A novel multispecies approach for the detection of ~~ecosystem~~ regime shifts in a plankton community - a case study in the North Sea

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Abstract.

The physical environment both above and below the ocean surface has changed dramatically during the last century. Changes in the marine environment induced by increased release of greenhouse gases and direct exploitation of resources include increased ocean temperature, decreased salinity and pH, and removal of apex-predators. The risk of ecological regime shifts occurring has similarly increased. A variety of methodologies to predict regime shifts have already been used in the North Sea, which has become an important case study for the analysis of regime shifts in a semi-enclosed water body. The North Sea is regarded as a case study in part due to the operation of the continuous plankton recorder, which has provided detailed abundance records of phyto- and zooplankton for over 60 years. Here, we propose a new methodology to calculate regime shift likelihood for every month between 1958 and 2020. This ~~methodology is unique as the model described~~ unique model produces a single time series of regime shift likelihood, using sequential abundance data of more than 300 plankton species. We show the model's ability to identify when regime shifts occurred in the past by comparing it to previous, less automated methodologies. We have validated the model for use in the North Sea by estimating how often false positives and false negatives are generated. Results from the model indicate evidence for three periods of high regime shift likelihood in various parts of the North Sea: between 1962 and 1972, between 1989 ~~until~~ and 1999, and ~~between~~ from 2002 until 2015. We show that these periods are consistent with previous estimates of North Sea regime shifts, and discuss possible applications of the model's output of a single time series.

1 Introduction

~~In 2024, the International Commission on Stratigraphy voted against the proposal to define the Anthropocene as a new geological epoch which began in 1952 (Zalasiewicz et al., 2024). Although a contentious decision, it is generally agreed that our global environment is changing.~~ The global ocean ~~is fundamental~~ plays a critical role in regulating climate on Earth ~~, but the marine environment can experience dramatic changes associated with increasing global mean temperatures. Potential modifications to~~ through heat and carbon redistribution. Global mean ocean temperature has increased since the Industrial Revolution, potentially inducing extreme events (IPCC, 2019). Changes in the oceanic environment ~~include increased incidence~~

~~of~~ associated with long-term temperature increase include more frequent marine heatwaves (Oliver et al., 2018, 2019), decreased

25 pH (Doney et al., 2009), loss of oxygen concentration (Heinze et al., 2021; IPCC, 2019), and changes to large scale ~~ocean~~ circulation patterns such as the Atlantic Meridional Overturning Circulation (AMOC) (Johnson et al., 2020; Robson et al., 2014), ~~changes to ocean~~ salinity (Curry et al., 2009; Skliris et al., 2014), ~~changes to~~ and stratification stability in the upper ocean (Hallegraeff, 2010; Sharples et al., 2006; Wells et al., 2020)~~, decreased ocean pH (Doney et al., 2009), and loss of oxygen content~~. The projected rate of ocean warming, acidification, and oxygen concentration ~~depend strongly~~ is strongly dependent on the rate

30 of greenhouse gas emissions (Kwiatkowski et al., 2020; Schmidtko et al., 2017). ~~This realization led to an attempt to reduce the impact anthropogenic influences are having.~~ In 2017, signatories to the Paris Climate Agreement agreed therefore to limit global temperature increase to less than 2 °C by the end of the 21st Century (Fox-Kemper et al., 2021). At current emission rates, it is likely that we will exceed these limits by 2050 (Fox-Kemper et al., 2021), which will potentially lead to the crossing of planetary boundaries~~and tipping points~~, tipping points and ecological regime shifts (Heinze et al., 2021; Rocha, 2022).

35 ~~Ecological regime shifts (hereafter called regime shifts) are somewhat analogous to tipping points in physical systems. Similar to tipping points, regime shifts are~~ Regime shifts are characterized by large, abrupt and persistent ~~change~~ changes in the function and structure of an ecosystem ~~(Scheffer et al., 2001; Reid et al., 2016). They~~ that are not easily reversible (Scheffer et al., 2001; Reid et al., 2016). Such reorganizations of the ecological system can be, but are not always, preceded by dynamics such as critical slowing down (Scheffer et al., 2001; Scheffer, 2009; Wouters et al., 2015). Regime shifts ~~are~~

40 ~~notoriously difficult to identify in~~ preceded by critical slowing down are associated with an erosion of dominant feedback mechanisms until a critical threshold, the so-called tipping point, is crossed (Biggs et al., 2018). Regime shifts are ecologically important, in part due to the possible presence of hysteresis or non-reversibility of changes (Sguotti et al., 2022). In open ocean systems ~~due to the need for time series~~of sufficient length and quality data collection ~~(Haines et al., 2024; Rudnick and Davis, 2003; Beaugr~~ regime shifts are notoriously difficult to identify (Haines et al., 2024; Rudnick and Davis, 2003; Beaugrand, 2004b; Scheffer et al., 2001)

45 , because statistical significant estimates of biodiversity changes require sufficiently long time series. For example, ~~evidence for several regime shifts has been identified in the~~ it is recommended that at least 50 years of measurements are needed to detect ecological changes driven by changing climate conditions, including regime shifts (Edwards et al., 2010), though there are studies which have used a shorter time frame (Hare and Mantua, 2000). Regime shifts in marine systems have therefore been documented most often in regions where in situ measurements and remote sensing data are relatively abundant, such as the

50 Northeast Pacific Ocean (Hare and Mantua, 2000), ~~the North Sea (Beaugrand and Reid, 2003; Edwards et al., 2001; Beaugrand et al., 2014; , and~~ along the Norwegian coast (Vollset et al., 2022)~~. However, there is considerable controversy~~, and the North Sea (Beaugrand, 2014; Djeghri et al., 2023; Beaugrand and Reid, 2003; Edwards et al., 2001; Sguotti et al., 2022). In fact, the North Sea has become a case study for detecting regime shifts in marine environments. The North Sea has undergone monitoring by the continuous plankton recorder (CPR), which constitutes one of the longest marine ecological time series, and diligent fishery

55 records. Despite this, considerable controversy remains around the identification of ~~these~~ regime shifts. ~~Numerous studies have found present~~

Abrupt changes in the abundance of a single species may be indicative of either a regime shift, which may be seen in multispecies communities and ecosystems, or representations of decadal variability. Different regime shift identification

methods are often applied to ecological or physical systems, but autocorrelation and critical slowing down signals have been

60 detected in both systems (Overland et al., 2006; Scheffer et al., 2001; Rudnick and Davis, 2003; Haines et al., 2024). In order to differentiate the presence of multiple climatic stable states from multidecadal fluctuations, Overland et al. (2006) applied different statistical signals, including white and red noise, to the context of regime shift identification. Classical detection methods have ~~falsely identified~~ been shown to falsely identify regime shifts in simulated time series data of species abundance, to which red noise ~~has~~ had been introduced (Haines et al., 2024; Rudnick and Davis, 2003). ~~Despite the ecological importance~~

65 ~~of regime shifts, in part due to the possibility that they are non-reversible (Sguotti et al., 2022), there is a need to demonstrate the robustness of identification methods.~~

~~Correctly identifying and simplifying~~ A correct and simple identification of regime shifts is crucial for ~~prediction and~~ future management of ecosystems~~and our interaction with them.~~. Previous studies have often focused on periods where specific species experienced an abrupt shift (Alvarez-Fernandez et al., 2012; Beaugrand, 2014; Djeghri et al., 2023; Reid et al., 2001; Vollset et al.,

70 , which can be identified using split-moving window boundary analysis (Alvarez-Fernandez et al., 2012; Beaugrand, 2014) or change-point analysis algorithms (Boulton and Lenton, 2019; Arellano-Nava et al., 2022).

In our study, we apply a specific change-point analysis algorithm to a group of species at once, in order to create a single time series of regime shift likelihood. Producing a single time series of regime shift likelihood must necessarily remove context. This is a major difference from previous methods like the split-moving window boundary analysis (Alvarez-Fernandez et al., 2012; Beaugrand, 2

75 or exploration of principle component analysis (Djeghri et al., 2023), which were concerned with indicating which species or functional groups were changed with apparent regime shifts. An advantage of new approach over previous methods is that construction of a single time series of regime shift likelihood can be the first step towards exploring potential drivers through linear analysis.

Knowledge of ecosystems requires reliable ~~abundance~~ time series from ~~(preferably)~~ preferably more than one trophic level,

80 for as many years as possible (Edwards et al., 2010; Wouters et al., 2015). Regime shifts in plankton are often detected in higher trophic levels first, despite signals possibly being present in lower trophic before (Reid et al., 2001; Vollset et al., 2022; Beaugrand, 2014). More data from higher trophic levels can be used to identify whether a system is controlled from the bottom up or through other means (Di Pane et al., 2022; Fauchald et al., 2011). Due to their relatively short lifespans and rapid generation time, planktonic organisms are especially useful for studying ecological responses to changing conditions in both the recent (Bowler

85 et al., 2010; Beaugrand, 2004b; Djeghri et al., 2023) and ancient past (Strack et al., 2022; Lowery et al., 2020). The idea of using plankton as a "canary in the coal mine" to provide early warnings of wider regime shifts is not unique (Bowler et al., 2010). For example, it has been well documented using ~~continuous plankton recorder (CPR)~~ CPR data that a regime shift occurred in the North Sea between the years of approximately 1982 and 1988, evidenced by the sudden change in abundance of calanoid copepods *Calanus finmarchicus* and *Calanus helgolandicus* (Beaugrand and Reid, 2003; Reid et al., 2016, 2001).

90 ~~Questions around methods used to identify regime shifts (Haines et al., 2024; Rudnick and Davis, 2003), and whether or not~~ Some studies have suggested a change in ~~plankton necessarily~~ the plankton community impacted higher trophic levels or ecosystem function~~(Djeghri et al., 2023; Reid et al., 2001) remain~~, but not all agree (Djeghri et al., 2023; Reid et al., 2001).

In our study, we have analyzed multiple time series of plankton abundance simultaneously. We here describe the process of generating a single time series representing the likelihood of a regime shift occurring at any point represented by the time series. The aim of designing a new automated methodology for detecting regime shifts was not simply to add to the growing list of statistical methods and models ~~used (see Beaugrand et al. (2014); Djeghri et al. (2023); Haines et al. (2024)~~ already in use (see Alvarez-Fernandez et al. (2012); Beaugrand et al. (2014); Djeghri et al. (2023); Haines et al. (2024)). The ~~key innovation of our approach lies in its ability to analyze multiple time series of plankton abundance simultaneously, and generate a single ecosystem time series representing~~ method described here does not necessitate the user to identify particular species of interest before analyzing a dataset, but rather uses all species in a dataset to estimate the likelihood of a regime shift occurring~~at any point represented by~~ . Figures can be made showing the time series ~~. This feature is particularly valuable for users who may lack detailed knowledge of~~ of species abundance showing the greatest difference in abundance over time, and which therefore likely contributed most to regime shift probability being high. These features are particularly valuable if the planktonic ecological history of the study area is not well known. We applied the new regime shift identification method to four areas of the North Sea. The method indicated regime shifts during periods and showed causative species were likely consistent with those found by previous methods. We discuss advantages and limitations of the new method, as well as possible future uses~~. By synthesizing these complex data into an accessible format, our method provides a practical tool for assessing ecosystem dynamics and detecting regime shifts in data-rich systems. We here describe a model which reduces a planktonic ecosystem to one time series, as a first step to designing an early warning system of regime shifts for the 21st Century.~~

2 Methods

2.1 Study area

The study area is comprised of the ~~CPR sampling areas bound by the~~ marine environment within 50° and 65° N and ~~-10~~10° W and 8° E (Fig. 1). Using ~~official~~ CPR sampling areas (also utilized by Montero et al. (2021); Alvarez-Fernandez et al. (2012); Djeghri et al. ( ) to search for evidence of regime shifts has been done previously, and allows results of our approach to be compared to other ~~methods (see Montero et al. (2021); Alvarez-Fernandez et al. (2012); Djeghri et al. (2023))~~previous results.
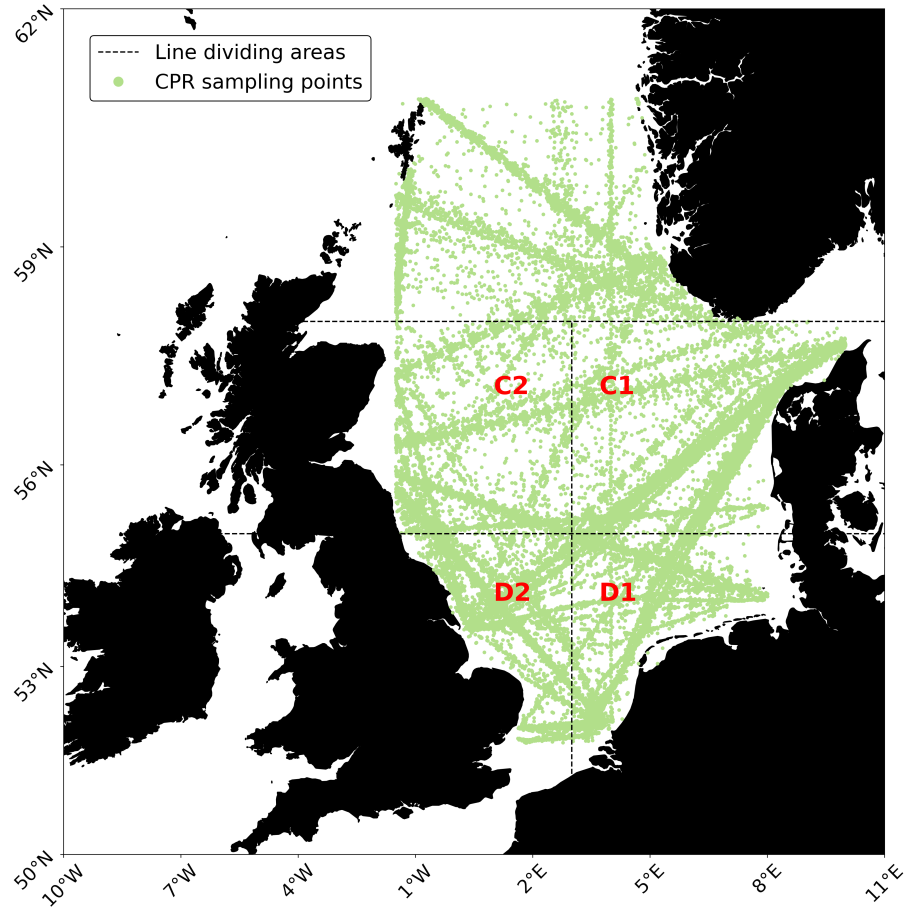
Figure 1. The North Sea study area with sampling points displayed in green, and CPR ~~official~~ areas C1, C2, D1 and D2 denoted by dashed lines and area names in red. Map was built using Met Office (2010 - 2015)

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2.2 ~~CPR~~ Ecological data

Abundance data concerning phytoplankton and zooplankton from 1958 until 2019 were obtained from the CPR (see Reid et al. (2003) for detailed methodology). ~~Seasonality trends of abundance time series of~~ Abundance data from the CPR for the over 200 phytoplankton species and ~~over~~ 80 zooplankton species ~~captured by the CPR were removed by converting~~ are given in captured organisms per 10 nautical miles of towing (Reid et al., 2003). Removing the seasonality trends of these data was accomplished by converting abundances into monthly anomalies for each year using Eq. 1 and Eq. 2.

