



Original Article

Time-variant productivity in biomass dynamic models on seasonal and long-term scales

Tobias K. Mildenerger ^{1*}, Casper W. Berg¹, Martin W. Pedersen^{1,2}, Alexandros Kokkalis ¹, and J. Rasmus Nielsen¹

¹National Institute of Aquatic Resources, Technical University of Denmark, Kemitorvet, 2800 Kgs. Lyngby, Denmark

²ENFOR A/S, Lyngsø Allé 3, Hørsholm 2970, Denmark

*Corresponding author: e-mail: t.k.mildenerger@gmail.com.

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The productivity of fish populations varies naturally over time, dependent on integrated effects of abundance, ecological factors, and environmental conditions. These changes can be expressed as gradual or abrupt shifts in productivity as well as fluctuations on any time scale from seasonal oscillations to long-term changes. This study considers three extensions to biomass dynamic models that accommodate time-variant productivity in fish populations. Simulation results reveal that neglecting seasonal changes in productivity can bias derived stock sustainability reference levels and, thus, fisheries management advice. Results highlight the importance of biannual biomass indices and their timing relative to the peaks of the seasonal processes (i.e. recruitment, growth, mortality) for the estimation of seasonally time-variant productivity. The application to real-world data of the eastern Baltic cod (*Gadus morhua*) stock shows that the model is able to disentangle differences in seasonal fishing mortality as well as seasonal and long-term changes in productivity. The combined model with long-term and seasonally varying productivity performs significantly better than models that neglect time-variant productivity. The model extensions proposed here allow to account for time-variant productivity of fish populations leading to increased reliability of derived reference levels.

Keywords: eastern Baltic cod (*Gadus morhua*), fisheries management, fish stock assessment, maximum sustainable yield, population dynamics, seasonality, SPiCT, surplus production model

Introduction

Increasing evidence suggests that the productivity of fish populations is time-variant (Hollowed *et al.*, 2013; Petitgas *et al.*, 2013; Hare *et al.*, 2016; Tommasi *et al.*, 2017): two recent studies using >200 stocks from the RAM Legacy Stock Assessment Database (Ricard *et al.*, 2012) and different modelling approaches revealed that around 68% of the assessed fish stocks (230 and 276 respectively) showed significant non-stationary behaviour (Vert-pre *et al.*, 2013; Britten *et al.*, 2017). The productivity of fish populations describes the rate of generation of biomass and is determined by the combined effects of three physiological processes: (i) somatic growth (growth of individuals in weight and length), (ii) recruitment (numbers of individuals recruiting to population), and (iii) the survival rate (number of fish surviving from

one point in time to the next). Time-variant productivity can be attributed to the dependency of the physiological processes and thus productivity on environmental conditions, such as temperature, precipitation, currents, eutrophication, or oxygen conditions (Pauly, 1980; Brander, 1995; Köster *et al.*, 2005), as well as ecological factors such as predator–prey relationships (Kempf *et al.*, 2009) or food availability (Ursin, 1963, 1967; Ross *et al.*, 2018). As environmental conditions are not constant over time (Belkin, 2009; Gruber, 2011; Boyce *et al.*, 2014), neither are the individual physiological processes nor the productivity of a fish population. Variability of productivity is usually described by stepwise shifts between “productivity regimes” or gradual changes in productivity over long time scales such as inter-annual variability (Peterman *et al.*, 2000; Vert-pre *et al.*, 2013; Britten *et al.*,

2017). However, all physiological processes contributing to stock productivity show also within year variability, in particular, in temperate regions, where seasonal differences in environmental conditions are large (Fretwell, 1972; Pauly, 1980): seasonal varying growth (Ursin, 1963, 1967; Lambert *et al.*, 2009; Frisk *et al.*, 2015), maturity (Lambert *et al.*, 2009), and recruitment (Payne *et al.*, 2008; Kempf *et al.*, 2009; Lobón-Cerviá and Bradford, 2014; Pécuchet *et al.*, 2015) have been observed and described for many species. Natural mortality is an important parameter in stock assessment, but notoriously difficult to measure and estimate in practice (Pauly, 1980; Mertz and Myers, 1997; Quinn and Deriso, 1999; Jennings *et al.*, 2009; Curti *et al.*, 2013; Maunder and Punt, 2013). Few studies have shown seasonality of natural mortality (Carlson *et al.*, 2008; Nielsen *et al.*, 2012).

As the productivity of a stock is directly related to its MSY (Fletcher, 1978)—an important reference level in fisheries management and advice (Russell, 1931; Graham, 1935; Larkin, 1977; Jennings *et al.*, 2009), seasonal and long-term fluctuations of fish productivity have direct consequences for fisheries management (Caddy and Gulland, 1983; Jennings *et al.*, 2009, and references therein). Not accounting for time-variant productivity might lead from sub-optimal harvesting and incorrectly specified recovery times to mismanagement and in some cases even stock collapse (Britten *et al.*, 2017; Nesslage and Wilberg, 2019), as the example of Gulf of Maine cod shows (Pershing *et al.*, 2015). In particular, in light of ongoing climate change, accounting for environmentally driven time-variant productivity in stock assessments is crucial. Stock assessment methodologies, such as Stock Synthesis (Methot and Wetzel, 2013), Gadget (Begley and Howell, 2004), or the state-space assessment model (Nielsen and Berg, 2014; Berg and Nielsen, 2016), allow for the estimation of time-variant parameters related to catchability, natural mortality, and stock recruitment. Nonetheless, the number of assessments with time-variant parameters is still limited (Britten *et al.*, 2017), which is especially the case for data-limited stock assessment methods. The prevalence of time-invariant parameters in most stock assessments might be attributed to the higher data requirements (quality and quantity) for the estimation of time-variant parameters, in particular regarding individual physiological processes. Models with a simpler population structure, such as biomass dynamic models [as Hilborn and Walters (1992) coined surplus production models] ease the inclusion of time-variant parameters, in particular considering limited information available, as potentially contrasting non-stationary patterns in the physiological processes do not have to be entangled individually, but are jointly described by the productivity of the population.

Biomass dynamic models are based on the theory of the biomass production of fish populations in relation to population size (Graham, 1935; Schaefer, 1954) assuming a dome-shaped relationship between surplus production—the net production of biomass per year—and the stock size in biomass (so-called production curve). Due to their simplicity (no age or length structure of the stock) and low data requirements (only catch and biomass index time series), this class of models is a commonly used stock assessment model for data-limited and data-moderate stocks.

Within the working groups of the International Council for the Exploration of the Sea (ICES), biomass dynamic models are used to assess the stock status relative to MSY proxy reference levels for data-limited stocks, such as the eastern Baltic cod stock (ICES subdivisions 24–32; ICES, 2018c), hereafter referred to as Baltic cod. With landings of >25 thousand metric tonnes in 2017

(ICES, 2018c), Baltic cod is commercially the most important fish species of the Baltic proper (Casini *et al.*, 2016). From a stock assessment point of view, Baltic cod is a problematic stock, because age readings seem unreliable (ICES, 2018c) and the stock is exposed to very variable environmental conditions (Köster *et al.*, 2005; Casini *et al.*, 2016). In the Baltic, cod is distributed according to the salinity tolerance threshold of the species, and the salinity conditions in the different Baltic basins fluctuates extensively due to high periodical variability in inflows of saline Atlantic water to the Baltic proper (Köster *et al.*, 2005). The Baltic Sea underwent significant environmental and ecological changes over the last century (Möllmann *et al.*, 2009; Reusch *et al.*, 2018), such as an increase in seal worm parasites due to increasing seal abundance, shifts in the dominating clupeid species and their spatial distribution patterns, and an increase in hypoxic zones, all of which challenge many Baltic fish stocks and particularly demersal predators such as cod (Eero *et al.*, 2015; Casini *et al.*, 2016). It has been shown that the nutritional condition of Baltic cod decreased substantially starting in the mid-1990s (Eero *et al.*, 2015; ICES, 2015). Baltic cod experts hypothesize that somatic growth has decreased and natural mortality has increased based on the decrease in nutritional condition, reduction of maturation size and ecosystem changes, such as higher seal predation, extension of hypoxic areas, cannibalism, and parasite infestation (ICES, 2017a, b). As claimed already by Walters (1987) and again by Britten *et al.* (2017), such temporal fluctuations in environmental and ecosystem conditions support the need for assessment models that can integrate between years and within year variability in stock productivity.

Here, we extend a biomass dynamic model to account for time-variant productivity by three different approaches, of which two allow to account for between years variability in productivity, with either stepwise shifts between productivity regimes, or gradual varying productivity, and one allows for within year variability, by a seasonally oscillating productivity. Within a simulation study, we evaluate the precision and accuracy of the models with and without within year variability in productivity under different scenarios. The scenarios focus on the seasonal model since little is understood about the implications and requirements of seasonal oscillating (or within year variability in) productivity in biomass dynamic models. We apply all three models (stepwise, gradual, and seasonal) and their combinations to the Baltic cod stock and discuss management implications of the time-variant productivity.

