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

Paul Dees[1,2], Friederike Fröb[1,2], Beatriz Arellano-Nava[3], David G. Johns[4], and Christoph Heinze[1,2]

[1]Geophysical Institute, University of Bergen, Norway
[2]Bjerknes Center for Climate Research, Bergen, Norway
[3]University of Exeter, Laver Building, North Park Road, Exeter, EX4 4QE, UK
[4]Continuous Plankton Recorder Survey, Marine Biological Association, Citadel Hill, Plymouth PL1 2PB, UK

Correspondence: Paul Dees (paul.dees@uib.no)

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 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 1999, and between 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 in regulating climate on Earth, but the marine environment can experience dramatic changes associated with increasing global mean temperatures. Potential modifications to the oceanic environment include increased incidence of marine heatwaves (Oliver et al., 2018, 2019), changes to large scale ocean circulation patterns such as the Atlantic Meridional Overturning Circulation (AMOC) (Johnson et al., 2020; Robson et al., 2014),

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changes to ocean salinity (Curry et al., 2009; Skliris et al., 2014), changes to 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 on the rate 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 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 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 (Heinze et al., 2021; Rocha, 2022).

Ecological regime shifts (hereafter called regime shifts) are somewhat analogous to tipping points in physical systems. Similar to tipping points, regime shifts are characterized by large, abrupt and persistent change in the function and structure of an ecosystem (Scheffer et al., 2001; Reid et al., 2016). They 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 notoriously difficult to identify 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; Beaugrand, 2004; Scheffer et al., 2001). For example, evidence for several regime shifts has been identified in the Pacific Ocean (Hare and Mantua, 2000), the North Sea (Beaugrand and Reid, 2003; Edwards et al., 2001; Beaugrand et al., 2014; Djeghri et al., 2023), and along the Norwegian coast (Vollset et al., 2022). However, there is considerable controversy around the identification of these regime shifts. Numerous studies have found present detection methods have falsely identified regime shifts in simulated time series data, to which red noise has been introduced (Haines et al., 2024; Rudnick and Davis, 2003). Despite the ecological importance 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 identification of regime shifts is crucial for prediction and future management of ecosystems and our interaction with them. Knowledge of ecosystems requires reliable abundance time series from (preferably) more than one trophic level, for as many years as possible (Edwards et al., 2010; Wouters et al., 2015). 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 et al., 2010; Beaugrand, 2004; 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) 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). Questions around methods used to identify regime shifts (Haines et al., 2024; Rudnick and Davis, 2003), and whether or not a change in plankton necessarily impacted higher trophic levels or ecosystem function (Djeghri et al., 2023; Reid et al., 2001) remain.

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)). The key innovation of our approach lies in its ability to analyze multiple time series of plankton abundance simultaneously, and

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generate a single ecosystem time series representing the likelihood of a regime shift occurring at any point represented by the time series. This feature is particularly valuable for users who may lack detailed knowledge of the planktonic ecological history of the study area. 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° and 8° E (Fig. 1). Using official CPR sampling areas 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)).

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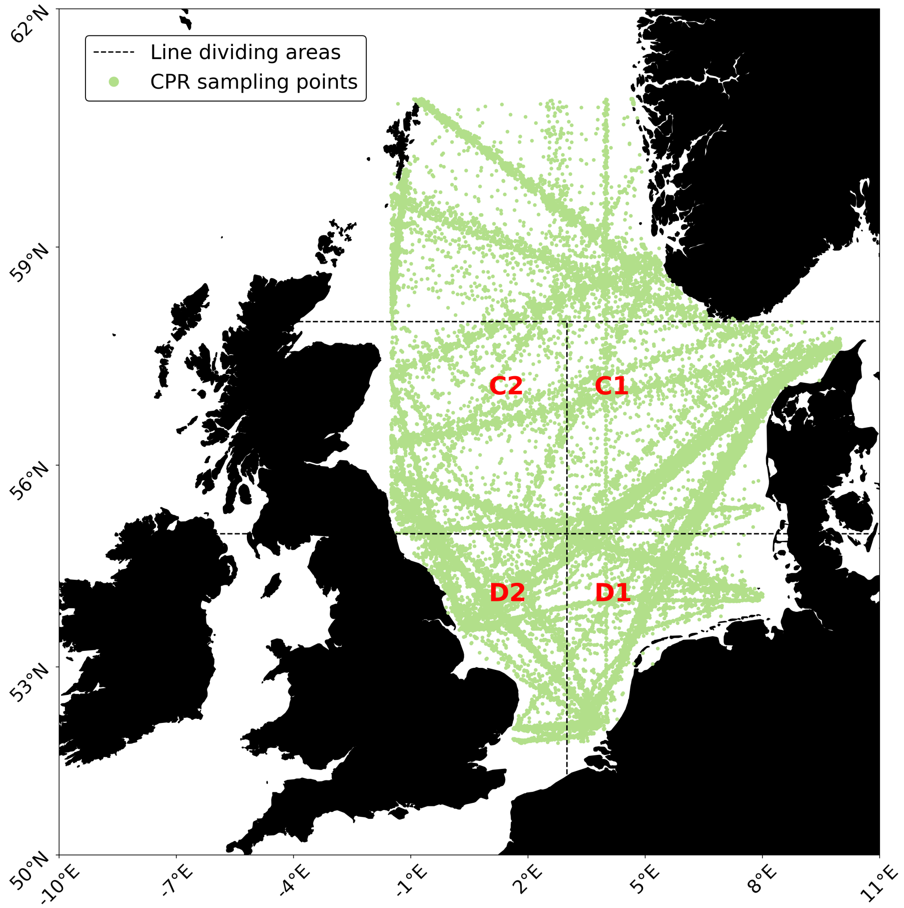

Figure 1. The North Sea study area with sampling points displayed in green, and CPR official areas C1, C2, D1 and D2 denoted by dashed lines and area names in red. Map was built using Met Office (2010 - 2015)

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2.2 CPR 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 over 200 phytoplankton species and over 80 zooplankton species captured by the CPR were removed by converting 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 (PCI), which is the logarithmic graded color scale estimated by the Sir Alister Hardy Foundation for Ocean Science (SAHFOS) group. The logarithmic transformation was applied before the mean abundance was calculated. The mean abundance was then calculated using the equations:

$$x' = \log(x_i + \frac{cm}{2}) \tag{1}$$

where x is the species abundance as measured by the CPR at time point i and cm is the CPR limit of quantification, and

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

where: $\Delta x(t)$ is the mean abundance anomaly at year-month t which includes every month of every year between 1950 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.

