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Response of the meso- and macro-zooplankton community to long-term environmental changes in the southern North Sea

R. Marques ^{1,*}, S. A. Otto ², J. Di Pane ^{3,4}, M. Boersma ^{3,5}, C. L. Meunier ³,
K. H. Wiltshire ⁶, C. Möllmann ², and J. Renz ¹

¹Senckenberg am Meer, German Centre for Marine Biodiversity Research (DZMB), Martin-Luther-King Platz 3, D-20146 Hamburg, Germany

²Institute of Marine Ecosystem and Fisheries Science (IMF), Center for Earth System Research and Sustainability (CEN), University of Hamburg, 22767 Hamburg, Germany

³Alfred-Wegener-Institut Helmholtz-Zentrum für Polar- und Meeresforschung, Biologische Anstalt Helgoland, 27498 Helgoland, Germany

⁴Aix Marseille Univ, Université de Toulon, CNRS, IRD, MIO, 13288 Marseille, France

⁵University of Bremen, FB2 28359 Bremen, Germany

⁶Alfred-Wegener-Institut Helmholtz-Zentrum für Polar- und Meeresforschung, Wattenmeerstation, 25992 List auf Sylt, Germany

*Corresponding author: tel: +49(0)40 42838 2294; e-mail: raquel.marques@senckenberg.de.

The North Sea (NS) is changing rapidly. Temporal variations in fishing intensity and eutrophic conditions, along with the ongoing impact of climate change, act in synergy resulting in modifications in marine communities. Although zooplankton has been extensively investigated, studies often ignore the large-sized meso- and macro-zooplankton (>500 µm), including holoplankton and meroplankton taxa. Here, we examined changes in abundances and community structure of these organisms between 1975 and 2018, using univariate and multivariate analysis, at different taxonomic levels. Abrupt changes in the abundances of (sub)communities occurred during different time periods and resulted in a significant restructuring of the entire community in 2006. These changes were consistent with the regime shifts reported in the NS and were a consequence of the environmental pressures on the whole community or on specific subcommunities. In the long term, the community shifted from higher abundances of hydrozoans and holoplankton taxa to an increasing abundance of decapods. Furthermore, we reveal the environmental variables that most explain the variability in the community dynamics, highlighting the importance of temperature and top-down processes. Our study underlines the relevance of investigations at different taxonomic levels, which elucidates how distinct responses to environmental changes ultimately shape the entire community structure.

Keywords: community structure, decapods, helgoland, hydrozoans, meroplankton.

Introduction

The North Sea (NS) is one of the marine “hotspots” of cumulative anthropogenic impacts, including fishing, climate change, and ocean- and land-based stressors (Halpern *et al.*, 2015), which affect its communities and ecosystem functioning. Sea surface temperatures have increased by >1°C since 1960s in the NS (Wiltshire *et al.*, 2008; Høyer and Karagali, 2016), naturally affecting the whole pelagic ecosystem, from lower to higher trophic levels (Müren *et al.*, 2005; du Pontavice *et al.*, 2020). Increasing riverine nutrients loads since the 1960s led to eutrophic conditions in coastal areas during the 1980s, but management policies reversed this trend and nutrients loads were substantially diminished resulting in current de-eutrophication (van Beusekom *et al.*, 2019). In the southern NS (SNS), these climatic and anthropogenic changes resulted in modifications in the nitrogen to phosphorus (N:P) ratios (van Beusekom *et al.*, 2019; Balkoni *et al.*, 2023), in water transparency (McQuatters-Gollop *et al.*, 2007; Dupont and Aksnes, 2013; Wilson and Heath, 2019) and in primary productivity (Xu *et al.*, 2020), with contrasting regional trends due to the complex hydrography conditions in this area (Tett and Walne, 1995). For instance, at Helgoland Roads, water transparency and primary productivity, in particular diatoms

abundance, have been increasing since the 1980s (Wiltshire *et al.*, 2008, 2010, 2015), while N:P ratio have been declining since the 1990s, due to differing decreasing rates in nutrient concentration (Raabe and Wiltshire, 2009; Balkoni *et al.*, 2023). In parallel with changes at the basis of the NS marine food webs, fisheries exploitation and management have affected fish stocks (Blöcker *et al.*, 2023). For example, the NS herring stock collapsed in the 1970s, but fishery management resulted in increasing biomass since the 1980s (Dickey-Collas, 2016). Considering the central role of herring in the functioning of planktonic food webs (Lynam *et al.*, 2017), these temporal variations at the top of the food web can potentially regulate zooplankton communities (Papworth *et al.*, 2016; Lynam *et al.*, 2017).

These modulations of bottom-up and top-down processes, induced changes in all marine trophic levels and triggered the reorganization of the NS marine ecosystems, often called “regime shifts” (abrupt changes in the structure and functioning of ecosystems, e.g. Möllmann *et al.*, 2015). In the NS, three main regime shifts have been identified since the mid-1970s. The first occurred in late 1980s, when the system changed from a cold to a warm dynamic regime (Reid *et al.*, 2001; Beaugrand *et al.*, 2008) causing a reorganiza-

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tion in the phytoplankton community towards higher abundances of dinoflagellates and lower of diatoms (Di Pane *et al.*, 2022). A concomitant reorganization of the zooplankton communities occurred, with higher relative contribution of warm water species, a reduction in the larval abundance of benthic bivalves as well as increases in jellyfish, echinoderms, and decapod larvae (Kirby *et al.*, 2008, 2009; Kirby and Beaugrand, 2009; Lindley and Kirby, 2010; Lindley *et al.*, 2010). This regime shift occurred simultaneously with the collapse of predatory ground fish stocks such as the Atlantic cod (*Gadus morhua*) and a growing biomass of forage fish including herring (Dickey-Collas, 2016; Sguotti *et al.*, 2022). The second regime shift occurred between 1996 and 2003, which was reflected in nearly all planktonic groups (Alvarez-Fernandez *et al.*, 2012; Beaugrand *et al.*, 2014). Diatoms replaced dinoflagellates as the dominating group in the phytoplankton community (Wiltshire *et al.*, 2008; Meunier *et al.*, 2018), and in parallel most copepod species decreased in abundance (Boersma *et al.*, 2015). Eventually, when considering the entire trophic structure, from plankton to predatory fish, a recent regime shift was identified in 2003, characterized by high diatoms biomass and an increase in saithe, plaice, sprat, and herring (Sguotti *et al.*, 2022). The latter author further identified the period between late 1980s and 2008 as an instable period, after which the NS community reached a new irreversible stable state.

While zooplankton play a central role in pelagic systems and are significantly affected by changing environmental conditions, most of the studies focused on the most common zooplankton organisms, very often copepods (e.g. Beaugrand *et al.*, 2008; Boersma *et al.*, 2015; Capuzzo *et al.*, 2018). When studying the entire zooplankton community, large-sized organisms are usually considered at a low taxonomic resolution (e.g. Kirby *et al.*, 2009; Beaugrand *et al.*, 2014), due to difficulties in identification, active avoidance of net sampling devices (e.g. WP2, Skjoldal *et al.*, 2013) or unsuitable preservation (i.e. gelatinous zooplankton, Harris *et al.*, 2000). However, large zooplankton play a critical role in the ecosystem, since they are not only a link in marine food webs, but also key players in the benthopelagic coupling and in ocean's biogeochemical cycles (Beaugrand *et al.*, 2010; Cavan *et al.*, 2017). Communities of large zooplankton comprise a great diversity of species, among which many are life stages of benthic organisms (i.e. meroplankton), including from economically important species, such as the edible crab (*Cancer pagurus*, Tonk and Rozemeijer, 2019), or gelatinous zooplankton, with strong impacts on several ecosystem services (Richardson *et al.*, 2009). Thus, assessing long-term changes in the larger size component of the zooplankton at high taxonomic resolution is critical to fully understand how the ongoing environmental changes affect the zooplankton community and the associated ecosystem processes (Lomartire *et al.*, 2021; Pitois and Yebra, 2022).

