Major declines in NE Atlantic plankton contrast with more stable populations in the rapidly warming North Sea

Matthew M. Holland [a,*], Arnaud Louchart [b], Luis Felipe Artigas [b], Clare Ostle [c], Angus Atkinson [c], Isabelle Rombouts [d], Carolyn A. Graves [e], Michelle Devlin [e], Birgit Heyden [f], Margarita Machairopoulou [g], Eileen Bresnan [g], Jos Schilder [h], Hans H. Jakobsen [i], Hannah Llody-Hartley [j], Paul Tett [k], Mike Best [l], Eric Goberville [m], Abigail McQuatters-Gollop [a]

[a] Marine Conservation Research Group, University of Plymouth, Drake Circus, Plymouth PL4 8AA, United Kingdom
[b] Laboratoire d'Océanologie et Geosciences, UMR 8187 LOG, Centre National de la Recherche Scientifique, Université du Littoral Côte d'Opale, Université de Lille, IRD, Wimereux, France
[c] The Marine Biological Association (MBA), The Laboratory, Citadel Hill, Plymouth PL1 2PB, United Kingdom
[d] Flanders Marine Institute (VLIZ), Marine Observation Centre (MOC), InnovOcean Campus, Jacobsenstraat 1, 8400 Oostende, Belgium
[e] Centre for Environment, Fisheries and Aquaculture Science (Cefas), Barrack Rd, Weymouth DT4 8UB, United Kingdom
[f] AquaEcology GmbH & Co. KG, Steinkamp 19, 26125 Oldenburg, Germany
[g] Marine Scotland Science, 375 Victoria Road, AB11 9DB Aberdeen, Scotland, United Kingdom
[h] Waterkwaliteit en Natuurbeheer, Rijkswaterstaat, Postbus 2232, 3500 GE Utrecht, Netherlands
[i] Department of Ecoscience, Aarhus University, Frederiksborgvej 399, 4000 Roskilde, Denmark
[j] Dove Marine Laboratory, Newcastle University, Front Street, Cullercoats, North Shields NE30 4PZ, United Kingdom
[k] Scottish Association for Marine Science, Oban, PA37 1QA, Scotland, United Kingdom
[l] Environment Agency, Kingfisher House, Goldhay Way, Peterborough PE2 5ZR, United Kingdom
[m] Unité Biologie des Organismes et Ecosystèmes Aquatiques (BOREA), Muséum National d'Histoire Naturelle, CNRS, IRD, Sorbonne Université, Université de Caen Normandie, Université des Antilles, Paris, France

HIGHLIGHTS

- The functional diversity of plankton in the NE Atlantic is changing.
- Regional variation in time-series trajectories due to anthropogenic pressures
- K-means clustering of abundance time-series identified spatially coherent patterns.
- Abundance typically increased in the North Sea and decreased offshore.
- Diatoms and copepods decreased in offshore areas, a concern for pelagic food webs.

GRAPHICAL ABSTRACT
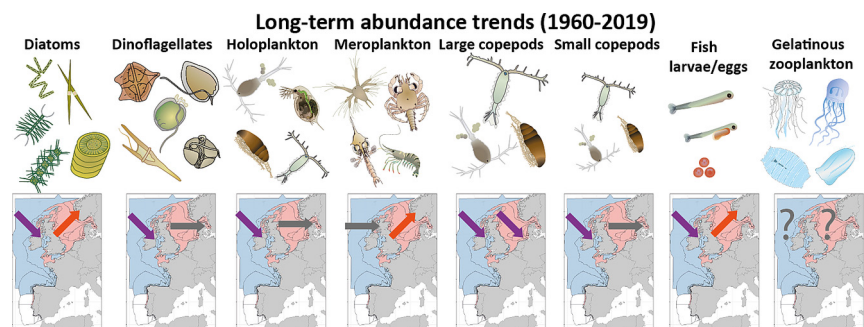
Long-term abundance trends (1960-2019)

ARTICLE INFO

ABSTRACT

Plankton form the base of marine food webs, making them important indicators of ecosystem status. Changes in the abundance of plankton functional groups, or lifeforms, can affect higher trophic levels and can indicate important shifts in ecosystem functioning. Here, we extend this knowledge by combining data from Continuous Plankton Recorder and fixed-point stations to provide the most comprehensive analysis of plankton time-series for the North-East Atlantic and North-West European shelf to date. We analysed 24 phytoplankton and zooplankton datasets from 15 research institutions to map 60-year abundance trends for 8 planktonic lifeforms. Most lifeforms decreased in abundance (e.g. dinoflagellates: −5 %, holoplankton: −7 % decade^{-1}), except for meroplankton, which increased 12 % decade^{-1}, reflecting widespread changes in large-scale and localised processes. K-means clustering of assessment