~~A logarithmic transformation was applied to all time series captured by the CPR, excluding the phytoplankton color index~~ Because the CPR survey is conducted by ships of opportunity, data from the CPR are highly variable in spatial and temporal resolution (Reid et al., 2003; Richardson et al., 2006). Sampling devices are towed behind ships at an average depth of 7 m, but this is also variable. There are some groups of plankton which are not routinely collected by the CPR survey, primarily large zooplankton (Marques et al., 2024) and some smaller species of phytoplankton (Richardson et al., 2006; Mengs et al., 2024). However, the distance covered and the period of operation provided by the CPR survey is unmatched by other plankton datasets, and is thus a highly valuable source of ecological data (Beaugrand, 2004a; Beaugrand et al., 2014; Djeghri et al., 2023).

The Phytoplankton Color Index (PCI) ~~, which is the~~ is a logarithmic graded color scale estimated by the ~~Sir Alister Hardy Foundation for Ocean Science (SAHFOS) group. The~~ CPR Survey Group, and has been been used as a proxy for chlorophyll concentration (Beaugrand, 2014; Reid et al., 2003). The PCI is a color scale completely separate from phytoplankton cells counted per sample, although high cell counts are likely correlated with high PCI. A logarithmic transformation was ~~applied before the mean abundance was calculated. The~~ also applied to phytoplankton and zooplankton species captured by the CPR (Eq. 1), before mean abundance was ~~then calculated using the equations:~~ calculated (Eq. 2):

$$x' = \log_{10}(x_i + \frac{cm}{2} \frac{LOQ}{2})$$ (1)

where x is the species abundance as measured by the CPR at time point i and ~~cm~~ LOQ is the CPR limit of quantification, ~~and~~ a constant of 20 cells per 10 nautical mile sample. The logarithmic transformation was applied to reduce the strong seasonal contrasts in abundance, particularly during bloom periods, and to stabilize variance across time series. This approach is commonly used for plankton data, where values can span several orders of magnitude (Djeghri et al., 2023; Beaugrand et al., 2014; Bedford. Logarithmic transformation necessitates the additional manipulation of adding half the limit of quantification to avoid calculating logs of zero. Changing original data in two ways instead of one, such as in square root transformations, is not ideal but logarithmic transformations were chosen because of the exponential difference in seasonal range observed in plankton abundance data, and due to its use in previous studies (Beaugrand et al., 2014; Dees et al., 2017).

Mean abundance at each time step was calculated using Equation 2, which also removed the seasonality signal from abundance time series:

$$\Delta x(t) = x(t) - \overline{x}_m$$ (2)

where: $\Delta x(t)$ is the mean abundance anomaly at year-month t which includes every month of every year between ~~1950~~ 1958 and 2019. $x(t)$ is the mean abundance of each species after the transformation detailed in Eq. 1 has been applied, calculated over time step t. $\overline{x}_m$ represents the mean abundance when the month m is the same as t, but calculated over all years.

150 ## 2.3 Detection and identification of regime shifts

~~We develop here a method that builds on the approach introduced by Boulton and Lenton (2019)~~The regime shift detection algorithm implemented here follows the method described by Boulton and Lenton (2019). Boulton and Lenton (2019)'s method was designed for use on detrended data, which required the removal of a seasonal signal from abundance time series (see Eq. 2). Converting raw data into logarithmically transformed anomalous means using Eq. 1-2 is a necessary step before detecting
155 abrupt shifts, as described in the following section. There is a risk that important features of the dataset, such as maxima and minima, are removed with this transformation. This is likely to result in more conservative estimates of abrupt changes in abundance. The largest driving force of plankton abundance throughout the year in temperate oceans is seasonality, but this was not the primary concern of this study. This model may not be suitable for identification of regime shifts exhibiting as changes to phenology, or the timing of phytoplankton blooms.

160 The core idea behind this approach is to detect anomalous rates of change in a time series, based on the premise that regime shifts correspond to unusually steep increases or decreases in the gradient over short periods. The algorithm begins by dividing the time series into fixed-length, ~~which detects abrupt shifts in individual time series by identifying anomalous~~ non-overlapping segments. Within each segment, a simple linear regression is applied to estimate the slope, representing the local rate of change. These slopes are then compared across all segments. To identify anomalous trends, the algorithm calculates the median slope
165 and the median absolute deviation (MAD). Slopes that deviate from the median by more than three MADs are flagged as anomalous. In this context, linear regression is used solely to quantify rates of change; since no statistical inference is involved, assumptions such as normality and homoscedasticity are not required (Schmidt and Finan, 2018). We adapted and refined the Python version (Arellano-Nava et al., 2022) of this method to estimate the likelihood of a regime shift across multiple species and trophic levels, presenting the results as a single time series. Our approach is referred to as the RST (Regime Shift Time-
170 series) model throughout this paper.

~~The algorithm published by Boulton and Lenton (2019) divides a time series into fixed-length, non-overlapping segments.~~ ~~For each segment, a linear regression is applied to calculate the rate of change. Rates that fall outside three median absolute~~ ~~deviations from the median of all slopes are deemed anomalous.~~ To track these anomalies, a ~~new detection~~ regime shift indicator time series is ~~created, initially filled with zeros, where each position corresponding to an anomalous rate is incremented or~~
175 ~~decremented by one~~ initialized with zeros. At each time step corresponding to the center of an anomalous segment, the indicator is updated with +1 (for a steep positive slope) or -1 (for a steep negative slope). This process is repeated ~~for various~~ across ~~a range of~~ segment lengths, from a user-defined minimum to a maximum of one-third of the ~~original time~~ total series length. ~~Finally, the resulting values are~~ The cumulative indicator values are then divided by the number of segment lengths used, ~~producing an~~ yielding a continuous regime shift likelihood index ranging from ~~-1~~ -1 to 1. ~~The algorithm thus returns a time~~
180 ~~series of regime shift likelihood indices, with each value indicating the likelihood of a regime shift occurring at that point in~~

~~the original time series: a result of~~ Values near 0 ~~suggests~~ suggest a low likelihood of abrupt ~~shifts~~change, while values ~~close to -1~~ approaching -1 or 1 indicate a high ~~probability of an abrupt change occurring at that point. Negative or positive numbers show whether the change is a decreasing or increasing trend~~likelihood of a regime shift, with the sign reflecting the direction of change.

We applied this single-series regime-shift detection algorithm to identify abrupt changes on each species across the entire ~~planktonic ecosystem~~ plankton community from the CPR dataset. The RST model is able to identify abrupt changes when assessing time series with regular time steps. This required the CPR dataset to be converted to a time series of mean anomaly abundances for each month in every year that the CPR has been in operation (see section 2.2). Regime shift likelihood time series were generated for the logarithmically transformed time series of mean abundance per month per year ($\Delta x(t)$) and logarithmically transformed time series of zooplankton abundance anomaly. The resulting time series indicates the likelihood of an abrupt change occurring at each time step for each species of zooplankton and phytoplankton captured by the CPR.

A low-pass filter was applied to abrupt change likelihood time series of each species. Distinct abrupt changes for species were determined by the abrupt shift likelihood exceeding the mean and standard deviation of the entire abrupt change likelihood time series. After an abrupt change was identified, Eq. 3 was used to check if the mean abundance of the species was different after the abrupt shift:

$$-2\sigma_A < (\bar{x}_0 - \bar{x}_1) < 2\sigma_A \tag{3}$$

where $\bar{x}_0$ and $\bar{x}_1$ are the mean abundance of species before and after an abrupt change, respectfully, as determined by Boulton and Lenton (2019)'s algorithm~~, respectively~~. The low-pass filter removed abrupt changes from the results if the mean abundance before and after a supposed abrupt shift did not differ by at least two standard deviations.

Next, we constructed a probability table to estimate the probability of an ~~ecosystem-wide abrupt change being detected~~ abrupt change for the entire sampled plankton community at each time point. For each species analyzed, the standard deviation of the regime shift likelihood time series was calculated. We then applied a series of weights to the likelihood of a regime shift occurring at every time step throughout the study period.

A rolling mean with a window length of 24 months was applied to the ~~time-series~~ time series of abrupt shift likelihood, for each species. The length of this rolling window was chosen because changes in the phytoplankton community are assumed to influence the zooplankton community (Capuzzo et al., 2018; Marques et al., 2024) and we assumed that two annual cycles would be long enough to capture this influence. After making this assumption, a series of figures were made to test the effect of iteratively changing the number of months in the rolling window. The code provided here allows the user to explore alternative rolling window lengths, and we encourage future studies to do so (see Supplemental Material).

Weights, based on the duration of sustained anomalies, were added to the relative importance of the ~~abrupt shift likelihood time series if the time series~~ time series of the likelihood of abrupt change if the time series exceeded one absolute standard deviation for an extended period (~~see~~ Eq. 4). This meant the added weight grew exponentially for species where standard deviation was exceeded for a longer time over the course of a ~~24 month~~ 24-month rolling window. Sustained deviation away

from a beginning point ~~therefor~~ therefore had a greater effect than sudden changes which did not last longer than five months:

$$w = \begin{cases} 1 & \text{if } n < 5 \\ 2 & \text{if } 5 \leq n < 10 \\ 4 & \text{if } 10 \leq n < 20 \\ 10 & \text{if } n \geq 20 \end{cases} \tag{4}$$

Here, n is equal to the number of times the probability of an abrupt change was greater than one standard deviation away from 0, and w is the weight added to the total probability of a regime shift occurring. Again, the weights added in this study assume bottom-up control of North Sea plankton populations, as found by previous studies (Marques et al., 2024; Capuzzo et al., 2018). Not all plankton populations are bottom-up controlled. Regime shifts may sometimes be caused by removal of predators (Eklöf et al., 2020), and we encourage future studies to explore modifying the weights described here.

These weighted series were then summed across species to generate community-level indices for zooplankton ($P_{zoo}(t)$) and phytoplankton ($P_{phy}(t)$). The total probability of ~~an ecosystem regime shift was~~ a regime shift in the plankton community was then calculated by adding the probability of an abrupt change in phytoplankton and zooplankton together.

$$P_{RS}(t) = P_{zoo}(t) + 2 \sum_{t-23}^{t} P_{phy}(t) \text{ x } P_{zoo}(t) \tag{5}$$

Here, $P_{RS}(t)$ is the total probability of ~~an ecosystem-wide regime shift~~ a regime shift in the plankton community at time t, $P_{zoo}(t)$ is the summed abrupt change likelihood for all zooplankton species at time t, and $\sum_{t-23}^{t} P_{phy}(t)$ is the summed abrupt change likelihood for all phytoplankton species between time t and the previous 23 months. ~~Following previous studies determining that zooplankton populations are controlled by~~ The product $P_{phy}(t) \times P_{zoo}(t)$ captures co-occurring abrupt changes in both phytoplankton and zooplankton, reflecting potential bottom-up ~~processes (Capuzzo et al., 2018; Marques et al., 2024), here we assume that~~ propagation of regime shifts. Doubling this interaction term emphasizes the influence of phytoplankton variability on zooplankton dynamics within a 24-month window. We reiterate that the relative strength of bottom-up controls (Di Pane et al., 2022) and wasp-waist controls (Fauchald et al., 2011) on zooplankton in the North Sea is debated. However, we here assume a change in phytoplankton could induce sustained changes in zooplankton, ~~allowing~~ which allowed us to quantify $P_{RS}(t)$.

Adding the chosen weights (Eq. 4), and including results from the previous ~~23~~ 24 months of the phytoplankton probability time series, means that results from the first two years of the RST time series will be inaccurate (see Supplemental Material). We encourage future studies to explore different ways of calculating $P_{RS}(t)$, and how $P_{RS}(t)$ changes under greater top-down control.

The time series of regime shift likelihood for all species was then converted into a percentage, so as to force the weighted scores for regime shift likelihood into a comparable estimate. Making RST model output a percentage means the estimated likelihood of a regime shift always reaches 100, even if the pre-percentage likelihood remains relatively low. This is an important limitation of the RST model, and must be taken into account when interpreting output which does not appear to

vary for extended periods of time. In order to allow for a degree of uncertainty around the estimated percentage likelihood of a regime shift, the absolute deviation around the mean percentage was also calculated at each time step. The results of this time series were plotted with the PCI, used as a proxy for chlorophyll concentration, and the two most abundant phytoplankton and zooplankton species.

The model code allows the user to choose whether regime shifts are indicated when the percentage change of a regime shift occurring rises above a chosen threshold, or when the rate of change in percentage likelihood increases above a chosen threshold in too short of a time period. In the present study, we opted to indicate possible regime shifts ~~when the threshold of a higher gradient change than~~ using the critical gradient of 20~~% was exceeded~~%. We here define a critical gradient as the change in percentage likelihood of a regime shift occurring between months. The choice to use a critical gradient to identify regime shifts was made because the percentage likelihood of a regime shift can remain above 50-60% for prolonged periods when abrupt changes are induced in only a small percentage of species (see Fig. 2). Large changes in regime shift likelihood are more indicative of abrupt changes occurring in multiple species simultaneously. ~~This choice can have potentially important implications, and will be discussed in Sections and .~~We chose to use the critical gradient of 20% in the present study, as validation tests indicated this resulted in an acceptable balance between false positive and false negative rates (Fig. 8). The limitation of the RST model producing time series that always reach 100% has thus been mitigated somewhat.

