

# Identification of tipping years and shifts in mesozooplankton community structure using multivariate analyses: a long-term study in southern North Sea

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Many previous studies on the changes in zooplankton communities considered only subsets of the total community. In this study, we investigated the temporal dynamics of the mesozooplankton community structure, considering all taxa (holo- and meroplankton) sampled over the last five decades at Helgoland Roads. We identified two tipping years. The first one occurred in 1983, which is consistent with previous studies conducted on copepods. The second shift, even more pronounced, took place in the mid-2000s. During the first shift, most taxa significantly increased in abundance and kept high densities until the end of the 1990s. Then, we observed in the mid-2000s a sharp decrease in community diversity and abundances of almost all taxa. One of the aims of the study was to test the robustness depending on the choice of taxa. To test this, we selected different subsets of the total zooplankton community, both randomly as well as based on functionality. We observed very similar trends over time for all groups, showing the complete community experienced the same changes. However, the timing of the tipping years depended on the organisms considered. These results highlight that the observed changes in the planktonic community are surprisingly robust and visible in most planktonic organisms.

**Keywords:** helgoland roads time series, holoplankton, meroplankton, multivariate regression tree, tipping point.

## Introduction

The southern North Sea has undergone considerable change over the last decades (Edwards *et al.*, 2002; Wiltshire *et al.*, 2010). Increasing water temperatures (Høyer and Karagali, 2016) accompanied by, first, a period of eutrophication followed by a decrease in nutrient inputs due to mitigation strategies (Meyer *et al.*, 2018) have influenced marine communities and food web structures (Beaugrand, 2004; Alheit *et al.*, 2005a). For instance, the plankton assemblages of the North Sea went through changes in taxonomic structure, abundances (Boersma *et al.*, 2015), and phenology (Scharfe and Wiltshire, 2019). Such changes can lead to sudden shifts in ecosystem status caused by passing a tipping point, beyond which core ecosystem functions, structures, and processes are fundamentally changed. Such events are commonly defined as regime shifts (Andersen *et al.*, 2009).

In the North Sea, two regime shifts, marked by abrupt changes across several physical and biological compartments, were identified for the last 50 years (Reid *et al.*, 2001, 2016; Beaugrand *et al.*, 2013, 2014). The first regime shift happened in the late 1980s (Reid *et al.*, 2001; Beaugrand and Ibanez, 2004; Alheit *et al.*, 2005a; McQuatters-Gollop *et al.*, 2007) and was linked to rapid warming (Reid *et al.*, 2016). Changing environmental conditions led to higher phytoplankton biomass (Reid *et al.*, 1998, 2001) and bloom duration after the shift (Wiltshire *et al.*, 2008). Also, the diversity of calanoid

copepods increased (Beaugrand and Ibañez, 2002; Beaugrand, 2003). Between 1996 and 2003, the North Sea experienced a second regime shift (Beaugrand *et al.*, 2014), marked by higher diatom and lower dinoflagellate abundances post-shift (Alvarez-Fernandez *et al.*, 2012; Hinder *et al.*, 2012; Bedford *et al.*, 2020; Di Pane *et al.*, 2022), which were accompanied by lower abundances of most copepod species (Alvarez-Fernandez *et al.*, 2012; Boersma *et al.*, 2015; Di Pane *et al.*, 2022). This second regime shift was attributed to an increase in temperature and wind speed (Hinder *et al.*, 2012), as well as to a change in the concentration and balance of dissolved nutrients (Alvarez-Fernandez *et al.*, 2012; Boersma *et al.*, 2015; Di Pane *et al.*, 2022).

Structural changes in planktonic communities can have profound impacts on ecosystem functioning. For instance, copepod abundances affect the recruitment of fish species in the North Sea (Reid *et al.*, 2001; Beaugrand and Reid, 2003; van Deurs *et al.*, 2009; Alvarez-Fernandez *et al.*, 2015; Cappuzzo *et al.*, 2018; Perälä *et al.*, 2020). Higher trophic levels, such as fish and their larvae, do not only consume copepods but rather have a quite diverse diet (Nunn *et al.*, 2011). However, only a few studies investigating changes in planktonic communities have so far considered zooplankton organisms other than copepods (Beaugrand *et al.*, 2003, 2014; Kirby *et al.*, 2008). Potentially, this represents a serious shortfall given the diversity of ecological functions and strategies

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**Table 1.** Description of the three functional group subsets used in the analyses.

Subset	Description	Taxa
Copepods	All adult copepod taxa identified	Cyclopoida, <i>Calanus</i> spp., <i>Harpacticoida</i> , <i>Oithona</i> spp., <i>Centropages</i> spp., <i>T. longicornis</i> , <i>Pseudo Paracalanus</i> spp., <i>Acartia</i> spp.
Non-copepods	Meroplankton and holoplankton other than copepods	Echinod. juveniles, Platyhelminthes, Chaetognatha, Ctenophora, Echinodermata larvae, Mollusca, Hydrozoa, Appendicularia, Phoronida, Cirripedia, Cladocera, Annelida, Decapoda zoea
Top-10	The ten most abundant taxa	<i>T. longicornis</i> , Annelida, Copepoda Nauplii, <i>Pseudo Paracalanus</i> spp., <i>Acartia</i> spp., Mollusca, Harpacticoida, <i>Oithona</i> spp., Appendicularia, Cirripedia

that the zooplankton compartment displays (Litchman *et al.*, 2013). Moreover, focusing on holoplankton and essentially ignoring meroplankton could impact research findings. The recruitment of fish and other organisms that feed on plankton is strongly influenced by the abundance and diversity of plankton, and focusing on just a few zooplankton species can lead to misunderstandings when studying the causes of fluctuations in higher trophic level recruitment. Hence, studies on mesozooplankton shifts require a more comprehensive assessment of the changes in the whole compartment to understand ecosystem-level implications.

