LIMNOLOGY and OCEANOGRAPHY

ASLO

Limnol. Oceanogr. 9999, 2025, 1–15

doi: 10.1002/lno.70258

RESEARCH ARTICLE

Food web modifications shifted the functional structure of zooplankton

Raquel Marques[1*,a], **Saskia A. Otto**[2], **Maarten Boersma**[3,4], **Christian Möllmann**[2], **Karen Wiltshire**[5,6], **Jasmin Renz**[1]

[1]Deutsches Zentrum für Marine Biodiversitätsforschung, Senckenberg am Meer, Hamburg, Germany; [2]Institute of Marine Ecosystem and Fisheries Science (IMF), Center for Earth System Research and Sustainability (CEN), University of Hamburg, Hamburg, Germany; [3]Biologische Anstalt Helgoland, Shelf Sea System Ecology, Alfred-Wegener-Institut Helmholtz-Zentrum für Polar- und Meeresforschung, Helgoland, Germany; [4]FB2, University of Bremen, Bremen, Germany; [5]Alfred-Wegener-Institut Helmholtz-Zentrum für Polar- und Meeresforschung, List/Sylt, Germany; [6]Trinity College Dublin, Faculty of Science, Technology, Engineering and Mathematics (STEM), Dublin, Ireland

Abstract

The North Sea has been undergoing long-term transformations driven by shifts in human activities and climate change, which have jointly reshaped the composition of marine communities. Despite existing studies, the functional mechanisms driving community changes remain poorly understood. Here, we analyzed a 43-year time series of meso- and macro-zooplankton (> 500 μm) monitored at Helgoland Roads to assess long-term changes in functional biodiversity. We applied functional diversity indices and trait-based uni- and multivariate analyses to (1) investigate the temporal variability in functional biodiversity components, (2) relate structural community changes to environmental drivers, and (3) interpret patterns in the context of community assembly mechanisms. Our results reveal asynchronous changes across biodiversity components, with pronounced structural shifts occurring in the early 2000s. These shifts were tightly linked to modifications in the food web: feeding traits together with predation-risk traits contributed most to diversity changes, shaped by the abundance of diatoms and fish biomass. Environmental filtering processes could be identified as key mechanisms driving the reorganization of the community, leading to a significantly altered functional structure after 2005, with potential implications for food web dynamics and energy transfer to higher trophic levels. Our findings underscore the value of trait-based approaches in gaining a comprehensive understanding of the mechanistic processes driving community change and support their integration into ecological models to improve projections of ecosystem responses under future conditions.

Marine ecosystems are undergoing profound transformations due to climate change and anthropogenic pressures, with cascading effects on biodiversity, ecosystem functioning, and the services they provide (Gattuso et al. 2015). The North Sea (NS) is a well-documented example, recognized as one of the marine "hotspots" of cumulative anthropogenic impacts (Halpern et al. 2015), which has been restructured over recent decades. Anthropogenic impacts have resulted in increased sea surface temperatures of at least 0.3°C per decade (de Amorim et al. 2023) and a decrease in riverine nutrient loads by more than half since the 1980s (van Beusekom et al. 2019). These changes have been linked to shifts in water transparency (Nohe et al. 2020), nutrient stoichiometry—particularly lower N : P ratios after the mid-1990s, which indicate higher food quality for zooplankton (Raabe and Wiltshire 2009)—as well as primary productivity (Wiltshire et al. 2008, 2015), and plankton community structure (Boersma et al. 2015; Di Pane et al. 2023; Marques et al. 2023). In parallel, changes in fisheries exploitation management led to an increase in pelagic fish biomass in recent years, with biomass of herring more than doubling between 2011 and 2016 (Dickey-Collas 2016).

*Correspondence: raquel.marques@setec.com

[a]Present address: Setec énergie environnement—setecinvivo, Toulon, France

Associate editor: Thomas Kiørboe

These modulations of bottom-up and top-down processes induced changes in all marine trophic levels from plankton to predatory fish and triggered the reorganization of the NS marine ecosystems. Three main regime shifts have been identified since the mid-1970s: (1) in the late 1980s, when the system changed from a cold to a warm regime (Reid et al. 2001); (2) between 1996 and 2003 (Beaugrand et al. 2014), with diatoms replacing dinoflagellates as the dominating group in the phytoplankton community (Wiltshire et al. 2008), and a decrease in the abundance of most copepods (Boersma et al. 2015); and (3) between 2003 and 2008, including several trophic levels (e.g., plankton, fish and benthos), after which the NS community reached a new irreversible state (Sguotti et al. 2022). However, despite extensive research on taxonomic shifts in the NS plankton community (Beaugrand et al. 2014; Di Pane et al. 2023; Marques et al. 2023), we still lack a mechanistic understanding of the functional processes that have shaped these changes and their ecological consequences.

Zooplankton, as key intermediates in the marine food web, play a crucial role in linking primary producers to higher trophic levels. So far, very few studies focused on large sized zooplankton organisms (> 500 μm), which are often ignored or included at very low taxonomic resolution. Marques et al. (2023) described a significant reorganization of this community on taxonomic level over time, concurrent with the reported regime shifts. However, taxonomic changes do not necessarily translate into shifts in functional diversity (Djeghri et al. 2023). Trait-based approaches, focusing on the functional structure of communities, have proven to offer a simple and comprehensive description of the structure of biological communities, and exhibit stronger connections with ecosystem processes compared to taxonomic methods alone. Functional diversity indices can therefore be used to assess the response of marine communities to environmental changes and the effects on ecosystem processes (Mouillot et al. 2013).

Community assembly mechanisms provide key insights into how biological communities are structured. Four main processes are recognized (Götzenberger et al. 2012): environmental filtering (species with functional traits less adapted to a given environmental condition are "filtered out," the community is composed of species with similar traits, resulting in functional convergence), limiting similarity (leads to functional divergence as coexisting species are expected to have different traits, allowing them to exploit different ecological niches) and, under neutral theory (Hubbel 2001), ecological drift and speciation (the local community structure results from random processes and all species are functionally equivalent).

Building upon Marques et al. (2023), this study aims to determine whether these shifts were accompanied by functional restructuring. Specifically, we assess the long-term variation in functional biodiversity, identify its environmental drivers and explore whether community assembly mechanisms have influenced these shifts. For that, we analyzed a 43-year time series of zooplankton abundances and constructed a trait database to complement taxonomic-based approaches. Based on a selection of 13 key traits, we hypothesize that changes in prey availability and predation pressure drive functional restructuring. We further hypothesize that, as environmental conditions shift, certain functional traits (e.g., size, feeding strategy) change or become more prevalent due to selective pressures (Götzenberger et al. 2012). By integrating these hypotheses, we move beyond taxonomic descriptions to uncover the mechanistic processes shaping long-term zooplankton community dynamics and provide critical insights into the role of functional diversity in ecosystem responses to environmental change.

Materials and methods

Zooplankton data

Zooplankton samples were obtained from a long-term monitoring sampling program from 1975 to 2018, at Helgoland Roads (depth 6–8 m, 54°11′18″N, 7°54′E), situated in the Southern North Sea (SNS). Zooplankton were collected 2–14 times per month by oblique hauls (Supporting Information Table S1), using a Hydrobios CalCOFI net (100 cm aperture, length 4 m, mesh size 500 μm). The sampled community comprises macro- and mesozooplankton organisms > 500 μm, hereafter called "large zooplankton" (see Marques et al. (2023) for details on sampling, preservation, and data base preparation). Taxa abundances were averaged per year to remove inequality in sampling effort and seasonal effects. The robustness of annual means was confirmed by comparing them with bootstrapped estimates (Supporting Information Fig. S1), which showed negligible differences. Although assembly mechanisms may also occur at seasonal time scales, here we focus only on the long-term trends of community structure, in response to long-term trends in environmental changes. The final taxonomic database was composed of 73 taxa and 44 years.

Environmental data

The analysis of the long-term variability in environmental conditions in the SNS was comprehensively performed by Marques et al. (2023), using breakpoint analysis to identify significant changes in the mean over time (Zeileis et al. 2002). In short, annual sea surface temperature (SST) and NAO (North Atlantic Oscillation) index were used to test for long-term effects of ocean warming and climate parameters, respectively. SST was obtained from the Helgoland Roads monitoring program and averaged by year. The annual NAO index was obtained from the Climate Data Guide (https://climatedataguide.ucar.edu/climate-data/overview-climate-indices). Copepod (all species except *Calanus* sp., as they are included in the analyzed community) and diatom abundance (making up 90% of the total microalgae community at Helgoland; Wiltshire et al. 2015) were used to test for the potential impact of the availability of zooplankton and phytoplankton prey, respectively. To account for an additional effect of food quality, the N : P ratio of the dissolved nutrients was used as a proxy, as nutrient stoichiochemistry in primary producers reflects that of their environment and significantly affects zooplankton growth rates (Malzahn and Boersma 2012). Secchi depth was used as an indicator of water turbidity. These parameters were all obtained from the Helgoland Roads monitoring program (Wiltshire et al. 2008). To test for the potential impact of predation pressure, the biomass of the most common zooplanktivorous predators in the NS, herring (*Clupea harengus*), mackerel (*Scomber scombrus*) and sprat (*Sprattus sprattus*) (ICES 2022), was used. Fish biomass of these species was obtained from catch per unit of effort (CPUE) data from the North Sea International Bottom Trawl Survey, quarter 1, from the ICES area IVb, that is, the SNS (https://www.ices.dk/data/data-portals/Pages/DATRAS.aspx). For each species, spatially resolved CPUE data were averaged per year and the biomass of the three species was summed up to create a proxy of total zooplanktivore biomass.