Pelagic habitats
Plankton

units according to abundance trends revealed largely opposing trend direction between shelf and oceanic regions for most lifeforms, with North Sea areas characterised by increasing coastal abundance, while abundance decreased in North-East Atlantic areas. Individual taxa comprising each phytoplankton lifeform exhibited similar abundance trends, whereas taxa grouped within zooplankton lifeforms were more variable. These regional contrasts are counterintuitive, since the North Sea which has undergone major warming, changes in nutrients, and past fisheries perturbation has changed far less, from phytoplankton to fish larvae, as compared to the more slowly warming North-East Atlantic with lower nutrient supply and fishing pressure. This more remote oceanic region has shown a major and worrying decline in the traditional food web. Although the causal mechanisms remain unclear, declining abundance of key planktonic lifeforms in the North-East Atlantic, including diatoms and copepods, are a cause of major concern for the future of food webs and should provide a red flag to politicians and policymakers about the prioritisation of future management and adaptation measures required to ensure future sustainable use of the marine ecosystem.

1. Introduction

Plankton form the base of pelagic food webs and play an integral bio-geochemical role in carbon cycling and sequestration (Guidi et al., 2016). Short generational times, small size, dependence on currents/hydrodynamics and, for phytoplankton, direct dependence on dissolved nutrients and solar energy make them well-suited for detecting impacts of environmental change (McQuatters-Gollop et al., 2015). Changes in plankton communities affect higher trophic levels, including shellfish, fish, and seabirds, which are supported either directly or indirectly by plankton (Frederiksen et al., 2006) with consequential impacts for the industries reliant on a healthy marine ecosystem (Hays et al., 2005).

The North-East Atlantic and North-West European shelf are experiencing rapid warming and other environmental changes attributable to climate change (Emeis et al., 2015). While warming can be a direct physiological pressure on plankton (Sarker et al., 2020), it can also drive physical changes in hydrology, including water currents, vertical mixing, and stratification regime (Behrenfeld et al., 2006). At the regional scale, significant changes in the plankton community have been recorded and strongly linked to changes in environmental conditions, most notably temperature (Bedford et al., 2020b), salinity (Edwards et al., 2002), nutrients (Desmit et al., 2020), and in the dynamics of higher trophic levels (Beaugrand et al., 2003; Heath and Lough, 2007; Olin et al., 2022). These widespread environmental changes have occurred alongside shorter-term variation in direct human impacts, including changes in riverine nutrient input (Capuzzo et al., 2018) and fishing pressure (Murgier et al., 2021) and it is often challenging to disentangle this myriad of impacts on the plankton community. This rapidly changing marine region supports important fisheries, encompasses a range of contrasting pelagic habitat types, including river plumes, coastal, shelf, and oceanic areas, and also benefits from some of the longest and highest density biological time series in the world (McQuatters-Gollop et al., 2022), making it a perfect location to investigate how climate change and variation in anthropogenic pressures have impacted plankton communities.

To detect important changes in ecosystem functioning, complex long-term plankton monitoring datasets can be summarised into ecologically meaningful lifeforms (i.e. planktonic organisms which fulfil the same important functional role in their environment) (Margalef, 1978; McQuatters-Gollop et al., 2019; Smayda and Reynolds, 2003; Tett et al., 2008) and indicators derived from these lifeforms can be useful for informing the location of critical changes occurring in pelagic ecosystems (McQuatters-Gollop et al., 2019). Numerous studies have highlighted trends in plankton within this region (Beaugrand et al., 2010; Bedford et al., 2020b; Schmidt et al., 2020) and a suite of mechanisms have been proposed to explain these changes, such as northward range shifts (Chivers et al., 2017), phenology shifts (Hinder et al., 2012), and changes in stratification and nutrient supply (Capuzzo et al., 2018). Few studies, however, have examined the regionality of large scale, long-term trends of multiple phytoplankton and zooplankton lifeforms by combining both inshore and offshore data (Bedford et al., 2020b).