In this study, we investigated potential structural changes in the mesozooplankton compartment over the last five decades in the southern North Sea by considering a high diversity of taxa and life strategies. Our two main aims were to (1) identify potential tipping years in the structure of the mesozooplankton community and (2) compare the results obtained from the complete mesozooplankton community to those obtained from several subsets of taxa in order to investigate how taxonomic selection affects tipping year identification and trends over time. To do so, we analysed a broad diversity of zooplankton groups, including both holo- and meroplankton, using the long-term dataset of Helgoland Roads (Greve *et al.*, 2004). Using multivariate statistical analyses, we identified periods during which the zooplankton community composition was drastically changed and numerically characterized the ecological success of individual zooplankton at these different time periods. Then, we showed how the selection of functional and random subsets of taxa impacted the identification of tipping years. Finally, we discussed whether using subsets has the potential to accurately describe changes in the zooplankton community or whether the whole community is needed to estimate major structural changes.

## Material and methods

### Data sources

In this study, we analysed the long-term time series of Helgoland Roads (54°11'18"N 7°54'E), in which zooplankton organisms have been sampled three times per week since 1974 (Greve *et al.*, 2004). The data can be found on PANGAEA: doi: 10.1594/PANGAEA.873032 (Boersma *et al.*, 2017). The sampling was done through oblique hauls with the HYDROBIOS quantitative collection device net (150 µm mesh size, aperture 17 cm, net length 100 cm). For a more detailed description of the sampling protocol, we refer the reader to Greve *et al.* (2004). We used data from 1975 to 2018. During this period, all species encountered were identified at 38 constant taxonomic levels. We selected 22 taxa that individually accounted for >0.1% of the total abundance. This selection

permitted to remove very rare (zero-inflated) taxa while retaining a substantial share of the complete community, representing 99.7% of total abundance. We acknowledge that this criterion may have some limitations in terms of capturing the full diversity and evenness of the community. However, this criterion was necessary to focus on the most ecologically relevant and abundant taxa and to reduce noise and variability in the data that can arise from very rare and sporadic taxa. Selected taxa (see Table 1) ranged from species (e.g. *Temora longicornis*) to a broader resolution (e.g. Appendicularia). It must be mentioned that broad resolutions may result in a lack of information regarding changes in dominance within taxa, but the main focus of this study is at the community level, and the use of appropriate multivariate analyses allows the identification of structural changes at the level of the whole plankton community (Beaugrand *et al.*, 2003).

### Data analysis

All analyses were performed under the R environment (R Core Team, 2022). The threshold for significance was set at 5%.

### Data preparation

We first calculated monthly mean abundances for each taxon. This was done in order to smooth the data and obtain a constant time step, necessary for time series analyses. Thus, the fauna datasets had 528 rows (12 months for 44 years). Taxon abundances were then log transformed [ $\log(\text{nb.m}^{-3} + 1)$ ; nb = number of individuals] and decomposed into three constituent components, namely, seasonality, trend, and random (package *stats*). The function isolates the fixed seasonal component using a moving average method, while the trend component is obtained by applying a locally weighted regression to the data after removing the seasonal component (Shumway and Stoffer, 2017). The trend component was used for further analysis.

### Changes in zooplankton community structure

Temporal dynamics of the zooplankton community trends were first studied by calculating total abundances (log transformed), diversity (i.e. Shannon), and evenness (i.e. Pielou) indices over time. The existence and timing of potential shifts in community structure were assessed by chronological clustering using a multivariate regression tree (MRT; package *mvpart*). The MRT of the taxa matrix was built and constrained by time, providing a chronological clustering suitable for detecting tipping points in multivariate time series (Andersen *et al.*, 2009; Legendre and Legendre, 2012; Auber *et al.*, 2015). In the context of the current study, a tipping year refers to a critical threshold beyond which the system undergoes a rapid and potentially irreversible change in its state (Lenton, 2013).

For tipping year detection, we decided to pick the minimum number of significant groups (multivariate analysis of variance, 999 permutations) needed to explain at least 50% of the total variation in order to identify the main shifts and to avoid producing too many small groups. The abundance of each taxon was then compared between periods by Pairwise Wilcoxon Rank Sum Tests, which calculate pairwise comparisons between group levels (i.e. periods) with Holm's corrections for multiple testing. We then calculated indicator values (IndVals, Dufrene, and Legendre, 1997) by carrying out indicator species analyses to uncover links between periods and taxa. This method allows identifying discriminant taxa and the best clustering level (or leaf) they belong to. The IndVal of an "x" taxon, in relation to a "y" period, is defined within each cluster as follows:  $\text{IndVal}_{xy} = \text{Specificity}_{xy} * \text{Fidelity}_{xy}$ , where  $\text{Specificity}_{xy}$  is the proportion of time steps (months) of the period "y" having the taxon "x", and  $\text{Fidelity}_{xy}$  is the proportion of the number of individuals of taxa "x" that are in a "y" period. IndVals vary from 0 to 1, in accordance with the level of association between periods and taxa. The higher the value, the more the taxon is linked to the period. For each taxon, the sum of each IndVal within each period is equal to 1. IndVals were tested by a permutation test (999 permutations) to identify significant associations, with the *p*-value corrected for multiple testing by Holm correction (Borcard et al., 2011). Finally, the mean abundances ( $\pm SD$ ) of each taxon for each previously obtained period were calculated and plotted.

In order to see how the overall community has changed, a principal coordinates analysis (PCoA) was performed on the seasonally detrended fauna matrix. The Bray-Curtis distance was used to calculate the dissimilarity matrix from the fauna matrix. The contributions of taxa in accounting for the variability in the two first axes (PCoA1 and PCoA2) were calculated. PCoA1 and PCoA2 were then used as indices of community structure changes over time.

### Change in tipping year identification

The second main objective was to investigate whether taxonomic selection, such as focusing on a specific group like copepods as an example, affects tipping year identification (MRT) and trend over time (PCoA) and ultimately research conclusions. We repeated the previously described analyses for subsets of functional groups (Table 1).

In addition to these functional subsets, we created several subsets of randomly selected taxa. These subsets were created in order to (1) highlight the minimum number of taxa necessary to observe previously identified tipping years and to (2) compare variations in tipping year identifications and trends over time depending on the taxa considered. To do so, we first created three subsets of ten, six, and three randomly selected taxa. Based the results, we repeated the random selection of six taxa ten times. The outcomes were then compared between subsets and with the results obtained from the complete dataset.

