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Shifts in North Sea forage fish productivity and potential fisheries yield

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Abstract

1. Forage fish populations support large scale fisheries and are key components of marine ecosystems across the world, linking secondary production to higher trophic levels. While climate-induced changes in the North Sea zooplankton community are described and documented in literature, the associated bottom-up effects and consequences for fisheries remain largely unidentified.
2. We investigated the temporal development in forage fish productivity and the associated influence on fisheries yield of herring, sprat, Norway pout and sandeel in the North Sea. Using principal component analysis, we analysed 40 years of recruitment success and growth proxies to reveal changes in productivity and patterns of synchroneity across stocks (i.e. functional complementarity). The relationship between forage fish production and *Calanus finmarchicus* (an indicator of climate change) was also analysed. We used a population model to demonstrate how observed shifts in productivity affected total forage fish biomass and fisheries yield.
3. The productivity of North Sea forage fish changed around 1993 from a higher average productivity to lower average productivity. During the higher productivity period, stocks displayed a covariance structure indicative of functional complementarity. *Calanus finmarchicus* was positively correlated to forage fish recruitment, however, for growth, the direction of the response differed between species and time periods. Maximum sustainable yield (MSY) and the associated fishing mortality (F_{msy}) decreased by 33%–68% and 26%–64%, respectively, between the higher and lower productivity periods.
4. *Synthesis and applications*. The results demonstrate that fisheries reference points for short-lived planktivorous species are highly dynamic and respond rapidly to changes in system productivity. Furthermore, from an ecosystem-based fisheries management perspective, a link between functional complementarity and productivity, indicates that ecosystem resilience may decline with productivity. Based on this, we advise that system productivity, perhaps monitored as forage fish growth, becomes an integral part of management reference points; in both single species and ecosystem contexts. However, to retain social license of biological advice when fish catch opportunities are reduced, it is crucial that shifts in productivity are thoroughly documented and made apparent to managers and stakeholders.

KEYWORDS
bottom-up effects, fisheries management, fisheries yield, forage fish, functional complementarity, maximum sustainable yield, portfolio effect, recruitment, small pelagic fisheries, system productivity

1 | INTRODUCTION

Changes in ecosystems are often gradual and smooth and follows, for example, large-scale climatological fluctuations. However, sudden rapid changes are not uncommon (Scheffer, Carpenter, Foley, Folke, & Walker, 2001), and the detection of such shifts is pivotal in responsive ecosystem based management (Casini, Bartolino, Molinero, & Kornilovs, 2010; King, McFarlane, & Punt, 2015; Pikitch et al., 2004). In the North Sea, the zooplankton community underwent considerable changes in the late 1980s and early 1990s, with the decline of the subarctic calanoid copepod *Calanus finmarchicus* being one of the most well-documented examples (Beaugrand, Brander, Lindley, Souissi, & Reid, 2003; Defriez, Sheppard, Reid, & Reuman, 2016; Pitois & Fox, 2006). While several authors have interpreted these changes as evidence of a major system wide regime-shift (Barange et al., 2008; Beaugrand et al., 2003; McQuatters-Gollop et al., 2007), resulting bottom-up effects on the fish stocks are still not well understood (Reid, de Fatima Borges, & Svendsen, 2001; Ware & Thomson, 2005).

The North Sea has a combined standing stock of commercially exploited forage fish equalling *c.* 7.6 million tonnes and annual yields averaging 1.5 million tonnes in the 1990s (Dickey-Collas et al., 2014; Engelhard et al., 2013). The forage fish biomass includes species such as herring (*Clupea harengus*), sprat (*Sprattus sprattus*), Norway pout (*Trisopterus esmarkii*), and lesser sandeel (*Ammodytes marinus*), which together consume *c.* 110 million tonnes of zooplankton annually (derived from data in Greenstreet, Bryant, Broekhuizen, Hall, & Heath, 1997; ICES, 2015a, 2015b; Van Deurs, Christensen, & Rindorf, 2013). The combination of a central position in the food chain and large responsiveness to climate change and environmental variability makes the management of forage fisheries a major challenge (Fauchald, Skov, Skern-Mauritzen, Johns, & Tveraa, 2011; Fiechter, Rose, Curchitser, & Hedstrom, 2015; Smith & Jarre, 2011).

