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An age- and length-structured statistical catch-at-length model for hard-to-age fisheries stocks

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Abstract

It is challenging in fisheries stock assessment to estimate cohort dynamics from length-based data for hard-to-age stocks, and existing approaches, for example, age-structured catch-at-length models (ACL) are unable to account for length-dependent processes within each cohort. Fisheries-dependent data are usually considered the default input to stock assessment models. However, with widespread recognition of the uncertainty of fisheries-dependent data and the increasing availability of high-quality survey data, a new situation emerges in some fisheries where a stock assessment model based only on survey data can provide good estimation of population dynamics. We develop an age- and length-structured statistical catch-at-length model (ALSCL) to estimate age-based dynamics from survey catch-at-length data. This approach also provides a good basis to then integrate fisheries-dependent data in the model. ALSCL can explicitly include length-dependent mortality and growth within each cohort by simultaneously tracking the three-dimensional dynamics across time, age, and length. We first use simulations of yellowtail flounder (*Limanda ferruginea*, Pleuronectidae) and bigeye tuna (*Thunnus Obesus*, Scombridae) to demonstrate that ALSCL outperforms ACL by providing more accurate estimates of age-based population dynamics when length-dependent processes are important. Next, we apply ALSCL to estimate the cohort dynamics of female yellowtail flounder on the Grand Bank off Newfoundland using survey catch-at-length, weight-at-length, and maturity-at-length data. We consider ALSCL as a hybrid between ACL and length-structured stock assessment models that keeps the advantages of both, and its ability to simultaneously track age and length dynamics is an important step toward the next-generation of fisheries stock assessment models.

KEYWORDS

age and length structured, length-based data, length-dependent mortality, next-gen stock assessment model, survey-based assessment

1 | INTRODUCTION

Fisheries stock assessment provides scientific foundations for fisheries management to achieve sustainable exploitation of fisheries resources, and population dynamics models are essential components of fisheries stock assessment. Over the past few decades, a wide range of population dynamics models have been developed, which

may be classified into biomass dynamics models, length-structured models and age-structured models (Hilborn & Walters, 1992). Among these models, age-structured models tend to produce more accurate estimates of population dynamics, and they are now the “preferred” methodology among stock assessment packages applied in fisheries management (Punt et al., 2020). A great challenge for implementing age-structured models is to collect accurate age data.

For example, crustaceans and molluscs are often difficult (if not impossible) to age (Smith & Addison, 2003). For many long-lived teleost species, the aging accuracy often decreases with age, leading to poor age estimates of older individuals (Marriott & Mapstone, 2006). Furthermore, common methods to age fish (e.g., otolith analysis) are usually expensive and time consuming to implement (Campana & Thorrold, 2001), and many fisheries may not have the capacity to age a large number of fish for stock assessment. It is also difficult to derive reliable age-based catches and stock size indices at appropriate spatial scales for stock assessments with complex or uncertain spatial (and stock) structure.

An innovative approach to deal with this challenge is the age-structured statistical catch-at-length (ACL) model (Fournier et al., 1998), which utilizes length/size data that are typically cheaper and more realistic to acquire with relatively high accuracy across the spatiotemporal scales of interest. ACL uses age-length transition matrices to transform abundance at age to abundance at length, so that age-based population dynamics can be estimated by fitting the model to length-based data. Many popular fisheries stock assessment software packages (e.g., MULTIFAN-CL, Fournier et al., 1998; SS3, Methot & Wetzel, 2013; and CASAL, Bull et al., 2012) are able to construct and implement ACLs, which are widely applied in fisheries without sufficient age data (e.g., world tuna fisheries). One major limitation of ACLs is they are unable to deal with length-dependent processes within age classes (Punt et al., 2013). For example, when the length distribution at age expands across a relatively wide range of lengths and fisheries are length-selective, then the fishing mortality may vary dramatically within the same age class. ACLs typically assume constant fishing mortality within age classes (Bull et al., 2012; Fournier et al., 1998; Methot & Wetzel, 2013), which may introduce bias in parameter estimation and reduce the accuracy of the stock assessment. Although this limitation is well acknowledged, there have been few successful attempts to integrate length-dependent fishing mortality into ACLs (but see McGarvey et al., 2007).

Fisheries-dependent data (e.g., total catch, age/size composition in catch samples) are usually the primary data source for fisheries stock assessment, because these data are usually easier and cheaper to acquire than fisheries-independent survey data. As a result, most fisheries stock assessment models treat fisheries-dependent data as the default and essential model input, and these models use fisheries-independent data as "bonus" information to improve the accuracy of model estimation (Hilborn & Walters, 1992). However, it is widely recognized that fisheries-dependent data are affected by many factors (e.g., markets, weather) other than stock dynamics, and these data may be highly uncertain and biased due to misreporting, which strongly affects the accuracy of stock assessment (Beare et al., 2005; Van Beveren et al., 2017). In contrast, fisheries-independent survey data may be more reliable because they are collected through well-designed surveys that are usually systematically and consistently implemented over time and space. With increasing amounts of fisheries-independent data and our increasing knowledge of the problems in inferring stock dynamics from fisheries-dependent data (e.g., Cadigan et al., 2017),

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a new situation is emerging in some fisheries where a stock assessment model based only on fisheries-independent data can provide good estimation of population dynamics (e.g., Kumar et al., 2020). Although the survey-only age-based assessment (SURBA) model has been around for a while (Beare et al., 2005; Cadigan, 2010; Cook, 2013), to our knowledge, no study has examined how much we can achieve in fisheries stock assessment by only using survey catch-at-length data, and this type of data is much more widely available than survey catch-at-age data.

In this paper, we propose an age- and length-structured statistical catch-at-length model (ALSCL) that can estimate age-based population dynamics from survey catch-at-length indices. ALSCL simultaneously tracks three-dimensional population dynamics across time, age and length, which integrates length- and age-based fishing mortality. We treat ALSCL as a "hybrid" between an ACL and a length-based population dynamics model, which keeps the advantages of both; that is, 1) estimate age-based population dynamics from length-based data and 2) use length-dependent processes to drive population dynamics. In the following sections, we first describe the model structure of ALSCL. Next, we use a simulation study to test whether ALSCL outperforms ACL when length-dependent processes are important. To generalize the results, the simulation is designed based on two species with drastically different dynamics, i.e., yellowtail flounder (*Limanda ferruginea*, Pleuronectidae) as a benthic flat fish that spawns once a year and has a relatively low growth rate, and bigeye tuna (*Thunnus Obesus*, Scombridae) as a pelagic predatory fish that spawns throughout the year and has a relatively high growth rate. Finally, we apply ALSCL in a case study to estimate the population dynamics of female yellowtail flounder on the Grand Banks off Newfoundland, Canada.

2 | METHODS

2.1 | Model structure

The key concept of ALSCL is the three-dimensional population dynamics across length, age, and time, so that the model can track the temporal variations of abundance-at-length for each cohort (Punt et al., 2017). The variation in the length distribution within each cohort is modelled using a length-dependent total mortality rate (Z), which is the sum of length-dependent fishing (F) and natural (M) mortality rates, and a growth transition matrix similar to that used in length-based models (Cronin-Fine & Punt, 2020). The temporal variations of age-based and length-based stock abundance are derived by summing the three-dimensional abundance across length and age dimensions, respectively.

The three-dimensional population dynamics across length bins ($l = 1, \dots, L$), age classes ($a = 2, \dots, A-1$), and time steps ($t = 2, \dots, T$) are modelled by length-based survival and growth within each cohort,

$$\mathbf{n}_{l|a,t} = \mathbf{G} \times (\mathbf{n}_{l|a-1,t-1} \circ e^{-\mathbf{z}_{l|t-1}}), \quad (1)$$

where $\mathbf{n}_{l|a,t}$ is a $L \times 1$ vector of length-specific abundance for individuals at age class a in time step t , $\mathbf{z}_{l|t}$ is the same dimension vector of length-specific total mortality rates in time step t , \mathbf{G} is the growth transition matrix (see below), \circ denotes element-wise multiplication (the Hadamard product), and $*$ indicates matrix multiplication. The number of time steps in our model is determined by the number of time steps of data available. We set the maximum age class (A) to be large enough to cover the majority of captured fish, because setting A at too small a value will result in a loss of survey information about cohort strength and growth rates. However, setting A too large increases computing time so a reasonable choice for A is more useful. To further reduce the uncertainty in choosing the maximum age, a plus group is added for the maximum age,

$$\mathbf{n}_{l|A,t} = \mathbf{G} \times (\mathbf{n}_{l|A-1,t-1} \circ e^{-\mathbf{z}_{l|t-1}} + \mathbf{n}_{l|A,t-1} \circ e^{-\mathbf{z}_{l|t-1}}). \quad (2)$$

The number of length bins (L) and the length bin widths are specified based on the range of length data, species life history, and computation time, which we consider further in the Discussion.

