



Original Article

Spatial and temporal variability in somatic growth in fisheries stock assessment models: evaluating the consequences of misspecification

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Distinct types of fish species experience variation in somatic growth rates over their life span; however, growth has historically been assumed to be invariant across time and space in integrated analysis-based stock assessment. A few previous studies have reported biased and imprecise assessment model outcomes when variability in somatic growth was ignored. In this study, we used a simulation-estimation framework to expand previous analyses and to examine the consequences of ignoring or incorporating spatial and temporal (year- and cohort-specific) variability in somatic growth in stock assessment models. The study included three life history types: small pelagic (e.g. sardine), gadids (e.g. cod), and long-lived (e.g. rockfish). In general, ignoring any type of variability in somatic growth led to biased and imprecise estimates of stock spawning biomass and management quantities. Unequal distribution of fishing mortality across space had large impacts on the performance of estimation models as well. Conversely, accounting for somatic growth variability, either by including an environmental index, estimating annual deviates, or implementing a spatially explicit model, produced unbiased and precise results. This study shows that somatic growth variability might produce large effects in stock assessments when ignored and provides pertinent information for stock assessment best practice guidelines.

Keywords: mean size-at-age, somatic growth, spatial and temporal variability, stock assessment, stock synthesis

Introduction

A stock assessment model is a mathematical representation of a fish population dynamic (e.g. birth, natural and fishing death, growth, maturation, and movement) used to evaluate the effects of harvest policies on its biological status relative to biological reference points (Beverton and Holt, 1957; Methot and Wetzel, 2013). Integrated analysis (IA) is a type of stock assessment model that became popular at the end of the 20th century and fits the model to several sources of data simultaneously in a single analysis (Fournier and Archibald, 1982; Maunder and Punt, 2013). One of the most used IA tools is Stock Synthesis (SS), a flexible statistical catch-at-age modelling framework applied to numerous fish stocks worldwide (Methot and Wetzel, 2013). SS's main strength is to estimate

numerous biological parameters at once to capture the complexity of a fish population; however, it is susceptible to model misspecification as any stock assessment model (Maunder and Punt, 2013). To further evaluate impacts of model misspecification in statistical catch-at-age models, SS and *ss3sim*, an R package to perform simulation experiments (Anderson *et al.*, 2014), have been used to study the performance of stock assessment models under different assumptions about natural mortality, somatic growth, and data quantity (Johnson *et al.*, 2015; Ono *et al.*, 2015; Monnahan *et al.*, 2016; Lee *et al.*, 2018; Stawitz *et al.*, 2019).

Fish populations experience variations of biological parameters due to intra- and interspecific interactions, or changes in environmental conditions (Shelton and Mangel, 2011), which may negatively impact the performance of a stock assessment method if they

are neglected (Keyl and Wolff, 2008). Variation in somatic growth is an important driver of population fluctuations, in some cases as important as variability in recruitment (Stawitz and Essington, 2018), and has been documented for many fish taxa (Gertseva *et al.*, 2017; Adams *et al.*, 2018; Ciannelli *et al.*, 2020). To study variations in somatic growth, changes in mean size-at-age across time and space are usually examined, which are generally caused by variations in the Brody growth coefficient (k) or asymptotic length (L_∞) of the von Bertalanffy growth function (Gertseva *et al.*, 2017; Adams *et al.*, 2018).

There are two main ways of how the mean size-at-age can vary temporally within a stock: changing systematically for all ages of fish individuals born in a particular year, known as cohort-specific (Feltrim and Ernst, 2010), or for all fish during a particular year, known as year-specific (Arnekleiv *et al.*, 2006). Triggers of these types of variability are not typically known and are not easily discerned, but some contributing factors may be (i) conditions in early-life stages, which might determine cohort growth rates in the future (Ciannelli *et al.*, 2020); (ii) genetic, where slow-growing ancestry might likely have a slow-growing offspring; (iii) density dependence, high biomass might reduce growth rates for a cohort or year class (Rijnsdorp and van Leeuwen, 1996); (iv) fishing pressure, through the selection of larger individuals, which decreases the mean length-at-age of the population but increases per-capita resource availability leading to plastic, compensatory increase in juvenile somatic growth (Lester *et al.*, 2014; Wilson *et al.*, 2019); and (v) environmental conditions, temperature, and high food supply increases the metabolism; and therefore also increases growth rates within a particular year (Kreuz *et al.*, 1982; Baudron *et al.*, 2014).

Historically, fish stock assessment models have rarely accounted for variations in somatic growth rates, assuming it was static through time (Whitten *et al.*, 2013). Previous studies have demonstrated that ignoring temporal variations in somatic growth rates may lead to serious bias in spawning biomass and management quantities for some species (Lee *et al.*, 2018; Stawitz *et al.*, 2019). Likewise, stock assessment models have commonly assumed that the region to be assessed contains a single homogeneous stock (Cadrin, 2020), seldom a valid assumption. There is scarce information about how the misspecification of spatial variability in somatic growth might affect estimates of the status of stock despite the increasing evidence of spatial variability in growth for a wide variety of species (Silva *et al.*, 2008; Gertseva *et al.*, 2010, 2017). Two previous studies reported large bias in biomass estimates when spatial variability in somatic growth was ignored for pink ling (*Genypterus blacodes*) off southern Australia (Punt *et al.*, 2015, 2016). The implementation of spatially explicit stock assessment models to account for spatial variability in biological traits has become a topic of study in recent years, with several studies showing scenarios where estimation performance was improved compared to single-area models (McGilliard *et al.*, 2015; Vigier *et al.*, 2018; Punt, 2019). Nevertheless, it is still unclear how ignoring spatial variation in biological parameters such as somatic growth and other model components (e.g. fishing mortality) may affect model outcomes for different types of species.

The main goal of this study is to evaluate the consequences of ignoring spatial or temporal variability in somatic growth in stock assessment models across three types of life histories: small pelagic (e.g. sardine), gadids (e.g. cod), and long-lived (e.g. rockfish). To accomplish our goal, we implemented a simulation experiment that consisted of comparing key variables from the operating model (OM), which represents the true population dynamics, with those

from the estimation models (EMs), which were fit to data sampled from the OM. Mean size-at-age was assumed to vary temporally based on the annual Pacific Decadal Oscillation (PDO) index or spatially between two areas. We also evaluated the impacts of (i) year- and cohort-specific temporal variability, (ii) the estimation method when the EM accounted for temporal variability (inclusion of an observed environmental index or estimation of annual deviates), and (iii) the distribution of fishing mortality between areas. This study provides guidelines for stock assessment scientists and expands previous investigations in somatic growth variability and stock assessment models by including diverse life histories, types of temporal variability, estimation methods, and spatial variability scenarios, making it useful for a wide range of study cases.

Material and methods

Simulation approach

We implemented a simulation experiment as done in previous studies (Johnson *et al.*, 2015; Ono *et al.*, 2015; Lee *et al.*, 2018). Each combination of OM and EM is referred to as a scenario and consists of the following four steps: (i) simulate the true population dynamics with process error in recruitment (and growth in some cases) across years by the OM, (ii) sample from the OM dynamics with observation error, (iii) fit the EM to sampled data, and (iv) compare estimates of relevant quantities with the true values simulated by OM. These steps were repeated many times (replicates) with different process and observation errors for each scenario. This simulation-estimation approach was performed using SS (version V3.30.14; Methot and Wetzel, 2013) for both the OM and the EM. Full details on SS can be found in Methot and Wetzel (2013) and Methot *et al.* (2020). We conducted our analysis in R (version 3.6.1; R Core Team, 2019), using the stock assessment simulation framework *ss3sim* (Anderson *et al.*, 2014). The model configurations and code to run and process these analyses are available online (https://github.com/gmoroncorrea/spatiotemporal_growth).

