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Climate change and fisheries affect benthic composition and diversity in the North Sea — investigations at the Dogger Bank during three decades (1991–2021)

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Abstract
This study investigates the long-term trends and potential drivers of changes in the epibenthic community at the "Dogger Bank" to clarify the effects of rising sea temperatures and trawling activities on epibenthic species composition and biodiversity. Over three decades (1991–2021), the epibenthic megafauna (> 1 cm) has been regularly sampled in summer with a 2-m beam trawl at five stations at the Dogger Bank tail end, and the epibenthic species abundances were quantitatively recorded. Furthermore, sea temperature and trawling effort datasets for the corresponding area were used to check for correlations with the species composition and abundances. The study relies on long-term data analysis and the application of multivariate statistical methods to discern temporal trends and the relative contributions of environmental and anthropogenic factors to community changes. This study hypothesizes that the benthic species community at the MPA on the Dogger Bank has undergone significant shifts over three decades due to rising sea temperatures and pressure from bottom contact fisheries. While local summer temperatures of the bottom water layer increased by up to 4 °C throughout the research period, trawling efforts rather decreased continuously in the area. Despite low interannual differences in species composition between the stations, we found the faunal regime to be under constant change (MDS, CCA), with a decrease in biodiversity (Shannon–Wiener indices) along with a general faunal regime shift around the turn of the millennium. We did not detect a linear correlation between biodiversity and temperature/trawling effort; however, we did find certain species positively or negatively correlating with these factors when using Spearman's rank analysis. Our results provide a solid benchmark for future research in the German and neighboring Exclusive Economic Zone.

Keywords Epibenthic megafauna · Long-term analysis · Trawling activity · Temperature rise · Exclusive economic zone · Marine biodiversity

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Introduction

The North Sea is a shallow, semi-enclosed shelf sea (Wieking and Kröncke 2005; Ducrotoy et al. 2000). Especially in coastal and shallow areas like the North Sea, marine biodiversity seems to be threatened as a result of conflicting, anthropogenic uses of coastal habitats (Gray 1997). Multiple factors such as industrial and agricultural pollution (Ducrotoy et al. 2000), marine traffic (Gislason 1994), offshore wind farms (Krone et al. 2013), and pipelines (Lacey and Hayes 2020) have led to a loss of marine biodiversity in general (Coleman and Williams 2002; Worm et al. 2006). An increasing number of studies, ranging from local to global scales, have demonstrated the apparent effects of climate change on the diversity of marine species (Worm and Lotze 2021), with ocean warming being a major driver (Williamson and Guinder 2021). For

the North Sea, long-term studies have highlighted that the sea is subject to significant changes, including rising temperatures and associated shifts in marine communities (Kröncke et al. 2011; Clarc and Frid 2001).

For the benthic fauna, fisheries mean another major impact factor (Tillin et al. 2006). Benthic fauna in the North Sea, especially in fished areas, has been subject to changes since the beginning of the twentieth century, partly due to changes in fishing intensity and methodology (Frid et al. 2000). This has had an impact on the size, occurrence, avoidance strategies, and feeding behavior of benthic species (Callaway et al. 2007; Groenewold and Fonds 2000). At the Dogger Bank, fisheries (and climate) have likely induced macrofaunal changes and regime shifts (Kröncke 2011). Since the early nineteenth century, prolonged declines in fish abundance have been observed, likely to be caused by fisheries (Plumeridge and Roberts 2017). At the two marine protected areas (MPAs) "Sylt Outer Reef" and "Borkum Reef Ground" in the German Exclusive Economic Zone (EEZ), we have found biodiversity to be slightly higher at areas with lower fishing effort (Hahn et al. 2022).

These changes underline the need for detailed investigations into the combined impacts of climate change and human activities on marine biodiversity. As both fisheries and ocean warming appear to be two of the key drivers of change to benthic biodiversity, an example area at the North Sea, the Dogger Bank, was chosen for investigating if changes in trawling effort and water temperature can be directly related to changes in benthic biodiversity.

The Dogger Bank (Fig. 1) is an isolated (Cotterill et al. 2017) 300-km-wide sandbank (Kröncke and Knust 1995) in the central-southern North Sea. According to Sonnewald and Türkay (2012a), it is considered a representative area for conducting long-term studies as it has a predominantly uniform, sandy, and shallow sediment structure. This homogeneity minimizes confounding factors, allowing for clearer interpretations of environmental and anthropogenic effects on benthic communities. There are only marginal differences

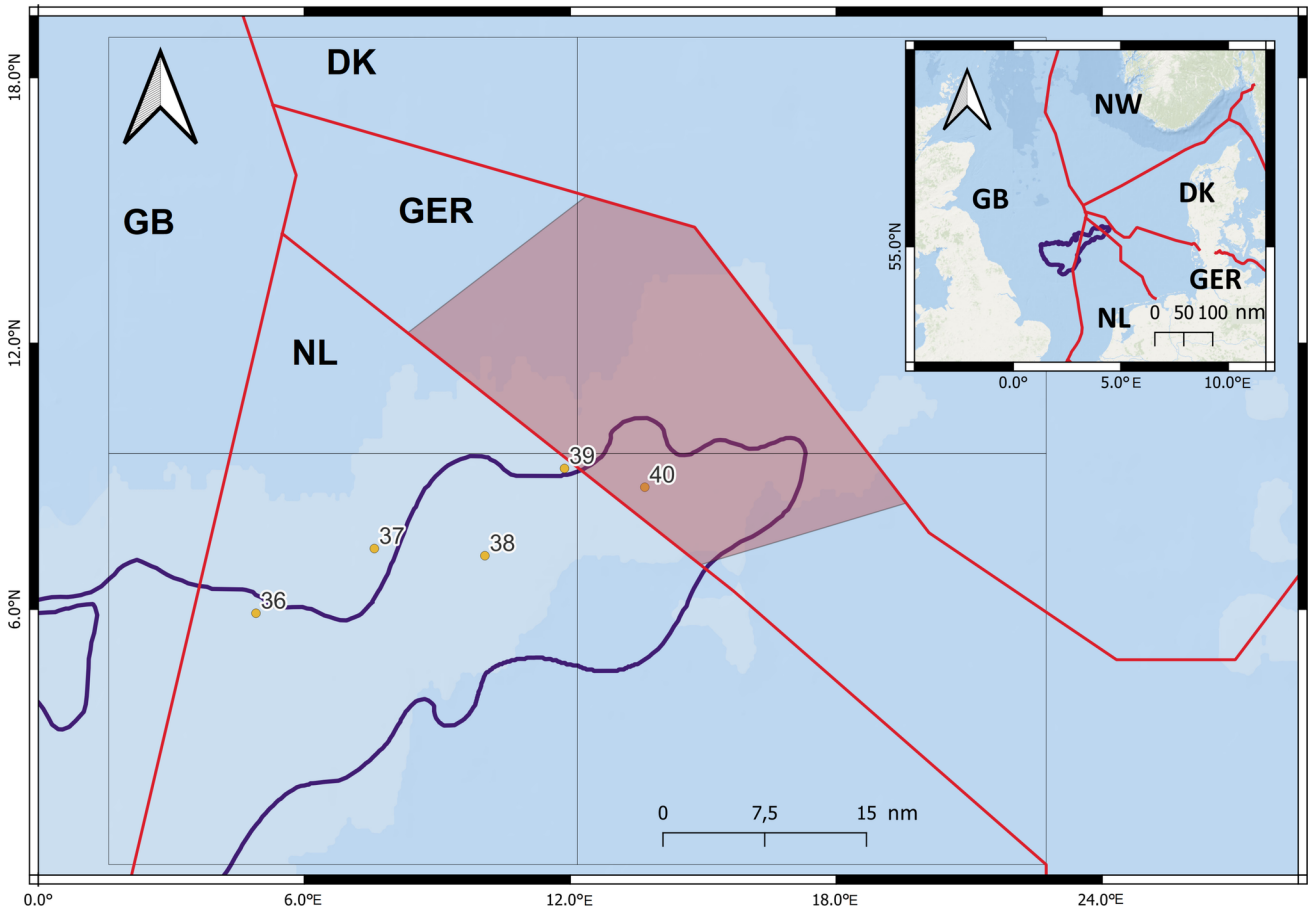


Fig. 1 Overview of the Dogger Bank with the sampling stations 36–40 in the central North Sea (small map). Red lines: Boundaries of the EEZs of the UK (GB), the Netherlands (NL), Denmark (DK), Norway (NW), and Germany (GER); blue line: 30 m depth line; thin gray squares: ICES statistical rectangles from which the fishery and water parameters were extracted—from top left to bottom right: 40F3, 40F4, 39F3, and 39F4. Red-shaded polygon: Natura2000 protected area. The map was compiled in QGIS 3.22.10

in depth and sediment composition at the Dogger Bank tail end, and the selected stations are comparable with respect to their benthic species composition.

