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ARTICLE

Evaluation of alternative modelling approaches to account for spatial effects due to age-based movement[1]

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Abstract: Spatial patterns due to age-specific movement have been a source of unmodelled process error. Modeling movement in spatially explicit stock assessments is feasible, but hampered by a paucity of data from appropriate tagging studies. This study uses simulation analyses to evaluate alternative model structures that either explicitly or implicitly account for the process of time-varying age-based movement in a population dynamics model. We simulated synthetic populations using a two-area stochastic population dynamics operating model. Simulated data were fit in seven different estimation models. Only the model that includes the correct spatial dynamic results in unbiased and precise estimates of derived and management quantities. In a single-area assessment model, using the fleets-as-area (FAA) approach may be the second best option to estimate both length-based and time-varying age-based selectivity to implicitly account for the contact selectivity and annual availability. An FAA approach adds additional observation error performed nearly as well. Future research could evaluate which stock assessment method is robust to uncertainty in movement and is more appropriate for achieving intended management objectives.

Résumé : Les motifs spatiaux qui découlent des déplacements dépendants de l'âge constituent une source d'erreur associée à un processus non modélisé. La modélisation des déplacements dans les évaluations des stocks spatialement explicites est possible, bien que limitée par la rareté de données provenant d'études de marquage adéquates. L'étude fait appel à des analyses par simulation pour évaluer différentes structures de modèle qui intègrent explicitement ou implicitement le processus de déplacement variable dans le temps selon l'âge dans un modèle de dynamique des populations. Nous avons simulé des populations synthétiques en utilisant un modèle opératoire stochastique à deux régions de dynamique des populations. Les données simulées ont été calées sur sept modèles d'estimation différents. Seul le modèle qui inclut la bonne dynamique spatiale produit des estimations précises biaisées et non biaisées des quantités dérivées et de gestion. Dans un modèle d'évaluation à une seule région, une approche de flottes-comme-région (FCR) qui estime tant la sélectivité basée sur la longueur que celle variable dans le temps selon l'âge pour tenir implicitement compte de la sélectivité de contact et de la disponibilité annuelle pourrait être la deuxième meilleure option. Une approche FCR qui ajoute une erreur d'observation supplémentaire a donné des résultats presque aussi bons. Des travaux futurs pourraient évaluer quelle méthode d'évaluation des stocks est robuste en présence d'incertitude associée aux déplacements et conviendrait le mieux aux objectifs de gestions visés. [Traduit par la Rédaction]

Introduction

The movement of fishes has been studied for decades, but detailed knowledge of the patterns, motivation, and implication of this biological process is far from complete. Fish migration has been defined as either within (microscale) or between (macroscale) habitat movements (Nakamura 1969; Humston et al. 2000). Microscale movements are often seasonal and associated with changes in the local environment (Sippel et al. 2011). Macroscale migrations have been linked with ontogenetic changes (Jacobson and Vetter 1996) and are thought to be related to reducing density-dependent effects (Royer and Fromentin 2006) and increasing population reproductive fitness (Leggett 1985; Holland et al. 2006).

Pelagic fish stocks often exhibit substantial microscale (Laurs and Lynn 1977) and macroscale movements (Polovina 1996). Pelagic sharks in the North Pacific show macroscale spatial patterns related to life stages (Nakano 1994). Pacific bluefin tuna (PBF; *Thunnus orientalis*) exhibit ontogenetic trans-Pacific migrations that may be linked to oceanic temperatures, food availability, and ultimately maturation (Polovina 1996). Recent work has documented that age-based processes are responsible for some large-scale fish movements (Francis 2016; McDaniel et al. 2016), though the potential for length-based processes should not be ignored (Nøttestad et al. 1999). Whether age- or length-based or a combination of processes, macroscale movements will lead to nonuniform spatial distribution of both size- and age-classes.

Spatial patterns resulting from macroscale movement have been a source of error due to an unmodelled process in many, if not most, stock assessments. Spatial patterns in size and age (e.g., sampling from juvenile areas) could bias estimation of life history parameters unless those spatial patterns are considered in the estimation (Xu et al. 2016; Lee et al. 2017). Spatial patterns in regional abundance due to size- or age-based movement may

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cause perceived variation in the selectivity pattern (referred to as "availability": the probability that a fish of a given age or size is available to the gear) even when the contact selectivity (the probability that a fish of a given age or size is caught by the gear) is unchanging (Waterhouse et al. 2014; Sampson 2014). Unmodelled changes in fishery selectivity may invalidate the assumption of a constant proportionality of indices to stock abundance. Unless adequately addressed, these spatial issues may result in biased estimates of the population dynamics.

Modelling all the relevant systems and observation processes, such as movement, is feasible, as several stock assessment programs (MULTFAN-CL (Fournier et al. 1998; Hampton and Fournier 2001), CASAL (Bull et al. 2005), Stock Synthesis (Methot and Wetzel 2013)) explicitly model spatial structure and age-dependent movement typically by incorporating tagging data into the integrated assessment model. For many applications the routine fisheries data alone are thought insufficient to estimate a process such as movement. However, Fournier et al. (1998) estimated age-dependent movement rates of albacore using routine fisheries data only because of the clear spatial segregation of the population by size evident in catch size composition data. Their approach employed an implicit solution to a first-order differential equation using an implicit finite difference scheme, producing a solution that incorporates characteristics of advective and diffusive movement. Recent simulation studies (Hulson et al. 2011; Goethel et al. 2015; McGilliard et al. 2015) have shown that incorporation of movement in spatially explicit models with or without tagging data may be feasible under certain conditions. Because of the difficulty in modelling the spatial dynamics caused by movement (i.e., spatially explicit models), there is no clear consensus on the most appropriate approach to deal with the effects of movement in stock assessment models. Thus, a fleets-as-areas (FAA) approach (also known as "areas-as-fleets") is commonly used to account for spatial processes (Cope and Punt 2011; Hurtado-Ferro et al. 2014; Waterhouse et al. 2014). This approach assumes each fleet represents a combination of gear and area with its own selectivity pattern estimated (i.e., spatially implicit models).

Studies of the FAA approach often do not consider movement of adults, with spatial heterogeneity caused instead by regional differences in fishing patterns (Cope and Punt 2011) or variation in biological rates (Punt et al. 2015). Relatively few studies (Hurtado-Ferro et al. 2014; O'Boyle et al. 2016) have explored migratory (rather than dispersive) movement patterns, and these have not compared the spatially implicit FAA models with spatially explicit alternatives. There are even fewer FAA studies that have explored more flexible selectivity patterns (e.g., temporal changes) to attempt to account for differences in availability due to heterogeneous impact of fishing pressure or movement (Hurtado-Ferro et al. 2014). In general, simulation analyses of the FAA approach have found trade-offs between bias and imprecision, where simplification of movement processes can result in more stable models, but at the cost of biased estimates of quantities of interest (McGilliard et al. 2015; Goethel et al. 2015). FAA models also have been found to perform better than more aggregated models (Cope and Punt 2011), especially when provided with adequately informative data.

Another common approach to deal with the effects of movement in stock assessment models, or any effect of unmodeled processes, is simply to add additional observation error (Francis 2011) in the data components of the model. This approach, however, may only prevent the lack of fit to particular data sources from unduly influencing model results, but does not address model misspecification causing the lack of fit (Wang et al. 2015) and prevents those data from providing useful information. The situation is further complicated because within a statistical modelling framework, it can be difficult to know if the lack of fit is due to misspecification related to that data component or to another model process, as all data and parameters are linked under the population dynamics (Piner et al. 2011).

