

Stochastic modelling and synthesis of dynamic fish recruitment productivity in the Celtic Seas ecoregion

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Abstract

The Celtic Seas ecoregion (CSE) is undergoing climatic and ecosystem changes, which can induce changes in fish productivity. Globally, the productivity of many stocks has shown evidence of change over decadal timescales. Varying factors might drive these dynamics in the CSE, but for many stocks, these mechanisms have not been fully understood to be included in management advice. We study dynamic productivity for 28 stocks in the Celtic Seas by tracking integrated stochastic signals in the relationship between stock size and recruitment using state-space modelling applying Peterman's Productivity Method. Our research objectives were to (i) fit Ricker stock–recruitment models with time-varying parameters to all age- or length-based assessed stocks in the CSE, (ii) evaluate which parameters vary in time, (iii) examine temporal characteristics of historical recruitment productivity, and (iv) evaluate productivity correlation across stocks. For 22 out of 28 stocks, at least one of the three time-varying parameter models had a better fit than the time-invariant model. In the CSE, fish productivity has diverse temporal patterns, with some stocks displaying relevant long-term decreasing productivity trends. Getting insight into temporal changes in recruitment productivity is very valuable and has important implications for sustainable fisheries.

Keywords: dynamic reference points; ecosystem approach; non-stationarity productivity; Peterman's productivity method; time-varying parameters

Introduction

The ICES Celtic Seas ecoregion (CSE) covers a major part of the northwestern European continental shelf. This ecoregion also includes areas of the deeper eastern Atlantic Ocean as well as coastal waters that are heavily influenced by oceanic inputs (ICES, 2021a). Previous studies in the area suggest that marine communities respond to the combined effect of fisheries and climate (Lynam *et al.*, 2010). Environmental changes, such as changes in the North Atlantic Oscillation, can produce temporal changes in oceanographic conditions, which, in turn, can cause ecological responses such as changes in the reproduction timing, abundance, growth, spatial distribution, mortality, and inter-specific relationships (Ottersen *et al.*, 2001). Climate change and extreme events could potentially cause important changes in the ecoregion (Richardson and Schoeman, 2004; Drinkwater *et al.*, 2010). While broad environmental variability and trends are evident, the mechanisms affecting the ecosystem and the populations are complex (Sugihara *et al.*, 2012; Fogarty *et al.*, 2016). Thus, although it is known that environmental drivers affect recruitment (e.g. Kristiansen *et al.*, 2011), these relationships are not fully understood and tend to be unstable over time (Myers, 1998; Stige *et al.*, 2006; Ottersen *et al.*, 2013).

Recruitment productivity is vital for the renewal of the population. In stock assessments, understanding the relationship between recruits and spawner biomass is key for the sustainable management of fisheries but notoriously variable

and traditionally difficult to understand (Hilborn and Walters, 1992; Myers, 1994). The stock–recruitment relationship, used to estimate maximum sustainable yield fishing mortality and biomass reference points, is typically modelled as a stationary process where the parameters are fixed based on historically constant estimates (time-invariant; Collie *et al.*, 2012, 2021; Silvar-Viladomiu *et al.*, 2022). However, population dynamics processes, on top of operating over different density ranges, may operate at different times (Zeng *et al.*, 1998). Globally many stocks' productivity has shown evidence of non-stationarity (Vert-pre *et al.*, 2013) and displayed evidence of temporal variation in parameters of the stock–recruitment relationship (Peterman *et al.*, 2003; Dorner *et al.*, 2008; Minto *et al.*, 2014; Britten *et al.*, 2016; Tableau *et al.*, 2019). Temporal changes in productivity have important implications for reference points (Kell *et al.*, 2016; Clausen *et al.*, 2018; Holt and Michielsens, 2020; Zhang *et al.*, 2021; Silvar-Viladomiu *et al.*, 2022), upon which fishing opportunities advice is based. Stock–recruitment models with time-varying parameters developed by Peterman and colleagues [Peterman's productivity method (PPM); Peterman *et al.*, 2000; Silvar-Viladomiu *et al.*, 2022] can track integrated underlying signals of change in productivity and identify trends (Peterman *et al.*, 2003).

For sustainable management of the CSE stocks, it is critically important that temporal trends in recruitment productivity are detected in a timely and reliable manner (Dorner *et al.*,

2008). Understanding the temporal dynamics of recruitment is crucial as recruitment determines future productivity for long-lived stocks, mediated by natural mortality, and proximal productivity for short-lived recruitment-driven stocks. This understanding also contributes to identifying long-term trends and abrupt changes such as regime shifts (Perälä *et al.*, 2020). To better understand how -rather than why- recruitment productivity has varied over decadal timescales, we applied PPM and extracted filtered and smoothed time series patterns for multiple species and stocks in the CSE. Our objectives were to (i) fit stock–recruitment models with different time-varying parameter configurations, (ii) evaluate which parameters vary in time, (iii) examine temporal characteristics of historical recruitment productivity, and (iv) evaluate productivity correlation across stocks.

Material and methods

Recruitment and spawning stock biomass estimates

We used the time series of spawning stock biomass (*SSB*) and recruitment (*R*) estimates from the most recent stock assessments issued by the International Council for the Exploration of the Sea (ICES). For stocks residing at least partially in the CSE, we extracted the data via XML from the ICES Stock Assessment Graphs database (ICES, 2022). From that list, the stocks her.27.1-24a514a (Norwegian spring-spawning herring) and lin.27.5b (Faroe grounds ling) were excluded from the analysis because the boundaries of the stock showed only a minor overlap with the CSE. We filtered for assessments that estimated spawning stock biomass and used “SSB” in the stock size description. Twenty-nine stocks were selected, most of which were category 1 (i.e. stocks with quantitative assessments), except for cod.27.7a and her.27.6a7bc, which at the time of data extraction were category 3 (i.e. stocks for which survey-based assessments or exploratory assessments indicate trends). However, we used data from the 2018 assessment, when the stocks were considered category 1, so a full analytical stock assessment was carried out. One stock with a short time series (<20 years) was excluded from the analysis (bli.27.5b67, blue ling in the Celtic Seas and Faroes grounds). Assessment methodologies were typically age- or length-structured (Table 1). While some assessments contain a stock–recruitment model to develop initial estimates of recruitment, if recruitment deviations are included, the annual recruitment estimates are informed by the available length and age data. Most of the assessments in this study did not assume a stock–recruitment relationship and included a large standard deviation (Supplementary Table S1). Stock assessments in this study that use extended survivors analysis (XSA), Gadget, and a4a models do not assume any stock–recruitment relationship. Assessments that use state-space assessment model (SAM) here assume no stock-recruit relationship and parameterized logarithm of recruitment with a random walk with high process variation, effectively estimating log recruitment as a free parameter. Some assessments that use age-structured assessment program (ASAP) in this study do not assume a stock–recruitment relationship (had.27.7a, her.27.irls, her.27.irls); the other ASAP assessment (cod.27.7a) assumes a Beverton–Holt stock–recruitment relationship with an annual recruitment CV of 0.5 that allows largely unconstrained variation in recruitment. The SS3 assessments in this study, assume a Beverton–Holt stock–recruitment relation-

ship with fixed steepness, equal to 0.9 and included recruitment variation big enough to give flexibility to the model to estimate recruitment deviations adequately for this stock, and steepness was estimated for hke.27.3a46-8abd. The spurdog assessments included a recruitment variability parameter of 0.2 (De Oliveira *et al.*, 2013). This lower deviation might constrain the magnitude of the time variation, but the patterns should remain similar. Stocks were classified using metadata from the assessment by region (northern CSE, central CSE, southern CSE, and northeast Atlantic wide area). The Northeast Atlantic wide area classifies stocks that cover a wide part of the Northeast Atlantic.