The operating model

OM configurations were generally based on simplified versions of recent stock assessment models of the Pacific sardine (*Sardinops sagax*) in the California Current System (CCS; Hill *et al.*, 2015), Pacific cod (*Gadus macrocephalus*) in the eastern Bering Sea (EBS; Thompson and Thorson, 2019), and splitnose rockfish (*Sebastes diploproa*) in the CCS (Gertseva *et al.*, 2009) (referred as sardine, cod, and rockfish hereafter for simplicity). These and similar species have shown significant spatiotemporal variability in somatic growth (Silva *et al.*, 2008; Black, 2009; Feltrim and Ernst, 2010; Gertseva *et al.*, 2010; Dorval *et al.*, 2015; Ciannelli *et al.*, 2020), which makes them suitable examples to represent a wide variety of life histories for this study. The intention in using a simplified version of stock assessments for these three species was to capture a variety of typical life history traits in OM configurations, each of which may affect the performance of various stock assessment approaches, rather than focusing on modelling any specific species. All OM configurations were age-structured with sexes combined and assumed a Beverton–Holt stock–recruitment relationship. One fishery and one survey were assumed when the OM simulated a single area (e.g. base and temporal variability cases), and two fisheries and two surveys were assumed when the OM simulated a two-area model (e.g. spatial variability cases; Figure S1). For the latter case, no

Table 1. Life history, fishery, and modelling parameters used in the OM and specified as initial values in the EM.

Parameter	Symbol	Sardine	Cod	Rockfish	Estimated?	Lower bound	Upper bound
Number of simulated years	–	40	75	120	–	–	–
Burn-in period (year)	–	1–10	1–25	1–40	–	–	–
Natural mortality (year ⁻¹)	<i>M</i>	0.4	0.36	0.048	Yes	0	2
Mean length-at-age <i>a</i> ₁ (cm)	<i>L</i> ₁	11.77	15.41	10.3	Yes	1	100
Youngest age well represented in data (year)	<i>a</i> ₁	0.5	1.5	1.66	–	–	–
Asymptotic length ¹ (cm)	<i>L</i> _∞	23.46 [22.5–24.5]	117.9 [120–116]	29 [27.5–30.5]	Yes	1	200
Growth rate ¹ (year ⁻¹)	<i>k</i>	0.38 [0.43–0.33]	0.11 [0.09–0.13]	0.16 [0.18–0.14]	Yes	0	2
Accumulator age (year)	<i>a</i> _{max}	15	20	100	–	–	–
SD of <i>L</i> ₁ -at- <i>a</i> ₁ (cm)	<i>SD</i> ₁	1.41	3.43	1.82	Yes	0	10
SD of <i>L</i> _∞ -at- <i>a</i> _{max} (cm)	<i>SD</i> ₂	1.17	10.31	6	Yes	0	10
Link parameter: <i>Env</i> _{index}	<i>par</i> _{env}	1	1	1	Yes	–10	10
Link parameter: deviates	<i>dev</i> _{se}	0.5	0.5	0.5	No	–	–
Scaling constant for weight-length (kg.cm ^{-0.2})	<i>Ω</i> ₁	7.52e-06	5.59e-06	2e-05	No	–	–
Allometric factor weight-length (–)	<i>Ω</i> ₂	3.23	3.19	3.01	No	–	–
Length-at-50% maturity (cm)	<i>Ω</i> ₃	15.44	50	21.84	No	–	–
Maturity slope (cm ⁻¹)	<i>Ω</i> ₄	–0.89	–0.95	–0.57	No	–	–
Steepness (–)	<i>h</i>	0.8	1	0.58	No	–	–
Log mean recruitment at unfished level (–)	<i>lnR</i> ₀	15.39	13.15	9.54	Yes	4	40
Recruitment deviation (–)	<i>σ</i> _R	0.75	0.72	1	No	–	–
Log survey catchability coefficient	<i>lnQ</i>	0	0	0	Yes	–20	20
Mean fishery size-at-50% selectivity (cm)	<i>β</i> _{1,f}	18	59.5	25	Yes	0	200
Fishery size selectivity slope (cm)	<i>β</i> _{2,f}	3	15	5	Yes	0	200
Mean survey size-at-50% selectivity (cm)	<i>β</i> _{1,s}	13	16	15	Yes	0	200
Survey size selectivity slope (cm)	<i>β</i> _{2,s}	3	2	1.5	Yes	0	200
Sample size for fishery length composition data	<i>η</i> _{fish}	100	100	100	–	–	–
Sample size for survey age composition data	<i>η</i> _{surv}	100	100	100	–	–	–
Coefficient of variation for the survey index of abundance (–)	<i>CV</i> _{surv}	0.2	0.2	0.2	–	–	–
Overdispersion parameter for the fishery length composition data	<i>c</i> _{par}	2	2	2	–	–	–

Values in brackets are specified when the OM simulated spatial variability (two-areas models) for Area 1 and 2, respectively.

differences in fleets features (e.g. catchability, observation error structure and variance, selectivity) were simulated between areas. Process error was included in the OM by adding independent, bias-corrected lognormal random deviates to the recruitment time series. Selectivity was assumed to be logistic, size-based, and time and space-invariant. Survey catchability was assumed to be 1. Parameters for each life history configuration were based on values specified in stock assessment models and are reported in Table 1.

We modelled somatic growth using the specialized von Bertalanffy growth function (Schnute, 1981), as parametrized in SS. Mean size-at-age at the initial population (i.e. unfished equilibrium population) is calculated from

$$L_a = L_\infty + (L_{min} - L_\infty) e^{-k(a-a_1)}, \tag{1}$$

where *k* is the Brody growth coefficient (year⁻¹), *L*_∞ is the asymptotic length (cm), *L*_{*a*} is the mean size (cm) of fish at age *a*, *a*₁ is the youngest age that is well-represented in the data, and *L*_{min} is the size (cm) at *a*₁. SS linearly interpolates the size of fish younger than *a*₁, adjusts the mean size of fish within the accumulator age, and normally distributes lengths at each age around a mean size (Appendix A in Methot and Wetzel, 2013). Then, mean size is incremented across years as

$$L_{y+1,a+1} = L_{y,a} + (L_{y,a} - L_\infty) (e^{-k} - 1) \gamma_c, \tag{2}$$

where *y* stands for years and *γ*_{*c*} is a cohort-specific multiplier (cohort *c* = *y* – *a*), which is assumed to be 1 unless cohort-specific variability is modelled.

Spatial variability in somatic growth

To simulate changes in mean size-at-age in space, we varied *k* and *L*_∞ between two areas (Table 1). For these cases, the OM simulated two-area models that assumed no movement post-settlement with global recruitment, followed by equal distribution of new recruits across the two areas (Figure 1A). Fish individuals in Areas 1 and 2 always had smaller and larger mean size-at-age at any age, respectively (Figure 2).

Temporal variability in somatic growth

To create temporal changes in mean size-at-age, *k*, or *L*_∞ varied across years for year-specific temporal variability (*k* turned into *k*_{*y*} and *L*_∞ into *L*_{∞*y*} in Equation 2). *k*_{*y*} and *L*_{∞*y*} were simulated as

$$k_y = k * \exp(PDO_{st_y}) \quad \text{and} \quad L_{\infty_y} = L_\infty * \exp(PDO_{st_y}),$$

where *PDO*_{*st*} is the annual Pacific Decadal Oscillation (PDO, Figure 1C) index (Newman et al., 2016) standardized between defined ranges to obtain minimum and maximum mean sizes-at-ages over years as shown in Figure 2.

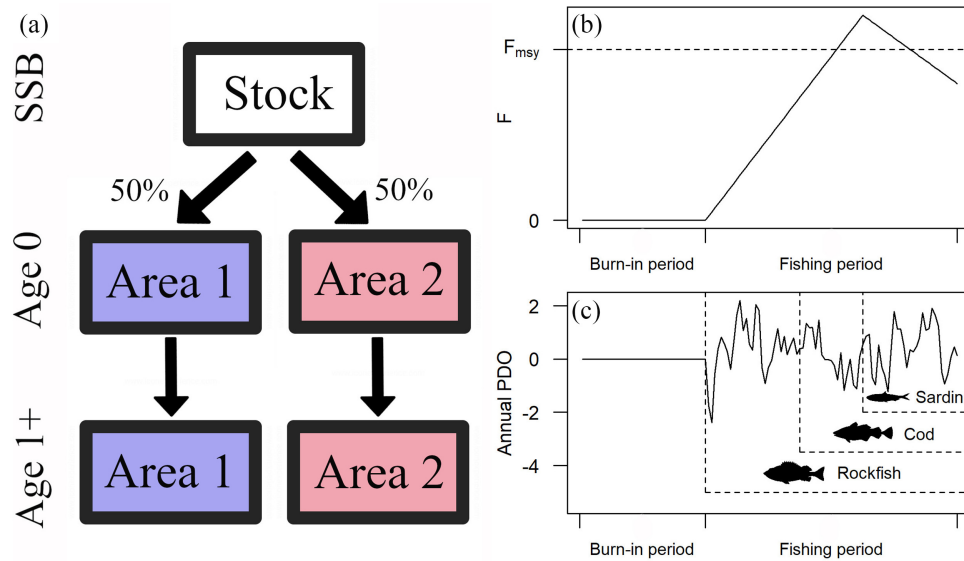


Figure 1. (a): Spatial structure assumed in the OM when simulating two areas: recruitment is distributed evenly between areas (50–50%). Area 1 (blue) had smaller individuals while Area 2 (red) had larger individuals at any age. There is no movement between areas after settlement. (b): Pattern of instantaneous fishing mortality (F) over time for the three types of life history. (c): The annual PDO index, used to simulate year and cohort-specific temporal growth variability in the OM. Distinct life histories used different parts of the PDO time series, but the burn-in period always had zero values (i.e. no variability).