In this simulation study we explore different stock assessment model configurations that attempt to account for the process of time-varying age-based movement explicitly or implicitly. The operating model is based on PBF, which is an iconic species that has a relatively simple ontogenetic macroscale migration pattern. A variable proportion of juvenile PBF migrate from the natal waters in the Western Pacific Ocean (WPO) to feeding grounds in the productive Eastern Pacific Ocean (EPO) where they reside for up to 4 years. Fish from the EPO then return to the WPO prior to spawning and remain there for life. These simple, macroscale age-based movements allow the testing of different modelling approaches in a relatively uncomplicated spatial model. A series of estimation models were conducted to approximate time-varying age-based movement by (*i*) estimating time-invariant movement, (*ii*) estimating length-based selectivity to account for contact selectivity and availability, (*iii*) adding additional observation error, (*iv*) aggregating fleets to account for the spatial heterogeneity of individuals arising from the movement, and (*v*) estimating both length- and time-varying age-based selectivity to account for contact selectivity and availability. Results of these approaches are compared with the model that explicitly (and correctly) models the spatial dynamics by estimating time-varying movement. The impact of the modelling approaches on derived and management quantities of interest are used to offer guidance on the efficacy of these modeling choices.

Materials and methods

Overview

Synthetic populations and corresponding fisheries data were simulated using a spatially explicit, two-area stochastic population dynamics operating model. The simulated fisheries data were subsequently used in seven different estimation modeling approaches to either explicitly or implicitly account for the process of time-varying age-based movement. A series of derived and management quantities from each model were compared with the true values from the operating model. The methods are explained starting with (*i*) the simulation of the PBF-like synthetic populations and generation of data, (*ii*) alternative estimation models, and (*iii*) calculation of performance metrics.

Simulation of PBF-like data

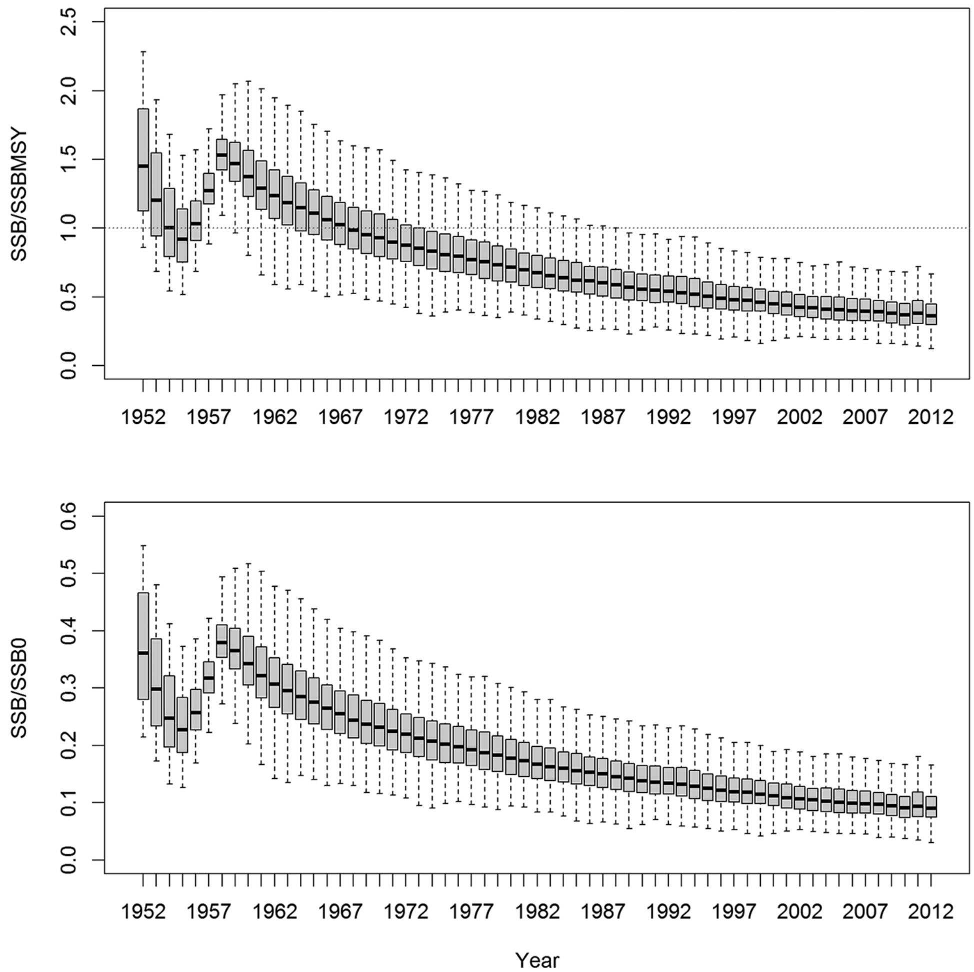
Operating model

We used the Stock Synthesis (SS3.24S; Methot and Wetzel 2013) stock assessment program to both create 1000 simulated data sets and estimate model parameters based on simulated data. The simulated populations approximated the population dynamics of PBF, which is a highly exploited and depleted stock (Fig. 1). Each generated data set was analyzed by all seven estimation models described under "Estimation models" below.

Stock Synthesis (SS) is a widely used forward-simulating integrated population dynamics model capable of fitting a wide variety of data types and can be used to generate simulated data from the same data types using its bootstrap functionality. The model keeps track of numbers at age by area and can transform the sampled age distribution into the associated length-at-age and length distributions. We used SS to create synthetic populations based on stochastically generated key parameters controlling the system (Table 1) and observation processes. Synthetic data were generated by sampling from parametric distributions with the same sample size and uncertainty assumptions of the underlying model (Methot and Wetzel 2013). More detail on the assumed distributions used in the sampling are described under "Observation model" below.

The operating model was developed and parameterized based on the 2014 PBF stock assessment with four seasons from 1952 to

Fig. 1. Box plot illustrating the distributions of spawning stock biomass (SSB) relative to its maximum sustainable yield (MSY)-based reference points (upper panel) and SSB relative to its unfished level (lower panel) from the simulated (true) populations. The horizontal line in the box represents median of the quantities, the box represents the lower and upper quartiles (25% and 75%), and the whiskers extend 1.5 times the interquartile range.



2012 (Anonymous 2014) but structured as spatially explicit, with movement between the two areas (WPO and EPO) assumed to occur instantaneously at the start of the year. Maximum age bin defined as an accumulator for all older ages was 20 years. Recruitment and spawning processes were assumed to take place only in the WPO with recruitment occurring in summer based on spawning biomass in spring. Biological processes (natural mortality, growth, and maturity) are seasonal assuming the same processes for the two areas and were simulated to be consistent with the 2014 assessment (Table 1). The key system process parameters (movement and recruitment) were generated randomly from distributions described in Table 1. Recruitment deviations with the same variability as assumed in the 2014 assessment were randomly generated to incorporate model process error.

To reflect incomplete knowledge of PBF movement, some aspects of movement were randomly generated. Age-based eastward movement rates from the WPO area to the EPO area (Fig. 2) were determined by the fraction of fish moving out of the WPO to the EPO at two reference ages, age 1 and $A_{\text{max\_WPO}\to\text{EPO}}$, where $A_{\text{max\_WPO}\to\text{EPO}}$ was assumed to be time-invariant but vary among each simulated population following a uniform distribution on the integer interval [3, 4]. The fraction of fish moving from the WPO to the EPO at age 1 was assumed to vary over time within each simulated population with mean rate at 40%, whereas the fraction of fish moving from the WPO to the EPO at age $A_{\text{max\_WPO}\to\text{EPO}}$ was fixed at 0.1% to approximate no older fish moving from the WPO to the EPO at $A_{\text{max\_WPO}\to\text{EPO}}$. Movement rates at each age a were calculated as values in the (0, 1) range through the transformation: movement rate$_a$ = $e^{p_a}/(e^{p_a} + 1)$, where the p_a are the underlying movement parameters chosen to achieve the rates described above. This inverse-logit transformation is the two-area realization of the generalized formula used by SS, in which the denominator contains the sum of the exponentiated parameters across all areas in the model, where the parameter for movement to the source area (fish staying in the same area) is fixed at 0. The movement rates for the integer ages between age 1 and age $A_{\text{max\_WPO}\to\text{EPO}}$ were the result of linearly interpolating the p_a parameters prior to the transformation described above. The parameter transformation was also the reason for the approximation to zero noted above, as no finite parameter value could provide a zero rate.