The growth transition matrix is a $L \times L$ stochastic matrix (i.e., a real square matrix with each column summing to one) that changes the cohort length distribution over time,

$$\mathbf{G} = \begin{bmatrix} p_{11} & \cdots & p_{1L} \\ \vdots & \ddots & \vdots \\ p_{L1} & \cdots & p_{LL} \end{bmatrix}. \quad (3)$$

Each element of the matrix (p_{ij}) represents the probability of moving from length bin j to i after one time step,

$$p_{ij} = \int_{l_{j-1}}^{l_j} \int_{l_{i-1}}^{l_i} f_{\Delta}(y - u | \theta) f_u(u | \theta) du dy, \quad (4)$$

where $f_{\Delta}()$ is the pdf of the growth increment $y - u$ to be length y after growth over one time step and $f_u()$ is the probability density function (pdf) of the initial length u before growth. For simplicity, we assume all individuals in length bin j have the same starting mean value of length bin j . In this case, Equation 3 simplifies to,

$$p_{ij} = \int_{l_{j-1}}^{l_j} f_{\Delta}(y - \bar{l}_j | \theta) dy. \quad (5)$$

The Von Bertalanffy (VonB) equation for the growth increment (Fabens, 1965) is often used for $f_{\Delta}()$. However, an implicit assumption of this method is that the L_{∞} must be greater than the maximum length bin; otherwise, the growth increment is negative. To overcome this limitation, we model the growth increment as a decreasing logistic equation (Millar & Nottingham, 2019). We assume the growth increment $(y - x) | x \sim N(\mu_x, \sigma_x^2)$ where $\sigma_x = \mu_x \times cv_{inc}$ and cv_{inc} is the coefficient of variation of the growth increment. The mean growth increment of length x is,

$$\mu_x = \frac{\Delta_{max}}{1 + e^{-\log(19) \times \frac{x - l_{50}}{l_{95} - l_{50}}}}, \quad (6)$$

where Δ_{max} is the maximum growth increment (which may be derived from the VonB model parameters as $\Delta_{max} = (1 - e^k)L_{\infty}$), and l_{50} and l_{95} denote the lengths at which the growth increment is 50% and 95% of Δ_{max} , respectively.

The total mortality rate for length bin l fish in time step t ($Z_{l,t}$) is the sum of the length-dependent fishing mortality rate ($F_{l,t}$) and the natural mortality rate (M), $Z_{l,t} = F_{l,t} + M$. We assume the $F_{l,t}$'s are stochastic and correlated across lengths and time steps. For simplicity, we assume $\log(F_{l,t})$ has a multivariate normal (MVN) distribution with the same mean for all l and t , (i.e., μ_F) and a separable covariance matrix Σ_F with elements,

$$\text{Cov}(\Sigma_{F,l,t}, \Sigma_{F,l-i,t-j}) = \frac{\sigma_F^2 \phi_L^{l|i} \phi_T^{t|j}}{(1 - \phi_L^2)(1 - \phi_T^2)}, l = 1, \dots, L \text{ and } t = 1, \dots, T. \quad (7)$$

Note that $\text{Corr}(\Sigma_{F,l,t}, \Sigma_{F,l-i,t-j}) = \phi_L^{l|i} \phi_T^{t|j}$, where ϕ_L and ϕ_T are the length and time autocorrelation coefficients, respectively. The F parameters to estimate are μ_F , σ_F^2 , ϕ_L and ϕ_T , although our model can be easily modified to contain multiple μ_F parameters that could account for abrupt changes in F due to known substantial management actions such as a fishing moratorium. For simplicity, we assume that M is known and constant (i.e., $M = 0.2/\text{year}$), although length-dependent M 's could also be assumed. We consider this further in the Discussion.

We assume that the initial size of each cohort (i.e., recruitment, r_t) is also stochastic and follows a first-order autoregressive process (AR(1)),

$$r_t = \bar{r}e^{\epsilon_t}, t = 1, \dots, T, \quad (8)$$

where \bar{r} is the median recruitment and ϵ_t is MVN with mean 0 and AR(1) covariance with correlation ϕ_r and stationary

variance $\sigma_r^2/(1 - \phi_r^2)$. Although we model the mean recruitment with a constant parameter, we can easily extend our model to include mean recruitment time-blocks or a stock-recruitment relationship. We assume the length distribution of recruitment is normal and we partition r_t to each length bin based on the probability of being in a length bin; that is,

$$r_{l,t} = r_t \times p_{l,r,t}, \quad (9)$$

where $p_{l,r,t}$ is a vector of probabilities for each length bin, and each element of $p_{l,r,t}$ is based on the distribution of size at the recruitment age class a_r in time step t . If we denote this length as X_t , then the probability that a recruited fish is in length bin l is $p_{l,r,t} = \Pr(LB_l < X_t \leq UB_l)$ where $X_t \sim N(\mu_{r,t}, \sigma_{r,t})$ and LB_l and UB_l are the lower and upper boundaries of length bin l . To handle recruitment that are predicted to have negative length, we set LB_1 to be negative infinity. The mean size at recruitment is derived using the VonB parameters, $\mu_{r,t} = L_\infty (1 - e^{-k(a_r - a_0)})$, and the standard deviation is $\sigma_{r,t} = \mu_{r,t} \times cv_{init}$ where cv_{init} is the coefficient of variation and is also a parameter to estimate.

Similarly, in the first model time step, the length distribution at each age class is assumed to be normal with coefficient of variation equal to cv_{init} . We partition stock number-at-age to length bins using Normal probabilities, where the mean length at each

age class in the first time step is $\mu_{a,1} = L_\infty (1 - e^{-k(a - a_0)})$ and the standard deviation is $\sigma_{a,1} = \mu_{a,1} * cv_{init}$. That is, the vector of length-specific abundance for individuals at age class a in the first time step is

$$n_{l,a,1} = n_{a,1} \times p_{l,a,1}, \quad (10)$$

where the elements of the vector $p_{l,a,1}$ are $p_{l,a,1} = \Pr(LB_l < X_a \leq UB_l)$ and $X_a \sim N(\mu_{a,1}, \sigma_{a,1})$. Similar to the recruitment case, LB_1 is set to negative infinity to deal with predictions of negative length. The $n_{a,1}$'s are derived from age-dependent stochastic equilibrium distribution,

$$n_{a,1} = r_1 e^{-Z_{init}(a-1)} e^{\epsilon_a}, a = 1, \dots, A \quad (11)$$

where r_1 is the recruitment in the first model time step, Z_{init} is a parameter to specify the age structure in the first model time step, and ϵ_a are independent Normal random variables with mean 0 and standard deviation σ_{init} which are assumed to be constant across ages.

If weight and maturity in length bin l and time step t ($wt_{l,t}$ and $mat_{l,t}$) are known, the biomass ($b_{l,a,t}$) and spawning biomass ($sb_{l,a,t}$) in length bin l , age class a and time t can also be derived using length-dependent weight and length-dependent maturity: $b_{l,a,t} = n_{l,a,t} wt_{l,t}$, $sb_{l,a,t} = b_{l,a,t} mat_{l,t}$. Note that we have assumed that the weight-at-length in the stock and in the fishery catches are the same, which will often be reasonable, whereas it is often not reasonable to assume weights-at-age in the stock and catches are the same because

of the length selectivity of the fishing fleets. The stock abundance in length bin l and time step t is $n_{l,t} = \sum_a n_{l,a,t}$ and the stock abundance at age class a is $n_{a,t} = \sum_l n_{l,a,t}$. The stock biomass and spawning biomass at length or at age can also be derived: $b_{l,t} = \sum_a b_{l,a,t}$, $b_{a,t} = \sum_l b_{l,a,t}$, $sb_{l,t} = \sum_a sb_{l,a,t}$, $sb_{a,t} = \sum_l sb_{l,a,t}$.

2.2 | Parameter estimation

The ALSCL and ACL models were implemented in R (R Core Team, 2020). Parameters are estimated using the maximum likelihood method (MLE), and the marginal negative loglikelihood (nll) function was minimized using the “*nllminb*” optimization function. The “TMB” template model builder package (Kristensen et al., 2016) was used to construct the nll functions. Random effects such as $\log(F_{l,t})$, log-recruitment deviations ϵ_t , and the initial log-number at age deviation ϵ_a are integrated out of the joint density of the data and random effects. TMB uses the Laplace approximation of the integrals over the high-dimensional random-effects. TMB also provides the “SEPARABLE” function to compute the separable extension of two multivariate normal (MVN) densities and we used this to compute the loglikelihood of the $\log(F_{l,t})$'s. We encountered problems using TMB to compute length bin probabilities, and our solution is described in the Appendix S1A.

The joint nll involves components for the MVN $\log(F_{l,t})$'s, the MVN recruitment ϵ_t 's in Equation (7), and MVN initial number at age ϵ_a 's in Equation (10). The only data used to estimate model parameters is a time-series of length-based survey indices ($I_{l,t}$). We assume independent and identically distributed (*iid*) lognormal survey measurement errors,

$$\log(I_{l,t}) = \log(q_l) + \log(n_{l,t}) + \epsilon_{l,t}, \epsilon_{l,t} \sim iid N(0, \sigma_l), \quad (12)$$

where, $I_{l,t}$ is the relative abundance (may be indexed by average survey catch when the fishing effort of a survey is constant over time) in length bin l and time step t , q_l is the catchability in length bin l which we assume is constant over time, and σ_l is the survey index standard deviation parameter to be estimated. Similar to the age-based SURBA stock assessment model (Beare et al., 2005), we cannot estimate the q_l 's using only survey information. The scale of the stock numbers cannot be estimated with only survey indices. Hence, ALSCL only estimates trends in stock size and fishery catches, but it does provide absolute estimates of F 's. We simply fix the maximum of the q_l 's to be one and specify the survey catchability at length using a logistic function that is parameterized in terms of sel_{50} and sel_{95} , which are the lengths at 50% and 95% catchability, or define survey catchability at length based on expert knowledge. Under this assumption, the scale of the ALSCL stock size estimates is the same as the scale of the fully selected survey indices.

2.3 | Simulation study

A simulation study is implemented to examine the accuracy of ALSCL and ACL estimation of age-specific population dynamics from survey catch-at-length data, which comprises operating models, assessment models, and performance evaluation (Figure 1). The simulation is based on biological data of two species with drastically different life histories (yellowtail flounder and bigeye tuna, *Thunnus obesus*) and three types of length- or age-dependent fishing selectivity (flat, asymptotic, and dome-shape) (Figure 2). Altogether, the simulation consists of 12 operating models (Table 1).

