ICES Journal of Marine Science, 2025, Vol. 82, Issue 3, fsaf021
https://doi.org/10.1093/icesjms/fsaf021
Received: 4 September 2024; **revised:** 12 February 2025; **accepted:** 13 February 2025
Original Article

ICES CIEM
International Council for the Exploration of the Sea
Conseil International pour l'Exploration de la Mer

Unmasking contrasting regime shift dynamics across three substocks of Atlantic cod in the North Sea

Enrico Cecapolli[1,2,3], Giovanni Romagnoni[4,5,6], Alexandra M. Blöcker[1], Christian Möllmann[1], Camilla Sguotti[1,7,*]

[1]Institute of Marine Ecosystem and Fishery Science (IMF), Center for Earth System Research and Sustainability (CEN), University of Hamburg, Grosse Elbstrasse 133, 22767 Hamburg, Germany
[2]National Research Council- Institute for Marine Biological Resources and Biotechnologies (CNR-IRBIM), Largo Fiera della Pesca 2, 60125, Ancona, Italy
[3]Department of Life and Environmental Sciences, Polytechnic University of Marche, Via Brecce Bianche 1, 60131 Ancona, Italy
[4]Centre for Ocean and Society (CeOS), Christian-Albrechts-University, Fraunhofer Str. 16, 24118 Kiel, Germany
[5]Department of Agricultural Economics, Christian-Albrechts-University, Olshausenstrasse 40, 24118 Kiel, Germany
[6]Leibniz Centre for Tropical Marine Research (ZMT), Fahrenheitsrasse 6, 28359 Bremen, Germany
[7]Department of Biology, University of Padova, Via U. Bassi 58/B, 35131 Padova, Italy
*Corresponding author. Department of Biology, University of Padova, via U. Bassi 58/B, 35131 Padova, Italy. E-mail: camilla.sguotti@unipd.it

Abstract

The Atlantic cod (*Gadus morhua*) in the North Sea has experienced a regime shift and is now considered to be in a persistent depleted state. Recent scientific evidence confirmed the presence of multiple populations of Atlantic cod in the North Sea through genetic evidence. Here, we investigated if the regime shift detected for North Sea cod manifested differently across areas [Southern, Northwestern-, and Viking (North–East)], revealing different dynamics and recovery potential for the corresponding populations. Methods from driver–state plots to stochastic cusp models were applied to detect the regime shifts. We found that cod in the Southern North Sea has undergone a regime shift and is now in a persistent depleted state. The Viking population is in a high resilience state, and it is recovering. Finally, the Northwestern North Sea population did not show signs of a regime shift and is showing a rising biomass level. Several abiotic and biotic drivers (e.g. fishing and warming) contribute to these differences. Our study provides useful information for the restructuring of management units of cod in the North Sea and highlights the importance of looking at regime shifts spatially.

Keywords: North Sea cod; discontinuous population dynamics; fisheries management; spatio-temporal scales; stochastic cusp model; regime shifts

Introduction

Regime shifts, i.e. unexpected and often sudden changes between system states, are among the most debated dynamics of marine ecosystems and populations (Scheffer et al. 2001, Rocha et al. 2014, Hillebrand et al. 2020). Systems (from an individual to the full ecosystem) that undergo regime shifts change from a past to a new state, characterized by different ecological structures and functions and by a certain degree of persistence (i.e. hysteresis) over time (Beisner et al. 2003, Scheffer and Carpenter 2003, Moellmann et al. 2009, 2015). Resilience, another fundamental property of systems that experience regime shifts, is defined as the capability of a system to maintain its structure and functions even when impacted. A system goes through a regime shift when its resilience is eroded. Regime shifts are still difficult to characterize because, following nonlinear discontinuous dynamics, they are highly unpredictable and often not easily detectable using simple statistical methods and models (Andersen et al. 2009, Bestelmeyer et al. 2011, Dakos and Kéfi 2022, Haines et al. 2024).

Two inherent limitations regarding regime shifts lie also in the usage of appropriate temporal and spatial (or hierarchical) scales when trying to detect them (deYoung et al. 2008, Fisher et al. 2015, Rocha et al. 2018, Eklöf et al. 2020). While the temporal dynamics of regime shifts are often considered, the spatial/hierarchical differences are generally neglected (Sguotti et al. 2022a). This limitation resides in the difficulty of identifying the study unit of the system and what its limits are. For instance, while it is rather easy to study physically bound entities such as an individual coral reef, it can be difficult to determine the spatial boundaries of an ecosystem or a population. Indeed, a regime shift detected within a larger area could in fact reflect a change occurring locally, or could involve only specific habitats within the overall area, or a subpopulation within a population complex. Therefore, within a spatial or hierarchical unit different states of the system could exist, with different hysteresis (persistence) levels (Scheffer et al. 2001, Beisner et al. 2003). The spatial context of regime shifts is extremely important to explore, especially when developing management measures (Blenckner et al. 2015, Levin and Möllmann 2015, Selkoe et al. 2015). Thus, a key for a good understanding of regime shifts should also include a punctual consideration of the proper spatial resolution (SI), to avoid misleading interpretations of the results.

The North Sea is a paradigmatic example of a large-scale ecosystem that underwent regime shifts encompassing most of its trophic web from plankton to large predatory fishes (Reid et al. 2001, Beaugrand 2004, Alheit et al. 2005,

---

Lynam et al. 2017). The first documented regime shift occurred in the 1980s and was attributed to large-scale climatic changes including increase of temperature and changes in hydro-climatic forces. Intense fishing pressure especially on some target fish species might have contributed to the regime shift (Beaugrand 2004, Beaugrand et al. 2019). The regime shift started at the bottom of the trophic web with changes in composition and abundances of the phytoplankton and zooplankton communities, and later affected upper trophic levels such as economically important fishes (Reid et al. 2001, Beaugrand et al. 2003, Beaugrand 2004, Ibanez et al. 2008, Llope et al. 2012). Another regime shift was detected in the plankton community in 1996 and is associated with a decrease in biomass and productivity of phytoplankton (Djeghri et al. 2023). A new regime shift of the North Sea community, from plankton to fishes, occurred in 2012 (Sguotti et al. 2022b). This shift was linked to increasing temperature due to climate changes and a reduction of fishing pressure. The fish community completely changed in composition, with species such as saithe and plaice becoming dominant and Atlantic cod being substantially reduced (Sguotti et al. 2022b).

During the 1980s regime shift, North Sea Atlantic cod (*Gadus morhua)*, was strongly depleted due both to overexploitation and the disappearance of zooplankton species that are its main prey during the larval stage (Hislop 1996, Beaugrand et al. 2003, Fernandes et al. 2020). Regime shifts analyses conducted only on the North Sea cod stock have demonstrated that the stock underwent regime shift dynamics characterized by irreversibility as also demonstrated for the entire ecosystem. The stock is at present in a depleted state characterized by low resilience, as also indicated in the community-wide study that explored the shift in 2012 (Sguotti et al. 2018, 2022b, Koul et al. 2021). The decline of Atlantic cod in the North Sea started around the 1980s, and the stock reached a very low biomass level in the 2000s (Walker et al. 2018). At present times (as of 2024), the stock shows limited recovery compared to previous abundances (Sguotti et al. 2018), still being below sustainable reference levels (ICES 2023) despite the reduction in fishing pressure. The recovery potential of Atlantic cod in the North Sea is low: changes in temperature due to climate change, and the reorganization of the full trophic assemblage in the new 2012 regime shift, contribute to the creation of hysteresis. Moreover, the temperature increase is also eroding the resilience of the stock with the stock being at present at low resilience. Management efforts aimed at recovery of the North Sea Cod may have been hindered by considering it as a single stock.

The consideration of a single stock unit for North Sea cod might be inappropriate since the populations inhabiting the Southern, Northwestern, and Viking (Northeastern) areas show contrasting patterns in population dynamics: an increase of the population is occurring in the northern areas of the North Sea, likely because of locally lower sea temperatures, while in the warmer southern areas the species seems to suffer (Wright et al. 2006, Hutchinson 2008, Engelhard et al. 2014, Heath et al. 2014, Walker et al. 2018, Romagnoni et al. 2020, Trifonova et al. 2021). Previous studies have shown that regime shifts can occur differently in large marine ecosystems due to the heterogeneity of the area and to different patterns of biotic and abiotic drivers (Fisher et al. 2015). In this light, the regime shift previously detected at the scale of the entire cod stock in the North Sea could have occurred differently among the different geographical locations considered, resulting in contrasting recovery potential and hysteresis patterns, and ultimately rendering management measures applied to the full basin mostly ineffective. In this context, management units utilized for stock assessment have been reviewed and the most recent benchmark proposes a multistock assessment model application (ICES 2023). While the inclusion of stock structure allows specific dynamics to be captured, the individual stocks' past dynamics, their current proximity to irreversible thresholds and their resilience to multiple pressures is still unexplored. Thus, a comprehensive analysis of regime shifts in the putative cod populations in contrast to the entire North Sea cod stock is fundamental to understand how recovery could be enhanced, and what populations are more likely to respond positively to management measures.

Here, we analyse whether the three putative populations of the cod stock [the Southern, Northwestern, and Viking (Northeastern) North Sea] underwent different dynamics (linear, nonlinear, and discontinuous), and especially regime shift dynamics. This division has been defined based on genetic, ecological, and behavioural evidence (summarized in ICES WGNSSK report; ICES 2023). First, we analysed the populations' development over time. Afterwards, we detected a number of possible drivers of the changes, and we tested for regime shifts dynamics using the stochastic cusp model, an approach deriving from catastrophe theory. We also explored the regime shift using alternative SI. The approach used in this investigation could result in useful hints for management purposes, as it gives a clearer overview of the status of the populations of cod and their dynamics over time in the spatial units considered, supporting the need to switch to a more effective strategy to favour the recovery of Atlantic Cod in the North Sea. Our study opens up new perspectives about the importance of spatial heterogeneity in regime shifts and the consequences for management measures.

