RESEARCH ARTICLE

Reinterpreting two regime shifts in North Sea plankton communities through the lens of functional traits

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Abstract

Aim: The so-called regime shifts in North Sea plankton communities provide an important historical case study to understand marine regime shifts. Previous studies characterized regime shifts using a variety of community metrics (e.g., indicator species abundances, taxonomic composition and chlorophyll biomass) but left the functional traits of plankton unassessed. Here, we explicitly re-assess the historically recognized North Sea regime shifts through the lens of plankton functional traits to gain a better understanding of these events.

Location: The North Sea (NW European shelf).

Time period: 1958–2018, focusing on the 1980s and 1996–2003 regime shifts.

Major taxa studied: Marine phyto- and zooplankton.

Methods: We compute trait spaces for both phyto- and zooplankton of the North Sea using traits from the literature and a Gower's distance-based method. Using abundance data from the Continuous Plankton Recorder Survey, we then compute monthly time series of the centroids of the communities, an indicator of functional composition. We then use principal component analysis on the centroids to assess the main temporal changes in plankton functional composition associated with the 1980s and 1996–2003 regime shifts.

Results: Little change in plankton functional composition was associated with the 1980s regime shift. In contrast, the functional composition of plankton communities changed markedly after the 1996–2003 regime shift, with an increase in the summer relative abundance of non-motile autotrophs (i.e., diatoms) and the spring relative abundance of meroplankton.

Main conclusions: The North Sea regime shifts were not associated systematically with changes in functional composition, calling into question the definition of regime shifts and illustrating the importance of taking different metrics into account to interpret ecological events accurately. Taking into account functional composition, we interpret the 1980s so-called regime shift as a latitudinal shift in communities that was insufficient to impact functional composition and the 1996–2003 so-called regime shift as a period of change in bentho-pelagic coupling.

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1 | INTRODUCTION

Plankton communities are changing world-wide, altering the functions and services of the ecosystems they support (e.g., primary productivity, fisheries; Benedetti et al., 2021; Henson et al., 2021). These changes can take the form of abrupt discontinuities, often termed regime shifts, where communities change rapidly and markedly in their composition, abundances and functioning (Scheffer et al., 2001). For regime shifts in marine plankton communities, the North Sea is considered to be an important case-study ecosystem because its plankton communities have undergone at least three so-called regime shifts over the last six decades, in the 1960s, the 1980s and between 1996 and 2003 (Alvarez-Fernandez et al., 2012; Beaugrand et al., 2014; Weijerman et al., 2005).

The three North Sea regime shifts differed from each other in that they manifested in different groups within the plankton communities and have different environmental causes. Owing to a lack of data at the start of the period, the 1960s regime is less known, but appears to be most pre-eminent in the phytoplankton, with changes apparent in the seasonality of the important diatom *Chaetoceros* (Beaugrand et al., 2014; Reid, 1975). The 1980s regime shift is the most well reported of the three regime shifts. It is generally framed as a complex shift from a "cold dynamic equilibrium" to a "warm dynamic equilibrium", where subpolar communities have been replaced by more temperate communities (Beaugrand, 2004). This is exemplified by the replacement of the subpolar copepod *Calanus finmarchicus* by its temperate congeneric, *Calanus helgolandicus* (Helaouët et al., 2013; Reid et al., 2003). In phytoplankton, the 1980s regime shift was marked by an increase in biomass at *c.* 1985 (Beaugrand, 2004). The primary cause of the 1980s regime shift appears to be an increase in temperature (Beaugrand, 2004). This transition did not occur in a single event; the 1980s regime shift presented two periods of rapid changes (1982–1985 and 1987–1988; Beaugrand, 2004) and was preceded by an important, but transient, cold ecological event at *c.* 1978 (Alvarez-Fernandez et al., 2012; Reid et al., 2003). Finally, the third regime shift occurred over the period 1996–2003 (Beaugrand et al., 2014). This shift was driven by the combined effects of increasing temperatures and decreased riverine nutrient inputs (Alvarez-Fernandez et al., 2012; Burson et al., 2016; Capuzzo et al., 2018; Desmit et al., 2020; Di Pane et al., 2022). This 1996–2003 regime shift is associated with a decrease of the biomass and productivity of phytoplankton (Capuzzo et al., 2018; Desmit et al., 2020), with changes in the relative importance of diatoms to dinoflagellates (Alvarez-Fernandez et al., 2012; Bedford et al., 2020; Di Pane et al., 2022). In zooplankton, the 1996–2003 regime shift is associated with a decrease in the abundances of copepods (Alvarez-Fernandez et al., 2012; Capuzzo

et al., 2018; Di Pane et al., 2022), accompanied by an increase in the abundances of sea urchin and decapod larvae (already started at the beginning of the 1990s but increasing further at *c.* 2000; see Bedford et al., 2020; Kirby et al., 2008).

Although these events undoubtedly represent important changes in the plankton communities of the North Sea, their characterization as "regime shifts" is a subject of debate (Sguotti et al., 2022). In the case of the North Sea, a regime shift is generally described as a large-scale, sudden and durable change in the abundance and/or composition of the community of interest (see e.g., Beaugrand, 2004). Such large changes are generally expected to have important consequences in terms of ecosystem functioning (Beaugrand et al., 2014). This definition, however, presents important limitations. For instance, the definition of what constitutes a "large" change is rendered highly complex by the fact that not all metrics of ecological communities (e.g., taxonomic compositions, species or functional group abundances, diversity) change synchronously. For example, Taylor (2002), using total copepod abundances, found no regime shift in the 1980s. However, Beaugrand (2004) argued that total copepod abundance is not an adequate metric to detect regime shifts because different species would react differently to environmental changes, making taxonomic composition a better metric. In addition, different metrics often present different timing in their shifts. To resolve this issue, one can consider different shifts in different ecosystem metrics as different regime shifts, perhaps at the cost of the idea of a single large-scale event often associated with the term "regime shift". An alternative way to resolve that issue, which was seemingly favoured in previous studies on the North Sea regime shifts, is to consider regime shifts as periods of several years needed for the ecosystem to reach a new stable state (Beaugrand, 2004), somewhat contradicting the idea of a regime shift being "sudden". Here, we argue that the different behaviours of different metrics, although they raise questions surrounding the definition of "regime shifts", might be highly informative on the nature of the ecological changes (Pavoine & Bonsall, 2011). From that perspective, the so-called regime shifts in the North Sea plankton communities should be investigated with different metrics to be understood better.