3   Validation of the model

In order to validate the RST model for its ability to detect regime shifts, a series of realistic data frames ~~were~~ was constructed and subsequently analyzed. The RST model was designed to convert time series data into monthly mean anomalies. In validation tests this function was removed, and anomalous monthly means of species abundance were simulated using Eq. 6:

$$x(t) = \alpha(x(t-1) \text{ x } AR) + \sigma z \tag{6}$$

where: $x(t)$ represents the abundance of each simulated species at time step t, α is an auto-regressive coefficient to prevent the series from moving too far from 0, kept at $\alpha = 0.99$, AR is the strength of autocorrelation in the time series, σ is a constant standard deviation, set to ~~$\sigma = 0.2$~~$\sigma = 0.1$, and z is a random number between -1 and 1, generated at each time step.

Regime shifts were induced into a chosen proportion of the simulated data frame using Eq. 7:

$$x(t+1) = (x(t)AR) + \frac{-x(t)^3 + x(t) + m_t}{2} + \sigma z \tag{7}$$

where: $x(t+1)$ is the simulated abundance at time step $t+1$, m_t is a time-varying parameter that controls the regime shift dynamics which is defined by one of three separate equations, depending on the time period, σ is a constant standard deviation, set to $\sigma = 0.2$, and z is a random number between -1 and 1, generated at each time step.

The standard deviation for species in which abrupt shifts were induced was larger than for species in which shifts were not induced. The original reason for adding this effect was because it has been shown variation is increased before regime shifts
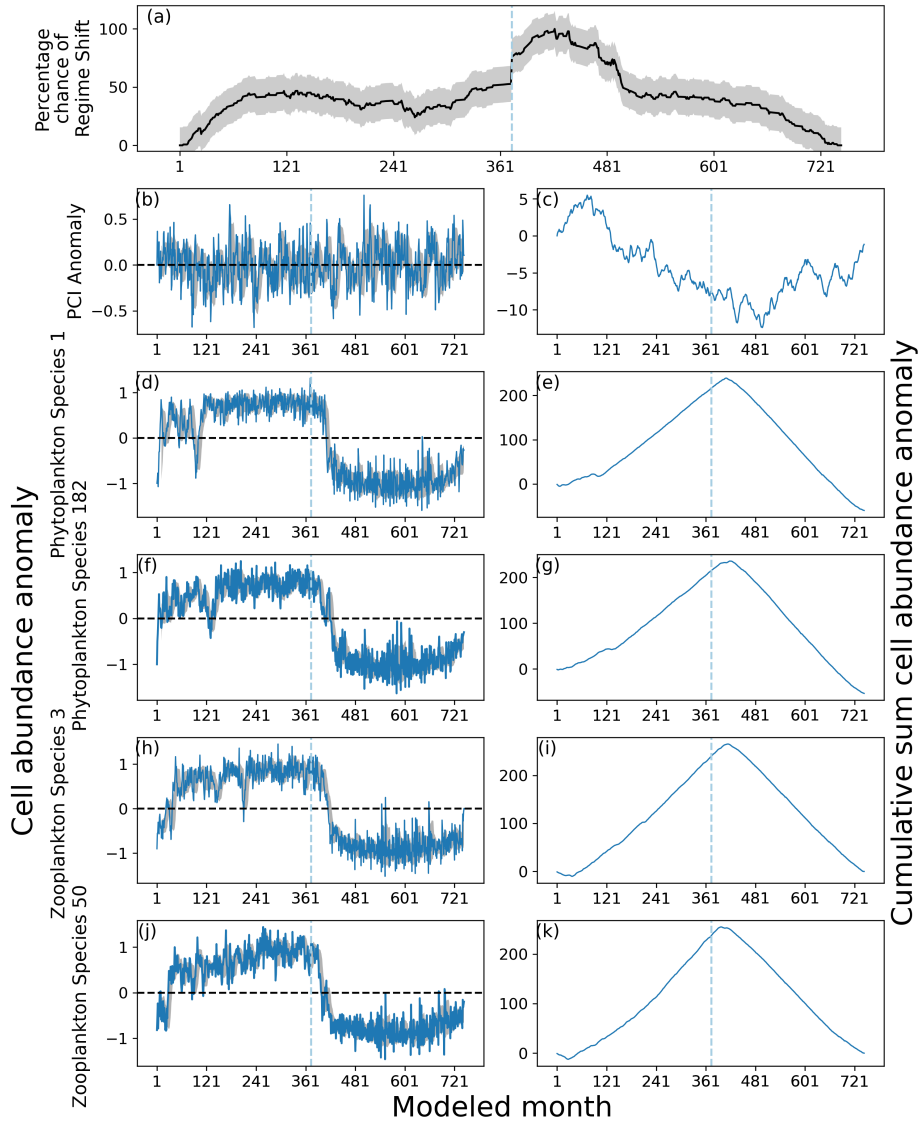
Figure 2. Output of the RST model for simulated data, where a regime shift was induced in 10% of 220 simulated phytoplankton species and 10% of 80 simulated zooplankton species. Time series of (a) the percentage chance of a regime shift occurring, with translucent shading around the line indicating the mean absolute deviation around the percentage chance; (b) time series ~~of simulated PCI anomaly~~ and (~~b~~c) associated cumulative ~~sum of simulated~~ PCI anomaly~~sum~~; ~~abundance anomalies of the greatest~~ (d) ~~time series~~ and ~~second greatest~~ (~~f~~e) ~~range displayed in anomalies~~ cumulative sum of simulated phytoplankton species ~~and their associated cumulative sum time series~~ showing the greatest range in abundance anomalies, (~~e~~f) time series and (g) cumulative sum of simulated phytoplankton species showing the second greatest range in abundance anomalies, ~~and~~ (h) time series and (~~j~~i) cumulative sum of simulated zooplankton species ~~with their associated cumulative sum time series~~ showing the greatest range in abundance anomalies, and (~~i~~j) time series and (k) cumulative sum of simulated zooplankton species showing the second greatest range in abundance anomalies. Vertical dashed lines indicate whenever the percentage likelihood of a regime shift occurring increases or decreases by over 20% in a single month, and the gray translucent area in plots (b), (d), (f), (h) and (j) show the standard deviation around the rolling 12-month mean.

caused by critical slowing down (Scheffer et al., 2001; Scheffer, 2009). It became clear that our interest should not be limited
275   to regime shifts preceded by critical slowing down, but increasing variation for simulated species experiencing abrupt shifts resulted in increased range and a greater chance of their time series appearing in graphs (Fig. 2-7). Before any abrupt shift impacts x, ~~m~~ m_t is equal to zero. From the beginning of the period when abrupt shifts are induced until the end of the shift, ~~m~~ m_t gradually increases from zero until it reaches the bifurcation parameter μ:

$$\mu = \frac{2\sqrt{3}}{9} \tag{8}$$

280 The bifurcation parameter (Eq. 8) was taken from Arellano-Nava et al. (2022) in order to obtain greater control over the timing of abrupt changes. From the end of the shift until simulated abundance x returns to previous levels, m is equal to μ. In examples ~~when RS_SP~~ where x has a different behavior or abundance after an abrupt shift has taken place, m decreases gradually from the bifurcation parameter μ until -5. When m_t is equal to μ, an abrupt shift in simulated abundance is likely to occur. When m_t is decreased, abrupt shifts are unlikely.

285   These formulae were adapted from the original $regimeshifts$ Python package by Arellano-Nava et al. (2022). Changes were made in Eq. 6 to allow the strength of autocorrelation to be modified, remove the bifurcation parameter and allow for realistic time series which do not show a regime shift. The changes added to Eq. 7 allow for greater control of when and how long induced regime shifts take place. We performed different experiments to validate the model.

3.1   Number of species experiencing regime shifts

290 First, the model was tested with respect to the percentage of species experiencing a regime shift. While autocorrelation was kept at a constant level of 0.6, the proportion of simulated phytoplankton and zooplankton species in which ~~a regime~~ an abrupt shift was induced were changed incrementally to show the effect of this on the ~~ecosystem wide~~ percentage likelihood that a regime shift took place.

  When 10% of simulated phytoplankton and zooplankton species experienced an abrupt transition, the percentage likelihood
295 of a regime shift remained around 50% with little variation for the majority of the time series (Fig. 2). A regime shift was still identified just after ~~year 30~~modeled month 361, when percentage likelihood of a regime shift occurring increased from approximately 50% to 75% before continuing to increase more slowly (Fig. 2).

  When an abrupt shift was induced in approximately ~~90~~70% of simulated phytoplankton and zooplankton species, more dramatic increases in percentage regime shift likelihood were observed (Fig. 3). A regime shift was identified by the RST model
300 just before the abundance of simulated PCI, phytoplankton, and zooplankton decreased (Fig. 3). The regime shift percentage likelihood increased ~~during approximately year 31 of the~~ soon after time step 361 of the simulated time series, and decreased during approximately ~~year 38~~ time step 460-500 (Fig. 3).

3.2   Time period between induced regime shifts

  Second, the effect that changing the time between induced abrupt shifts had on the percentage likelihood of a regime shift was
305 tested. Here, the amount of autocorrelation was constantly high (0.6), and the proportion of species which experienced a regime
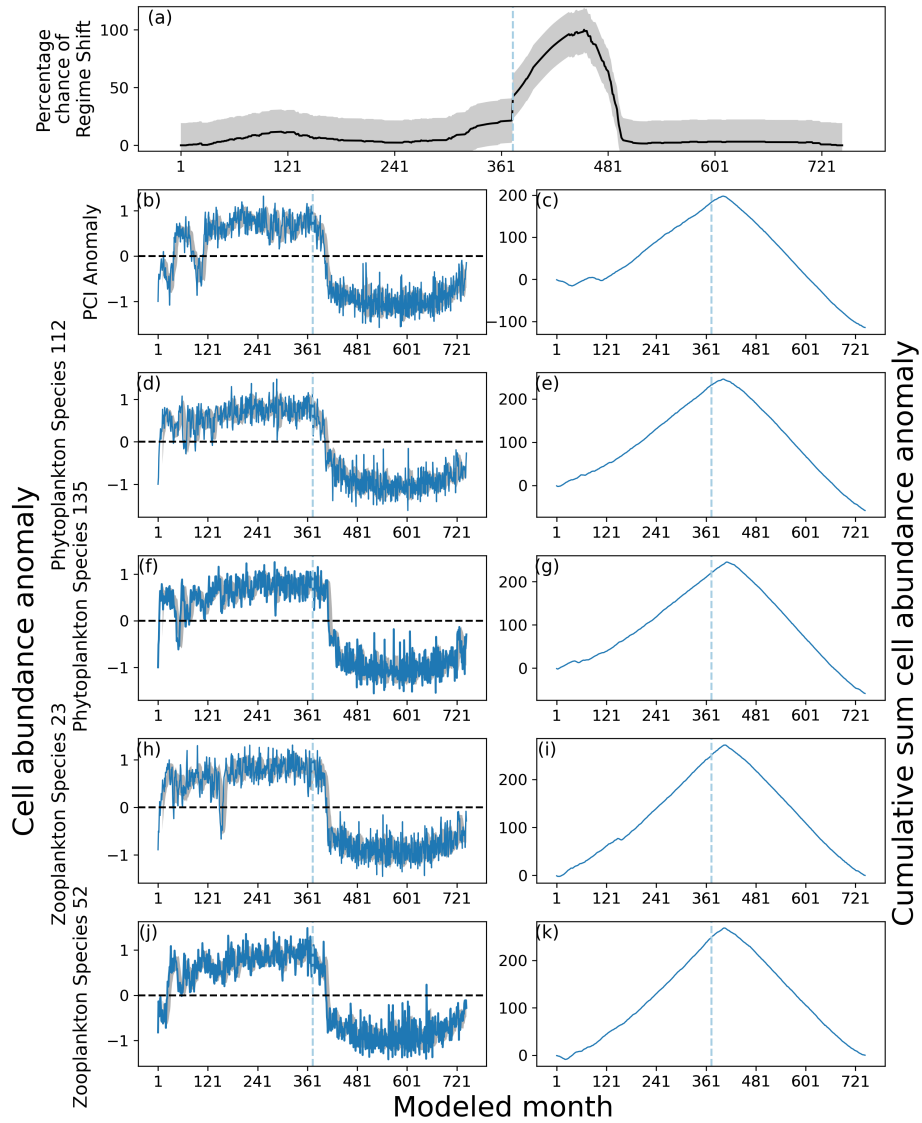
Figure 3. As for Fig. 2, except for regime shifts were induced in ~~90~~70% of simulated phytoplankton species and 90% of simulated zooplankton species. The percentage likelihood of predicted a regime shift increased by greater than the critical gradient ~~before 1990~~ after simulated month 360 and continued to increase until ~~mid-1990.~~ approximately month 420. Abrupt shifts in simulated PCI anomaly and simulated phytoplankton and zooplankton species can be observed between ~~1970~~ simulated months 0 and ~~1980~~150, and after ~~1990.~~360.

shift was kept at a constant 0.4 while the length of time between the first and second induced abrupt changes ~~(or regimes)~~ was changed incrementally.

When the period between the first and last induced changes to simulated species abundance was restricted to lasting a maximum of 20% of the time series, or 12.4 simulated years, the model was barely able to detect two separate regime shifts (Fig. 4). The percentage likelihood of a regime shift occurring did not decrease by more than 10% between induced abrupt shifts (Fig. 4). When the period between the first and last induced abrupt changes was increased to being at least 22.5% of the time series, or just less than 14 modeled years, two distinct regime shifts can be observed as the percentage likelihood fell by more than 20% between the two induced shifts (Fig. 5).

3.3 Lag-one autocorrelation strength

In a final validation experiment, we tested the effect of lag-one autocorrelation strength on regime shift detectability. The proportion of species which experienced a regime shift was kept at a constant 0.4 and the time period between induced abrupt changes was also kept consistent, while autocorrelation strength was increased incrementally from 0.1 to 1.0 in steps of 0.1.

The percentage likelihood of a regime shift occurring was less variable when the strength of lag-1 autocorrelation was restricted to $AR = 0.1$ (Fig. 6). This is especially visible at the beginning of the time series when the first abrupt change was induced, as the percentage likelihood did not increase dramatically before approximately year 25 (or month 300) of the simulation (Fig. 6). The regime shift percentage likelihood increased most dramatically after ~~year 30~~modeled month 361, when abrupt changes were induced in 40% of phytoplankton and zooplankton species ~~in the population~~ (Fig. 6).