## Results

### Changes in overall zooplankton community structures

The first objective of our study was to describe the temporal dynamics of the zooplankton community at Helgoland Roads over the past five decades. For this purpose, the monthly

total zooplankton abundance and three diversity indices were calculated from the seasonally detrended fauna matrix (Figure 1a). From 1975 to the early 1990s, we observed an increase in the log of the sum of the abundances and Shannon indices, followed by a relatively stable period until 2007, and a sharp decrease after 2007. Conversely, Pielou's evenness index indicates the opposite pattern, with a strong increase until 1985 followed by a sharp decrease until 1990, then a relatively stable period until 2007 before finally increasing again.

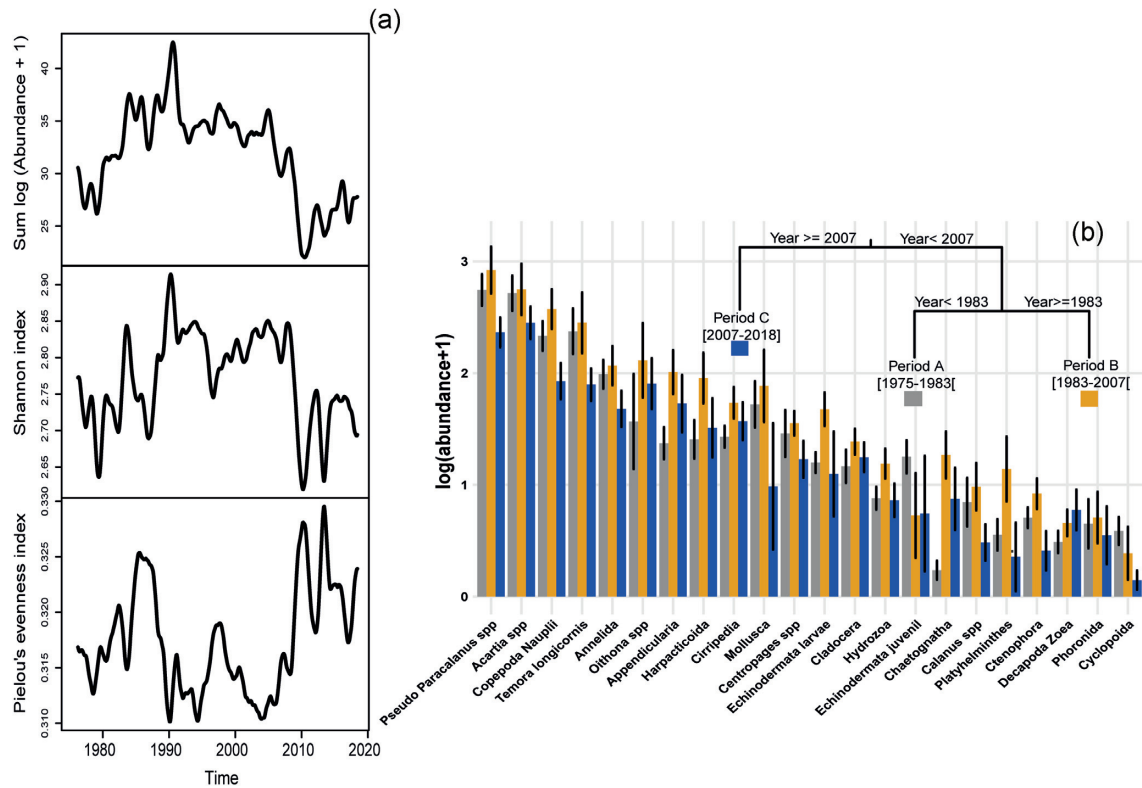
The MRT analysis detected two tipping years and, consequently three time periods. These changes in community structure over time accounted for 52% of total structure variation over the study period. These three periods are characterized by statistically different (permutation test, 999 permutations,  $p < 0.05$ ) taxonomic compositions and abundances (Figure 1b), namely Period A (1975–1983), Period B (1983–2007), and Period C (2007–2018). Beside Echinodermata juvenile and Cyclopoida, which were linked to Period A, and Decapoda zoea to Period C, most taxa were significantly linked to Period B, during which they displayed the highest and most significant indicator values (Figure 1b, Table 2).

Changes in community structure over the time period were then studied by computing a PCoA on the faunal matrix (Figure 2a). It allowed the visualization of the change in the overall community over time within a 2-D axis system. The first two axes explained 64% of the variations observed in the dataset (47% and 17%, respectively). Most taxa (12 taxa) were affiliated with PCoA 1 (Figure 2b), all of them in the positive part of the axis. Decapoda zoea, Appendicularia, *Oithona* spp., Cirripedia, and Chaetognatha were affiliated with the positive part of the second axis, while Echinodermata juvenile, *Temora longicornis*, and *Acartia* spp. to its negative part. The taxa Mollusca and Phoronida were affiliated with neither the first nor second axis (contribution to axes lower than average). Subsequently, PCoA coordinates (months of each year) along both axes were plotted over time (Figure 2c). The two axes showed different trends over time. The community represented by the first PCoA axis increased in abundance until the beginning of the 1990s, followed by a decline, especially sharp after the mid-2000s. The taxa represented by the positive part of the second PCoA axis have generally increased in abundance throughout the past five decades.

### Tipping year identification and trend comparison

The previous analyses carried out on the complete dataset were repeated on different subsets in order to compare the trend and timing of significant tipping years in community change depending on the taxa considered (Table 3).

