

Common trends in recruitment dynamics of north-east Atlantic fish stocks and their links to environment, ecology and management

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Abstract

Recruitment dynamics are challenging to assess or predict because of the many underlying drivers that vary in their relevance over time and space. Stock size, demographic and trait composition, condition and distribution of spawning fish and the spatio-temporal dynamics of trophic and environmental interactions all influence recruitment processes. Exploring common patterns among stocks and linking them to potential drivers may therefore provide insights into key mechanisms of recruitment dynamics. Here, we analysed stock-recruitment data of 64 stocks from the north-east Atlantic Ocean for common trends in variation and synchrony among stocks using correlation, cluster and dynamic factor analyses. We tested common trends in recruitment success for relationships with large-scale environmental processes as well as stock state indicators, and we explored links between recruitment success and demographic, environmental and ecological variables for a subset of individual stocks. The results revealed few statistically significant correlations between stocks but showed that underlying common trends in recruitment success are linked to environmental indices and management indicators. Statistical analyses confirmed previously suggested relationships of environmental-ecological factors such as the subpolar gyre and Norwegian coastal current with specific stocks, and indicated a large relevance of spawning stock biomass and demographics, as well as predation, whereas other suggested relationships were not supported by the data. Our study shows that despite persistent challenges in determining drivers of recruitment due to poor data quality and unclear mechanisms, combining different data analysis techniques can improve our understanding of recruitment dynamics in fish stocks.

KEYWORDS

early life stages, marine fish, population dynamics, recruitment dynamics, trophic interactions

1 | INTRODUCTION

In marine fish, recruitment dynamics have been recognized as fundamental to population dynamics and fluctuations in stock size for

more than a century (Hjort, 1914), yet the underlying drivers and mechanisms have been scarcely understood. The relationship between spawning stock and recruitment, which is widely used in fisheries models, has been particularly unsuccessful in explaining

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recruitment variability (Myers & Barrowman, 1996; Walters, 1987), despite the fact that density-dependent recruitment can be detected in most stocks (Zimmermann, Ricard, & Heino, 2018). The major reason is the complex interplay among environmental and ecological variables that influence the reproductive output of the spawning stock and the development of early life stages until recruitment. Besides the demographics and fecundity of the spawning stock (Longhurst, 2002; Marshall, Kjesbu, Yaragina, Solemdal, & Ulltang, 1998; Rickman, Dulvy, Jennings, & Reynolds, 2000), its distribution and subsequent drift of eggs and larvae are crucial because they determine the environment and trophic interactions experienced during the early life stages and, thus, growth and survival.

Linking the state of stocks, environmental processes and ecological interactions to recruitment success may help to explain the dynamics of fish populations and their productivity. Especially, large-scale oceanographic processes (Castillo-Jordán et al., 2015; Trenkel et al., 2014) and spatio-temporal overlap (e.g., the match-mismatch hypothesis; Cushing, 1990) have been identified as key drivers. Oceanic currents and wind influence drift, dispersal and settlement of fish at early life stages (Edwards, Hare, Werner, & Seim, 2007; Pineda, Hare, & Sponaugle, 2007) and, together with temperature and salinity, define the habitat that enables the survival and growth of eggs and larvae (MacKenzie, Hinrichsen, Plikshs, Wieland, & Zezera, 2000). The degree of overlap between drift patterns and the timing of important events such as algal blooms or predator migration is key in terms of both food availability (Beaugrand, Brander, Alistair Lindley, Souissi, & Reid, 2003; Kristiansen, Drinkwater, Lough, & Sundby, 2011; Van Poorten, Korman, & Walters, 2018) and predation (Huse, Salthaug, & Skogen, 2008; Skaret, Bachiller, Langøy, & Stenevik, 2015). Similarly to the recruiting cohort, the abundance and presence of prey or predators are also subjected to (often the same) climatic and oceanographic processes (notably direction and strength of ocean currents, upwelling, temperature, freshwater inflow, salinity, sunlight and turbidity) as well as food web dynamics and therefore linked among each other.

Because underlying physical conditions, large-scale processes and bottom-up productivity are shared among fish stocks residing in the same ecosystem or even across ecosystems, a linkage between recruitment success of different fish stocks and thus synchrony can be expected. In the north-east Atlantic system, climatic oscillations known as the Atlantic Multidecadal Oscillation (AMO; Edwards, Beaugrand, Helaouët, Alheit, & Coombs, 2013; Knight, Folland, & Scaife, 2006) and the North Atlantic Oscillation (NAO; Drinkwater et al., 2003; Ottersen et al., 2001) are considered to act as the major forcing factors of environmental processes. These climatic indices are directly linked to sea surface temperature (SST), wind direction and strength, ocean currents and thus also upwelling and water mixing. Large-scale ocean circulations may be particularly important as they have a major influence on the distribution of water masses and nutrients and thus the productivity of ecosystems. The extent of the subpolar gyre (SPG), its interplay with the more southern subtropical gyre and the effects on the North Atlantic Current (NAC) have been

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identified as important drivers of temperature, salinity, nutrient distribution and primary production (González-Gil, Taboada, Höfer, & Anadón, 2015; Hátún et al., 2009; Llope et al., 2006), affecting recruitment in species such as blue whiting (*Micromesistius poutassou*, Gadidae; Kloppmann, Mohn, & Bartsch, 2001; Miesner & Payne, 2018; Payne et al., 2012), European hake (*Merluccius merluccius*, Merlucciidae; Sánchez, Sánchez, & Gil, 2003), Atlantic cod (*Gadus morhua*, Gadidae) and haddock (*Melanogrammus aeglefinus*, Gadidae; ICES, 2015). Another prime example of an oceanographic key process is the Norwegian Coastal Current (NCC; Skagseth, Slotte, Stenevik, & Nash, 2015), which is tightly linked to the North Atlantic Current, precipitation and wind-induced upwelling and has a crucial impact on the recruitment dynamics of a range of species that spawn along the Norwegian Coast within the current, including several large stocks of gadoids, Atlantic herring (*Clupea harengus*, Clupeidae) and capelin (*Mallotus villosus*, Osmeridae).

Identifying synchrony and shared trends among fish stocks could help to determine the key drivers behind ecosystems dynamics and improve the predictability of recruitment (Stachura et al., 2014). Determining common trends and interactions from data will thus shed some light on the many open questions about recruitment dynamics and contribute to an ecosystem-based approach to management of fish stocks. In the present study, we tested the hypothesis that shared recruitment dynamics exist within a large dataset of north-east Atlantic fish stocks by exploring the synchrony of recruitment success, common underlying trends in the time series and their potential relationships with environmental indices and management indicators. Synchrony in recruitment has been previously explored with partially conflicting conclusions (e.g., Cohen, Mountain, & O'Boyle, 1991; Myers, Mertz, & Barrowman, 1995). However, the

large increase in available data, time-series length and computational power allows now for a much broader approach that includes novel methods beyond direct correlations between fish stocks. Here, we focused on trends in the data set to detect major underlying patterns that allow for novel insights on recruitment fluctuations within noisy data. Furthermore, we analysed a subset of stocks from three spawning ecoregions for their relationships with ecological and environmental indices, testing previously established or hypothesized connections between recruitment dynamics and possible drivers in these specific fish stocks. This provided a comparison between possible common underlying trends and predictors of recruitment dynamics in specific stocks.

2 | METHODS

2.1 | Data

In our analysis, we used stock and recruitment data from European fish stocks with time series longer than 25 years published in stock assessment reports from the International Council for the Exploration of the Sea (ICES). Stock and recruitment data were based on annual spawning stock biomass (SSB) and recruitment numbers from stock summary tables. The assessments of the selected stocks contained no structural assumptions regarding the relationship between spawning stock biomass and recruitment. The study included in total 64 different stocks from the entire north-east Atlantic Ocean (Figure 1; stock names are detailed in Supporting information Table S1).

As potential explanatory variables, we included a range of population and environmental data. Environmental data used in the present study consist of indices of climatic oscillations, including the AMO (Trenberth & Zhang, 2017) and NAO (National Center for Atmospheric Research, 2017a), regional SST (NOAA/IMR) and water flow as well as temperature and salinity indices of currents and gyres. Available time series of zooplankton abundance in the Barents and Norwegian Sea (Dalpadado et al., 2014) were also included. Table 1 lists all explanatory variables tested in this study and the justifications of including them.

2.2 | Statistical analysis

Recruitment was divided by SSB to calculate time series of recruits per spawning stock biomass

$$R/SSB(t) = \frac{R(t)}{SSB(t)},$$

where t corresponds to the year when each cohort was spawned; that is, $R(t)$ was adjusted by recruitment age a_{rec} to correct for $a_{rec} > 0$ in assessment reports.