Most North Sea fisheries are presently managed using harvest control rules targeting the fisheries maximum sustainable yield (MSY; Kell, Pilling, & O'Brien, 2005; Mohn & Chouinard, 2007). In the EU, MSY is defined as the highest yield that can be taken on average from a stock under existing average environmental conditions without significantly affecting reproduction (EU, 2013). If all forage fish stocks in the North Sea show synchronous responses to climate-driven changes in the zooplankton community, this will impact the combined forage fish biomass and MSY of these stocks. While scientific single-species advice on catch opportunities will likely reflect this within a span of less than 5 years, the decreasing catch potential of the individual stocks may not be as easily accepted by stakeholders (Kelly, Pecla, & Fleming, 2017). On the other hand, if the responses are asynchronous (i.e. inverse correlations between species), the overall biomass and yield may remain relatively stable over time, providing a basis a multispecies approach to management and likely enhancing acceptance among stakeholders. These stabilizing mechanisms are known as the portfolio effect (Tilman, Lehman, & Bristow, 1998) or functional complementarity (Lindegren, Checkley, Ohman, Koslow, & Goericke, 2016) and have been demonstrated in several ecosystems around the world (Lluck et al., 1992; Lindegren et al., 2016).

In the present study, we analysed time series of two productivity metrics, length anomalies and recruitment success, for the major forage fish stocks in the North Sea, and tested the hypothesis that overall forage fish productivity has changed alongside with the changes in the zooplankton community described in the literature. Alternatively, some stocks have responded negatively and others positively (i.e. functional complementarity). Lastly, we simulated stock development to demonstrate implications for MSY and the potential forage fish biomass in the North Sea.

2 | MATERIALS AND METHODS

2.1 | Metrics of fish productivity

The analyses combined data from five major forage fish stocks in the North Sea: herring, Norway pout, sprat, northern sandeel and southern sandeel (the southern and northern sandeel stock correspond to stock assessment area 1 and 3, respectively; see ICES, 2015b). Growth and recruitment success were used as metrics of fish productivity (Kell, Nash, Dickey-Collas, Mosqueira, & Szuwalski, 2016). A pre-analysis revealed that annual growth effects exceeded cohort effects. Hence, growth was derived from average annual length anomalies of consistently sampled ages, rather than as cohort specific estimates. Length at age data for herring, sprat and Norway pout were derived from the ICES International Bottom Trawl Survey Database (February 1967–2014). The surveys contributing to this database use demersal trawls to sample the abundance of fish. The survey catch rates are used in both herring, sprat and Norway pout stock assessments in the area, and for herring and sprat, the results from this survey shows high consistency with data from acoustic surveys when used to estimate abundance indices. In contrast to, e.g. acoustic surveys, the sampling does not target aggregations of fish and hence avoids possible bias if high aggregations tend to contain, e.g. smaller individuals. Total catch and length composition of the majority of species is recorded in each haul. Haul duration generally varies between 15 and 35 min, and on average two trawl hauls are conducted within each ~30 × 30 nm statistical rectangle in a grid covering the entire North Sea, although not all rectangles were monitored prior to the 1980s. The length of the time series differed between the three stocks as sprat and Norway pout were not aged up until 1976 and 1984 respectively.

Age-length keys were estimated using continuation-ratio logits (Gerritsen, McGrath, & Lordan, 2006; Rindorf, Jensen, & Schrum, 2008; Rindorf & Lewy, 2001). All fish ages were measured in years from 1 January in the year of spawning. The mean length of each stock s at age a in year y, ($l_{a,y,s}$), was calculated by estimating average length of all fish caught in a given age group. Unfortunately, the data are often recorded in plus-groups for older ages and hence, age segregated data for older ages are not consistently reported.

Sandeel are not representatively caught in the trawl surveys, and therefore length at age data for sandeel were derived from fish sampled from the commercial fishery in the second quarter, which roughly captures the fishing season. The samples are a combination of on-board samples (samples organized by control agencies) and port samples. Sample size is *c.* 1 kg taken randomly from the catch. Mean length at age in each statistical rectangle was estimated by combining sampled length distributions with age-length keys. Length at age in a given year was estimated as the average mean length in the commercial catches. Samples were available from 1978 to 2014 for the southern sandeel stock (except from 1990) and from 1982 to 2014 for the northern stock. These procedures provided yearly estimates of mean length at age of northern and southern sandeel, sprat and Norway pout of ages 2–4 and herring of ages 2–5. Fish of age 0 and 1 were not included as these were only partially recruited to the survey sampling gear. The estimated mean lengths at age were then used to estimate the annual mean length anomalies. Length at ages 2+ was highly correlated between ages within years for all stocks (Pearson′s product moment correlation: coefficients >0.60, $p < .001$ for all ages and stocks). This indicates that a common factor is influencing the length of all ages in a given year. Reducing complexity of data by computing the anomalies was therefore desirable. The mean length anomaly of fish, $\lambda_{y,s}$, was computed as:

$$\lambda_{y,s} = \left(\frac{l_{2,y,s} - \bar{l}_{2,s}}{\bar{l}_{2,s}} + \frac{l_{3,y,s} - \bar{l}_{3,s}}{\bar{l}_{3,s}} + \ldots + \frac{l_{\max,y,s} - \bar{l}_{\max,s}}{\bar{l}_{\max,s}} \right) / \left(\max - 1 \right),$$

where $l_{a,y,s}$ is the length at age a in year y of stock s, $\bar{l}_{a,s}$ is the average length at age a of stock s across all years and max denotes the oldest age included in the analysis for stock s (max is 5 for herring and 4 for other stocks; max − 1 is used in the denominator, since age 1 fish is not included in the analysis, as explained above).