To model cohort variability in growth, γ_c in Equation 2 varied over years as

$$\gamma_c = \exp(PDO_{st}),$$

where PDO_{st} was standardized accordingly to obtain a minimum and maximum variability over cohorts as shown in Figure 2.

The magnitude of simulated variability in mean size-at-age varied across life histories and was based on published literature (Silva *et al.*, 2008; Gertseva *et al.*, 2010; Dorval *et al.*, 2015; Ciannelli *et al.*, 2020) (Figure 2).

Data generation

The OM generated four types of data: catches, survey index of abundance, fishery length composition, and survey age composition (Figure S1). Fishing was initiated after a “burn-in” period that varied across life histories (see Table 1); and catches were reported for all years without error. Catches were specified using an instantaneous fishing mortality time series (referred F_{vals} hereafter, vals stands for “F values”) that increased linearly in time to F_{high} , the value that led to catch at equilibrium of 0.9 MSY on the right limb of the production curve ($F_{high} > F_{MSY}$), and then decreased linearly to F_{low} , the value which leads to an equilibrium catch of 0.9 MSY on the left limb of the production curve ($F_{low} < F_{MSY}$) (“two-way trip” pattern, Magnusson and Hilborn, 2007) (Figure 1b). For two-area OM configurations, distinct F_{vals} between areas were evaluated:

(i) F_{vals} is the same for both areas (100–100% case, equal distribution).

(ii) F_{vals} is multiplied by 0.1 for Area 2 (100–10% case, unequal distribution).

(iii) F_{vals} is multiplied by 0.1 for Area 1 (10–100% case, unequal distribution).

The abundance index was generated using a lognormal distribution with a standard deviation (Table 1). Fishery length compositions were simulated for all years with positive catches and

sampled from a Dirichlet distribution to account for non-random, overdispersed catch-at-length samples. The overdispersion sample size multiplier, c , was set to 2 for sample sizes of 100. Survey age compositions were generated from a multinomial distribution that assumed homogeneous capture probabilities across ages and perfect mixing of fish individuals. Age composition was simulated for all years with abundance index information and sample sizes set to 100.

The estimation model

Estimated parameters in EM configurations were growth parameters, natural mortality (M), unfished recruitment (R_0), survey catchability, and selectivity parameters (see Table 1 for details). All other parameters were fixed at their true values. We applied a procedure to correct for bias in estimated recruitment deviations that can arise in a penalized likelihood framework (Methot and Taylor, 2011). To do this, we first ran 25 replicates and estimated bias adjustment parameters, and then used the average of those parameters for all replicates of a scenario (e.g. Monnahan *et al.*, 2016). Proportions of replicates with an invertible Hessian are reported in Table S1. EM sample sizes were configured with the correct effective sample size: $100/2^2$ for the fishery (sampled from a Dirichlet distribution; Aanes and Pennington, 2003; Ono *et al.*, 2015) and 100 for the survey (sampled from a multinomial distribution). EM parameters were initialized at the true parameter value, except for the recruitment deviations (initialized at zero). No other priors were specified for any parameters other than the bounds (uniform priors).

Spatial variability in somatic growth

The EM configurations used three approaches when the OM simulated spatial variability in somatic growth:

(i) *Aggregated approach*: the EM ignored spatial variability in mean size-at-age by implementing a single area model that aggre-

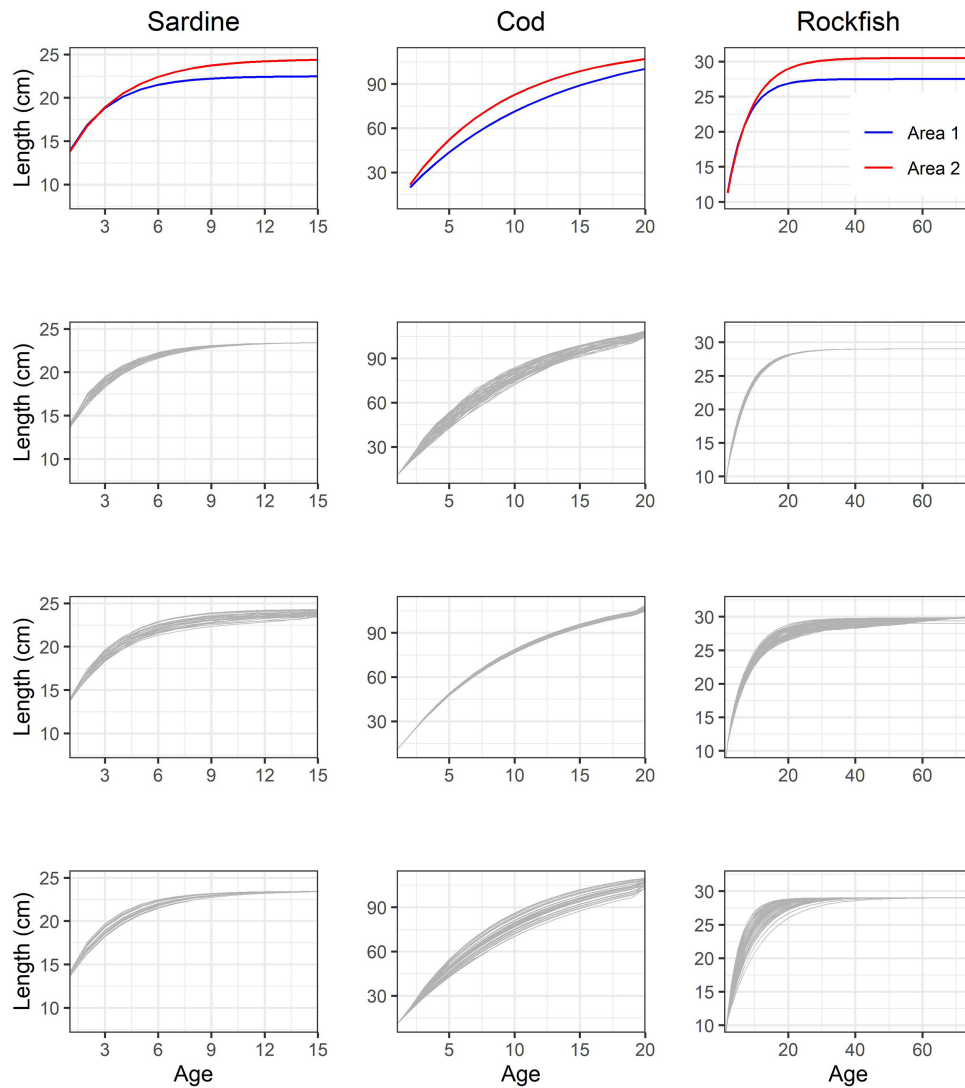


Figure 2. Simulated difference in the mean size-at-age in the OM. Row 1: spatial variability. Row 2: year-specific temporal variability (k). Row 3: year-specific temporal variability (L_{∞}). Row 4: cohort-specific temporal variability (γ_c). Gray lines are the mean size-at-ages for different years (rows 2 and 3) and cohorts (row 4).

gated data generated data by the OM before fitting: (a) catches were summed, (b) abundance indices were summed, and (c) length and age compositions were summed per bin, weighted by their respective catch or index of abundance (Punt *et al.*, 2015). Therefore, a unique k and L_{∞} were estimated.