For the three functional group subsets, the MRT analysis showed that three periods were sufficient to reach 50% of explained variation in the structure composition over time. The first significant tipping year was identified in 1981 for the copepod subset, 1983 for non-copepods, and 1989 for the ten most abundant taxa, showing a detection of changes varying up to 8 years. In the copepod and non-copepod subsets, only cyclopoids and echinoderm juveniles were linked to the first period, respectively, as in the analyses of the whole data set. Interestingly, in the top-10 subset, the copepods *T. longicornis*, *Pseudo Paracalanus* spp., and *Acartia* spp. were linked to the first period (1975; 1989), while these same taxa had a sig-



**Figure 1.** Zooplankton community temporal dynamics. (a) Total zooplankton abundance ( $\log \text{nb.ind.m}^{-3}$ ), taxonomic richness (Shannon index), and Pielou's evenness over the time period. (b) Mean abundance ( $\text{nb.m}^{-3}$  log transformed  $\pm$  SD) of each taxon for each period defined by the MRT. All comparisons were found to be significantly different at the 5% threshold, except for *Acartia* spp. Period A versus B; Echinodermata larvae Period A versus C; Hydrozoa Period A versus C; and Echinodermata juvenile Period B versus C. See Appendix 1 for Pairwise Wilcoxon Rank Sum Tests  $p$ -value results.

**Table 2.** Affiliation of taxa to the periods defined by the MRT.

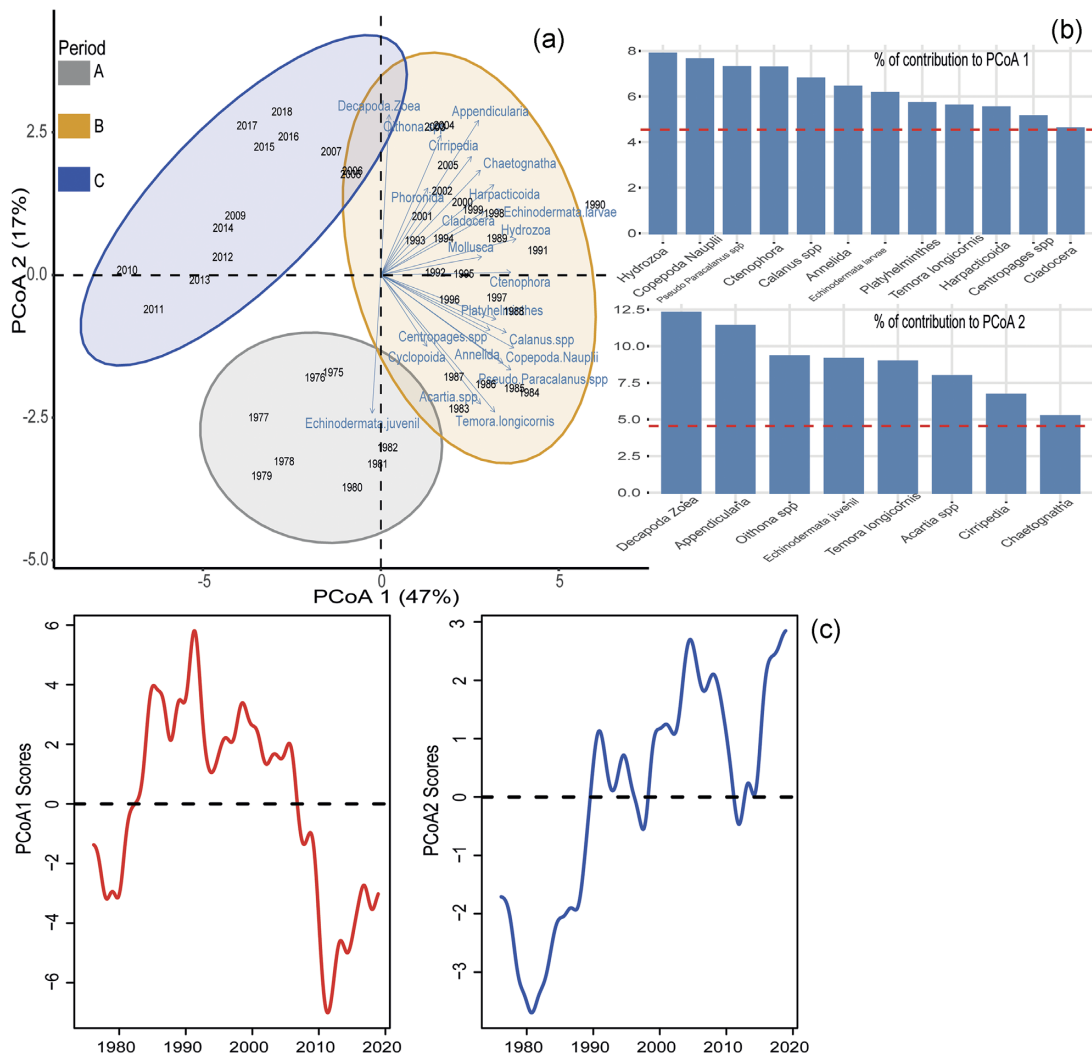
Taxa	Period	Indicator value	$p$ value
Cyclopoida	A	0.53	<0.01***
Echinodermata juvenile	A	0.46	<0.01***
Platyhelminthes	B	0.56	<0.01***
Chaetognatha	B	0.54	<0.01***
Ctenophora	B	0.46	<0.01***
<i>Calanus</i> spp.	B	0.43	<0.01***
Echinodermata larvae	B	0.43	<0.01***
Mollusca	B	0.42	<0.01***
Hydrozoa	B	0.41	<0.01***
Harpacticoida	B	0.41	<0.01***
Appendicularia	B	0.4	<0.01***
<i>Oithona</i> spp.	B	0.38	<0.01***
Copepoda Nauplii	B	0.38	<0.01***
Phoronida	B	0.38	<0.01***
Cirripedia	B	0.37	<0.01***
<i>Centropages</i> spp.	B	0.37	<0.01***
Cladocera	B	0.37	<0.01***
<i>Temora longicornis</i>	B	0.37	<0.01***
<i>Pseudo Paracalanus</i> spp.	B	0.37	<0.01***
Annelida	B	0.37	<0.01***
<i>Acartia</i> spp.	B	0.35	<0.01***
Decapoda zoea	C	0.41	<0.01***

For each taxon, the cluster (or period) i.e. statistically linked (permutation test; 999 permutations) is given along with the indicator value (ranged from 0 to 1). Period A (1975–1983); Period B (1983–2000); Period C (2007–2018).