Materials and methods

Data

Our study aims at understanding the dynamics of Atlantic cod (*G. morhua*) in three areas of the North Sea, which are believed to represent three distinct populations of the stock (from now on called substocks) (ICES 2023). The three areas of focus are: the Southern, Northwestern, and Viking (Northeastern), and were defined according to stock assessment reports (ICES 2023). All the analyses described below were conducted separately for the three areas in order to analyse the different substocks. We also repeated the same analyses by aggregating together the Southern and the Northwestern area since, while the assessment is currently run on three units, it is still debated whether they can be treated together or separated due to their similarities in genetic traits and habitats (ICES 2023) (see Supporting Information).

Cod population data

The estimates of cod abundance in the different areas were obtained using survey data (fishery-independent) coming from the North Sea International Bottom Trawl Survey (NS-IBTS), available from the International Council for the Exploration of the Sea (ICES; DATRAS, http://www.ices.dk/data/data-portals/Pages/DATRAS.aspx). This survey is carried out twice a year (first and third quarters) since 1997 by ICES, but started already with at least one survey in quarter 1 from the 1960s, performed using a standard otter trawl as sampling gear for each vessel involved. Focusing on the data presenting consistent sampling, we extracted the first quarter data (Q1, from January to March). We created a dataset of Catch per Unit of Effort (CPUE) of cod per area per year. To do so, we first summed specimens in every station. Then we averaged the CPUE per ICES statistical rectangle (which are ICES geographical units), and finally we summed the values per area. We restricted the dataset from 1985 to 2015 (years from which we had data for all the drivers).

Biotic variables

As biotic factors possibly related to cod dynamics, we used the abundance of big copepods, which included mainly *Calanus finmarchicus* and *Calanus helgolandicus*, since they are fundamental prey items for cod larvae (Beaugrand 2004). Big copepods data came from the Continuous Plankton Recording, supplied by the Continuous Plankton Recorder program (www.cprsurvey.org) (McQuatters-Gollop et al. 2015). The values were provided by ICES rectangles; thus we averaged them to obtain estimates of their abundance per area per year.

Environmental drivers

As abiotic factors we used three environmental indices, which are well known to impact cod populations: sea surface temperature (SST), that was used as a proxy of climate change, sea bottom temperature (SBT), which is most influential for adult cod since it is a demersal species, and Sea Surface Salinity (SSS), that can have an impact on a variety of fish species, even if direct effects on cod are not extensively reported. Data were available per rectangle, and we averaged all the values to obtain one estimate per area per year. These data were produced by the oceanographic model by Núñez-Riboni and Akimova (Núñez-Riboni and Akimova 2015).

Fishing effort

Finally, we checked whether different patterns of fishing effort could influence the dynamics of cod. Fishing effort data were taken from Couce et al. (2019) and covered the 31-year series from 1985 to 2015. These data are estimates of the hours fished by beam and otter trawler per ICES rectangle in the North Sea, and are therefore a good estimate of spatial fishing effort (Couce et al. 2019). In order to obtain yearly estimates per area we summed the hours trawled every year per area. Fishing mortality, considered a more direct proxy of impact of fisheries, is provided at substock level in the latest assessment; however, due to model assumptions, it may not reflect actual patterns of exploitation. Fishing effort was thus considered a more robust proxy.

Methods

All analyses were performed in the three areas (Southern, Northwestern, and Viking). We applied a range of analyses in order to be able to detect the presence of discontinuous dynamics and confirm the presence of hysteresis in cod's substocks (Sguotti et al. 2022a).

First, we looked at the dynamics of Atlantic cod in the different areas by plotting its survey CPUE per year, to gain a first overview of the three substocks considered in the analyses.

Detecting hysteresis, driver–state plot

As a second step, in order to investigate the presence of regime shift dynamics in each cod substock and to detect the presence of possible hysteresis, we graphically investigated the driver–state plots (Bestelmeyer et al. 2011, Sguotti et al. 2022a). Hysteresis is the property for which, after a regime shift, the return path from the state B to the state A is different compared to the path that led to the shift from A to B. This means that when the driver is removed, the state variable does not recover in the same way as it collapsed. The driver–state plots are therefore the first step to identify hysteresis: if a linear relationship was found, i.e. for every level of the driver there was just one level of the state variable, then the dynamic of the population was considered linear. Conversely, if for a given level of the driver, multiple states of the state variable exist and thus a loop emerges, this was considered an indication of discontinuous dynamics, and thus a regime-shift-like behaviour (Andersen et al. 2009). We plotted as the state variable the survey CPUE of cod in the three areas and fishing effort as the driver, being the most relevant driver responsible for the decrease of the substocks (but see the section 'Discussion' for a better interpretation) (Engelhard et al. 2014, Sguotti et al. 2018).

The stochastic cusp model

Finally, to confirm the presence of discontinuous dynamics we performed stochastic cusp models for each area (Thom 1977). The stochastic cusp model, derived from the catastrophe theory, models the presence of a cusp bifurcation in a state variable depending on two control variables (Petraitis and Dudgeon 2016, Sguotti et al. 2018, 2024, Dakos and Kéfi 2022). This model is increasingly applied in ecological studies to detect regime shift dynamics following a cusp. Moreover, it allows to statistically compare and detect three alternative dynamics in the system: linear, nonlinear continuous (in the form of a logistic model), and nonlinear and discontinuous (i.e. regime shift behaviour in the form of a cusp bifurcation) (Petraitis and Dudgeon 2015, Sguotti et al. 2018, 2024, Möllmann et al. 2021). The model was formulated by Thom in the 1970s and was enriched with a stochastic process (the Wiener process) in order to make it usable in natural systems (Grasman et al. 2009, Diks and Wang 2016). The model is based on the differential equation:

$$-V(z_t,\ \alpha, \beta) = -\frac{1}{4}z_t^4 + \frac{1}{2}\beta_t^2 + \alpha z_t, \qquad (1)$$

where $V(z_t,\ \alpha, \beta)$ is a potential function, whose slope represents the rate of change of the system (the system state variable is called Z_t), depending on the two control variables (α, β).

This equation is then extended with the Wiener process in order to render the model able to account for stochasticity:

$$-\frac{\delta V(z,\ \alpha, \beta)}{\delta z} = \left(-z_t^3 + \beta z_t + \alpha\right) dt + \sigma_z dW_t = 0. \qquad (2)$$

This equation models how a state variable (z_t) abruptly changes depending on potential small changes of two control variables (α, β) (Grasman et al. 2009, Petraitis and Dudgeon 2015, Diks and Wang 2016, Sguotti et al. 2018). In our case, the state variable is modelled as a function of the cod substock abundance (survey CPUE), since our aim was to understand if all the three separate substocks of the North Sea present discontinuous, regime shift dynamics (Equation 3a). Alpha is the so-called asymmetry parameter and controls the dimension of the state variable (the transition from high to low state). In our study, alpha is a function of the fishing effort since fishing is believed to be the main controller of the dimension of the cod substocks (Equation 3b). Beta is the so-called bifurcation parameter, that, by changing, can modify the relationship between the state variable and the asymmetry parameter from linear to nonlinear discontinuous, and thus can induce hysteresis in the interaction between the state variable and the asymmetry variable. In our model, beta was modelled as a function of the environmental drivers (i.e. SST, SBT, and SSS) and the big copepods resulting in many different models to compare (Equation 3c). All the mentioned drivers were previously tested looking at possible correlations using Spearman's rank-order correlation test using Hmisc R package (see Fig. S1) (Hollander et al. 2013). The stochastic cusp model equation is then solved using the Cobb's maximum-likelihood method (Diks and Wang 2016).

$$z_t = w_0 + w_1 \textit{cod substock abundance}. \tag{3a}$$

$$\alpha = \alpha_0 + \alpha_1 \textit{fishing effort}. \tag{3b}$$

$$\beta = \beta_0 + \beta_1 \textit{ environmental drivers/big copepods}. \tag{3c}$$

To detect the presence of discontinuous dynamics a Cardan's discriminant (δ) needs to be solved (Equation 4):

$$\delta = 27\alpha^2 - 4\beta^3. \tag{4}$$

If the Cardan discriminant is smaller than, or equal to 0, then the state variable follows discontinuous dynamics and presents multiple equilibria. Instead, if it is bigger, it presents linear dynamics. Thus, the model is able to detect different dynamics of the system (Grasman et al. 2009, Diks and Wang 2016, Sguotti et al. 2018). The model can be represented in 2D using a cusp plain. The cusp plain is built using the combination of the asymmetry and bifurcation variable. The combination of these two that produce a negative Cardan's discriminant, results in the tipping point or bifurcation area. This area corresponds to the area below the fold and is an area of low resilience, and therefore, where the state variable could potentially be highly variable (Sguotti et al. 2024). Finding the state variable in this area indicates that regime shifts have occurred or are about to occur, but the system did not yet reach a stable state and thus still presents low resilience. The position of the state variable depends on the combination of the two control drivers and their historical time path. If the variable does not show regime shifts depending on the two stressors, then it will be far away from the instability area.

The routine automatically fits two alternative models, a linear model (Equation 5) and a logistic model (Equation 6) in order to provide a model comparison and test which type of dynamic better represents the system.

$$z_t = g_0 + g_1 \cdot \textit{Capacity} + g_2 \cdot \textit{SST} + \epsilon, \tag{5}$$

where g_0 is the intercept of the model, and g_1 and g_2 the slopes coefficients of the two control variables and ϵ is the normally distributed random error (mean = 0, variance=σ^2).

$$z_t = \frac{1}{1 + e^{\left(-\frac{\alpha}{\beta^2}\right)}} + \epsilon, \tag{6}$$

where Z, α, β are canonical variables of the observed state and control variables defined in Equation (3) and ϵ is the zero mean random disturbance.