Age-based westward movement rates from the EPO to the WPO (Fig. 2) were determined by the specified fraction of fish returning to the natal area to spawn as increasing from 5% at age 1 to 99.9% at the second reference age ($A_{\text{max\_EPO}\to\text{WPO}}$), where $A_{\text{max\_EPO}\to\text{WPO}}$ was assumed to be time-invariant but vary among each simulated population following a uniform distribution on the integer interval [3, 4]. These rates produce the observed pattern of younger fish present in the EPO but few remaining in that area after maturation (where the parameter transformation noted above prevented the rate from being set to 100%). As with the westward movement described above, the westward rates were linearly interpolated

Table 1. Characterization of the data types and distributions that were used to develop each simulated population and derive all catch, catch per unit effort (CPUE), and length observations.

Description	Operating model
Data	
Dynamics calculated	1952–2012, quarterly
No. of areas	2
No. of fleets	6
No. of indices	4 (3 for F1, 1 for F4)
No. of fleets with length data	6
Parameter or variable	
Growth	
Maximum age	20 years
Length at age 0 (L_0, cm)	Fixed at 21.5
CV of length at age 0	Fixed at 0.262
Length at age 3 (L_3, cm)	Fixed at 109.194
CV of length at age 3	Fixed at 0.05
Growth coefficient (K)	Fixed at 0.157
Movement	
Minimum age with estimated fraction of fish moving from the WPO to the EPO ($A_{\mathrm{min\_WPO \rightarrow EPO}}$)	Fixed at age 1
Maximum age with fixed fraction of fish moving from the WPO to the EPO ($A_{\mathrm{max\_WPO \rightarrow EPO}}$)	Uniform (3, 4)
Fraction of fish moving from the WPO to the EPO at age $A_{\mathrm{min\_WPO \rightarrow EPO}}$ (1952–2011)	State 1: temporal process follows Uniform (0.1, 0.7) State 2: temporal process follows low-frequency signal (PDO-like) (see Fig. 3)
Fraction of fish moving from the WPO to the EPO at age $A_{\mathrm{max\_WPO \rightarrow EPO}}$	Fixed at 0.1%
Minimum age with fixed fraction of fish moving from the EPO to the WPO ($A_{\mathrm{min\_EPO \rightarrow WPO}}$)	Fixed at age 1
Maximum age with fixed fraction of fish moving from the EPO to the WPO ($A_{\mathrm{max\_EPO \rightarrow WPO}}$)	Uniform (3, 4)
Fraction of fish moving from the EPO to the WPO at age $A_{\mathrm{min\_EPO \rightarrow WPO}}$	Fixed at 5%
Fraction of fish moving from the EPO to the WPO at age $A_{\mathrm{max\_EPO \rightarrow WPO}}$	Fixed at 99.9%
Recruitment	
Log unfished recruitment ($\ln(R_0)$; thousands of fish)	Fixed at 9.09
Standard deviation for recruitment in log space (σ_R)	Fixed at 0.6
Spawner–recruit steepness	Fixed at 0.95
Annual recruitment deviations in log space (1942–1951)	Fixed annual values at 0.037, 0.0024, −0.0057, 0.3628, 1.5099, 0.1313, −0.2651, −0.5902, −0.1308, and −0.0373
Annual recruitment deviations in log space (1952–2011)	Normal (0, σ_R = 0.6)
Mortality	
Natural morality (age-specific M, year^{-1})	Fixed (1.6 at age 0; 0.386 at age 1; 0.25 at age 2 and older)
Seasonal fishing mortality (F, year^{-1}) for each fleet (1952–2012)	Generated (see Fig. 4)
Initial fishing mortality	Fixed at 0.42 for F1 and 10.37 for F4
Reproduction	
Proportion maturity at age	Fixed (0.2 at age 3, 0.5 at age 4, 1 at age 5 and older)
Selectivity patterns	Time-invariant and length-based selection assuming asymptotic pattern for F1 and domed shapes for F2–F6; values fixed at the estimates from the 2014 assessment

Note: All parameter values (except for recruitment deviations and fishing mortality, F) were drawn once from the distribution or fixed to produce a single simulated population. Parameter values that were fixed are based on the 2014 stock assessment (Anonymous 2014). Annual recruitment deviations and F values were drawn from the appropriate distribution for each year of the simulation. Uniform random variables are represented by Uniform (minimum bound, maximum bound) and Gaussian random variables are represented by Normal (mean, standard deviation).

between the two reference ages prior to transformation (also described above).

Two different states of nature governing the time-varying movement process were evaluated in the simulation (Fig. 3). The first assumed that an additive deviation from the mean of the movement parameter from the WPO to the EPO at age 1 for each year was a random event from a uniform distribution to achieve the movement rate ranging from 10% to 70%. The second assumed that an additive deviation from the mean of the movement parameter from the WPO to the EPO at age 1 for each year followed low frequency variability that is similar to the Pacific Decadal Oscillation (PDO) with persistence in the same warm or cold phase for 20 to 30 years using a sinusoidal function (Latif and Barnett 1996; Hare 1996; Zhang 1996). The time-varying movement parameters were calculated by adding these deviations to the mean movement parameter and transformed to time-varying movement rates in the 0–1 range based on the transformation noted above.

A variety of mean fishing mortality trajectories were used to generate fisheries catch for each fleet (Fig. 4) following the methods of Carruthers et al. (2012). Annual fleet-specific fishing mortality

Fig. 2. Age-based movement rates (percentage that move) between areas assumed in the simulation analyses. The movement rates from the Western Pacific Ocean (WPO) to the Eastern Pacific Ocean (EPO) at age 1 was further modified by additional time-varying variability as shown in Fig. 3.