Traits database

Traits were selected following the de Bello et al. (2021) framework, by first identifying the main ecological processes of interest that have shaped the long-term change in the NS. For each process, associated environmental stressors were identified, hypotheses formulated on how organisms are expected to respond, and response traits that influence performance under those stressors were selected (Table 1). Trait selection was also influenced by data availability and consistency of information across taxa. Among the taxa considered, 76% were meroplankton and several traits associated with the (often benthic) adult stages were included to account for the influence of environmental stressors on the full life cycle (Table 2 and Supporting Information File S2). For holoplanktonic organisms, larval-related traits were considered to be representative of adult stages. From 13 traits selected, seven traits were associated with larval/pelagic stages and five with adult/benthic stages (Table 2). Trait information was primarily obtained from literature sources. Some morphological traits were complemented with additional measurements (see Supporting Information for further information).

Data analysis

Functional diversity indices

Long-term changes in macro-/mesozooplankton biodiversity were assessed through the analysis of temporal variation in functional alpha-diversity indices (Mouillot et al. 2013), which were computed based on the distribution of taxa in the multidimensional trait space according to their similarities in terms of trait composition, taking into consideration taxa abundances. The dissimilarity among taxa was computed using Gower distances between each pair of taxa. Bias in dissimilarity values was reduced following de Bello et al. (2021) and by excluding highly correlated traits (Pearson correlation). Numerical traits were log-transformed to avoid the influence of extreme values in non-normally distributed traits. Binary and factorial traits have only extreme values, disproportionately influencing the final dissimilarity values. The weight of numerical traits on the final average dissimilarity matrix was increased by 50%, to increase their influence in relation to factorial traits. Gower distance dissimilarity matrix was computed for each individual trait or group of fuzzy traits, followed by an average of all dissimilarity matrices (de Bello et al. 2021). Gower distance dissimilarity matrix was computed by the "gowdis" function of the FD package (v 1.0.12.1; Laliberté et al. 2014). The final Gower distance matrix was used to compute several functional alpha-diversity indices (Table 3). Functional diversity indices were calculated by the function "alpha.fd.multidim," from the package "mFD" (Magneville et al. 2022). The functional space was computed by principal coordinate analysis based on the best number of principal components (PCs), determined by the quality measure mean absolute deviations (Maire et al. 2015). For visualization and interpretation of the functional dissimilarity among taxa, a k-means cluster analysis was performed on the taxa coordinates of the first two axes of the principal coordinate analysis functional space, using the "factoextra" package (Kassambara and Mundt 2020). The optimal number of clusters was defined as the one most frequently suggested by the indices calculated using the NbClust package (v 3.0.1; Charrad et al. 2014).

To identify if and when abrupt changes in functional diversity indices occurred over time, a univariate analysis was used to test for breakpoints in the mean, which indicated structural changes in linear regression models (Zeileis et al. 2002). Breakpoints were estimated by minimizing the residual sum of squares of the regression, with a minimum segment length of 15% of the time series (ca. 7 years), allowing us to identify long-term changes without the loss of too much information. The best number of breakpoints was selected based on the Bayesian Information Criterion. The breakpoint analysis was performed using the "strucchange" package (v1.5.2; Zeileis et al. 2002).

Environmental drivers of changes

The relationship between the functional community structure of large zooplankton and environmental conditions in the SNS was assessed using redundancy analysis (RDA) based on community-weighted means of functional traits. Community-weighted mean corresponds to the average trait values in the community, weighted by the abundance of taxa (log $[x + 1]$) (de Bello et al. 2021). The RDA analyses were performed using the "vegan" package (v2.6-2; Oksanen et al. 2022), after testing for collinearity among the explanatory variables by Pearson's correlation and variance inflation factor ("faraway" package, v1.0.7;

Table 1. Traits included in the functional analysis and the associated hypothesis used for traits selection in relation to each environmental stressor.

Environmental changes	Stressor	Hypothesis	Traits
Larval/pelagic stages			
De-eutrophication	Change in food availability	Herbivorous and omnivorous taxa, that are able to feed on phytoplankton, benefit from higher food availability (Verity and Smetacek 1996).	Trophic regime
	Decrease of copepods	Active current feeding is the best overall feeding strategy, when considering energy costs to capture food and predation vulnerability. This strategy targets non-motile prey, like diatoms (Kiørboe 2011).	Feeding strategy
	Increase of phytoplankton	Under conditions with higher availability of small prey (phytoplankton vs. copepods), those that are able to feed on smaller prey will prevail (Cohen et al. 1993; Kiørboe and Hirst 2014).	Prey size
		Gelatinous organisms will prevail in low food availability as they increase prey encounter surface by inflation, have wider trophic niche and need less food per unit of biomass (Pitt et al. 2013).	Body type
	Increase in visibility	Visual predators will benefit from higher light intensity and visibility conditions (Kiørboe 2011; Kiørboe and Hirst 2014).	Feeding strategy
		Higher water visibility is expected to increase the vulnerability of prey for visual predators. Invisibility due to tissue transparency is an advantage (Litchman et al. 2013).	Body type
		Larger organisms are more conspicuous and more vulnerable to predation under higher visibility conditions (Pechenik 1999).	Size
Ocean warming	Increase of temperature	Warming, directly or indirectly, at intra- or interspecific level, is expected to reduce phytoplankton cell size. This is expected to decrease the trophic transfer efficiency and benefit smaller predators (Sommer et al. 2017).	Size
Decrease of fishing pressure	Increase of predators	Higher number of spines provides better protection against predators (Morgan 1989). It is expected that taxa with longer and/or more spines will have higher probability of survival.	Spine length
		Predation is one of the most important sources of mortality for early life stages of zooplankton and the vulnerability to predation increases for smaller organisms (Allen 2008). Larger early life stages are expected to have a decreased vulnerability to predation and have higher probability of survival.	Size of first stage
		Inflation capacity (bigger size) and lower carbon per unit of biomass reduce the vulnerability and appealing of gelatinous organisms to predators (Pitt et al. 2013).	Body type
Adult/benthic stages			
De-eutrophication	Change in food availability Decrease of copepods Increase of phytoplankton	Higher availability of phytoplankton food sources is expected to benefit benthic species that feed directly or indirectly on these sources, i.e., suspension and deposit feeders (Thompson 2005)	Adult feeding strategy
	Increase visibility	Visual predators will benefit from higher light intensity and visibility conditions (Kiørboe 2011)	Adult feeding strategy
Ocean warming	Increase of temperature	Species with higher reproduction frequency are expected to have better ability to cope with predator–prey phenology changes (Richardson 2008) and environmental variability (Reznick et al. 2002)	Reproduction frequency

(Continues)

Table 1. Continued

Environmental changes	Stressor	Hypothesis	Traits
Decrease of fishing pressure	Increase of predators	Species with higher ability to avoid predators by burrowing or swimming escaping behavior are expected to increase their survival (Hinz et al. 2021)	Mobility
		Larger species are less vulnerable to predation (Cohen et al. 1993)	Size
Ocean warming	Increase of temperature	Higher temperatures accelerate larval development in meroplankton, reducing planktonic duration and potentially desynchronizing dispersal with optimal settlement conditions. This could affect recruitment success and benthic population dynamics, ultimately altering community composition (Kirby et al. 2008).	Life cycle

Faraway 2022). To find the most parsimonious models, RDA model selection was done by the "ordistep" (backward and forward selection, using the "vegan" package). The significance of the model, of the individual RDA axis, as well as of the retained explanatory variables, was examined using permutation tests with 1000 iterations. The amount of variance in the response data explained by the environmental variables was quantified by the adjusted R^2. RDA analysis allowed us to identify the main environmental drivers as well as the traits that contributed most to the observed changes in community structure.

Detecting community assembly mechanisms

Null models were used to investigate potential assembly mechanisms shaping the large zooplankton community composition (Götzenberger et al. 2012), by randomizing community abundances or trait values, followed by re-calculation of functional diversity indices, and the comparison to observed

Table 2. Traits, traits categories and the associated code (in parenthesis) included in the functional analysis.

