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Environmentally induced functional shifts in phytoplankton and their potential consequences for ecosystem functioning

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Abstract

Phytoplanktonic organisms are particularly sensitive to environmental change, and, as they represent a direct link between abiotic and biotic compartments within the marine food web, changes in the functional structure of phytoplankton communities can result in profound impacts on ecosystem functioning. Using a trait-based approach, we examined changes in the functional structure of the southern North Sea phytoplankton over the past five decades in relation to environmental conditions. We identified a shift in functional structure between 1998 and 2004 which coincides with a pronounced increase in diatom and decrease in dinoflagellate abundances, and we provide a mechanistic explanation for this taxonomic change. Early in the 2000s, the phytoplankton functional structure shifted from slow growing, autumn blooming, mixotrophic organisms, towards earlier blooming and faster-growing microalgae. Warming and decreasing dissolved phosphorus concentrations were linked to this rapid reorganization of the functional structure. We identified a potential link between this shift and dissolved nutrient concentrations, and we hypothesise that organisms blooming early and displaying high growth rates efficiently take up nutrients which then are no longer available to late bloomers. Moreover, we identified that the above-mentioned functional change may have bottom-up consequences, through a food quality-driven negative influence on copepod abundances. Overall, our study highlights that, by altering the phytoplankton functional composition, global and regional changes may have profound long-term impacts on coastal ecosystems, impacting both food-web structure and biogeochemical cycles.

KEYWORDS
climate change, de-eutrophication, diatoms, dinoflagellates, functional traits, Helgoland Roads time series, North Sea

1 | INTRODUCTION

Phytoplanktonic organisms form the base of aquatic food webs, representing the essential link between the abiotic environment and higher trophic levels (Sommer et al., 2002). Because phytoplankton species differ in their metabolic requirements and in their modes of nutrient acquisition (Falkowski, 2004), environmental conditions can directly influence community structure of phytoplankton, which in turn, affects the biogeochemical cycles of many elements (e.g. carbon, nitrogen, phosphorus). Because of this sensitivity to environmental change, the impact that global and regional change has on phytoplankton communities may in turn affect the entire food web and the associated ecosystem services, from nutrient turnover to fisheries (Beaugrand et al., 2003; Capuzzo et al., 2018; Reid et al., 2001).

The simultaneous impacts of global and regional change are particularly visible in coastal regions such as the North Sea, which have undergone particularly rapid warming, and are, thus, considered global warming hotspots (Simpson et al., 2011; Wiltshire & Manly, 2004). Over the past decades, warming of the coastal North Sea has been accompanied by changes in dissolved nutrient concentrations characterized first by a eutrophication phase in the 1960s and 1970s. In the period 1985–2000, the implementation of policy measures targeting terrestrial nutrient runoffs (Grizzetti et al., 2012) decreased total phosphorus inputs into the North Sea by 50–70% and nitrogen inputs by 20–30% (Burson et al., 2016; Lenhart et al., 2010; Passy et al., 2013; Skogen et al., 2004). Although most environmental changes occur gradually, natural variability and anthropogenically induced changes can act concurrently and cause sudden non-linear changes in marine community composition, which are indicative of ecological regime shifts.

Complex systems may have critical thresholds, or tipping points, at which the system shifts abruptly from one state to another (Scheffer et al., 2009). In its ecological definition, a regime shift is a rapid change in community structure, including replacement or even loss of key species (Conversi et al., 2015). For instance, Reid et al. (1998, 2001) described a sudden increase in phytoplankton biomass in the North Sea for the late 1980s, which they linked to concurrent increases in temperature and inflows of Atlantic water. At roughly the same time, the abundance of calanoid copepods also significantly increased (Beaugrand, 2003; Beaugrand & Ibañez, 2002). Hence, this regime shift was characterized by an increase in planktonic abundances rather than by a change in taxonomic structure. A second regime shift was identified for the late 1990s-early 2000s (Beaugrand et al., 2014). During this period, diatom densities rapidly increased (Alvarez-Fernandez et al., 2012; Bedford et al., 2020; Wiltshire et al., 2008), seasonal diatom blooms started to occur earlier (Wiltshire et al., 2008), whereas the abundances of dinoflagellates (Hinder et al., 2012; Meunier et al., 2018) and most copepod species declined (Alvarez-Fernandez et al., 2012; Boersma et al., 2015). This shift in planktonic structure of the North Sea was linked to the continuing increase of temperature and stronger summer wind speed (Hinder et al., 2012), as well as to a decrease in dissolved nutrient concentrations (Alvarez-Fernandez et al., 2012; Boersma et al., 2015; Meunier et al., 2018). Although these sudden taxonomic changes have been well described, their consequences for the functioning of the system have been rather implicit, and a functional understanding of North Sea regime shifts is missing.

Most studies on phytoplankton community changes have thus far used a taxonomic approach (e.g. Alvarez-Fernandez et al., 2012; Beaugrand & Reid, 2003; Hinder et al., 2012; Scharfe & Wiltshire, 2019; Wiltshire et al., 2008; Wiltshire & Manly, 2004). Although these studies have increased our understanding of the North Sea ecosystem, taxonomic approaches do not provide a mechanistic understanding of community changes and do not assess how these changes can be linked to ecological functions (Litchman & Klausmeier, 2008; McGill et al., 2006). Here, by focusing on traits (i.e. biological characteristics), functional approaches, also called trait-based approaches, we hope to provide an ecological understanding of the complex changes occurring in species assemblages. In these approaches, traits are defined as any morphological, physiological or phenological characteristic that reflects fitness indirectly via its effects on growth, reproduction, and survival (Litchman et al., 2013; Violle et al., 2007). Thus, functional approaches allow the identification of the traits, which drive community composition changes, or, alternatively, those that are most affected by alterations in environmental conditions.

Here, using the trait-based approach we explored the potential influence of changing environmental conditions on the functional structure (i.e. trait composition) of the southern North Sea phytoplankton. We applied multivariate analyses to the unique long-term Helgoland Roads data set for the period 1975 to 2018. We aimed to (1) characterise the functional structure of a representative and consistent part of the phytoplankton community in the North Sea; (2) study how this functional structure changed over time; (3) identify the potential environmental drivers of functional structure changes and (4) assess the potential repercussions of these functional changes for the ecosystem.

2 | MATERIALS AND METHODS

2.1 | Data origins

Our analyses were based on the long-term data set of Helgoland Roads (Wiltshire et al., 2008; PANGAEA, 2004; http://www.pangaea.de). Since 1962, phytoplankton has been sampled and counted on a work-daily basis. Additionally, temperature, salinity, nutrient concentrations (SiO_4^{4-}, PO_4^{3-}, NH_4^+, NO_3^-, NO_2^-) and Secchi-depth have been monitored (see Hickel et al., 1993 for method description). The identification of phytoplankton organisms was carried out to the lowest taxonomic level possible, which was often the species level (see Wiltshire and Dürselen (2004) for a complete list of counted categories), and counted using the Utermöhl method (Lund et al., 1958). In 1975, the zooplanktonic compartment was added to the sampling, three times a week (Greve et al., 2004). For more

details of the sampling and analytical methods used at Helgoland Roads, see Greve et al. (2004) and Boersma et al. (2015) for zooplankton, Wiltshire and Dürselen (2004) for phytoplankton, and Raabe and Wiltshire (2009) for nutrients.