Model details

We applied PPM, which is a state-space dynamic model for estimating time-varying parameters of the stock–recruitment relationship (see Silvar-Viladomiu *et al.*, 2022). We focused on the univariate (single-population) PPM to study the recruitment productivity of CSE stocks. We described the stock–recruitment relationship with the linearized version of the Ricker model (Ricker, 1954), which depends on two parameters: a maximum productivity and a density-dependent coefficient (Peterman *et al.*, 2000). We use the natural logarithm of the survival ratio *R/S* (also termed the “killing power”, Myers 2001). The linearized Ricker model follows the function below:

$$\ln\left(\frac{R_t}{S_{t-\tau}}\right) = a + bS_{t-\tau} + v_t$$

$$v_t \sim N(0, \sigma_v^2), \quad (1)$$

where R_t is the recruitment in year t , $S_{t-\tau}$ is the spawning stock biomass in time t (lag by the age of recruitment τ), a is the maximum productivity, b is the density-dependent mortality, and v_t is an amalgam of process and observation errors.

We evaluated four different models as follows: (i) time-invariant Ricker model, (ii) time-variant maximum productivity Ricker model, (iii) time-variant density-dependent mortality Ricker model, and (iv) time-covariant maximum productivity and density-dependent mortality Ricker model. We fitted the models by maximization of the likelihood within the DLM package (Petris *et al.*, 2009) in the statistical software R. To estimate time-varying parameters, the Kalman filter was implemented.

First, we estimated the time-invariant linearized Ricker model. This model is stationary in its parameters because it assumes that the parameters are constant across the entire time series of spawner and recruit data (Equation 1). The maximum-productivity coefficient (a) is the natural logarithm of α in the traditional Ricker formulation, which is the maximum reproductive rate and represents the product of the fecundity and density-independent mortality integrated over time from spawning to recruitment (Ricker, 1954). The density-dependent mortality (b) gives the rate at which recruitment is reduced by density-dependent mortality.

For the second model, we estimated the time-varying maximum-productivity parameter. We allow the stochastic parameter(s) to vary via a random-walk process:

$$\ln\left(\frac{R_t}{S_{t-\tau}}\right) = a_t + bS_{t-\tau} + v_t, \quad (2)$$

Table 1. Details of the CSE stocks investigated.

Stock key label	Description	Scientific name	Age-at-R	Assessment	Series length	Region
aru.27.5b6a	Greater silver smelt in divisions 5.b and 6.a (Faroes grounds and west of Scotland)	<i>Argentina silus</i>	5	SAM	22	Northern CSE
bli.27.5b67	Blue ling in subareas 6-7 and division 5.b (Celtic Seas and Faroes grounds)	<i>Molva dypterygia</i>	9	MYCC	17	NEA wide area
bss.27.4bc7ad-h	Seabass in divisions 4.b-c, 7.a, and 7.d-h (central and southern North Sea, Irish Sea, English Channel, Bristol Channel, and Celtic Sea)	<i>Dicentrarchus labrax</i>	0	SS3	37	Central CSE
cod.27.6a	Cod in division 6.a (West of Scotland)	<i>Gadus morhua</i>	1	SAM	40	Northern CSE
cod.27.7a	Cod in division 7.a (Irish Sea)	<i>Gadus morhua</i>	0	ASAP	51	Central CSE
cod.27.7e-k	Cod in divisions 7.e-k (eastern English Channel and southern Celtic Seas)	<i>Gadus morhua</i>	1	SAM	41	Southern CSE
dgs.27.nea	Spurdog in Subareas 1-10, 12 and 14 (the northeast Atlantic and adjacent waters)	<i>Squalus acanthias</i>	0	^a	116	NEA wide area
had.27.46a20	Haddock in Subarea 4, division 6.a, and subdivision 20 (North Sea, West of Scotland, Skagerrak)	<i>Melanogrammus aeglefinus</i>	0	SAM	50	Northern CSE
had.27.6b	Haddock in division 6.b (Rockall)	<i>Melanogrammus aeglefinus</i>	1	XSA	30	Northern CSE
had.27.7a	Haddock in division 7.a (Irish Sea)	<i>Melanogrammus aeglefinus</i>	0	ASAP	29	Central CSE
had.27.7b-k	Haddock in divisions 7.b-k (southern Celtic Seas and English Channel)	<i>Melanogrammus aeglefinus</i>	0	SAM	29	Southern CSE
her.27.6a7bc	Herring in divisions 6.a and 7.b-c (West of Scotland and West of Ireland)	<i>Clupea harengus</i>	1	SAM	62	Northern CSE
her.27.irls	Herring in divisions 7.a South of 52°30'N, 7.g-h, and 7.j-k (Irish Sea, Celtic Sea, and southwest of Ireland)	<i>Clupea harengus</i>	1	ASAP	63	Southern CSE
her.27.nirs	Herring in division 7.a North of 52°30'N (Irish Sea)	<i>Clupea harengus</i>	1	SAM	41	Central CSE
hke.27.3a46-8abd	Hake in subareas 4, 6, and 7, and divisions 3.a, 8.a-b, and 8.d, northern stock (Greater North Sea, Celtic Seas, and the northern Bay of Biscay)	<i>Merluccius merluccius</i>	0	SS3	44	NEA wide area
hom.27.2a4a5b6a7a-ce-k8	Horse mackerel in subarea 8 and divisions 2.a, 4.a, 5.b, 6.a, 7.a-c, e-k (the northeast Atlantic)	<i>Trachurus trachurus</i>	0	SS3	40	NEA wide area
mac.27.nea	Mackerel in subareas 1-8 and 14 and division 9.a (the northeast Atlantic and adjacent waters)	<i>Scomber scombrus</i>	0	SAM	42	NEA wide area
meg.27.7b-k8abd	Megrim in divisions 7.b-k, 8.a-b, and 8.d (west and southwest of Ireland, Bay of Biscay)	<i>Lepidorhombus whiffiagonis</i>	1	^b	37	Southern CSE
mon.27.78abd	White anglerfish in subarea 7 and divisions 8.a-b and 8.d (Celtic Seas, Bay of Biscay)	<i>Lophius piscatorius</i>	0	a4a	36	Southern CSE
ple.27.7a	Plaice in division 7.a (Irish Sea)	<i>Pleuronectes platessa</i>	1	SAM	40	Central CSE
pok.27.3a46	Saithe in subareas 4, 6, and division 3.a (North Sea, Rockall and West of Scotland, Skagerrak, and Kattegat)	<i>Pollachius virens</i>	3	SAM	52	Northern CSE
reg.27.561214	Golden redfish in subareas 5, 6, 12, and 14 (Iceland and Faroes grounds, West of Scotland, North of Azores, East of Greenland)	<i>Sebastes norvegicus</i>	5	Gadget	46	Northern CSE
sol.27.7a	Sole in division 7.a (Irish Sea)	<i>Solea solea</i>	2	XSA	50	Central CSE
sol.27.7e	Sole in division 7.e (western English Channel)	<i>Solea solea</i>	2	XSA	51	Southern CSE
sol.27.7fg	Sole in divisions 7.f and 7.g (Bristol Channel, Celtic Sea)	<i>Solea solea</i>	1	SAM	50	Southern CSE
whb.27.1-91214	Blue whiting in subareas 1-9, 12, and 14 (the northeast Atlantic and adjacent waters)	<i>Micromesistius poutassou</i>	1	SAM	40	NEA wide area
whg.27.6a	Whiting in division 6.a (West of Scotland)	<i>Merlangius merlangus</i>	0	SAM	41	Northern CSE
whg.27.7a	Whiting in division 7.a (Irish Sea)	<i>Merlangius merlangus</i>	0	ASAP	42	Central CSE
whg.27.7b-ce-k	Whiting in divisions 7.b-c and 7.e-k (southern Celtic Seas and eastern English Channel)	<i>Merlangius merlangus</i>	0	SAM	22	Southern CSE