We used R/SSB instead of absolute recruitment to remove effects of SSB on absolute recruitment, enabling a clearer view

on density-independent drivers of recruitment variability. This is important because SSB affects absolute recruitment but tends to be less relevant for recruitment success than environmental factors (Szuwalski, Vert-Pre, Punt, Branch, & Hilborn, 2015). R/SSB provides, thus, a proxy for actual recruitment success, given that there is a significant relationship between SSB and recruitment (Cardinale & Hjelm, 2006). Here, this condition is fulfilled as statistically significant density dependence has been found for all stocks used in this study (Zimmermann et al., 2018). Furthermore, by restricting our analysis to comparatively long time series (median length of 38 years), we excluded stocks with clear, unidirectional trends in the time series of SSB that could cause erroneous signals in R/SSB . Because there can be additional density dependence in recruitment success (Cardinale & Hjelm, 2006), we tested for significant effects of SSB in our analysis, as detailed in the specific approaches below.

R/SSB data were compartmentalized into three groups: the lowest quartile (<25%), the highest quartile (>75%) and the intermediate quartiles (25%–75%). Quartile distribution was used as an indicator for years with normal (intermediate) recruitment success (i.e., number of recruits are in the range of average recruitment success) and years with exceptionally low or high recruitment success (i.e., weak or strong year classes that deviate distinctly from the average recruitment success). To determine the correlation between stocks, Pearson's correlation coefficients and their significance levels were calculated. To correct for multiple testing, p -values were adjusted with the method of Benjamini and Hochberg (1995) that controls the expected proportion of false discoveries amongst the rejected hypotheses.

To identify common trends among the time series of R/SSB , we applied dynamic factor analysis (DFA; Zuur, Fryer, Jolliffe, Dekker, & Beukema, 2003). DFA is a technique to estimate common underlying trends from multivariate time series (Zuur, Tuck, & Bailey, 2003) by modelling multiple, non-stationary time series of observed data as a function of n common trends, formulated as:

$$Y_{i,t} = \alpha_{1,t} \cdot Z_{i,1} + \alpha_{2,t} \cdot Z_{i,2} + \dots + \alpha_{n,t} \cdot Z_{i,n} + \varepsilon_{i,t}.$$

$Y_{i,t}$ is the time series of R/SSB of stock i at time t , α the common trend j , z the corresponding factor loading for a specified number of trends $j = 1, 2, \dots, n$, and $\varepsilon_{i,t}$ a random noise term. Time series were normalized to their mean and standard deviation prior to further analysis. The models tested included different combinations of numbers of trends ($n_j = 1, 2, \dots, 5$) and different variance and covariance structure (same variance and covariance; same variance, no covariance; different variance, no covariance) of observation errors. Models with $n_j > 5$ were tested but discarded because they failed to converge when fitted to our dataset. Goodness of fit was determined with the second-order Akaike's information criterion (AICc). We gave preference to AICc over AIC because AICc performs better for low to moderate sample sizes (Hurvich & Tsai, 1991), which applied to our study due to the low number of observations compared to the number of parameters, especially for the models with

several trends and observation to parameter ratios of <10 (e.g., up to 374 parameters for five trends compared to 2,442 observations). Because the interpretation of differences in absolute AICc values is

not straight-forward, we used AICc weights that represent conditional probabilities for each model (Wagenmakers & Farrell, 2004) to select the best-fitting model.

TABLE 1 List of environmental variables included in the analysis and possible relevance for recruitment dynamics. The specific environmental indices and proposed hypotheses relating them to general or stock-specific recruitment success are detailed

Variables	Indices	Hypotheses
Atlantic Multidecadal Oscillation	AMO index (Trenberth & Zhang, 2017)	Major forcing factor of climatic and ecological processes in the Northern Atlantic (Edwards et al., 2013; Knight et al., 2006), temperature-based and thus closely connected to SST
Currents (based on water flow or wind stress)	Denmark strait (temperature, salinity, water flow; internal data, IMR), Faroe-Shetland channel (temperature, salinity, water flow; internal data, IMR), Irminger current (I. Nunez-Riboni, von Thünen Institut, personal communication), Iceland-Faroe ridge (internal data, IMR), NCC (Skagseth et al., 2015)	Currents determine nutrient distribution, ecosystem productivity, drift patterns of early life stages and recruitment (Checkley, Raman, Maillet, & Mason, 1988), for example, Icelandic and Faroese circular current (Astthorsson & Gislason, 1995; ICES, 2015), NCC (Skagseth, Drinkwater, & Terrile, 2011; Skagseth et al., 2015); beneficial transport effects for egg and larval development (Opdal & Jørgensen, 2015)
East Atlantic Pattern	EAP index (National Oceanic and Atmospheric Administration, 2017)	Major forcing factor in the eastern Atlantic Ocean (Stenseth et al., 2003), linked to, for example, down-/upwelling in the Bay of Biscay and off the Iberian coast with effects on recruitment in European hake (Sanchez, Sánchez, Landa, & Fernandez, 2003; Sánchez et al., 2003), megrim and four-spotted megrim (Sanchez et al., 2003), horse mackerel and sardine (Guisande, Cabanas, Vergara, & Riveiro, 2001; Santos, de Fátima Borges, & Groom, 2001) and anchovy (Borja, Fontan, Sáenz, & Valencia, 2008; Borja, Uriarte, Egaña, Motos, & Valencia, 1998)
Food availability	Zooplankton indices (Dalpadado et al., 2014), stock biomass and cohort abundance	Food availability crucial for growth and survival of early life stages and therefore recruitment (Bergenius, Meekan, Robertson, & McCormick, 2002; Cushing, 1990; Garrido et al., 2017; Hüseyin, St. John, & Böttcher, 1997; Le Pape & Bonhommeau, 2015)
North Atlantic Oscillation	NAO index (National Center for Atmospheric Research, 2017a)	Major forcing factor that drives ecosystem dynamics (Stenseth et al., 2003), linked to, for example, recruitment in gadoids, especially Atlantic cod (Jarre-Teichmann et al., 2000; Köster et al., 2005; Nissling, Kryvi, & Vallin, 1994; Stige et al., 2006)
Northern Annular Mode	NAM index (National Center for Atmospheric Research, 2017b)	Closely connected to NAO (Ambaum, Hoskins, & Stephenson, 2001; Overland et al., 2010) with proposed similar effects on ecosystem productivity and recruitment
Predation	Stock biomass and cohort abundance of possible predators	Cannibalism and predation on early life stages drive recruitment variability (Bailey, 1994; Bailey & Houde, 1989; Huse et al., 2008; Jarre-Teichmann et al., 2000; Neuenfeldt & Köster, 2000; Nilsson, 2006; Ricard et al., 2016)
Sea Surface Temperature	SST indices (NOAA/IMR), Northern Atlantic and regionalized (including index of Kola section)	Temperature affects recruitment success, as shown by case studies in the Baltic Sea (Baumann et al., 2006; Cardinale et al., 2009; Dodson et al., 2018; Köster et al., 2005), Barents Sea (Gjøsæter & Bogstad, 1998; Ottersen & Loeng, 2000), North Sea stocks (Arnott & Ruxton, 2002; Kempf, Floeter, & Temming, 2009; van der Veer, Pihl, & Bergman, 1990), on Atlantic cod (Kempf et al., 2009; Olsen et al., 2010; Planque & Fox, 1998; Planque & Frédou, 1999) and flatfish stocks (Fox, Planque, & Darby, 2000; Henderson & Seaby, 2005; Nash & Geffen, 2000; Rijnsdorp et al., 1992); mechanistic link through food availability in the North Sea (Beaugrand et al., 2003; Payne et al., 2009)
Spawner demographics	Diversity index based on age-specific abundance in mature stock	Age and size composition linked to reproductive output of spawning stock and thus recruitment (Barneche et al., 2018; Hixon et al., 2014; Marteinsdottir & Thorarinsson, 1998)
Spawner condition	Mean weight-at-age of mature stock	Weight-at-age as a proxy for condition of spawning stock, affecting reproductive output and thus recruitment (Hjermann et al., 2007; Kjesbu et al., 1998; dos Santos Schmidt et al., 2017; Stige et al., 2006)
Subpolar Gyre	Surface-height based gyre index (Hátún et al., 2016)	Key driver of salinity, temperature, nutrient distribution and thus productivity in north-east Atlantic Ocean (Hátún et al., 2016), linked to recruitment dynamics in Atlantic cod stocks (ICES, 2015), spawning distribution and larval drift in blue whiting (Kloppmann et al., 2001; Miesner & Payne, 2018; Payne et al., 2012)

To correct for possible density effects of SSB on R/SSB , we tested all 64 time series of R/SSB for statistically significant correlations with SSB and used the linear relationship where detected to detrend the time series. By applying the same DFA approach as detailed above for absolute R/SSB to the detrended data set, we were able to determine the potential impact of density effects on the detection of underlying common trends. Furthermore, we compared our results to those of the same approach applied to simulated data sets of randomized time series, with the goal to exclude the possibility that emerging patterns and number of trends may be a random result. Simulated data sets were obtained by combining randomized time series of all 64 stocks.