Different species are found north and south of the Dogger Bank; at the central North Sea, and thus also on the Dogger Bank, there is a mixture of benthic species communities (Heip and Craeymeersch 1995).

Herein, a long-term dataset on the abundances of the mega-epibenthic species (1991–2021) at the eastern part of the Dogger Bank, the so-called "tail end" (Kröncke 1990), is investigated and correlated with corresponding data on fisheries and water temperature. Thus, this research contributes to understanding how synergistic stressors influence benthic biodiversity. Moreover, it has implications for marine conservation and management strategies, as at the German EEZ, parts of the NATURA2000 marine protected area "Dogger Bank" are likely to be closed for fisheries in the future, and this study serves as a baseline for future studies after a potential closure (Marine Management Organisation 2022).

Material and methods

Benthos sampling

During three decades (1991 to 2021), the benthos was sampled almost yearly (Tab. A1) in summer using RV "Senckenberg" at the Dogger Bank (Fig. 1). Five stations in the German and Dutch EEZ (36 (55.30669 N, 3.31324 E), 37 (55.38456 N, 3.56565 E), 38 (55.37632 N, 3.80124 E), 39 (55.48234 N, 3.97183 E), and 40 (55.45932 N, 4.14359 E)) were visited 26 times. All species over 1 cm in size that live on the seafloor in and on the uppermost sediment layer (first 5 cm), including demersal fishes that could be captured, were examined. The term "benthos" or "benthic fauna" is used to describe these species. At each station, marine benthic species were collected with a 2-m beam trawl (cod-end mesh size 1 cm^2) that was towed over the seafloor for a distance of 1 nautical mile (~ 1.85 km) in one direction at a speed of 2 knots (~ 3.7 km/h). The catch was photo-documented and its volume determined. Afterwards, the catch was sieved over two different mesh sizes (1 cm^2, 1 mm^2), with a part of the fine fraction (> 1 mm) immediately preserved but not used in the later data analysis of this work. Species of the larger fraction (> 1 cm) were identified to the species level as quickly as possible, and the abundance of all non-colonial forms was recorded in a list. During this procedure, we always endeavored to keep the animals alive in buckets of seawater. After their identification at the species level, the living animals were released back to the sea again if they were not of further scientific interest. Undetermined species and fine fractions were preserved either in a formaldehyde-seawater solution or predominantly, in more recent years, in 96% EtOH for later determination and analyses. After identification, the count data of the preserved specimens from the larger fraction (> 1 cm) of the beam trawl were added to the diversity dataset already obtained on board. The rate of species discoveries over time was determined and shown in a species accumulation curve (Fig. 3).

Trawling dataset

A dataset by Couce et al. (2020) was used which contains the compiled data of trawled hours per year and the ICES (International Council for the Exploration of the Sea) rectangle covered by bottom-contacting fishery. The stations were assigned to the ICES rectangle(s) in which they are geographically located to extract the respective trawling hours for statistical analyses from the dataset by Couce et al. (2020). Stations 36–39 were assigned to the mean beam and bottom trawling hours from the ICES rectangle 39F3, and for station 40, the average between the yearly mean beam and bottom trawling hours for the two ICES rectangles 39F4 and 40F4 was calculated. For statistical analysis, the corresponding benthic and trawling hours data from 1991 to 2012 (2012: last year of the dataset by Couce et al. (2020) were used. No trawl data were available for the years after 2012, and, hence, any trawling-related analysis was limited to the period 1991–2012.

Temperature dataset

The water temperature was measured at each station with a CTD probe. Our dataset was complemented using publicly available CTD data from ICES (https://data.ices.dk/viewmap?area=35), covering the same time period (June 1–Aug 31, 1991–2021) and region (3–5° E, 55–56° N, Fig. 2) as the benthic dataset. The temperature in the summer seasons was averaged for the period 1991 to 2001 and 2002 to 2021 with the program Ocean Data View 5.5.2. As stratification was detected, only temperature data from depths below 25 m were considered to be directly relevant to the benthos and were included in the statistical analyses (see below).

Statistical analyses

The packages *psych* (v. 2.2.5), *stats* (4.2.0), *car* (v. 3.1–2), and *vegan* (v. 2.6–2) were used in R (v. 4.3.2, 2023) for statistical analyses (except for the Spearman's rank correlations). A linear regression model was used to determine a potential temporal trend in the temperature data. Biodiversity was determined using the Shannon–Wiener biodiversity index (Spellerberg and Fedor 2003). To identify a linear trend in the change in the Shannon–Wiener Index over the years, the significance of the relationship between the years and the Shannon–Wiener indices was tested by performing a

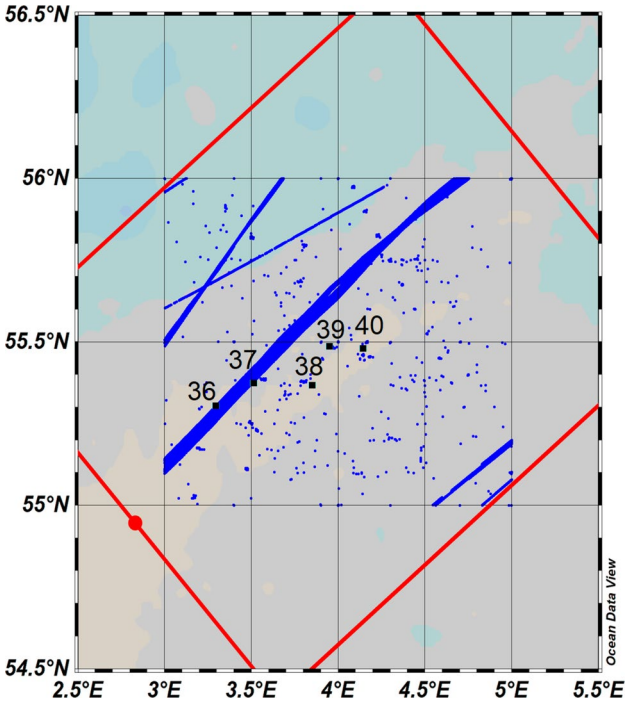


Fig. 2 Locations of available data points of publicly available CTD data from ICES (blue spots and lines) of the CTD data for the study area. Black dots mark our sampled stations. The map was compiled in Ocean Data View (v. 5.5.2)

linear regression and determining the *p*-values for the slope of the regression coefficient. To identify potential changes in community composition, we scaled and rounded the mean abundance per species and per year, applied dispersion-based weighting (Clarke et al. 2006) to account for differences in variability, and performed a Bray–Curtis similarity analysis (Bray and Curtis 1957), which we visualized using a multidimensional scaling (MDS) plot. In order to detect potential relationships between the Shannon–Wiener biodiversity indices per year and the mean temperature and trawling hours individually, two linear regressions were made. In addition, a series of canonical correspondence analyses were performed for each of the five stations, using the individual species abundances per year as response variables, while the corresponding mean temperature per season and trawling hours per year were used as explanatory variables. The same input variables of only those species with a minimum of ten individuals found throughout the research period were used in the software Primer (v. 6.1.11) to perform Spearman's rank correlations between species data and trawling activity as well as temperature, respectively. The first correlation consisted of yearly, mean benthos species abundances and trawling hours from 1991 to 2012, and the second of yearly, mean benthos species abundances and mean bottom water temperatures in summer from 1991 to 2021. An x–y matrix of mean species abundance data, trawling hours, and temperature was square-root transformed (Bishara and Hittner 2012), and the Spearman's rank correlation coefficients were computed. The correlations "abundance— temperature" and "abundance—trawling hours" were checked for their significance ($p = 0.05$) in relation to the number of pairings according to Zar (1972).