2.3 Detection and identification of regime shifts

We develop here a method that builds on the approach introduced by Boulton and Lenton (2019), which detects abrupt shifts in individual time series by identifying anomalous rates of change. 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-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 time series is created, initially filled with zeros, where each position corresponding to an anomalous rate is incremented or decremented by one. This process is repeated for various segment lengths, from a user-defined minimum to a maximum of one-third of the original time series length. Finally, the resulting values are divided by the number of segment lengths used, producing an index ranging from -1 to 1. The algorithm thus returns a time 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 0 suggests a low likelihood of abrupt shifts, while values close to -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.

We applied this single-series regime-shift detection algorithm to identify abrupt changes on each species across the entire planktonic ecosystem from the CPR dataset. The RST model is able to identify abrupt changes when assessing time series with

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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 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 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 of abrupt shift likelihood, for each species. Weights were added to the relative importance of the abrupt shift likelihood time series if the time series of abrupt change 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 rolling window. Sustained deviation away from a beginning point therefor 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.

The total probability of an ecosystem regime shift was calculated by adding the probability of an abrupt change in phytoplankton and zooplankton together.

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

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Here, $P_{RS}(t)$ is the total probability of an ecosystem-wide regime shift 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 bottom-up processes (Capuzzo et al., 2018; Marques et al., 2024), here we assume that a change in phytoplankton could induce sustained changes in zooplankton, allowing us to quantify $P_{RS}(t)$.

Adding the chosen weights (Eq. 4), and including results from the previous 23 months of the phytoplankton probability time series, means that results from the first two years of the RST time series will be inaccurate. 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. 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 20% was exceeded. 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 Determination of Type I and Type II errors and Robustness of regime shift detection.

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 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 $\sigma = 0.2$, 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:

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

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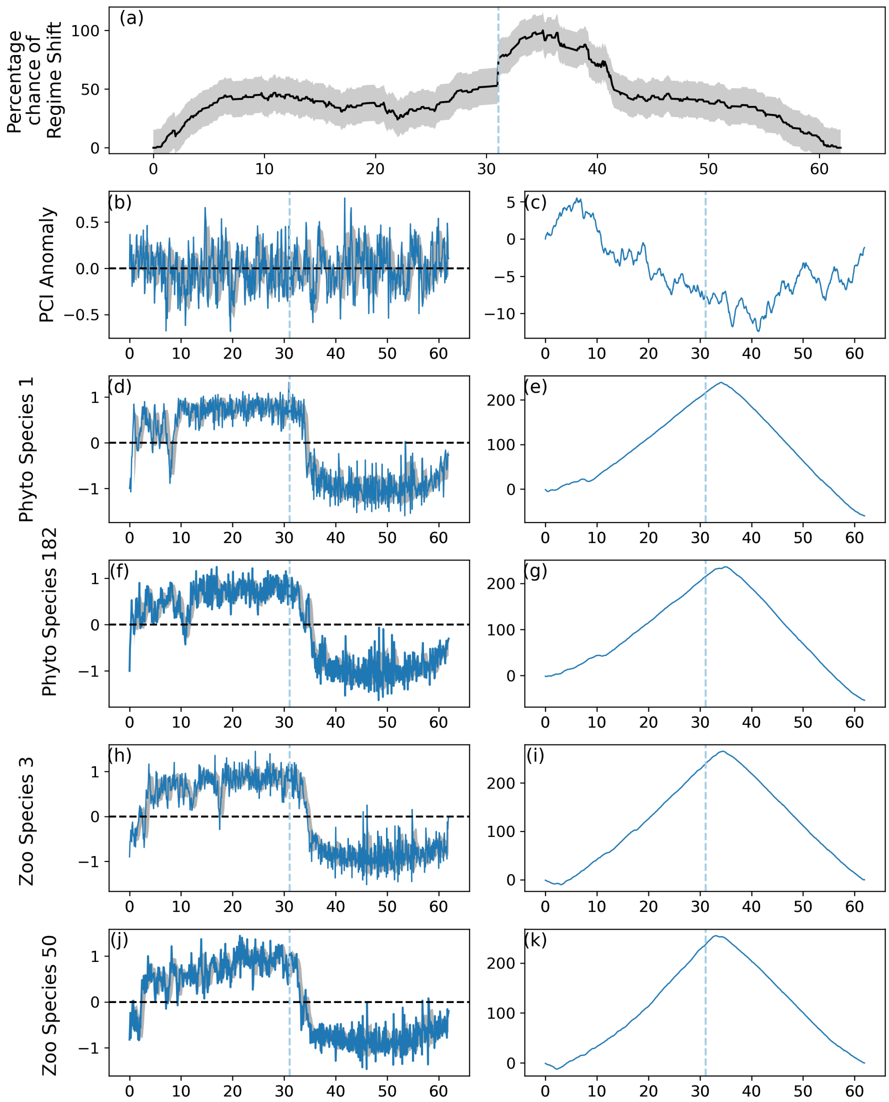

Figure 2. Output of the RST model for simulated data, where a regime shift was induced in 10% of 220 simulated phytoplankton species and 10% of 80 simulated zooplankton species. Time series of (a) the percentage chance of a regime shift occurring, with translucent shading around the line indicating the mean absolute deviation around the percentage chance; (b) time series of simulated PCI anomaly and (b) associated cumulative PCI anomaly sum; abundance anomalies of the greatest (d) and second greatest (f) range displayed in anomalies of simulated phytoplankton species and their associated cumulative sum time series (e) and (g), and (h) and (j) simulated zooplankton species with their associated cumulative sum time series (i) and (k). 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.

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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, and z is a random number between -1 and 1, generated at each time step.

Before any abrupt shift impacts x, m is equal to zero. From the beginning of the period when abrupt shifts are induced until the end of the shift, m gradually increases from zero until it reaches the bifurcation parameter μ:

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

From the end of the shift until simulated abundance x returns to previous levels, m is equal to μ. In examples when RS_SP has a different behavior or abundance after an abrupt shift has taken place, m decreases gradually from the bifurcation parameter μ until -5.

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

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 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 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, 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% 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 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 time series, and decreased during approximately year 38 (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 tested. Here, the amount of autocorrelation was constantly high (0.6), and the proportion of species which experienced a regime 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.

