

Major shift in the copepod functional community of the southern North Sea and potential environmental drivers

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Copepods form the bulk of secondary production in marine ecosystems and are a major resource for higher trophic levels. Copepods are highly sensitive to environmental changes as they are ectotherms with a short life span whose metabolism and development depend on abiotic conditions. In turn, changes in their functional structure (i.e. functional trait composition) can have impacts on ecosystems. We examined changes in the copepod functional community in the North Sea over the past five decades, using a trait-based approach. We observed a shift around 1986–1988: the copepod community was initially dominated by larger herbivores, with a long development time, diapause ability, and highest abundances in summer. This community changed abruptly after 1986–1988, to a dominance of smaller carnivore taxa, with shorter development times, less ability to enter diapause, and that display higher abundances in autumn. This rapid reorganization could be driven by higher water temperatures, lower dinoflagellate abundances, and lower nutrient concentrations. These changes could impact adjacent trophic levels, such as phytoplankton on which several species graze or fish larvae, leading to a mismatch situation with consequences for fish recruitment. Our results emphasize the impact that global and regional changes could have on coastal ecosystems through the role played by copepods.

Keywords: climate change, functional traits, Helgoland Roads Time Series, marine ecosystems, multivariate analyses, regime shifts, zooplankton.

Introduction

In marine ecosystems, plankton represents the base of the food web. Changes in the composition and abundance of primary (i.e. phytoplankton) and secondary (i.e. zooplankton) producers impact the entire food web and associated ecosystem services. In the plankton, mesozooplankton (i.e. zooplankton from 0.2 to 20 mm), form a key trophic group with a central role in the trophodynamics of pelagic ecosystems (Helaouët and Beaugrand, 2007). These organisms also play a fundamental role in nutrient recycling and export of material to depth (Steinberg and Landry, 2017). In mesozooplankton communities, copepods are responsible for the bulk of secondary production and are a major food source for zooplanktivorous organisms (Kjørboe, 2011). In addition to their important ecological roles, copepods are highly sensitive to environmental changes as they are ectotherms with a short life span whose metabolism and development depend on abiotic conditions (Richardson, 2008). Therefore, it is important to understand how these organisms respond to multiple and concurrent changes in the environment.

The North Sea has undergone considerable environmental change over the last decades (Wiltshire *et al.*, 2010). Warming and increasing salinity (Edwards *et al.*, 2002) are among some of the most important ones. As an example, at Helgoland Roads, annual mean temperature increased by 1.9°C between 1962 and 2019 (Amorim *et al.*, 2023). Besides this, due to the success of policy measures targeting nutrient runoffs and phosphorus removal from domestic and industrial wastewa-

ter, the coastal environment of the North Sea has experienced de-eutrophication since the 1980s, after a period of high nutrient inputs that started in the 1950s (Grizzetti *et al.*, 2021). These measures decreased total phosphorus inputs by 50–70% and nitrogen inputs by 20–30% between 1985 and 2002 (Burson *et al.*, 2016). Physical and chemical changes in the North Sea led to the reorganization of marine communities and food web structures and induced shifts in several species (Beaugrand, 2004; Alheit *et al.*, 2005). Such changes have been widely reported for all trophic levels, and particular attention has been paid to planktonic communities in terms of phenology (Scharfe and Wiltshire, 2019), biomass (Wiltshire and Manly, 2004), and functional community structure (Di Pane *et al.*, 2022) for phytoplankton. For zooplankton communities, Alvarez-Fernandez *et al.* (2012) showed abrupt changes in the copepod community marked by a decrease in the abundance of neritic species and a decrease in the proportion of cold-adapted copepods relative to warm-adapted ones. Boersma *et al.* (2015) demonstrated changes in copepod community composition and abundance over the last decades, especially marked by a decline in the calanoid copepod percentage compared to the total abundance, along with an increase in copepod diversity during the late 1980s. The authors specifically observed a significant decrease in the calanoids *Temora longicornis*, *Acartia* spp., and *Pseudo/Paracalanus* spp., while the opposite trend was observed for the cyclopoids *Oithona* spp. and *Corycaeus* spp. While taxonomic changes have been well described (Beaugrand and Ibanez, 2004; Alvarez-Fernandez *et*

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al., 2012; Boersma *et al.*, 2015), these approaches are limited in explaining biological responses and their consequences for ecosystems. Indeed, taxonomic approaches can describe major changes in communities but cannot identify the functional mechanisms that explain why and how some organisms are doing better in a changing environment since they do not allow for direct ecological interpretation (Jansson *et al.*, 2020). Moreover, a taxonomic shift may not necessarily lead to a major functional loss in the community if there is functional redundancy (different species sharing similar traits) (Rosenfeld, 2002). In contrast, if functional redundancy is not present, a small loss of species can lead to a significant change in the functional structure (Auber *et al.*, 2022). Thus, a proper functional understanding of community changes in the North Sea is currently missing. Since the set of traits of an individual determines its success in a given environment and how it can impact ecosystem functioning (McGill *et al.*, 2006), trait-based approaches provide mechanistic information in community ecology (Violle *et al.*, 2007). By definition, functional traits refer to any morphological, physiological, behavioural, or life-history characteristic measured at the individual level that impacts fitness through its consequences on the three fundamental ecological functions of an organism: growth, reproduction, and survival (Violle *et al.*, 2007; Litchman *et al.*, 2013). This reduces the complexity of ecosystems by focusing on a few traits linked to ecological strategies (Litchman *et al.*, 2013), rather than on a potentially long list of species. Therefore, trait-based approaches allow a better understanding of why the environment selects some species at the expense of others (i.e. response traits) and the consequences that changes in traits will have on ecosystem functioning (i.e. effect traits).

Our study uses a trait-based approach to investigate shifts in the copepod functional community of the southern North Sea over the last five decades and their potential links to the changing environment. Using the Helgoland Roads Time Series, a unique data set and one of the richest marine time series in the world (Wiltshire *et al.*, 2010), we aim to (i) characterize the functional structure of the copepod community, (ii) study how this functional structure changed over time, (iii) identify the potential environmental drivers of functional structure changes, and (iv) discuss the potential repercussions of these changes in traits on the food web. We expect to observe major shifts in the copepod functional community linked to changes in species composition previously documented in the literature. Finally, we present potential explanations for the success or decline of species based on the traits they display and the consequences for the ecosystem.

Material and methods

Data origins

The helgoland road time series

Copepod counts from the Helgoland Roads dataset (Greve *et al.*, 2004; Wiltshire *et al.*, 2008) were used in this study. We focused on the copepod rather than on the whole mesozooplankton community, because they account for ~65% of the total mesozooplankton abundance at Helgoland Roads. Additionally, unlike many other taxa of the community, copepods are identified at the genus/species levels making them the ideal target for trait-based approaches.