(ii) *Areas-as-fleets approach*: the EM ignored spatial variability in somatic growth by implementing a single-area model, but fishery and survey data generated by the OM were not aggregated and the data for each area were assumed to be associated with a different fleet, each with its selectivity parameters (Waterhouse *et al.*, 2014). Therefore, a unique k and L_{∞} was estimated.

(iii) *Spatially explicit approach*: the EM implemented spatially explicit models (areas matched to those simulated in the OM); therefore, data aggregation was not required and spatial variability in mean size-at-age was accounted for (i.e. k and L_{∞} were estimated by area). Catchability and selectivity parameters were estimated by fleet (Figure S1) and the distribution of recruitment between areas was fixed at the true values (0.5 for each area).

Trends in the differences in simulated abundance indices between areas used by the EM were also explored to examine how the

distribution of fishing mortality and the spatial variability in mean size-at-age impact these indices.

Temporal variability in somatic growth

We evaluated three approaches when the OM simulated temporal variability in somatic growth:

(i) *Constant assumption*: temporal variations in mean size-at-age was ignored by assuming constant k or L_{∞} over time.

(ii) *Including an observed environmental index*: included an environmental index (*Env index*), which was linked to k or L_{∞} for the year-specific variability as

$$k_y = k * \exp(par_{env} * Env\ index_y) \quad \text{or} \\ L_{\infty_y} = L_{\infty} * \exp(par_{env} * Env\ index_y)$$

and to the γ_c parameter for the cohort-specific variability as

$$\gamma_c = \exp(par_{env} * Env\ index_y).$$

Table 2. Main scenarios evaluated for the three types of life histories.

	Operating model	Estimation model
Spatial variability only in fishing mortality	Equal F	Constant Areas-as-fleets Spatially explicit
	F: 100–10%	Constant Areas-as-fleets Spatially explicit
	F: 10–100%	Constant Areas-as-fleets Spatially explicit
Spatial variability in fishing mortality and somatic growth	Equal F	Constant Areas-as-fleets Spatially explicit
	F: 100–10%	Constant Areas-as-fleets Spatially explicit
	F: 10–100%	Constant Areas-as-fleets Spatially explicit
Temporal variability in somatic growth	Year-specific: variability in k	Constant Env index Deviates
	Year-specific: variability in L_∞	Constant Env index Deviates
	Cohort-specific: variability in γ_c	Constant Env index Deviates

The par_{env} parameter is estimated by the EM and *Env index* is an “observed” environmental index (see Appendix A for more details about its derivation).

(iii) *Estimating deviates*: We estimated multiplicative deviates for every year or cohort as follows:

$$k_y = k * \exp(dev_{se} * dev_y) \quad \text{or}$$

$$L_{\infty,y} = L_\infty * \exp(dev_{se} * dev_y)$$

for the year-specific variability and

$$\gamma_c = \exp(dev_{se} * dev_y)$$

for the cohort-specific variability. dev_y values were estimated by year and dev_{se} was fixed at 0.5.

Scenarios

We grouped scenarios as “Spatial variability” or “Temporal variability,” summarized in Table 2. We also evaluated a “base” scenario (or “self-test”), that consisted of comparing a single-area OM that assumed no variability in somatic growth to an EM that was correctly specified. Likewise, the “Spatial variability” scenarios was divided in two groups: in the first group, the OM simulated variability in fishing mortality but not in somatic growth, and, in the second group, the OM simulated variability in somatic growth and fishing mortality. We did this with the aim to separate effects of fishing mortality and growth variability on model outcomes.

Model convergence and performance

As in Monnahan et al. (2016), convergence checks used in real cases (e.g. inverting Hessian as done when we estimated bias adjustment parameters) are impractical at the scale of this simulation experiment. Therefore, we considered a model to have converged if it reached a maximum gradient less than 0.01 and no parameters were estimated to be on bounds.

Every scenario consisted of 100 convergent replicates, checking that stability was reached for quantiles 2.5, 50, and 97.5% of SSB estimates. For each replicate, we calculated the relative error (% RE) by comparing, between the OM and EM, spawning biomass time series (SSB), L_∞ , k , M , recruitment at unfished levels (R_0), and two management quantities: B/B_{msy} , spawning biomass in the terminal year (B) over spawning biomass at the maximum sustainable yield (B_{msy}), and F/F_{msy} , harvest rate (in biomass) in the terminal year (F) over harvest rate at the maximum sustainable year (F_{msy}). B_{msy} and F_{msy} were calculated using parameters in the last year. RE was calculated as

$$RE = \frac{(\hat{\theta} - \theta)}{\theta} * 100\%$$

where $\hat{\theta}$ represents the value estimated by the EM and θ the true value specified in the OM. To evaluate the EM performance, we summarize the 100 RE values in these two metrics: median RE (a measure of bias), and coverage of the 95% of the RE distribution (a measure of precision). When comparing area-specific outcomes between the two-area OM and single-area EM, the EM estimates

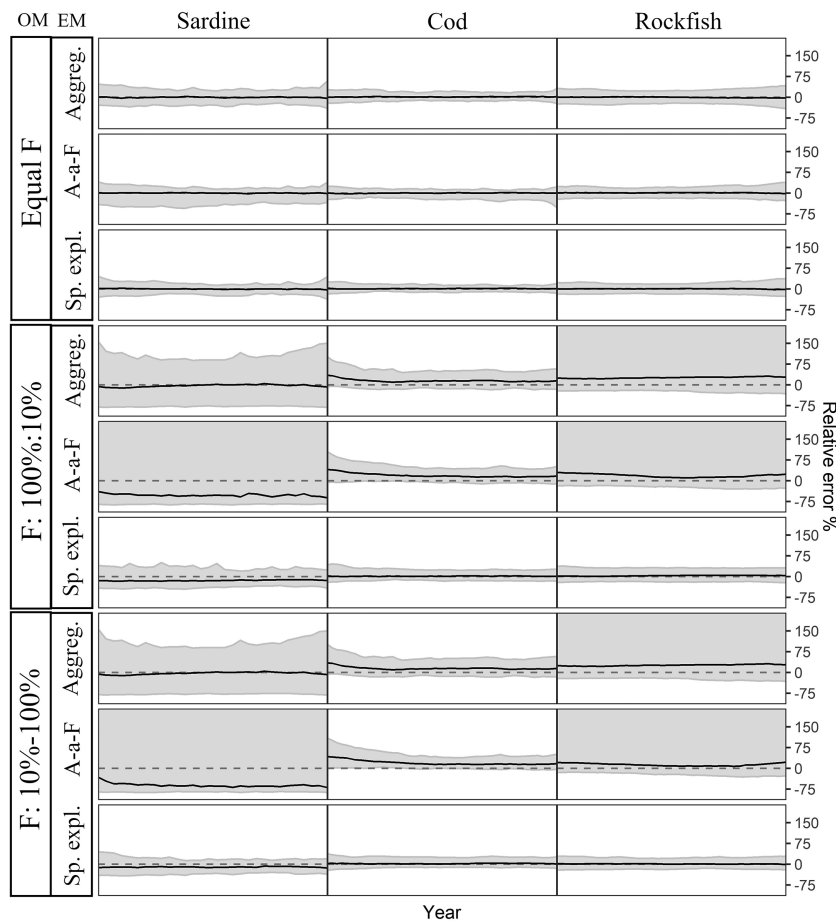


Figure 3. Time series of RE in estimated spawning stock biomass (SSB) over time for scenarios when the OM simulated two areas with only variability in fishing mortality. The black line represents the median, while the gray shaded area represents the 95% quantile. The horizontal dotted line represents no bias over the time series would occur. The OM and EM configurations are on the left. “Aggreg” = Aggregated approach. “A-a-F” = Areas-as-fleet approach. “Sp. expl.” = Spatially explicit. Years do not include the burn-in period and vary by life-history (see Table 1).

were repeated twice, i.e.

$$RE_1 = \frac{(\hat{\theta}_1 - \theta_1)}{\theta_1} * 100\%, \quad RE_2 = \frac{(\hat{\theta}_1 - \theta_2)}{\theta_2} * 100\%,$$

where the subscripts stand for areas.

Results

The EM configurations that ignored spatial or temporal variability in somatic growth generally led to biased and imprecise estimates. When the EM accounted for these types of variability, by implementing a spatially explicit model, including an environmental index, or estimating annual deviates, their performance was substantially improved.

