

# Recruitment regime shifts and nonstationarity are widespread phenomena in harvestable stocks experiencing pronounced climate fluctuations

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## Abstract

Methods to reliably identify jump discontinuities in biological time series and to assess the specific contribution of various covariates are rapidly progressing. Here, we took advantage of these statistical improvements as well as those seen in complementary, down-scaled climate and biogeochemical models to investigate causes of the substantial interannual variability observed in recruitment strength in hindcast analyses. This systematic meta-analysis included 23 data-rich, commercially valuable, warm- and cold-temperate stocks in the North, Norwegian and Barents Seas. Since this study focuses on recruitment strength variability, we have used the term “recruitment regime shift” to distinguish from the concept of ecosystem regime shift. The breakpoint analysis revealed that the former criterion applied to more than half of the time series, mainly with respect to North Sea stocks but also to those in the Norwegian Sea. The exploratory analysis using vcGAM indicated that 1–3 shifts per stock were real, when using five drivers spanning spawning stock biomass to large-scale climatic processes. Thus, non-stationary relationships were extensively prevalent, indicating that each stock is uniquely adapted to its locally varying conditions. Outputs from the stationary GAM resembled those from the vcGAM but not after the threshold year. In-depth case studies showed that the proxy of a given driver for the process which was to be included should be critically considered in a spatiotemporal context. Furthermore, the stock-specific uncertainty associated with the given recruitment figures as such should also be an in-built component of the model construct and thereby in the evaluation of the output.

## KEYWORDS

biophysical drivers, meta-analysis, Northeast Atlantic, time series, turning point, year-class strength

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## 1 | INTRODUCTION

Climate fluctuations, including both climate change and variability, have profound effects on marine ecosystems at various organizational levels, including individual organisms, assemblages and communities. Changes can disrupt the structure and stability of ecosystems, ultimately altering their functions and the services they provide to humans (Doney et al., 2012; Hoegh-Guldberg & Bruno, 2010; Poloczanska et al., 2013). The Northeast Atlantic, encompassing the North, Norwegian and Barents Seas, is particularly susceptible to climate change (Paasche et al., 2015). For instance, the North Sea is placed second on the list of those large marine ecosystems (LMEs) that have already warmed the most worldwide (Belkin, 2009), whilst the Barents Sea exhibits “Arctic Ocean Amplification”, with a warming rate 2.3 times higher than the global mean (Shu et al., 2022) and “Atlantification” (Ingvaldsen et al., 2021). Moreover, climate variability, driven by phenomena like the North Atlantic Oscillation (NAO), exerts substantial influence on regional environmental factors such as wind patterns, ocean currents and temperature, resulting in considerable changes within the ecosystems of the Northeast Atlantic (Loeng & Drinkwater, 2007; Parsons & Lear, 2001). Given its significance for global seafood production, this area has been the focal point in a series of studies examining climate impacts on fish stocks and fisheries (Fosshem et al., 2015; Gullestad et al., 2020; Kjesbu et al., 2022; Payne et al., 2021). Therefore, an understanding of climate-induced variability in fish populations dynamics is critical for the sustainable management of fisheries.

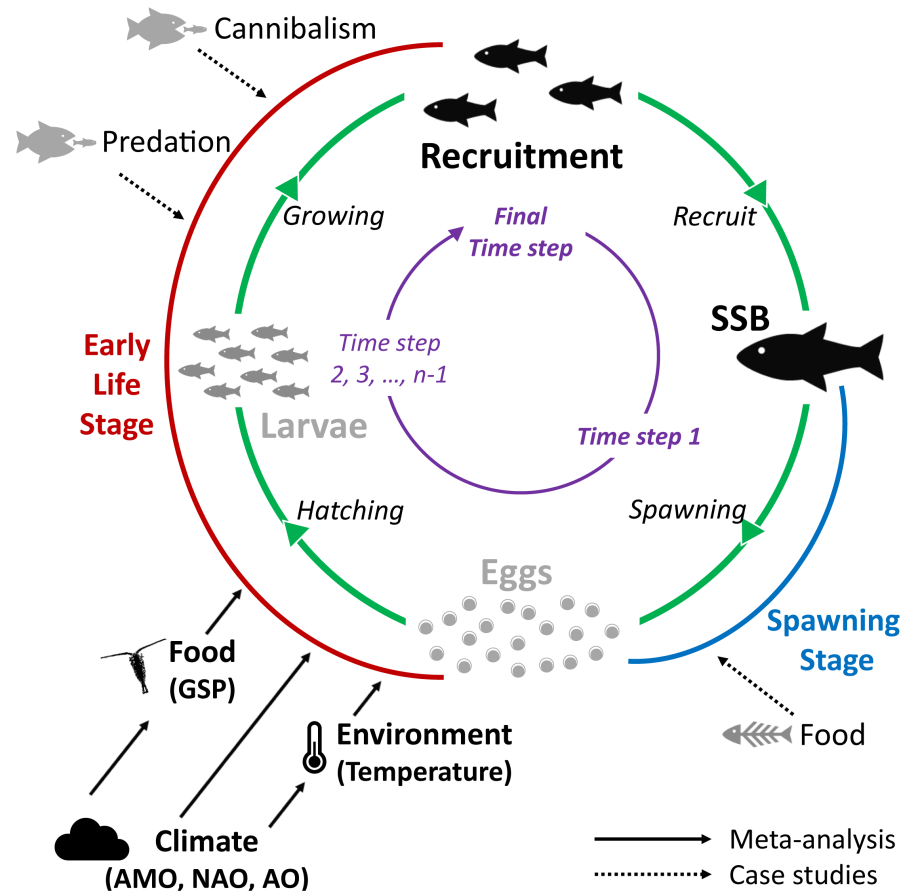
Recruitment plays a vital role in population dynamics as it reflects the number of young individuals entering the harvestable population (stock). It involves complex processes influenced by a plethora of various biotic and abiotic effectors (drivers), which have been the subject of fisheries investigation for over a century since the pioneering work of Hjort (1914). A higher spawning stock biomass (SSB) is expected to lead to better recruitment; however, this is not always the case (Szuwalski et al., 2015), as only small percentages of the variance from a relationship between SSB and recruitment can typically be explained (Cury et al., 2014; Myers & Barrowman, 1996). This inability to generally find significant relationships indicates a potential stronger influence of environmental factors on the formation of year-class strength compared to SSB per se. As an example, Munch et al. (2018) using empirical dynamical modelling found that recruitment was not related to the SSB at all in 43% out of the 185 examined stocks. Therefore, while such extensive analyses and reviews provide valuable insights into the universal principles underlying recruitment dynamics, other influential drivers than SSB obviously need to be examined. Exceptions may exist for overfished stocks which could show impaired recovery due to additional compensatory mechanisms, i.e. undergoing an Allee effect (Perälä et al., 2022).

Recruitment is the culmination of, and a critical process in the life history of marine populations, affected by complex set of external drivers which occur at different stages of ontogeny (Figure 1). Despite the shortcomings mentioned above, SSB can be considered a proxy for the stock reproductive potential but can also influence the extent of

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intraspecific competition and cannibalism, if relevant (Kell et al., 2016). Food availability (prey) significantly affects individual fecundity (Kjesbu et al., 1998) cascading to the stock reproductive potential

**FIGURE 1** Conceptual diagram illustrating how multiple drivers may impact recruitment. Terms in black bold represent factors that are consistently considered in the meta-analysis, whereas terms in grey represent factors that are additionally evaluated in the case studies. The other colours applied are for ease of reading only.



(Cooper et al., 2013). Local biotic and abiotic conditions, such as plankton productivity and temperature, can exert substantial effects on natural mortality of egg and larval stages (Cushing, 1990; Le Pape & Bonhommeau, 2015; Pepin, 1991). Moreover, large-scale climate variability, representing integrated and relatively low-frequency modes, also have considerable effects on recruitments success ( $R/SSB$ , where  $R$  is recruitment) (Lehodey et al., 2006; O'Brien et al., 2000). Finally, predation during the early-life-history stage can play a critical role in regulating recruitment levels (Bailey & Houde, 1989). All these factors contribute to the complex nature of recruitment dynamics, posing significant challenges in understanding the functional mechanisms which result in variability on survivorship of early life history stages to the eventual recruitment.

It is increasingly recognized that non-linear population dynamics are ubiquitous in animals, such as in fishes with faster-reproducing characteristics, due to the complex interactions among a long suite of biotic and abiotic drivers (Clark & Luis, 2020). The non-linear nature, particularly in recruitment fluctuation, as underlined by Munch et al. (2018) and Zimmermann et al. (2019), significantly hampers our understanding of fish population dynamics in response to multiple drivers, including climate change and variability, which have been of great concern in recent decades. In effect, traditional linear models used to explore climate–biology relationships appear inadequate when projecting long-term trends as part of management strategies. Moreover, linear methods used for short-term predictions, e.g. Northeast Arctic (NEA) cod (*Gadus morhua*, Gadidae) recruitment for the next few years

have shown large discrepancies, highlighting problems with the advice decision-making (Årthun et al., 2018; Kjesbu, Tiedemann, et al., 2023; Stiansen et al., 2005). In addition to the non-linear effects of multiple drivers on population dynamics, the relationships tend to exhibit non-stationary patterns over time. These non-stationary driver–response relationships, which involve potentially changing drivers, directions and strengths, have been observed worldwide across multiple populations and communities (Litzow et al., 2018, 2019; Ma et al., 2021, 2023). Undoubtedly, non-stationary relationships further limit the utility of conventional statistical models based on stationary assumptions to explore driver–response relationships and make forecasts, particularly in the context of climate-induced population dynamics (Dormann et al., 2013; Williams & Jackson, 2007). Therefore, exploring the non-linear effects of multiple drivers and their non-stationary characteristics should be a research priority to enable more accurate forecasting of population dynamics and the development of effective management strategies.

Understanding the impacts of multiple drivers, particularly those related to climate, on recruitment variability is crucial for informing fisheries management strategies. A potential approach is to use process-based ecosystem models, which synthesizes existing observational and experimental knowledge into a numerical framework (Hjøllo et al., 2021). However, these are often unavailable due to their extremely high level of sophistication. Also, statistically advanced studies that systematically examine the observed patterns in recruitment strength across different stocks, especially in the context of

biophysical drivers, are generally scarce in the existing literature. Our study aims to fill the latter knowledge gap by focusing on the Northeast Atlantic, an area characterized by its unique history of continued, extensive accumulation of fishery, environment and climate data (Kjesbu et al., 2022; Trenkel et al., 2014). To achieve our objectives, we explore a range of models, including climate, biogeochemical and statistical models. A meta-analysis across 23 stocks was conducted to identify stock-specific responses to hypothesized important drivers. More specifically, this investigation examined long-term trends, any discontinuities and non-stationary relationships in a coherent fashion. Additionally, case studies – selecting one key stock in each LME, as specified below – were undertaken to reveal finer-scale responses to biotic and abiotic drivers over different time scales. These case studies allow us to explore elusive and unexpected responses that were first identified in the meta-analysis. By combining these approaches, this study aims to advance the principal understanding of the statistical role of recognised key covariates (Figure 1) in determining the recruitment dynamics of harvestable marine stocks.

## 2 | METHODS AND MATERIALS

### 2.1 | Study areas and targets

The geographical area examined is the Northeast Atlantic, with the North, Norwegian and Barents Seas (Figure 2). A total of 23 harvestable stocks were analysed; 6 stocks distributed in the Barents Sea (consisting of 4 stocks in Atlantic waters and 2 stocks in Arctic waters), 5 stocks in the Norwegian Sea (consisting of 2 stocks in coastal waters and 3 stocks in oceanic waters) and 12 stocks in the North Sea (see Table S1).

### 2.2 | Data

#### 2.2.1 | Biological data

Biological data, including recruitment age, recruitment abundance (hereafter recruitment) and spawning stock biomass (SSB), were extracted from ICES Stock Assessment Database (ICES Stock Assessment Database, 2022) and IMR-PINRO reports (<https://www.hi.no/hi/nettrapper?query=&serie=imr-pinro>). Recruitment success was calculated as recruitment divided by SSB (Zimmermann et al., 2019). The associated length of the examined time series varied from about one- to three-quarters of a century, including recent assessments (2020–2021) (Table S1).

#### 2.2.2 | Environmental data

Water temperature ( $T$ , °C) and gross secondary production (GSP,  $\text{gC}/\text{m}^2$ ) were considered key explanatory factors (Kjesbu et al., 2022).  $T$  values were taken from Nemo-NAA10km, which is a regional configuration

of the ocean model NEMO (Nucleus for European Modelling of the Ocean), forced by physics from the global Norwegian Earth System Model version NorESM2-MM (Bentsen et al., 2013), covering in this case the North Atlantic north of 40°N (including also the North Sea and the Arctic Ocean) at 10km resolution (Hordoir et al., 2022). GSP values, defined as annual zooplankton (including Calanidae) production excluding loss processes (i.e. total amount of phytoplankton eaten), originated from the biogeochemical model NORWECOM.E2E (The NORwegian ECOlogical Model system End-To-End) (Skogen et al., 2018) forced by the NEMO physics. Time series for eight (geographical) polygons (Figure S1) from January 1970 to December 2019 were established. Winter (December–March)  $T$ , averaged from 0 to 200m (within each polygon), was used as proxy for thermal conditions, whereas annual (January–December) GSP, integrated from 0 to bottom (within each polygon), reflected zooplankton productivity.

### 2.2.3 | Climatic data

The Atlantic Multidecadal Oscillation (AMO), North Atlantic Oscillation (NAO) and Arctic Oscillation (AO) were chosen to represent large-scale climate variability patterns in the North Atlantic and Arctic oceans at different temporal scales (Knight et al., 2006; Rigor et al., 2002; Wanner et al., 2001), i.e. with AMO referring to multidecadal-scale variability, while NAO and AO to decadal-scale variability (Table S2). Once again, winter averages (December–March) were calculated and used in the following analyses, extended backwards to 1950 (from 2021).

## 2.3 | Data analyses – meta-analysis

A suite of statistical approaches – differing in script complexity and focal outputs (Table S3) – were consulted in R (R Core Team, 2022) to primarily explore recruitment regime shift and nonstationarity across 23 stocks, taking into account uncertainty in the data.

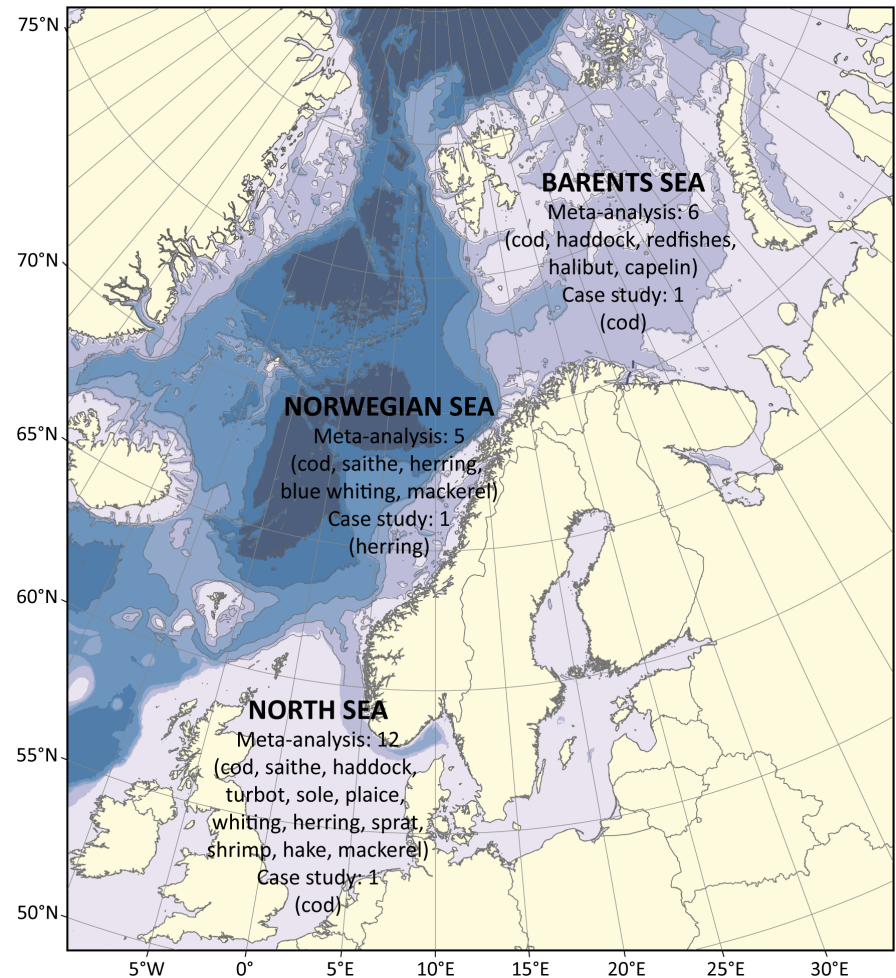
### 2.3.1 | Correlation analysis

Pearson correlation analyses were applied to detect any linear relationships among climatic, environmental and biological parameters. Any potential presence of autocorrelation (in all variables used for correlation analysis) was consistently evaluated, and the number of degrees of freedom obtained from significance tests were adjusted accordingly (Pyper & Peterman, 1998). Analyses were conducted by the “psych” package (Revelle, 2017).

### 2.3.2 | Breakpoints analysis

To identify any “recruitment regime shift” across years, defined as a dramatic and abrupt change in recruitment which remains

**FIGURE 2** The Northeast Atlantic, encompassing the North, Norwegian and Barents Seas. Text inserts show the stocks considered in the meta-analysis and case studies.



persistent over time, adjusted from the concept of ecological regime shift by Conversi et al. (2015), we applied the “strucchange” package (Zeileis et al., 2002, 2003). Within this breakpoint analysis, the minimal segment size ( $h$ ) was set to 20% of the time series (Table S1). The number of recruitment regime shifts, restricted to 0–4, were quantified using the Bayesian Information Criterion (BIC). The 95% confidence intervals were also estimated and used for auxiliary judgment of the reliability of the noted recruitment regime shift in question. The breakpoints analysis was also applied to climatic indices and environmental variables for identification of any phase change and abrupt state shift, respectively. Hence, for climatic indices, the annotated phase change was more gradual over time than for a shift.

### 2.3.3 | Stock–recruitment relationship

Ricker (1954) and Beverton–Holt (Beverton & Holt, 2012) models were fitted to evaluate stock–recruitment relationships and any density-dependent effects, an underlying principle within both model constructs. The data were fitted by the “FSA” package (Ogle et al., 2022).

### 2.3.4 | General additive model (GAM) and variable coefficient GAM (vcGAM)

To further explore relationships between recruitment dynamics and density-dependent and density-independent drivers, GAMs were fitted in the first instance, i.e. assuming a stationary and additive relationship between the response variable and the selected explanatory variables. The former was set to be recruitment and the latter were SSB, T, GSP, AMO, NAO and AO (Section 2.2), with time lags equal to recruitment age of the stock, formulated as

$$\text{Recruitment} = \alpha + \sum_{i=1}^n s(x_i) + \varepsilon \quad (1)$$

where  $s$  is smooth function with a thin plate regression spline and an effective degree of freedom less than 3 to avoid overfitting (relaxed to 4 and 5 in case studies, Section 2.4) (Wood, 2003),  $\alpha$  and  $\varepsilon$  are intercept and error terms, respectively, and  $x_i$  is the explanatory variables under examination. Model specification was achieved by running a full GAM, keeping thereafter those explanatory variables with a significant effect on recruitment, considering the level of uncertainty (Section 2.3.5). Variables with 95% of bootstrap-derived  $p$  value ( $p_{95}$ ) less than .10 were identified as significant ones.

To handle any non-stationary and non-additive relationships, we subsequently moved to vcGAM, formulated as

$$\text{Recruitment}_t = \begin{cases} \alpha_1 + \sum_{i=1}^n s_1(x_i) + \varepsilon_t, & t \leq \text{threshold year}_1 \\ \alpha_1 + \sum_{i=1}^n s_2(x_i) + \varepsilon_t, & \text{threshold year}_1 < t \leq \text{threshold year}_2 \\ \dots & \dots \\ \alpha_1 + \sum_{i=1}^n s_j(x_i) + \varepsilon_t, & t > \text{threshold year}_{j-1} \end{cases} \quad (2)$$

where the threshold years separate different periods with different driver-response relationships, with the other term definitions and initial settings being the same as in the corresponding GAM. The number of threshold years ranged from 1 to the number of detected recruitment regime shifts (if no recruitment regime shift occurred, the number was set to 1). Candidates of threshold year were required to ensure that the separated periods represented at least 20% of the length of the time series (e.g. candidates ranged from the 20th to the 80th of the whole time series in the case of one threshold year). Threshold years were estimated by traversing all candidates, based on considerations of square of  $R$  ( $R^2$ ), adjusted square of  $R$  ( $R_{adj}^2$ ), corrected Akaike information criterion ( $AIC_c$ , accounting for any small sample size) and the generalized cross validation score (GCV) of the model run (Casini et al., 2009). Generally, threshold years were identified as the years which got consensus by at least three of these four information criteria. In exceptional cases,  $AIC_c$  and GCV were given priority, as specified. Best model (among models with different numbers of threshold years) was also selected based on the aforementioned principles.