Methods

Stochastic production model in continuous time

The stochastic surplus production model in continuous time (SPiCT; Pedersen and Berg, 2017) is a fully stochastic version of the traditional Pella–Tomlinson biomass dynamic model (Pella and Tomlinson, 1969). It uses the reparametrization of Fletcher (1978) and is formulated as a stochastic differential equation (SDE) including process noise:

$$dB_t = \left(\gamma m \frac{B_t}{K} - \gamma m \left[\frac{B_t}{K} \right]^n - F_t B_t \right) dt + \sigma_B B_t dW_t, \quad (1)$$

where $\gamma = n^{n/(n-1)}/(n-1)$, B_t is the exploitable biomass at time t , K is the carrying capacity, m is the productivity parameter and represents the MSY (maximum attainable surplus production Fletcher, 1978), n determines the shape of the production curve,

σ_B is the standard deviation of the process noise, and dW_t is Brownian motion. In SPiCT, the fishing mortality F_t is modelled as a stochastic process:

$$F_t = S_t^{(F)} G_t^{(F)}, \quad (2)$$

where $S_t^{(F)}$ represents the seasonal component, and $G_t^{(F)}$ the diffusion component. The diffusion component follows:

$$d \log(G_t^{(F)}) = \sigma_F dV_t, \quad (3)$$

where σ_F is the standard deviation of the process noise and dV_t is standard Brownian motion. If seasonal catches are unavailable, $S_t^{(F)} = 1$ and thus $F_t = G_t^{(F)}$. In this study, seasonal fishing mortality was modelled by $S_t^{(F)} = \exp(D_{s(t)})$, representing a cyclic B-spline (de Boor, 1978) with a period of 1 year with $s(t) \in [0, 1]$ being a mapping from t to the proportion of the current year that has passed. The annual variation allowed by the cyclic B-spline is determined by the number of knots, which must be smaller than or equal to the number of catch observations per year. The values of the cyclic B-spline are defined by the parameter vector φ of length equal to the number of knots minus one. Note that the seasonal process represented by the spline ($S_t^{(F)}$) is repeated every year. Pedersen and Berg (2017) implemented an approximation of a seasonal correlation structure in continuous time with a system of coupled SDEs that is known analytically to have oscillatory solutions, i.e. solutions with a sinusoidal repeating signal (Gardiner, 1985). This can accommodate changes in the fishing pattern over time, however using this approach for Baltic cod did not converge to a realistic solution, while significant auto-correlation in the catch residuals was detected when using the cyclic spline (Figure D13 in the Supplementary). To circumvent these problems an extension to SPiCT was developed, which adds an auto-correlated (discrete-time) process H on top of the cyclic spline S and the diffusion component G and to Equation (2) ($F_t = S_t^{(F)} G_t^{(F)} \exp(H_{j(t)})$).

$$H_{j(t)} = \varphi_H H_{j(t-1)} + \epsilon_{H,j(t)}, \quad (4)$$

where j maps t to a quarter of the year (dependent on the time-resolution of the catch data), φ_H is the coefficient of the auto-correlation with the process 1 year ago (here lag 4 since catches are by quarter), and $\epsilon_{H,j(t)} \sim N(0, \sigma_H^2)$, with σ_H being the standard deviation of the observation noise term. This represents an important addition to the original SPiCT model, allowing for an alternative way to estimate deviations from a constant seasonal fishing pattern over time. In other words, the H process describes a step function that is constant in time within quarters and auto-correlated with a lag of 1 year, and may be thought of as deviations from the mean seasonal process described by $S_t^{(F)}$ which can adapt to changes in amplitude and timing (phase) of the real seasonal fishing pattern. The biomass index and catch observations are respectively modelled by:

$$I_t = qB_t \cdot e^{\nu_t}, \quad (5)$$

$$C_t = \int_t^{t+\Delta} F_s B_s ds \cdot e^{\epsilon_t}, \quad (6)$$

where q is the catchability, $\nu_t \sim N(0, \sigma_\nu^2)$ and $\epsilon_t \sim N(0, \sigma_\epsilon^2)$, σ_ν and σ_ϵ are the standard deviations of the observation noise terms,

and Δ is the time-interval for the catch (typically a year or quarter of a year).

The Pella–Tomlinson biomass dynamic model allows for skewed production curves (see Figure C7 in the Supplementary for two examples) and includes the Schaefer ($n = 2$; Schaefer, 1954) and Fox ($n = 1$; Fox, 1970) models as special cases. The assumptions are (i) the analysed stock is not subject to migration (i.e. closed population), (ii) B_t is the exploitable stock biomass, (iii) there are no lagged effects in dynamics of B_t , and (iv) the catchability in the survey and fishery are constant over the years. Furthermore, fishing gear selectivity and natural mortality are not explicitly modelled.

Time-variant productivity

Time-variant productivity is modelled by the combination of a mean productivity parameter, a seasonal component, and an additional component determining the long-term changes in productivity:

$$m_t = \bar{m} \hat{S}_t^{(m)} G_{l(t)}^{(m)}, \quad (7)$$

where \bar{m} is the mean m parameter, $\hat{S}_t^{(m)}$ is the scaled seasonal term, and $G_{l(t)}^{(m)}$ corresponding to the long-term changes. The seasonal productivity is implemented as a yearly repeating seasonal process and is modelled as a sinus curve with a known period of 1 year.

$$\hat{S}_t^{(m)} = \exp(A \sin(2\pi t + \varphi_S)), \quad (8a)$$

$$\hat{S}_t^{(m)} = \frac{S_t^{(m)}}{E(S_t^{(m)})}, \quad (8b)$$

where A is the amplitude and φ_S the phase of the sinus curve. The long-term productivity changes $G_{l(t)}^{(m)}$ correspond to either one of the following three cases: (i) no long-term changes [Equation (9)], (ii) stepwise changes [Equation (10)], or (iii) gradual changes over time [Equation (11)].

$$G_t^{(m)} = 1, \quad (9)$$

$$\log(G_{l(t)}^{(m)}) = \log(\Delta m_{l(t)}), \quad (10)$$

$$d \log(G_t^{(m)}) = -\psi \log(G_t^{(m)}) dt + \sigma_m dW_t^m, \quad (11)$$

where $\Delta m_{l(t)}$ is the difference in the productivity parameters between regimes with $l(t)$ being a mapping from t to the corresponding regime and ψ is the mean reversion rate, defining the speed with which the process approaches the long-term mean (here 0), σ_m the standard deviation of the Ornstein–Uhlenbeck (OU; Uhlenbeck and Ornstein, 1930) process errors. The gradual model [Equation (11)] corresponds to the OU process, which is a stationary Gauss–Markov process and can be considered the continuous time analogue of the discrete time first-order Auto-Regressive process. The OU process tends to drift towards its long-term mean over time and represents random auto-correlated deviations from the average production \bar{m} . The most likely time point for the regime shift of the stepwise model [Equation (10)] can be determined by minimizing the Akaike information criterion ($AIC = 2k - 2 \log \hat{L}$, where k is number of estimated parameters and \hat{L} is the maximum value of the likelihood function; Akaike, 1998).

Table 1. Model extensions regarding time-variant productivity on short- and long-term scales based on the original SPiCT.

Model code	Seasonal model	Stepwise model	Gradual model	Equations
C-C				Equation (9) and $\hat{S}_t^{(m)} = 1$
S-C	✓			Equation (9) and $\hat{S}_t^{(m)} \neq 1$
C-Vs		✓		Equation (10) and $\hat{S}_t^{(m)} = 1$
S-Vs	✓	✓		Equation (10) and $\hat{S}_t^{(m)} \neq 1$
C-Vg			✓	Equation (11) and $\hat{S}_t^{(m)} = 1$
S-Vg	✓		✓	Equation (11) and $\hat{S}_t^{(m)} \neq 1$

These equations allow to model within year variability in productivity as seasonal (S) changes or as constant (C) and between years variability by the variable stepwise model (Vs), the variable gradual model (Vg), or as constant (C). The combination of these aspects allows to derive the original SPiCT (C-C) and five extensions accounting for time-variant productivity (Table 1). All model extensions are available at the GitHub repository under <https://github.com/tokami/spict/tree/seaprodTVP> and example applications at: <https://github.com/tokami/pubs/tree/master/TVP>.

Reference levels

SPiCT estimates three reference levels: MSY, the fishing mortality required to attain MSY (F_{MSY}), and the biomass of the stock if fished at F_{MSY} (B_{MSY}). Traditionally, reference levels are time-invariant, however, the equations for the reference levels [Equations (A1)–(A3) and Appendix] imply that MSY and F_{MSY} are time-variant if the productivity (in terms of m) is time-variant, but B_{MSY} is not because it does not depend on m . The seasonal component of the productivity is of a lesser interest for fisheries management as the advice is usually based on reference levels representative for a year (or management period). Therefore, the seasonal components of m_t and F_t ($\hat{S}_t^{(m)}$ and $S_t^{(F)}$, respectively) are omitted in the estimation of the reference levels.

$$MSY_t = m_t^c, \quad (12)$$

$$B_{MSY} = K \left(\frac{1}{n} \right)^{1/n-1}, \quad (13)$$

$$F_{MSY_t} = MSY_t / B_{MSY}, \quad (14)$$

where m_t^c represents the non-seasonal component of m_t ($m_t^c = \bar{m}G_{I(t)}^{(m)}$). These reference levels represent the non-seasonal deterministic reference levels, the non-seasonal stochastic ones can be derived by substituting the corresponding equations in Pedersen and Berg (2017) with above deterministic levels (cf. Appendix). For the stepwise productivity model, this implies a constant MSY and F_{MSY} level for each regime, while for the gradual model, the two reference levels become continuous.

Simulation study

The simulation study is parametrized according to the results of the SPiCT assessment of the Baltic cod stock with the S-Vg model (see below) and allows the evaluation of the seasonal production relative to seasonal patterns, data quality and the non-seasonal SPiCT assessment. Table 2 summarizes the parameter values and

simulation settings. The framework comprises 500 simulations and extends over a simulation period of 30 years and 4 seasons, which is in line with the occurred data conditions in the North Sea. Five different scenarios combine seasonal fishing mortality and productivity with variable phases (Figure 1) and biannual biomass indices with different timing (rugs in Figure 1; Table 3).