The analysis of the functional response of phytoplankton was carried out for the time period 1975–2018, to include the potential impact of grazers. Phytoplankton species for this analysis were chosen following Scharfe and Wiltshire (2019), representing the subset of the phytoplankton community which has been consistently identified and counted during the whole observational period, without any taxonomical issues. Furthermore, this subset represents around half of the total yearly phytoplankton abundance at Helgoland roads, and includes the most dominant marine phytoplankton groups, representing a seasonal cross section of all observed species, with a wide variety of life history strategies. In Sarker et al. (2018), the authors estimated the representativeness of this subset and concluded that as a representation of long-term changes in phytoplankton diversity at Helgoland Roads, the use of this subset is relevant. Most importantly, the data necessary to fill the trait table for these species were available in the literature. This, in fact is one of the main bottlenecks in trait-based approaches, as described by Martini et al. (2021), who state 'The main caveat [..] is that only a limited number of species and/or traits have been reported so far, thus not yet allowing for a generalization of findings across taxa, the definition of fitness landscapes, and/or the characterization of ecological niches or responses to environmental change'. Our representative selection allowed us to create a complete trait table after an extensive review of the literature to identify trait characteristics or modalities for all species (Table 1). This table comprised the four trait categories as defined by Litchman et al. (2013), namely morphological, life history, behavioural and physiological traits. In total, the trait table gathered 15 traits of different types (i.e. numerical, binomial, nominal and ordinal). The trait values assigned to each species are given in the Appendix S1.

2.2 | Data analyses

Analyses were performed under the R environment (R Core Team, 2020). The threshold of significance for all tests was set at 5%.

2.2.1 | Data preparation

We first calculated the average monthly values for the abundance of each species and for environmental parameter values. This was done to smooth the data and obtain a homogeneous time step, necessary for time series analyses. The complete environmental matrix comprised sea surface temperature (SST, °C), Secchi depth (m) and salinity as well as nutrient concentrations ($\mu mol.L^{-1}$) for silicate (SiO_4^{4-}), phosphate (PO_4^{3-}) and dissolved inorganic nitrogen (DIN) as the sum of ammonium (NH_4^+), nitrate (NO_3^-) and nitrite (NO_2^-). As copepods are important grazers of phytoplankton (Frost, 1987), we considered

the sum of copepod abundances ($ind.m^{-3}$) as proxy for grazing pressure. Copepod abundances were then composed by the harpacticoid *Euterpina acutifrons*, the cyclopoid *Oithona spp.*, and five calanoids, that is, *Acartia spp.*, *Calanus spp.*, *Centropages spp.*, *Pseudocalanus-Paracalanus spp.* and *Temora longicornis*. All these variables measured at Helgoland Roads have changed substantially over the last decades (Wiltshire et al., 2010) and have a strong potential to drive phytoplankton functional structure.

Each time series (each monthly species abundance and environmental parameters) was then decomposed into three constituent components, seasonality, trend and random (package *stats*). The trend component represents the seasonally detrended, or de-seasonalized data, that is, the general trend once the seasonal variations (i.e. repeating short-term cycle in the series) are removed (Shumway & Stoffer, 2011). Thus, the trend of each species and environmental parameter over the time period was isolated and used for further analysis. It permitted the removal of the signal of seasonal variations and to focus on general trends over the time period (Metcalfe & Cowpertwait, 2009). Environmental parameter trends are given in Appendix S2.

2.2.2 | Functional space

The first aim was to characterise the phytoplankton functional structure. To do so, we defined the functional space which represents the relative distance and position of species in relation to each other, according to their traits. The functional space can be represented into a multidimensional ordination and represents the functional similarity/dissimilarity among species; that is the extent to which the traits of different species differ (Villéger et al., 2008). The abundance of the different species does not contribute to the shape or size of the functional space.

We created a distance matrix based on the trait's dissimilarity between all pairs of species. We used Gower's distance metric, which is capable of handling mixed data types (i.e. numerical and categorical). Then, a PCoA was computed to transform pairwise species distances into a multi-dimensional space that best represents the overall traits variation among species (Borcard et al., 2018). Only traits driving species position significantly (permutation test, 999 permutations) along the first two PCoA axes were represented. We then analysed temporal dynamics within the functional space by examining the mean position (i.e. centroid) within the functional space, and how this position changes over time. This centroid is the mean position of the species in the functional space, weighted by their abundance (Laliberté & Legendre, 2010). A movement of the centroid along the axes of the PCoA reflects a relative increase in the representativeness of the traits positioned in the direction that the centroids take. Finally, to highlight changes in centroid positions, a Euclidian distance matrix was calculated for annual centroid coordinates within the bi-dimensional space and plotted as a heat map where colour intensity represents dissimilarity among years. Rapid change of colour intensity marks a period of functional structure change.

TABLE 1 List of the traits used in the study. The table gathers four trait categories for 15 traits of different types. The citations given are either articles or book (Kraberg et al., 2010) for which a large amount of information from a wide variety of sources has been used

Type (Litchman et al., 2013)	Trait	Description	Variable's type	Variable's levels/ranges	Literature source
Morphological	Spines	Presence of spines	Binomial	Yes/No	(Kraberg et al., 2010)
	Chain former	Ability to form chains	Binomial	Yes/No	(Klais et al., 2017)
	Cell shape	Cell geometry	Nominal	Triangular prism/elliptic cylinder/ cylinder/conical/ flattened ellipsoid/ rhomboid prism	(Kraberg et al., 2010)
	Cell volume	Mean volume of the cell (μm^3)	Continuous	[199–653000]	(Harrison et al., 2015)
	Cell variation	Coefficient of variation of cell volume	Continuous	[22–80]	(Harrison et al., 2015)
Life history	Resting stage	Ability to survive as spores, resting cells, hypnozygotes or cysts	Binomial	Yes/No	(Kraberg et al., 2010)
	Bloom	Ability to form blooms. 0: not bloom forming; 1: Rarely in moderate biomass; 2: Frequently in moderate biomass; 3: Frequently in high biomass	Ordinal	0/1/2/3	(Kraberg et al., 2010)
	Seasonal preference	For each season. 0: no appearance; 1: occasionally, 2: moderate; 3: Peak occurrence	Ordinal	0/1/2/3	(Harrison et al., 2015)
Behavioural	Motility	Ability to swim three-dimensionally	Binomial	Yes/No	(Klais et al., 2017)
Physiological	Silica	Ability to use silica as cell wall material	Binomial	Yes/No	(Klais et al., 2017)
	Mu max	Maximum growth rate (d^{-1})	Continuous	[0.35–2.47]	(Edwards et al., 2012, 2015)
	Alpha (α)	Slope of the photosynthesis-irradiance curve	Continuous	$[3.23.10^{-3}–0.37]$	(Edwards et al., 2015)
	Optimal irradiance	Irradiance at the maximum photosynthesis rate (µmol photons m^{-2} s^{-1})	Continuous	$[72.63–2.72.10^{10}]$	(Edwards et al., 2015)
	Trophic mode		Binomial	Autotrophy/mixotrophy	(Klais et al., 2017)
	Toxicity	Ability to produce toxins	Binomial	Yes/No	(Kraberg et al., 2010)

2.2.3 | Functional structure changes

The second aim of our study was to identify changes in the functional structure over the sampling period, that is, the relative contribution of each trait to the total structure. To do so, we calculated the community-weighted means (CWMs) as the abundance-weighted average trait values of all species in the community. CWMs allow the evaluation of how trait structure varies, over time in our case, as changes in species composition and abundance lead to changes in the mean trait values of the community (McLean et al., 2018). A centred-scaled principal component analysis (PCA) was then performed on the CWM table, and the contribution of each trait to the creation of the first two axes of the PCA was calculated. We then used PCA1 (axis explaining most variation) as an index of structural change over time. To define the timing of potential phytoplankton functional structure shifts, we graphically analysed the outcome of the PCA, whereby a shift in data distribution from the positive to the negative side of the principal component axis would indicate a significant change in the structure of the data set, here functional community composition. To verify that the traits responsible for changes in functional structure over the time period are also those discriminating species most, thereby indicating a functional change, we correlated PCoA 1 centroids scores and PCA 1 loadings before checking whether the correlation is significant.

