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Incorporating intra-annual variability in fisheries abundance data to better capture population dynamics

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ABSTRACT

To reduce the risk of overexploitation and the ensuing conservation and socio-economic consequences, fisheries management relies on receiving accurate scientific advice from stock assessments. Biomass dynamics models used in stock assessment tend to rely primarily on indices of abundance and commercial landings data. Standard practice for calculating the indices used in these models typically involves taking averages of survey tow data over large, diverse spatial domains. There is a lot of variability in the choice of methodologies used to propagate index uncertainty into the assessment model, many of which require specifying it through expert knowledge or prior distributions. Here we propose an alternative approach that treats each individual survey tow as an independent estimate of the true underlying biomass in the stock assessment model itself. This reduces information loss and propagates uncertainties into the model directly. A simulation study demonstrates that this approach accurately captures underlying population dynamics and reliably estimates variance parameters. We further demonstrate its utility with data from the Inshore Scallop Fishery of south-west Nova Scotia. Results show significant improvements in parameter estimation over previous models while providing similar predictions of biomass with less uncertainty. This reduced uncertainty can improve the resulting scientific advice and lead to improved decision-making by fisheries managers.

1. Introduction

Fisheries scientists have long used statistical models to quantify population status and associated demographic variability in harvested populations. Typically, the primary goal of these models is to estimate population parameters to help provide reliable science advice for fisheries management. The scientific advice provided must be as accurate as possible to lower the risk of overexploitation or implementation of undue socio-economic restrictions. This risk is exemplified by numerous examples of stocks which have collapsed despite the use of complex assessment techniques and detailed scientific advice (e.g. Northern cod (*Gadus morhua*) in Hutchings and Myers, 1994; Myers et al., 1996). To this end, much effort has gone into creating stock assessment frameworks capable of accounting for multiple sources of uncertainty (e.g.

Schnute and Richards, 1995; Aeberhard et al., 2018).

State-space models (SSMs) are one such framework: they are able to account for both measurement error, which occurs in the observation of data, and process error, which comes from the imperfect knowledge of the underlying dynamical processes of interest (De Valpine, P, 2002; Cressie et al., 2009; Aeberhard et al., 2018). These models can be built to account for noisy data (e.g. Punt et al., 2000), complex non-linear population dynamics (e.g. Froese, 2006; Linton and Bence, 2008) and non-Gaussian distributions (e.g. Martin et al., 2005; Cressie et al., 2009), all of which are common with fisheries data. Estimation frameworks for SSMs, traditionally difficult to fit in practice, have become more easily accessible through innovations facilitating the approximation of intractable integrals. Multiple approaches have been developed, such as Bayesian methods usually involving Markov Chain Monte Carlo

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(MCMC) (Meyer and Millar, 1999; Linton and Bence, 2008), and frequentist methods employing automatic differentiation and the Laplace approximation (Skaug and Fournier, 2006; Kristensen et al., 2016). These approaches have been used extensively when incorporating traditional stock assessment models into SSM frameworks (e.g. Nielsen and Berg, 2014; Smith et al., 2017; Pedersen and Berg, 2017).

Biomass dynamics models are a common type of stock assessment model used by fisheries scientists (Hilborn, 1992). Requiring only an index of population abundance and commercial landings, their implementation in SSM frameworks has led to their widespread use (e.g. Smith and Hubley, 2014; Xu et al., 2019; Best and Punt, 2020). A common example is the delay-difference model, developed to be a compromise between intractably complex models and overly simplistic ones (Deriso, 1980; Schnute, 1985). However, since biomass dynamics models use relatively few inputs, it is imperative that these inputs be reliable and that their uncertainty is quantified.

These models tend to utilize two different types of data as part of their indices: fishery-dependent (e.g. commercial landings, fishing log-books, etc) and fishery-independent (e.g. surveys) data. Although significant work often goes into developing better methods to obtain reliable indices, such as stratification approaches and sampling designs for survey data (e.g. Smith, 1996; Kimura and Somerton, 2006) or improved estimates from fishery-dependent sources (Harley et al., 2001; Maunder and Punt, 2004; Maunder et al., 2006b), the uncertainty around them is often specified or approximated using prior assumptions (e.g. Smith and Lundy, 2002; Winker et al., 2020) or simply estimated

using expert judgement (e.g. Cook, 2013; Nielsen and Berg, 2014; Yin et al., 2019). Additionally, the data used to generate the indices for these models contain a wealth of information that is obscured or aggregated during the development of a population index. Somewhat surprisingly, there has not been a great deal of research attempting to quantify how directly incorporating individual observations (e.g. survey tows) into existing model frameworks would impact the model inference.

To directly utilize individual survey observations stock assessment SSMs must be modified to deal with a common difficulty associated with these types of data: zero inflation. This can be achieved through the use of delta distributions, wherein the probabilities of zero catches and positive ones are modeled separately before being combined to obtain the final estimates (Stefánsson, 1996; Martin et al., 2005; Thorson et al., 2015). This type of approach has recently been used to obtain reliable indices of abundance (Kimura and Somerton, 2006; Thorson et al., 2015), but incorporation of this approach directly into a biomass dynamics model has not been thoroughly explored.

This work aims to demonstrate how to incorporate fishery-independent survey data directly into an SSM in order to reduce the information loss associated with traditional indices that aggregate data spatially. Referred to as the Tow-Level Model (TLM), we modify the SSM proposed in (Yin et al., 2019) for the Inshore sea scallop (*Placopecten magellanicus*) fishery, Scallop Production Area 3 (SPA 3), Nova Scotia, Canada, to directly incorporate individual survey tow data. We undertake a simulation study to explore the estimability and identifiability of TLM. We then fit TLM to SPA 3 and compare its parameter estimates to