Results

Species composition

From 1991 to 2021, a total of 117 benthic species were recorded across five sampling stations. These belonged to the phyla Chordata (43 species), Mollusca (26 species), Arthropoda (22 species), Echinodermata (12 species), Annelida (6 species), Bryozoa (5 species), Porifera (1 species), and Nemertea (1 species). The most common species over the entire research period was the Mediterranean scaldfish *Arnoglossus laterna* (Walbaum, 1792)*, the common starfish Asterias rubens* (Linnaeus, 1758), the solenette *Buglossidium luteum* (Chabanaud, 1930), the common dab *Limanda limanda* (Linnaeus, 1758), and the common hermit crab *Pagurus bernhardus* (Linnaeus, 1758). A species accumulation curve indicated that in the first few years, there was still a rapid increase in the number of species being detected with each additional sampling visit to Dogger Bank (Fig. 3), demonstrating that the diversity of a certain area is, generally, likely to be higher than shown in the samples. While individual species richness data points remained virtually unchanged after 2011, the curve fit has not yet shown signs of approaching an asymptote.

Biodiversity

The Shannon–Wiener index (Hs) showed a negative trend from 1991 to 2021. It ranged from 2.2 in 1996 to 0.8 in 2017 (Fig. 4). The linear regression of Hs over time was significant ($p < 0.001$). The extent to which the conspicuously low Hs value in 2017 influenced the general trend was analyzed. A separate analysis without this outlier showed that the negative trend remains significant ($p = 0.005$). The year 2017 is conspicuous with a very low average biodiversity and this may be a link to the comparatively lower mean summer temperatures of that year (Fig. 8). The average Shannon–Wiener index value over the entire study period is 1.74.

The epibenthic community showed some variability from year to year. The MDS plot shows that the development of species composition and diversity in the study area can be clearly separated into two time periods: 1991 to 2001 and 2002 to 2021 (Fig. 5). This separation is clearly recognizable in the MDS diagram, as the communities of the first period

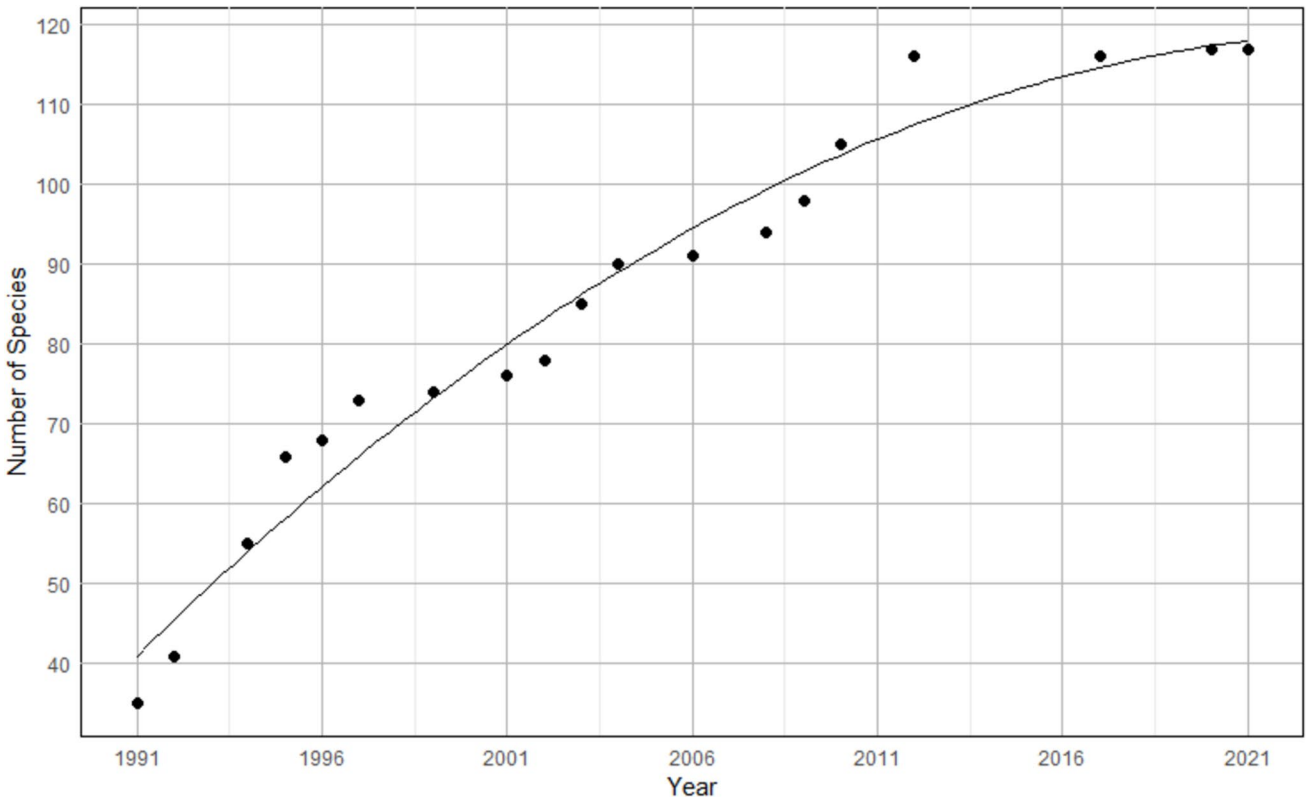


Fig. 3 Species accumulation curve of the mean values from stations 36 to 40 in the period 1991–2021. First value: Number of species detected in 1991. Following values: Number of species from the previous year plus the number of newly detected species from the present year

(1991 to 2001) are grouped in the lower part of the diagram, while the communities of the second period (2002 to 2021) are clustering in the upper part of the diagram. This spatial separation indicates differences in species composition and biodiversity between the two periods.

Effects of trawling activities

Trawling activity decreased sharply in the study area from 1991 to 2012 (Fig. 6). While around 30,000 h/year were fished in the corresponding ICES rectangles at the initial phase of our study period (Fig. 1), under 10,000 h/year were fished in the same area with beam and otter trawls in recent years. However, the correlation coefficient between the Shannon–Wiener index values and trawling activity showed a low r of -0.0217, and the linear regression was not significant ($p = 0.9365$). The relationship between Hs and water temperature was not significant either ($r = -0.0595$, $p = 0.8089$).

The analysis of the Spearman's rank coefficient between trawling activity and the mean number of individuals from stations 36–40 showed some significant correlations (Table 1). Three species, the brittle star *Ophiura albida* (Forbes, 1839), the common whelk *Buccinum undatum* (Linnaeus, 1758), and the common hermit crab *Pagurus bernhardus*, show a significant positive correlation with increasing trawling activity. The strongest negative correlation is associated with the lemon sole *Microstomus kitt* (Walbaum, 1792), the sea star *Luidia sarsii* (Düben and Koren in Düben, 1844), and the Mediterranean scaldfish *Arnoglossus laterna*. Other species such as the European plaice *Pleuronectes platessa* (Linnaeus, 1758) also show significant negative correlations. In general, more species correlate negatively than positively with increased trawling activity.