NEA stands for Northeast Atlantic. Age-at-R stands for age at recruitment. Assessment types: SAM (state-space assessment model), MYCC (multi-year catch curves), SS3 (stock synthesis 3), XSA (extended survivors analysis), and ASAP (age-structured assessment program).

^a Age and length-structured model with separate sexes.

^b Bayesian statistical catch at age using statsmanstats

$$\begin{aligned} a_t &= a_{t-1} + \omega_t \\ \omega_t &\sim N(0, \sigma_\omega^2), \end{aligned} \quad (3)$$

where ω_t is the process error. Allowing the parameters to vary over time permits the separation of process variation in the parameters from measurement error in survival (Minto *et al.*, 2014). We assumed a random-walk process for the system equation because we had no a priori knowledge of temporal patterns in the parameter. Besides, a random-walk model performed well at tracking a wide variety of underlying temporal trends (Peterman *et al.*, 2000; Dorner *et al.*, 2008; Minto *et al.*, 2014). The density-dependent parameter, b , in this model, is time-invariant.

For the third model, we estimated time-varying density-dependent mortality, following stochastic variation with a random walk process:

$$\ln\left(\frac{R_t}{S_{t-\tau}}\right) = a + b_t S_{t-\tau} + v_t, \quad (4)$$

$$\begin{aligned} b_t &= b_{t-1} + \omega_t \\ \omega_t &\sim N(0, \sigma_\omega^2), \end{aligned} \quad (5)$$

where ω_t is the process error. The maximum-productivity parameter, a , in this model, is time-invariant.

For the fourth model, we estimate time-varying maximum productivity and density-dependent mortality by allowing both parameters to covary, following a correlated random walk:

$$\ln\left(\frac{R_t}{S_{t-\tau}}\right) = a_t + b_t S_{t-\tau} + v_t, \quad (6)$$

$$\begin{bmatrix} a_t \\ b_t \end{bmatrix} \sim \mathcal{N}\left(\begin{bmatrix} a_{t-1} \\ b_{t-1} \end{bmatrix}, \begin{bmatrix} \sigma_a^2 & \rho\sigma_a\sigma_b \\ \rho\sigma_a\sigma_b & \sigma_b^2 \end{bmatrix}\right), \quad (7)$$

where ρ is the correlation between the process deviations of a and b .

Model comparison

To identify the best model for the given time series, we used goodness-of-fit statistics. We evaluated the models based on the model selection criterion Akaike information criterion (AIC; Burnham and Anderson 2004). The AIC was calculated using the analytical solution for the log-likelihood from the Kalman filter algorithm including the number of variance parameters and the dimension of the state vector. The best-fitting model was judged by the difference (δ) between the AIC values of the models. The most parsimonious of the four model fits was the model with the lowest AIC value. Models within 2 AIC units of the lowest were considered equally plausible models. Models with the lowest AIC with a difference of equal or more than 2 units were considered to have substantial support or evidence.

CSE productivity trends

We continue the analysis focusing on stocks displaying evidence of time-varying parameters. To understand temporal patterns in dynamic recruitment productivity, we plotted the parameter time series of the model with the lowest AIC, e.g. the estimated a_t time series from the time-variant maximum-productivity model or the estimated b_t time series from the time-variant density-dependent mortality model. Additionally,

we plotted the relationship between the time-invariant estimate and the mean of the time-varying maximum productivity for the full-time series and the last 5 years of the time series.

Correlation analysis between stock's maximum productivity patterns

We estimated the Spearman rank pairwise correlation between stock-specific time-varying trends in productivity (for the stock where the time-varying maximum productivity model had a better fit). The estimated time series of a_t values constituted our measure of productivity. We compared correlations across stocks to quantify the extent to which similar patterns in the a_t parameter are shared among stocks. To cluster the stocks that have similar patterns, we performed a hierarchical cluster analysis on the pairwise correlations using *hclust* using the "complete linkage" method in R.

Results

Results are divided into two sections. First, we compare the goodness-of-fit of the time-invariant and the three time-variant stock-recruitment models. For the second part, we focus on the parameter temporal variation of the best-fitting models and describe the trends and correlations between stocks.

Model comparison and selection

For 22 out of 28 stocks, at least one of the three time-varying parameter models had a better fit than the time-invariant model (based on the difference between the two models' AIC values). The best-fitting model results were unchanged using AICc (Burnham and Anderson, 2004), a method used to address small sample sizes. For six stocks, the time-invariant model had more support but equally plausible as the AIC differences were small ($\delta < 2$; Table 2), except for two stocks (had.27.7a, hom.27.2a4a5b6a7a-ce-k8), which showed more support for the time-invariant model (with $\delta = 2$).