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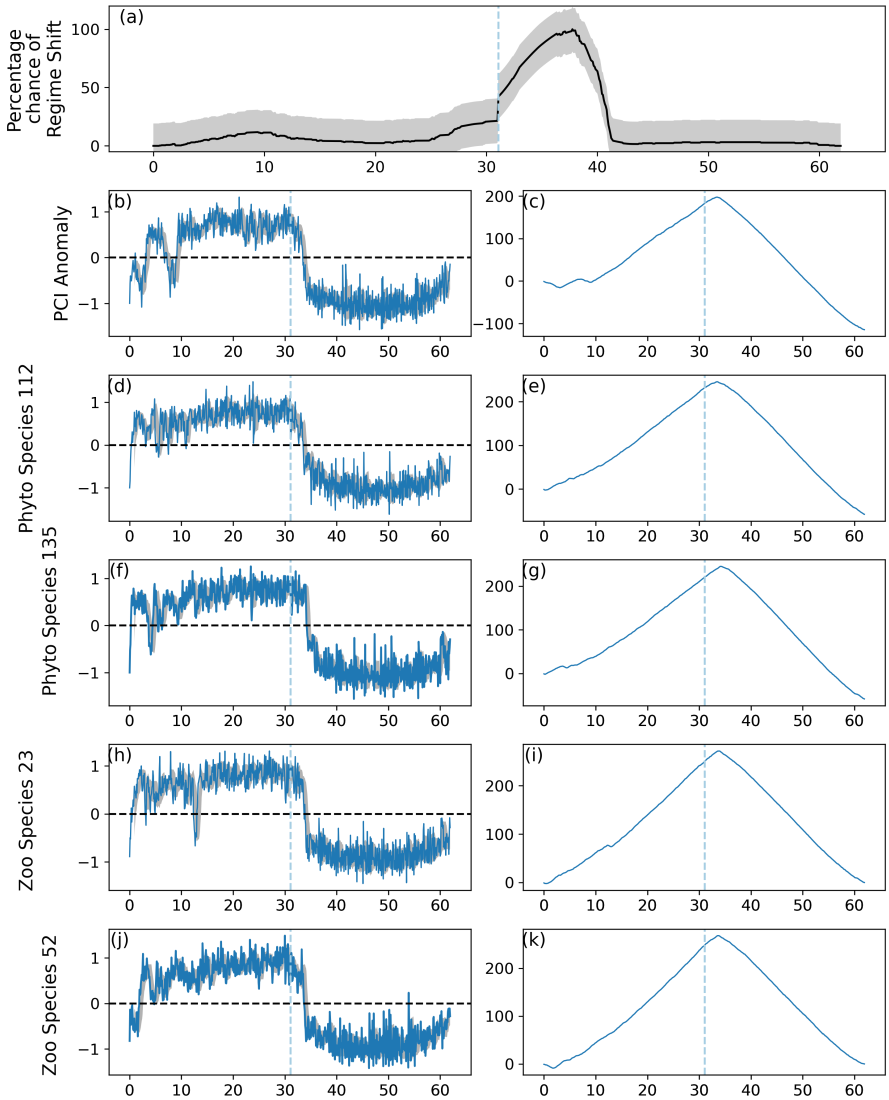

Figure 3. As for Fig. 2, except for regime shifts were induced in 90% of simulated phytoplankton species and 90% of simulated zooplankton species. The percentage likelihood of predicted a regime shift increased by greater than the critical gradient before 1990 and continued to increase until mid-1990. Abrupt shifts in simulated PCI anomaly can be observed between 1970 and 1980, and after 1990.

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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 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 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 of the simulation (Fig. 6). The regime shift percentage likelihood increased most dramatically after year 30, 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 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 (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 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. 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

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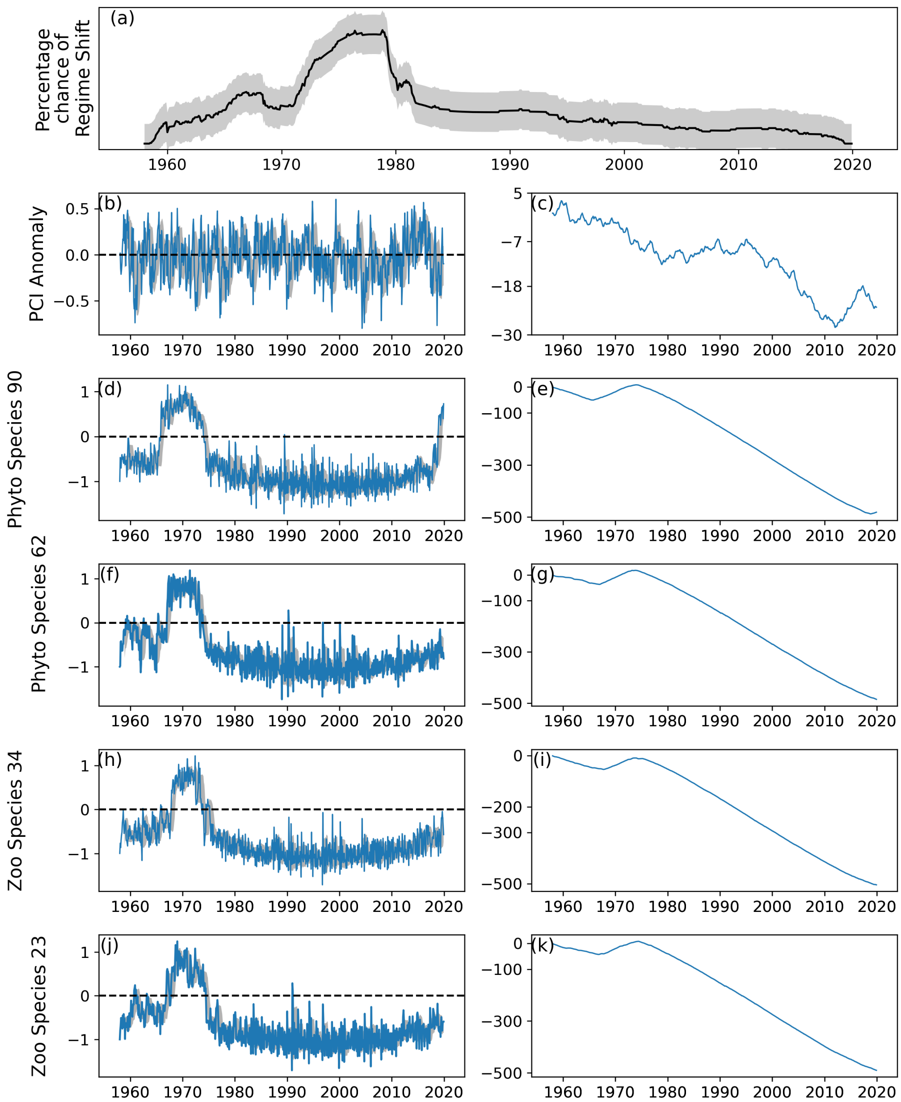

Figure 4. As for Fig. 2, except for the period between first and last induced abrupt changes was restricted to last 20% of the time series, or 12.4 years. Two abrupt changes in simulated PCI anomaly can be observed.