Estimated common trends were correlated with large-scale environmental indices (AMO, East Atlantic Pattern [EAP], Northern Annular Mode [NAM], NAO, SPG, SST) as well as indicators of stock state (geometric mean of SSB/B_{LIM} and F/F_{MSY} over all stocks included in the study; Zimmermann & Werner, 2019) to test for possible links between recruitment and environment or management. We tested both linear and generalized additive models (GAMs) to account for possible nonlinear relationships.

For a detailed analysis of individual stocks, we selected the following spawning ecoregions: (a) NCC including capelin, north-east Arctic cod, haddock and saithe (*Pollachius virens*, Gadidae), and Norwegian spring-spawning herring; (b) Icelandic currents including Icelandic capelin, cod, haddock, herring, ling (*Molva molva*, Lotidae), saithe and tusk (*Brosme brosme*, Lotidae); (c) Faroese circular currents including cod on Faroese plateau, haddock and saithe. GAMs were applied to try to explain the variation in R/SSB in these stocks with Gaussian distribution using combinations of all potentially plausible covariates for each stock, based on assumptions derived from literature research. Covariates included climatic and water circulation indices (large-scale and region specific), biomasses or cohort abundances of possible prey, predator or competitor populations, total biomass, mean body weight and demographic diversity of the spawning stock, and time as proxy for unaccounted variables with a trend over time. To calculate mean weight and spawner diversity, we used stock-specific weight-at-age and abundance-at-age data from the corresponding stock assessments to calculate indices of weight and demographic distribution in the mature part of each stock.

The best fitting GAM including smooth terms was selected based on a comparison of GCV and AICc values (Wood, 2001). Following Stige, Ottersen, Brander, Chan, and Stenseth (2006), model selection was conducted in an upward approach, testing for the addition of each term at a time, starting with year effects representing temporal trends, followed by internal physical and ultimately ecological covariate. Smoothing functions were used to account for nonlinearity in explanatory variables and their knots restricted to five to avoid overfitting and implausible patterns. If smoothing did not result in a better fit, a linear relationship was assumed. Variance inflation factor was used to test for collinearity among explanatory variables.

Time series of covariates we tested were aligned with the years when recruits were spawned and additionally with negative (prior to spawning year) or positive (after spawning year) time lags where appropriate. Lags can be relevant when a specific factor either

influences reproductive output before the year when spawning occurs or when the period between spawning and recruitment lasts several years. Although the earliest life stages have been often considered as particularly critical, environmental conditions and ecological interactions affect also the development and survival of juvenile fish in the subsequent years. Many gadoid stocks, for instance, recruit at ages 2–4, which implies that recruitment can be affected by environmental and ecological conditions during up to 4 years of pre-recruit stages. Also, demographic structure and condition of a spawning stock that determine number and quality of spawned eggs are typically built up during the year(s) before spawning, creating delayed effects that are potentially relevant (dos Santos Schmidt et al., 2017).

Weighted mean body weights of the mature component of each stock were calculated from weight-at-age data, using abundance-at-age data as weights. Following Marteinsdottir and Thorarinnsson (1998), Shannon diversity index H was used as an indicator of spawning stock diversity based on abundance-at-age data in the mature component of each stock:

$$H_t = x_t \cdot \log(x_t) - \sum_{n=1}^{a_{\max}} a_{n,t} \log(a_{n,t})/x_t,$$

with x_t as the total number of mature fish and a_n number of fish in age class n at time t for all age classes from ages until maximum age a_{\max} .

All analyses were conducted using R version 3.5.1 (R: Development Core Team, 2018) and the packages MARSS (Holmes, Ward, & Wills, 2012) and mgcv (Wood, 2001).

3 | RESULTS

Qualitative analysis revealed partial alignments in recruitment variability and years with clusters of particularly strong or weak recruitment among several stocks (Figure 2). Of those stocks with similar time series in quartiles of recruitment success, there were many with close ecological and geographic proximity, such as capelin, north-east Arctic and coastal cod that all spawn along the coast of northern Norway; Faroese and Icelandic saithe, and Faroese cod and haddock; sprat (*Sprattus sprattus*, Clupeidae) and herring stocks in the Baltic Sea; herring in the North Sea and west of Scotland; plaice (*Pleuronectes platessa*, Pleuronectidae) in the North Sea and the English Channel; or North Sea cod and sandeel (*Ammodytes sp.*, Ammodytidae). The years with highest recruits per spawning biomass across all 64 stocks were 1983, 1991 and 1999–2001 (Figure 2), in terms of both mean of quartile scores and relative number of stocks in the highest quartile. These are contrasted by the years 1977 and 2010–2012 with the weakest year classes across all stocks in terms of R/SSB (Figure 2). Although in most of these years stocks with particularly strong or weak year classes could be found across all ecoregions, there were clear spatial patterns. In 1983, 80% of the stocks spawning along the Norwegian coast and 67% of the stock spawning around Faroe

Islands had high recruitment. In 2000, this applied to all Icelandic and two-thirds of Faroese stocks, and in 2001, five of six sole (*Solea solea*, Soleidae) stocks showed increased recruitment. Spatial accumulations of weak R/SSB occurred in 1977 (100% of Faroese and 75% of Norwegian stocks), 2010 (63% of Icelandic stocks) and 2011 (69% of stocks spawning in the North Sea, 67% along the Norwegian coast and 57% around Iceland). Furthermore, these coinciding, particularly strong or weak years contributed to the clustering of stocks and occurred therefore mostly in stocks that clustered closely together, that is, showed similar R/SSB patterns in general (Figure 2).

3.1 | Correlations between stocks

We found statistically significant correlations in R/SSB and R/SSB quartiles between stocks in all spawning ecoregions (Supporting information Figure S1) and taxonomic groups (Supporting information Figure S2), both negative and positive, including strong ones. Many significant positive correlations were between stocks with a close taxonomic and/or geographic proximity to each other, resulting in direct ecological links and shared dynamics or overlapping spawning or nursery areas: for example, cod stocks west of British Isles; Baltic cod stocks; Icelandic tusk and ling; Faroese cod and haddock; cod, Norway pout and sandeel

in the North Sea; megrim (*Lepidorhombus whiffiagonis*, Scopthalmidae) and four-spotted megrim (*Lepidorhombus boscii*, Scopthalmidae); among Norwegian coastal cod and north-east Arctic capelin, cod, haddock and saithe. For few stocks, for example, between Baltic cod and Baltic herring or sole in the Skagerrak and western Baltic Sea, negative correlations were detected. We also found a range of statistically significant correlations within taxonomic groups (Supporting information Figure S2) across adjacent ecoregions, for example, cod and herring stocks west of British Isles and in the North Sea or Icelandic and Faroese saithe, but also across distinct ecoregions, for example, herring stocks in the Baltic Sea and Icelandic or Norwegian spring-spawning herring, or plaice stocks in the English channel and megrim on the Iberian shelf. Overall, the proportion of stocks with statistically significant correlations was low and signals were not fully consistent between absolute recruitment success (R/SSB quartiles) and years with exceptionally strong or weak recruitment (R/SSB quartiles).

3.2 | General trends in recruitment success

Based on an AICc weight of 0.98, a DFA model with four common trends and equal variance-covariance structure explained best the variability in R/SSB among all the 64 time series (Supporting