The operating models with length-dependent F 's were constructed to match the model structure of ALSCL, except that F 's were specified as the product of fully selected F and length-dependent selectivity, i.e., $F_{l,t} = F_t s_l$. Recruitment was modeled by the Beverton-Holt function with autocorrelated process error, i.e., $R_{t+a_r} = \frac{\alpha \times SSB_t}{\beta + SSB_t} e^{\epsilon_t}$, and all of the ϵ_t are MVN with mean 0 and AR(1) covariance with correlation ϕ_r and stationary variance $\sigma_r^2 / (1 - \phi_r^2)$. The operating models with age-dependent F 's were constructed to match the model structure of ACL (model structure described in Appendix S1B), except that F 's were specified as the product of fully selected F and age-dependent selectivity, i.e., $F_{a,t} = F_t s_a$, and recruitment was also modeled by the Beverton-Holt function with autocorrelated process error. We specified $\log(F_t) = \log(\bar{F}) + \epsilon_{Ft}$, where the ϵ_{Ft} were MVN with AR(1) covariance parameters ϕ_F and σ_F . The weight-at-length ($w_{l,t}$) and maturity-at-length ($mat_{l,t}$) were derived from a length-weight relationship ($W = x_0 \times Len^{x_b}$) and maturation ogive (a logistic function specified by L_{50} and L_{95}) of the two species, which were

fixed over time. The initial age structure was specified to decline exponentially over age, and the biological parameters were specified based on empirical data of yellowtail flounder on the Grand Bank off Newfoundland (Parsons et al., 2021) and bigeye tuna in the western and central Pacific Ocean (Ducharme-Barth et al., 2020) (Table 2). Particularly, quarterly time steps are used to model the continuous recruitment of bigeye tuna while yearly time steps are used to model the annual recruitment of yellowtail flounder. We used the same number of length bins (to control the computation time for simulation purpose) but different bin width for the two species to test the robustness of the model comparison results for different choices of bin width.

For each of the operating models, we generated 100 datasets of true population dynamics and observed survey catch-at-length (an index of relative abundance at length). For yellowtail flounder that follows annual population dynamics, each simulation run was 100 years and the data in the last 20 years were used to fit the assessment models (i.e., 80 years burn-in period to reduce the effects of assumptions about initial age- and length-structure on population dynamics). For bigeye tuna that follows quarterly population dynamics, each simulation run was 100 years and the data in the last 5 years (20 quarterly steps) were used to fit the assessment models. Hence, the survey indices, length-dependent survey catchability and length-dependent weight and maturity during the last 20 time-steps (20 years for yellowtail flounder and 20 quarters for bigeye tuna) were used as inputs to the assessment models.

We examined the performance of ALSCL and ACL for several stock quantities. Specifically, we examined the estimation accuracy and

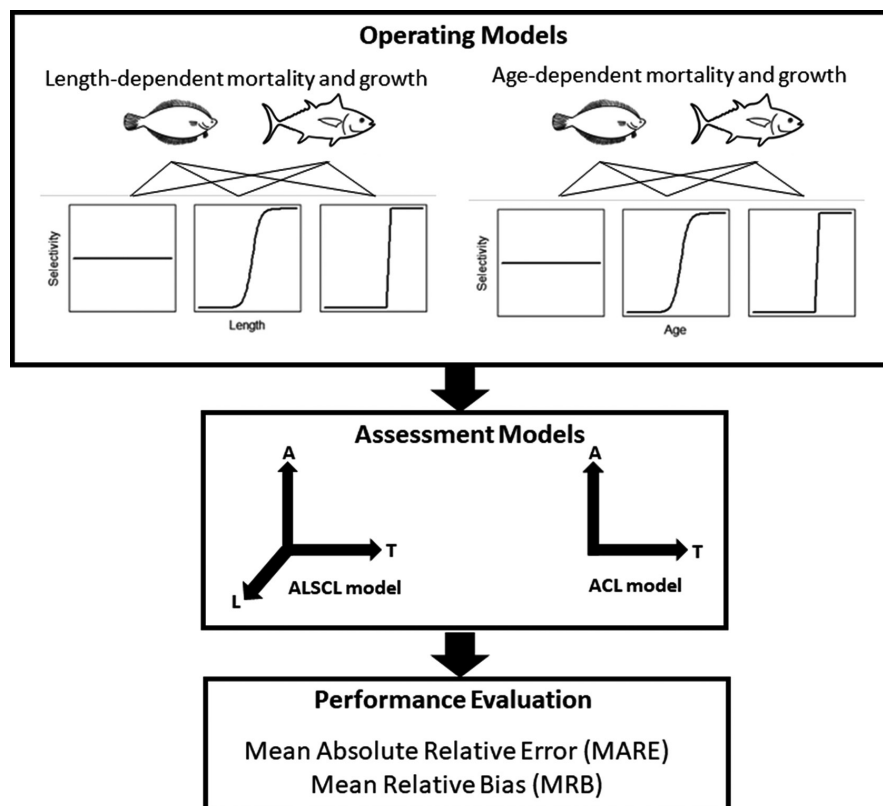


FIGURE 1 Simulation framework

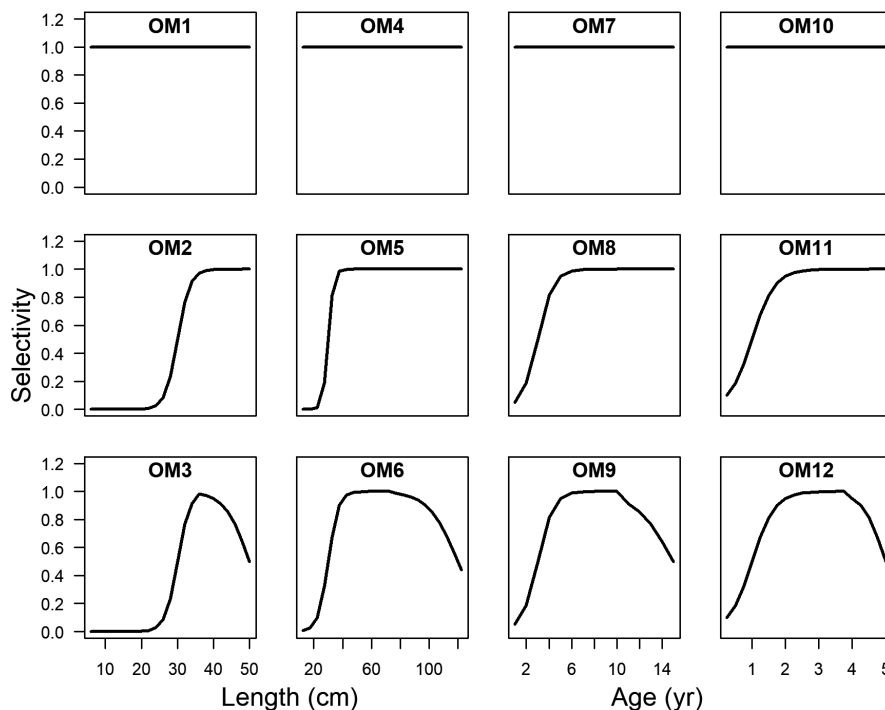


FIGURE 2 Length- or age-dependent fishing selectivity assumed in different operating models (OMs)

Operating model	Biological parameters	Fishing selectivity	Fishing mortality/growth rate within cohort
OM1	Yellowtail flounder	Flat	Length-dependent
OM2	Yellowtail flounder	Asymptotic	Length-dependent
OM3	Yellowtail flounder	Dome shape	Length-dependent
OM4	Bigeye tuna	Flat	Length-dependent
OM5	Bigeye tuna	Asymptotic	Length-dependent
OM6	Bigeye tuna	Dome shape	Length-dependent
OM7	Yellowtail flounder	Flat	Age-dependent
OM8	Yellowtail flounder	Asymptotic	Age-dependent
OM9	Yellowtail flounder	Dome shape	Age-dependent
OM10	Bigeye tuna	Flat	Age-dependent
OM11	Bigeye tuna	Asymptotic	Age-dependent
OM12	Bigeye tuna	Dome shape	Age-dependent

TABLE 1 Configuration of 12 operating models (OMs) with different assumptions of biological characteristics, fishing selectivity, and fishing mortality/growth within each age class

relative bias of recruitment, spawning stock biomass, total abundance, total biomass, and abundance at age for the two assessment models,

$$\text{MARE} = \frac{\sum_l \sum_a \sum_t \sqrt{\left(\frac{y_{\text{est},l,a,t} - y_{\text{true},l,a,t}}{y_{\text{true},l,a,t}} \right)^2}}{L \times A \times T}$$

$$\text{MRB} = \frac{\sum_l \sum_a \sum_t \frac{y_{\text{est},l,a,t} - y_{\text{true},l,a,t}}{y_{\text{true},l,a,t}}}{L \times A \times T}$$

where MARE is mean absolute relative error, MRB is the mean relative bias, $y_{\text{est},l,a,t}$ is the estimated value of stock quantity y for length bin l , age class a and time step t by fitting ALSCL and ACL, $y_{\text{true},l,a,t}$ is the true value of quantity y for length bin l , age class a and time step t

generated from the operating models, L , A and T are the total number of length bins, ages, and time steps.