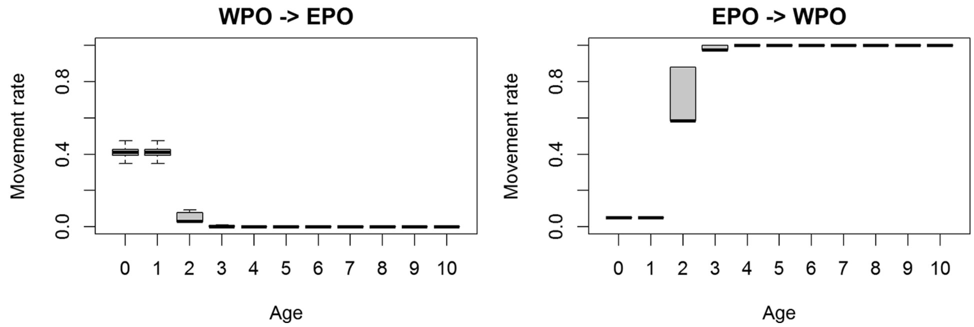
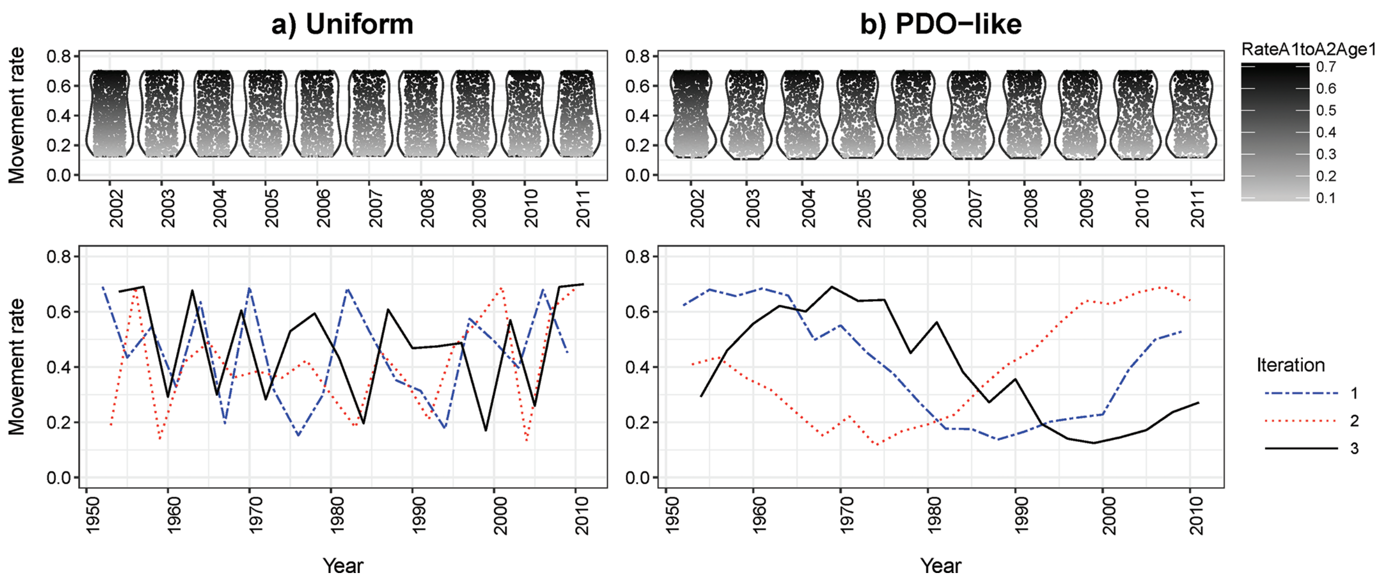


Fig. 3. Violin plot of the generated movement rates (percentage that move) for age 1 fish moving from area 1 (WPO) to area 2 (EPO) in the last 10 years (upper panels) and three examples of iteration-specific, time-varying movement rates (lower panels). Two discreet states of nature were used to describe movement: (*a*) uniform (left panels) and (*b*) Pacific Decadal Oscillation (PDO)-like (right panels).



rates were generated based on this overall mean and trend from the 2014 assessment (Anonymous 2014), increasing for 38 years then varying from decreasing to increasing thereafter. These annual fishing mortality rates were then proportionated into quarter based on the mean proportion of catch across years for each quarter from the 2014 assessment. We assumed the non-equilibrium initial conditions by starting the model at the depleted level estimated from the 2014 assessment and including recruitment deviations for 10 years prior to the first year of the modeling time period. This initial condition was set without variability in a consistent manner to that in the 2014 assessment; however, the rapid decline followed by a rapid increase of spawning stock biomass in the initial years of simulated period was generated (Fig. 1). This pattern might be related to the transition of this initial age structure toward the new equilibrium condition associated with the depleted state. Nevertheless, our quantities of interest are all at the end of the time series, so this pattern is unlikely to have a strong impact on the results.

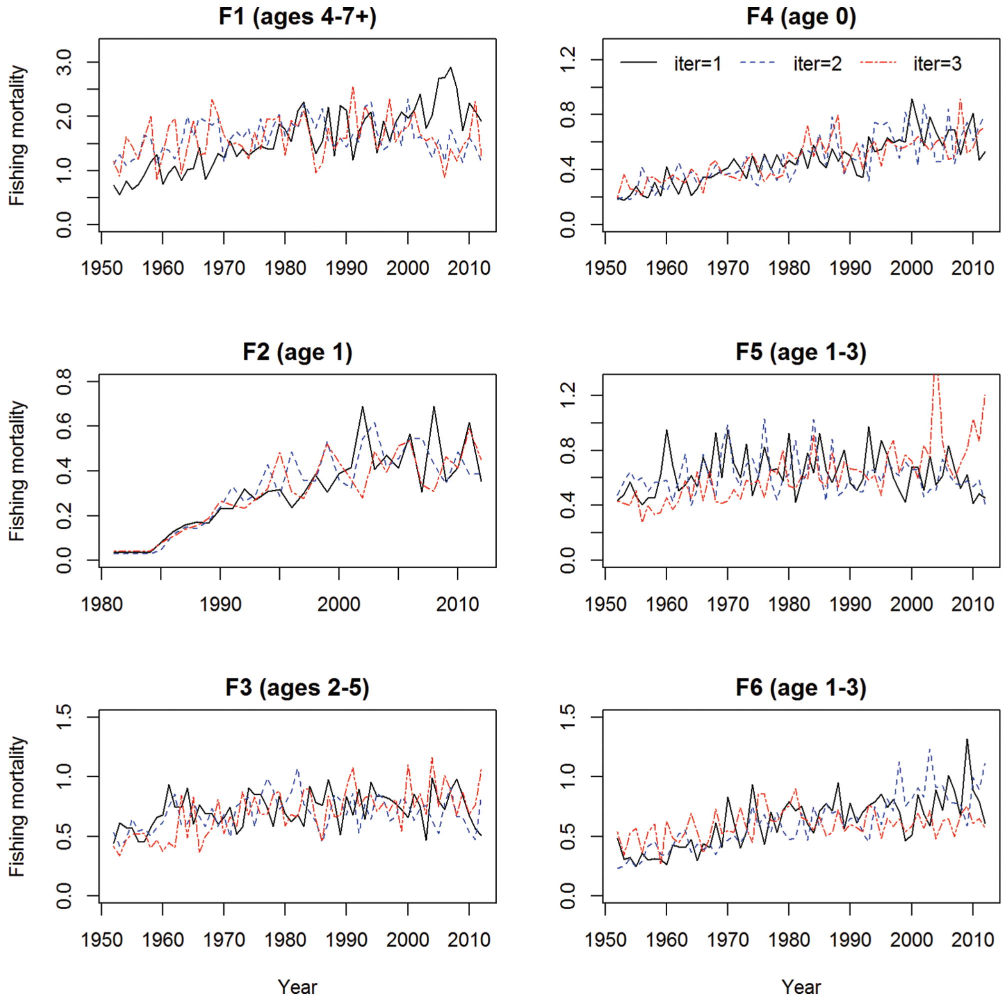
Selectivity for each of the six fleets was time-invariant and length-based so that the probability of capture was based on fish length, but the selected fish is also impacted by the age structure present in the spatial area. Selectivity patterns were simulated to be consistent with the 2014 assessment (Anonymous 2014). Selectivity follows a double-normal function with smooth transitions. This function is composed of three components: an ascending limb for small fish (asc), a flat top where selectivity equals 1.0 (top), and a descending limb for large fish (dsc). The three components are connected at two intersections using steep logistic functions (Methot and Wetzel 2013). Values for all three components were fixed at the estimates from the 2014 assessment. For the WPO fleet taking adults (F1), the selectivity pattern was assumed to be a logistic curve in the operating model but allowed to deviate from this curve in the estimation models.

Observation model

The observation component of the operating model included six fishing fleets: one WPO fleet taking adults (F1), one WPO fleet taking age 0 (F4), three WPO fleets taking ages 1–5 (F2, F3, F5), and one EPO fleet taking ages 1–3 (F6). Each fleet was assigned to one spatial region. Data generated for each fleet included quarterly catch, annual fishery-dependent indices of relative abundance, and quarterly length composition of the catch.