All models include seasonal fishing mortality (cyclic B-spline), but do not include the auto-correlated process H [Equation (4)] nor long-term changes in productivity ($G_t^{(m)} = 1$). The simulation study uses a modified version of the SPiCT simulation model used in Pedersen and Berg (2017). Each scenario is estimated using the models C-C and S-C. Section B in the Supplementary includes more details to the simulations study and ten additional scenarios.

Performance metrics

The results of the simulations are evaluated based on several performance metrics, which are estimated for the reference levels and the last observations of the relative biomass and fishing mortality, $(B/B_{MSY})^{\text{last}}$ and $(F/F_{MSY})^{\text{last}}$, respectively. The relative states in the last year have an important role within stock assessment and management advice. Here, the biomass and fishing mortality values represent the last instances of the baseline trajectories omitting the seasonal factors. The performance metrics are: (i) the proportion of converged model fits, where a model is defined as converged if the optimizer `nlm` (R Core Team, 2014) reports a successful completion and if confidence intervals (CIs) can be estimated and are finite. For converged fits, (ii) the median bias (MB) is estimated by following equation:

$$MB = \text{median} \left(\frac{\hat{\theta} - \theta}{\theta} \right), \quad (15)$$

where $\hat{\theta}$ is the estimated value and θ the true or target value. In addition, (iii) the coverage fraction (CF), i.e. the fraction of simulations where the CI includes the true value (target is equal to 95%), and (iv) the coefficient of variation (CV) are estimated. The combination of these metrics allows inference about the precision and accuracy of the different scenarios. The relative errors for the two quantities are compared between the two models (C-C and S-C) and between the scenarios for each model based on the Wilcoxon signed-rank test.

Application to Baltic cod

All six model combinations (Table 1) are fitted to the Baltic cod data: seasonal catches from all commercial fleets targeting Baltic cod and the biannual (quarter 1 and quarter 4) biomass index from the Baltic International Trawl Survey for the years 1991–2018 are taken from ICES (ICES, 2018c). All models include the seasonal fishing mortality (cyclic B-spline) and the auto-correlated process H [Equation (4)] and are fitted by a two-step fitting process: first, to stabilize the optimizer, the model is fitted using all default priors (n , $\alpha = \sigma_I/\sigma_B$, $\beta = \sigma_C/\sigma_F$ for the Vs models, and additional ψ and σ_m for the Vg models). In the second step, the point estimates are used as the initial values for the second fit without any priors. This process stabilizes the optimization and allows to remove the impact of priors on the likelihood of the models and thus the calculation of the likelihood ratio test for nested models.

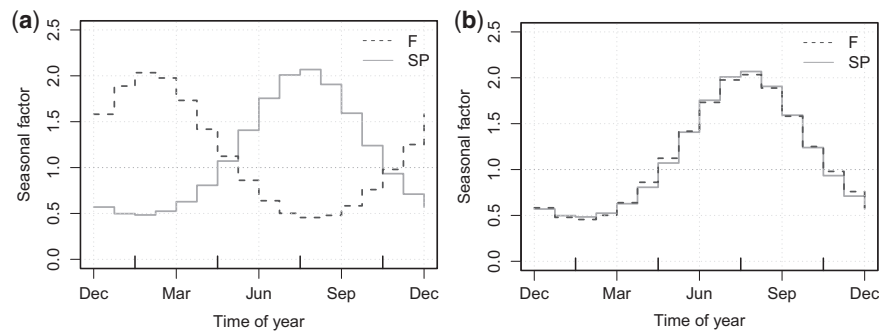


Figure 1. Different scenarios of the seasonal pattern of fishing mortality (dashed) and productivity (solid) with equal amplitudes: (a) contrasting pattern of fishing mortality and productivity; (b) identical pattern of two seasonal processes. The rugs on the x axis show the timing of the survey indices, where the first and third rug correspond to the survey in the North Sea, the second and fourth to a case where the indices miss the maxima and minima of the seasonal factors, and the first and fourth to the survey in the Baltic Sea.

Table 2. Parameters used for the simulation study.

Parameter	Description	Value
dt [year]	Euler time step	1/16
K [ktonnes]	Carrying capacity	148.9 (CV = 0.1)
m [ktonnes]	Stock productivity	59.78 (CV = 0.1)
n	Shape parameter of production curve	0.62 (CV = 0.1)
q	Catchability	0.02–0.04
$bkfrac$	Fraction of B/K	0.9–1
F_0 [year ⁻¹]	Initial fishing mortality	0.01
F_{max} [year ⁻¹]	Maximum fishing mortality	2
σ_B	SD of biomass process error [Equation (1)]	0.1
σ_I	SD of index observation error [Equation (5)]	0.1
σ_F	SD of fishing mortality process error [Equation (3)]	0.1
σ_C	SD of catch observation error [Equation (6)]	0.1
φ	Parameter vector of cyclic B-spline of seasonal fishing mortality process [Equation (2)]	1.4, 1, 0.7/2.5, 1.2, 0.34/0.7, 1, 1.4/0.34, 1.2, 2.5
φ_S	Phase of seasonal productivity process [Equation (8)]	1.28
A	Amplitude of seasonal productivity process [Equation (8)]	0.73/0.25

Values are based on the results of the SPiCT assessment of the Baltic cod stock with the S-Vg model (Table 4). Values separated by a backslash correspond to different scenarios.

CV, coefficient of variation; SD, standard deviation.

Table 3. Scenarios of the simulation study with the properties of the simulation framework as well as the number of converged runs for each scenario.

Scenario code	Pattern F vs. P	Seasonal factors	Num indices	$t_{indices}$	Converged runs (%)
CE2N	Contrasting	Equal	2	NS	96.2/99.8
CE2X	Contrasting	Equal	2	X	50.6/91.4
IE2N	Identical	Equal	2	NS	100/99.8
IE2X	Identical	Equal	2	X	95.4/99.8
CE2NX	Contrasting	None	2	NS	97.2/99.6

All scenarios are estimated with and without the seasonal productivity model. The column “seasonal factors” indicates if the amplitudes of the two seasonal factors (F and P) are equal or if there is no seasonal productivity, i.e. “none” and the column $t_{indices}$ indicates the timing of the indices, where NS corresponds to a North Sea like timing (first and third quarter) and X corresponds to a mismatch between indices and the maxima and minima of the seasonal factors (second and fourth quarter; cp. Figure 1). The first number in the “Converged runs” column represents the values for the seasonal model and the second for the non-seasonal model.

Results

Simulation study

The simulation study revealed that results of the SPiCT assessment are biased if underlying seasonal productivity is not

accounted for (e.g. scenario CE2N; Figure 2). The MB of the non-seasonal model is 21% for $(B/B_{MSY})^{last}$ and -10.9% for $(F/F_{MSY})^{last}$ and is significantly higher than of the seasonal model (7.3 and -5.3% , respectively) according to the Wilcoxon signed-

Table 4. Results of the Baltic cod assessment.

Quantity	Models					
	C-C	S-C	C-Vs	S-Vs	C-Vg	S-Vg
B_{MSY}	14.09 0.01 – > 1e ³	68.39 11.43 – 409.13	72.06 40.06 – 129.63	65.38 38.1 – 112.18	3.58 < 0.01 – > 1e ³	42.35 18.11 – 99.02
F_{MSY}^a	6.34 < 0.01 – > 1e ³	0.66 0.11 – 4.04	1.29 0.73 – 2.27	1.4 0.8 – 2.44	19.83 < 0.01 – > 1e ³	1.68 0.71 – 3.95
F_{MSY}^b			0.55 0.28 – 1.09	0.64 0.34 – 1.21		
MSY^a	89.29 47.31 – 168.54	45.32 35.24 – 58.27	92.66 80.3 – 106.93	91.13 78.81 – 105.36	70.92 49.47 – 101.67	71.03 61.21 – 82.43
MSY^b			39.42 31.2 – 49.81	41.86 33.89 – 51.72		
$(B/B_{MSY})^{last}$	3.61 < 0.01 – > 1e ³	0.68 0.07 – 6.54	0.38 0.25 – 0.59	0.31 0.22 – 0.45	4.47 < 0.01 – > 1e ³	0.28 0.15 – 0.52
$(F/F_{MSY})^{last}$	0.09 < 0.01 – 280.54	0.83 0.08 – 8.64	2.13 1.17 – 3.87	2.1 1.28 – 3.47	0.25 < 0.01 – 787.69	2.61 1.33 – 5.13
	LR(2) = 15.05, $p < 0.001$		LR(2) = 14.02, $p < 0.001$		LR(2) = 11.28, $p < 0.001$	

Bold numbers represent point estimates with the respective 95% CIs below. For the Vg models, values for the time-variant MSY and F_{MSY} represent averages over the whole time period. For Vs models, the estimates and CIs of both regimes are presented. The last row shows the results of the likelihood ratio test for each model pair. The grey columns highlight the most suitable models.

^aCorresponds to the first productivity regime (1991–2009) for the Vs models.

^bCorresponds to the second productivity regime (2010–2017) for the Vs models.

rank test ($p < 0.001$ and $p < 0.05$ for the two quantities respectively). However, if no seasonal productivity was simulated, MBs are comparable (scenario CE2NX; Figure 2) and there is no significant difference between the two models for the two quantities ($p = 0.561$ and $p = 0.708$, respectively), even though the precision of C-C is slightly better than of S-C (Figure 2).