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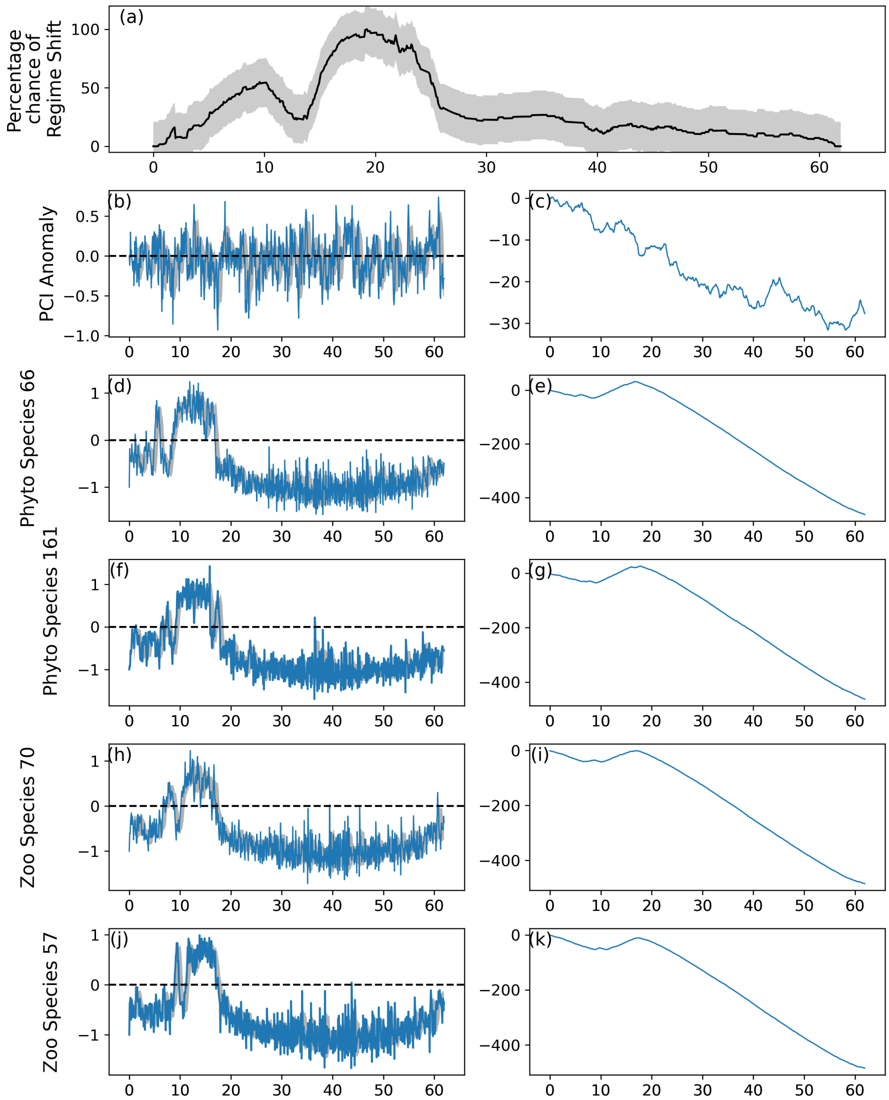

Figure 5. As for Fig. 2, except for the period between first and last induced abrupt changes was restricted to last 22.5% of the time series, or 13.95 years. The percentage likelihood of a regime shift can be observed to increase until mid-1970 until it decreased before increasing again after 1980.

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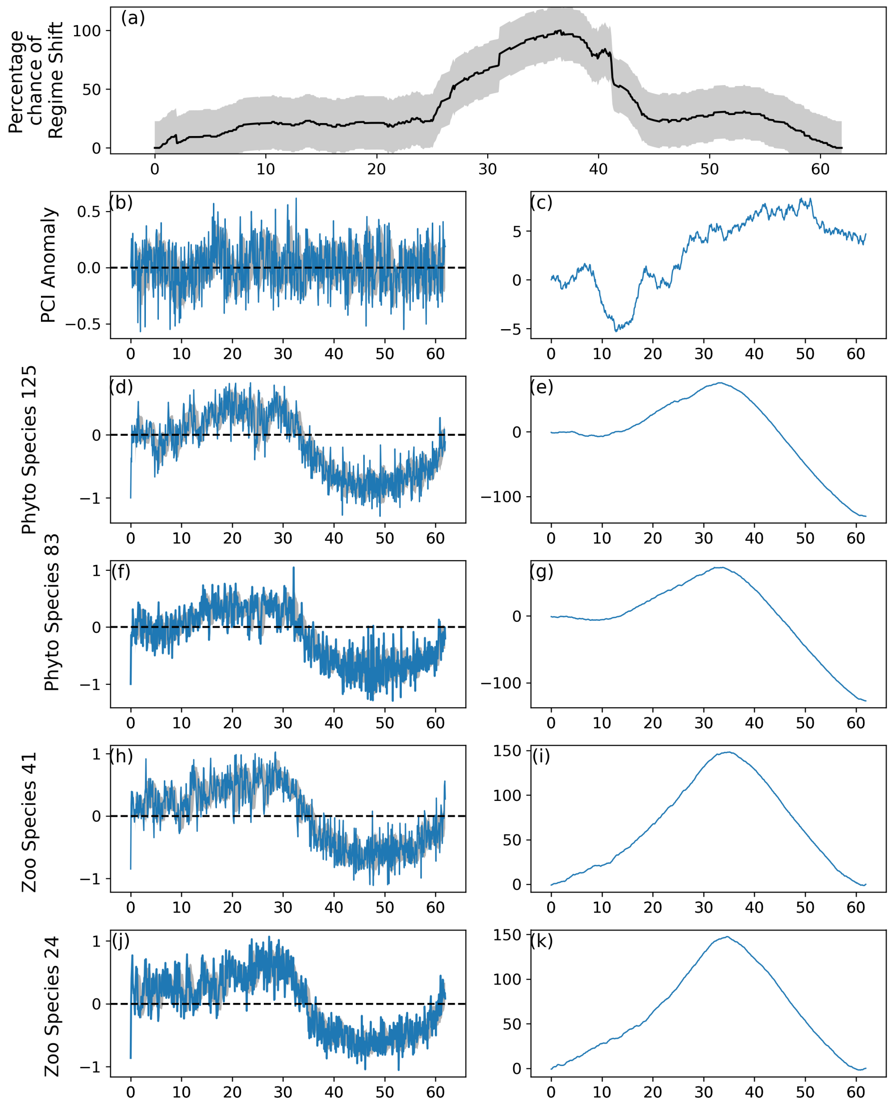

Figure 6. As for Fig. 2, except for the strength of lag-1 autocorrelation was equal to 0.1.