We fit the stochastic cusp models and then we performed a model selection based on four criteria (as discussed in Sguotti et al. 2024) to confirm whether the data presented a cusp bifurcation and thus an irreversible regime shifts:

- The pseudo R-squared [calculated as 1-(error variance/var(z)], where the error variance is defined as the difference between the observed values and the mode of the distribution closest to these values) had to be higher than 0.3.
- The corrected Akaike Information Criterion (AICc) of the cusp model had to be lower than the AICc of the linear model (by at least 2 units).
- The percentage of points inside the bifurcation area had to be more than 10%
- The estimate of the state variable parameter had to be significant.

If these conditions were met then the dynamics of the substocks could be well represented by a cusp model (a discontinuous model representing a cusp bifurcation) (Grasman et al. 2009). If the conditions were not met, then the substocks did not presented a regime shift depending on the external pressures. The residuals were also plotted in order to check the model. Since the cusp model represents a bifurcation of the state variable moving from a 'high' state to a 'low' state the residuals plots show a bimodal distribution of the variable.

All the analyses were performed using R Version 4.3.2 (R Core Team 2023). The cusp model was performed with the cusp package (Grasman et al. 2009).

Results

Dynamics of the North Sea Atlantic cod

Using the NS-IBTS data, we reconstructed the time series of the CPUE of three Atlantic substocks of cod in the North Sea: Northwestern, Viking, and Southern (Fig. 1a). The time series of the survey CPUE of cod showed different dynamics in the three substocks. Northwestern cod showed a strong decline in CPUE around 1998 followed by relatively low abundances. After 2010, a recovery to almost precollapse levels occurred at the end of the time series (Fig. 1b). A similar but more oscillatory pattern can be seen for the Viking substock: cod declined around 1998 as well and remained low, with a recovery towards the end of the time series (Fig. 1c). In contrast, the dynamics of Southern cod appeared completely differently, with the CPUE values constantly declining without showing any sign of recovery (Fig. 1d).

Possible drivers of cod dynamics in the North Sea

To compare the dynamics observed in the cod substocks with anthropogenic, biotic, and abiotic drivers we explored whether differences could be noted between the time series of the drivers in every area considered. The patterns were generally quite similar between the area of the Northwestern and Viking substocks and in some cases different for the Southern substock (Fig. 2). For instance, while effort drastically declined in the areas of the Northwestern and Viking substocks (Fig. 2a and b), in the Southern substock area it increased strongly until 2000, and just then started to decline (Fig. 2c). Moreover, the magnitude of the effort, thus the number of hours of trawling, was twice as high in the Southern compared to the Northwestern substocks. In all the three areas

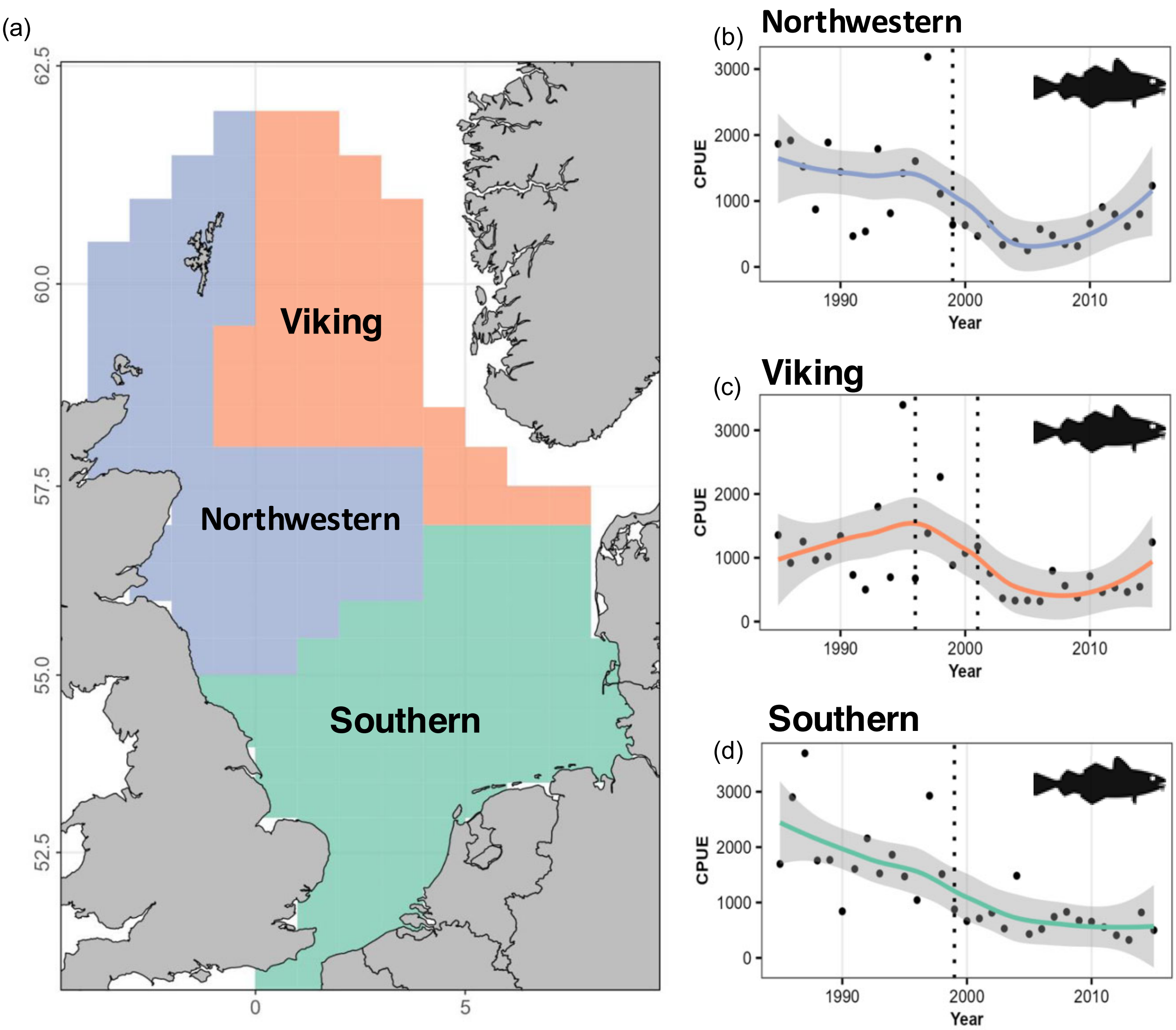

Figure 1. Time series of the three populations/substocks of cod in the North Sea. (a) Map of the distribution of the three different cod populations in the North Sea as identified by the ICES Stock Assessment Group. Time series of CPUE of (b) The Northwestern cod, (c) the Viking cod, and (d) the Southern cod. The line passing through the dots is the smoothed trend done by fitting a loess to better visualize the trend of the populations. In grey is the confidence interval of the line.

copepods oscillated substantially, with the highest abundances present in the Viking and the lowest in the Southern substocks areas (Fig. 2d–f). Finally, temperature (both surface and bottom) and salinity showed similar dynamics in all the three areas (Fig. 2g–o). However, temperature was higher in the area occupied by the Southern substock by almost 2°C.

Driver–state plots

We applied driver–state plots using fishing effort as the driver, since it is the driver in our study that directly influence the CPUE of cod. The three substocks showed different hysteresis patterns according to the state–driver plot (Fig. 3). The Northwestern cod substock and the Viking substock showed a sign of hysteresis, but the hysteresis loop created by the presence of multiple levels of the state variable for the same level of the drivers, was closed at the end of the time series when the level of the survey CPUE reached past levels (Fig. 3a). Instead, for the Southern substocks the hysteresis loop is not yet closed (CPUE levels lower compared to the beginning of the time series) and the hysteresis is strong (Fig. 3b and c). These results could indicate that the cod substocks present a range of dynamics in the three areas, with Southern cod presenting regime shifts, while Northwestern and Viking cod presenting more linear and continuous dynamics. Identifying the prevalent types of dynamics is fundamental to understand the different recovery patterns and potential among the three substocks.

Stochastic cusp models

To finally confirm the presence of regime shifts and different dynamics in the three cod substocks in the North Sea, we performed a number of stochastic cusp models (Table 1; Figs S1–S3. To select the models, we used the four criteria suggested in Sguotti et al. (2024) (and detailed in the method sections): pseudo R-squared, AICc, percentage of points inside the cusp area, and significance of the estimate of the state variable