2.4 | Case study

Yellowtail flounder is a commercially important species on the Grand Banks off Newfoundland. The fishery is managed in Northwest Atlantic Fisheries Organization (NAFO) divisions 3LNO (Figure S1). Since 1990, annual stratified-random bottom trawl surveys have been conducted in the spring (April to June) and fall (September to November) by the Canadian Department of Fisheries and Oceans (DFO) in 3LNO. The survey gear changed from an Engel 145' high-rise groundfish trawl to a more efficient

TABLE 2 Parameters of operating models in the simulation study

Parameter	Meaning	Yellowtail flounder	Bigeye tuna
T	number of time steps used for model diagnostic	20 years	20 quarters
A	number of age classes	15	20
L	number of length bins	23	23
$\{LB_1, LB_2, \dots, LB_L\}$	lower bounds of length bins (cm)	{-inf, 7, 9..., 49}	{-inf, 15, 20..., 120}
$\{UB_1, UB_2, \dots, UB_L\}$	upper bounds of length bins (cm)	{7, 9..., 49, inf}	{15, 20..., 120, inf}
k	growth rate parameter	0.2/year	0.38/year
L_∞	asymptotic length parameter	60 cm	152 cm
a_0	growth parameter	0.017	0.0066
a_r	age class of recruitment	1 year	1 quarter
\bar{r}	mean recruitment	500	10,000
ϕ_r	log recruitment autocorrelation	0.1	0.1
σ_r	standard deviation of log recruitment	0.3	0.3
Z_{init}	initial mortality to determine age structure in initial time step	0.5/year	0.1/quarter
σ_{init}	standard deviation of log number at age in the initial time step	0.2	0.3
cv_{init}	cv of the length distribution at the age for recruitment and age classes in initial time step	0.2	0.2
cv_{inc}	cv of the growth increment	0.2	0.3
M	natural mortality	0.2/year	0.2/quarter
\bar{F}	mean fully selected fishing mortality	0.2/year	0.2/quarter
ϕ_F	autocorrelation in log fully selected fishing mortality	0.75	0.75
σ_F	standard deviation log fully selected fishing mortality	0.2	0.2
σ_{SN}	standard deviation of the survey measurement error	0.1	0.1
x_a	parameter to define length-weight relationship	e^{-12}	$2e^{-5}$
x_b	parameter to define length-weight relationship	3	3
α	Beverton-Holt model parameter	400	15,000
β	Beverton-Holt model parameter	10	150
L_{95}	Length of 95% maturity	40 cm	120 cm
L_{50}	Length of 50% maturity	35 cm	100 cm
sel_{95}	Length of 95% survey catchability	20 cm	50 cm
sel_{50}	Length of 50% survey catchability	15 cm	30 cm

Note: Parameter values are specified based on empirical data of yellowtail flounder on the grand Bank off Newfoundland and bigeye tuna in the western and Central Pacific Ocean.

Campelen 1800 shrimp trawl in 1995 (Parsons et al., 2021). The survey collects various types of data for yellowtail flounder, including total number caught per tow, length composition, body weight, maturity, etc. However, few age data were acquired for this species.

Due to the lack of age information, the current stock assessment for 3LNO yellowtail flounder uses a Bayesian surplus production model (Parsons et al., 2021). Surplus production models can only estimate the dynamics of total population biomass/abundance using survey catch per unit effort and total catch data. The

cohort dynamics of the population are not estimated, although survey and fishery catch at length data and some aging information are available. Surplus production models are unable to explicitly account for transient age and size dynamics in growth, maturation, age/length-dependent fishery selectivity, and natural mortality, which may lead to unreliable estimates of stock size and sustainable harvest rates (Punt & Szuwalski, 2012; Wang et al., 2014). These models perform poorly if data contrast is low and process and observation errors are large (e.g., Geng et al., 2020). To illustrate how to address these deficiencies, we used ALSCL and the spring survey female catch-at-length (standardized by survey effort to index relative abundance at length), maturation-at-length, and weight-at-length data between 1996 and 2017 (the period when the survey uses the Campelen trawl). Modifying the model to deal with the older Engels survey data and data for males is beyond the scope of this paper. Based on our understanding of the gear selectivity of the Campelen trawl, asymptotic catchability-at-length was specified and assumed to be constant over time (Figure S1). We used 9 age classes and 22 length bins with 2 cm bin widths: {<11.5, 11.5–13.5, 13.5–15.5, ..., 49.5–51.5, >51.5}. The last age class represents fish at age 9 and older.

3 | RESULTS

3.1 | Simulation study

ALSCL outperformed ACL for all operating models with length-dependent selectivity, regardless of the species or patterns of fishing selectivity at length. For the six operating models (OM1–6) based on the biological traits of yellowtail flounder and bigeye tuna and three types of length-dependent fishing mortality, the MAREs and MRBs of estimated recruitment, spawning stock biomass, total abundance, total biomass and growth parameters were generally smaller for ALSCL than ACL (Figures 3 and 4). Similarly, for age-specific abundance, ALSCL had smaller MAREs and MRBs than ACL in most age classes, especially for older age classes (Figures 5 and 6).

The opposite pattern was observed when fishery selectivity was age-dependent, which was consistent across species and patterns of fishing selectivity at age. In the six operating models (OM7–12) simulating population dynamics of yellowtail flounder and bigeye tuna under three types of age-dependent fishing mortality rates, the MAREs and MRBs of estimated recruitment, spawning stock biomass, total abundance, total biomass and growth parameters were generally smaller for ACL than ALSCL (Figures 3 and 4). For age-specific abundance, ACL had smaller MAREs and MRBs than ALSCL in most age classes, especially for older age classes (Figures 5 and 6).

The MAREs and MRBs of total abundance estimates were similar between ALSCL and ACL (Figures 3 and 4), but the MAREs and MRBs of age-specific abundance estimates were quite different. When fishery selectivity was length-dependent, ACL underestimated the

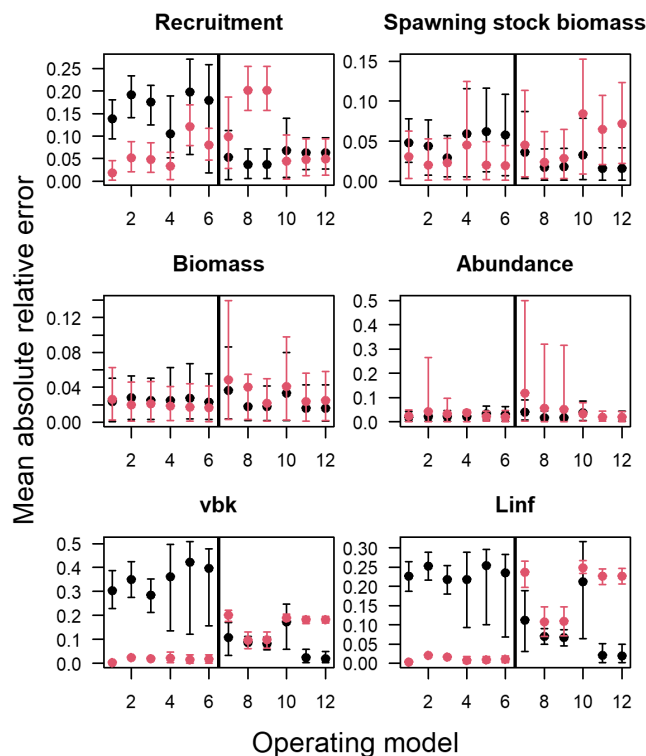


FIGURE 3 Mean absolute relative errors for recruitment, spawning stock biomass, total abundance, total biomass and growth parameters estimated by ALSCL (red points) and ACL (black points) using data from 12 operating models. Error bars indicate the 5% and 95% quantiles over 100 simulations. The vertical lines separate operating models using length-based and age-based mortality and growth within age classes

abundance of younger age classes while overestimated the abundance of older age classes (Figure 6). Hence, when summing over all age classes, the bias of different age classes tended to cancel out and led to similar MARE and MRB of total abundance estimates. Therefore, although ALSCL and ACL had similar MAREs and MRBs of total abundance estimates, ALSCL could more accurately estimate the cohort dynamics. The opposite was observed when fishery selectivity was age-dependent, i.e., ACL had more accurate estimates of cohort dynamics than ALSCL (Figure 6).

3.2 | Case study

The ALSCL was fit to the spring survey number-at-length of female yellowtail flounder in NAFO Divisions 3LNO, and used weight-at-length and maturity-at-length data as inputs, to estimate their relative abundance and biomass between 1996 and 2017. The model converged well with relatively good fit (Figure S1, S4).

The total abundance and recruitment fluctuated between 1996 and 2017, and remained low during recent years (Figure 7a), while the total biomass and spawning stock biomass increased overall during 1996–2013 but decreased since then (Figure 7b). No clear stock-recruitment relationship was identified, with relatively

constant recruitment over a wide range of spawning stock biomass levels (Figure 7C). The mean F showed cyclic variations over time with three peaks around 2002, 2008, and 2015 (Figure 7D).