The critical role of plankton to ecosystem health and sustainable use also makes them integral to policy-related reporting (Aubert et al., 2017; Brander et al., 2003; Rombouts et al., 2019; Tett et al., 2008). The OSPAR Convention is an international agreement among 15 "contracting parties" (including 14 nation states and the European Union) for protecting this shared marine environment and co-managing human activities sustainably. To assess the status of pelagic habitat biodiversity, contracting parties routinely submit plankton monitoring data to OSPAR. Our study summarises data submitted to OSPAR by eight contracting parties, expanding on spatial patterns of long-term change described in Bedford et al. (2020b), incorporating additional plankton datasets over a broader spatial extent, and using an improved set of ecologically relevant assessment units to divide the North-East Atlantic. The aims of our study were to perform the most comprehensive assessment to date, to (1) detect and quantify long-term changes in the abundance of plankton lifeforms across the North-East Atlantic; (2) identify any consistent spatial patterns of change in lifeform abundance; and (3) explore similarities and differences in the way plankton communities have changed across pelagic habitats.

2. Materials and methods

2.1. Plankton monitoring datasets

Datasets were submitted to OSPAR by contracting parties through a 2021 data call to support OSPAR's Quality Status Report 2023 (QSR 2023), which aims to assess the environmental and biodiversity status of the North-East Atlantic. Each dataset was subjected to institute-specific quality control procedures to ensure consistency and accuracy of counting and methodology (see Supplemental methods: Quality control for plankton datasets). Once received by OSPAR, datasets were uploaded to the online Plankton Lifeform Extraction Tool (PLET), allowing for taxa and samples to be aggregated into monthly-averaged lifeform abundances, as described in Ostle et al. (2021). While biomass can often be a more informative metric than abundance for detecting changes in plankton communities, particularly for measuring impacts on the food web, determination of biomass based on standardised estimates of organism volume or carbon content were beyond the scope of this paper due to incomplete size information for the >1800 taxonomic groups assessed. Even so, due to the shared functional role of taxonomic groups within each lifeform it is likely that large variation in their abundance will still generate important impacts on marine food webs. The data that support the findings of this study are openly available from The Archive for Marine Species and Habitats Data (DASSH), at https://www.dassh.ac.uk/lifeforms/.

Two types of data were used to support this analysis. Spatially extensive open water surveys, such as the Continuous Plankton Recorder (CPR), are useful for examining the direction and magnitude of changes in selected lifeform abundances over time across large pelagic habitats, revealing spatial patterns of change (Bedford et al., 2020b). Additionally, fixed-point, full depth time-series stations provide complementary information on a larger fraction of the plankton size spectrum and in the more nearshore habitats that are particularly valuable for studying anthropogenic pressures such as eutrophication (McQuatters-Gollop et al., 2019) and pollution (Serranito et al., 2016).

To use datasets from multiple sources effectively, procedures were implemented to ensure the comparability of results. Datasets were not

combined due to differences in sampling, analysis, and enumeration methods. Instead, all datasets were analysed separately, using an identical set of methods. This way it was possible to compare trends derived across multiple datasets since each dataset maintained an internally consistent sampling and enumeration methodology. The analysis was primarily restricted to OSPAR Regions II (Greater North Sea), III (Celtic Seas) and IV (Bay of Biscay and Iberian Coast). Datasets were required to contain samples collected during and before a contemporary "assessment period" to represent current conditions. For this analysis, we selected the period between 2015 and 2019. Time-series were limited to the end of 2019 to maintain consistency among datasets, although initial date varied. Due to interannual variability in plankton monitoring data, time-series needed to be of sufficient length (i.e. ≥10 years) to facilitate identifying statistically significant trends. While the CPR data typically covered 1960 to 2019, many of the coastal time-series commenced in the 1980s or later. Histograms displaying the distribution of samples through time for each time-series can be located in the Supplementary Materials for phytoplankton (Fig. S 1) and for zooplankton (Fig. S 2).

While 19 institutions from 9 contracting parties submitted datasets to be used for the QSR 2023, analysis was limited to 24 datasets from 15 institutions in 8 countries (Fig. 1; Table S 1). The table in Supplementary Materials contains DOI links to detailed metadata for each dataset, wherever this was available. Unused datasets were all determined to be out of scope for this assessment due to limited length (<10 years) or poor coverage of the assessment period.