Overall, the MBs are smallest for MSY and the relative reference levels and higher for B_{MSY} and F_{MSY} (Table B2 in the Supplementary). Absolute levels, however, vary substantially between the different scenarios and are dependent on the number of indices per year, their timing and the properties of the seasonal processes, one of which is their relative pattern: contrasting vs. identical. While S-C generally outperforms C-C for the contrasting pattern, the C-C model seems to perform better for the identical pattern (Figure 2). However, the smaller MB in $(B/B_{MSY})^{last}$ for C-C is the result of highly overestimated B_{MSY} and underestimated biomass (Figure B4 in the Supplementary). In addition, the MB in $(B/B_{MSY})^{last}$ and $(F/F_{MSY})^{last}$ is comparable between the contrasting and identical pattern for S-C ($p = 0.541$ and $p = 0.767$ for the two quantities respectively), even though, the seasonal productivity process was overestimated to a larger extent in some simulations of the contrasting scenarios in comparison to the identical pattern (Figure 3). In contrast, C-C shows significant differences between the contrasting and identical pattern of the seasonal processes ($p < 0.001$ for $(B/B_{MSY})^{last}$ and $(F/F_{MSY})^{last}$). The relative strength of the seasonal processes is less important (additional scenarios in Section B of the Supplementary). Another important factor affecting model performance is the number of indices and their timings. While there is no significant difference in the MB of $(B/B_{MSY})^{last}$ between 4 and 2 indices ($p = 0.24$ and $p = 0.09$ for the contrasting and identical pattern, respectively; cf. additional scenarios CE4A and IE4A in Figure B3 and Table B1 in the Supplementary), the MB of $(F/F_{MSY})^{last}$ is significantly larger with 2 indices (–5.3%) than with 4 indices

(–0.3%) for the contrasting pattern ($p < 0.001$) as well as for the identical pattern with –4% vs. 2.5% for 2 and 4 indices, respectively ($p < 0.001$). In addition, the number of simulations overestimating the seasonal productivity pattern is larger for the scenario with 2 indices than for the one with 4 (Figure B5 in the Supplementary). If the timing of the indices does not capture any peak of the seasonal processes (scenarios CE2X and IE2X), the MB in both quantities is significantly higher than if both peaks of the seasonal processes are captured (scenarios CE2N and IE2N in Figure 2) or when at least one peak is captured (cf. additional scenarios CE2B and IE2B in Figure B3 and Table B1 in the Supplementary). Although the bias in $(F/F_{MSY})^{last}$ for scenarios CE2X and IE2X is smaller than the other scenarios (Figure 2), Figure B4 in the Supplementary reveals that the bias in the individual reference levels is highest for these scenarios and the resulting MB in $(F/F_{MSY})^{last}$ is only the consequence of a highly overestimated F_{MSY} and underestimated F .

Across all scenarios, between 90 and 100% of all simulations converged, except for scenario CE2X, which shows a high proportion (50.6%) of non-converged runs for the seasonal model (Table 3). Also C-C shows convergence problems for this scenario but the convergence ratio was substantially higher (91.4%). Overall, the proportion of converged non-seasonal fits is higher than the seasonal fits (Table 3). The CF is generally quite high with values around 80% for B/B_{MSY} and around 95% for F/F_{MSY} for most scenarios (Figure 2). The CV is around or below 0.1 and 0.2 for B/B_{MSY} and F/F_{MSY} , respectively and similar across all scenarios and C-C and S-C (Figure 2). Figure 3 shows that the seasonal pattern was generally well estimated, albeit with some outlying simulations, in particular for the scenarios with contrasting seasonal patterns. For CE2NX, the amplitude of the seasonal process [parameter A in Equation (8)] was with 0.2 (median over all simulations) estimated to be much smaller than for the comparative scenario CE2N (0.73).

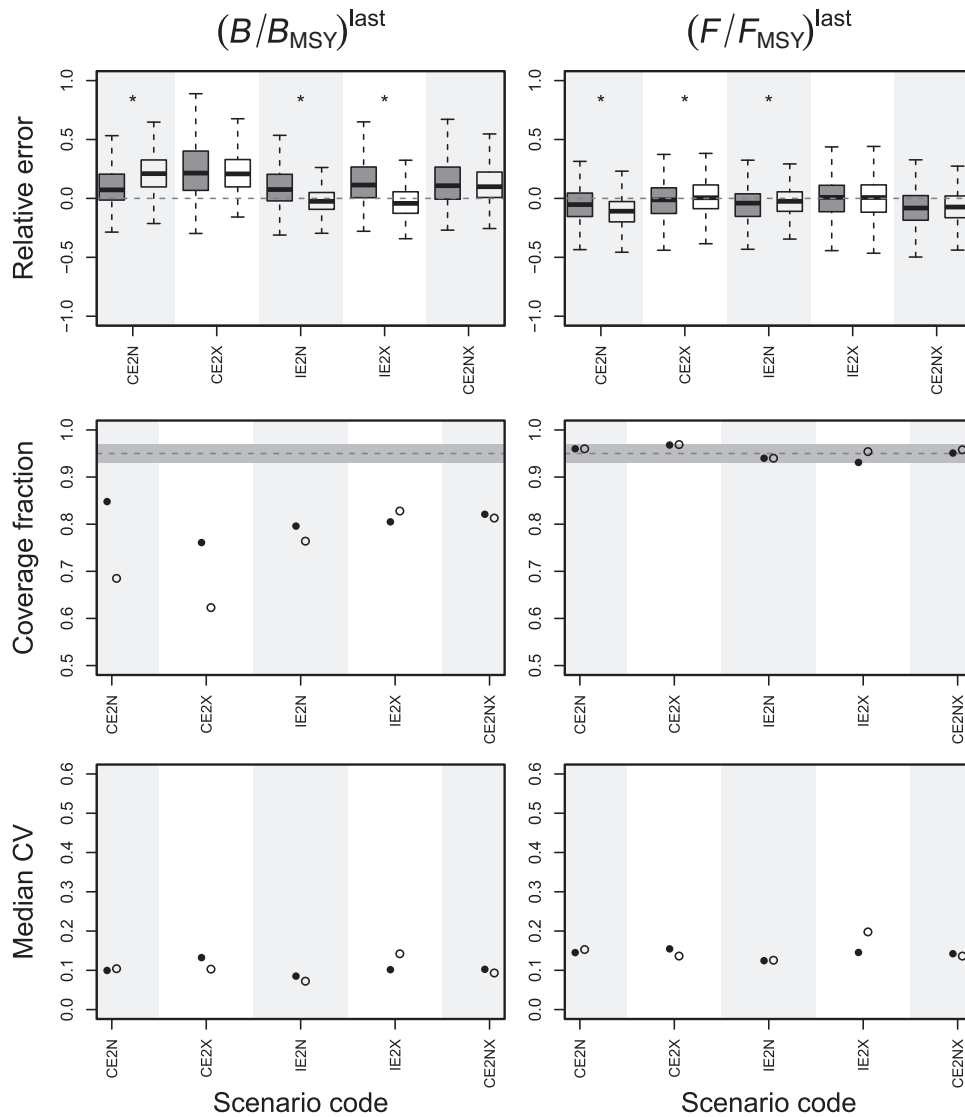


Figure 2. Results of the simulation study for the two quantities $(B/B_{MSY})^{last}$ and $(F/F_{MSY})^{last}$ for all scenarios. Dark filled bars and circles represent seasonal model (S-C), while white bars and circles represent the non-seasonal model (C-C). The boxplots do not include outliers. The second row shows the CF, where the horizontal line represents the reference line for the 95% CIs at 0.95 with expected uncertainty for the reference line dependent on the number of simulations as the shaded area. The stars above the boxplots in the first row indicates for which scenario the differences between the two models (C-C and S-C) are significant based on the Wilcoxon signed-rank test (Table B2 in the Supplementary).

Baltic cod

Beside S-C, all models applied to Baltic cod converged and resulted in reasonable parameter estimates (Section D3 in the Supplementary) and derived quantities (Table 4). However, estimated CIs for derived quantities (Table 4) of the models C-C, S-C, and C-Vg span up to five orders of magnitude, indicating that these models may be unsuitable for the given data. The remaining three models C-Vs, S-Vs, and S-Vg gave reasonable CIs (maximum difference between upper and lower CI limits of one order of magnitude) and show similar biomass and fishing mortality trajectories (Figure 4) and the same stock perception (Table 4): over-fishing in terms of biomass ($B/B_{MSY} < 0.5$) and fishing mortality ($F/F_{MSY} > 2$) at the last assessment time point.

The optimum break point of the Vs models was estimated based on model comparison with different break points

(Figure D14 in the Supplementary), resulting in two productivity regimes: (i) 1991–2009 and (ii) 2010–2017. The MSY of the first productivity regime (~ 91 ktonnes) is more than two times higher than the second regime (~ 40 ktonnes) for both models. The average productivity parameter of the Vg models is ~ 70 ktonnes, however, decreased from ~ 100 ktonnes in 1995 to ~ 40 ktonnes in 2018 (Figure 4f). The uncertainty of the biomass and fishing mortality trajectories in the S-Vg model are higher than in the S-Vs model (Figure 4). For the stepwise models, the seasonal and non-seasonal gave similar point estimates and CIs. For the gradual models, however, the model without seasonality did not give reasonable results (cf. Section D7 in the Supplementary) and indicates the opposite stock perception than of the S-Vg. Although the trajectory of the MSY of the S-Vs and the S-Vg models are different, the absolute value in the last