The aim of this study is to assess how the meso- and macro-zooplankton community responded to the observed long-term environmental changes in the SNS. Our approach was to (1) identify if and when step-wise changes in the abundance of large-sized zooplankton occurred, (2) detect shifts in the community structure, and (3) uncover the environmental variables that explain most of the variability in abundances and community structure over time. To achieve these goals, a combination of univariate and multivariate statistical analyses was employed, using a unique 44-year time series of meso- and

macro-zooplankton community ($> 500 \mu\text{m}$), monitored in the SNS. This was performed at different taxonomic resolution, to disentangle how the distinct responses ultimately shape the structure of the whole community. These results were then put into context with the regional described regime shifts, uncovering how the long-term changes in the NS environment affected the large-sized zooplankton community.

Material 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, $54^{\circ}11'18''\text{N}$ $7^{\circ}54'\text{E}$), situated in the SNS. Zooplankton were collected 2 to 14 times per month by oblique hauls, using a Hydrobios CalCOFI net (100 cm aperture, 4 m long) with a mesh size of $500 \mu\text{m}$. Samples were preserved with formaldehyde (4%), counted and identified to the lowest possible taxonomic level under dissecting microscope (see also Greve *et al.*, 2004 for further details). Since early 1980s, ctenophores were counted immediately upon arrival at the laboratory to avoid formaldehyde fixation problems, which are known to cause the disintegration of the organisms and bias their abundance values. The sampled community is, therefore, composed of macro- and meso-zooplankton organisms with sizes $> 500 \mu\text{m}$, which will hereafter be called “large zooplankton”.

The taxonomic database was first carefully inspected to obtain the most quantitatively accurate representation of the large zooplankton community over time. Species with total length $< 500 \mu\text{m}$ can still be collected in the net, but their abundances are biased, due to incomplete retention (Skjoldal *et al.*, 2013). To reduce this bias, all taxa with reported minimum sizes $< 500 \mu\text{m}$ were eliminated from the database (e.g. all copepods except adult *Calanus* sp., echinoderms, bivalves, and polychaeta larvae). Species that were not consistently identified during the whole sampling period were eliminated or, when possible, merged at higher taxonomic level. To reduce the effect of differences in the resolution of species identifications performed by different technicians over time, all species were merged to genus level. Rare species, i.e. those that were present in $< 10\%$ of all samples or those that are not considered planktonic but sporadically collected in the samples (e.g. cumaceans), were eliminated. Taxa abundances were averaged per year to remove the seasonal effect and focus only on the long-term trends. The final taxonomic database was composed of 73 taxa and 44 years (Supplementary Table SI).

Environmental data

Sea surface temperature and the NAO (North Atlantic Oscillation) index were used to test for interannual effects of climate change and, in particular, ocean warming in the SNS. Sea surface temperature was measured at the Helgoland sampling station (see Wiltshire *et al.*, 2010 for further details) and averaged by year. The annual NAO index was obtained from the Climate Data Guide (<https://climatedataguide.ucar.edu/climate-data/overview-climate-indices>), as the variation in pressure between the Icelandic low area and the Azores high area in the northern North Atlantic. Copepods (excluding *Calanus* sp.) and diatoms abundance (making up 90% of the total microalgae community at Helgoland, Wiltshire *et al.*, 2015) were used to test for the impact of availability of zooplank-

ton and phytoplankton food, respectively. To account for an additional effect of food quality, the environmental N:P ratio was used as a proxy. As an indicator of water clarity reflecting the eutrophication status, we used Secchi depth, which was measured together with diatoms abundance, copepods abundance, and nutrients concentration (NO₃ and PO₄) as part of the Helgoland Roads monitoring programme (see Wiltshire *et al.*, 2010). To test for the impact of predation pressure, the biomass of the most common zooplanktivorous predators in the NS was used, namely the herring (*Clupea harengus*), mackerel (*Scomber scombrus*), and sprat (*Sprattus sprattus*) (ICES, 2022). 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, i.e. the SNS (<https://www.ices.dk/data/data-portals/Page/s/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 fish biomass.

Data analysis

The analyses were performed in four main steps: (1) the evaluation of gradual or step-wise changes in environmental conditions, (2) the assessment of gradual or step-wise changes in abundances, (3) the detection of shifts in community structure, and (4) the identification of environmental variables most correlated with the observed changes in abundances and community structure. The overall community was composed of two main taxonomic groups, i.e. Decapods and Hydrozoans, representing 38.4 and 37.0% of all taxa considered, respectively. Therefore, these analyses were performed for the whole community (*Total*) and for three subcommunities within the whole community: the dominant taxonomic groups *Decapods* and *Hydrozoans* and a group termed the *Others*, which represents 24.7% of the analysed taxa and comprises a mix of different taxa, such as copepods (i.e. *Calanus* sp.), chaetognaths, ctenophores, or scyphozoans (Supplementary Table S1).

To identify if and when abrupt changes in environmental conditions and abundances occurred over time, a univariate analysis was used to test for breakpoints, which indicate structural changes in linear regression models (Zeileis *et al.*, 2002, 2003). We tested for breakpoints in both the mean (i.e. the intercept, Bm) and the trend (i.e. the relationship between the variable and time, Bt). Breakpoints are 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). The best number of breakpoints was selected based on Bayesian information criterion (BIC). The breakpoint analysis was performed using the “strucchange” package (v1.5.2, Zeileis *et al.*, 2002, 2003). Shifts in (sub)community structure were tested using multivariate regression trees (MRT), with time (i.e. years) as the constraint for the partitioning of the data. The number of clusters was selected based on the minimum cross-validated relative error (Borcard *et al.*, 2011, Supplementary Figure S1). MRT was performed using the “mvpart” package (v1.6.2, Therneau *et al.*, 2014).

Univariate statistical models were used to uncover the correlation between the environmental variables and the abundances of the whole community (*Total*) and of each subcommunity (*Decapods*, *Hydrozoans*, and *Others*). Generalized additive models (GAMs) were used, by modelling their

log-transformed abundances ($\log(x + 1)$) as a smoothing function of the different environmental variables. We set the effective degrees of freedom restricted to a maximum of 4, to extract only the main changes, and temporal autocorrelation of residuals was tested by ACF plots. To achieve the best fixed terms for the model, we used backwards selection, by eliminating the least significant covariate until all terms were significant. The best supported model was selected based on the Akaike's information criterion (AIC) and parsimony (Zuur *et al.*, 2009). Standardized residuals were plotted against fitted and observed values to validate the models. GAMs were fitted using the “mgcv” R package (v1.8.40, Wood, 2023).

The relationship between the environmental stressors and the subcommunity structure was assessed by transformed redundancy analysis (RDA), after applying Hellinger transformation on the individual taxa abundances to reduce the influence of double-zeros (Borcard *et al.*, 2011; Legendre and Legendre, 2012). RDA analyses were performed with 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, 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 global 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 . These analyses allowed us not only to identify the main environmental drivers, but also the taxa that contributed most to the observed changes in subcommunity structure.