The composition of a community in functional traits (i.e., its functional composition) is now recognized as an important community metric because it can give important insights into the drivers of community composition (Mouillot et al., 2013) or into the relationship between the community composition and ecosystem functioning (van der Plas, 2019). Functional composition has also been applied successfully to study abrupt shift in communities (Di Pane et al., 2022; McLean et al., 2018). For marine plankton specifically, functional traits are increasingly documented and associated with databases making functional trait-based approaches available (Litchman

& Klausmeier, 2008; Litchman et al., 2013; Martini et al., 2021; Ostle et al., 2021). Yet so far, the only long-term functional insight on the change of plankton functional composition associated with the North Sea regime shifts is derived from a single coastal time series and focused on phytoplankton (Di Pane et al., 2022). An assessment at the scale of the whole North Sea and including zooplankton remains to be done.

In this paper, we aim to assess whether and how the historically recognized North Sea regime shifts are associated with changes in the functional composition of plankton communities across the whole North Sea. We acknowledge the debate and difficulties around the characterization of the plankton community changes as "regime shifts", but use the term and the results from previous studies to contextualize the present paper. We use the monthly phytoplankton and zooplankton community composition data from the Continuous Plankton Recorder (CPR) survey over the 1958–2018 period in conjunction with a functional trait-based approach (e.g., Mammola et al., 2021; Mouillot et al., 2013). Given that the 1960s regime shift is less well known and close to the start of our time series, we focus on the better-documented regime shifts from the 1980s and 1996–2003. Changes in the functional composition of the plankton communities are then interpreted to gain new insight into the causes and consequences of the North Sea regime shifts. More specifically, we (1) assess whether the North Sea regime shifts were associated systematically with changes in the functional composition of plankton, (2) discuss the likely drivers of the differences between the two regime shifts and (3) discuss the repercussions of our results for our understanding of the North Sea regime shifts.

2 | MATERIALS AND METHODS

2.1 | Community composition data

The plankton community data used here (Djeghri, 2022) were obtained from the Continuous Plankton Recorder (CPR) Survey operated by the Marine Biological Association of the United Kingdom. The CPR sampling is done by merchant ships towing CPR samplers along their routes. The standard tow depth is 7 m, and plankton is captured on a 270 μm mesh silk and preserved in formalin. Each sample represents *c*. 10 nautical miles of tow and 3 m^3 of filtered seawater, and abundances are evaluated semi-quantitatively (Richardson et al., 2006). The methodology has been consistent since 1958, allowing comparisons over decades and large geographical areas.

We focus our analysis on four CPR standard areas in the North Sea and over the period 1958–2018 (Figure 1). These areas are the best studied in the context of the 1980s and 1996–2003 regime shift (e.g., Alvarez-Fernandez et al., 2012). Their size allows the capture of enough samples in each area to reach near-complete monthly time series (except for the period around 1980 in the southern North Sea) while preserving some spatial information (Figure 1). Monthly time series of averaged abundances were calculated for each plankton taxon in each CPR standard area. The CPR data contain rare species that might not be representative of the local community. These were removed by keeping only taxa present in >1% of samples in at least one of the four CPR standard areas. Taxa not counted systematically since 1958 by the CPR survey were also removed. A last step of taxa screening was performed on zooplankton (i.e., metazoan plankton) taxa by removing
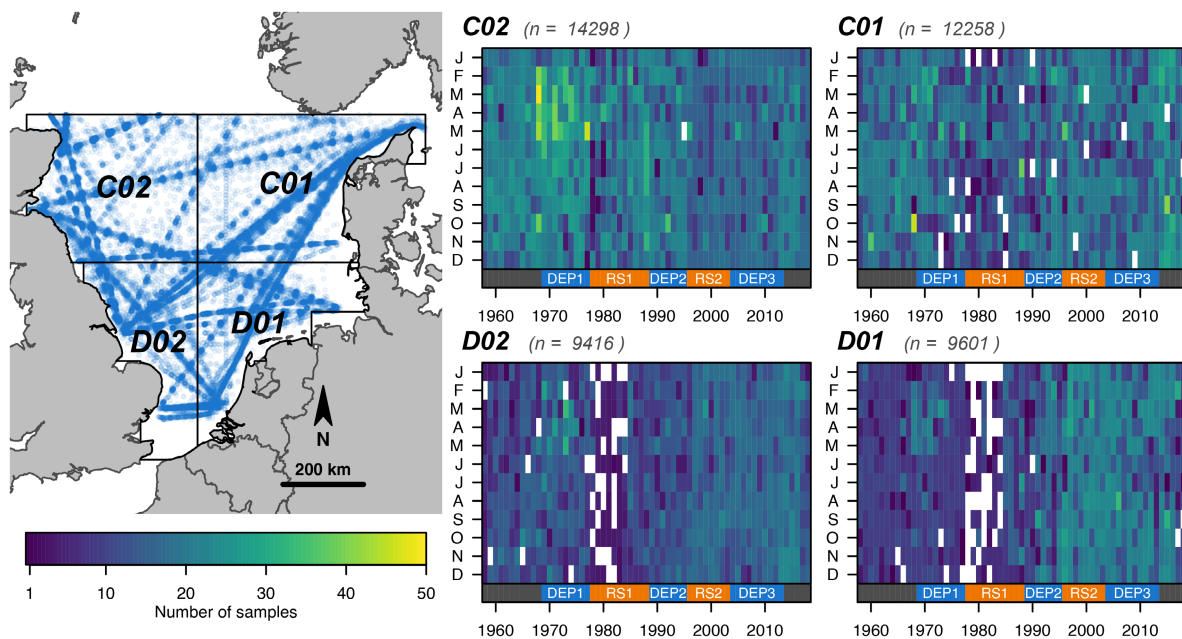

FIGURE 1 Map of the Continuous Plankton Recorder standard areas from the North Sea included in this study (blue points are individual samples) and associated biplots representing the monthly sampling effort over the period 1958–2018, with both so-called regime shifts (RS; in orange) and dynamic equilibrium periods (DEP; in blue) represented. The number *n* in parentheses is the total number of samples per area.

thycoplankton (organisms primarily benthic, found in the plankton only when advected from the seabed, e.g., caprellids) and eggs because they are rare in CPR samples and not active in the plankton. We also removed copepod nauplii owing to the high uncertainty in trait attribution. This selection process allowed us to have the same list of consistently counted taxa for all the CPR standard areas and throughout the whole period studied here. The complete list of taxa included is given in the Supporting Information (Appendix S1).

2.2 | Functional trait data and selection

Because of differences in biology (e.g., uni- vs. muticellularity), phytoplankton and zooplankton were assigned a different set of functional traits and analysed separately. The traits included in this study are given in Table 1 and were obtained primarily from three databases (Benedetti et al., 2016; Brun et al., 2017; Ramond et al.,

2018), completed using varied literature sources to reach a complete traits × taxa table (detailed in Supporting Information Appendix S1). The functional traits used were either continuous (i.e., sizes) or categorical. Categorical traits of which modalities are mutually exclusive (e.g., the cover of phytoplankton organisms is either silicate or organic) were simply attributed one modality (i.e., one-hot encoded). Categorical traits of which modalities are not mutually exclusive were attributed a mixture of modalities (i.e., fuzzy coded). For example, an omnivorous copepod is considered 50% carnivorous and 50% herbivorous (for more details, see Table 1; Supporting Information Appendix S1).