Effects of temperature change

Surface temperatures were higher than bottom water temperatures (Fig. 7a and b). At about 25 m, a thermocline was detected. It can also be seen that the temperature in the deeper layers has risen in the years since 2001, particularly in the east of the studied area (Fig. 7b), and the thermocline appears to be deeper. In winter, the water column is mixed (Fig. 7c and d). A slight increase in temperature can also be seen in the temperature analysis for the winter months from 2001 onwards, while temperatures of up to 12 °C can also be seen in the deep layers (Fig. 7 d), which were not yet present in the years leading up to 2001 (Fig. 7c).

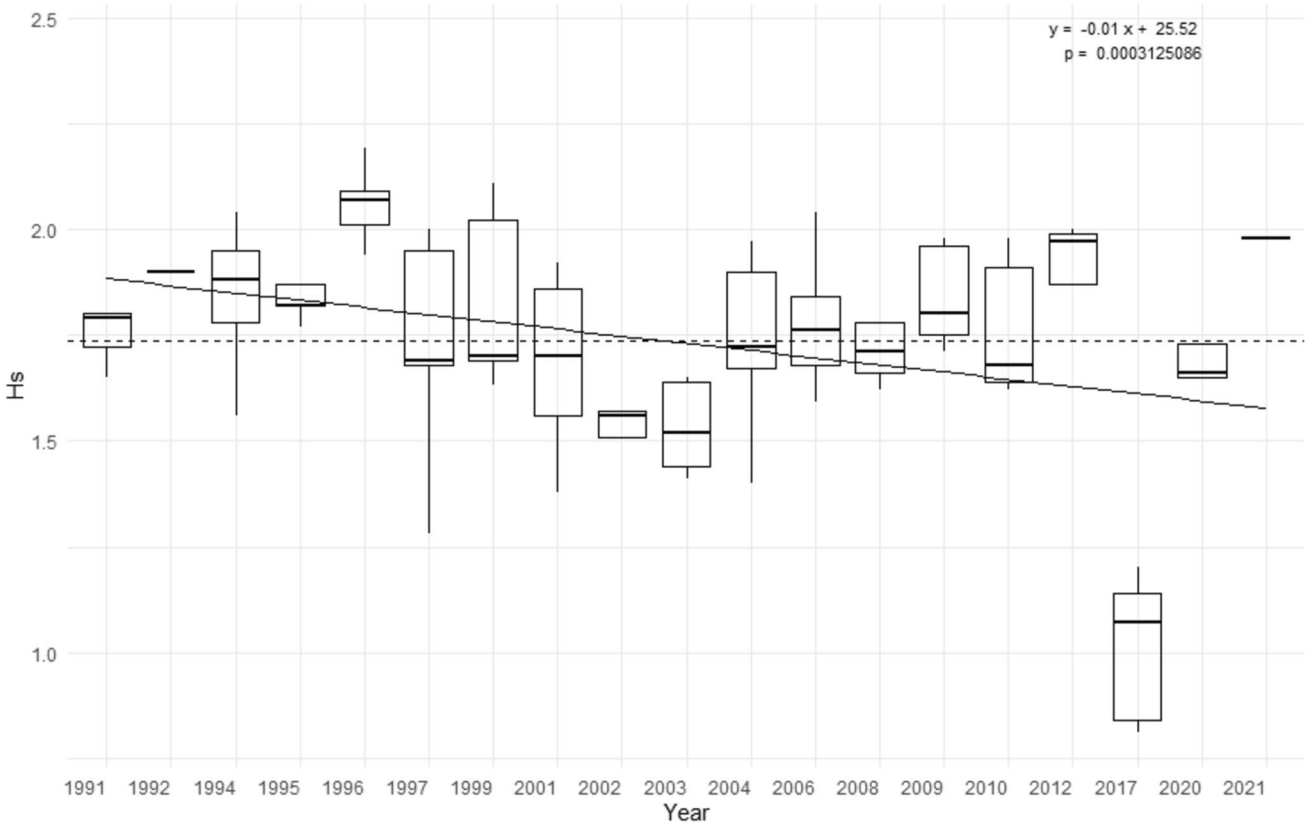


Fig. 4 Shannon–Wiener (Hs) biodiversity index for stations 36–40 over the period 1991–2021 with a linear trend line. The dotted line marks the mean Hs from all stations over this period (1.74). The boxplots show the variability of Hs values between stations for each year, with the box showing the interquartile range (IQR) and the error bars covering the range of minimum and maximum values

Using a linear regression model, it was possible to prove with $p = 0.0006083$ that the temperature increases statistically significantly over the years. Mean water temperatures from 1991 to 2021 for the summer months of June–August for all stations (ICES transects 40F3, 40F4, 39F3 and 39F4) below 25 m depth increased by about 4 °C (Fig. 8). Years where the bottom temperature did not follow the trend but were much lower included 1996, 2001, and 2017.

By investigating the relationship between temperature and abundance, we aim to understand whether rising temperatures might lead to shifts in population size. The Spearman's rank correlation analysis between bottom water temperature and mean abundance at stations 36–40 also showed that some species had significant positive and others had negative correlations (Table 2). Here, remarkably more species correlated positively than negatively to temperature, especially *Luidia sarsi*, *Microstomus kitt*, and *Arnoglossus laterna*. In contrast, other species such as *Ophiura albida*, *Gadus morhua* (Linnaeus, 1758), and *Corystes cassivelaunus* (Pennant, 1777) correlated negatively with the water temperature.

CCA

Figure 9 shows a canonical correspondence analysis (CCA) for stations 36–39 and station 40 for the years 1991–2012. As the CCAs of stations 36–39 resulted in virtually the same patterns, these stations are shown in one CCA (for separated CCAs see Fig. A1). Station 40 showed slightly different patterns. The CCA for stations 36–39 shows that fishing pressure drove the pattern of the benthic community in the 1990s–early 2000 s, while temperature was more influential thereafter. The stronger dissimilarity of communities at station 40 in the two time periods suggests a stronger influence of temperature than at the other stations.

Discussion

This study focused on the benthic diversity of the Dogger Bank and investigated whether species composition and abundance showed responses related to trawling activity and sea temperature. Benthos plays a crucial role in marine ecosystems and has diverse ecological and economic

