



Discontinuous dynamics in North Sea cod *Gadus morhua* caused by ecosystem change

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ABSTRACT: Marine ecosystems worldwide experience abrupt changes and regime shifts in structure and functioning due to the interacting effects of multiple stressors. North Sea cod *Gadus morhua* is a key example of a species being strongly overexploited for decades, causing an abrupt stock decrease below scientifically advised sustainable levels. Despite reductions in fishing pressure in recent years, populations of North Sea cod have not yet recovered. Why recovery is hindered and especially how ecosystem dynamics interacted with fishing to create a stable low cod stock is an open question. Here, we sequentially apply change point and principle component analyses as well as stochastic cusp modelling to a long-term time series (1963–2018) to show that North Sea cod recovery is limited due to an interaction of fishing pressure, internal stock dynamics and external environmental changes. We found that cod biomass experienced nonlinear, discontinuous dynamics, given the interaction of fishing pressure and climate change-induced increases in temperatures, wind magnitude and the North Atlantic Oscillation. Our results further demonstrate discontinuity in cod biomass due to low recruitment caused by a discontinuous relationship between stock biomass and environmental changes characterized by climate and zooplankton variables. Our study indicates that climate-induced changes in the environment have trapped North Sea cod in a depleted state, limiting the probability that the population will regain its role as a main target species for fisheries. Hence, we highlight the importance of incorporating discontinuous dynamics in fisheries management approaches to achieve sustainable exploitation levels and to identify thresholds of drivers to favour policies to prevent regime shifts.

KEY WORDS: Recovery · Collapse · Regime shift · Stochastic cusp model

1. INTRODUCTION

People and communities worldwide depend strongly on the services oceans provide. Livelihoods are built upon the provision of food, the cultural benefits of tourism and the trade of marine commodities. The awareness that these goods are under enormous anthropogenic pressures is increasing and efforts are being made to recover those losses (Palmer et al. 2004, Ingeman et al. 2019). Recovery of deteriorated marine ecosystems is defined differently depending on who is involved, what is being assessed and which

goals are being formulated (Lotze et al. 2011). Definitions of recovery comprise the restoration of underlying ecosystem functions and processes, recovery goals such as system stability (Ingeman et al. 2019) or the recuperation of marine populations and their habitats (Duarte et al. 2020). In fisheries management, recovery is considered to be achieved if biomass levels reach a level consistent with the maximum sustainable yield concept (B_{MSY}), which enables sustainable fishing (Duarte et al. 2020). The European Union (EU) applies the MSY approach through the common fisheries policy. Achieving MSY is considered recov-

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ery, where management implements reference levels with respect to fishing mortality and biomass (i.e. F_{MSY} and $MSY B_{trigger}$; ICES 2012a). F_{MSY} is the rate of F at which the long-term average catch corresponds to MSY and the long-term average biomass to B_{MSY} (the expected biomass if F is at F_{MSY}). $MSY B_{trigger}$ relates to a threshold at which F is advised to be reduced relative to F_{MSY} (ICES 2022b).

Ecosystems can recover from different levels of disturbance, where (1) a complete recovery restores the system to its initial state or (2) a partial recovery results in an alternative state. However, if the system remains damaged in the long term, its state may become irreversible (Lotze et al. 2011, Duarte et al. 2020). Limited recovery is theoretically enforced if drivers are not reversed and may be associated with the appearance of abrupt shifts in system dynamics; so-called 'regime shifts'. Regime shifts occur if the resilience of a system (or population) is low and its structure and functioning are being altered (Beisner et al. 2003, Conversi et al. 2015). The underlying theory of regime shifts involves the characteristics of abrupt changes and alternative stable states (Scheffer et al. 2001, Beisner et al. 2003). However, the detection of abrupt changes by itself does not necessarily imply discontinuous dynamics. Additional analyses are required to detect underlying drivers, alternative states and hysteresis (Sguotti et al. 2022). Depending on the relationship between a pressure and the response variable, a shift can occur logistically or discontinuously. Discontinuity implies the occurrence of hysteresis, where the path of reaching a new alternative stable state differs from the path of returning to the original state (Scheffer et al. 2001, Conversi et al. 2015, Sguotti et al. 2019).

Regime shifts are a well-documented phenomenon in the marine realm, in particular within the North Sea ecosystem, and have been observed over several trophic levels (Weijerman et al. 2005, Kenny et al. 2009). Regime changes were mainly reported for phytoplankton and zooplankton and related hydro-climatic changes such as the North Atlantic Oscillation (NAO) and the Atlantic Multidecadal Oscillation (AMO) (Fromentin & Planque 1996, Reid & Edwards 2001, Edwards et al. 2013) as well as local temperature (Capuzzo et al. 2018, Edwards et al. 2020, Nohe et al. 2020). A major regime shift was detected during the 1980s, including pronounced changes in phytoplankton due to increasing temperature (Beaugrand & Reid 2003, Beaugrand 2004, Lynam et al. 2017). Phytoplankton biomass has increased steadily in recent decades (McQuatters-Gollop et al. 2011), and a change in the ratio between diatoms and dinoflagel-

lates has been observed (Hinder et al. 2012). Recently, further warming, combined with a decrease in eutrophication since the 1990s, has caused a change in bloom patterns and an increase in diatom and dinoflagellate biomass (Nohe et al. 2020). Changes in primary production have been further related to shifts in the zooplankton community affecting the productivity of fish populations (Kenny et al. 2009, Lynam et al. 2017), in particular where changes in secondary production may increase stress on already depleted fish stocks (Edwards et al. 2020).

An instructive case for studying recovery and regime shift dynamics is Atlantic cod *Gadus morhua*. Atlantic cod populations are key examples of overfishing, and many collapsed cod stocks have not recovered even though fishing pressure has often been greatly reduced (Rose 2019, Sguotti et al. 2019). In the North Sea, cod increased dramatically during the so-called 'gadoid outburst', characterized by favorable feeding conditions for gadoid species in the North Atlantic during the 1960s (Cushing 1980). Subsequently, fishing pressure was increased to very high levels, causing the stock to decline sharply (Cook et al. 1997). This decrease, combined with the reduced production of young cod and a decrease in optimal thermal habitat due to increased warming of the North Sea (O'Brien et al. 2000, Blanchard et al. 2005, Rindorf & Andersen 2008), resulted in the stock collapsing and falling below scientifically advised safety levels in the late 1980s (ICES 2022a). Furthermore, the decrease in thermal range combined with fishing pressure led to a northward shift of the cod stock (Engelhard et al. 2014). Since the North Sea stock consists of 3 distinct populations centered around the Viking bank, the Dogger bank (the South proper) and the north-west (Romagnoni et al. 2020), it can be assumed that the southern population is affected most by these stressors. A recovery plan was established in the 1990s to stop cod from declining and to enhance recovery (ICES 2012b). Still, the North Sea cod stock has not recovered and recruitment has remained at historically low levels since 1998 (ICES 2022a). This failed recovery, despite a strong reduction in fishing pressure, points to hysteresis in cod dynamics, a typical sign of a regime shift in the fish stock or its supporting ecosystem (Sguotti et al. 2019).

In this study, we examined whether regime changes in the North Sea ecosystem can be linked to the failed cod recovery. We explored cod–ecosystem links using stochastic cusp modelling (Grasman et al. 2009), a modelling approach based on catastrophe theory. Catastrophe theory became popular in the 1970s

(Zeeman 1979) but was largely ignored afterwards (Sguotti et al. 2019). However, recently, stochastic cusp modelling has been increasingly applied in diverse scientific fields such as economics (Diks & Wang 2016), sociology and psychology (Guastello et al. 2012, Sideridis et al. 2016), as well as in fisheries (Sguotti et al. 2019, 2020, Möllmann et al. 2021). The theory's scope comprises investigating sudden changes in dynamic systems in response to multiple interactions of external drivers (Poston & Stewart 1978, Grasman et al. 2009, Sguotti et al. 2019). Importantly, the stochastic cusp modelling approach allows for (1) evaluating discontinuity in system dynamics implying hysteresis in response to external drivers and (2) testing for stability of system states at any point in time (Zeeman 1979, Grasman et al. 2009). Even though regime shifts in North Sea cod stocks are being intensively studied, the drivers of these shifts are not fully understood (Sguotti et al. 2019).