Results

Environmental conditions

The average annual temperature at Helgoland Roads ranged from 8.3 to 11.9°C, showing an overall increasing trend over time (Figure 1a), with a significant breakpoint in the mean (Bm) in 2002 (Table 1), when the temperature increased from 9.7 to 10.7°C. NAO did not show any significant Bm, fluctuating from −5.96 to 4.09 (mean of 0.57), but showed a positive overall trend over time (Figure 1b). An increasing trend in N:P ratios was observed until 1995 (breakpoint in trend, Bt), decreasing thereafter, with higher mean values of 41.4 between the Bm 1986 and 1995, compared with lower values before (16.6) and after (19.1) this period (Figure 1c). An increasing trend was observed for both the Secchi depth and the diatoms abundance, with one Bm. Secchi depth increased from 3.1 to 3.8 m in 1986 (Figure 1d), while diatom abundance increased from 11.3×10^4 to 20.5×10^4 ind.L^{−1} in 1998 (Figure 1e). The abundance of copepods increased until 1990, when a Bt was identified, decreasing afterwards (Figure 1f, Table 1). This resulted in four periods with significant differences in their mean abundance: until 1982 (3.9×10^3 ind.m^{−3}), between 1982 and 1990, when their 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 abundance was lowest (2.2×10^3 ind.m^{−3}). Finally, fish biomass increased over time without any Bt, from a minimum of 1.14×10^5

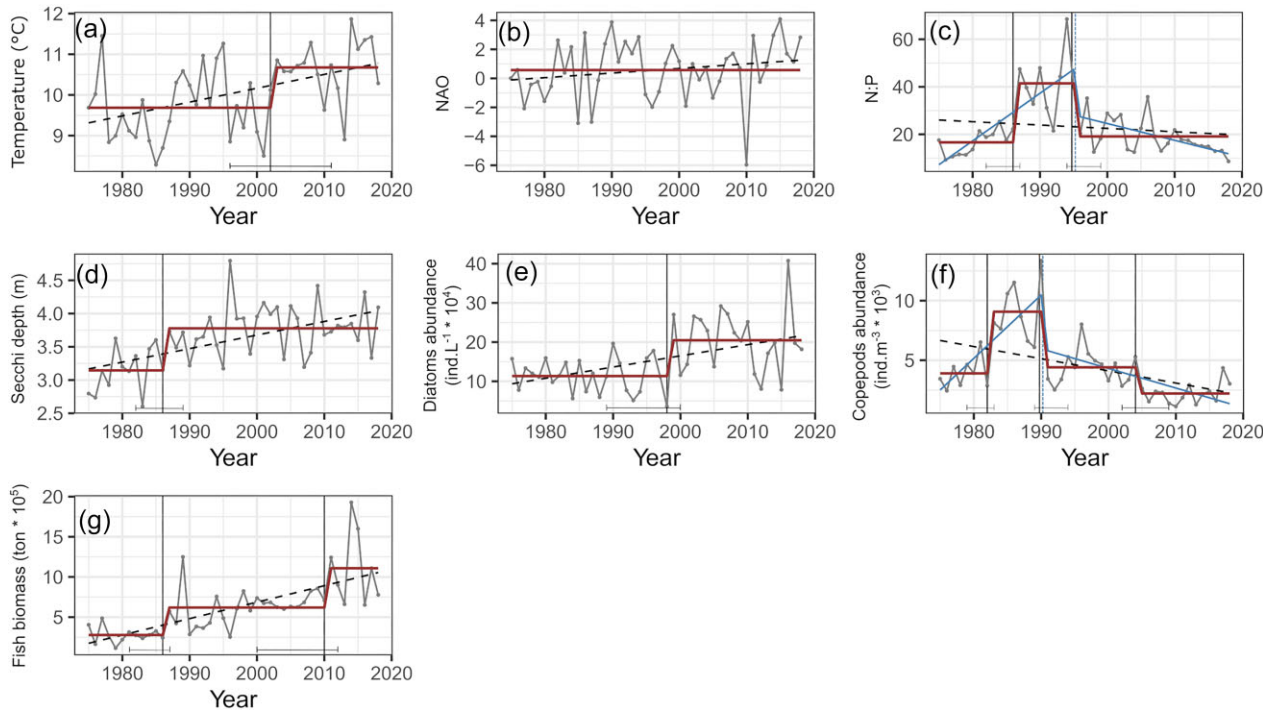


Figure 1. Temporal interannual variation of the environmental variables (grey lines). Solid red lines represent the mean of the variable per period, delimited by breakpoints (Bm, vertical black lines), with 95% CIs. Solid blue lines represent the trend of the variable per period, delimited by breakpoints (Bt, vertical-dashed blue lines, if existent). Dashed black line is the overall linear trend of the whole time series.

Table 1. Timing of identified step-wise changes in the environmental variables.

Variable	Breakpoint mean (Bm)	Breakpoint trend (Bt)
Temperature	2002	NC
Diatoms abundance	1998	NC
Copepods abundance	1982, 1990, 2004	1990
Secchi depth	1986	NC
NAO	NC	NC
Fish biomass	1986, 2010	NC
N:P	1986, 1995	1995

Changes in the mean (Bm) and trend (Bt) were detected by univariate breakpoint analysis. NC: no changes.

tons in 1979 to a maximum of 19.3×10^5 tons in 2014 (Figure 1g, Table 1). This resulted in three periods of increasing biomass with significant Bm in 1986 and 2010 (means of 2.7 , 6.2 , and 11.1×10^5 tons, respectively).

Long-term changes in abundances of (sub)communities of large zooplankton

The overall abundance (*Total*) of the large zooplankton community decreased over time with three periods identified by the breakpoint analysis (Bm) (Figure 2a, Table 2): until 1986 the abundance remained low (mean 27.3 ind.m^{-3}) increasing then to a mean of 41.6 ind.m^{-3} until 1995, when a Bt was found, after which the abundance drastically decreased until the end of the study period (mean of 24.1 ind.m^{-3}). *Decapods* was the only subcommunity that did not show any significant change in mean abundance over time (no Bm), although an overall increasing trend could be observed (Figure 2b, Table 2). Indeed, decapods abundance showed two periods of increasing trend in abundance, separated by a Bt in 1995. In the first period, the abundance increased from a minimum

of 0.37 (in 1979) to 22.3 ind.m^{-3} (in 1995), but it drastically decreases to 2.2 ind.m^{-3} in 1996, recovering again in the second period to the overall maximum abundance of 42.2 ind.m^{-3} in 2017. For the *Hydrozoans*, the breakpoint analysis identified two main periods in their mean abundance, before and after the Bm in 1996 (Figure 2c). During the first period, their abundance fluctuated at higher levels (mean of 8.2 ind.m^{-3}), with two conspicuous peaks in 1981 and 1989 (18.4 and 20.4 ind.m^{-3} , respectively), resulting in two Bt (1983 and 1989). After 1989, hydrozoan abundance decreased to 3.1 ind.m^{-3} until the end of the study period, resulting in a significant Bm in 1996, with values below 1.2 ind.m^{-3} in the last 5 years of the survey. The abundance of the *Others*, also decreased over time (overall trend), especially after 1986, when a Bt was identified (Figure 2d, Table 2). A Bm was detected in 2007, when the mean abundance decreased from 12.7 to 3.5 ind.m^{-3} (Figure 2d). Overall, these results indicate that the first shift in *Total* abundance in 1986 cannot be attributed to a shift of a single group but rather to an increase of individual taxa across all three subcommunities, while the strong decline observed in 1995 represents the cumula-