Data on recruitment (R) and spawning stock biomass (S) were derived from stock assessments (ICES, 2015a, 2015b). Recruitment success was estimated as $\ln(R/S)$ and the annual anomaly of all-time series was estimated as described for length at age. However, to avoid erroneous conclusion, the type of analysis was repeated with residuals from a Ricker relationship (see Supporting information).

2.2 | Statistical analysis of data time series

Data were analysed both within each stock and across stocks. Analyses carried out within each stock served to identify time trends in length anomaly and recruitment success, and was conducted using Pearson′s product moment correlation tests. The across stock analyses focused on the more general correlation structure and was conducted using principle components analyses (PCA) in line with the approach described in Lindegren et al. (2016).

Initial spectral analyses showed periodicities in data. Data were therefore also analysed as 3-year running averages to differentiate between correlation patterns resulting from multiannual trends and correlation patterns resulting from year-to-year fluctuations. Applying running averages, rather than the underlying annual values, can potentially introduce an artificial autocorrelation in the data reducing the effective number of degrees of freedom below the number of observations. To remove this source of bias, the degrees of freedom was reduced in tests in accordance with the method described in Pyper and Peterman (1999).

As PCA estimates a common correlation structure throughout the dataset, we analysed whether there were significant changes in the correlation structure over time. The analysis was used to identify the most likely single year breakpoint in the time series (across stocks). The breakpoint analysis was performed by estimating the parameters in the following model:

$$X[t] \sim N(Z[t], I \times s^2)$$

where the observation at time t is $X[t] = (x[t1], \ldots, x[t5])$, with $x[t1]$ being the observed productivity value for stock 1 at time t and so forth. $Z[t] = (z[t1], \ldots, z[t5])$ denotes the underlying process describing productivity and I is a matrix with 1 in the diagonal and 0 elsewhere, and s^2 is the variance parameter. The underlying process model for Z is assumed to be a multivariate random walk with a common correlation parameter ρ_1 for all pairs up to time τ after which point the common correlation parameter is ρ_2. The log likelihood of each possible breakpoint τ is then evaluated to determine if there is a clear change point in the correlation structure.

Lastly, a PCA analysis for each productivity metric was conducted. Based on the results from the breakpoint analysis described above, the PCA for length anomalies was split into the period before and including 1993 and the period after 1993. The contribution of the different stocks to the first and second principal component (PC1 and PC2, respectively) and the time trends of PC1 and PC2 were examined.

2.3 | Zooplankton

To investigate if trends in forage fish productivity were correlated to changes in the zooplankton, the PC1 from all three PCAs was related to an annual *C. finmarchicus* North Sea index using Pearson′s product moment correlation tests. *Calanus finmarchicus* abundance (numbers/m^3) was derived from the continuous plankton recorder (CPR) survey (Batten et al., 2003; Reid, Colebrook, Matthews, Aiken, & Team, 2003) and provided by the Sir Alister Hardy Foundation for Ocean Science (Richardson et al., 2006; Stevens & Johns, 2017), where it was delivered in the CPR standard format of monthly values for each of the four CPR standard areas within the North Sea (c1, c2, d1 and d2). The annual index was subsequently calculated by first deriving the median value across all months and then the median across all areas.

2.4 | The effect of fish stock productivity on the fisheries and potential forage fish biomass