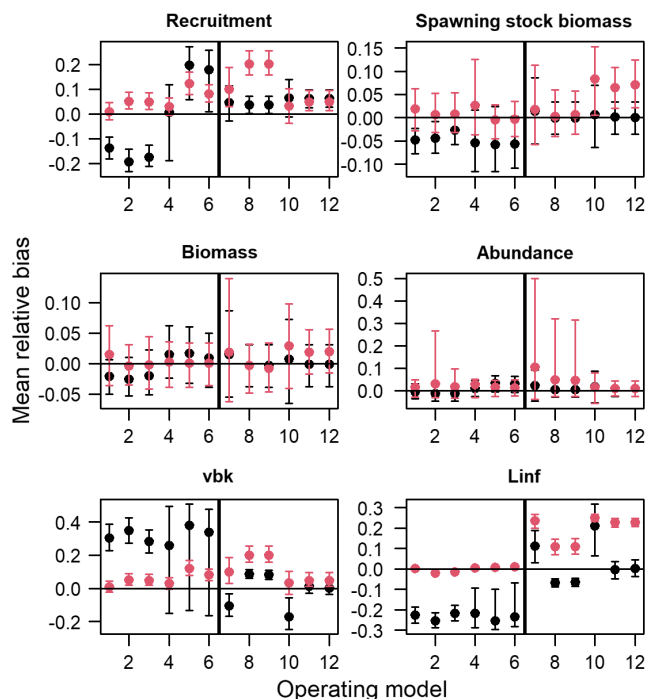


FIGURE 4 Mean relative bias for recruitment, spawning stock biomass, total abundance, total biomass and growth parameters estimated by ALSCL (red points) and ACL (black points) using data from 12 operating models. Error bars indicate the 5% and 95% quantiles over 100 simulations. The vertical lines separate operating models using length-based and age-based mortality and growth within age classes. The horizontal lines indicate no bias

The different trends between abundance and biomass suggest strong variation of age/length structure over time. Indeed, the model estimates showed substantially different temporal variation patterns among age classes, with younger and older age classes (e.g., ages 1, 2, 8, and 9) decreasing while middle age classes (e.g., ages 4 and 5) increased over time (Figure 8).

4 | DISCUSSION

4.1 | ALSCL as an improved ACL

It has been a challenge in stock assessment to estimate cohort dynamics from length-based data for fisheries that have insufficient or unreliable age data. Although the development of ACLs has been a milestone in estimating age-based population dynamics from length-based data (Fournier et al., 1998), these models cannot account for length-dependent mortality within the same age (Punt et al., 2013). The length-dependent mortality is often associated with length-dependent fishing mortality, although natural mortality also likely varies across length. Fishing gears typically have different length selectivity, for example, a trawl net usually has asymptotic selectivity with poor ability to catch small fish, while a gillnet has dome-shaped selectivity by passing small fish and rejecting large ones. Length-dependent fishing selectivity causes length-dependent fishing mortality rates, so it is unrealistic to assume constant fishing mortality for fish with different lengths even if they are of the same age.

To overcome this challenge, McGarvey et al. (2007) proposed a “slices” method to account for length-dependent fishing mortality in ACLs, but this method was specifically designed for fish stocks that are subject to knife-edge fishing selectivity imposed

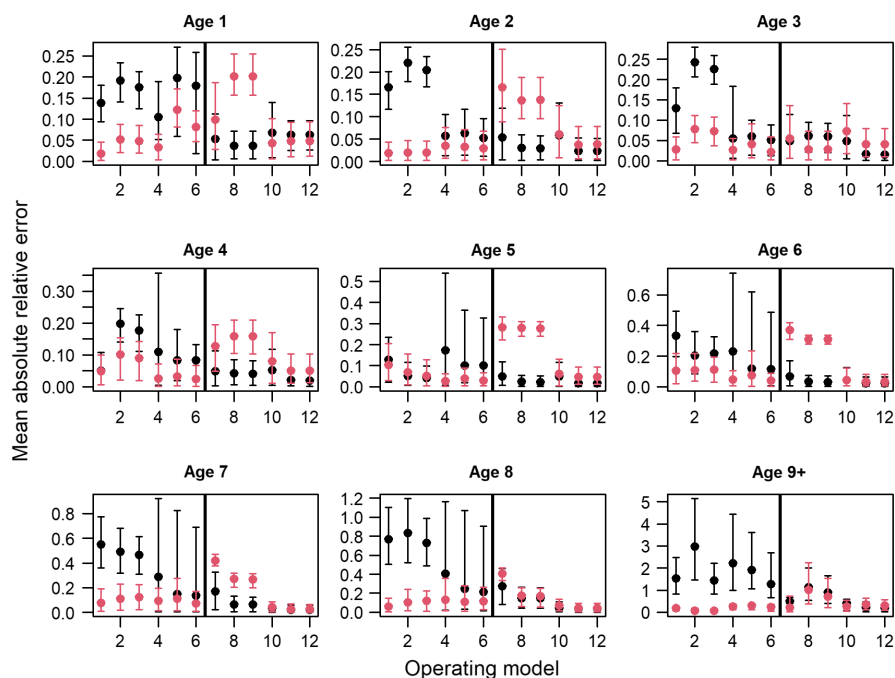


FIGURE 5 Mean absolute relative errors for number at age estimated by ALSCL (red points) and ACL (black points) using data from 12 operating models. Error bars indicate the 5% and 95% quantiles over 100 simulations. The vertical lines separate operating models using length-based and age-based mortality and growth within age classes

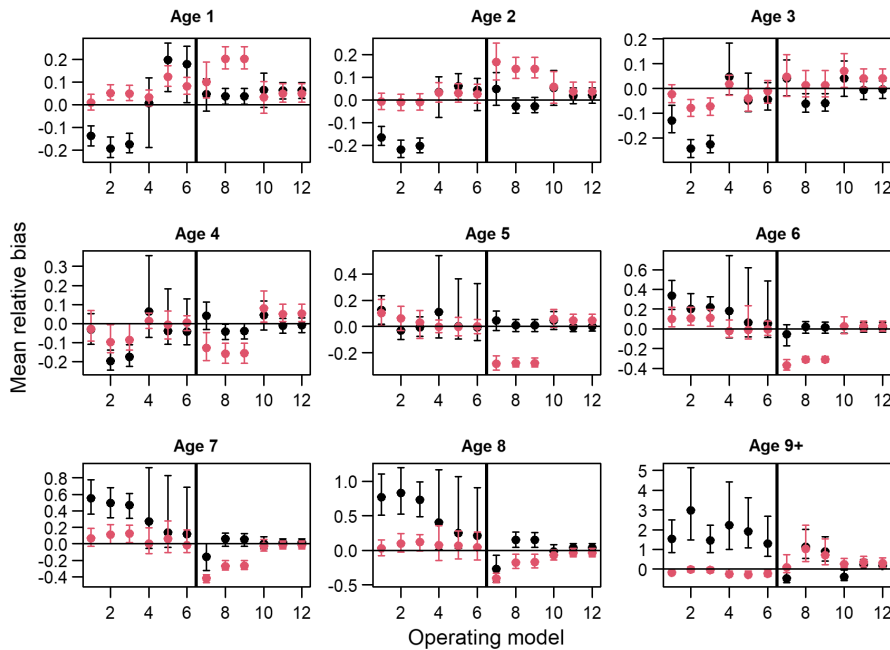


FIGURE 6 Mean relative bias for number at age estimated by ALSCL (red points) and ACL (black points) using data from 12 operating models. Error bars indicate the 5% and 95% quantiles over 100 simulations. The vertical lines separate operating models using length-based and age-based mortality and growth within age classes. The horizontal lines indicate no bias

by a minimum landing size, which may not be suitable for other shapes of length-dependent selectivity. Stock synthesis has another approach to integrate length-dependent fishing mortality within cohorts via the “growth platoon” (Taylor & Methot, 2013). Nevertheless, only a small number of growth platoons are allowed due to computational considerations (currently only 3 or 5 platoons are allowed in stock synthesis), and the fishing mortality rate is assumed to be constant over length within each growth platoon. Hence, this “growth platoon” method may not be an ideal solution to account for length-dependent fishing mortality rates in stock assessment. We developed the ALSCL that simultaneously tracks the age and length structure of fish stock, so that length-dependent mortality can be explicitly accounted for via length-structured survival and growth within each cohort. This three-dimensional (i.e., length, age, and time) model structure is similar to the assessment framework proposed by Akselrud et al. (2017) and consistent with the demand to simultaneously capture age and size dynamics in the next-generation fisheries stock assessment models (Punt et al., 2020). We consider ALSCL as a hybrid of classical ACL and length-based models, and demonstrated via simulation that ALSCL had much smaller estimation error and bias than ACL when fishing mortality was length-dependent. The superior performance of ALSCL over ACL is consistent between species with very different biological characteristics (yellowtail flounder vs. bigeye tuna) and among various patterns of fishing selectivity at length (constant, asymptotic, and dome-shape).

Particularly, we found that ALSCL outperformed ACL even when fishing mortality was constant over length. This revealed a largely overlooked limitation of ACL which ignores length-dependent growth rates. ACLs usually assume a normal or log-normal distribution of length at age. If we assume new-born fish follows a normal distribution across length and growth increments decrease with length (the fundamental assumption of the VonB growth model),

the length distribution of these new-born fish after growth will be skewed away from the normal distribution due to the uneven growth increments across length. This skew process will continue as the fish grow older, which will further deviate from the assumption of a normal distribution of length at age assumed in ACLs (e.g., Lv & Pitchford, 2007; Russo et al., 2009). The same problem applies when the length distribution at age is assumed to be lognormal or gamma. Therefore, ALSCL is an improvement of ACL by explicitly accounting for length-dependent growth rate.

Both length-dependent mortality and growth rates within age contributed to the superior performance of ALSCL than ACL. Not surprisingly, when we assume length-dependent mortality and growth rates were not important within each age class, ACL outperformed ALSCL. Hence, the choice between ACL and ALSCL depends on the importance of length-dependent processes within age. ALSCL should be selected for species that exhibit relatively wide distribution of length at age, while ACL may be acceptable when the length variation within age is relatively small.