2.2.4 | Identification of environmental drivers and potential consequences of functional structure changes

After having identified the functional structure dynamics, we explored the relation between the changes in functional structure and environmental parameters through Granger causality tests (package *vars*; Pfaff, 2008). This analysis provides a stringent criterion for causation (Damos, 2016; Zhang, 2011) and has already demonstrated its relevance to ecology (e.g. Hinder et al., 2012; McLean et al., 2018). In a nutshell, it adds a causal term to the linear prediction model and compares this to a similar linear model without that term. Causality must satisfy two criteria: (i) a causal factor should precede an effect in time and (ii) incorporating historical values of a causal factor leads to significantly improved prediction of the observed effect. Subsequently, a comparison of residual sum of squares is carried out by a F-test. This value is then translated to a *p*-value using the F-distribution. The strength of the causality is expressed in the F-value: the higher the value, the stronger the causality. When a significant causality is identified, the causal factor is said to 'Granger cause' the effect variable since causality can never be proven in the absence of well-controlled experiments (Granger, 1969).

In our study, Granger causality tests were used to identify potential causal links between environmental parameters and functional structural changes (represented by PCA 1), with potential time lags. We also tested reverse causations, that is, whether the changes in community structure could have affected environmental

conditions. From the definition of the Granger causality, a direct correlation without time lag does not qualify. Hence, Granger causality tests showed the time that a variable trend needs to Granger cause the trend of another one. Because phytoplankton organisms have short life spans and high growth rates, and their community composition can change rapidly, we defined an arbitrary minimum lag of two months and a maximum of 24 months based on a trade-off of bias versus power. With too few lags, residual autocorrelation can be found, providing a biased test. With too many, the null hypotheses might be incorrectly rejected due to spurious correlations (Thurman & Fisher, 1988).

To avoid overestimating causalities, as a result of correlations between explanatory variables, we reduced potential redundancy, by selecting only those variables that explained the highest variation following the method proposed by Borcard et al. (2018). This method also permitted the removal of variables unrelated to functional structure changes. A redundancy analysis (RDA) was performed between the CWM and the complete de-seasonalized environmental matrix followed by subsequently performing a forward selection based on the null RDA and a backward selection based on the full RDA, simultaneously. The simplified parsimonious model was then tested by a permutation test (999 permutations), along with the remaining variables. Finally, we used the monthly trend of PCA 1 loading and environmental variables selected by the parsimonious model for Granger causality tests.

Furthermore, we performed a variation partitioning analysis between significant potential drivers and traits affiliated to PCA 1, using the time lags identified above. This analysis quantifies the part of variation in the trait values explained by each variable when controlling for the effect of other variables, as well as the amount of explained variation shared by the different variables (Anderson & Cribble, 1998). Ecologically, it permits to identify the main drivers of functional structure changes (Borcard et al., 2018). The significance of the variation explained by each variable was assessed by a Monte-Carlo permutation test (999 permutations). For environmental parameters potentially affected by functional structure changes, we performed a linear regression between PCA 1 and environmental parameters, considering the significant time lag highlighted.

3 | RESULTS

3.1 | Characterisation of phytoplanktonic functional space

Using the traits of each species, we defined the functional space of the phytoplankton community (Figure 1a,b). The first and second axes of the PCoA explained 39% and 16% of the trait variation between species, respectively (Figure 1c; permutation test, 999 permutations). Cell volume, cell volume variation, ability to form blooms and optimal irradiance did not significantly contribute to species discrimination (permutation test, $p > .05$). The positive part of axis
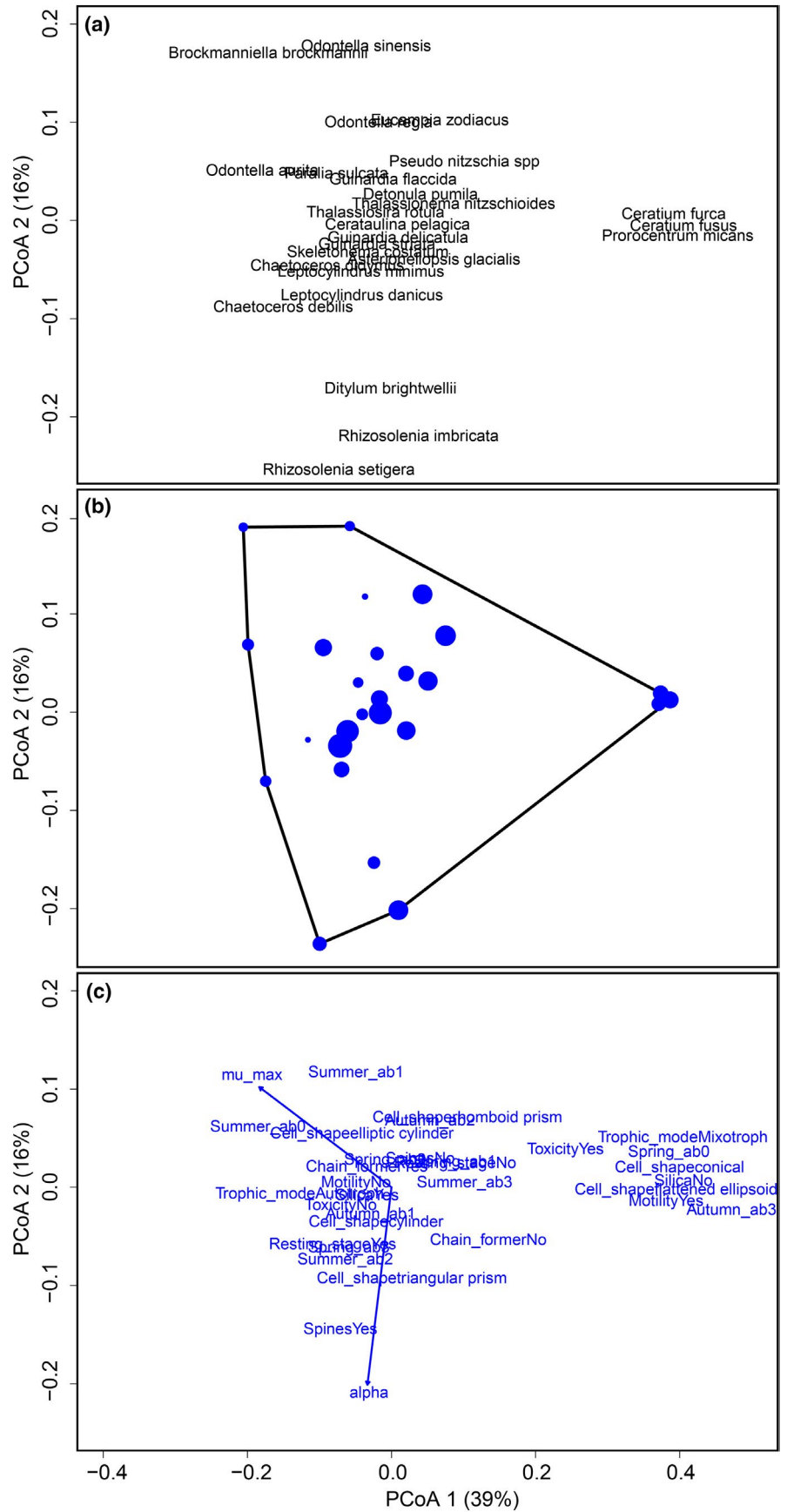
1 was associated with low maximum growth rate (mu_max), mixotrophic mode, no silica and peak of occurrence during autumn. The second axis mainly discriminated species depending on alpha (ability to grow under low light).