nificant Indval in the second period (1981; 2003) within the copepod subset, indicating a strong association to the years comprised between 1981 and 1989. The same schema was observed for Annelida, affiliated to the top-10 subset during

the first period but to the second period (1983; 2008) within the non-copepod subset. The second tipping year appeared closer between subsets, as observed in 2003 for copepods, 2008 for non-copepods, and 2007 for the ten most abundant





**Figure 2.** Changes in zooplankton community structures. (a) PCoA is performed on log-transformed monthly abundances. Ellipses represent the elliptical contours of each period defined by MRT (as a Supplementary variable) at a probability of 95%. For clarity, individual data points (months of each year) were not represented, but the year's barycentre was added. (b) Taxa contribution to the first and second axes. The red dotted lines represent the mean contribution of all taxa. Only taxa having a contribution superior to the mean are represented. (c) PCoA1 and PCoA2 individual data points (months) coordinates.

taxa subset, showing a detection of tipping years varying up to 5 years. During the third period, the only significantly affiliated taxon was Decapoda zoea within the non-copepods subset, being in line with the results from the complete community (Table 2).

Regarding random subsets, two significant tipping years were always identified, one during the 1980s and another during the 2000s, with tipping year identification varying up to 2–3 years, respectively (Table 3). At the threshold of at least 50% of the variation explained by two tipping years, the use of only three random taxa did not permit to identify major changes, explaining only 39% of the total variation. In other words, this result means that a higher number of periods is needed to reach 50% of total variations. However, taxa affiliation within periods was consistent among all subsets.

To explore the effect of taxa selection on trend over time, we repeated PCoA analyses on the functional and random subsets. Additionally, we created ten random subsets of six taxa, which was the minimum number of taxa fulfilling the

threshold of 50% of variation explained by two tipping years.

The changes in PCoA 1 and PCoA 2 coordinates over time graphically illustrated the changes in community structure (Figure 3). Along the first axes (Figure 3b and c), all subsets followed a similar trend over time, showing a homogeneity in the response of most taxa over time. However, the magnitude and timing of observable changes were determined by the number and composition of taxa considered. For the functional subsets (Figure 3a), copepods were the first group to experience substantial changes, while the non-copepod subset showed a delayed response. The three random subsets (Figure 3b) allowed us to see the impact of the number of taxa on the magnitude of the changes. The random subset with ten taxa was the furthest from the origin, while the random subset with three taxa was the closest. Figure 3c shows the trend for the ten random subsets of six taxa. This graph shows, therefore, the variation that can be observed for the same number of randomly selected taxa. As with the other subsets, all fol-

**Table 3.** Multivariate regression trees (MRT) and species indicator analyses outcomes for each subset.

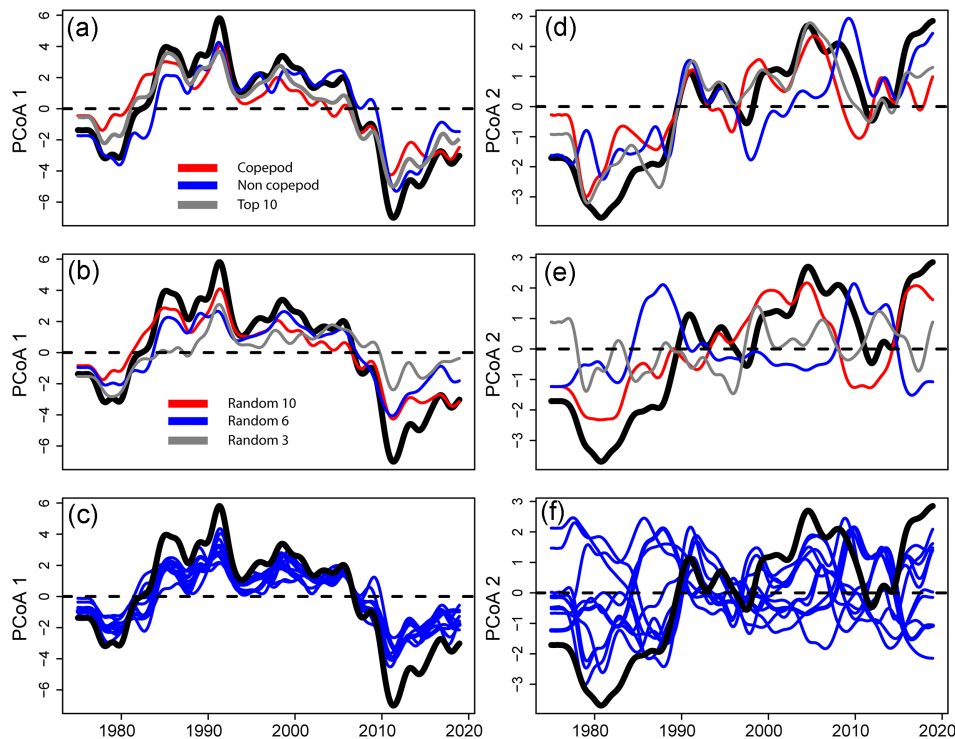
Subset	MRT		Species indicator analyses	
	Variation explained	Periods	Affiliated taxa	IndVal
Copepod	54%***	(1975; 1981) (1981; 2003)	Cyclopoida	0.53***
			<i>Calanus</i> spp.	0.44***
			<i>Harpacticoida</i>	0.40***
			<i>Oithona</i> spp.	0.38***
			<i>Centropages</i> spp.	0.38***
			<i>T. longicornis</i>	0.37***
			<i>Pseudo Paracalanus</i> spp.	0.37***
			<i>Acartia</i> spp.	0.35***
			-	-
			-	-
non-copepod	51%***	(2003; 2018) (1975; 1983) (1983; 2008)	Echinod. juveniles	0.46***
			Platyhelminthes	0.56***
			Chaetognatha	0.54***
			Ctenophora	0.45***
			Echinod. larvae	0.43***
			Mollusca	0.41***
			Hydrozoa	0.41***
			Appendicularia	0.40***
			Phoronida	0.38***
			Cirripedia	0.37***
			Cladocera	0.37***
			Annelida	0.36***
			Decapoda zoea	0.40***
			<i>T. longicornis</i>	0.37***
			Annelida	0.37***
			Copepoda Nauplii	0.36***
			<i>Pseudo Paracalanus</i> spp.	0.36***
			<i>Acartia</i> spp.	0.36***
			Mollusca	0.44***
Harpacticoida	0.39***			
<i>Oithona</i> spp.	0.38***			
Appendicularia	0.38***			
Cirripedia	0.37***			
-	-			
Top 10	54%***	(2003; 2018) (1975; 1989)	Decapoda zoea	0.40***
			<i>T. longicornis</i>	0.37***
			Annelida	0.37***
			Copepoda Nauplii	0.36***
			<i>Pseudo Paracalanus</i> spp.	0.36***
			<i>Acartia</i> spp.	0.36***
			Mollusca	0.44***
			Harpacticoida	0.39***
			<i>Oithona</i> spp.	0.38***
			Appendicularia	0.38***
Cirripedia	0.37***			
-	-			
Random 10	55%***	(2007; 2018) (1975; 1983) (1983; 2009)	Cyclopoida	0.54***
			Echinod. juveniles	0.47***
			Platyhelminthes	0.43***
			<i>Calanus</i> spp.	0.43***
			Echinod. larvae	0.4***
			Harpacticoida	0.37***
			Cirripedia	0.37***
			<i>T. longicornis</i>	0.36***
			<i>Acartia</i> spp.	0.35***
			-	-
Random 6	50%***	(2009; 2018) (1975; 1983) (1983; 2006)	-	-
			-	-
			Platyhelminthes	0.55***
			Harpacticoida	0.40***
			Appendicularia	0.40***
			<i>Oithona</i> spp.	0.38***
			<i>T. longicornis</i>	0.37***
			Cladocera	0.37***
			-	-
			-	-
Random 3	39%***	(2006; 2018) (1975; 1981) (1981; 2009)	-	-
			-	-
			Hydrozoa	0.42***
			<i>Oithona</i> spp.	0.39***
			Cirripedia	0.37***
			-	-
-	-			
-	-			