We found stable results for SSB estimates when running 100 convergent replicates per scenario (Figures S2–S10). The base (self-test) scenario displayed unbiased and relatively precise estimates for the three types of life histories (Figure S11), although the precision was generally lower for sardine and rockfish.

Spatial variability

We observed that spatial distribution of fishing mortality and somatic growth impacted the indices of abundance simulated by the OM. When variability in somatic growth was absent, an even fishing mortality distribution produced similar indices of abundance in both areas, but an unequal distribution decreased the index of abundance in the area with higher fishing mortality (Figures S12–S14). When somatic growth variability was present, the area with smaller or larger mean size-at-ages produced a lower or higher index of abundance, respectively.

Aggregated approach

When fishing mortality was equally distributed, this approach led to unbiased and precise estimates in all model outcomes for the three types of life histories, regardless of whether spatial variability in somatic growth was present (Figures 3–6). However, only when variability in somatic growth was present, growth parameters (L_∞ and k) were estimated in-between the true values (Figures 4 and 6).

An uneven distribution in fishing mortality negatively impacted the performance of this approach. When somatic growth was not

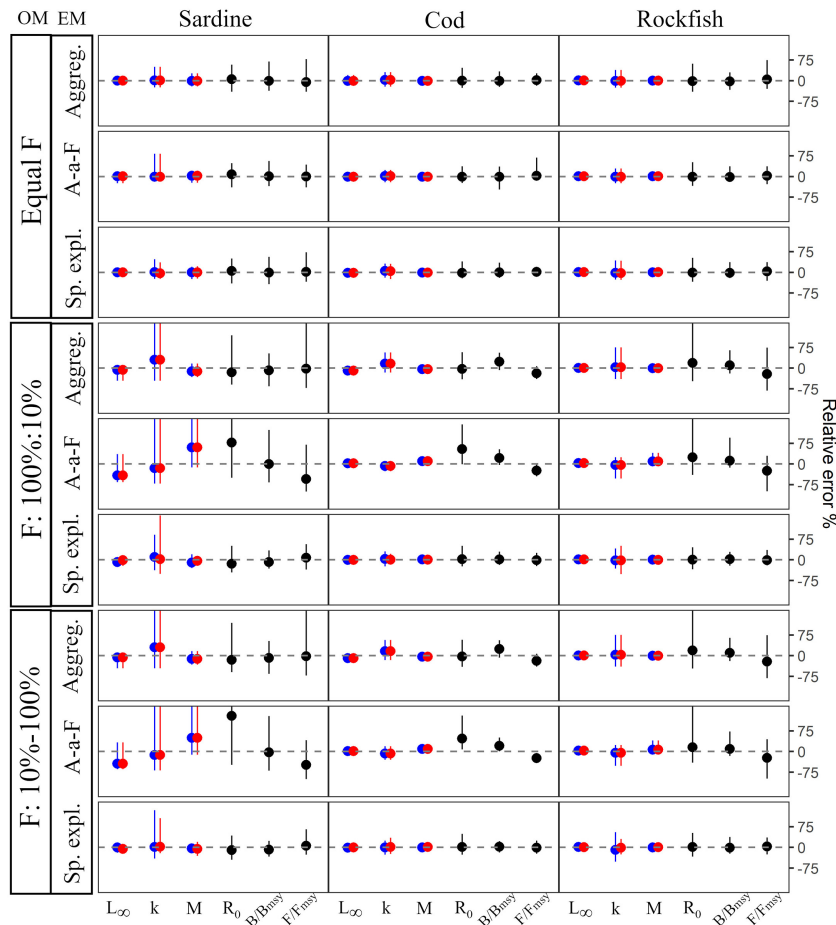


Figure 4. Median (point) and 95% quantiles (lines) of RE in compared model outcomes. The OM simulated two areas with only variability in fishing mortality. The horizontal dotted line represents no bias over the time series would occur. The OM and EM configurations are on the left. “Aggreg” = Aggregated approach. “A-a-F” = Areas-as-fleet approach. “Sp. expl.” = Spatially explicit. Blue, red, and black colour represent RE values for Area 1, Area 2, and the entire area, respectively.

simulated, the F:100%:10% and F:10%:100% cases led to very similar results, reporting imprecise SSB estimates for sardine and rockfish and overestimation in SBB for rockfish ($\sim +20\%$) (Figure 4). We also observed overestimation ($\sim +25\%$) in k for sardine and cod, and overestimation ($\sim +20\%$) in B/B_{msy} and underestimation ($\sim -20\%$) in F/F_{msy} for cod and rockfish (Figure 4). When somatic growth was present, the imprecision in SSB estimates increased and k was generally overestimated, especially for sardine and cod. Also, large bias in R_0 was detected for cod cases ($\sim \pm 50\%$). Management quantities continued reporting biased estimates ($< 40\%$), where B/B_{msy} was generally overestimated and F/F_{msy} underestimated (Figure 6).

Areas-as-fleets approach

Like the aggregated approach, when fishing mortality was equally distributed, the areas-as-fleets approach led to unbiased and precise estimates in model outcomes for the three types of life histories, regardless of somatic growth variability (Figures 3–6). Only when variability in somatic growth was present, L_∞ and k were estimated in-between the true values and R_0 was overestimated ($\sim +20\%$) for cod cases (Figures 4 and 6).

An uneven distribution in fishing mortality produced very imprecise SSB estimates for sardine and rockfish (Figures 3 and 5). SSB

was largely underestimated ($\sim -70\%$) for sardine and usually overestimated for rockfish. An overestimation in SSB ($\sim +30\%$) was also observed for cod cases. L_∞ was underestimated ($\sim -50\%$) and M overestimated ($\sim +50\%$) for sardine. R_0 was generally overestimated and F/F_{msy} underestimated for the three types of life histories, and this was aggravated when spatial variability in somatic growth was present (Figures 4 and 6). Likewise, B/B_{msy} was overestimated for cod and rockfish (F:10%:100%) but underestimated for sardine cases.

Spatially explicit approach

A spatially explicit model always produced precise and unbiased model outcomes for the three types of life-histories regardless of the fishing mortality distribution between areas or the presence of somatic growth variability (Figures 3–6).

Temporal variability

We observed that varying L_∞ , k , or γ_c produced different degrees of variability in mean size-at-age for each type of life history (Figure 2). For example, varying k produced negligible variations but varying L_∞ led to large variability in mean size-at-age for rockfish.

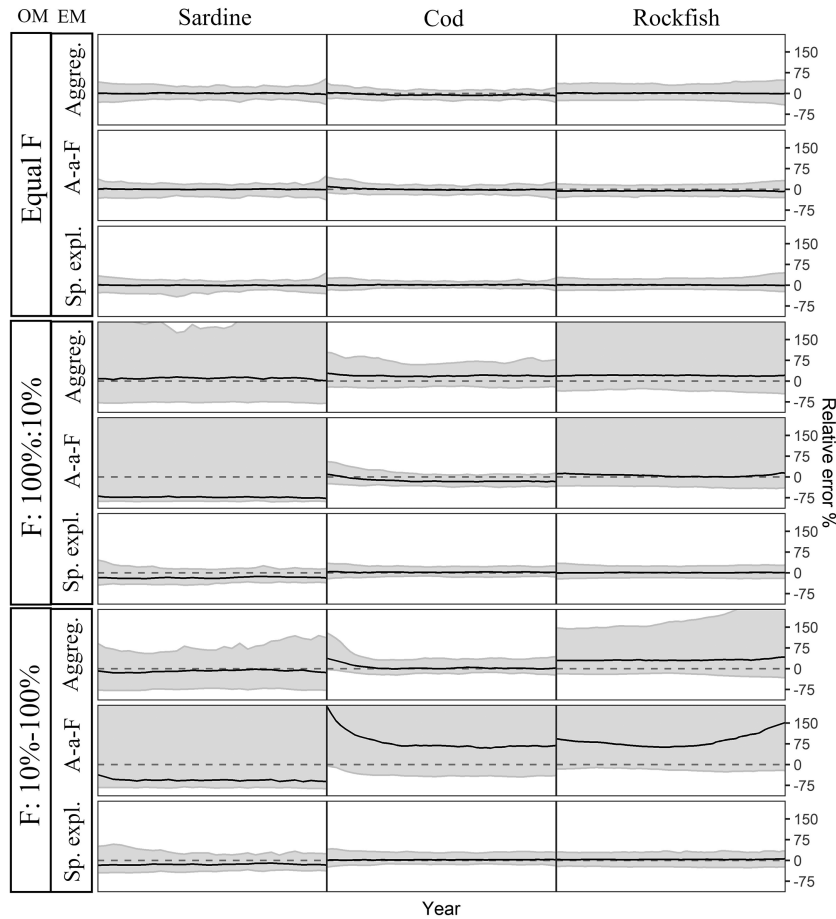


Figure 5. Time series of RE in estimated spawning stock biomass (SSB) over time for scenarios when the OM simulated spatial variability in fishing mortality and somatic growth. The black line represents the median, while the gray shaded area represents the 95% quantile. The horizontal dotted line represents no bias over the time series would occur. The OM and EM configurations are on the left. “Aggreg” = Aggregated approach. “A-a-F” = Areas-as-fleet approach. “Sp. expl.” = Spatially explicit. Years do not include the burn-in period and vary by life history (see Table 1).