GAM and vcGAM were run by the “mgcv” package (Wood, 2011; Zuur et al., 2009). The 3-year-moving-average datasets were used to decrease interannual variability and improve model fitness (Walters & Hilborn, 2005). The detection of a recruitment regime shift was solely based on the corresponding recruitment time series (cf. Section 2.3.2), whereas for nonstationarity and the associated threshold, this detection was achieved by examining the specific relationship between recruitment and driver time series (cf. Section 2.3.4).

### 2.3.5 | Dealing with uncertainty

To, as far as possible, handle any potential bias within the stock assessment as such (Brooks & Deroba, 2015), the recruitment and SSB datasets were resampled 1000 times from their confidence intervals using bootstrapping to get the candidate time series, and then the candidate time series were used in the above analyses to get the statistical distributions of critical information criteria. In addition, these randomly resampled candidate time series should reduce the risk of detecting spurious significance resulting from autocorrelation, where the statistical distributions of critical information criteria provided additional support for evaluating the significance of explanatory variables. These uncertainties analyses

formed an integral part of the above-mentioned breakpoints analysis, GAM and vcGAM.

## 2.4 | Data analyses – case studies

One key stock – in terms of ecosystem functioning and fisheries interests – was selected from each of the three LMEs in question: Northeast Arctic (NEA) cod in the Barents Sea, Norwegian spring-spawning (NSS) herring (*Clupea harengus*, Clupeidae) in the Norwegian Sea and North Sea (NS) cod in the North Sea (Gullestad et al., 2020). In the case of North Sea cod, the data used here are from the pre-2023 perception of this stock (ICES, 2023). The successively undertaken comprehensive analyses within each case study were based on to the availability of overlapping time series for both the stock and the drivers of interest, labelled as time series of relatively long, intermediate and short length. Therefore, in addition to the data used in the meta-analysis, extra datasets were collated to provide more in-depth understandings on recruitment dynamics of the targeted stock.

### 2.4.1 | Northeast Arctic (NEA) cod

In the long-term investigation on recruitment dynamics of NEA cod (at age 3 years), the before-during-World War 2 (WW2) recruitment and SSB data of Hysten (2002) (1913–1945) were added to the corresponding post-WW2 data of ICES (IMR-PINRO) (1946–2021) (Table S1), altogether a time series covering the period from 1913 to 2021. The time series of Hysten (2002), however, does not have any estimation of uncertainty which limits its usefulness in certain model situations (see below). Annual mean temperatures at 0–200 m depth in the Kola Section (Kola temperature) – running along the 33°30' E meridian from 70°30' to 72°30' N and covering the period from 1921 to 2020 – were extracted as an index for the long-term thermal change in the Barents Sea (Boitsov et al., 2012; Kjesbu, Alix, et al., 2023). Winter AMO and NAO from 1921 to 2021 were added to this data inventory to represent large-scale climate variability (Section 2.2.3). Moving (rolling) correlations (1921–2021) were estimated to reveal any non-stationary pattern between recruitment and SSB, between recruitment and Kola temperature, as well as between Kola temperature and climatic indices. Different moving windows, i.e. 9, 11, 15, 21 and 25 years were used to provide robust inference (Kjesbu et al., 2014; Litzow et al., 2018).

For the intermediate perspective (1973–2019) on NEA cod recruitment, we conducted GAM and vcGAM bringing in modelled T (instead of Kola temperature) and GSP as additional explanatory variables. Thus, this study mimicked the one undertaken in the meta-analysis but strengthened by the extended use of bootstrapping techniques (Section 2.3.5) to explore the robustness of each curve fitting, split in the vcGAM by any associated threshold value (Section 2.3.4). As in the meta-analysis, 3-year-moving-average datasets were used.

In the further updated GAM, applied to a shorter time span (1992–2019), we included seven additional, likely relevant explanatory variables: (i) NEA cod 0-group abundance and (ii) 0-group total length from field surveys (Skjoldal et al., 2022); (iii) total biomass of capelin (*Mallotus villosus*, Osmeridae) divided by SSB of NEA cod (food availability) (Kjesbu et al., 1998); cannibalism represented by either (iv) consumption of cod by cod (Bogstad & Mehl, 1997; ICES Stock Assessment Database, 2022) or by (v) immature cod, estimated as TSB (total stock biomass) minus SSB and, finally, (vi) predation represented by SSB of Northeast Atlantic mackerel (*Scomber scombrus*, Scombridae) or (vii) Norwegian spring-spawning herring. Thus, we assumed that mackerel – due to their recent extended poleward migration, including along the Norwegian coast – would include cod larvae in their diet along with, e.g. herring larvae as proven by genetic markers (Allan et al., 2021), i.e. in the drift part of both stock's offspring (Endo et al., 2023). Furthermore, we assumed that young and adult herring could possibly feed upon cod larvae in the overlapping distribution area (Hamre, 1994; Tiedemann et al., 2021). Original datasets (without any moving average) were consulted, a forward-step model specification was constructed and the maximum number of explanatory variables set to 3 to avoid overfitting. The vcGAM was not conducted in the sub-case study because of the short time length available.

## 2.4.2 | Norwegian spring-spawning (NSS) herring

For the long-term investigation on NSS herring, the full recruitment (at age 2 years) time series covered the period from 1907 to 2017 (Stenevik et al., 2022). These data, however, did not include any estimation of uncertainty, in contrast with those from the ICES assessment outputs (1988–2021) (Table S1). In the overlapping time segment, the reported, overall figures on recruitment strength per year appear similar ( $r = .99, p < .001$ ). In effect, the full time series was applied to address any recruitment regime shift by the breakpoints analysis (Section 2.3.2), but thereafter giving special attention to those results given with confidence intervals.

The following in-more-depth examination of NSS herring recruitment dynamics was applied to the time series of relatively short length (1990–2019). As a start, the usual “quintet” of drivers was considered using GAM and vcGAM fitting procedures, with 3-year-moving-average data sets, as for the meta-analysis. After that, the influences of NSS herring 0-group abundance and total length (Skjoldal et al., 2022), food availability indicated by GSP

divided by SSB of NSS herring, and predation represented by SSB of Northeast Atlantic mackerel (Section 2.4.1) were collectively analysed, using original data sets. The same type of forward-step model specification was undertaken as in Section 2.4.1. The vcGAM was not conducted because of the short time length.

## 2.4.3 | North Sea (NS) cod

As pointed out by Beaugrand et al. (2003) and Kjesbu, Alix, et al. (2023), recruitment of NS cod (at age 1 year) is closely related to the abundance of *Calanus finmarchicus* (Calanidae). We therefore replaced the above modelled GSP outputs (Section 2.2.2) with corresponding observations on *C. finmarchicus* abundance given by the Continuous Plankton Recorder (CPR) survey (<https://doi.org/10.17031/1758>), followed by running revised GAM and vcGAM of intermediate time length (1971–2019), using 3-year-moving-average data sets. In advance, we tested any presence of recruitment regime shifts in a longer perspective (1963–2021), complemented with recruitment versus SSB plots, i.e. using an analogous methodology as in the two previous case studies (Sections 2.4.1 and 2.4.2).

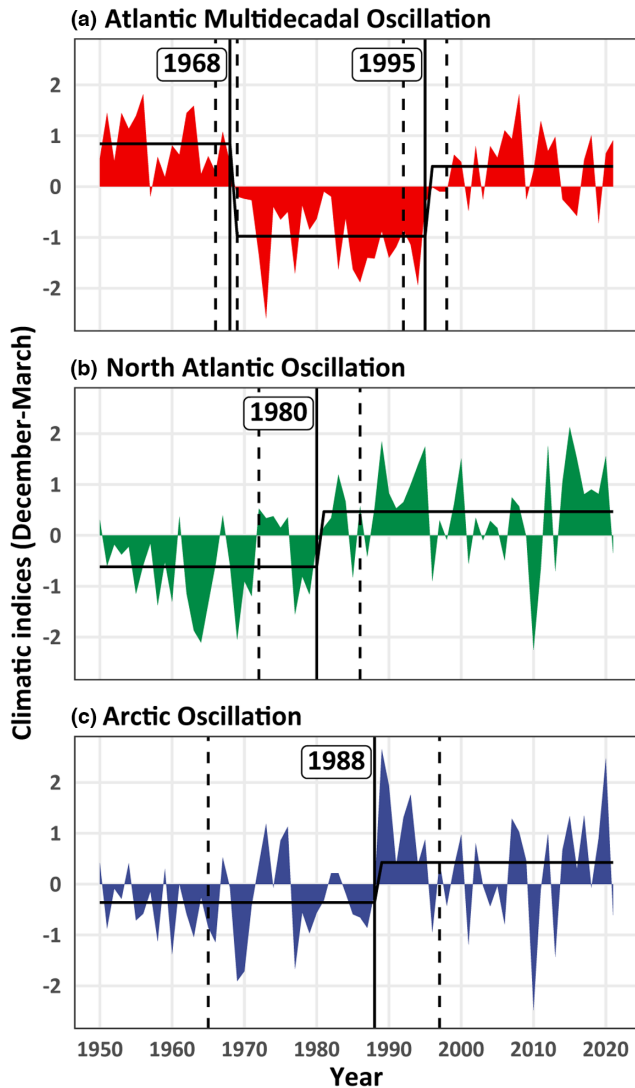
# 3 | RESULTS

## 3.1 | Biophysical drivers

The observed, longer-term modal variability (1950–2021) of the AMO, NAO and AO (Table S2) naturally come with phases of varying time length that are below or above the historic mean (Figure 3). For T and GSP, this sort of BIC defined breakpoint indicated step-wise increases (1970–2019), in several cases taking place abruptly (Figure 4).

Each of the three climatic indices showed considerable variability, both within and between phases (Figure 3). Overall, the AMO exhibited a positive phase in the 1950s and 1960s, becoming a negative phase which lasted until the mid-1990s, and then was followed by a predominately positive phase. Superimposed on these multi-decadal patterns, two phase changes were statistically identified, around 1968 and 1995. Both had narrow confidence intervals (CI), suggesting confidence in their presence. There was a phase change in the NAO around 1980 but with a relatively broad CI. The change was going from a generally negative to a generally positive phase and the latter reflects more persistent westerly winds in the Northeast Atlantic (Table S2). For the AO, a phase change appeared to have occurred around 1988. This was associated with an extremely broad CI. In principle, this type of change should indicate an increased prevalence of a stronger belt of wind around the Arctic (Table S2). So, the more recent climatic situation in the Northeast Atlantic is comparatively windy, coinciding with a warm phase.

Within the Northeast Atlantic (1970–2019), T in the eight polygons (Figure S1) cooled until the mid-1980s but then started to warm (Figure 4a). This bifurcated pattern was not detected within



**FIGURE 3** Trajectories and phase change patterns of climatic indices (1950–2021). Horizontal lines represent the phase means of the index, and vertical solid and dashed lines indicate the years of phase change and their corresponding 95% confidence intervals, respectively. All climatic indices are presented on relative y-axis scales.

the Barents Sea Polar, however there has been a recent increase in T. The alternative use of T averaged over 0–50m instead of over 0–200m gave similar insights (Figure S2). The eight T curves presented here could be grouped into three categories: cold (Barents Sea Polar and Barents Sea Arctic), moderately warm (Barents Sea Coast, Barents Sea Atlantic and Norwegian Sea Oceanic) and warm (Norwegian Sea Coast, North Sea Oceanic and North Sea Coast) (Figure 4a). Abrupt shifts in the eight polygons were detected either once (in six cases) or twice (in two cases), depending upon polygon, and higher latitudes featured the larger relative increase in T (Figure 4a). The T values within the same geographical region mimicked each other ( $r \geq .76$ ,  $p < .001$ ), e.g. between Norwegian Sea Oceanic and Norwegian Sea Coast ( $r = .76$ ,  $p < .001$ ) and between North Sea Oceanic and North Sea Coast ( $r = .92$ ,  $p < .001$ ).

All polygon-specific GSP estimates displayed a positive trend (1970–2019), except for the North Sea Coast (of Norway) showing no clear trend. Single abrupt shifts dominated, as this event was seen in 5 out of 8 polygons (Figure 4b). Generally, GSP levels ( $\approx 30\text{--}300\text{ gC/m}^2/\text{year}$ ) decreased in a northward direction; however, the Norwegian Sea Coast had the highest values. Barents Sea Polar and Barents Sea Arctic presented the strongest increase, with marked abrupt shifts in the late 1980s and mid-2000s. In the Barents Sea Coast, an abrupt shift occurred in the early 2000s, about twenty years after the one that occurred in the Barents Sea Atlantic. The latter largely coincided with the synchronous shifts in the mid-1980s in the Norwegian Sea Oceanic. For the Norwegian Sea Oceanic, yet another abrupt shift occurred in the early 2000s, which also happened in the Norwegian Sea Coast and North Sea Oceanic. The single, negative abrupt shift seen for North Sea Coast occurred in the late 1990s. Overall, GSP shifts along the main route of the North Atlantic Current occurred at the same time in the 1980s, spreading a few years later to the North Sea and, finally, to the coastal and farthest northern part of the Barents Sea in the 2000s (Figure 4b). This chronology resembles what was observed for the abrupt shifts of T (Figure 4a).

Statistical collinearity clearly existed between several of the climatic indices or environmental variables (Figure S3). NAO and AO appeared highly positively correlated while not significantly associated with AMO (Figure S3a). Consequently, AO was excluded in the subsequent model runs to reduce the collinearity issues. Furthermore, NAO (and AO) showed significant relationships with 5 polygon-specific T and GSP (Figure S3b). The correlation coefficient between T in different polygons generally became less with geographical distance (Figure S3c). This pattern was less clear in the between-GSP comparisons (Figure S3d). Except for Barents Sea Atlantic, the results on GSP in this high-latitude ocean basin indicated widespread links with those for T elsewhere in the Northeast Atlantic study region, though not so with the North Sea Coast T (Figure S3e).

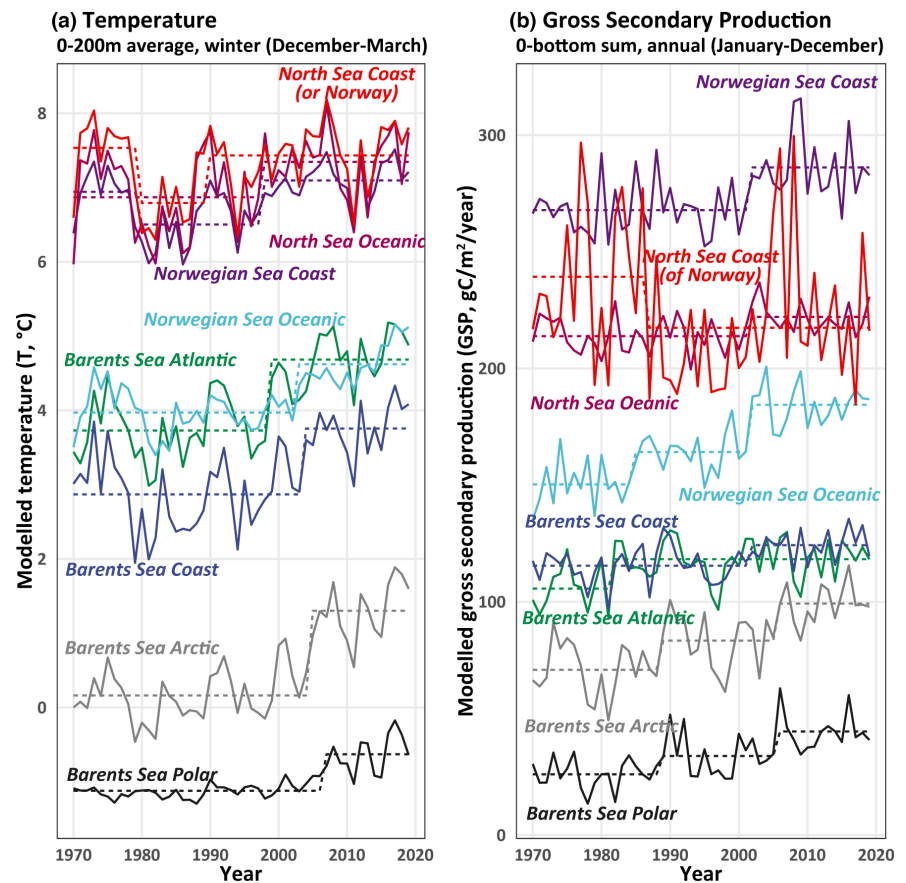
## 3.2 | Meta-analysis

### 3.2.1 | Recruitment regime shift and direction

In total, 15 out of the 23 stock time series contained recruitment regime shifts, reflecting either improved or reduced recruitment strength or alternations over time (Figure 5a). Recruitment regime shift years were relatively robust to the associated uncertainty in recruitment estimates from the stock assessment, since consistency (high frequency of the shift year) was detected when using bootstrapped recruitment time series (Figure S4). Stocks in the North Sea showed the highest proportion of recruitment regime shifts, with 9 out of 12 stocks showing this statistically defined phenomenon within the available length of the time series. However, most of these stocks displayed only one shift, concentrated either around 1980 or 2000. In this shelf sea, negative and positive recruitment regime shifts generally took place in parallel



**FIGURE 4** Modelled temperature (a) and gross secondary production (b) in eight polygons covering the study areas in the Northeast Atlantic (1970–2019, Figure S1). Solid and dotted lines represent original trajectories and state means, respectively.

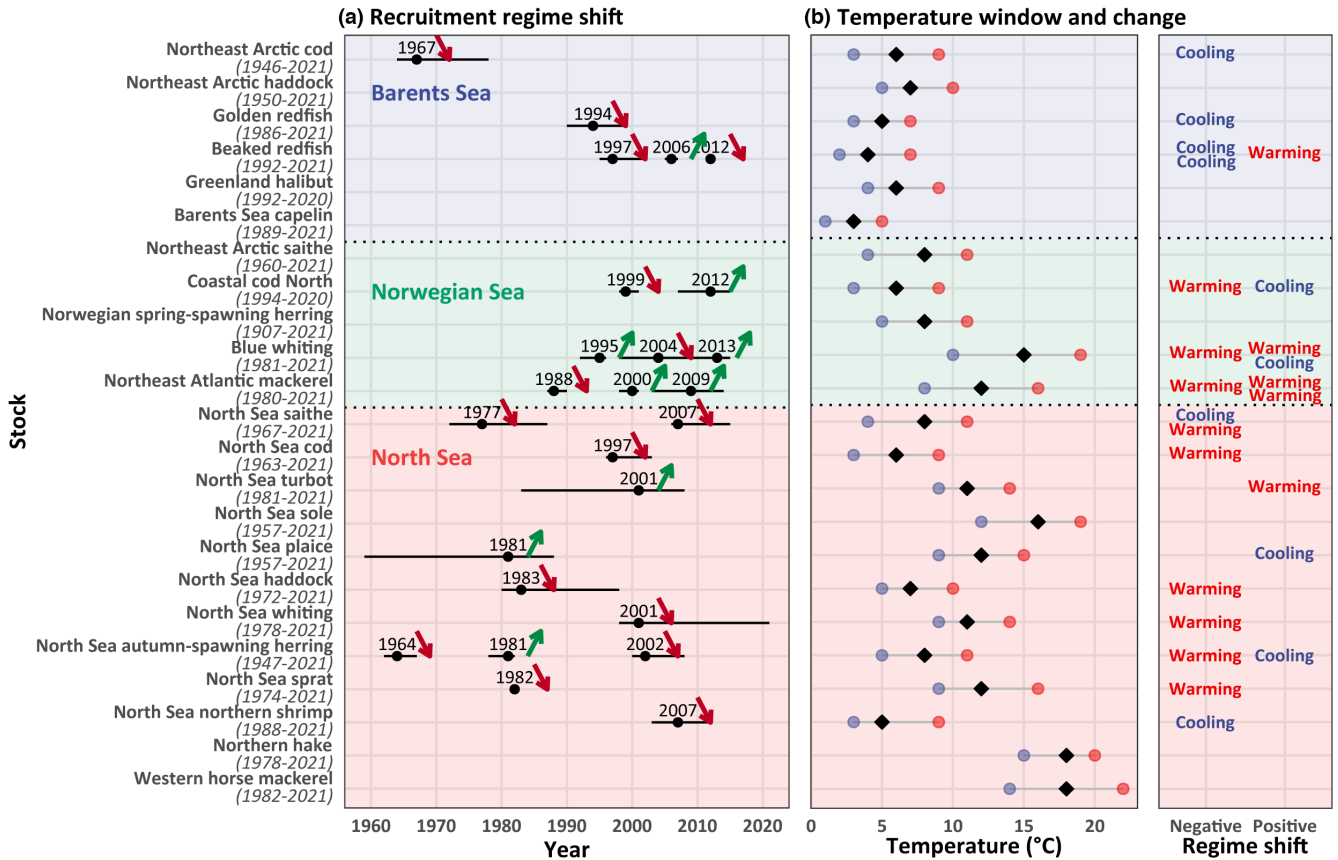


with warming and cooling  $T$ , respectively (Figure 5b). In contrast, 3 out of 5 stocks in the Norwegian Sea showed recruitment regime shift two or three times and then most frequently around 2000 and 2010. The generality of these recruitment regime shifts was more difficult to discern in relation to changes in  $T$ , but, as always, depended upon the stock in question (Figure 5b). For the Barents Sea, 3 of 6 stocks were identified with recruitment regime shifts over approximately the same two recent time windows as indicated for the Norwegian Sea, with negative recruitment regime shifts typically coinciding with cooling  $T$  (Figure 5b). This was the reverse of pattern outlined for the North Sea. The single recruitment regime shift of NEA cod occurred as early as in 1967. In addition, other stocks with exceedingly long time series ( $\geq \approx 75$  years), North Sea autumn-spawning herring underwent a regime shift in 1964 followed by another two later, whereas NSS herring showed no trace of any recruitment regime shift.