We found strong evidence that 22 stocks had time-varying parameters because time-invariant models had considerably less support (with AIC $\delta > 2$; Table 2). Comparisons of model fit showed that the model with time-varying maximum productivity had the strongest support for 18 stocks, and the model with time-varying density-dependent mortality had the strongest support for four stocks. For six stocks both time-varying parameter models were equally plausible because they had similar AIC support ($\delta < 2$; Table 2). For 14 stocks, the time-varying maximum productivity had substantially more support relative to the time-varying density-dependent mortality ($\delta \geq 2$; Table 2), and for two stocks time-varying density-dependence mortality had substantially more support relative to the time-varying maximum productivity (ple.27.7a, pok.27.3a46; Table 2).

The models with both parameters covarying in time estimated a high correlation between parameters for 60% of the stocks (Supplementary Table S2). These models never showed better AIC support because AIC penalized the use of a higher number of parameters (Table 2). For most stocks, results of the time-variant maximum-productivity model and the model with both parameters covarying showed similar trends for the a_t parameter (Supplementary Figure S1). The fixed parameter in the time-varying models often had scaling differences from the time-invariant value (Supplementary Figures S1 and

Table 2. Summary of model fits. The AIC model difference is represented by δ , for example δ_{a-at} is the AIC difference between the time-invariant model minus the time-varying a model.

Stock	Time-invariant			Time-varying b			Time-varying a			Time-varying a and b			
	1			2			2			4			
	LogL	AIC	δ_{a-at}	LogL	AIC	δ_{a-bt}	LogL	AIC	δ_{a-bt}	LogL	AIC	δ_{a-cov}	δ_{b-cov}
aru.27.5b6a	14.57	-23.14	30.01	29.33	-50.67	27.53	-2.48	13.35	-14.70	-8.43	-38.45	-35.96	
bss.27.4bc7ad-h	-45.75	97.51	4.04	-41.79	91.59*	5.92	1.88	-41.79	95.59	1.92	-2.12	-4	
cod.27.6a	31.64	69.28*	-1.42	-31.32	70.65	1.37	0.06	-31.02	74.04	-4.76	-3.34	-4.39	
cod.27.7a	-46.06	98.12	19.46	-41.08	90.15	7.97	-11.49	-35.33	82.66	15.46	-4.00	7.49	
cod.27.7e-k	-40.65	87.24	5.44	-37.83	83.66	3.57	-1.87	-36.62	85.24	2.00	-3.44	-1.57	
dgs.27.nea	275.75	-545.51	100.88	281.38	-646.39*	9.26	-91.63	327.20	-642.39	96.88	-4.00	87.62	
had.27.46a20	-64.75	135.51	26.44	-54.06	116.12	19.39	-7.05	-50.43	112.87	22.64	-3.80	3.25	
had.27.6b	-54.18	114.36	17.07	-49.55	107.10	7.26	-9.81	-44.64	101.29	13.07	-4.00	5.81	
had.27.7a	-42.35	90.70*	-2.00	-41.58	91.16	-0.47	1.53	-42.35	96.70	-6.00	-4.00	-5.53	
had.27.7b-k	-37.07	80.14*	-1.99	-37.07	82.14	-2.00	-0.01	-37.06	86.13	-5.99	-4.00	-3.99	
her.27.6a7bc	-19.83	45.66	3.42	-19.83	47.66	2.00	-46.51	-3.43	5.15	40.52	-3.99	42.52	
her.27.irls	-31.44	68.87*	1.93	-31.44	70.87	2.00	-0.07	-31.40	74.80	-5.93	-4.00	-3.93	
her.27.nirs	-18.33	42.66	4.94	-15.90	39.79	2.86	-2.08	-14.86	41.71	0.94	-4.00	-1.92	
hke.27.3a46-8abd	-14.56	35.12	-0.14	-13.29	34.57*	0.55	0.69	-13.25	38.50	3.38	-3.24	-3.92	
hom.27.2a4a5b6a7a-ce-k8	-43.68	93.35*	-2.00	-43.68	95.35	-2.00	0.00	-43.68	99.35	-6.00	-4.00	-4.00	
mac.27.nea	9.03	-12.05	64.01	9.03	-10.05	2.00	-66.01	42.03	-72.06	60.01	-4.00	62.00	
meg.27.7b-k8abd	11.93	-17.87	18.18	18.52	-29.04	11.18	-7.01	22.02	-32.05	14.18	-4.00	3.01	
mon.27.78abd	-18.28	42.56	6.19	-14.39	36.78	5.78	-0.41	-14.18	40.36	2.19	-4.00	-3.58	
ple.27.7a	7.91	-6.81	6.65	14.23	-20.46*	10.65	4.00	14.23	-16.46	6.65	0.00	-4.00	
pok.27.3a46	-29.01	64.02	39.30	-6.24	20.49*	43.54	4.23	-6.24	24.47	39.55	0.25	-3.98	
reg.27.561214	-50.72	107.44	26.93	-36.37	80.74	26.69	-0.26	-36.04	84.08	23.35	-3.58	-3.34	
sol.27.7a	-29.97	65.95	6.50	-29.97	67.94	1.99	-8.49	-25.73	63.45	2.50	-4.00	4.48	
sol.27.7e	9.71	-13.42*	1.42	10.07	-12.13	1.29	0.13	10.07	-8.13	5.29	-3.87	-4.00	
sol.27.7fg	3.79	-1.57	4.96	5.39	-2.78	1.21	-3.76	7.27	-2.54	0.96	-4.00	-0.24	
whb.27.1-91214	-40.63	87.25	23.45	-40.63	86.25	2.00	-25.45	-27.78	67.57	19.68	-3.77	21.68	
whg.27.6a	-22.70	41.51	8.19	-19.76	47.52	3.89	-4.30	-17.61	47.22	4.19	-4.00	-0.29	
whg.27.7a	-17.35	40.69	10.34	-12.96	33.39	6.76	-3.58	-11.17	34.34	6.35	-0.41	-0.41	
whg.27.7b-ce-k	-25.06	56.13	15.72	-17.34	42.68	13.44	-2.27	-16.20	44.41	-11.72	-4.00	-1.72	

Model AIC for the different models, lower AIC values signalled with an asterisk, and grey highlights the best or the best fitting models within 2 units. Stock descriptions are provided in Table 1.



Figure 1. Estimated time series trends in maximum productivity (a_t) and 95% confidence intervals for stocks in the CSE, ordered by northern CSE, central CSE, southern CSE, and northeast Atlantic (NEA) wide area. The horizontal dashed line is the time-invariant maximum productivity parameter. Stock descriptions are provided in Table 1.

S2), typically being higher fixed maximum productivity in the time-varying density-dependent model and lower fixed density-dependent in the time-varying maximum productivity model. When the best-fitting model was the time-invariant one (Table 2), some stocks did not show temporal trends in the parameters (e.g. had.27.7b-k and hom.27.2a4a5b6a7a-ce-k8; Supplementary Figures S1 and S2).