Trait	Description	Trait category	Trait levels
Larval/pelagic stages			
Trophic regime (TrophRd)	Main diet	Factorial	Omnivores (omn); Carnivores (carn)
Feeding strategy (FeedSd)	Strategy used to find and capture prey	Factorial	Cruise feeding hydromechanical (CruH); Cruise feeding visual (CruV); Current feeding (CurrT); Deposit feeding (dep); Passive ambush (PassAmb)
Prey size (PreySd)	Minimum prey size included in their diet	Factorial	Mesoplankton (meso); Microplankton (micro); Nanoplankton (nano); Picoplankton (pico)
Body type (BodyTd)	Body tissue texture	Ordinal	Hard exoskeleton (0); Soft body (1); Gelatinous (2)
Size (SizeMedd)	Median body length (mm)	Numerical	
Spine's length (LgthSd)	Index of number and length of spines	Numerical	
Size of first stage (Size1d)	Size (total length or bell diameter) of first larval stage (mm)	Numerical	
Adult/benthic stages			
Adult feeding strategy (FeedSi)	Strategy used to find and capture prey	Fuzzy coding	Deposit feeding (Dep); grazer (Gra); Predator (Pred); Scavenger (Sca); suspension feeding (Sus); Symbiont (Symb)
Reproduction frequency (RepFi)	Number of spawning events	Factorial	Annual episodic (Ae); Annual protracted (Ap); Biannual episodic (Be); Semelparous (S)
Mobility (Mobi)	Type of mobility	Fuzzy coding	Burrower (B); Crawler (C); Permanent attachment (PA); Swimmer (S)
Adult size (SizeMaxi)	Maximum body size (mm)	Numerical	
Body protection (BodyPi)	Body protection type	Ordinal	Unprotected soft tissue (0); Thin exoskeleton or shell (1); Hard exoskeleton or shell (2)
Life cycle (LifeC)	Type of life cycle	Factorial	Holoplankton (h); Meroplankton (m)

Table 3. Computed taxonomic and functional alpha-diversity indices (Magneville et al. 2022).

Name	Code	Definition
Taxonomic richness	Tric	Number of taxa
Functional richness	Fric	Total volume of the functional space occupied by the community
Functional identity	Fide	Weighted average position of taxa along principal components 1 and 2 axis
Functional evenness	Feve	Regularity of abundance distribution along the minimum spanning tree that links all taxa ensuring the lowest cumulative branch length
Functional divergence	Fdiv	Deviation of the abundance distribution from the center of gravity of the functional space occupied by the community in each year, reflecting the proportion of the abundance that is supported by the taxa with the most extreme functional traits

values. If the observed index values are higher than those obtained by null models, co-occurring species are more functionally dissimilar than expected by chance (functional divergence), which can be interpreted as evidence for limiting similarity processes. In contrast, lower-than-expected values indicate functional convergence, suggesting environmental filtering processes, as co-occurring taxa are more likely to share similar traits that enable persistence under similar conditions.

We computed null models for two complementary indices: Fric and Fdiv. Fdiv is based on species traits and relative abundances, and has been shown to be a particularly powerful index for detecting community assembly processes (Mouchet et al. 2010). For Fdiv, two types of null models were used (Götzenberger et al. 2016): randomization of taxa abundances within samples across all taxa while preserving taxonomic richness of samples (C1) and randomization of sample abundances within each taxon across all samples, preserving the occurrence frequency of taxa (C2). C1 is considered to be powerful in detecting limiting similarity processes, while C2 is most appropriate to detect environmental filtering and/or weaker competitor exclusion (Götzenberger et al. 2016). Both types of models were computed using the "richness" (C1) and "frequency" (C2) algorithms, implemented via the randomizeMatrix() function in the "picante" package (Kembel et al. 2010).

A different randomization procedure was applied for Fric due to its known dependency on species richness. Fric quantifies the volume of trait space and increases mechanically with the number of taxa. To ensure meaningful comparison, taxonomic richness needs to remain constant across observed and randomized communities. We used the independent swap (IS) algorithm (Gotelli 2000) in the randomizeMatrix function, which simultaneously preserves both row sums (annual species richness) and column sums (species occurrence frequency). This approach allowed us to isolate deviations in functional richness that could not be explained by variation in taxonomic richness, enabling direct comparison between Fric and Tric across years.

All null model simulations were run with 999 iterations. For both indices, standardized effect sizes (SES) were calculated as SES = (observed value − mean of randomized values)/standard deviation of randomized values. Values of SES < -1.645 and SES > 1.645 were considered significantly lower or higher than expected by chance, indicating functional divergence and convergence, respectively (Götzenberger et al. 2016).

Results

Environmental conditions

The average annual sea surface temperature at Helgoland Roads ranged from 8.3°C to 11.9°C and showed a clear increasing trend over time. In contrast, NAO did not exhibit any significant long-term trend, fluctuating between −5.96 and 4.09, with a mean value of 0.57 throughout the study period. The N : P ratio showed markedly elevated mean values (41.4) between 1986 and 1995, compared to lower mean values before (16.6) and after (19.1) this period. Water transparency, as indicated by Secchi depth, increased from a mean of 3.1 before 1986 to 3.8 m afterwards, while mean diatom abundance increased from 11.3×10^4 to 20.5×10^4 ind.L^{-1} after 1998. Four periods with significant differences in their mean abundances were observed for copepods: until 1982 (3.9×10^3 ind.m^{-3}), between 1982 and 1990, when their mean abundance was highest (9.1×10^3 ind.m^{-3}), between 1990 and 2004 (4.4×10^3 ind.m^{-3}) and during the last years of the survey when their mean abundance was lowest (2.2×10^3 ind.m^{-3}). Finally, fish biomass increased over time from a mean of 2.7×10^5 tons before 1986 to 11.1×10^5 tons after 2010. For a detailed description of the long-term variation in these variables, we refer to Marques et al. (2023).

Functional diversity indices

Functional diversity indices were computed based on five principal components (mean absolute deviation = 0.028); however, the first two axes captured the main differences among taxa well (Fig. 1), with three main clusters identified (see Supporting Information Fig. S2). Cluster 1 was mainly composed of holoplanktonic taxa (LifeCh) with a soft body type (BodyTd1), a hydromechanical cruise feeding strategy (FeedSdCruH), larger median body size, and adult stages with the ability to swim (Mobi.S). Cluster 2 mainly represented taxa with a gelatinous body type (BodyTd2), a carnivorous feeding mode (TrophRdcarn), a passive ambush strategy (FeedSdPassAmb), and permanently attached adult stages (Mobi.PA). Cluster 3 assembled the taxa with more and/or longer spines (LgthSd), a hard exoskeleton (BdyTd0),

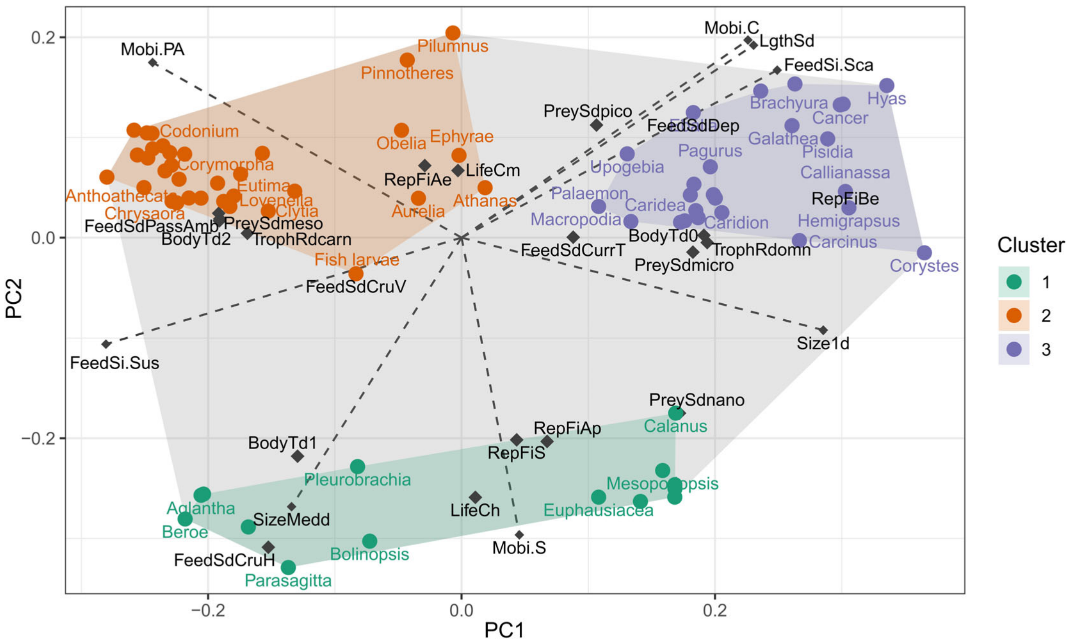

Fig. 1. Position of the taxa in the functional multivariate space used to compute functional diversity indices. Only the first two axes (principal component [PC]1 and PC2) are presented. The color of points indicates their respective k-means cluster. For clarity, some taxon names are not shown. Traits that contributed most to the positioning of the taxa along PC1 and PC2 (based on post hoc permutation tests, p value ≤ 0.001) are indicated by dashed gray lines (quantitative traits) or diamond-shaped gray points (averages of factor levels). Polygons represent the convex hull encompassing all taxa from the entire community (in gray) and from each cluster (colored).

omnivorous organisms (TrophRdomn), organisms feeding on a smaller prey type (pico- and micro-plankton, PreySdpico and PreySdmeso, respectively), taxa with crawling adult stages (MobiC), and those with a scavenging feeding strategy (FeedSi.Sca). The taxa in the vertices of the convex hull (in the six-dimensional space) of the whole community define the total functional richness. They have the most extreme combination of traits and are considered "specialists," such as the decapod species *Pilumnus* sp., and *Corystes* sp., the chaetognath *Parasagitta* sp. and the hydrozoan *Codonium* sp. (Fig. 1).