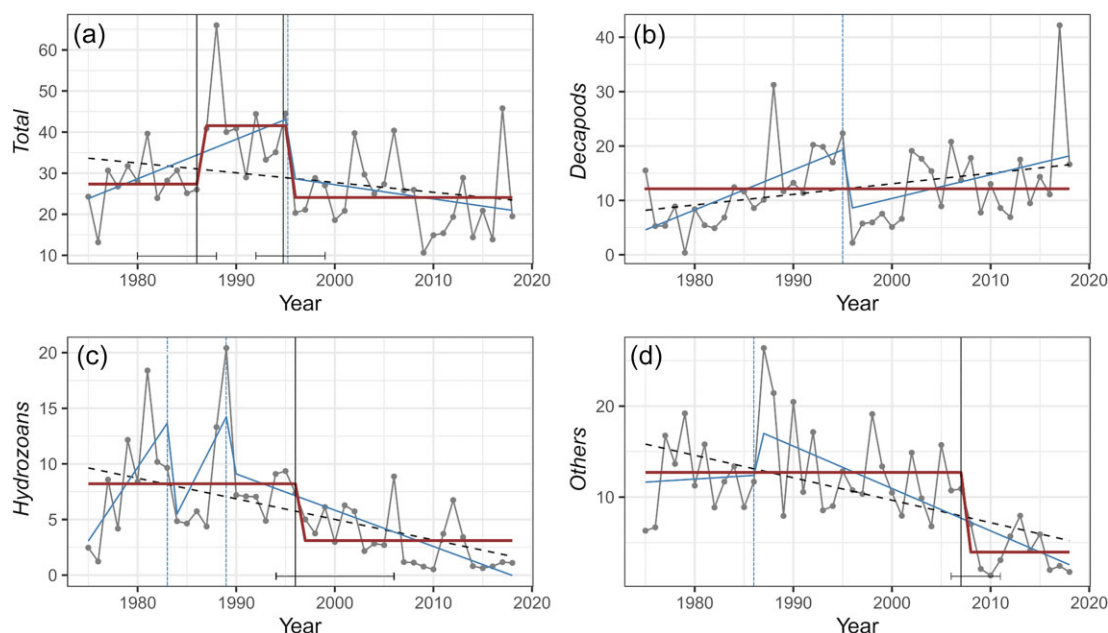


Figure 2. Temporal interannual variation of abundance (grey lines, ind.m^{-3}) of large zooplankton community at Helgoland Roads: (a) whole community (Total), (b) Decapods, (c) Hydrozoans, and (d) Others. Solid red lines represent the mean of abundance per period, delimited by breakpoints (Bm, vertical black lines, Table 2), with 95% CIs. Solid blue lines represent the trend of abundance per period, delimited by breakpoints (Bt, vertical-dashed blue lines, Table 2). Dashed black line is the overall linear trend of the whole time series.

Table 2. Timing of identified step-wise changes in abundances and community structure of the community and subcommunities.

(Sub)community	Breakpoint mean (Bm)	Breakpoint trend (Bt)	MRT
Total	1986, 1995	1995	2006
Decapods	NC	1995	2002
Hydrozoans	1996	1983, 1989	2001
Others	2007	1986	NC

Changes in the mean (Bm) and trend (Bt) of abundances were detected by univariate breakpoint analysis, while changes in community structure were identified by MRT analysis. NC: no changes.

tive effect of a general decrease in *Decapod* and *Hydrozoan* taxa.

Long-term changes in (sub)communities structure of large zooplankton

The MRT analysis identified significant changes in the overall community structure in 2006, but within each subcommunity, shifts occurred earlier: in 2001 for *Hydrozoans* and in 2002 for *Decapods* (Table 2, Supplementary Figure S1). No significant changes in community structure were detected for the *Others*, indicating that the decline in mean abundance in 2007 appeared to be widespread among all its members. Given the timing of this decline, any changes in the overall community structure reflect the changes in the relative abundances within the *Decapods* and *Hydrozoans* subcommunities, further amplified by the decline in the overall abundance of *Others*.

The most overall abundant taxa were *Parasagitta* sp., *Polybiidae*, *Upogebia* sp., *Calanus* sp., *Pleurobrachia* sp., *Pisidia* sp., *Carcinus* sp., and *Rathkeidae* (Supplementary Table S1). The decapods *Upogebia* sp. (mud shrimp) and *Pisidia* sp. (porcelain crab) showed important increases in the relative abundance over time, not only within the *Decapods* subcommunity but also for the entire community (Figure 3a and Supplementary Figure S2). These taxa were nearly absent until late 80s, but accounted together for >40% of *Total* and

30% of *Decapods* abundance in the last years of the survey, when their abundances reached maximum values of 12.7 and 9.9 ind.m^{-3} , respectively (both in 2017, Supplementary Figure S4). In contrast, *Carcinus* sp. showed the greatest decrease in relative abundance within the *Decapods*, from a maximum of 60% in 1976 to <10% since 2008. *Cancer* sp., *Hemigrapsus* sp., *Crangon* sp., and *Galathea* also showed conspicuous increase or decrease in abundances over time (Supplementary Figure S4). Within *Hydrozoans* subcommunity *Rathkeidae* (mainly *Lizzia blondina* and *Rathkea octopunctata*) and *Obelia* sp. decreased markedly in relative abundance, from maximum of 96 and 55%, respectively, in late 70s to <5% in the last years of the study (Figure 3b). In contrast, *Clytia* sp. and *Eucheilota* sp. increased their representation among hydrozoans (up to 71 and 41%, respectively, after 2000s). However, their abundances also decreased, especially since early 90s (Supplementary Figure S4), suggesting that changes in relative abundance among hydrozoans were a consequence of stronger decreasing trend of the most abundant taxa (i.e. *Rathkeidae* and *Obelia* sp.). *Calanus* sp. (Copepoda), *Parasagitta* sp. (Chaetognatha), and *Pleurobrachia* sp. (Ctenophora), were the most abundant taxa within the subcommunity *Others*, representing for most years > 80% of the abundance, with no evident long-term changes in community structure (Table 2).