The temporal dynamics within the functional space was studied over time (Figure 2a). The centroid moved from the top, via the right, to bottom left of the graph, with displacements especially rapid (i.e. long distance between centroids) from 1989 to 2004, and the functional space is especially distinct between two periods, before and after 2004 (Figure 2b). In view of the range of variation of the two axes, the temporal change within the functional space was mainly along the first axis (i.e. ranged from 0.04 to −0.01), indicating that species which increased in relative abundance were located in the

left half of the functional space, corresponding to silica, autotrophy or high growth rate traits.

3.2 | Changes in phytoplankton functional structure

Temporal dynamics of the phytoplankton functional structure were examined by generating a CWM matrix using the functional traits and the detrended monthly species abundances, ordinated in a PCA (Figure 3a). The first two axes of the PCA gathered 60% of the trait composition changes over time, with PCA 1 explaining 46% of the temporal dynamic and PCA 2 only 14%. The percentage contribution
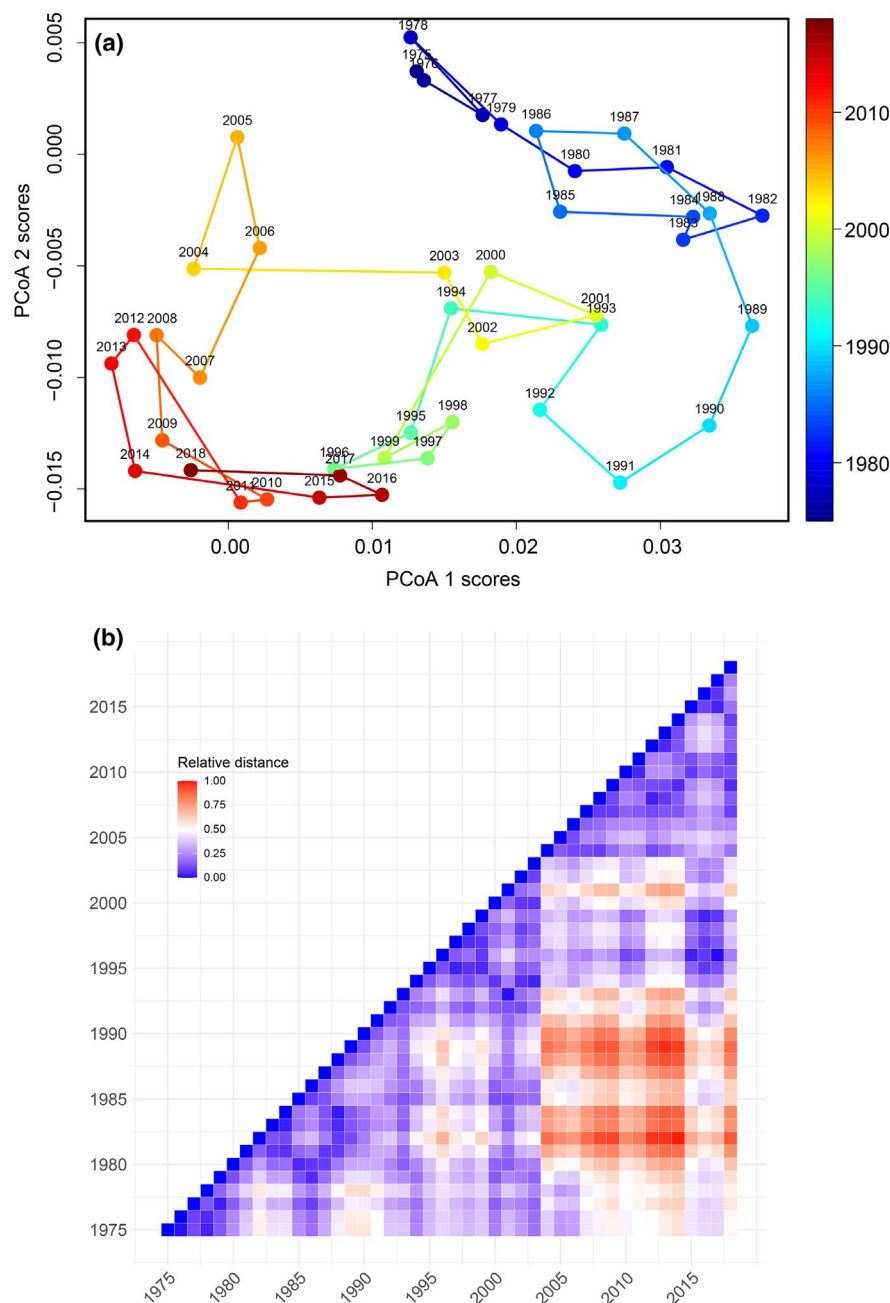