\*\*\* :  $p < 0.001$ .

lowed a similar trend, showing similar major changes for most taxa, although with some lag.

The second axis (Figure 3d, e, and f) summarizes additional changes that have occurred in a few taxa and shows different trends over time depending on the taxa used in the subsets. This is explained by the fact that very few taxa have not undergone the same changes as the vast majority of other zooplank-

ton (e.g. *Oithona* spp., Decapoda zoeae, appendicularia), and are therefore participating in axis 2 computation (see Figure 2). Thus, this axis was more impacted by taxon selection and showed the specific trend of some taxa that did not follow the rest of the community. At least one of the taxa affiliated with axis 2 was always found in the functional and random subsets (Table 3), explaining a certain consistency in the trend shown



**Figure 3.** PCoA1 (a, b, c) and PCoA2 (d, e, f) individual data year (month) coordinates for the functional group (a, d) and the random (b, e) subsets. The Panels C and F display the results for the ten random subsets of six taxa (the list of taxa is given in Appendix 2). The black line corresponds to the result from the complete community (Figure 2c).

with an overall increase throughout the period, albeit with strong fluctuations (Figure 3d, e). By running a random selection of six taxa ten times, variations along the second axis between subsets were highlighted (Figure 3f), with some trends particularly different from the PCoA 2 of the complete community.

## Discussion

In this study, we aimed to highlight the major changes that the southern North Sea mesozooplankton community has undergone between 1975 and 2018. Our study considered the dynamics of the whole community and identified contrasting periods characterized by different community structures. We showed two substantial changes, marked by an increase in abundance of most taxa during the 1980s and a sharp decline in abundance and biodiversity after the mid-2000s. We also aimed to highlight how the taxa considered in such analyses can impact research conclusions, especially tipping year identification and trends over time. Interestingly, we observed very similar patterns among subsets composed of taxa contrasting in terms of life history traits. In other words, the high majority of taxa experienced similar, or opposite, responses to changes in their environment, illustrating major shifts in the total zooplankton community structure. However, the tipping year identification showed some differences between functional groups, which were likely due to the interplay between abundance and life strategy, impacting rates of change in community structure. These results highlight that organisms can exhibit delays in their responses and that there is no single year in which the whole community has changed but rather a period of change, more or less extended depending on the degree of perturbation in the system. This result stresses the

importance of integrating a diverse mesozooplankton community to study zooplankton shifts in a more holistic manner.

## Changes in overall zooplankton community structures

Chronologically, the first pronounced change that the complete mesozooplankton community underwent happened in the early 1980s. With the exception of cyclopoids and echinoderm juveniles, which decreased in abundance, a significant increase in the abundances of all taxa occurred after 1983. This general increase in abundance led to a higher total planktonic abundance and richness but a decrease in evenness, referring to a lower similarity of frequencies among taxa. The 1980s are known to be a transitional period from a cold to a warm regime, along with high variations in the biotic and abiotic environment in the North Sea during the period 1982–1988 (Beaugrand, 2004). During this decade, studies using data from the Continuous Planktonic Recorder reported a significant increase in calanoid copepod abundances (e.g. Beaugrand and Ibanez, 2004; Alvarez-Fernandez *et al.*, 2012). Our results are in line with these studies but show that, in addition to copepods, most of zooplankton taxa displayed sharp increase in abundances during this period. The global impact of this shift was studied by Reid *et al.* (2016), who demonstrated that this event was triggered by rapid global warming from anthropogenic and natural forcing. Environmentally induced abrupt changes in plankton composition and size structure could have then affected fish recruitment, with consequences for fisheries (Reid *et al.*, 2003). For instance, these events showed close correlations with a large increase in catches the horse mackerel (Reid *et al.*, 2001), sand eel larvae abundances (Frederiksen *et al.*, 2006), and an increase in flatfish recruit-

ment (Beaugrand, 2004), but a decrease in cod recruitment (Beaugrand, 2003).

