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PRIMARY RESEARCH ARTICLE

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A decline in primary production in the North Sea over 25 years, associated with reductions in zooplankton abundance and fish stock recruitment

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Abstract

Phytoplankton primary production is at the base of the marine food web; changes in primary production have direct or indirect effects on higher trophic levels, from zooplankton organisms to marine mammals and seabirds. Here, we present a new time-series on gross primary production in the North Sea, from 1988 to 2013, estimated using in situ measurements of chlorophyll and underwater light. This shows that recent decades have seen a significant decline in primary production in the North Sea. Moreover, primary production differs in magnitude between six hydrodynamic regions within the North Sea. Sea surface warming and reduced riverine nutrient inputs are found to be likely contributors to the declining levels of primary production. In turn, significant correlations are found between observed changes in primary production and the dynamics of higher trophic levels including (small) copepods and a standardized index of fish recruitment, averaged over seven stocks of high commercial significance in the North Sea. Given positive (bottom-up) associations between primary production, zooplankton abundance and fish stock recruitment, this study provides strong evidence that if the decline in primary production continues, knock-on effects upon the productivity of fisheries are to be expected unless these fisheries are managed effectively and cautiously.

KEYWORDS

bottom-up effects, climate change, fish recruitment, North Sea, nutrients, phytoplankton, primary production

1 | INTRODUCTION

Phytoplankton primary production is at the base of the marine food web. Primary production is a key driver of zooplankton and ichthyoplankton dynamics and hence influences small planktivorous fish and, in turn, larger predatory fish, marine mammals and seabirds that are dependent on these. Changes in primary production have indirect effects on commercial fish stocks that help support the world's human protein requirements (Chassot et al., 2010), and are relevant to society because of our dependency on marine food products. In fact, worldwide marine primary production, estimated between 44 and 67 Pg of carbon per year (44–67 × 10^{15} gC/year;

Westberry, Behrenfeld, Siegel, & Boss, 2008), has been shown to constrain fisheries catches at a global level, as well as at regional scales (Chassot, Mélin, Le Pape, & Gascuel, 2007; Chassot et al., 2010).

Coastal and shelf seas, such as the North Sea, have higher production than open oceans and they supply 80% of the world's wild-captured seafood (Watson, Green, Tracey, Farmery, & Pitcher, 2016). Their proximity to land also makes coastal and shelf seas more susceptible to human pressures including fishing, shipping, seabed degradation and changes in water characteristics. The impacts of these pressures include nutrient enrichment and "darkening" of water (Dupont & Aksnes, 2013; Roulet & Moore, 2006).

The North Sea represents a clear demonstration of these pressures. Fish stocks have shown substantial changes, with declines especially in the 1980s–1990s. Several stocks have recently recovered, thanks to improved fisheries management especially since 2000 (Engelhard, Lynam, García-Carreras, Dolder, & Mackinson, 2015), but levels of recruitment have generally remained low (Pécuchet, Nielsen, & Christensen, 2015). In addition to the effects of sustaining fisheries and other maritime industries (shipping, oil and gas extraction) for many centuries (Engelhard, 2008), the North Sea receives inputs from river systems that drain densely populated and intensively farmed areas. Widespread use of fertilizers led to increased nutrient loads from the 1950s to the 1980s; with stricter policies, this was succeeded by nitrogen and phosphorus input reductions in recent decades (Burson, Stomp, Akil, Brussaard, & Huisman, 2016; Painting et al., 2013). Water clarity of the North Sea has decreased during the past half-century driven largely by increased suspended sediment (Capuzzo, Stephens, Silva, Barry, & Forster, 2015; Dupont & Aksnes, 2013). In addition, surface water temperature has increased by 0.2–0.4°C/decade (Dye et al., 2013), particularly from the late 1980s (Beaugrand, 2004).

Changes in phytoplankton growth and primary production can be driven by various factors including nutrient and light availability, temperature, and grazing (Behrenfeld et al., 2006; Cadée & Hegeman, 2002; Cloern, Foster, & Kleckner, 2014). It is unclear, due to a lack of direct observations, whether changes in nutrient levels and light availability in the North Sea, combined with the recent marked temperature increase, have influenced the area's primary production.

In spite of the importance of primary production for understanding the dynamics of higher trophic levels, in situ long-term datasets of primary production are limited and available for relatively few sites, for example, the Marsdiep (Cadée & Hegeman, 2002) and Oosterschelde estuary (Smaal, Schellekens, van Stralen, & Kromkamp, 2013). This is because traditional methods for measuring primary production, such as the ^{14}C method (Steemann Nielsen, 1952) and light/dark bottle oxygen method (Williams, Raine, & Bryan, 1979), have generally been time-consuming and expensive with limited spatial coverage. Due to this lack of in situ primary production data, researchers have often relied on models (based on chlorophyll or carbon); proxies, such as phytoplankton biomass (e.g. Phytoplankton Colour Index, as sampled by the Continuous Plankton Recorder; McQuatters-Gollop et al., 2015); and satellite remote sensing data, to obtain insight in spatial and temporal patterns of primary production, particularly at the global scale (for a review, see Westberry et al., 2008).

In this paper, we reconstruct a time-series of primary production based on an empirical relationship including in situ measurements of chlorophyll concentration and light climate (K_d, light attenuation coefficient and surface irradiance), from 1988 to 2013. We do so for the entire North Sea (excluding the deepest parts; see Figure 1), as well as for six different hydrodynamic regions (based on van Leeuwen, Tett, Mills, & van der Molen, 2015), given expected differences in primary production between these regions. To our knowledge, this is the first primary production time-series of this kind estimated for the North Sea, and it could be used to validate model predictions and estimates of primary production from satellite ocean colour images.

Specifically, we answer the following questions:

Q1. How has primary production fluctuated in the North Sea's different hydrodynamic regions?
Q2. Which environmental drivers may account for observed changes in primary production?
Q3. Do changes in primary production have bottom-up effects on higher trophic levels with implications for zooplankton dynamics and/or fisheries productivity?