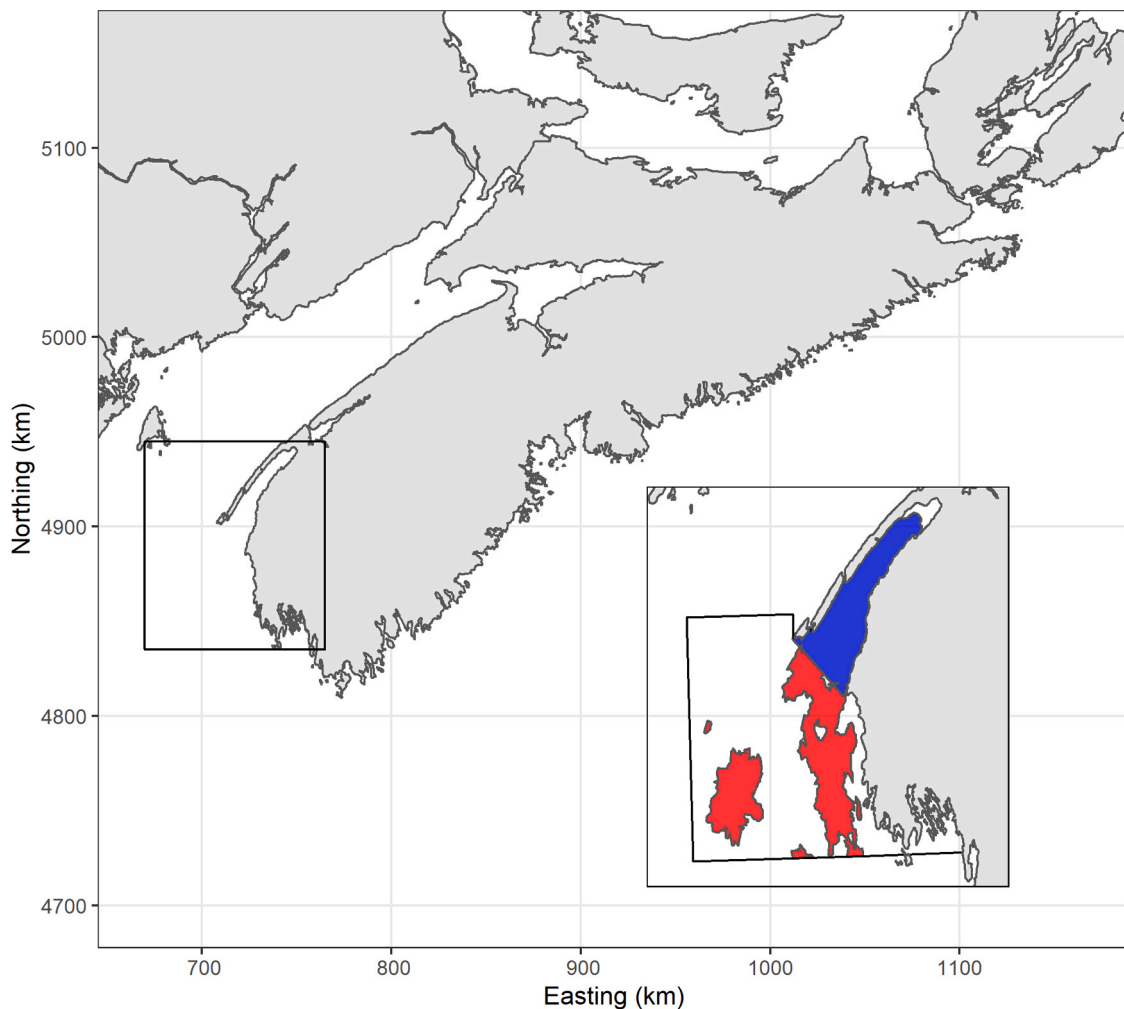


Fig. 1. Map of Nova Scotia with Scallop Production Area 3 (SPA 3) inset. Black borders represent management borders of SPA 3, red represents the Inside VMS stratum and blue represents the St-Mary's Bay stratum.

those obtained with the current operational model by Fisheries and Oceans Canada (DFO) (referred to as the Aggregated Index Model (AIM)) (Nasmith et al., 2016). Finally, we compare the predictions of the underlying processes (commercial size biomass, recruit biomass and instantaneous natural mortality) and associated uncertainties.

2. Implementation

2.1. Data

DFO conducts annual scallop surveys in SPA 3, which is a scallop management area in the Bay of Fundy, Canada (Fig. 1). The number of tows per year ranges from 100 to 162 during the study period (1997–2018). This area is spatially heterogeneous and has historically been challenging to model, as exemplified by the 2012 restratification of the area to strata based on fishing effort as a proxy for habitat (Nasmith et al., 2016). DFO uses a stratified random sampling design where the sample size in a given strata is proportional to its area. There are 3 strata: the St. Mary's Bay stratum, the Inside VMS stratum, and the Outside VMS stratum (Fig. 1; Nasmith et al., 2016). The area is managed using a Total Allowable Catch (meats) which is informed based on the operational model used by DFO.

At sea, all live and dead scallops (clappers: dead scallops whose shells are still hinged) are counted and sorted into 5 mm bins. Commercial size scallops are defined as having shell heights greater than or equal to 80 mm, and recruits are those between 65 mm and 79 mm, which are expected to grow to be commercial size the following year. Clappers are used to obtain an estimate of instantaneous natural mortality and only commercial size clappers are included in the model. A subset of live scallops (3 per 5 mm bins that are 50 mm and larger) is dissected in order to record their individual shell height and meat weight (weight of the adductor muscle, Glass, 2017). A linear model based on a cube law (Froese, 2006) with depth as a covariate is fitted to these data in order to estimate the commercial and recruit biomass per tow. The start and end position of each tow are recorded at sea using the commercial vessel navigational system Olex AS (Olex marine survey and navigation, www.olex.no); survey catches are standardized to 800 m length x 5.334 m width.

The operational population model currently used by DFO considers only two stratum: St. Mary's Bay and the Inside VMS strata (Fig. 1, Nasmith et al., 2016). Annual survey indices of commercial biomass, recruit biomass, commercial numbers, and clapper numbers, corresponding to the modelled area are calculated by obtaining the means per tow for both the St. Mary's and Inshore VMS strata, then scaling up to the respective stratum by multiplying the mean value by the number of towable units (number of tows that would be necessary to cover the whole stratum), and then the totals for St. Mary's Bay and the Inside VMS strata are added together. All landings are 100% dockside monitored and commercial landings are obtained from individual commercial logbooks. All commercial landings are assumed to come from the St. Mary's Bay and Inside VMS strata, an assumption supported by previous analyses (Nasmith et al., 2016).