When strength of lag-1 autocorrelation was increased to $AR = 0.725$, the earlier regime shift which began after ~~year 30~~ modeled month 361 was detected, as the critical gradient threshold was exceeded (Fig. 7). The maximum percentage change of a regime shift was still detected at approximately the same time as when lag-one autocorrelation was lower, ~~just before year 40~~ before month 481 (Fig. 6-7). A greater variation is shown throughout the time series, as percentage likelihood was lower during periods with no induced regime shifts (Fig. 7).

3.4 Determination of Type I and Type II errors

Additional tests to determine the likely number of Type I errors, or false positives, were completed using a bootstrapping model. Simulated datasets exhibiting different levels of red noise were made. This was accomplished using 100 repetitions of Eq. 6 using the same value of AR and σ, but different values of the random variable z. After every 100 repetitions of Eq. 6, AR and σ were incrementally changed. AR and σ ranged between 0 and 1 ~~,~~ and changed by steps of 0.1 and 0.2, respectively. Redness of noise was calculated using Eq. 9:

$$redness = \frac{AR}{\sigma} \tag{9}$$

and redness of noise thus ~~varied~~ varied between 0.0 and 5.0.

A similar test was carried out to approximate the percentage of Type II errors, or false negatives. In this example, the same bootstrapping method was used, but abrupt shifts were induced in 40% of phytoplankton and zooplankton species using Eq. 7.
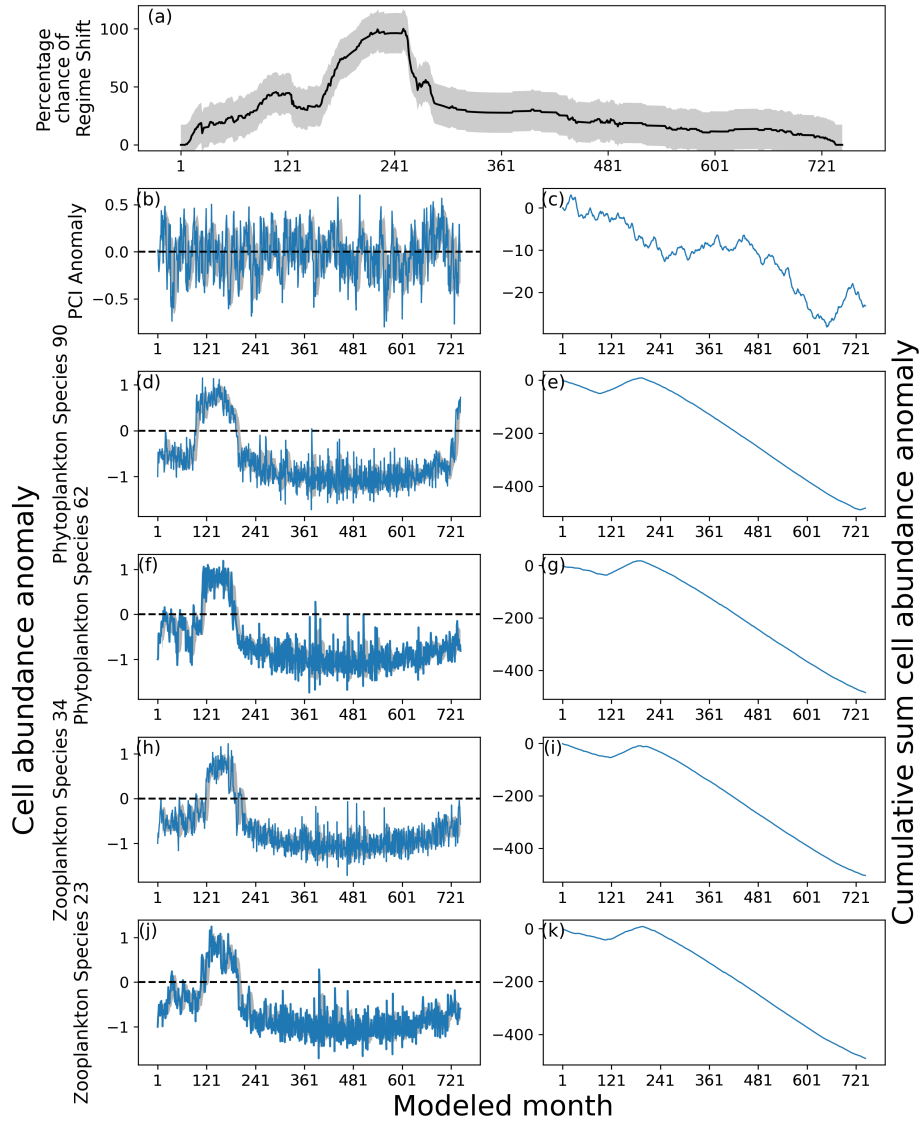
Figure 4. As for Fig. 2, except for the period between first and last induced abrupt changes was restricted to last 20% of the time series, or ~~12.4 years. Two abrupt changes in~~ nearly 150 simulated ~~PCI anomaly can be observed~~months.
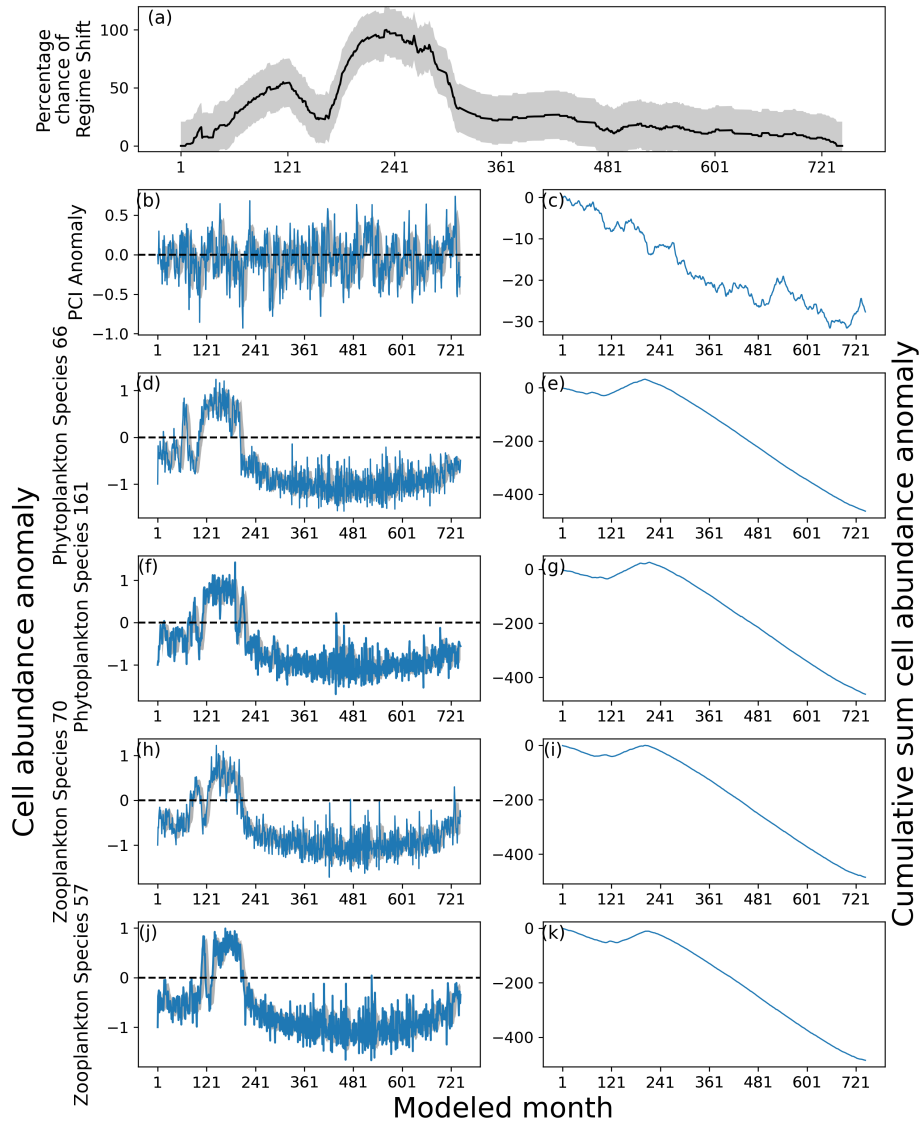
Figure 5. As for Fig. 2, except for the period between first and last induced abrupt changes was restricted to ~~last~~ 22.5% of the time series, or ~~13.95 years~~162 simulated months. The percentage likelihood of a regime shift can be observed in plot (a) to increase from month 150 until ~~mid-1970 until it decreased before increasing again~~ decreasing after ~~1980.~~approximately month 300.
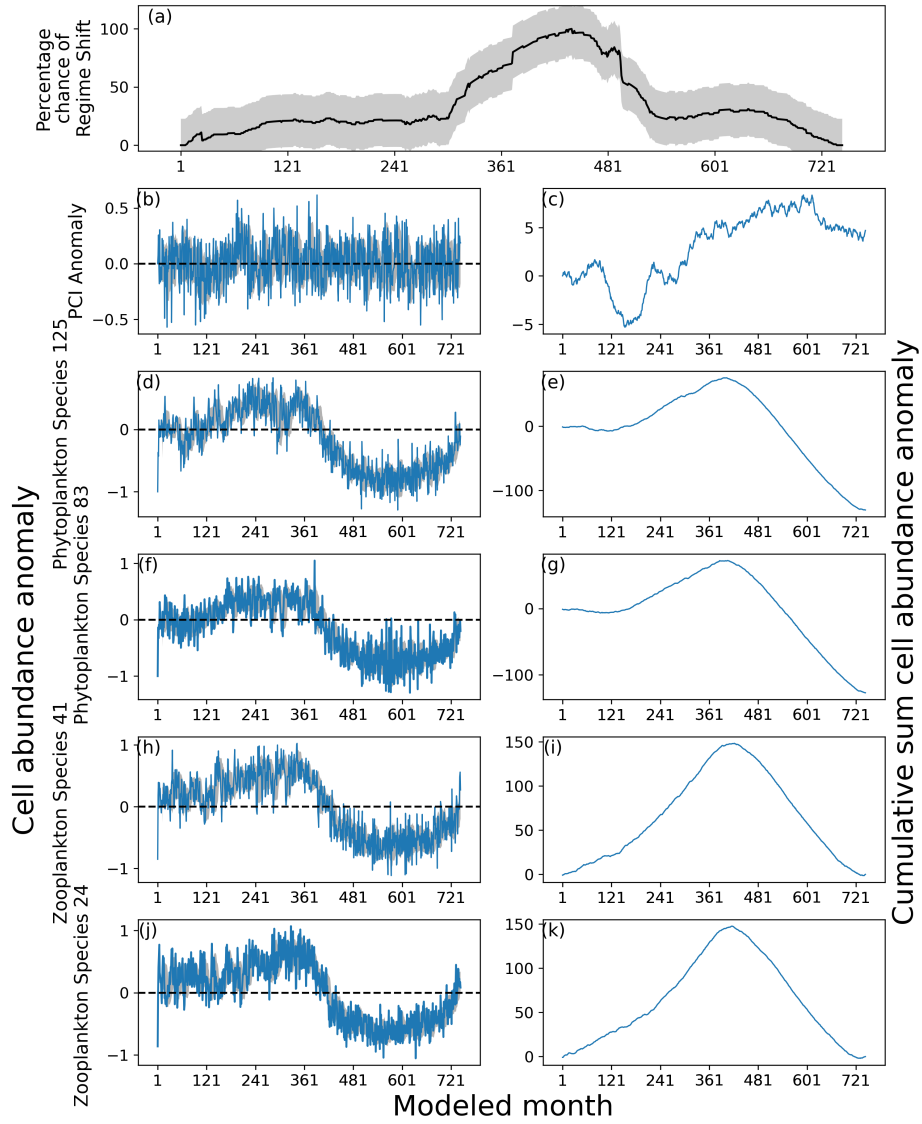
Figure 6. As for Fig. 2, except for the strength of lag-1 autocorrelation was equal to 0.1. An abrupt change was not induced in PCI anomaly (b-c), but changes were induced in species represented in plots (d-k).
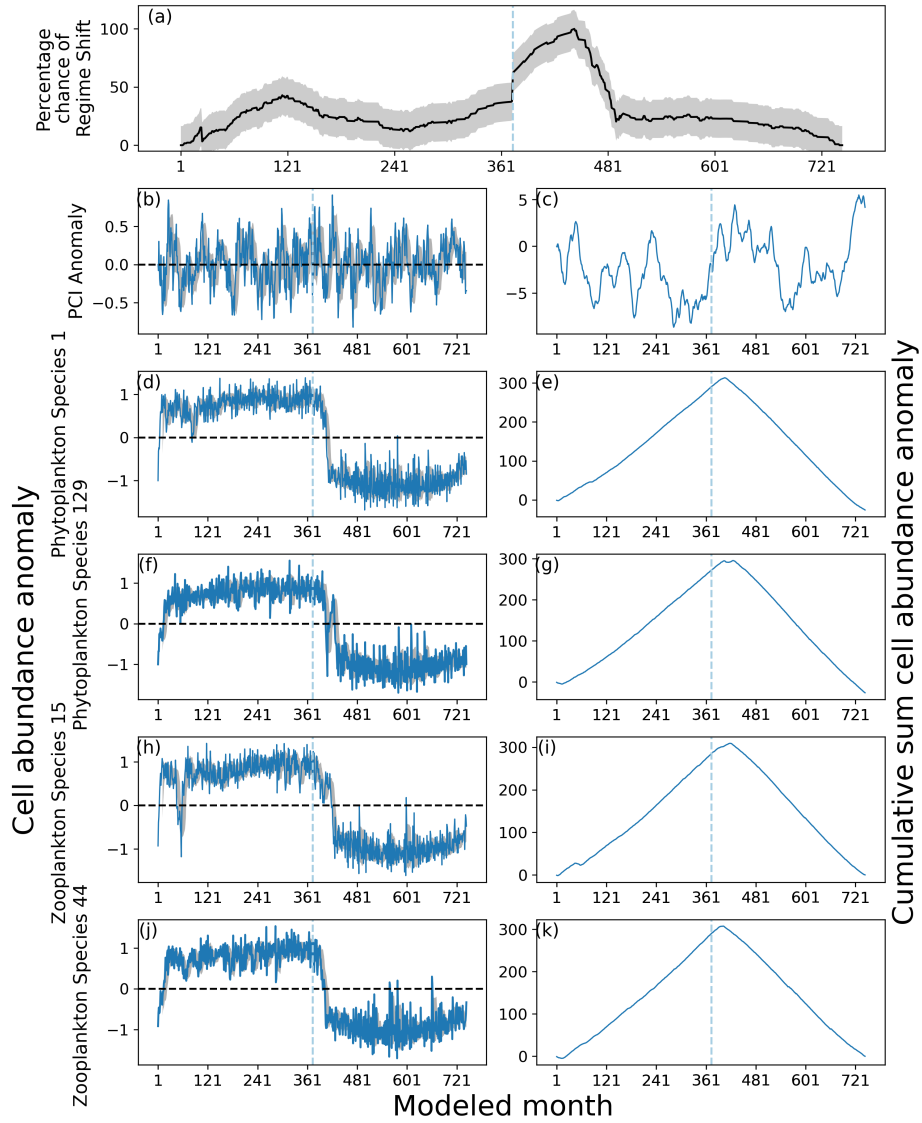
Figure 7. As for Fig. 2, except for the strength of lag-1 autocorrelation was equal to 0.725. ~~Sudden~~ A regime shift can be seen in (a) when abrupt changes can be observed in (d) - (k)~~.~~, just after simulated month 360.