The catch data were assumed to be known without error. CPUE-based indices of relative abundance were only included for the fleets taking adults (F1) and age 0 (F4) from the WPO. Each index of relative abundance was assumed to occur in the season when the majority of catch was recorded. Each index of relative abundance data was assumed to be proportional to the available biomass with a scaling factor (catchability coefficient) and was generated with a bias-corrected lognormal error distribution with standard

Fig. 4. Three examples of simulated fishing mortality for each of six fleets (F1–F6). The ages taken by each fleet are given in parentheses.



deviation based on the 2014 assessment (Anonymous 2014). Quarterly size data for each fleet were assumed to follow a multinomial error structure with variance described by the quarterly sample size = 50 for simplicity.

Estimation models

The fisheries data generated in the simulations described above were utilized by seven alternative estimation models. The initial parameter values were based on the estimates from the 2014 stock assessment and the generated values in the operating model. Each alternative model attempted to account for the spatial patterns caused by time-varying age-based movement using a different combination of alternative model processes, adding additional observation error, or levels of data aggregation (Table 2; the first part of the abbreviation is the number of areas and second part of the abbreviation is the initial of the model name):

1. Correctly specified model (2A_CS) is spatially explicit containing two spatial areas by estimating time-varying movement rates fixed at the correct ages and estimating time-invariant, double-normal length-based selectivity (asc, top, and dsc) for each fleet to account for contact selectivity. The model included all six fleets as separate fleets, and the relevant processes in the operating model and data were given the same sample weights as in the operating model. Parameterization of the 2A_CS estimation model is identical to the operating model except that rates for the processes are estimated. In this regard the model is the least realistic model, as it assumes perfect understanding of the system.
2. Naive spatial model (2A_NI) is spatially explicit containing two spatial areas by estimating time-invariant movement rates fixed at the correct ages and estimating time-invariant, double-normal length-based selectivity (asc, top, and dsc) for each fleet to account for contact selectivity. The model included all six fleets as separate fleets, and data were given the same sample weights as in the operating model. Parameterization of the 2A_NI estimation model is similar to the operating model, but rates for the processes are estimated, with the exception that movement processes are time-invariant. This model would likely be applied when estimating spatial dynamics is important, but information on movement is limited.
3. Time-invariant model (1A_TI) is spatially implicit (a single area) by estimating time-invariant, double-normal length-based selectivity (asc, top, and dsc) for each fleet to attempt to account for both contact selectivity and availability. Because each fleet represents a combination of gear and area, spatial patterns in the fish biomass due to fish movement (i.e., availability) are implicitly accounted for by the length-based selectivity. All six fleets in the operating model were treated separately, as was also the case in the first two models, but in this model the fleets all operate in a single area. This approach is referred to as FAA approach to deal with spatial issues (Hurtado-Ferro et al. 2014; Waterhouse et al. 2014). Data from

Table 2. Summary of parameterization for recruitment, movement, and selectivity among the seven estimation models.

	Estimation model						
	1-2A_CS	2-2A_NI	3-1A_TI	4-1A_TVlen	5-1A_DW	6-1A_AG	7-1A_TVage
Recruitment							
Log unfished recruitment $\ln(R_0)$ (thousands of fish)	Est.	Est.	Est.	Est.	Est.	Est.	Est.
Recruitment deviations in log space (1952–2011)	Est.	Est.	Est.	Est.	Est.	Est.	Est.
Movement parameters							
Fraction of fish moving from the WPO to the EPO at age 1	Est., TV (1952–2011)	Est., TI	NA	NA	NA	NA	NA
Fraction of fish moving from the EPO to the WPO at age 1	Est., TI	Est., TI	NA	NA	NA	NA	NA
Selectivity patterns							
F1	WPO adults	WPO adults	WPO adults	WPO adults	WPO adults	WPO adults	WPO adults
Length-based contact	Est., TI	Est., TI	Est., TI	Est., TI	Est., TI	Est., TI	Est., TI
Age-based availability	NA	NA	NA	NA	NA	NA	NA
F2	WPO ages 1–5	WPO ages 1–5	WPO ages 1–5	WPO ages 1–5	WPO ages 1–5	WPO age 0	WPO ages 1–5
Length-based contact	Est., TI	Est., TI	Est., TI	Est., TI	Est., TI	Est., TI	Est., TI
Age-based availability	NA	NA	NA	NA	NA	NA	Est. jointly for F2, F3, and F5, TV (1952–2012, ages 1 to 4)
F3	WPO ages 1–5	WPO ages 1–5	WPO ages 1–5	WPO ages 1–5	WPO ages 1–5	WPO + EPO ages 1–5	WPO ages 1–5
Length-based contact	Est., TI	Est., TI	Est., TI	Est., TI	Est., TI	Est., TI	Est., TI
Age-based availability	NA	NA	NA	NA	NA	Est., TV (1952–2012, ages 1 to 7)	Est. jointly for F2, F3, and F5, TV (1952–2012, ages 1 to 4)
F4	WPO age 0	WPO age 0	WPO age 0	WPO age 0	WPO age 0	NA	WPO age 0
Length-based contact	Est., TI	Est., TI	Est., TI	Est., TI	Est., TI		Est., TI
Age-based availability	NA	NA	NA	NA	NA		NA
F5	WPO ages 1–5	WPO ages 1–5	WPO ages 1–5	WPO ages 1–5	WPO ages 1–5	NA	WPO ages 1–5
Length-based contact	Est., TI	Est., TI	Est., TI	Est., TI	Est., TI		Est., TI
Age-based availability	NA	NA	NA	NA	NA		Est. jointly for F2, F3, and F5, TV (1952–2012, ages 1 to 4)
F6	EPO ages 1–3	EPO ages 1–3	EPO ages 1–3	EPO ages 1–3	EPO ages 1–3	NA	EPO ages 1–3
Length-based contact	Est., TI	Est., TI	Est., TI	Est., TV (1952–2012)	Est., TI		Est., TI
Age-based availability	NA	NA	NA	NA	NA		Est., TV (1952–2012, ages 1 to 4)
No. of estimated parameters	164	104	102	285	102	531	605

Note: The cell defines if estimated parameters (Est.) were time-invariant (TI) or time-varying (TV). "NA" denotes that the parameter is not applicable to the process.

each fleet were given the same sample weights as in the operating model.

4. Time-varying model (1A_TVlen) builds on the 1A_TI model by allowing for and estimating a time-varying, double-normal length-based selectivity (i.e., incorporating an additional model process) to attempt to account for the annual spatial age-class availability due to movement. The model is the same as the 1A_TI model except that selectivity parameters (asc, top, and dsc) are estimated annually for the EPO fleet (F6).
5. Down-weighted model (1A_DW) builds on the 1A_TI model by down-weighting the assumed samples size for the composition data to attempt to account for the unmodeled process of time-varying movement. The model is the same as the 1A_TI model except that the length composition data for each of the non-CPUE fleets (F2, F3, F5, and F6) are given 10% of the weights of the CPUE fleets (i.e., they are down-weighted by 90%) because those fleets do not fish on the whole population for the respective ages.
6. Fleet aggregated model (1A_AG) builds on the 1A_TI model by aggregating four fleets taking the migrating age-classes (ages 1–4) into a single fleet so the number of fleets was reduced to three (two CPUE fleets and one non-CPUE fleet). This approach subsumes spatial issues within an aggregate fleet by combining catch and composition data, which were weighted by their catch in numbers. For this aggregate fleet, the model estimates time-invariant, double-normal length-based selectivity (asc, top, and dsc) and time-varying age-based selectivity (age-specific parameters) to approximate the length-based and age-based processes, respectively. The age-based selectivity for this aggregate fleet is parameterized as a random walk from ages 1 to 7 (transformed to remain in the 0–1 range), with the parameters for each age allowed to vary of time (see Taylor et al. 2014 or the online Supplementary material[2] for details). The model also estimates a separate time-invariant, double-normal length-based selectivity (asc, top, and dsc) for the two CPUE fleets. These CPUE fleets were given the same sample weights as in the operating model, and the aggregate fleet was given the sample weights that were weighted by their catch (in numbers; i.e., roughly 50).
7. Time-varying age-based model (1A_TVage) builds on the 1A_TI model by estimating a time-varying age-based selectivity (i.e., incorporating an additional model process) to attempt to account for the annual spatial age-class availability due to movement. The time-varying age-based selectivity is shared among all fleets in the same area and parameterized as a random walk from ages 1 to 4 (transformed to remain in the 0–1 range), with the parameters for each age allowed to vary of time (see Taylor et al. 2014 or the online Supplementary material[2] for details). All fleets in the operating model were treated separately. Each fleet has its own time-invariant length-based selectivity estimated (asc, top, and dsc) to account for differences in the contact selectivity, assuming that no significant changes have accrued in the fisheries to change the contact selectivity. Data from each fleet were given the same sample weights as in the operating model.