Alternatively, each individual survey tow can be considered as a separate observation. Only data from St. Mary's Bay and the Inside VMS strata are used, and are treated as if from a single combined stratum. The observed commercial biomass and recruit biomass in each tow are multiplied by the number of towable units in the total modelled area. In this way, each individual tow can be thought of as a replicate of the traditional single index of abundance.

2.2. Models

State-space models (SSMs) are hierarchical models defined by two stochastic processes: \mathbf{X}_t , $t = 1, \dots, T$, representing the unobserved dynamic state process (e.g. that describing the real population dynamics) at discrete time-steps t , and the observation process \mathbf{Y}_t , $t = 1, \dots, T$,

which links the observations to the true underlying dynamic processes of interest (Aeberhard et al., 2018). Model parameters are combined in a p -vector $\theta \in \Theta \subseteq \mathbb{R}^p$, and fixed covariates are indicated by \mathbf{z}_t .

θ is considered a vector of fixed effects and $\mathbf{X}_{1:T}$ a vector of random effects predicted from estimates of θ . These variables can be combined into the following joint likelihood $L(\cdot)$ and marginal log-likelihood $\mathcal{L}(\cdot)$:

$$L(\theta, \mathbf{Y}_{1:T}, \mathbf{X}_{1:T}) = p(\mathbf{Y}_1 | \mathbf{X}_1, \theta) \prod_{t=2}^T p(\mathbf{Y}_t | \mathbf{X}_t, \theta) p(\mathbf{X}_t | \mathbf{X}_{t-1}, \theta) \quad (1)$$

$$\mathcal{L}(\theta, \mathbf{Y}_{1:T}) = \log \int L(\theta, \mathbf{Y}_{1:T}, \mathbf{X}_{1:T}) d\mathbf{X}_{1:T} \quad (2)$$

Approximations for these high-dimensional integrals are obtained using the Laplace method as implemented in the TMB package in R (Kristensen et al., 2016). TMB's use of automatic differentiation has been shown to be computationally more efficient than most other packages without loss of accuracy (Kristensen et al., 2016; Auger-Méthé et al., 2017). Nomenclature follows the style of (Yin et al., 2019), where $\overset{Ind}{\sim}$ indicates that the data are independently distributed and $u/N(\sigma^2)$ describes a lognormal distribution with $\mathbf{mean} = \mathbf{0}$ on the log scale and variance σ^2 on the log scale.

2.2.1. TLM

Our TLM represents the population dynamics of sea scallops through the following equations:

$$B_t = [\exp(-m_t)g_{t-1}(B_{t-1} - C_{t-1}) + \exp(-m_t)g_{t-1}^R R_{t-1}] \tau_t \quad (3)$$

$$R_t = R_{t-1} \phi_t, \quad \phi_t \overset{Ind}{\sim} u/N(\sigma_\phi^2) \quad (4)$$

$$m_t = m_{t-1} \eta_t, \quad \eta_t \overset{Ind}{\sim} u/N(\sigma_\eta^2) \quad (5)$$

where $\tau_t \overset{Ind}{\sim} u/N(\sigma_\tau^2)$ for $t = 2, \dots, T$. Eq. 3 moves the underlying scallop biomass in year $t - 1$, B_{t-1} , to year t by removing the commercial landings C_{t-1} , adjusting for instantaneous natural mortality m_t , growth g_{t-1} and recruitment where R_{t-1} represents the recruits surviving to time $t - 1$ and g_{t-1}^R their growth rate. This is a simplification of the delay-difference model (Deriso, 1980; Schnute, 1985), originally presented in Smith and Lundy (2002) and more recently described in Nasmith et al. (2016). While the growth rates are usually obtained as part of the model itself, we instead use direct estimates. These are based on the ratios between the observed average meat weight of commercial size scallop in a given year and in the following year (see Nasmith et al., 2013 for details). Equation 4 and 5 allow some temporal dependency in the recruitment and mortality processes. No distributions were assumed for the initial states of all 3 processes (B_1 , R_1 and m_1) and they were instead left free to vary based on the observations.

The following equations connect the underlying population dynamics to the observations:

$$I_{i,t} = \frac{q_I B_t}{p_I} \epsilon_{i,t}, \quad \epsilon_{i,t} \overset{Ind}{\sim} u/N(\sigma_\epsilon^2) \quad (6)$$

$$I_{i,t}^R = \frac{q_R R_t}{p_I^R} v_{i,t}, \quad v_{i,t} \overset{Ind}{\sim} u/N(\sigma_v^2) \quad (7)$$

$$L_{i,t} \overset{Ind}{\sim} \text{Binomial}(n_{i,t}, m_t S) \quad (8)$$

where Eq. 6 links the observed survey commercial size scallop biomass $I_{i,t}$ in tow i at time t , $t = 1, \dots, T$ to the underlying population biomass B_t by adjusting for commercial size catchability q_I and the probability of observing a non-zero survey tow, p_I . Using the delta approach, p_I is assumed to follow a binomial distribution based on the number of tows with positive commercial size scallop catches. $\epsilon_{i,t}$ is a lognormal error term with associated variance parameter σ_ϵ^2 . Eq. 7 follows a similar approach, replacing each term with their recruit

equivalent so that $I_{i,t}^R$ is the observed survey recruit biomass in tow i at time t , R_t is the underlying recruitment, q_R is the recruit catchability, p_i^R is the probability of positive recruit catches and $v_{i,t}$ is a lognormal error term with associated variance σ_v^2 . p_i^R is also assumed to follow a binomial distribution based on the number of tows with positive recruit scallop catches. Eq. 8 links the number of clappers in a given tow $L_{i,t}$ to instantaneous natural mortality m_t scaled by clapper catchability S using a binomial distribution based on the total number of live scallops plus clappers caught $n_{i,t}$. This approach assumes that the ratio of clappers to clappers plus live scallops is a proxy for the instantaneous natural mortality i.e., the probability of death of any individual scallop, instead of a proxy for the cumulative mortality over the previous year. $p_l, p_l^R, q_l, q_R, \text{ variances } \sigma_{\epsilon,t}^2 \text{ and } \sigma_v^2, \text{ and } S$ are parameters to be estimated from the data. The observations are assumed to be independent from one another under these equations.