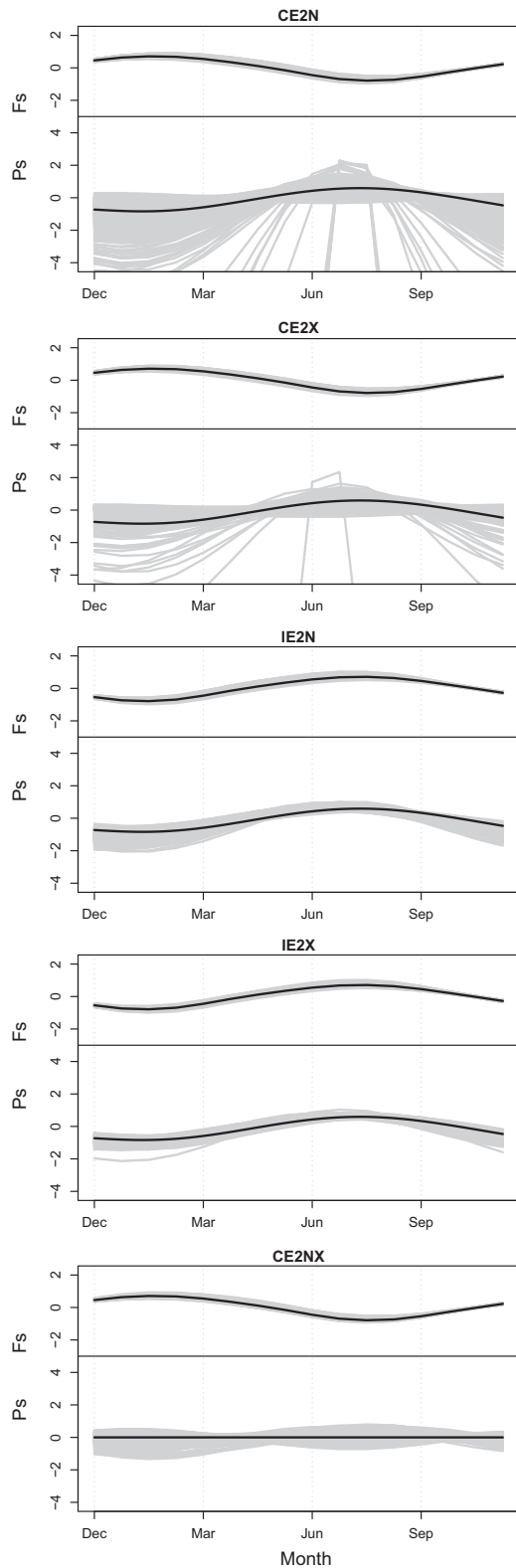


Figure 3. Estimated and true seasonal processes. The black line represents the true seasonal pattern used in the simulation and the grey lines represent the estimated patterns for each simulation. F_s indicates the seasonal F process and P_s the seasonal productivity process.

assessment year of both models is close: 42 and 37.4 tonnes, respectively.

The likelihood ratio test indicates that for all nested models the addition of the two parameters of the seasonal model improves the model fit significantly (Table 4). All models estimated a similar seasonal fishing mortality pattern, with a maximum between April and May and minimum around August (Figure 5a and b). Also the seasonal productivity pattern is similar between the S-Vs and S-Vg, with the maximum around May–June and the minimum between November and December (Figure 5c and d). The slight difference in timing of maxima and minima between models is also shown in the phase parameter: -0.36 and -0.09 for S-Vs and S-Vg, respectively. The amplitude of the seasonal productivity is 1.55 and 0.92 for the stepwise and gradual model, respectively. The uncertainty of the seasonal production factors estimated with S-Vs is almost twice as high as for the gradual model. The C-Vg model gives comparable results to S-Vg if a vague prior for the reversion rate (ψ) is used.

Discussion

Productivity is not constant over time, but shows time-dependent variability due to intra-specific and ecological processes, and environmental conditions (Caddy and Gulland, 1983; Peterman *et al.*, 2000; Mullon *et al.*, 2005; Vert-pre *et al.*, 2013; Britten *et al.*, 2016, 2017). The proposed extensions to a biomass dynamic model allow to account for time-variant productivity both within and between years, i.e. on both short-term seasonal and long-term inter-annual basis. The new models (S-C, C-Vs, S-Vs, C-Vg, S-Vg) were simulation tested (Section C in the Supplementary) and did not reveal any error or dependence on life-history traits, showing expected declining error and CIs with increasing length of the time series (Figures C8–C12 in the Supplementary).

Simulation study

The simulation study reveals that reference levels are not only biased when neglecting seasonal productivity but that the biases depend on the properties of the seasonal processes quantitatively and qualitatively. Thus, not accounting for within year variability in productivity might have similar negative effects on management as it was shown for between years variability in productivity (Peterman *et al.*, 2000; Britten *et al.*, 2017; Nesslage and Wilberg, 2019). Furthermore, the simulation study shows how unaccounted seasonal productivity can lead to large biases in absolute reference levels (B_{MSY} and F_{MSY}) and states (B and F), while the bias in MSY and relative reference levels (B/B_{MSY} and F/F_{MSY}) is relatively small, e.g. for scenario I2EN. This underpins the recommendation of using the relative reference levels for fisheries management (Pedersen and Berg, 2017) as they are the least biased quantities even if seasonal productivity is not accounted for.

Overall, the biases are smaller with the identical pattern in comparison to the contrasting pattern. This can be attributed to the fact that the two seasonal processes are overlapping and that the effect on biomass (and thus on the observed indices) is multiplicative. It appears that it is more complicated for the model to resolve the seasonal trends in catch and biomass and allocate them correctly to the seasonal productivity when the patterns are

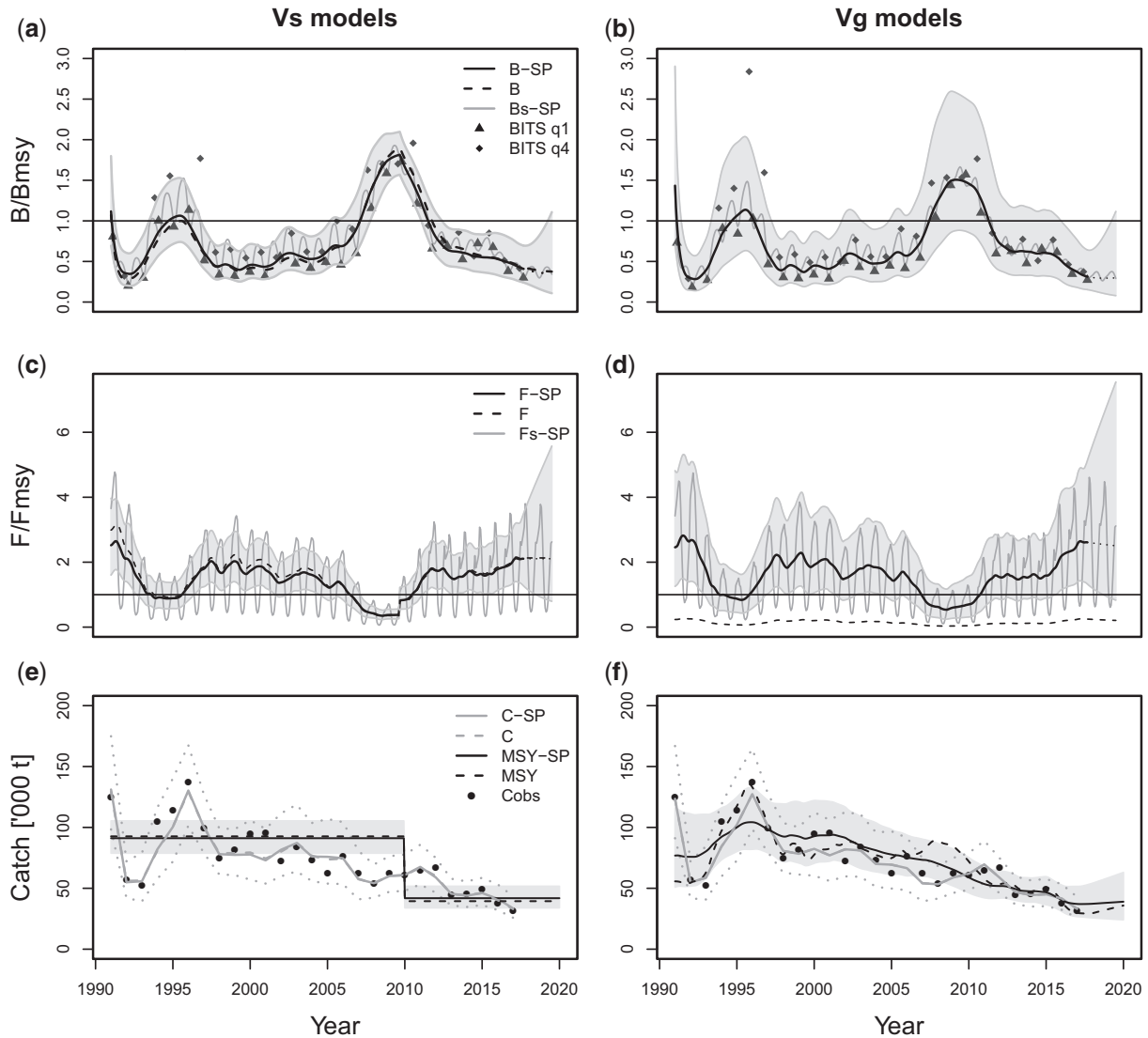


Figure 4. Results of the Batic cod assessment in terms of relative biomass (a, b), fishing mortality (c, d), and catch (e, f) for the regime-shift (Vs) and gradual models (Vg), respectively. Bold black lines in the two top rows represent the relative mean biomass and fishing mortality from the seasonal models, respectively, while the grey lines include the seasonal processes. Dashed lines represent estimated trajectories from non-seasonal models. Shaded areas represent the 95% CIs of the relative mean trajectories of the seasonal models (without seasonality). The relative biomass trajectory of C-Vg is outside of the plotting region with an average value of 8.4. The third row shows catch trajectories and estimated MSY of the seasonal models (solid grey and solid black lines, respectively) and of the non-seasonal model (dashed grey and dashed black lines, respectively). The different symbols represent the observations of the two surveys and catches, respectively.

contrasting (more deviations from the true seasonal productivity curve for the contrasting scenarios in comparison to the identical patterns in Figure 3). While two indices can be sufficient for the estimation of seasonal productivity, the simulation study revealed the importance of the timing of the indices relative to the peaks of the seasonal processes. Scenarios with the timing close to at least one peak of the seasonal productivity process perform better than if the timing is in between peaks. In this case, the biomass index cannot inform the model about the amplitude or phase of the seasonal productivity process.