In order to demonstrate how changes in recruitment and growth impact MSY, the associated mortality F_{msy} and the potential forage fish spawning stock biomass (i.e. spawning stock biomass at a fishing mortality of zero), we simulated stock dynamics for the period before and after 1993 (see estimation of time-series breakpoints above). Calculations were based on a dual simulation model where the yield resulting from a given fishing mortality is determined based on a "perceived stock" and subsequently removed from a "true" stock, which receives a stochastic annual recruitment. The model framework is in accordance with the models described in Butterworth and Punt (1999) and Butterworth (2007) and ICES (2013). F_{msy} is defined as the fishing mortality resulting in the highest long-term average yield that can be obtained while at the same time ensuring that probability of the spawning stock (S) falling below the lower limit biomass reference point, represented by B_{lim}, does not exceed 5% (ICES, 2014). Simulations of stocks development when managed according to F_{msy} were carried out for a period of 20 years and repeated 1,000 times. The probability of achieving a spawning stock below B_{lim} (adopted from the ICES reports ICES, 2015a, 2015b) was calculated as the number of simulated years with $S < B_{lim}$ divided by the total number of simulated years. To demonstrate the effects of reduced productivity on the potential combined forage fish biomass, we also simulated the potential combined forage fish spawning stock before and after 1993 in a no-fishing scenario ($F = 0$). Simulations were carried out for each stock for the two periods identified in the breakpoint analysis described above (1983–1993 and 1994–2013). Period-specific stock-recruitment relationships and mean weight at age were calculated from values in the ICES reports for the respective stocks (ICES, 2015a, 2015b). For simplicity, we applied stock-recruitment relationships of the hockey-stick type (Barrowman & Myers, 2000) with time invariant breakpoints at B_{lim}. Hence, only the upper level of the hockey stick and mean weight at age varied between the two periods (before and after 1993). As a simplification and to avoid making prejudiced assumptions, correlations between stocks were not accounted for. Hence, the focus of the simulations were merely to establish the overall change between the two periods defined above. A more detailed description of the model and input data can be found in Supporting information.

3 | RESULTS

3.1 | Time trends in productivity within stocks

All stocks displayed decreasing trends in production, reflected in either length anomalies, recruitment success or both. Length anomalies showed a significant declining trend in four out of five stocks, sprat being the exception (Table 1, Figure 1). Using 3-year running averages, significant trends were detected for herring and northern sandeel, although all stocks but southern sandeel showed a tendency toward lower recruitment success late in the time series (Table 1, Figure 2). Overall, these results demonstrate a shift from a period of high forage fish productivity (across all species and stocks) to a period of considerably lower productivity.

TABLE 1 Time trends. Pearson′s product moment coefficients and p-values (in parenthesis) are provided for the correlations of time vs. recruitment success and length anomalies, respectively. Tests was made for both annual values and 3-year averages (see Section 2). Significant correlations are in bold font

Stock	Recruitment success	Length anomaly
Herring		
Trend in annual values	−0.21 (0.092)	**−0.45 (0.001)**
Trend in 3-year running mean	**−0.75 (0.009)**	−0.53 (0.079)
n	67	49
Norway pout		
Trend in annual values	−0.14 (0.4616)	**−0.51 (<0.001)**
Trend in 3-year running mean	−0.47 (0.0616)	**−0.62 (0.014)**
n	30	41
Southern sandeel		
Trend in annual values	0.02 (0.894)	**−0.41 (0.013)**
Trend in 3-year running mean	0.10 (0.688)	−0.42 (0.202)
n	31	37
Northern sandeel		
Trend	−0.20 (0.282)	**−0.34 (0.037)**
Trend in 3-year running mean	**−0.52 (0.037)**	−0.31 (0.179)
n	31	37
Sprat		
Trend in annual values	−0.12 (0.468)	−0.30 (0.060)
Trend in 3-year running mean	−0.41 (0.161)	−0.34 (0.255)
n	40	41

3.2 | Covariation patterns in productivity across stocks

The across stock covariation structure in the length anomaly data changed significantly over time, with the most likely breakpoint being in 1993. In contrast, the covariation structure of recruitment success remained the same throughout the time series. The PC1 for length anomaly up to 1993 explained most of the variation (PC1: 80%, PC2: 11%; Table 2), hence, the across stock correlation structure was strong. Until 1993, PC1 was positively correlated to length anomaly of sprat and the two sandeel stocks and negatively correlated to herring and Norway pout.