In summary, TLM contains the observed states $\mathbf{Y}_t = (I_t, I_t^R, L_t)^T$, the unobserved states $\mathbf{X}_t = (B_t, R_t, m_t)^T$, the fixed covariates $\mathbf{z}_t = (N_t, C_t, g_t, g_t^R)^T$ and the parameters $\theta = (p_l, p_l^R, q_l, q_R, S, \sigma_{\epsilon,t}^2, \sigma_v^2, \sigma_{\tau}^2, \sigma_{\phi}^2, \sigma_{\eta}^2)^T$.

2.2.2. AIM

AIM utilizes a Bayesian framework which incorporates prior knowledge (such as expert opinion and historical experience) (Meyer and Millar, 1999) through what are known as prior distributions $\pi(\theta)$. The full model formulation is described in Yin et al. (2019). A Markov Chain Monte Carlo (MCMC) algorithm, which samples from the posterior distribution for the purpose of inference (Best and Punt, 2020), is used to fit AIM in R using the WinBUGS package (Lunn et al., 2000). The population dynamics are captured in the following way:

$$\frac{B_t}{K} = [\exp(-m_t)g_{t-1} \frac{B_{t-1} - C_{t-1}}{K} + \exp(-m_t)g_{t-1}^R \frac{R_{t-1}}{K}] \tau_t \quad (9)$$

Here, $\tau_t \sim \text{Ind} u/N(\sigma_{\tau}^2) \mathbf{1}_{[0,8]}$ for $t = 2, \dots, T$. K is a scaling parameter, while $\mathbf{1}_{[a,b]}$ is an indicator function indicating censoring within interval $[a, b]$. Both are present for numerical stability and to facilitate convergence (Yin et al., 2019). B_1 is specified as $B_1/K \sim u/N(\sigma_{\tau}^2)$. All other variables are identical to those of TLM.

There are no underlying process equations for recruitment R_t and instantaneous natural mortality m_t . Instead, both the ratio R_t/K and m_t are assumed to be independently and identically distributed (i.i.d.) following log-normal distributions with mean -1.9 and variance 2 on the natural logarithm scale. The following equations connect the underlying population dynamics to the observations:

$$I_t = qB_t \epsilon_t, \quad \epsilon_t \sim \text{Ind} u/N(\sigma_{\epsilon,t}^2) \quad (10)$$

$$I_t^R = qR_t R_t v_t, \quad v_t \sim \text{Ind} u/N(\sigma_{v,t}^2) \quad (11)$$

$$L_t = m_t S (\frac{S}{2} N_{t-1} + (1 - \frac{S}{2}) N_t) \kappa_t, \quad \kappa_t \sim \text{Ind} u/N(\sigma_{\kappa}^2) \quad (12)$$

Both commercial size and recruit indices are linked to their respective processes by a single catchability parameter q . For recruits, this catchability is adjusted by r_t , which is the ratio of commercial size scallops caught in lined and unlined survey drags with the lined gear meant to capture recruits. Furthermore, the variances for both equations $\sigma_{\epsilon,t}^2$ and $\sigma_{v,t}^2$ are allowed to vary through time because of the availability of survey coefficients of variations (CVs) used in the prior distributions (Yin et al., 2019). A single index per year is used.

Equation 12, called the ‘‘popcorn’’ model (Smith and Lundy, 2002), links the clapper index L_t to the live scallop index N_t and instantaneous natural mortality m_t using parameter S , which represents the average hinge separation time in years for a clapper (known as dissolution rate) instead of a simple catchability as in Equation 8. Equation 12 assumes a fixed lifespan for clappers (see Smith and Lundy, 2002 for details).

In summary, AIM contains the observed states $\mathbf{Y}_t = (I_t, I_t^R, L_t)^T$, the unobserved states $\mathbf{X}_t = (B_t, R_t, m_t)^T$, the fixed covariates $\mathbf{z}_t = (N_t, C_t, g_t, g_t^R, r_t, CV_{\epsilon,t}, CV_{v,t})^T$ and the parameters $\theta = (K, q, S, \sigma_{\epsilon,t}^2, \sigma_{v,t}^2, \sigma_{\kappa}^2, \sigma_{\tau}^2)^T$. Identifiability issues exist for AIM, wherein priors intended to be non-informative have a strong impact on the model output, which motivated its reformulation using a frequentist framework as proposed by Yin et al. (2019).

2.3. Simulation Study

Five simulation experiments were conducted to assess the estimability and identifiability of TLM with the focus on parameter estimation and random effects prediction. Both data simulation and model fitting were performed using TMB. The first simulation experiment estimated q_l . To assess how much of the uncertainty in the predicted processes was related to the variance parameters and how much to the catchability parameters, the second experiment informed q_l using a beta distribution. These first two simulations spanned 22 years (the same time length as the SPA 3 data). To see if the length of the time-series was impacting parameter estimation, a third simulation experiment mimicked the first but extended the data to 50 years. Finally, to test the effect of higher variances, a fourth experiment mimicked the second (informing q_l) but increased the observation variances by an order of magnitude while a fifth experiment did the same for the process variances. Table 1.

Eqs. 3 to 8 were used to simulate $\mathbf{Y}_{1:T}$ and $\mathbf{X}_{1:T}$ 1000 times. g_t and g_t^R were fixed at 1.1 and 1.5 in every year t , values that are very close to the mean values in this area, the number of tows n_t^{tows} was set to 100 every year, and the total number of live scallops and clappers caught ($n_{i,t}$) in every tow was simulated from a Poisson distribution with $\lambda = 100$. B_1 was set to 1000 metric tonnes, R_1 was set to 100 metric tonnes and m_1 was set at 0.1.

Commercial landings C_t were simulated from a log-normal distribution with a mean of 20% of B_t in every year and a variance of 0.1 on the log scale. Simulating the commercial catch as a direct proportion of the biomass avoids the possibility of simulating negative biomass, which is a common issue with these type of models (Yin et al., 2019; Best and Punt, 2020).