Phytoplankton, nutrient concentrations, and hydrographic parameters were monitored since 1962 on a work daily basis

near the island of Helgoland in the German Bight (54°11'18" N 7°54' E; DEIMS.iD: <https://deims.org/1e96ef9b-0915-4661-849f-b3a72f5aa9b1>). Due to strong tidal currents and shallow depth (i.e. 6–8 m), the water column at the sampling site is always well mixed, which allows the use of a bucket for a representative water sample of the entire water column (Wiltshire *et al.*, 2010). Salinity and nutrient concentrations ($\mu\text{mol L}^{-1}$) are measured on a filtered aliquot of the water sample using a salinometer and standard colorimetric techniques (Grasshoff *et al.*, 2009), respectively. Sea surface temperature (SST, °C) is measured directly from the bucket and turbidity (quantified as Secchi depth in metres) is measured from the research vessel at the sampling site.

The Helgoland Roads time series was expanded from 1975 onwards, to include meso- and macro-zooplankton (Greve *et al.*, 2004). Zooplankton, including copepods, is sampled three times a week and counted. The mesozooplankton species compartment is sampled using a Nansen net (150 μm , aperture 17 cm, and net length 100 cm) fitted with a flowmeter. The complete monitoring method was described by Greve *et al.* (2004).

The functional response analysis of copepods was performed for the time period 1975–2018. Copepod taxa counts were extracted from the Helgoland Roads dataset, namely, the harpacticoid *Euterpina acutifrons*, the cyclopoids *Corycaeus (Ditrichocorycaeus) anglicus*, and *Oithona* spp. (mainly *O. similis* and *O. nana*), and five calanoids, i.e. *Acartia* spp. (a combination of *A. tonsa* and *A. clausi*), *Calanus* spp. (a combination of *C. finmarchicus* and *C. helgolandicus*), *Centropages* spp. (a combination of *C. hamatus* and *C. typicus*), *Pseudocalanus-Paracalanus* spp. (composed of *Pseudocalanus elongatus* and *Paracalanus parvus*), and *Temora longicornis*. The taxa listed above represent all the copepod species of the Helgoland Roads dataset and almost all of the Southern North Sea. The data can be found on PANGAEA: doi: 10.1594/PANGAEA.873032 (Boersma *et al.*, 2017).

Functional trait matrix

A copepod traits database was developed using a set of traits described by Brun *et al.* (2017). In total, 11 functional traits were gathered, corresponding to the four trait types defined by Litchman *et al.* (2013), i.e. morphological, physiological, behavioural, and life history traits and to the three fundamental and ecological functions of an organism in which they are involved (Figure 1). We included the trait “phenology” as potential trait, which refers to the season at which the maximum abundance of each taxa is observed at Helgoland Roads. Although Brun *et al.* (2017) did not include this trait in their framework, we consider it to be a valuable source of information, especially regarding synchrony in the seasonal timing between copepod community and adjacent trophic levels. Moreover, the phenology is closely associated with various environmental factors, including light availability, wind, and temperature. Instead of solely considering the season, the trait “phenology” encompasses all season-related environmental changes. The trait table consisted of five continuous traits and six qualitative traits of two different types: binary traits with two modalities (e.g. diapause ability: yes/no), and nominal traits with more than two modalities (e.g. dietary preference: herbivory/carnivory/detritivory).

Functional trait data for the eight copepod taxa used in this study were collected either from previous data compilations

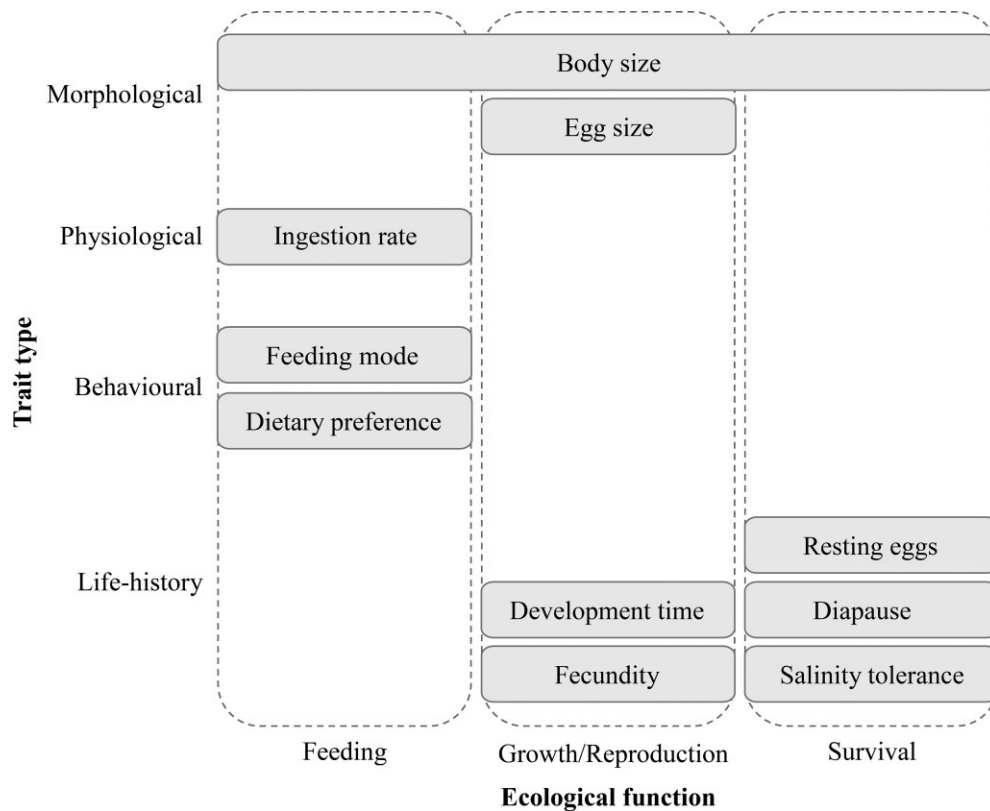


Figure 1. Copepod traits selected for our study and classified according to function and type based on the framework of Brun *et al.* (2017). Body size is considered a “master trait” and transcends all three functions.

on traits or from primary literature (Table 1). When the taxonomic rank was limited to genus in the literature, only trait data of taxa from the genus that are known to occur on Helgoland Roads were extracted from the literature. For continuous traits, the average was calculated when multiple values for the same taxa were found in the literature (Appendix 1). Some taxa such as *Corycaeus* spp. and *Euterpina acutifrons* are poorly documented in the North Sea, and certain traits (e.g. ingestion and egg production rate), remain unrecorded. As a result, our trait table displays 4% of missing values. All data were collected for adults only since early life stages (i.e. nauplii and copepodites) were not identified at Helgoland Roads.