CSE time-varying maximum productivity

The stocks examined exhibit various temporal trends and patterns in the maximum-productivity parameter. The amplitudes of the time-varying productivity (in logarithmic scale) vary from <1 (e.g. Faroes grounds and West of Scotland greater silver smelt, aru.27.5b6a) to around 5 (e.g. northeast At-

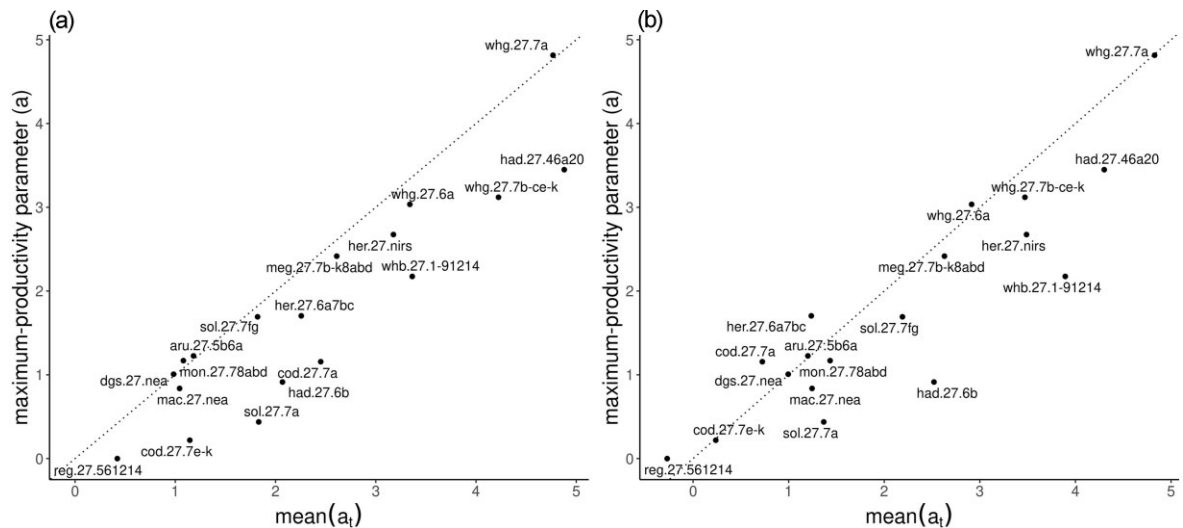


Figure 2. Time-invariant estimates of maximum productivity (a) related to mean time-varying estimates of maximum productivity for (a) full-time series and (b) the last 5 years. Stock descriptions are provided in Table 1.

lantic blue whiting, whb.27.1-91214) (Figure 1). This variability corresponds to the recruitment number per metric ton of the spawning stock biomass on a logarithmic scale. The longest series available for the northeast Atlantic spur-dog (1905–2020), in Figure 1, we truncated this time series because for most species the time series were considerably shorter.

For some stocks, the current productivity level was substantially lower than at the beginning of the time series (e.g. West of Scotland whiting, whg.27.6a), but for other stocks current productivity was higher (e.g. Irish Sea herring, her.27.nirs) than or similar to historical productivity (Figure 1). For most stocks, estimates of time-invariant maximum productivity were similar to or lower than the mean time-varying maximum productivity (Figure 2a). However, for some stocks, recent time-varying maximum productivity was lower than the time-invariant one (Figure 2b); for example, Irish Sea cod (cod.27.7a) and West of Scotland and West of Ireland herring (her.27.6a7bc).

With regard to northern CSE stocks, maximum productivity has declined considerably for many stocks (Figure 1), e.g. West of Scotland whiting (whg.27.6a) and West of Scotland and West of Ireland herring (her.27.6a7bc). The North Sea and West Scotland haddock (had.27.46a20) also displayed declining productivity until 2012 with productivity increasing thereafter. West of Scotland whiting showed a steep decrease until 2009 and stabilization since. West of Scotland and West of Ireland herring displayed fluctuations with an overall declining long-term trend. Productivity of Faroes grounds and West of Scotland greater silver smelt (aru.27.5b6a) declined until the early 2000s and increased after with a peak around 2009. Rockall haddock (had.27.6b) fluctuated, with a lower productivity point around 2010 (Figure 1).

In the central CSE, stocks showed a diversity of patterns (Figure 1). A decreasing trend was observed for Irish Sea cod (cod.27.7a) for the entire time series. Irish Sea whiting (whg.27.7a) had a low productivity level in the early 1990s, productivity increased until the early 2000s and decreased since 2013 to levels similar to those at the beginning of the time series. Irish Sea sole (sol.27.7a) displayed decreasing pro-

ductivity but with some increase in recent years. Irish Sea herring (her.27.nirs) productivity was fairly stable at a low level for the start of the time series and in the late 1990s had a marked increase with a fairly stable period at a higher level since the mid-2000s.

Southern CSE stocks had higher levels of currently time-varying productivity than the time-invariant one (Figure 1). Celtic Sea cod (cod.27.7e-k) productivity increased with a peak in the mid-1990s and has been decreasing since to levels lower than those observed at the start of the series, with a short increase in the last year of the time series. Similarly, Celtic Sea whiting (whg.27.7b-ce-k) displayed an erratic decline in productivity since 1990. This productivity trend differed from those for other stocks in the southern CSE. Bristol Channel and Celtic Sea sole (sol.27.7fg) displayed erratic fluctuations in productivity with an increase in the most recent years. Productivity of West and Southwest of Ireland and Bay of Biscay megrim (meg.27.7b-k8abd) displayed fluctuations but did not display a clear long-term trend. Celtic Sea and Bay of Biscay white anglerfish (mon.27.78abd) fluctuated with a slow long-term increasing trend.

Northeast Atlantic widely distributed stocks typically displayed erratic fluctuations (Figure 1). Iceland and Faroes grounds, west of Scotland, north of Azores, and east of Greenland golden redfish (reg.27.561214) displayed a decreasing long-term trend in productivity. Northeast Atlantic blue whiting (whb.27.1-91214) displayed an erratic long-term trend in productivity slowly increasing. Northeast Atlantic spur-dog (dgs.27.nea) displayed relatively constant productivity until the late 1950s and has subsequently fluctuated erratically with no long-term directional trend (Figure 1). Northeast Atlantic mackerel (mac.27.nea) displayed relatively constant productivity until 2000, a subsequent marked increase and fluctuated around a higher productivity level since (Figure 1).

Correlation analysis between stock's productivity patterns

The correlation of time-varying maximum productivity across stocks showed patterns in productivity within and among regions and species. Correlations within northern and southern CSE stocks were mostly positive, showing also positive correlations with some stocks in the central region and north-

east Atlantic widely distributed stocks (Figure 3). This suggests that regional-scale factors might be important drivers of changes in recruitment productivity. Among central CSE stocks, some correlations were positively strong between Irish Sea whiting and herring, and between sole stocks (Bristol Channel, Celtic Sea, and Irish Sea sole) and Irish Sea cod. These groups were negatively correlated with each other (Figure 3).