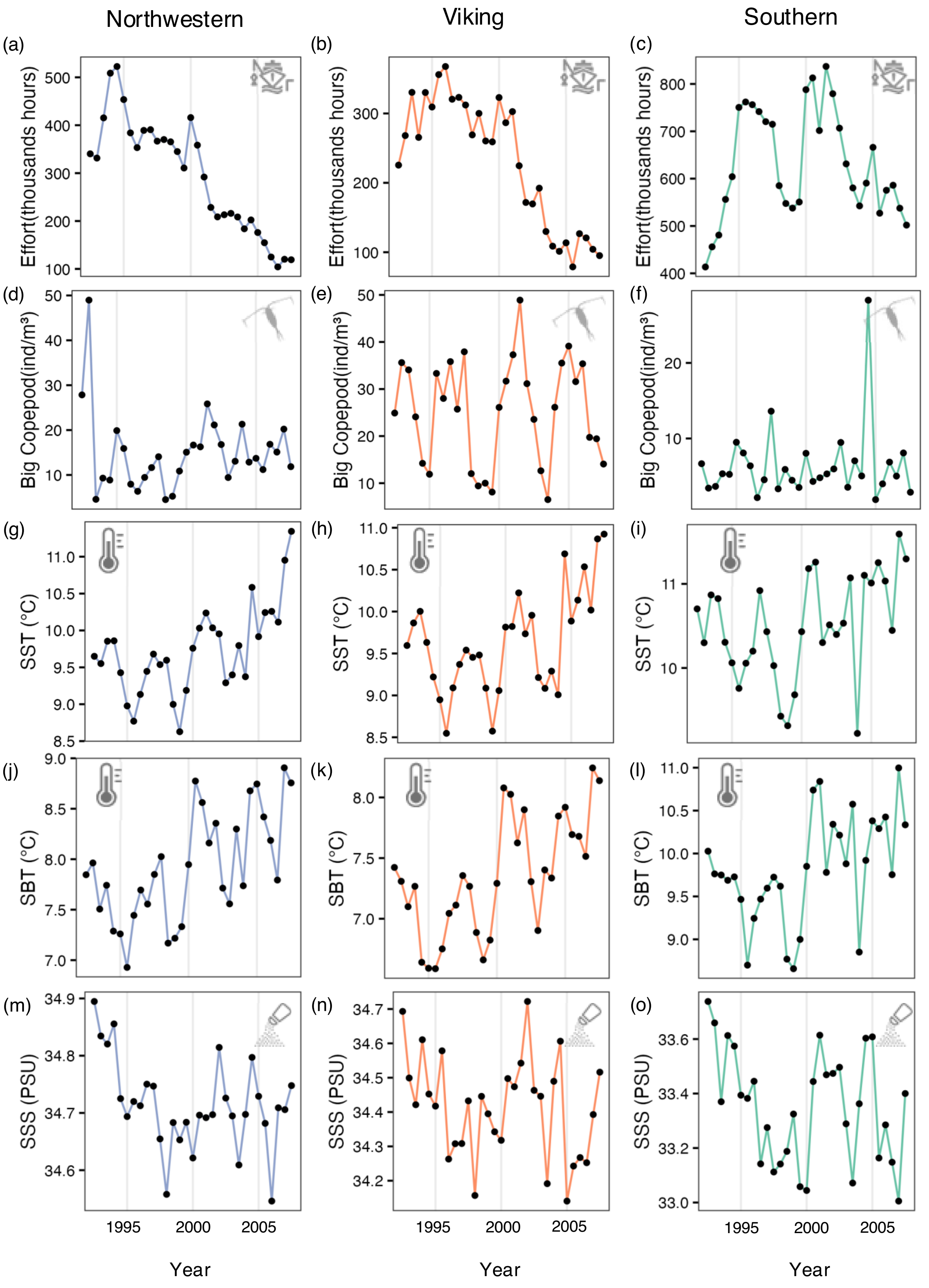

Figure 2. Anthropogenic biotic and abiotic drivers of cod in the three areas of the North Sea. Time series of effort (a, b, and c), big copepods (counts, d, e, and f), SST (g, h, and i), SBT (j, k, and l), and SSS (m, n, and o) in the three areas (Northwestern, Vikings, and South) of the North Sea. The colour of the lines represents the areas as reported in Fig. 1.

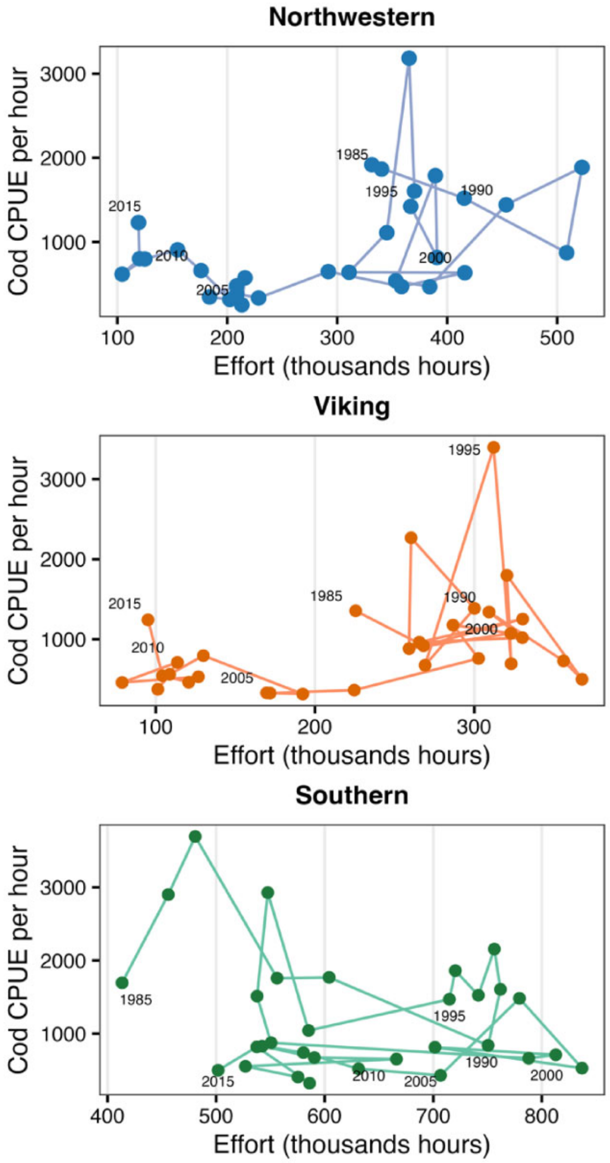

Figure 3. Hysteresis patterns of the three cod substocks. The driver–state plot using as dependent variable CPUE of cod and as explanatory variable fishing effort for the (a) Northwestern, (b) Viking, and (c) Southern populations.

Table 1. Results of the stochastic cusp model.

	NW	Vik	South
SST	Logistic 1 9.6%	Cusp 0.58 38%	Cusp 0.54 48%
SSS	Logistic 0.42 6.4%	Cusp 0.58 35%	Cusp 0.62 45%
SBT	Logistic 0.36 6.4%	Cusp 0.58 38%	Cusp 0.58 58%
Big copepods	Logistic 0.45 6.4%	Cusp 0.61 38%	Cusp 0.61 41%

The table shows the alternative stochastic cusp models that were performed for the three areas using different variables as beta (SST = sea surface temperature, SSS = sea surface salinity, and SBT = sea bottom temperature). The different bifurcation factors are indicated in the first column since the state variable and the asymmetry variable remained the same in all the models (CPUE and effort, respectively). For each area the best pseudo-R squared among the three alternative models, cusp, logistic and linear, are reported and the % of points within the cusp area.

Table 2. Results of the cusp models for the three areas using SST as beta.

Parameters	SST NW	SST Vik	SST South
$\alpha1$	-1.64^{*}	-1.76^{*}	-0.97^{**}
$\alpha2$	0.94^{*}	0.95	-0.37
$\beta1$	7.47	1.19	-10.5
$\beta2$	-0.68	0.09	1.17^{*}
w1	-1.04^{***}	-1.47^{**}	-1.08^{***}
w2	0.81^{***}	0.78^{***}	0.94^{***}
R^2 linear	0.20	0.17	0.15
R^2 logistic	1	0.31	0.42
R^2 cusp	0.06	0.58	0.54
%points	9.6	38	48
deltaAIC	-9	-17	-12

Estimates of the parameters of the stochastic cusp model. $\alpha1$ and $\alpha2$ are respectively the intercept and slope of the splitting parameter depending on fishing. $\beta1$ and $\beta2$ are respectively the intercept and slope of the bifurcation parameter that changes in all the models. w1 and w2 are the intercept and the slope of the state variable, the abundance of cod. The significant levels of the estimates are indicated with a star ($^{*}P < .05$, $^{**}P < .005$, and $^{***}P < .0005$). The R^2 are pseudo Cobb R^2 computed to compare the model using the cusp formulation or a linear or a logistic model. The other criteria for the selection of the cusp model are also shown. The percentage of point in the cusp area needs to be higher than 10% for an accepted cusp model, and the deltaAIC needs to be lower than 0 (AIC of the cusp model smaller than AIC of the linear model).

parameter (Table 2). Through these criteria, the cusp model was selected or rejected against the alternative linear model.

For the Northwestern substock the cusp model was always rejected based on the pseudo R-squared and the percentage of points in the bifurcation area, and the best model was a logistic model, thus a continuous model. This suggested that the Northwestern substock did not undergo regime shifts represented by a cusp bifurcation (Tables 1 and 2, Table S1, Fig. S1). This result is in contrast with previous study on North Sea cod stock as a whole, showing that the basin-wide stock underwent an irreversible regime shift. Conversely, for the Viking and the Southern substocks, the cusp was systematically the best model (and all the criteria of the evaluation were always passed), so discontinuous dynamics were prevalent (Tables 1 and 2, Table S2, Fig. S2 and Tables 1 and 2, Table S3, Fig. S3). These results indicate that while Northwestern cod did not undergo regime shifts and present only continuous dynamics, Viking and Southern cod indeed underwent regime shifts (in the shape of a cusp model) due to fishing and the biotic and abiotic drivers. These results indicate that the dynamics are different at different SI of the population.