### 3.2.2 | Recruitment patterns vs. drivers

For 20 stocks at least one of the selected drivers (SSB,  $T$ , GSP, NAO and AMO) contributed significantly to recruitment strength, set at  $p_{95} < .10$  to take into consideration the uncertainty in the stock assessments, as indicated above. Out of the two model choices, vcGAM performed better than GAM in all situations, as the former non-stationary approach resulted in higher  $R^2$  and  $R^2_{adj}$ , and, in

parallel, generally showed lower GCV and  $AIC_c$  values (Figure 6a, Table S4). For stocks which exhibited multiple recruitment regime shifts, the subsequent, corresponding implementation of several threshold years did not result in improved model fits, particularly when compared to the enhancement achieved by introducing one threshold year as opposed to none (e.g. Coastal cod North and Northeast Atlantic mackerel, Table S4). An exception was observed in the case of North Sea autumn-spawning herring, where the vcGAM with two threshold years was the best model. In the Barents and Norwegian Seas, the threshold years occurred after 2000, whereas those in the North Sea mainly concentrated in the 1980s and 1990s (Figure 6b). GAM outputs largely mirrored those given by vcGAM before but not after the vcGAM-defined threshold year (Figure 7). The passing of a given threshold year resulted in decoupled relationships in 15 stocks and the detection of reorganized driver importance in 4 others (Figure 7). In addition, for 8 stocks at least one significant driver remained but where the specific response curves changed type, going, as an example, from a positive to negative linear influence of AMO on the recruitment of blue whiting (*Micromesistius poutassou*, Gadidae) (Figure 7). Also, this standardized overview, considering any varying influence of the same quintet of drivers throughout the meta-analysis, implied that three stocks were left with an unpredictable recruitment dynamic ( $p_{95} > .10$ ): Greenland halibut (*Reinhardtius hippoglossoides*, Pleuronectidae), North Sea turbot (*Scophthalmus maximus*, Scophthalmidae) and Barents Sea capelin.



**FIGURE 5** Recruitment regime shift patterns across the 23 Northeast Atlantic stocks examined in the meta-analysis (a) and temperature window and change of each stock at recruitment regime shift (b). In (a), dots and horizontal lines indicate the years and their 95% confidence intervals, respectively. Arrow shows the shift direction. Years in parentheses associated with each stock name specify the time series used in the breakpoints analysis. In (b), blue, black and red points represent 25th, 50th and 75th of temperature preference extracted from Cheung et al. (2013). Temperature change is calculated based on 5-year averages before and after recruitment regime shift. For Northeast Arctic cod, the temperature change around 1967 was calculated based on Kola temperature only. For North Sea autumn-spawning herring, the temperature change around 1964 could not be calculated as no matching temperature time series was available.

The various SSB time series trajectories of the 23 stocks were highly diverse, and with large within-stock variability across years (Figure S5). Accordingly, past the currently defined stock-specific threshold year given by the vcGAM, SSB could markedly increase or decrease, or roughly level off, but also seeing apparent lag effects, as for North Sea plaice (*Pleuronectes platessa*, Pleuronectidae) and Northern hake (*Merluccius merluccius*, Merlucciidae) (Figure S5). Fishing mortality (F) and SSB were generally inversely related for 16 stocks of which this coupling was significant for nine stocks (Figure S5).

### 3.2.3 | Pseudovalidation

Generally, the appearance of recruitment regime shift years (Figure 5) was significantly correlated with threshold years (Figure 6) over the same window of 50 years (1970–2019) ( $n=14$ ,  $r=.872$ ,  $p<.001$ , Figure 8a). In addition, years characterized by regime shifts without the presence of thresholds were identified ( $n=8$ , Figure 8b).

An increasing number of threshold years generally resulted in these being more closely adjacent to regime shift years, though these models were not the best fitted ones (Table S4). In contrast, years featuring thresholds without accompanying regime shift were also detected ( $n=6$ , Figure 8c). With respect to the temporal alignment between biological response (recruitment regime shifts and thresholds) and phase change/abrupt shift, both synchronous and asynchronous patterns were observed (Figure S6), in which one example of the former would be the simultaneous occurrence of intensive recruitment regime shifts of North Sea stocks – though in different direction depending on stock – and the phase shift of NAO around 1980. To complement the formal test based on overlapping time series, we noticed that the single, negative recruitment regime shift seen in 1967 for NEA cod (Figure 8d) coincided with the AMO going from a warm to a cold phase (Figure 3). The earliest recruitment regime shift (out of three) of North Sea autumn-spawning herring in 1964, classified as negative (Figure 8d), occurred at a fast-falling SSB and sharply increasing F (with culminated in a recognized stock collapse in the early 1970s) (Figure S5).

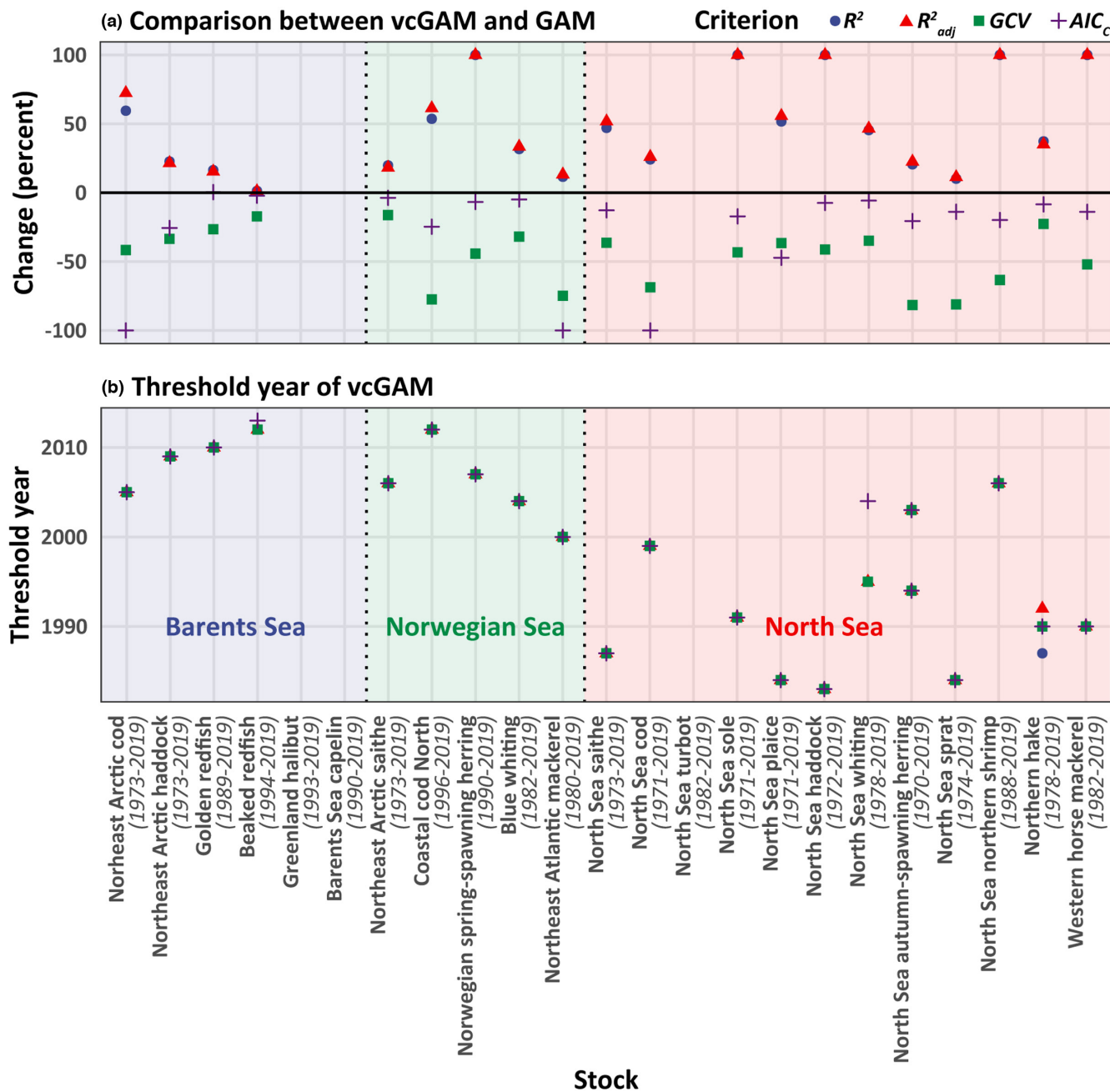


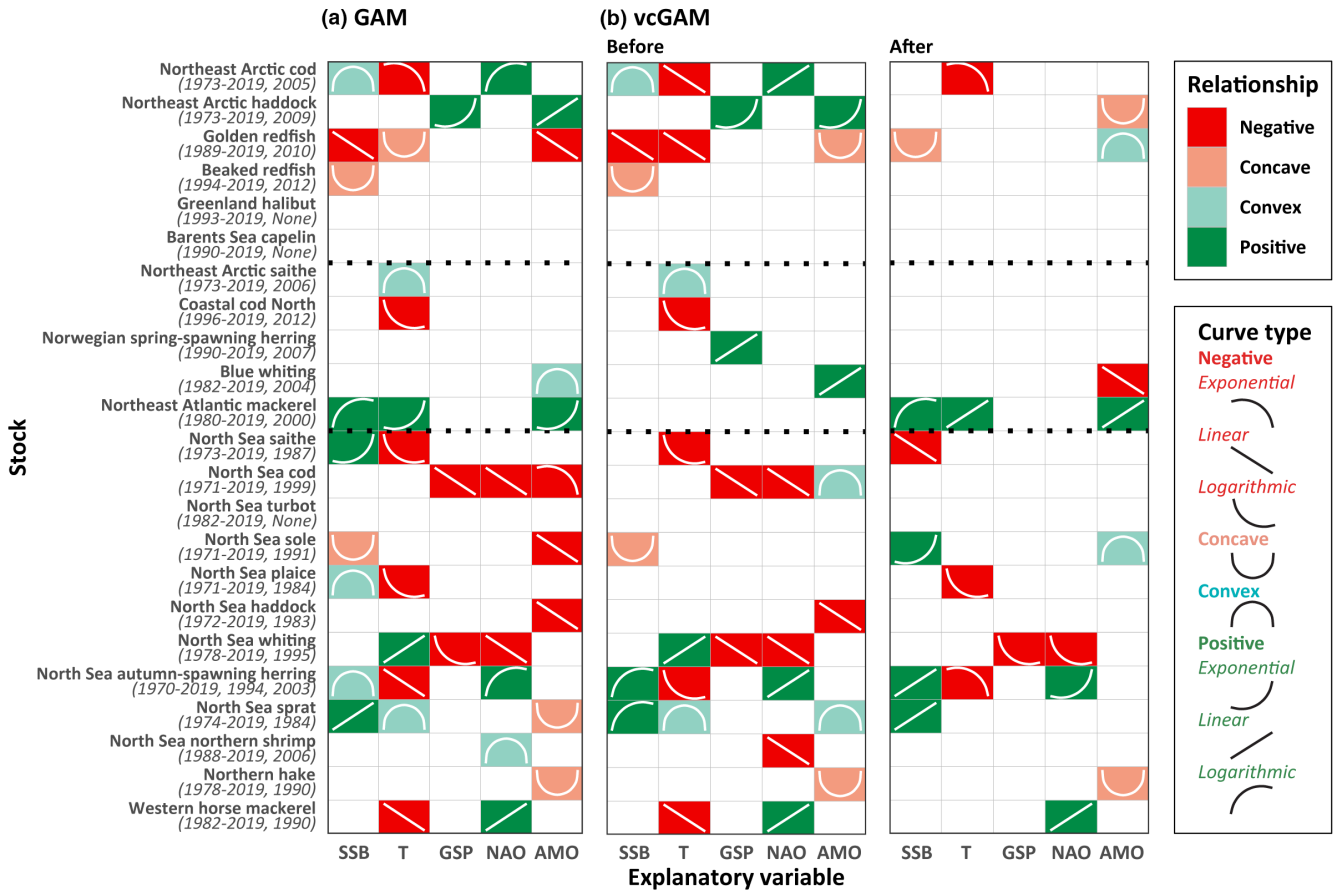
FIGURE 6 Comparison between GAM and vcGAM regarding explanatory power and vcGAM-defined threshold year for each of the 23 stocks in the meta-analysis. (a) The relative explanatory power of vcGAM versus GAM – i.e.  $100 \times (\text{vcGAM} - \text{GAM}) / \text{GAM}$  (in percentage) – in which increases or decreases above 100% are capped at 100% for better visibility and (b) the respective threshold years. Years in parentheses associated with each stock name specify the time series used in the models.

### 3.3 | Case studies

#### 3.3.1 | Northeast Arctic (NEA) cod

Moving correlation over the long-term time series (1921–2021) of NEA cod revealed wave-formed correlation patterns between SSB and the subsequent recruitment at age 3 years (Figure 9a), or between the latter and Kola temperature (Figure 9b). Such systematically varying significance levels over time were also seen for Kola temperature versus NAO (Figure 9c) and Kola temperature versus

AMO (Figure 9d). Thus, this rhythm included in all four combinations clearly significant, positive relationships (Figure 9). However, relationships could become negative, but not significant, as seen for Kola temperature versus AMO in the 1950s to the 1980s. SSB was significantly related to recruitment during four, relatively short periods up to the late 1990s, although this finding was dependent upon the length of moving window. For Kola temperature, such a strong statistical association with recruitment existed between the late 1970s and late 1990s. NAO was positively related to Kola temperature in the late 1970s to mid-1990s, whereas this link in the 1930s was less



**FIGURE 7** Curve fitting of GAM (a) and vcGAM before and after the threshold years (b) to investigate the effects of SSB, T, GSP, NAO and AMO on recruitment strength for the 23 tested stocks in the meta-analysis. Filled rectangles indicate significant explanatory variables and the superimposed lines stand for the type of relationship in question. Years in parentheses specify the time series used in the models, accompanied by the estimated threshold year(s) given from the vcGAM. The North Sea autumn-spawning herring formed an exception displaying two threshold years instead of one; the “after” refers in this particular situation to the period in-between, with no significant relationship being identified after the second threshold year.

robust, i.e. again affected by the length of moving window. AMO correlated with Kola temperature around 2000, at a time when there was no apparent relationship for the NAO versus Kola temperature.

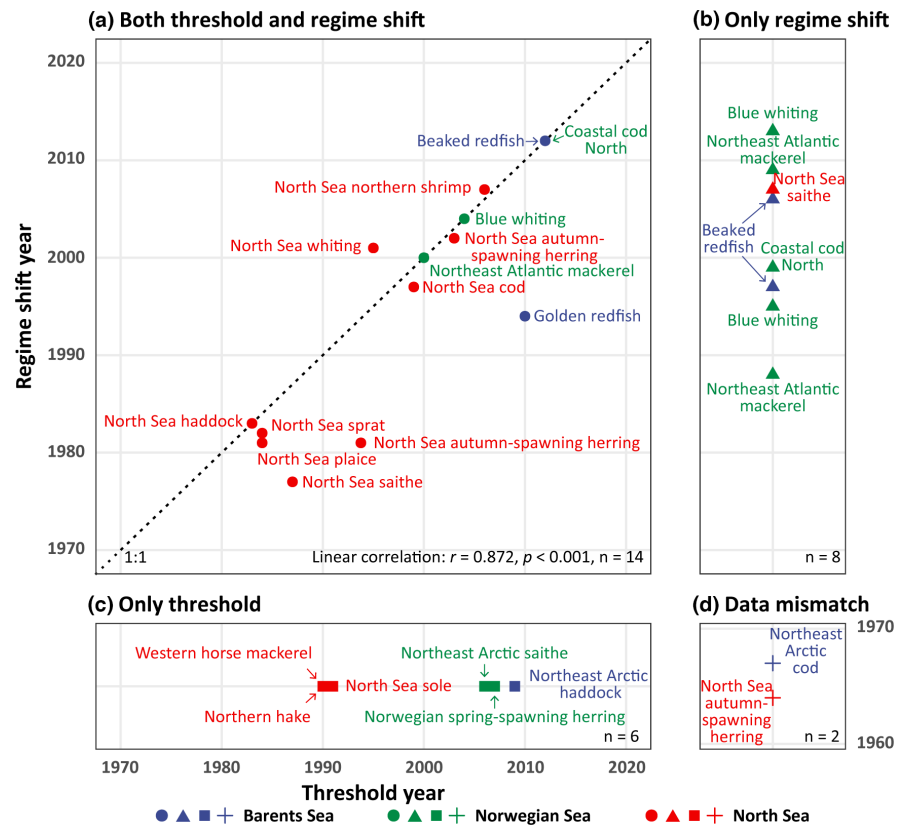
Considering only the recruitment data with uncertainty (1946–2020) (Figure S7), the year-class strength was at a generally lower level from the late 1960s onwards (Figure 10a). The estimated recruitment regime shift in 1967 was robust to the associated uncertainty expressed in the stock assessment (Figure S4), though coupled to a rather broad CI (Figure 10a). A density-dependent effect of SSB on recruitment was present (Figure 10b), and this was coincident with an extraordinarily high SSB (Figure S7). Thus, the shape of this post-WW2 plot agrees with the perception of the Ricker model ( $R^2 = .21, p < .001$ ) rather than of the Beverton-Holt model ( $p = .07$ ) (Figure 10b). The recruitment success, i.e. number of recruits per unit of biomass, exhibited significant fluctuations prior to the 1980s, followed by a subsequent dampening to consistently low levels since the 2000s (Figure 10c).

Considering the GAM for the period 1973–2019 (cf. Figure 7), the bootstrap-derived  $p$  indicated that SSB, T and NAO should be considered significant drivers of NEA cod recruitment dynamics (Figure S8a). Thus, GSP and AMO did not contribute significantly

( $p_{95} > .10$ ) in combination with these three other drivers. Relaxing the effective degree of freedom to 4 and 5 gave similar results, though, for better visualization the results with an effective degree of freedom equal to 3 were kept. The associated bootstrap GAM curve fits showed a density-dependent effect of SSB on recruitment, with an apparent negative effect originating at  $SSB > 1.1$  million tonnes (Figure 11a). For T and NAO, both the earlier schematic negative exponential and positive logarithmic relationships, respectively (Figure 7), were very close to linear (Figure 11a).

Scrutiny with vcGAM instead explained 74.3% (95% CI: 59.5%–80.5%) of the variance in recruitment (represented by  $R^2$ ) compared to 46.6% (31.3%–54.8%) for the baseline GAM (Figure 11). Jointly, the four information criteria for model strength ( $R^2, R^2_{adj}, GCV$  and  $AIC_c$ ) reflected a markedly better explanatory power of vcGAM than of GAM (Figure S8b). The bootstrapping revealed that the shape of the significant relationship between recruitment and SSB before 2005 was convex ( $p_{95} < .01$ ) (Figure 11b). The corresponding fitting procedure behind the negative, linear curve with T and the positive, linear curve with NAO appeared robust ( $p_{95} < .01$ ) (Figure 11b). After 2005, the effects of SSB and NAO on recruitment were seemingly

**FIGURE 8** Scatter plot between threshold years from vcGAM and recruitment regime shift years from breakpoints analysis across all 23 stocks in the meta-analysis. (a) Stocks with both threshold(s) and regime shift(s); (b) and (c) with only regime shift(s) and threshold, respectively and (d) data mismatch between vcGAM and breakpoints analysis outcomes. Coloured points and accompanying labels reflect stocks belonging to the same ocean basins.



trivial ( $p_{95} \geq .334$ ) (Figure 11b). Thus, we noted decoupled relationships compared to those seen before 2005. The effect of T was still significant ( $p_{95} < .01$ ) but with curve type changed to negative exponential (Figure 11b).