Constant assumption

Ignoring year-specific temporal variability, either by varying k or L_∞ in the OM, generally led to cyclic patterns of biased SSB estimates over time (Figure 7) when the simulated variability in mean size-at-age was large. This was observed for sardine and cod cases when k varied in the OM, and for rockfish when L_∞ varied. This cyclic pattern in biased SSB estimates was also observed for the cohort-specific variability, although not as large as the year-specific case, and only for cod and sardine. Biological parameters estimates were unbiased and precise when variability mean size-at-age was small but led to over- and underestimation (< 20%) in k and management quantities when the variability became large either for year- and cohort-specific temporal variability (Figure 8).

Including an environmental series

We noticed that observed mean size-at-age (ML^a) was highly correlated with the true simulated variability in the OM (Figure S15). When this index was included in the EM to account for temporal variability in mean size-at-age, the cyclic patterns of bias in SSB estimates observed for the constant approach disappeared but preci-

sion was not improved (Figure 7). In some cases, SSB was constantly underestimated over time (~ 10%), especially when the simulated variability in somatic growth was small. Biological parameters estimates were unbiased and precise when k and γ_c varied over time in the OM, but there was still over- and underestimation (<20%) in k and management quantities when the variability in mean size-at-age was simulated by changing L_∞ (Figure 8).

Estimating deviates

When deviates were estimated in the EM, it generally led to unbiased SSB estimates over time, although a constant overestimation (<10%) was observed for cod and rockfish when k varied temporally in the OM (Figure 7). Biological parameters estimates were precise and unbiased in most cases, but we observed a large overestimation (~ 45%) in k and small underestimation (~ 10%) in L_∞ for rockfish when the OM simulated variability in L_∞ (Figure 8). Likewise, overestimation (~ 25%) was reported for the same parameter when L_∞ varied temporally in the OM. Management quantities reported small bias (<10%), especially for the cohort-specific variability.

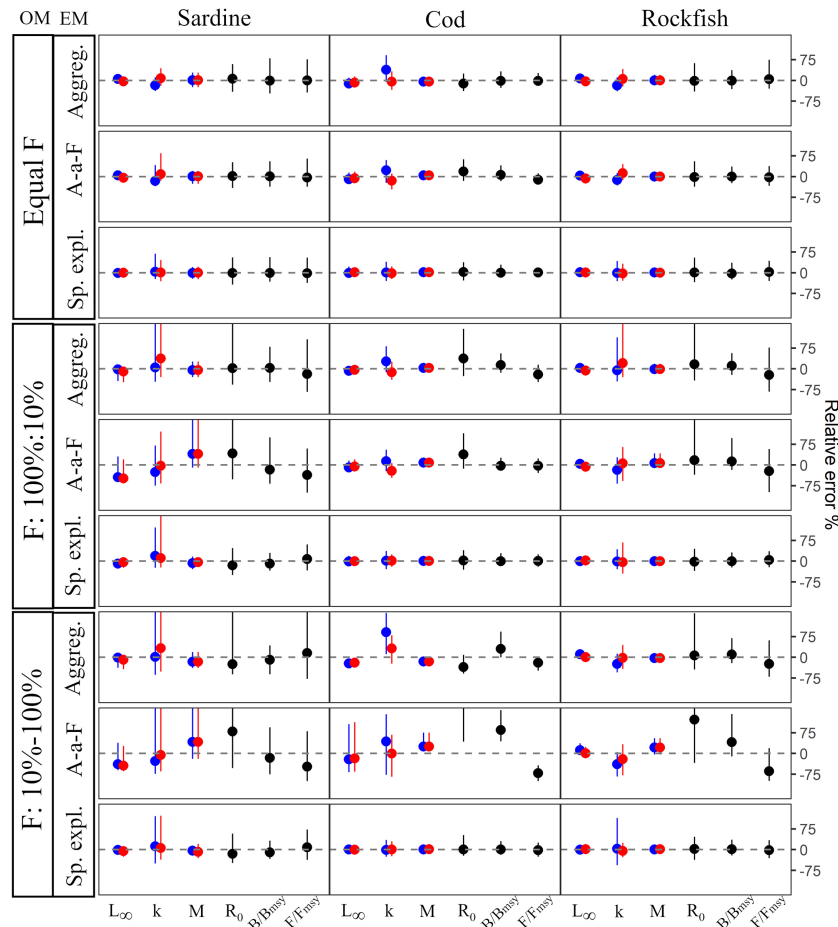


Figure 6. Median (point) and 95% quantiles (lines) of RE in compared model outcomes. The OM simulated two areas with variability in fishing mortality and somatic growth. The horizontal dotted line represents no bias over the time series would occur. The OM and EM configurations are on the left. “Aggreg” = Aggregated approach. “A-a-F” = Areas-as-fleet approach. “Sp. expl.” = Spatially explicit. Blue, red, and black colour represent RE values for Area 1, Area 2, and the entire area, respectively.

Discussion

Our results suggest that, in some cases, ignoring spatial or temporal variability in somatic growth may lead to serious bias in biological parameter estimates and management quantities for the three types of life histories. These findings can be applicable to a wide range of study cases, especially because variability in somatic growth is more common than rare. A survey conducted in the United States found out that most fish stocks have some kind of spatial structure, usually in somatic growth; however, it is not commonly modelled in stock assessment models (Berger et al., 2017). We found that accounting for somatic growth variability through diverse strategies (e.g. implementing a spatially explicit model, calculating an environmental index from observed data, or estimating annual deviates) may solve this problem, which can be useful for fisheries scientists when implement a stock assessment model. However, they might potentially lead to other challenges that are discussed in this section.

Spatial variability

The aggregated approach completely ignores any type of spatial structure and combines information from areas that have different biological traits or fishing patterns. Using a simulation approach,

Punt et al., (2015, 2016) investigated how different assessment configurations performed when there was spatial heterogeneity in recruitment, fishing mortality, and somatic growth for pink ling. They found that aggregated models produced biased and imprecise SSB estimates, such as was observed in this study. Similar results were also found in Cope and Punt (2011) for spatial heterogeneity in catch histories. In our study, we noticed that when fishing mortality was equally distributed between areas, the aggregated approach reported quiet good performance for the three types of life histories regardless somatic growth variability. This result highlights that spatial variation in somatic growth might not be enough to cause bias or bad precision in stock assessment outcomes. Conversely, an uneven distribution of fishing mortality affected considerably the performance of this approach and was aggravated when somatic growth was also present, leading to bias in important management quantities that may affect the correct evaluation of the status of a stock. This poor performance may be principally caused by the aggregation of contrasting compositional data produced by quite different fishing intensities instead of variations in mean size-at-age caused by spatial changes in growth parameters.

The areas-as-fleet approach has been applied previously to account for the spatial structure of fishery selection in stock assessment models (Hurtado-Ferro et al., 2014; Waterhouse et al., 2014).