FIGURE 2 Temporal dynamics of phytoplankton functional space centroid. (a) The graph is a zoom in the range of variation within the functional space (Figure 1). Dots represent the centroid position of each year in a colour gradient following the time evolution. The line is shown to help tracking changes over time. (b) Heat map of the Euclidian distance matrix between PCoA centroid coordinates of each year. The relative distance extends from 0 to 1, the latter being the maximal distance observed between 2 years
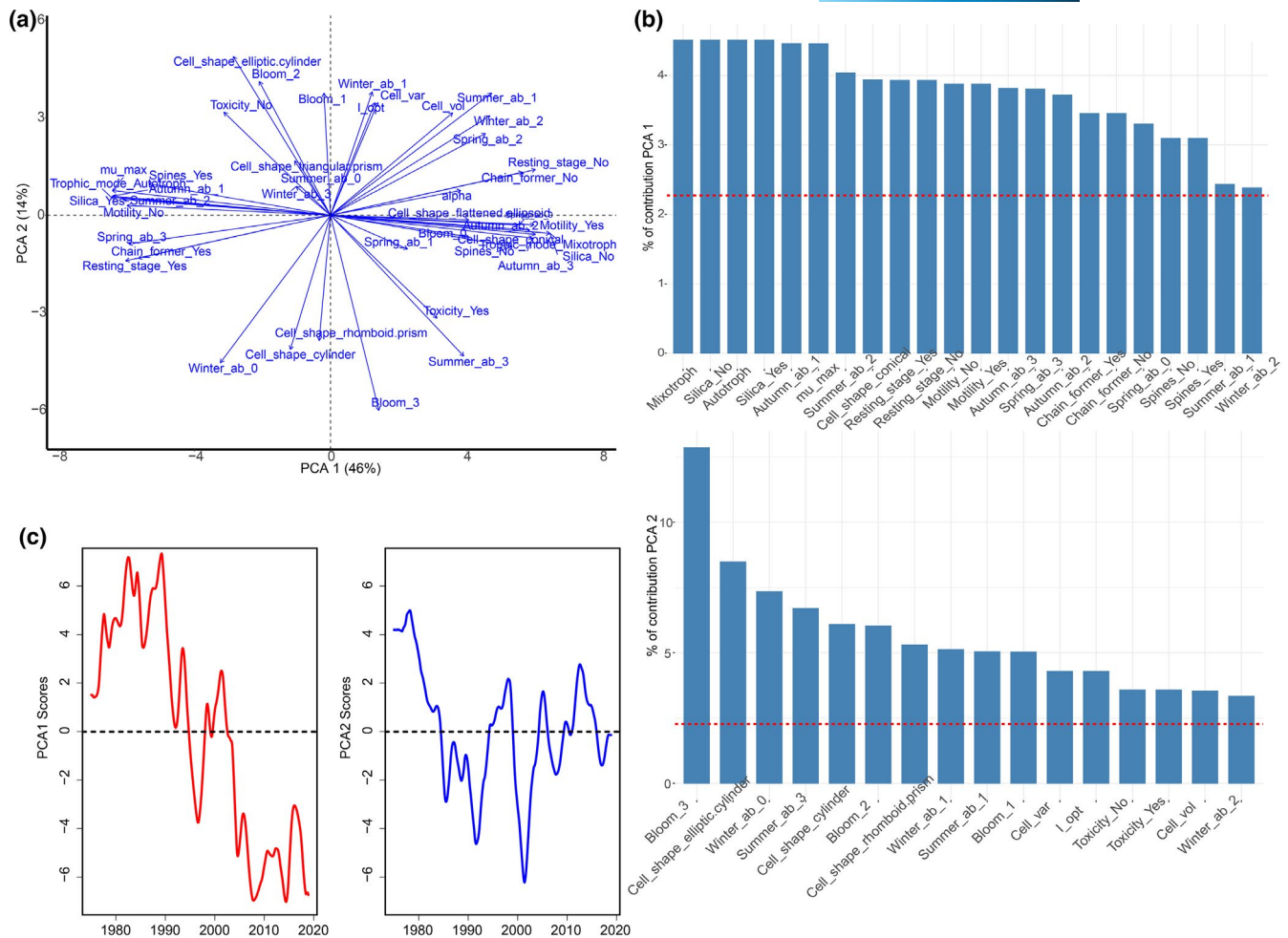
FIGURE 3 Functional structure changes between 1975 and 2018. (a) Principal component analysis (PCA) of the community-weighted mean matrix. Individual data points (months of each year, $n = 528$) are not represented for the sake of visibility. (b) Relative contribution of each trait and modalities to the first and second PCA axes. The red dotted lines represent the mean contribution of all traits. Only traits having a contribution higher than the mean are represented. (c) PCA 1 and PCA 2 individual data points coordinates. For the definition of the traits and their modality, please refer to Table 1

of each trait was calculated for both axes (Figure 3b). Time separation along axis 1 was mainly related to the functional structure changes in terms of trophic mode, presence of silica or maximum growth rate. PCA 2 mainly separated years depending on the blooming ability trait. Examination of the change of the PCA loadings with time revealed temporal changes in the functional structure (Figure 3c). PCA 1 coordinates showed a major drop starting in 1990 and ending in 2008. Coordinates switched from the positive to the negative part of the axis between 1998 and 2004, representing a significant shift in the functional structure of the phytoplankton community. These temporal dynamics were mainly explained by relative decreases of mixotrophy and autumnal bloomers, and a relative increase in fast growing and siliceous organisms. Fluctuations over time also occurred along PCA 2 with two major drops, in the 1980s and the late 1990s. These fluctuations between the negative and positive sides of axis 2 provide information about periods of time either characterised by high bloom-forming communities dominated by cylindrical-shaped cells (negative part) or highly variable cells size (cell_var) with

elliptic cylindrical-shaped cells. The proportion of organisms capable of forming blooms increased at the end of the 1980s, the average position of the coordinates being in the negative part, or fluctuating around zero after this period. Using regression analyses, PCoA 1 and PCA 1 loadings showed a highly significant correlation ($R^2 = .87$; $p < .01$), meaning that the traits that best differentiate species are also the traits that best differentiate years, namely trophic mode, siliceous theca, maximum growth rate and high autumnal versus spring abundance.

3.3 | Drivers of functional structure changes and environmental implications

An analysis of Variance Inflation Factors and forward/backward selection carried out on the complete RDA (all variables) identified SST, DIN, PO_4^{3-} and grazing as variables related to variations in trait composition, removing salinity, SiO_4^{4-} and Secchi. Then, we

used Granger causality tests to investigate potential causalities between these environmental time series and PCA 1 loadings as an index of structural changes, explaining by itself almost half of the total observed variation (Figure 4). The results of all Granger causality tested at the 23-time lags (from 2-month to 24-month lag) are given in Appendix S3.

The series of Granger causality identified that changes in functional structure were significantly related first to PO_4^{3-} ($F_{11,986} = 2.53$; $p < .01$) and, secondly, to SST ($F_{16,956} = 1.84$; $p < .05$), both roughly a year earlier (11 and 16 months, respectively). Neither DIN nor grazing pressure had significant causal influence on phytoplanktonic functional changes at any time lag. Following these results, a variation partitioning was performed, considering time lags, to highlight the amount of variation in the functional structure explained by the two identified drivers (Figure 5).

The variation partitioning results show that 63% of the total annual trait composition variation was explained by the SST, PO_4^{3-} concentration and their shared variation. The dissolved PO_4^{3-} component accounted for 53% of trait variation while SST explained 45%. In terms of pure effect (i.e. variation explained when controlling for the effect of the other variables), PO_4^{3-} concentration explained still the most with 18% of variation explained and 10% for SST. However, the largest amount of variation was shared between SST and PO_4^{3-} concentration, accounting for 35% of the functional composition changes.