Although, the biases in derived quantities for the best informed scenario (CE4A, see Section B in the Supplementary) are small and the distributions include zero, the CF for all quantities (except F/F_{MSY}) is smaller than the nominal 95%. The small biases

and low CF can be attributed to the differences of the fishing mortality process in the simulation and estimation and/or data limitations. The simulated roller-coaster pattern for the fishing mortality violates the assumptions of the random walk model used in the estimation procedure. The maximum likelihood estimator and Laplace approximation might introduce a bias, in particular for short time series. A time series of 30 years is far from the asymptotic limit [cf. Figures C8 and C9 in this study and Supplementary Figure S5 in Pedersen and Berg (2017)] and thus, might be insufficient in regard to the complexity of the model additions.

This study contributes to a growing body of research demonstrating how time-variant parameters in surplus production models can improve model performance (Prager, 1994; Vert-pre et al.,

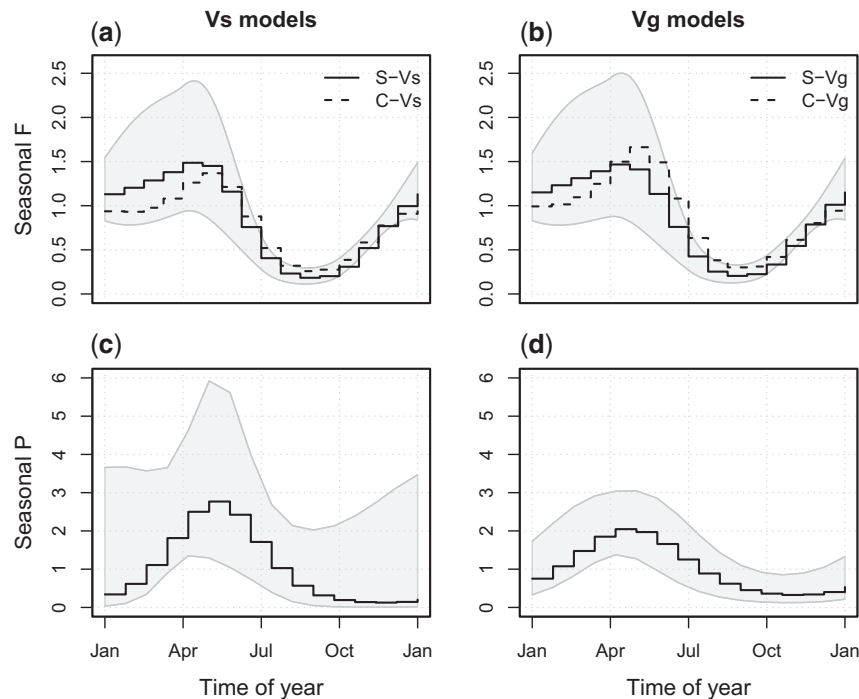


Figure 5. Seasonal processes of the Baltic cod assessment: (a, b) The seasonal fishing mortality processes and (c, d) the seasonal productivity processes for the regime-shift models (Vs) and the gradual models (Vg), respectively. Shaded areas represent the 95% CIs. The first row includes the seasonal fishing mortality process for the non-seasonal models (dashed lines).

2013; Nakayama *et al.*, 2017; Nesslage and Wilberg, 2019), however, this study is the first to model time-variant parameters of surplus production models with the Fletcher parametrization (Fletcher, 1978) rather than the original parametrizations (Graham, 1935; Schaefer, 1954; Pella and Tomlinson, 1969) and particularly quantifying short-term seasonal productivity fluctuations. As previous studies, we considered time-dependent variability in the intrinsic population growth rate (or its analogue ‘ m ’ in the Fletcher parametrization) rather than the carrying capacity K . While processes affecting the carrying capacity of fish populations take place (e.g. habitat contraction; Orensanz *et al.*, 2005; Worm and Tittensor, 2011), they are more difficult to detect based on a biomass index time series alone and due to the weak dynamical connection between biomass and carrying capacity when biomass is low (Britten *et al.*, 2017).

Baltic cod

The models fitted to Baltic cod show a consistent and clear pattern of long-term changes in stock productivity, with either a continuously decreasing productivity pattern or a high and subsequent low productivity regime and none of the models with constant long-term productivity converged without problems. The estimated long-term productivity changes of Baltic cod correlate well with observed changes in the condition of Baltic cod that started in the mid-1990s (Eero *et al.*, 2015; ICES, 2015). The decreasing condition and productivity of Baltic cod can be explained by the individual processes contributing to stock productivity (somatic growth, recruitment, and survival): the peak of the continuous productivity (and the high first productivity regime) fits to the peak abundance of sprat in the Baltic Sea in the mid-1990s (Casini *et al.*, 2016), which was the most abundant

pelagic prey in the stomachs of Baltic cod (Neuenfeldt and Beyer, 2003). Although the subsequent decline of sprat abundance does not have the same reduction rate as the decrease in modelled productivity, the increased spatial mismatch between the core sprat and cod distribution areas in the Baltic poses another cause for productivity decrease (Casini *et al.*, 2016). Similarly, the sharp decline of the productivity of the Northwest Atlantic cod (*Gadus morhua*) stocks at levels of high stock density in 1985 was attributed mainly to the decline of available forage fish (Shelton *et al.*, 2006; Rothschild, 2007; Hilborn and Litzinger, 2009). In addition, according to Casini *et al.* (2016) the increase in hypoxic zones in the Baltic Sea since the 1990s (Conley *et al.*, 2011) has affected cod productivity negatively due to physiological stress, benthos productivity decrease, and habitat compression. Also the increasing seal abundance and, thus, the increase in seal parasites which affect the somatic growth and survival of Baltic cod negatively increased over the last two decades (Mehrdana *et al.*, 2014).

As for long-term changes in productivity, seasonal variations result from seasonal patterns in somatic growth, recruitment, and/or survival. The feeding level of Baltic cod peaks in the third and fourth quarter (Baranova and Uzars, 1986). However, the maximum feeding level does not correspond to the maximum somatic growth rate, as the individuals have an energy deficit after spawning which has to be balanced out before energy can be allocated to somatic growth. The peak in somatic growth is, thus, delayed and to be expected in the first quarter (S. Neuenfeldt, DTU Aqua, pers. comm.), fitting well to the estimated pattern in seasonal productivity. Also the low lipid content of the main pelagic prey species (sprat and herring) from November to March (Røjbek *et al.*, 2014) matches the pattern of the seasonal productivity. The second individual-level process, recruitment and, thus, spawning also shows a seasonal tendency for Baltic cod: although,

Baltic cod has a prolonged spawning period from February to November, spawning peaks in May–August (Wieland, 2000; Bleil *et al.*, 2009), which is expressed in the estimated seasonal productivity pattern in two ways: (i) individuals recruiting to the fishery in May in the third year after spawning (biomass in SPiCT corresponds to exploitable biomass), and (ii) weight-loss after peak spawning in May–August (S. Neuenfeldt, DTU Aqua, pers. comm.). Less is known about the third component, seasonal patterns of the survival of Baltic cod, but the natural mortality of Baltic cod might be high right after spawning (K. Hüsey, DTU Aqua, pers. comm.).

The assumption of the SPiCT assessment that the Baltic cod stock is not subject to migration is likely violated as individuals are not only migrating within the Baltic Sea and mixing with the western Baltic cod stock (particularly in the Arkona Basin; Aro, 1989; Nielsen *et al.*, 2013), but the migration rate also varies over time (Hüsey *et al.*, 2016). Furthermore, we made the assumption that the seasonal productivity pattern is constant over time although some inter-annual variability has been observed (Wieland, 2000; Bleil *et al.*, 2009). This should be seen as an assumption necessary to facilitate the analysis rather than representing the truth, since we are approaching the limit of what can be estimated from the data. Random deviations from a constant pattern would likely increase the uncertainty but not introduce bias, whereas systematic trends are likely to introduce biases in the assessment. Extending the model to allow the seasonal productivity pattern to change over time is an avenue for future research.

According to the assessments with reasonable fits and uncertainties (C-Vs, S-Vs, S-Vg), the Baltic cod stock is depleted ($B < B_{MSY}$) and subject to over-fishing ($F > 2F_{MSY}$). The models with seasonal productivity are significantly better at describing the data compared to models without seasonality, although the estimates of $(B/B_{MSY})^{last}$ and $(F/F_{MSY})^{last}$ are almost identical. However, the simulation study showed that this may not be the case in other cases. The time-variant reference levels (MSY and F_{MSY}) do not affect the classification of the stock in terms of these relative states historically or in the current year. Taking assessment uncertainty into account, useful management advice can be given based on the relative states in the last time step ($(B/B_{MSY})^{last}$ and $(F/F_{MSY})^{last}$) as demonstrated for the original SPiCT (ICES, 2018b).

Conclusion

This study introduces a novel approach to incorporate environmental change into stock assessments without the need of complex and data-demanding (ecosystem) models and defines time-variant reference levels for fisheries management and advice. Although the extensions of biomass dynamic models introduced here, increase requirements for data quality and quantity (seasonal catches and biannual survey indices required), accounting for time-variant productivity is important as stocks in low-productivity regimes cannot support the same yield as stocks in high-production regimes and neglecting seasonality might severely bias estimated reference levels and relative states and, therefore, management advice. Accounting for a combination of time-variant productivity on seasonal and long-term scales improves the assessment of the Baltic cod stock significantly.