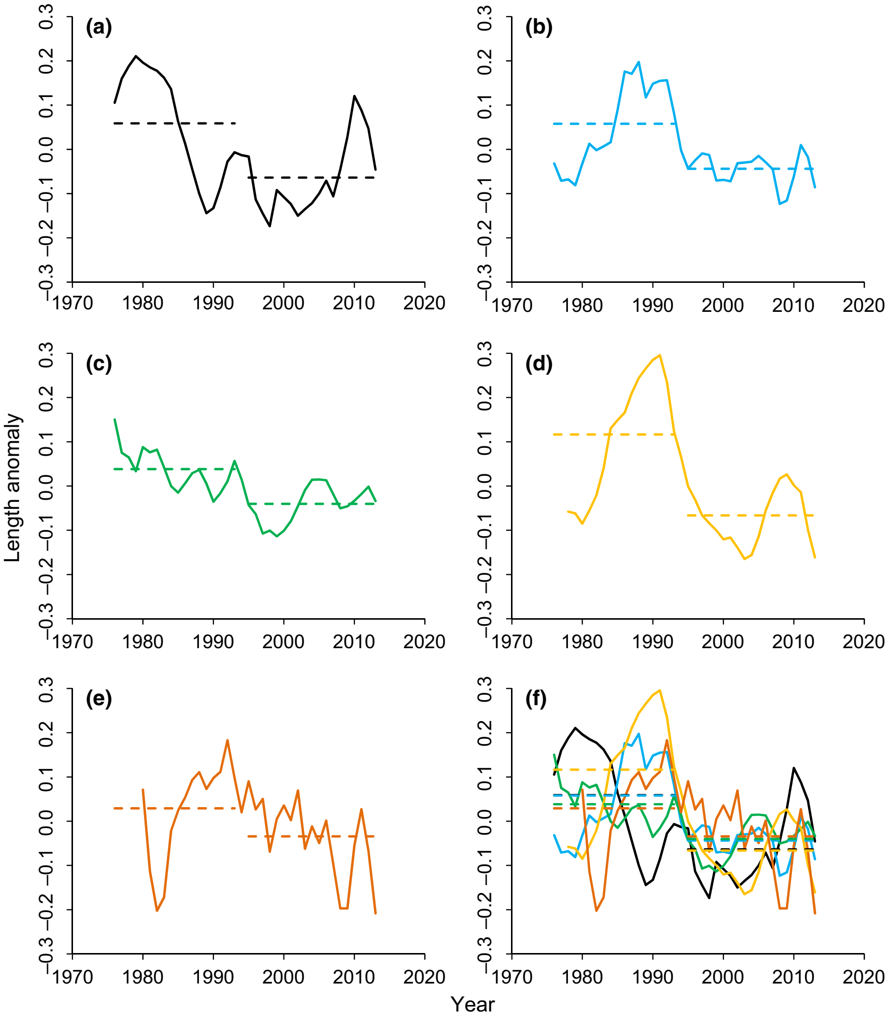

FIGURE 1 Development in length anomaly (solid line) of herring (a), sprat (b), Norway pout (c), southern sandeel (d), northern sandeel (e) and all stocks together (f). Broken lines show averages before and after 1993

After 1993, the across stock correlation structure in the length anomaly data was weaker, as indicated by the relatively low proportion of variation explained by PC1 (PC1: 37%, PC2: 31%) (Table 2). PC1 was now negatively correlated to length anomaly of sprat and the northern sandeel stock but positively correlated to herring, Norway pout and the southern sandeel stock. Hence, a high value of PC1 prior to 1993 corresponds to high growth of sprat and sandeel of both stocks and a low growth of herring and Norway pout, whereas a high value of PC1 after 1993 corresponds to low growth of sprat and northern sandeel and a high growth of herring, Norway pout and southern sandeel. To make the results from the two periods more intuitively comparable, we used PC1 in analyses of the period before 1993. Using this method, a high value of PC1 corresponds to a high growth of herring and Norway pout and a low growth of sprat and northern sandeel in both periods.

PC1 for recruitment success explained 42% of the total variation and PC2 added another 33%. PC1 was positively correlated to the recruitment success of all stocks, although the correlation with southern sandeel was weak (Table 2). PC2 was positively correlated to southern sandeel and negatively correlated to sprat, indicating that years of high recruitment success for one of these stocks matched up with years of poor recruitment success for the other. PC1 showed an overall significant decreasing trend over time (Pearson's product moment correlation: correlation −0.76, $p = .002$), indicating a general decrease in forage fish recruitment success. Further information about correlations between individual stocks can be found in Table S3.

3.3 | Zooplankton

The annual *C. finmarchicus* index was positively correlated to PC1 for recruitment ($c = 0.41$, $t = 2.32$, $df = 26$, $p = .029$), PC1 for growth (i.e. length anomalies) in the late period (after 1993) ($c = 0.51$, $t = 2.54$, $df = 18$, $p = .021$) and PC1 for growth in the early period (until 1993) ($c = 0.59$, $t = -2.52$, $df = 12$, $p = .027$; Figure 3). Hence, a higher density of *C. finmarchicus* was consistent with higher growth of herring and Norway pout and lower growth of sprat and northern sandeel in both periods.