Reverse causations were also tested. This time, the series of Granger causality tests identified PO_4^{3-} ($F_{12,980} = 2.48$; $p < .01$), DIN ($F_{14,968} = 2.04$; $p < .01$), both with roughly 1-year time lag, and grazing pressure ($F_{24,908} = 1.96$; $p < .01$) (2 years) as potentially driven by phytoplanktonic functional structure changes. We then calculated
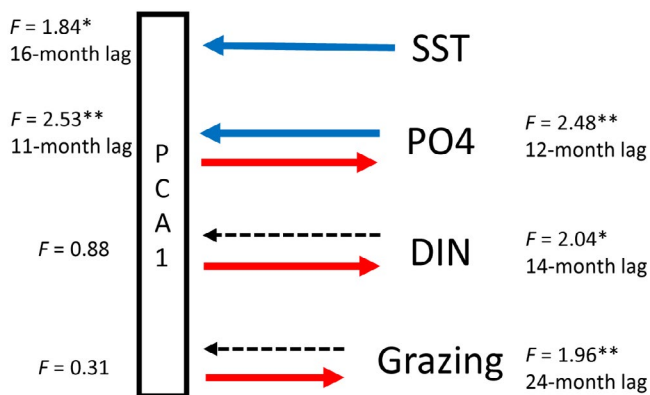

FIGURE 5 Variance partitioning analysis. Venn diagram showing the percentage of variation in the functional structure explained by each of the potential driver identified by Granger causality test (see Figure 4). ***: $p < .01$ (Monte-Carlo test; 999 permutations). Only traits affiliated to PCA 1 were used, namely trophic mode, siliceous theca, maximum growth rate, motility, chain forming, resting stage, autumnal and spring abundance. The explanatory variables are placed to their time of effect (SST: −16 months; PO_4^{3-}: −11 months)

linear regressions between annual PCA 1 loading and these three variables considering the most significant time lags (Figure 6). The three regressions performed were significantly correlated to PCA 1 loading at different magnitudes. Grazing was most correlated to functional structure changes after 24 months ($p < .01$; $R^2_{adj} = .69$) followed by DIN concentration (14 month-lag; $p < .01$; $R^2_{adj} = .47$) and PO_4^{3-} (12-month lag; $p < .01$; $R^2_{adj} = .41$). This implies that the time needed by the nutrient trends to respond substantially to the functional structure shift is around 1 year, while grazing as the sum of copepods abundance, reacted more slowly, with 2 years needed to be substantially impacted.

4 | DISCUSSION

In this study, we investigated changes in the functional structure of North Sea phytoplankton during the past five decades, and their relation to changing environmental conditions. Phytoplankton showed an increase in blooming ability at the end of the 1980s, followed by a rapid shift in functional structure between 1998 and 2004. This functional change was characterised by a switch from mixotrophic, slow growers and autumnal bloomers, to autotrophic fast-growing cells and spring bloomers. This functional restructuring was associated mostly, in terms of explained variation, with decreasing phosphate concentrations, followed by increasing temperatures. This functional restructuring of the phytoplankton in turn had consequences for the nutrient concentrations roughly 1 year later, and for the grazer-densities 2 years later.

FIGURE 4 Results of Granger causality test between environmental variables and PCA 1 axis. Most significant time lags (lowest p value and highest F-value) are indicated. * = $p < .05$, ** = $p < .01$. The direction of the arrow indicates the hypothesis being tested. Arrow from right to left; H0: environmental parameter variations do not Granger-cause functional structure variations. When blue, the null hypothesis is rejected. Arrow from left to right; H0: PCA variation do not Granger-cause environmental parameter variations. When red, the null hypothesis is rejected. Dotted arrows indicate no granger causality at the threshold of 5%
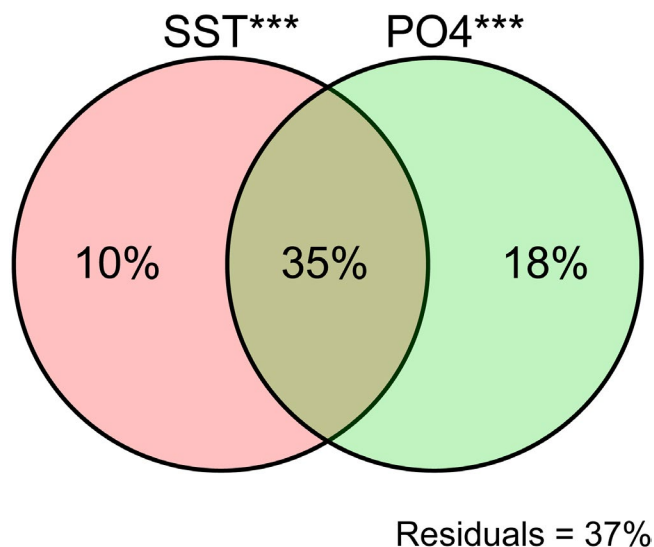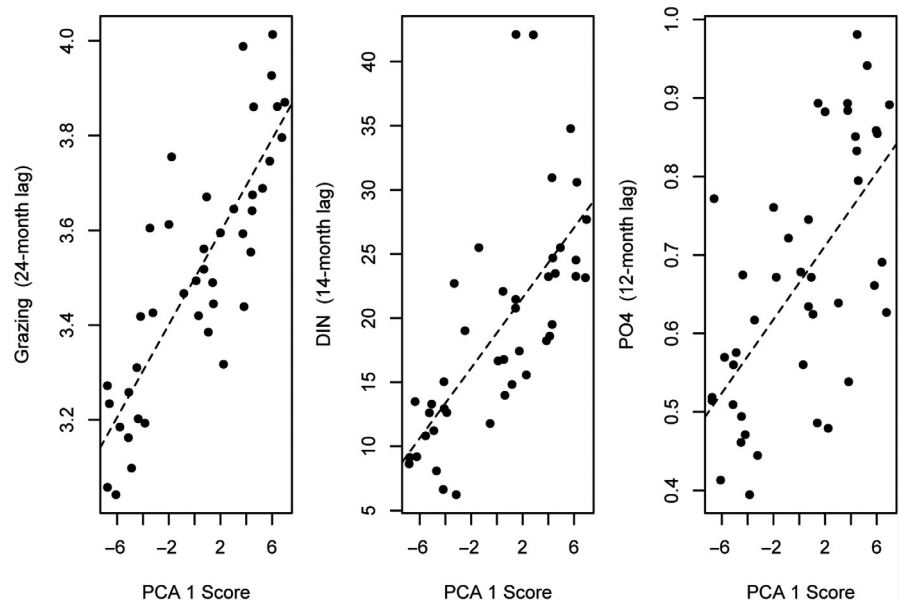
FIGURE 6 Lag-plot between PCA 1 loading as explanatory variable and dependent variables highlighted by Granger causality tests. Each point corresponds to the annual trend value of PCA 1 and the dependent variable at its relevant time lag

4.1 | Shift in phytoplankton functional structure

Towards the end of the 1980s, the coastal North Sea experienced a substantial increase in phytoplankton biomass, both in absolute amounts as well as seasonal extent (Reid et al., 1998; Wiltshire et al., 2008). Edwards et al. (2001) also reported after this period a phytoplanktonic biomass higher than the long-term average, with a particularly strong increase in winter (Reid & Edwards, 2001). Our study provides a potential mechanistic explanation for this increase in phytoplankton biomass, as we also identified a sharp increase of phytoplankton with strong bloom-forming characteristics at the end of 1980s. Thus, increased abundances of organisms forming large blooms likely lead to higher chlorophyll concentrations, which suggests an increase in primary productivity in the North Sea ecosystem at the end of the 1980s. Although this relative increase in the importance of high bloomers seems significant, this trait represented a relatively small percentage of the total variation observed in functional structure composition. We, therefore, cannot characterize the late 1980s as having experienced a shift in functional structure *sensu stricto*. Therefore, we focused our attention on the dramatic change in the functional structure, which occurred around 10 years later.