2.3 | Functional composition of the plankton community

To assess changes in the functional traits of the plankton of the North Sea we first characterize functional compositions of plankton

TABLE 1 Ecological significance and implementation details of the functional traits of phytoplankton and zooplankton included in this study (see also Litchman et al., 2013; Litchman & Klausmeier, 2008).

Trait	Ecological effects		Implementation
	Individual scale	**Ecosystem scale**	
Phytoplankton			
Cell size	Physiological rates, predator–prey interactions etc.	Size structure, trophodynamics, carbon export	Continuous: $\log_{10}$-transformed maximum and minimum of the intrataxa variability in cell size (longest section) each having a weighting $w = \frac{1}{2}$ (reaching $w = 1$ for the trait)
Cover	Nutritive needs (e.g., silicates), predation risk, sinking speed	Nutrient dynamics, trophodynamics, carbon export	Categorical (levels: siliceous, organic) $w = 1$
Shape	Nutrient uptake, sinking speed	Nutrient dynamics, carbon export	Fuzzy-coded categorical, with a total = 1 coding scheme (modalities: long, round, irregular) $w = \frac{1}{3}$ for each modality, hence $w = 1$ for the trait
Coloniality	Predation risk and sinking speed	Trophodynamics, carbon export	Categorical (levels: solitary, colonial) $w = 1$
Motility	Prey finding, predation risk, position in water column	Trophodynamics	Categorical (levels: motile, non-motile) $w = 1$
Nutritive strategy	Energy acquisition	Primary production, nutrient dynamics, trophodynamics	Fuzzy-coded categorical, with a total = 1 coding scheme (modalities: phototrophic, heterotrophic) $w = \frac{1}{2}$ for each modality, hence $w = 1$ for the trait
Zooplankton			
Body size	Physiological rates, predator–prey interactions etc.	Size structure, trophodynamics, carbon export	Continuous: $\log_{10}$-transformed maximum and minimum of the intrataxa variability[a] in body size (longest section) each having a weighting $w = \frac{1}{2}$ (reaching $w = 1$ for the trait)
Life cycle	Reproductive output, phenology	Seasonality, bentho-pelagic coupling	Categorical (levels: holoplanktonic, meroplanktonic) $w = 1$
Feeding mode	Prey selectivity, predation risk	Trophodynamics	Fuzzy-coded categorical, with a total = 1 coding scheme (modalities: active, passive) $w = \frac{1}{2}$ for each modality, hence $w = 1$ for the trait
Trophic regime	Trophic level	Trophodynamics	Fuzzy-coded categorical, with a total = 1 coding scheme (modalities: carnivore, herbivore) $w = \frac{1}{2}$ for each modality, hence $w = 1$ for the trait
Cover/support	Motility, predation risk	Trophodynamics	Categorical (levels: shell, naked, internal skeleton, exoskeleton) $w = 1$

[a]Excluding ontogeny. Instead, different ontogenic stages can be represented as different "taxa"; for more details, see the Supporting Information (Appendix S1).
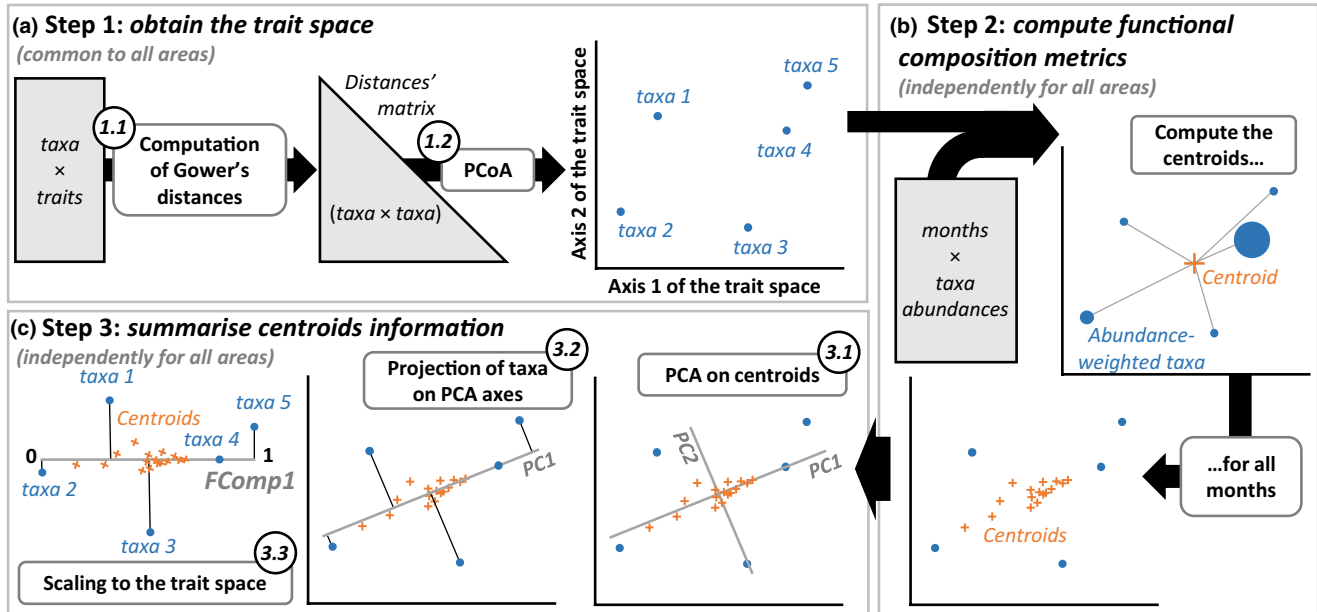
FIGURE 2 Methodology followed in this study. (a) Step 1, obtain a multidimensional trait space (only two dimensions are represented here) by performing a principal coordinates analysis (PCoA) on taxa-to-taxa Gower's distances computed from the taxa × traits matrix. (b) Step 2, compute community centroids for all available months of the time series (1958–2018) by combining trait space and abundance data. (c) Step 3, summarize the information on centroids using principal component analysis (PCA; only the firsts axes are represented). To help ecological interpretation, taxa (and their associated traits) are then projected on PCA axes as additional variables, and PCA axes are scaled to the trait space (between zero and one). For simplicity, we refer to these scaled, centroid-based PCA axes as "functional composition axes" (FComp1, FComp2, etc.).

communities using the methodology proposed by Villéger et al. (2008) and Laliberté and Legendre (2010). This methodology ordinates the taxa from the targeted community in a multidimensional space according to their similarities in terms of functional traits. The space obtained is referred to as a "trait space", in which properties of the community can be computed and tracked over time.