To standardize continuous traits regarding the divergence in experimental design among literature sources, some conversions were performed. Maximum ingestion rate and egg production rate were computed to a standard reference temperature of 15°C by assuming a Q_{10} of 2.8 (Kjørboe and Hirst, 2014), from those cases where the measurements had been taken at different temperatures. The same was done for development time, using Bělehrádek’s empirical equation (Mauchline, 1998) shown below:

$$D = a(T - \alpha)^b.$$

Whereby D is the development time from egg to adult in days, T is the standard reference temperature in °C i.e. 15°C, a is a constant related to body size, α is a constant related to the embryonic duration, and b is a constant set at -2.05 for copepods (Mauchline, 1998). With regard to egg size, when information on carbon biomass was not available in the literature, outer diameter (μm) was converted into volume. Volume was

then converted into $\mu\text{g C}$ by assuming $0.14 \times 10^{-6} \mu\text{g C } \mu\text{m}^{-3}$ (Kjørboe and Sabatini, 1995).

Data preparation

First, we calculated the average monthly values of environmental parameters and taxa abundances. This was done in order to smooth the data and obtain a homogeneous time step, which is necessary for time series analyses.

Local environmental factors monitored at Helgoland Roads were used as explanatory variables: sea surface temperature (SST), salinity, Secchi depth, and nutrient concentrations, namely silicate (SiO_4^{4-}), phosphate (PO_4^{3-}), nitrate (NO_3^-), nitrite (NO_2^-), and ammonium (NH_4^+). In addition, the abundance of potential food, dinoflagellates, and diatoms (cells L^{-1}) were also used as explanatory variables.

As turbulence may enhance the encounter rate between copepods and their prey, wind speed (m s^{-1}), and direction were also examined and were obtained from the DWD Climate Center (<https://cdc.dwd.de/portal/>). The complete environmental matrix comprised then 11 parameters.

Monthly taxa abundances and environmental parameters time series were created using “ts()” function from the R *stats* package, starting in 1975 and with a frequency of 12 (i.e. monthly data). All time series showed seasonal patterns. As seasonality was not the focus of our study, each time series was initially decomposed through moving averages in order to extract the trend using “decompose()” function from the R *stats* package. The decomposition process calculates the three main components of a time series, i.e. seasonality, random, and trend by estimating and subtracting each component from the original data. Given that the seasonal variation

Table 1. Copepod functional traits selected for this study.

Type	Traits	Description	Unit	Variable	Level/Range	Reference
Morphological	Body size	Mean total length	mm	Continuous	[0.3; 5]	Brun <i>et al.</i> (2017)
	Egg size	Mean μg Carbon	$\mu\text{g C}$	Continuous	[0.014; 0.320]	Marcus (1996); Razouls <i>et al.</i> (2005); Brun <i>et al.</i> (2017)
Physiological	Ingestion rate (Ingestion R)	Mean specific ingestion rate converted at 15°	$\mu\text{g C mg C}^{-1} \text{ h}^{-1}$	Continuous	[8.35; 162.58]	Kjørboe and Hirst (2014)
Behavioural	Feeding mode	Whether feeding current, ambush feeding, or both	–	Binomial	Yes/No	Barton <i>et al.</i> (2013); Brun <i>et al.</i> (2017)
	Dietary preference	Omnivores with a preference for either herbivorous detritivorous or carnivorous diet	–	Nominal	Herbivore/Detritivore/Carnivore	Greve <i>et al.</i> (2004)
Life-history	Egg production rate (EPR)	Mean egg production rate converted at 15°	egg female ⁻¹ day ⁻¹	Continuous	[0.14; 173.20]	Hirst and Kjørboe (2002)
	Diapause	Potential to express the diapause trait as copepodite or adult stages	–	Binomial	Yes/No	Mauchline (1998); McGinty <i>et al.</i> (2018)
	Salinity tolerance	Whether stenohaline or euryhaline	–	Nominal	Steno/Euryhaline	Collins and Williams (1982)
	Development time (Dev time)	Generation duration (from egg to adult stage) at 15°C	day	Continuous	[19.30; 31.56]	Mauchline (1998)
	Resting eggs	Potential to produce resting eggs	–	Binomial	Yes/No	Marcus (1996)
Other	Phenology	Season associated with the maximum abundance	–	Nominal	Summer/Autumn/Summer–Autumn	Boersma <i>et al.</i> (2017)

remained relatively stable over time within each time series, the choice of additive decomposition was appropriate. In order to perform the decomposition, missing data were imputed beforehand via linear interpolation using “na_seadec()” function from the R *imputeTS* package. Trends in abundance and environmental parameters (i.e. seasonally detrended data) were extracted and used in our analysis (Figure 2). Because wind direction is circular in nature, the mean was calculated using the “circ.mean()” function from the *CircStats* R package before decomposition. Therefore, trend in wind direction ranged from around -90° to 25° corresponding to a wind range from West to North East.

Data analyses

All analyses were conducted in the R environment (R Core Team, 2020) with a threshold of significance set at 5%.

Functional structure of the copepod community

One approach that provides essential information on the functional community structure is the use of ordination methods

that allow to examine the functional structure of biological communities by projecting their constituting species in a multidimensional functional space based on the species’ trait combinations (Mouillot *et al.*, 2013). The first step was to quantify traits dissimilarity between taxa by using distance-based measures (Figure 2). Because we had different traits in our dataset (i.e. binomial, continuous, and nominal), a Gower distance matrix, which allows mixing qualitative and quantitative data (Villéger *et al.*, 2008), was computed by calculating pairwise dissimilarities between traits using “daisy()” function from the *cluster* package. Missing values in a row are not included in the dissimilarities involving the row. A Principal Coordinates Analysis (PCoA) based on the distance matrix obtained was then performed to evaluate the trait difference between taxa (Figure 2). A Cailliez correction was applied to fix the negative eigenvalues (Borcard *et al.*, 2018). To assess temporal changes in the functional space, the centroids of the community were computed for each year by using the abundance-weighted positions of all the taxa on the first two PCo axis. Each centroid was plotted in the ordination space (PCoA), and the trajectory was then examined (Figure 2).