Comparison of model results

We evaluated the performance of the estimation models based on convergence of the model (determined by proportion of runs with positive-definite Hessian matrices) and the distribution of relative errors in the quantities of interest for the PBF stock assessment: depletion, spawning biomass, fishing mortality, unfished spawning biomass, maximum sustainable yield (MSY), spawning biomass at MSY, spawners-per-recruit at MSY, and fishing mortality at MSY. Equilibrium MSY was calculated by assuming the distribution of fishing effort among fleets and areas remains constant at the mean over the last 3 years. Percent relative error (RE_d^j) is defined as the percentage difference between estimated value (Est_d^j) and true value ($True_d^j$) divided by true value for quantity (j) for a given simulation run (d).

$$RE_d^j = \frac{Est_d^j - True_d^j}{True_d^j} \times 100$$

Bias and imprecision were expressed as the median of relative error (MRE) and the standard deviation of relative error (StdRE) for each method, respectively.

Results

Derived quantities

Model configurations have consequential impacts on the estimates for three out of four derived quantities (Fig. 5). The estimates of the unfished spawning biomass (SSB0) are robust to the model configurations under both hypotheses of time-varying movement (MREs between −1% and 2%; StdRE ≤ 10%) except for the 1A_AG model (MREs between 5% and 6%; Fig. 5 and Table 3). The estimates of the derived quantities related to the terminal year(s) (i.e., the ratio of spawning biomass in 2012 to unfished biomass (Depletion2012), the mean of estimated spawning biomass in the last 5 years (SSB0812), and the mean of the instantaneous fishing mortalities in the last 5 years (F0812)) were more median-biased than those of SSB0 with the exceptions of the 1A_DW and 1A_TVage models under the PDO-like movement. However, imprecision for these three quantities increased when the movement process was PDO-like.

Among the seven model configurations, the 2A_CS model performed the best based on both bias and imprecision for these three quantities related to the terminal year(s) under both hypotheses of time-varying movement (MREs between −1% and 2%; StdRE ≤ 10%). The accuracy and precision of the estimates for these three quantities deteriorate when the time-varying movement process was not correctly modelled. The 1A_TVage (MREs between −6% and 2%) and 1A_DW (MREs between −6% and 5%) models are the second-best based on the bias for the three quantities related to the terminal year(s) under both hypotheses of time-varying movement, whereas the 2A_NI (MREs between −6% and 14%) and 1A_AG (MREs between −16% and 13%) models performed the worst. The 1A_AG (531 parameters) and 1A_TVage (605 parameters) models had about twice the number of parameters as the next most parameterized model (1A_TVlen, 285 parameters). These two models with the most parameters were also the only ones that had any convergence issues (as indicated by a small fraction of nonpositive-definite Hessian matrices; Fig. 5).

An apparent bimodality was noticeable in estimates of some derived quantities under PDO-like movement for all incorrectly specified models (Fig. 5). The apparent bimodality was related to the proportion of scenarios with either high or low movement rates near the terminal years of the model (Figs. 3 and 6). The movement rates generated from the low-frequency signal (PDO-like) are autocorrelated between years. When the movement rates are low in the terminal years, the spawning biomass was overestimated with high variability. Conversely, when the movement rates are moderate to high, the spawning biomass was less biased with less variability. The bias in the derived quantities was likely the result of the model having few observations of cohorts near the end of the model and the inability of the structure of the alternative models to adequately account for the observed size composition data.

[2]Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2016-0294.

Fig. 5. Relative error values of estimated derived quantities for the seven estimation models applied to simulated populations for uniform (left panels) and PDO-like (right panels) movement. The open grey circles indicate converged estimates, and the violin depicts kernel probability density of all converged runs. Depletion2012 is the ratio of spawning biomass in 2012 to unfished level. SSB0812 is the mean of estimated spawning biomass in the last 5 years. F0812 is the mean of the instantaneous fishing mortalities in the last 5 years. SSB0 is the estimated unfished spawning biomass. The number of runs where final Hessian matrix is positive-definite for each of estimation models is given in the bottom of each panel. [Colour online.]