To test the effect of different dataset sizes on false positive and false negative rates, experiments were repeated for datasets of 220 phytoplankton and 80 zooplankton species, 110 phytoplankton and 40 zooplankton species, and 55 phytoplankton and 20 zooplankton species. The effect of Type I and Type II error generation under different critical gradients was assessed by repeating these tests using critical gradients of 18% and 20% (Fig. 8).

The choice to use critical gradients of identifying regime shifts was made after validation tests showed Validation tests showed that the percentage likelihood of a regime shift was nearly constantly high remained high throughout nearly the whole time series when fewer species experienced abrupt changes shifts to their abundance (Fig. 2 -compared to Fig. 3). Therefore, we chose to identify regime shifts using critical gradients instead of finding times when percentage likelihood of a regime shift exceeded a threshold. The assumption was made that using critical gradients to identify regime shifts would result in fewer Type I errors. Normalizing the results of the RST model to between 0 and 100 makes made time series of regime shift likelihood in different North Sea regions more comparable, but results resulted in the time series being less variable and remaining high for a long time when fewer species experience experienced an abrupt shift (Fig. 2-3). When it is unknown how many species in an ecosystem If the number of species in a community or ecosystem which have experienced an abrupt shift is unknown, or when there is a suspicion that relatively few species have changed suddenly, it is therefore more appropriate to use critical gradient thresholds to identify regime shifts.

We show that for datasets of 220 simulated phytoplankton species and 80 simulated zooplankton species the false positive rate is less than 5% (Fig. 8a). The rate of false positives for datasets with fewer species is significantly higher than for larger datasets (Fig. 8). For datasets of only 55 phytoplankton and 20 zooplankton species, the choice of critical gradient results in significantly different false positive rates and false negative rates (Fig. 8). Box plots notches suggest that for smaller datasets, when a critical gradient of 20% is used the rates of false negatives are significantly higher, while false positive rates are significantly lower (Fig. 8). Differences between critical gradients of 18% or 20% do not appear to be significant for sample sizes of 110 phytoplankton species and 40 zooplankton species or larger (Fig. 8).

Estimates of false positive rate production demonstrates that using time series from fewer species will yield less robust results (Fig. 8). In the current example, we use time series of approximately 110 phytoplankton and 40 zooplankton species, which proved to be a sufficiently large dataset. This should be taken as an indication of the robustness of the RST model when used in the current study, rather than an absolute minimum limit of the number of time series which should be used.

The original $regimeshifts$ function by Boulton and Lenton (2019) was designed to be used by non-expert users, and we have tried to keep the same rationale. Without knowing anything about a particular community of plankton, a non-expert user could potentially input many time series into the RST model in order to identify the two most abundant phytoplankton species and whether there is a high probability of any regime shifts having taken place during the time period the dataset exists in. Apart from allowing this process to be used by non-experts, another advantage to including all possible species is minimizing the risk of Type I and Type II errors by keeping sample sizes as large as possible (Fig. 8). We now show an example of using the RST model on phytoplankton and zooplankton abundance data from the CPR.
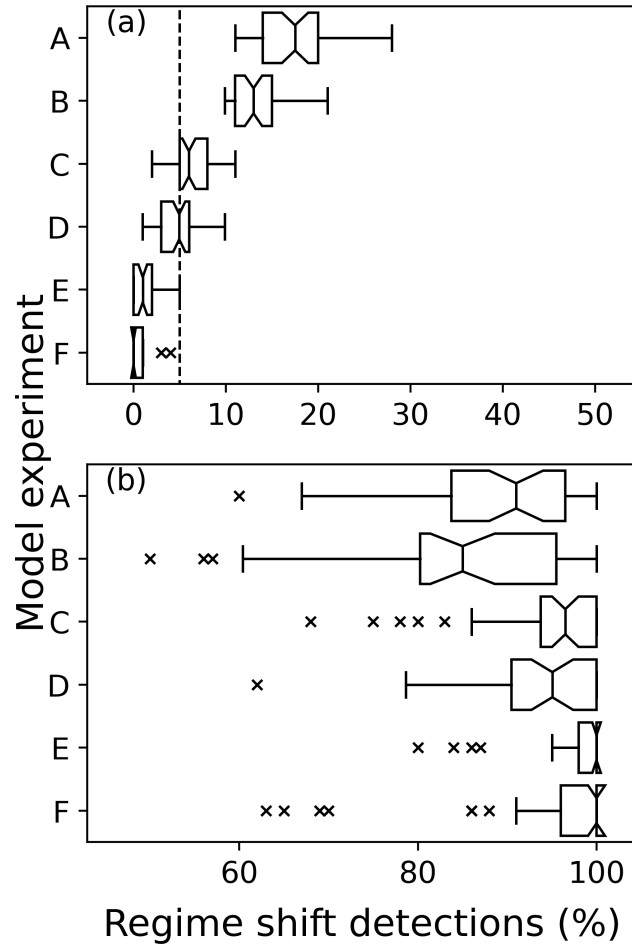
Figure 8. (a) Box plots showing the percentage of datasets of varying levels of red noise where regime shifts were identified where no abrupt changes were induced. A dashed line has been drawn at 5%. Notches on box plots which do not overlap indicate a significant difference. Different plots show datasets of 55 phytoplankton and 20 zooplankton species where critical gradients of A 20% and B 18% were used to identify regime shifts, 110 phytoplankton and 40 zooplankton species where critical gradients of C 20% and D 18% were used to identify regime shifts, and 220 phytoplankton and 80 zooplankton species where critical gradients of E 20% and F 18% were used to identify regime shifts. (b) Abrupt changes were induced in 40% of species.

4   Case study: North Sea

After validation, the RST model was used to generate time series showing likelihood of regime shifts occurring for each of the four ~~regions~~ areas in the North Sea (Fig. 1). Abundance anomalies for each month of the time series between 1958 and 2020 were also plotted, and indications of regime shifts were plotted in each graph (Fig. 9-13). The threshold of a higher gradient change than 20% was chosen to show when regime shifts occurred.

4.1   Predicted regime shifts in Area C1

A total of four regime shifts were identified in ~~region~~ Area C1, located in the center east North Sea (Fig. 1), by the RST model (Fig. 9a). These were also periods when the percentage likelihood of a regime shift occurring increased above 50% (Fig. 9a). The four regime shifts identified were in 1989, 1997, 2002 and 2013, although of these only the identified regime shifts in 1989 and 2002 were associated with an increasing percentage chance (Fig. 9a).

No large variations in PCI anomaly were detected over the study period. However, before 1990 the mean PCI anomaly was mostly just below zero (Fig. 9b-c). After 1990, PCI anomaly was more positive (Fig. 9b-c).

Larger variations over time were detected in the abundances of the most variable phytoplankton groups, *Ceratium furca* and *Ceratium fusus* (Fig. 9d-g). Abundances of both these *Ceratium* species were largely above zero until 2002, when the second regime shift was identified (Fig. 9). After 2002, mean abundance of these species was below the mean abundance of the study period (Fig. 9d-g).

In contrast, the mean anomalous abundance of *C. finmarchicus* decreased from being mostly positive to being mostly negative in 1989, when the first regime shift was identified (Fig. 9). After 1989, the mean anomalous abundance of *C. finmarchicus* remained below zero (Fig. 9). At the same time, the mean anomalous abundance of *C. helgolandicus* increased from below zero to approximately zero in 1989 (Fig. 9). The anomalous abundance of *C. helgolandicus* became positive after the second regime shift began in 2003 (Fig. 9).

4.2   Predicted regime shifts in Area C2

Six regime shifts were detected by the RST model in Area C2, located in the center west North Sea (Fig. 1); in 1963, 1980, 1989, twice in 1992, and 2003 (Fig. 10a). Of these, three were identified when the gradient of the percentage chance of a regime shifts occurring was positive; 1963, 1989 and 1992 (Fig. 10a). The percentage chance of a regime shift occurring was highest in the period between 1991 and 2003, as it remained above 75% for most of the time (Fig. 10a).

PCI anomaly remained below zero for most of the time before 1990, after which it stayed approximately equal to zero (Fig. 10b-c). The two most variable phytoplankton species were *Ceratium macroceros* and *C. furca* (Fig. 10d-g). The mean abundance anomaly of *C. macroceros* was positive until the mid-1970s, after which it remained mostly negative until approximately 2003 (Fig. 10d-e). The only change in anomalous *C. macroceros* abundance associated with an identified regime shift occurred in 2003 (Fig. 10e). The anomalous abundance of *C. furca* remained around zero for most of the time series until 2003 (Fig. 10f-g). After 2003, the mean anomalous abundance of *C. furca* was largely below zero (Fig. 10f-g).
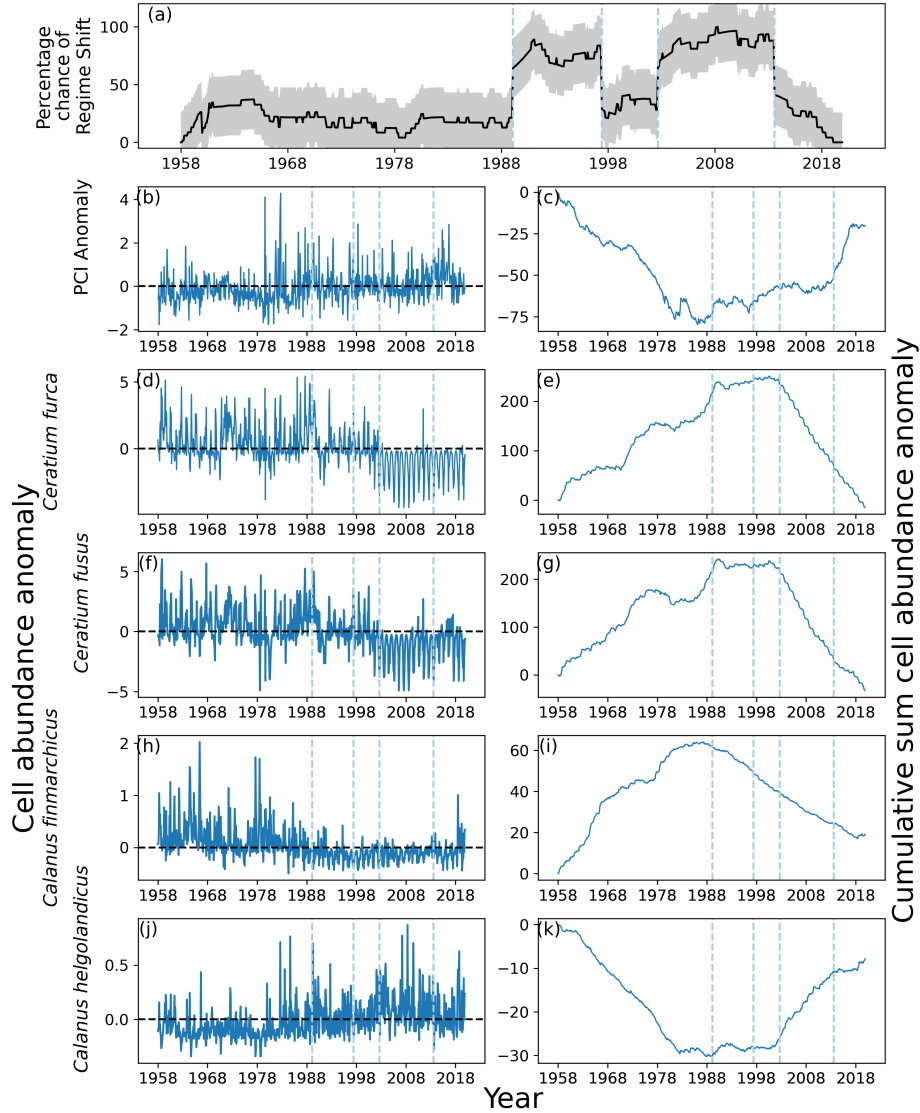
Figure 9. (a) Percentage likelihood of regime shift as estimated by the RST model for Area C1 (see Fig. 1), located between 54° and 58° North and 3° and 12° East~~. Individual plots show~~; (b) monthly mean anomaly and (c) cumulative sum of PCI; (d) monthly mean anomaly ~~, abundance time series~~ and (e) cumulative sum of ~~the~~ phytoplankton species abundance exhibiting greatest range; (~~b~~f) ~~most~~ monthly mean anomaly and (~~c~~g) ~~second most abundant~~ cumulative sum of phytoplankton species ~~,~~ abundance ~~time series~~ exhibiting second greatest range; (h) monthly mean anomaly and (i) cumulative sum of *Calanus finmarchicus*; and (~~d~~j) ~~*C. finmarchicus*~~ monthly mean anomaly and (~~e~~k) cumulative sum of *C. helgolandicus*. The sample size for the entire study period in this area is ~~11976.~~11976 (see Methods section).
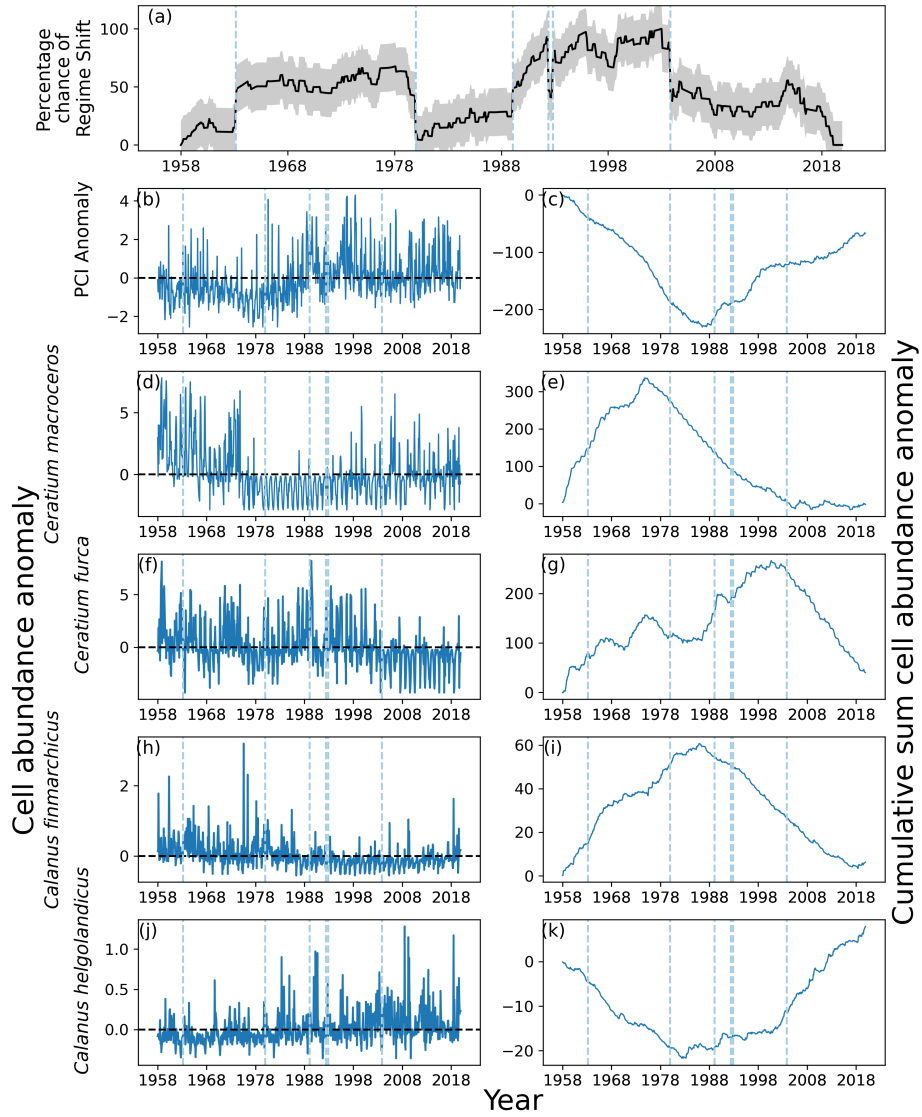
Figure 10. As for Fig. 9, but the region of interest here is Area C2 (see Fig. 1), between 54° and 58° North and between -2° and 3° East. The sample size for the entire study period in this area is 8737.