We then explored the results of the modelling approach by plotting the models' output (Figs 4 and 5). Since the output of the different models across environmental variables were very similar for the same substocks (see Figs S1–S3), for simplicity, here we just show the results of the models using as bifurcation variable SST. The output of the model shows the position of the state variable (survey CPUE, the dots) depending on the two control drivers. The combination of the two drivers creates the bifurcation area (i.e. transition area), where the regime shifts occur (blue area in Fig. 4). This area corresponds to the area below the fold (Fig. 5), in which three equilibria are possible. State variables that are inside this area present a very low resilience, i.e. are at risk of new transitions (Grasman et al. 2009, Sguotti et al. 2018). A given combination of the two control drivers could provide three levels of state variable (the survey CPUE), and the realised one depends on the previous position, i.e the historical trajectory. The state variable can move in or out of the area or can be far away, depending

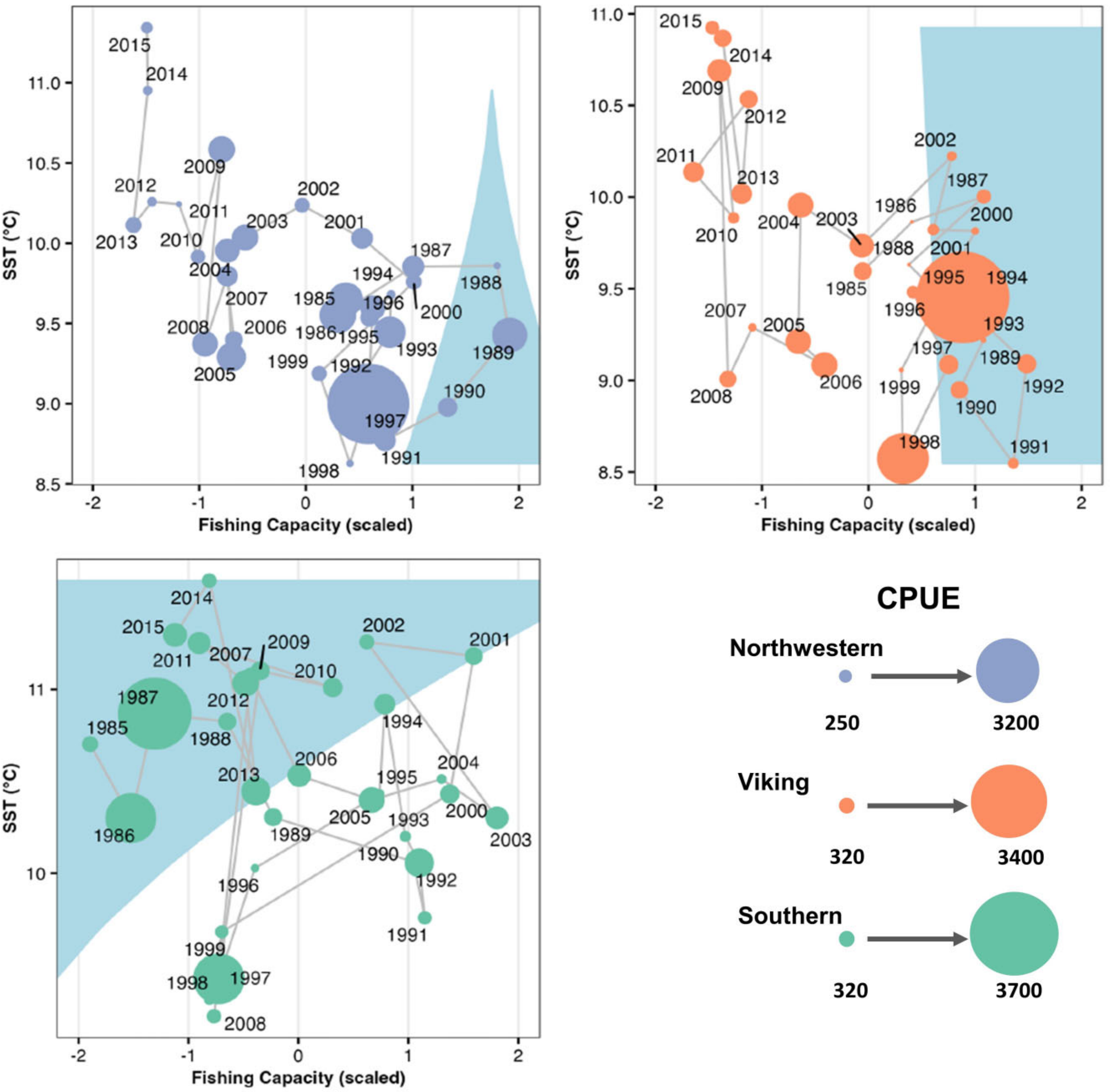

Figure 4. The stochastic cusp models. Output of the stochastic cusp models for (a) the Northwestern substock, (b) the Viking, and (c) the Southern substock. On the *x*-axis, the asymmetry variable, fishing capacity expressed in hours and scaled. On the *y*-axis, the bifurcation factors in this case SST. The blue shaded area corresponds to the instability area, the area where three equilibria of the systems are present: two stable and one unstable. The dimension of the dots is proportional to the CPUE of the cod population (big dot = high CPUE, small dots = low CPUE).

on whether it presents regime shifts or not. The Northwestern substock was close to the tipping point (partially inside the blue area) around the 1990s, but the immediate decline of fishing effort coupled with an increase in SST and in general of the other drivers, pushed the stock away from the tipping point into a stable and resilient (far away from the bifurcation area) state (Fig. 4a). Therefore, the plot confirms that this substock did not undergo a regime shift. Moreover, the substock has recently shown a recovery towards past levels. The Viking substock crossed a tipping point in 2000 (before it was inside the bifurcation area and in 2000 exited the tipping point). Nonetheless, the decline of fishing and the increase of SST allowed the substocks to move away from the bifurcation area and become more resilient. (Fig. 4b, small dots outside the area). The stocks is also recovering towards past levels. The difference between the Viking and the Northwestern substocks is that in the former, discontinuous dynamics were highlighted (since generally the best model was a model with bifurcation). Therefore, to eventually be able to return to the same state as before (i.e. in this case, reach the highest biomass level) a further decline of fishing should be applied, and fishing should drop far below past and current levels to be able to induce a new tipping point. Instead, since Northwestern cod shows continuous dynamics, management actions could still bring the population back towards the highest past abundances. Finally, the Southern substock showed a very different situation. Here, the system underwent a regime shift and always presented a low resilience to fishing and temperature or

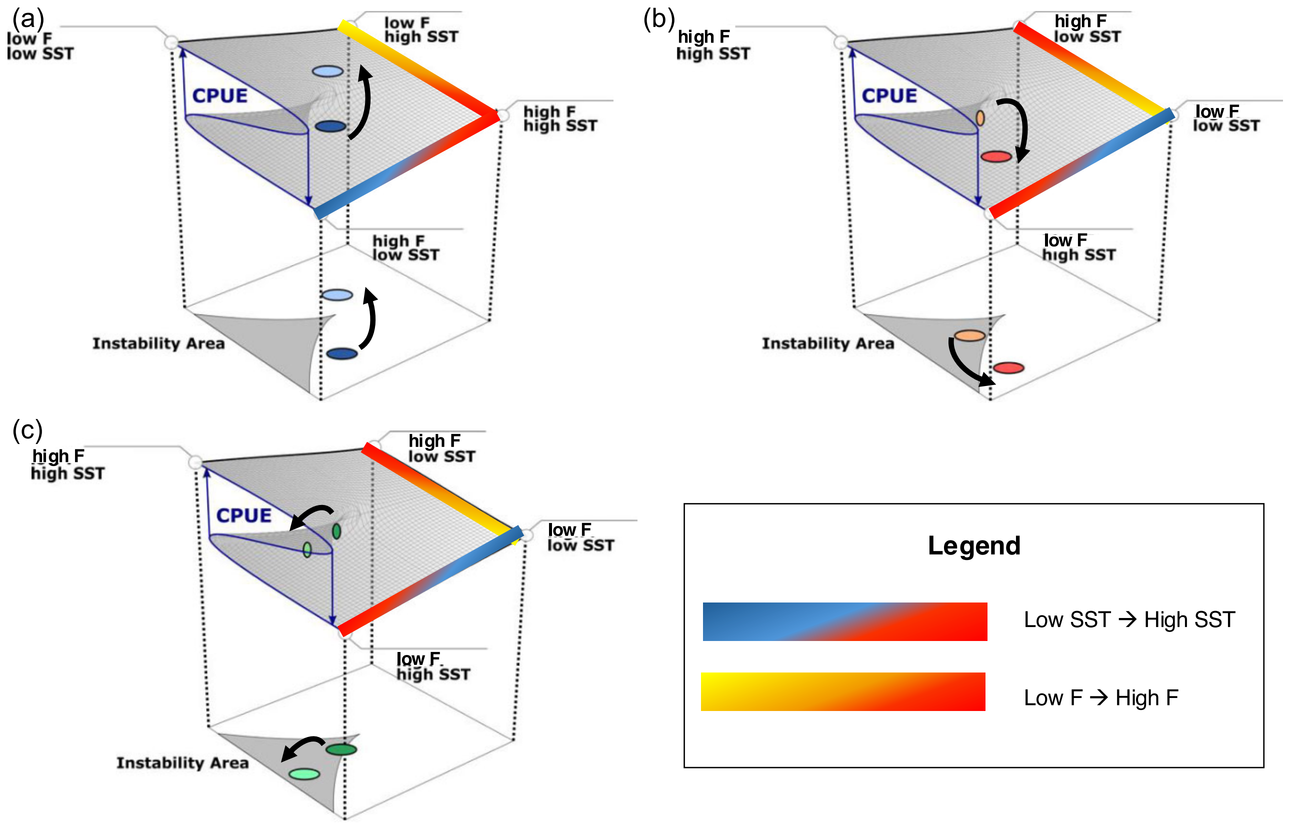

Figure 5. Stochastic cusp model representation for (a) the Northwestern North Sea cod, (b) the Viking North Sea cod, and (c) the Southern North Sea cod. 3D representation of the cusp model, where North Sea Cod CPUE (state variable) depends on the two variables: fishing capacity (expressed in hours and scaled) representing the asymmetry variable (α), and SST, representing the bifurcation variable (β). The representation are a summary of the model output presented in Fig. 4. The discontinuous path pictured within the folding area represents unstable equilibria, also visible in the grey area of the 2D projection. The (a) blue and light blue, (b) orange and red, and (c) dark green and lights green circles represent the CPUE respectively of Northwestern, Viking, and Southern cod at the beginning and at the end of the time series to show the development. The arrow shows the 'trajectories' of the substocks on the 3D cusp plain and the 2D projection. The effect of temperature depends on the results of the modelling approach (Fig. 4) and is represented by a blue–red gradient. For Northwestern substock, temperature increase push the stock towards a resilient state, while for Viking and Southern is the opposite. The effect of fishing is represented by the yellow to red gradient. In all the stocks fishing has declined over the last decades.

the other drivers going in and out the bifurcation area (the blue area). This substock presents low resilience, and a low CPUE state (Fig. 4c, small green dots). Thus, for this substock no return to previous condition seems possible since it underwent a regime shift and is negatively affected by ongoing temperature increase. Moreover, being this substock stuck deep under the fold, it is expected that it will not respond to management measures (reduction in fishing pressure) with any major increase in biomass, least so with a return to the previous stable state.