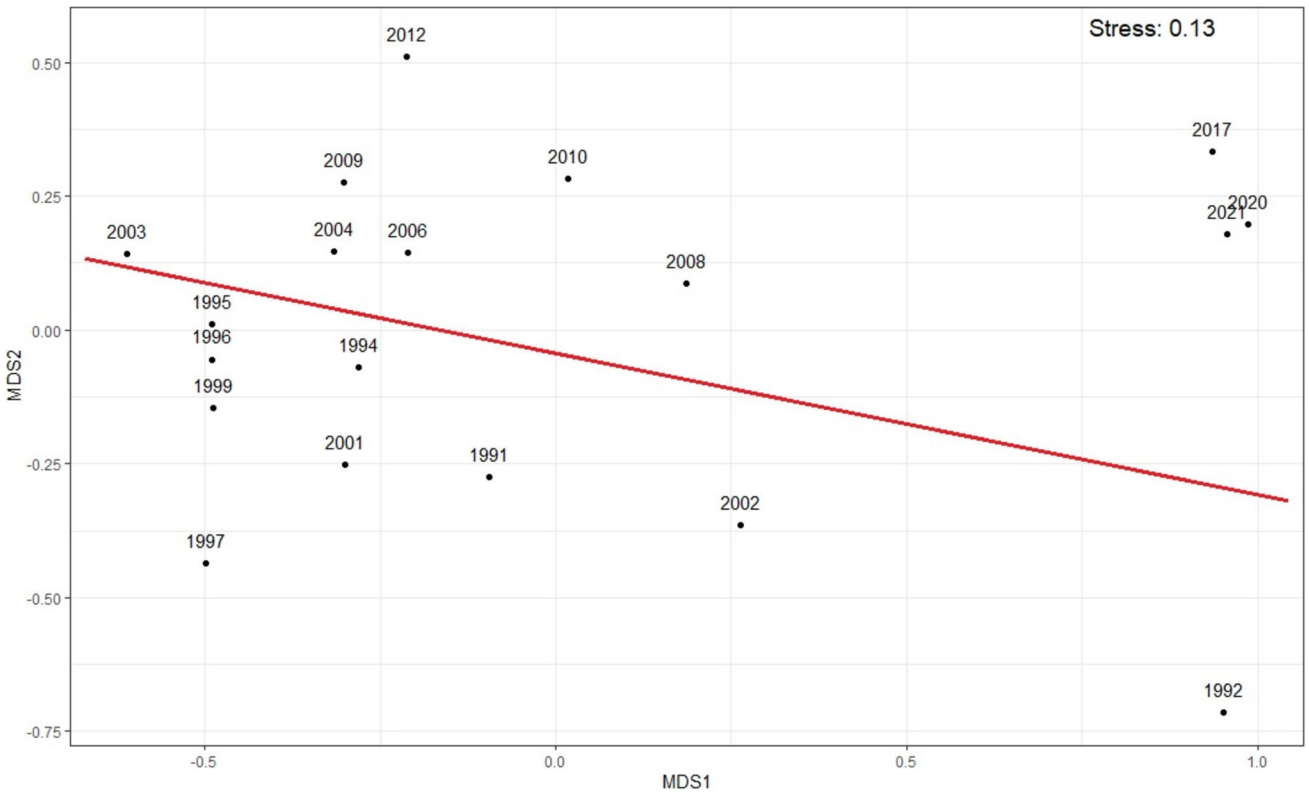


Fig. 5 Bray–Curtis community similarity evaluation in an MDS plot based on the dispersion-based weighted mean species abundances of stations 36–40. The red line marks the threshold at which a separation of time periods in the MDS plot can be recognized

significance. It serves as food for commercially utilized fish species in the North Sea and forms the basis for food webs, which also include crustaceans such as shrimps, crabs, and mussels (Ehrnsten et al. 2019). In addition, the benthos is involved in the process of carbon remineralization, whereby organic carbon in the sediments is broken down and released back into the nutrient cycle (Szczepanek et al. 2024). Benthic fauna in the North Sea, especially in fished areas, has been subject to changes for about 100 years, partly due to changes in fishing intensity and methodology (Frid et al. 2000). In addition to historical fishing pressure, temperature records from the region indicated a consistent warming trend over the past three decades, with documented impacts on benthic and pelagic communities (Beare et al. 2004).

Species composition and diversity

The results of our time series analysis of benthic macrofauna communities revealed significant shifts in community structure from 1991 to 2021, as observed in the MDS plot. The canonical correspondence analysis (CCA, Fig. 9) showed that the influence of fishing was more dominant for all stations in the 1990 s and early 2000 s, while in later years, a stronger influence of rising temperatures became apparent. Station 40 in particular, located in the Natura2000 area, shows a more pronounced shift towards temperature, indicating that water warming may play a stronger role here than at the other stations. These results indicate that station 40 is more strongly influenced by large-scale temperature changes, while the stations outside the Natura2000 area respond to fishing changes for longer. Species responses to these environmental factors varied: trawling predominantly led to declines in species abundance, while the temperature effects were more diverse, with approximately equal proportions of positive and negative abundance trends. This indicates that while temperature has become more influential in recent years, its effects on species abundances are more complex than the impact of trawling.

Effects of trawling activity on epibenthic community structure

From 1991 to 2021, there was a sharp decline in bottom-contacting fisheries at the Dogger Bank in the North Sea (Fig. 6). This decline in trawling was partly due to the increasing number of regulations and restrictions imposed on fishermen (Arnason 2013) but was also certainly due to a change in the distribution of target fish stocks (Engelhard et al. 2014). The correlations found between the trawling hours and species may reflect the ecological traits and behaviors of individual

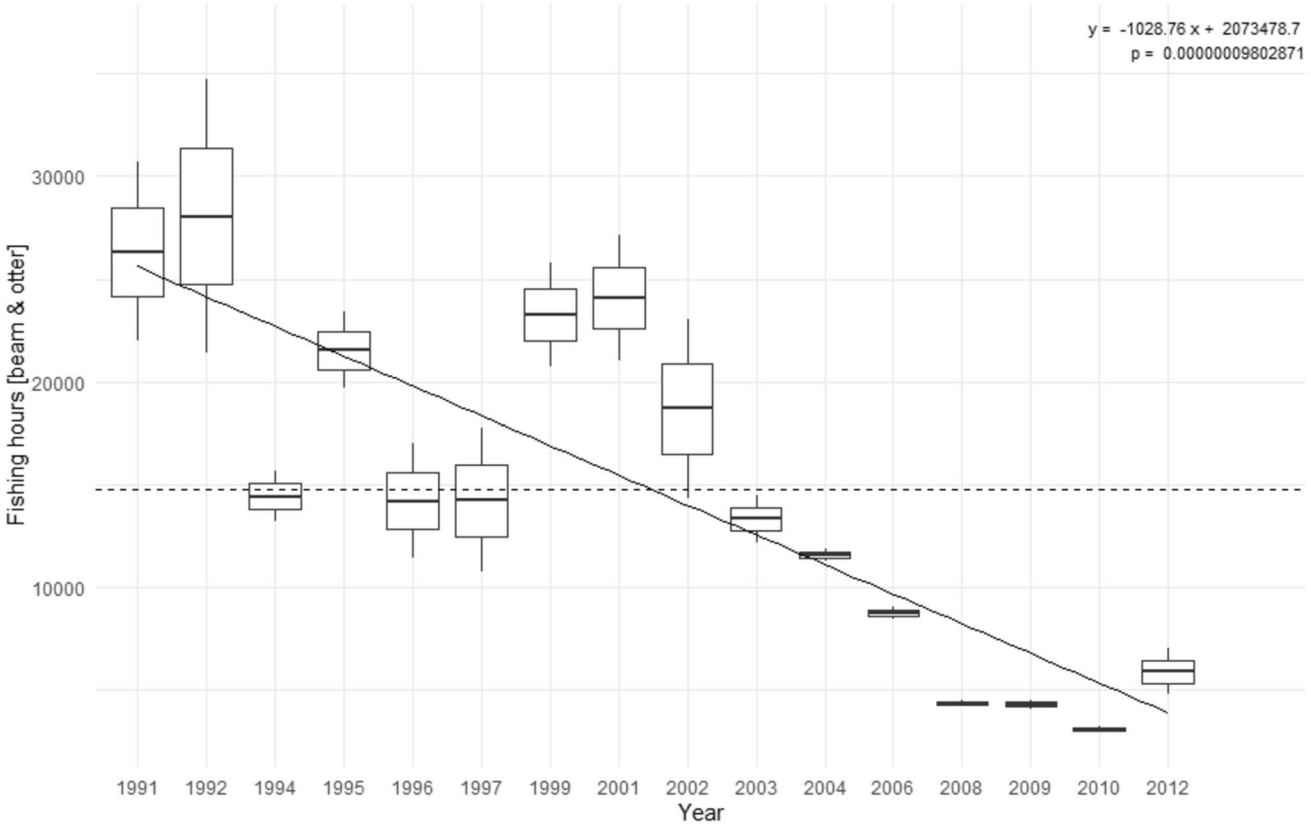


Fig. 6 Mean hours of trawling for the ICES statistical rectangles 39F3, 39F4, and 40F4 (Fig. 1) with linear regression (solid) and mean (dotted) lines from 1991 to 2012. Data are from the Couce et al. (2019) dataset