From the beginning of the study period until 1989, the mean anomaly of *C. finmarchicus* was above zero (Fig. 10h-i). After 1989, mean anomalous *C. finmarchicus* abundance was mostly below zero for the remainder of the time series (Fig. 10h-i). The opposite pattern was observed in the mean anomalous abundance of *C. helgolandicus*; from the beginning of the study period until 1980 the abundance anomaly was below zero (Fig. 10j-k). Between 1980 and 2001, the mean anomalous abundance of *C. helgolandicus* and the variation around it became larger (Fig. 10j-k). After 2001, mean anomalous abundance of *C. helgolandicus* increased further and was almost always above zero (Fig. 10j-k).

4.3 Predicted regime shifts in Area D1

Two regime shifts were identified in Area D1, in the southeast of the North Sea (Fig. 1). These regime shifts occurred in 1997, when there was a positive gradient, and 2008, when there was a negative gradient (Fig. 11a). The percentage likelihood between these regime shifts remained above 50%, and was below 40% the remainder of the time series (Fig. 11a).

PCI anomaly was less than zero for much of the time series until 1997 (Fig. 11b). After 2008, the mean PCI anomaly increased to above zero for the rest of the time series (Fig. 11b-c). The two most variable phytoplankton species, *C. furca* and *C. macroceros*, show positive anomalous abundance at the start of the time series until the mid-1970s (Fig. 11d-g). The mean abundance anomaly of *C. furca* then remained around zero until 2000 after which it decreased (Fig. 11d-e). The mean abundance of *C. macroceros* remained below zero from the mid-1970s until the end of the time series (Fig. 11f-g).

The anomalous abundance of *C. finmarchicus* was largely above zero until approximately 1988, after which it remained below zero until the end of the time series (Fig. 11h-i). The anomalous abundance of *C. helgolandicus* followed the opposite trend, as it stayed below zero until approximately 1988 and subsequently remained around zero until 1997 (Fig. 11j-k). After 1997, the mean anomalous abundance of *C. helgolandicus* increased to being mostly above zero for the remainder of the time series (Fig. 11j-k).

4.4 Predicted regime shifts in Area D2

A lot of the patterns seen in Area D1 were also seen in Area D2, situated in the southwest region of the North Sea (Fig. 1). Two regime shifts were detected; during 1994, when the percentage chance gradient was positive, and 2005 when gradient was negative (Fig. 12a). Between these identified regime shifts, the percentage likelihood of a regime shift occurring remained above 50%, whilst it remained below 50% for most of the rest of the time series (Fig. 12a).

PCI anomaly was less than zero for much of the time series until 1994 (Fig. 12b). After 1994, the mean PCI anomaly increased to above zero for the rest of the time series (Fig. 12b-c). The anomalous abundance of *C. macroceros* was positive at the start of the time series until the mid-1970s (Fig. 12d-e). The mean abundance of *C. macroceros* remained below zero until nearly the end of the time series (Fig. 12f-g). The mean abundance anomaly of *C. furca* remained above zero until 2005 after which it decreased to below zero (Fig. 12d-e).

The anomalous abundance of *C. finmarchicus* was largely above zero until the mid-1980s, after which it remained below zero until the end of the time series (Fig. 12h-i). The anomalous abundance of *C. helgolandicus* followed the opposite trend
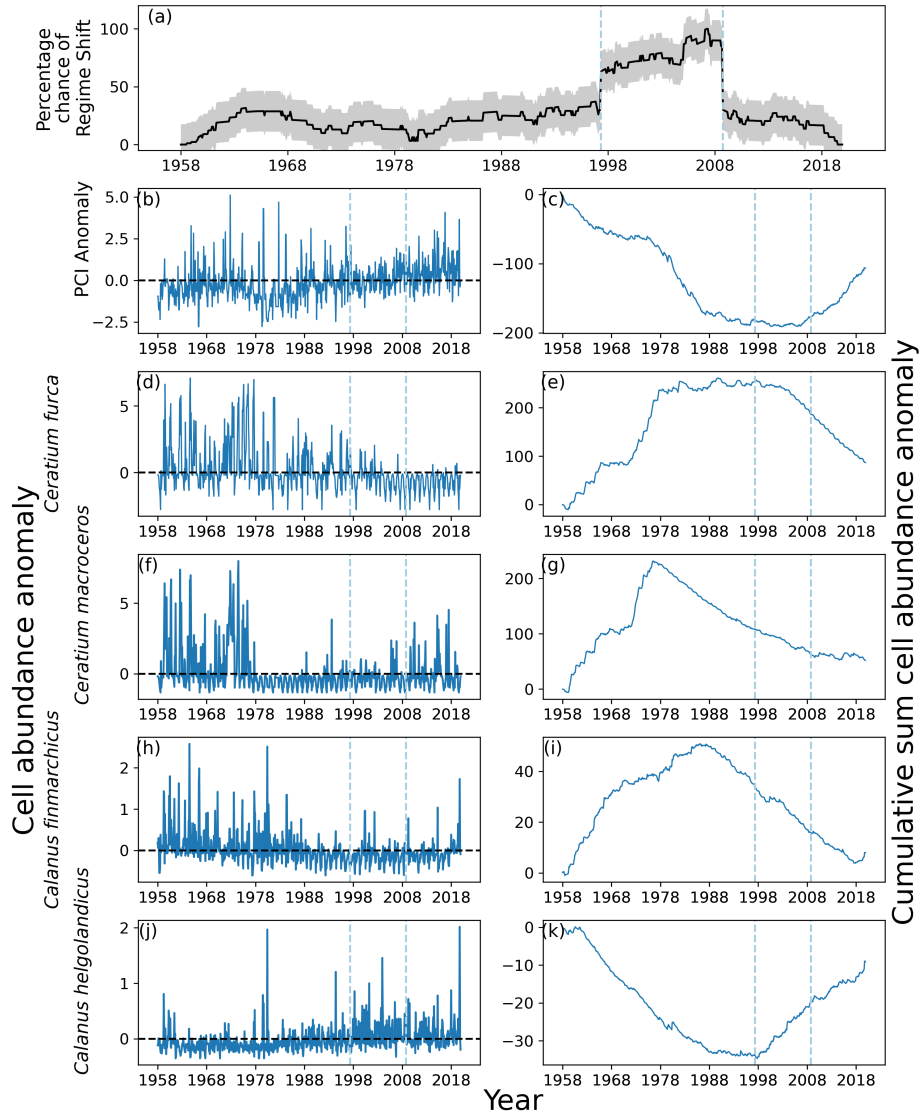
Figure 11. As for Fig. 9, but the region of interest here is Area D1 (see Fig. 1), south of 54° North and between 3° and 12° East. The sample size for the entire study period in this area is 5566.
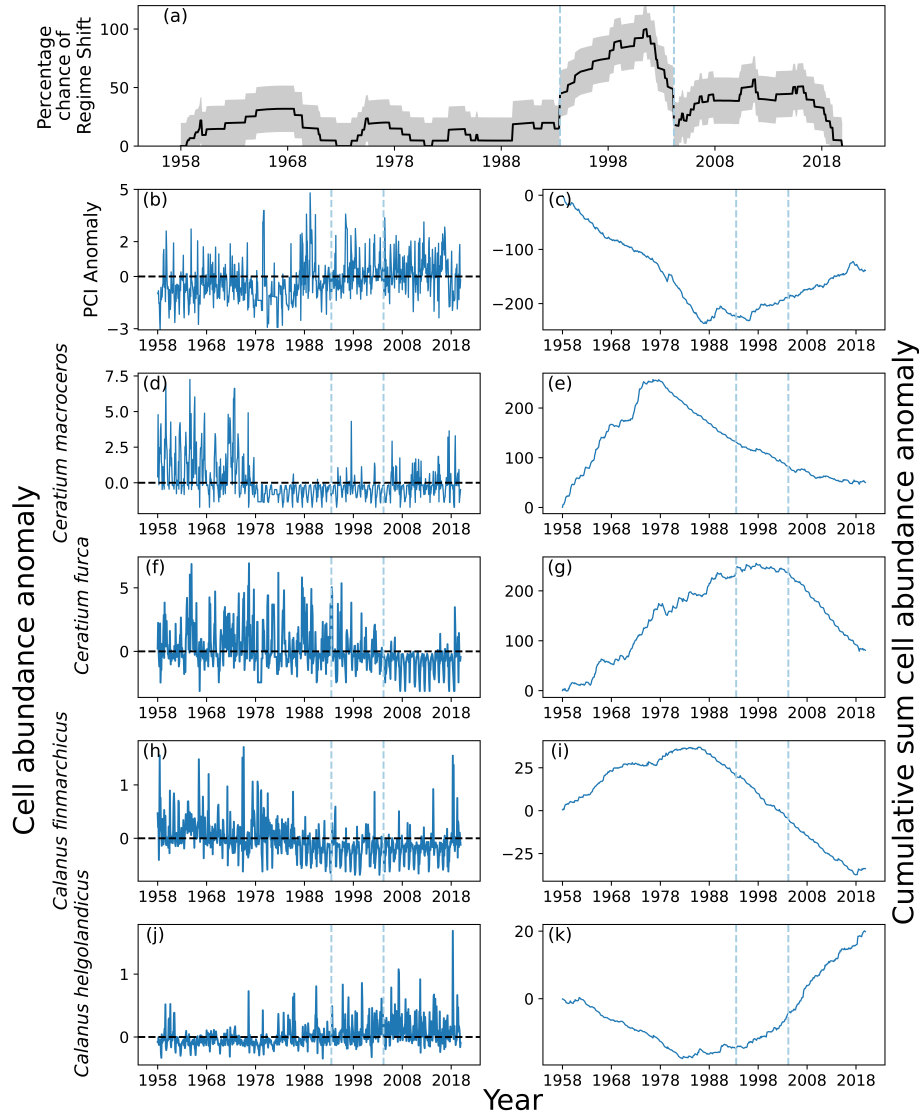
Figure 12. As for Fig. 9, but the region of interest here is Area D2 (see Fig. 1), south of 54° North and between –2° and 3° East. The sample size for the entire study period in this area is 9743.

as it stayed below zero until approximately 1994, after which it increased to being mostly above zero for the remainder of the time series (Fig. 12j-k).

4.5 Entire North Sea

Seven regime shifts were identified for the entire North Sea (Fig. 1) by the RST model, if the first is omitted for happening at the beginning. These were detected during 1962, 1972, 1979, 1998, 2003, 2008, 2015 (Fig. 13a). Of these identified regime shifts, four of them occurred while the percentage likelihood gradient was positive: 1962, 1972, 1998 and 2003 (Fig. 13a). The percentage chance of a regime shift occurring between regime shifts was not noticeably higher or lower compared to other periods in the time series (Fig. 13a). The RST model indicated that the likelihood of a regime shift having occurred in the North Sea remained above 50% for the majority of the time series (Fig. 13).

The mean PCI anomaly in the North Sea began to increase above zero at approximately 1980 (Fig. 13). From approximately 1990 until the end of the study period, PCI anomaly remained relatively steady.

The two most variable phytoplankton species *C. furca* and *C. macroceros* exhibited more dramatic changes in abundance. These changes occurred just after 2000 for *C. furca*, and between 1970 and 1980 for *C. macroceros* (Fig. 13d-g). Each of these abrupt shifts were associated with regime shifts identified by the RST model (Fig. 13d-g).

Abundance of *C. finmarchicus* began to decrease between 1980 and 1990, at approximately the same time that PCI anomaly started to increase (Fig. 13). The decrease in *C. finmarchicus* was preceded by the abundance of *C. helgolandicus* starting to increase (Fig. 13). It is difficult to attribute any of these changes to regime shifts identified by RST, but when *C. helgolandicus* started to increase from just before 2000, the probability of a regime shift occurring increased by more than 20% per month several times (Fig. 13).