2 | MATERIALS AND METHODS

2.1 | Study areas

Primary production was investigated for six hydrodynamic regions within the North Sea, based on van Leeuwen et al.'s (2015) classification of water masses according to the length of the mixing/stratification periods. Stratification characteristics of a region are mainly determined by air temperature (onset and strength of stratification), wind (mixing and break-up of stratification), local depth and rainfall (determining fresh water flow into the North Sea; van Leeuwen et al., 2015). While four regions—the seasonally stratified, permanently mixed, intermittently stratified and freshwater influence regions (Figure 1a)—present stable density stratification characteristics (both in space and time), a part of the North Sea (here termed "transitional") was not classified by van Leeuwen et al. (2015) owing to its interannual variability in stratification characteristics. This transitional region, although not fully meeting the assumption of a stable mixing/stratification regime, was included in the present analysis as it accounts for a substantial proportion of primary production in the North Sea. We distinguish a "transitional east" and "transitional west" region (separated by 2°E longitude), in consideration of the different light regimes in these areas, with higher turbidity in the east compared to the west (Gohin, 2011). The deeper, north-easternmost waters of the North Sea (permanently stratified region in van Leeuwen et al., 2015) were not included in our study owing to a lack of data on chlorophyll and light climate.

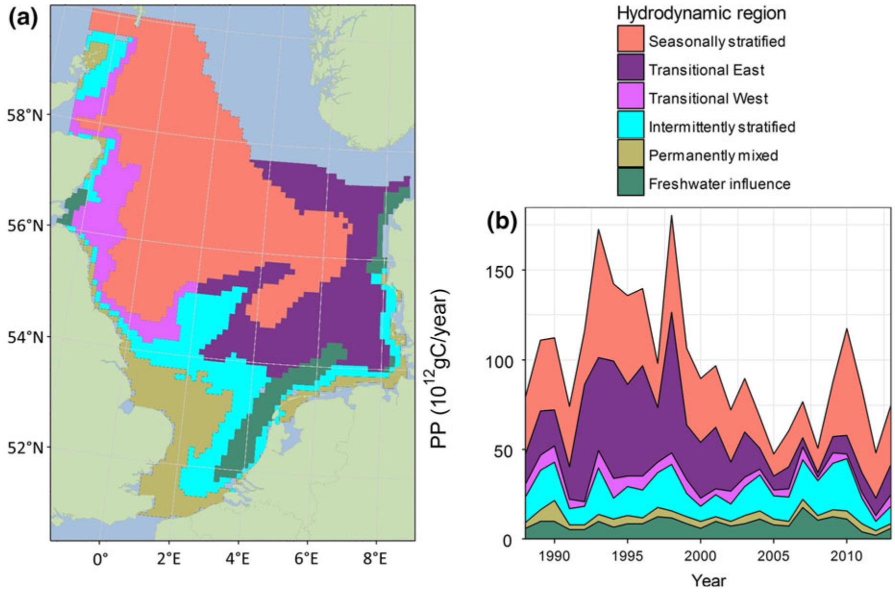

FIGURE 1 (a) Map of the North Sea showing the six hydrodynamic regions examined (based on van Leeuwen et al., 2015, with their transitional region split in “west” and “east”). (b) Changes in total annual primary production, PP (10^{12} gC/year), in each hydrodynamic region

2.2 | Collation of data underlying primary production estimates

For each region, time-series of primary production were reconstructed based on collations of all data available for chlorophyll concentration, light attenuation and surface irradiance from 1988 to 2013. Only measurements further than 6 nautical miles from the coast were included.

2.2.1 | Chlorophyll

We collated in situ measurements of chlorophyll concentration (determined using standard fluorimetric technique) for the upper 20 m of the water column, collected during ship-based surveys, from databases held at ICES, the NERC North Sea Project, and Cefas, the Centre for Environment, Fisheries & Aquaculture Science (Capuzzo et al., 2015; and see Fig. S1). Possible duplicates between these different databases were checked and eliminated. Measurements collected at the same location on the same day were averaged, as well as measurements from different depths in the upper 20 m of the water column. This depth was chosen as it includes the euphotic layer in the southern and central North Sea (Capuzzo et al., 2013) and broadly coincides with the surface mixed layer in the seasonally stratified area of the North Sea (Weston, Fernand, Mills, Delahunty, & Brown, 2005). Measurements from calibrated fluorescence sensors on automated “SmartBuoy” moorings were also included in the database but were averaged weekly, to reduce temporal autocorrelation of data (Capuzzo et al., 2015). Potential spatial autocorrelation was addressed averaging observations that were collected within 0.1 decimal degree in the same day.

2.2.2 | Light attenuation

Data on the light attenuation coefficient (K_d) were estimated using two approaches: (i) from in situ PAR (Photosynthetically Available Radiation) profiles (1997–2013), and (ii) from in situ measurements of SPM (suspended particulate materials; 1988–2013), which is known to have an empirical relationship with K_d (Devlin et al., 2008). The PAR profiles were collected during Cefas surveys using a LI-COR LI-192 cosine-corrected underwater quantum sensor, either mounted on a CTD rosette system or on a solid-state data logger (ESM-2; Greenwood et al., 2010). Here, K_d was calculated from the linear regression of natural log-transformed PAR profiles versus depth, between circa 2 m and the depth at which $\text{PAR} = 1\ \mu\text{mol photons m}^{-2}\ \text{s}^{-1}$ (Capuzzo et al., 2013). Only profiles collected during full daylight (i.e. excluding the crepuscular periods) were considered in this analysis. The in situ SPM measurements were obtained from the same sources as the chlorophyll observations described above and likewise included the upper 20 m of the water column only. SPM measurements collected on surveys were determined by gravimetric analysis; measurements from SmartBuoys were obtained from calibrated backscatter (Capuzzo et al., 2015). As for chlorophyll, SPM data from SmartBuoys were averaged weekly to reduce temporal autocorrelation (Capuzzo et al., 2015). Observations within 0.1 decimal degree, collected in the same day, were averaged to correct potential spatial autocorrelation. SPM data were converted to estimates of K_d, using the relationship for coastal and offshore UK waters described by Devlin et al. (2008), and combined with estimates of K_d calculated from PAR profiles (Fig. S1).

2.2.3 | Surface irradiance

To estimate daily surface irradiance (E_0), data on total solar radiance per day were obtained from the National Centers for Environmental Prediction (NCEP, Boulder, CO, USA) Reanalysis II dataset (Kanamitsu et al., 2002), downloaded from https://www.esrl.noaa.gov/psd/data/gridded/reanalysis/. Daily estimates for the North Sea area were downloaded on a 2.5° × 2.5° grid and averaged based on the hydrodynamic regions. Net shortwave radiation flux at surface or surface irradiance, in W/m^2, was converted to mol photons m^{-2} day^{-1}, as described in Capuzzo et al. (2013).