Discussion

In this study we applied different techniques, from driver–state plots to the stochastic cusp model to investigate whether regime shifts can be found in three substocks of Atlantic cod in the North Sea depending on a range of external drivers. This study explores an urgent question, because the stock of Atlantic cod in the North Sea has been considered as a single unit from a management point of view until very recently (Hutchinson 2008, Heath et al. 2014, Fisher et al. 2015, Walker et al. 2018), despite growing evidence of the presence of multiple units with diverse dynamics and ecology (Heath et al. 2014). Recently, the management unit has undergone a review process, and it was proposed to split it into three substocks, consistent with genetics and ecological evidence (Heath et al. 2014), in the attempt to provide more accurate management measures (ICES 2023). A clear understanding of the presence of regime shifts in the three units however, could not yet be determined in a structural way (Fredslund 2023). Our results clearly and unequivocally show that the three substocks of cod indeed experienced contrasting dynamics (Fig. 5). While all the substocks showed evident CPUE decline around the year 2000, the dynamics of the decline and the recovery are very different between substocks. The Northwestern substock presents nonlinear but continuous dynamics (i.e. not regime shifts) while the Viking and the Southern substocks show regime shift dynamics. This difference is fundamental from a management point of view since it indicates that contrasting recovery patterns might be found among the three substocks. When sustainably managed, the Northwestern substock could be able to return to previous highest abundances: the continuous dynamics identified indicate that if the driver of change, and in particular fishing, is reverted, the population can potentially return to the past state (Andersen et al. 2009, Selkoe et al. 2015). At the moment, in fact, the Northwestern substock shows encouraging signs of recovery (Dulvy et al. 2008, Engelhard et al. 2014, Beukhof et al. 2019, ICES

2023), with the latest assessment showing a rise in Spawning Stock Biomass (SSB) above the Maximum Sustainable Yield (MSY) threshold (ICES 2023).

Different is instead the fate of the Viking and Southern substocks. These two units present discontinuous dynamics and underwent regime shifts, thus hysteresis hinders the recovery towards the previous state, and the substocks will likely be trapped in a new state in the immediate future. Still, important differences can be found between the two substocks. The Viking cod is resilient to low fishing and to the other drivers: this means that its dynamics are expected to be more stable, and thus easier to manage in order to maintain it a stable level. In the last years of the analyses, this substock shows encouraging signs of recovery even if it is still far away from the previous highest biomass. Therefore, if fishing will decline even further (far below past and current levels), the Viking population should be able to remain robust and stable in the face of other external stressors, such as temperature and could potentially increase. The recent stock assessment for Viking cod show an agreement with our results. Indeed, fishing pressure did not decline further and thus the stock has further declined and it is far below the level reached in 2015 (last year of our study). Instead, the Southern substock shows a very low resilience to external drivers and is thus more unstable. Even when regulating fishing pressure, stock size will fluctuate due to changes in environmental stressors. Managing this stock that is neither robust nor stable will be very challenging and, in fact, management measures have proven so far ineffective (Drinkwater 2005, Engelhard et al. 2014, Beukhof et al. 2019). While our analyses show the presence of regime shifts in the Southern and Viking substocks, the modelling approach is not able to mechanistically explain how the regime shift occurred. Possible mechanisms could be linked with recruitment failure due to changes in available food, predation, or competitions mediated by climate change and especially, temperature increase (Sguotti et al. 2022b, Blöcker et al. 2023). Consequences of fishing such as truncated age and size in populations or Allee effects could also act as possible mechanisms of the regime shifts.

Notably, our results complement and advance the analysis on regime shifts in the recruitment productivity of the three substocks performed at the latest Benchmark meeting (Fredslund 2023) to identify the emergence of novel recruitment regimes. Our detailed investigation on the drivers of the regime shifts following the methodological guidelines of Sguotti et al. (2022b), confers a more robust understanding of the occurrence of regime shifts in the three substocks showing that eventually the Northwestern population did not undergo a regime shift characterized by hysteresis but rather a continuous, nonlinear dynamic defined as phase shift (Sguotti et al. 2022a).

Even if the three substocks show contrasting patterns, the trends of the drivers used as bifurcation factors and impacting them are rather similar. Indeed, similarities can be seen in the trends of temperature (both surface and bottom) with steady increase, but also in the time series of copepods and salinity. The magnitude of the drivers is, however, different in the three areas. The average SST in the Southern North Sea is 2°C higher compared to temperature in the Northern areas. This indicates that Southern cod is exposed to higher temperatures that are closer to the maximum thermal tolerance of the species, as well known from previous studies (Drinkwater 2005, Pörtner et al. 2008, Pörtner and Peck 2010, Righton et al. 2010, Butzin and Pörtner 2016). Temperature can directly act on cod through changes in recruitment or growth, or indirectly by changing the time or occurrence of their preys (Kempf et al. 1870, Pörtner et al. 2008, Olsen et al. 2011, Butzin and Pörtner 2016, Sguotti et al. 2018). Therefore, the environment in the Southern North Sea is more hostile for cod compared to the other areas (Engelhard et al. 2014, Akimova et al. 2019). Instead, temperature in the Northern North Sea is further away from the maximum thermal tolerance for cod, allowing it to thrive and recover (Righton et al. 2010, Butzin and Pörtner 2016). Moreover, cod seems to exploit deeper, colder and more stable areas in the Northern North Sea, which may act as refugia, that are not available in the shallow Southern North Sea (Neat et al. 2014). The quantities of large copepods are also lower in the Southern North Sea compared to the other areas. Being large copepods fundamental prey for cod larvae, the low abundances might represent another limiting factor for the Southern substock (Beaugrand et al. 2003).

Fishing effort is the other driver that presents different trends among the three areas. Indeed, fishing effort has been higher in the Southern North Sea for centuries and this could have chronically impacted fish populations since longer times, again causing the southern population to be less resilient from other stressors (Engelhard 2009, Couce et al. 2019). Similar patterns of recovery and disappearance can be found in shark and ray populations, that are absent or extirpated from the Southern North Sea but are showing recovery in the Northern areas (Perry et al. 2005, Dulvy et al. 2008, Sguotti et al. 2016), arguably because of the difference in fishing pressure in the two areas. Thus, past fishing trends could have a strong effect on fish population dynamics even in the present, and, coupled with environmental drivers and community changes, cause the presence of discontinuous dynamics of cod at lower latitudes in the North Sea.

Our study presents some limitations that need to be taken into account when interpreting the results. First of all, the resolution of the substocks in the North Sea used in our study is not univocal. The latest cod stock benchmark (Fredslund 2023) recognizes connectivity between the Northwestern area and the West of Scotland population, which we have not included in our study. Our distribution follows the North Sea stock subdivision that has been proposed in the latest assessment available at the time of writing (ICES 2023), but limited to North Sea proper. A further confirmation of the presence of spatial regime shift and the importance of scale derives from consideration about alternative substock resolution: in fact, it has been debated whether the Southern and Northwestern substocks should be considered separately or as one unit, given their genetic homogeneity (ICES 2023). For this reason, we repeated the analyses also considering just two substocks instead of three (i.e. merging these two units), and we showed that the emergent dynamics are masked if we aggregate these substocks together since the two areas present opposite dynamics (Tables S5C–S8C, Table 4). Indeed, the large substock ('Dogger' substock in the literature) presents no recovery, strong hysteresis, and discontinuous dynamics (Figs S5C–S8C, Table 4). This indicates that the dynamics of the larger Dogger substock match the dynamics of the Southern substock, but completely masks the positive status of the Northwestern substock evidenced by our results. Our study thus reveals that the use of three substocks, matching the recognized structure for assessment, allows to better highlight and unmask contrasting dynamics that might be useful for management compared to the utilization of a single stock unit for all the North Sea proper. Indeed, Sguotti et al. (2018) documented a regime shift characterized by hysteresis and with low recovery potential for the whole stock of Atlantic cod in the North Sea, that however masked important and contrasting spatial dynamics.

Another bias lies in the use of fishing effort instead of fishing mortality as driver of the substock. The most recent stock assessment reports provide values of fishing mortality (F) per substock, highlighting however that, at the moment, these are not reliable. Therefore, the only available driver that we had that was spatially resolved and for which we had data from 1985 until present was fishing effort. This indicator is additionally limited by the fact that fishing pressure is the result of hours of fishing of beam trawls and otter trawls (Couce et al. 2019). Cod is not targeted by beam trawls and is also not always the target of otter trawls. However, using this nonspecific fishing pressure, we capture both direct (extraction) and indirect effects of fishing such as bycatch and habitat destruction that can impact the cod substocks (Jennings et al. 1998, Halpern et al. 2015). Another possible issue could be caused by the mixing between substocks. Cod is a mobile species and substocks are known to intermingle in feeding grounds, to then migrate to the respective areas during the spawning season. To limit this problem, we selected IBTS data from Quarter 1 (winter), a season in which mixing between the substocks should be very limited due to the spawning migration taking place, so that each stock is restricted to its respective reproduction areas. Finally, some inherent bias resides in the use of the stochastic cusp model. Indeed, this model, as generally all statistical models, entails a simplification of reality, but can nonetheless provide important information about contrasting dynamics and detect regime shifts occurring in the form of a cusp bifurcation (Sguotti et al. 2018, Dakos and Kéfi 2022). Moreover, both state–driver plots and the cusp model confirmed and contributed to explain the results obtained, conferring robustness to the conclusions.