Over a short time scale (1992–2019), with data on 0-group abundance and total length, food availability (capelin for the adults), cannibalism (consumption of cod by cod, or by immature biomass) and predation (on drifting larvae by mackerel and herring) (Figure S9), the best GAM was with food availability and cannibalism (immature biomass) as explanatory variables, explaining 50.5% (31.9%–60.2%) of the total variance (Figure 12). Although the originally fitted curve with cannibalism gave  $p < .05$ , the  $p_{95}$  was .136, indicating large uncertainty. The uncertainty was relatively low for food availability as both  $p$  and  $p_{95}$  fell in the significant range, i.e.  $< .01$  and  $< .05$ , respectively. Food availability showed a concave relationship with recruitment, with the turning point at 10 times more mass of capelin than of adult cod (Figure 12). Except for the years around 1990 and 2000, all figures for food availability were below 10 (Figure S9b), corresponding to the descending limb of the fitted curve. Recruitment decreased logarithmically with increasing cannibalism to some-sort-of a turning point around 1.5 million tonnes of immature cod biomass (Figure 12).

### 3.3.2 | Norwegian spring-spawning (NSS) herring

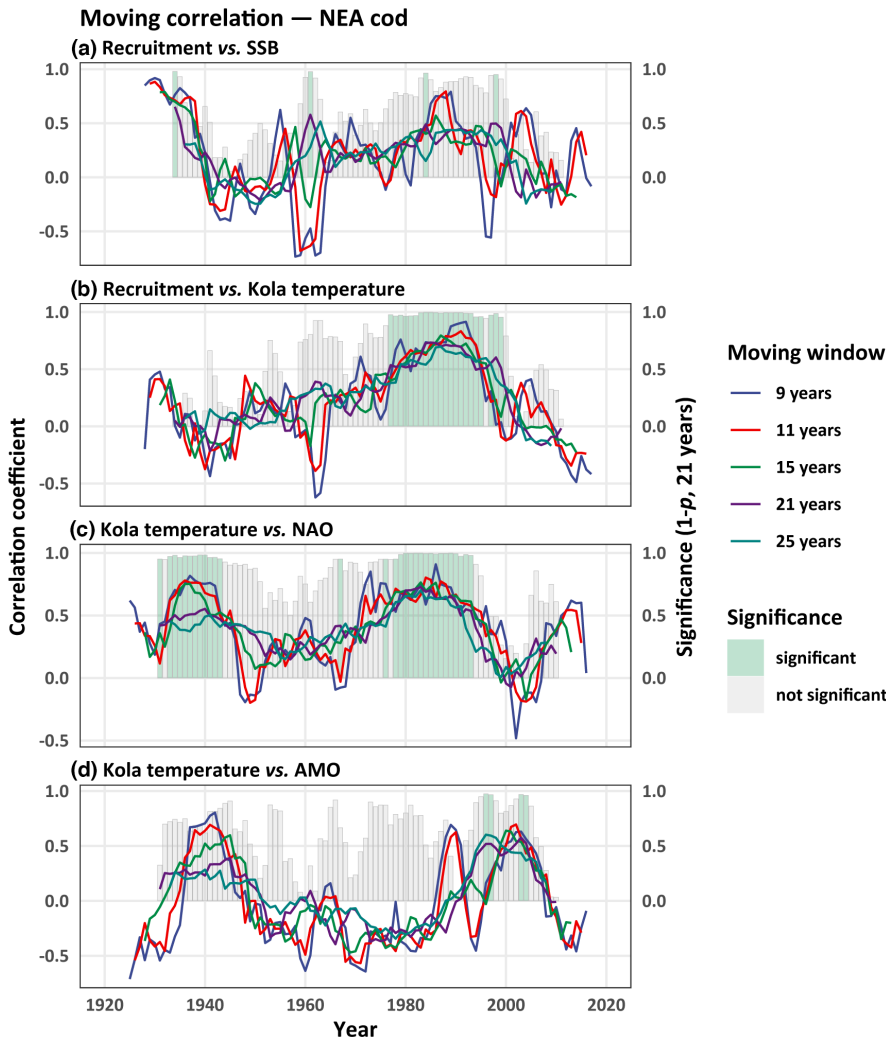
The recruitment of NSS herring at age 2 years (1907–2021) showed large interannual fluctuations but also a relatively stable and low-level period from the late 1960s to the early 1980s during the

enforced fishing moratorium, ending with the production of the strong year class in 1983 (Figure S10). Neither any recruitment regime shift (Figure 13a) nor density-dependent effect (Figure 13b) was detected, even after splitting up this time series into before and after the fishing moratorium (Figure S10). The recruitment success was characterized by three distinct peaks over the past three decades: one in the mid-1990s, another in the mid-2000s and the most recent one in the late 2010s (Figure 13c).

The GAM (1990–2019) identified GSP as the only potential influential driver of NSS herring recruitment dynamics within this explanatory setting (SSB, T, GSP, NAO and AMO), considering estimation uncertainty (Figure S11a). Using an effective degree of freedom of 4 or 5 rather than 3 made no difference. However, bootstrapping indicated that a large degree of uncertainty remained, even for the effect directions ( $p = .948$ ,  $p_{95} = .991$ , Figure 14a).

The vcGAM (Figure S11b) resulted in marked improvements in the model fitness in view of the baseline GAM. The best vcGAM, with a threshold year of 2007, explained 53.5% (46.1%–60.0%) of the variance compared to 0.2% (0.1%–0.5%) with GAM (Figure 14). GSP showed a positive relationship with recruitment up to 2007 ( $p_{95} < .01$ ) but then its statistical contribution disintegrated ( $p_{95} = .756$ ) (Figure 14b), when GSP, represented by the Norwegian Sea Oceanic polygon (Figure S1), reached relatively high levels (Figure 4b).

With 0-group abundance and total length as well as proxies for adult food availability and larval predation (Figure S12) included in the model selection, the best GAM referred to the two explanatory



**FIGURE 9** Long-term moving correlations (1921–2021) in the NEA cod case study between recruitment at age 3 years and SSB (a), or with Kola temperature (b), and between Kola temperature and NAO (c), or with AMO (d). Coloured lines show the correlation coefficients for different moving windows, whereas bars (placed in the middle of the 21-years moving window) indicate the level of significance ( $1 - p$ , adjusted considering autocorrelation), where green and grey fill refers to significant and insignificant correlations, respectively. The current definition of the level of significance was applied for illustration purposes only.

variables characterizing the 0-group, explaining 62.0% (55.1%–66.9%) of the total variance (Figure 15). The relationship between 0-group abundance and recruitment was of a logarithmic type ( $p_{95} < .05$ ), indicating a density-dependent effect. The 0-group size formed a clear, positive linear relationship with recruitment ( $p_{95} < .001$ ).

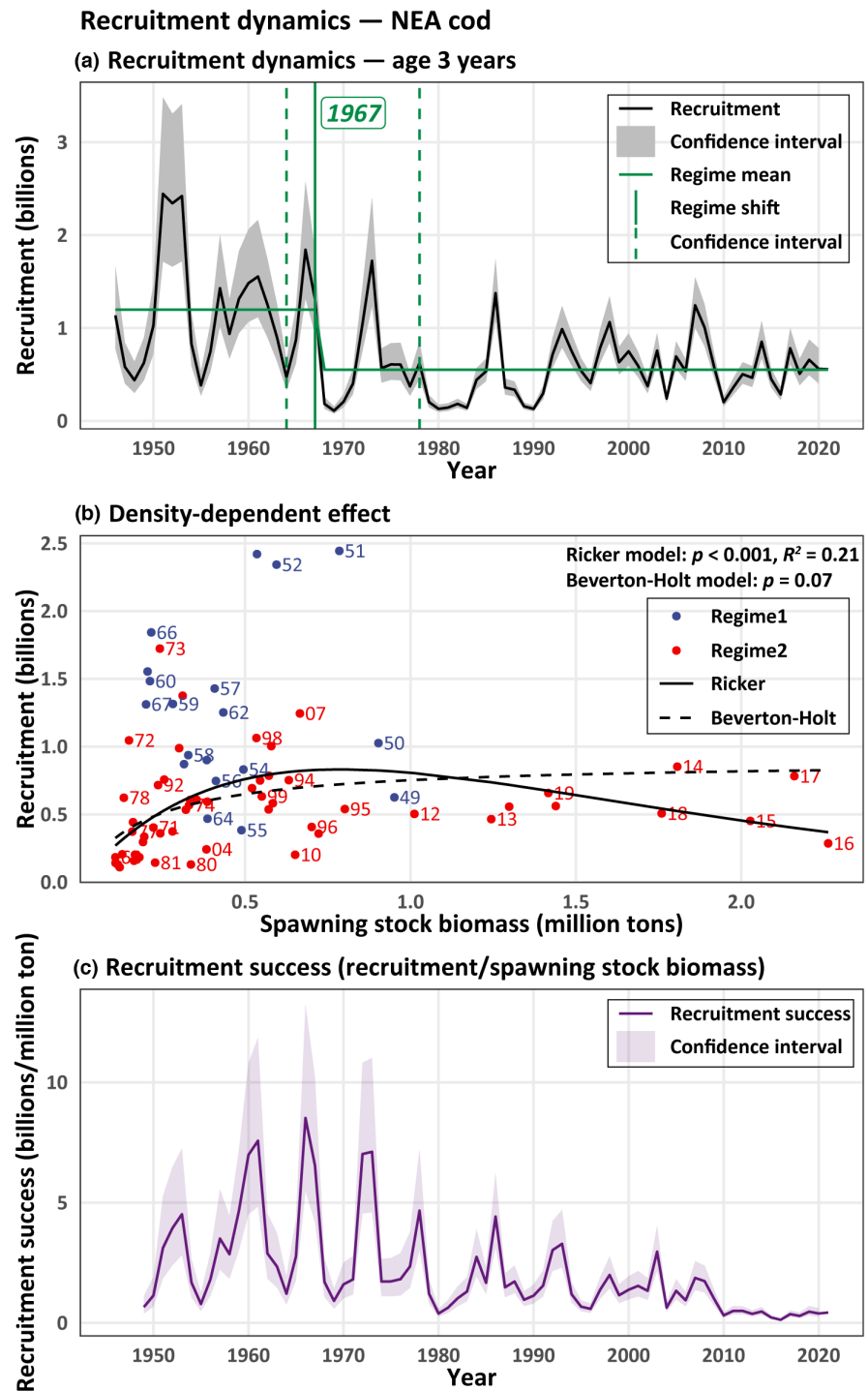
### 3.3.3 | North Sea (NS) cod

Examinations of the recruitment patterns of NS cod at age 1 year (1963–2021) revealed a recruitment regime shift around 1997, though with some precision uncertainty based on CI (Figure 16a). This switching implied moving from a high-level, large interannual fluctuation situation to a low-level, stable situation (Figure 16a). Both the recruitment and the SSB were low after the switch (Figure 16b; Figure S5). No significant density-dependent effect could be detected (Figure 16b); both the Ricker and Beverton-Holt model performed poorly ( $p = .87$  and  $.89$ , respectively) in explaining recruitment as a function of SSB. In essence, these two models resulted in identical, but unreliable curve fitting. The recruitment success demonstrated substantial interannual variability, characterized by a notable decline in the late 1990s, remaining at relatively low levels, except for a single peak in the mid-2000s (Figure 16c).

The replacement of GSP (Figure 7) with the abundance of *C. finmarchicus* for the shorter period from 1971 to 2019 was substantiated by the lack of any significant correlation ( $p = .28$ ) between the modelled biomass of zooplankton in the whole water column and the corresponding CPR-given observational set for this single, key copepod in the upper water layer (Figure S13). *C. finmarchicus* appeared negatively related to T ( $p < .001$ ) and NAO ( $p < .001$ ) but there did not appear to be any link with AMO ( $p = .13$ ) (Figure S13). Nevertheless, the best GAM identified *C. finmarchicus*, NAO and AMO as significant drivers of NS cod recruitment, explaining 77.0% (67.8%–82.7%) of the total variance (Figure 17a, Figure S14a). Thus, T and SSB were left out as insignificant drivers ( $p_{95} > .10$ ). Here in this case, we also kept the effective degree of freedom at 3; using 4 and 5 had no effect. In contrast to the negative effect of GSP seen earlier (Figure 7), *C. finmarchicus* abundance had an exponential, positive effect on recruitment, whereas NAO and AMO were negative in an approximately linear fashion (Figure 17a).

When applying vcGAM, the explanatory power further increased to 92.1% (85.7%–94.7%), with a threshold year at 1998 (Figure 17b; Figure S14b). The threshold year in 1998 was identified by GCV and AIC<sub>c</sub>; the alternative use of  $R^2$  and  $R^2_{adj}$  as information criteria suggested 1982 (Figure S14b). Before 1998, the effect of abundance of *C. finmarchicus* and NAO were similar to those detected by the baseline GAM,

**FIGURE 10** Case-study recruitment dynamics ( $\pm 95\%$  CI) of NEA cod at age 3 years across years (1946–2021) with any incidence of recruitment regime shift indicated (a), corresponding explorations of any density-dependent effect of SSB on recruitment, represented by the Ricker and Beverton-Holt models (b) and trajectories of recruitment success, calculated as recruitment divided by SSB (c).



but AMO was a convex relationship with recruitment. These effects disappeared statistically after 1998 ( $p_{95} \geq .547$ ) (Figure 17b).

## 4 | DISCUSSION

### 4.1 | Premises

The key purpose of this investigation was to explore, better understand and contrast in a standardized way the recruitment dynamics of 23 stocks of commercial interests in the Northeast Atlantic.

This approach utilised overlapping time series of recruitment, SSB and biophysical drivers using state-of-the-art statistics. As special focus was given to any marked changes (jump discontinuities) in these different series and their relationships, the applied terminology required special attention. Any as-far-as-possible verification of the results was also important to increase the informative value in a broader context. In essence, during this investigation we not only examined numerous temporally resolved relationships between recruitment and covariates but also consulted various types of data sources and, not at least, applied different statistical methodology.

### GAM and vcGAM results — NEA cod

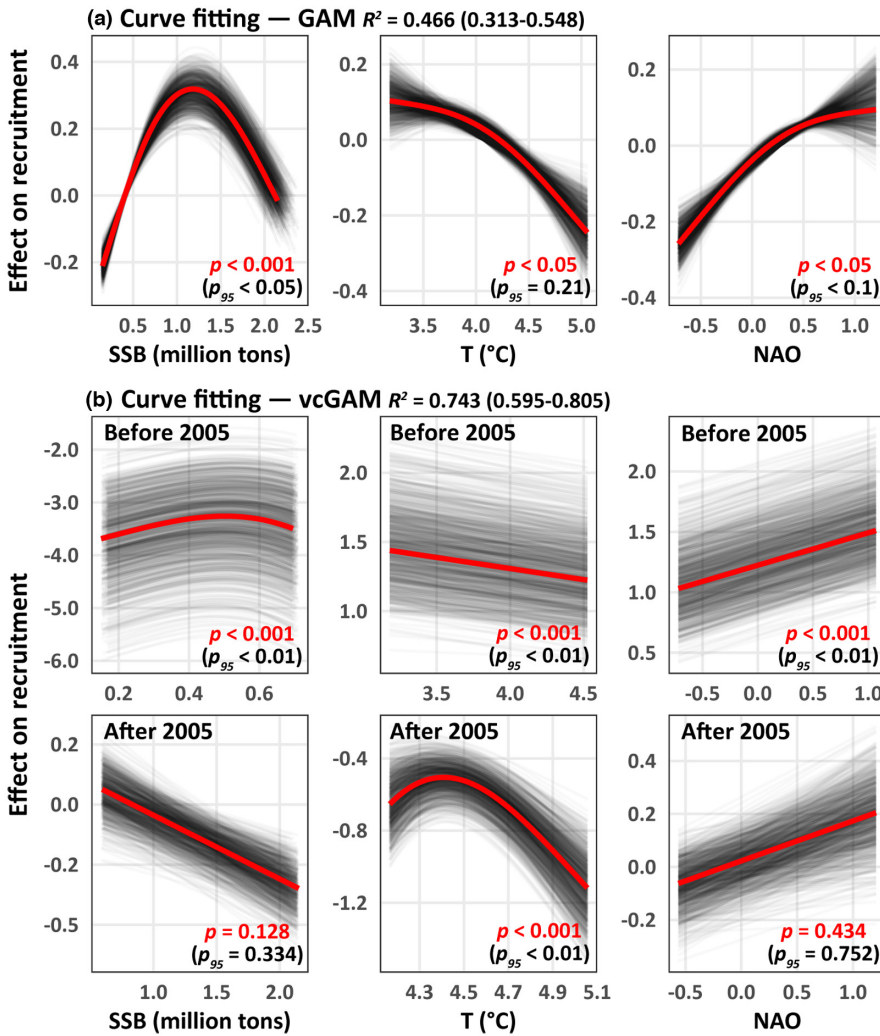


FIGURE 11 Results of GAM (a) and vcGAM (b, split into before and after 2005) from the NEA cod case study (1973–2019). Red and black lines show fitted curves, using original and resampled recruitments, respectively. The  $p$  and  $p_{95}$  (95% of bootstrapped  $p$ ) stand for the significance of the fitted curves using original (red) and resampled (black) recruitments, respectively. The  $R^2$ , with 95% confidence intervals in the parentheses, indicates model explanation of recruitment dynamics. Note that different scales are used in each panel for visibility. NAO unit: relative scale.

### Updated GAM — NEA cod $R^2 = 0.505$ (0.319-0.602)

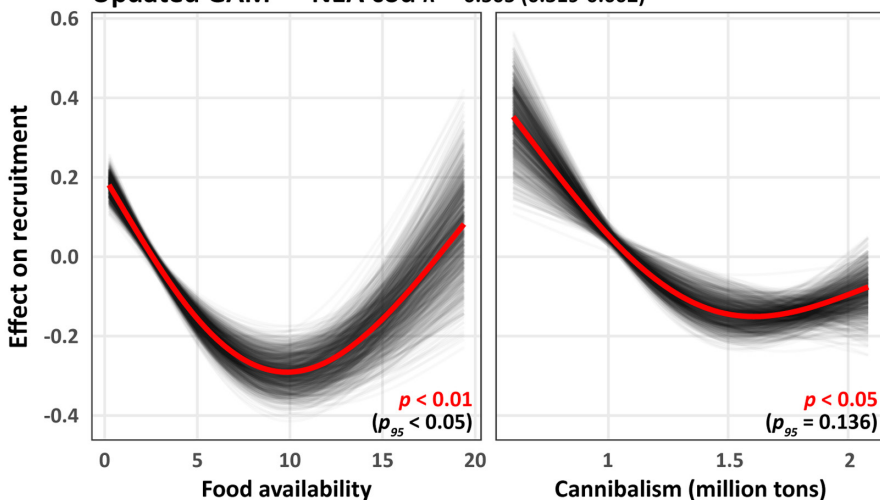


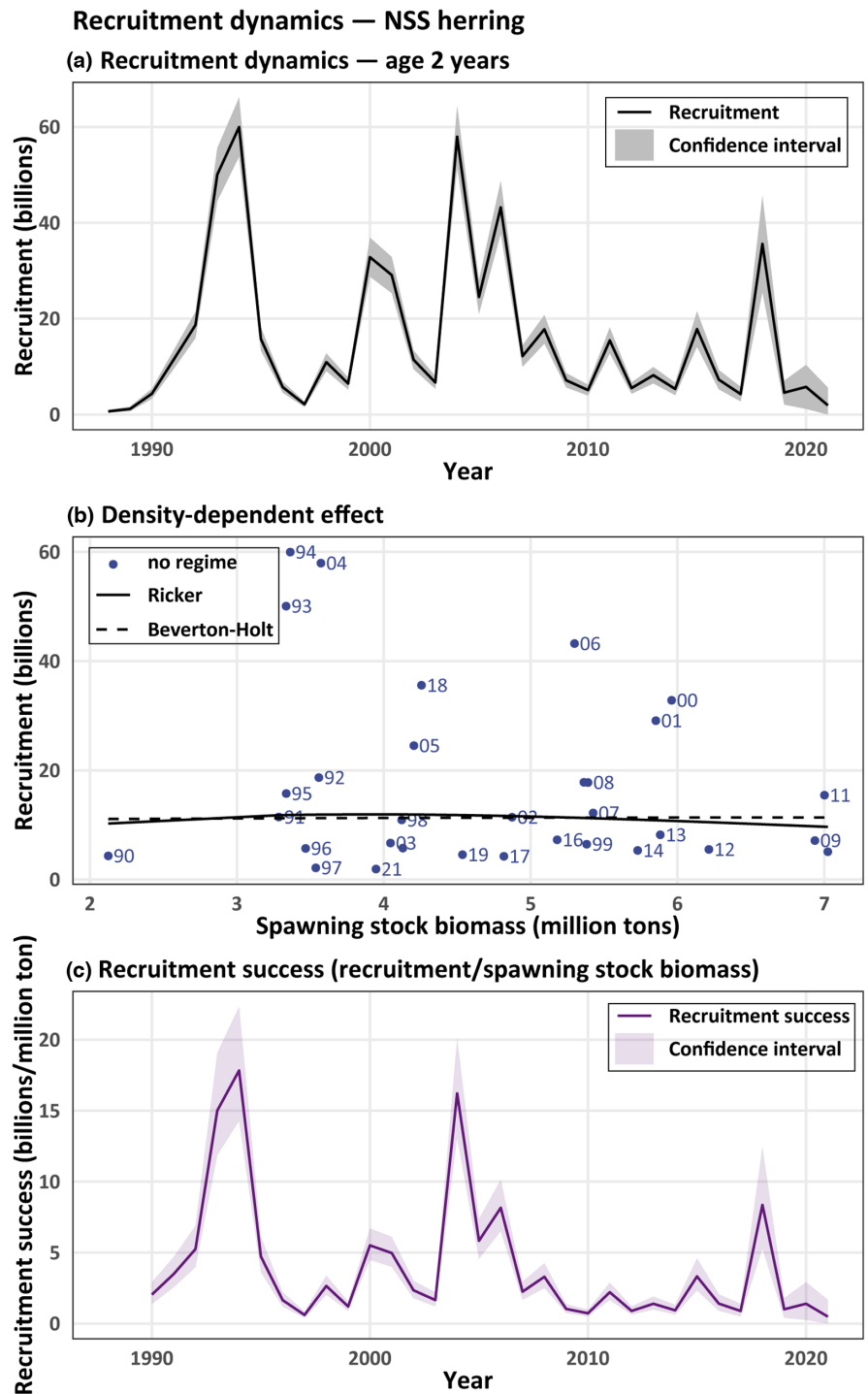
FIGURE 12 Updated (1992–2019) GAM results in the NEA cod case study with either food availability (total biomass of capelin divided by SSB of NEA cod) or cannibalism (immature biomass) as explanatory variable. Red and black lines show fitted curves, using original and resampled recruitments, respectively. The  $p$  and  $p_{95}$  (95% of bootstrapped  $p$ ) stand for the significance of the fitted curves using original (red) and resampled (black) recruitments, respectively. The  $R^2$ , with 95% confidence intervals in the parentheses, indicates model explanation of recruitment dynamics. Food availability unit: relative scale.