Table 1 Spearman's rank correlation (rs) of the trawling data and mean species abundances of stations 36–40 from 1991 to 2012. Only species with statistically significant correlations ($p < 0.05$) are shown. Positive values (marked in red) indicate a positive correlation between epifaunal abundance and trawling activity, while negative values (marked in blue) indicate a negative correlation

Species	rs
Ophiura albida	0.48
Buccinum undatum	0.33
Pagurus bernhardus	0.28
Merlangius merlangus	−0.25
Asterias rubens	−0.29
Echiichthys vipera	−0.32
Limanda limanda	−0.32
Merlangius merlangus	−0.34
Pomatoschistus minutus	−0.34
Ascidiella scbra	−0.45
Callionymus lyra	−0.48
Echinocardium cordatum	−0.48
Buglossidium luteum	−0.52
Pleuronectes platessa	−0.60
Arnoglossus laterna	−0.66
Luidia sarsi	−0.75
Microstomus kitt	−0.78

species. For example, scavenger species such as *Ophiura albida*, *Buccinum undatum*, and *Pagurus bernhardus*, which show a positive correlation with trawling activity, benefit from trawled areas and the associated destroyed epibenthos (Groenewold and Fonds 2000). Species such as *Luidia sarsi* and *Arnoglossus laterna* that show a negative correlation with trawling activity may be more sensitive to the effects of trawling, whether through direct physical damage to their habitat or the disruption of their food web. For species like *Microstomus kitt* and *Pleuronectes platessa*, the reason for a negative correlation can simply be that they are target species of the fishing industry. However, since there has been a decline in trawling over the past two decades, these target species should have become more abundant again in recent years or in the future, as long as they are not affected by rising sea temperatures or other stressors (Blöcker 2022). These interpretations suggest that different species may respond differently to the effects of trawling depending on their ecological characteristics, habitat preferences, and adaptations to their environment.

The intensity of fishing with small trawlers was greatest in the regions of the Wadden Sea in 2010 to 2012 (Eigaard et al. 2017). The Dogger Bank, which is located at the northwestern end of the German EEZ, shows a lower intensity. Considering there are other areas which are much more

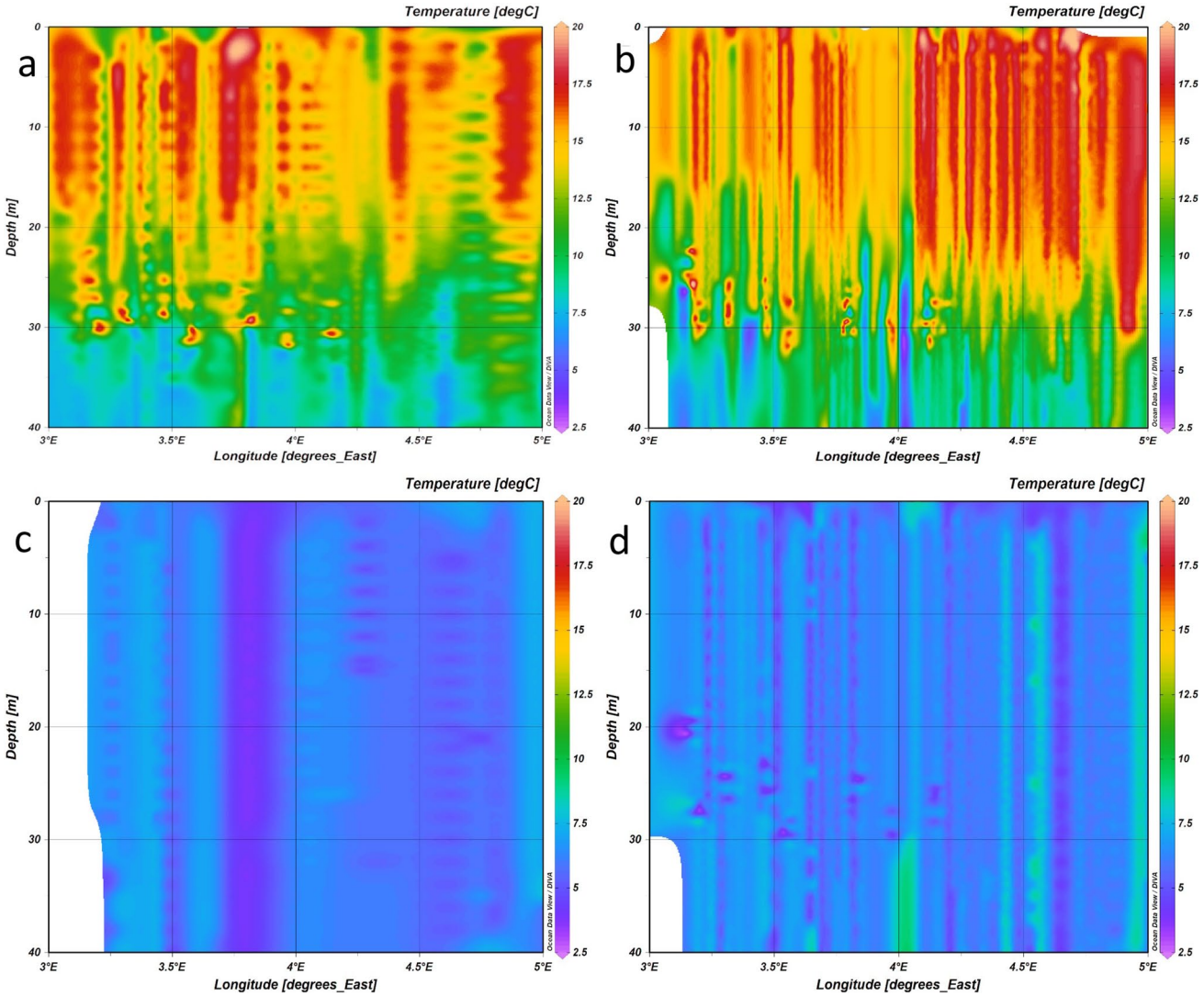


Fig. 7 Latitudinal section of publicly available mean temperature data from ICES of all available data points for the study area (Fig. 2) at depths of 0–40 m, recorded with the CTD probe. **a** Summer (Jun 1–Aug 31) during 1991–2001; **b** Summer (Jun 1–Aug 31) during 2002–2021; **c** Winter (Nov 1–Mar 31) during 1991–2001; **d** Winter (Nov 1–Mar 31) during 2002–2021

intensely fished in the North Sea, even more drastic changes can be expected there with regard to the epifauna. Several studies confirm that epifauna communities in the Wadden Sea have changed over the years long before the present time series from 1924 to 1986 (Reise and Schubert 1987; Buhs and Reise 1997). Regular fishing with bottom-touching gear increases the possibility that this fished area will have permanent changes in ground-living fauna (Jones 1992). Therefore, limiting bottom-contact fishing in designated zones (as has happened recently in the German NATURA2000 areas of the Sylt Outer Reef, Borkum Reef Ground, and Amrumbank) is useful to ensure the recovery of marine ecosystems and their benthic fauna. It is important that periods between trawling are sufficiently long since studies have already shown that recovery in benthic fauna is not observed at fished sites after 1 year; thus, it may take several years for these species to recover (Cook et al. 2013).