4.2 | ALSCL as a flexible and integrated stock assessment model

Since the seminal work of Fournier and Archibald (1982), integrated models have become the preferred approach in fisheries stock assessment due to their ability to utilize multiple types of fisheries-dependent and -independent data (Punt et al., 2020). In this paper, we only fit ALSCL to survey-based length data and only relative population dynamics were estimated, which demonstrates the applicability of ALSCL to data-limited fisheries. However, ALSCL is not only designed for data-limited situations, it can also fit to survey-based age data (random or length-stratified), fisheries-dependent length and age data, as well as

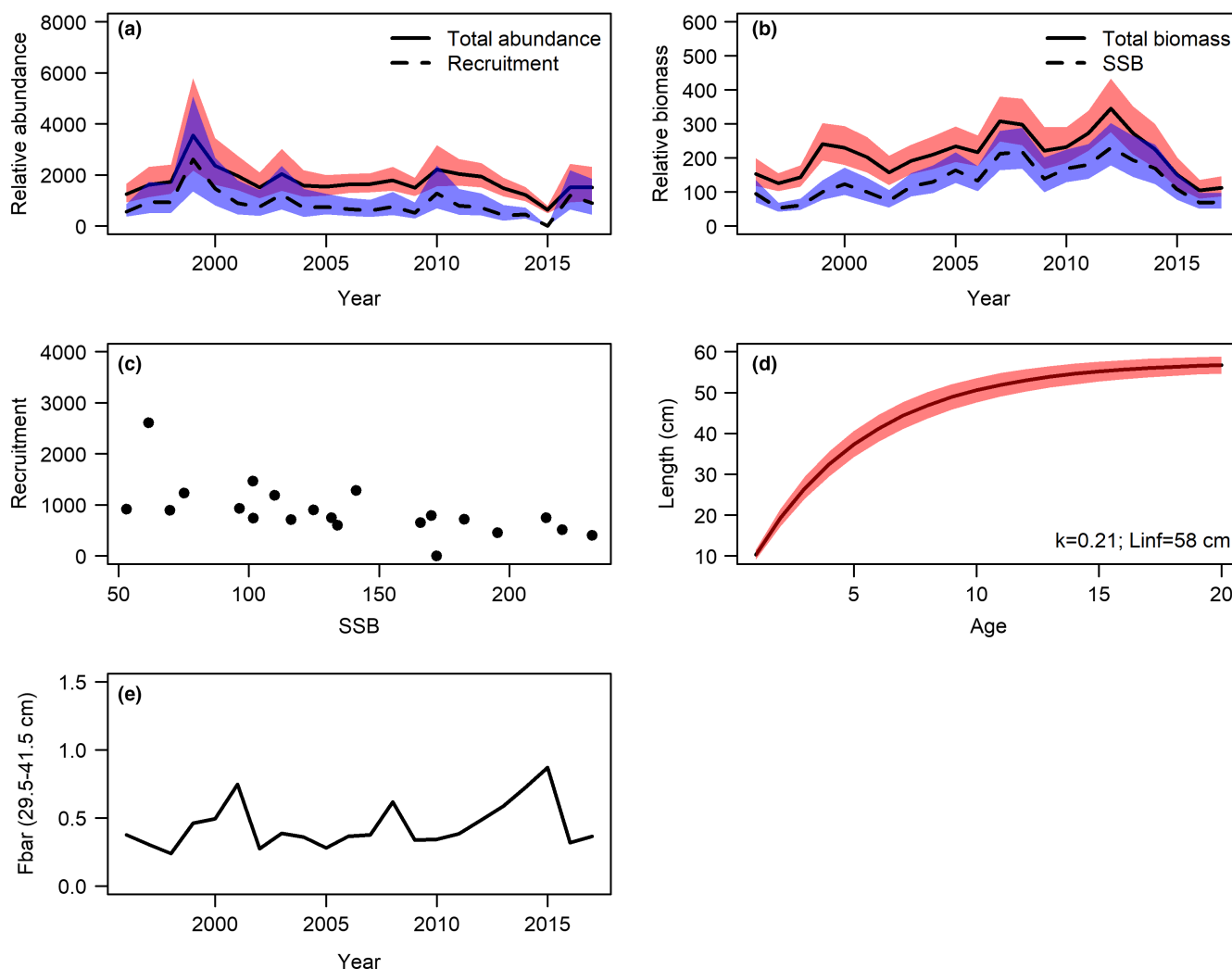


FIGURE 7 Estimated recruitment and total abundance (a), spawning stock biomass (SSB) and total biomass (b), stock-recruitment relationship (c), growth curve (d) and mean fishing mortality (e) of female yellowtail flounder (at relative scale) on grand Bank off Newfoundland between 1996 and 2017. Red and blue shaded areas are 95% confidence intervals

total fisheries catch and tagging data depending on availability. For example, ALSCL model can estimate catch number-at-length, age, and time from the three-dimensional abundances using the Baranov catch equation $c_{l,a,t} = n_{l,a,t} (1 - e^{-Z_{l,t}}) \frac{F_{l,t}}{Z_{l,t}}$, where $c_{l,a,t}$ and $n_{l,a,t}$ are the catch and stock number in length bin l , age class a , and time step t , respectively. The catch at length or at age can also be derived: $c_{l,t} = \sum_a c_{l,a,t}$, $c_{a,t} = \sum_l c_{l,a,t}$. For parameter estimation, this only requires adding appropriate loglikelihood functions for these catch data, as functions of stock size, mortality rates, and ancillary parameters (variances, correlations, etc.), to the joint loglikelihood in the state-space estimation framework for ALSCL. It is also possible to include process errors in population dynamics if more data are included when fitting ALSCL. When fitting to fisheries-dependent length and/or age data, ALSCL would be able to estimate the absolute population dynamics. By combining different types of data, ALSCL may produce more accurate estimates of population dynamics. Hence, ALSCL is a rather flexible stock assessment model that can meet the requirements of

various fisheries ranging from data-limited to data-rich situations (Punt et al., 2020).

The three-dimensional structure gives ALSCL extra flexibility compared to most existing integrated models that are based on two-dimensional (i.e., age-time or length-time) dynamics. For some species, different age classes may reside in different habitats due to ontogenetic shifts (Ciannelli et al., 2022), which may cause them to be subject to different levels of fishing pressure. Additionally, fish growing to asymptotic size may have different natural mortalities among ages due to senescence. As a result, fishing mortality may be both age- and length-dependent. This can create a great challenge for age-based or length-based stock assessment models. The three-dimensional structure of ALSCL actually provides an easy solution to this problem by allowing fishing mortality to vary across length, age, and time. Hence, ALSCL could be a useful tool for fisheries stocks subject to age- and length-dependent mortality. Similarly, many key population traits (e.g., maturation) may also be both age- and length-dependent (Andersen, 2020; Ernande

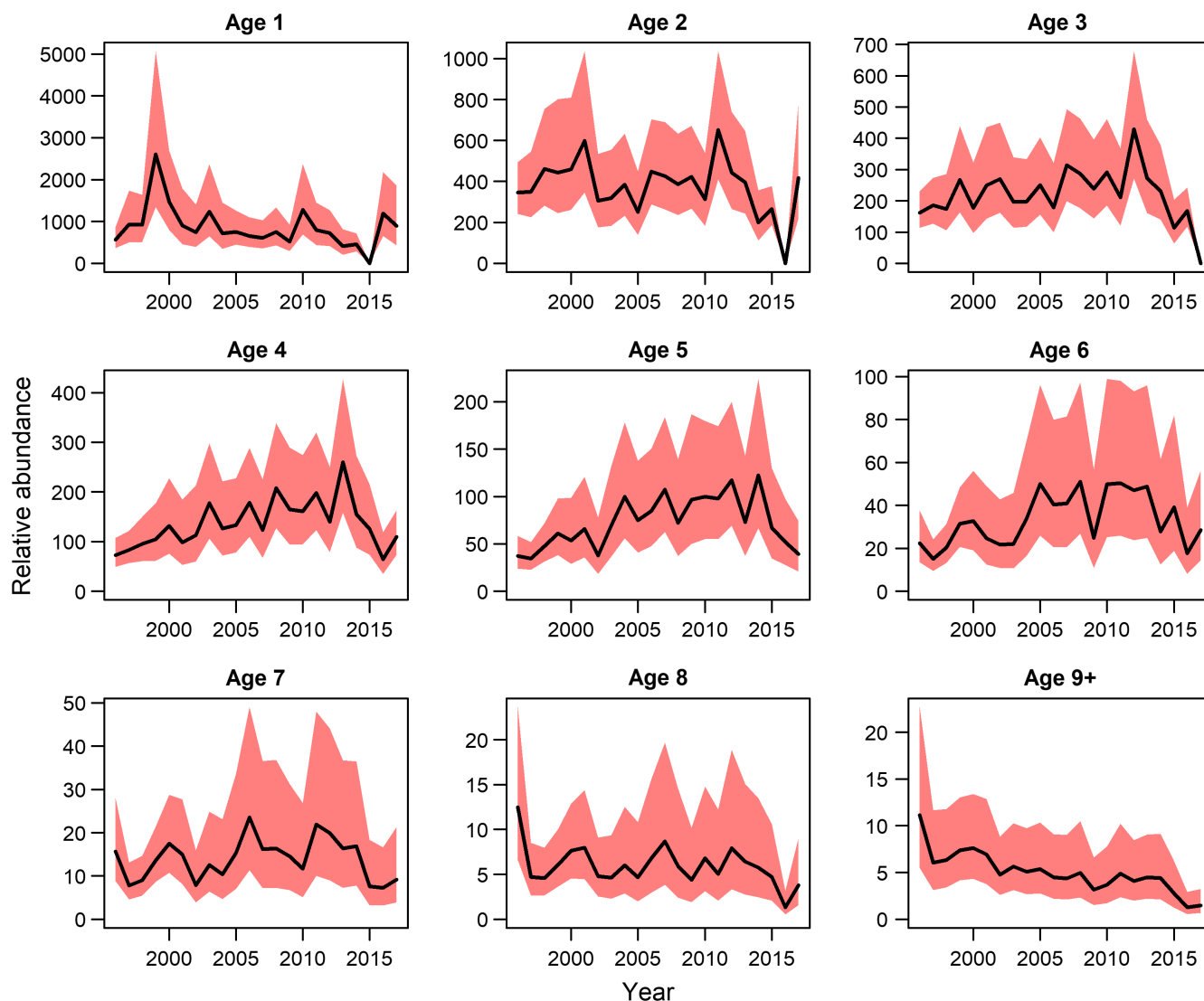


FIGURE 8 Estimated abundance at age (panels) of female yellowtail flounder on grand Bank off Newfoundland between 1996 and 2017. Shaded areas are 95% confidence intervals. The abundances are relative but they are comparable among age classes, because they are all scaled relative to the survey catch number

et al., 2004), and ALSCL is able to explicitly integrate such age- and length-based data.