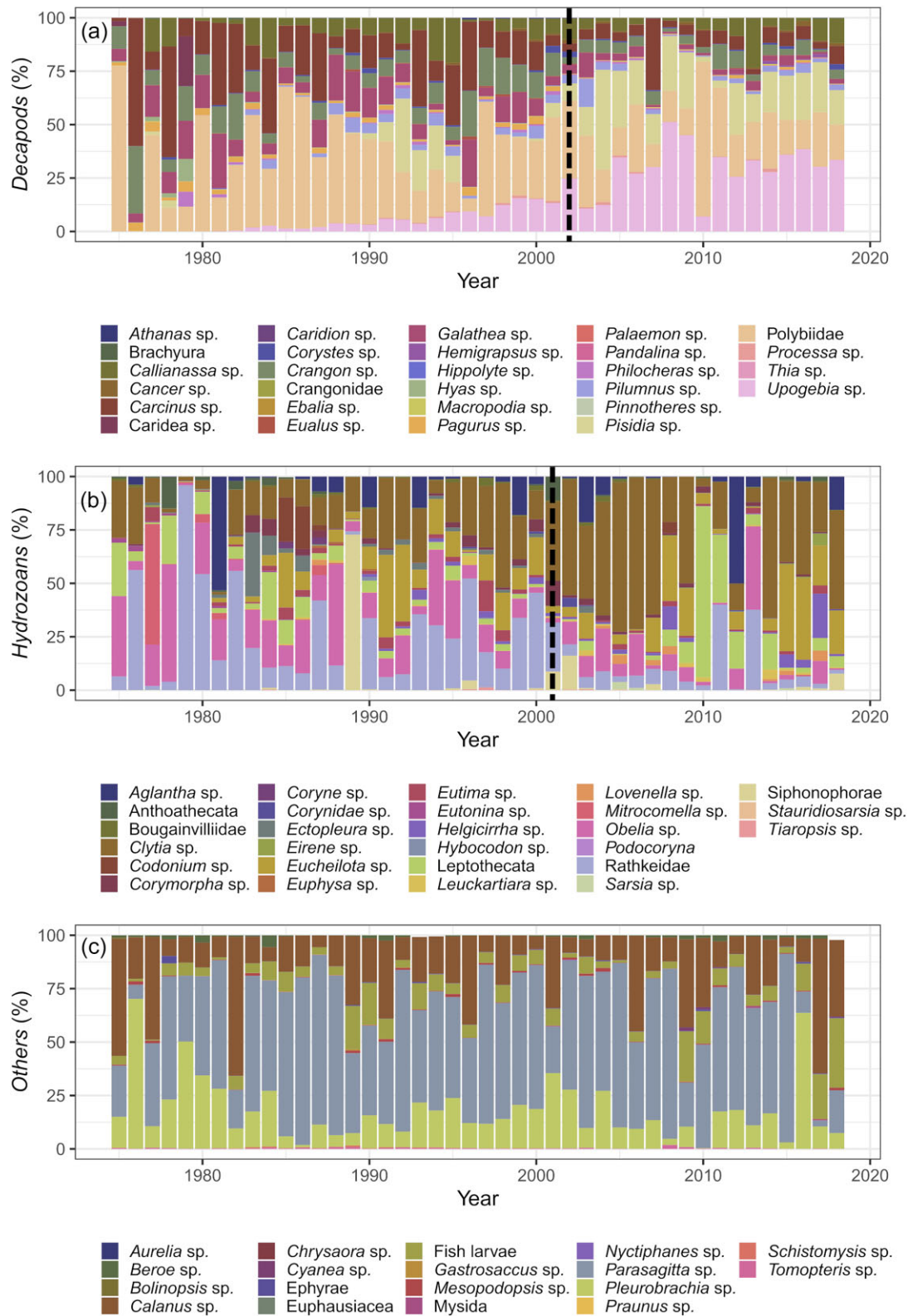


Figure 3. Relative abundance of the different taxa within each subcommunity at Helgoland Roads: (a) *Decapods*, (b) *Hydrozoans*, and (c) *Others*. Vertical black-dashed lines indicate the year of significant changes in community structure identified by MRT.

Table 3. Overview of the final GAMs fitted to the abundances of the (sub)communities, including the predictors retained in the final model, the associated AIC, and explained deviance.

(Sub)community	Predictors retained	AIC	Explained deviance (%)
<i>Total</i>	Temp⁺ + Cop⁺ + Secchi^o + Fish⁻	19.0	53.0
<i>Decapods</i>	Diat ^{ns} + Secchi⁻ + Fish⁺	59.4	60.4
<i>Hydrozoans</i>	Cop ^o + Fish⁻ + N:P⁺	70.8	59.9
<i>Others</i>	Diat ⁻ + Cop ⁺ + Fish⁻	58.7	53.9

Superscripts indicate their partial effect: positive (+), negative (-), nonlinear (o), and not significant (ns). In bold are those with stronger effects (see Supplementary Figure S5).

The relationship between environmental conditions and large zooplankton dynamics

Relationship with abundances

The univariate statistical models used to uncover the environmental variables most correlated with the abundance of the different taxonomic groups, revealed that the tested predictors significantly explained >50% of deviances in all cases (Table 3 and Supplementary Table SII and Figure S5). *Total* abundance was negatively affected by fish biomass Effective degrees of freedom (edf) = 1, $F = 7.8$, $p = 0.008$, positively by temperature (edf = 1, $F = 7.0$, $p = 0.012$) and copepods abundance (edf = 1.9, $F = 5.8$, $p = 0.005$), and a nonlinear effect of Secchi disk depth with higher abundances expected at intermediate levels of water transparency (edf = 2.4, $F = 4.4$, $p = 0.011$). *Decapods* were the only taxa positively affected by fish biomass (edf = 3.9, $F = 8.0$, $p < 0.001$), particularly at lower biomass levels ($< 50 \times 10^4$ tons) after which the abundance of decapods appear to be less affected (Supplementary Figure S5). *Decapods* abundance was also negatively affected by Secchi disk depth (edf = 1.3, $F = 5.4$, $p = 0.034$) and by diatoms abundance, although not significantly (but retained in the final model, edf = 3.0, $F = 2.6$, $p = 0.087$). The effect of the predictors on the *Hydrozoans* abundance was consistently nonlinear, but while the fish biomass effect was generally negative (edf = 3.1, $F = 3.0$, $p = 0.034$), the N:P ratio effect was generally positive (edf = 2.0, $F = 5.3$, $p = 0.008$). In contrast, higher hydrozoans abundance is expected to occur at intermediate levels of copepods abundance (edf = 2.2, $F = 4.4$, $p = 0.013$). Finally, the *Others* appeared to be negatively correlated with diatoms (edf = 1, $F = 9.2$, $p < 0.004$) and positively correlated with copepods abundances (edf = 1, $F = 5.2$, $p = 0.028$, respectively), while fish biomass had a nonlinear effect (edf = 3.6, $F = 4.4$, $p = 0.005$), especially at higher biomass levels ($> 50 \times 10^4$ tons), when the abundance of *Others* is expected to substantially decrease (Supplementary Figure S5).

Relationship with community structure

The environmental variables considered in this study significantly affected the structure within *Decapods* and *Hydrozoans* subcommunities (significant global RDA models, Table 4), but not the *Others* ($F = 0.79$, $p = 0.711$). The environmental variables explained 30.5 and 12.0% of the variability in the data for *Decapods* and *Hydrozoans*, respectively. The changes within these communities were significantly summarized by only one axis (significant RDA1, Table 4), which represented most of the explained variability in the data (25.7 and 10.1%, respectively, Table 4). The RDA1 revealed a substantial modification in community structure over time for both the *Decapods* and *Hydrozoans* (Figure 4a and b, respectively).

In both cases, temperature and Secchi depth were selected by the models. However, *Decapods* were also affected by the increasing trend in fish biomass and by the decreasing trend in copepods abundance (Figure 4c). For the *Hydrozoans* community, fish biomass was highly correlated with RDA1 but not retained in the full model (Figure 4d). This apparent contradictory result is a consequence of the model selection process. Model selection is based mainly on permutation tests and the variance explained by the model. When fish biomass is included in the model, the permutation test indicate that the overall explained variance only slightly increases in comparison with a model without fish biomass (Adj. $R^2 = 12.6$ vs. 12.0%), but this predictor does not significantly explain the variation in the data ($F = 1.28$, $p = 0.214$). In contrast, removing Secchi depth from the model would result in a noticeable decrease in the overall variance explained (Adj. $R^2 = 9.1$ %). The key taxa identified by the RDA analysis shaping the variability in subcommunity structure over time were *Upogebia* sp., *Pisidia* sp., and *Carcinus* sp. for *Decapods*, and Rathkeidae, *Obelia* sp., *Clytia* sp., and *Eucheilota* sp. for *Hydrozoans*. Further RDA analysis on the whole community (Supplementary Figure S6) confirmed the importance of *Upogebia* sp., *Pisidia* sp., Rathkeidae, and *Obelia* sp., as the key taxa driving the structural changes in the whole large zooplankton community.