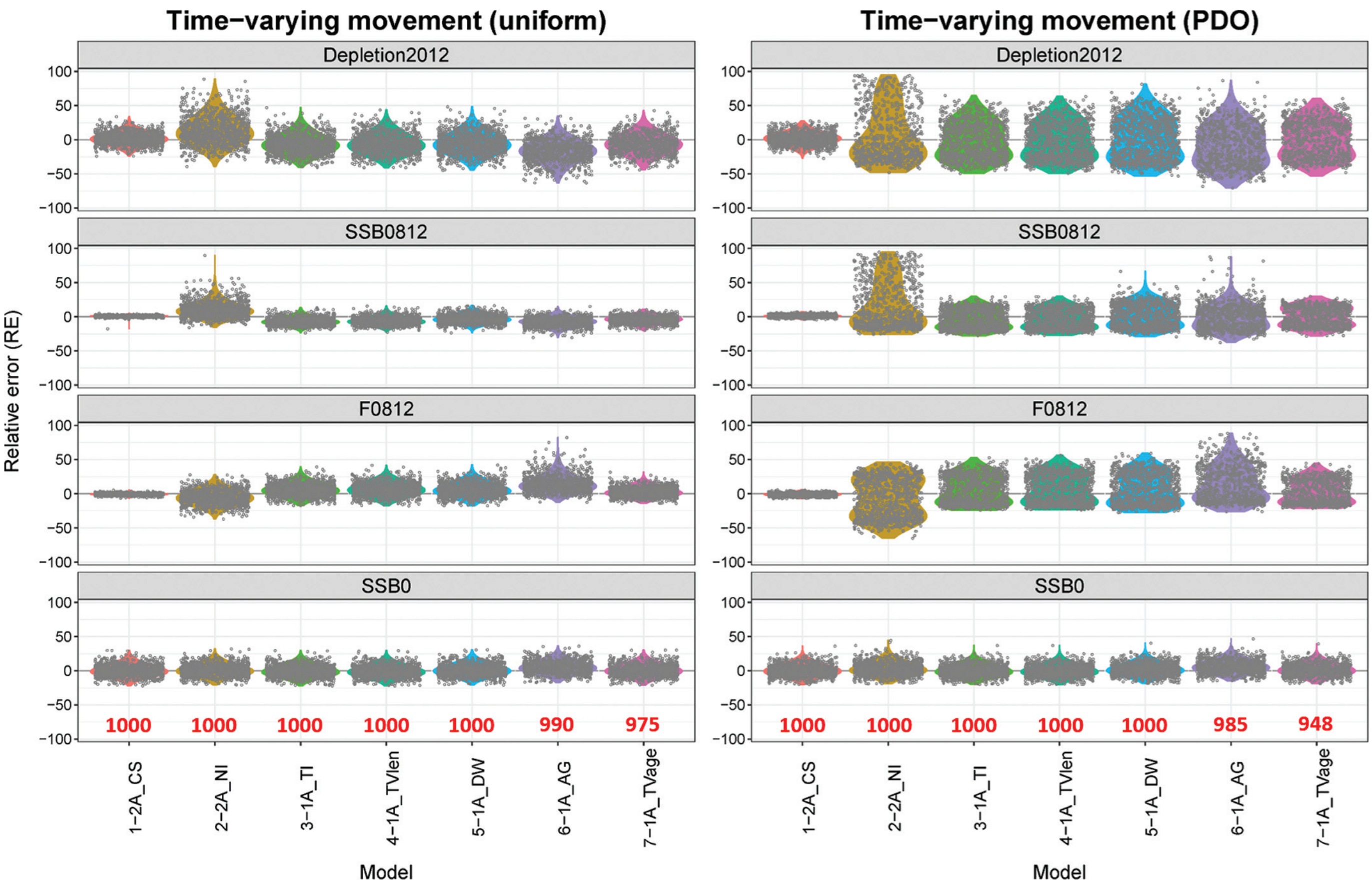


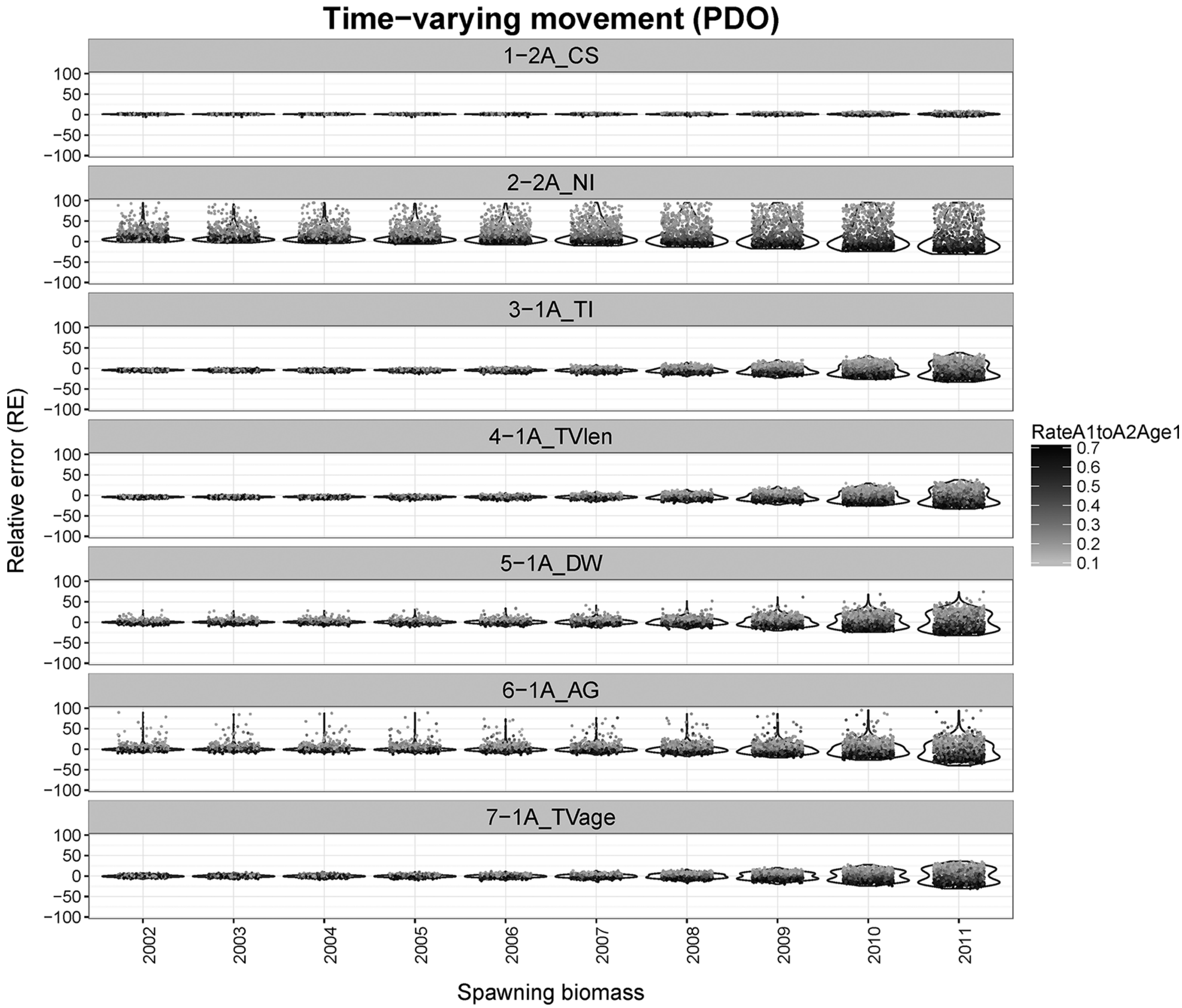
Table 3. Median and standard deviation (in parentheses) of relative error values of estimated derived and management quantities for the seven estimation models.

	Estimation model						
	1-2A_CS	2-2A_NI	3-1A_TI	4-1A_TVlen	5-1A_DW	6-1A_AG	7-1A_TVage
Time-varying movement (uniform)							
Depletion2012	2 (9)	12 (21)	−7 (14)	−7 (14)	−6 (15)	−16 (16)	−6 (14)
SSB0812	1 (1)	9 (12)	−7 (6)	−7 (6)	−4 (6)	−8 (7)	−4 (5)
F0812	−1 (2)	−6 (11)	5 (9)	6 (10)	5 (10)	13 (13)	2 (7)
SSB0	0 (8)	1 (9)	−1 (8)	−1 (8)	1 (9)	5 (9)	0 (9)
SSBMSY	2 (9)	0 (9)	8 (9)	8 (9)	6 (9)	8 (9)	4 (9)
SPRMSY	2 (1)	−1 (2)	8 (2)	8 (2)	5 (2)	3 (2)	4 (2)
FMSY	−2 (1)	1 (5)	−9 (4)	−8 (4)	−4 (4)	1 (4)	−5 (3)
MSY	−1 (8)	−2 (9)	4 (10)	3 (10)	3 (10)	3 (10)	2 (9)
Time-varying movement (PDO)							
Depletion2012	2 (9)	14 (72)	−5 (26)	−5 (26)	−2 (29)	−10 (30)	−1 (26)
SSB0812	1 (2)	10 (60)	−5 (14)	−5 (14)	0 (16)	−2 (19)	0 (14)
F0812	−1 (2)	−6 (28)	4 (20)	5 (21)	3 (22)	9 (26)	0 (17)
SSB0	1 (8)	2 (10)	0 (9)	0 (9)	2 (9)	6 (9)	1 (9)
SSBMSY	2 (9)	0 (9)	9 (9)	9 (9)	7 (9)	8 (9)	5 (9)
SPRMSY	2 (1)	−2 (3)	9 (1)	9 (1)	5 (2)	2 (3)	3 (3)
FMSY	−2 (1)	3 (4)	−9 (4)	−8 (4)	−3 (4)	2 (4)	−3 (2)
MSY	0 (8)	−3 (9)	4 (9)	4 (9)	2 (9)	3 (10)	2 (9)