The idea of three-dimensional dynamics across length, age, and time is not new, and a few single-species, multi-species, and ecosystem models (e.g., MULTISPEC, BORMICON and FLEKSIBEST) have adopted this idea (Akselrud et al., 2017; Bogstad et al., 1997; Guldbrandsen Frøysa et al., 2002; Stefánsson & Pálsson, 1997). However, these are mostly simulation models rather than stock assessment models, and they are not designed to provide estimates of population dynamics for fisheries management. FLEKSIBEST is a stock assessment model, but it is designed to fit age- and length-specific catch and survey data (Guldbrandsen Frøysa et al., 2002), which may not be feasible for cases where reliable age data are missing. The contribution of our paper is to develop a stock assessment model that can readily use length-based data for stock assessment, and this makes our model flexible and compatible with

common requirements of fisheries management (including data-limited situations).

4.3 | Challenges of ALSCL

The key input of ALSCL when only survey indices are used is the specification of survey catchability, which is also a major challenge. The absolute value of catchability is not estimable without fisheries catch information, but the pattern of length-dependent catchability may be specified based on the selectivity of survey gears. Additionally, since fisheries-independent surveys are usually systematically and consistently implemented through time, the length-dependent catchability may be assumed to be constant over time. In the case study, we assumed catchability to increase asymptotically with increasing length, which is based on the type of trawl gear used

in surveys on the Grand Bank. We also assumed that the availability of yellowtail flounder to survey gear was constant over length, because the survey coverage relative to the distribution of yellowtail flounder was relatively high. However, in cases where fish availability differs greatly among length, both gear selectivity and fish availability should be considered when calculating catchability at length.

Modelling growth transition matrix is another challenge of ALSCL, and this challenge is shared among most length-structured models (Cronin-Fine & Punt, 2020). We assumed constant growth parameters and the annual growth is specified to start from the middle length within each length bin. These are common assumptions adopted among length-structured models but may not be realistic enough to account for variations of growth parameters among individuals. Millar and Nottingham (2019) developed a method to allow the length at the beginning of growth to be uniformly distributed within each length bin but did not account for variation of growth parameters among individuals. Cronin-Fine and Punt (2020) proposed a method to numerically integrate variation of growth parameters among individuals, but this method is too computationally intensive to be included in the current version of ALSCL. We also assumed growth rates and parameters did not change over time, and there are many cases where this assumption will not be appropriate (Thorson et al., 2015). Future studies are needed to develop a more efficient way to account for variation of growth parameters among individuals as well as over time when modelling the growth transition matrix.

The natural mortality rate is often considered to be one of the most important parameters in a fish stock assessment, but it is also among the most difficult parameters to estimate using commonly available data (Punt et al., 2021). When only survey data is used, we can only estimate the total mortality rate, and fishing and natural mortality rates cannot be separated without an assumption for the natural mortality rate. Historically, the natural mortality rate has been assumed to be 0.2/year across ages and lengths for many stock assessments. By adopting this assumption, we can derive the fishing mortality rate and predict fishery catch at length and age. If there are additional information on natural mortality, length- and/or age-dependent natural mortality rates can be input to ALSCL as data.

It is also important to define an appropriate number of length bins and length bin widths for ALSCL. The range and width of length bins are often dependent on the resolution of length data, fish biology, and management objectives. In addition, computation efficiency should also be considered when making these decisions, because computing time will increase greatly for models with more length bins.

4.4 | Case study

ALSCL was fit to the survey catch-at-length, weight-at-length, and maturity-at-length of female yellowtail flounder on the Grand Bank off Newfoundland, and the model successfully converged. ALSCL was able to estimate the growth parameters of female yellowtail flounder ($L_{\infty} = 58\text{cm}$, $k = 0.21/\text{year}$; Figure 7D), which are consistent

with the results from independent studies on the growth curves of this stock (Dwyer et al., 2003). Compared to the current surplus-production model used for stock assessment that can only estimate total biomass dynamics and overall fishing mortality rate (Parsons et al., 2021), ALSCL is able to estimate age-based population dynamics, including age-specific fishing mortality rate, abundance, biomass and spawning biomass. The estimated biomass shared similar trends between ALSCL and the surplus-production model, both of which showed dome-shape variations between 1996 and 2017 (Parsons et al., 2021). Additionally, the three peaks of estimated mean fishing mortality rate by ALSCL roughly matched the time when there were high catches of yellowtail flounder (Parsons et al., 2021). However, the scale of the ALSCL F estimates ($F_{bar} \approx 0.5$; Figure 7e) is much higher than that of the production model ($F_{bar} \approx 0.08$; Parsons et al., 2021). Even though the F of production model, which is really harvest rate or fractions of biomass removed, is not directly comparable to the fishing mortality rate in ALSCL, the differences in estimates for yellowtail flounder are substantial and imply much different fishery impacts on the stock. The low-production model F seems inconsistent with the lack of large fish ($>45\text{cm}$) in survey catches (Figure S1) and the growth parameters of this stock. If harvest rates are as low as the production model indicates then we should see more fish around the asymptotic size of 56–58 cm. The lack of fish at these sizes in survey catches indicates higher mortality rates. ALSCL also identified strong variations of stock age structure over time that cannot be estimated from the current surplus-production model, implying the importance to estimate the cohort dynamics of yellowtail flounder.

The case study application of ALSCL only uses survey-based length data of female yellowtail flounder, so only relative abundance/biomass can be estimated. The integration of male yellowtail flounder may further increase the accuracy of model estimates, especially if there are strong variations of sex ratio over time. In the future, an integrated ALSCL with both survey and catch-based length data and both sexes may be recommended to improve the current stock assessment of yellowtail flounder. We anticipate that short-term stock projections based on ALSCL will provide more reliable evaluations of the impacts of future catch options that fisheries managers may consider.

Overall, ALSCL is a flexible and realistic stock assessment model that is able to explicitly account for length-dependent mortality and growth. The three-dimensional structure is the key for ALSCL to fit to length-based, age-based, or length- and age-based data, which is consistent with the recommended features of the so-called “next-gen” stock assessment models (Punt et al., 2020). In this paper, we only demonstrated the potential of ALSCL to deal with situations where age data is missing and survey-based number at length data are available, which may be applicable to fisheries with regular survey but unreliable catch data. Another common situation is when fisheries-dependent catch-at-length data is available but reliable fisheries-independent surveys are missing (e.g., most tuna fisheries). In such cases, as previously discussed, ALSCL can be readily adapted to fit to fisheries-dependent catch-at-length data. The flexibility of ALSCL enables it to deal

with various data situations for stock assessment. In the context of management strategy evaluation (MSE) practices (Punt et al., 2016), the flexibility and realism of ALSCL may make it a strong candidate of operating models that can explicitly track both age- and length-dependent processes.

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DATA AVAILABILITY STATEMENT

The data and code that support the findings of this study are available from the corresponding author upon reasonable request.