Besides the direct impact of bottom-contacting fisheries, trawlers also have indirect effects on the behavior of various commercial fish species, for example, by activating escape behavior (Heino and Godø 2002). In a second step, this could lead to behavioral adaptations that affect fish stocks by causing unnecessary escape reactions. These escape responses can result in an inefficient distribution of resources, either by disrupting the natural foraging patterns of fish (e.g., leading to suboptimal use of food resources) or by influencing the availability of fish for the fishery, thereby affecting both predator–prey dynamics and the distribution of fishing efforts among fishers (Heino and Godø 2002). Thus, the complete exclusion of mobile bottom-touching fisheries in certain

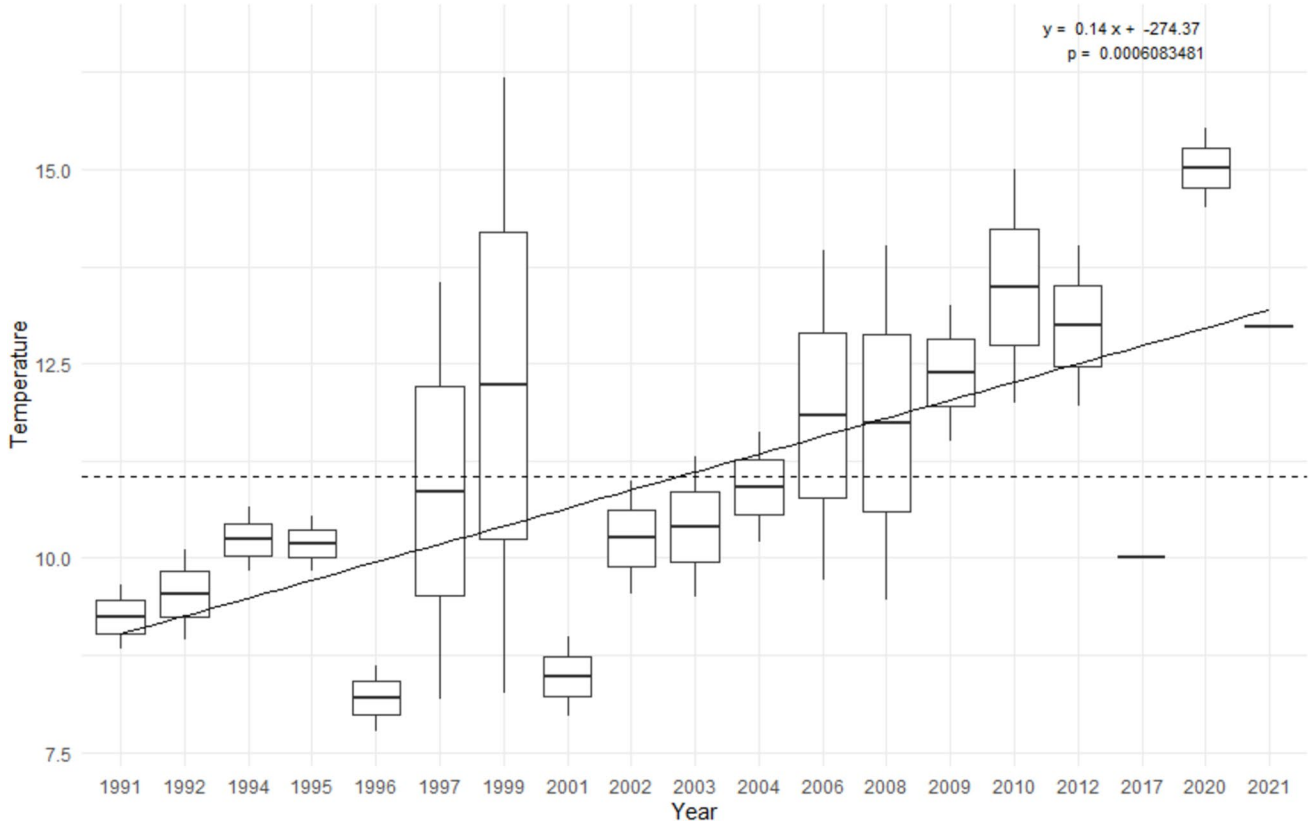


Fig. 8 Mean summer temperatures (June 1–August 31) of all measured data at depths below 25 m in the ICES statistical transects 39F3, 39F4, and 40F4 (Fig. 1) with linear regression (solid) and mean (dotted) lines from 1991 to 2021

protected areas in the North Sea is more advisable than just a reduction in fishing pressure. In order to promote ecosystem-friendly fisheries, previous studies have focused on indicators related to ecosystem status, trawling pressure, and management progress (Jennings 2005). These studies have recommended the use of specific ecological indicators to monitor and reduce fishing impacts, improve management practices, and ensure long-term sustainability of fish stocks. The present study builds on these recommendations by investigating the relationship between trawling activity and ecosystem health, aiming to provide further insights into effective management strategies.

Effects of temperature change on epibenthic community structure

Advancing climate change is resulting in an increase in water temperature (Bijma et al. 2013), an effect that is not stopping at the North Sea. The average temperature increases of 4 °C from 1991 to 2021 in the water layers from 25 m and deeper are dramatic compared to the global change of less than 1° for the 0–700 m water layer from 1993 to 2019 (Johnson and Lyman 2020)! This temperature increase can be attributed to climate change (Clark et al. 2003), a phenomenon that has also affected benthic species in marine ecosystems across broad ocean regions (Birchenough et al. 2015). In 2017, water temperatures at depths of 25 m and below were considerably lower than in the years before and after this time, which also applies to biodiversity according to the Shannon–Wiener index for the year 2017. Strong temperature fluctuations can cause stress for marine organisms, especially if they are not able to adapt quickly enough to these changes (Neumann et al. 2009). Temperature changes can affect the growth and distribution of plankton which, in turn, can affect the entire food chain (Winder and Sommer 2012). If the availability of planktonic species changes due to temperature changes, then this can affect the food base for various marine organisms and lead to a shift in biodiversity (Weyhenmeyer et al. 2012).

In general, the effects of elevated temperature on a species depends on their specific temperature sensitivity (Freitas et al. 2007). The species *Luidia sarsii*, *Microstomus kitt*, and *Arnoglossus laterna* show a strong positive correlation with increasing temperatures; for *Ludidia sarsii*, a positive correlation with summer bottom temperatures has already been demonstrated by Sonnewald and Türkay (2012b). Based on the ecological preferences, a model was developed that can be used to make future predictions on abundance and distribution of a given species; *Microstomus kitt* is one of the species that may be found in greater numbers in the future

Table 2 Spearman's rank correlation (rs) of the temperature data and mean species abundances of stations 36–40 from 1991 to 2021. Only species with statistically significant correlations ($p < 0.05$) are shown. Positive values (marked in red) indicate a positive correlation between epifaunal abundance and trawling activity, while negative values (marked in blue) indicate a negative correlation

Species	rs
Luidia sarsi	0.69
Microstomus kitt	0.67
Arnoglossus laterna	0.67
Pleuronectes platessa	0.39
Alcyonium digitatum	0.36
Alcyonidium diaphanum	0.35
Merlangius merlangus	0.26
Buglossidium lureum	0.25
Pomatoschistus minutus	0.22
Ascidiella scabra	0.21
Echiichthys vipera	−0.20
Asterias rubens	−0.26
Eutrigla gurnadus	−0.27
Liocarcinus holsatus	−0.29
Euspira pulchella	−0.34
Psammechinus miliaris	−0.38
Buccinum undatum	−0.42
Pagurus bernhardus	−0.43
Corystes cassivelaunus	−0.43
Gadus morhua	−0.51
Ophiura albida	−0.63

due to the increase in temperature (Maltby et al. 2020). The negative correlation patterns of the species *Ophiura albida*, *Gadus morhua*, and the masked crab *Corystes cassivelaunus* with temperature suggest that these species are either sensitive to higher temperatures or prefer colder environments. *Gadus morhua* is known for its preference for cooler waters as the temperature tolerance during the spawning period is approx. 1–8 °C (Righton et al. 2010) and may, therefore, be less successful in warmer conditions (Drinkwater 2005), and modeling has already calculated a decline for *Gadus morhua* in the future (Maltby et al. 2020) Species with tolerance for high temperatures may show a lower or no direct response to sea temperature fluctuations, while other species that are less adaptable may be negatively affected by temperature change. A study of long-term data from the North Sea from 1978 to after 1987 already shows that trawling has an effect on fish stocks, although changes in environmental conditions may exacerbate this effect (Reid and Edwards 2001).