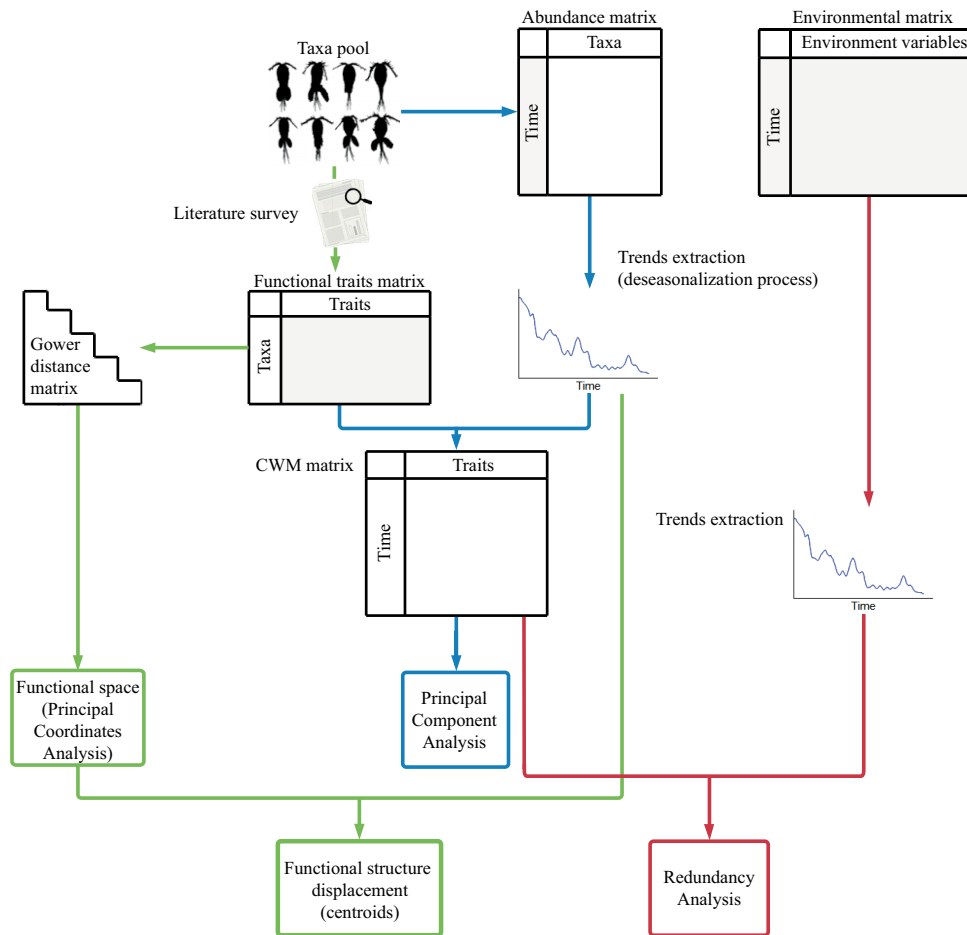


Figure 2. Workflow diagram for the different analyses of this study. The three main steps are represented by the coloured arrows. Green: characterization of the functional community structure. Blue: change in the functional community structure. Red: environmental drivers of the changes in the functional community structure.

Shift in the functional community structure

To assess potential shifts in the functional community structure over time, a Community Weighted Mean (CWM) was generated by combining the monthly copepod abundance table and the functional trait table. The CWM is the average value of the traits weighted by the abundance of all taxa present in the community. For binomial and nominal traits, the CWM is the proportion of each modality within the community. Therefore, the value of each modality ranged between 0 and 1. A centred-scaled Principal Component Analysis (PCA) was then performed on the CWM table, displaying the temporal dynamics of the functional community when all the traits are considered simultaneously (Figure 2). Traits that contributed more than the mean contribution were considered important enough to contribute to axis creation. To assess the existence and timing of potential sudden changes in the copepod functional community, a Sequential *t*-test Analysis of Regime Shift (STARS) was performed (Rodionov, 2004). STARS was conducted on the PC1 and PC2 scores with a 10-year moving window (i.e. cut-off length) using the “Rodionov()” function from the *rshift* package. This method computes a Regime Shift Index (RSI) used to statistically accept or reject the presence of a sudden change in the community that persists over time. As regime shift detection can be achieved using a diverse range of quantitative techniques (Andersen *et*

al., 2009), other methods were explored (e.g. multiple change point, single change point, and chronological clustering). Results for each method are provided in Appendix 2.

Spearman correlation coefficients were used to examine the correlation between the traits that differentiate taxa the most (i.e. PCo1 and 2 scores), and those that changed the most over time (i.e. PC1 and 2 scores). It is worth noting that PC1 scores were recalculated using yearly abundance, in contrast to the previous monthly analysis. This adjustment was made with the aim of investigating if the traits differentiating taxa the most were the same as those differentiating the years. Hence, a significant correlation indicates a shift in the functional structure, whereas the absence of correlation indicates that the functional change over time is associated with traits of lesser importance in structuring the functional community.

Environmental drivers of the functional community structure changes

Once the temporal dynamics of the functional copepod community were assessed, the main question was to know which traits are most likely to dominate in the copepod community under different environmental conditions. At a community scale, the Community-Weighted Mean-Redundancy Analysis (CWM-RDA) is one of the most suitable methods to study the response of CWM traits to environmental gradients (Figure 2).

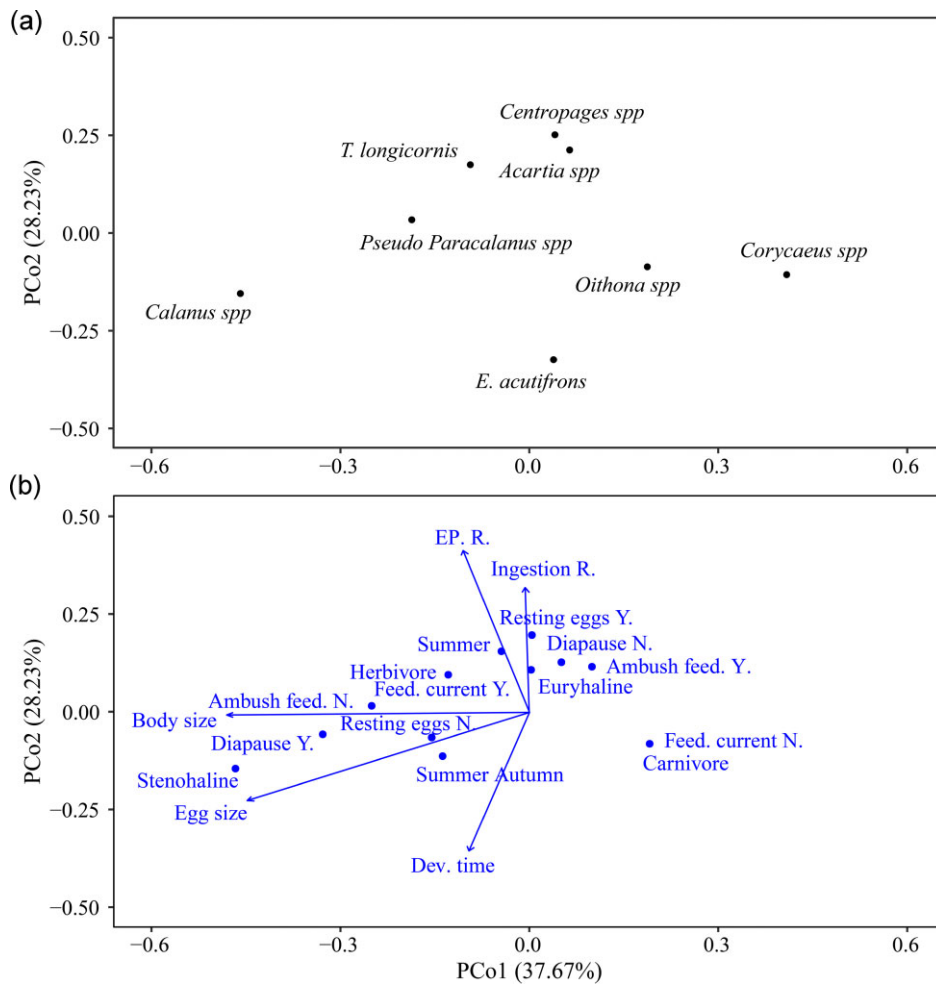


Figure 3. Functional space of the copepod community. (a) With the position of the eight taxa. Points are plotted in the space according to the trait values of the corresponding taxa. (b) With the traits driving the position of taxa along PCoA axes 1 and 2. Results of PCoA showing the first two principal coordinates, which explain 37.67 and 28.23% of the variation between taxa. Arrows and points correspond to quantitative and qualitative traits, respectively. EP = egg production; R = rate; Dev = development; Feed = feeding; Y = yes; N = no.