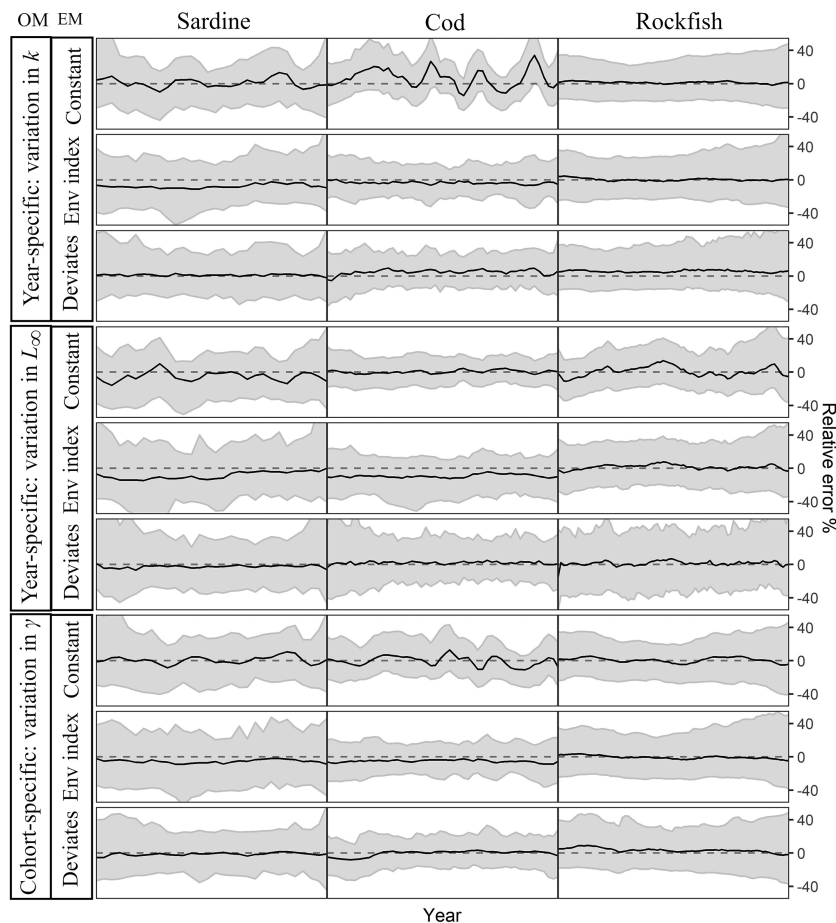


Figure 7. Time series of RE in estimated spawning stock biomass (SSB) over time. The black line represents the median, while the gray shaded area represents the 95% quantile. The horizontal dotted line represents no bias over the time series would occur. The OM and EM configurations are on the left. Years do not include the burn-in period and vary by life-history (see Table 1).

It does not aggregate data and keeps fleets separated; therefore selectivity parameters are estimated independently. This approach has also been used to test for spatial variability in somatic growth for pink ling (Punt *et al.*, 2015, 2016), finding poor performance when spatial variability in growth, recruitment, and fishing mortality were present. In our study, this approach reported the worst performance, especially for sardine and rockfish, when variability in fishing mortality was present and was exacerbated when variability in somatic growth was also simulated. This bad performance is likely due to the stock assessment model tries to estimate unique biological parameters to fit observed compositional data that is simulated from distinct growth parameters. Therefore, the areas-as-fleets approach may not be appropriate to account for spatial heterogeneities in model components.

Spatially explicit models led to the best estimates and it is the recommended approach to account for differences in mean size-at-age in space, although it might lead to other issues such as low convergence rates or long run times, especially for long-lived species (e.g. rockfish) in which a large number of parameters is estimated. In general, stock assessment models that ignore the spatial structure of a population perform worse in comparison to models that include it (Cope and Punt, 2011). There have been efforts to migrate from single to multiple-area stock assessment models in recent years and

results have been promising (Punt *et al.*, 2018; Vigier *et al.*, 2018). It is known that their implementation is important to account for spatial variability in fishing patterns between areas that can arise due to political, economic, or area closures reasons (Cope and Punt, 2011), but also to account for spatial variability in biological traits such as somatic growth, which can also exacerbate the bias produced by other model components. Nevertheless, implementing a spatially explicit model might not be an easy task since there should be a good amount of data and research about how different biological processes vary in space and time, which might only be suitable for well-studied fish stocks.

Analysing observed data to recognize spatial differences in fishing mortality and growth might also be useful. We observed that simulated CPUE was highly impacted by differences in fishing intensity, but also by somatic growth for cod and rockfish cases. The analysis of compositional data and age-length information might also be important to detect spatial variability in other biological traits. To conclude, when there is no evidence of spatial variability in fishing mortality, any evaluated approach might produce good model outcomes. However, only a spatially explicit model may lead to precise and unbiased results when spatial variability in fishing mortality and somatic growth are present for any type of life history.

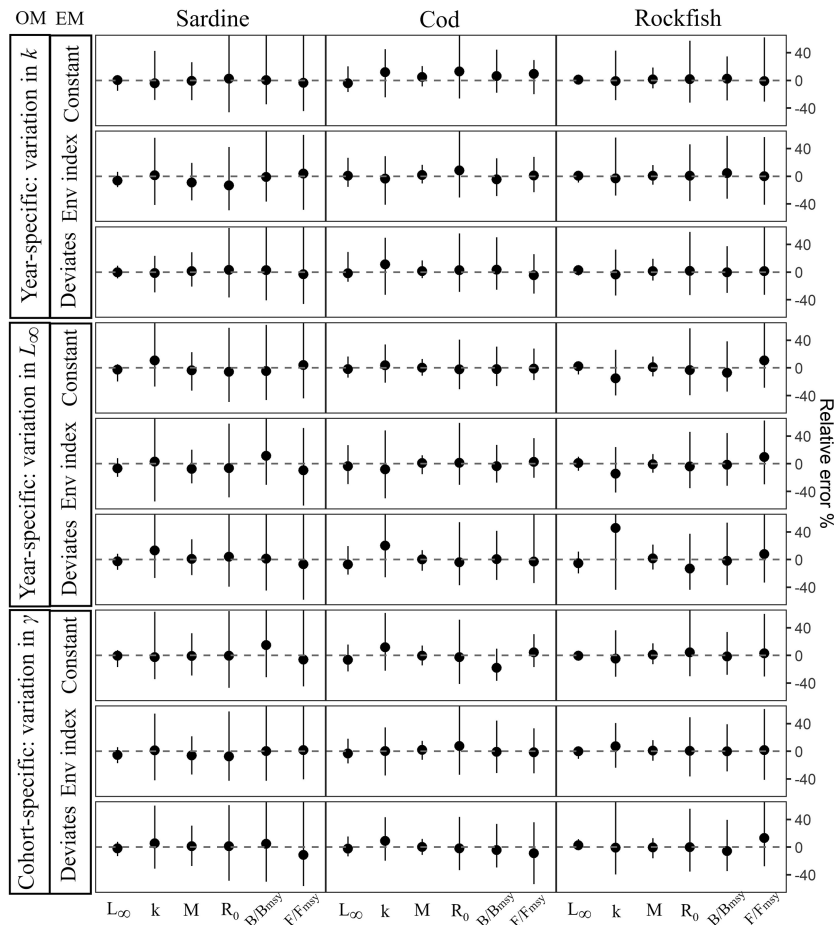


Figure 8. Median (points) and 95% quantiles (lines) of RE in important estimated parameters. The horizontal dotted line represents no bias over the time series would occur. The OM and EM configurations are on the left.

Temporal variability

Variations in mean size-at-age influence directly the total biomass of a stock by changing the weight of individuals. Therefore, low-biomass periods are expected when small mean size-at-ages dominate the population and vice versa, and if this variability is not considered, bias in biomass estimates may be usual as observed in our results. Only two previous studies have explored the consequences of somatic growth temporal misspecification in stock assessment models using a simulation approach, exclusively focused on the year-specific temporal variability (Lee et al., 2018; Stawitz et al., 2019). They also found imprecise and biased stock assessment estimates when year-specific temporally variable growth was ignored. For example, Lee et al. (2018), based on rockfish life-history parameters, observed large bias in SSB and recruitment estimates when year-specific temporal variability in growth was ignored, but this was improved by including an environmental index linked to growth parameters (k and L_∞) in the EM. However, this environmental index should be precise enough because, if not, it might not improve the model performance (Lee et al., 2018).