4.6 Summary of North Sea results

The RST model successfully identified regime shifts in the North Sea, and their variance over time, space and species involved (Tables 1-2). Regime shifts identified by the RST model in the beginning of the study period appear to have been accompanied by changes in phytoplankton species abundance, though not necessarily PCI anomaly (Table 1). Regime shifts in the 1980s and 1990s appear to have been accompanied by changes in copepods *C. finmarchicus* and *C. helgolandicus*, and PCI anomaly (Table 1). Regime shifts after 2000 appear to be associated with changes in phytoplankton species abundance (Table 1).

In the south of the North Sea identified regime shifts were first observed in the West in area D2 before the East in area D1 (Tables 1-2). In the center of the North Sea it is more difficult to determine whether the same regime shifts are being detected at similar times, as more were detected by the RST model than in the South (Table 2).

Abrupt changes in PCI anomaly, abundance anomaly of either of the two most variable phytoplankton species, or at least one of *C. finmarchicus* or *C. helgolandicus* were detected when the majority of regime shifts were identified if the gradient of regime shift likelihood was positive (Table 2). Exceptions occurred in D2 during 1994, and the North Sea during 1962 and 1972 (Fig. 12-13; Table 2). Similarly, regime shifts were identified when the likelihood time series gradient was negative which were not accompanied by abrupt changes to PCI anomaly or the other four time series shown. An example of this was in area
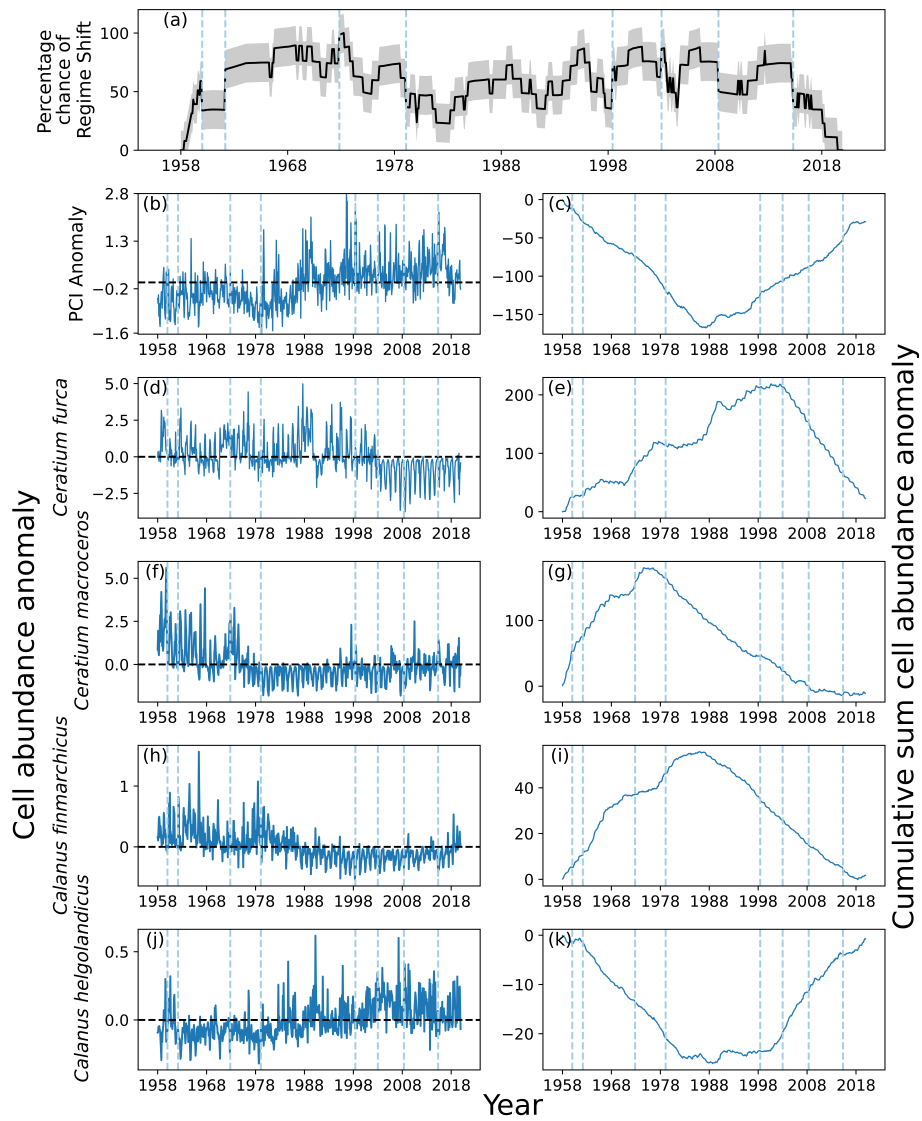
Figure 13. As for Fig. 9, but showing results of the entire North Sea (Fig. 1). The sample size for the entire study period in this area is 56745.

Table 1. Regime shifts identified by RST model, divided into 20 year periods. The species involved column indicates whether the PCI anomaly, the two most variable phytoplankton species or either *C. finmarchicus* or *C. helgolandicus* experienced noticeable changes associated with the identified regime shift.

Period	Species involved	C1	C2	D1	D2	North Sea
1960 - 1979	*C.macroceros*, *C.furca*	1963				1962, 1972, 1979
1980 - 1999	PCI *C.helgolandicus*, *C.finmarchicus*	1989, 1997	1980, 1989, 1992	1997	1994	1998
2000 - 2019	*C.furca*, *C.fusus*, *C.macroceros*	2002, 2013	2003	2008	2005	2003, 2008, 2015

Table 2. Comparison of regime shifts found in North Sea areas during the present study. ~~Positive and negative columns indicate whether the gradient of percentage chance of a regime shift occurring was positive or negative.~~

Area	~~(positive~~ (positive gradient)	Regime shifts detected by RST model ~~(negative~~ (negative gradient)
C1	1989, 2002	1997, 2013
C2	1963, 1989, 1992	1980, 1992, 2003
D1	1997	2008
D2	1994	2005
North Sea	1962, 1972, 1998, 2003	1979, 2008, 2015

C2 during 1989 (Fig. 10). Exceptions appear to occur whether the RST gradient is positive or negative, so all times when the critical gradient was exceeded have been noted (Tables 1-2).

5 Discussion

Our analysis presents a novel ~~multi-species~~ multispecies approach to quantify the likelihood of a regime shift ~~in marine ecosystems occurring~~ occurring in marine plankton communities. We find that by constructing a single time series of regime shift likelihood from abundance data of different phytoplankton and zooplankton species, our model is able to reliably detect ~~past~~ previous regime shifts in the North Sea (Table 1). ~~Our results point to future opportunities of automated detections of regime shifts and their driving mechanisms in various marine systems across spatial and temporal scales~~ Distinguishing regime shifts in North Sea plankton from changes in abundance due to advection is a limitation of this approach. Future work could address this limitation by incorporating spatial patterns from hydrodynamic models, helping to separate genuine ecological shifts from transport-driven variability. A step towards this would be to divide the North Sea into hydrodynamically appropriate regions van Leeuwen et al. (2015), but this is beyond the scope of the present study. A single time series of regime shift likelihood may lead to the future development of automated detection algorithms. Comparison of regime shift likelihood to potential drivers in a single-variate model is likely to be less challenging to implement than multivariate models or principal component analyses.

5.1 Proof of concept

As noted by multiple ~~studies of ecology~~ ecological studies, validation of new methods and models is a necessary first step (Dees et al., 2023; Mateus et al., 2019; Groesser and Schwaninger, 2012). We therefore constructed artificial abundance data that mimic the characteristic of observed CPR data that allowed an extensive validation of our model. This approach had previously been successfully applied in a previous study using the novel multi-scale multivariate split moving window methodology to identify North Sea regime shifts (Beaugrand et al., 2014). Further, we estimated the probability of our model producing Type 1 and 2 errors in order to quantify the robustness of our model's ability to detect regime shifts, which Haines et al. (2024) have identified as a frequent limitation to regime shift detection models.

Validation tests showed that regime shift likelihood variation during induced regime shifts was much larger when a greater proportion of species experienced an abrupt change ~~(Fig. 2-3).~~ . When only a small proportion of species experience an abrupt abundance shift, the percentage of regime shift likelihood remained high for a large part of the time range and only deviated by just over 20% ~~(Fig. 2).~~ . This is important to know for interpretation of RST output when ecological data are used. Previous studies have shown that for plankton populations in the North Sea, approximately 40% of species were involved in ~~ecosystem identified~~ regime shifts (Beaugrand et al., 2014). We have shown ~~the model is able to~~ that the model can detect regime shifts when fewer species are involved, but care must be taken when interpreting model output as the 20% critical gradient is not always exceeded.

The minimum amount of time between abrupt shifts that the RST model was able to distinguish between, was between 12 and 14 years. The time period between abrupt changes was therefore kept at 40% of the time series, or just under 25 years, to remove all possibility of time taken for the community to be established having an impact on model performance. It is likely that for abrupt changes with a smaller time period between them than 12 years, the predicted likelihood of a regime shift will be elevated over an extended time period. Another limitation of the model observed is the length of time between the start of the time series and when the earliest regime shift can be detected. In Fig. 7, abrupt changes to the abundance of two phytoplankton species can be observed but were not accompanied by an increase in the regime shift probability time series above the critical gradient. This is similar to Beaugrand et al. (2014), where results suggested a regime shift near the beginning of their study period which could not be confirmed.

Autocorrelation in time series data can lead to increased false positive rates (Haines et al., 2024). Removal of the effect of autocorrelation has previously been accomplished using statistical means such as the modified Chelton method, which reduces the number of degrees of freedom (Pyper and Peterman, 1998; Hinder et al., 2014; Bedford et al., 2020a; Dees et al., 2017), or by applying an auto-regressive-moving average (ARMA) model to the data (Alvarez-Fernandez et al., 2012). The original regimeshifts model, incorporated within the RST model described here, does not remove autocorrelation but instead detects anomalous rates of change (Boulton and Lenton, 2019; Arellano-Nava et al., 2022). Similar to tipping points, regime shifts can be preceded by increasing autocorrelation and variance (Dakos et al., 2015; Scheffer et al., 2001). Preserving autocorrelation within the analyzed dataset is therefore preferential when looking for early warning signals for regime shifts. Regime shift detection by the RST model is improved when autocorrelation is stronger, although in silico validation tests have shown that regime shifts are still identified when autocorrelation before abrupt shifts is weak or absent. Preserving more of the dataset's original structure appears to allow the RST model to identify regime shifts with a low false positive rate, relative to other methods (Fig. 8) (Haines et al., 2024; Rudnick and Davis, 2003).

The in silico experiments described here show that the RST model is capable of identifying regime shifts with similar numbers of species as is collected by the CPR, but care should be taken if the time series of regime shift likelihood does not deviate dramatically. Changes in regime shift likelihood of approximately 20% should be investigated individually by looking at accompanying time series and cumulative sum graphs, as it is possible that these are false positives or false negatives.

The RST model identified likely regime shifts in different regions of the North Sea, which can be grouped by species and timing. Regime shifts observed at the beginning and end of the study period appear to have been caused primarily by changes in the most abundant species of phytoplankton. Regime shifts in the 1980s and 1990s appear to have been driven by changes in PCI and copepods *C. finmarchicus* and *C. helgolandicus*. These results are consistent with previously identified regime shifts in the North Sea (Beaugrand et al., 2014; Djeghri et al., 2023; Bedford et al., 2020a; McQuatters-Gollop et al., 2007), although it is difficult to make a direct comparison due to differences in spatial areas chosen.

As noted in a comprehensive review, the most important governing factors of ecological systems are space and time (Wolkovich et al., 2014). The North Sea is a body of water which experiences a lot of advection (van Leeuwen et al., 2015; Fransz et al., 199
535   and the distribution of any plankton within are influenced by advection (Hjøllo et al., 2009; Fransz et al., 1991; Bartsch et al., 1989), and it is premature to conclusively identify a particular date a regime shift occurred without comparing neighboring areas. For example, results from the RST model show an apparent regime shift involving *C. finmarchicus* and PCI occurred in the mid-west of the North Sea (area Area C2) during 1992, and subsequently the southwest of the North Sea (area Area D2) during 1994, and then in the southeast North Sea (area Area D1) during 1997 (Table 1, Fig. 11-12). 1997. Again, a regime shift

540   involving the most variable phytoplankton species *C. macroceros, C. furca* and *C. fusus* was identified in area Area C2 in 2003, then in D2 during 2005, before being detected in D1 in 2008 (Table 1, Fig. 11-12). In the present analyses 2008. An important limitation of the RST model is that it is difficult to confirm whether regime shifts have taken place at different times or whether plankton was advected , or whether abrupt changes in plankton were due to advection around the North Sea system.

5.2   Apparent early warning for imminent regime shifts

545   Contrary to our expectations, the RST model appeared able to predict regime shift before they occurred. The RST time series increased above the rate of the critical gradient before a One of the first investigations of ecological regime shifts in the North Sea focused on the shift from a zooplankton community dominated by *C. finmarchicus* to one where *C. helgolandicus* was more dominant in the between 1982 and 1989 (Beaugrand and Reid, 2003; Reid et al., 2016, 2001). Other studies have suggested this regime shift began later in the 1980s (Wouters et al., 2015; Beaugrand, 2014; Alvarez-Fernandez et al., 2012).

550   More investigations into North Sea plankton communities revealed another likely regime shift which ended in 1968, though as this was the near the beginning of the ecological time series used there is less confidence (Beaugrand, 2014). A final ecological regime shift was detected in simulated species (Fig. 3, 7) and , to a lesser extent, biological time series data. Examples include area D1 when identified between 1996 and 2003, though whether there was an impact to ecosystem function is uncertain (Beaugrand et al., 2014; Djeghri et al., 2023; Alvarez-Fernandez et al., 2012). When analysis into separate Northern

555   and Southern North Sea areas took place, a regime shift was identified before changes in the abundance of *C. furca* and *C. helgolandicus* (Fig. 11), and area detected around 1978 (Alvarez-Fernandez et al., 2012). Using the RST method we have shown three periods of increased regime shift likelihood, though likelihood differs by North Sea area.