This method is a Redundancy Analysis (RDA), with a CWM table as a response matrix. Collinearity between environmental variables was checked through a Variance Inflation Factor analysis (VIF) with a threshold value set at 10 (Legendre *et al.*, 2011). None of the variables showed collinearity. A forward selection procedure was then applied to find the most parsimonious model. The procedure was based on a double-stopping criterion involving *P*-values and an adjusted R^2 [“ordiR2step()” function from the *vegan* package] to avoid a type I error and an overestimation of the amount of variance explained (Blanchet *et al.*, 2008). The significance of the model was then tested through an Anova-like procedure with 999 permutations (Legendre *et al.*, 2011). Environmental parameter trends used to compute the RDA are given in Appendix 3.

Results

Characterizing copepod functional space

Our first objective was to define the functional space of the copepod community by using the traits of dissimilarity between each taxon (Figure 3).

Together, the first two axes of the PCoA explained 65.9% of the trait variation between taxa (37.67 and 28.23%, respectively). The first axis of the functional space was broadly characterized by differences between taxa with a larger body and egg size (negative part of PCo1) and taxa with smaller body and egg size (positive part of PCo1) (Figure 3b). The negative part of axis 1 was also characterized by herbivorous current feeding taxa, with an ability to enter diapause, and taxa with low tolerance to salinity variations (i.e. stenohaline). Conversely, the positive part of axis 1 was represented by carnivorous ambush feeding taxa. In Figure 3b, the second axis reveals a clear distinction between two groups of taxa. The first group, characterized as “ambush feeders”, exhibit high egg production, high maximum ingestion rate, and short development time (positive part). The second group, on the other hand, displays lower egg production and lower maximum ingestion rate, coupled with longer development time (negative part).

Temporal dynamic in the functional space (i.e. in the relative contribution to trait differences among taxa) were then assessed by examining the movement of functional space centroids over time (Figure 4). Centroid’s movement within the functional space ranged from -0.03 to 0.03 along the first

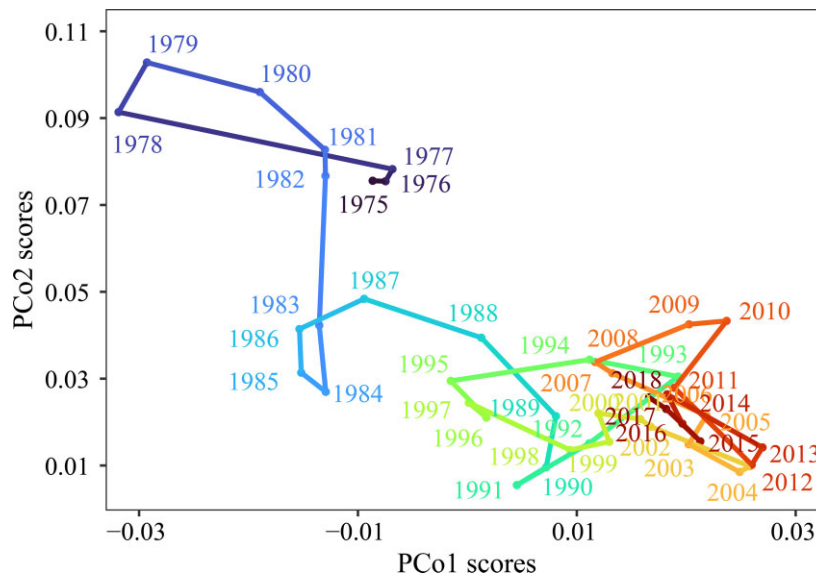


Figure 4. Temporal displacement of the copepod functional space centroid between 1975 and 2018. Centroids (coloured points) are positioned in the PCoA ordination space along the two main axes. A shift of the centroid along the axes of the PCoA indicates a shift in the representation of traits towards the direction taken by the centroid. This indicates a relative increase in the significance of those traits. Rapid colour intensity changes indicate a period of fast functional structure change.

axis and 0 to 0.10 along the second axis. From 1975 to 1982, centroids were located in the top left and moved sharply from 1982 to 1984 toward the bottom. Originally located in the positive part of PCo2, the displacement of the centroid towards the origin showed that the functional community structure shifted from a community with a high maximum ingestion rate, egg production rate, and short development time toward a more balanced community regarding traits affiliated with axis 2. Between 1987 and 1989, a second displacement of the centroids was observed along the first axis from the left to the right part. After these years, especially after 1988, the community centroids were all placed in the bottom right, characterized by smaller, carnivorous copepods with smaller eggs.

Shift in the functional community structure

Our second objective was to study the temporal dynamics of the copepod functional community. For this purpose, we generated a CWM matrix using functional traits and monthly taxon abundances and then performed a PCA (Figure 5).

The first two axes of the PCA represented 87.76% of the total functional structure variation over time (Figure 5a), with the first axis accounting for 67.75% of the temporal trait variability. Nine traits (with a total of 14 modalities) contributed to PC1 creation, namely, body size, diet preference (i.e. herbivory and detritivory), seasonal occurrence (autumn and summer), maximum ingestion rate, development time, diapause ability, resting eggs, salinity tolerance, and egg production rate (Appendix 4a). PC1 scores (i.e. the first index of community structure changes over time) displayed high variability with scores ranging from -9.70 to 4.70 . Negative values were observed from 1975 to 1988, with a minimum value in 1979 (Figure 5b). This period was characterized by a functional community dominated by larger herbivorous copepods with a long development time, a high egg production rate, a low maximum ingestion rate, and a peak of occurrence in summer. These organisms were also characterized by an abil-

ity to enter diapause or to produce resting eggs and to tolerate high salinity variation (Figure 5a). PC1 scores started to move from 1980 on and switched from negative to positive in 1988. These temporal dynamics indicated a shift toward a functional community dominated by smaller, detritivorous copepods with a shorter development time, a lower egg production rate, a higher maximum ingestion rate, and a maximal abundance in autumn. Unlike the 1970–1980's community, the new community was less able to enter diapause or to produce resting eggs and to tolerate larger variations in salinity. The sequential *t*-test analysis of regime shifts aligns with the observations of PC1 scores and identified a strong shift in the copepod functional community between 1986 and 1988 (Figure 5b; Appendix 5).

