0.033
3	4.26	9.24	0.007	0.031	5.14	10.34	0.005	0.050
4	5.43	9.06	0.026	0.065	5.38	10.19	0.008	0.073
5	6.31	8.88	0.076	0.131	6.22	10.03	0.022	0.107
6	7.27	8.71	0.238	0.245	7.19	9.88	0.068	0.153
7	7.73	8.53	0.447	0.413	7.97	9.72	0.173	0.215
8	7.92	8.36	0.645	0.603	8.48	9.57	0.338	0.292
9	7.94	8.18	0.789	0.767	8.70	9.41	0.492	0.384
10	7.77	8.00	0.796	0.877	8.68	9.26	0.561	0.485
11	7.75	7.83	0.930	0.939	8.61	9.10	0.609	0.588
12	7.60	7.65	0.946	0.971	8.56	8.95	0.681	0.683
13	7.38	7.47	0.912	0.986	8.51	8.79	0.752	0.765
14	7.16	7.30	0.875	0.994	8.39	8.64	0.784	0.831
15	7.04	7.12	0.920	0.997	8.16	8.48	0.727	0.881
16	7.07	6.95	1.134	0.999	8.24	8.33	0.917	0.918

[1] Catch curve results are presented as log(frequency).

APPENDIX F

RAW INPUT DATA FORMATS

The full list of raw input data is available in Table 1. Below are example records of un-tagged captures released without a mark (Table F1), marked releases with a recapture (Table F2), newly marked releases without a recapture (Table F3), user-supplied selectivity-at-age overrides (Table F4), and regional boat trips (Table F5). These raw input files are then used to create the aggregate tables inputted into the ADMB model (Appendix G).

Table F1. Example records of individuals caught un-tagged and released un-tagged within the assessment period.

Rel_Date	Rel_Zone	Rel_Age
30/05/2000	A	6.0
05/06/2000	B	4.9
07/06/2000	B	5.9
⋮	⋮	⋮

Note: Release events contain details on the date, zone and relative age. These records are then aggregated before inclusion into the model as a component of the total un-tagged captures (Table G1). No unique individual identifiers are included in this raw input data.

Table F2. Example data showing individual release/recapture event records for tagged releases with a subsequent recapture event within the assessment period.

PIT_tag	*Rel_Date*	*Rel_Zone*	*Rel_Age*	*Recap_Date*	*Recap_Zone*	*Recap_Age*
0A1309313	04/10/2011	C	16.3	27/10/2013	C	19.4
0A1309313	13/04/2012	D	33.3	10/05/2013	D	34.1
0A1309313	10/05/2013	D	34.1	20/07/2013	D	34.3

Note: Fields associated with the release events use the "*Rel_*" prefix, while recapture events contain the "*Recap_*" prefix. Release and recapture events contain details on the date, zone and relative age. These records were then aggregated before inclusion into the model as a component of the total un-tagged captures (Table G1) and marked releases with a recapture (Table G2). The oldest record for each PIT tag is also used in summary of the final releases (Table G3). PIT tag codes are unique to each individual.

Table F3. Example data showing individual release event records for newly marked releases without a subsequent recapture event within the assessment period.

PIT_tag	*Rel_Date*	*Rel_Zone*	*Rel_Age*
0A1309313D	27/07/2012	A	14.3
0A1309313F	25/09/2011	C	15.2
0A13093140	27/09/2011	C	12.5
⋮	⋮	⋮	⋮

Note: Release events contain details on the date, zone and relative age. These records were then aggregated before inclusion into the model as a component of the total untagged catch (Table G1) and newly marked releases without recaptures (Table G3). PIT tag codes are unique to each individual.

Table F4. Example data showing selectivity-at-age overrides for the assessment period.

$y = 1$	$y = 2$	...	$y = Y$
0.000	0.000	...	0.000
0.006	0.006	...	0.019

⋮	⋮	...	⋮
1.00	1.00	...	1.00

Note: User-supplied selectivity values must range from 0 to 1, with rows indicating age class values (A rows in total) for each assessment year (Y columns in total).

Table F5. Example data showing the regional boat trip records, by season, year, and sampling region.

Yr	*Season*	*RegionL*	*BoatTrips*
1999	Fall	A	24
1999	Fall	B	2
1999	Fall	C	47
⋮	⋮	⋮	⋮

Note: Recorded boat trips primarily include the recreational fishery and the Albion test fishery.

APPENDIX G

AGGREGATED DATA INPUTTED INTO ADMB

The raw input data is then aggregated by the R codebase (Figure 5) into frequency data for inclusion in the ADMB data input file. These aggregates include the total number of un-tagged captures (Table G1), total number of marked releases with a recapture (Table G2), final releases (Table G3) and total boat trips by year and sampling region (Table G4). Raw input data used by the R codebase can be found in Appendix F.

Table G1. Example of aggregated number of the total number of individuals caught without a tag, used by the untagged catch component of the ISAMR model.