The true values for the parameters θ and the starting values are provided in Table 2. Starting values for the random effects were 2000 metric tonnes for B_b , 200 metric tonnes for R_t and 0.3 for m_t . The maximization of the likelihood was performed using the quasi-Newton optimizer *nlmminb* in R. The beta distribution used to inform q_l in experiments 2, 4 and 5 had its shape parameters set at 10 and 12 (generalized from the distribution used in assessments for the inshore fishery, see Yin et al., 2019). For experiment 4, the true values of σ_{ϵ} and σ_v are increased to 1, while for experiment 5 the same is done for σ_{τ} and σ_{ϕ} . Due to the use of log-normal random walks, the simulated processes tended to decrease over time (Lewontin and Cohen, 1969). This was not an issue for the commercial size and recruit biomass, since simulated populations only reached unrealistic numbers on much longer time-scales (over 100 years), but was more difficult for the instantaneous natural mortality which sometimes rapidly decreased to a very small value when larger variances were tested. Due to this, the simulation value for σ_{η} was fixed at 0.1 for all settings. Code for all simulations is available upon request.

Table 1
Simulation experiments.

Experiment	q_l estimation	Time-Series Length	Observation Variance	Process Variance
1	Free	22 Years	Low	Low
2	Informed	22 Years	Low	Low
3	Free	50 Years	Low	Low
4	Informed	22 Years	High	Low
5	Informed	22 Years	Low	High

Table 2
Parameters used for first three simulation experiments and their starting values.

Parameter	True Value	Starting Value
σ_τ	0.1	exp(-1)
σ_ϕ	0.1	exp(-1)
σ_η	0.1	exp(-1)
σ_e	0.1	exp(-1)
σ_v	0.1	exp(-1)
q_I	0.4	exp(-1)
q_R	0.2	exp(-1)
S	0.6	exp(-1)
p_I	0.8	0.5
p_I^R	0.4	0.5

2.4. Application

To compare parameter estimates and predictions, both the TLM and AIM were fitted to SPA 3 data from St-Mary's Bay and the Inside VMS stratum. TLM was fitted twice, once freely estimating q_I and once informing q_I with the same beta distribution as for the simulations. This distribution is a slightly modified version of the one used in the current assessment, itself based on experiments regarding gear efficiency (Smith et al., 2012). To further test its flexibility, TLM was fitted to all of the data from SPA 3 (see Supplementary Materials). Since detailed commercial logbook data are only available from 1998 onwards, the models were fitted to data from 1997–2018. AIM was fitted using the custom DFO R package SSModel, which uses WinBUGS (Lunn et al., 2000), while TLM was fitted using the Template Model Builder (TMB) package in R. Optimization starting values are provided in Table 2 and random effects starting values set to $10 * \max(I_{i,t})$ for B_v , $10 * \max(I_{i,t}^R)$ for R_t and 0.3 for m_t . As indicated above, TLM assumes that the survey tows are independent. While the delay-difference equation should account for temporal correlations, this approach is unable to account for spatial correlation. The use of a stratified random sampling design, if the strata are appropriate, should help compensate for this potential issue. To examine how appropriate this assumption is, one-step prediction residual plots as described in Thygesen et al. (2017) are calculated using the *oneStepPredict* function in TMB for all three types of observations.

3. Results

3.1. Simulation

Over 96% of simulations converged for all 5 experiments (see Column 1 of Table 3). Almost all variance parameters were captured with a very high accuracy for all experiments without affecting the estimability of other parameters (see Supplementary materials). The only exceptions are σ_τ and σ_ϕ in experiment 4 where they are sometimes estimated arbitrarily close to zero (usually when the simulated data are variable to the point of being unrealistic).

Informing q_I through a beta distribution (Experiments 2, 4, and 5) substantially improves both its own estimability and that of q_R , removing the density at 0 for both, and has no visible impacts on the estimability of other parameters (see Fig. 2). This indicates that a single assumption about q_I can result in more accurate and precise estimation

Table 3
Number of simulations that converged, gave false convergence, gave singular convergence, or failed to converge.

Experiment	Convergence	False Convergence	Singular Convergence	Failed to converge
1	999	0	1	0
2	1000	0	0	0
3	1000	0	0	0
4	967	24	0	9
5	960	0	4	36

in TLM. If q_I is misspecified in the prior distribution, the model tends to move to this incorrect value (see Supplementary Materials). Histograms of parameter estimates for individual experiments are available in the supplementary materials.

The predicted underlying biomass has minimal bias and improved accuracy when q_I is informed, with over 98.5% of the predictions being at most 31% away from the simulated value in experiment 4 and even more precise in experiment 2 and 5. (Fig. 3). S and q_R are generally underestimated, and there is a strong correlation between instantaneous natural mortality and recruitment estimates (e.g. $r = 0.718$ in experiment 2). These results are indicative of confounding between the estimate of recruitment and instantaneous natural mortality. However, the model is able to reliably capture their combined effect since the consistent biases in both these processes do not lead to biased biomass predictions (Fig. 3).

3.2. Application

Both TLM and AIM successfully converged when fitted to data from the modelled area. Furthermore, TLM also successfully converged for the entirety of SPA 3 (see Supplementary Materials). Estimates for the few directly comparable parameters were very similar (see Table 4). The standard error of σ_τ is more than 3 times lower when estimated by TLM than AIM, indicating substantially less uncertainty in the estimated patterns of population biomass change. Informing q_I increases its estimate from 0.24 to 0.43 in comparison to when it is freely estimated, and its standard error declines from 145% to 25% of the point estimate. It also reduces the standard error of q_R but does not impact any other parameter (Table 4). Residual plots generally do not raise any concerns regarding model assumptions, although a spatial pattern in the biomass residuals is present in years where part of the areas were not sampled (see Supplementary materials).

The 95% confidence intervals for the biomass obtained from TLM (prediction ± 1.96 standard error) are 6.7% smaller on average than the 95% credible intervals from AIM (Fig. 4). The uncertainty declines despite the much larger uncertainties around the recruitment and instantaneous natural mortality estimates in TLM; this aligns with the behavior of these estimates observed in the simulation experiments. The TLM biomass predictions are on average 11% below the estimates from the AIM model and the maximum difference in any year was 32%. The overall trends for the TLM model were always within the 95% credible interval of the AIM model. These similarities arise despite the significant reduction in the number of parameter constraints in TLM (1 vs dozens for AIM).