The first step is to produce the trait space in which functional metrics of the communities can be assessed (Figure 2a). Taxa-to-taxa Gower's distances (Gower, 1971) were computed from the taxa × traits matrix (1.1 in Figure 2a). We chose Gower's distance because of its ability to accommodate both continuous and categorical traits (Table 1). Gower's distances also accommodate weightings, used here to ensure that each trait would have a final weight equal to one in the analysis despite the fact that some traits have several entries (e.g., fuzzy-coded traits; Table 1). A principal coordinates analysis (PCoA) was then performed on the distance matrix to obtain a Euclidean space, in which taxa are positioned relative to each other according to their Gower's distances (1.2 in Figure 2a). PCoA axes with negative eigenvalues were corrected using Cailliez's method, which has the advantage of yielding a linear relationship between the original Gower's distances and the Euclidean distances obtained after the PCoA (Legendre & Anderson, 1999). All the axes of the PCoA are retained and constitute the trait space used in this study. Given that we use a common species list for the four CPR standard areas, the trait space is the same in all areas, ensuring comparability.

The second step (Figure 2b) is to compute the abundance-weighted centroid of communities (Laliberté & Legendre, 2010). The centroid (c) is an indicator of the average position of the community in the trait space and is thus an indicator of mean functional composition (it is also called functional identity; Mouillot et al., 2013). It is computed as the centre of gravity of abundance-weighted taxa in the trait space:

$$c = [c_i] = \frac{\sum a_j x_{ji}}{\sum a_j}.$$

The centroid c is a position in the trait space defined by a set of coordinates c_i on the i axes of the trait space, where a_j is the abundance of taxon j and x_{ji} the position of taxon j on the axis i of the trait space. Centroids were computed using the time series of averaged monthly abundances for the period 1958–2018 in each of the four standard areas.

Given that the monthly centroids are a set of points within the multidimensional trait space (Figure 2b), the third step (Figure 2c) of our analysis is to perform a principal components analysis (PCA) on centroids coordinates to summarize the information (3.1 in Figure 2c). The PCA is performed without scaling, in order to conserve the proportions of the trait space, and thus consists only of centring and rotation. Given that the centroid coordinates and the position of the taxa are defined within a shared trait space, it is possible to project the taxa from the trait space to the PCA axes (3.2 in Figure 2c). Given that the taxa are directly associated

with their functional traits, this projection allows the visualization of trait distribution along PCA axes, hence ecological interpretations. This procedure is repeated independently in each standard area. To compare axes obtained by the different PCAs done for the different standard areas more conveniently, we scaled these axes between zero and one using minimal and maximal projected taxa coordinates (the limits of the trait space; *3.3* in Figure 2c). For simplicity, we will refer to these scaled, centroid-based PCA axes as "functional composition axes" (FComp1, FComp2 etc.) in the following sections.

2.4 | Assessment of the effects of the regime shifts on plankton functional composition

To assess whether the 1980s and 1996–2003 regime shifts were associated with changes in functional composition of plankton, we compared the periods before and after each regime shift. If the functional composition of plankton changed markedly during a regime shift, the periods before and after this regime shift should present differences in their first functional composition axes (FComp1, FComp2, etc.). We divided the time series into three groups of periods (Figure 1), as follows.

1. The periods 1958–1968 and 2014–2018 are considered as margins of our time series and not formally included. These margins comprise 5 years at the beginning and end of the time series and the 1960s regime shift (ending in 1968; Beaugrand et al., 2014), which cannot be included because of lack of data on the ecosystem state before the event.
2. The periods 1978–1988 and 1996–2003 correspond to the regime shifts (RS1 and RS2; Figure 1). The temporal limits of the regime shifts are taken from the literature, where previous studies have found important ecological changes: RS1 comprises mainly the 1980s regime shift (from 1982 to 1988; Beaugrand, 2004) but starts in 1978 to include the 1978 cold event that had important but transient impacts on plankton communities (Alvarez-Fernandez et al., 2012; Reid et al., 2003). RS2 delimitation follows Beaugrand et al. (2014).
3. The remaining periods (1969–1977, 1989–1995 and 2004–2013) are considered as "dynamic equilibrium periods" (DEP1, DEP2 and DEP3, respectively; Figure 1) and correspond to periods not reported to include important changes in the plankton community in the literature (e.g., Beaugrand et al., 2014). A period of dynamic equilibrium is thus expected to be more stable in community composition than a period of regime shift.

We then compare annual means of the coordinates on functional composition axes (thus aggregating seasonal variability) of DEP1 and DEP2 to assess whether plankton functional composition changed during RS1, and of annual means of DEP2 and DEP3 to assess whether plankton functional composition changed during RS2 using Kruskal–Wallis tests.

3 | RESULTS

3.1 | Ecological interpretation of the first functional composition axes

In both phytoplankton and zooplankton, a large part of the variance in centroids was captured by FComp1 (>65% in phytoplankton and between 44 and 74% in zooplankton). In comparison, FComp2 generally explained five to six times less variance (often *c.* 10%), with the exception of FComp2 in zooplankton from C02 (21%). Although FComp2 might present some patterns associated with the North Sea regime shifts (Supporting Information Appendix S2), we choose to focus here on Fomp1 owing to the high proportion of variance explained in the four standard areas and in the two plankton communities. The values of FComp1 obtained by four independent PCAs for each of the four standard areas of the North Sea were very similar to each other within either phytoplankton or zooplankton communities, as indicated by matching repartition of projected taxa and traits along them (Figure 3; see also Supporting Information Appendix S3). This indicates that patterns in centroids across the North Sea and within a group (i.e., phytoplankton or zooplankton) were generally driven by variations in the same functional traits, irrespective of the standard area considered.

In phytoplankton, taxa projected on FComp1 were separated on the basis of their cover, motility and nutritive strategy but not on the basis of shape or size (Figure 3a). The FComp1 in phytoplankton can thus be interpreted as an axis distinguishing communities dominated by non-motile autotrophs from communities dominated by motile mixotrophs. This grouping corresponded mostly to the well-known taxonomic and ecological distinction between diatoms and dinoflagellates.

In zooplankton, taxa projected on FComp1 were separated on the basis on their type of life cycle, feeding mode and type of cover or support (Figure 3b). In particular, taxa with an internal skeleton were isolated from taxa with an exoskeleton. In contrast, patterns in body size were less obvious (Figure 3b). In our dataset, meroplanktonic taxa are predominantly active feeders and comprise many kinds of cover or support owing to their diversity in body plans (Supporting Information Appendix S1). The FComp1 in zooplankton can therefore be interpreted as separating primarily communities dominated by crustacean holoplankton (i.e., mostly copepods) from communities dominated by meroplankton.