In our study, we observed that including an observed environmental index (ML^a) to account for both types of temporal variability (year and cohort-specific) in mean size-at-age generally reduced bias in SSB estimates, but it did not produce any effect when there was not a large variability in the OM (e.g. changes in L_∞ for cod or changes in k for rockfish). The relative good performance of ML^a

might be due to that indicator is precise enough to account for the simulated variability as observed in Lee et al. (2018). We found that ML^a for younger ages were more correlated with the true variability, either when k , L_∞ , or γ_c varied, due to the changes in growth parameters affect directly younger ages. For older ages, observed mean size-at-age is not only a cause of variation in growth parameters at the last year, but also from previous years and that may produce noise in the ML^a time series. ML^a is also an indicator relatively easy to estimate (Silva et al., 2008; Hunter et al., 2016) as long as length and age data are appropriately sampled and treated (e.g. selectivity effects on sampled data); therefore, calculating ML^a and using it as an indicator of somatic growth variability might be recommended.

Stawitz et al. (2019), based on petrale sole (*Eopsetta jordani*) life-history parameters, found bias in management reference quantities when interannual or regime-like year-specific temporal variability in growth parameters (k and L_∞) was ignored, but that bias was generally eliminated by estimating deviates in the EM. In our study, we also evaluated estimating deviates rather than including an environmental index to account for temporal variability in somatic growth. Estimating deviates improved the accuracy of SSB, biological parameter, and management quantities estimates for the three types of life-history, reporting a better performance than including an environmental index. However, estimating deviates increases considerably the model complexity since an extra parameter per year is estimated within the model, which might increase run times or

decrease convergence rates, especially for long-lived species such as rockfish. However, it might be suitable for short or medium-lived species, especially when there is evidence of temporal variability in somatic growth but there is no knowledge about its environmental driver.

Impacts of cohort-specific temporal variability in somatic growth on the performance of stock assessment models have received less attention in comparison to the year-specific case (Whitten *et al.*, 2013). Whitten *et al.*, (2013) observed that estimating deviates that varied mean size-at-age by cohort improved model fitting in comparison to models that assumed constant growth for blue grenadier (*Macruronus novaezelandiae*). In our study, when cohort-specific variability was ignored, we observed bias in SSB estimates over years for sardine and cod cases, but not as large as the year-specific case. The smaller bias for the cohort-specific case may be caused by a “buffering effect,” where consecutive years or short periods with slow and fast somatic growth across cohorts might buffer their impacts on annual SSB estimates. This can also explain why ignoring cohort-specific temporal variability for rockfish did not lead to bias in SSB since this buffering effect might be more marked for long-lived species. Therefore, accounting for cohort-specific variability in somatic growth may be important for short and medium-lived species and should be considered in stock assessment models.

Caveats and future research

A common caveat in simulation-estimation experiments is that parameters are fixed at their true value (assumed to be known) or their starting points are the true values. This hardly ever happens in real cases and needs further research to understand if that improves or degrades the EM performance. For example, steepness (h), a parameter of the stock–recruitment relationship that provides information about the stock productivity, was assumed to be known; however, it is one of the most uncertain and critical quantities in stock assessment models and it is not easily estimated in real cases (Lee *et al.*, 2012).

Simulated data types might impact model performance. In our study, length and age compositional data were considered, which may be playing an important role to estimate biological parameters (Magnusson and Hilborn, 2007; Ono *et al.*, 2015). However, conditional age-at-length data (CAAL) or weight-at-age may be also available for some stocks, being the former particularly informative to estimate growth parameters (Piner *et al.*, 2016). The quantity of data is another factor to be considered, longer or shorter periods of data might impact the estimation of important biological parameters (Ono *et al.*, 2015; Stawitz *et al.*, 2019). For example, having a long time series of age compositions might help to estimate natural mortality and recruitment precisely (Magnusson and Hilborn, 2007). In our study, we simulated data for most years; however, this might not hold for many fish stocks and caution should be taken in those cases.

In some cases, the assumed boundaries among areas with different biological parameters lack a biological basis and are set due to management or political reasons (e.g. boundaries between countries or states) (e.g. Williams *et al.*, 2012; Adams *et al.*, 2018). In this study, we assumed that the boundary between areas with distinct somatic growth was known; however, this ecological limit might not be totally identified in some cases or wrongly assumed as political boundaries. Some new methods have been proposed to identify these boundaries when spatial somatic growth variability is present

and have shown promising results that might be applied to real cases (Kapur *et al.*, 2020). However, it is still unknown how an incorrect boundary between areas with a distinct growth parameter can affect the performance of spatially explicit models.

The main challenges in implementing spatially explicit stock assessment models are the lack of information on movement rates and patterns, reproductive isolation, and stock composition (Cadrin and Secor, 2009). Here, we assumed no movement between areas post settlement, which applies fairly generally, including some rockfish, but is simplified for other species. Movement patterns are diverse and particular for every stock, which might affect our results in several ways. For instance, movement of individuals from slow-to fast-grow areas and/or vice versa might mitigate or aggravate the consequences of ignoring spatial variability in growth observed in our study. The study of movement and how it affects spatially explicit stock assessment models is an active area of research in fisheries sciences and future studies might consider different movement patterns and their interactions with spatial variability in somatic growth and fishing mortality simultaneously.

Currently, spatially explicit stock assessment models usually incorporate more than two areas (Punt *et al.*, 2015, 2018; Vigier *et al.*, 2018). The inclusion of more areas and different recruitment distribution among them need also be evaluated, which can lead to complexities and further non-linearities in results. Also, we only evaluated changes in classic growth parameters such as k and L_{∞} ; however, other parameters in the growth equation might also vary the mean size-at-ages substantially. For example, L_{\min} [see (1)] might produce larger variations for species such as sardines due to variation in growth in early life stages.

Conclusion

This study extends previous analyses on the consequences of ignoring spatial and temporal variability in somatic growth, commonly observed for many fish stocks, in stock assessment models for three types of life histories. We principally found that ignoring temporal and spatial growth variability, in some cases, can lead to biased biological parameter estimates and management quantities. We also explored various ways of taking into account this variability that can be considered by fisheries scientists when implementing a stock assessment model.

Supplementary data

Supplementary material is available at the ICES/JMS online version of the manuscript.

Data availability statement

The data underlying this article will be shared on reasonable request to the corresponding author.

Acknowledgments

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Appendix A: observed environmental index (*Env index*) derivation

We derived the observed environmental index (*Env index*) included in the EM that accounted for temporal variability in somatic growth. Including the annual PDO index, used to simulate the true variability in OM, would implicitly assume that fisheries scientists precisely know what environmental variable drives temporal changes in somatic growth, an unrealistic case that would overestimate the performance of the EM. Fisheries scientists usually examine variations in somatic growth by analysing ring widths of otoliths (e.g. Black, 2009) or length and age data collected by fishery-independent or dependent sources. Then, they (i) fit a von Bertalanffy growth curve to size-at-age data and look at changes in the k or L_∞ parameter (e.g. Adams *et al.*, 2018; Li *et al.*, 2018), or (ii) look at changes in mean size-at-age over time or space (e.g. Feltrim and Ernst, 2010; Ciannelli *et al.*, 2020). These indicators of somatic growth might be then related to one or several environmental variables (e.g. temperature, primary productivity; Arnekleiv *et al.*, 2006), which is finally included in the stock assessment model and linked to a growth parameter (e.g. k , L_∞ , or γ_c) to alter the mean size-at-age relationship within the model.

We followed the next steps to obtain a realistic environmental index that can be included in the EM to account for temporal variation in mean size-at-age (based on Pardo *et al.*, 2013):

(i) Using numbers-at-age, mean sizes-at-ages, and standard deviation of sizes-at-ages information generated by the OM that simulated year or cohort-specific temporal variability in somatic growth, we simulated lengths of fish individuals by age (in the population).

(ii) To simulate observed data, we randomly drew length samples by age from data generated in (i). The sizes of these samples ranged from 200 individuals for younger ages to a single individual for older ages.

(iii) We calculated the mean size-at-ages (ML^a) from sampled size data obtained in (ii).

(iv) Steps (i)–(iv) were repeated for all years (y) in a replicate, obtaining ML_y^a .

(v) We calculated the Pearson correlation coefficient of ML_y^a with either k_y or $L_{\infty y}$ to identify which was the age that led ML_y^a to the closest the true variability in the OM.

We noted that the correlation was stronger between k or L_∞ and ML^a for younger ages (results not shown). Therefore, we decided that using the mean size at a young age was a suitable indicator of somatic growth variability. Also, it can be used for year and cohort-specific cases. We selected ages 1.5, 2.5, and 2.5 for sardine, cod, and rockfish, respectively. Finally, ML^a was standardized between -1 and 1 and then included in the EM as an environmental time series.

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