Supplementary data

Supplementary material is available at the ICESJMS online version of the manuscript.

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References

- Akaike, H. 1998. Information theory and an extension of the maximum likelihood principle. *In* Selected Papers of Hirotugu Akaike, pp. 199–213. Ed. by E. Parzen, K. Tanabe, and G. Kitagawa. Springer Series in Statistics (Perspectives in Statistics). Springer, New York, NY.
- Aro, E. 1989. A review of fish migration patterns in the Baltic. *Rapports et procès-verbaux des réunions/Conseil Permanent International pour l'Exploration de la Mer*, 190: 72–96.
- Baranova, T., and Uzars, D. 1986. Growth and maturation of cod (*Gadus morhua callarias* L.) in the eastern Baltic. ICES Council Meeting, 7.
- Begley, J., and Howell, D. 2004. An Overview of Gadget, the Globally Applicable Area-disaggregated General Ecosystem Toolbox. ICES CM 2004, 13.
- Belkin, I. M. 2009. Rapid warming of Large Marine Ecosystems. *Progress in Oceanography*, 81: 207–213.
- Berg, C. W., and Nielsen, A. 2016. Accounting for correlated observations in an age-based state-space stock assessment model. *ICES Journal of Marine Science*, 73: 1788–1797.
- Bleil, M., Oeberst, R., and Urrutia, P. 2009. Seasonal maturity development of Baltic cod in different spawning areas: importance of the Arkona Sea for the summer spawning stock. *Journal of Applied Ichthyology*, 25: 10–17.
- Boyce, D. G., Dowd, M., Lewis, M. R., and Worm, B. 2014. Estimating global chlorophyll changes over the past century. *Progress in Oceanography*, 122: 163–173.
- Brander, K. M. 1995. The effect of temperature on growth of Atlantic cod (*Gadus morhua* L.). *ICES Journal of Marine Science*, 52: 1–10.
- Britten, G. L., Dowd, M., Kanary, L., and Worm, B. 2017. Extended fisheries recovery timelines in a changing environment. *Nature Communications*, 8: 15325.
- Britten, G. L., Dowd, M., and Worm, B. 2016. Changing recruitment capacity in global fish stocks. *Proceedings of the National Academy of Sciences*, 113: 134–139.
- Caddy, J. F., and Gulland, J. A. 1983. Historical patterns of fish stocks. *Marine Policy*, 7: 267–278.
- Carlson, S. M., Olsen, E. M., and Vllestad, L. A. 2008. Seasonal mortality and the effect of body size: a review and an empirical test using individual data on brown trout. *Functional Ecology*, 22: 663–673.
- Casini, M., Käll, F., Hansson, M., Plikshs, M., Baranova, T., Karlsson, O., Lundström, K. *et al.* 2016. Hypoxic areas, density-dependence and food limitation drive the body condition of a heavily exploited marine fish predator. *Royal Society Open Science*, 3: 160416.
- Conley, D. J., Carstensen, J., Aigars, J., Axe, P., Bonsdorff, E., Eremina, T., Haahti, B. M. *et al.* 2011. Hypoxia is increasing in the coastal zone of the Baltic Sea. *Environmental Science and Technology*, 45: 6777–6783.
- Curti, K. L., Collie, J. S., Legault, C. M., and Link, J. S. 2013. Evaluating the performance of a multispecies statistical

- catch-at-age model. *Canadian Journal of Fisheries and Aquatic Sciences*, 70: 470–484.
- de Boor, C. 1978. A practical guide to splines. *Mathematics of Computation*, 28: 1191–1194.
- Eero, M., Hjelm, J., Behrens, J., Buchmann, K., Cardinale, M., Casini, M., Gasyukov, P. *et al.* 2015. Eastern Baltic cod in distress: biological changes and challenges for stock assessment. *ICES Journal of Marine Science*, 72: 2180–2186.
- Fletcher, R. I. 1978. On the restructuring of the Pella–Tomlinson system. *U.S. Fisheries Bulletin*, 76: 515–534.
- Fox, W. W. 1970. An exponential surplus-yield model for optimizing exploited fish populations. *Transactions of the American Fisheries Society*, 99: 80–88.
- Fretwell, S. 1972. *Populations in a seasonal environment*, Vol. 5. Princeton University Press.
- Frisk, C., Andersen, K. H., Temming, A., Herrmann, J. P., Madsen, K. S., and Kraus, G. 2015. Environmental effects on sprat (*Sprattus sprattus*) physiology and growth at the distribution frontier: a bioenergetic modelling approach. *Ecological Modelling*, 299: 130–139.
- Gardiner, C. W. 1985. *Handbook of Stochastic Methods*. Springer, Berlin. 4 pp.
- Graham, M. 1935. Modern theory of exploiting a fishery, and application to North Sea trawling. *ICES Journal of Marine Science*, 10: 264–274.
- Gruber, N. 2011. Warming up, turning sour, losing breath: ocean biogeochemistry under global change. *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences*, 369: 1980.
- Hare, J. A., Morrison, W. E., Nelson, M. W., Stachura, M. M., Teeters, E. J., Griffis, R. B., Alexander, M. A. *et al.* 2016. A vulnerability assessment of fish and invertebrates to climate change on the Northeast U.S. Continental Shelf. *PLoS One*, 11: e0146756.
- Hilborn, R., and Litzinger, E. 2009. Causes of decline and potential for recovery of Atlantic cod populations. *The Open Fish Science Journal*, 2: 32–38.
- Hilborn, R., and Walters, C. J. 1992. Quantitative fisheries stock assessment: choice, dynamics and uncertainty. *Reviews in Fish Biology and Fisheries*, 2: 177–178.
- Hollowed, A. B., Barange, M., Beamish, R. J., Brander, K., Cochrane, K., Drinkwater, K., Foreman, M. G. *et al.* 2013. Projected impacts of climate change on marine fish and fisheries. *ICES Journal of Marine Science*, 70: 1023–1037.
- Hüssy, K., Hinrichsen, H. H., Eero, M., Mosegaard, H., Hemmer-Hansen, J., Lehmann, A., and Lundgaard, L. S. 2016. Spatio-temporal trends in stock mixing of eastern and western Baltic cod in the Arkona Basin and the implications for recruitment. *ICES Journal of Marine Science*, 73: 293–303.
- ICES. 2015. Report of the Benchmark Workshop on Baltic Cod Stocks (WKBALTCOD), 26 March 2015, Rostock, Germany. *ICES CM 2015/ACOM:35*, 172 pp.
- ICES. 2017a. Report of the Baltic Fisheries Assessment Working Group (WGBFAS), 19–26 April 2017, Copenhagen, Denmark. *ICES CM 2017/ACOM:11*, 810 pp.
- ICES. 2017b. Report of the Workshop on Biological Input to Eastern Baltic Cod Assessment (WKBEBCA), 12 March 2017, Gothenburg, Sweden. *ICES CM 2017/SSGEPD:19*, 40 pp.
- ICES. 2018a. Baltic Fisheries Assessment Working Group (WGBFAS), 6–13 April 2018, ICES HQ, Copenhagen, Denmark. *ICES CM 2018/ACOM:11*, 748 pp.
- ICES. 2018b. Report from the Workshop on the Development of Quantitative Assessment Methodologies based on Life-history traits, exploitation characteristics, and other relevant parameters for stocks in categories 3-6, 2–6 October 2017, Lisbon, Portugal. *ICES CM 2017/ACOM:43*, 221 pp.
- Jennings, S., Kaiser, M., and Reynolds, J. 2009. *Marine Fisheries Ecology*. Blackwell Scientific, Oxford.
- Kempf, A., Floeter, J., and Temming, A. 2009. Recruitment of North Sea cod (*Gadus morhua*) and Norway pout (*Trisopterus esmarkii*) between 1992 and 2006: the interplay between climate influence and predation. *Canadian Journal of Fisheries and Aquatic Sciences*, 66: 633–648.
- Köster, F., Möllmann, C., Hinrichsen, H.-H., Wieland, K., Tomkiewicz, J., Kraus, G., Voss, R. *et al.* 2005. Baltic cod recruitment—the impact of climate variability on key processes. *ICES Journal of Marine Science*, 62: 1408–1425.
- Lambert, G., Nielsen, J. R., Larsen, L. I., and Sparholt, H. 2009. Maturity and growth population dynamics of Norway pout (*Trisopterus esmarkii*) in the North Sea, Skagerrak, and Kattegat. *ICES Journal of Marine Science*, 66: 1899–1914.
- Larkin, P. A. 1977. An epitaph for the concept of maximum sustained yield. *Transactions of the American Fisheries Society*, 106: 1–11.
- Lobón-Cerviá, J., and Bradford, M. 2014. Recruitment and survival rate variability in fish populations: density-dependent regulation or further evidence of environmental determinants? *Canadian Journal of Fisheries and Aquatic Sciences*, 71: 290–300.
- Maunder, M. N., and Punt, A. E. 2013. A review of integrated analysis in fisheries stock assessment. *Fisheries Research*, 142: 61–74.
- Mehrdana, F., Bahlool, Q. Z., Skov, J., Marana, M. H., Sindberg, D., Mundeling, M., Overgaard, B. C. *et al.* 2014. Occurrence of zoonotic nematodes *Pseudoterranova decipiens*, *Contracaecum osculatium* and *Anisakis simplex* in cod (*Gadus morhua*) from the Baltic Sea. *Veterinary Parasitology*, 205: 581–587.
- Mertz, G., and Myers, R. A. 1997. Influence of errors in natural mortality estimates in cohort analysis. *Canadian Journal of Fisheries and Aquatic Sciences*, 54: 1608–1612.
- Methot, R. D., and Wetzel, C. R. 2013. Stock synthesis: a biological and statistical framework for fish stock assessment and fishery management. *Fisheries Research*, 142: 86–99.
- Möllmann, C., Diekmann, R., Müller-karulis, B., Kornilovs, G., Plikshs, M., and Axe, P. 2009. Reorganization of a large marine ecosystem due to atmospheric and anthropogenic pressure: a discontinuous regime shift in the central Baltic Sea. *Global Change Biology*, 15: 1377–1393.
- Mullon, C., Fréon, P., and Cury, P. 2005. The dynamics of collapse in world fisheries. *Fish and Fisheries*, 6: 111–120.
- Nakayama, S. I., Akimoto, S., Ichinokawa, M., and Okamura, H. 2017. Incorporating accessibility limitation into the surplus production model. *Fisheries Science*, 83: 353–365.
- Nesslage, G. M., and Wilberg, M. J. 2019. A performance evaluation of surplus production models with time-varying intrinsic growth in dynamic ecosystems. *Canadian Journal of Fisheries and Aquatic Sciences*, 2018–0292, doi: 10.1139/cjfas-2018-0292.
- Neuenfeldt, S., and Beyer, J. E. 2003. Oxygen and salinity characteristics of predator–prey distributional overlaps shown by predatory Baltic cod during spawning. *Journal of Fish Biology*, 62: 168–183.
- Nielsen, A., and Berg, C. W. 2014. Estimation of time-varying selectivity in stock assessments using state-space models. *Fisheries Research*, 158: 96–101.
- Nielsen, B., Hüssy, K., Neuenfeldt, S., Tomkiewicz, J., Behrens, J. W., and Andersen, K. H. 2013. Individual behaviour of Baltic cod *Gadus morhua* in relation to sex and reproductive state. *Aquatic Biology*, 18: 197–207.
- Nielsen, J. R., Lambert, G., Bastardie, F., Sparholt, H., and Vinther, M. 2012. Do Norway pout (*Trisopterus esmarkii*) die from spawning stress? Mortality of Norway pout in relation to growth, sexual maturity, and density in the North Sea, Skagerrak, and Kattegat. *ICES Journal of Marine Science*, 69: 197–207.
- Orensanz, J. M., Ernest, B., Armstrong, D. A., Stabeno, P., and Livingston, P. 2005. Contraction of the geographic range of distribution of snow crab (*Chionoecetes opilio*) in the eastern Bering Sea: an environmental ratchet? *CalCOFI Report*, 45: 65–79.