2.2. Plankton lifeforms

We selected eight plankton lifeforms (diatoms, dinoflagellates, holoplankton, meroplankton, large copepods, small copepods, fish larvae and eggs, gelatinous zooplankton) for their ecological-relevance and the high confidence in their classification (McQuatters-Gollop et al., 2019). Diatoms and dinoflagellates represent major components of the larger phytoplankton in temperate seas. While both contribute primary productivity to pelagic food webs, diatoms are exclusively autotrophic and require the

nutrient silicate (Raven and Waite, 2004), while dinoflagellates exhibit broader nutritional modes (i.e. autotrophy, mixotrophy, or heterotrophy) (Sherr and Sherr, 2007). These lifeforms are functionally distinct due to differences in motility (Ross and Sharples, 2007) and sinking rates (Durkin et al., 2016), and likely contribute in unique ways to trophic pathways and biogeochemical cycling.

Holoplankton are a diverse non-taxonomic group of zooplankton which spend their entire lifecycle in the pelagic ecosystem, and include copepods, appendicularians, cladocerans, chaetognaths and euphausiids. By contrast, meroplankton (another diverse non-taxonomic group) are zooplankton which spend only part of their lifecycle in the pelagic ecosystem before recruiting to benthic habitats. Meroplankton contains organisms including cirripedes, decapods, echinoderms, bryozoans, some polychaetes and molluscs, and several other groups.

We defined large copepods as any copepod with a total adult length ≥ 2 mm and small copepods as <2 mm in adult total length. Large copepods can be nutritionally dense and are an essential component of the diets of many fish, such as Atlantic mackerel (*Scombrus scomber*), in their larval, juvenile and even adult stages (Kvaavik et al., 2019). Small copepods are typically the most abundant zooplankton lifeform. Their high abundance and small size makes them readily consumable by larval fish and they are essential for transferring energy from phytoplankton to higher trophic levels (Turner, 2004). While copepods also contribute to holoplankton abundance, the separate lifeforms reveal different aspects of ecosystem functioning.

Fish larvae and eggs represent the next step in the pelagic food web, as fish larvae rely heavily on copepods for their growth and survival. For Atlantic cod (*Gadus morhua*), a year-class's recruitment success depends on whether small copepods are in high abundance during the period when larval fish emerge from their eggs (Platt et al., 2003).

Gelatinous zooplankton are defined here as organisms belonging to the phyla Cnidaria and Ctenophora. They exert strong predation pressure on larval fish, eggs, and crustacean zooplankton. Due to their non-quantitative capture by common sampling methods and poor fixation in formaldehyde, this group is not counted or underrepresented in some key zooplankton datasets including the spatially extensive CPR survey
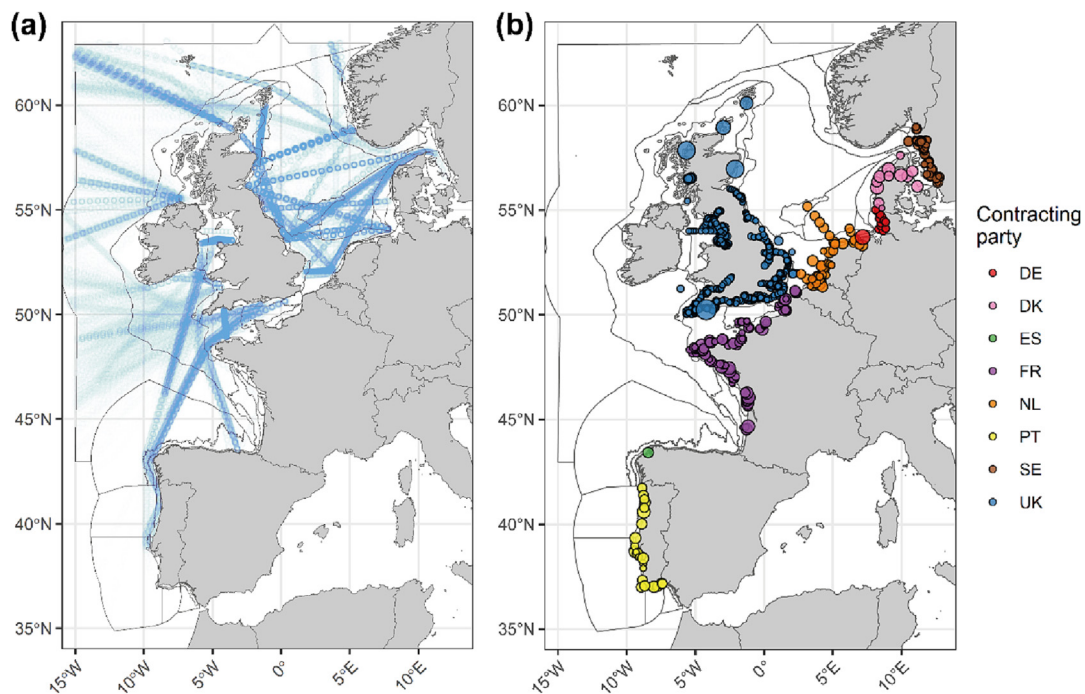
Fig. 1. CPR routes (a) and the locations of samples from all other datasets used in the assessment (b). Points are overlaid on the assessment units used to aggregate samples. Points are coloured according to the contracting party of the institute that provided the data. The total number of samples taken at each location is proportional to point opacity in (a) and point size in (b).