Management quantities

Model configurations and the hypotheses of time-varying movement have less impacts on the estimates for all four MSY-based management quantities (MREs between −9% and 9%; StdRE ≤ 10%) than those for the derived quantities (MREs between −16% and 14%; StdRE ≤ 72%) (Fig. 7 and Table 3). The estimates of all four management quantities were less sensitive to hypotheses of time-varying movement without the terminal year bimodality seen in

Fig. 6. Relative error values of 2002 to 2011 spawning biomass estimated from the seven estimation models applied to simulated populations for PDO-like movement. The dots indicate converged estimates, and the violin depicts kernel probability density of all converged runs. Shading of the dots represents the movement rate from area 1 (WPO) to area 2 (EPO) at age 1 ranging from dark representing high movement rate (0.7) to light representing low movement rate (0.1). The gradient is scaled from the mean movement rate (0.4) to the two endpoints.



the derived quantities. Among the seven model configurations, the 2A_CS (MREs between −2% and 2%) and 2A_NI (MREs between −3% and 3%) models are the best based on bias for the estimates of all four MSY-based management quantities under both hypotheses of time-varying movement. Both 1A_AG (MREs between 1% and 8%) and 1A_TVage (MREs between −5% and 5%) models performed better than other one-area models (MREs between −9% and 9% for 1A_TI, −8% and 9% for 1A_TVlen, −4% and 7% for 1A_DW) to estimate management quantities.

Discussion

For most applied population dynamics modelling of systems where fish migration occurs, spatially explicit models with estimated movement have not been used. Our results suggest that estimating the correct process of spatial dynamics with time-varying movement may be the only method that can assure unbiased and precise estimates of both derived and management quantities. In contrast, the naive spatial model (2A_NI) that overly simplifies the movement process poorly estimates derived quantities in the terminal years but estimates well MSY-based management quantities. For cases such as PBF where movement patterns are relatively simple, it may be worth the resources to devote more effort to well-designed studies that provide direct observations of the movement process (e.g., tagging).

When considering a single-area assessment model to account for time-varying age-based movement (spatially implicit), a model that estimates both length-based and time-varying age-based selectivity to approximate the stationary contact selectivity and time-varying availability may be the best alternative (1A_TVage). Both the fleet-aggregated (1A_AG) and time-varying age-based (1A_TVage) models substituted estimating time-varying age-based selectivity to approximate time-varying age-based movement. The time-varying age-based model was demonstrably better than all other single-area models at estimating derived quantities related to the terminal years, while both the fleet-aggregated and the time-varying age-based models estimated MSY-based manage-

Fig. 7. Relative error values of estimated MSY-based management quantities for the seven estimation models applied to simulated populations for uniform (left panels) and PDO-like (right panels) movement. The open grey circles indicate converged estimates, and the violin depicts kernel probability density of all converged runs. The number of runs where final Hessian matrix is positive-definite for each of estimation models is given in the bottom of each panel. [Colour online.]

ment quantities better than all other singe-area models. One lesson learned in the study was that care must be taken to incorporate variability in all important processes, and aggregation of data led to a particular form of process variability. Aggregating several fleets (1A_AG) with annual changes in catch proportions among fleets led to unmodelled annual changes in the contact selectivity. Even when individual contact selectivity patterns are time-invariant, aggregating several fleets with temporal variability in catch results in the aggregate contact selectivity changing. Ignoring this process variability in the length-based contact selectivity for a fast-growing fish with high fishing mortalities on juveniles led to both bias and imprecision for the derived quantities. In contrast, the time-varying age-based model that maintained individual contact selectivity and shared regional availability did not suffer from the changing contact selectivity at the cost of increased number of parameters.

Less complex single-area models that used length-based selectivity to account for both contact selectivity and time-varying availability (1A_TI and 1A_TVlen) were not able to capture important aspects of the population dynamics, similar to the findings in Hurtado-Ferro et al. (2014). This may be because the exclusive use of length-based selectivity does not correctly mimic the age-based process of movement. An additional confounding misspecification for the 1A_TVlen model was partially due to allowing only fleets operating in one area to have time-varying selectivity parameters. Age-based movement between areas changes the age structure of both areas; thus, in a single area model, the availability component of selectivity will need to account for movement in all fleets and both areas that catch the migrating age-classes. However, modelling time-varying length-based selectivity in all fleets that catch the migrating age-classes would have resulted in a considerable numbers of estimated parameters (800+), increased confounding among the parameters, and ignored that the process of movement was age-based and not length-based.

More generally, when attempting to model populations with spatial structure, researchers need to consider that lack of fit to data arises when all relevant model processes are not included or those processes are modeled with an incorrect structure. Whether it is preferable to add additional but potentially incorrect model process or simply to treat the unmodelled process error as observation error for less prioritized data are not clear (Francis 2011; Lee et al. 2014). In situations where we lack biological understanding, adding additional model process to approximate movement requires more parameters without guaranteeing a correctly specified model. The simplest modelling approach of including the unmodeled process error as part of the observation error (1A_DW) performed almost as well as the best alternative model (1A_TVage) with far less complexity and faster run times. Because of the simplicity of this model configuration, it could be produced relatively easily in applied research and may perform as well as more complex alternatives in a one-area model. This approach may be reasonable when causes of misspecification are not known; however, because the misspecification causing the lack of fit has not been addressed, bias and imprecision in model estimates are likely. More research aimed at diagnostic methods to determine the actual model processes misspecified are needed (Carvalho et al. 2017; Maunder and Piner 2017).

As is the case for many simulation studies, many caveats should be included in the interpretation of the findings. The best-performing model (2A_CS) was based on perfect knowledge of the system and the simplification that age-based movement followed a functional form. Because the 2A_CS model is perfectly specified, it is not surprising that the model is able to estimate movement rates without any parameter confounding. In addition, specifying many biological parameters (natural mortality, steepness, growth, and fecundity) likely reduced the uncertainty on some quantities such as SPRMSY and FMSY. Intentionally generating better data than should be expected in real-world applications allowed for more interpretable comparisons of specific changes in model structure but at the cost of realism. If all potential real-world sources of error were included, the study might have captured more of the real variability in estimates that should be expected but also likely would obscure the relative differences in performance between alternative models. The implications of this are especially relevant to the correctly specified model, which almost certainly would not perform as well in actual applications. It is also reasonable to assume that in real-world applications the magnitude of both bias and imprecision as well as model convergence probability could be very different. Because we assumed a length-based model, results informed by other types of data (age compositions, tagging data, etc.) might be different (Hulson et al. 2011; Goethel et al. 2015). Beyond the simplifications discussed above, there are certainly a number of other alternative models that could have been considered. However, to keep the study manageable, the range was limited to a variant of those under consideration for the provision of advice for this migratory species.

Spatial issues arising from nonuniform movements continue to be a source of bias and uncertainty in the modelling of population dynamics (Hurtado-Ferro et al. 2014; Carruthers et al. 2015). This study attempted several model configurations, including those that attributed all the variability to length-based processes (ignoring age-based processes), but only models that included the correct combination of both processes performed well. Despite the study limitations, the results of this and other recent work (Hurtado-Ferro et al. 2014; McGilliard et al. 2015) provide guidance on possible solutions when a spatially explicit model is not feasible. In particular, the FAA approach depends on providing adequately flexibility to selectivity, not only in the degree of dome shape (Waterhouse et al. 2014; O'Boyle et al. 2016) but also in the degree of variation over time. We recommend that research should continue on developing and testing spatial models (McGilliard et al. 2015) on a case-by-case basis and that biological research should focus on designing and conducting the appropriate studies to collect the data needed to estimate movement rates. If unbiased models are unlikely to be developed, management strategies that are robust to these types of assessment biases need to be developed (Rochet and Rice 2009; Bunnefeld et al. 2011).

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