All functional diversity indices fluctuated over time, but significant changes in long-term means occurred at different times, depending on the index (Fig. 2). Both, the taxonomic (Tric) and functional richness (Fric) increased in the early 1980s, with a simultaneous breakpoint in the mean detected in 1981 (Fig. 2a, b). Taxonomic richness increased from a mean of 41.6 to 56.0, while functional richness increased from 0.59 to 0.73. Between 1995 and 1996, taxonomic richness decreased from 59 to 52 taxa, which was followed by a sharp decrease in functional richness to below 0.5 in 1996 and 1997. In 2003, mean taxonomic richness significantly decreased to 47.9, which was not reflected in the functional richness that remained high until the end of the study period. The functional identity (Fide) on principal components 1 and 2, showed an overall increase over time (Fig. 2c), with a significant breakpoint in the mean in 2002 and 2007, respectively, reflecting a long-term change in the mean functional composition of the community. Likewise, although highly variable, the functional evenness increased over time with breakpoints detected in 1981 and in 1995, and mean values of 0.26, 0.32, and 0.37 in the three different periods (Fig. 2d). In contrast, functional divergence decreased over time, with a significant breakpoint in 2005, when the mean changed from 0.90 to 0.82 (Fig. 2e). These results reflect the decrease in relative abundance of those taxa with the most extreme combination of traits among the global community (i.e., the specialists), particularly in recent years, leading to a distinct community with more evenly represented generalists and an overall less diverse functional community.

The effect of environmental variables and important traits

The RDA analysis showed that the environmental variables significantly affected the functional structure of the large zooplankton community (significant final global model, $F = 7.38$, p value = 0.001). The model explained 22.9% of the total variation in the data (Fig. 3a), with only the first RDA axis contributing significantly (22.3%, $F = 14.38$, p value = 0.001) to the change. The temporal variation in RDA1 scores, which shifted from negative values until the late 1990s to positive values in more recent years (Fig. 3a, b), illustrates the reorganization of the community over time. Initially, the community of large zooplankton was characterized by higher mean abundances of gelatinous plankton (BodyTd_2), carnivorous organisms

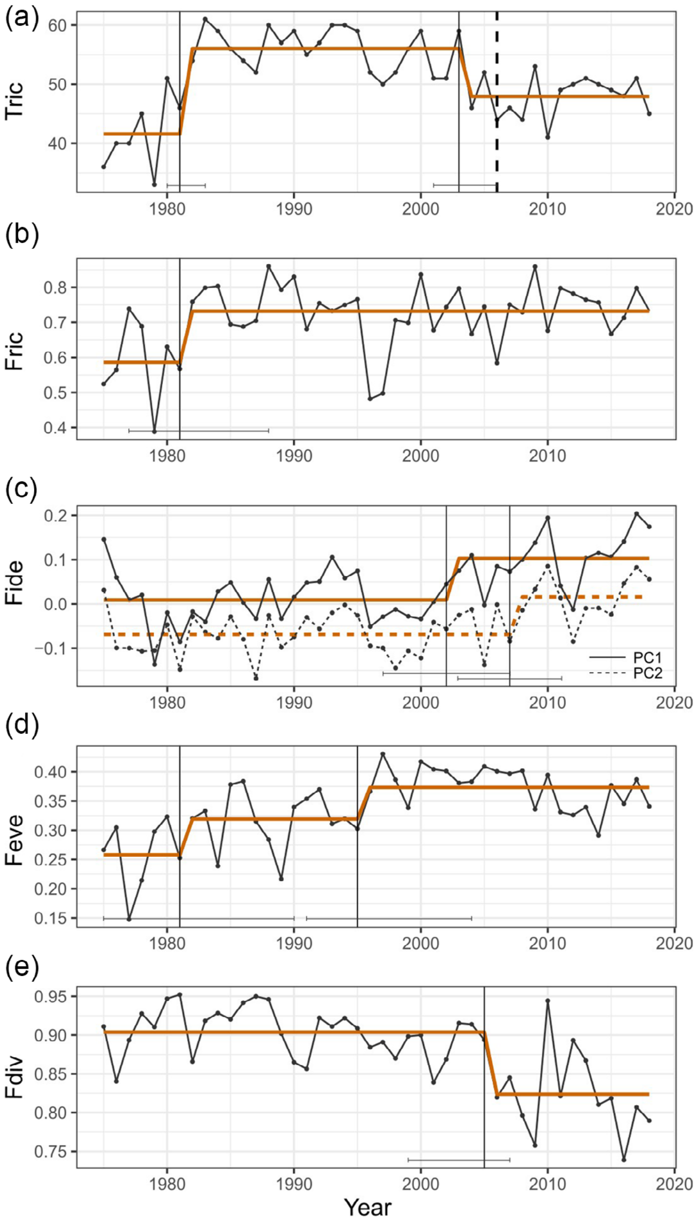

Fig. 2. Temporal variation (black lines) of diversity indices: (**a**) taxonomic richness, (**b**) functional richness, (**c**) functional identity, (**d**) functional evenness, and (**e**) functional divergence. Solid orange lines represent the mean of the index, delimited by breakpoints (vertical black lines), with 95% confidence intervals (gray horizontal lines). Thick dashed vertical line in (**a**) indicates significant changes in taxonomic community structure (Marques et al. 2023).

(TrophRd_carn), with permanently attached adult stages (Mobi_PA), that feed on mesozooplankton prey size (PreySd_meso) and have a passive ambush feeding strategy. Over time, this structure shifted to a community dominated by organisms with hard exoskeletons (BodyTd_0), protected with longer and/or more spines (LghtSd), possessing an omnivorous trophic regime (TrophRd_omn), and capturing their prey through a current feeding strategy (FeedSd_CurrT) (Fig. 3a, c). Only diatom abundance and fish biomass were retained in the final model (Fig. 3d). However, the declining trend in copepod abundance and the increase in temperature likely also affected the community structure over time, as indicated by their high absolute RDA1 scores. Indeed, when temperature was included in the model alongside diatom abundance and fish biomass, the explained variance increased slightly (adjusted $R^2 = 24.5\%$), but the effect of this predictor was not significant ($F = 1.81$, $p = 0.14$ based on permutation tests) and was therefore excluded during the selection process.

Community assembly mechanisms

The results of the null model analyses based on Fdiv and Fic suggest that environmental filtering and limiting similarity both likely contributed to shaping the community structure over time, but patterns were not consistent across indices or time periods. For Fdiv, both randomization processes (C1 and C2) yielded generally similar results, pointing to two periods with different dominant mechanisms (Fig. 4): before 2005, standardized effect size (SES) was mostly positive, particularly in model C1, suggesting that limiting similarity may have been more influential during that time. However, no significant divergence was detected. After 2005, SES values became more negative, and significant convergence was detected in a few individual years (2008, 2009, and after 2016), but only in the C2 model. Although environmental filtering processes were stronger in more recent years, evidence for this remains limited to specific years and is model-dependent.

Observed and simulated Fric values were positively correlated with Tric (Fig. 5a), and most years fell within the 95$^{\text{th}}$ percentiles indicating a non-significant difference from the null model distribution. Only 2 years, 1996 and 1997, showed significant convergence (SES < -2.69), indicating potential environmental filtering during this brief episode (Fig. 5b). In contrast, 1977 exhibited significant divergence (SES $= 2.12$), pointing to a possible effect of limiting similarity. However, outside of these isolated years, SES values remained within non-significant bounds. Taken together, these findings suggest that the community may have been shaped by both environmental filtering and limiting similarity processes at different times, but neither mechanism clearly dominated throughout the study period. Moreover, the two indices (Fdiv and Fric) appear to capture different aspects of the community structure, with Fdiv reflecting changes in relative abundance distributions and Fric responding more to the loss or retention of extreme trait combinations.

Discussion

Changes in the functional structure of zooplankton

The trait-based analysis provided detailed insights into how, why and when the zooplankton community in the SNS changed, revealing major functional changes over the last four decades. The first clear change was observed in 1981, when