Occasionally, productivity time series had strong positive correlations among stocks from different regions, strong correlations are shown between cod stocks (Celtic Sea and Irish Sea cod), Celtic Sea whiting, and West of Scotland and West of Ireland herring (Figure 3), which had marked decreasing productivity trends (Figure 1). In other cases, productivity correlations with most stocks were weak, e.g. for northeast Atlantic mackerel, Celtic Sea and Bay of Biscay white angler fish, and West and Southwest of Ireland and Bay of Biscay megrim, suggesting unique patterns in recruitment productivity for these stocks.

We found that productivity correlations within stocks of the same species were mostly positive. Productivity patterns for cod, haddock, and sole stocks in the ecoregion showed strong positive correlations. Productivity patterns of whiting stocks show positive correlations between West of Scotland and southern Celtic Seas stocks but were negatively correlated with Irish Sea whiting (Figure 3).

CSE time-varying density-dependent mortality

The four stocks that showed evidence of time-varying density-dependent mortality displayed different patterns (Figure 4). For most stocks, the average time-varying density-dependent mortality was lower than the time-invariant density-dependence level. The time-varying model shows stronger density-dependent processes (more negative), especially at recent and current levels. North Sea, Irish Sea, English Channel, Bristol Channel, and Celtic Sea seabass (bss.27.4bc7ad-h) displayed increasing density-dependent mortality at the beginning of the time series with a peak in the early 2000s and a decrease since then (Figure 4). Northern hake stock (hke.27.3a46-8abd) density-dependent mortality increased with a peak around 2009 and has declined since then (Figure 4). Irish Sea plaice (ple.27.7a) displayed fluctuations in density-dependent mortality with no clear long-term trend (Figure 4). North Sea, Rockall and West of Scotland saithe (pok.27.3a46) time-varying density-dependent mortality displays fluctuations but overall declined considerably over the time series, displaying significant differences with the time-invariant density-dependent mortality (Figure 4).

Discussion

We found evidence of non-stationary maximum productivity and density-dependent mortality for many stocks in the CSE manifested as important changes in the temporal trends in recruitment productivity parameters. In this section, we consider the important biological insights of PPM models, examine productivity dynamics in the CSE, explain data and method caveats, and remark on implications for management.

Biological insight of PPM models

PPM enabled the identification of temporal patterns in the parameters of the stock–recruitment model. PPM permits esti-

mation of the integrated effects of underlying processes influencing recruitment while reducing the confounding from random sources of noise or variability independent of the trend (Peterman *et al.*, 2003; Holt and Peterman, 2004). Applying PPM, we can model how recruitment productivity changes over time. This improves estimates of systematic underlying changes in productivity—revealing the underlying signal (Peterman *et al.*, 2000; Dorner *et al.*, 2008). We showed that parameters of the stock–recruitment relationship often vary over time, which offers valuable insight into complex temporally variable regulation processes in changing ecosystems.

In the Ricker model, the parameters have differentiated density-dependent effects of spawner abundance on productivity and density-independent effects. The maximum productivity is the mean productivity at low stock sizes and captures variations in recruitment separating environmental effects and maternal effects from the effects of density in adult biomass. Being the density-independent parameter, time-varying maximum productivity influences stock recruitment regardless of spawner abundance (Dorner *et al.*, 2008) and integrates the direct environmental signal. Changes in the density-dependence mortality parameter impact recruitment related to the stock size. Detecting which parameter varies in time, which is of great ecological interest, is difficult. For some stocks, goodness fit differences between the time-variant models (time-varying maximum productivity and time-varying density-independent mortality) were small. In these cases, it would be useful to evaluate the behaviour of the model that allows both parameters to covary in time. Also, applying ensemble modelling (Jardim *et al.*, 2021) could be useful in cases when the understanding of the dynamics is incomplete (i.e. averaging the weight of each time-variant model based on AIC).

Our analysis indicated that, for most stocks in the CSE individual stock–recruitment parameters changed. Evidence of time-varying maximum productivity was found for many stocks in the CSE, and changes in density dependence were also important for some stocks. Changes in the maximum-productivity parameter would impact recruitment at all stock sizes. Changes that result in reduced maximum productivity might be problematic, and changes that result in stronger density dependence have consequences for the stability of the population (Britten *et al.*, 2016). Our results did not find evidence of both parameters covarying in time. Previous univariate implementations of PPM indicated that models with time-varying maximum productivity and constant density-dependent mortality fitted best (Peterman *et al.*, 2003; Dorner *et al.*, 2008). Additionally, multivariate implementations also show improved goodness of fit of the time-varying maximum productivity and density-dependence being relatively stable in time (Minto *et al.*, 2014).

Dynamics in the CSE

For most stocks in the CSE, recruitment productivity has varied over time, which suggests that the productivity of many stocks is non-stationary, as found also by Minto *et al.* (2014) for Atlantic cod stocks and by Tableau *et al.* (2019) for New England stocks. The observed changes in productivity might be caused by external (i.e. environment) or internal changes and multiple direct and indirect drivers and mechanisms. These changes might depend on fish species or even stocks as life-history characteristics of populations might differ (Subbey *et al.*, 2014). Additionally, the effects of these processes may