Therefore, the main goal of our study was to investigate the potential existence of discontinuous dynamics in North Sea cod and to understand the underlying mechanisms limiting cod stock recovery. Our

study provides evidence for non-linear discontinuous population dynamics in North Sea cod, implying hysteresis in the recovery of the fish stock to reduced F . We relate the failed cod recovery to low recruitment in response to changes in phytoplankton and zooplankton productivity in the North Sea ecosystem as a result of climate-induced temperature rise. Our study demonstrates how climate-induced ecosystem dynamics can limit the recovery of a depleted fish stock, which is important information for ecosystem-based fisheries management.

2. METHODS

2.1. Data

We gathered a wide range of biotic and abiotic data (1963–2018) to obtain a more comprehensive picture of ecosystem dynamics and to identify potential external pressures on the stock. The data were selected based on their known effects on cod stock dynamics (Table 1).

Table 1. Relevance of abiotic and biotic variables for North Sea cod stock dynamics. As the North Atlantic Oscillation (NAO) is only an index for wind, we additionally included both wind and current speeds to include direct yearly changes in the environment of North Sea cod. AMO: Atlantic Multidecadal Oscillation; SBT: sea bottom temperature; SST: sea surface temperature; Sv: Sverdrup

Variable	Rationale	Reference(s)
NAO	Reflects strong westerly winds causing variabilities in seasonal phytoplankton production and zooplankton, hence, changes in lower trophic levels, altering the food web of cod	Hurrell (1995), Reid & Edwards (2001), Drinkwater et al. (2003), Alvarez-Fernandez et al. (2012)
AMO	Long-term dynamics and variability in temperature affects phytoplankton and zooplankton abundances, hence, changes in lower trophic levels, altering the food web of cod	Edwards et al. (2013), Alheit et al. (2014)
SST (°C)	Increasing SST affects recruitment negatively through changes in prey abundances and distribution, and changes the distribution of adult North Sea cod	Drinkwater (2005), Righton et al. (2010), Engelhard et al. (2014), Baudron et al. (2020)
SBT (°C)	Increasing SBT affects demersal, cold-water-preferring cod, causing, e.g. faster growth, decreasing age of maturity	Drinkwater (2005), Righton & Metcalfe (2019)
Inflow (Sv)	Zooplankton (e.g. <i>Calanus finmarchicus</i>)-rich water and changes in deep water temperatures affects cod recruitment. The inflow is also positively related to the NAO during winter	Hjøllo et al. (2009), Alvarez-Fernandez et al. (2012), Akimova et al. (2016), Gao et al. (2021)
Wind (m s ⁻¹)	Wind speed; see NAO	Hurrell (1995), Drinkwater et al. (2003)
Current (m s ⁻¹)	The direction and strength is influenced by the inflow	Reid & Edwards (2001)
Phytoplankton (phytoplankton colour index)	Food web at trophic level 1	Alheit et al. (2005), Alvarez-Fernandez et al. (2012)
Diatoms	Food web at trophic level 1	Alheit et al. (2005), Alvarez-Fernandez et al. (2012)
Dinoflagellates	Food web at trophic level 1	Alheit et al. (2005), Alvarez-Fernandez et al. (2012)
Small copepods	Food web at trophic level 2 and important food source for cod larvae	Alheit et al. (2005), Alvarez-Fernandez et al. (2012)
Large copepods	Food web at trophic level 2 and important food source for cod larvae	Beaugrand et al. (2003)

To analyze stock dynamics, we retrieved estimates of North Sea cod spawning stock biomass (SSB), recruitment (R) at age 1 and F from the International Council for the Exploration of the Sea (ICES) Stock Assessment Database (ICES 2019). We investigated climate effects on cod using indices of the NAO (Climate Prediction Center 2020) and the AMO (Enfield et al. 2001), provided in monthly values from the Climate Prediction Center of the National Oceanic and Atmospheric Administration (NOAA). Both NAO and AMO are hydro-climatic indices known to be related to oceanographic changes in the North Sea (Drinkwater et al. 2003, Knight et al. 2006). The NAO index is based on atmospheric pressure differences at sea level between the Azores High and the Icelandic Low (Drinkwater et al. 2003), whereas the AMO index builds upon Atlantic sea surface temperature (SST) variations in the Northern Hemisphere (Knight et al. 2005). We used the NAO winter index, which is computed based on the mean pressure difference from December to March. Mechanisms related to the NAO are considered to have their greatest effect on the boreal environment during these months, where a positive NAO reflects high westerly winds (Hurrell 1995, Drinkwater et al. 2003). The AMO has been identified as a coherent mode of natural variability occurring in the North Atlantic Ocean with an estimated period of 60–80 yr, and it is based on SST anomalies in the North Atlantic basin, typically averaged over 0–80° N. In general, the AMO is an index for the climate of the Northern Hemisphere and is connected to the variability in rainfall and SST in northwestern Europe (Knight et al. 2006, Edwards et al. 2013, Alheit et al. 2014). We used the yearly mean of the AMO.

Since local temperature greatly affects the ecosystem, we also gathered annual SST (°C) and sea bottom temperature (SBT; °C) data (Nunez-Riboni & Akimova 2015). We further explored the effect of the North Sea Inflow (in Sverdrup [Sv]) on cod dynamics. The inflow of zooplankton-rich water and simultaneous changes in the temperatures of deep waters are expected to affect North Sea cod R (Akimova et al. 2016). Monthly inflow data were derived from simulations with the NORWECOM model (Hjøllo et al. 2009). These inflow data cover the longitudinal Orkney-Utsir transect along 59.17° N over the entire water column (Hjøllo et al. 2009). As NAO and AMO are also related to local changes in winds and currents, we also obtained the latter data from NOAA and the Integrated Climate Data Center, University of Hamburg. We calculated annual mean wind mag-

nitude from daily u - and v -wind data at a level of 10 m (Kalnay et al. 1996), and yearly mean current magnitude from daily u - and v -current data (Mogensen et al. 2012, Balmaseda et al. 2013), aggregated across the whole North Sea, using the following Pythagorean equation:

$$\text{magnitude} = \sqrt{u^2 + v^2} \quad (1)$$

where magnitude is the overall wind or current speed (m s^{-1}), and u and v are its eastward and southward components, respectively. The wind and currents come from the west if u is positive and from the east if u is negative, and from the south if v is positive and from the north if v is negative.

We furthermore used phytoplankton and zooplankton abundance indicators derived from the continuous plankton recorder (CPR) survey (Johns 2019) to characterize North Sea ecosystem changes, specifically the phytoplankton colour index, the abundance of diatoms and dinoflagellates and the abundance of small and large copepods (Capuzzo et al. 2018, Bedford et al. 2020). We used annual means for the complete North Sea from spatially resolved monthly data across the entire North Sea for each of the biotic variables.

All data were combined into a data matrix, with annual values covering the entire North Sea for the period 1963–2018; i.e. the period covered by the cod stock assessment data we used.

2.2. Statistical analyses

We applied a combination of statistical modelling approaches to analyze the potential effects of biotic and abiotic variables on the recovery of the North Sea cod stock. We first applied statistical change point analyses to the SSB time series to identify the first regime shift characteristic: abrupt changes. For subsequent analyses, we checked for possible collinearity among variables by applying the Pearson correlation and a variance inflation factor (VIF) analysis, using a VIF value threshold of ≤ 3 (Zuur et al. 2010). To further understand common trends in abiotic, biotic and cod stock dynamics, we conducted a principal component analysis (PCA) (Kassambra 2017) and constrained clustering (Diekmann et al. 2012, Juggins 2020).

Finally, we used the stochastic cusp model, an approach that identifies the effect of 2 external drivers and their interactions on a state variable (in our case, SSB or R) in causing discontinuous dynamics (Grasman et al. 2009).

2.2.1. Change point analyses

We identified abrupt changes in North Sea cod stock dynamics using statistical change point analyses applied to the time series of SSB. Different change point approaches exist that encompass distinct statistical concepts and, hence, often the change points identified in a time series vary slightly. Therefore, we applied 2 common methods and only accepted change points if both methods detected a change point at approximately the same time (± 1 yr). The Bayesian change point analysis (Erdman & Emerson 2007) uses a Bayesian approach to estimate the probability of change in a specific year of a time series. The 'bcp' function (Erdman & Emerson 2007) uses the Markov chain Monte Carlo approach to calculate the posterior probability that the posterior means before and after the change point differ significantly (Erdman & Emerson 2007). Given large yearly oscillations in the SSB time series, we define years with a posterior probability > 0.7 to be a significant change point. Secondly, we used the 'cpt.mean' function (Killick & Eckley 2014) using the 'BinSeg' method (Scott & Knott 1974). 'BinSeg' searches for a maximum number of change points using a multiple change point search. A statistical single change point test is then performed for the entire data series. The method encompasses splitting the time series into 2 at the detected change point. The procedure is repeated until no further change points are found in the time series (Killick & Eckley 2014).