4. Discussion

There are traditionally two main areas of focus around biomass dynamics models. To improve assessment advice, the focus is often on creating the best possible index using survey stratification, sampling designs or novel modelling approaches (Chyan-Huei Lo et al., 1992; Smith, 1996; Kimura and Somerton, 2006; Kotwicki et al., 2014; Nasmith et al., 2016), or to explore demographic parameters of the stock assessment model itself (e.g. catchability) with little attention paid to the model indices (Wilberg et al., 2010; Pedersen and Berg, 2017). While understanding both of these aspects is essential for reliable stock assessment, the disconnect between the two has resulted in overlooking an alternative model formulation. Here we demonstrate that using tow-level data directly improved the model fit and lowered the uncertainty for the biomass predictions and several key parameters, while drastically reducing the number of assumptions required by AIM (i.e. informative priors and fixing the parameters for the distributions of recruitment and instantaneous natural mortality).

TLM was able to reliably predict biomass and track biomass changes over time without the use of an aggregated index. The TLM biomass predictions had less uncertainty than the existing stock assessment

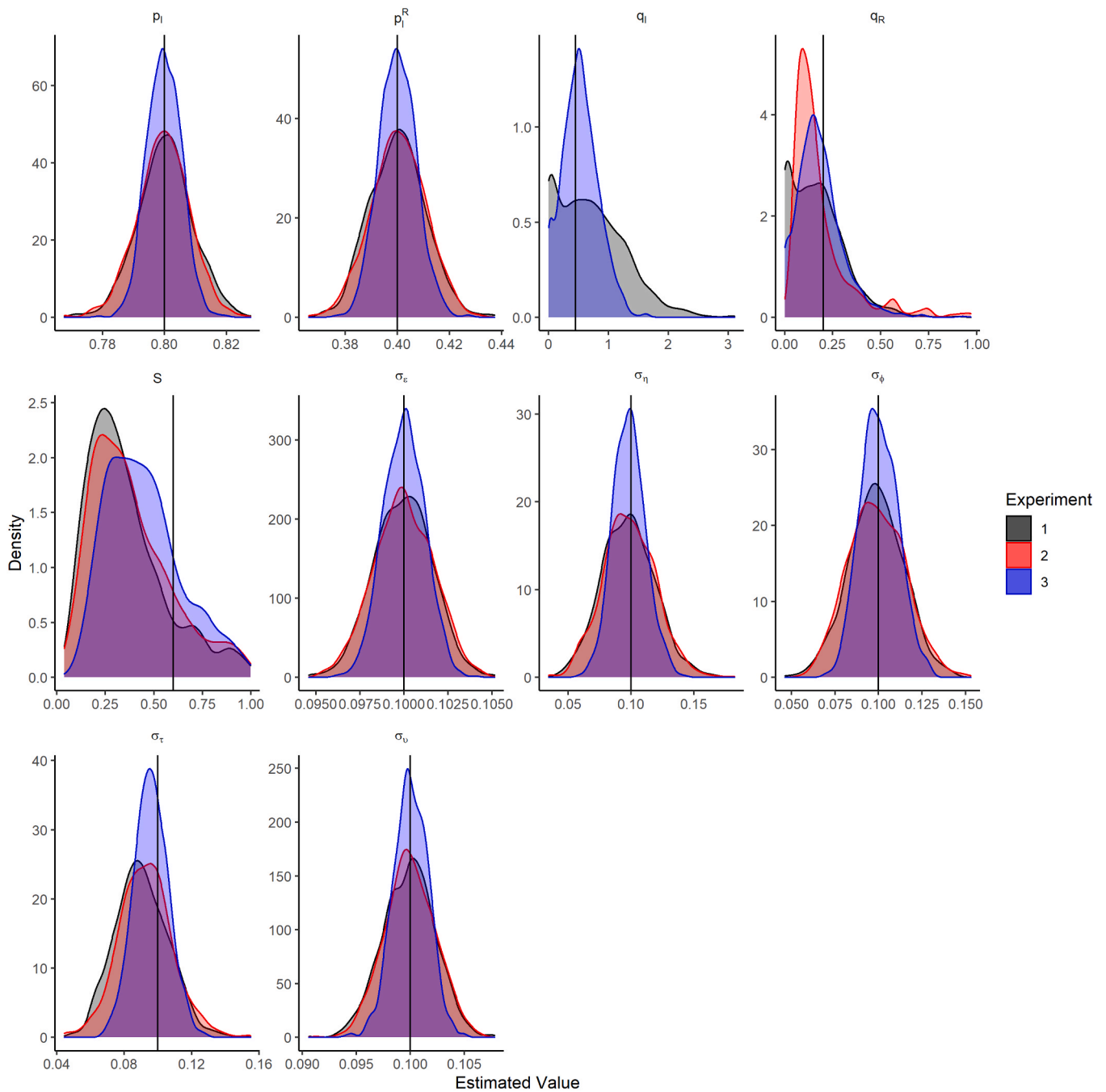


Fig. 2. Density plots of parameter estimates from first three simulation experiments (black line denotes true value). Estimates of S larger than 1 and estimates of q_l for experiment 2 are not shown.

model while capturing the temporal dynamics observed in the area. Furthermore, the combined effect of recruitment and instantaneous natural mortality was well captured in both the simulations and the case study. This conceptually straightforward modification to a traditional delay difference stock assessment model improved estimation and prediction, maintained the advantages traditionally associated with these models and avoided the separation of the stock assessment models and their indices. Furthermore, the apparent difficulties related to catchability parameters, recruitment and instantaneous natural mortality wherein they are estimated with very large standard errors were unrelated to the incorporation of tow-level data, but were instead related to the removal of strict assumptions implicitly used in AIM.

Our approach was able to propagate uncertainties directly from the raw data into the final model outputs while accounting for zero-inflation

and providing results in line with the operational stock assessment all while using a single informative prior distribution in q_l . In comparison, AIM required dozens of prior distributions (a number of which are informative or semi-informative) and an expected mean level for both the instantaneous natural mortality and recruitment. The simulation study confirmed the accuracy of the relative biomass predictions while clearly demonstrating the ability of TLM to capture the relative overall productivity, despite some confounding between recruitment and instantaneous natural mortality. Incorporating all of these processes inside a unified framework strengthens the confidence in the model predictions and should improve the science advice provided to managers.