The definition of “regime shift” seems to be generally accepted as “a dramatic and abrupt change that remains persistent over time” (Conversi et al., 2015); however, this normally refers to

complex ecosystem processes and often specifically considered as an ecosystem regime shift (Levin & Möllmann, 2015). As demonstrated by our study and others (Perretti et al., 2017; Tirronen



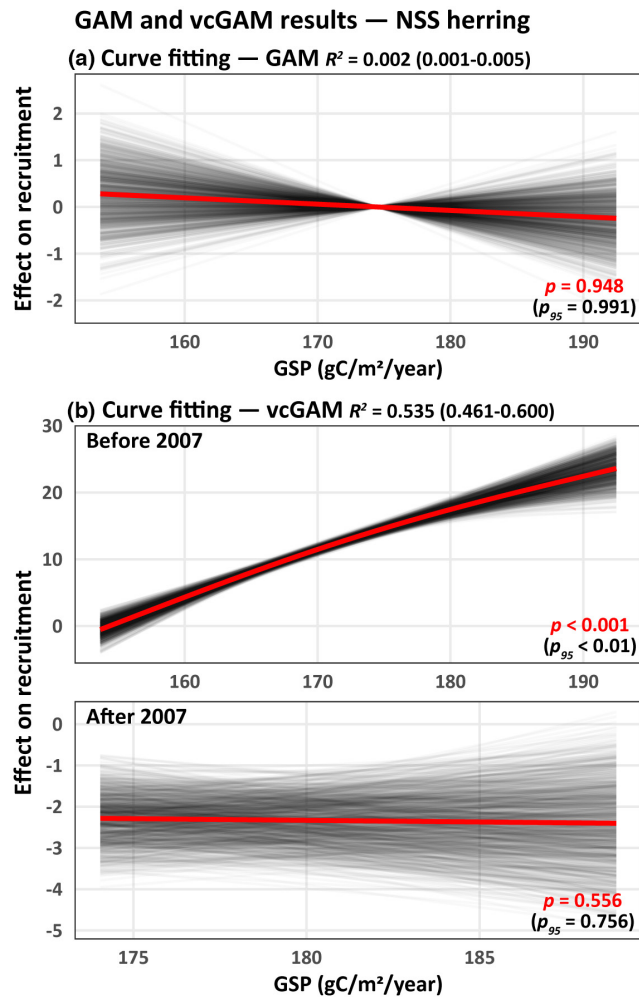
**FIGURE 13** Case-study recruitment dynamics ( $\pm 95\%$  CI) of NSS herring at age 2 years across years (1988–2021) (no incidence of recruitment regime shift was detected) (a), and corresponding explorations of any density-dependent effect of SSB on recruitment, represented by the Ricker and Beverton-Holt models (b), and trajectories of recruitment success, calculated as recruitment divided by SSB (c).



et al., 2023), the dynamics of year-class strength often showed characteristic patterns over varying periodicity, leading us to select the term recruitment regime shifts. However, the AMO, NAO and AO series are basically cyclic (modal) in fashion, whereas the T and GSP series often exhibited several, successive, stepwise changes. Therefore, in addition to the term recruitment regime shift, we went for, provided the statistics indicated so, the wording “gradual change” and “abrupt shift”, respectively. Consequently, the discontinuities and their corresponding time series segments were referred to as “regime”, “phase” and “state”. In effect, a given

recruitment regime was a function of the corresponding phase and state covariates. This also included the status of the stock (SSB) and subsequently the pre-recruit stage, represented by 0-group data.

The identification of the breakpoint-analysis-detected recruitment regime shift(s) was tested by comparison with the threshold year from the vcGAM, using estimated SSB, observed AMO and NAO and modelled T and GSP data as explanatory factors (drivers). These were included as a part of the wider understanding of recruitment dynamics. We named this comparative effort “pseudovalidation”



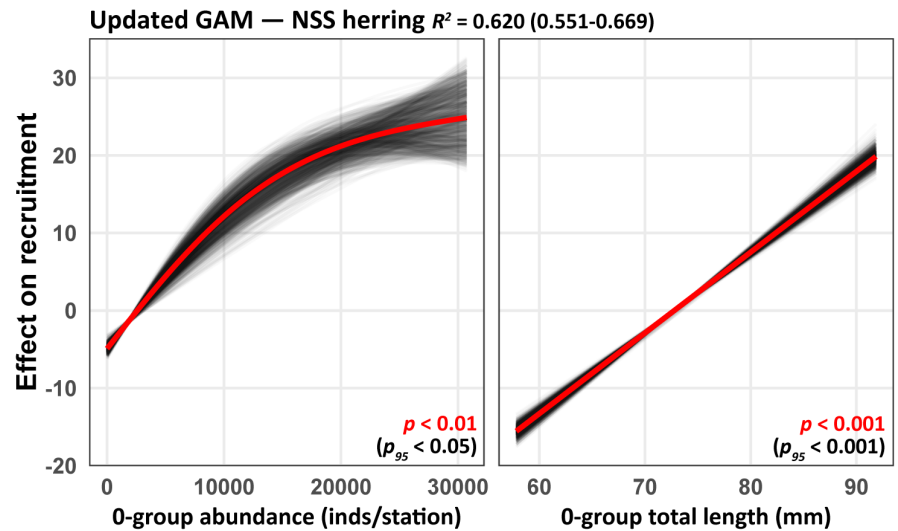
**FIGURE 14** Results of GAM (a) and vcGAM (b, split into before and after 2007) from the NSS herring case study (1990–2019) with GSP as explanatory variable. Red and black lines show fitted curves, using original and resampled recruitments, respectively. The  $p$  and  $p_{95}$  (95% of bootstrapped  $p$ ) stand for the significance of the fitted curves using original (red) and resampled (black) recruitments, respectively. The  $R^2$ , with 95% confidence intervals in the parentheses, indicates model explanation of recruitment dynamics. Note that different scales are used in each panel for visibility.

rather than true validation. This is because both recruitment regime shift years and threshold years were de facto model outputs, though the recruitment data, as those for SSB, are founded on extensive field efforts, typically both from fisheries independent and dependent sources. Overall, there were reasons to believe that the presences of recruitment regime shifts are real, especially when the recruitment regime shift year and threshold year appeared close in time. However, the direct causality between recruitment regime shift and threshold in recruitment-driver relationship is elusive. For instance, the recruitment regime shift can happen without any corresponding threshold in the relationship with the chosen variables investigated, or vice versa. Theoretically, recruitment regime shift should be the “effect” as it only considers fluctuations in recruitment, and nonstationarity (thresholds) may be the possible “cause”.

However, statistically, the occurrence of one can lead to, or not lead to, the occurrence of the other one. Furthermore, it is essential to acknowledge that, despite looking for comprehensive possible drivers on recruitment, certain key drivers may have been overlooked. This could be due to data limitations or the inherent complexity of mechanisms governing species interactions and trophic dynamics which could lead to asynchrony. Additionally, the statistical identification of recruitment regime shifts places emphasis on the amplitude and speed of change, whereas for threshold the criteria refer to the variability of the established relationships. Logically, these methodological differences make it challenging to ensure synchronicity between recruitment regime shifts and threshold years. In addition, this study illustrated substantial variability in the temporal alignment of phase changes in climatic indices compared to abrupt shifts in environmental variables. Therefore, expecting to find a complete synchrony between shifts in biological responses and a given biophysical driver, out of many in operation across different processes and life history stages (Figure 1), seems unrealistic. For instance, parametrization of the significant effect of in-situ wind conditions (cf. micro-turbulence) and light conditions for larval survival is yet beyond reach in present model constructs (Kjesbu, Tiedemann, et al., 2023).

The length of the available time series for drivers and recruitment were often different. These differences were dealt with by restricting the time series so they fully overlapped, which is a specific requirement in all exploratory analyses. The protocol for time series selection was particularly pronounced in the case studies on NEA cod, NSS herring and NS cod. These were typically split into analyses on time series of long, intermediate or short length due to the successive addition of less “data-rich” drivers of potential high influence for local stock recruitment dynamics. These case-study series varied from 28 (cf. updated GAM on NEA cod) to 49 years (cf. GAM and vcGAM on NSS herring). Likewise, in the meta-analysis, the length of the time series ranged from minimum 28 years (Coastal cod North) up to a maximum of 115 years (NSS herring). The in-built issue of autocorrelations was either explicitly considered by adjusting the significance level in the undertaken correlation analysis or implicitly by bootstrapping for GAM and vcGAM. However, the often-used practice of moving average (window) to remove “noise” within these long time series undoubtedly causes extra autocorrelation. To reduce this unwanted, complex effect, we selected the minimum period for moving-average in the relevant statistical analyses, i.e. using a moving window of 3 years. The Northeast Atlantic stocks considered here consist of either warm- or cold-temperate species. Over the latitudinal range, 50–80°N, cold-temperate stocks in the south should be inclined to show a negative directional effect in terms of stock productivity proxies when the waters warm, whereas the opposite should be the case for cold-temperate stocks in the north, as well as for the widely distributed, warm-temperate species (Kjesbu et al., 2022). Our findings essentially fit into the same climate-environmental-latitudinal cline impact framework; however, our findings are based on advanced statistical tools instead of expert

**FIGURE 15** Updated (1990–2019) GAM results on recruitment dynamics in the NSS herring case study with either 0-group abundance or 0-group total length as explanatory variable. Red and black lines show fitted curves, using original and resampled recruitments, respectively. The  $p$  and  $p_{95}$  (95% of bootstrapped  $p$ ) stand for the significance of the fitted curves using original (red) and resampled (black) recruitments, respectively. The  $R^2$ , with 95% confidence intervals in the parentheses, indicates model explanation of recruitment dynamics. 0-group abundance unit: number of individuals (inds) per (trawl) station.



evaluations (scorings). The advantage of the latter approach is that data-poor stocks can be included along with a wider range of potential influential drivers (Hare et al., 2016). The disadvantage is the lack of statistically based uncertainties and probabilities, the main issues addressed in this study.

## 4.2 | Recruitment regime shift

Of the stock-specific time series analysed, 65% revealed 1–3 recruitment regime shift(s). Therefore, we conclude their existence to be a regular phenomenon in the Northeast Atlantic harvestable stocks.

In the North Sea, the recruitment regime shifts were concentrated around 1980 and 2000. Those seen in the 1980s principally co-occurred with the T trends turning from a relatively sharp decrease to a relatively sharp increase. In parallel, NAO went from a negative to a positive phase. Parallel ecological changes in bottom-up processes were evidently happening, i.e. from phytoplankton via zooplankton to higher trophic levels, including fishes (Beaugrand, 2004; Weijerman et al., 2005). A few years later the SSB of the warm-temperate North Sea sole (*Solea solea*, Soleidae) showed a major increase, although without any preceding recruitment regime shift. The last group of recruitment regime shifts seen in this shelf sea in the 2000s happened at generally higher levels of GSP in clearly warmer water compared to the 1980s, accompanied by widespread examples of declines in recruitment strength. An exception was another warm-temperate flatfish, the North Sea turbot, which also exhibited a positive response. It should be noted that this was the only studied stock in these waters with a fully unpredictable recruitment dynamic with respect to the suite of drivers considered. Whether another ecosystem regime shift was interacting with or responsible for these more recent local recruitment regime shifts remains unknown. Furthermore, North Sea sole, Northern hake (*Merluccius merluccius*, Merlucciidae) and Western horse mackerel (*Trachurus trachurus*, Carangidae) have so far not shown any sign of recruitment regime shift. Looking beyond these assessment stock

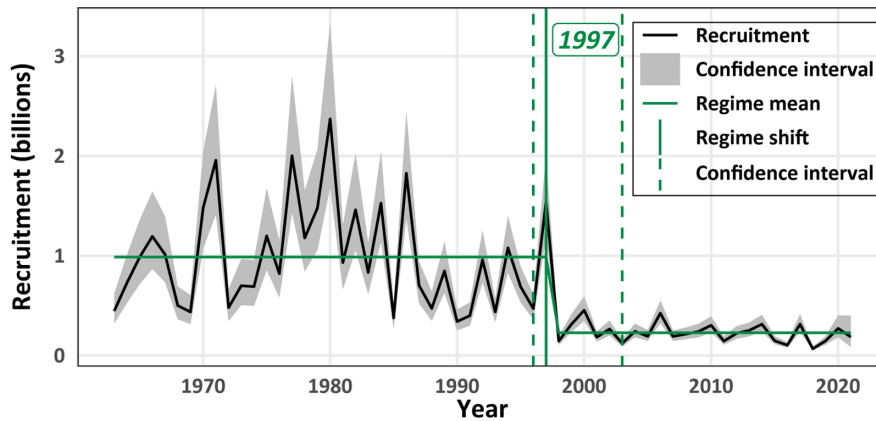
units, all three species are exceedingly widely distributed in southern parts of the present region.

The T in the Norwegian Sea increased rapidly after the late 1990s. For fish stocks inhabiting or seasonally migrating northwards into this vast geographical area, there is no mention of recruitment regime shifts. However, such events were prevalent from 2000 onwards. The robust shift for the widely distributed blue whiting around 1995 may be linked to a widening and strengthening of the subpolar gyre in the Northeast Atlantic (Hátún et al., 2009). For NEA mackerel, SSB reached a historically high level in 2014 (dos Santos Schmidt et al., 2023), agreeing with the present detection of two positive recruitment shifts, one in 2000 and another in 2009. No trace of any recruitment regime shift was, however, found for NSS herring, despite the exceedingly long time series at hand (1907–2021). A plausible explanation is that there is a tendency for periodic large year classes which may be associated with a suite of environmental drivers (Skagseth et al., 2015). The variability in recruitment strength in NSS herring is generally a magnitude of order higher than for NEA mackerel and blue whiting (ICES Stock Assessment Database, 2022).

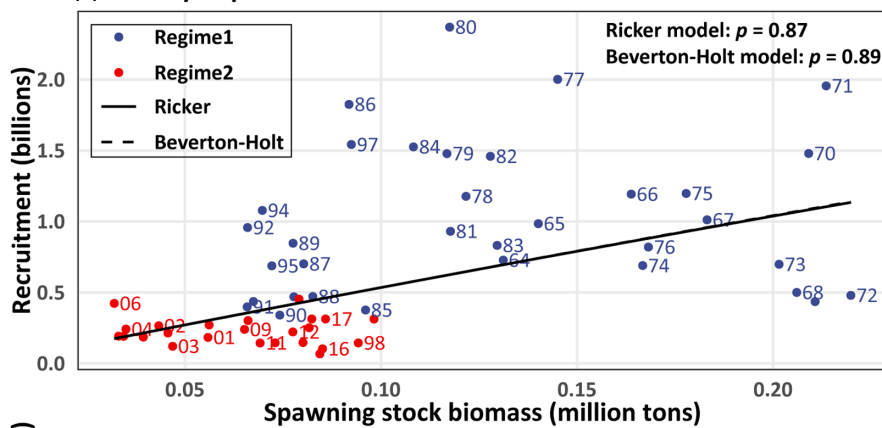
The environmental conditions in the Barents Sea have markedly changed over the past decades, but Johannesen et al. (2012) found no clear evidence for any ecosystem regime shift between 1970 and 2009. Furthermore, we noticed that the corresponding fluctuations in recruitment strength for NEA cod and haddock (*Melanogrammus aeglefinus*, Gadidae) did not feature any recruitment regime shift as such. However, the identified recruitment regime shifts for the two redfishes (*Sebastes* spp.) in the mid-2000s coincided with the increase in T and GSP to unprecedented levels. Back in time, the recruitment regime shift of NEA cod in 1967 may possibly be a result of the gradual change of the AMO into a cold phase, although certainly a complex biophysical interplay as we found NAO to be the significant climate index contributor in the subsequently undertaken GAM-vcGAM case study. To complement, a statistical analysis on NEA cod employing various methods to detect jump discontinuities for one of the longest, systematic biological series existing, “the Hjort liver index time series” (1859–2012) revealed that a significant,

## Recruitment dynamics — NS cod

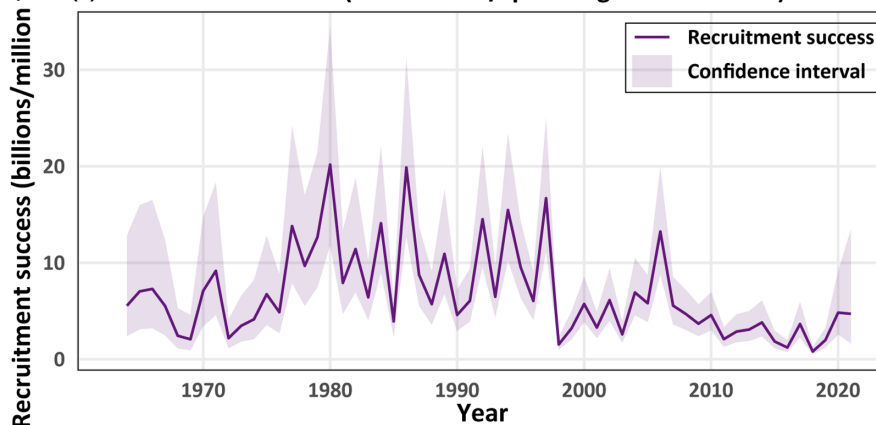
### (a) Recruitment dynamics — age 1 year



### (b) Density-dependent effect



### (c) Recruitment success (recruitment/spawning stock biomass)



**FIGURE 16** Case-study recruitment dynamics ( $\pm 95\%$  CI) of NS cod at age 1 year across years (1963–2021) with any incidences of recruitment regime shift indicated (a), and corresponding explorations of any density-dependent effect of SSB on recruitment, represented by the Ricker and Beverton-Holt models that provided practically identical regression curves (b), and trajectories of recruitment success, calculated as recruitment divided by SSB (c).