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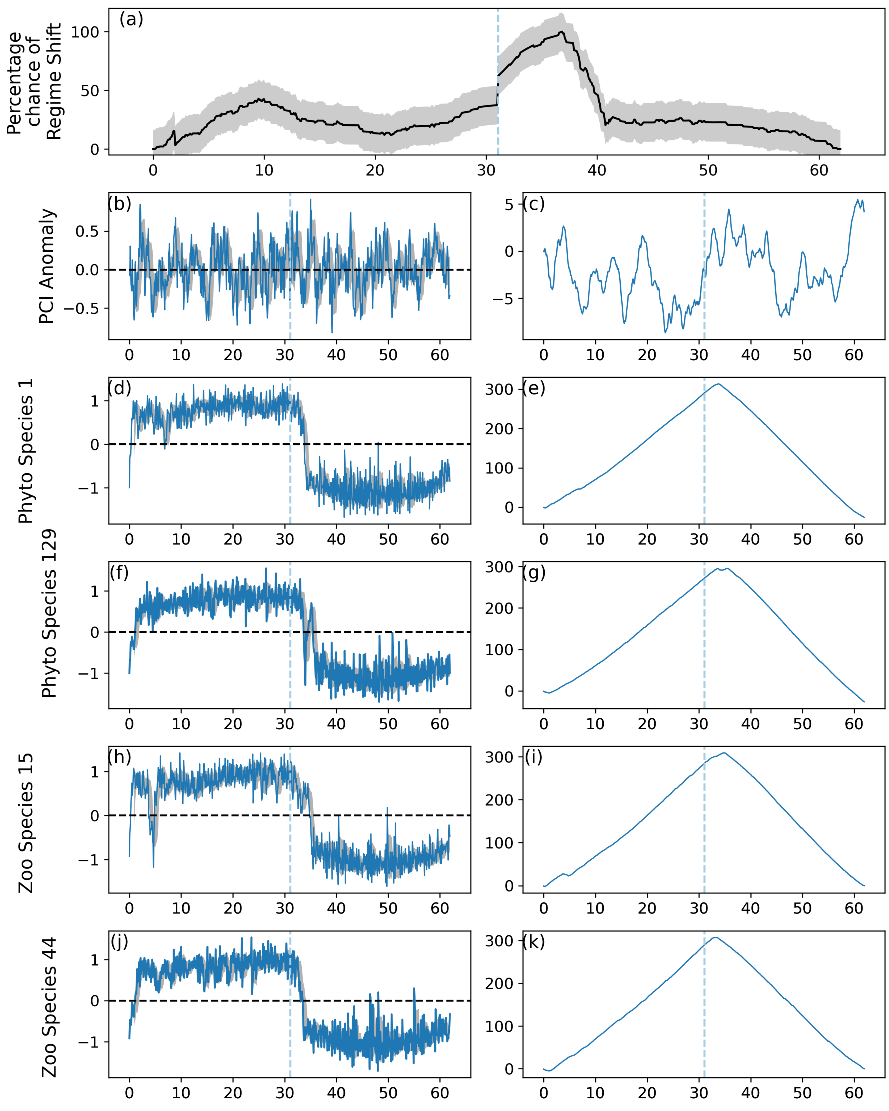

Figure 7. As for Fig. 2, except for the strength of lag-1 autocorrelation was equal to 0.725. Sudden changes can be observed in (d) - (k).

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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 percentage likelihood of a regime shift was nearly constantly high fewer species experienced abrupt changes (Fig. 2-3). 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 time series of regime shift likelihood in different North Sea regions more comparable, but results in the time series being less variable and remaining high for a long time when fewer species experience an abrupt shift (Fig. 2-3). When it is unknown how many species in an ecosystem have experienced an abrupt shift, 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.

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 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 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).

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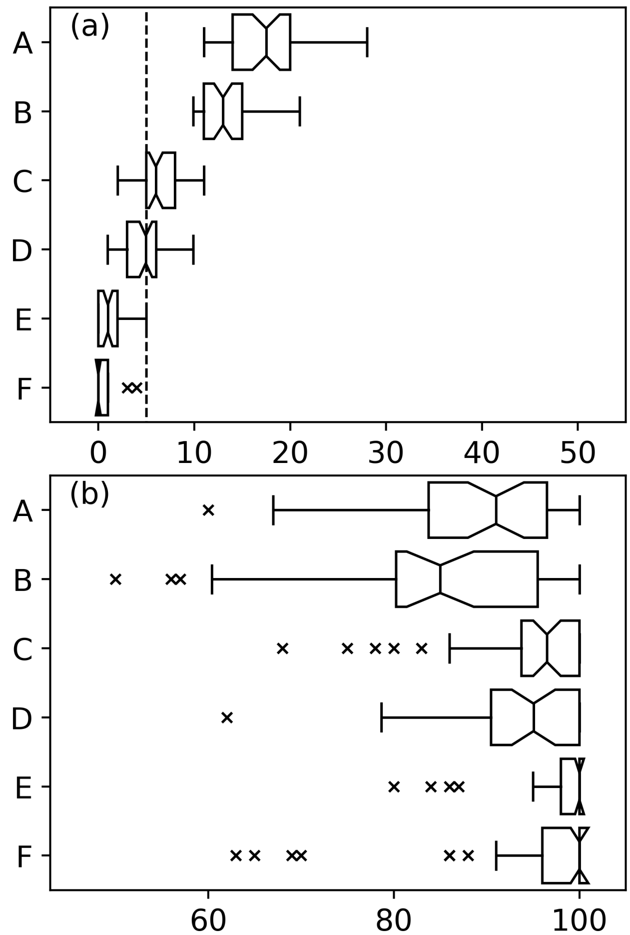

Figure 8. (a) Box plots showing the percentage of datasets of varying levels of red noise where regime shifts were identified where no abrupt changes were induced. A dashed line has been drawn at 5%. Notches on box plots which do not overlap indicate a significant difference. Different plots show datasets 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.