2.3 | Modelling time-series of chlorophyll concentration and K_d

Based on all available observations, daily averaged values of chlorophyll and K_d were calculated for each hydrodynamic region (Figs S2 and S3). However, data were not available for all days and all years in each region, and in some cases data were missing for longer periods, particularly for K_d (notably for the seasonally stratified area in the early 1990s, and transitional east in the late 1990s; Fig. S3). As we aimed to estimate daily values of gross production for each hydrodynamic region, the following modelling approach was used to impute missing observations and reconstruct full time-series. For each chlorophyll and K_d time-series, a Gaussian kernel smoother has been used to smooth the raw data, as implemented in the R function ksmooth() (R Core Team, 2016). A fairly wide bandwidth (1 year) was used, which means that the interquartile range of the kernel will be 0.5 years. This wide bandwidth is necessary to span some of the gaps in the data.

For the region of freshwater influence, limited K_d observations were available. Therefore, the trends were calculated based on observations from neighbouring hydrodynamic regions.

2.4 | Calculation of gross annual primary production

The smoothed time-series of chlorophyll concentration, K_d, and surface irradiance (E_0) were used to calculate daily estimates of gross primary production for each hydrodynamic region, according to the empirical model by Cole and Cloern (1987):

$$P = a + b * \left[\mathrm{chl} * \frac{4.61}{K_d} * E_0\right], \tag{1}$$

where P is gross daily primary production (mgC m^{-2} day^{-1}), and chl is chlorophyll concentration (mg/m^3). The parameters a and b, used for these calculations, were equal to 45.6 and 0.76, respectively; they were estimated from the linear regression of measurements of primary production obtained using the ^{14}C method, versus the corresponding composite term [chl*(4.61/K_d)*E_0]. Measurements of carbon fixation were carried out at two sampling stations (one at Oyster Grounds and one north of the Dogger Bank), in correspondence of two SmartBuoys, at 5 time points throughout 2007. Further details on the calculation of the coefficients a and b are given in the Supporting Information (Fig. S4, Methods S1 and S2).

Gross annual primary production (gC m^{-2} year^{-1}) in a given region was calculated integrating the daily primary production estimates for that region over a year. The total annual production of the area investigated (tonnes C/year) was then estimated by multiplying the (per-area) annual production estimates with the total area size (in km^2) of the region.

2.5 | Relationships between primary production and environmental variables

As potential environmental drivers of North Sea primary production, time-series were collated on climatic variables and proxies for nutrient inputs into the North Sea. As an indicator for temperature variations within the North Sea, we used the interpolated sea surface temperature dataset (HadISST) held by the Hadley Centre of the UK Meteorological Office (Rayner et al., 2003; see http://www.metoffice.gov.uk/hadobs/hadisst). The dataset was available in a 1° × 1° latitude–longitude grid on a global scale, and annual mean sea surface temperatures were calculated for the study area (between 51° and 61°N, and 2°W and 9°E).

As a broad-scale climate indicator, we used the North Atlantic Oscillation (NAO) winter index (December of the previous year to March of the focal year). The NAO is defined here as the normalized atmospheric sea level pressure difference between Gibraltar (high) and Iceland (low). A positive winter index is characterized by stronger westerly winds bringing relatively warm conditions to western Europe; the NAO has previously been linked with primary production (Ottersen et al., 2001). Data were obtained from the Climatic Research Unit of the University of East Anglia (http://www.cru.uea.ac.uk/cru/data/nao).

As proxies for riverine nutrient inputs into the North Sea, time-series on nutrient loads in the river Rhine at Lobith, Netherlands, were used (the Dutch Ministry of Infrastructure and the Environment, Rijkswaterstaat; http://live.waterbase.nl.ipaddress.com). The Rhine represents the major riverine input source of nutrients to the southern and central North Sea (Painting et al., 2013). Specifically, data on phosphate concentrations (PO_4, expressed in mg P/L of river surface water after filtration), and on combined nitrate and nitrite levels ($NO_3 + NO_2$, or NO_x; expressed in mg N/L of river surface water after filtration) were collated.

Correlations between the above-mentioned environmental variables and trends in primary production were tested. Specifically, the Pearson's cross product–moment correlation (r_p) was used as one-sample Kolmogorov–Smirnov test did not detect any departures from normality ($p > .05$). There was moderate temporal autocorrelation within several of the time-series variables examined. To account for this, the test procedure for significance of correlations was adjusted conservatively (Pyper & Peterman, 1998) by reducing the effective degrees of freedom (increasing the p values) according to the degree of autocorrelation; adjusted p values are hereafter referred to as p_{adj}.

2.6 | Relationships between primary production and higher trophic levels

To assess possible bottom-up effects of changes in primary production on higher trophic levels, we collated time-series on zooplankton and fish recruitment dynamics. Zooplankton data came from the Continuous Plankton Recorder (CPR) survey, which is managed by the Sir Alister Hardy Foundation for Ocean Science (SAHFOS) and has operated in the North Atlantic and North Sea since 1931 (McQuatters-Gollop et al., 2015), measuring the abundance of approximately 500 plankton taxa (Richardson et al., 2006). The collection and analysis of CPR samples have followed a consistent methodological approach since 1958; full details have been published extensively elsewhere (Batten et al., 2003; Warner & Hays, 1994) but are summarized here. The CPR collects samples using a high-speed plankton recorder that is towed behind "ships of opportunity" through the surface layer of the ocean (~10 m depth). Water passes through the recorder, and plankton are filtered by a slow moving silk layer (mesh size 270 μm). A second layer of silk covers the first and both are reeled into a tank containing 4% formaldehyde, and so preserved for later analysis.

Here, primary production is examined in relation to smaller and larger copepods which, in addition to playing a key trophic role, are among the most ubiquitous of zooplankton taxa. In the North Sea, the CPR collects 104 copepod taxa, 42 of which are small (<2 mm in length) and 62 of which are large (>2 mm in length). Small copepods are identified and counted during the "traverse" stage of analysis where 1/50 of the CPR sample silk is analysed. Large copepods are not subsampled; instead each individual is identified and counted (Richardson et al., 2006). Here, we present copepod abundance as individuals/m^2, for the upper 20 m of the water column.