3.2 | Changes in plankton functional composition associated with the 1980s and the 1996–2003 regime shifts

From 1958 to *c.* 2000, and in the four standard areas of the North Sea, the FComp1 of phytoplankton communities showed a seasonal pattern, with non-motile autotrophs dominating in spring, whereas motile mixotrophs dominated in summer and autumn (Figure 4a). This pattern was generally conserved across the 1980s regime shift
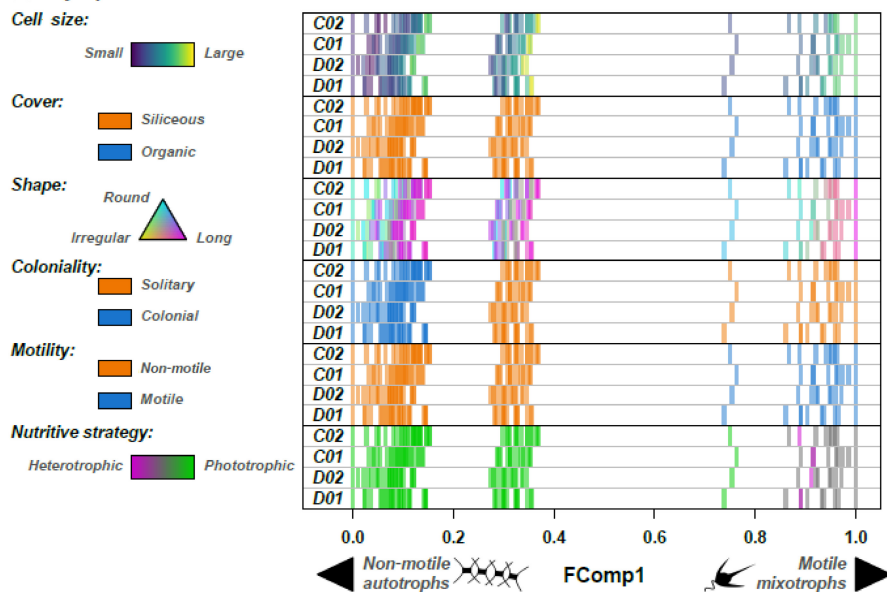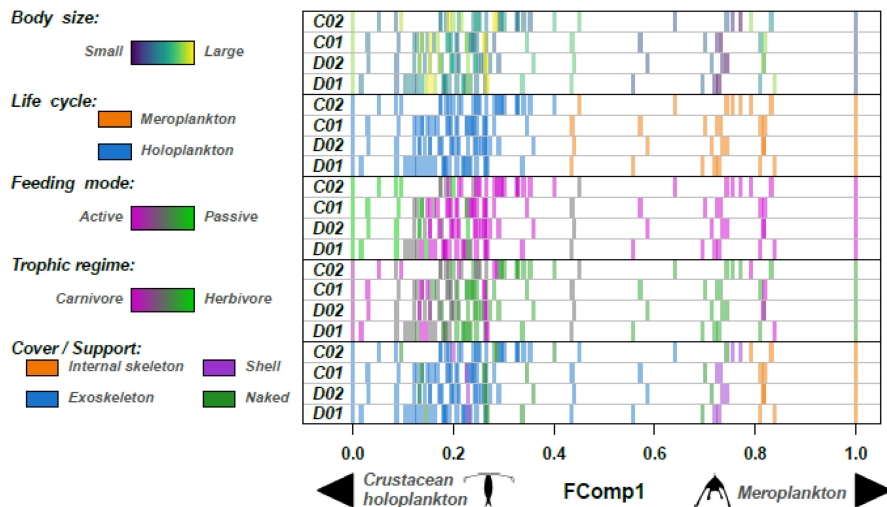
FIGURE 3 Projection of taxa (vertical bars) and associated traits on the first functional composition axis (FComp1) in (a) phytoplankton and (b) zooplankton in the four standard areas of the North Sea (C02, C01, D02 and D01). An ecological interpretation of the types of communities separated by FComp1, based on trait repartition, is given below the graphics (see main text for more details). To simplify the figure, cell and body sizes are presented as an average between the minimum and maximum sizes used in the analyses.

(RS1). However, the summer–autumn relative abundance of motile mixotrophs diminished during the 1996–2003 regime shift (RS2) in all standard areas of the North Sea, although this is less clear in the North-East (C01) area.

Zooplankton communities generally tended to be dominated by crustacean holoplankton, with a seasonal increase in meroplankton relative abundance in summer from 1958 to *c*. 1985 (Figure 4b). After RS1, this increase in meroplankton relative abundance happened earlier in the year. After RS2, the seasonal increase in meroplankton relative abundance became more pronounced and it dominated the zooplankton communities of the North Sea in the end of spring and beginning of summer. These changes were most pronounced in the East standard areas (C01 and D01) of the North Sea.

Annual averages in FComp1 (Figure 5) suggest that the functional composition of the phytoplankton and zooplankton communities changed more clearly after RS2 than after RS1. Except for the zooplankton community of C02 (Figure 5b), the difference between

FComp1 in the DEPs before and after the regime shift is always larger for RS2 than for RS1. In all areas and in phytoplankton and zooplankton taken together, we found three of eight (four areas × two groups) significant differences between FComp1 of DEP1 and DEP2 linked to RS1 (Figure 5; Kruskal–Wallis tests). In contrast, for RS2, seven of eight differences in FComp1 between DEP2 and DEP3 were significant (Figure 5; Kruskal–Wallis tests).

The patterns found in the annual averages (Figure 5) confirm those found in monthly data (Figure 4). The changes in plankton functional composition associated with RS2 are clearer than the changes associated with RS1. In phytoplankton, this takes the form of a decrease in the summer–autumn relative abundance of motile mixotrophs (i.e., dinoflagellates) in favour of non-motile autotrophs (i.e., diatoms). In zooplankton, the seasonal increase in meroplankton relative abundance tended to happen earlier in year after RS1. However, the change associated with RS2 was again clearer, with an important seasonal increase in meroplankton relative abundance, particularly in the eastern North Sea.