Discussion

Long-term changes in the large zooplankton community

The NS is one of the most human-impacted marine ecosystems in the world (Halpern *et al.*, 2015) and its environment underwent relevant changes over decades. The community of large zooplankton in the SNS responded to these changes and experienced a reorganization during the 1990s and 2000s. In addition to a general decline of the entire community abundance, changes in the relative abundance of each taxa over time resulted in a different overall community structure after 2006 (Figure 5). In general, the community changed from being composed by higher abundances of hydrozoans and holoplanktonic taxa, to an increase in decapods. Here, we were able to uncover the main environmental factors underpinning these changes, highlighting the critical role of temperature, pelagic fish biomass, and water turbidity. However, the final outcome of these changes is rarely a result of a few parameters, but instead, of the complex interaction of multiple stressors, affecting differently the individual taxa and at different timings. This underlines the relevance of addressing the impact of environmental changes at different community levels, which elucidate how the complexity of interactions ultimately shape the entire community structure.

Table 4. Main results of the RDA analysis on each subcommunity.

	Adj. R ² (%)	F (global)	p-value (global)	RDA1 (%)	F (RDA1)	p-value (RDA1)	Variables retained
Decapods	30.5	5.72	0.001	25.7	19.30	0.001	Temp + Cop + Secchi + Fish
Hydrozoans	12.0	3.92	0.001	10.1	6.64	0.001	Temp + Secchi
Others	-	0.79	0.711	-	-	-	None

Variables retained in the final selected model: Temp: temperature, Diat: diatoms abundance, Secchi: Secchi depth, Fish: fish biomass, Cop: copepods abundance.

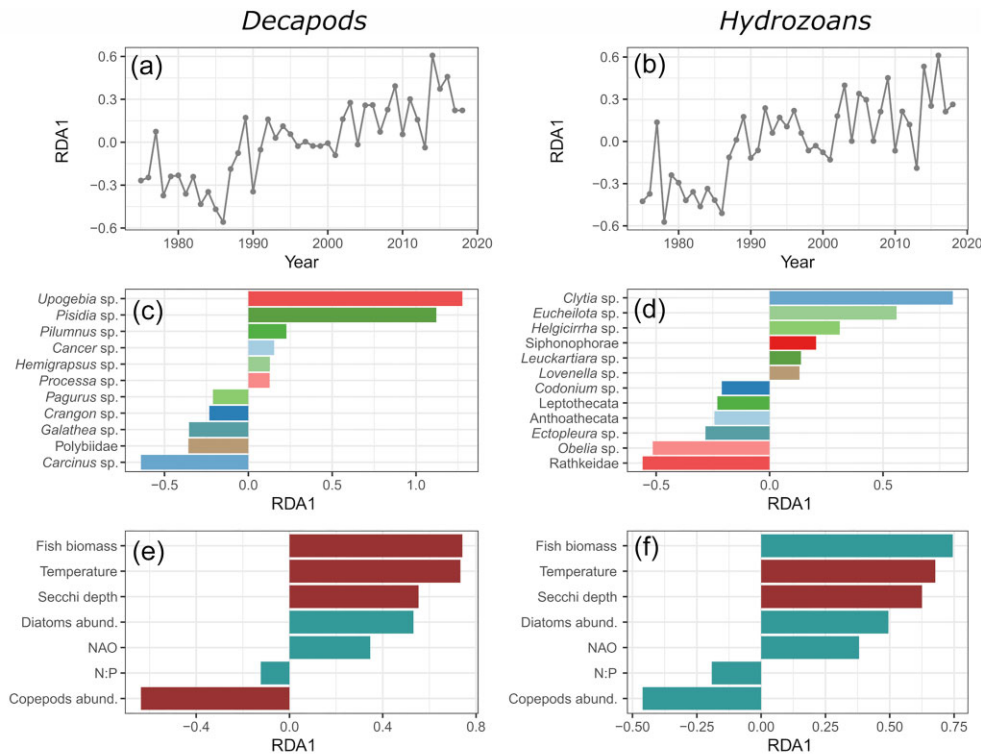


Figure 4. RDA of *Decapods* (b, c, e) and *Hydrozoans* (b, d, f) subcommunities: (a) and (b) temporal variability of RDA1 scores; (c) and (d) taxa that most contributed to the main changes in the respective subcommunity structure. Only the taxa with high positive and negative RDA1 scores are presented; (e) and (f) environmental variables that affected the structure of subcommunities, with negative and positive effects. In red are the variables retained in final selected model.

The described changes in the large zooplankton community in this study matched the previously described regime shifts in the NS (Figure 5). During the first regime shift in late 80s (Reid *et al.*, 2001; Beaugrand *et al.*, 2008), an overall increase in the abundance across all taxa reinforced a step-wise boost in the abundance of the entire community, although with little impact on its structure. Increasing water temperature along with high abundances of copepods and low levels of fish predation likely supported these changes. The simultaneous step-wise increase in water transparency and N:P ratios suggests that these growth in the large zooplankton abundance was bottom-up driven through the enhancement of the productivity of the whole planktonic food web (Sguotti *et al.*, 2022). In 1995/1996, the abundance of the whole large zooplankton community decreased drastically and continue to decline until the end of the study period. This drastic decline in 1995/1996 immediately preceded the regime shift identified between 1996 and 2003 (Alvarez-Fernandez *et al.*, 2012; Beaugrand *et al.*, 2014) and was mainly a consequent of the cumulative step-wise drop in the abundance of meroplanktonic organisms, i.e. *Decapods* and *Hydrozoans*.

Within these two subcommunities, significant changes in their structure were detected in early 2000s, in conjunction with the described regime shift. However, significant changes in the community structure of the whole community were only detected in 2006, due to the combination of these subcommunity changes and the simultaneous step-wise decrease in the abundance of mainly holoplanktonic taxa (i.e. *Others*). This agrees with Di-Pane *et al.* (2023), who identified a shift in the structure of the mesozooplankton community (including smaller size fractions, >150 μ m) at Helgoland in 2007 and with the third reported regime shift in the NS (Sguotti *et al.*, 2022). The distinct timing of changes in abundance and structure within (sub)communities, highlight the importance of integrating high taxa diversity and resolution in community structure analysis (Di Pane *et al.*, 2023). Shifts in the structure of marine communities occur over a period of change instead of a single year, due to the variability in life history strategies among zooplankton organisms. For instance, meroplankton species have typically longer (>1 year) life cycles than holoplankton and the effect of environmental changes on their growth, maturation, and embryonic development of