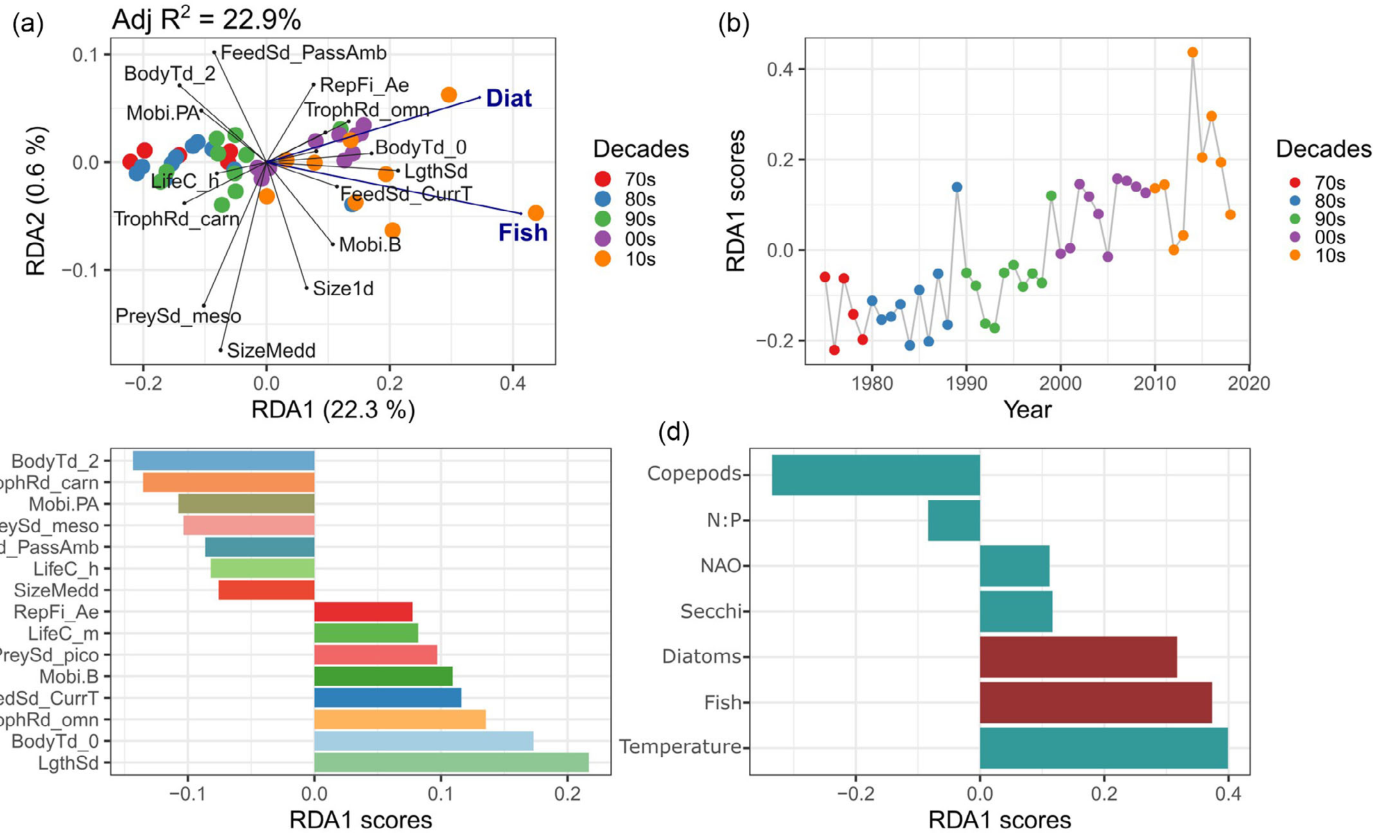

Fig. 3. Redundancy analysis (RDA) results on the functional community structure (community-weighted mean): (**a**) RDA distance triplot, showing the Euclidean distances between years and their relationship with traits, constrained by the explanatory variables retained in the final model. Only traits with high (positive and negative) RDA1 scores are shown. Dots—individual years, colored by decades; black lines—individual traits or trait levels; blue lines—explanatory variables; (**b**) temporal variability of the RDA1 distance scores of the final model; (**c**) RDA1 correlation scores of traits with high positive and negative values, indicating which traits contribute most to changes in community structure, with increasing or decreasing trends over time, respectively. See Table 1 with codes of traits and trait levels; (**d**) RDA1 correlation scores of the environmental variables from the full model (i.e., including all explanatory variables). Variables retained in the final selected model are shown in red.

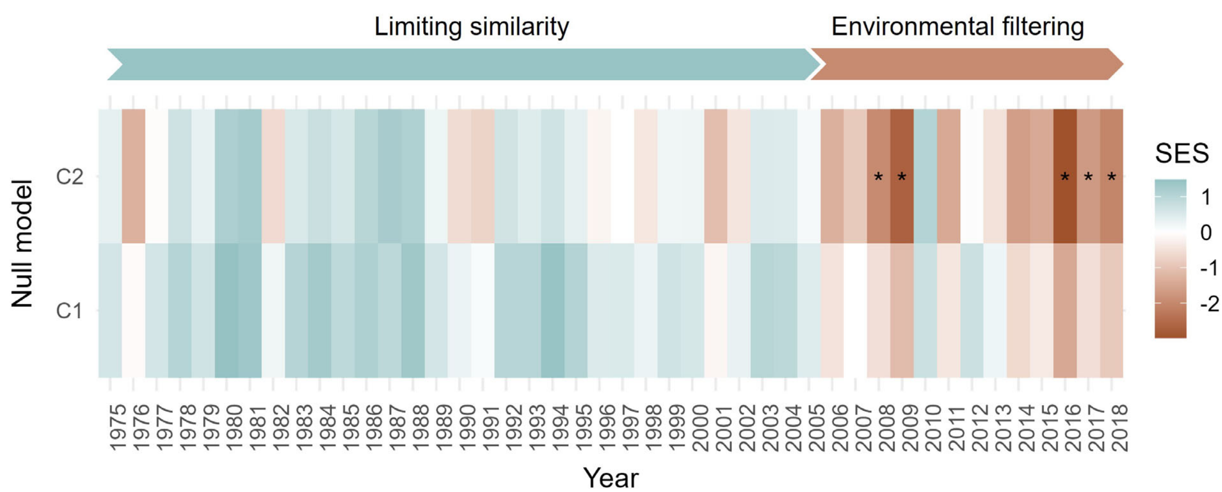

Fig. 4. Null model results based on the functional divergence index (Fdiv) to detect community assembly mechanisms. Standardized effect sizes (SES) were obtained using two types of null models: C1 (suitable for detecting limiting similarity) and C2 (suitable for detecting environmental filtering). Significant functional divergence or convergence is indicated by an asterisk (*). Above, a schematic representation of the two periods with different dominant community assembly mechanisms is shown.

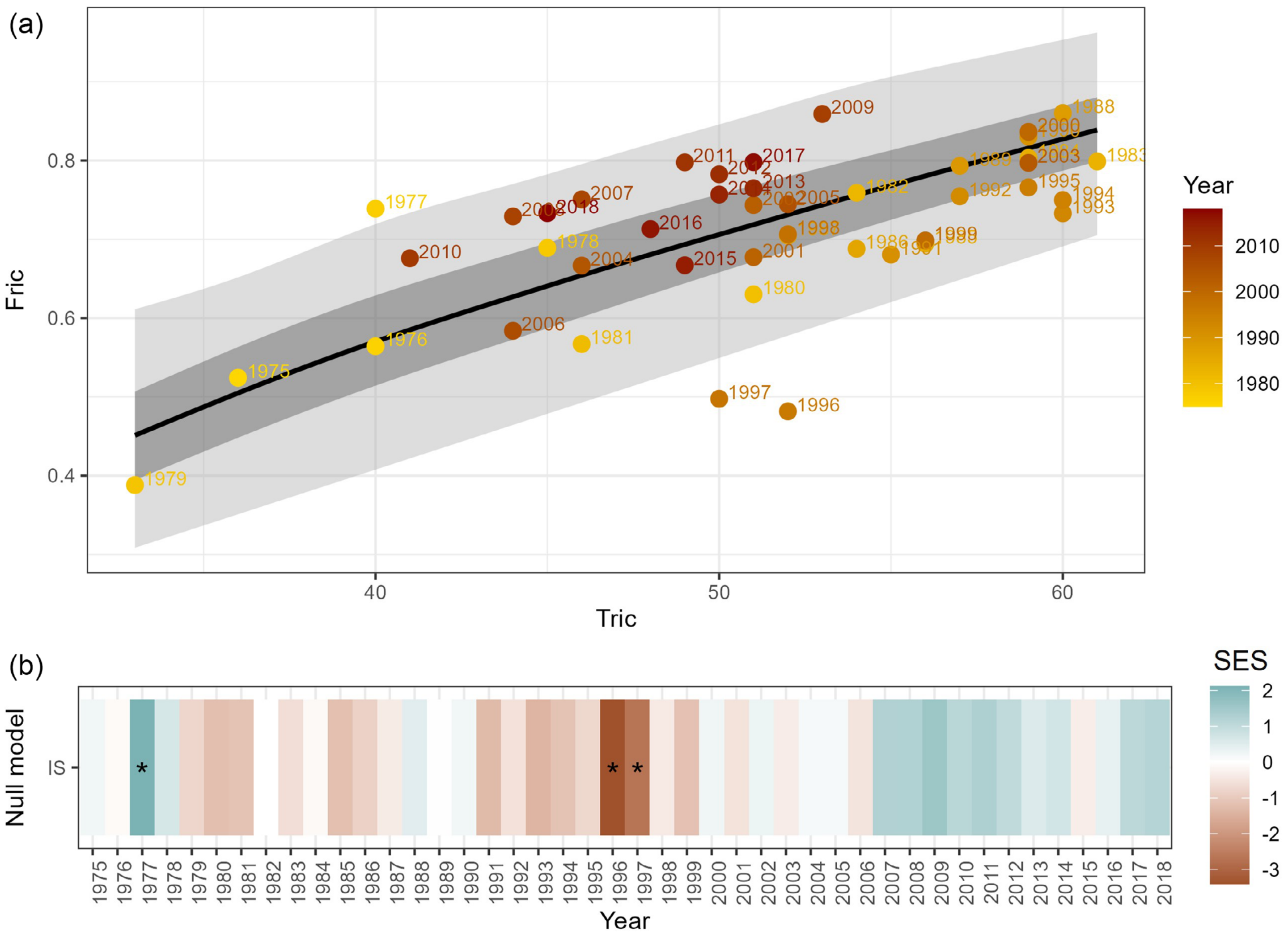

Fig. 5. Comparison between taxonomic richness (Tric) and functional richness (Fric). (**a**) Observed (colored dots) and simulated Fric values based on the independent swap (IS) null model. The bold black line represents the mean of 999 random permutations; shaded areas indicate the 50th (dark gray) and 95th (light gray) percentiles, smoothed using a generalized additive model (GAM) function. (**b**) Standardized effect sizes (SES) of Fric over time, obtained from the IS null model. Significant functional divergence or convergence is indicated by an asterisk (*).