In addition, we examined primary production in relation to a standardized index of fish recruitment averaged over seven stocks of high commercial significance. These were as follows: cod *Gadus morhua*, haddock *Melanogrammus aeglefinus*, whiting *Merlangius merlangus*, Norway pout *Trisopterus esmarkii*, herring *Clupea harengus*, sprat *Sprattus sprattus*, and sandeel *Ammodytes marinus*. For each species, recruitment time-series were compiled from the ICES stock assessment reports (ICES, 2016a,b), for the period 1988–2014 (for sandeel, recruitment was combined for Sandeel Areas 1, 2 and 3). The recruitment time-series for each species were standardized (i.e. the overall mean was subtracted and the result was divided by the standard deviation); next, annual scores were averaged across the seven species, each of which was thus given equal weighting in the standardized recruitment index.

We examined relationships between primary production and higher trophic levels (small copepods, large copepods, fish recruitment) using Pearson's cross product–moment correlation (r_p). As there was evidence for temporal autocorrelation within time-series, all p values obtained were adjusted using Pyper and Peterman's (1998) correction procedure according to the level of autocorrelation, as described above for the environmental variables tested against primary production; again, adjusted p values were reported as p_{adj}.

3 | RESULTS

3.1 | North Sea primary production by hydrodynamic region

Gross annual primary production (PP) in the North Sea was estimated at 97.3 ± 6.9 × 10^{12} gC/year (mean ± *SE* over period 1988–2013, n = 26 years; range 48.4–180.1 × 10^{12} gC/year). On a per-area basis, this equated to 234 ± 17 gC m^{-2} year^{-1}. There were differences in average annual primary production between the six hydrodynamic regions examined (Figure 1). Average primary production (per-area) was highest in the freshwater influence, transitional east and intermittently stratified regions; intermediate in the seasonally stratified and transitional west regions; and considerably lower in the permanently mixed region (Table 1). Given that regions differed in size, this implied that on average 36% and 28% of North Sea gross primary production came from the seasonally stratified and transitional east regions, respectively; the region of freshwater influence because of its small size, accounted for 9% of total primary production (Table 1).

3.2 | Primary production: long-term trend

There was a declining trend in PP in the North Sea over the period 1988–2013, in spite of substantial annual fluctuations (Figure 1b); this decline is statistically significant (Table 1; r^2 = 0.261, p = .0076). Whereas in the 1990s, PP tended to be in the region of 100–150 × 10^{12} gC/year, since 2000 it has generally been between 50 and 100 × 10^{12} gC/year. The decline, however, was not evenly distributed throughout the North Sea but principally evident for two hydrodynamic regions: the transitional east (p = .0039) and transitional west (p = .0057). Between 1988 and 1999, these two regions together on average accounted for 40% of PP in the North Sea; since the 2000s this has been substantially lower (mean 24%). In none of the hydrodynamic regions did primary production increase.

3.3 | Environmental drivers and changes in primary production

In the North Sea, sea surface temperatures (SST) have recently warmed although a few recent years (2010–2013) were fairly cold (Figure 2b); in turn, warmer annual SST was associated with lower levels of gross primary production (Fig. S6a). The negative relationship of the North Sea PP with annual SST was significant (Table 2: r_p = −.520, p_{adj} < .05); particularly, the transitional east and the seasonally stratified regions showed a significant negative relationship with SST (Table S1; r_p = −.581, p < .01 for seasonally stratified; r_p = −.493, p < .01 for transitional east). The relationship between PP and SST (Table 2) was not evident for each season: no significant correlations were found with winter or spring SST (p_{adj} > .1), but those with summer SST (r_p = −.434, p_{adj} < .05) and autumn SST (r_p = −.568, p_{adj} < .005) were found to be significant, and negative.

The North Atlantic Oscillation (NAO) winter index fluctuated considerably over the study period with a declining trend and was mainly positive, with strong negative values in 1996 and 2010 (Figure 2a; Table 2). There was no evidence that the NAO was significantly associated with levels of PP (Fig. S6b; Table 2; p_{adj} > .5).

Two proxies for riverine nutrient inputs into the North Sea—Rhine PO_4 and NO_x concentrations as monitored in Lobith, Netherlands—decreased significantly over the study period (Figure 2c,d; Table 2). We did not find a significant correlation between Rhine

TABLE 1 Mean gross primary production and temporal trends over 1988–2013, by hydrodynamic region

	PP (gC m^{-2} $year^{-1}$)		Area PP (10^{12} gC/year)		Annual change in PP (gC m^{-2} $year^{-1}$)			
Region	Mean	*SE*	Mean (%)	*SE*	r^2	*p*	Slope	*SE*
Seasonally stratified	200	15	34.9 (36)	2.75	0.091	.134		
Transitional East	354	54	27.6 (28)	4.24	0.299	.0039**	−19.78	6.19
Transitional West	187	15	5.8 (6)	0.47	0.278	.0057**	−5.38	1.77
Intermittently stratified	268	20	16.3 (17)	1.24	0.001	.884		
Permanently mixed	82	7	4.0 (4)	0.35	0.128	.073		
Freshwater influence	382	28	8.7 (9)	0.65	0.001	.903		
North Sea	**234**	**17**	**97.34 (100)**	**6.92**	**0.261**	**.0076****	**−5.67**	**1.94**
Varela et al. (1995)	200–400							
van Leeuwen et al. (2013)			90.3[a]					
Marshall et al. (2016)	259[a]						−0.3	0.02

Gross primary production in six hydrodynamic regions of the North Sea and in all regions combined, averaged over 1988–2013 (with *SE* over the 25-year period), and test statistics examining for temporal trends. Descriptive statistics are shown for PP per unit area (gC m^{-2} $year^{-1}$) and for the entire area encompassed by each region (in 1,012 gC/year, and as percentage of the total area production of the North Sea). Where long-term trends are significant (**$p < .01$), we also show the annual change in PP (in gC m^{-2} $year^{-1}$). Earlier, published estimates of annual production for the North Sea are also given for comparison.

[a] Phytoplankton net annual primary production.