3.4 | Productivity and MSY

Weight at age in the catch decreased by 13% on average across age classes and stocks between the early period and the late period (before and after 1993), and mean recruitment dropped nearly 30% on average (Table 3). These reductions led to a decrease in MSY and F_{msy} of around 47% and 46% respectively (ranging from 26% to 69%,

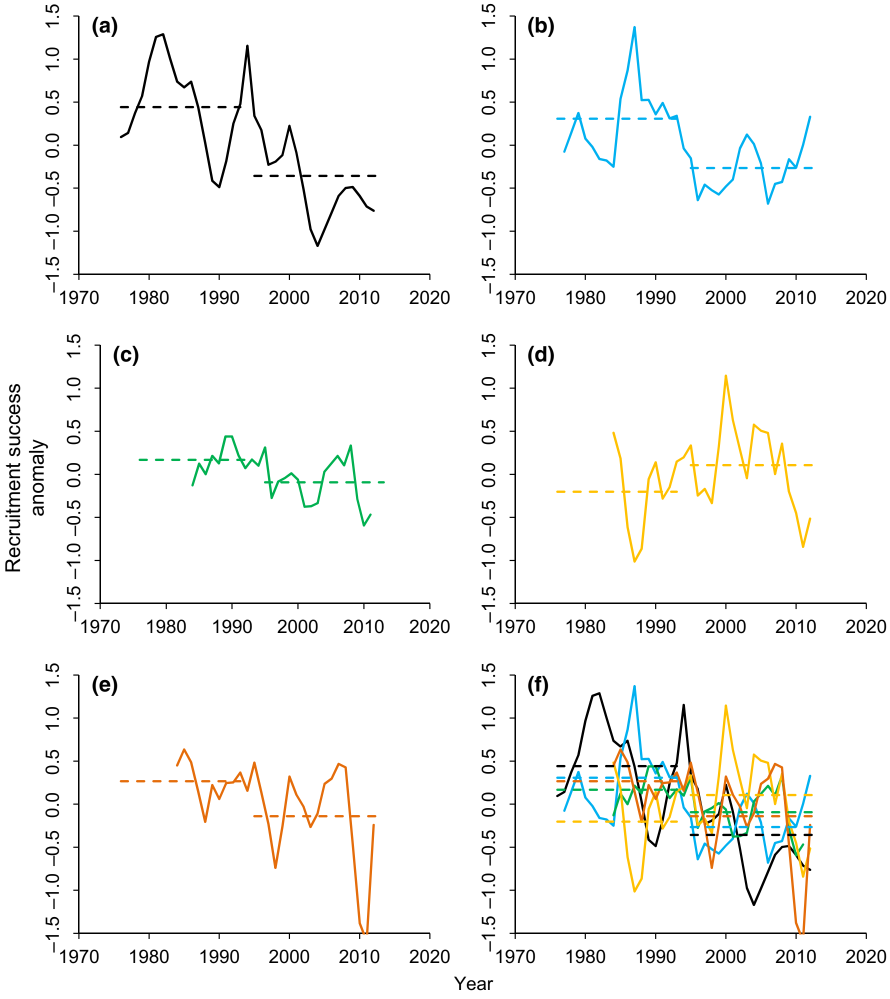

FIGURE 2 Development in recruitment success (solid line) of herring (a), sprat (b), Norway pout (c), southern sandeel (d), northern sandeel (e) and all stocks together (f). Broken lines show averages before and after 1993

Table 3). In comparison the reduction in the potential forage fish spawning stock biomass (given a fishing mortality of zero) amounted to *c.* 25% (Figure 4). The greater decrease in MSY is caused by the necessity to sustain the stock above the unchanged biomass limit reference point B_{lim}.

4 | DISCUSSION

Our results revealed that a shift in North Sea forage fish productivity (reflected in recruitment to the stocks or the growth of individuals) occurred in succession with the well-documented shifts in the plankton community (McQuatters-Gollop et al., 2007; Pitois & Fox, 2006). The year of 1993 represented the statistically most likely single-year breakpoint between a period of higher correlation in forage fish productivity and a subsequent lower correlation.

The shift in productivity around 1993 was consistent across stocks. Hence, the functional complementarity hypothesis was not supported over the entire time period. However, in the period before 1993, productivity (represented by growth) was inversely correlated between two different subsets of forage fish stocks (sprat and sandeel vs. herring and Norway pout), indicating that functional complementarity may have existed when productivity was high. Different species within the same functional group, respond in different ways to environmental drivers (Chavez, Ryan, Lluch-Cota, & Ñiquen, 2003; Lindegren et al., 2016). The stocks experience different prey fields, prefer different prey (Albert, 1994; Last, 1987; Raab et al., 2012; Van Deurs, Koski, & Rindorf, 2013), and may be expected to display different responses to changes in food availability (Defriez et al., 2016). Prior to 1993, years favouring growth of herring and Norway pout were different from those favouring sandeel and sprat, creating a synchrony among some segments of the forage fish community and an asynchrony among others. Thus, in periods with high forage fish productivity, the different spatial distributions and life histories may result in divergent growth patterns, facilitating overall stability in the forage fish community (i.e. functional complementarity). However, below a certain threshold, the functional complementarity was no longer be sustained (i.e. after 1993).