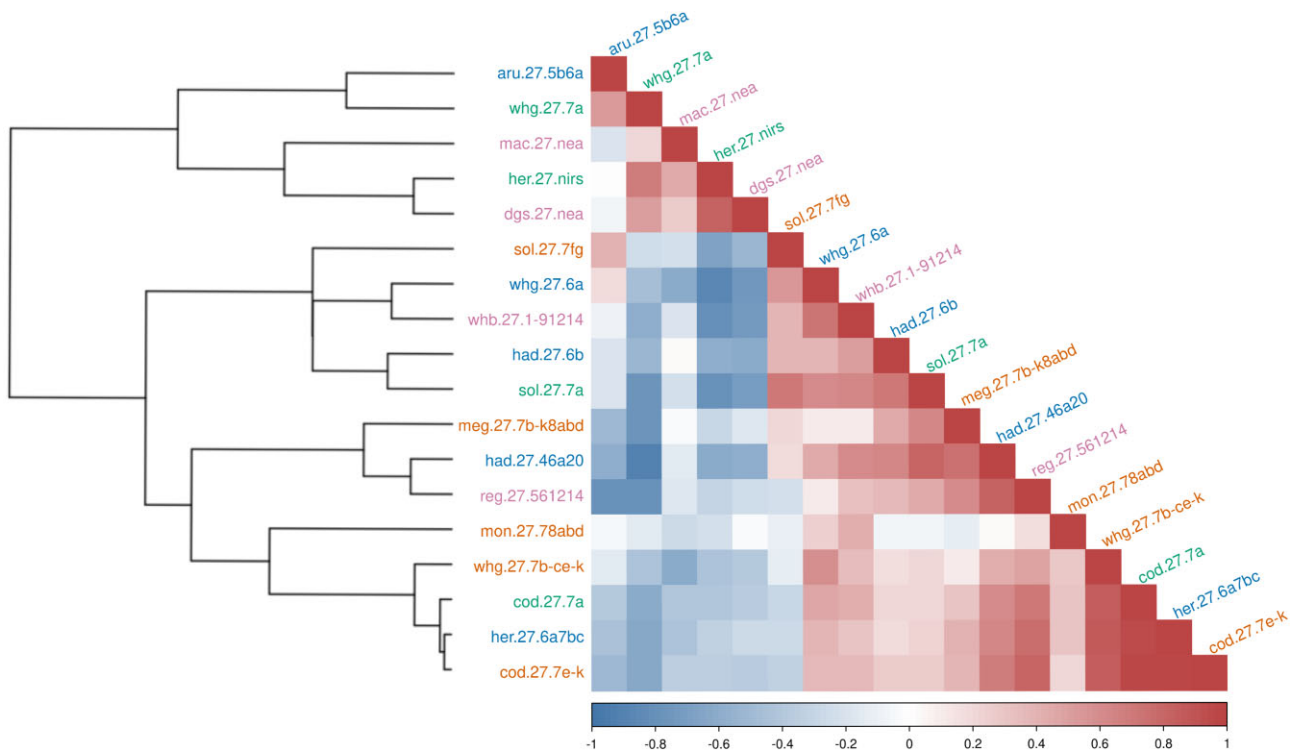


Figure 3. Estimated pairwise productivity correlation for stocks in the CSE (significance level of 0.01). Red represents positive correlations, and blue represents negative correlations. Stocks are hierarchically clustered by complete linkage method. Stock descriptions are provided in Table 1. Stock labels in blue are for northern CSE stocks, in green for central CSE stocks, in orange for southern CSE stocks, and in pink for NEA widely distributed stocks.

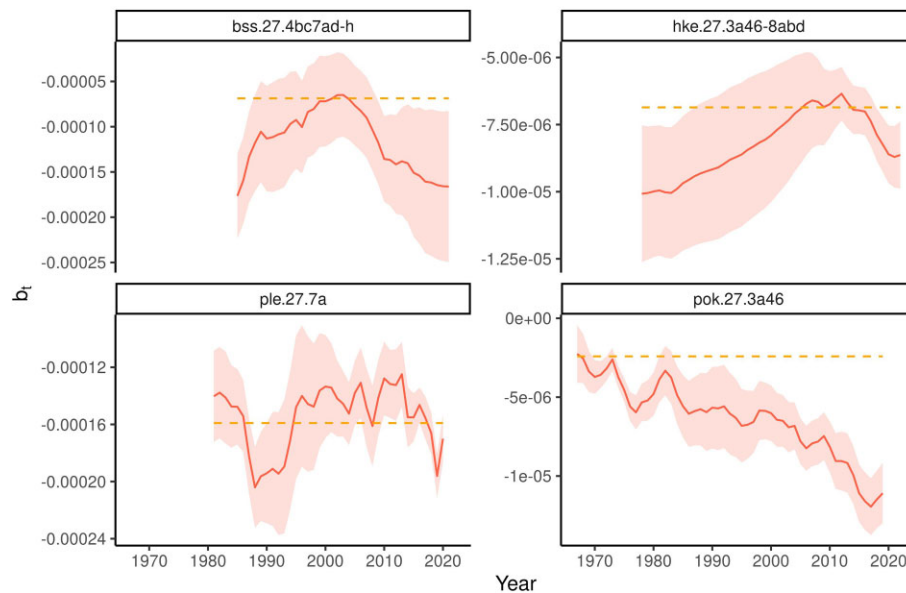


Figure 4. Estimated time series trends in density-dependent mortality (b_t) and 95% confidence intervals for stocks in the CSE. The horizontal dashed orange line is the time-invariant density-dependent mortality parameter. Stock descriptions are provided in Table 1.

change over time (Stige *et al.*, 2006; Ottersen *et al.*, 2013). Hence, change patterns and timing are very stock dependent. A mechanistic understanding of why Celtic Sea stock productivity has changed is beyond the scope of this study, but it would be crucial to investigate in the future. In this section, we discuss productivity temporal patterns and hypothesize some of the possible reasons for changes in productivity.

We observed long-term shared trends, for example, the overall decline in productivity for many stocks in the CSE with a considerable positive correlation, suggesting that regional factors might be important drivers of changes in productivity. The consistent patterns in productivity observed between some stocks indicate that common factors (e.g. environmental conditions) may influence those populations. Alternatively,

some stocks responded differently, particularly for the central region and northeast Atlantic widely distributed stocks. This might reflect that fish populations are affected by more than one driver or react differently to the same drivers. For example, the effects of climate variability on fish productivity can vary between regions (Parsons and Lear, 2001). Furthermore, current and historical levels of fishing pressure might have been different for different stocks.

Internal stock changes such as changes in age structure influence stock productivity (Stenseth *et al.*, 1999; Wright and Gibb, 2005; Ohlberger *et al.*, 2022). These changes in stock structure can be caused by fishing or climate change, and the CSE has had high levels of fishing pressure historically (Zimmermann and Werner, 2019). Northern and southern whiting stocks' productivity had a positive correlation but was negatively correlated to the productivity of the central stock (Irish Sea whiting). For Irish Sea whiting historically high levels of fishing mortality caused a considerable reduction in spawning stock biomass; however, this did not result in significant earlier maturation (Gerritsen *et al.*, 2003). Since the 1980s, the decline in biomass, and the reduction in length- and weight-at-age might have reduced the potential for compensatory changes in reproductive output (Gerritsen *et al.*, 2003), which could have caused the low peak in productivity for the Irish Sea whiting.

We found mainly consistent patterns within stocks of the same species. Patterns in productivity were strongly positively correlated for neighbouring CSE stocks of the same species for cod, sole, and haddock. For cod stocks, there is a general decline in productivity with a strong correlation, which suggests common processes might be operating. The decline in productivity might have been caused by overexploitation (Myers *et al.*, 1996). Additionally, cod survival during early life stages could be affected by temperature, as survival was found to decline with increasing temperatures in the northeastern USA (Fogarty *et al.*, 2008). The consequences of environmental-related regime shifts on cod productivity were found to be accentuated when fishing mortality is high and populations are small (Perälä *et al.*, 2020). Relationships between maturation, recruitment, and sea temperature can differ for regionally different cod populations (Armstrong *et al.*, 2004). For Irish sea cod, maturity and growth changed over time, showing an increase over time in proportion mature and reduced size-at-age which coincided with rising sea surface temperature and a decline in recruitment and stock biomass and high fishing mortality (Armstrong *et al.*, 2004). While being different populations, a combination of these effects could be contributing to the downward productivity trend of all the CSE cod stocks.