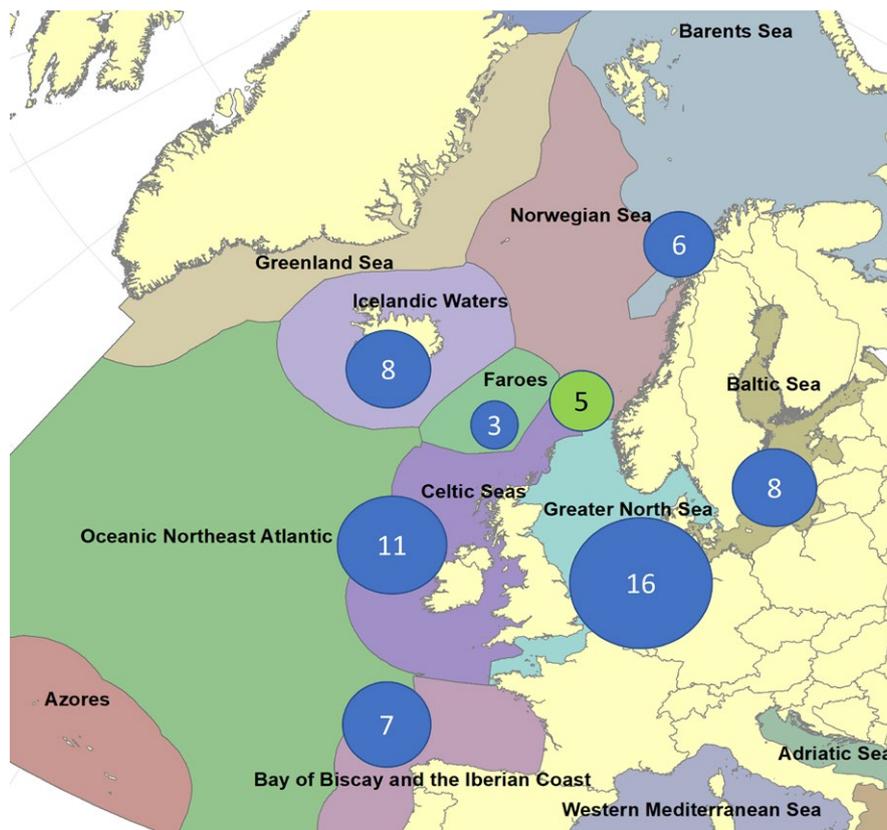


FIGURE 1 Map of the north-east Atlantic Ocean detailing the ecoregions and number of stocks with their main spawning areas associated to the specific ecoregion (blue circles) used in the present analysis. Stocks with substantial spawning areas across more than one ecoregion are listed separately (green circle). Size of circles is scaled relative to the number of stocks in each ecoregion. The full stock list is presented in Supporting information Table S1. Map provided by the International Council for the Exploration of the Sea (www.ices.dk/wileyonlinelibrary.com) [Colour figure can be viewed at wileyonlinelibrary.com]

information Table S2, Figure S3). Prior correcting for density effects did not affect the model selection (Supporting information Table S3); that is, the same model was selected with an AICc weight of 0.87.

On the other hand, model selection results for DFA applied to the original data sets (Supporting information Tables S2 and S3) were clearly different from those of randomized data sets (Supporting

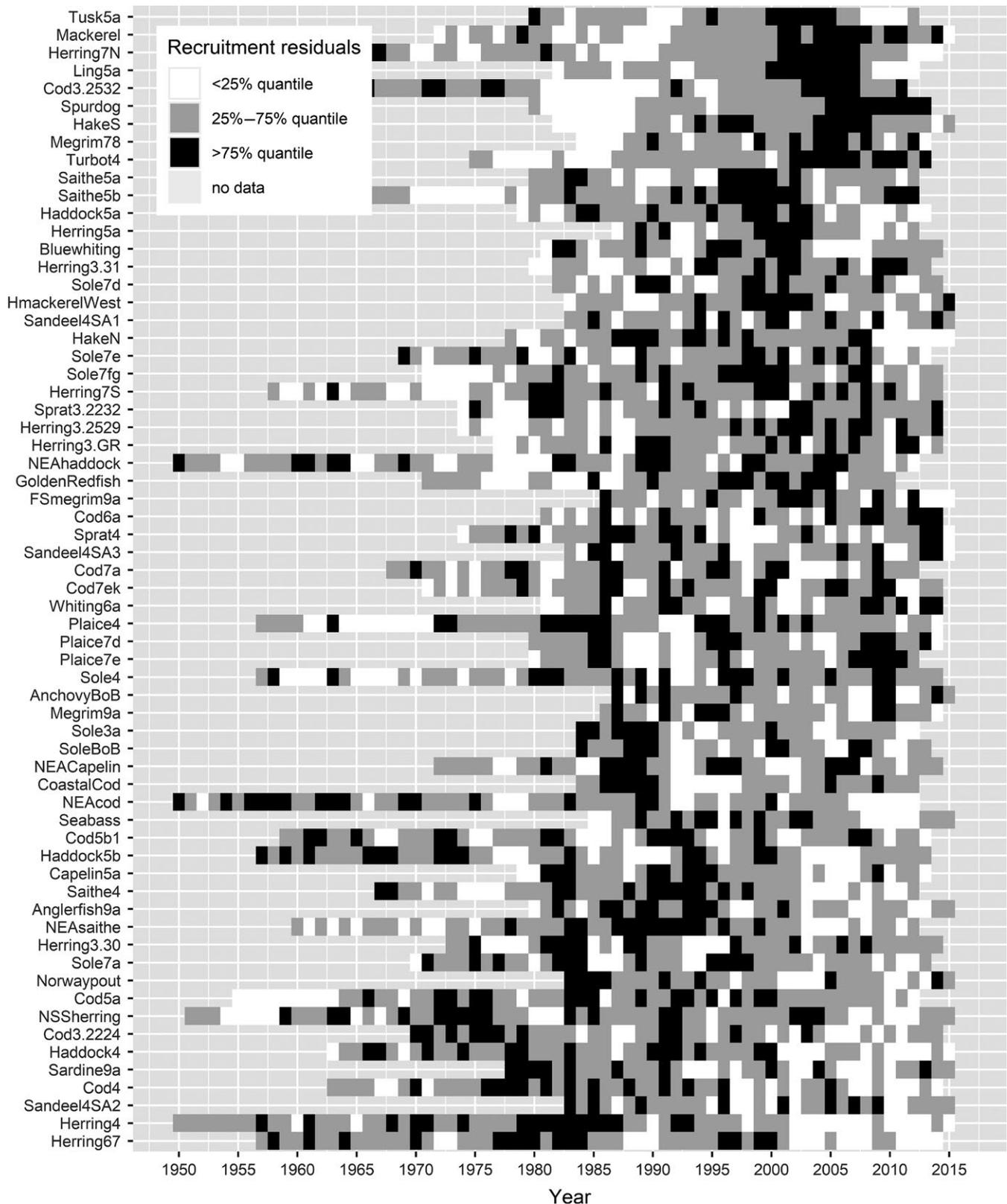


FIGURE 2 Recruitment success (R/SSB) quartiles (white = low (<25%), grey = medium (25%–75%), black = high (>75%)) over the entire time series of each stock. Stocks are ordered based on cluster analysis distance using Euclidian distance and Ward's method as clustering method; that is, the closer the position of stocks the more similar they are and vice versa

information Table S4). In randomized data sets, AICc values were generally higher and increased throughout with additional trends, indicating no benefit of adding trends and thus showing a clearly distinct pattern compared to the original data set. The fitted DFA model explained R/SSB well in most stocks except for outliers of very strong or weak recruitment success (Supporting information Figure S4).

In the selected DFA model, the four trends could be partially attributed to specific geographic or taxonomic groups based on factor loadings. Trend 1 indicates a strong link to stocks spawning along the Norwegian coast and Iceland, notably different gadoids and capelin, as well as various stocks of sole. The three other trends showed more ambiguity and broader distributions, although tendencies towards stocks associated with the (south-)western shelf from the Iberian coast to west of British Isles (trend 2) or the Baltic and North Sea (trend 3) could be detected.

For each of the four common trends, linear models and GAMs showed statistically significant correlations with two or more environmental as well as management indices (Table 2, Figures 3 and 4). GAMs outperformed linear models throughout, although overall results were consistent with only very few exceptions of strongly nonlinear relationships (e.g., SSB/B_{LIM} and trend 3). Based on the explanatory power, AMO and SPG indices dominated as environmental predictors followed by NAM and the closely related NAO index. The variable with highest prediction power explained between 21% (SPG of trend 4) and 64% (SPG of trend 3) of the total deviance. For trend 1 and trend 3, strong negative relationships with a high goodness of fit (deviance explained > 50%) to AMO, SPG and SST indices were found (Table 1).

Each of the four trends showed statistically significant, strong correlations with one of the mean indicators of stock state, SSB/B_{LIM} or F/F_{MSY} (Figure 4, Table 1). The total deviance explained by GAM models ranged from 37% (trend 4) to 54% (trend 1). The best explanatory variable was in all trends but trend 2 SSB/B_{LIM} . The relationships are clearly positive for trend 1 and moderately positive for trend 2, whereas the smooth functions were more complex and not unidirectional for trends 3 and 4.

When correcting for effects of SSB on R/SSB , the trends and correlations remained consistent (Supporting information Table S4). The results showed quantitative differences, that is, in most cases, a decrease in explanatory power, compared to the relationship of the explanatory variables with the common trends derived from absolute R/SSB , but did not deviate qualitatively. Exceptions were trends 2 and 3 where the environmental variables that explained most variability switched order of importance: the explanatory power of the NAO index increased above the one of the closely linked NAM index for trend 2, and SST performed better than SPG for trend 3. The same also applied for SSB/B_{LIM} and F/F_{MSY} in respect to trend 2. However, the statistical significance and relevance of explanatory variables for the specific trends were confirmed overall.