FIGURE 4 Seasonal (*y*-axes) and long-term (*x*-axes) variations in the first functional composition axis (FComp1) in (a) phytoplankton and (b) zooplankton communities in the four standard areas of the North Sea (C02, C01, D02 and D01), with both so-called regime shifts (RS; in orange) and dynamic equilibrium periods (DEPs; in blue) represented. The proportion of variance explained by FComp1 is given in parentheses.
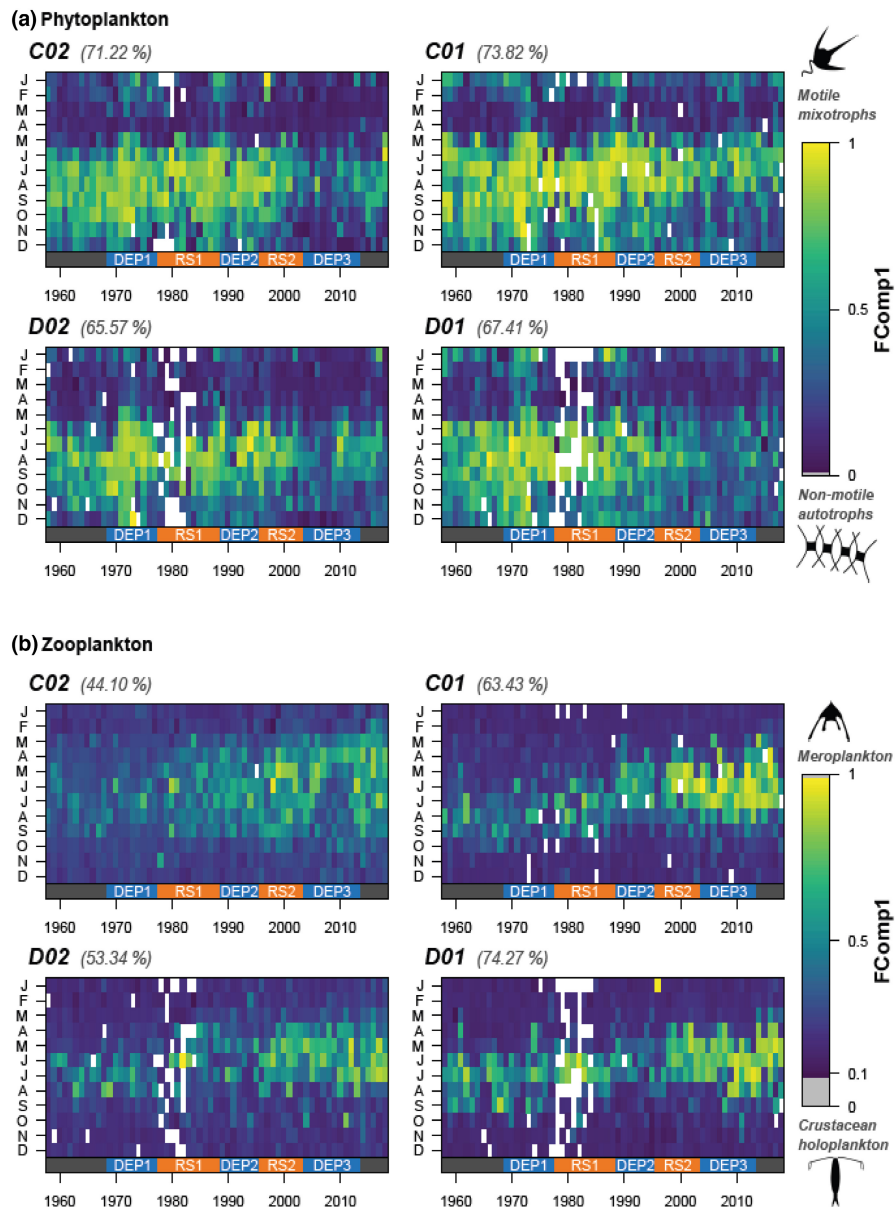
3.3 | Variations outside of regime shift periods

Some important changes in FComp1 do not occur during either RS1 or RS2. Most pre-eminently, phytoplankton communities in all standard areas show a common pattern of increase and decrease of the relative abundance of motile mixotrophs during DEP1 (Figure 5a), calling into question whether these periods represent a true equilibrium with regard to plankton functional composition.
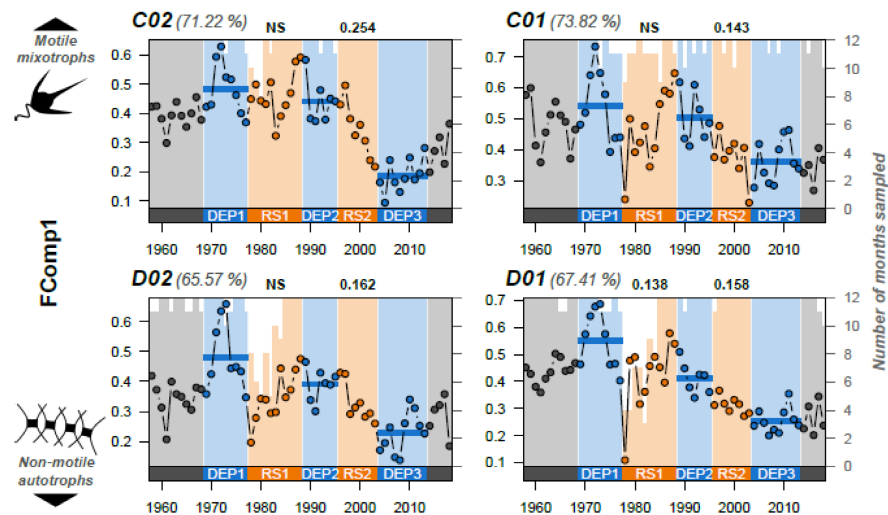
4 | DISCUSSION

Our approach shows that the functional composition of both phytoplankton and zooplankton across the whole North Sea changed more after the 1996–2003 regime shift than after the 1980s regime shift, confirming and broadening conclusions from more local studies

(Di Pane et al., 2022). In previous works using different metrics of community composition and abundances, the two regime shifts have often been presented as events of similar importance (e.g., Alvarez-Fernandez et al., 2012; Beaugrand et al., 2014), which might seem to contradict our results obtained with functional trait-based approaches. However, different metrics assess different aspects of ecosystems and communities with potentially different ecological drivers (Pavoine & Bonsall, 2011). Bringing together the different conclusions reached through the use of different metrics might thus reveal new ecological mechanisms underlying the North Sea regime shifts.
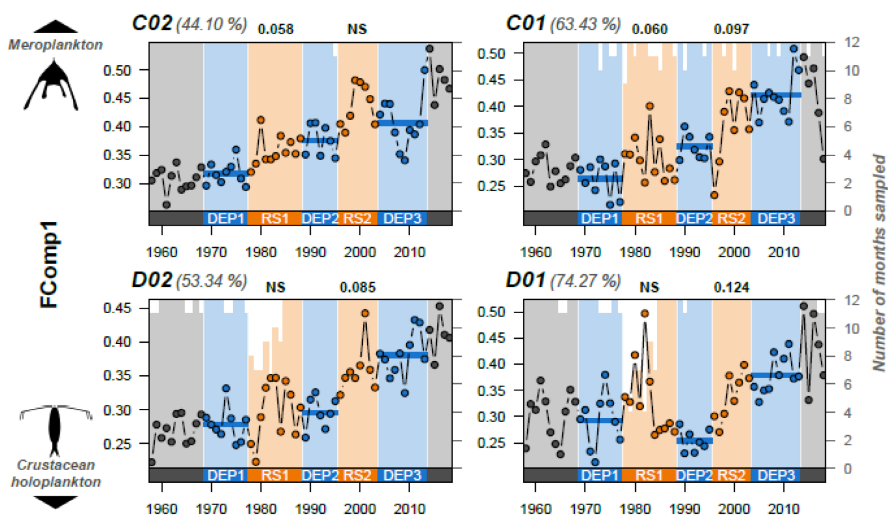
4.1 | New insights into the 1980s regime shift