The density-dependent mortality relates to stock size but can be affected by many factors, e.g. competition, juvenile habitat, and age structure (Myers, 2001), and thus changes in density-dependent mortality might be stock dependent. The northern hake stock has had a decrease in fishing mortality and an increase in spawning stock biomass, since around 2010, which might be related to the strengthening of density-dependent mortality. Similarly, the increase in spawning biomass of the North Sea, Rockall and West of Scotland, Skagerrack, and Kattegat saithe since the late 1990s might be affecting the strengthening of the density dependence.

Data and method caveats

The Ricker stock–recruitment model used for this study has overcompensation (declining recruitment) at higher spawner abundances, which does not happen for all species. Time-varying Ricker parameters have been widely used for salmon populations (Peterman *et al.*, 2003; Holt and Peterman, 2004; Peterman and Dorner, 2012). The Ricker model has been considered to provide a reasonable model for estimating the slope at the origin of stocks (Myers *et al.*, 1999). Minto *et al.* (2014) applied PPM with time-varying parameters in a Ricker model for cod populations, and Tableau *et al.* (2019) applied it to New England fish populations. Britten *et al.* (2016) used the Ricker model to perform a global analysis of time-varying productivity trends of 262 stocks worldwide. The Ricker model has the advantage of its easy linearization, which allows the use of the Kalman filter to estimate the time-varying parameters. Additionally, the parameter separation into density-independent and density-dependent components of the Ricker makes for a more straightforward interpretation. Both the parameter α in Ricker models and the slope at the origin for the Beverton–Holt can be interpreted as the maximum annual reproductive rate directly or by standardization (Myers, 2001). The main difference between these models would be caused by the different forms of density-dependent mortality assumed by the model. Nonetheless, more research and development are needed to be able to implement the PPM in other stock–recruitment models such as the Beverton–Holt.

Data used to estimate recruitment productivity, i.e. recruits and spawner abundance, are estimated from stock assessment models and have considerable associated uncertainty and correlation between estimates (Brooks and Deroba, 2015). Most assessments in this study do not assume a stock–recruitment relationship and allow for large estimated recruitment deviations. The majority of the stocks in this study were category 1, i.e. stocks with analytical assessments. Estimated recruitment variability in data-rich stocks with recruitment indices is thought to be more robust to recruitment assumptions, and so the recruitment variability signal in the data is sufficiently strong (Dickey-Collas *et al.*, 2015). Additionally, many of the stocks studied were historically overexploited, which provided resolution and contrast on population dynamics at low population abundance. The method would be improved by investigating the inclusion of assessment uncertainty and covariance of the recruitment and spawning stock biomass estimates. There could be two profitable ways forward with this: (i) for recruitment uncertainty, this could be added to the measurement-error variance matrix of the Kalman filter such that the minimal measurement error variance is no lower than the estimated recruitment uncertainty; and (ii) bootstrapping from the joint posterior distribution of the SSB and recruitment estimates and running the Kalman filter for each bootstrap replicate.

The univariate PPM approach might fail to separate the measurement error and the process variability for some of the stocks' time series. This issue is related to a flat likelihood around its maximum in the estimation process (Petris *et al.*, 2009; Tableau *et al.*, 2019). Although this might be resolved with longer time series, when longer time series are not available, estimating the time-varying parameters collectively using a multivariate model could be a solution (Minto *et al.*, 2014). Moreover, estimating a common signal-to-noise ratio reduces the number of parameters to estimate and is thought

to be more robust to shorter time series (Tableau *et al.*, 2019). However, the univariate approach, used in this study, is useful for assessing a single stock and getting a population's view on recruitment productivity variability in time. Potentially, knowing the region's signal-to-noise ratio could be used to inform the model and might help in cases where the separation of observation error from process error is not robust. More generally, understanding how the signal-to-noise ratio varies across regions may provide insights into the nature of change more globally.

Implications for management

Currently, time-invariant stock–recruitment parameters over the available time series are typically used to derive reference points for management advice (ICES, 2021b). This approach assumes a stationary stock–recruitment relationship and accounts for average environmental and fishing conditions but is not robust if the ecosystem changes (Silvar-Viladomiu *et al.*, 2022). Stock–recruitment parameters are critical in many problems in fisheries management because they affect the estimation of reference points and sustainable harvest rates (Holt and Michielsens, 2020; Zhang *et al.*, 2021). We discovered long-term trends and mismatches between time-invariant and time-varying maximum productivity and density-dependent mortality parameters. We showed temporal patterns in the recruitment productivity of CSE stocks, which is relevant for sustainable advice, especially in the presence of long-term trends in productivity levels. For example, stocks that have continuously declined in maximum productivity would be immediate red flags of time-invariant reference points, hence their implications for sustainable management should be explored.

Advice frameworks typically consider stock productivity regime shifts. When regime shifts are detected, ICES guidelines recommend using a data window of spawner and recruit pairs or truncating the time series (ICES, 2021b). Choosing recruitment windows to derive reference points can be problematic because shorter time series lead to disregarding earlier dynamics and increase uncertainty in reference points (Deurs *et al.*, 2021). Productivity changes are often gradual making it difficult to choose a time window (Collie *et al.*, 2021). Incorporation of ecosystems and climate information into stock assessments and advice has shown to be necessary but challenging (Punt *et al.*, 2014; Bentley *et al.*, 2021). We argue that in the context of ecosystem changes affecting productivity, tracking time-varying stock recruitment productivity, estimating dynamic reference points, and measuring current productivity levels are crucial for management (Collie *et al.*, 2021; Silvar-Viladomiu *et al.*, 2022). Tableau *et al.* (2019) demonstrated that the short-term forecast power for time-varying productivity models generally outperformed time-invariant models. Beyond forecasting, time-varying productivity models can directly inform sustainable harvest practices (Collie *et al.*, 2012, 2021). Stochastic dynamic programming studies have shown that the time-invariant harvest control rule based on average productivity performed similarly to the dynamic harvest control rule except at low productivity (Collie *et al.*, 2021). This occurs because changes in maximum productivity at low productivity have a stronger effect on the optimal harvest rate than changes in the same parameter at high productivity. Consequently, special care is needed at low productivity levels.

Implementations of time-varying productivity frameworks have shown the ability to improve on time-invariant management (Collie *et al.*, 2012), with particular importance for management in the context of climate change (Collie *et al.*, 2021). Dynamic methods such as the PPM, capable of tracking changes in stock productivity, are outstanding because although a mechanistic understanding of the processes that affect productivity is important, ultimately, is not needed for tactical decision-making now (Minto *et al.*, 2014; Collie *et al.*, 2021; Silvar-Viladomiu *et al.*, 2022). Further research is needed to study non-stationary productivity with management strategy evaluations to test the implementation of time-varying recruitment productivity. In view of the evidence that CSE fish recruitment productivity is changing over time, fisheries science and advice should take it into account, and management must respond to be robust to these productivity changes.

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Supplementary material

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

Conflict of interest: There is no conflict of interest

Data availability

All data and code we used for analysis are available on our GitHub repository: https://github.com/paulasv/CSE_stochastic_recruitment.

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