The Dogger Bank is an elevation that at its maximum is 40 m deep, and, thus, temperature changes may have a stronger impact on epifauna communities in that region compared to deeper areas. In the deeper northern part of the North Sea, few benthic species appear to be affected by warming water temperatures; this contrasts with benthos in the shallower, southern North Sea (Neumann et al. 2009). Climate change–induced introductions of benthic, invasive species, such as the angular crab *Goneplax rhomboides* (Linnaeus 1758), are causing a repopulation and ecosystem restoring due to overlapping niches (Neumann et al. 2013), while species'

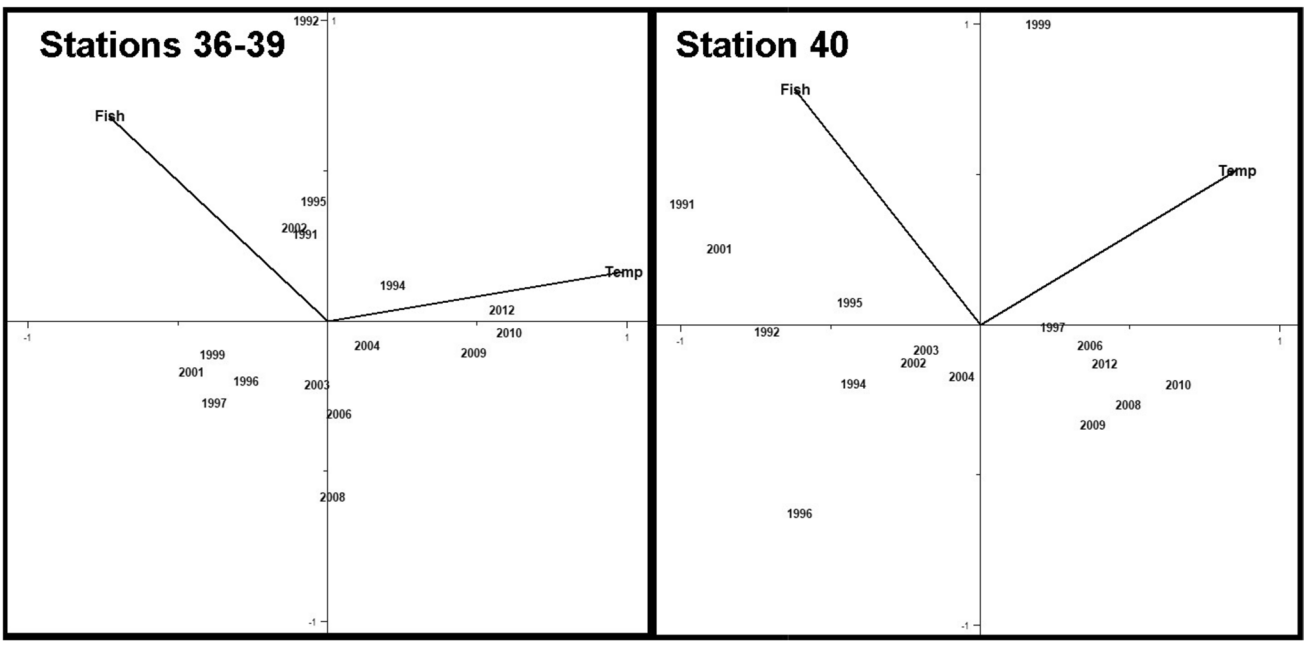


Fig. 9 Canonical correspondence analysis (CCA) of individual species abundances with the mean summer bottom water temperature and the mean trawling activity (fishing hours per year, derived from Couce et al. 2020) of stations 36–39 versus station 40

range shifts occur (Lord 2014). A long-term study of epifauna communities in the North Sea has shown that reproduction success, in particular, is affected by temperature anomalies (Neumann and Kröncke 2011). As bottom-associated fishes move to deeper areas in response to temperature change (Dulvy et al. 2008), the shallow areas of the North Sea in particular could expect to lose species richness or a species shift.

Combination of temperature and trawling effects on benthic fauna

The interpretation of the results from the present and published studies shows that both water temperature and trawling activity can have a significant impact on the abundance and diversity of benthic communities, and on the ecological relationships and behavior of the species studied, emphasizing the importance of studying the combined influence of temperature and trawling on the ecology of marine communities. In general, it can be assumed that the food webs and, thus, also the energy flow in the near-bottom layers will change in the future with changing temperature and trawling activity, as they already have done, evidently, in our research area. Although no significant correlation between the Shannon–Wiener Index and temperature or trawling activity could be detected, it is clear that there are distinct, positive or negative effects of both factors at the species level. Both multi-variate analyses indicated a clear shift in community structure from 1991 to 2001 and the years 2002 to 2021; during the same period, trawling continued to decline and the sea temperatures increased.

This finding supports the hypothesis that a change of multiple factors, among them trawling and temperature, must have taken place around the turn of the century. The faunal community of the years 2020 and 2021, in particular, showed a greater correlation with temperature; therefore, it can be assumed that the influence of temperature will become even greater and more significant as the sea temperature is expected to continue to rise in the coming years.

Summary and outlook

During the study period of 30 years between 1991 and 2021, the local summer temperatures in the lower water layer increased by up to 4 °C, while trawling activity in the area continuously decreased. Despite minimal annual variation in species composition between the stations, our analysis revealed a continuous change in the benthic fauna characterized by the decreasing species diversity and an overall faunal regime shift around the turn of the millennium. Although we did not find a direct relationship between biodiversity and temperature or trawling effort, we identified certain species that show positive or negative correlations with these factors.

Since 2012, the annual sampling of the stations with the RV "Senckenberg" has regrettably diminished due to canceled expeditions and/or bad weather conditions. It will be vital to resume regular sampling so that future changes in the benthos in the area can be compared with historical records. Further biodiversity change can be expected in the coming years. Therefore, in order to be able to study this anticipated change, annual surveys of the area are essential. Since the exclusion of mobile, bottom-dwelling fisheries is planned around station 40 in the coming years, it is particularly important to monitor both that station and the stations outside the protected area. Long-term studies such as these are now, and will continue to be, increasingly important. Climate change and other environmental factors continue to impact benthic biodiversity (Clark et al. 2003). Hence, such long-term studies are important for future measures in ecosystem restorations. The outcomes of this study serve as a foundation for future research and monitoring efforts, particularly within the Dogger Bank study area. Long-term, fisheries-independent studies are needed to inform conservation and fisheries management, as they can document the time frames required for the recovery of benthic communities and provide deeper insights into the long-term consequences of environmental changes caused by human activities on marine ecosystems.

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Declarations

Conflict of interest The authors declare no competing interests.

Ethical approval The use and care of experimental animals complied with German animal welfare laws, guidelines, and policies as approved by § 7a Sect."Introduction"No. 1–8 Animal Welfare Act. Care was taken to ensure that no animal suffered unnecessarily and that all animals were released back into their natural habitat after a quick identification, as long as they could be properly identified on board. All applicable international, national, and/or institutional guidelines for animal testing, animal care, and use of animals were followed by the authors.

Sampling and field studies All necessary permits for sampling and observational field studies were obtained by the authors from the

respective authorities. The study complies with the Convention on Biological Diversity and the Nagoya protocol.

Data availability Generated data are available in the appendix. Sample metadata (if samples were transferred to the collection) will be available via the scientific collection portal AQUILA (https://search.senckenberg.de/aquila-public-search/search).

Author contribution SJH and MS conceived and designed the research and experiments conducted. SJH and MS analyzed the data. SJH, AB, and MS wrote the manuscript. All authors read and approved the manuscript. Artificial intelligence (https://chatgpt.com/) was used to finally check the grammar and spelling of the scientific English.

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