both Tric, Fric, and Feve increased, likely reflecting the arrival of new taxa (e.g., *Pilumnus* sp., *Corystes* sp., and *Pisidia* sp.), promoting coexistence and enhancing trait complementarity. Indeed, the 1980s regime shift was suggested to be associated with large-scale climatic variations and the consequent expansion of species distributions (Reid et al. 2001; Beaugrand and Ibanez 2004), a common response reported for several pelagic (Reid et al. 2003) and benthic species (Neumann et al. 2013). A short-lived but notable disruption occurred in 1996–1997, when Fric dropped sharply. This period coincided with a documented extreme winter that strongly affected benthic populations (Kröncke et al. 2013) and was accompanied by a significant decline in the abundance of decapod larvae and hydrozoans (Marques et al. 2023). This likely impacted species with lower tolerance to extreme temperatures (e.g., *Corystes* sp., *Pisidia* sp., and *Macropodia* sp., were absent during these years), and resulted in decreasing functional richness. Although this fluctuation was not associated with significant long-term shifts, it underscores how episodic environmental disturbances can temporarily alter functional community properties. More persistent structural changes began to unfold in the early 2000s, marked by a decrease in Fdiv and a concurrent increase in Fide, suggesting a shift toward communities increasingly dominated by generalists. This aligns with earlier reports of asynchronous timing of biodiversity changes and supports the view that the post-1996 regime shifts reported in the NS were prolonged, multi-year reorganizations of communities rather than abrupt tipping points (Beaugrand and Ibanez 2004; Sguotti et al. 2022).

The analysis of assembly mechanisms provides further context for the post-2005 changes in community structure. Patterns in functional divergence suggest that limiting similarity may have prevailed before 2005, consistent with a functionally diverse community supported by high productivity and niche partitioning. After 2005, signals of environmental filtering became more apparent, evidenced by significant convergence in selected years and a decline in the abundance of functionally extreme gelatinous and carnivorous taxa (e.g., Rathkeidae, *Parasagitta* sp.). Although these signals were not uniformly strong across all years or models, the overall shift in trait composition, coupled with changing assembly processes, supports the interpretation of a major structural reorganization after 2005. This agrees with the potentially irreversible regime shift identified in the mid-2000s (Sguotti et al. 2022), and underscores the need to integrate multiple dimensions of biodiversity when identifying and interpreting ecosystem dynamics.

Drivers for changes in functional structure

The observed changes in the functional community structure of large zooplankton were primarily associated with resource- and predator-driven bottom-up and top-down processes. Diatom abundance and fish biomass, used as indicators of phytoplankton availability and predation pressure, respectively, were the most important environmental variables affecting long-term changes in the community structure, together with traits influencing trophic interactions. Omnivorous organisms using current-feeding strategies and possessing protective traits against predators (e.g., hard exoskeletons, numerous or long spines) increased. This may partially explain the long-term decrease in hydrozoans and increase in decapod larvae (Marques et al. 2023). Gelatinous organisms are susceptible to fish predation due to soft tissues, high digestion rates and limited escape capabilities (Marques et al. 2016), making them important prey for various fish species (Marques et al. 2019; Brodeur et al. 2021). In contrast, organisms with hard exoskeletons and spines, common in decapod larvae, are less attractive to fish. Their larger size and spines hinder ingestion, especially for gape-limited feeders (Allen 2008). Accordingly, *Pisidia* sp., characterized by conspicuous large spines, has increased in abundance in recent years (Marques et al. 2023). This aligns with Kiørboe (2011), who argued that the success of a taxon depends on the trade-offs between feeding efficiency, predation mortality, and metabolism, constrained by the environment.

Our results suggest that high productivity and diverse prey before the early 2000s promoted niche partitioning and coexistence of functionally diverse taxa, consistent with limiting similarity. High abundances of motile phytoplankton and copepods (Boersma et al. 2015; Di Pane et al. 2022) and relatively low predation pressure may have enabled coexistence of functionally diverse populations by reducing interspecific competition (Götzenberger et al. 2012). However, despite overall higher SES during this period, significant overdispersion was rarely detected, indicating the influence of often underestimated ecological drift effects (Gilbert and Levine 2017). After 2005, environmental filtering processes became more evident, likely reducing the abundance of species with traits less suited to contemporary environmental conditions (Götzenberger et al. 2012, 2016). The decline in motile prey (copepods and dinoflagellates, Di Pane et al. 2022), may have reduced food availability for carnivores and passive ambush feeders. At the same time, increasing predation pressure on vulnerable species likely led to a reduction in the available niche size. In parallel, the rise in non-motile prey (i.e., diatoms) provided sufficient resources for active current feeders with a better ability to escape predators.

While these trait–environment relationships highlight the dominant role of food availability and predation, the influence of temperature—often cited as a major driver of plankton change—was surprisingly limited in our analysis. Poleward distribution shifts of warm-water species (Lindley et al. 2010; Benedetti et al. 2023), and the effect of temperature on species' reproduction, development, and survival (Kirby et al. 2007), are known to shape zooplankton communites. The direct effect of temperature on the taxonomic community structure has been documented for phytoplankton (Di Pane et al. 2022), copepods (Deschamps et al. 2024), and for meso- and macrozooplankton communities at Helgoland (Marques et al. 2023). However, at the functional level, temperature had only minor explanatory power compared to diatom abundance and fish biomass. This suggests that temperature may act more indirectly—by altering food web dynamics—rather than being a dominant direct driver of functional composition. Indeed, such trophic amplification of climate warming has been previously suggested for the NS (Lindley et al. 2010).

Caveats of the study

While our findings offer valuable insights, several caveats warrant consideration. Trait selection was influenced by data availability for the entire community, and certain important traits could not be included (e.g., fecundity, swimming speed, feeding, and metabolic rates). The traits considered in our study may differ in their sensitivity to different environmental parameters and/or be associated with other stressors not explicitly addressed in our hypotheses. For instance, traits related to metabolic scaling may respond more directly to temperature, while categorical traits (e.g., reproduction mode, mobility) may be less sensitive. Body size is a fundamental trait influencing swimming speed, lipid storage, prey and predator size, and various vital rates (Litchman et al. 2013), all of which may be affected differently by different environmental factors. Furthermore, considering trade-offs is central to defining ecological strategies and omitting them may oversimplify the complexity of trait-mediated responses to environmental stressors (Litchman et al. 2013). Therefore, it is imperative to acknowledge that no trait-based analysis can ever be entirely comprehensive or free from bias and it might overlook critical mechanisms.

Our results did not reveal a strong influence of traits associated with benthic adult stages, although we cannot ignore the importance of bentho-pelagic dynamics in our system. The reduction of decapod adults, by predators such as cod (Frank et al. 2005), habitat modifications through the addition of hard substrates from windfarms (Janßen et al. 2013), and fluctuations in bottom trawling pressure (Hinz et al. 2021) have been shown to affect the size and structure of benthic communities, and thus their larval populations.

Finally, our results reflect zooplankton community changes in the southern NS only. Although our results are consistent with broader NS reports (Djeghri et al. 2023), the low spatial resolution of our dataset, based on a single long-term monitoring station, limits the generalizability of our conclusions across larger spatial scales.

Conclusion

The response of marine communities to multiple stressors is complex, and the interaction of biotic and abiotic factors can complicate the interpretation of changes in community structure. Our study shows that trait-based approaches help simplify this complexity and reveal the principal processes underlying observed changes. Trophic mechanisms emerged as particularly influential in shaping the functional structure of meso- and macrozooplankton. The role of prey-type stands out, with long-term changes in both lower and higher trophic levels mechanistically linked to internal shifts within zooplankton communities. Given the central role of trophodynamic processes, future modeling efforts should move beyond biomass-based representations and incorporate trait-based formulations of zooplankton allowing for more mechanistic responses to both resource availability and predation pressure. To better capture top-down control, models should incorporate dynamic, trait-mediated predation rather than fixed mortality rates. This includes accounting for predator–prey size relationships and selective feeding behaviors of higher trophic levels that differentially impact zooplankton functional groups.

Author Contributions

Raquel Marques: Conceptualization; formal analysis; investigation; methodology; visualization; writing. Saskia A. Otto: Conceptualization; methodology; validation; writing. Maarten Boersma: Data curation; writing. Christian Möllmann: Resources; writing. Karen Wiltshire: Data curation. Jasmin Renz: Conceptualization; data curation; funding acquisition; resources; supervision; validation; writing.

Acknowledgments

We thank all the technicians that were instrumental in the analysis and counting of the samples over time, in particular the support by numerous technicians from AWI and DZMB—Senkenberg am Meer. A special acknowledgement goes to Wulf Greve, the founder of this monitoring program. We thank the crews of the research vessel “Aade” for their unfailing provision of samples and the two reviewers for their valuable comments and suggestions, which helped improve the quality of this work. This work was conducted within the framework of the project BioWeb (BMBF grant number 03F0861A), with support from the DFG initiative 1991 “Taxon-omics” (RE2808/3-1 andRE2808/3-2). Open Access funding enabled and organized by Projekt DEAL.