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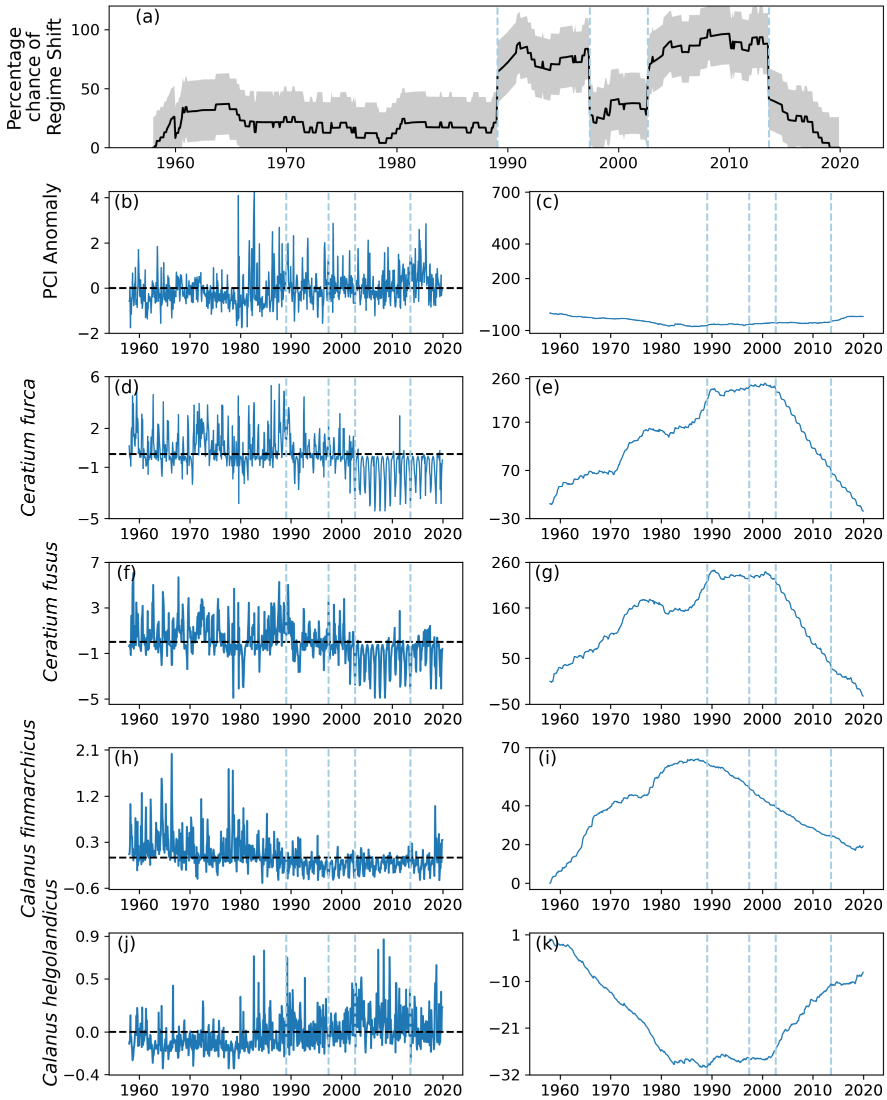

Figure 9. (a) Percentage likelihood of regime shift as estimated by the RST model for Area C1 (see Fig. 1), located between 54° and 58° North and 3° and 12° East. Individual plots show (b) PCI anomaly, abundance time series of the (b) most and (c) second most abundant phytoplankton species, abundance time series of (d) *C. finmarchicus* and (e) *C. helgolandicus*. The sample size for the entire study period in this area is 11976.

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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).

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).

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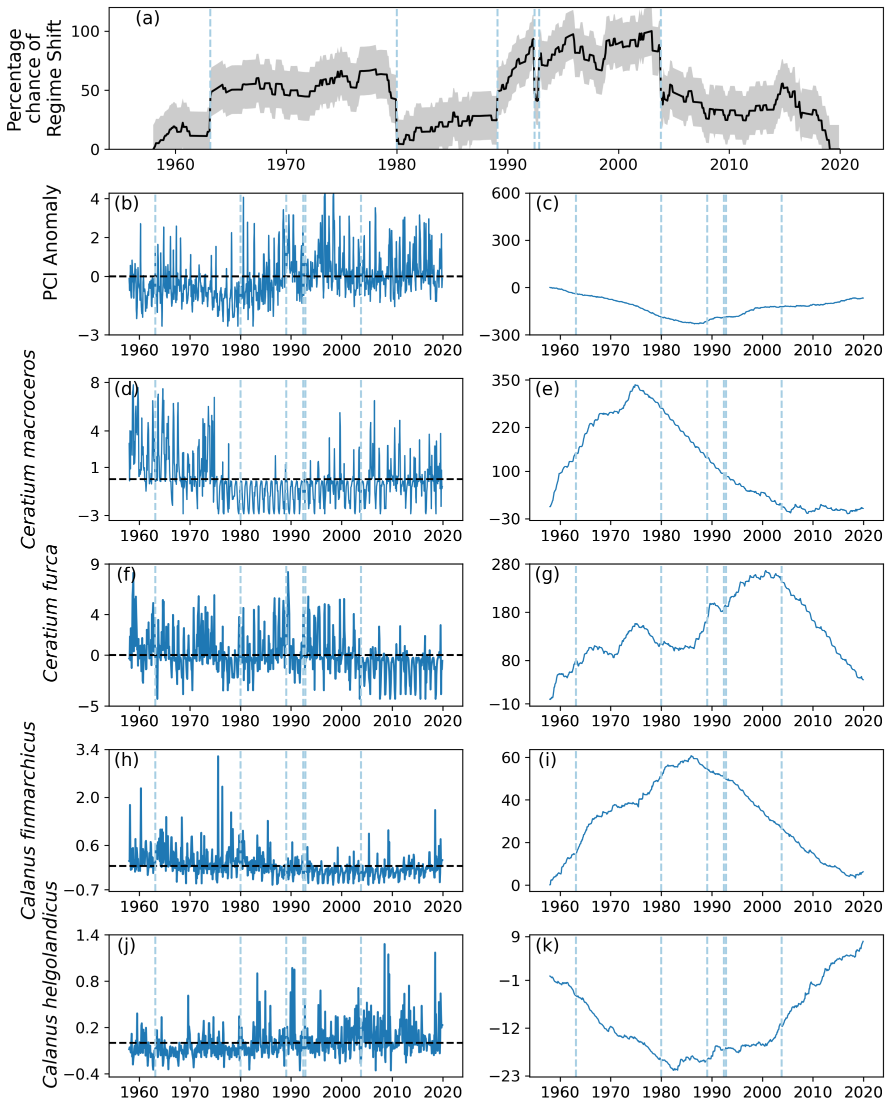

Figure 10. As for Fig. 9, but the region of interest here is Area C2 (see Fig. 1), between 54° and 58° North and between -2° and 3° East. The sample size for the entire study period in this area is 8737.