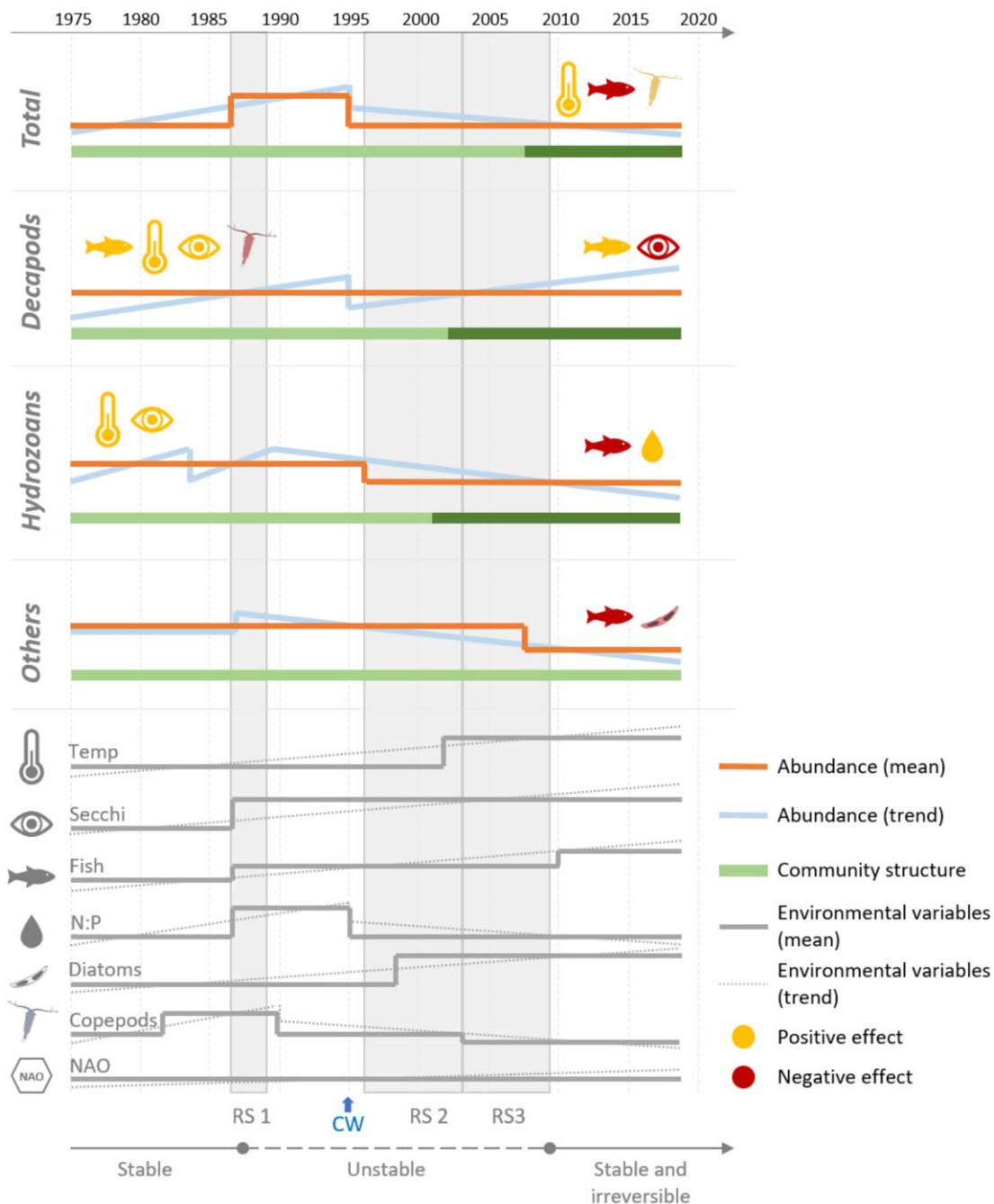


Figure 5. Schematic representation of the main results of the univariate and multivariate analyses. Solid orange and blue lines show the step-wise changes in the mean and trend abundances of the different (sub)communities, respectively. Green bars show the significant changes in community structure of the respective (sub)communities. Solid and dashed grey lines show the step-wise changes in the mean and trend of the environmental variables, respectively. The environmental variables with stronger correlation with community structure and abundances are represented by a respective symbol, on the left and right side of the scheme, respectively, with the colour of the symbols representing the type of effect. Vertical grey-shaded areas represent the reported periods of regime shifts (RS) in the NS (Reid *et al.*, 2001; Beaugrand *et al.*, 2008, 2014; Alvarez-Fernandez *et al.*, 2012), including the periods of stable and unstable states (Sguotti *et al.*, 2022). The blue arrow indicates the cold winter (CW) that affected the NS benthic community (Neumann *et al.*, 2008; Kröncke *et al.*, 2013).

the benthic stages (e.g. Azra *et al.*, 2020) might induce a time lag response in the abundance of the pelagic stages. In addition, mounting evidence of high evolutionary potential of zooplankton organisms (e.g. Peijnenburg *et al.*, 2006; Yebra *et al.*, 2011) under environmental changes support the hypothesis that different genetic adaptation capacities and rates among zooplankton populations might affect their response

time to those changes (Dam, 2013; Peijnenburg and Goetze, 2013). This holds particularly true at a comprehensive ecosystem level, when multiple trophic levels are included. Sguotti *et al.* (2022) reviewed and analysed temporal changes of several components of the NS marine community, from plankton to fish, and showed that the NS ecosystem experienced a period of instability between late 80s and late 2000s, when an

apparent “slow regime shift” occurred. These changes resulted in an irreversible regime shift, with a complete restructuring of the community after 2003, which only stabilized in a new state after 2008. The dynamics of the large zooplankton community in the SNS appeared to match these periods, with internal changes occurring at different timings during the unstable period, establishing a distinct community structure after mid-2000s.

The influence of environmental variables

The described long-term changes in abundances and structure of the large zooplankton community in the SNS were likely an outcome of the long-term interaction of multiple stressors. However, here, we uncover the role of some environmental variables and the potential effect of their short-term abrupt variations, particularly in temperature, fish predation, and water turbidity. At long-term, the increasing trend in temperature likely explain the success of *Decapods* over time. Temperature has been identified as one of the main regulators of decapods abundance by affecting their reproductive efficiency (Kirby *et al.*, 2007, 2008), survival and development (Rumrill, 1990; Hoegh-Guldberg and Pearse, 1995) at different stages of their life cycle (Zeiss and Kroncke, 1997; Reiss *et al.*, 2006; Neumann *et al.*, 2008), as well as their distribution (Lindley and Kirby, 2010). For instance, *Pisidia* sp., one of the key identified taxa in our results, is strongly affected by increasing temperatures and expected to increase in the NS (Lindley *et al.*, 1993), which was confirmed in our results. Despite the overall increasing trend in temperature, severe cold temperatures might also affect the community. The winter of 1995/1996 was exceptionally cold, which caused an unusual high mortality of benthic macrofauna organisms, including decapods, and significantly changed the benthic community structure (Neumann *et al.*, 2008; Kröncke *et al.*, 2013). This mortality was likely reflected in the abundance of decapods larvae in the pelagic environment and explain the observed drastic drop in their abundance. To our knowledge, similar studies are not available for hydrozoans in the NS, but a similar effect could be speculated. Indeed, under unfavourable conditions, like cold winters, benthic hydrozoan colonies might be severely reduced to resting hydrorhizae or produce cysts in order to survive (Bavestrello *et al.*, 2006; Martell *et al.*, 2017), or they can switch to less effective reproduction strategies, which ultimately affect the production of medusae (Boero *et al.*, 2008). Therefore, we speculate that the shift in the community structure of these two subcommunities might reflect the reorganization of the benthic community after the cold winter in 1995/1996, which after a post disturbance succession stage (Neumann and Kröncke, 2011), resulted in a significant shift in their internal structure in early 2000s (Kröncke *et al.*, 2013; Kröncke *et al.*, 2019).