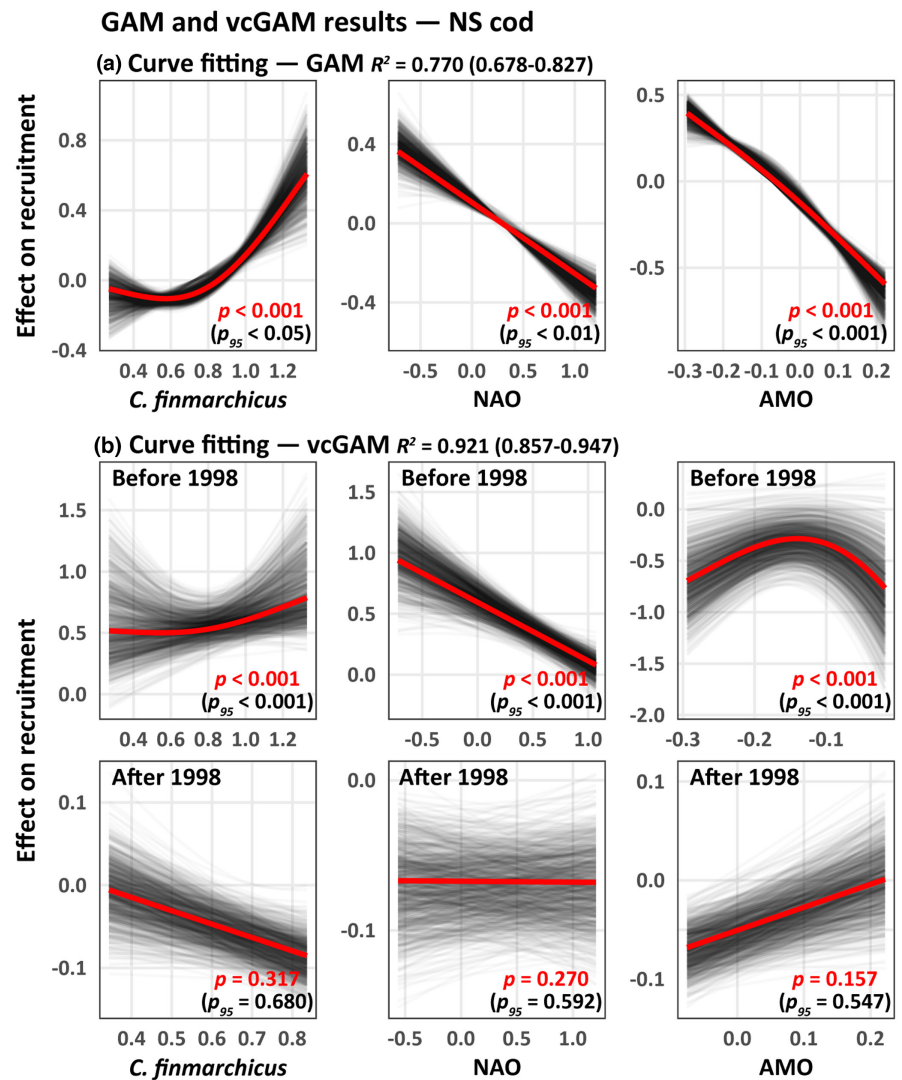
negative shift occurred around 1990, which was likely mediated via the complex ways the liver (hepatosomatic) index responds to winter temperatures (Hermansen et al., 2016).

## 4.3 | Recruitment dynamics

To get comparative insights into regulatory mechanisms behind recruitment dynamics (Figure 1), we systematically undertook both stationary (GAM) and non-stationary (vcGAM) approaches and the

above-mentioned, likely plausible explanatory factors (SSB, T, GSP, NAO and AMO). The resulting recruitment responses per driver and stock were thereafter ultimately placed in a thermal window of tolerance and change (cf. warming vs. cooling), split by each of the three LMEs. First of all, we found in this meta-analysis that each stock is uniquely adapted to the local conditions (environmental niche) within the LME, as expected from an eco-evolutionary perspective (Facon et al., 2006). Thus, there were hardly any consistent pattern for a given driver across stocks, e.g. the role of SSB could range from being (1) undetectable via (2) significant but hard

**FIGURE 17** Updated (1971–2019) results on recruitment dynamics in the NS cod case study with *Calanus finmarchicus*, NAO and AMO as successive explanatory variables, using GAM (a) and vcGAM (b), split into before and after 1998. Red and black lines show fitted curves, using original and resampled recruitments, respectively. The  $p$  and  $p_{95}$  (95% of bootstrapped  $p$ ) stand for the significance of the fitted curves using original (red) and resampled (black) recruitments, respectively. The  $R^2$ , with 95% confidence intervals in the parentheses, indicates model explanation of recruitment dynamics. Note that different scales are used in each panel for visibility. *C. finmarchicus* unit:  $\ln(\text{abundance} + 1)$ , NAO and AMO units: relative scales.



to explain mechanistically, e.g. concave instead of convex, to (3) significant and easily understandable, e.g. positive linear. Although the response patterns varied greatly by stock, it is also so that improved biophysical conditions would be expected to heighten stock productivities throughout the whole ocean basin. Examples are the clear cyclicity in the aggregated catch statistics in the Barents Sea over the last century (Haug et al., 2017) and by the Gadoid Outburst in the North Sea in the colder 1960s and 1970s (Cushing, 1984).

The explanatory power was clearly better with vcGAM than with GAM. The importance of realizing that nonstationarity is an issue was exemplified by the outcome of a given run in GAM typically resembling the corresponding one from vcGAM before but not after the vcGAM-defined threshold year. Thus, this article demonstrates that any established model should be expected to do poorly or collapse in a longer perspective, i.e. at so far untested parameter combinations (Kjesbu, Tiedemann, et al., 2023). Rightly so, we did not disentangle the separate influence of  $F$  per se; we instead incorporated SSB data. Such a choice was on the assumption that SSB represents the stock reproductive potential (Kell et al., 2016) but also due to the

lack of generality in SSB versus  $F$  statistical relationships: SSB was negatively impacted by  $F$  in 41% cases. Expressed differently, we determined that it was outside the scope of this study to examine the robustness of the given assessment figures. Anyway, the observation that recruitment regime shift(s) often coincided for various stocks with highly different trends and magnitudes of  $F$ , strengthens that environmental conditions in a broad sense largely define year-class strength. This is reported in numerous publications, however, then without indicating strong stock compensatory effects (Ottersen & Holt, 2023), such as a detrimental Allee effect (Perälä et al., 2022). Care should be taken when considering overfished stocks, such as Western horse mackerel (ICES Stock Assessment Database, 2022), since only NAO contributed statistically to its recruitment dynamics but was not present after the threshold year. It should be noted that we did not include two other vital variables formally required to estimate stock productivity, i.e. body growth and natural mortality (Maunder et al., 2023; Rindorf et al., 2022). We argue that the inclusion of GSP should, however, be a good proxy for linkages body growth of planktivores (Heath, 2005) and early-life-history stages in general (Houde, 2008), whereas cannibalism, as included in the

NEA cod case study, is an expression of natural mortality (Yaragina et al., 2009).

In regarding to gaining a better understanding of recruitment dynamics, one should first of all realize the extreme complexity involved as multiple biotic and abiotic variables are influential (Figure 1) but also that these intra- and interconnections might function highly differently over time (Houde, 2016). However, due to the complexity of the prerecruitment processes and the multiple biotic and abiotic variables that have an influence, the underlying parametrizations should be updated in the future. Not only so, the usefulness of the current selection of drivers in the meta-analysis – in terms of their explanatory power and likely mechanistic role – included also examples of debatable results. Because of this, the variable in question might fail in properly reflecting the process aimed to be incorporated, as exemplified below.

SSB is generally considered the principal covariate in studies on recruitment dynamics in marine stocks due to its key role in defining stock status and thereby total allowable catch (TAC) (Walters & Martell, 2004). A global meta-analysis on 364 stocks showed that the relationship between SSB and recruitment (S-R relationships) is typically close to being positively linear (Myers & Barrowman, 1996). The highest (lowest) recruitment tends to occur when SSB is high (low), implying that recruitment generally is better above the median SSB. A subsequent complementary study exploring S-R relationships for 211 fish stocks, concluded on the existence of an universal asymptotic curve but with generally weak predictive power (Cury et al., 2014). In our study, we found examples where these S-R relationships provided little insight, such as in Golden redfish (*Sebastes norvegicus*, Scorpaenidae) where a negative relationship changing to a concave curve after the threshold year in 2010. This corresponded to high and falling SSB values, respectively. Furthermore, the impact of SSB disintegrated statistically at high levels for NEA cod, Coastal cod North and beaked redfish (*Sebastes mentella*, Scorpaenidae). This indicates that the effect of SSB depends on its actual mass in relation to the climate phase and environmental state situation. Therefore, the role of SSB in recruitment dynamics requires multiple cause-effect considerations of density dependency and density independence (Rothschild, 1986).

Another prime candidate as an environmental proxy of driver of recruitment dynamics is temperature. Our meta-analysis supports the notion that a higher T is expected to improve the recruitment strength of commercial stocks located in the higher-latitude Barents Sea (Bogstad et al., 2013; Øiestad, 1994). The opposite is the case in the lower-latitude North Sea (Kjesbu, Alix, et al., 2023) but in that ocean basin also observing smaller body sizes (cf. Bergmann's rule) (Baudron et al., 2014). Overall, these results agree with Myers (1998), concluding that recruitment-environment relationships tend to be positive (negative) for stocks in the northern (southern) limit of a species range. Such varied responses should be linked to the thermal niches of the species (Beaugrand, 2015). The observed (Kola temperature) and modelled (hindcasted) temperatures (T) in the Barents Sea are apparently positioned under the ascending limb of the convex (bell-shaped) "dose-response curve" (Drinkwater, 2005),

whereas the corresponding T series in the North Sea under the descending limb, with the analysed Norwegian Sea stocks being in a mixed situation. However, as illustrated by NEA cod (1921–2019), the situation may be much more complex. Here, the moving correlation of recruitment-temperature was generally periodic, as was the Kola temperature regressed on AMO, or NAO. This recruitment-temperature rhythm became a negative, insignificant trend with the current extreme warming in the Barents Sea. Historically, a warmer temperature has been considered a requirement but not a sufficient one for improved recruitment in this stock (Ellertsen et al., 1989; Kjesbu, Tiedemann, et al., 2023). Whilst this perception was valid in the 1980s, it is now not statistically valid. Therefore, it can reasonably safely be assumed that the ambient temperature is still positioned under the above-mentioned ascending limb of the dose-response plot for NEA cod but other influential factors have gained further strength.

Climatic indices, typically as large-scale teleconnection and atmospheric patterns over basins, may perform better than local environmental variables in the present exploration exercises since they represent integrated physical processes (Forchhammer & Post, 2004; Hallett et al., 2004). NAO refers to a redistribution of atmospheric mass between the Arctic and the subtropical Atlantic, leading to large changes in surface air temperature, winds, storminess and precipitation over the North Atlantic (Hurrell & Deser, 2010). Specifically, the presence of the positive NAO phase since the 1980s, not only caused pronounced changes in the physical conditions but also ecological communities in the North Atlantic (Alheit et al., 2012). The NAO appeared as a significant driver in half of the stocks studied in the North Sea, with T and NAO being positively correlated. Elsewhere, we only detected a significant effect of the NAO on NEA cod recruitment before 2005. The relevance of NAO through the increase in the advection of water along the western edge of the European shelf coincided with a northward migration of Western horse mackerel, which increased feeding opportunities for the adults (Reid et al., 2001). Conversely, the negative implications of a stronger NAO on NS cod recruitment seemingly operate via less *Calanus finmarchicus* being advected into the North Sea from the deep Norwegian Sea (Gao et al., 2021; Sundby, 2000) – we noted a significant inverse relation between the abundance of this copepod and NAO – reducing cod offspring growth rates and subsequent year class strength (Sirabella et al., 2001).

Acting simultaneously with the decadal-scale NAO, the multidecadal-scale AMO is based on detrended sea surface temperature anomalies averaged over the North Atlantic, thereby representing the long-term effect of low-frequency variability in thermal conditions (excluding global warming) on the ecosystems (Alheit et al., 2019). AMO is related in various ways with the other drivers considered here, but its cascading influence could not be statistically ascertained due to the issue of autocorrelation. Despite that, the negative or non-linear impacts of AMO on North Sea stocks were striking. Generally, AMO has a major influence on defining the longer-term, geographical displacement of regional stocks, as demonstrated for Northern hake and NEA mackerel

(Gullestad et al., 2020). Additionally, AMO is known to be important for the population dynamics of pelagic species as well as community structures (Tsikliras et al., 2019). Overall, recruitment success in the Northeast Atlantic stocks appears to be linked to large-scale climate variability patterns, primarily AMO and the subpolar gyre (Zimmermann et al., 2019). However, it should be noted that recent studies argue that AMO under on-going climate change fails to isolate the true internal variability in Northern Hemisphere mean temperature (Mann et al., 2014, 2022). So, although AMO functioned as an effective driver for several stocks, its current relevance might be less than before.

Food availability is well known to be vital for the recruitment success of marine fishes (Okamoto et al., 2012; Olsen et al., 2011). This can be manifested in adult investment in reproduction (McBride et al., 2015) or growth and survival of larvae (Cushing & Horwood, 1994). This implied that the principal stock-specific prey was divided by SSB in the NEA cod and NSS herring studies, whereas GSP lagged to the year the larvae were hatched for the meta-analysis. For NSS herring the ratio, i.e. GSP/SSB, appeared statistically irrelevant with respect to a better understanding of its recruitment dynamics. However, for NEA cod the updated GAM revealed a significant concave pattern, where the turning point was around 10 times more capelin than NEA cod SSB. More in-depth explorations show that the negative trend seen to the left in this curve principally refer to data after 2005, suggesting that the recent higher migration costs, due to a more northward displacement in the Barents Sea (Kjesbu, Alix, et al., 2023), might have negatively affected the fecundity (dos Santos Schmidt et al., 2017). Therefore, the current version of food availability for the adults of NEA cod lacks the spatial perspective. Moreover, the influence of cannibalism was a significant aspect but with high uncertainty, using immature biomass as an indicator. This was based on the notion that mortality resulting from cannibalism in NEA cod is primarily attributed to 3- to 6-year-olds, because the sexually mature NEA cod predominantly feed on capelin (Yaragina et al., 2009). For the NS cod, GSP statistically failed to represent the local abundance of *C. finmarchicus*; GSP tends to reflect the production of all types of zooplankton throughout the water column, whilst the CPR data show the near-surface abundance of *C. finmarchicus* (and other copepods not considered here). Our finding of an evidently reduced role of *C. finmarchicus* after 1998 compared to before this year agrees with the on-going northward displacement of this key copepod (Beaugrand et al., 2002; Kjesbu, Alix, et al., 2023). In addition, we found a robust, negative effect of NAO on *C. finmarchicus* abundance, linked to the westerly-wind-induced variability in temperature and inflow (Fromentin & Planque, 1996; Gao et al., 2021; Hjøllø et al., 2009).

0-group abundance and growth are anticipated to give a first indication of the subsequent recruitment strength (Eriksen et al., 2011). Our case study on NSS herring corroborates this assertion, revealing a positive link between 0-group abundance in combination with 0-group growth (measured as total length) and recruitment strength at age 2 years. In particular, the contribution of the latter trait was statistically strong, seeing direct proportionality, where the fitted curve

depicting the effect of 0-group abundance displayed an asymptotic pattern. This curve shape indicates that density-dependent effects are in place for NSS herring already about 6 months post hatch (Dingsør et al., 2007). It is, however, worth noting that the unsuccessful, parallel application of the 0-group variables for NEA cod could relate to that the juveniles of NEA cod are in the process of settling to the bottom when this statutory ecosystem survey runs in the Barents Sea, with those captured near the bottom typically being significantly larger (Irgens et al., 2017). Thus, the adopted survey design of trawling to a maximum depth of 80 m (mostly to 60 m) (Skjoldal et al., 2022) might provide relatively less quantitative insight in the actual 0-group situation for the demersal NEA cod than for the pelagic NSS herring. However, the potential large influence of variability in cannibalism over the first years of life may mask any influences of 0-group abundance and growth on NEA cod recruitment strength (Bergstad et al., 1987).

#### 4.4 | Non-stationary recruitment-climate relationships

Our results – consistently avoiding any prefixed S-R relationships – provided evidence for the prevalent existence of non-stationary recruitment-climate relationships in stocks inhabiting the Northeast Atlantic, consistent with results reported in Ottersen et al. (2013) based on the Ricker model. Non-stationary biology-climate relationships are emerging worldwide, e.g. in the Northeastern Pacific (Litzow et al., 2018, 2019), Northwestern Pacific (Ma et al., 2021, 2023), Northwestern Atlantic (Perälä et al., 2017) and, as documented here, in the Northeastern Atlantic. However, there is no clear consensus about the rationale behind these sudden changes. Studies in the Pacific attributed the nonstationarity to variability in atmospheric systems, altered relationships between large-scale atmospheric forcing and local-scale environmental responses (Litzow, Hunsicker, et al., 2020; Litzow, Malick, et al., 2020). In our study, the use of moving window revealed highly significant correlations between NAO and Kola temperature from the mid-1970s to the late 1990s, corresponding to the period with strong positive phases of NAO, indicating an intense Icelandic Low and a strong Azores High (Ottersen et al., 2001). Using the data-rich NEA cod as example, tight correlations were observed between recruitment at age 3 years and Kola temperature during that time window. It is reasonable to infer that strong atmospheric forcing drives homogeneity in regional physical variables in the Barents Sea, and thereby poses marked effects on this stock's recruitment dynamics. After 2000, accompanying decoupled Kola temperature-NAO relationship, recruitment-Kola temperature also decoupled. Ottersen and Holt (2023) hypothesized that recruitment from a truncated spawning stock, i.e. dominated by younger individuals and few age classes, is more vulnerable to environmental fluctuations. It would be an effective explanation for the uncorrelated recruitment and Kola temperature in the 1930s, when the Kola temperature was highly associated with NAO, but the demographic structure of NEA cod being highly rich (mean age

of spawners >12 years old) thereby overruling the statistical detection of the temperature influence. Additionally, novel climates, which were primarily represented by unparalleled T and GSP after 2000, would also be an important driver behind the decoupled relationships.

Concerning modelling strategies, the emerging recognition on non-stationary biology–climate relationship requires updated statistical approaches, especially for threshold models. In this study, comparisons between stationary and non-stationary relationships were achieved by GAM and vcGAM. Although no fitted formula is given by these models, high flexible model structures benefit integration of the changeable effective drivers and types of their effects (Ma et al., 2023). However, modelling strategies concerning non-stationary relationships include plentiful of choices. Based on this work, the first consideration should be time-dependent effects of invariant drivers showing different influences (direction and strength) within various time frames. Then one should incorporate variant drivers that make a measurable contribution in different time frames. Furthermore, asynchronous threshold years should be considered, i.e. different drivers might introduce threshold years at unlike time points instead, as here, limiting the script to contain the same threshold year(s). In addition to fitting relationships based on historical data, threshold models show promising prospects under climate change scenarios. However, a difficulty is the accurate prediction of future threshold years. Except for the characterization and forecast of specially worrying regional climate change patterns (for example, the emergency of novel climate), “early warning signals” derived from critical transition theories (Scheffer et al., 2009, 2012) could also possibly be used to provide references for expected threshold years in years to come.

## 5 | CONCLUSIONS

Our hindcast meta-analysis aimed to give an overview of how the recruitment of commercial stocks in the Northeast Atlantic has responded to variability in biophysical drivers as well as in SSB, with a particular focus on recruitment regime shifts and nonstationarity in recruitment–climate relationships. These extensive exploratory analyses revealed prevalent recruitment regime shifts in this region of the world's ocean but also stock- and area-specific patterns. Furthermore, these shifts were reflected in the recruitment responses as such, underlining the point that comprehensive considerations about both stock traits and habitat conditions are needed when investigating recruitment dynamics. Non-stationary recruitment–climate relationships were often recorded in the Northeast Atlantic. These markedly altered formulations could be triggered by climate-induced homogeneity and heterogeneity in local-scale environmental condition, changes in dominating age class of spawning stocks, and as well as novel climate. Both synchronicity and asynchronicity exist between recruitment regime shifts, nonstationarity (threshold) in recruitment–climate relationships as well as abrupt state shift and phase change in biophysical drivers, emphasizing

that the recruitment of a stock may not react to a shift/change of external drivers in a regime-like manner. To enhance the finer-scale understanding of recruitment responses, especially those that are elusive or unexpected in the meta-analysis, we included case studies on key stocks. By incorporating additional candidate variables that capture critical aspects of life history or vital processes, we were able to portray recruitment dynamics in greater detail, underlining the requirements for even more stock-specific analyses, especially for stocks whose key drivers may not be adequately represented by the large-scale variables used in the meta-analysis. This two-step analytic design highlighted the necessity for more in-depth understandings of the representatives of biotic and abiotic drivers. Considering the anticipated increase in the frequency and severity of climate change and variability in the future, evolving advice and managing strategies for commercial stocks seems an imperative task to support the sustainability in fisheries.

## AUTHOR CONTRIBUTIONS

S.M. and O.S.K. involved in conceptualization, as well as visualization; A.B.S. and S.S.H. provided the modelled climatic (environmental) data; S.M. did analysis; O.S.K. provided suggestions on analysis; K.O. provided instructions on formal analysis; R.D.M.N., K.N., S.S., T.C. and J.H.V. provided feedback on results; O.S.K. and G.H. acquired the funding; S.M. and O.S.K. wrote the original draft; all co-authors reviewed and edited the manuscript.

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## CONFLICT OF INTEREST STATEMENT

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## DATA AVAILABILITY STATEMENT

All sources of data are specified in the Methods and Materials section in this article, either from ICES ([www.ices.dk](http://www.ices.dk)), the published literature or online databases.