The second axis accounted for a smaller percentage of the trait temporal variability (20.01%). Ambush feeding, feeding current, carnivore, seasonal peak in summer/autumn, and salinity tolerance contributed significantly to the axis creation (Appendix 4b). Fluctuations over time also occurred along PC2, despite a much lower variability than PC1 (i.e. PC2 scores ranging from -5.48 to 4.29) and sequential *t*-test did not identify any shift in the functional copepod community for the traits associated with PC2.

The correlation between axes scores was then tested to see if the traits differentiating taxa the most (PCo1 and 2) are the same than those differentiating the years (PC1) depending on their trait's composition. PC1 scores were highly correlated with PCo1 scores ($\rho = 0.84$; $p < 1.0 \times 10^{-3}$) and PCo2 scores ($\rho = -0.92$; $p < 1.0 \times 10^{-3}$). This shows that the trait differentiating species the most (PCo1 and 2) are also traits that are responsible for major changes over the year (PC1). These traits include body size, dietary preference, development time, egg production and ingestion rates, and abundance in spring compared to autumn. Additionally, correlations between PCo1 and 2 with PC2 scores, which accounted for a lower percentage of traits temporal variability, were also tested. Correlation between PCo1 and PC2 were weaker but

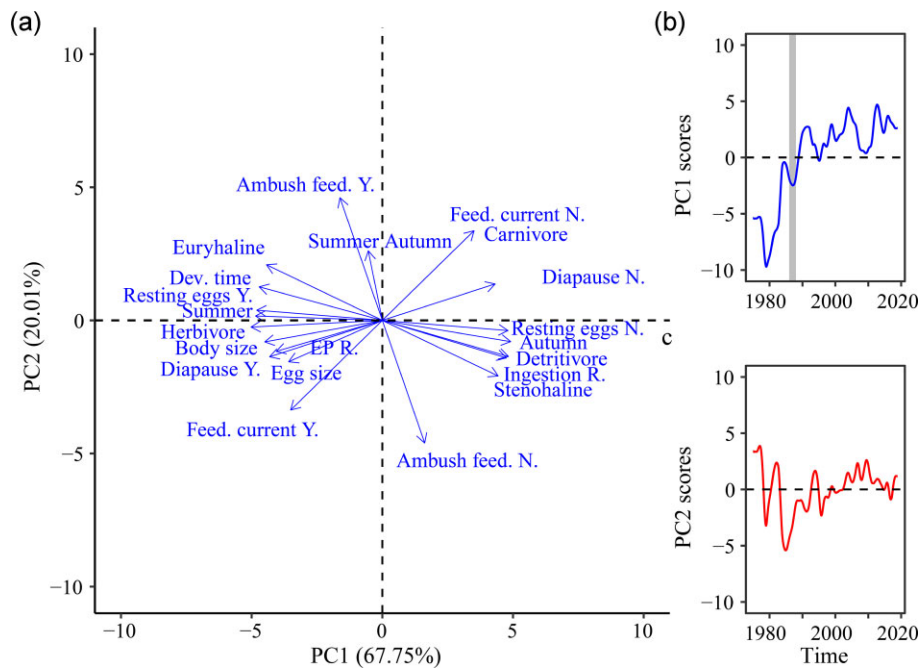


Figure 5. PCA on CWM matrix. (a) Results of PCA showing the first two principal components, which explain 67.75 and 20.01% of the temporal variation in the community trait composition. (b) Temporal dynamics (monthly) of the first axis of the PCA. The grey rectangle indicates significant shifts. (c) Temporal dynamic (monthly) of the second axis of the PCA. EP = egg production; R = rate; Dev = development; Feed = feeding; Y = yes; N = no.

still significant ($\rho = 0.44$; $p < 0.01$), while the correlation between PCo2 and PC2 was not significant ($\rho = 0.15$; $p = 0.33$).

Link between environment and functional community changes

The variance in copepod trait structure was attributed to fluctuations in diatom and dinoflagellate abundances, wind speed and direction, as well as variations in nitrate (NO_3^-), ammonium (NH_4^+), phosphate (PO_4^{3-}), sea surface temperature (SST), and salinity ($p < 0.001$) (Figure 6). Based on R2 and p -value, silicate (SiO_4^{4-}), nitrite (NO_2^-), and Secchi depth were excluded from the final model.

The first axis represented 56.41% of the variance constrained by the environment (Adj-R2 = 0.73) and was mainly described by NH_4^+ (correlated at -0.94 with the first axis), PO_4^{3-} (correlated at -0.82), SST (correlated at 0.68), and wind speed (correlated at 0.69). Wind direction (correlated at -0.52), salinity (correlated at 0.46), and dinoflagellates (correlated at -0.44) described this axis to a lesser extent. As the environmental parameters were standardized, canonical factors may be used to compare the relative weight of initial variables. Thus, NH_4^+ contributed 5 and 8 times more to the first axis than wind speed and SST, respectively, and over 100 times more than PO_4^{3-} (Appendix 6).

The CWM traits of the copepod community were projected along the first axis of the RDA. Along this axis, herbivory, diapause ability, production of resting eggs, slow development time, high egg production rate, body size, seasonal peak in summer, and egg size were positively correlated with NH_4^+ , PO_4^{3-} , and dinoflagellate abundance, and negatively correlated with SST, salinity, and wind speed.

The second axis represented 9.70% of the CWM traits variation constrained by the environment and was mainly described by NO_3^- (correlated at -0.49 with the second axis) and SST (correlated at 0.45). These two variables contributed

equally to this axis. Along this axis, feeding current was positively correlated with NO_3^- concentration, while carnivory was negatively correlated with the latter. For both axes 1 and 2, diatom abundance is not well represented, indicating a very low correlation between this variable and the traits affiliated with the two axes.

Discussion

Shift in the copepod functional structure

In this study, we investigated the copepod community functional structure of the southern North Sea over the past five decades. We found that the functional community shifted during the end of the 1980s. Prior to 1986–1988, the functional copepod community was characterized by larger herbivorous copepods with a long development time, a high egg production rate, an ability to enter diapause or to produce resting eggs, to tolerate high variation in salinity with high abundance in summer. In contrast, after 1986–1988, the community shifted towards a community dominated by smaller carnivorous or detritivorous copepods, more abundant in autumn, with shorter development times, lower egg production rates, less able to enter diapause or to produce resting eggs as well as to tolerate high variations in salinity. These traits were the same as the ones differentiating taxa the most. This illustrates a complete reversal of the functional structure from one trait structure dominance to its opposite. This shift can be directly associated with two distinct life history strategies, with different trade-offs between body size, development time, and fecundity (Kjørboe and Hirst, 2008; Barton *et al.*, 2013). Indeed, copepod displaying a short development time will mature earlier resulting in a higher number of reproduction events, although with smaller egg production rates per event. However, as they mature at a smaller size, they may be more vulnerable and prone to higher mortality compared to