(Aubert et al., 2018; Boero et al., 2008). The limited data available for gelatinous zooplankton have been included to highlight their poor representation in plankton datasets in comparison to other life-forms.

2.3. Spatial and temporal scale of analysis

While pelagic habitats are primarily open systems with no clearly definable boundaries, they can be roughly delineated according to key water column features, such as bathymetry, freshwater influence, and stratification, and based on spatially consistent patterns in phytoplankton dynamics (Enserink et al., 2019; van Leeuwen et al., 2015). The analysis of distributed datasets was performed across distinct pelagic habitats or "assessment units" (Fig. 2). Discrete fixed-point times series were each analysed separately and not extrapolated to any larger spatial scale. To identify regional variation in lifeform trends we used the "COMP4 assessment units" (Common Procedure for the Identification of the Eutrophication Status of the OSPAR Maritime Area, 4th application), an OSPAR data product, to spatially subdivide plankton samples (Enserink et al., 2019). These assessment units are a geographical representation of the conditions most likely to drive plankton distribution, dynamics, and community composition.

For further information, refer to Supplemental methods: Deriving COMP4 assessment units.

2.4. Lifeform abundance trends

All analyses were performed using R-programming language (R Core Team, 2020). For each dataset and sample, total lifeform abundances were grouped by assessment unit or fixed-point station to generate a distinct subset for each lifeform. Each record of a taxon, including very rare taxa, was classified into lifeforms based on a Masterlist of trait information, and subsequently the total abundance of each lifeform was summed for each sample (Ostle et al., 2021). Before total lifeform abundance could be log_{10} transformed, a nominal value equivalent to half the minimum non-zero observed value for each time-series was added to each sample to remove zeros (Ives, 2015). Rather than simply adding 1 to every value, this approach was used to ensure the magnitude of the adjustment matched the scale of each time-series, particularly for time-series which had many zeros recorded in winter months. Common time resolution averaging for both data types was monthly, even when finer temporal resolution was available. For distributed CPR data, this occasionally resulted in localised