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REFERENCES

- Akselrud, C. A., Punt, A. E., & Cronin-Fine, L. (2017). Exploring model structure uncertainty using a general stock assessment framework: The case of Pacific cod in the eastern Bering Sea. *Fisheries Research*, 193, 104–120. <https://doi.org/10.1016/j.fishres.2017.03.016>
- Andersen, K. H. (2020). Size-based theory for fisheries advice. *ICES Journal of Marine Science*, 77, 2445–2455. <https://doi.org/10.1093/icesjms/fsaa157>
- Beare, D. J., Needle, C. L., Burns, F., & Reid, D. G. (2005). Using survey data independently from commercial data in stock assessment: An example using haddock in ICES division VIa. *ICES Journal of Marine Science*, 62(5), 996–1005. <https://doi.org/10.1016/j.icesjms.2005.03.003>
- Bogstad, B., Hauge, K. H., & Ulltang, Ø. (1997). MULTISPEC—a multi-species model for fish and marine mammals in the Barents Sea. *Journal of Northwest Atlantic Fishery Science*, 22, 317–341. <https://doi.org/10.2960/J.v22.a23>
- Bull, B., Francis, R. I. C. C., Dunn, A., McKenzie, A., Gilbert, D. J., Smith, M. H., Bian, R., & Fu, D. (2012). CASAL (C++ algorithmic stock assessment laboratory): CASAL User Manual v2.30–2012/03/21 (No. 275).
- Cadigan, N. (2010). Trends in Northwest Atlantic fisheries organization (NAFO) subdivision 3Ps cod (*Gadus morhua*) stock size based on a separable total mortality model and the Fisheries and Oceans Canada research vessel survey index. *Can. Sci. Advis. Sec. Sci. Advis. Rep.*, 2010/015.
- Cadigan, N. G., Wade, E., & Nielsen, A. (2017). A spatiotemporal model for snow crab (*Chionoecetes opilio*) stock size in the southern gulf of St. Lawrence. *Canadian Journal of Fish and Aquatic Sciences*, 74, 1808–1820. <https://doi.org/10.1139/cjfas-2016-0260>
- Campana, S. E., & Thorrold, S. R. (2001). Otoliths, increments, and elements: Keys to a comprehensive understanding of fish populations? *Canadian Journal of Fisheries and Aquatic Sciences*, 58(1), 30–38. <https://doi.org/10.1139/cjfas-58-1-30>
- Ciannelli, L., Neuheimer, A. B., Stige, L. C., Frank, K. T., Durant, J. M., Hunsicker, M., Rogers, L. A., Porter, S., Ottersen, G., & Yaragina, N. A. (2022). Ontogenetic spatial constraints of sub-arctic marine fish species. *Fish and Fisheries*, 23(2), 342–357. <https://doi.org/10.1111/faf.12619>
- Cook, R. M. (2013). A fish stock assessment model using survey data when estimates of catch are unreliable. *Fisheries Research*, 143, 1–11. <https://doi.org/10.1016/j.fishres.2013.01.003>
- Cronin-Fine, L., & Punt, A. E. (2020). There is no best method for constructing size-transition matrices for size-structured stock assessments. *ICES Journal of Marine Science*, 77(1), 136–147. <https://doi.org/10.1093/icesjms/fsz217>
- Ducharme-Barth, N., Vincent, M., Hampton, J., Hamer, P., Williams, P., & Pilling, G. (2020). Stock assessment of bigeye tuna in the western and Central Pacific Ocean (issue WCPFC-SC16-2020/SA-WP-03).
- Dwyer, K. S., Walsh, S. J., & Campana, S. E. (2003). Age determination, validation and growth of grand Bank yellowtail flounder (*Limanda ferruginea*). *ICES Journal of Marine Science*, 60, 1123–1138. [https://doi.org/10.1016/S1054-3139\(03\)00125-5](https://doi.org/10.1016/S1054-3139(03)00125-5)
- Ernande, B., Dieckmann, U., & Heino, M. (2004). Adaptive changes in harvested populations: Plasticity and evolution of age and size at maturation. *Proceedings of the Royal Society B: Biological Sciences*, 271(1537), 415–423. <https://doi.org/10.1098/rspb.2003.2519>
- Fabens, A. J. (1965). Properties and fitting of the von Bertalanffy growth curve. *Growth*, 29, 265–289.
- Fournier, D. A., & Archibald, C. P. (1982). A general theory for analyzing catch at age data. *Canadian Journal of Fisheries and Aquatic Sciences*, 39(8), 1195–1207. <https://doi.org/10.1139/f82-157>
- Fournier, D. A., Hampton, J., & Sibert, J. R. (1998). MULTIFAN-CL: A length-based, age-structured model for fisheries stock assessment, with application to South Pacific albacore, *Thunnus alalunga*. *Canadian Journal of Fisheries and Aquatic Sciences*, 55(9), 2105–2116. <https://doi.org/10.1139/f98-100>
- Geng, Z., Punt, A. E., Wang, Y., Zhu, J., & Dai, X. (2020). On the dangers of including demographic analysis in Bayesian surplus production models: A case study for Indian Ocean blue shark. *Fisheries Research*, 230, 105636. <https://doi.org/10.1016/j.fishres.2020.105636>
- Guldbrandsen Frøysa, K., Bogstad, B., & Skagen, D. W. (2002). Fleksibest—an age-length structured fish stock assessment model. *Fisheries Research*, 55(1–3), 87–101. [https://doi.org/10.1016/S0165-7836\(01\)00307-1](https://doi.org/10.1016/S0165-7836(01)00307-1)
- Hilborn, R., & Walters, C. J. (1992). Quantitative fisheries stock assessment: Choice, dynamics and uncertainty. In *Quantitative fisheries stock assessment: Choice, dynamics, and uncertainty* (Vol. 2, Issue 2). Chapman and Hall. <https://doi.org/10.1007/BF00042883>
- Kristensen, K., Nielsen, A., Berg, C. W., Skaug, H., & Bell, B. M. (2016). TMB: Automatic differentiation and Laplace approximation. *Journal of Statistical Software*, 70(5), 1–21. <https://doi.org/10.18637/jss.v070.i05>
- Kumar, R., Cadigan, N. G., Zheng, N., Varkey, D. A., & Morgan, M. J. (2020). A state-space spatial survey-based stock assessment (SSURBA) model to inform spatial variation in relative stock trends. *Canadian Journal of Fisheries and Aquatic Sciences*, 21(June), 1–21. <https://doi.org/10.1139/cjfas-2019-0427>
- Lv, Q., & Pitchford, J. W. (2007). Stochastic von Bertalanffy models, with applications to fish recruitment. *Journal of Theoretical Biology*, 244(4), 640–655. <https://doi.org/10.1016/j.jtbi.2006.09.009>

- Marriott, R. J., & Mapstone, B. D. (2006). Consequences of inappropriate criteria for accepting age estimates from otoliths, with a case study for a long-lived tropical reef fish. *Canadian Journal of Fisheries and Aquatic Sciences*, 63(10), 2259–2274. <https://doi.org/10.1139/F06-109>
- McGarvey, R., Feenstra, J. E., & Ye, Q. (2007). Modeling fish numbers dynamically by age and length: Partitioning cohorts into “slices”. *Canadian Journal of Fisheries and Aquatic Sciences*, 64(9), 1157–1173. <https://doi.org/10.1139/F07-080>
- Methot, R. D., & Wetzel, C. R. (2013). Stock synthesis: A biological and statistical framework for fish stock assessment and fishery management. *Fisheries Research*, 142, 86–99. <https://doi.org/10.1016/j.fishres.2012.10.012>
- Millar, R. B., & Nottingham, C. D. (2019). Improved approximations for estimation of size-transition probabilities within size-structured models. *Canadian Journal of Fisheries and Aquatic Sciences*, 76(8), 1305–1313. <https://doi.org/10.1139/cjfas-2017-0444>
- Parsons, D. M., Rideout, R., & Rogers, R. (2021). 2021 assessment of yellowtail flounder in NAFO divisions 3LNO using a stock production model in a Bayesian framework. NAFO Scientific Council Research Document, 21/018, 1–47.
- Punt, A. E., & Szuwalski, C. (2012). How well can F_{MSY} and B_{MSY} be estimated using empirical measures of surplus production? *Fisheries Research*, 134–136, 113–124. <https://doi.org/10.1016/j.fishres.2012.08.014>
- Punt, A. E., Huang, T., & Maunder, M. N. (2013). Review of integrated size-structured models for stock assessment of hard-to-age crustacean and mollusc species. *ICES Journal of Marine Science*, 70(1), 16–33. <https://doi.org/10.1093/icesjms/fss185>
- Punt, A. E., Butterworth, D. S., de Moor, C. L., De Oliveira, J. A. A., & Haddon, M. (2016). Management strategy evaluation: Best practices. *Fish and Fisheries*, 17(2), 303–334. <https://doi.org/10.1111/faf.12104>
- Punt, A. E., Akselrud, C. A., & Cronin-Fine, L. (2017). The effects of applying mis-specified age- and size-structured models. *Fisheries Research*, 188, 58–73. <https://doi.org/10.1016/j.fishres.2016.11.017>
- Punt, A. E., Dunn, A., Elvarsson, B. P., Hampton, J., Hoyle, S. D., Maunder, M. N., Methot, R. D., & Nielsen, A. (2020). Essential features of the next-generation integrated fisheries stock assessment package: A perspective. *Fisheries Research*, 229, 105617. <https://doi.org/10.1016/j.fishres.2020.105617>
- Punt, A. E., Castillo-Jordan, C., Hamel, O. S., Cope, J. M., Maunder, M. N., & Ianelli, J. N. (2021). Consequences of error in natural mortality and its estimation in stock assessment models. *Fisheries Research*, 233, 105759.
- R Core Team. (2020). *R: A language and environment for statistical computing* (1.2.5042). R Foundation for Statistical Computing.
- Russo, T., Baldi, P., Parisi, A., Magnifico, G., Mariani, S., & Cataudella, S. (2009). Lévy processes and stochastic von Bertalanffy models of growth, with application to fish population analysis. *Journal of Theoretical Biology*, 258(4), 521–529. <https://doi.org/10.1016/j.jtbi.2009.01.033>
- Smith, M. T., & Addison, J. T. (2003). Methods for stock assessment of crustacean fisheries. *Fisheries Research*, 65(1–3), 231–256. <https://doi.org/10.1016/j.fishres.2003.09.017>
- Stefánsson, G., & Pálsson, Ó. K. (1997). BORMICON: A boreal migration and consumption model. In *Marine research institute report* (Vol. 58). Marine Research Institute.
- Taylor, I. G., & Methot, R. D. (2013). Hiding or dead? A computationally efficient model of selective fisheries mortality. *Fisheries Research*, 142, 75–85. <https://doi.org/10.1016/j.fishres.2012.08.021>
- Thorson, J. T., Monnahan, C. C., & Cope, J. M. (2015). The potential impact of time-variation in vital rates on fisheries management targets for marine fishes. *Fisheries Research*, 169, 8–17. <https://doi.org/10.1016/j.fishres.2015.04.007>
- Van Beveren, E., Duplisea, D., Castonguay, M., Doniol-Valcroze, T., Plourde, S., & Cadigan, N. (2017). How catch underreporting can bias stock assessment of and advice for Northwest Atlantic mackerel and a possible resolution using censored catch. *Fisheries Research*, 194, 146–154. <https://doi.org/10.1016/j.fishres.2017.05.015>
- Wang, S. P., Maunder, M. N., & Aires-da-Silva, A. (2014). Selectivity's distortion of the production function and its influence on management advice from surplus production models. *Fisheries Research*, 158, 181–193. <https://doi.org/10.1016/j.fishres.2014.01.017>

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