2.2.2. PCA and constrained clustering

We performed a PCA to understand how the biotic community and abiotic variables changed over time, which variables are most strongly associated with these changes and to identify the main mode of variability for these changes. A PCA extracts the main modes of variability from a multivariate data set by creating new variables, the so-called principal components, which represent a linear combination of the original variables (Kassambra 2017). Here, we first scaled the data for normalizing and then applied the PCA on 3 data matrices: (1) all abiotic and biotic variables combined, (2) abiotic variables only and (3) biotic variables only. Cod SSB and R were treated as supplementary quantitative variables in the analyses, meaning they were not included in the PCA calculations but are still shown in the results. For each case, we extracted principal components 1 (PC1) and PC2 to represent general abiotic and biotic trends over time. To determine clusters of years with similar

patterns in abiotic and biotic variables, we applied constrained hierarchical clustering (Diekmann et al. 2012, Juggins 2020) to the time series, using pairwise Euclidean distances among years. Clusters were distinguished using graphical interpretation of constrained incremental sum of squares clustering (CONISS) broken stick and CONISS cluster plots.

2.2.3. Stochastic cusp modelling

As a focus of our analysis, we used the stochastic cusp model to test for discontinuous dynamics in North Sea cod. The model is based on catastrophe theory implying a canonical cusp form and describes abrupt changes between equilibria of a state variable (z_t) due to changes in 2 control parameters (α , β). In this way, the cusp is efficient in finding abrupt changes despite continuous and small changes in these control parameters. Parameter α is the so-called asymmetry parameter and affects the dimension of the state variable (e.g. SSB) directly and can be managed through policy; e.g. F (Fig. 1) (Grasman et al. 2009, Sguotti et al. 2019). The control parameter β , the so-called bifurcation variable or splitting factor (e.g. R or SST), determines the path of the relationship between the state variable and the asymmetry parameter, which can change from linear to non-linear continuous (logistic) to discontinuous (Fig. 1a) (Grasman et al. 2009, Sguotti et al. 2019). Hence, by using the stochastic cusp model, the interactive effect of 2 simultaneous or cumulative drivers on the state variable can be determined (Diks & Wang 2016, Sguotti et al. 2019).

The rate of change of this relationship is represented by the following cubic equation:

$$V(z_t; \alpha, \beta) = \frac{1}{4}z_t^4 - \frac{1}{2}\beta z_t^2 - \alpha z_t \quad (2)$$

where $V(z_t; \alpha, \beta)$ is a potential function with the 2 control parameters (α , β) affecting the system state (z_t). The function provides a scalar for each state of z_t and vector of the control variables (Wagenmakers et al. 2005). The function's slope represents the rate of change of the system z_t depending on α and β (Grasman et al. 2009, Sguotti et al. 2019).

Given stochasticity in empirical data and natural processes (Sguotti et al. 2020), white noise in the form of a Wiener process is added to transform Eq. (2) into a stochastic differential equation. It is assumed that Eq. (2) governs the state variable (z_t) and that the driving noise includes the variance σ_z^2 . If the derivative of Eq. (2) equals 0, the system is at equilibrium:

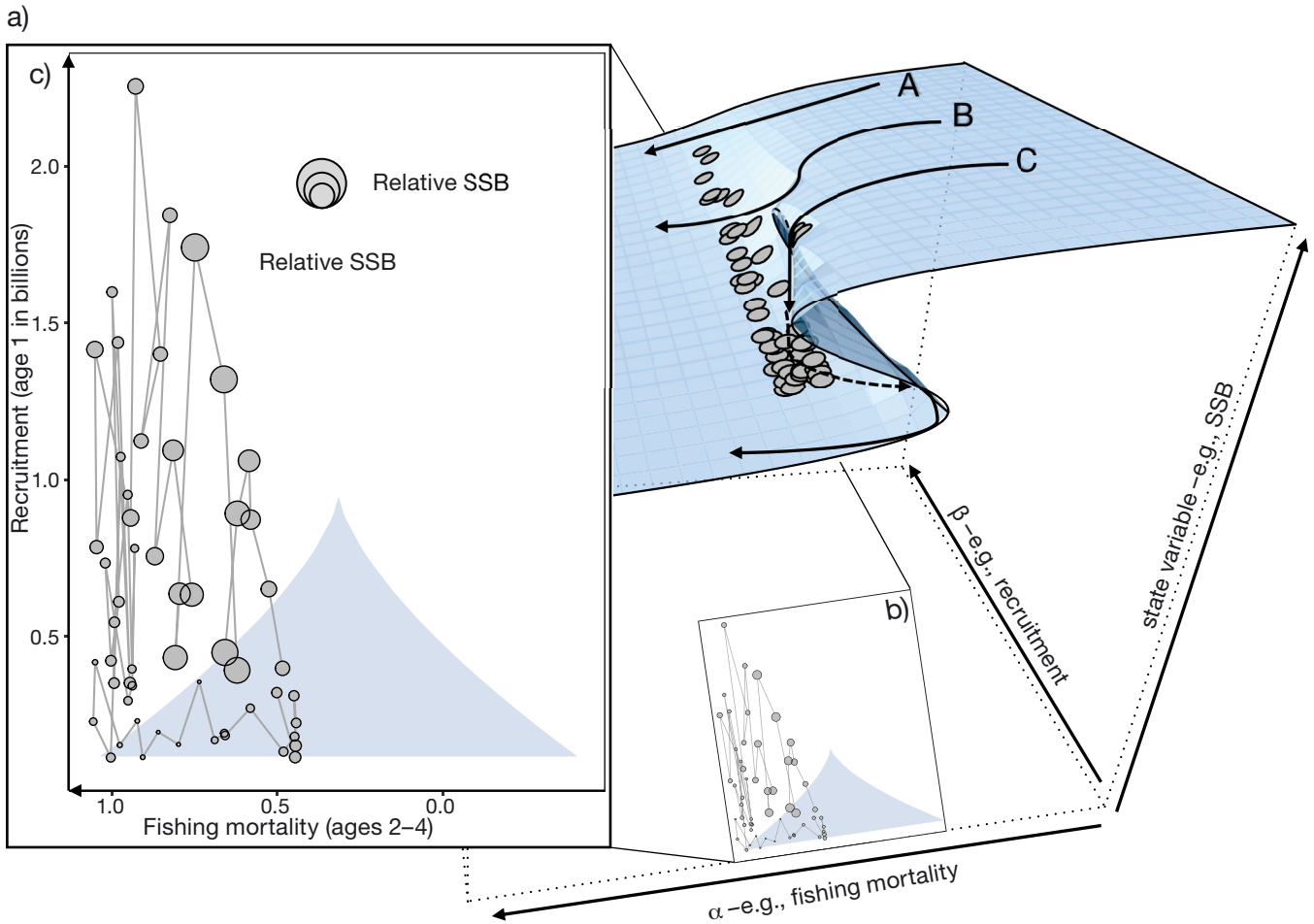


Fig. 1. Stochastic cusp model representation. (a) 3D representation of the cusp model where North Sea Cod spawning stock biomass (SSB; state variable) depends on the 2 variables fishing mortality set by management (α) and recruitment (β), with the latter controlling the path of SSB (A: the linear path, B: the logistic path, or C: the discontinuous path; dashed arrow represents unstable equilibria). (b,c) 2D representation of the cusp model. Light blue area: the bifurcation area under folded 3D plane; size of points: size of SSB, with the radius scaled relative to stock size

$$-\frac{\delta V(z, \alpha, \beta)}{\delta z} = (-z_t^3 + \beta z_t + \alpha) dt + \sigma_z dW_t = 0 \quad (3)$$

The left-hand side represents the drift term, σ_z is the diffusion parameter and W_t is the Wiener process (Grasman et al. 2009, Diks & Wang 2016, Sguotti et al. 2019).

Here, we applied the model twice, using SSB and R as the state variable, respectively. To analyze changes in SSB, SSB was lagged by 1 to obtain R at age 0, as the SSB in a given year directly affects the number of recruits in that year. The manageable asymmetry parameter α was either represented by fishing pressure for SSB, or by SSB for R . The splitting factor β was represented by the abiotic and biotic parameters as well as trends of the full community given by PC1s and PC2s. In addition, the splitting factor was predicted by a combination of abiotic and biotic PCs to investigate the effects of combined abiotic and biotic

changes on the relationship between the state variable and the asymmetry parameter.