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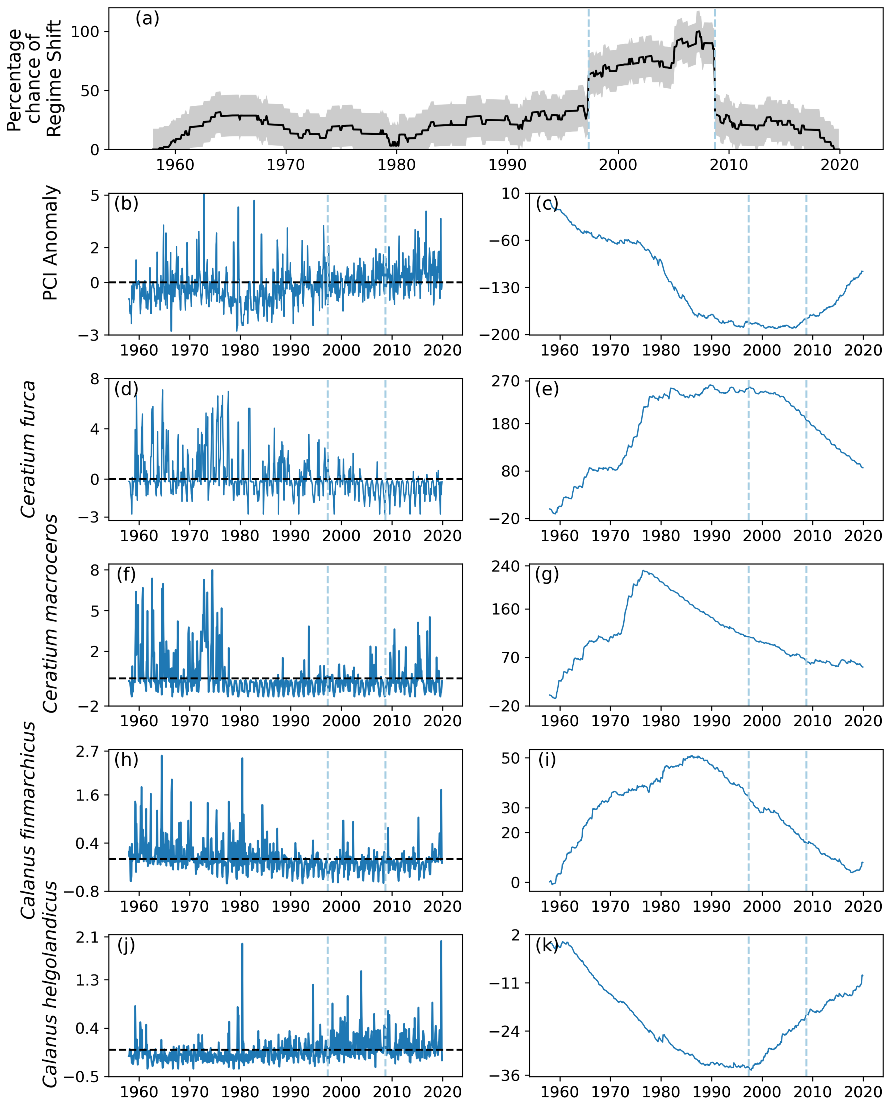

Figure 11. As for Fig. 9, but the region of interest here is Area D1 (see Fig. 1), south of 54° North and between 3° and 12° East. The sample size for the entire study period in this area is 5566.

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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 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, 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.

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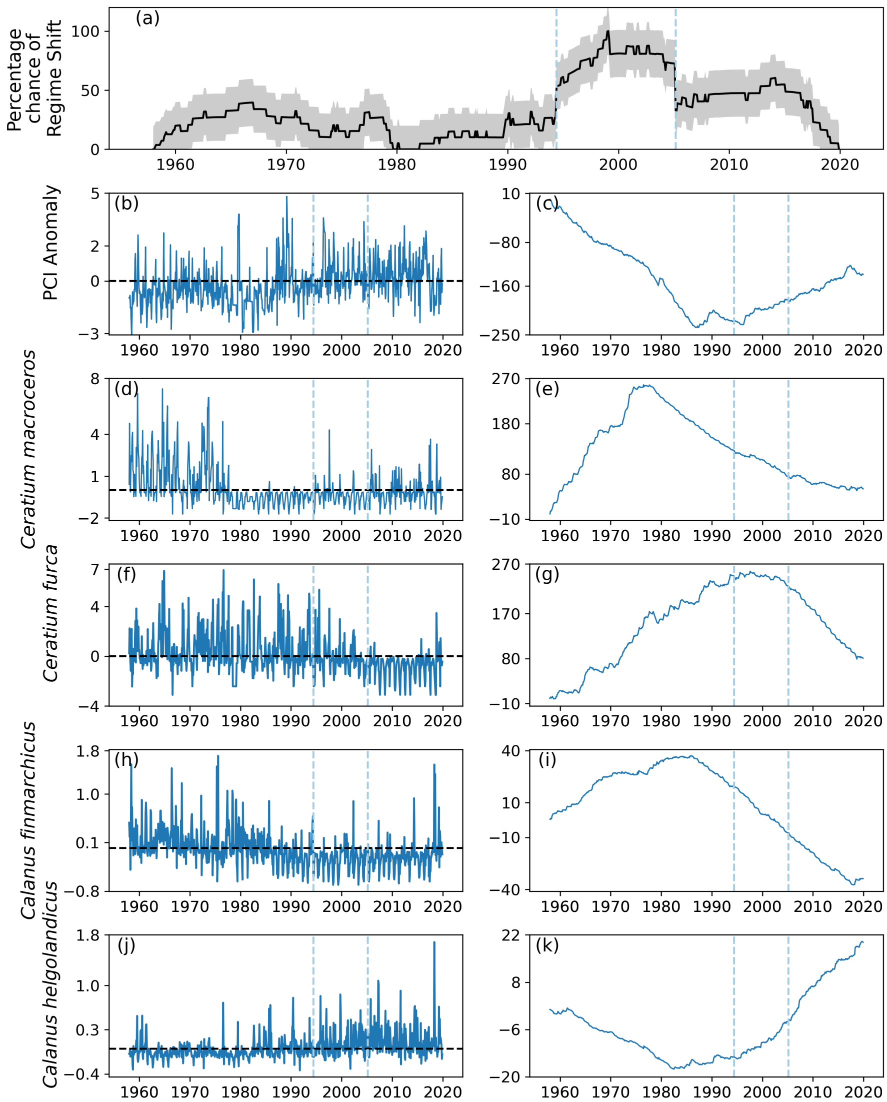

Figure 12. As for Fig. 9, but the region of interest here is Area D2 (see Fig. 1), south of 54° North and between –2° and 3° East. The sample size for the entire study period in this area is 9743.