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## REFERENCES

- Alheit, J., Gröger, J., Licandro, P., McQuinn, I. H., Pohlmann, T., & Tsikiras, A. C. (2019). What happened in the mid-1990s? The coupled ocean-atmosphere processes behind climate-induced ecosystem changes in the Northeast Atlantic and the Mediterranean. *Deep Sea Research Part II: Topical Studies in Oceanography*, 159, 130–142. <https://doi.org/10.1016/j.dsr2.2018.11.011>
- Alheit, J., Pohlmann, T., Casini, M., Greve, W., Hinrichs, R., Mathis, M., O'Driscoll, K., Vorberg, R., & Wagner, C. (2012). Climate variability drives anchovies and sardines into the north and Baltic seas. *Progress in Oceanography*, 96(1), 128–139. <https://doi.org/10.1016/j.pocean.2011.11.015>
- Allan, B. J. M., Ray, J. L., Tiedemann, M., Komyakova, V., Vikebø, F., Skaar, K. S., Stiasny, M. H., Folkvord, A., Nash, R. D., Stenevik, E. K., & Kjesbu, O. S. (2021). Quantitative molecular detection of larval Atlantic herring (*Clupea harengus*) in stomach contents of Atlantic mackerel (*Scomber scombrus*) marks regions of predation pressure. *Scientific Reports*, 11(1), 5095. <https://doi.org/10.1038/s41598-021-84545-7>
- Årthun, M., Bogstad, B., Daewel, U., Keenlyside, N. S., Sandø, A. B., Schrum, C., & Ottersen, G. (2018). Climate based multi-year predictions of the Barents Sea cod stock. *PLoS One*, 13(10), e0206319. <https://doi.org/10.1371/journal.pone.0206319>
- Bailey, K., & Houde, E. (1989). Predation on eggs and larvae of marine fishes and the recruitment problem. *Advances in Marine Biology*, 25, 1–83. [https://doi.org/10.1016/S0065-2881\(08\)60187-X](https://doi.org/10.1016/S0065-2881(08)60187-X)
- Baudron, A. R., Needle, C. L., Rijnsdorp, A. D., & Tara Marshall, C. (2014). Warming temperatures and smaller body sizes: Synchronous changes in growth of North Sea fishes. *Global Change Biology*, 20(4), 1023–1031. <https://doi.org/10.1111/gcb.12514>
- Beaugrand, G. (2004). The North Sea regime shift: Evidence, causes, mechanisms and consequences. *Progress in Oceanography*, 60(2–4), 245–262. <https://doi.org/10.1016/j.pocean.2004.02.018>
- Beaugrand, G. (2015). Theoretical basis for predicting climate-induced abrupt shifts in the oceans. *Philosophical Transactions of the Royal Society, B: Biological Sciences*, 370(1659), 20130264. <https://doi.org/10.1098/rstb.2013.0264>
- Beaugrand, G., Brander, K. M., Alistair Lindley, J., Souissi, S., & Reid, P. C. (2003). Plankton effect on cod recruitment in the North Sea. *Nature*, 426(6967), 661–664. <https://doi.org/10.1038/nature02164>
- Beaugrand, G., Reid, P. C., Ibanez, F., Lindley, J. A., & Edwards, M. (2002). Reorganization of North Atlantic marine copepod biodiversity and climate. *Science*, 296(5573), 1692–1694. <https://doi.org/10.1126/science.1071329>
- Belkin, I. M. (2009). Rapid warming of large marine ecosystems. *Progress in Oceanography*, 81(1–4), 207–213. <https://doi.org/10.1016/j.pocean.2009.04.011>
- Bentsen, M., Bethke, I., Debernard, J. B., Iversen, T., Kirkevåg, A., Seland, Ø., Drange, H., Roelandt, C., Seierstad, I. A., Hoose, C., & Kristjansson, J. E. (2013). The Norwegian earth system model, NorESM1-M—part 1: Description and basic evaluation of the physical climate. *Geoscientific Model Development*, 6(3), 687–720. <https://doi.org/10.5194/gmd-6-687-2013>
- Bergstad, O., Jørgensen, T., & Dragesund, O. (1987). Life history and ecology of the gadoid resources of the Barents Sea. *Fisheries Research*, 5(2–3), 119–161. [https://doi.org/10.1016/0165-7836\(87\)90037-3](https://doi.org/10.1016/0165-7836(87)90037-3)
- Beverton, R. J., & Holt, S. J. (2012). *On the dynamics of exploited fish populations* (Vol. 11). Springer Science & Business Media.
- Bogstad, B., Dingsør, G. E., Ingvaldsen, R. B., & Gjørseter, H. (2013). Changes in the relationship between sea temperature and recruitment of cod, haddock and herring in the Barents Sea. *Marine Biology Research*, 9(9), 895–907. <https://doi.org/10.1080/17451000.2013.775451>
- Bogstad, B., & Mehl, S. (1997). Interactions between Atlantic cod (*Gadus morhua*) and its prey species in the Barents Sea. *Proceedings of the International Symposium on the Role of Forage Fishes in Marine Ecosystems, Report No. 97-01(97-01)*, 591–615.
- Boitsov, V. D., Karsakov, A. L., & Trofimov, A. G. (2012). Atlantic water temperature and climate in the Barents Sea, 2000–2009. *ICES Journal of Marine Science*, 69(5), 833–840. <https://doi.org/10.1093/icesjms/fss075>
- Brooks, E. N., & Deroba, J. J. (2015). When “data” are not data: The pitfalls of post hoc analyses that use stock assessment model output. *Canadian Journal of Fisheries and Aquatic Sciences*, 72(4), 634–641. <https://doi.org/10.1139/cjfas-2014-0231>
- Casini, M., Hjelm, J., Molinero, J.-C., Lövgren, J., Cardinale, M., Bartolino, V., Belgrano, A., & Kornilovs, G. (2009). Trophic cascades promote threshold-like shifts in pelagic marine ecosystems. *Proceedings of the National Academy of Sciences*, 106(1), 197–202. <https://doi.org/10.1073/pnas.0806649105>
- Cheung, W. W. L., Watson, R., & Pauly, D. (2013). Signature of ocean warming in global fisheries catch. *Nature*, 497(7449), 365–368. <https://doi.org/10.1038/nature12156>
- Clark, T., & Luis, A. D. (2020). Nonlinear population dynamics are ubiquitous in animals. *Nature Ecology & Evolution*, 4(1), 75–81. <https://doi.org/10.1038/s41559-019-1052-6>
- Conversi, A., Dakos, V., Gårdmark, A., Ling, S., Folke, C., Mumby, P. J., Greene, C., Edwards, M., Blenckner, T., Casini, M., Pershing, A., & Möllmann, C. (2015). A holistic view of marine regime shifts. *Philosophical Transactions of the Royal Society, B: Biological Sciences*, 370(1659), 20130279. <https://doi.org/10.1098/rstb.2013.0279>
- Cooper, W. T., Barbieri, L. R., Murphy, M. D., & Lowerre-Barbieri, S. K. (2013). Assessing stock reproductive potential in species with indeterminate fecundity: Effects of age truncation and size-dependent reproductive timing. *Fisheries Research*, 138, 31–41. <https://doi.org/10.1016/j.fishres.2012.05.016>
- Cury, P. M., Fromentin, J.-M., Figuet, S., & Bonhommeau, S. (2014). Resolving Hjort's dilemma: How is recruitment related to spawning stock biomass in marine fish? *Oceanography*, 27(4), 42–47. <https://doi.org/10.5670/oceanog.2014.85>
- Cushing, D. (1984). The gadoid outburst in the North Sea. *ICES Journal of Marine Science*, 41(2), 159–166. <https://doi.org/10.1093/icesjms/41.2.159>
- Cushing, D. (1990). Plankton production and year-class strength in fish populations: An update of the match/mismatch hypothesis. *Advances in Marine Biology*, 26, 249–293. [https://doi.org/10.1016/S0065-2881\(08\)60202-3](https://doi.org/10.1016/S0065-2881(08)60202-3)
- Cushing, D., & Horwood, J. (1994). The growth and death of fish larvae. *Journal of Plankton Research*, 16(3), 291–300. <https://doi.org/10.1093/plankt/16.3.291>
- Dingsør, G. E., Ciannelli, L., Chan, K.-S., Ottersen, G., & Stenseth, N. C. (2007). Density dependence and density independence during the early life stages of four marine fish stocks. *Ecology*, 88(3), 625–634. <https://doi.org/10.1890/05-1782>

- Doney, S. C., Ruckelshaus, M., Emmett Duffy, J., Barry, J. P., Chan, F., English, C. A., Galindo, H. M., Grebmeier, J. M., Hollowed, A. B., Knowlton, N., Polovina, J., Rabalais, N. N., Sydeman, W. J., & Talley, L. D. (2012). Climate change impacts on marine ecosystems. *Annual Review of Marine Science*, 4, 11–37. <https://doi.org/10.1146/annurev-marine-041911-111611>
- Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J. R. G., Gruber, B., Lafourcade, B., Leitão, P. J., Münkemüller, T., McClean, C., Osborne, P. E., Reineking, B., Schröder, B., Skidmore, A. K., Zurell, D., & Lautenbach, S. (2013). Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. *Ecography*, 36(1), 27–46. <https://doi.org/10.1111/j.1600-0587.2012.07348.x>
- dos Santos Schmidt, T., Slotte, A., Olafsdottir, A. H., Nøttestad, L., Jansen, T., Jacobsen, J. A., Bjarnason, S., Lusseau, S. M., Ono, K., Hølleland, S., Thorsen, A., Sandø, A. B., & Kjesbu, O. S. (2023). Poleward spawning of Atlantic mackerel (*Scomber scombrus*) is facilitated by ocean warming but triggered by energetic constraints. *ICES Journal of Marine Science*, fsad098. <https://doi.org/10.1093/icesjms/fsad098>
- dos Santos Schmidt, T. C., Slotte, A., Kennedy, J., Sundby, S., Johannessen, A., Óskarsson, G. J., Kurita, Y., Stenseth, N. C., & Kjesbu, O. S. (2017). Oogenesis and reproductive investment of Atlantic herring are functions of not only present but long-ago environmental influences as well. *Proceedings of the National Academy of Sciences*, 114(10), 2634–2639. <https://doi.org/10.1073/pnas.1700349114>
- Drinkwater, K. F. (2005). The response of Atlantic cod (*Gadus morhua*) to future climate change. *ICES Journal of Marine Science*, 62(7), 1327–1337. <https://doi.org/10.1016/j.icesjms.2005.05.015>
- Ellertsen, B., Fossum, P., Solemdal, P., & Sundby, S. (1989). Relation between temperature and survival of eggs and first-feeding larvae of the Northeast Arctic cod (*Gadus morhua* L.). *Rapports et Procès-Verbaux Des Réunions du Conseil International Pour l'Exploration de la Mer*, 191, 209–219.
- Endo, C., Skogen, M., Stige, L., Hjøllø, S., & Vikebø, F. (2023). The effects of spatial and temporal variations in spawning on offspring survival in Northeast Arctic cod. *ICES Journal of Marine Science*, fsad034. <https://doi.org/10.1093/icesjms/fsad034>
- Eriksen, E., Bogstad, B., & Nakken, O. (2011). Ecological significance of 0-group fish in the Barents Sea ecosystem. *Polar Biology*, 34, 647–657. <https://doi.org/10.1007/s00300-010-0920-y>
- Facon, B., Genton, B. J., Shykoff, J., Jarne, P., Estoup, A., & David, P. (2006). A general eco-evolutionary framework for understanding bioinvasions. *Trends in Ecology & Evolution*, 21(3), 130–135. <https://doi.org/10.1016/j.tree.2005.10.012>
- Forchhammer, M. C., & Post, E. (2004). Using large-scale climate indices in climate change ecology studies. *Population Ecology*, 46, 1–12. <https://doi.org/10.1007/s10144-004-0176-x>
- Fossheim, M., Primicerio, R., Johannessen, E., Ingvaldsen, R. B., Aschan, M. M., & Dolgov, A. V. (2015). Recent warming leads to a rapid borealization of fish communities in the Arctic. *Nature Climate Change*, 5(7), 673–677. <https://doi.org/10.1038/nclimate2647>
- Fromentin, J.-M., & Planque, B. (1996). *Calanus* and environment in the eastern North Atlantic. II. Influence of the North Atlantic oscillation on *C. finmarchicus* and *C. helgolandicus*. *Marine Ecology Progress Series*, 134, 111–118. <https://doi.org/10.3354/meps134111>
- Gao, S., Hjøllø, S. S., Falkenhaug, T., Strand, E., Edwards, M., & Skogen, M. D. (2021). Overwintering distribution, inflow patterns and sustainability of *Calanus finmarchicus* in the North Sea. *Progress in Oceanography*, 194, 102567. <https://doi.org/10.1016/j.pocean.2021.102567>
- Gullestad, P., Sundby, S., & Kjesbu, O. S. (2020). Management of transboundary and straddling fish stocks in the Northeast Atlantic in view of climate-induced shifts in spatial distribution. *Fish and Fisheries*, 21(5), 1008–1026. <https://doi.org/10.1111/faf.12485>
- Hallett, T., Coulson, T., Pilkington, J., Clutton-Brock, T., Pemberton, J., & Grenfell, B. (2004). Why large-scale climate indices seem to predict ecological processes better than local weather. *Nature*, 430(6995), 71–75. <https://doi.org/10.1038/nature02708>
- Hamre, J. (1994). Biodiversity and exploitation of the main fish stocks in the Norwegian-Barents Sea ecosystem. *Biodiversity and Conservation*, 3, 473–492. <https://doi.org/10.1007/BF00115154>
- Hare, J. A., Morrison, W. E., Nelson, M. W., Stachura, M. M., Teeters, E. J., Griffis, R. B., Alexander, M. A., Scott, J. D., Alade, L., Bell, R. J., Chute, A. S., Curti, K. L., Curtis, T. H., Kircheis, D., Kocik, J. F., Lucey, S. M., McCandless, C. T., Milke, L. M., Richardson, D. E., ... Griswold, C. A. (2016). A vulnerability assessment of fish and invertebrates to climate change on the northeast US continental shelf. *PLoS One*, 11(2), e0146756. <https://doi.org/10.1371/journal.pone.0146756>
- Hátún, H., Payne, M., Beaugrand, G., Reid, P., Sandø, A., Drange, H., Hansen, B., Jacobsen, J., & Bloch, D. (2009). Large bio-geographical shifts in the North-Eastern Atlantic Ocean: From the subpolar gyre, via plankton, to blue whiting and pilot whales. *Progress in Oceanography*, 80(3–4), 149–162. <https://doi.org/10.1016/j.pocean.2009.03.001>
- Haug, T., Bogstad, B., Chierici, M., Gjøsæter, H., Hallfredson, E. H., Høines, Å. S., Hoel, A. H., Ingvaldsen, R. B., Jørgensen, L. L., Knutsen, T., Loeng, H., Naustvoll, L.-J., Røttingen, I., & Sunnanå, K. (2017). Future harvest of living resources in the Arctic Ocean north of the Nordic and Barents seas: A review of possibilities and constraints. *Fisheries Research*, 188, 38–57. <https://doi.org/10.1016/j.fishres.2016.12.002>
- Heath, M. R. (2005). Changes in the structure and function of the North Sea fish foodweb, 1973–2000, and the impacts of fishing and climate. *ICES Journal of Marine Science*, 62(5), 847–868. <https://doi.org/10.1016/j.icesjms.2005.01.023>
- Hermansen, G. H., Hjort, N. L., & Kjesbu, O. S. (2016). Recent advances in statistical methodology applied to the Hjort liver index time series (1859–2012) and associated influential factors. *Canadian Journal of Fisheries and Aquatic Sciences*, 73(2), 279–295. <https://doi.org/10.1139/cjfas-2015-0086>
- Hjøllø, S. S., Skogen, M. D., & Svendsen, E. (2009). Exploring currents and heat within the North Sea using a numerical model. *Journal of Marine Systems*, 78(1), 180–192. <https://doi.org/10.1016/j.jmarsys.2009.06.001>
- Hjøllø, S. S., van Leeuwen, S. M., & Maar, M. (2021). Marine research and management topics addressed by process-based ecosystem models. *Marine Ecology Progress Series*, 680, 1–6. <https://doi.org/10.3354/meps13963>
- Hjort, J. (1914). Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. *Rapports et Procès-verbaux des Réunions du Conseil International pour l'Exploration de la Mer*, 20, 1–228.
- Hoegh-Guldberg, O., & Bruno, J. F. (2010). The impact of climate change on the world's marine ecosystems. *Science*, 328(5985), 1523–1528. <https://doi.org/10.1126/science.1189930>
- Hordoir, R., Skagseth, Ø., Ingvaldsen, R. B., Sandø, A. B., Löptien, U., Dietze, H., Gierisch, A. M., Assmann, K. M., Lundesgaard, Ø., & Lind, S. (2022). Changes in Arctic stratification and mixed layer depth cycle: A modeling analysis. *Journal of Geophysical Research: Oceans*, 127(1), e2021JC017270. <https://doi.org/10.1029/2021JC017270>
- Houde, E. D. (2008). Emerging from Hjort's shadow. *Journal of Northwest Atlantic Fishery Science*, 41, 53–70. <https://doi.org/10.2960/J.v41.m634>
- Houde, E. D. (2016). Recruitment variability. In *Fish reproductive biology: Implications for assessment and management* (pp. 98–187). John Wiley & Sons.
- Hurrell, J. W., & Deser, C. (2010). North Atlantic climate variability: The role of the North Atlantic oscillation. *Journal of Marine Systems*, 79(3–4), 231–244. <https://doi.org/10.1016/j.jmarsys.2009.11.002>