Using a likelihood approach, the canonical state variable (z_t) and parameters α and β are estimated as linear functions of one or more observable state variables (Eq. 4a) or independent variables (Eqs. 4b and 4c), respectively (Grasman et al. 2009, Diks & Wang 2016):

$$z_t = w_0 + w_1 \text{ SSB} \quad (4a)$$

$$\alpha = \alpha_0 + \alpha_1 \text{ Fishing pressure} \quad (4b)$$

$$\beta = \beta_0 + \beta_1 \text{ Abiotic and/or Biotic Driver} \quad (4c)$$

where w_0 , α_0 and β_0 are the intercepts and w_1 , α_1 and β_1 are the slopes of the models.

These estimated parameters were substituted into Eq. (3). The canonical form of the cusp function contains equilibrium points, which are defined by a

function of the control parameters (Grasman et al. 2009, Sguotti et al. 2019):

$$-\frac{\delta V(z, \alpha, \beta)}{\delta z} = -z_t^3 + \beta z_t + \alpha = 0 \quad (5)$$

Eq. (5) has one solution if:

$$\delta = 27\alpha^2 - 4\beta^3 \quad (6)$$

δ is Cardan's discriminant, which distinguishes the different possible solutions in the number of equilibria, i.e. one equilibrium if $\delta > 0$ and 3 if $\delta < 0$ (Grasman et al. 2009, Diks & Wang 2016, Sguotti et al. 2019).

The 'cusp' model R package computes linear, logistic and cusp models simultaneously. For the linear model, a simple linear regression is performed (Grasman et al. 2009):

$$z_t = \beta_0 + \beta_1 \text{ Abiotic and/or Biotic Driver} + \varepsilon_t \quad (7)$$

where z_t and β are as defined in Eqs. (4a) and (4c) and ε reflects the statistical noise.

The logistic curve is fitted to the data using the maximum likelihood under the assumption of normal errors (Grasman et al. 2009), using the following equation:

$$z_t = \frac{1}{1 + \exp(-\alpha/\beta^2)} + \varepsilon_t \quad (8)$$

where z_t , α and β are defined as in Eqs. (4a), (4b) and (4c), and ε represents the statistical noise.

The 'cusp' model R package produces a 3D surface as an outcome, which shows linear, logistic and discontinuous relationships between the state variable and the control parameters (Fig. 1). These 3 relationships are tested statistically against each other. In addition, the discontinuous path includes a folded area, the so-called bifurcation set (Grasman et al. 2009, Sguotti et al. 2019). The 3D surface can be visualized in 2D, where the bifurcation set (area of instability) is highlighted in blue and the α and β parameters are on the x - and y -axis, respectively (Fig. 1b,c). Points within the bifurcation area represent the unstable state of the system ($\delta > 0$). At the boundary of the bifurcation set, Cardan's discriminant (δ) equals zero. Points outside of the bifurcation area indicate the stable alternate states and high resilience to pressures. If the relationship is indeed discontinuous, the path runs through the bifurcation area and might indicate the presence of hysteresis (Diks & Wang 2016, Petraitis & Dudgeon 2016).

Given the high number of covariates and their combinations representing β , we performed a model-selection procedure using a combination of an infor-

mation-theoretic approach (Burnham & Anderson 2002) and the classical stepwise model selection. Five models each were specified *a priori* for SSB and R and then modified using backward and forward selection. A total of 14 and 13 models for SSB and R were tested, respectively (see Table S1 for all model outcomes).

We validated the cusp model outcomes according to criteria recommended by Grasman et al. (2009) and developed by Cobb (1998). First, we assessed whether the cusp fit is superior to a linear or a logistic regression based on the goodness of fit, using Cobb's pseudo- R^2 and Akaike's information criterion (AIC). Secondly, we determined the significance of the state variable slope coefficient, which should be significantly different from zero. Thirdly, the percentage of observations (α and β pairs) within the bifurcation area should at least be 10% (Cobb 1998, Grasman et al. 2009). In addition, we looked at the diagnostic plots, which show a residual versus fitted plot, and density estimates of the state variable in the 2D plane (Grasman et al. 2009). Eventually, we chose the best-fitting cusp models based on the highest R^2 value and based on our focus on discontinuity and hysteresis presence in the state variables SSB and R to detect the occurrence of true regime shifts.

We performed all analyses within the statistical and programming environment of R (R Core Team 2018). The change point analyses were performed with the packages 'bcp' (Erdman & Emerson 2007) and 'changepoint' (Killick & Eckley 2014). The PCA was conducted using the packages 'stats' (R Core Team 2018) and 'factoextra' (Kassambra & Mundt 2019), the constrained clustering method was supported by the packages 'vegan' (Oksanen et al. 2020) and 'rioja' (Juggins 2020) and the stochastic cusp modelling was implemented with the package 'cusp' (Grasman et al. 2009).

3. RESULTS

3.1. North Sea cod stock dynamics

North Sea cod stock experienced a strong decline in SSB and R beginning the early 1970s (Fig. 2). We determined major abrupt changes in SSB in 1975 and 2006 using statistical change point analysis, indicating 3 regime periods (Fig. 2a). The first regime was characterized by a steep increase in SSB followed by a decline. The initial regime was the only period within the study period where the SSB was above all biomass management reference points, indicating a

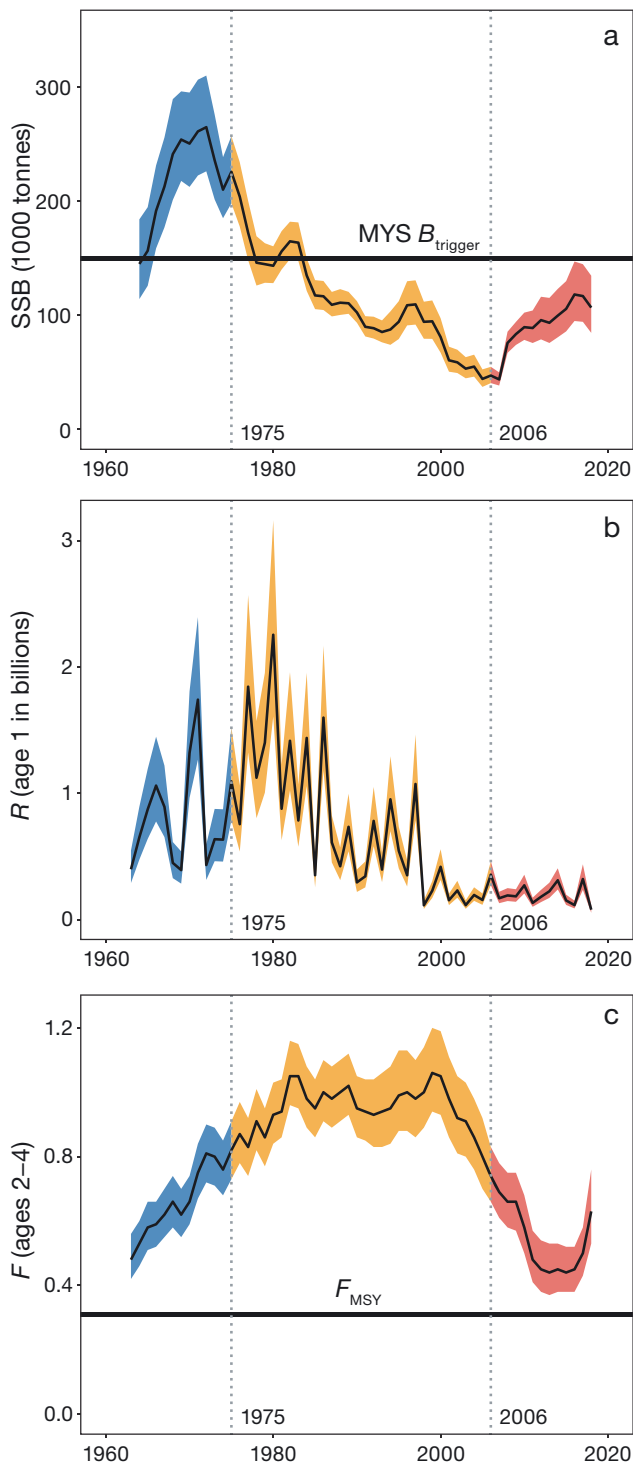


Fig. 2. (a) Spawning stock biomass (SSB), (b) recruitment (R), and (c) fishing mortality (F) of North Sea cod. Vertical lines in (a–c) indicate abrupt changes in SSB identified by statistical change point analyses; colours distinguish the 3 regimes identified; horizontal lines in (a) and (c) indicate management reference points (i.e. level of SSB triggering specific action in management [$MSY B_{trigger}$], F level aiming at maximum sustainable yield [F_{MSY}]) (ICES 2012a)

sustainable stock size. Within the second regime, SSB declined continuously until 2005, crossing all reference points. After 2006, SSB increased slightly but did not recover above $MSY B_{trigger}$. R showed a similar development as SSB until the end of the second regime (Fig. 2b). F was above the reference point F_{MSY} during the whole assessment period (Fig. 2c). Fishing pressure constantly increased until the late 1990s and subsequently declined in the early 2000s, but never reached the present management target of F_{MSY} . In recent years, F has increased again.