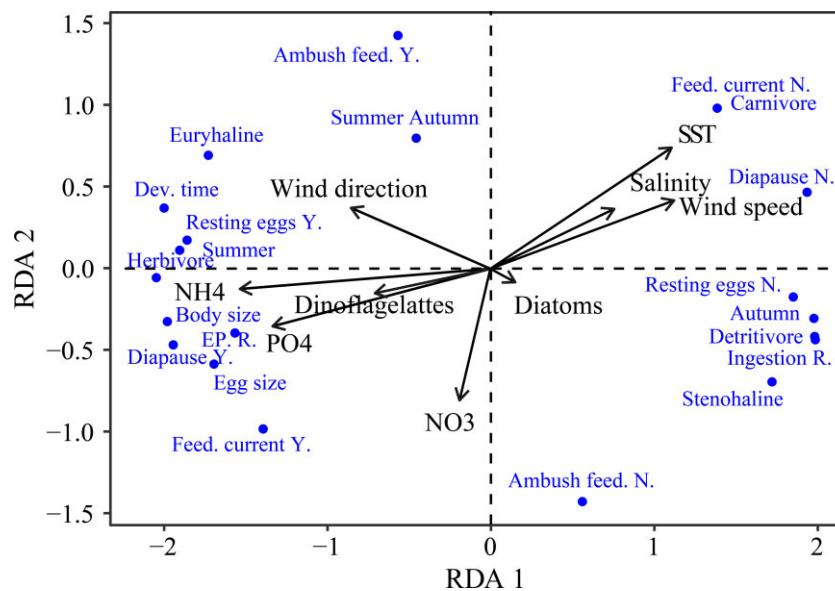


Figure 6. RDA applied on the CWM matrix using the environmental table as explanatory matrix. Adj-R2 = 0.73. Results of RDA, showing the first two principal components, that explain 56.41 and 9.70% of the CWM traits variation. CWM traits are represented in blue and environmental variables selected by the forward selection procedure are represented by the black arrows. The angles between CWM trait variables and those representing environmental variables reflect their linear correlation (type II scaling). EP = egg production; R = rate; Dev = development; Feed = feeding; Y = yes; N = no.

copepods displaying long development time. Thus, we suggest that the community after 1986–1988 invests more in reproduction than in survival, while the opposite was observed for the community before 1986–1988.

Copepod functional structure shift in relation to environment

Our analysis of the link between environmental variables and the copepod functional structure revealed a strong temporal structuring in the North Sea. The period prior to 1986–1988 was characterized by lower SST and wind speed, as well as higher dinoflagellate abundances, NH_4^+ and PO_4^{3-} concentrations. A significant contrast can be observed with the period after 1986–1988, where the conditions were characterized by higher SST, salinity, and wind speed as well as lower dinoflagellate abundance, NH_4^+ and PO_4^{3-} concentrations.

The decrease in dinoflagellates observed in the late 1990s and early 2000s (Di Pane *et al.*, 2022) could have negatively impacted the food availability for herbivorous taxa as they are an important nutritional resource for copepods (Gentsch *et al.*, 2009). In addition to this decrease in dinoflagellates, the North Sea ecosystem experienced an increase in diatom abundance, resulting in an increase in primary production and in the contribution of diatoms to the overall algal biomass during the late 1980s (Reid and Edwards, 2001; Boersma *et al.*, 2015). However, dinoflagellates are considered a better food source for copepods compared to diatoms (Ban *et al.*, 1997). Diatom traits such as the presence of spines or siliceous protective structures can act as a protective mechanism against copepod grazing (Ryderheim *et al.*, 2022). Although diatom abundances were less associated with changes in copepod community structure than dinoflagellate abundances, it is conceivable that the availability of diatom prey played a role in the shift towards a carnivore and detritivore-dominated community. Even if there is a degree of variation between taxa with a preference for carnivory, detritivory, or

herbivory (McGinty *et al.*, 2018), caution should be taken in interpreting the shift in dietary preferences, given the potential for taxa to display omnivorous feeding and therefore adapting their dietary strategies according to resource availability.

We also observed a negative influence of SST on body size and development time, consistent with the Bergmann's rule that proposes a negative relationship between marine ectotherms' body size and temperature (Campbell *et al.*, 2021). This rule applies at both intraspecific and interspecific levels. As our study focuses on the interspecific level, the decrease observed in body size due to global warming occurs when small species replace larger ones (Rice *et al.*, 2015; Benedetti *et al.*, 2023). This manifests itself as a transition in the taxa composition, with smaller taxa such as *Corycaeus* spp. and *Oithona* spp. replacing larger ones such as *Calanus* spp.

The links found between the environmental parameters, temperature and dinoflagellates, and the traits, size, development time, and food preference, are in line with the study of Benedetti *et al.* (2018), which showed that carnivorous taxa were affiliated with a warmer environment. Similarly, Barton *et al.* (2013) demonstrated that herbivorous taxa that store lipids via diapause will be disadvantaged by warmer waters. The authors did not provide a potential explanation for the link between temperature and these traits. However, body size is considered to be a master trait that transcends all ecological functions (Litchman *et al.*, 2013; Brun *et al.*, 2017). Thus, body size influences other traits such as metabolic rates, egg production rate, feeding mode, and even diapause ability (McGinty *et al.*, 2018). Therefore, the fact that temperature determines the size of the individuals in the community could lead to an indirect change in these related traits.

Decreases in NH_4^+ and PO_4^{3-} concentrations could also indirectly impact the functional community of copepods through phytoplankton food-quality reduction. Indeed, a positive correlation between nutrients (i.e. nitrogen and phosphate) and calanoid copepods abundance has been ob-

served in the North Sea (Boersma *et al.*, 2015). Because of decreasing nutrient concentrations, phytoplankton species will contain more carbon relative to nutrients, which would result in a decrease in food quality for zooplankton (Sterner *et al.*, 1993; Meunier *et al.*, 2018). Thus, the reduction in food quality may have had a significant impact on the observed shift in the copepod community's life strategy around 1986–1988, affecting development, size (Litchman *et al.*, 2013), and consequently, egg production rate. Thus, it would be more advantageous to specialize in food sources other than phytoplankton. Carnivory could be an option, as an intermediate step in the food chain (i.e. herbivorous copepods) can enhance predator productivity when phytoplankton have a low nutritional quality (Yang *et al.*, 2011).

On another note, changes in wind patterns also have the potential to impact the copepod community through changes in water mass movements (Pershing *et al.*, 2004). However, even though wind patterns at Helgoland display significant seasonal variations (e.g. easterly winds prevailing in spring), there has been no substantial change in the wind regime over the past 70 years (Rubinetti *et al.*, in press). Consequently, we cannot accurately attribute the observed shifts in the copepod functional community to changes in water mass movements.

Although the link between copepod functional communities and environmental variables such as temperature and nutrient concentration are consistent with the literature, it is important to note that with our analysis of the relationships between functional traits and environmental variables, we took a correlative approach. Experiments in controlled environments are needed to establish true causality.