The simulated population dynamics revealed that the reduction in forage fish productivity around 1993 roughly halved the MSY and F_{msy} (the fishing mortality associated with MSY) and reduced the potential forage fish spawning stock biomass by *c.* 25%. This drop in productivity is comparable to a study conducted on North Sea cod (Kell et al., 2016). However, Shephard et al. (2014) found that the forage fish

TABLE 2 Principal component contributions of different stocks. Contribution indicates the correlation between the species specific metric and the principal component. Large contributions are present where the principal component closely follows the species specific metric, small contributions indicate that the principal component does not reflect variation in the species specific metric

Productivity metric	Stock	PC1 contribution	PC2 contribution
Recruitment success	Herring	0.44	−0.20
	Norway pout	0.55	0.07
	Sandeel (southern)	0.11	0.73
	Sandeel (northern)	0.61	0.29
	Sprat	0.35	−0.59
Length anomaly before 1993	Herring	−0.48	−0.12
	Norway pout	−0.40	0.73
	Sandeel (southern)	0.49	−0.19
	Sandeel (northern)	0.40	0.62
	Sprat	0.46	0.18
Length anomaly after 1993	Herring	0.56	0.36
	Norway pout	0.21	0.51
	Sandeel (southern)	0.46	0.31
	Sandeel (northern)	−0.51	0.39
	Sprat	−0.42	0.60

biomass in the North Sea has remained relatively stable between 1983 and 2012, it may therefore be so that productivity changes amongst the forage fish stocks after all have been successfully counteracted by appropriate management action (Dickey-Collas et al., 2014). Recruitment and spawning stock is often poorly correlated (Kell et al., 2016; Szuwalski, Vert-Pre, Punt, Branch, & Hilborn, 2015). Hence, we chose to use a simple hockey stick relationship for the simulations, rather than making assumptions about more complicated relationships (Chen & Irvine, 2001). Another simplification made here was that reference points were kept constant across the period of change, as opposed to having dynamic reference points (Punt et al., 2013).

Our analysis suggested a positive relationship between *C. finmarchicus* and forage fish recruitment. The importance of *C. finmarchicus* eggs and nauplii as food for fish larvae has been highlighted in relation to sandeel and cod (Arnott & Ruxton, 2002; Beaugrand et al., 2003; Van Deurs, Van Hal, Tomczak, Jónasdottir, & Dolmer, 2009). For sprat and Norway pout, recruitment success has not formerly been linked to *C. finmarchicus*. However, sprat recruitment is reportedly positively correlated to temperature (Baumann et al., 2006). Hence, variation in temperature in the southern North Sea could potentially explain the inverse patterns in recruitment success of sandeel in the southern area and sprat. The substantial downward shift in key elements of the plankton (McQuatters-Gollop et al., 2007; Pitois & Fox, 2006) and stock production across a range of zooplanktivorous species (results presented here), seem to indicate a declining primary production (Ware & Thompson, 2005). However, other studies point to changes in zooplankton species composition as the cause of reduced fish growth (Beaugrand et al., 2003; Van Deurs, Jørgensen, & Fiksen, 2015). Factors such as spawning site diversity or the frequency of unlikely events governing extreme recruitment outburst (Lowerre-Barbieri et al., 2016; Pepin, 2015) have also been proposed as drivers of variation in fish stock production. However, such mechanisms would not be expected to influence growth as found in the present study.

With the growing interest in implementing ecosystem-based fisheries management (Pikitch et al., 2004), the regime-shift subject is gradually becoming an integral part of the scientific endeavours in fisheries biology and management (Anderson & Piatt, 1999; Barange et al., 2008; King et al., 2015). Several studies have argued that the North Sea underwent a major regime-shift in the late 1980s, manifested first as changes in primary and secondary production (McQuatters-Gollop et al., 2007; Reid et al., 2001). This is just a few years earlier than the break point identified in the present study and therefore credible