3.2. North Sea ecosystem changes

A major question in our study was how cod stock dynamics are embedded in overall ecosystem developments in the North Sea. We divided the ecosystem into biotic (Fig. 3) and abiotic (Fig. 4) dynamics. Major changes in large and small copepods took place around the 1980s, implying a strong decrease in their abundance (Fig. 3a,c). A strong increase in phytoplankton (Fig. 3b) in the late 1980s was followed by a strong decline and increase in dinoflagellates (Fig. 3d) and diatoms (Fig. 3e), respectively, from the 2000s onwards.

Similar developments with major changes in the 1980s and 2000s took place in the abiotic environment (Fig. 4). The NAO, the inflow and overall wind and current speeds increased steadily from 1980 onwards, shown by a switch from a negative to a positive anomaly (Fig. 4a,c,e,g). The AMO, SBT and SST (Fig. 4b,d,f) showed increases later in time, around 2000.

For an overall understanding of the ecosystem developments, we conducted a comprehensive assessment of North Sea ecosystem changes using PCA based on these biotic and climatic variables (Fig. 5). Our correlation and VIF analyses revealed that SST and AMO could be removed from the analysis. The analysis, including all relevant biotic and abiotic variables (Fig. 5), revealed a main ecosystem component (PC1) that increased continuously over the entire study period (Fig. 5a, see Fig. S1 & S2 in the Supplement at www.int-res.com/articles/suppl/m713_p133_supp.pdf for distinct biotic and abiotic PCA). The main variables contributing to PC1 were phytoplankton (represented by the phytoplankton colour index), the North Sea inflow and the NAO. Both phytoplankton and the inflow showed an abrupt increase in the early 1980s and the 1990s, respectively (Fig. 4). PC2 remained relatively stable until the late 1990s and subsequently experienced an

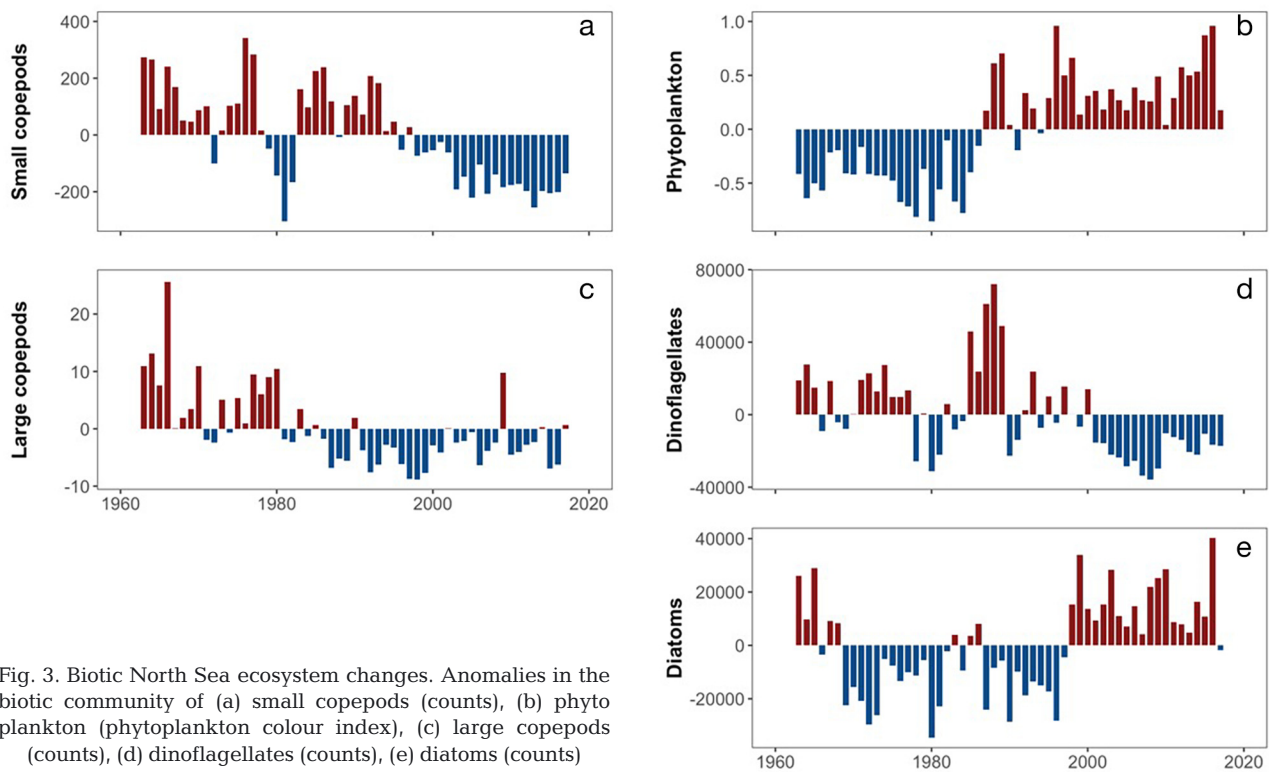


Fig. 3. Biotic North Sea ecosystem changes. Anomalies in the biotic community of (a) small copepods (counts), (b) phytoplankton (phytoplankton colour index), (c) large copepods (counts), (d) dinoflagellates (counts), (e) diatoms (counts)

abrupt change to a lower level (Fig. 5b). Variables mainly associated with PC2 were climatic and lower trophic level variables like SBT, diatoms and small copepods. In particular, the temperature variables were negatively correlated with PC2.

We separated 3 main periods in the North Sea ecosystem using constrained clustering on these PCA results (Fig. 5c,d). These periods coincided with the major changes in the abiotic and biotic variables. A first (1963–1984) and a third cluster (2001–2017) demonstrated opposite configurations in the ecosystem. A large and productive cod stock (high SSB and strong R) and high abundances of copepods were characteristic of the first period, but all variables have recently shown low values. The recent period was characterized by increased AMO, wind and current magnitudes, inflow and temperatures in the North Sea, while the initial period could be described as a cold regime. The second cluster (1985–2000) represented the transition between the 2 more extreme periods.

3.3. Discontinuous cod stock dynamics

The main aim of our study was to understand North Sea cod SSB and R dynamics and detect potential

regime shift dynamics. We modelled the interactive effects of biotic and abiotic changes with (1) F on SSB and (2) SSB on R . We used the stochastic cusp model approach to investigate the effect of the interactions between these drivers on SSB and R and also to test for regime stability and potential irreversibility or hysteresis of the system. Our model-selection procedure revealed for SSB, 5 and for R , 2 relevant cusp models, implying discontinuous dynamics (Table 2). All models display heterogeneous distributions of the residuals and have a low AIC compared to the linear and logistic models. The discontinuous dynamics in the models with SSB as the state variable were strong since the R^2 values of the cusp models were much larger than those of the logistic models. In contrast, the cusp models with R have R^2 values that were only slightly larger than those of the logistic models (Table 2, Cobb's pseudo- R^2).