How can these results be useful for management? Here we show, aligning with the existing literature but from a novel point of view and approach, that considering just one stock of Atlantic cod for the whole North Sea might lead to incorrect assumptions, which may result in inappropriate management measures since the three substocks of cod show contrasting dynamics and recovery potential. Our results align with, and support the conclusions of the latest ICES benchmark (2023) (Fredslund 2023). We highlight that separated management should be applied in the three areas considering that, based on our analysis, the Northwestern cod could potentially recover to previous high abundances with the current reduction of fishing, Viking cod should be managed even in a more precautionary way to avoid declines and to improve biomass; and Southern cod appears to be in state that is difficult to recover from even through accurate management measures due to the low resilience it exhibits to the current stressors. These results are confirmed by the present state of the substocks, as evidenced by the latest ICES advices. These dynamics could create conflict among the fishers, potentially inducing spatial redistribution of fisheries from the Southern part of the North Sea to the northern, or changes of target species (Pinsky and Fogarty 2012, Pinsky et al. 2018, Rogers et al. 2019).

Our study highlights the importance of looking at regime shifts from a spatial point of view, and how contrasting dynamics can emerge at different SIs (Fisher et al. 2015, Rocha et al. 2018). It shows the difficulty of detecting regime shifts especially in large marine ecosystems that can present a variety of habitats, communities, and anthropogenic impacts. More research is needed to understand how to tackle the problem of spatial heterogeneity in regime shift science and to understand which scales are meaningful to use for management approaches (Sguotti et al. 2022a). Our analyses revealed that using smaller management units in the case of the North Sea helped to unravel important patterns that might be useful for management. Understanding the impact of regime shifts on individual species and populations is important in order to enable meaningful and effective management measures (Blenckner et al. 2015, Levin and Möllmann 2015, Selkoe et al. 2015, Thrush et al. 2016). New avenues should be pursued to make regime shifts science more applicable for management and to integrate it in policy frameworks (Sguotti et al. 2022a).

Acknowledgements

This study benefitted from exchanges and discussion at the ICES WGCOMEDA. The work reflects only the author's/authors' view; the European Commission and their executive agency are not responsible for any use that may be made of the information the work contains. We thank the scientists that collected the data that were used for this study.

Author contributions

C.S., G.R., and C.M. conceptualized the study and the methodology, E.C. and C.S. conducted the formal analysis, the visualization of the manuscript, and wrote the original draft. All the authors helped with validation and the writing - review and editing - of the manuscript.

Supplementary data

Supplementary data is available at *ICES Journal of Marine Science* online.

Conflict of interest: The authors declare no conflict.

Funding

This study was conducted within the course of the project SeaUseTip, Spatio-temporal analysis of tipping points in the socio-ecological system of the North Sea (funding code: 01LC1825A-C), and the bilateral project 'SocialEcological Tipping Points of the Northern Humboldt Current Upwelling System, Economic Repercussions and Governance Strategies', (Humboldt Tipping—Phase I, funding code: 01LC1823E), both projects sponsored by the German Federal Ministry of Education and Research (BMBF), within the framework of the international and interdisciplinary programme 'Eco-Biological Tipping Points' (BioTip, https://www.fona.de/en/me asures/funding-measures/biotip.php). E.C. was funded with the support of the Erasmus + programme of the European Union. C.S. was also funded by the EU HORIZON RESET (Resilience Estimation to SET management goals in marine ecosystems) Project (101065994) under the HORIZON-MSCA-2021-PF. G.R. was additionally funded by Biodiversa+, the European Biodiversity Partnership, in the context of the MUrFor (Managing sustainable sea Urchin fishery and marine FORest conservation) project under the

2021–2022 BiodivProtect joint call. It was cofunded by the European Commission (GA number 101052342) and the German Federal Ministry of Education (BMBF; project grant number 16LW0331). The work reflects only the author's/authors' view; the European Commission and their executive agency are not responsible for any use that may be made of the information the work contains.

Data availability

The data on survey CPUE of Atlantic cod are openly available at ICES DATRAS, http://www.ices.dk/data/data-portals/Pages/DATRAS.aspx. The data on copepods were collected from the Continuous Plankton Recorder program (www.cprsurvey.org). The environmental drivers were obtained from oceanographic model by Núñez-Riboni and Akimova (Núñez-Riboni and Akimova 2015). Finally, historical fishing effort data were collected from Couce et al. (2019).

References

Akimova A, Hufnagl M, Peck MA. Spatiotemporal dynamics of predators and survival of marine fish early life stages: Atlantic cod (*Gadus morhua*) in the North Sea. *Prog Oceanogr* 2019;**176**:102121. https://doi.org/10.1016/j.pocean.2019.102121

Alheit J, Moellmann C, Dutz J *et al.* Synchronous ecological regime shifts in the central Baltic and the North Sea in the late 1980s. *ICES J Mar Sci* 2005;**62**:1205–15. https://doi.org/10.1016/j.icesjms.2005.04.024

Andersen T, Carstensen J, Hernandez-Garcia E *et al.* Ecological thresholds and regime shifts: approaches to identification. *Trends Ecol Evol* 2009;**24**:49–57. https://doi.org/10.1016/j.tree.2008.07.014

Beaugrand G, Brander KM, Alistair Lindley J *et al.* Plankton effect on cod recruitment in the North Sea. *Nature* 2003;**426**:661–4. https://doi.org/10.1038/nature02164

Beaugrand G, Conversi A, Atkinson A *et al.* Prediction of unprecedented biological shifts in the global ocean. *Nat Clim Change* 2019;**9**:237–43. https://doi.org/10.1038/s41558-019-0420-1

Beaugrand G. The North Sea regime shift: evidence, causes, mechanisms and consequences. *Prog Oceanogr* 2004;**60**:245–62. https://doi.org/10.1016/j.pocean.2004.02.018

Beisner BE, Haydon DT, Cuddington K. Alternative stable states in ecology. *Front Ecol Environ* 2003;**1**:376–82. https://doi.org/10.1890/1540-9295(2003)001%5b0376:ASSIE%5d2.0.CO;2

Bestelmeyer BT, Ellison AM, Fraser WR *et al.* Analysis of abrupt transitions in ecological systems. *Ecosphere* 2011;**2**:art129. https://doi.org/10.1890/ES11-00216.1

Beukhof E, Dencker T, Pecuchet L *et al.* Spatio-temporal variation in marine fish traits reveals community-wide responses to environmental change. *Mar Ecol Progr Ser* 2019;**610**:205–22.

Blenckner T, Kannen A, Barausse A *et al.* Past and future challenges in managing European seas. *Ecol Soc* 2015;**20**:40.

Blöcker AM, Sguotti C, Möllmann C. Discontinuous dynamics in North Sea cod *Gadus morhua* caused by ecosystem change. *Mar Ecol Progr Ser* 2023;**713**:133–49.

Butzin M, Pörtner HO. Thermal growth potential of Atlantic cod by the end of the 21st century. *Global Change Biol* 2016;**22**:4162–8. https://doi.org/10.1111/gcb.13375

Couce E, Schratzberger M, Engelhard G. Reconstructing three decades of total international trawling effort in the North Sea. *Earth Syst Sci Data* 2019;**12**:1–19.

Dakos V, Kéfi S. Ecological resilience: what to measure and how. *Environ Res Lett* 2022;**17**:043003.

deYoung B, Barange M, Beaugrand G *et al.* Regime shifts in marine ecosystems: detection, prediction and management. *Trends Ecol Evol* 2008;**23**:402–9.

Diks C, Wang J. Can a stochastic cusp catastrophe model explain housing market crashes?. *J Econ Dyn Cont* 2016;**69**:68–88. https://doi.org/10.1016/j.jedc.2016.05.008

Djeghri N, Aurélien B, Ostle C *et al.* Reinterpreting two regime shifts in North Sea plankton communities through the lens of functional traits. *Global Ecol Biogeogr* 2023;**32**:1–14.

Drinkwater KF. The response of Atlantic cod (*Gadus morhua*) to future climate change. *ICES J Mar Sci* 2005;**62**:1327–37. https://doi.org/10.1016/j.icesjms.2005.05.015

Dulvy NK, Rogers SI, Jennings S *et al.* Climate change and deepening of the North Sea fish assemblage: a biotic indicator of warming seas. *J Appl Ecol* 2008;**45**:1029–39. https://doi.org/10.1111/j.1365-2664.2008.01488.x

Eklöf JS, Sundblad G, Erlandsson M *et al.* A spatial regime shift from predator to prey dominance in a large coastal ecosystem. *Commun Biol* 2020;**3**:1–9.

Engelhard GH, Righton DA, Pinnegar JK. Climate change and fishing: a century of shifting distribution in North Sea cod. *Global Change Biol* 2014;**20**:2473–83. https://doi.org/10.1111/gcb.12513

Engelhard GH. One hundred and twenty years of change in fishing power of English North Sea trawlers. In: *Advances in Fisheries Science: 50 years on from Beverton and Holt*. Hoboken, NJ: John Wiley & Sons, Inc, 2009, 1–25.

Fernandes JA, Rutterford L, Simpson SD *et al.* Can we project changes in fish abundance and distribution in response to climate?. *Global Change Biol* 2020;**26**:3891–905.

Fisher JA, Casini M, Frank KT *et al.* The importance of within-system spatial variation in drivers of marine ecosystem regime shifts. *Philos Trans R Soc B Biol Sci* 2015;**370**:1–8. https://doi.org/10.1098/rstb.2013.0271

Fredslund J. Benchmark workshop on Northern Shelf cod stocks (WKBCOD). ICES Scientific Reports. Copenhagen: ICES, 2023. /articles/report/Benchmark_workshop_on_Northern_Shelf_cod_stocks_WKBCOD_/22591423/1 (29 January 2024, date last accessed).

Grasman RPPP, Van Der Maas HLJ, Wagenmakers E-J. Fitting the cusp catastrophe in R: a cusp package primer. *J Stat Softw* 2009;**32**:1–27.

Haines H, Planque B, Buttay L. Poor performance of regime shift detection methods in marine ecosystems. *ICES J Mar Sci* 2024;**00**:1–14.

Halpern BS, Frazier M, Potapenko J *et al.* Spatial and temporal changes in cumulative human impacts on the world's ocean. *Nat Commun* 2015;**6**:7615.