3.3 | Predictors of recruitment success in individual stocks

To explore observed patterns in more detail, we carried out an analysis of individual stocks that spawn within the NCC and the Icelandic

and Faroese circular currents. From the GAM models with the best fit based on GCV and AICc, more than 50% of the variance could be explained by the included explanatory variables in 12 of 15 stocks (Figure 5, Table 3). Among those, values ranged from 51% (NEA saithe) to 91% (Icelandic ling). In all stocks but Icelandic saithe, the best fitting model included two or more explanatory variables from different categories, that is, combinations of internal, climatic or oceanographic factors as well as potential food web links and trends over time. The specific covariates varied among stocks but showed substantial overlap. Internal covariates were particularly common, with spawning stock biomass and spawner diversity in seven stocks each and mean weight of spawners in five stocks. Furthermore, NAO and the closely linked Northern Annual Mode were found statistically significant explanatory variables in a total of six stocks and SPG in four. From the regionalized environmental variables included in this study, the NCC was relevant in four of five models for stocks spawning in the NCC, either as NCC intensity or stability or combination of both. Ecological covariates were common and found with positive, negative or nonlinear relationships in 10 stocks, including negative effects of corresponding cod stocks on NEA capelin, Icelandic ling and Faroese saithe. In many cases, time lags were associated with these covariates, both negative (i.e., 1–2 years before spawning year) for internal variables and positive for environmental and ecological variables (i.e., 1–2 years after spawning). Additionally, time trends were found in a total of five stocks.

4 | DISCUSSION

Our analysis showed synchronies and shared trends in recruitment success among a range of north-east Atlantic fish stocks and that the underlying trends can be linked with large-scale environmental processes, most notably AMO and SPG, and changes in stock status. Furthermore, statistical models explained a substantial proportion of the variability in recruitment success in most individual stocks from a subset of three specific spawning ecoregions. In several cases, this confirmed previously suggested relationships of recruitment success with spawning stock biomass and demographics as well as environmental or ecological drivers. It also demonstrated that other, partly understudied interactions may be more important for recruitment success than assumed, especially trophic ones. Our analysis highlighted the role of considering time lags between recruitment and possible drivers, since the reproductive potential of stock is shaped in the years before spawning and external factors can affect survival of pre-recruits in many stocks up to several years after spawning. Clustering among stocks indicated that year class variation between stocks tends to align, even though the overlap is incomplete and blurred by the large overall variation.

The results demonstrate the complex, multilayered nature of recruitment success. Even though the patterns in clustering and correlation analysis overlap, recruitment success over the entire time series can be partially distinct from underlying trends or the occurrences of exceptional year classes. The latter occur as typically

TABLE 2 Modelling DFA trends of absolute recruitment success with environmental and management indices as predictors: listed are the outputs of linear and generalized additive models with the correlation coefficient or the degrees of freedom, respectively, the corresponding *p*-value and deviance explained. Statistically significant (*p* < 0.05) correlations are shown in *italic* and in **bold** the explanatory variables that explain the trends best

DFA trend	Environmental index	Linear model			GAM model		
		Coef.	<i>p</i> -value	% expl.	<i>df</i>	<i>p</i> -value	% expl.
Trend 1	<i>AMO</i>	-9.62	<0.01	0.53	2.90	<0.01	0.59
	<i>EAP</i>	-2.54	<0.01	0.20	1.00	<0.01	0.22
	<i>NAM</i>	-0.01	0.98	-0.02	1.00	0.98	0
	<i>NAO</i>	0.60	0.12	0.03	1.01	0.12	0.06
	<i>SPG</i>	44.10	<0.01	0.28	1.22	<0.01	0.31
	<i>SST</i>	-2.78	<0.01	0.18	2.18	0.01	0.26
	<i>F/F_{MSY}</i>	-0.84	0.63	-0.02	2.11	0.14	0.14
	<i>SSB/B_{LIM}</i>	9.62	<0.01	0.48	1.89	<0.01	0.53
Trend 2	<i>AMO</i>	1.29	0.28	0.00	1.89	0.27	0.09
	<i>EAP</i>	0.35	0.49	-0.01	1.32	0.60	0.03
	<i>NAM</i>	0.78	<0.01	0.26	1.95	<0.01	0.33
	<i>NAO</i>	0.60	0.01	0.13	1.58	0.02	0.18
	<i>SPG</i>	13.76	0.08	0.05	1.00	0.08	0.08
	<i>SST</i>	-0.28	0.63	-0.02	2.27	0.18	0.13
	<i>F/F_{MSY}</i>	3.43	<0.01	0.22	2.71	<0.01	0.4
	<i>SSB/B_{LIM}</i>	-2.56	0.04	0.07	2.90	<0.01	0.3
Trend 3	<i>AMO</i>	5.17	<0.01	0.17	3.58	<0.01	0.45
	<i>EAP</i>	1.24	0.09	0.04	2.07	0.03	0.19
	<i>NAM</i>	0.10	0.75	-0.02	1.00	0.75	0
	<i>NAO</i>	-0.07	0.83	-0.02	1.00	0.83	0
	<i>SPG</i>	-46.99	<0.01	0.51	3.68	<0.01	0.64
	<i>SST</i>	4.14	<0.01	0.51	1.00	<0.01	0.52
	<i>F/F_{MSY}</i>	-4.62	<0.01	0.18	1.00	<0.01	0.2
	<i>SSB/B_{LIM}</i>	-0.71	0.71	-0.02	3.44	<0.01	0.44
Trend 4	<i>AMO</i>	3.11	<0.01	0.15	1.00	<0.01	0.17
	<i>EAP</i>	0.84	0.07	0.05	1.00	0.07	0.07
	<i>NAM</i>	0.06	0.78	-0.02	1.87	0.34	0.08
	<i>NAO</i>	-0.07	0.75	-0.02	1.64	0.59	0.04
	<i>SPG</i>	-18.04	0.01	0.13	1.80	0.02	0.21
	<i>SST</i>	0.72	0.18	0.02	1.00	0.18	0.04
	<i>F/F_{MSY}</i>	-0.27	0.79	-0.02	3.55	0.25	0.15
	<i>SSB/B_{LIM}</i>	-2.80	0.01	0.11	3.18	<0.01	0.37

few to singular outliers within recruitment time series and are likely based on the optimal combination of several drivers. These events are therefore not necessarily comparable with the overall dynamics and especially difficult to predict, as illustrated in the stock-specific DFA fits and GAMs that predict most of the time series well but fail to fully capture the peak years of exceptional recruitment success (or failure). Common trends and major drivers therefore explain variation in recruitment success over the entire time series but not necessarily the singular events of very strong (or weak) year classes. This also implies that large-scale drivers such as AMO and SPG may

be necessary but not sufficient to explain recruitment dynamics; that is, their state provides the basis for recruitment success in a given year yet other factors need to be in place too to result in an exceptional year class. Additionally, environmental variables such as temperature or currents may have contrasting effects on different species, for example, have positive effects for one stock and negative one for another, further complicating the overall picture. Our study therefore also underlines the nonlinearity of recruitment dynamics, which are inadequately described by one single statistical method alone, especially classic linear correlations, and require