Further implications: potential consequences on the food web

The functional changes we reported may have had a knock-on effect on the entire food web. Changes in copepod functional structure may influence fish community through impact on planktivorous fish fitness (Perälä *et al.*, 2020) and larval fish survival (Payne *et al.*, 2009). For example, Payne *et al.* (2009) demonstrated that the timing of recruitment failure of North Sea herring *Clupea harengus* in 2000 coincided with the change in plankton community structure detected in 1998. Moreover, cod recruitment was negatively affected by the changes in the copepod community in the late 1980s (Beaugrand *et al.*, 2003). We show that the post-1986–1988 community was predominantly characterized by smaller taxa, with a faster development time, a delayed peak of occurrence, and less able to enter diapause. Among these traits, phenological traits may alter fish communities. Following the match/mismatch hypothesis (Cushing, 1990), larval fish survival and, consequently, their recruitment success, rely on a spatial and temporal coincidence with their trophic resources. Within the North Sea, most of the fish species spawn during spring (Munk and Nielsen, 2005). Thus, a copepod community displaying a shorter development time and a peak of occurrence during autumn, can lead to mismatch situations between larvae of spring-spawning fish species and the maximal abundance of their prey. Indeed, Beaugrand *et al.* (2003) suggested a mechanism involving the mismatch hypothesis by which temperature change affects the survival of cod larvae. They concluded that the increase in temperature since the mid-1980s has altered the copepod community (i.e. abundance,

size, and timing) in ways that reduce the survival of early life stages of cod.

The shift from a large diapausing to a small non-diapausing taxa-dominated community could be accompanied by a major change in the nutritional quality of copepods for zooplanktivorous fish. Unlike diapausing copepods, non-diapausing ones do not accumulate lipid reserves and are therefore less energetic for their predators (Schnack-Schiel and Hagen, 1994). Smaller taxa could accentuate this phenomenon since small zooplankton are considered a poorer source of energy for their predators (Brooks and Dodson, 1965). In support of this hypothesis, van Deurs *et al.* (2015) showed that when smaller copepods replaced larger ones, the potential growth rate of the sandeel, *Ammodytes marinus*, was reduced by half. Therefore, a shift to smaller copepods could increase natural mortality or reduce growth, which could also lead to a reduction in fish stock renewal (van Deurs *et al.*, 2015).

We hypothesized that the change in copepod diet was probably due to a change in dinoflagellate abundance. However, the 1986–1988 shift in the copepod functional structure may also have directly impacted lower trophic levels. It is well known that copepods may exert a top-down effect on phytoplankton communities through the grazing pressure, especially at the onset of the bloom (Sommer *et al.*, 2001; Jagadeesan *et al.*, 2017). It has been shown that warmer years lead to a delay in the phytoplanktonic spring bloom in the coastal North Sea (Wiltshire and Manly, 2004). The authors discussed that the observed delay could be related to the fact that, due to warmer temperature, copepods may be able to remain present in the environment in autumn and winter making their top-down pressure higher during the phytoplankton biomass building phase (Wiltshire *et al.*, 2008). Our study provides further evidence for this hypothesis. The current copepod community is dominated by individuals with a seasonal peak in autumn and less able to enter diapause. Therefore, the environmental selection of these traits allowed copepods to maintain populations in the environment during the biomass building phase of the phytoplankton bloom, thereby delaying it by exerting a grazing pressure.

While the results of this study provide valuable insights on a shift in the copepod functional community and the environmental variables driving it, it is important to acknowledge some limitations and potential confounding factors that should be considered. Our study focuses solely on the copepod community as they account for 65% of the mesozooplankton community at Helgoland Roads. Consequently, we do not cover the entire spectrum of traits and ecological functions within the zooplankton community. At Helgoland Roads, two taxonomic shifts within the mesozooplankton communities have been documented, occurring in 1983 and 2006–2007, involving nearly all mesozooplankton taxa (Di Pane *et al.*, 2023; Marques *et al.*, 2023). Notably, Appendicularia and Hydrozoans exhibited significant fluctuations in their abundance, characterized by increases and decreases during the first and second shifts, respectively (Di Pane *et al.*, 2023; Marques *et al.*, 2023). Tunicates and hydrozoans are known to exhibit a wide range of traits and contribute to the overall functional diversity of the ecosystem. Consequently, by expanding trait-based approaches to encompass these organisms and, on a larger scale, the entire zooplankton community, we could gain a more comprehensive understanding of the complex interactions and dynamics within the zooplankton community.

Furthermore, an additional limitation arises from the challenge of identifying taxa at the lower taxonomic rank. While some taxa were identified at the species level, such precision is not always possible (Greve *et al.*, 2004; Boersma *et al.*, 2015). Thus, the Helgoland Road dataset considers species of the genus *Paracalanus* and *Pseudocalanus* as a single taxon, as well as *Calanus helgolandicus* and *Calanus finmarchicus* groups as *Calanus* spp. Lower taxonomic resolution can result in some hidden patterns such as change in dominance between two species grouped as one taxon or changes in functional traits that could not be described in this study. Although leading to a loss of precision, the functional trait approach avoids a potential error of judgement, as the traits are inherent to the taxa used, allowing the use of high taxonomic levels (Jansson *et al.*, 2020).

Conclusion

This study represents a systematic and robust approach investigating the changes observed in the copepod functional community, their reasons, and potential consequences. As such, it is an important step forward in understanding how a plankton group, considered as a keystone in marine food web responds to environmental changes. Our findings explained why some species were doing better than others in a changing environment and permitted to link it to the cascading effects on the marine food web. Our study examined trait composition for copepods only. However, because of its crucial place in the marine food web, it would be particularly interesting in future studies to examine trophic trait cascades and how different trophic levels, adjacent to copepods, might affect each other's trait composition, and how these changes in traits can feedback on their environmental drivers. Due to the high complexity of communities, it is particularly difficult to predict their reorganization under global change. Trait-based approaches are therefore interesting tools to solve this problem by grouping organisms according to their functional traits rather than their taxonomy. Hence, we are confident that the use of a trait-based approach could provide a powerful way to evaluate climate change impacts on organisms through a selection of key functional traits.

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Data availability

The data underlying this article are available in the Data Publisher for Earth & Environmental Science PANGAEA, at <https://doi.org/10.1594/PANGAEA.873032>, <https://doi.pangaea.de/10.1594/PANGAEA.960375>, <https://doi.pangaea.de/10.1594/PANGAEA.960407>, or will be shared on reasonable request to LTER.HRSR@awi.de.

Supplementary data

Supplementary material is available at the ICESJMS online version of the manuscript.

Conflict of interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Author contributions

MMD: Conceptualization, Formal Analysis, Investigation, Methodology, Writing. MB: Conceptualization, Data Curation, Writing, Validation, Supervision. CLM: Conceptualization, Supervision, Validation, Writing. IVK: Data Curation, Resources, Writing. KHW: Data Curation, Resources, Writing. JDP: Conceptualization, Methodology, Writing, Validation, Supervision.

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