Previous work established that the 1980s regime shift is primarily a temperature-driven, northward community shift, with a

FIGURE 5 Annual averages in the first functional composition axis (left axes; FComp1) in (a) phytoplankton and (b) zooplankton communities in the four standard areas of the North Sea (C02, C01, D02 and D01), with both so-called regime shifts (RS; in orange) and dynamic equilibrium periods (DEP; in blue) represented. The proportion of variance explained by FComp1 is given in parentheses. Bar plots in the background indicate sampling effort as the number of months sampled (right axes). Blue lines indicate the mean of FComp1 during DEP. The absolute difference between the mean FComp1 during DEP before and after each RS is given above each panel (NS = non-significant at α = .05, Kruskal–Wallis test).

temperate community replacing a subpolar community (Alvarez-Fernandez et al., 2012; Beaugrand, 2004; Helaouët et al., 2013). In other words, the 1980s regime shift is associated with a change in the thermal niche of plankton organisms (Beaugrand & Ibanez, 2004). At large biogeographical scales, it is well established that the thermal niche of organisms can be correlated with certain functional traits (e.g., Bergmann's rule empirically links body sizes and environmental temperature; Meiri & Dayan, 2003). In marine plankton, strong relationships between large-scale temperature gradients and functional traits in copepods emerge when contrasting tropical, temperate and polar communities (Becker et al., 2021; Campbell et al., 2021). However, the subpolar and temperate copepod species present in the North Sea before and after the 1980s regime shift generally have similar traits (i.e., dominantly herbivorous and actively feeding crustacean holoplankton; Supporting Information Appendix S1). The extent of the northward shift in the copepod community within the North Sea during the 1980s regime shift was therefore not sufficient to elicit an important change in the functional traits assessed here (for a similar lack of change in functional composition in spite of change in taxonomic composition in Mediterranean Sea copepods, see Benedetti et al., 2019). The same reasoning can be applied more generally to phytoplankton and zooplankton, as supported by the relatively small changes in functional composition (present study; Di Pane et al., 2022) despite important temperature-driven taxonomic changes (Beaugrand, 2004; Beaugrand et al., 2014). Overall, the 1980s regime shift might therefore be interpreted as a temperature-driven northward community shift insufficient to affect the functional composition of plankton significantly.

Interestingly, despite its small signal in plankton functional composition, the 1980s regime shift had important plankton-mediated impacts on the whole North Sea ecosystem, from phytoplankton biomass (Reid et al., 2001) to the recruitment and functional traits of fish (Beaugrand et al., 2003; Beukhof et al., 2019; McLean et al., 2019). At the community scale, large ecological events, such as regime shifts, consist of changes in both the composition (i.e., relative abundances of species and/or traits) and absolute abundances of species and/or traits. Changes in both composition and absolute

abundances can then affect ecosystem functioning, but disentangling their relative importance remains a challenge. For the 1980s regime shift, the fact that the functional composition of plankton communities remained generally stable suggests that the change of plankton community composition had little impact on ecosystem functioning. Therefore, the plankton-mediated effects of the 1980s regime shift on ecosystems might be mostly attributable to changes in overall abundance or biomass. For example, phytoplankton biomass increased during the 1980s regime shift (Beaugrand, 2004) without significant changes in functional composition (Figures 4a and 5a; see also Di Pane et al., 2022). Nonetheless, this increase in phytoplankton biomass had consequences for ecosystem functioning by favouring planktivorous fish (Beukhof et al., 2019; McLean et al., 2019).

4.2 | New insights into the 1996–2003 regime shift

In contrast to the 1980s regime shift, the 1996–2003 regime shift shows marked changes in the functional composition of plankton. In zooplankton, the increase in seasonal meroplankton relative abundance at the expense of holoplanktonic copepods (Figure 4b) implies that a greater proportion of plankton organisms originally come from the benthos, suggesting an increase in bentho-pelagic coupling. Likewise, in phytoplankton, diatom-associated traits (e.g., siliceous cover, autotrophy, non-motility) that became prevalent year-round after the 1996–2003 regime shift (Figure 4a) tend to favour carbon export (possibly to the benthos) instead of recycling within the plankton (Di Pane et al., 2022; Margalef, 1978; Tréguer et al., 2018). This suggests that a higher proportion of the pelagic production might have been directed to the benthos after the 1996–2003 regime shift. The 1996–2003 regime shift might therefore be interpreted as a shift from a plankton community with relatively reduced connection to the benthos to a community characterized by a stronger bentho-pelagic coupling, both in terms of transfer of living organisms (meroplankton) and of transfer of the pelagic production to the benthos. Given that many important plankton traits respond to bentho-pelagic coupling or affect it (e.g., zooplankton type of life cycle, traits affecting carbon export in phytoplankton), this interpretation would explain the strong association of the 1996–2003 regime shift with changes in plankton functional composition. The strengthening of the bentho-pelagic coupling associated with the 1996–2003 regime shift appears to be attributable to a combined effect of climate-induced increase in temperature and stratification of the water column, in addition to a decrease in nutrient inputs from rivers linked to water quality policies across Europe (Alvarez-Fernandez et al., 2012; Burson et al., 2016; Capuzzo et al., 2018; Di Pane et al., 2022). The decrease in riverine nutrient inputs and increased stratification has been detrimental to primary production and, in particular, to dinoflagellate populations, explaining the increased diatom relative abundance (Alvarez-Fernandez et al., 2012; Burson et al., 2016; Capuzzo et al., 2018; Desmit et al., 2020; Di Pane et al., 2022). As a result, the quantity and quality of prey available to holoplanktonic

copepods decreased, potentially explaining their decreasing abundances (Alvarez-Fernandez et al., 2012; Capuzzo et al., 2018; Di Pane et al., 2022; Traboni et al., 2021). Concomitantly, increasing temperatures have favoured sea urchin (primarily *Echinocardium cordatum*) reproduction, increasing the abundance of their larvae in zooplankton after the 1980s and even more markedly after 2000 (Bedford et al., 2020; Kirby et al., 2007, 2008). The dominance of these meroplanktonic larvae in the zooplankton might also have been facilitated, after the 1996–2003 regime shift, by the relatively low abundance of holoplanktonic copepods that might act as competitors or predators.