Heath MR, Culling MA, Crozier WW *et al.* Combination of genetics and spatial modelling highlights the sensitivity of cod (*Gadus morhua*) population diversity in the North Sea to distributions of fishing. *ICES J Mar Sci* 2014;**71**:794–807.

Hillebrand H, Donohue I, Harpole WS *et al.* Thresholds for ecological responses to global change do not emerge from empirical data. *Nat Ecol Evol* 2020;**4**:1502–9. https://doi.org/10.1038/s41559-020-1256-9

Hislop JR. Changes in North Sea gadoid stocks. *ICES J Mar Sci* 1996;**53**:1146–56. https://doi.org/10.1006/jmsc.1996.0140

Hollander M, Wolfe DA, Chicken E. Nonparametric statistical methods. In: *Wiley Series in Probability and Statistics*. Vol. **848**. Hoboken, NJ: Wiley, 2013. https://www.wiley.com/en-us/Nonparametric+Statistical+Methods%2C+3rd+Edition-p-9780470387375 (9 July 2024, date last accessed).

Hutchinson WF. The dangers of ignoring stock complexity in fishery management: the case of the North Sea cod. *Biol Lett* 2008;**4**:693–5. https://doi.org/10.1098/rsbl.2008.0443

Ibanez F, Beaugrand G, Ibanez F *et al.* Monitoring marine plankton ecosystems: identification of the most relevant indicators of the state of an ecosystem. *J Mar Syst* 2008;**73**:138–54.

ICES. Working group on the assessment of demersal stocks in the North Sea and Skagerrak (WGNSSK). ICES Scientific Reports. Copenhagen: ICES, 2023. /articles/report/Working_Group_on_the_Assessment_of_Demersal_Stocks_in_the_North_Sea_and_Skagerrak_WGNSSK_/22643143/1 (29 January 2024, date last accessed).

Jennings MJ, Kaiser S, Jennings S *et al.* The effects of fishing on marine ecosystems. *Adv Mar Biol* 1998;**34**:201–352.

Kempf A, Huse G, Dingsør G *et al.* The importance of overlap—predicting North Sea cod recovery with a multi species fisheries assessment model. *ICES J Mar Sci* 1870;**67**:1989–97.

Koul V, Sguotti C, Årthun M *et al.* Skilful prediction of cod stocks in the North and Barents Sea a decade in advance. *Nat Commun* 2021;**2**:1–10.

Levin PS, Möllmann C. Marine ecosystem regime shifts: challenges and opportunities for ecosystem-based management. *Philos Trans R Soc B Biol Sci* 2015;**370**:20130275.

Llope M, Licandro P, Chan KS *et al.* Spatial variability of the plankton trophic interaction in the North Sea: a new feature after the early 1970s. *Global Change Biol* 2012;**18**:106–17.

Lynam CP, Llope M, Moellmann C *et al.* Interaction between top-down and bottom-up control in marine food webs. *Proc Natl Acad Sci* 2017;**114**:1952–7.

McQuatters-Gollop A, Edwards M, Helaouët P *et al.* The Continuous Plankton Recorder survey: how can long-term phytoplankton datasets contribute to the assessment of Good Environmental Status?. *Estuar Coast Shelf Sci* 2015;**162**:88–97. https://doi.org/10.1016/j.ecss.2015.05.010

Moellmann C, Diekmann R, Muller-Karulis B *et al.* Reorganization of a large marine ecosystem due to atmospheric and anthropogenic pressure: a discontinuous regime shift in the Central Baltic Sea. *Global Change Biol* 2009;**15**:1377–93. https://doi.org/10.1111/j.1365-2486.2008.01814.x

Moellmann C, Folke C, Edwards M *et al.* Marine regime shifts around the globe: theory, drivers and impacts. *Philos Trans R Soc B Biol Sci* 2015;**370**. https://doi.org/10.1098/rstb.2013.0260

Möllmann C, Cormon X, Funk S *et al.* Tipping point realized in cod fishery. *Sci Rep* 2021;**11**:1–12.

Neat FC, Bendall V, Berx B *et al.* Movement of Atlantic cod around the British Isles: implications for finer scale stock management. *J Appl Ecol* 2014;**51**:1564–74. https://doi.org/10.1111/1365-2664.12343

Núñez-Riboni I, Akimova A. Monthly maps of optimally interpolated in situ hydrography in the North Sea from 1948 to 2013. *J Mar Syst* 2015;**151**:15–34. https://doi.org/10.1016/j.jmarsys.2015.06.003

Olsen EM, Ottersen G, Llope M *et al.* Spawning stock and recruitment in North Sea cod shaped by food and climate. *Proc R Soc B Biol Sci* 2011;**278**:504–10.

Perry PJ, Low JR, Ellis JD *et al.* Climate change and distribution shifts in marine fishes. *Science* 2005;**308**:1912–5. https://doi.org/10.1126/science.1111322

Petraitis PS, Dudgeon SR. Cusps and butterflies: multiple stable states in marine systems as catastrophes. *Mar Freshwater Res* 2016;**67**:37–46. https://doi.org/10.1071/MF14229

Petraitis PS, Dudgeon SR. Variation in recruitment and the establishment of alternative community states. *Ecology* 2015;**96**:3186–96. https://doi.org/10.1890/14-2107.1

Pinsky ML, Fogarty M. Lagged social-ecological responses to climate and range shifts in fisheries. *Clim Change* 2012;**115**:883–91. https://doi.org/10.1007/s10584-012-0599-x

Pinsky ML, Reygondeau G, Caddell R *et al.* Preparing ocean governance for species on the move. *Science* 2018;**360**:1189–91.

Pörtner HO, Bock C, Knust R *et al.* Cod and climate in a latitudinal cline: physiological analyses of climate effects in marine fishes. *Clim Res* 2008;**37**:253–70. https://doi.org/10.3354/cr00766

Pörtner HO, Peck MA. Climate change effects on fishes and fisheries: towards a cause-and-effect understanding. *J Fish Biol* 2010;**77**:1745–79. https://doi.org/10.1111/j.1095-8649.2010.02783.x

R Core Team. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing. 2023.

Reid PC, Borges MD, Svendsen E. A regime shift in the North Sea circa 1988 linked to changes in the North Sea horse mackerel fishery. *Fish Res* 2001;**50**:163–71. https://doi.org/10.1016/S0165-7836(00)00249-6

Righton DA, Andersen KKH, Neat F *et al.* Thermal niche of Atlantic cod *Gadus morhua*: limits, tolerance and optima. *Mar Ecol Progr Ser* 2010;**420**:1–13.

Rocha JC, Biggs R, Peterson G. Regime shifts: what are they and why do they matter?. Regime Shifts Database. GitHub, 2014. www.regimeshifts.org

Rocha JC, Peterson G, Bodin Ö *et al.* Cascading regime shifts within and across scales. *Science* 2018;**362**:1379–83. https://doi.org/10.1126/science.aat7850

Rogers LA, Griffin R, Young T *et al.* Shifting habitats expose fishing communities to risk under climate change. *Nat Clim Change* 2019;**9**:512–6.

Romagnoni G, Kvile KØ, Dagestad KF *et al.* Influence of larval transport and temperature on recruitment dynamics of North Sea cod (*Gadus morhua*) across spatial scales of observation. *Fish Oceanogr* 2020;**29**:324–39.

Scheffer M, Carpenter S, Foley Ja *et al.* Catastrophic shifts in ecosystems. *Nature* 2001;**413**:591–6.

Scheffer M, Carpenter SR. Catastrophic regime shifts in ecosystems: linking theory to observation. *Trends Ecol Evol* 2003;**18**:648–56. https://doi.org/10.1016/j.tree.2003.09.002

Selkoe KA, Blenckner T, Caldwell MR *et al.* Principles for managing marine ecosystems prone to tipping points. *Ecosyst Health Sustain* 2015;**1**:1. https://doi.org/10.1890/EHS14-0024.1

Sguotti C, Färber L, Romagnoni G. Regime shifts in coastal marine ecosystems: theory, methods and management perspectives. In: *Reference Module in Earth Systems and Environmental Sciences*. Amsterdam: Elsevier, 2022a.

Sguotti C, Blöcker AM, Färber L *et al.* Irreversibility of regime shifts in the North Sea. *Front Mar Sci* 2022b;**9**:1830. https://doi.org/10.3389/fmars.2022.945204

Sguotti C, Lynam CPCP, García-Carreras B *et al.* Distribution of skates and sharks in the North Sea: 112 years of change. *Global Change Biol* 2016;**22**:2729–43. http://doi.wiley.com/10.1111/gcb.13316

Sguotti C, Otto SA, Frelat R *et al.* Catastrophic dynamics limit Atlantic cod recovery. *Proc R Soc B Biol Sci* 2018;**286**:20182877.

Sguotti C, Vasilakopoulos P, Tzanatos E *et al.* Resilience assessment in complex natural systems. *Proc R Soc B* 2024;**291**:20240089.

Thom R. Structural stability, catastrophe theory and applied mathematics. The John yon Neumann Lecture. *SIAM Rev* 1977;**19**: 189–201.

Thrush SF, Lewis N, Le Heron R *et al.* Addressing surprise and uncertain futures in marine science, marine governance, and society. *Ecol Soc* 2016;**21**:44.

Trifonova NI, Scott BE, De Dominicis M *et al.* Bayesian network modelling provides spatial and temporal understanding of ecosystem dynamics within shallow shelf seas. *Ecol Indic* 2021;**129**:107997.

Walker N, De Oliveira J. ICES Stock Annex: cod (*Gadus morhua*) in Subarea 4 and divisions 7.d and 20 (North Sea, English Channel and Skagerrak). Report of the ICES Advisory Committee, 2022. ICES Advice, 2018.

Wright PJ, Neat FC, Gibb FM *et al.* Evidence for metapopulation structuring in cod from the west of Scotland and North Sea. *J Fish Biol* 2006;**69**:181–99. https://doi.org/10.1111/j.1095-8649.2006.01262.x

Handling Editor: Rebecca Selden