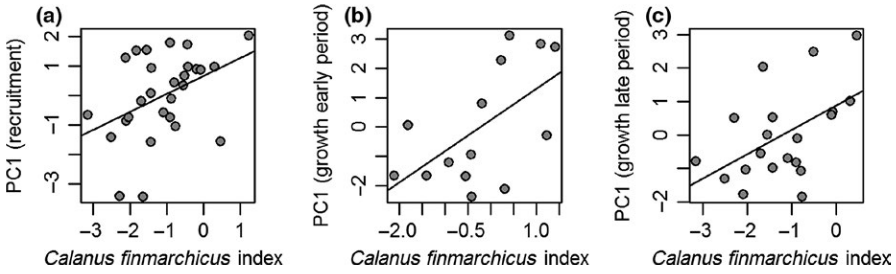

FIGURE 3 Correlations between *Calanus finmarchicus* and the first principal component of recruitment (a) and growth (b, c). Since the PCA analysis of growth was divided into an early period and a late period (see Section 2), the correlation analyses were also divided into two (b, c). All correlations were significant according to Pearson's product-moment correlation test (see Section 3)

TABLE 3 Relative change in weight at age, recruitment, Maximum sustainable yield (MSY), and F_{msy} for each stock. Values are given as % change between the period before 1993 and the period after 1993 (minus indicate a negative change). Data on mean weight at age and recruitment were adopted from the stock assessment reported by ICES and are the same data applied in the calculations of MSY and F_{msy} (see Section 2)

Stock	Weight at age (%)	Recruitment (%)	MSY (%)	F_{msy} (%)
Sandeel (southern)	−26	−23	−56	−50
Sandeel (northern)	−24	−52	−68	−64
Sprat	−6	−9	−34	−48
Herring	−3	−27	−33	−26
Norway pout	−8	−29	−45	−41

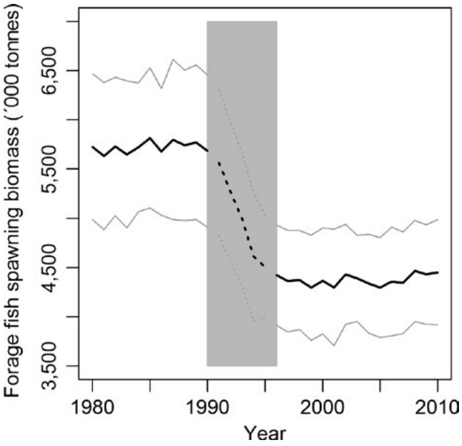

FIGURE 4 Model simulations of how the combined forage fish spawning stock biomass would have developed even without fishing ($F = 0$; i.e. the potential forage fish biomass). Black line is the mean of one thousand simulations and grey lines represents the standard deviations. Hence, the decline is caused by the introduction of the observed changes in stock recruitment and weight at age in the stocks into the model (see Table 3). The grey field defines the transition zone between the high productivity period and the low productivity period

that the shift in forage fish production is the consequence of such a regime-shift. However, based on the time series length presented here and the large inter-annual fluctuations in weight-at-age and recruitment, that even after converting to 3 years running averages were still distinctive for some stocks, it cannot be concluded if an abrupt regime-shift like transition from one state to another has truly taken place, or if the change we observed reflects climatic oscillations on a multidecadal time-scale, as reported for anchovy-sardine systems (Chavez et al., 2003). Such differentiation may, however, be worth pursuing in the future, as it would be a major asset in models of resource fluctuations and execution of ecosystem based management actions (King et al., 2015).

Here, we have shown that what appears to have been climate induced changes in productivity in the North Sea had substantial effects on MSY and F_{msy}. While, similar findings have previously been presented for cod, this is the first study to show how productivity in an entire forage fish community can shift in less than a decade, reducing the sustainable catches opportunities by a factor of two across all major forage fish stocks (Kell et al., 2005; Mohn & Chouinard, 2007; Morgan, Shelton, & Rideout, 2014). In addition, this study reveals a link between productivity and functional complementarity among stocks (the portfolio effect), supporting one of the recommendations put forward in Dickey-Collas et al. (2014), that a forage fish community cannot be managed as an overall resilient pool of biomass where one species take over the niche when another is in decline. Hence, we advocate against having a long-term maximum on the total removal of forage fish (i.e. a community MSY), which is in contrast to what has been suggested for some other systems (e.g. Lluck et al., 1992). At least, system productivity ought to be integrated into any long-term management plan and fisheries reference points should be kept dynamic, irrespective of whether it is made in a single species or multi species context. Furthermore, it is here demonstrated how already existing time series of forage fish growth and reproductive output can potentially be used as indicators of system productivity, and last but not least, to ensure social license, when catch opportunities are reduced as a result of declining productivity, documentation and communication to stakeholders is critical (Kelly et al., 2017).

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AUTHORS' CONTRIBUTIONS

All authors were involved in conceiving the ideas and designing methodology; A.R. and M.V.D. collected and analysed the data; L.W.C., A.R. and M.V.D. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

Data are available in the Dryad Digital Repository https://doi.org/10.5061/dryad.tq1f7 (Clausen, Rindorf, van Deurs, Dickey-Collas, & Hintzen, 2017).

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