Interpreting the 1996–2003 regime shift as a period of increasing bentho-pelagic coupling might give interesting ecological insights into the wider functioning of the North Sea. For example, many fish species showed marked changes in recruitment or abundance across and after the 1996–2003 period owing to different biotic and abiotic factors (for a complete discussion on herring, see e.g., Corten, 2013). Nonetheless, the fish community remained predominantly planktivorous (Beukhof et al., 2019; McLean et al., 2018, 2019) despite a decrease in pelagic primary productivity and holoplanktonic copepod abundances (Capuzzo et al., 2018; Desmit et al., 2020). In a general context of strengthening of the bentho-pelagic coupling, the loss of planktonic pelagic production might have been compensated by an influx of meroplanktonic prey from the benthos. More specifically, the meroplankton of the North Sea is dominated by the larvae of the sea urchin *Echinocardium cordatum* (Kirby et al., 2007, 2008). Interestingly, the distribution of the larvae and adult sea urchins (Weinert et al., 2016) is centred in the eastern North Sea, coinciding with a lower average trophic level in fish, probably associated with planktivory (Beukhof et al., 2019). *Echinocardium cordatum* larvae might thus have become an important food for planktivorous fish after the 1996–2003 regime shift. This mechanism of compensation might have acted in synergy with other mechanisms proposed to explain the dominance of planktivorous fish in the North Sea, such as density-dependent feedback loops (Fauchald, 2010).

4.3 | Comparing the two regime shifts

With reference to plankton communities, it is therefore possible to interpret the two successive North Sea regime shifts as follows. First, the 1980s regime shift was primarily a temperature-driven northward community shift, sufficient to affect the taxonomic composition and abundance of the plankton communities but insufficient to affect their functional composition significantly. Important plankton-mediated effects of the 1980s regime shift on ecosystem functioning are therefore likely to be attributable primarily to changes in overall plankton abundances or biomass rather than to changes in composition. Second, the 1996–2003 regime shift can be interpreted as a period of strengthening of the bentho-pelagic coupling driven mainly by increasing temperature and decreasing nutrient inputs. This regime shift significantly impacted the functional

composition of plankton communities, with potential consequences for ecosystem functioning, such as the maintenance of planktivorous fish in spite of decreasing pelagic production. The present interpretation of the two regime shifts suggests that temperature-induced redistribution of plankton species alone (as during the 1980s regime shift) might have little impact on plankton functional composition (see also Benedetti et al., 2019), at least on the temporal and spatial scales considered here (for larger scale perspectives, see Benedetti et al., 2021; Henson et al., 2021; McGinty et al., 2021). Instead, abrupt functional changes in plankton communities might emerge when environmental changes (e.g., changes in climate and/or nutrient inputs) alter the coupling between habitats (Griffiths et al., 2017; Weinert et al., 2016), as during the 1996–2003 regime shift. We suggest that a better understanding of these couplings and of their impacts on ecosystem functioning might be achieved by integrating different compartments of the North Sea ecosystem (i.e., plankton, nekton and benthos) under a unified functional approach (see e.g., Pecuchet et al., 2018).

4.4 | Caveats

Notwithstanding the new information on the North Sea regime shifts provided by our approach to the CPR data, some technical and conceptual limitations remain. Importantly, the CPR sampling and data do not resolve the full planktonic community. The CPR undersamples both the small size classes of phytoplankton, owing to the rather coarse (270 μm) mesh size, and the larger zooplankton, owing to its small mouth opening (for more details, see Richardson et al., 2006). In addition, because the CPR sampling operates at high towing speeds (20–30 km/h), the most fragile organisms are not well preserved. It is therefore possible that relevant changes in functional composition of poorly sampled compartments of plankton were missed by our analysis. This issue can be alleviated by comparing CPR sampling with other time series that use complementary methods, which reveals generally concordant results (see Di Pane et al., 2022). The CPR sampling also presents different degrees of taxonomic precision, in particular in zooplankton, with holoplanktonic copepods often being determined to the species, whereas meroplankton is determined to coarser levels (e.g., decapod larvae, echinoderm larvae; for detailed information, see Supporting Information Appendix S1). This varying degree of taxonomic precision propagates to the degree of precision of our trait attribution, limiting our ability to decipher fine patterns in change of functional composition. Nonetheless, the patterns discussed in this paper rest on robustly determined traits (e.g., meroplankton vs. holoplankton), which are unlikely to be affected by an improved taxonomic precision.

Finally, by splitting our time series into periods of regime shifts and periods of dynamic equilibrium, we have superimposed the results of previous studies on our functional composition metrics. This framing allowed us to propose a reinterpretation of these events, but it is important to recognize that some of the patterns found

in plankton functional composition do not align with the timing of regime shifts and dynamic equilibrium periods garnered from previous studies. Two points are particularly salient: first, the 1980s regime shift has a small signal in plankton functional composition; and second, some important variation in functional composition occurs during periods considered as periods of dynamic equilibrium (see phytoplankton functional composition in the 1970s; Figure 5a). Unsurprisingly, this illustrates that different metrics of communities and ecosystems can present asynchronous variations (see e.g., Beaugrand, 2004) that might then be studied usefully to reach a better understanding of ecological events (see our discussion on the 1980s regime shift).

4.5 | Conclusion: Plankton functional traits and North Sea regime shifts

The use of functional trait-based approaches to plankton communities allowed us to highlight new aspects of the historically recognized 1980s and 1996–2003 North Sea regime shifts, putting previous studies into a new perspective and highlighting anew the usefulness of functional trait-based approaches (Martini et al., 2021; Ostle et al., 2021). One of the most intriguing result of this work is our finding of a relative lack of change in the functional composition of plankton during the 1980s regime shift, despite the clear detection of the event using a variety of other metrics (absolute abundances of different groups, taxonomic composition etc.; see Beaugrand, 2004). This raises the general question of how to integrate different ecosystem and community metrics that do not present synchronous changes in concepts centred on single ecosystem-changing events, such as a "regime shift". For instance, given that taxonomic composition does not impact ecosystem functioning directly (Hooper et al., 2005), it is unclear whether a change of taxonomic composition alone can be considered as a regime shift or whether it must be associated with a change in total abundance or functional composition. With the development of new metrics describing ecological communities, such as functional composition, ecologists are likely to be confronted increasingly with this question of integration of different metrics. Answering this question is outside the scope of the present paper, but it is one of the many problems with the concept of regime shifts [other problems include detectability (Hillebrand et al., 2020) and the presence or absence of hysteresis (Sguotti et al., 2022)]. We suggest that achieving a better, more formal agreement on what is a regime shift is an important research agenda.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data and code that support the findings of this study are openly available in The Archive for Marine Species and Habitats Data (DASSH) at: https://doi.mba.ac.uk/data/2951.

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BIOSKETCH

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SUPPORTING INFORMATION

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