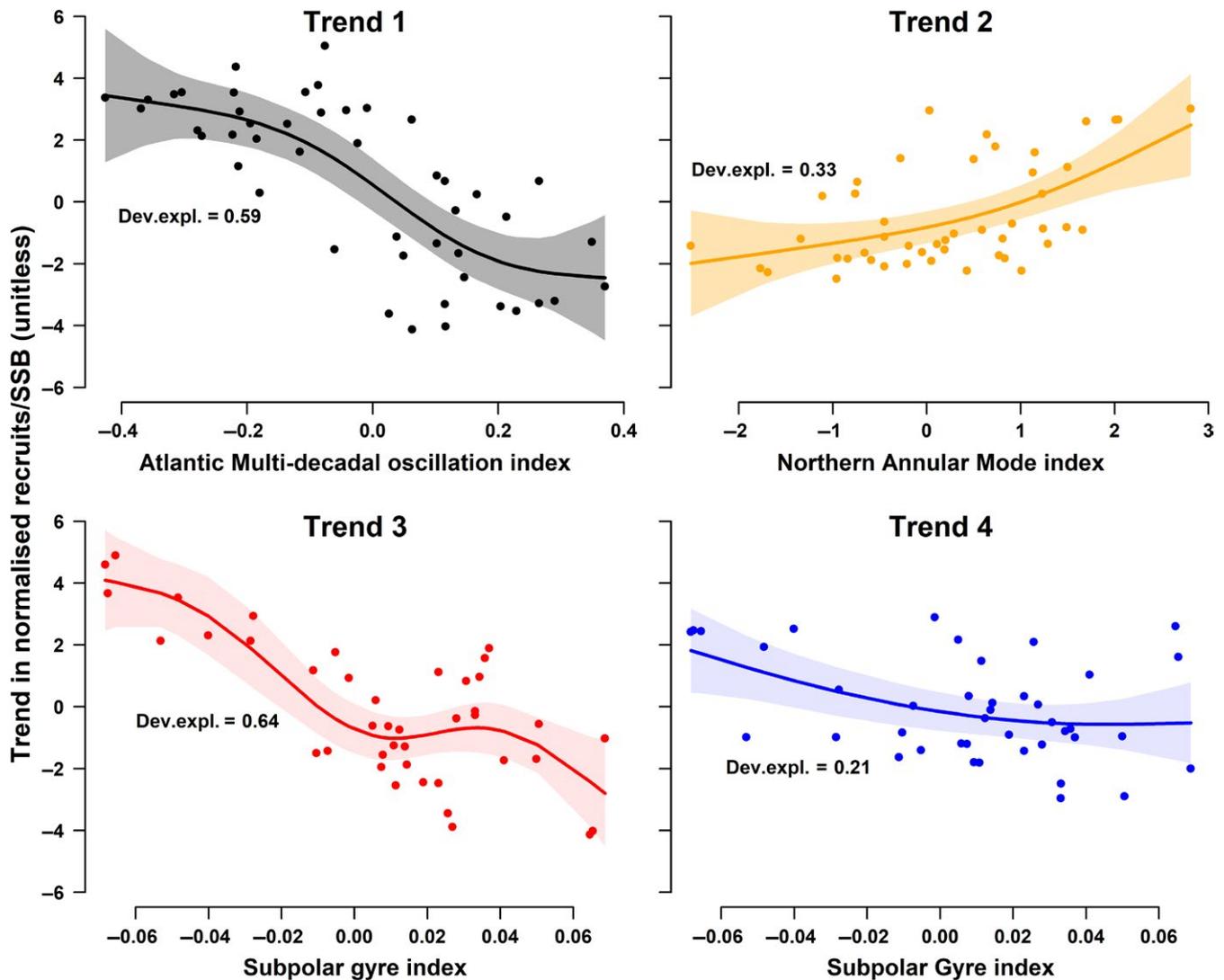


FIGURE 3 Scatterplots between the four common trends in R/SSB estimated by the DFA model and large-scale environmental indices and estimated GAM smoothers. Each dot represents a year in the time series and shows a data point of DFA trend and environmental variable. Shown are the environmental indices with a significant ($p < 0.05$) correlation and the highest explanatory power for each trend, determined by total deviance explained. Tested were indices of AMO, EAP, NAM, NAO (annual and summer/winter) and SST. DFA trends and loadings are presented in Supporting information Figure S2 and correlations listed in Table 1 [Colour figure can be viewed at wileyonlinelibrary.com]

therefore a combination of approaches for a complete picture. DFA may serve here as a powerful and, in this context, relatively novel tool to reveal underlying trends and environmental links beyond simple, linear relationships, despite the caveat that results may be difficult to translate into simple conclusions on a specific fish stock.

4.1 | Common trends and stock-specific drivers

The analysis of common trends and recruitment success in individual stocks aligned with each other and the literature, specifically regarding the role of atmospheric oscillations, ocean circulation (notably the subpolar gyre) and temperature. Our results corroborate therefore that processes related to these large-scale environmental indices likely explain a substantial proportion of the observed

recruitment variation, and they also highlight important links to fishing as a major driver of the state of fish stocks and, thus, their reproductive potential. Although it remains open whether correlations represent direct mechanistic links, our analysis demonstrates how trends in recruitment dynamics and the underlying drivers can be identified. Determining these major patterns shared among stocks helps to identify the processes and ecological links that are of actual relevance for population dynamics and thus fisheries management. The results from the DFA may provide insights beyond empirically ascertained synchrony through linear correlations, which was found in a low number of stocks despite substantially more data available and a much broader approach than in past studies (Myers et al., 1995). This suggests that underlying common trends and simultaneously occurring strong and weak year classes are masked by

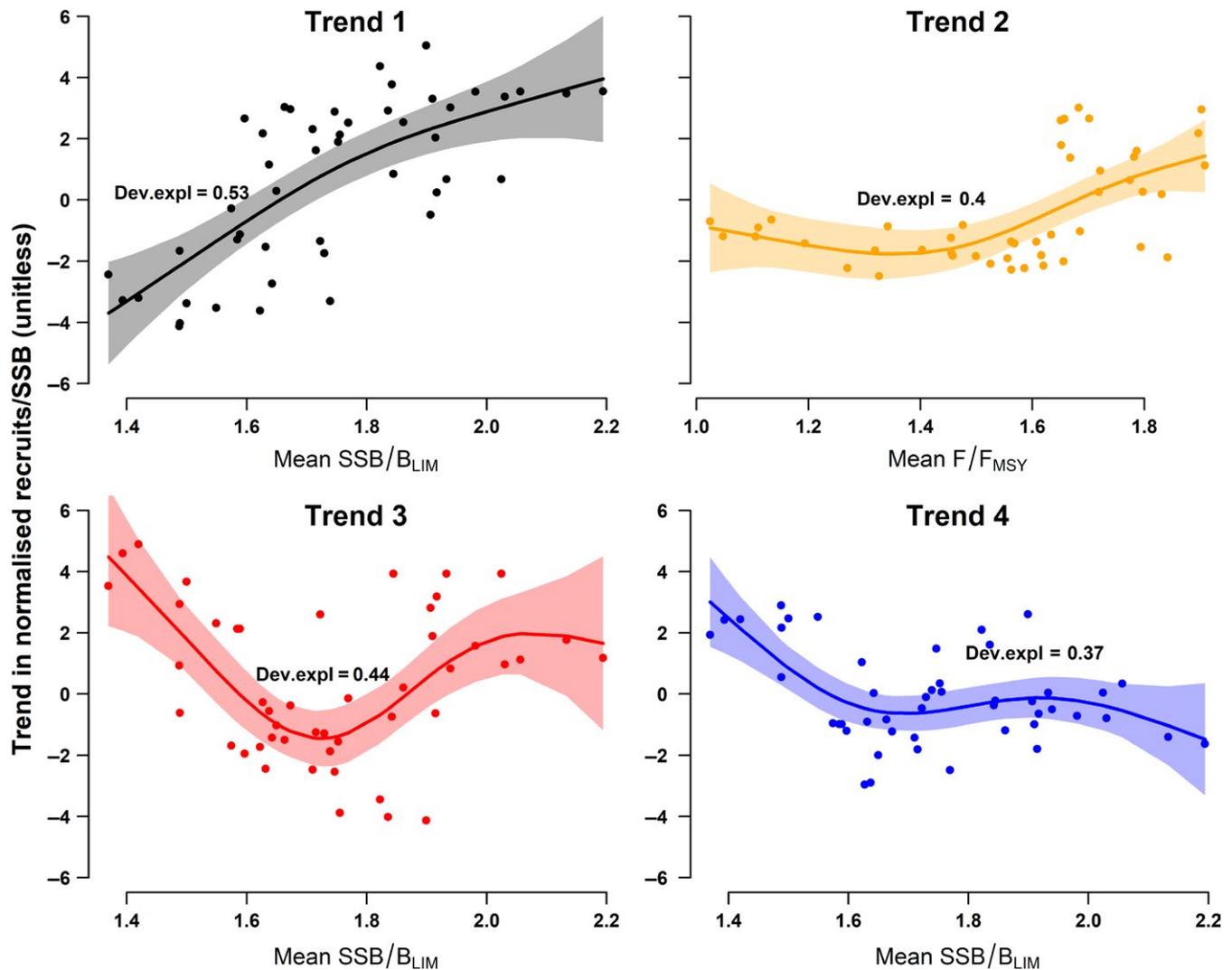


FIGURE 4 Scatterplots between the four common trends in R/SSB estimated by the DFA model and management indicators and estimated GAM smoothers. Each dot represents a year in the time series and shows a data point of DFA trend and management indicator. Shown are the management indices with a significant ($p < 0.05$) correlation that had the highest explanatory power for each trend, determined by total deviance explained. Tested were geometric mean of SSB/B_{LIM} and F/F_{MSY} over all stocks [Colour figure can be viewed at wileyonlinelibrary.com]

additional stock-specific dynamics and noise or have nonlinear characteristics that cannot be adequately detected by simple Pearson's correlations. The latter includes interactions between stocks that may increase competition or predation under favourable recruitment conditions, undermining synchronous recruitment success. Although we can conclude that direct synchrony between stocks may exist, it remains largely undetectable over entire recruitment time series except for few closely linked stocks.