Conflicts of Interest

Saskia A. Otto and Christian Möllmann have the same affiliation as the Deputy Editor Elisa Schaum from University of Hamburg.

Data Availability Statement

The datasets originated from the monitoring program at Helgoland Roads analyzed during the current study are available in PANGAEA® at https://www.pangaea.de/ and provided by Jasmin Renz, Maarten Boersma, and Karen Wiltshire on reasonable request. Fish biomass data are available at the International Bottom Trawl Survey (IBTS) program of ICES (https://www.ices.dk/data/data-portals/Pages/DATRAS.aspx).

References

Allen, J. D. 2008. “Size-Specific Predation on Marine Invertebrate Larvae.” *The Biological Bulletin* 214: 42–49. https://doi.org/10.2307/25066658.

Beaugrand, G., X. Harlay, and M. Edwards. 2014. “Detecting Plankton Shifts in the North Sea: A New Abrupt Ecosystem Shift Between 1996 and 2003.” *Marine Ecology Progress Series* 502: 85–104. https://doi.org/10.3354/meps10693.

Beaugrand, G., and F. Ibanez. 2004. “Monitoring Marine Plankton Ecosystems. II: Long-Term Changes in North Sea Calanoid Copepods in Relation to Hydro-Climatic Variability.” *Marine Ecology Progress Series* 284: 35–47. https://doi.org/10.3354/meps284035.

Benedetti, F., J. Wydler, and M. Vogt. 2023. “Copepod Functional Traits and Groups Show Divergent Biogeographies in the Global Ocean.” *Journal of Biogeography* 50: 8–22. https://doi.org/10.1111/jbi.14512.

Boersma, M., K. H. Wiltshire, S.-M. Kong, W. Greve, and J. Renz. 2015. “Long-Term Change in the Copepod Community in the Southern German Bight.” *Journal of Sea Research* 101: 41–50. https://doi.org/10.1016/j.seares.2014.12.004.

Brodeur, R. D., T. W. Buckley, G. M. Lang, D. L. Draper, J. C. Buchanan, and R. E. Hibpshman. 2021. “Demersal Fish Predators of Gelatinous Zooplankton in the Northeast Pacific Ocean.” *Marine Ecology Progress Series* 658: 89–104. https://doi.org/10.3354/meps13489.

Charrad, M., N. Ghazzali, V. Boiteau, and A. Niknafs. 2014. “NbClust: An R Package for Determining the Relevant

Number of Clusters in a Data Set." *Journal of Statistical Software* 61, no. 6: 1–36. http://www.jstatsoft.org/v61/i06/.

Cohen, J. E., S. L. Pimm, P. Yodzis, and J. Saldaña. 1993. "Body Sizes of Animal Predators and Animal Prey in Food Webs." *Journal of Animal Ecology* 62: 67–78. https://doi.org/10.2307/5483.

de Amorim, F. d. L. L., K. H. Wiltshire, P. Lemke, et al. 2023. "Investigation of Marine Temperature Changes across Temporal and Spatial Gradients: Providing a Fundament for Studies on the Effects of Warming on Marine Ecosystem Function and Biodiversity." *Progress in Oceanography* 216: 103080. https://doi.org/10.1016/j.pocean.2023.103080.

de Bello, F., C. P. Carmona, A. T. C. Dias, L. Götzenberger, M. Moretti, and M. P. Berg. 2021. Handbook of Trait-Based Ecology: From Theory to R Tools. Cambridge University Press. https://doi.org/10.1017/9781108628426.

Deschamps, M. M., M. Boersma, C. L. Meunier, I. V. Kirstein, K. H. Wiltshire, and J. Di Pane. 2024. "Major Shift in the Copepod Functional Community of the Southern North Sea and Potential Environmental Drivers." *ICES Journal of Marine Science* 81: 540–552. https://doi.org/10.1093/icesjms/fsad160.

Di Pane, J., M. Boersma, R. Marques, M. Deschamps, U. Ecker, and C. L. Meunier. 2023. "Identification of Tipping Years and Shifts in Mesozooplankton Community Structure Using Multivariate Analyses: A Long-Term Study in Southern North Sea." *ICES Journal of Marine Science* 81: fsad071. https://doi.org/10.1093/icesjms/fsad071.

Di Pane, J., K. H. Wiltshire, M. McLean, M. Boersma, and C. L. Meunier. 2022. "Environmentally Induced Functional Shifts in Phytoplankton and Their Potential Consequences for Ecosystem Functioning." *Global Change Biology* 28: 2804–2819. https://doi.org/10.1111/gcb.16098.

Dickey-Collas, M. 2016. "North Sea Herring: Longer Term Perspective on Management Science Behind the Boom, Collapse and Recovery of the North Sea Herring Fishery." In Management Science in Fisheries: An Introduction to Simulation-Based Methods, edited by C. T. T. Edwards and D. J. Dankel, 365–408. Routledge.

Djeghri, N., A. Boyé, C. Ostle, and P. Hélaouët. 2023. "Reinterpreting Two Regime Shifts in North Sea Plankton Communities Through the Lens of Functional Traits." *Global Ecology and Biogeography* 32: 962–975. https://doi.org/10.1111/geb.13659.

Faraway, J. 2022. faraway: Functions and Datasets for Books by Julian Faraway. R package version 1.0.9. https://CRAN.R-project.org/package=faraway.

Frank, K. T., B. Petrie, J. S. Choi, and W. C. Leggett. 2005. "Trophic Cascades in a Formerly Cod-Dominated Ecosystem." *Science* 308: 1621–1623. https://doi.org/10.1126/science.1113075.

Gattuso, J.-P., A. Magnan, R. Billé, et al. 2015. "Contrasting Futures for Ocean and Society From Different Anthropogenic CO_2 Emissions Scenarios." *Science* 349: aac4722. https://doi.org/10.1126/science.aac4722.

Gilbert, B., and J. M. Levine. 2017. "Ecological Drift and the Distribution of Species Diversity." *Proceedings of the Royal Society B: Biological Sciences* 284: 20170507. https://doi.org/10.1098/rspb.2017.0507.

Gotelli, N. J. 2000. "Null Model Analysis of Species Co-Occurrence Patterns." *Ecology* 81: 2606–2621. https://doi.org/10.1890/0012-9658(2000)081[2606:NMAOSC]2.0.CO;2.

Götzenberger, L., Z. Botta-Dukát, J. Lepš, M. Pärtel, M. Zobel, and F. de Bello. 2016. "Which Randomizations Detect Convergence and Divergence in Trait-Based Community Assembly? A Test of Commonly Used Null Models." *Journal of Vegetation Science* 27: 1275–1287. https://doi.org/10.1111/jvs.12452.

Götzenberger, L., F. de Bello, K. A. Bråthen, et al. 2012. "Ecological Assembly Rules in Plant Communities—Approaches, Patterns and Prospects." *Biological Reviews* 87: 111–127. https://doi.org/10.1111/j.1469-185X.2011.00187.x.

Halpern, B. S., M. Frazier, J. Potapenko, et al. 2015. "Spatial and Temporal Changes in Cumulative Human Impacts on the World's Ocean." *Nature Communications* 6: 7615. https://doi.org/10.1038/ncomms8615.

Hinz, H., A. Törnroos, and S. de Juan. 2021. "Trait-Based Indices to Assess Benthic Vulnerability to Trawling and Model Loss of Ecosystem Functions." *Ecological Indicators* 126: 107692. https://doi.org/10.1016/j.ecolind.2021.107692.

Hubbel, S. 2001. The Unified Neutral Theory of Biodiversity and Biogeography (MPB-32). Princeton University Press.

ICES. 2022. Greater North Sea Ecoregion—Fisheries Overview. ICES Advice: Fisheries Overviews. https://doi.org/10.17895/ices.advice.21641360.v1.

Janßen, H., C. B. Augustin, H. H. Hinrichsen, and S. Kube. 2013. "Impact of Secondary Hard Substrate on the Distribution and Abundance of Aurelia Aurita in the Western Baltic Sea." *Marine Pollution Bulletin* 75: 224–234. https://doi.org/10.1016/j.marpolbul.2013.07.027.

Kassambara, A., and F. Mundt. 2020. factoextra: Extract and Visualize the Results of Multivariate Data Analyses. CRAN: Contributed Packages.

Kembel, S. W., P. D. Cowan, M. R. Helmus, et al. 2010. "Picante: R Tools for Integrating Phylogenies and Ecology." *Bioinformatics* 26: 1463–1464. https://doi.org/10.1093/bioinformatics/btq166.

Kiørboe, T. 2011. "How Zooplankton Feed: Mechanisms, Traits and Trade-Offs." *Biological Reviews* 86: 311–339. https://doi.org/10.1111/j.1469-185X.2010.00148.x.

Kiørboe, T., and A. G. Hirst. 2014. "Shifts in Mass Scaling of Respiration, Feeding, and Growth Rates across Life-Form Transitions in Marine Pelagic Organisms." *The American Naturalist* 183: E118–E130. https://doi.org/10.1086/675241.