The second shift in the structure of the complete mesozooplankton community was identified for 2007, and it was the most dramatic shift that occurred over the past five decades. This shift was characterized by a sharp decrease in abundance of almost all taxa, which led to a lower total plankton abundance and richness but an increase in evenness. Our study is one of the first to report a mesozooplankton community structural shift during the 2000s and to highlight that the abundance of all taxa except Decapoda zoea has declined over the past two decades. In support of our results, another study considering the time period 1958–2007 found significant changes between 1996 and 2003 in the North Sea when considering multiple mesozooplankton taxa, which had the same magnitude in terms of species response as the well-documented shift detected in the 1980s. (Beaugrand *et al.*, 2014). However, their time series stopped in 2007, and temporal discontinuity is hardly detected towards the edge of a time series (Cornelius and Reynolds, 1991; Beaugrand, 2004).

While this study focuses on the shifts in the mesozooplankton community of the North Sea, it is worth noting that such shifts have been observed in other regions as well. For instance, Garcia-Comas *et al.* (2011) studied changes in zooplankton groups (i.e. copepod, chaetognath, decapod larvae, siphonophores, and jellyfish) from 1974 to 2003 in the Mediterranean Sea. They obtained similar results, with all zooplankton groups increasing in the early 1980s, decreasing during the 1990s, and then increasing again in the early 2000s. Beside the study area, trends over time and the timing of tipping years may vary depending on the species or taxonomic group considered. Indeed, species can react differently to hydro-climatic forcing depending on their specific physiological tolerances, processes, or life histories (Beaugrand and Reid, 2003; Beaugrand, 2004). Consequently, it is of utmost importance to consider a high diversity of taxa and lifeforms in community shift studies, as well as to consider groups of taxa separately to account for differences in life history traits.

### Comparison of different taxon subsets: similar trend with lag of response

In order to investigate the impact of taxonomic selection on community composition trends and tipping year identification, we repeated analyses considering different functional groups of taxa. Analysing different taxon subsets enabled us to identify that the vast majority of taxa followed a very similar trend over time, which was comparable to the trend of the whole community, i.e. abrupt abundance increase during the 1980s and decrease during the 2000s. This result highlights a major shift impacting zooplankton overall, since very dissimilar organisms in terms of life history traits were affected in a similar way. However, the timing of tipping years varied somewhat according to the plankton group. Therefore, there is no single year in which shifts happened but rather periods of time, more or less extended between groups depending on the shift intensity.

Regarding the first abrupt change, we identified a tipping year in 1981 for copepods and one in 1983 for the non-copepod subset. Concerning the ten most abundant zooplankton taxa, we identified the tipping year in community structure during 1989. All calanoid copepods were always linked to the

time period including the 1980s, either the first period (1975–1989) for the top 10 subset or the second period (1981–2003 and 1983–2007) for the copepod subset and the complete community. These results indicate that the 1980s were a dynamic period during which zooplankton abundances, especially those of calanoid copepods, increased. Beaugrand *et al.* (2014) identified changes in plankton abundance in the North Sea for several groups, including copepods, other holozooplankton, and meroplankton. This study also reports an abrupt increase of holoplankton other than copepods as well as meroplankton directly after a cold episodic event in 1978–1982, which is in line with our results. However, in their study, the tipping year for copepod abundances was found in the late 1980s, while we identified it in the early 1980s. In Beaugrand and Reid (2003), the tipping year was identified 1984–1985; and in Beaugrand (2004), it was between 1982 and 1984. We were able to show (1) an inter-study difference in tipping year identification for the same subset (e.g. copepods) and (2) tipping year variations for different groups of taxa (e.g. copepods versus the most abundant taxa).

We obtained similar results for the second tipping year. Regarding the 2000's shift, the shift in abundances of the copepod group was, as with the 1980's shift, observed earlier (i.e. 2003) compared to the whole community (i.e. 2007), the ten most abundant taxa (i.e. 2007), and the non-copepods (i.e. 2008). Here, the shift period was thus extended over 5 years, compared to the 8-year period of change in the 1980s. This gives information on the velocity of the shift, which seems to be faster during the 2000s, potentially due to more intense environmental changes during this period. In Beaugrand *et al.* (2014), authors suggested as well a shift in the 2000s for copepods and meroplankton, both displaying lower abundances after 2003. Moreover, the authors stated that the timing of the shift varied according to the planktonic group and even among taxa within a group, which was also the case in our study. Indeed, among copepods, the trend was different for harpacticoids and *Oithona* spp., copepods which showed an overall increasing abundance until the mid-2000s, while the calanoid copepods started to decline during the early 1990s. Compared to calanoid copepods, such as *T. longicornis* and *Acartia* spp., whose abundances started to decline in the 1990s (Alvarez-Fernandez *et al.*, 2012), the abundance of *Oithona* spp. increased from 1997 to 2005 (Martens and van Beusekom, 2008). Some organisms, such as appendicularia and cirripedia, followed the same increasing trend until the mid-2000s, which had not been investigated before.

Within an ecosystem such as the North Sea, the organisms considered (Beaugrand *et al.*, 2014), the study zone and its area extent (McGinty *et al.*, 2011), the statistical tools employed (Andersen *et al.*, 2009), as well as the time series edges (Cornelius and Reynolds, 1991), are all variables that can influence the tipping year detection. Beaugrand (2004) stated that for the 1980s ecological planktonic shift, the timing of the shift can vary greatly within a 5-year period when biological indicators (i.e. taxa) are considered individually. We do not aim here to redefine the well-studied 1980s shift, but our results highlight the delay that can be observed in tipping year identification depending on biological and statistical factors. The most abundant taxa were the latest group to show abrupt changes. This could mean that the more abundant a taxon is, the more inertia it has, i.e. it takes longer to move from one state to another. In ecology, inertia has been defined by time



lags in the responses of populations to changes in the environment (Cole, 1985). Population inertia, or the tendency not to show substantial change when environmental conditions do, can delay or even mask a response threshold (Milchunas and Lauenroth, 1995). On the other hand, the earlier tipping year identification for copepods compared to other organisms could come from differences in life histories. Mesozooplankton lifeforms generally have a short-lived and high-fecundity life history. That makes their recruitment, abundance, and spatial distribution highly responsive to environmental variability. However, holoplankton, such as copepods, have a generally faster life cycle than meroplankton. Indeed, many meroplanktonic organisms are essentially larvae of fairly long-lived organisms, where the life span of the adult and its reproductive success can be the defining response to environmental change. Then, a faster life cycle could lead to a faster response to environmental changes, which may explain the earlier tipping year detected for holoplankton. The reason why inertia may predominate over response potential remain however unclear.