First, we analyzed the dynamics of SSB as a function of the interaction between R and F (Fig. 6a). At the beginning of the time series, R was high, F was low and SSB was high and within the unstable area. Afterwards, the cod stock reached a stable state (outside the bifurcation or cusp area) characterized by high SSB values and high R and F . During the last period, F decreased, R reached constant low levels and SSB entered the unstable area where 3 equilibria are

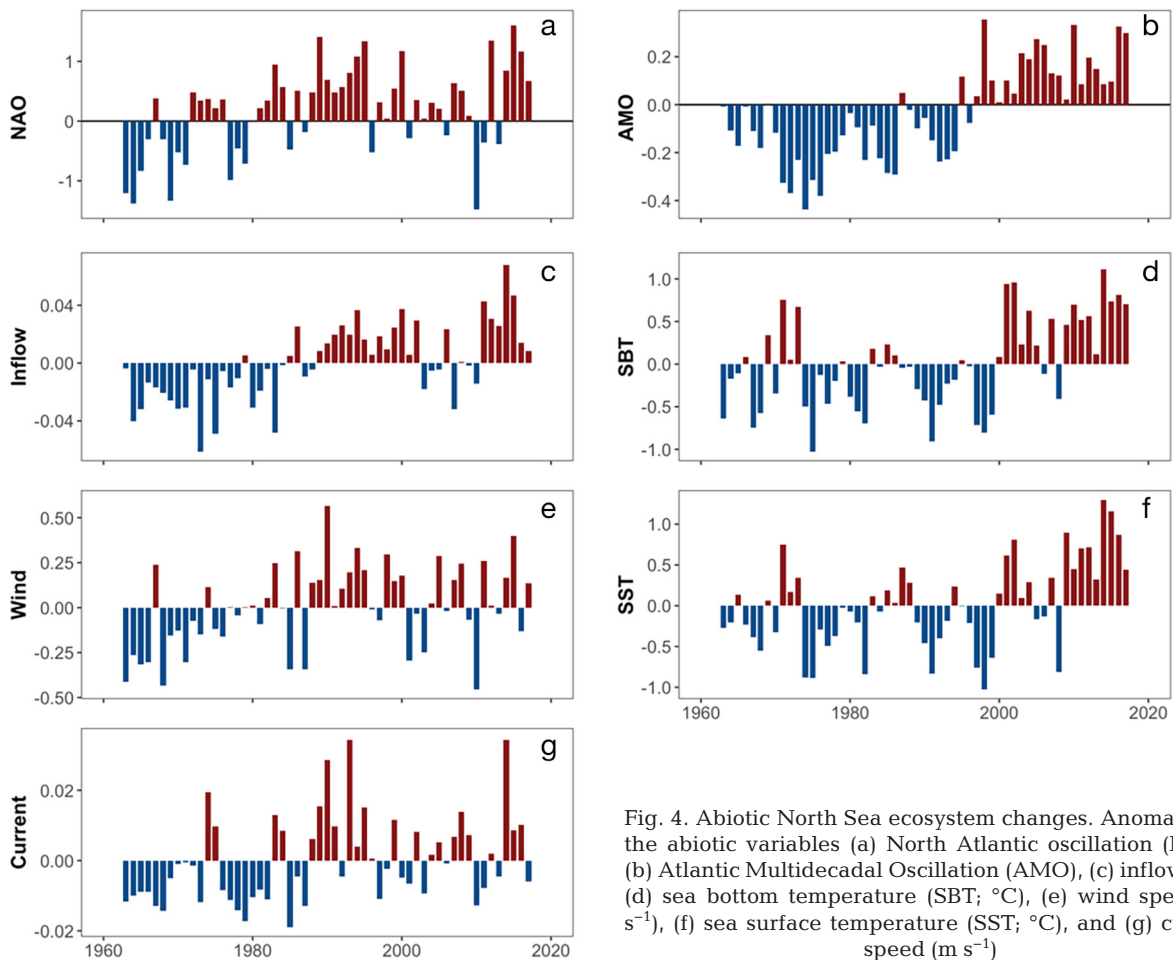


Fig. 4. Abiotic North Sea ecosystem changes. Anomalies in the abiotic variables (a) North Atlantic oscillation (NAO), (b) Atlantic Multidecadal Oscillation (AMO), (c) inflow (Sv), (d) sea bottom temperature (SBT; °C), (e) wind speed (m s^{-1}), (f) sea surface temperature (SST; °C), and (g) current speed (m s^{-1})

possible. These results show that SSB went through discontinuous dynamics, implying hysteresis.

In the next set of stochastic cusp models, we used indicators of abiotic and biotic variables as splitting factors to test how these indirectly interact with F to steer SSB dynamics (Fig. 6b–d). We identified 3 cusp models that show a similar pattern and highlight the importance of climatic influences such as wind magnitude and temperature through the overall PC2 (Fig. 6b) and SBT (Fig. 6d), which are strongly related to changes in NAO (Fig. 6c). In the first period, F and the climatic variables (overall wind speed, temperature, NAO) were low and SSB was high. Subsequently, F and the temperature, overall wind speed and the NAO index, representing stronger westerly winds, increased, whereas SSB reached slightly lower levels. Initially, the climatic variables continued to increase, F decreased and SSB resided in an unstable low state.

Our next model incorporated the interaction of large copepods (as important prey for cod develop-

ment) and F and their effect on SSB (Fig. 6e). During the first 2 periods, F increased, the levels of copepods remained high and SSB remained outside the cusp area. Subsequently, large copepods declined, F was reduced and SSB entered the cusp area. Here, again, SSB was trapped in an unstable state in the last period. All these models showed that SSB is presently in a low state and trapped in the unstable area.

Our first 4 models suggest that environmental drivers are important for the dynamics of North Sea cod and that low levels of R hinder the recovery of SSB. Thus, in a second set of models, we studied how environmental drivers affect R to determine the underlying causes that are keeping R low. First, we investigated the additional effect of PC1 (phytoplankton, inflow, NAO, large copepods) and PC2 (SBT, overall wind magnitude, SST) resulting from the common PCA of biotic and abiotic variables and SSB on R (Fig. 6f). The model showed an initial decrease of high SSB coupled with increases of the environmen-

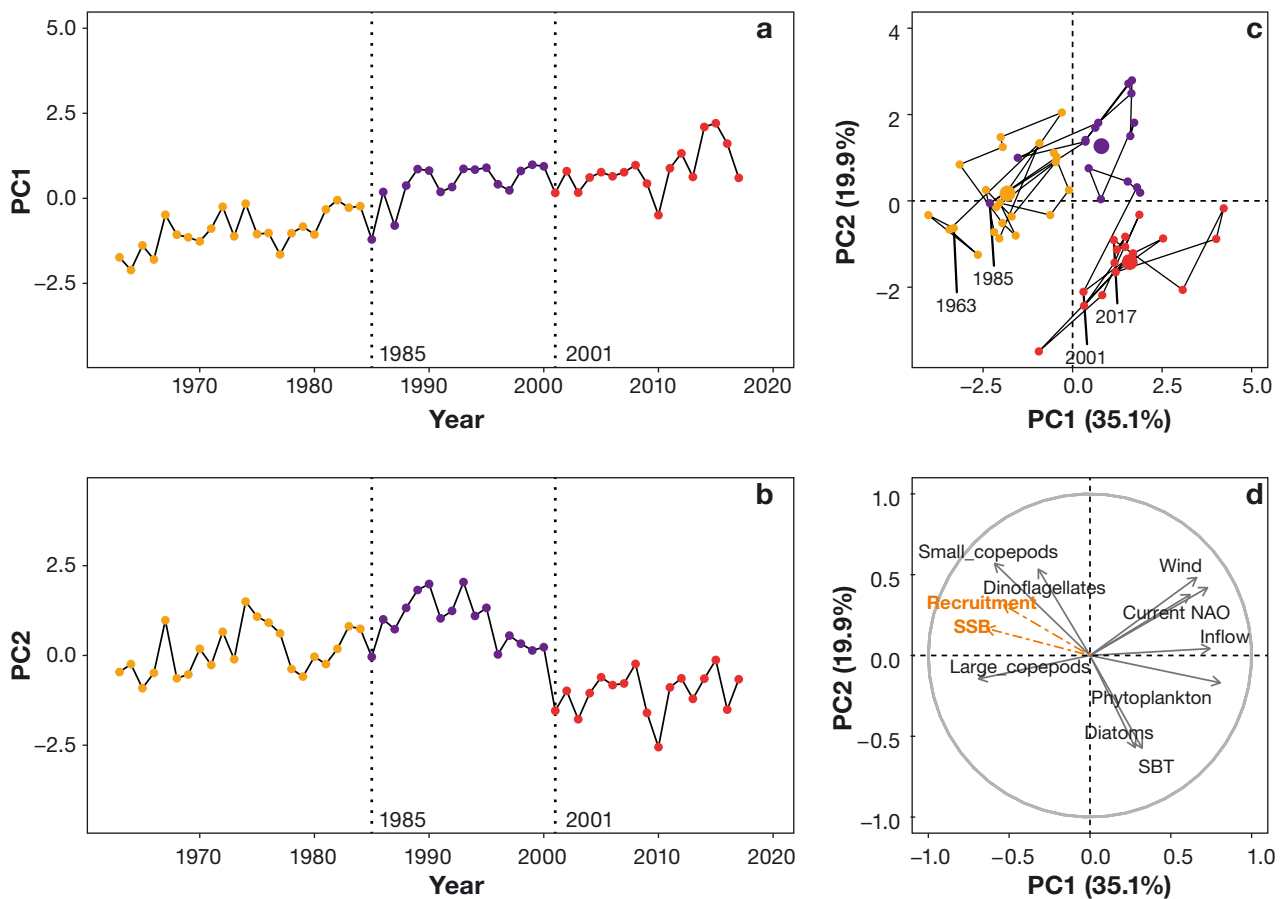


Fig. 5. Major trends in North Sea ecosystem dynamics. Results of principal component analysis (a) PC1 trajectory over time, (b) PC2 trajectory over time, (c) PCA individuals, (d) PCA variables (SSB: spawning stock biomass; SBT: sea bottom temperature; NAO: North Atlantic Oscillation; Phytoplankton [phytoplankton colour index]). SSB and recruitment are supplementary quantitative variables (orange); vertical lines in (a) and (b) indicate transitions between clusters identified by constrained clustering analyses in (c); cluster 1 in yellow (1963–1984), cluster 2 in purple (1985–2000), cluster 3 in red (2001–2017); icons represent main variables contributing to PC

tal variables, and decreasing R switching from outside the bifurcation area into the unstable bifurcation area. Within the last period, SSB levels increased slightly, whereas the PC variables increased further and R remained in the instability area.