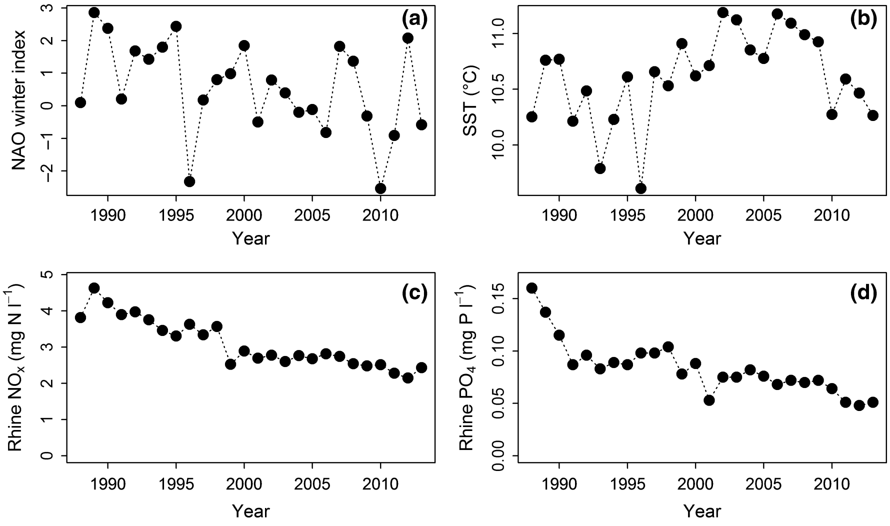

FIGURE 2 Trends of environmental variables: (a) NAO winter index, (b) annual average sea surface temperature (SST), (c) Rhine dissolved inorganic phosphate, PO_4 and (d) Rhine total oxidized nitrogen, NO_x (monitored at Lobith, Netherlands)

PO_4 levels and PP in the wider North Sea (Fig. S6c; Table 2: $r_p = .325$, $p_{adj} > .1$) and for various regions, except transitional west (Table S1; $r_p = .466$, $p < .05$). Contrarily, the Rhine NO_x levels had a significant, positive correlation with the wider North Sea primary production (Fig. S6d; Table 2: $r_p = .523$, $p_{adj} < .05$), as well as with transitional east and west regions (Table S1; $r_p = .502$, $p < .01$ and $r_p = .518$, $p < .01$, respectively).

3.4 | Primary production: relationships with higher trophic levels

Over the study period, a decline in the average annual abundance of small copepods in the North Sea was observed (Figure 3), which was significant (Table 2: $r^2 = 0.673$, $p < .0001$). Small copepod abundance was correlated with PP in the wider North Sea (Fig. S6e, Table 2); this correlation was significant (Table 2, $p_{adj} < .05$), and it appears it was driven by the transitional east region (Table S3). The abundance of large copepods fluctuated, but did not show a significant trend (Figure 3, Table 2: $p > .1$); neither was large copepod abundance significantly correlated with primary production in the winder North Sea or specific hydrodynamic regions (Table 2: $p_{adj} > .1$; Table S2: $p > .1$).

There was, moreover, a correlation of PP with the standardized index of fish stock recruitment in the North Sea. This index, in spite of substantial interannual variability, showed a significant decline over the study period (Figure 3, Table 2: $p < .005$). The correlation with primary production was positive and significant (Fig. S6g, Table 2: $p_{adj} < .05$).

TABLE 2 Temporal trends in North Sea environmental variables and higher trophic levels; and correlations of these variables with gross annual primary production

	Trend over 1988–2013				Correlation with PP	
	r^2	p	Slope	SE	r_p	p_{adj}
Environmental variables						
SST	0.105	.106			−.520	.012*
SST_{win}	0.045	.297			−.136	.509
SST_{spr}	0.042	.312			−.223	.278
SST_{sum}	0.170	.036*	0.038	0.017	−.434	.032*
SST_{aut}	0.161	.042*	0.028	0.013	−.568	.0043***
NAO_{win}	0.160	.043*	−0.073	0.034	.113	.585
PO_4	0.682	<.0001***	−0.0028	0.0004	.325	.122
NO_x	0.841	<.0001***	−0.0800	0.0071	.523	.020*
Higher trophic levels						
Small copepods (m^{-2})	0.661	<.0001***	−102.0	15.0	.533	.0148*
Large copepods (m^{-2})	0.066	.204			−.328	.102
Fish recruitment	0.329	.0022***	−0.0454	0.013	.445	.0317*

Environmental variables include: North Sea annual mean sea surface temperature (SST), SST averaged over winter, spring, summer and autumn (SST_{win}, SST_{spr}, SST_{sum}, SST_{aut}), NAO winter index (NAO_{win}), and PO_4 and NO_x (monitored at Lobith, Netherlands). Higher trophic levels include: small and large copepods, and a standardized index of fish stock recruitment.

Statistically significant correlations are indicated: *$p < .05$, **$p < .01$, ***$p < .005$. p Values in correlations adjusted (p_{adj}) for autocorrelation.

4 | DISCUSSION

To our knowledge, this was the first large-scale study on long-term trends in primary production across the North Sea, based on quantitative in situ observations. Since the late 1980s, primary production has not only fluctuated, but also shown a statistically significant decline (Table 1), particularly in two hydrodynamic regions. Correlations with temperature and riverine nutrient inputs suggest sea surface warming and anthropogenic nutrient inputs as likely drivers of the decline. There is, moreover, evidence of bottom-up effects of decreasing primary production on higher trophic levels including (small) copepods and average fish stock recruitment.

4.1 | Comparison with other studies

The primary production estimates averaged by hydrodynamic region were in line with in situ measurements by Joint and Pomeroy (1993), done in 1988–1989 in the southern North Sea using the ^{14}C method: high production in the south-east (freshwater influence and transitional east regions) and low production in the south-west (permanently mixed region; Fig. S5). Estimates for the region of freshwater influence (Fig. S5; Table 1) also agreed with in situ measurements in the Marsdiep (Netherlands), where phytoplankton production in the 1980s and early 1990s was high (300–450 gC m^{-2} $year^{-1}$: de Jonge, Bakker, & van Stralen, 1996; Cadée & Hegeman, 2002). Our primary production estimates for the whole North Sea (per-area: 234 ± 85 gC m^{-2} $year^{-1}$; total: 97 ± 35 × 10^{12} gC/year: Table 1) corresponded with estimates from the ERSEM model (gross production of 200–400 gC m^{-2} $year^{-1}$: Varela, Cruzardo, & Gabaldon, 1995) and from the coupled GETM-ERSEM-BFM model (total net production of 90.3 × 10^{12} gC/year: van Leeuwen, van der Molen, Ruardij, Fernand, & Jickells, 2013; per-area, 259 gC m^{-2} $year^{-1}$: Marshall et al., 2016). A decline in PP was, likewise, reported by Marshall et al. (2016) based on the GETM-ERSEM-BFM model, but was of considerably smaller magnitude (−0.3 ± 0.02 gC m^{-2} $year^{-1}$; here −5.5 ± 1.9 gC m^{-2} $year^{-1}$, see Table 1), which could be partly due to differences in the time-periods analysed (1980–2008; here 1988–2013).