- Pauly, D. 1980. On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. *ICES Journal of Marine Science*, 39: 175–192.
- Payne, M. R., Hatfield, E. M. C., Dickey-Collas, M., Falkenhaus, T., Gallego, A., Gröger, J., Licandro, P. *et al.* 2008. Recruitment in a changing environment: the 2000s North Sea herring recruitment failure. *ICES Journal of Marine Science*, 66: 272–277.
- Pécuchet, L., Nielsen, J. R., and Christensen, A. 2015. Impacts of the local environment on recruitment: a comparative study of North Sea and Baltic Sea fish stocks. *ICES Journal of Marine Science*, 72: 1323–1335.
- Pedersen, M. W., and Berg, C. W. 2017. A stochastic surplus production model in continuous time. *Fish and Fisheries*, 18: 226–243.
- Pella, J. J., and Tomlinson, P. K. 1969. A generalized stock production model. *Inter-American Tropical Tuna Commission*, 13: 421–488.
- Pershing, A. J., Alexander, M. A., Hernandez, C. M., Kerr, L. A., Le Bris, A., Mills, K. E., Nye, J. A. *et al.* 2015. Slow adaptation in the face of rapid warming leads to collapse of the Gulf of Maine cod fishery. *Science* (New York, N.Y.), 350: 809–812.
- Peterman, R. M., Pyper, B. J., and Grout, J. A. 2000. Comparison of parameter estimation methods for detecting climate-induced changes in productivity of Pacific salmon (*Oncorhynchus* spp.). *Canadian Journal of Fisheries and Aquatic Sciences*, 57: 181–191.
- Petitgas, P., Rijnsdorp, A. D., Dickey-Collas, M., Engelhard, G. H., Peck, M. A., Pinnegar, J. K., Drinkwater, K. *et al.* 2013. Impacts of climate change on the complex life cycles of fish. *Fisheries Oceanography*, 22: 121–139.
- Prager, M. H. 1994. A suite of extensions to a nonequilibrium surplus-production model. *Fishery Bulletin*, 92: 374–389.
- Quinn, T. J., and Deriso, R. B. 1999. *Quantitative Fish Dynamics*. Oxford University Press, Oxford.
- R Core Team. 2014. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Reusch, T. B., Dierking, J., Andersson, H. C., Bonsdorff, E., Carstensen, J., Casini, M., Czajkowski, M. *et al.* 2018. The Baltic Sea as a time machine for the future coastal ocean. *Science Advances*, 4: eaar8195.
- Ricard, D., Minto, C., Baum, J., and Jensen, O. 2012. Evaluating the stock assessment knowledge base and status of exploited marine populations with the RAM Legacy Stock Assessment Database. *Fish and Fisheries*, 13: 380–398.
- Røjbek, M. C., Tomkiewicz, J., Jacobsen, C., and Støttrup, J. G. 2014. Forage fish quality: seasonal lipid dynamics of herring (*Clupea harengus* L.) and sprat (*Sprattus sprattus* L.) in the Baltic Sea. *ICES Journal of Marine Science*, 71: 56–71.
- Ross, S. D., Nielsen, J. R., Gislason, H., Nielsen, A., and Andersen, N. G. 2018. Growth and food consumption of whiting *Merlangius merlangus*. *Journal of Fish Biology*, 93: 334–343.
- Rothschild, B. J. 2007. Coherence of Atlantic cod stock dynamics in the Northwest Atlantic Ocean. *Transactions of the American Fisheries Society*, 136: 858–874.
- Russell, E. S. 1931. Some theoretical considerations on the “Overfishing” problem. *ICES Journal of Marine Science*, 6: 3–20.
- Schaefer, M. B. 1954. Some aspects of the dynamics of populations important to the management of the commercial marine fisheries. *Inter-American Tropical Tuna Commission Bulletin*, 1: 25–56.
- Shelton, P. A., Sinclair, A. F., Chouinard, G. A., Mohn, R., and Duplisea, D. E. 2006. Fishing under low productivity conditions is further delaying recovery of Northwest Atlantic cod (*Gadus morhua*). *Canadian Journal of Fisheries and Aquatic Sciences*, 63: 235–238.
- Tommasi, D., Stock, C. A., Hobday, A. J., Methot, R., Kaplan, I. C., Eveson, J. P., Holsman, K. *et al.* 2017. Managing living marine resources in a dynamic environment: the role of seasonal to decadal climate forecasts. *Progress in Oceanography*, 152: 15–49.
- Uhlenbeck, G. E., and Ornstein, L. S. 1930. On the theory of Brownian motion. *Physical Review*, 36: 823–841.
- Ursin, E. 1963. On the seasonal variation of growth rate and growth parameters in Norway Pout (*Gadus esmarkii*) in the Skagerrak. *Meddelelser fra Danmarks Fiskeri—og Havundersogelser*, 4: 17–29.
- Ursin, E. 1967. A mathematical model of some aspects of fish growth, respiration, and mortality. *Journal of the Fisheries Research Board of Canada*, 24: 2355–2453.
- Vert-pre, K. A., Amoroso, R. O., Jensen, O. P., and Hilborn, R. 2013. Frequency and intensity of productivity regime shifts in marine fish stocks. *Proceedings of the National Academy of Sciences*, 110: 1779–1784.
- Walters, C. J. 1987. Nonstationarity of production relationships in exploited populations. *Canadian Journal of Fisheries & Aquatic Sciences*, 44: 156–165.
- Wieland, K. 2000. Changes in the timing of spawning of Baltic cod: possible causes and implications for recruitment. *ICES Journal of Marine Science*, 57: 452–464.
- Worm, B., and Tittensor, D. P. 2011. Range contraction in large pelagic predators. *Proceedings of the National Academy of Sciences*, 108: 11942–11947.

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Appendix: Estimation of the non-seasonal stochastic reference levels and relative states

The non-seasonal stochastic reference levels can be derived by substituting the corresponding equations in Pedersen and Berg (2017) with the deterministic reference levels [Equations (12)–(14)], resulting in:

$$MSY_t^s = MSY_t^d \left(1 - \frac{n/2}{1 - (1 - F_{MSY_t}^d)^2} \sigma_B^2 \right), \quad (A1)$$

$$B_{MSY_t}^s = B_{MSY}^d \left(1 - \frac{1 + F_{MSY_t}^d (n-2)/2}{F_{MSY_t}^d (2 - F_{MSY_t}^d)^2} \sigma_B^2 \right), \quad (A2)$$

$$F_{MSY_t}^s = F_{MSY_t}^d - \frac{(n-1)(1 - F_{MSY_t}^d)}{(2 - F_{MSY_t}^d)^2} \sigma_B^2, \quad (A3)$$

where the superscript d refers to the deterministic reference levels as defined in “Reference levels” section and σ_B refers to the standard deviation of the biomass process noise. Similarly, in the estimation of the relative states (B_t/B_{MSY} and F_t/F_{MSY}), the seasonal part of the biomass and fishing mortality is omitted as otherwise the quantities were strongly dependent on the time of the year one chooses to evaluate them. These relative states are estimated by removing the seasonal components of m_t and F_t ($\hat{S}_t^{(m)}$ and $S_t^{(F)}$, respectively) in Equations (1) and (2).