The late 1990s-early 2000s were marked by profound changes in the planktonic compartment of the North Sea (Beaugrand et al., 2014; Sarker et al., 2018). Hinder et al. (2012) and Alvarez-Fernandez et al. (2012) identified that after 1999, the North Sea ecosystem experienced a pronounced increase in diatom and decrease in dinoflagellate abundances, and Wiltshire et al. (2008) identified that seasonal diatom blooms started to occur earlier. These results are supported by Beaugrand et al. (2014) and Sarker et al. (2018) who highlighted an abrupt ecosystem shift in the planktonic assemblages of the North Sea between 1996 and 2003 and found similar trends for these two phytoplanktonic lifeforms. Furthermore, Sarker et al. (2018) found that ecosystem variability is an important predictor of phytoplankton diversity, and that low ecosystem variability yields higher species diversity due to niche differentiation, which tends to reduce competition. However, these studies did not provide a functional explanation for this taxonomic shift. Using our trait-based analysis, we addressed this issue and identified that the shift in functional structure we observed was driven by a few main traits. Indeed, from 1975 to 1990, the functional structure was characterised by slow growing species, having a mixotrophic feeding behaviour, no silica and displaying maximal abundance during autumn. While the 1990s was a transition period with high variations in the relative proportion of different traits, since the beginning of the 2000s, the functional structure is dominated by organisms with high growth rates, highly abundant in spring, often found in chains, able of resting stage production and having an autotrophic feeding mode. Those traits were the same as the traits differentiating species the most within the functional space, indicating a major shift in functional structure passing from one lifeform dominance to its functional opposite.

Although these results are ecologically significant, it is worth noting that we analysed a subset of all phytoplankton species that can be observed within the southern North Sea, which could limit our ability to capture patterns of community composition (Vellend et al., 2008). However, trait-based approaches address ecological strategies along trait continua, and the subset of phytoplankton we used covered a broad range for each trait considered, which gives us confidence in the relevance of the results we obtained. It must be mentioned that trait selection also can have direct impacts on research conclusions (Zhu et al., 2017). Trait choice must be based on the hypotheses of interest, they must holistically capture functional diversity, and reflect well-defined ecological functions (Dee et al., 2016; Lefcheck et al., 2015; McGill et al., 2006; Petchey & Gaston, 2006). We ensured that the traits used in this study match these requirements, representing the four main trait types defined by Litchman et al. (2013). Furthermore, the functional changes we identified are well in line with other studies focusing on taxonomic approaches.

Our analyses show that maximum growth rate, seasonal preference and trophic mode are the main traits related to the functional shift we observed. Compared with dinoflagellates, diatoms have generally higher growth rates, an earlier seasonal preference, and essentially autotroph, whereas dinoflagellates can be mixotrophs. These differences make diatoms and dinoflagellates successful in different environmental conditions as summarized by Margalef's Mandala (Glibert, 2016; Margalef, 1978), which predicts the occurrence of different taxonomic/functional groups of phytoplankton along environmental gradients. In the following, we expand on these aspects and discuss how changing environmental conditions in the North Sea may have led to this functional structure shift.

4.2 | Drivers of functional structure changes and effects on the environment

4.2.1 | Drivers of functional structure changes

In our study, warming appeared as one of the two main direct drivers of the late 1990s functional structure change. The study of Hinder et al. (2012) supports this result as it showed that, after the 1990s, the sharp increase in diatoms/dinoflagellates ratio was related to warming and increasingly windy conditions, causing higher degrees of turbulence. This finding is supported by the study of Berdalet et al. (2007) showing that turbulence impairs dinoflagellates cell-division and life-cycle processes. Such effects of turbulence may be even more marked in well-mixed systems such has the southern North Sea where stratification processes are restricted (Tett & Walne, 1995; Wiltshire et al., 2015). Similarly, Bedford et al. (2020) observed an offshore decline of dinoflagellate abundances in the North Sea, correlated with increasing temperatures at the same period. Temperature was positively correlated to the increase in diatoms, and therefore negatively to dinoflagellate abundances in the study of Beaugrand et al. (2014). Whereas these studies did not consider nutrient concentrations as a potential driver, here, we determined that decreasing phosphate concentrations in the North Sea since the 1980s was the main factor influencing the functional structure of phytoplankton communities. The time needed for the functional structure to respond to warming and de eutrophication was about 1 year. Many species of phytoplankton have very specific periods of the year that they can be found, so any reaction to changing environmental conditions is most likely only observable the next time the species is found in the plankton, which is typically 1 year later. Hence, the observed time lags of 1 year suggest the most rapid reaction we could have observed, and suggests that there is an almost instantaneous reaction of phytoplankton communities to environmental change. In fact, Hinder et al. (2012) observed a similar time lag effect of sea surface temperature on phytoplankton abundances. Hence, functional structure changes which occurred in the southern North Sea are driven by concurrent regional (dissolved phosphate concentrations) and global changes (temperature).

Disentangling the relative influence of different environmental drivers on biological systems is a useful but highly complex scientific exercise (e.g. Özkan et al., 2016; Winder & Cloern, 2010). Different processes involved in the structure of the phytoplankton community, such as climate-induced annual changes, human disturbance or aperiodic weather events can act on multiple time scales, making it difficult to disentangle their specific effects (Özkan et al., 2016). Information about the pre-industrial state of the phytoplanktonic community would be interesting to contrast the composition of a community under an historical, nutrient-poor and cooler temperature regime with the current community under also less nutrient-rich conditions but a higher water temperature. Using the continuous-plankton-recorder data set, Gieskes and Kraay (1977) studied North Sea plankton changes between 1948 and 1975. Over this period, diatoms contributed to a minor degree to the total community, while dinoflagellates were always the most abundant taxa in summer and autumn. Using back-tracking modelling approaches, some studies (e.g. Kerimoglu et al., 2018; Stegert et al., 2021) have shown a much lower phytoplankton biomass in the pre-industrial nutrient-poor coastal system. However, this type of approach does not allow the study of the taxonomic composition, and even less functional structure, but instead treats the phytoplankton community as a whole, either using chlorophyll a concentration or total abundance.

In our study, we found that decreasing phosphate could be the main driver of phytoplanktonic changes. Competition can be defined as the rivalry between lifeforms for access to limited environmental resources. Following Tilman's theory (Tilman, 1990), the lifeform with the lowest R^* (i.e. the minimal concentration of limiting resource that a lifeform requires to survive in a habitat) is predicted, at equilibrium, to displace all competitors (Craine, 2005). Because phosphorus is often the factor limiting phytoplankton growth in the North Sea (Pätsch & Radach, 1997; Wiltshire et al., 2010), one may expect that fast-growing organisms, having high phosphorus demands (Egge, 1998), should be outcompeted when dissolved phosphorus concentrations decrease. However, analyses of long-term data series, results from scientific expeditions, as well as laboratory experiments have all shown that dinoflagellates are negatively influenced by low dissolved phosphorus concentrations (Camarena-Gómez et al., 2021; Li et al., 2016; Meunier et al., 2018). Indeed, although earlier studies have shown that dinoflagellates can be more successful than diatoms in warm and relatively nutrient-poor conditions (Henson et al., 2012; Kamykowski & Zentara, 2003; Xiao et al., 2018), the study of Marañón et al. (2018) showed that nutrient limitation suppresses the temperature dependence of metabolic rates and growth of phytoplankton species, which may explain why dinoflagellates, which are rather dominant in autumn, did not benefit from warmer waters. This hypothesis stresses out the importance of bloom timing trait. We identified a shift from autumnal bloom-forming algae to a functional structure dominated by early-blooming (spring), fast growing algae. Spring phytoplankton bloom is a rapid event, which selects taxa, mainly diatoms, displaying a combination of traits fitting to the spatio-temporal environmental conditions, typically high growth rates, photoadaptation to low-light

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conditions, nutrient kinetics and grazing resistance (Lewandowska et al., 2015). Previous studies have shown that warming has significantly increased the length of the growing season for diatoms (Wiltshire et al., 2008, 2015; Wiltshire & Manly, 2004), and have shown large shifts in species occurrence and phenology (Scharfe & Wiltshire, 2019) which are in line with our results. We suggest that warming favours these early-blooming organisms, which efficiently deplete dissolved nutrients seasonally due to their fast-growing abilities, and thereby, in the de-eutrophication context of the area we studied, exacerbate the consequences of overall decreasing nutrient availability for autumn-blooming lifeforms.