For the coastal area off East Anglia (permanently mixed region), our results disagreed with modelled production estimates by Daewel and Schrum (2013), who suggested high levels of primary production. Contrarily, based on in situ measurements, the permanently mixed region is found to be least productive of the six hydrodynamic regions (Table 1), probably a consequence of light limitation. This part of the southern North Sea is turbid due to high concentrations of suspended solids, originating from the Thames estuary and due to coastal erosion (Fettweis, Monbaliu, Baeye, Nechad, & van den Eynde, 2012; Gohin, 2011); we suggest that low light availability limits primary production here (Capuzzo et al., 2013).

There was disagreement, in part, between the decline in primary production reported here over 1988–2013, and recent studies describing increasing trends in the Phytoplankton Colour Index (PCI) of the Continuous Plankton Recorder (CPR), from 1948 to 2007 in the North Sea (Raitsos et al., 2014) and from 1948 to 2010 on the Western European shelf (McQuatters-Gollop et al., 2011). Discrepancies might be due to the PCI being a proxy for phytoplankton biomass, rather than a direct measure of production. They may also be due to the much longer time-series of both CPR-based studies (>60 years; and ending slightly earlier). Notably, the earlier increase

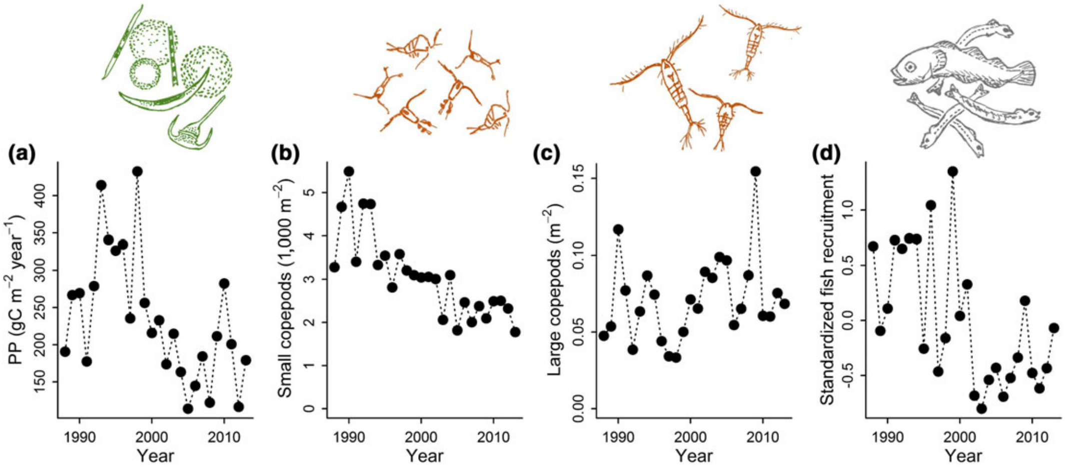

FIGURE 3 Interannual variation in annual primary production, PP (gC m^{-2} year^{-1}), mean abundance of small copepods (1,000 × m^{-3}) and large copepods (m^{-3}), and a standardized index of fish stock recruitment (including sandeel, sprat, herring, Norway pout, cod, haddock and whiting), in the North Sea

in phytoplankton biomass in the North Sea appears to have been stepwise, around 1988 (Raitsos et al., 2014), and has been characterized as a "regime shift" (Dippner, Möller, & Hänninen, 2012; Reid, Borges, & Svendsen, 2001). If both phytoplankton biomass and primary production indeed showed a stepwise increase in the late 1980s, then the current study suggests that in the following, more recent period, levels again declined substantially.

4.2 | Considerations on the method adopted for estimating primary production

The semi-empirical algorithm based on chlorophyll and light climate (Equation 1) explained 86% of variability in primary production (Methods S1), when compared with in situ estimates collected in 2007. This percentage is comparable with values obtained by Cole and Cloern (1987; over 80% of variability explained). Chlorophyll concentration on its own has been shown to explain approximately 70% of the variability in production (see e.g., example Gowen & Bloomfield, 1996; Joint & Pomeroy, 1993); however, in 2007, chlorophyll accounted for only 31% of the variability in production (Fig. S4b). Instead, surface irradiance (E_0) explained 46% of variation in production (Fig. S4c), hence the inclusion of the "light" term ($4.61/K_d{*}E_0$) in Equation 1, for estimating production.

Although the semi-empirical algorithm seemed producing reliable estimates of production, Equation 1 presents some limitations. Being estimated from data collected during a single year (2007) and at two locations (central and southern North Sea), it may not fully capture the interannual and spatial variability in the photosynthetic capacity of the phytoplankton community of the wider North Sea. In fact, phytoplankton maximum photosynthetic rate (P_{max}) and photosynthetic efficiency (α) are affected by factors such as nutrient regime, light history, time of the day, temperature, phytoplankton species composition, phytoplankton cell size, and volume (see review by Côté & Platt, 1983). The temporal and spatial variability of these factors, combined with other potential source of errors during sampling and analysis of in situ data, is a source of uncertainty; this is not accounted for in this study and could be the reason for the intercept of Equation 1 being significantly different from zero (Methods S1). Quantifying the uncertainty around the estimates of production is an important challenge for future works as it should also include the variations in the between and within year trends of chlorophyll and K_d, and the variation of the imputed data from the Gaussian kernel smoother.