This state-space hierarchical framework has widespread applicability since its only requirement for implementation is that the stock

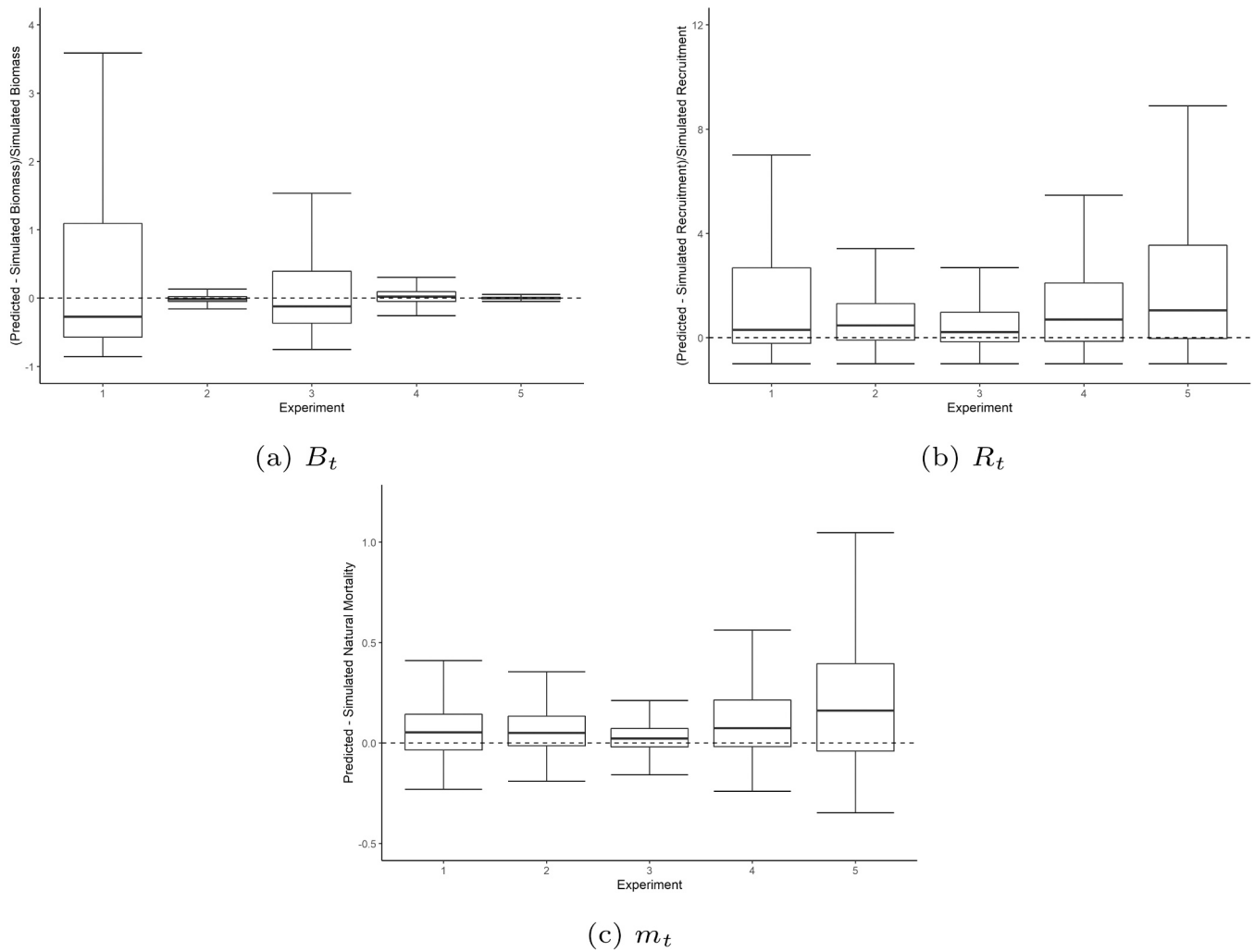


Fig. 3. Tukey boxplots of the difference between the predicted process and the true value for all 5 experiments (outliers not shown for visual clarity). B_t and R_t are shown as a percentage of the true value, while m_t is the point-wise difference.

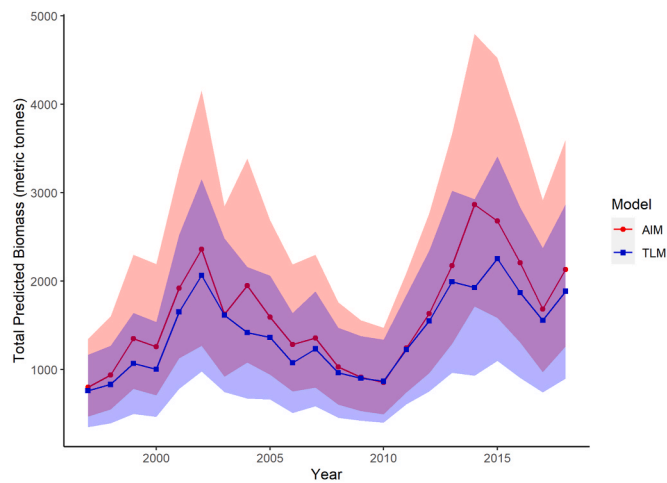
Table 4

Parameter estimates for AIM and TLM fitted to SPA 3 (standard error in parentheses). TLM was fitted twice, once freely estimating q_I and once constraining it with a beta distribution.