The results from both the common trends in recruitment success and the individual stocks suggest strong links to ocean currents and their physical properties, including temperature. This confirms findings of other recent studies that proposed the Norwegian coastal current (Skagseth et al., 2015) and in particular the subpolar gyre (Hátún et al., 2016; Payne et al., 2012) as major determinants of ecosystem productivity and recruitment success

in the north-east Atlantic Ocean. Previously, this role has often been associated with the NAO (Drinkwater et al., 2003; Ottersen et al., 2001), but this relationship may depend on the specific time series (Solow, 2002) and has in some cases increasingly dissolved in recent years (Drinkwater, Colbourne, Loeng, Sundby, & Kristiansen, 2013; Hátún et al., 2016). Weakened or broken-down relationships do, however, not rule out an important role of NAO or its arctic equivalent NAM in the north-east Atlantic system. In fact, our study found statistically significant relationships between recruitment success and NAO or NAM based on recent, comparatively long time series, reinforcing their relevance for recruitment dynamics. However, based on the literature and our results, we can conclude that it will be more promising for future research to focus on oceanographic processes such as those related to the subpolar gyre. Compared to atmospheric processes, the state of currents

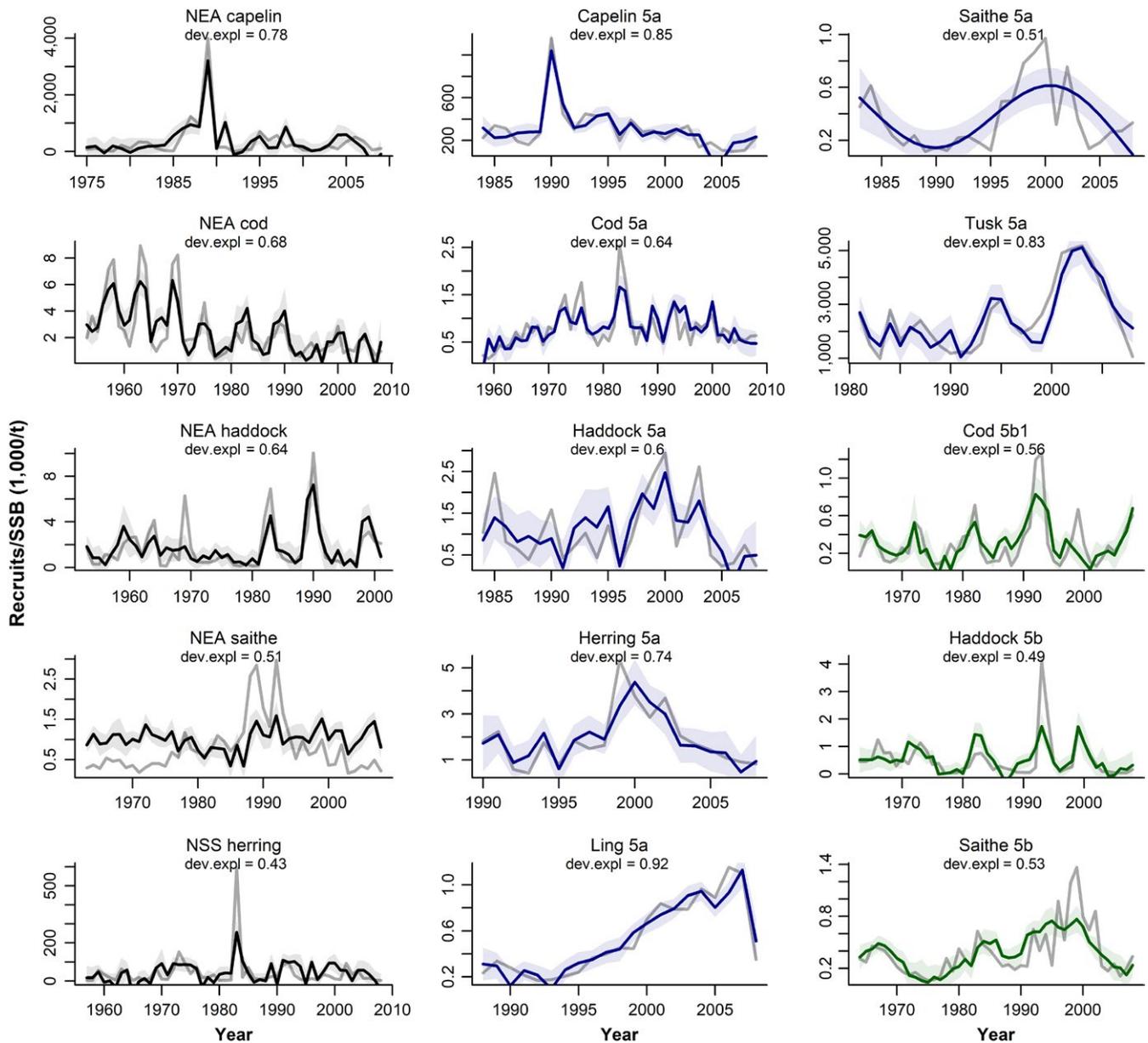


FIGURE 5 Recruitment success represented by R/SSB (1,000/tonnes) and corresponding GAM models of stocks spawning along the Norwegian coast (black), around Iceland (blue) and on Faroes grounds (green). Light grey lines indicated recruits per unit spawning stock biomass as estimated in the stock assessment, whereas dark lines show the model predictions and their 95% confidence intervals (shaded areas). Colours indicate the different spawning ecoregions (black = Norwegian coast [left], blue = Iceland [middle and top 2 on the right], green = Faroe Islands [bottom 3 on the right]). The selected models are detailed for each stock in Table 3

has more immediate effects on marine ecosystem functioning and thus recruitment success of fish stocks. Furthermore, our results also suggest that spawning stock biomass influences recruitment success but that these density effects do not affect the detection of underlying trends and explain only a minor fraction of the recruitment variability, confirming the existing literature (Szuwalski et al., 2015; Vert-pre, Amoroso, Jensen, & Hilborn, 2013).

The proportion of the variability explained in the common trends was moderate (around or below 50%), particularly when SSB was explicitly accounted for, and more than one variable was found to be relevant. This stresses that recruitment dynamics are complex and depend

on a set of different, possibly interdependent factors. The detected relationships between trends in recruitment success and indicators of stock status underline this and illustrate that also fishing has indirect effects on recruitment. These effects go beyond diminishing the spawning stock, notably by affecting stock demographics (Hixon, Johnson, & Sogard, 2014; Murawski, Rago, & Trippel, 2001) and thus productivity (Britten, Dowd, & Worm, 2016; Zimmermann & Jørgensen, 2017). We found significant relationships with SSB/B_{LIM} in all common trends, albeit with different directions and shapes. Because the recruitment success of a stock feeds back to its own stock biomass and through the food web also to dynamics of other stocks, this may be expected and

TABLE 3 Details of GAM models for individual stocks listing the variables of the best fitting model. Bold indicates statistically significant relationship ($p < 0.05$), italic marginal significance ($p < 0.1$), a plus (minus) sign before the variable a positive (negative) relationship, and asterisk an interaction, and s() a nonlinear relationship (i.e., whether a smoother has been applied). If not indicated with s(), a linear relationship was found. Food web interactions consist either of SSB (SSB) or recruits (R) of a specific stock, NAO was tested with annual, summer and winter indices. Subscripts represent the time lags to spawning year t , no subscript means that time series of covariate was aligned with R/SSB at year t . The last column lists the total deviance in the data explained by the model

Region	Stock name	Internal	Climatic	Circulation	Food web	Time	Dev. explained explained (%)
Norwegian coast	NEA capelin	s(SSB) + s(H_{t-1})		Kolaindex	s(Cod.SSB)		78
	NEA cod	s(SSB)	s(SST)	s(NCCstability)	Haddock.Rec + s(Herring. Rec _{t-1})	-Year	68
	NEA haddock		s(NAO)	s(NCC _{t+2})	s(Cod.SSB) + s(Herring.Rec)		64
	NEA saithe	SSB + s(H) + s(Weight_{t-2})	s(NAM _{t+1})	NCC			51
	NSS herring			SPG + NCC*NCCstability	s(Cod.R)		43
Iceland	Capelin 5a	s(SSB)		s(SPG)		s(Year)	85
	Cod 5a	s(Weight _{t-2}) + s(H)	s(NAOwinter)	s(SPG)			64
	Haddock 5a	s(H _{t-1}) - Weight _{t-1}	s(NAOsummer)		s(Ling.SSB)		60
	Herring 5a	s(SSB) + s(H) - Weight					74
	Ling 5a				s(Cod.SSB)	s(Year)	91
	Saithe 5a				s(Haddock.SSB _{t+2})	s(Year)	32
Faroes	Tusk 5a	s(SSB)	- NAO _{t+1}				83
	Cod 5b1	s(H _{t-2}) + s(Weight _{t-1})	NAOsummer _{t+2}		- Haddock.SSB _{t+2} - Saithe. SSB		56
	Haddock 5b			s(SPG _{t+1})	Saithe.Rec _{t-1}	s(Year)	49
	Saithe 5b	-SSB - H			s(Cod _{t+1})		53

explain the occurrence of positive as well as partially negative relationships. The partially positive relationship between F/F_{MSY} and trend 2, on the other hand, was mainly driven by overlapping years of high recruitment success and widespread overfishing in the 1990s. This could have been facilitated by compensatory effects; that is, strong fishing pressure reduced stock biomasses to low levels where density dependence maximizes R/SSB , at least in the short run. Other factors that may be relevant, such as zooplankton abundances, could simply not be detected in our study because corresponding time series are too short or lacking entirely for many areas, highlighting that data availability remains a major limitation for these types of analyses.