This study may also not account fully for variations in the cellular chlorophyll content of phytoplankton organisms: in the equation adopted for calculating PP (Equation 1), chlorophyll concentration is assumed proportional to phytoplankton biomass. The carbon-to-chlorophyll ratio (θ), however, may be affected by nutrient and light stress (Behrenfeld et al., 2016). Indeed, a mismatch between trends in chlorophyll and phytoplankton biomass has been observed in coastal and offshore waters off the Netherlands (decreasing chlorophyll but increasing biomass); this was attributed to changes in the phytoplankton community, and in the nutrient and light regimes over 20 years (Alvarez-Fernandez & Riegman, 2014). It is not known whether this trend in θ is limited to coastal waters of the southern North Sea or representative of the wider North Sea. However, as our estimates of PP are based on chlorophyll, an increase in θ (reduction in chlorophyll but increase in biomass) could result in our values of PP being underestimated.

Another reason that our analysis could underestimate total primary production is that it included the upper water layers but did not account for deep chlorophyll maxima, which are commonly observed in stratified areas of the North Sea during summer. At some locations during peak season, deep chlorophyll maxima may account for >50% of water column productivity (Fernand et al., 2013; Weston et al., 2005). Across the North Sea and across the year, however, simulations by the GETM-ERSEM-BFM model indicated that primary production below 15 m accounts for only 10% of annual production (van Leeuwen et al., 2013). Hence, our figures may only mildly underestimate total PP, and mainly in the seasonally stratified region.

One final consideration on the method adopted for calculating production is the definition of the hydrodynamic regions and their spatial variability between years. While the permanently mixed region is very well defined spatially, with sharp boundaries, the seasonally stratified, intermittently stratified and fresh water regions show more spatial variation. These regions extend into the transitional areas in different years depending on circumstances (see van Leeuwen et al., 2015). Consequently, depending on the governing conditions, parts of the transitional areas may be classified as seasonally stratified 1 year, but as intermittently stratified or even as freshwater influence area another year. At the same time, the defined areas of seasonally stratified, intermittently stratified and freshwater influence areas are themselves remarkably stable, with a near 100% occurrence (i.e. these areas always classified as this particular regime over all 51 simulated years; see figures 6 and 7 in van Leeuwen et al., 2015). Thus, some of the changes found in the two transitional areas may be linked to variability in the hydrodynamic conditions.

4.3 | Key drivers affecting primary production

The recent decline in primary production was statistically significantly related to a decrease in riverine dissolved nutrient concentrations (Table 2); this was particularly evident for the transitional east and west regions (Table S1). As phytoplankton organisms take up nutrients from water to create macromolecules (organic matter), lower nutrient levels in the water will restrict their uptake into the cell, in turn limiting cell growth and production (Moore et al., 2013). The degree of limitation depends on the organism's size and elemental requirements so that phytoplankton populations can differ in their responses to low nutrient availability; in the long-term, changes in nutrient levels can alter the composition of a phytoplankton community (Moore et al., 2013).

Since the late 1980s, policy changes with regard to agricultural fertilizers and detergents, aimed at limiting undesirable effects such as eutrophication, excessive algal growth and oxygen depletion, have led to reductions in phosphate and nitrogen inputs via the Rhine and other rivers into the North Sea (Lenhart et al., 2010; Tett et al., 2007). The reduction in phosphate inputs, however, has been far more effective than that of nitrogen (Burson et al., 2016; Lenhart et al., 2010; Passy et al., 2013). As a result, phytoplankton in the North Sea has not only experienced generally reduced nutrient availability, but also a change in the stoichiometric ratio of nutrients. Coastal waters of the southern North Sea, previously co-limited in both N and P, are now severely P limited, while offshore systems are mainly N limited (Burson et al., 2016). It is of note that the transitional east hydrodynamic region, where production declined most substantially (Figure 1 and Fig. S5), coincides with an area that mainly receives inputs from the river Rhine (Painting et al., 2013; their figure 4), as highlighted by the highly significant positive correlation between PP and NO_x (Table S1). Further work may shed light on whether reduced nutrient levels per se, or a change in the N:P ratio (and associated changes in phytoplankton communities) may have contributed to reduced primary production. Surprisingly, we did not find a significant correlation between NO_x and PP at the fresh water influence region (Table S1); this might be due to limited light climate data for this region which could have compromised primary production estimates (see Section 2).

Temperature and light climate can also influence primary production, alongside nutrient levels. Temperature changes can affect phytoplankton growth (and PP) through direct physiological changes (Eppley, 1972), and indirectly by influencing the phytoplankton environment, for example, through changes in stratification regimes (Behrenfeld et al., 2006). In laboratory experiments where light and nutrients are not limiting, phytoplankton species show maximum growth rates at an optimal temperature (which differs between species); above or below this, growth rates are less (Eppley, 1972). However, when considering the response of a whole phytoplankton community, interactions between species generally result in an increase in growth rate with temperature (Edwards, Thomas, Klausmeier, & Litchman, 2016; Eppley, 1972). Our results (decreasing production with increasing temperature: Fig. S6a; Table 2) are in contradiction with these observations, suggesting that other mechanisms are to be accounted for. Indeed, outside "ideal" laboratory conditions, the responses of phytoplankton to temperature changes were found to depend on the nutrient and light regimes (Edwards et al., 2016). For example, when light availability was not limiting (~100–200 μmol photons m^{-2} s^{-1}), PP of the phytoplankton community increased with temperature (as observed in the laboratory; Eppley, 1972); however, when irradiance was low (<20 μmol photons m^{-2} s^{-1}), production was temperature-insensitive and warming would not lead to an increase in growth (Edwards et al., 2016).

There is evidence that the light climate of the North Sea has changed in the last decades although with regional differences in water clarity trends. At Helgoland Roads in the German Bight (Wiltshire et al., 2008) and at sampling stations in Dutch waters (Alvarez-Fernandez & Riegman, 2014), light availability has increased. Contrarily in the wider North Sea, Dupont and Aksnes (2013) observed a reduction in light climate, also supported by in situ observations of suspended particulate materials by Capuzzo et al. (2015). We suggest that phytoplankton growth in the permanently mixed region, which is turbid, has been least affected by temperature increase, compared to the other, clearer, regions (Fig. S3; Capuzzo et al., 2013); in fact, annual primary production has been fairly constant here (Fig. S5). In the other coastal regions (freshwater influence and transitional), increased light availability in conjunction with increased temperature would have been expected to lead to an increase in phytoplankton community growth; however, the primary production estimates show the opposite trend (Fig. S5). This may well be due to the nutrient reductions in these regions (cf. Lenhart et al., 2010), which would have negatively impacted on production rates (Table 2).