Rel_Y	*Rel_A*	*Rel_R*	*N*
2	4	1	2
7	4	1	1
10	4	1	1
⋮	⋮	⋮	⋮

Note: Tabulated output indicates that *N* release events occurred (i.e., tagged and untagged) where an individual of age *Rel_A* was released in year *Rel_Y*, in sampling region *Rel_R*. Source data includes records individuals caught and released without a tag (Table F1), as well as the first record for tagged releases with a recapture (Table F2) and all records for newly marked releases that were never again observed (Table F3).

Table G2. Example tabulated output of for marked release recapture events with subsequent recaptures within the assessment period.

Rel_Y	*Rel_A*	*Rel_R*	*Cap_Y*	*Cap_R*	*N*
2	7	1	2	1	1
1	8	1	2	1	1
2	8	1	2	1	5
⋮	⋮	⋮	⋮	⋮	⋮

Note: Tabulated output indicates that *N* release events existed where a fish of age *Rel_A* was captured and released (with a tag) in assessment year *Rel_Y* in sampling region *Rel_R* where the next capture event occurred in assessment year *Cap_Y* in sampling region *Cap_R*. Data source is all records of marked individuals with a recapture (Table F2).

Table G3. Example of tabulated output for the final release events of marked individuals.

Rel_Y	*Rel_A*	*Rel_R*	*N*
15	4	1	2
2	5	1	2
3	5	1	6
⋮	⋮	⋮	⋮

Note: Tabulated output indicates that *N* release events existed where a fish of age *Rel_A* was captured and released (with a tag) in assessment year *Rel_Y* and sampling region *Rel_R*, but was not recaptured again within the remainder of the assessment period. Data sources the final recapture event for marked releases with a recapture (Table F2) along with all records for newly marked releases without a recapture (Table F3)

Table G4. Example of tabulated yearly regional boat trips (i.e., effort) directly used by the ISAMR model.

Y	*R*	*E*
1	1	65
1	2	220
1	3	555
⋮	⋮	⋮

Note: Tabulated output indicates the total number of boat trips, *E*, that occurred in sampling region *R* in assessment year *Y*. Data source is the number of boat trips by year, season and region (Table F5).