Dynamic factor analysis revealed common trends that are distinct from random patterns and indicate clear links to explanatory variables. Multivariate analyses of large datasets are prone to detect random patterns that are very similar to those found when applying the same method to an actual dataset (Planque, Arneberg, & James, 2018). Here, we showed that our results from the original dataset are very different from those of randomized datasets. The overlap between cluster analysis, correlations and DFA corroborated the results from the latter, as correlated stocks tended to share closely similar trend associations (e.g., links among flatfish or stocks spawning along the Norwegian coast). Nevertheless, the DFA results showed a complex picture, as for instance strong associations of some stocks with several trends. Furthermore, despite some associations between specific common trends and ecoregions or taxonomic groups, they are far from clear or even discrete. A simple differentiation of the data set into, e.g., southern and northern stocks or demersal and pelagic stocks by trend was not observed. This can, however, be expected considering that large-scale variables such as temperature- or gyre-driven water circulation impact physical conditions and ecosystem productivity across different ecoregions. The latter is illustrated by the SPG's influence on currents, temperature and nutrient distribution in the entire northern ranges of the study area (Hátún et al., 2016), which has been shown to effect spawning distribution and larval drift west of the British Isles and around Iceland of both demersal and pelagic gadoids (see Table 1). Our results confirm this by linking SPG to, among others, British, Faroese and Icelandic gadoids as well as capelin and blue whiting. Our results also confirm the widely described (see Table 1) effects of NAO (and the Northern Annual Mode) on gadoid stocks across the entire study region.

The species in our study have similar larval ontogeny across a wide taxonomic range. From spawning to recruitment, fish species move, literally and figuratively, through different habitats and ecological niches that are often very distinct from those they inhabit as adults. Especially in the early larval stages, different species such as herring and cod undergo similar planktonic stages and can share the same habitat. This may explain shared dynamics across species with very different adult lifestyles and is confirmed by our analysis that found, for instance, the NCC to be relevant for different species spawning along the Norwegian coast.

4.2 | The role of the spawning stock

Besides the SSB itself, which was confirmed as minor but significant driver of recruitment success, stock demographics and condition of

spawners are assumed to be relevant too for reproductive output and, subsequently, recruitment (Kjesbu, Witthames, Solemdal, & Walker, 1998; Marteinsdottir & Thorarinnsson, 1998). This is, however, not necessarily confirmed by statistical analysis (Stige et al., 2017). Brunel (2010) found for 39 stocks, of which 35 stocks were included in the present analysis, only few and overall not significant effects of age structure on recruitment. Our results are equally mixed, detecting mean weight or diversity of spawners as an explanatory variable in a range of stocks (Table 3) that explained large proportion of variability in some cases, such as NEA capelin. Because reproductive output is linked to the age and body size of spawning fish (Barneche, Robertson, White, & Marshall, 2018), this possibly confirms the expectation that demography and weight-at-age of the spawning stock are important for recruitment despite the key role of survival at early life stages. Furthermore, larval survival itself may also depend on egg quality, which is linked to body size and age of spawners (Berkeley, Chapman, & Sogard, 2004; O'Farrell & Botsford, 2006) and ties together the relevance of pre- and post-spawning processes. Consequently, the composition and condition of the spawning stock likely play an important role for stock productivity and resilience (Hixon et al., 2014). Our analysis also showed that time lags between condition, fecundity and spawning success can be detected, confirming previous findings (dos Santos Schmidt et al., 2017). It remains to be explored whether simplified proxies such as spawner demographics or mean weight are sufficiently capable of capturing these dynamics or whether better measurements are necessary. Additional attention should be also given to intraspecific interactions between cohorts that can create negative feedbacks and thus counteract positive effects of a large or diverse spawning stock (Ricard, Zimmermann, & Heino, 2016).

4.3 | Limitations

Despite the increasing data availability, most available time series are still comparatively short and represent a set of very specific historic states that may not always be representative for general population dynamics. Previous studies have shown that seemingly strong relationships between recruitment and explanatory variables can break down over time (Drinkwater et al., 2013; Solow, 2002), raising the question whether past statistically significant relationships were only an artefact of the specific time series or if the relevance of different drivers changes over time. Furthermore, explanatory variables are often correlated, complicating detection of functional relationships and the model selection. Interpretation of complex GAMs with several explanatory variables is therefore not straight-forward, as different combinations of variables may result in similarly good models. An example is the role of AMO for Icelandic stocks, which was suggested by the DFA and through significant correlations with three Icelandic stocks, but not reflected in the model selection as sets of other variables turned out to result in more parsimonious models.

Regime shifts due to, for example, environmental changes, shift in species distribution or stock collapses can alter the properties of recruitment dynamics (Chavez, Ryan, Lluch-Cota, & Niquen, 2003;

Perälä & Kuparinen, 2015). Non-stationarity has been identified as a major issue in stock-recruitment relationships (Minto, Mills Flemming, Britten, & Worm, 2013; Peterman, Pyper, & MacGregor, 2003; Walters, 1987), partly explaining their poor performance in many cases. This may also apply for environmental drivers since their effects can interact with density-dependent effects and may be stronger when stock sizes are low (Brander, 2005), implying that the role of environmental effects depends on the state of a fish stock and thus on other effects that can alter stock sizes. Strong fishing pressure, for instance, can alter stock productivity over time through changes in the demographic structure and evolutionary adaptation (Britten et al., 2016; Enberg, Jørgensen, & Mangel, 2010). A similar issue becomes evident when considering ecological interactions with other species, whose abundance and distribution also fluctuate due to natural and anthropogenic drivers. The impact of predation on recruitment, for instance, may vary depending on the spatio-temporal overlap of prey and predator (Durant et al., 2014; Huse et al., 2008). These fine-scale dynamics are difficult to observe and are rarely captured in currently available time series. Improving the spatio-temporal resolution is therefore an important pathway to deepen our understanding of recruitment dynamics.

Stock and recruitment data from stock assessments and environmental indices are not observed data but estimates from statistical models that are typically highly aggregated in time and space. The estimation uncertainty and the underlying assumptions can therefore bias the statistical analysis and their interpretation (Brander, Neuheimer, Andersen, & Hartvig, 2013; Brooks & Deroba, 2015). Using R/SSB can add further, potentially problematic assumptions (Cardinale & Hjelm, 2006; Stige et al., 2006) that need to be considered. Furthermore, aggregating recruitment to an annual total of an entire stock may oversimplify the true dynamics, since there is spatially or temporally diverse spawning behaviour or even discrete spawning units within most stocks. Different spawning components and their eggs and larvae may therefore experience different environmental conditions, yet stock assessment data do not resolve such fine-scale dynamics. Similarly, annual indices of environmental processes may not represent the specific conditions in critical periods between spawning and recruitment adequately, diluting potential statistical signals. Technical progress in data collection, such as satellite remote sensing, may therefore provide the necessary spatio-temporal resolution of environmental and habitat information to improve our understanding of ecosystem processes and recruitment dynamics (Chassot et al., 2011; Kacev & Lewison, 2016).

5 | CONCLUSIONS

Understanding recruitment dynamics and improving their predictability could help to reduce the forecast uncertainty in stock assessments and boost the quality of management advice and sustainability of the world's fisheries. Today, the physical and biological properties of ecosystems and their effects on population dynamics are almost entirely ignored in fisheries management

worldwide (Skern-Mauritzen et al., 2016). Implementing environmental and ecological interactions that all affect stock productivity and recruitment success into assessments would, thus, be a crucial step towards an ecosystem approach to fisheries management. However, this would ultimately require a much clearer understanding of the mechanistic processes and the capability to forecast them accurately. Without improved predictability, observing directly pre-recruit abundance on scientific surveys and responding to fluctuations with adaptive harvest strategies may remain the most cost-effective management strategy (Walters & Collie, 1988); that could potentially be even further simplified, see for instance Kelly and Codling (2006); Zimmermann and Enberg (2017). Future progress in collecting real-time information of ecosystems as well as novel statistical approaches such as empirical dynamic modelling (Munch, Giron-Nava, & Sugihara, 2018; Perretti, Sugihara, & Munch, 2013) will be fundamental to finding beneficial ways of integrating environmental and ecological data into assessment and management processes. Our study underlines this by demonstrating that there are shared, synchronous trends among fish stocks in the north-east Atlantic Ocean, and by identifying common underlying drivers, which provides an important basis for further research.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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