The previous model highlighted that the interaction of abiotic and biotic variables caused changes in R dynamics. Subsequently, we studied the effect of changes in small copepods as possible effects on cod R since they are important prey items (Fig. 6g). At the beginning of the time series, small copepods were highly abundant, SSB was high and R was in the unstable area but was high as well. In the next period, both SSB and the abundance of small copepods decreased and R entered the stable area. In the last period, SSB increased slightly, the abundance of small copepods remained low and R was in the unstable area, close to the border of tipping towards

stability. This supports the results of the previous model and highlights that biotic and abiotic variables are relevant to model R , which underwent hysteresis and is, at present, in a very low state and inside the instability area.

4. DISCUSSION

In our study, we demonstrated that North Sea cod experienced regime shifts in SSB and R , including hysteresis, despite reduced F . Low cod R together with unsustainable fishing pressure caused a failed cod recovery. Our results also suggest that low R was the result of North Sea ecosystem changes at lower trophic levels, e.g. in phytoplankton and zooplankton productivity, due to climate-induced temperature rise and global changes. We demonstrated how

Table 2. Stochastic cusp model outcomes. Statistical results of selected cusp analyses; z_t : state variable; α : asymmetry parameter; β : bifurcation parameter; AIC: Akaike's information criterion; SSB: spawning stock biomass; R : recruitment; F : fishing mortality. The number of parameters were 4, 5 and 6 for all linear, logistic and cusp models, respectively

z_t	α	β	Model	AIC	Δ AIC	Cobb's pseudo- R^2	% within bifurcation area
SSB	F	Recruitment	Linear	1350.29	1228.75	0.36	36.36
			Logist	1346.54	1225	0.43	
			Cusp	121.54	0	0.50	
SSB	F	PC2 biotic and abiotic	Linear	1371.17	1249.63	0.06	50.91
			Logist	1366.35	1244.81	0.17	
			Cusp	143.03	21.49	0.54	
SSB	F	NAO	Linear	1367.10	1245.54	0.13	45.45
			Logist	1365.46	1243.92	0.19	
			Cusp	144.76	23.22	0.56	
SSB	F	SST	Linear	1365.23	1243.69	0.16	40.00
			Logist	1364.09	1242.55	0.21	
			Cusp	142.67	21.13	0.46	
SSB	F	SBT	Linear	1364.50	1242.96	0.17	36.36
			Logist	1365.67	1244.13	0.18	
			Cusp	138.46	16.92	0.35	
SSB	F	Large copepods	Linear	1359.96	1238.42	0.24	52.72
			Logist	1361.59	1240.05	0.29	
			Cusp	132.90	Nov 36	0.40	
R	SSB	PC1 + PC2 biotic and abiotic	Linear	1552.08	1453.61	0.43	83.33
			Logist	1547.09	1448.62	0.50	
			Cusp	98.47	0	0.58	
R	SSB	Small copepods	Linear	1560.96	1462.49	0.31	50.00
			Logist	1550.31	1451.81	0.45	
			Cusp	166.80	68.33	0.49	

changes in the ecosystem context can limit the recovery of an already depleted fish stock, impeding management measures, which is important information for ecosystem-based fisheries management.

Our analyses of the ecosystem components (environment and lower trophic levels, i.e. phytoplankton and zooplankton) confirmed the major regime shift identified in the North Sea during the 1980s (Fromentin & Planque 1996, Reid & Edwards 2001, Alheit et al. 2005, Edwards et al. 2013, Reid et al. 2016). The regime shift was caused by an increase in water temperature, also reflected by positive changes in the global climate indices NAO and AMO (Beaugrand et al. 2002). These changes affected and increased the overall wind magnitude from the west and the North Atlantic inflow, which influence the lower trophic levels such as phytoplankton and zooplankton in the North Sea (Fromentin & Planque 1996, Reid et al. 2001, 2003). Phytoplankton biomass increased substantially and changed from a diatom-dominated to a dinoflagellate-dominated assemblage (Beaugrand &

Reid 2003, Beaugrand 2004, Alheit et al. 2005, Reid et al. 2016). Shifts in phytoplankton combined with the increase in water temperature induced changes in the zooplankton community. Specifically, a temperature-induced increase in warm-water species and a decrease in cold-water species took place, and the phytoplankton increase induced a reduction in *Calanus finmarchicus* and an increase in *C. helgolandicus* abundance. The former is a major prey species for young cod, wherefore the regime shift in the 1980s was the first to be recognized as being related to Atlantic cod survival in the North Sea (Beaugrand et al. 2002, 2003). However, the association between the NAO and changes in *Calanus* species in the North Sea were only detected for the shift in the 1980s (Fromentin & Planque 1996). After the shift, a space–time decoupling took place for *C. finmarchicus* and the effect of increasing temperatures overshadowed the effects of the NAO, leading to favourable conditions for *C. helgolandicus* (Montero et al. 2021).

Our results add to earlier studies revealing regime shifts and hysteresis in North Atlantic cod stocks related to the interaction of fishing pressure and temperature changes (Sguotti et al. 2019, 2020, Möllmann et al. 2021). In addition to temperature as a proxy for climatic changes, we used distinct environmental and biological drivers in the models to understand why the North Sea cod remained in a low state. We found that SSB recovery is limited by the interaction of F and external abiotic and biotic dynamics such as increasing temperature and decreasing abundance of large copepods. Increasing temperatures play an important role for the life history traits of cod, causing faster growth rates and a decrease in age of maturity (Drinkwater 2005, Righton & Metcalfe 2019). In addition, fecundity and cod condition increase with increasing bottom temperature (Rose 2019). The SSB is currently trapped in a low state and, given expected further increases in external drivers such as water temperatures (IPCC 2022), the recovery potential of SSB is low.

We have also shown that cod SSB recovery depends strongly on R . R has been at low levels within