Top-down pressure was likely one of the major environmental drivers of changes in large zooplankton community in this study, since the increasing biomass of zooplankton predators had a widespread negative correlation with the whole community abundances and structure, except for decapods. Top-down control of zooplankton communities was pointed to be one of the main regulators of key NS zooplankton taxa, such as *Calanus* sp. For instance, Papworth *et al.* (2016), did a comprehensive study that included 86 biological and physical drivers of *C. finmarchicus* abundance in the NS, and revealed that fish predation, in particular from herring, was one of the

most important drivers. The predation effect on *Hydrozoans* is, however, less expected. Gelatinous zooplankton has low nutritional value (e.g. Lucas *et al.*, 2011) and are, therefore, often considered as “dead ends” in the food webs. However, this paradigm has been recently disputed (Hays *et al.*, 2018) and recent reports have been showing that these organisms are a suitable source of food for a variety of fish species (Ayala *et al.*, 2018; Marques *et al.*, 2019; Brodeur *et al.*, 2021). Furthermore, the predation on gelatinous zooplankton by fish appear to be stronger when high quality food is less available, promoting a shift in fish selectivity towards less nutritional but more abundant preys (Marques *et al.*, 2016). This might be the case in our study site, where the decrease in the abundance of copepods might have forced zooplanktivorous fish to prey on alternative sources of food, like hydrozoans. This decrease in *Hydrozoans* abundance further support the hypothesis that the presumed global increase in jellyfish populations is biased towards scyphozoans and lack long-term data to substantiate a widespread trend for all gelatinous zooplankton (Sanz-Martín *et al.*, 2016). On the other hand, the success of decapods despite of the high predation pressure, might be, at least, partially explained by their combination of traits. Kjørboe (2011) argued that the fitness of a species is highly influenced by the trade-off of its traits associated with predation mortality and feeding efficiency. Therefore, their short pelagic larval duration (Anger *et al.*, 2015) and the presence of numerous and long spines, which is a typical feature of many decapod larvae (Morgan, 1989, 1992), likely reduce their vulnerability to zooplanktivorous predators (Rumrill, 1990; Hoegh-Guldberg and Pearse, 1995; Kirby *et al.*, 2007). One striking example is *Pisidia* sp. larvae, which has exceptionally long spines, providing them with a superior protection against zooplanktivorous predators.

Water turbidity was also found to be highly correlated with the observed restructuring of the large zooplankton community. However, here, we suspect that temporal changes in this physical environmental condition rather amplifies the impact top-down and bottom-up pressures. On one hand, low turbidity conditions would theoretically increase the vulnerability of zooplankton to visual predators, since high water visibility increases the fish euphotic habitat (Dupont and Aksnes, 2013). This could further endorse the negative impact of fish predation on the abundance of most taxa (except decapods) and it was even suggested to affect the competitive trophic relationship with tactile jellyfish (Aksnes, 2007; Haraldsson *et al.*, 2012), further sustaining the reduction in *Hydrozoans* abundance observed in our study. On the other hand, low water turbidity was one of the main drivers of high diatom abundances and longer bloom periods at Helgoland (Wiltshire *et al.*, 2015). This likely increased the food availability for decapod larvae, as well as for their newly settled or adult stages, such as for *Upogebia* sp. This taxon was shown to feed on planktonic and sedimented phytoplankton at both the pelagic (Faleiro and Narciso, 2009; Fileman *et al.*, 2014) and benthic (Dworschak, 1987; Lindahl and Baden, 1997) stages, respectively, and showed the most conspicuous increase in relative abundance over time, within the entire community.

Food quality (i.e. N:P ratios), although not identified as critical in changes in the community structure, it significantly affected the abundance of *Hydrozoans*, and its step-wise change in 1986 and 1995, interestingly match those observed in *Total* abundance. The impact of food quality on plankton communities have been extensively demonstrated (e.g. Danielsdottir

et al., 2007; Meunier *et al.*, 2018) and suggested as an important driver of herbivorous zooplankton abundance in the SNS (Meunier *et al.*, 2016). The strong relationship between N:P ratio and *Hydrozoans* is, however, unexpected. It could be speculated that the high nitrogen demand per unit of carbon of jellyfish, due to the particular composition of their body tissues (Pitt *et al.*, 2013), could explain these results, but the few existing studies on the response of jellyfish to nutrient-limited food sources revealed their tolerance to this stressor (Malzahn *et al.*, 2010; Schoo *et al.*, 2010; Chen and Li, 2017). Further studies are, thus, still required to fully understand this relationship.

Although we included multiple stressors in our analysis, rarely (if ever) is a study comprehensive enough to fully address the complexity of interactions affecting zooplankton communities. It is, therefore, not surprising that a large proportion of the variation in the statistical results (GAM and RDA models) remained unexplained. Here, we only investigated the temporal variability of the large zooplankton dynamics at one particular area of the SNS. Expansion or contraction of species-specific spatial distributions, was recognized as critical in community structural changes, including for many organisms considered in this study (e.g. Lindley *et al.*, 1993; Beaugrand *et al.*, 2008; Puce *et al.*, 2009; Lindley and Kirby, 2010), which was, thus, not considered in our study. In addition, changes in community structure are also a consequence of stochastic processes, such as ecological drift that causes species abundance to fluctuate randomly (Vellend, 2010; Gilbert and Levine, 2017). However, the performed analysis at high taxonomic resolution allow us to consider taxa-specific ecology and the potential effect of additional stressors not considered in this study. This is the case of the impact of beam trawls on some meroplankton organisms. *Upogebia* sp., a burrowing shrimp in their adult stages, live in tunnels that may extend down to 50 cm deep in the sediment (Dworschak, 1983). This particular trait is especially important in the NS where beam trawls are frequently used and can have a severe impact on the benthic community (Bergman and van Santbrink, 2000). The protection provided by the deep burrows can, therefore, help to explain the conspicuous increasing trend of *Upogebia* sp. larvae in our study site (Duineveld *et al.*, 2007; Hinz *et al.*, 2021).

The implications of changes in large zooplankton community to the ecosystem functioning might be important. The overall low zooplankton abundance might affect fish recruitment (e.g. Beaugrand *et al.*, 2003) and the efficiency of the biological carbon pump (e.g. Cavan *et al.*, 2017). Furthermore, the increasing in decapods abundance in the plankton, followed by higher recruitment to the benthos, might affect the trophodynamics of the associated communities, through their role as predators and prey, and potentially affect ecosystem services, such as fisheries (e.g. Kirby and Beaugrand, 2009; Lindley and Kirby, 2010; Boudreau and Worm, 2012). Understanding and predicting biodiversity changes and their impacts on ecosystem functioning at taxonomic level is, however, intricate. One possible approach to simplify the complexity of interactions at multivariate taxonomic level, is trait-based analysis. This approach not only facilitate our understanding of how communities respond to changes in the environment, but also how changes in communities affect ecosystem functioning (de Bello *et al.*, 2021). The complementary knowledge at both the taxonomic and functional community structures,

will provide a better understanding of the responses and the effects of biodiversity changes over time.

Conclusion

Here, significant changes in the community structure of meso- and macro-zooplankton in the SNS were reported, likely mediated by long-term changes in climatic and anthropogenic stressors. These changes followed the previously described regime shifts in the NS, in particular the periods of stable and unstable states of the ecosystem. Overall, the decrease in abundance of hydrozoans and holoplanktonic taxa, together with increasing trends in decapods abundance resulted in a significant change in the community structure in 2006, after an unstable period when internal subcommunity structural changes were identified. This highlights how internal responses shape the reorganization of the community and the potential ecological mechanisms sustaining such reconfiguration, in particular the role of temperature and predation pressure. This study further uncovers how complex these mechanisms are due to the variety of life histories among the large zooplankton organisms. Assessing community structure changes at different taxonomic levels allows to disentangle this complexity and, therefore, better understand how and when changes occur. Given their ecological importance in marine food webs and their role in connecting benthic and pelagic populations, we strongly emphasize the necessity of prioritizing and sustaining efforts to study and understand the often-overlooked large-sized zooplankton community.

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Supplementary Data

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

Author contributions

RM: conceptualization, formal analysis, investigation, methodology, visualization, and writing; SAO: conceptualization, methodology, validation, and writing; JDP: methodology and writing; MB: data curation and writing; CLM: writing; KW: data curation; CM: resources and writing; and JR: conceptualization, data curation, funding acquisition, resources, supervision, validation, and writing.

Data availability

The datasets originated from the monitoring program at Helgoland Roads analysed 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) programme of ICES (<https://www.ices.dk/data/data-portals/Pages/DATRAS.aspx>).

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Conflict of interest

The authors declare that they have no financial or personal conflict of interests.

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