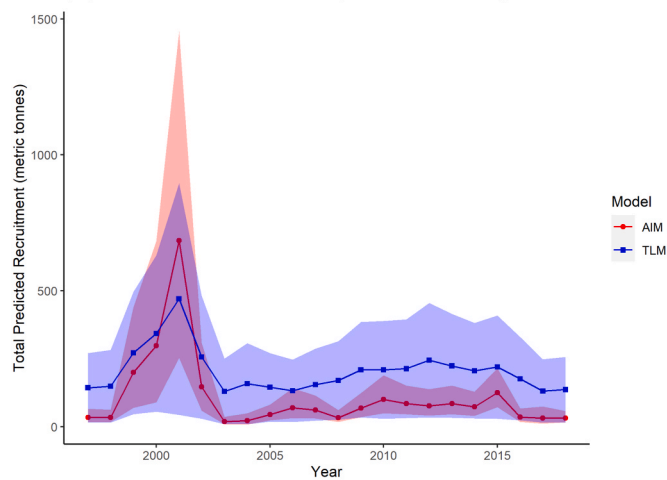
AIM		TLM		TLM (q_I informed)	
Parameter	Estimate	Parameter	Estimate	Parameter	Estimate
K	663.902(20.190)	σ_τ	0.213(0.058)	σ_τ	0.215(0.058)
q	0.328(0.083)	σ_ϕ	0.340(0.082)	σ_ϕ	0.337(0.081)
S	0.265(0.067)	σ_η	0.661(0.095)	σ_η	0.661(0.095)
σ_c	0.291(0.065)	σ_e	0.991(0.019)	σ_e	0.991(0.019)
σ_τ	0.246(0.188)	σ_o	1.065(0.028)	σ_o	1.066(0.028)
		q_I	0.240(0.342)	q_I	0.424(0.104)
		q_R	0.051(0.054)	q_R	0.066(0.027)
		S	0.220(0.099)	S	0.221(0.101)
		p_I	0.920(0.007)	p_I	0.921(0.007)
		p_I^R	0.497(0.013)	p_I^R	0.497(0.013)

assessment model utilizes indices. While the strata and stratified random sampling design (Nasmith et al., 2016) of SPA 3 appear to successfully help TLM overcome potential correlations between observations that are not incorporated (e.g. spatial correlations), modelling areas with less appropriate survey designs may prove problematic. However, this approach could easily be extended for almost any general case, including more difficult situations where a survey design does not account for correlated observations. For example, instead of modifying a

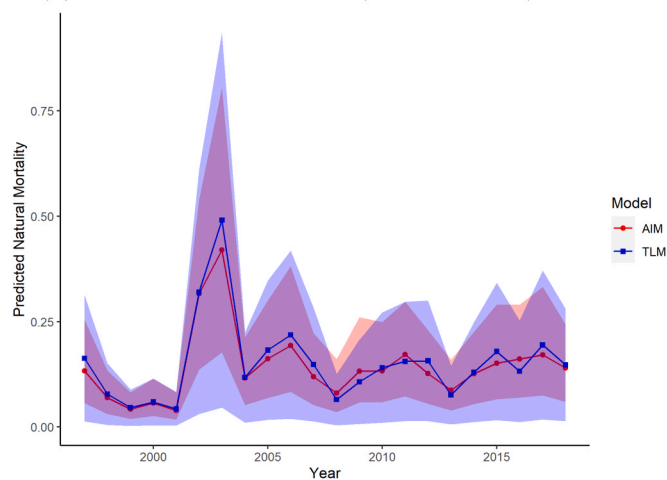
model that utilizes design-based indices (Smith, 1996; Nasmith et al., 2016), model-based methods to index standardization (e.g. Maunder et al., 2006a; Kotwicki et al., 2014) could replace the current observation equations and directly propagate uncertainties from these sub-models to the final stock assessment model outputs to account for correlated observations. Overall, the direct incorporation of tow-level data within a stock assessment model could be extended to virtually any type of stock assessment model that tends to aggregate information



(a) Predicted Biomass (metric tonnes)



(b) Predicted Recruitment (metric tonnes)



(c) Predicted Instantaneous Natural Mortality

Fig. 4. Predicted processes for the SPA 3 scallop data from AIM (red) and TLM (blue) when q_I is informed. Envelopes represent interpolated point-wise 95% credible intervals and 95% confidence intervals respectively.

prior to the modelling exercise. These models would inherently incorporate temporal and spatial patterns of population productivity.

One of the currently underutilized sources of information present in datasets used for fishery assessments are the locations of individual observations. Methods to incorporate spatial and spatio-temporal information have recently been developed to improve survey indices (e.g. Thorson et al., 2015), biomass predictions (e.g. Cadigan et al., 2017) and understanding of biological drivers (e.g. Pedersen et al., 2018) in relation to fisheries. A spatial pattern in the residuals is present in some years (see Supplementary Materials). While it is possible that this is caused by the lack of data in St. Mary's Bay in the early years, it also suggests that the inclusion of spatial structure could be of some benefit for this model. To build on the approach presented in this study, and in the broad move towards an ecosystem approach to fisheries (Ruckelshaus et al., 2008; Guo et al., 2019), future work could explicitly model these locations to get at the latent spatial information contained within them. This could implicitly capture the spatial variability in productivity due to environmental and ecological processes in which the population lives without requiring additional (expensive) data collection.

Since many management approaches to fisheries, from ecosystem-based multispecies approaches (Ruckelshaus et al., 2008) to the use of biological reference points (Caddy and Mahon, 1995; Shertzer et al., 2010), rely on models that accurately capture true population trends, the unbiased biomass predictions with reduced uncertainty in final predictions inherently lowers the risk associated with any decision-making process. This modelling framework demonstrates how stock assessments can better harness existing data in a simple and straightforward manner even in the presence of significant variation. Our approach enables the expansion of existing models to account for variability and zero-inflation, avoid averaging, and improves our ability to track changes in populations over time without requiring new investments in sampling intensity or the development of new conceptual tools. This approach has the potential to decrease uncertainty and subsequently increase the confidence that managers and stakeholders have in the science advice provided by these modelling frameworks, ultimately leading to better decision making in support of long-term sustainable fisheries.

CRediT authorship contribution statement

Raphael R. McDonald: Conceptualization - Methodology - Software - Validation - Formal analysis - Investigation - Data curation - Writing – original draft - Writing – review & editing - Visualization. David M. Keith: Conceptualization - Validation - Resources - Data curation - Writing – review & editing - Funding acquisition. Jessica A. Sameoto: Conceptualization - Resources - Data curation - Writing – review & editing - Project administration - Funding acquisition. Jeffrey A. Hutchings: Writing – review & editing- Writing – review & editing - Supervision. Joanna Mills Flemming: Conceptualization - Validation - Resources - Writing – review & editing - Supervision - Project administration - Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.fishres.2021.106152](https://doi.org/10.1016/j.fishres.2021.106152).

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