Predicting species or functional groups response to global change on a fixed environmental niche preference (i.e., optimal temperature or nutrient range) has its limits. Phytoplanktonic organisms and their traits can display resilience or plasticity, which would be beneficial for persisting under global change (Charmantier et al., 2008; Litchman et al., 2012; Nicotra et al., 2010; Reusch & Boyd, 2013). Chivers et al. (2017) addressed this issue, and showed that, compared with diatoms, dinoflagellates have a lower phenotypic plasticity, closely tracking the velocity of climate change. Although the authors could not explain the underlying mechanisms, this dichotomy may have influenced the restructuring of the phytoplankton community. Consequently, there is no single driver of phytoplanktonic community change, but a synergy between warming and other environmental parameters, in the case of our study dissolved phosphate concentrations, which drive the net impact that global change has at different spatial scales (Bedford et al., 2020).

4.2.2 | Consequences of functional structure changes on ecosystem functioning

We identified that the functional structure changes described above, had a significant influence on dissolved nutrient concentrations, as well as copepod abundance trend represented by the grazing pressure. Even if our results on the causal influence of phytoplankton functional shifts on nutrient concentrations and copepod abundances were statistically significant and in line with the existing literature, such causality links must be taken with caution, and well-controlled experiments are necessary to establish them. For instance, cryptic mechanisms could be unravelled when studying in situ communities and their complex interactions with the biotic and abiotic compartments in mesocosm experiments (Boyd et al., 2018).

In the North Sea, nitrogen inputs were reduced by 20 to 30% in the period 1985–2002 due to the success of policy measures addressing eutrophication (Burson et al., 2016; Lenhart et al., 2010; Passy et al., 2013), and since 2003, total nitrogen inputs to the North Sea have remained fairly constant (www.ospar.org/assessments). However, nitrogen concentrations at Helgoland Roads have decreased by more than 50% compared to the 1980s (see Appendix S2). We hypothesize that the sharp restructuring of the phytoplankton functional structure, and in particular the fast growing and early blooming characteristics of the post 1990's community, are

responsible for this nitrogen sink. The functional restructuring could have also led to a faster dissolved phosphate depletion, making this environmental parameter both a response and effect variable. After controlling for seasonal variations, the dissolved concentrations of nitrogen and phosphorus appeared to be influenced by phytoplankton functional structure changes with a time lag of 1 year. The combination of fast-growing performance, related to efficient nutrient uptake (Litchman et al., 2007) and, earlier blooming characteristics of the post 1990s functional structure, could lead to an earlier and faster flow of nutrients to the benthos through cellular senescence (Wasmund et al., 2017), thereby negatively impacting the concentration of dissolved nutrients from 1 year to the next. The efficient depletion of dissolved nitrogen may further influence the identity and strength of biological nutrient limitation. Hence, we hypothesize that nitrogen concentration, and the overarching phosphorus limitation at Helgoland roads (Wiltshire et al., 2015), and in coastal North Sea waters in general (Pätsch & Radach, 1997), is not only driven by seasonal variations of riverine inputs but is also influenced by the functional structure of the phytoplankton community. Growth rate and seasonal preference can, thus, be considered as effect-traits, having a direct influence on ecosystem processes (Pakeman, 2011).

Total copepod abundance (used here as an index of grazing pressure) appeared significantly and negatively impacted by the changes in phytoplankton functional structure, with a 2-year time lag. Their more complex ontogeny and longer life span may explain this longer response time compared to phytoplankton. This result is supported by previous studies indicating that the abundances of most copepod species have declined in the North Sea since the late 1990s (Alvarez-Fernandez et al., 2012; Beaugrand et al., 2014; Boersma et al., 2015). From the phytoplankton traits we used in this study, we could not isolate a specific trait of the post 1990s community which could have driven this decline in copepod abundance. Scharfe and Wiltshire (2019) also used copepod abundances as proxy of grazing pressure and identified a reduction, particularly pronounced after 2007, but could not identify a direct bottom-up nor top-down control exerted on this compartment.

Klausmeier and Litchman (2012) identified that decreasing nutrient input benefits spring bloomers and can lead to the decrease or complete absence of fall bloom dynamics and ultimately to a decrease in grazers biomass. The lower copepod abundance observed could also be directly related to the shift from dinoflagellates to diatoms, as reports exist that dinoflagellates are a better food source for many copepod species (Ianora et al., 2004), and even that diatoms may produce substances that inhibit copepod reproduction in some cases (Ban et al., 1997; Calliari & Tiselius, 2005; Miralto et al., 1999; Müller-Navarra et al., 2004). This could have led to a decrease in copepod abundances by reducing their larval survival success, and therefore their recruitment. However, changes in nutrient availability are also directly reflected in the elemental composition of phytoplankton (Meunier et al., 2014). As the relative carbon to nutrient ratios in copepods is less variable, as compared with that in phytoplankton (Van de Waal et al., 2010), changes in dissolved nutrient availability modifies the nutritional quality of phytoplankton and

creates room for nutritional mismatches. Hence, the shift observed in functional structure may have been associated with a change in food quality resulting in an elemental mismatch between copepods and their phytoplankton prey, leading to changes in copepod abundances.

5 | CONCLUSION

In this study, we used a trait-based approach to explain an environmental induced shift in North Sea coastal phytoplankton functional structure. Organismal traits appeared very useful to identify a functional shift during the 1990s. The changes in growth rate performance, seasonal preference, motility or trophic mode dominance of phytoplankton, likely emerged from the combined influence of decreasing phosphate concentrations and sea warming. These traits were related to the two dominant and contrasted phytoplanktonic lifeforms; dinoflagellates and diatoms, and more precisely, those that grow fast. By their great differences in life history traits, this abrupt 1990s shift between two functional structures likely had major ecosystem-level consequences, impacting both food-web structure and biogeochemical cycles. The functional structure dominated by fast-growing-spring bloomers since the mid-2000s could have, in addition to a change in food quality, lowered copepod fitness and led to an earlier and faster energy flow to the benthos. By impacting nutrient concentration (top-down control) and higher trophic levels (bottom-up control), the trait characteristics of the phytoplankton community could result in wasp-waist control on ecosystem functioning. These hypotheses still need more investigations to support or infer true causality. Overall, our results emphasize the profound impact that both global and regional change have on coastal ecosystems through the lever represented by phytoplankton. This compartment and the many life strategies it contains could therefore be the key component to marine food web stability in a context of a changing environment.

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