For the entire North Sea, the RST model detected regime shifts at similar times to Beaugrand et al. (2014). However, the split moving window method did not detect regime shifts after 2003 (Beaugrand et al., 2014). When just Area C1 of

560   the North Sea was considered, the RST model detected the regime shifts in the late 1980s, and between the late 1990s and early 2000s. Again, a later regime shift after 2010 was also identified. The RST model also detected the late 1980s shift in Area C2 when the model identified a regime shift before discernible changes in *C. helgolandicus* or . Interestingly, Alvarez-Fernandez et al. (2012) detected regime shifts in approximately 1978 which appear consistent with those detected by the the RST model in the entire North Sea in 1979 and Area C2 during 1980. The shift from *C. finmarchicus* abundance (Fig.

565   10). This was unexpected because there is no forecasting or early warning functionality in the baseline model that the RST was built around (Arellano-Nava et al., 2022; Boulton and Lenton, 2019). to *C. helgolandicus* appears to have occurred later in

Area D1 and D2. Further study of the plankton community and the apparent regime shifts suggested in many areas after 2003 is recommended.

~~A possible reason for this apparent early warning of regime shifts may have been caused by abrupt changes being induced~~

5.2 RST model output

The nature of the CPR database and the RST model's ability to detect regime shifts in multispecies communities means abrupt changes in phytoplankton and zooplankton species can be identified which were not displayed in the output's graphs. Equation 7 induces regime shifts in simulated time series, but the stochastic term m incorporated within Eq. 7 gradually increases the likelihood for simulated time series to experience an abrupt change. For example, minor differences in the timing of abrupt shifts in phytoplankton species 1 and 129 ~~can be observed (Fig. 7d-g), as well as~~ and zooplankton species 15 and 44 ~~(Fig. 7h-k).~~ can be observed. In this case, abrupt changes began to be induced in 40% of species just before 1990, ~~and this~~ which caused the percentage likelihood of a regime shift ~~occurring~~ to increase. ~~Not all abrupt changes occurred simultaneously, and the~~ The RST time series shows probability of the entire ~~ecosystem~~ plankton community captured by the CPR experiencing a regime shift~~rather than~~, and is influenced by abrupt shifts in individual species. ~~This shows only inspecting a limited number of abundance graphs visually can lead to errors, and exhibits the importance of the RST model to detect regime shifts or abrupt changes.~~

~~Another reason for the apparent early warning signal given by the RST model may have been caused by the exponential increase induced in the percentage likelihood of a regime shift time series when abrupt changes are detected at the same time, or within 24 months, across multiple trophic levels (Eq. 5). Having this potential for exponential increases in the RST time series programmed into the model is advantageous for making the identified regime shift appear more significant if it has influenced the ecosystem for a longer period. A possible disadvantage of the RST model is that it is possible for many regime shifts to be predicted in quick succession, even though only one occurred (as in Fig. 10). This reiterates why the time series must be assessed together with abundance time series graphs. It is also possible that for apparently preemptive regime shifts predicted from ecological data, changes in other abundance time series not displayed in the graphs were responsible for the regime shifts identified by the~~ The ability to calculate risk of regime shifts in the community by analyzing all species, instead of those assumed to be most important, exhibits the importance of the RST model.

~~The time series for regime shift probability in biological data is more variable than for simulated species. It is likely that some of the apparent mismatches in identified regime shifts and actual changes in abundance are for different reasons than the pseudo-detection of regime shifts observed in simulated data. In biological data, it is possible for large and~~ Large and dramatic changes in species abundance ~~to~~ can occur without an accompanying change in regime shift likelihood, as ~~seen~~ observed in *C. finmarchicus* abundance in the entire North Sea~~(Fig. 13), or~~, or either *Ceratium* spp. or PCI in Area D1~~(Fig. 11). Likely reasons for these mismatches are that the~~. The RST model is designed to predict regime ~~shifts for entire ecosystems~~shift likelihood for all species that are input, and changes ~~in single species are unlikely to~~ to single species do not always affect the entire ~~ecosystem. Only the most abundant species, or time series where the largest range was observed, are shown in the time series plots in Fig. 9-13.~~ community (Fauchald et al., 2011; Djeghri et al., 2023). This is an important difference from other

regime shift detection algorithms used in the North Sea (Beaugrand et al., 2014; Bedford et al., 2020b, a). Output from the original $regimeshifts$ function was multiplied by the mean abundance of species for that month, resulting in the RST model estimating regime shift likelihood for all species in a particular database rather than simply measuring the number of species exhibiting abrupt changes. In this way, the RST model was kept appropriate for non-expert users while scaling the proportion

605   that each species contributes to the percentage likelihood of a regime shift. Applying more specific weights to keystone species such as *C. finmarchicus* or *C. helgolandicus* may be an interesting avenue for future research.

5.3 ~~Regime shift detection across multiple trophic levels~~

In contrast to the present study, which used abundance records from every species recorded in the CPR dataset, previous studies predicting regime shifts in marine plankton datasets have looked at small groups of individual species. Example studies

610   include those analyzing the 1980s regime shift involving *C. finmarchicus* and *C. helgolandicus* (Beaugrand and Reid, 2003; Edwards et al., 2001; Reid et al., 2016), and those studies grouping species into functional groups of phyto- and zooplankton (Beaugrand et al., 2014; Bedford et al., 2020a; Hinder et al., 2012; McQuatters-Gollop et al., 2007; Haines et al., 2024). The advantage of this approach is the ability to show how certain groups of species have changed over time, possibly as a response to increased temperature or increases in other anthropogenic input (Bedford et al., 2020a; Beaugrand and Reid, 2003; Edwards

615   et al., 2001). However, by looking at only a limited number of species or groups, studies can miss changes to other species groups which were not specifically checked. It is particularly difficult to calculate major changes across multiple trophic levels in the marine environment ~~,~~ because different sampling methodologies are used for plankton and fish~~and these are often in effect~~, and data have often been collected over different scales of time and space (Haines et al., 2024; Beaugrand and Reid, 2003; Reid et al., 2001). Studies of ecological regime shifts have therefore traditionally been more common in closed systems

620   like lakes, where regular monitoring of across multiple regime shifts is easier (Bertani et al., 2016). Ecological regime shifts in marine ecosystems should be observed in more than one trophic level at a time (Beaulieu et al., 2016; Yletyinen et al., 2016; Haines et al., 2024). ~~It is generally agreed by previous studies of regime shifts in the North Sea that there have been at least three North Sea regime shifts; in the 1960s, the late 1980s and between 1996 and 2003 (Beaugrand et al., 2014; Djeghri et al., 2023)~~.

625   Assessing how many trophic levels are represented in a database of phytoplankton and zooplankton is challenging~~without undertaking an investigation of stable isotopes~~, as heterotrophic dinoflagellates can be an ecologically significant consumer of ciliates, diatoms and some smaller zooplankton species (Sherr and Sherr, 2007; Park et al., 2006). Accordingly, zooplankton can operate over a range of trophic levels depending on species, season, and region (Kürten et al., 2013; Décima, 2022). ~~In contrast to Beaugrand et al. (2014) who chose only 44 phytoplankton species and 29 zooplankton species in their method, following the selection~~ The methodology of Ibanez and Dauvin (1998) ~~which focused on representative species while~~ to select

630   species from the CPR dataset focused on choosing representative species and avoiding zero inflated presence-absence counts~~, our~~. Use of this selection methodology meant only 44 phytoplankton species and 29 zooplankton species were analyzed by Beaugrand et al. (2014)'s method. In contrast, the present method used data from all species collected by the CPR. ~~This meant including abundance data from at~~ At least three trophic levels were thus included: phytoplankton, zooplankton, and fish larvae

635 and eggs. ~~The original $regimeshifts$ function by Boulton and Lenton (2019) was designed to be used by non-expert users, and we have tried to keep the same rationale. Without knowing anything about a particular ecosystem, a non-expert user could potentially input many time series into the RST model in order to identify the two most abundant phytoplankton species and whether there is a high probability of any regime shifts having taken place during the time period the dataset exists in. Apart from allowing this process to be used by non-experts, another advantage to including all possible species is minimizing the risk~~

640 ~~of Type I and Type II errors by keeping sample sizes as large as possible (Fig. 8).~~

In order to take greater advantage of the valuable CPR dataset and all trophic levels included, the RST model used in this analysis explicitly placed exponentially greater weight on the percentage likelihood of a regime shift if abrupt changes were detected in both phyto- and zooplankton species within the window length of 24 months (see Methods). When data for the entire study area was analyzed by the RST, the percentage likelihood of a regime shift taking place was highest at

645 approximately 1968, the late 1980s, and between 1996 and 2003. These periods compare favorably with those predicted by Beaugrand et al. (2014) and provide some validation of the RST model described here. Explicitly adding differing weights to meroplanktonic organisms may be an interesting avenue of future research.

5.3 Robustness of regime shift detection

A recent paper looking at various different methodologies ~~designed to detect~~ for detecting regime shifts in marine ecosystems

650 showed that most methods generate false positives at such a high rate that it is impossible to determine whether ~~or not~~ regime shifts in the North Sea and along the west coast of Norway have really taken place ~~(Haines et al., 2024; Rudnick and Davis, 2003)~~ ~~.~~(Haines et al., 2024). Some regime shift detection methods produce false positive rates of 100%, though the majority are closer to around 20% (Haines et al., 2024). Although the present model does not always have a false positive rate below 5%~~(Fig. 8, as recommended by Haines et al. (2024), ,~~, the false positive rate when using the RST model is lower than those reported by

655 a range of previous studies (Haines et al., 2024; Rudnick and Davis, 2003). ~~Some regime shift detection methods produce false positive rates of 100%, though the majority are closer to around 20% (Haines et al., 2024). When~~ Results presented in the present study suggest when more species are ~~looked at~~analyzed, there is a reduced likelihood of generating false positives or negatives~~(Fig. 8)~~. The lower false positive rate shows the value of including all species collected by the CPR.

It has been assumed that the ~~danger~~ production of Type II errors ~~is greater than those of Type I errors~~detracts from model

660 usefulness more than Type I error production does, particularly as false positives have been reported more commonly (Haines et al., 2024; Rudnick and Davis, 2003). The rate of false negatives in the present study is higher than those for false positives~~(Fig. 8. This may be remedied by decreasing~~ ~~.~~ Decreasing the value of the critical gradient used to identify regime shifts in this study ~~, but the~~ will likely decrease false positive production, but validation tests performed in this study indicate doing so will increase the rate of false ~~positives (Fig. 8a). Generating false negatives also entails risks.~~ negatives. Having a

665 conservative estimate of regime shift likelihood should increase the certainty in identified regime shifts. If this method is used to predict regime shifts in future scenarios or management situations, further reducing false positives could lead policy makers to perhaps wrongly assume a regime shift is not imminent when one could occur in the near future. We therefore advise RST

model users to thoughtfully explore the use of different window lengths and critical gradients, especially if using the model to advise management.

670   Thoughtfully interpreting graphs generated by the RST model alongside species abundance data, instead of only noting times when the critical gradient indicates that a regime shift is likely, will also help identify false positives and negatives. The resultant time series generated by the RST of a dataset with no induced abrupt changes shows much less variation and fewer large changes over a study period compared to a dataset with more species experiencing abrupt changes(Fig. 2-3).. Using examples like this as a comparison can help users of the RST model to identify spurious regime shifts identified using
675 gradients or thresholds.

6   Conclusion

The RST model described here has shown success at identifying regime shift probability in a single time series based on patterns of species abundance, and whether abrupt changes in abundance are observed in more than one trophic level. Validation tests have demonstrated the robustness of the RST model and its ability to identify regime shifts with a relatively low error rate.
680 Recent advances in machine learning and deep learning algorithms mean that forecasting single time series into the future is a possibility which should be explored in future studies (Hewamalage et al., 2023). Success in this endeavor will show the RST model described here as a first step to designing a regime shift forecasting model for the 21st century.

    Reducing all CPR abundance data Although there are several advantages to condensing an estimate of regime shift likelihood into a single time series, limitations of this approach have also been discussed. These limitations include needing approximately
685 14 years between abrupt changes for the algorithm to detect regime shifts, and the inability to distinguish between apparent regime shifts caused by advection. Another potential disadvantage of reducing the rich data collected by the CPR into one time series of regime shift likelihood necessarily removes is removal of context, which can potentially introduce more uncertainty and biases into the estimation of whether a regime shift occurred (Nguyen, 2024). For example, a recent study of focused on the northwest European shelf has found no change in functional groups associated with past identified regime shifts (Djeghri
690 et al., 2023). Another study has found evidence that functional groups have changed, but did not link this to abrupt regime shifts (Bedford et al., 2020a). Links between regime shifts in plankton and fish do exist (Reid et al., 2001; Vollset et al., 2022) and there is even evidence to suggest regime shifts have affected the abundance of higher trophic levels, such as whales (Meyer-Gutbrod et al., 2021). Further studies of planktonic regime shifts regime shifts in plankton communities should elucidate whether regime shifts in plankton such regime shifts are drivers of regime shifts in higher trophic levels, or if whether abrupt
695 changes seen in more than one trophic level is coincidentalare caused by the same biotic or abiotic drivers.

    The relatively low variability observed in regime shift likelihood for the entire North Sea when compared to the smaller sub-regions, which have much smaller sample sizes, is likely to be due to regime shifts occurring in different parts of the North Sea at different times. The North Sea is a semi-enclosed body of water surrounded by high-populated areas, where the distribution of plankton is influenced by water advection (Kürten et al., 2013; Fransz et al., 1991)(Hjøllo et al., 2009; Bartsch et al., 1989; Fransz et al., 19
700 . There are also a diverse range of hydrodynamic regimes in the North Sea, distinguished by stratification patterns and fresh-

water influence (van Leeuwen et al., 2015). The standard regions used in most studies of CPR data (Djeghri et al., 2023; Beaugrand, 2014; Beaugrand et al., 2010; Bedford et al., 2020a), including the present study, are likely not as ecologically meaningful in comparison to regions divided based on similar ecohydrology or distance from inflow channels. A 21st century early warning system for regime shifts should make use of subareas divided by hydrology and distance from North or South entrances to the North Sea. This would improve our understanding of physical drivers of regime shifts and contribute to more advanced regime shift prediction.

Code availability. All data analysis was accomplished using Python (Python Software Foundation). In particular we have used the packages Pandas (Team, 2024) and NumPy version 1.26.4 (Harris et al., 2020). The regime shift code written in Python by Arellano-Nava et al. (2022) is publicly available under https://github.com/BeatrizArellano/regimeshifts. The code for our model is available at www.doi.org/10.5281/zenodo.14750039.

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