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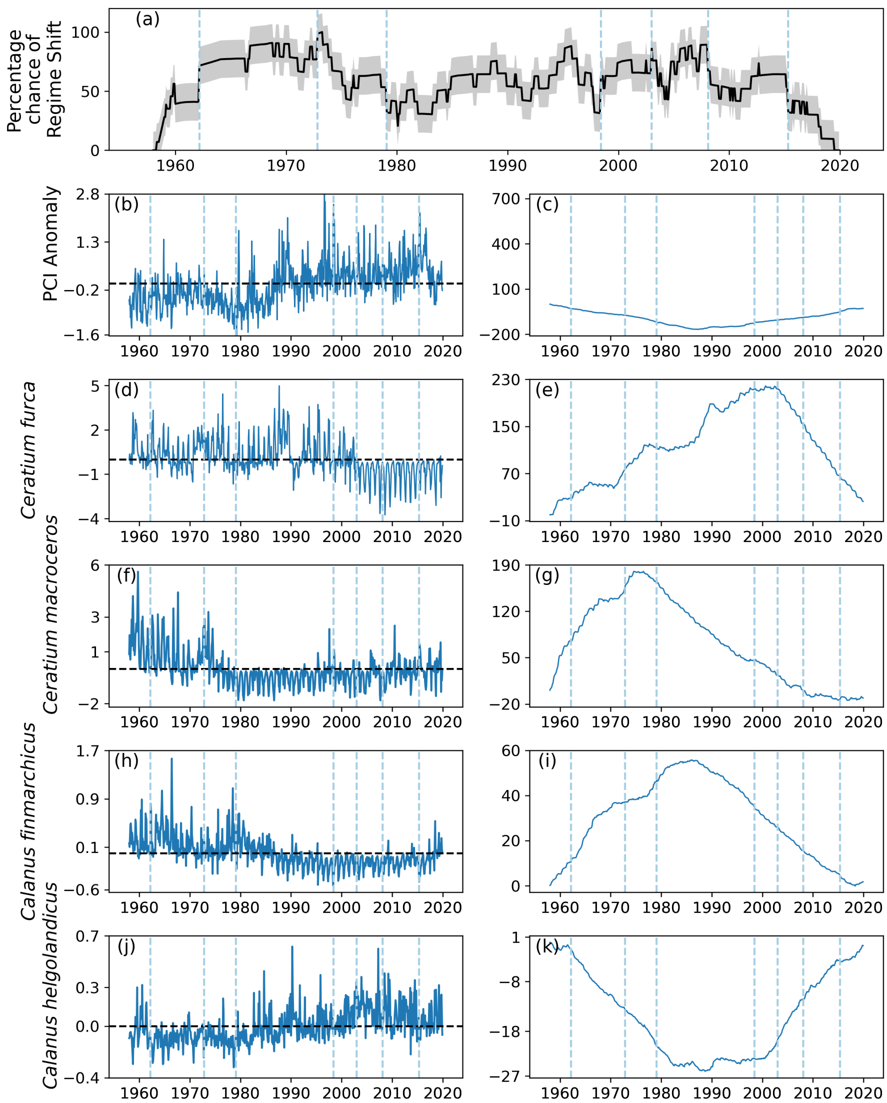

Figure 13. As for Fig. 9, but showing results of the entire North Sea (Fig. 1). The sample size for the entire study period in this area is 56745.

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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

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

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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	Regime shifts detected (positive)	Regime shifts detected (negative)
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

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 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 approach to quantify the likelihood of a regime shift in marine ecosystems occurring. 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 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.

5.1 Proof of concept

As noted by multiple studies of ecology, 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 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

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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 regime shifts (Beaugrand et al., 2014). We have shown the model is able to 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.

Approximately 14 years was found to be the minimum amount of time between abrupt shifts that the RST model was able to distinguish between different regimes (Fig. 4-5). 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 ecosystems to be established having an impact on model performance. It is likely that for abrupt changes with a smaller time period between them than this, the predicted likelihood of a regime shift will be elevated over an extended time period. Another potential issue 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 the study by Beaugrand et al. (2014), where results suggested a regime shift was present near the beginning of their study period but 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., 2020; 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 regime shifts are still identified when autocorrelation before abrupt shifts is weak or absent (Fig. 6-7). 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 validation 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 these are either false positives or false negatives (Fig. 8).

The RST model identified likely regime shifts in the North Sea, which differ slightly by area (Tables 1-2). These regime shifts 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 (Table 1). Regime shifts in the 1980s and 1990s appear to have been driven by changes in chlorophyll and the copepods *C. finmarchicus* and *C. helgolandicus* (Table 1). These

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results are consistent with previously identified regime shifts in the North Sea (Beaugrand et al., 2014; Djeghri et al., 2023; Bedford et al., 2020; McQuatters-Gollop et al., 2007), although it is difficult to make a direct comparison due to differences in methodology and 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., 1991; Kürten et al., 2013), and it is premature to conclusively identify a particular date a regime shift occurred without comparing neighboring areas. For example, an apparent regime shift involving *C. finmarchicus* and PCI occurred in the mid-west of the North Sea (area C2) during 1992, and subsequently the southwest of the North Sea (area D2) during 1994, and then in the southeast North Sea (area D1) during 1997 (Table 1, Fig. 11-12). Again, a regime shift involving the most variable phytoplankton species was identified in 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 it is difficult to confirm whether regime shifts have taken place at different times or whether plankton was advected around the North Sea system.

5.2 Apparent early warning for imminent regime shifts

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 regime shift was detected in simulated species (Fig. 3, 7) and, to a lesser extent, biological time series data. Examples include area D1 when a regime shift was identified before changes in the abundance of *C. furca* and *C. helgolandicus* (Fig. 11), and area C2 when the model identified a regime shift before discernible changes in *C. helgolandicus* or *C. finmarchicus* abundance (Fig. 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).

A possible reason for this apparent early warning of regime shifts may have been caused by abrupt changes being induced in phytoplankton and zooplankton species which were not displayed in 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 zooplankton species 15 and 44 (Fig. 7h-k). In this case, abrupt changes began to be induced in 40% of species just before 1990, and this caused the percentage likelihood of a regime shift occurring to increase. Not all abrupt changes occurred simultaneously, and the RST time series shows probability of the entire ecosystem experiencing a regime shift rather than 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

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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 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 dramatic changes in species abundance to occur without an accompanying change in regime shift likelihood, as seen in *C. finmarchicus* abundance in the entire North Sea (Fig. 13), or *Ceratium* spp. or PCI in D1 (Fig. 11). Likely reasons for these mismatches are that the RST model is designed to predict regime shifts for entire ecosystems, and changes in single species are unlikely to 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.

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 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., 2020; 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., 2020; Beaugrand and Reid, 2003; Edwards 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 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 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).

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

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the selection methodology of Ibanez and Dauvin (1998) which focused on representative species while avoiding zero inflated presence-absence counts, our method used data from all species collected by the CPR. This meant including abundance data from at least three trophic levels: phytoplankton, zooplankton, and fish larvae 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 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. When data for the entire study area was analyzed by the RST, the percentage likelihood of a regime shift taking place was highest at 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.

5.4 Robustness of regime shift detection

A recent paper looking at various different methodologies designed to detect regime shifts in marine ecosystems 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). 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 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 more species are looked at, there is a reduced likelihood of generating false positives or negatives (Fig. 8).

It has been assumed that the danger of Type II errors is greater than those of Type I errors, 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 the value of the critical gradient used to identify regime shifts in this study, but the validation tests performed in this study indicate doing so will increase the rate of false positives (Fig. 8a). Generating false negatives also entails risks. If this method is used to predict regime shifts in future scenarios, 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.

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

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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 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. 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 into one time series of regime shift likelihood necessarily removes 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 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., 2020). 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 should elucidate whether regime shifts in plankton are drivers of regime shifts in higher trophic levels, or if abrupt changes seen in more than one trophic level is coincidental.

The relatively low variability observed in regime shift likelihood for the entire North Sea when compared to the smaller subregions, 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). There are also a diverse range of hydrodynamic regimes in the North Sea, distinguished by stratification patterns and freshwater 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., 2020), 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 (pandas development 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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Competing interests. The authors have no competing interests to declare.

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