Indirectly, changes in temperature can affect production through changes in water column stratification: warming of the surface water causes a greater density difference between the surface and bottom layers, therefore increasing stratification (Behrenfeld et al., 2006). With bottom waters higher in nutrients, the increased stratification reduces vertical nutrient exchange to the surface nutrient-limited layer, therefore reducing phytoplankton growth and production (Behrenfeld et al., 2006). This would not only apply to the seasonally and intermittently stratified regions (where no trends in primary production were observed; Table 1), but also to both transitional (east and west) regions (where primary production declined); these regions show high interannual variability in the length of stratification/mixing periods (hence termed "transitional" by van Leeuwen et al., 2015) and the spatial extent of stratification within each may have increased with warming (Fig. S5). This is supported by the statistically significant negative correlation between PP and SST for the seasonally stratified and transitional east regions (Table S1).

Changes in stratification may also limit vertical phytoplankton movements through the water column, which can affect the onset of the spring bloom. For the stratified central North Sea, van Haren, Mills, and Wetsteyn (1998) showed that a minimum level of turbulence is required for the development of the phytoplankton spring bloom, as it maintains fast sinking phytoplankton organisms in the illuminated upper layer of the water column. During autumn, a stronger thermocline could also delay the breaking-up of the stratification, therefore occurring when light levels are lower and resulting in a reduced autumn bloom (van der Molen et al., 2013). This would also be supported by the particularly strong relationship of PP with summer/autumn temperature (Table 2).

We conclude that the negative relationship of temperature with primary production is better explained by indirect effects on the phytoplankton's environmental conditions (i.e. nutrient availability, light climate, movement through the water column) than by direct physiological responses to warming. Furthermore, production takes place at the phytoplankton community-level, and integrates the interactions of many different species that have different physiological responses and adaptability to climate change, and that have changed in relative abundances (Alvarez-Fernandez & Riegman, 2014; McQuatters-Gollop et al., 2011).

4.4 | Primary production: bottom-up effects on higher trophic levels

Decreasing primary production was mirrored by decreasing abundance trends of small copepods (albeit not of large copepods), particularly at the transitional east region (Table S2); this implies bottom-up control of zooplankton by primary production (Chassot et al., 2007; Kenny, Skjoldal, Engelhard, Kershaw, & Reid, 2009). Likewise, primary production of the wider North Sea was correlated with trends in average recruitment of seven commercially important fish stocks; again this suggests bottom-up control of fish stock productivity—in line with work on interactions between bottom-up and top-down control of the North Sea food web (Chassot et al., 2007; Lynam et al., 2017; Pitois, Lynam, Jansen, Halliday, & Edwards, 2012).

The lack of a relationship with large copepods may be surprising, but these only form a smaller fraction of total copepod biomass in the southern and central North Sea, where the four predominant taxa—*Temora*, *Acartia*, *Pseudocalanus* and *Paracalanus*—are all small (Pitois & Fox, 2006). It is in the northern North Sea where the larger copepods, for example *Calanus finmarchicus*, are more abundant (especially in the seasonally stratified region) although the smaller *Temora*, *Acartia*, *Pseudo-* and *Paracalanus* represent substantial fractions of copepod biomass also here (Pitois & Fox, 2006). In general, small copepods may be more representative of the copepod fauna in large parts of the North Sea, especially given a shift in copepod fauna from larger, boreal species to smaller, temperate species observed from the 1960s through late 1980s (Beaugrand & Reid, 2003; Pitois & Fox, 2006).

An integrated assessment of the North Sea ecosystem, which included climatic drivers as well as several trophic levels from plankton to fish, and fisheries (Kenny et al., 2009), concluded that the North Sea has moved from a top-down driven system in the 1980s–1990s, to a more bottom-up-driven system in the early 2000s. More recently, an analysis of change in the North Sea ecosystem by means of an interaction model (Lynam et al., 2017) concluded on-going, simultaneous bottom-up control (from physics to plankton, to planktivorous fish) and top-down exploitation pressure (mainly on demersal fish). Results from our study also provide strong evidence for bottom-up control—from climate and nutrients to primary production, and from primary production to zooplankton and fish recruitment.

4.5 | Implications

Projections of climate change and ecosystem responses for the end of the 21st century (2080–2100 vs. 1980–2000) indicate that net primary production of the Greater North Sea (and consequently zooplankton biomass) is expected to decline, due to increased stratification (Chust et al., 2014; van der Molen et al., 2013) although opposite trends might be expected at particular locations (van Leeuwen, le Quesne, & Parker, 2016). Implications of a further decline in PP would not be limited to the reduced carbon transfer to higher trophic levels, but would also affect the CO_2 flux from the atmosphere to the water. It has been observed that the southern North Sea acts as a source of CO_2 to the atmosphere during summer and autumn, due to respiration exceeding production (Thomas et al., 2005). A further reduction in PP could increase the flux of CO_2 from the sea surface to the air.

Confusingly, while primary production in the North Sea has declined since the late 1980s (and positive relationships with fish recruitment were found), many of the fish stocks are currently in a much better state than they were around the turn of the millennium (Cardinale et al., 2012; ICES, 2016b). Indeed, concern about overexploitation of many fish stocks during the 1990s led to the adoption of a range of measures to reduce fishing pressure, notably quota reductions and the EU fishing fleet reduction scheme adopted since 2000 (Engelhard et al., 2015). Fishing mortality rates on important fish stocks, such as cod, plaice, sole and whiting have decreased greatly since then, and many stocks have shown recoveries (ICES, 2016a,b).

This study, by pointing at relationships between PP and fish recruitment, and by also revealing a marked decline in PP, would suggest that, if fishing pressure had not declined while PP decreased, many fish stocks would currently not have been in the healthy state they are now. This underlines the importance of the cautious fisheries management of the past decade, and also for future years if the decline in primary production were set to continue (Behrenfeld et al., 2016; Chust et al., 2014). This is particularly relevant because of the global importance of shelf seas, often heavily fished, for world food security, notably protein production (Jennings et al., 2016), and the possibility that a warming climate may lead to a decrease in phytoplankton production also elsewhere in the world.

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