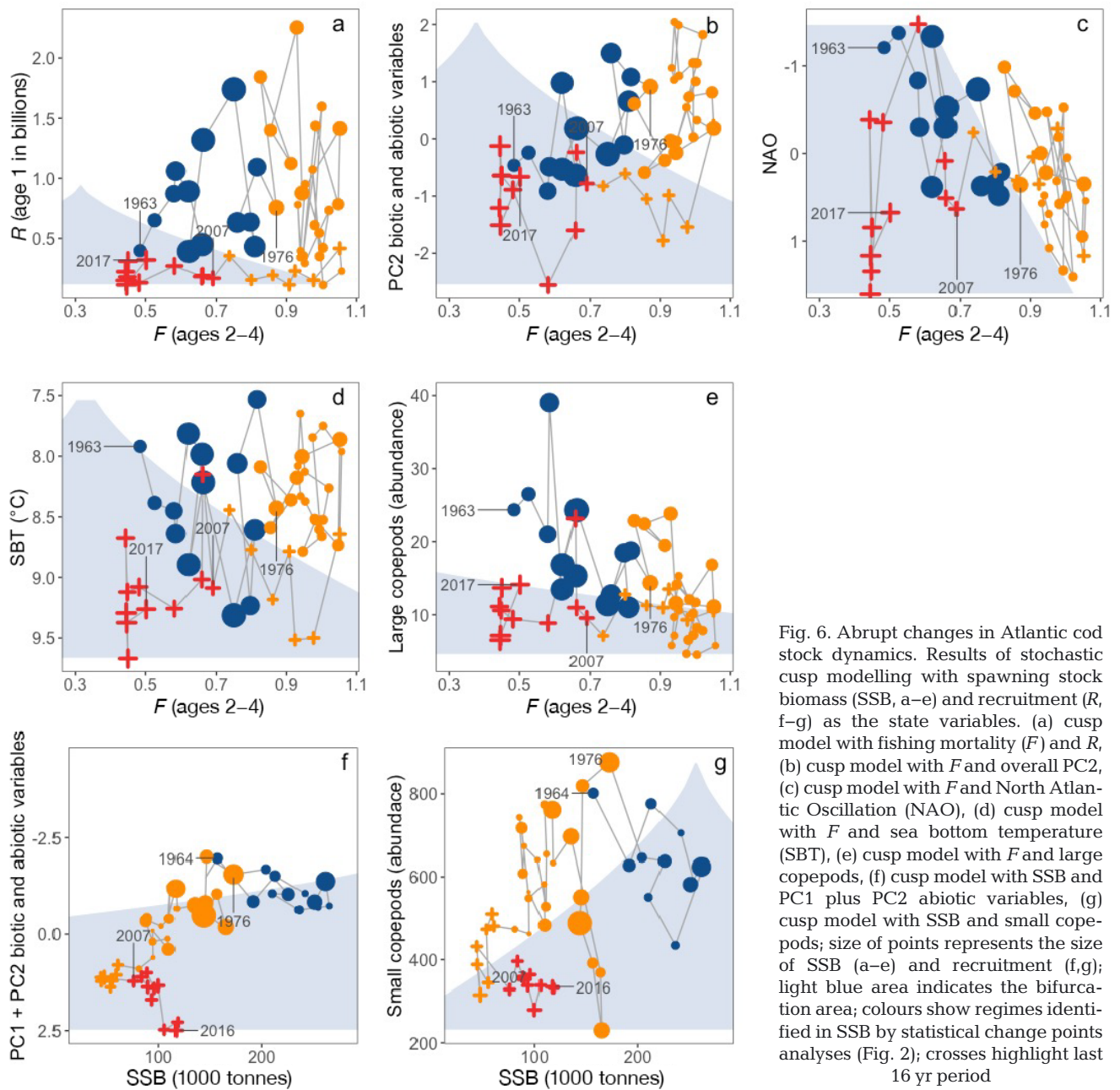


Fig. 6. Abrupt changes in Atlantic cod stock dynamics. Results of stochastic cusp modelling with spawning stock biomass (SSB, a–e) and recruitment (R , f–g) as the state variables. (a) cusp model with fishing mortality (F) and R , (b) cusp model with F and overall PC2, (c) cusp model with F and North Atlantic Oscillation (NAO), (d) cusp model with F and sea bottom temperature (SBT), (e) cusp model with F and large copepods, (f) cusp model with SSB and PC1 plus PC2 abiotic variables, (g) cusp model with SSB and small copepods; size of points represents the size of SSB (a–e) and recruitment (f,g); light blue area indicates the bifurcation area; colours show regimes identified in SSB by statistical change points analyses (Fig. 2); crosses highlight last 16 yr period

the unstable cusp area for 20 yr due to interactions between low SSB and increasing climate change effects. We found that not only did changes such as increases in wind speed (Stige et al. 2006) and sea temperature (Planque & Frédou 1999, Rindorf et al. 2020) related to the regime shift in the 1980s result in maintaining R in the low state, but also that an ecosystem shift in the 2000s hindered R recovery. The shift occurred due to warmer sea temperatures and an associated change from a dinoflagellate-dominated to a diatom-dominated phytoplankton community. In con-

trast to Lynam et al. (2017), who reported a decrease in diatoms given increased phytoplankton and decreased large copepods, we saw that an increase in diatoms is associated with increasing positive temperatures (AMO) and decreasing abundances of small copepods. The decrease primarily reflects a reduction in dinoflagellates, which are an important food source for small copepods (Alvarez-Fernandez et al. 2012). These changes in lower trophic levels have severe consequences for cod R . Given cascading effects through the food web, increased temperatures

not only cause a prey mismatch between prey size and young cod (Beaugrand et al. 2003) but also changes in the distribution and the abundance of prey (Righton et al. 2010). Hence, increasing temperatures affect cod larvae indirectly through changes in prey abundance and directly through reduced egg survival and reduced larval growth (Rose 2019).

Under more favourable environmental conditions, such as lower temperatures, these cascading effects could reverse, and R could increase to favour a recovery of the stock. In addition, the chance for recovery can be enhanced by further decreases in F . Environmental stressors have strong bottom-up effects in open ecosystems (Conversi et al. 2015), but the top-down impact of fisheries is stronger in benthic systems where cod are abundant (Kenny et al. 2009). Hence, reducing fishing further or even implementing a fishing ban for cod may push SSB into a stable area with higher SSB levels, and further declines in the stock could be prevented.

We have demonstrated the potential of the stochastic cusp model approach to consider interactions between abiotic and biotic drivers and hence broaden the understanding of underlying reasons causing limited recovery of North Sea cod. Our study has limitations, given known uncertainties within the stock assessment data we used (Sguotti et al. 2019). The stochastic cusp model approach is increasingly being applied in various scientific disciplines (Grasman et al. 2009, Diks & Wang 2016). It has only recently been used in ecology and, even more recently, applied in fisheries science (Sguotti et al. 2019, 2020, 2022, Möllmann et al. 2021). The approach requires improvement to account for autocorrelation in time series data, which is difficult due to the nature of the stochastic cusp model, which initially fits external variables to the asymmetry parameter, splitting and state variable before the potential function is fitted (Grasman et al. 2009). Furthermore, model comparison given uncertainties using AIC and Cobb's pseudo- R^2 needs to be improved (Sguotti et al. 2019). In our case, AIC and Cobb's pseudo- R^2 were always best for the cusp model outcome.

Here, we studied Atlantic cod in the North Sea as one stock and did not distinguish between the 3 sub-populations (Romagnoni et al. 2020). However, North Sea cod populations are affected differently in the different areas. In particular, the cod population in the southern North Sea is more negatively affected by changing temperatures given different preferences in the thermal niches between southern and northern cod (Righton et al. 2010). The increases in temperature result in a northward shift of the south-

ern boundary of cod and hence a decrease in its distribution area (Baudron et al. 2020). The combined effect of fishing pressure and temperature led to changes in the fish community's functionality in general, supporting an increase of functionally distinct species mainly in the south and an increase of functionally common species in the north (Murgier et al. 2021). The study of discontinuous dynamics in the spatial sphere of cod is novel and, hence, a useful approach to improve the understanding of North Sea cod dynamics and the North Sea fish community.

Finally, our study indicates that North Sea cod experienced non-linear discontinuous population dynamics. Despite decreased fishing pressure, climate-change-induced, long-term impacts have enhanced the effects of abiotic and biotic drivers on the stock and increased the likelihood that the stock will not recover. SSB and R underwent regime-shift-like, non-linear discontinuous dynamics and will likely stay in a state with low SSB and R and low resilience (Lotze et al. 2011). The definition of cod recovery includes an 'increase towards a specific target', corresponding to the MSY level in EU waters (Lotze et al. 2011). To reach the MSY, management at the EU level, which incorporates sustainable fishing at ICES reference levels, is required (ICES 2012b). Additionally, it is fundamental to understand discontinuous dynamics in fisheries management to prevent abrupt failures given linear management approaches. Decision-makers need to decide whether the newly reached state and its implications are desirable for the whole socio-ecological system depending on North Sea cod. Knowing that a new state is potentially irreversible, policies sustaining the new state should be put in place, rather than trying to restore it (Sguotti et al. 2022). Moreover, management is required to consider abrupt changes related to climate change, especially given the steady increase in ocean warming in the North Sea (IPCC 2022). Identifying regime shifts and tipping points indicate thresholds of driver effects, e.g. sea temperature, which could favour the implementation of policies avoiding shifts (Sguotti et al. 2022). Even though F was reduced greatly, cod did not recover due to profound and abrupt ecosystem changes and probably changes in prey species composition.

Management goals to 'increase towards a specified target', such as biomass towards an MSY level, should be implemented to enhance the restoration of a system to a more natural, robust or pristine structure (Lotze et al. 2011). Similar to cod, other North Sea species might experience abrupt discontinuous dynamics due to overfishing and climate change.

Hence, we highlight the importance of incorporating discontinuous dynamics in fisheries management approaches to achieve sustainable exploitation levels and to identify thresholds of drivers to favour policies that prevent regime shifts.

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