- Hysten, A. (2002). Fluctuations in abundance of Northeast Arctic cod during the 20th century. *ICES Marine Science Symposia*, 215, 543–550. <https://doi.org/10.17895/ices.pub.8898>
- ICES. (2023). *Benchmark workshop on Northern Shelf cod stocks (WKBCOD)*. [https://ices-library.figshare.com/articles/report/Benchmark\\_workshop\\_on\\_Northern\\_Shelf\\_cod\\_stocks\\_WKBCOD\\_/22591423](https://ices-library.figshare.com/articles/report/Benchmark_workshop_on_Northern_Shelf_cod_stocks_WKBCOD_/22591423)
- ICES Stock Assessment Database. (2022). Copenhagen, Denmark. ICES. <https://standardgraphs.ices.dk>
- Ingvaldsen, R. B., Assmann, K. M., Primicerio, R., Fossheim, M., Polyakov, I. V., & Dolgov, A. V. (2021). Physical manifestations and ecological implications of Arctic Atlantification. *Nature Reviews Earth and Environment*, 2(12), 874–889. <https://doi.org/10.1038/s43017-021-00228-x>
- Irgens, C., Kjesbu, O. S., & Folkvord, A. (2017). Ontogenetic development of otolith shape during settlement of juvenile Barents Sea cod (*Gadus morhua*). *ICES Journal of Marine Science*, 74(9), 2389–2397. <https://doi.org/10.1093/icesjms/fsx088>
- Johannesen, E., Ingvaldsen, R. B., Bogstad, B., Dalpadado, P., Eriksen, E., Gjøsaeter, H., Knutsen, T., Skern-Mauritzen, M., & Stiansen, J. E. (2012). Changes in Barents Sea ecosystem state, 1970–2009: Climate fluctuations, human impact, and trophic interactions. *ICES Journal of Marine Science*, 69(5), 880–889. <https://doi.org/10.1093/icesjms/fss046>
- Kell, L. T., Nash, R. D., Dickey-Collas, M., Mosqueira, I., & Szuwalski, C. (2016). Is spawning stock biomass a robust proxy for reproductive potential? *Fish and Fisheries*, 17(3), 596–616. <https://doi.org/10.1111/faf.12131>
- Kjesbu, O., Witthames, P., Solemdal, P., & Walker, M. G. (1998). Temporal variations in the fecundity of Arcto-Norwegian cod (*Gadus morhua*) in response to natural changes in food and temperature. *Journal of Sea Research*, 40(3–4), 303–321. [https://doi.org/10.1016/S1385-1101\(98\)00029-X](https://doi.org/10.1016/S1385-1101(98)00029-X)
- Kjesbu, O. S., Alix, M., Sandø, A. B., Strand, E., Wright, P. J., Johns, D. G., Thorsen, A., Marshall, C. T., Bakkeplass, K. G., Vikebø, F. B., Myksvoll, M. S., Ottersen, G., Allan, B. J. M., Fossheim, M., Stiansen, J. E., Huse, G., & Sundby, S. (2023). Latitudinally distinct stocks of Atlantic cod face fundamentally different biophysical challenges under on-going climate change. *Fish and Fisheries*, 24, 297–320. <https://doi.org/10.1111/faf.12728>
- Kjesbu, O. S., Bogstad, B., Devine, J. A., Gjøsaeter, H., Howell, D., Ingvaldsen, R. B., Nash, R. D., & Skjæraasen, J. E. (2014). Synergies between climate and management for Atlantic cod fisheries at high latitudes. *Proceedings of the National Academy of Sciences*, 111(9), 3478–3483. <https://doi.org/10.1073/pnas.1316342111>
- Kjesbu, O. S., Sundby, S., Sandø, A. B., Alix, M., Hjøllø, S. S., Tiedemann, M., Skern-Mauritzen, M., Junge, C., Fossheim, M., Thorsen Bross, C., Søvik, G., Zimmermann, F., Nedreaas, K., Eriksen, E., Höffle, H., Hjelset, A. M., Kvamme, C., Reece, Y., Knutsen, H., ... Huse, G. (2022). Highly mixed impacts of near-future climate change on stock productivity proxies in the north East Atlantic. *Fish and Fisheries*, 23(3), 601–615. <https://doi.org/10.1111/faf.12635>
- Kjesbu, O. S., Tiedemann, I., Alix, M., Thorsen, A., & Sundby, S. (2023). Half a century of high-latitude fisheries oceanography research on the “recruitment problem” in Northeast Arctic cod (*Gadus morhua*). *ICES Journal of Marine Science*, 80, 1179–1201. <https://doi.org/10.1093/icesjms/fsad073>
- Knight, J. R., Folland, C. K., & Scaife, A. A. (2006). Climate impacts of the Atlantic multidecadal oscillation. *Geophysical Research Letters*, 33(17), L17706. <https://doi.org/10.1029/2006GL026242>
- Le Pape, O., & Bonhommeau, S. (2015). The food limitation hypothesis for juvenile marine fish. *Fish and Fisheries*, 16(3), 373–398. <https://doi.org/10.1111/faf.12063>
- Lehodey, P., Alheit, J., Barange, M., Baumgartner, T., Beaugrand, G., Drinkwater, K., Fromentin, J.-M., Hare, S., Ottersen, G., Perry, R., Roy, C., van der Linden, C. D., & Werner, F. (2006). Climate variability, fish, and fisheries. *Journal of Climate*, 19(20), 5009–5030. <https://doi.org/10.1175/JCLI3898.1>
- Levin, P. S., & Möllmann, C. (2015). Marine ecosystem regime shifts: Challenges and opportunities for ecosystem-based management. *Philosophical Transactions of the Royal Society, B: Biological Sciences*, 370(1659), 20130275. <https://doi.org/10.1098/rstb.2013.0275>
- Litzow, M. A., Ciannelli, L., Puerta, P., Wettstein, J. J., Rykaczewski, R. R., & Opiekun, M. (2018). Non-stationary climate–salmon relationships in the Gulf of Alaska. *Proceedings of the Royal Society B*, 285(1890), 20181855. <https://doi.org/10.1098/rspb.2018.1855>
- Litzow, M. A., Ciannelli, L., Puerta, P., Wettstein, J. J., Rykaczewski, R. R., & Opiekun, M. (2019). Nonstationary environmental and community relationships in the North Pacific Ocean. *Ecology*, 100(8), e02760. <https://doi.org/10.1002/ecy.2760>
- Litzow, M. A., Hunsicker, M. E., Bond, N. A., Burke, B. J., Cunningham, C. J., Gosselin, J. L., Norton, E. L., Ward, E. J., & Zador, S. G. (2020). The changing physical and ecological meanings of North Pacific Ocean climate indices. *Proceedings of the National Academy of Sciences*, 117(14), 7665–7671. <https://doi.org/10.1073/pnas.1921266117>
- Litzow, M. A., Malick, M. J., Bond, N. A., Cunningham, C. J., Gosselin, J. L., & Ward, E. J. (2020). Quantifying a novel climate through changes in PDO-climate and PDO-salmon relationships. *Geophysical Research Letters*, 47(16), e2020GL087972. <https://doi.org/10.1029/2020GL087972>
- Loeng, H., & Drinkwater, K. (2007). An overview of the ecosystems of the Barents and Norwegian seas and their response to climate variability. *Deep Sea Research Part II: Topical Studies in Oceanography*, 54(23–26), 2478–2500. <https://doi.org/10.1016/j.dsr2.2007.08.013>
- Ma, S., Fu, C., Li, J., Sun, P., Liu, Y., Ye, Z., Watanabe, Y., & Tian, Y. (2023). Non-stationary effects of multiple drivers on the dynamics of Japanese sardine (*Sardinops melanostictus*, Clupeidae). *Fish and Fisheries*, 24(1), 40–55. <https://doi.org/10.1111/faf.12708>
- Ma, S., Tian, Y., Fu, C., Yu, H., Li, J., Liu, Y., Cheng, J., Wan, R., & Watanabe, Y. (2021). Climate-induced nonlinearity in pelagic communities and non-stationary relationships with physical drivers in the Kuroshio ecosystem. *Fish and Fisheries*, 22(1), 1–17. <https://doi.org/10.1111/faf.12502>
- Mann, M. E., Steinman, B. A., Brouillette, D. J., Fernandez, A., & Miller, S. K. (2022). On the estimation of internal climate variability during the preindustrial past millennium. *Geophysical Research Letters*, 49(2), e2021GL096596. <https://doi.org/10.1029/2021GL096596>
- Mann, M. E., Steinman, B. A., & Miller, S. K. (2014). On forced temperature changes, internal variability, and the AMO. *Geophysical Research Letters*, 41(9), 3211–3219. <https://doi.org/10.1002/2014GL059233>
- Mauder, M. N., Hamel, O. S., Lee, H.-H., Piner, K. R., Cope, J. M., Punt, A. E., Ianelli, J. N., Castillo-Jordán, C., Kapur, M. S., & Methot, R. D. (2023). A review of estimation methods for natural mortality and their performance in the context of fishery stock assessment. *Fisheries Research*, 257, 106489. <https://doi.org/10.1016/j.fishres.2022.106489>
- McBride, R. S., Somarakis, S., Fitzhugh, G. R., Albert, A., Yaragina, N. A., Wuenschel, M. J., Alonso-Fernández, A., & Basilone, G. (2015). Energy acquisition and allocation to egg production in relation to fish reproductive strategies. *Fish and Fisheries*, 16(1), 23–57. <https://doi.org/10.1111/faf.12043>
- Munch, S. B., Giron-Nava, A., & Sugihara, G. (2018). Nonlinear dynamics and noise in fisheries recruitment: A global meta-analysis. *Fish and Fisheries*, 19(6), 964–973. <https://doi.org/10.1111/faf.12304>
- Myers, R., & Barrowman, N. J. (1996). Is fish recruitment related to spawner abundance. *Fishery Bulletin*, 94, 707–724.
- Myers, R. A. (1998). When do environment–recruitment correlations work? *Reviews in Fish Biology and Fisheries*, 8, 285–305. <https://doi.org/10.1023/A:1008828730759>

- O'Brien, C. M., Fox, C. J., Planque, B., & Casey, J. (2000). Climate variability and North Sea cod. *Nature*, 404(6774), 142. <https://doi.org/10.1038/35004654>
- Ogle, D. H., Doll, J. C., Wheeler, P., & Dinno, A. (2022). FSA: Fisheries Stock Analysis. R package version 0.9.3. <https://github.com/fishR-Core-Team/FSA>
- Øiestad, V. (1994). Historic changes in cod stocks and cod fisheries: Northeast Arctic cod. ICES Marine Science Symposia. Copenhagen.
- Okamoto, D. K., Schmitt, R. J., Holbrook, S. J., & Reed, D. C. (2012). Fluctuations in food supply drive recruitment variation in a marine fish. *Proceedings of the Royal Society B: Biological Sciences*, 279(1747), 4542–4550. <https://doi.org/10.1098/rspb.2012.1862>
- Olsen, E. M., Ottersen, G., Llope, M., Chan, K.-S., Beaugrand, G., & Stenseth, N. C. (2011). Spawning stock and recruitment in North Sea cod shaped by food and climate. *Proceedings of the Royal Society B: Biological Sciences*, 278(1705), 504–510. <https://doi.org/10.1098/rspb.2010.1465>
- Ottersen, G., & Holt, R. E. (2023). Long-term variability in spawning stock age structure influences climate–recruitment link for Barents Sea cod. *Fisheries Oceanography*, 32(1), 91–105. <https://doi.org/10.1111/fog.12605>
- Ottersen, G., Planque, B., Belgrano, A., Post, E., Reid, P. C., & Stenseth, N. C. (2001). Ecological effects of the North Atlantic oscillation. *Oecologia*, 128, 1–14. <https://doi.org/10.1007/s004420100655>
- Ottersen, G., Stige, L. C., Durant, J. M., Chan, K.-S., Rouyer, T. A., Drinkwater, K. F., & Stenseth, N. C. (2013). Temporal shifts in recruitment dynamics of North Atlantic fish stocks: Effects of spawning stock and temperature. *Marine Ecology Progress Series*, 480, 205–225. <https://doi.org/10.3354/meps10249>
- Paasche, Ø., Østerblom, H., Neuenfeldt, S., Bonsdorff, E., Brander, K., Conley, D. J., Durant, J. M., Eikeset, A. M., Goksøyr, A., Jónsson, S., Kjesbu, O. S., Kuparinen, A., & Stenseth, N. C. (2015). Connecting the seas of Norden. *Nature Climate Change*, 5(2), 89–92. <https://doi.org/10.1038/nclimate2471>
- Parsons, L., & Lear, W. (2001). Climate variability and marine ecosystem impacts: A North Atlantic perspective. *Progress in Oceanography*, 49(1–4), 167–188. [https://doi.org/10.1016/S0079-6611\(01\)00021-0](https://doi.org/10.1016/S0079-6611(01)00021-0)
- Payne, M. R., Kudahl, M., Engelhard, G. H., Peck, M. A., & Pinnegar, J. K. (2021). Climate risk to European fisheries and coastal communities. *Proceedings of the National Academy of Sciences*, 118(40), e2018086118. <https://doi.org/10.1073/pnas.2018086118>
- Pepin, P. (1991). Effect of temperature and size on development, mortality, and survival rates of the pelagic early life history stages of marine fish. *Canadian Journal of Fisheries and Aquatic Sciences*, 48(3), 503–518. <https://doi.org/10.1139/f91-065>
- Perälä, T., Hutchings, J. A., & Kuparinen, A. (2022). Allee effects and the Allee-effect zone in Northwest Atlantic cod. *Biology Letters*, 18(2), 20210439. <https://doi.org/10.1098/rsbl.2021.0439>
- Perälä, T. A., Swain, D. P., & Kuparinen, A. (2017). Examining nonstationarity in the recruitment dynamics of fishes using Bayesian change point analysis. *Canadian Journal of Fisheries and Aquatic Sciences*, 74(5), 751–765. <https://doi.org/10.1139/cjfas-2016-0177>
- Perretti, C. T., Fogarty, M. J., Friedland, K. D., Hare, J. A., Lucey, S. M., McBride, R. S., Miller, T. J., Morse, R. E., O'Brien, L., Pereira, J. J., Smith, L. A., & Wuenschel, M. J. (2017). Regime shifts in fish recruitment on the northeast US continental shelf. *Marine Ecology Progress Series*, 574, 1–11. <https://doi.org/10.3354/meps12183>
- Poloczanska, E. S., Brown, C. J., Sydeman, W. J., Kiessling, W., Schoeman, D. S., Moore, P. J., Brander, K., Bruno, J. F., Buckley, L. B., Burrows, M. T., Duarte, C. M., Halpern, B. S., Holding, J., Kappel, C. V., O'Connor, M. I., Pandolfi, J. M., Parmesan, C., Schwing, F., Thompson, S. A., & Richardson, A. J. (2013). Global imprint of climate change on marine life. *Nature Climate Change*, 3(10), 919–925. <https://doi.org/10.1038/nclimate1958>
- Pyper, B. J., & Peterman, R. M. (1998). Comparison of methods to account for autocorrelation in correlation analyses of fish data. *Canadian Journal of Fisheries and Aquatic Sciences*, 55(9), 2127–2140. <https://doi.org/10.1139/f98-104>
- R Core Team. (2022). *A language and environment for statistical computing*. In R Foundation for Statistical Computing. <https://www.R-project.org/>
- Reid, P. C., de Fatima Borges, M., & Svendsen, E. (2001). A regime shift in the North Sea circa 1988 linked to changes in the North Sea horse mackerel fishery. *Fisheries Research*, 50(1–2), 163–171. [https://doi.org/10.1016/S0165-7836\(00\)00249-6](https://doi.org/10.1016/S0165-7836(00)00249-6)
- Revelle, W. R. (2017). Psych: Procedures for personality and psychological research.
- Ricker, W. E. (1954). Stock and recruitment. *Journal of the Fisheries Research Board of Canada*, 11(5), 559–623. <https://doi.org/10.1139/f54-039>
- Rigor, I. G., Wallace, J. M., & Colony, R. L. (2002). Response of sea ice to the Arctic oscillation. *Journal of Climate*, 15(18), 2648–2663. [https://doi.org/10.1175/1520-0442\(2002\)015<2648:ROSITT>2.0.CO;2](https://doi.org/10.1175/1520-0442(2002)015<2648:ROSITT>2.0.CO;2)
- Rindorf, A., van Deurs, M., Howell, D., Andonegi, E., Berger, A., Bogstad, B., Cadigan, N., Elvarsson, B. P., Hintzen, N., Savina Roland, M., Taylor, M., Trijoulet, V., van Kooten, T., Zhang, F., & Collie, J. (2022). Strength and consistency of density dependence in marine fish productivity. *Fish and Fisheries*, 23(4), 812–828. <https://doi.org/10.1111/faf.12650>
- Rothschild, B. J. (1986). *Dynamics of marine fish populations*. Harvard University Press.
- Scheffer, M., Bascompte, J., Brock, W. A., Brovkin, V., Carpenter, S. R., Dakos, V., Held, H., Van Nes, E. H., Rietkerk, M., & Sugihara, G. (2009). Early-warning signals for critical transitions. *Nature*, 461(7260), 53–59. <https://doi.org/10.1038/nature08227>
- Scheffer, M., Carpenter, S. R., Lenton, T. M., Bascompte, J., Brock, W., Dakos, V., Van de Koppel, J., Van de Leemput, I. A., Levin, S. A., Van Nes, E. H., Pascual, M., & Vandermeer, J. (2012). Anticipating critical transitions. *Science*, 338(6105), 344–348. <https://doi.org/10.1126/science.1225244>
- Shu, Q., Wang, Q., Årthun, M., Wang, S., Song, Z., Zhang, M., & Qiao, F. (2022). Arctic Ocean amplification in a warming climate in CMIP6 models. *Science Advances*, 8(30), eabn9755. <https://doi.org/10.1126/sciadv.abn9755>
- Sirabella, P., Giuliani, A., Colosimo, A., & Dippner, J. W. (2001). Breaking down the climate effects on cod recruitment by principal component analysis and canonical correlation. *Marine Ecology Progress Series*, 216, 213–222. <https://doi.org/10.3354/meps216213>
- Skagseth, Ø., Slotte, A., Stenevik, E. K., & Nash, R. D. (2015). Characteristics of the Norwegian coastal current during years with high recruitment of Norwegian spring spawning herring (*Clupea harengus* L.). *PLoS One*, 10(12), e0144117. <https://doi.org/10.1371/journal.pone.0144117>
- Skjoldal, H. R., Eriksen, E., Gjøsæter, H., Skagseth, Ø., Prozorkevich, D., & Lien, V. S. (2022). Recruitment variability of fish stocks in the Barents Sea: Spatial and temporal variation in 0-group fish length of six commercial species during recent decades of warming (1980–2017). *Progress in Oceanography*, 206, 102845. <https://doi.org/10.1016/j.pocean.2022.102845>
- Skogen, M. D., Hjøllø, S. S., Sandø, A. B., & Tjiputra, J. (2018). Future ecosystem changes in the Northeast Atlantic: A comparison between a global and a regional model system. *ICES Journal of Marine Science*, 75(7), 2355–2369. <https://doi.org/10.1093/icesjms/fsy088>
- Stenevik, E. K., Hølleland, S., Enberg, K., Høines, Å., Salthaug, A., Slotte, A., Vatnehol, S., & Aanes, S. (2022). Predicting density-dependent somatic growth in Norwegian spring-spawning herring. *ICES Journal of Marine Science*, 79(4), 1340–1352. <https://doi.org/10.1093/icesjms/fsac057>

- Stiansen, J. E., Aglen, A., Bogstad, B., Loeng, H., Mehl, S., Nakken, O., Ottersen, G., & Svendsen, E. (2005). Including climate into the assessment of future fish recruitment, using multiple regression models. ICES CM 2005/O:25 Connecting Physical-Biological Interactions to Recruitment Variability, Ecosystem Dynamics, and the Management of Exploited Stocks.
- Sundby, S. (2000). Recruitment of Atlantic cod stocks in relation to temperature and advection of copepod populations. *Sarsia*, 85(4), 277–298. <https://doi.org/10.1080/00364827.2000.10414580>
- Szuwalski, C. S., Vert-Pre, K. A., Punt, A. E., Branch, T. A., & Hilborn, R. (2015). Examining common assumptions about recruitment: A meta-analysis of recruitment dynamics for worldwide marine fisheries. *Fish and Fisheries*, 16(4), 633–648. <https://doi.org/10.1111/faf.12083>
- Tiedemann, M., Nash, R. D., Stenevik, E. K., Stiasny, M. H., Slotte, A., & Kjesbu, O. S. (2021). Environmental influences on Norwegian spring-spawning herring (*Clupea harengus* L.) larvae reveal recent constraints in recruitment success. *ICES Journal of Marine Science*, 78(2), 640–652. <https://doi.org/10.1093/icesjms/fsaa072>
- Tirronen, M., Depesstele, J., & Kuparinen, A. (2023). Can regime shifts in reproduction be explained by changing climate and food availability? *Frontiers in Marine Science*, 10, 1167354. <https://doi.org/10.3389/fmars.2023.1167354>
- Trenkel, V. M., Huse, G., MacKenzie, B. R., Alvarez, P., Arrizabalaga, H., Castonguay, M., Goñi, N., Grégoire, F., Hátún, H., Jansen, T., Jacobsen, J. A., Lehodey, P., Lutcavage, M., Mariani, P., Melvin, G. D., Neilson, J. D., Nøttestad, L., Óskarsson, G. J., Payne, M. R., ... Speirs, D. C. (2014). Comparative ecology of widely distributed pelagic fish species in the North Atlantic: Implications for modelling climate and fisheries impacts. *Progress in Oceanography*, 129, 219–243. <https://doi.org/10.1016/j.pocean.2014.04.030>
- Tsikliras, A. C., Licandro, P., Pardalou, A., McQuinn, I. H., Gröger, J. P., & Alheit, J. (2019). Synchronization of Mediterranean pelagic fish populations with the North Atlantic climate variability. *Deep Sea Research Part II: Topical Studies in Oceanography*, 159, 143–151. <https://doi.org/10.1016/j.dsr2.2018.07.005>
- Walters, C. J., & Hilborn, R. (2005). Exploratory assessment of historical recruitment patterns using relative abundance and catch data. *Canadian Journal of Fisheries and Aquatic Sciences*, 62(9), 1985–1990. <https://doi.org/10.1139/f05-105>
- Walters, C. J., & Martell, S. J. (2004). *Fisheries ecology and management*. Princeton University Press.
- Wanner, H., Brönnimann, S., Casty, C., Gyalistras, D., Luterbacher, J., Schmutz, C., Stephenson, D. B., & Xoplaki, E. (2001). North Atlantic oscillation—concepts and studies. *Surveys in Geophysics*, 22(4), 321–381. <https://doi.org/10.1023/A:1014217317898>
- Weijerman, M., Lindeboom, H., & Zuur, A. F. (2005). Regime shifts in marine ecosystems of the North Sea and Wadden Sea. *Marine Ecology Progress Series*, 298, 21–39. <https://doi.org/10.3354/meps298021>
- Williams, J. W., & Jackson, S. T. (2007). Novel climates, no-analog communities, and ecological surprises. *Frontiers in Ecology and the Environment*, 5(9), 475–482. <https://doi.org/10.1890/070037>
- Wood, S. N. (2003). Thin plate regression splines. *Journal of the Royal Statistical Society, Series B: Statistical Methodology*, 65(1), 95–114. <https://doi.org/10.1111/1467-9868.00374>
- Wood, S. N. (2011). Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *Journal of the Royal Statistical Society, Series B: Statistical Methodology*, 73(1), 3–36. <https://doi.org/10.1111/j.1467-9868.2010.00749.x>
- Yaragina, N. A., Bogstad, B., & Kovalev, Y. A. (2009). Variability in cannibalism in Northeast Arctic cod (*Gadus morhua*) during the period 1947–2006. *Marine Biology Research*, 5(1), 75–85. <https://doi.org/10.1080/17451000802512739>
- Zeileis, A., Kleiber, C., Krämer, W., & Hornik, K. (2003). Testing and dating of structural changes in practice. *Computational Statistics & Data Analysis*, 44(1–2), 109–123. [https://doi.org/10.1016/S0167-9473\(03\)00030-6](https://doi.org/10.1016/S0167-9473(03)00030-6)
- Zeileis, A., Leisch, F., Hornik, K., & Kleiber, C. (2002). Strucchange: An R package for testing for structural change in linear regression models. *Journal of Statistical Software*, 7, 1–38. <https://doi.org/10.18637/jss.v007.i02>
- Zimmermann, F., Claireaux, M., & Enberg, K. (2019). Common trends in recruitment dynamics of north-east Atlantic fish stocks and their links to environment, ecology and management. *Fish and Fisheries*, 20(3), 518–536. <https://doi.org/10.1111/faf.12360>
- Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A., & Smith, G. M. (2009). *Mixed effects models and extensions in ecology with R* (Vol. 574). Springer.

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