Kirby, R. R., G. Beaugrand, and J. A. Lindley. 2008. "Climate-Induced Effects on the Meroplankton and the

Benthic-Pelagic Ecology of the North Sea." *Limnology and Oceanography* 53: 1805–1815. https://doi.org/10.4319/lo.2008.53.5.1805.

Kirby, R. R., G. Beaugrand, J. A. Lindley, A. J. Richardson, M. Edwards, and P. C. Reid. 2007. "Climate Effects and Benthic–Pelagic Coupling in the North Sea." *Marine Ecology Progress Series* 330: 31–38. https://doi.org/10.3354/meps330031.

Kröncke, I., H. Reiss, and J. W. Dippner. 2013. "Effects of Cold Winters and Regime Shifts on Macrofauna Communities in Shallow Coastal Regions." *Estuarine, Coastal and Shelf Science* 119: 79–90. https://doi.org/10.1016/j.ecss.2012.12.024.

Laliberté, E., P. Legendre, and B. Shipley. 2014. FD: Measuring Functional Diversity from Multiple Traits, and Other Tools for Functional Ecology. R Foundation for Statistical Computing.

Lindley, J. A., G. Beaugrand, C. Luczak, J.-M. Dewarumez, and R. R. Kirby. 2010. "Warm-Water Decapods and the Trophic Amplification of Climate in the North Sea." *Biology Letters* 6: 773–776. https://doi.org/10.1098/rsbl.2010.0394.

Litchman, E., M. D. Ohman, and T. Kiørboe. 2013. "Trait-Based Approaches to Zooplankton Communities." *Journal of Plankton Research* 35: 473–484. https://doi.org/10.1093/plankt/fbt019.

Magneville, C., N. Loiseau, C. Albouy, et al. 2022. "mFD: An R Package to Compute and Illustrate the Multiple Facets of Functional Diversity." *Ecography* 2022: e05904. https://doi.org/10.1111/ecog.05904.

Maire, E., G. Grenouillet, S. Brosse, and S. Villéger. 2015. "How Many Dimensions Are Needed to Accurately Assess Functional Diversity? A Pragmatic Approach for Assessing the Quality of Functional Spaces." *Global Ecology and Biogeography* 24: 728–740. https://doi.org/10.1111/geb.12299.

Malzahn, A. M., and M. Boersma. 2012. "Effects of Poor Food Quality on Copepod Growth Are Dose Dependent and Non-reversible." *Oikos* 121: 1408–1416. https://doi.org/10.1111/j.1600-0706.2011.20186.x.

Marques, R., C. Bouvier, A. M. Darnaude, et al. 2016. "Jellyfish as an Alternative Source of Food for Opportunistic Fishes." *Journal of Experimental Marine Biology and Ecology* 485: 1–7. https://doi.org/10.1016/j.jembe.2016.08.008.

Marques, R., A. M. Darnaude, S. Crochemore, C. Bouvier, and D. Bonnet. 2019. "Molecular Approach Indicates Consumption of Jellyfish by Commercially Important Fish Species in a Coastal Mediterranean Lagoon." *Marine Environmental Research* 152: 104787. https://doi.org/10.1016/j.marenvres.2019.104787.

Marques, R., S. A. Otto, J. Di Pane, et al. 2023. "Response of the Meso- and Macro-Zooplankton Community to Long-Term Environmental Changes in the Southern North Sea." *ICES Journal of Marine Science* 81: fsad121. https://doi.org/10.1093/icesjms/fsad121.

Morgan, S. G. 1989. "Adaptive Significance of Spination in Estuarine Crab Zoeae." *Ecology* 70: 464–482. https://doi.org/10.2307/1937551.

Mouchet, M. A., S. Villéger, N. W. H. Mason, and D. Mouillot. 2010. "Functional Diversity Measures: An Overview of their Redundancy and their Ability to Discriminate Community Assembly Rules." *Functional Ecology* 24: 867–876. https://doi.org/10.1111/j.1365-2435.2010.01695.x.

Mouillot, D., N. A. J. Graham, S. Villéger, N. W. H. Mason, and D. R. Bellwood. 2013. "A Functional Approach Reveals Community Responses to Disturbances." *Trends in Ecology & Evolution* 28: 167–177. https://doi.org/10.1016/j.tree.2012.10.004.

Neumann, H., I. de Boois, I. Kröncke, and H. Reiss. 2013. "Climate Change Facilitated Range Expansion of the Non-Native Angular Crab Goneplax Rhomboides into the North Sea." *Marine Ecology Progress Series* 484: 143–153. https://doi.org/10.3354/meps10299.

Nohe, A., A. Goffin, L. Tyberghein, et al. 2020. "Marked Changes in Diatom and Dinoflagellate Biomass, Composition and Seasonality in the Belgian Part of the North Sea between the 1970s and 2000s." *Science of the Total Environment* 716: 136316. https://doi.org/10.1016/j.scitotenv.2019.136316.

Oksanen, J., G. L. Simpson, F. G. Blanchet, et al. 2022. vegan: Community Ecology Package. https://cran.r-project.org/package=vegan.

Pechenik, J. A. 1999. "On the Advantages and Disadvantages of Larval Stages in Benthic Marine Invertebrate Life Cycles." *Marine Ecology Progress Series* 177: 269–297. https://doi.org/10.3354/meps177269.

Pitt, K. A., C. M. Duarte, C. H. Lucas, et al. 2013. "Jellyfish Body Plans Provide Allometric Advantages beyond Low Carbon Content." *PLoS One* 8: e72683. https://doi.org/10.1371/journal.pone.0072683.

Raabe, T., and K. H. Wiltshire. 2009. "Quality Control and Analyses of the Long-Term Nutrient Data from Helgoland Roads, North Sea." *Journal of Sea Research* 61: 3–16. https://doi.org/10.1016/j.seares.2008.07.004.

Reid, P. C., M. de F. Borges, and E. Svendsen. 2001. "A Regime Shift in the North Sea Circa 1988 Linked to Changes in the North Sea Horse Mackerel Fishery." *Fisheries Research* 50: 163–171. https://doi.org/10.1016/S0165-7836(00)00249-6.

Reid, P. C., M. Edwards, G. Beaugrand, M. Skogen, and D. Stevens. 2003. "Periodic Changes in the Zooplankton of the North Sea During the Twentieth Century Linked to Oceanic Inflow." *Fisheries Oceanography* 12: 260–269. https://doi.org/10.1046/j.1365-2419.2003.00252.x.

Reznick, D., M. J. Bryant, and F. Bashey. 2002. "r- and k-Selection Revisited: The Role of Population Regulation in Life-History Evolution." *Ecology* 83: 1509–1520. https://doi.org/10.1890/0012-9658(2002)083[1509:RAKSRT]2.0.CO;2.

Richardson, A. J. 2008. "In Hot Water: Zooplankton and Climate Change." *ICES Journal of Marine Science* 65: 279–295. https://doi.org/10.1093/icesjms/fsn028.

Sguotti, C., A. M. Blöcker, L. Färber, et al. 2022. "Irreversibility of Regime Shifts in the North Sea." *Frontiers in Marine Science* 9: 945204. https://doi.org/10.3389/fmars.2022.945204.

Sommer, U., K. H. Peter, S. Genitsaris, and M. Moustaka-Gouni. 2017. "Do Marine Phytoplankton Follow Bergmann's Rule Sensu Lato?" *Biological Reviews* 92: 1011–1026. https://doi.org/10.1111/brv.12266.

Thompson, J. K. 2005. "One Estuary, One Invasion, Two Responses: Phytoplankton and Benthic Community Dynamics Determine the Effect of an Estuarine Invasive Suspension-Feeder." In The Comparative Roles of Suspension-Feeders in Ecosystems, 291–316. Springer Netherlands.

van Beusekom, J. E. E., J. Carstensen, T. Dolch, et al. 2019. "Wadden Sea Eutrophication: Long-Term Trends and Regional Differences." *Frontiers in Marine Science* 6: 370. https://doi.org/10.3389/fmars.2019.00370.

Verity, P. G., and V. Smetacek. 1996. "Organism Life Cycles, Predation, and the Structure of Marine Pelagic Ecosystems." *Marine Ecology Progress Series* 130: 277–293. https://doi.org/10.3354/meps130277.

Wiltshire, K. H., M. Boersma, K. Carstens, A. C. Kraberg, S. Peters, and M. Scharfe. 2015. "Control of Phytoplankton in a Shelf Sea: Determination of the Main Drivers Based on the Helgoland Roads Time Series." *Journal of Sea Research* 105: 42–52. https://doi.org/10.1016/j.seares.2015.06.022.

Wiltshire, K. H., A. M. Malzahn, K. Wirtz, et al. 2008. "Resilience of North Sea Phytoplankton Spring Bloom Dynamics: An Analysis of Long-Term Data at Helgoland Roads." *Limnology and Oceanography* 53: 1294–1302. https://doi.org/10.4319/lo.2008.53.4.1294.

Zeileis, A., F. Leisch, K. Hornik, and C. Kleiber. 2002. "strucchange: An R Package for Testing for Structural Change in Linear Regression Models." *Journal of Statistical Software* 7: 1–38. https://doi.org/10.18637/jss.v007.i02.

Supporting Information

Additional Supporting Information may be found in the online version of this article.

Submitted 08 October 2024
Revised 27 June 2025
Accepted 19 October 2025