APPENDIX H

EXAMPLE MODEL FIT DIAGNOSTICS

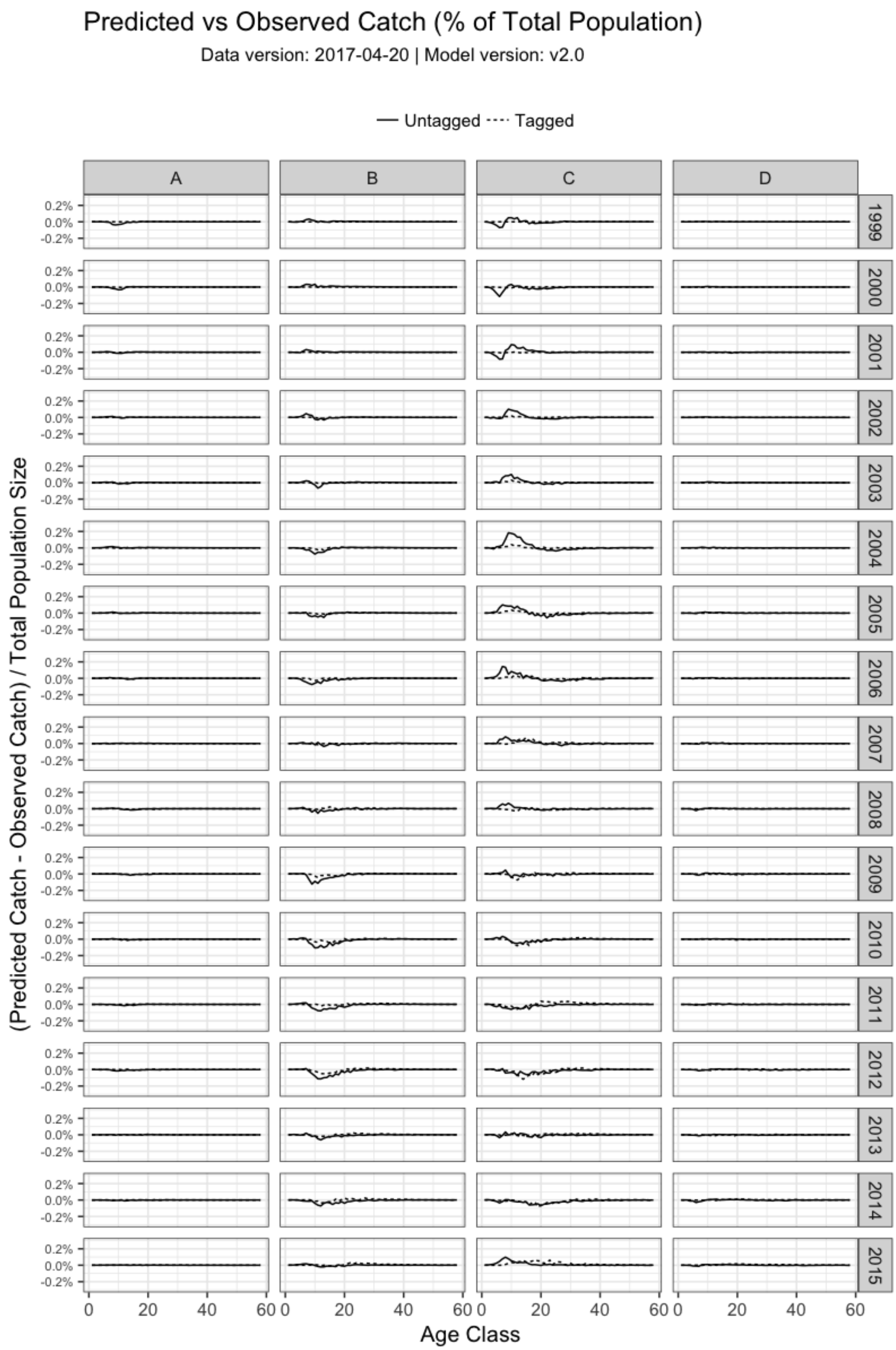

Figure H1. Example diagnostic plot that shows the raw discrepancy between observed and predicted catch for the un-tagged and tagged populations as a percentage of the total population estimate.

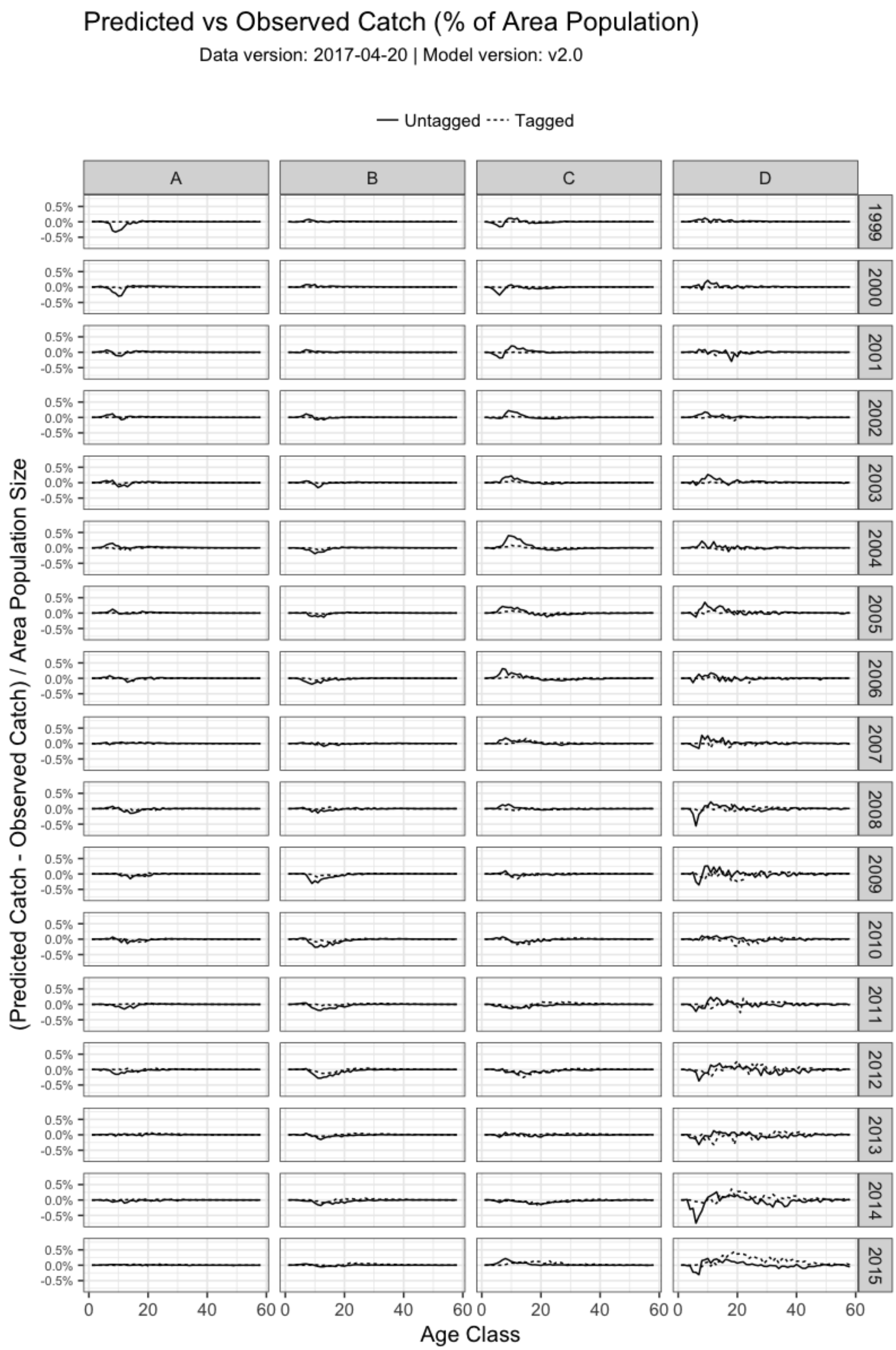

Figure H2. Example diagnostic plot showing the discrepancy between observed and predicted catch for the un-tagged and tagged populations as a percentage of the regional population estimate.