We have thus shown that in order to best identify tipping years, the analysis should at best incorporate a wide variety of organisms and not focus solely on one group or the most abundant taxa. However, due to technical reasons, the availability of highly diverse time series at high taxonomic resolution and on a relevant time scale is rarely possible. A restricted number of biological indicators has to be used. To investigate the effect of such selection, we set up several subsets of randomly selected taxa. Here, we showed that six taxa were enough to describe tipping years accurately. Under this threshold, the analyses failed to show abrupt changes in community structure since they were more impacted by taxa-specific tendencies. With any set of six taxa, the trend over time was always very similar to that of the complete community. We do not suggest here that only six taxa are sufficient for shift studies, but this result reinforces the fact that in our case, the majority of organisms used in the analysis displayed a relatively consistent trend over the time period.

Interestingly, meroplankton played a significant role in the detection of community changes, potentially due to a close coupling between their benthic and pelagic life stages. Although our study only investigated the pelagic part of the ecosystem, previous research indicates changes in benthic organisms in the area over the last few decades. For instance, Kröncke *et al.* (2011) examined the changes that occurred in the benthic macrofauna communities in the North Sea between 1986 and 2000. They showed that almost all species exhibited rising abundances during this time period, which is in line with our results on their planktonic stages. Kröncke *et al.* (2011) attributed the changes observed to seawater warming and increasing primary production. Investigating the connections between changes in pelagic and benthic organisms could yield valuable insights into the ecosystem's overall functioning, and we encourage future research to explore this further.

In summary, the 1980s and 2000s can be considered periods of major change for the zooplankton community. The vast majority of zooplankton followed a similar trend with few lags in their tipping year, possibly due to the interplay of life history strategies and abundances. The identification of a major change in the community benefits from a representative cross-section of all taxa. By reducing the number of taxa considered, analyses lose their power to identify these major changes, as the community analyses were more impacted by

specific trends. Comparing tipping years and trends among different subsets can as well help identifying velocity of the shift periods and the chronology of response between contrasted functional units.

### Potential implications of the 2000's shift

The early 2000s were marked by numerous changes within North Sea plankton, such as a sharp decline in dinoflagellate abundances and an increase in diatoms in the coastal North Sea (Hinder *et al.*, 2012; Bedford *et al.*, 2020), driven by both increasing temperature and windy conditions (Hinder *et al.*, 2012), as well as de-eutrophication (Di Pane *et al.*, 2022). The microzooplankton compartment was also negatively influenced by decreasing phosphate concentrations (Meunier *et al.*, 2018), and copepods showed decreasing abundances during this period (Payne *et al.*, 2009; Alvarez-Fernandez *et al.*, 2012; Capuzzo *et al.*, 2018; Di Pane *et al.*, 2022). While this was only suggested by Beaugrand *et al.* (2014), our study is the first to report a marked tipping year for mesozooplankton at community scale during the 2000s in the North Sea.

This abrupt change in zooplankton community structure may have had major consequences for upper trophic levels and, consequently, for food web dynamics in the southern North Sea. The 2000s were characterized by changes in fish abundances, and, for instance, a particularly low recruitment of the North Sea herring has been observed between 2002 and 2010 (Corten, 2013). Payne *et al.* (2009) showed a close temporal agreement between the poor recruitment observed for this species and the significant changes in the plankton community identified during the 2000s, the authors stating: “*It is, therefore, possible that we are observing the first consequences of this planktonic change for higher trophic levels*”. This recruitment depression in herring was concomitant with the one observed by Frederiksen *et al.* (2006) for lesser sandeels, while at the same time the abundance of snake pipefish substantially increased (Harris *et al.*, 2007). Climate-driven changes in plankton communities have been suggested as one of the mechanisms explaining these alterations in fish recruitment success (Frederiksen *et al.*, 2006; Lindegren *et al.*, 2018), with further impacts on seabird breeding success (Harris *et al.*, 2007). We showed that, in addition to copepods, the abundance of other holoplankton and meroplankton, which are consumed by planktivorous fish, also abruptly changed in the 2000s, which could have participated to these observed changes in upper trophic levels.

In conclusion, our study highlights the need for more integrative and holistic approaches to identify and understand the changes that ecosystems can experience. Using the complete mesozooplankton assemblage sampled at Helgoland Roads for more than four decades, we could identify two main shifts in its structure, one during the 1980s, and a second one, less studied, during the 2000s. The timing of the shift can vary greatly within an 8-year period depending on the taxes considered. However, similar trends were observed during a period of increasing abundances for most of the holo- and meroplanktonic taxa after 1983, which lasted until the mid-1990s. In this paper, we did not attempt to explain changes observed within the mesozooplankton compartment. However, regarding the very similar trend that all groups displayed and the climate-driven changes that the phytoplankton compartment

underwent during these shift periods (Alheit *et al.*, 2005b; Di Pane *et al.*, 2022), it is likely that bottom-up processes are the main structuring mechanisms. While the causes and consequences of these changes may be complex and require further investigation, we suggest that exploring the links between changes in the environment and lower trophic levels could provide important insights into the functioning of the overall ecosystem. Therefore, we encourage future studies to investigate these links in more detail.

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## Supplementary data

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

## Conflict of Interest statement

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

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## Author contributions

Julien Di Pane: (conceptualization, formal analysis, investigation, methodology, and writing), Maarten Boersma: (conceptualization, data curation, writing, validation, and supervision), Raquel Marques: (conceptualization, methodology, and writing), Margot Deschamps: (investigation, and writing), Ursula Ecker: (data curation and resources), Cédric Léo Meunier: (conceptualization, supervision, validation, and writing).

## Data availability statement

The data underlying this article are available in PANGAEA, at <https://dx.doi.org/10.1594/PANGAEA.873032>.

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