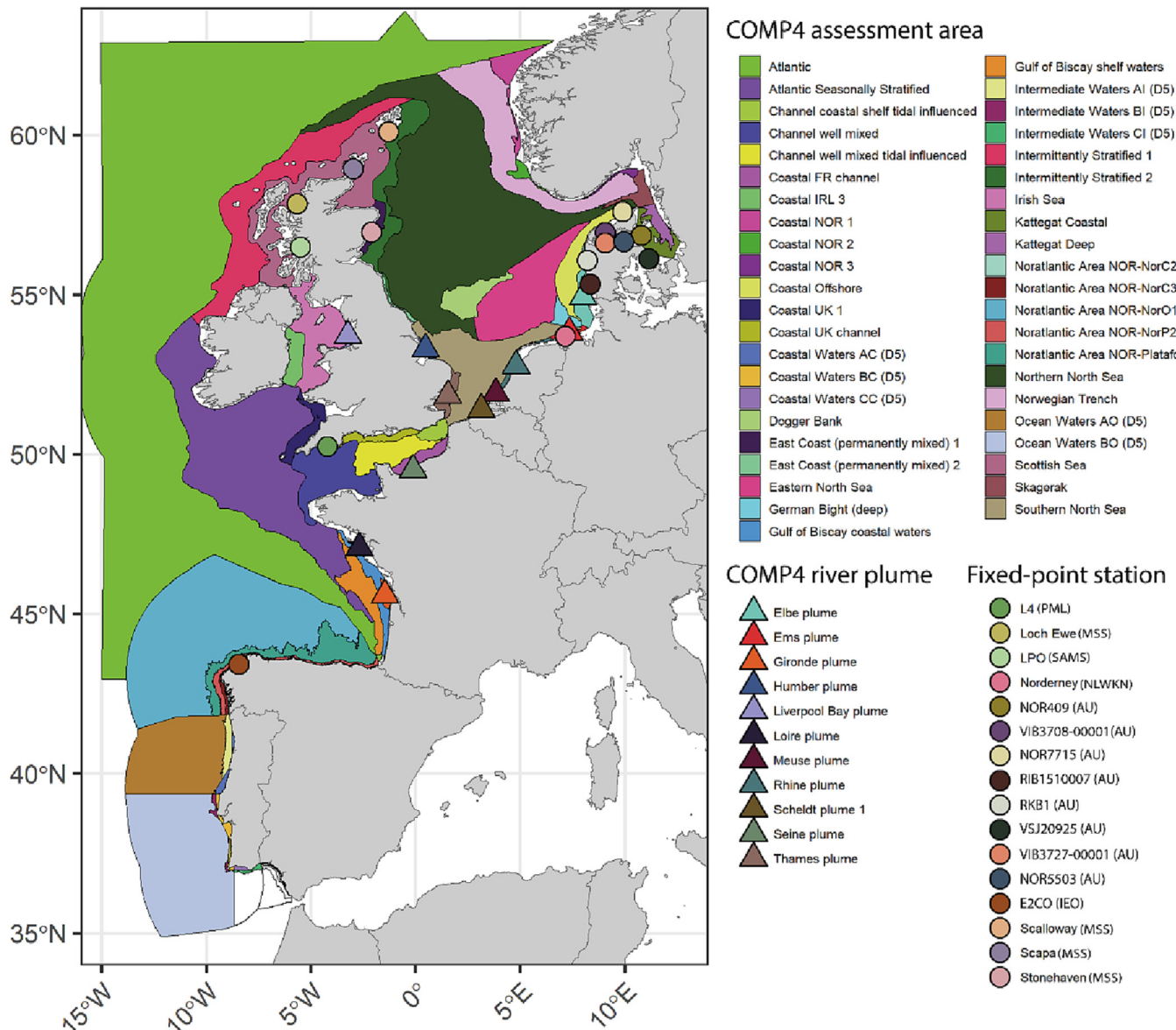

Fig. 2. COMP4 assessment units developed by JMP-EUNOSAT (Enserink et al., 2019) and OSPAR as polygons. Triangle symbols highlight the small COMP4 assessment units which contain river plumes, and round symbols indicate the locations of the fixed-point plankton monitoring stations used in this study.

groupings of samples being extrapolated across larger assessment units (see the distribution of CPR samples in Fig. 1(a)), as was the case for CPR data along the west of Scotland (Intermittently Stratified 1) and Ireland (Atlantic Seasonally Stratified).

For months when there were no distributed samples within an assessment unit, gaps in the time-series constructed from spatially distributed datasets were filled by extracting a mean value from an inverse distance weighted (IDW) interpolated surface generated from samples adjacent to the assessment unit (<250 nmi) from the same dataset. IDW surfaces were generated across a 0.5° square grid based on monthly binned values with land areas clipped. Values for cells intersecting each polygon were averaged with equal-area weighting. This spatial interpolation step accounted for 30 % of months in distributed time-series, on average. No spatial interpolation was applied to fixed-point station time-series. For all time-series, years containing fewer than eight distinct months of samples were excluded from the trend analysis (Bedford et al., 2020b). This step removed on average 11 % of years from each time-series. Remaining gaps of three months or less were filled with linear interpolation from adjacent months. On average, this final step resulted in an additional 3 % of months being added to each time-series. The direction of lifeform abundance trends was determined with the Kendall trend test (see Supplemental methods: Calculating trends in lifeform abundance). Sen's slope estimates were calculated to determine the median percent change in abundance per decade for each lifeform across all assessment units.

Considering the range of start dates among datasets (e.g. 1960 for CPR, 1992 for PML, 1999 for NLWKN; Table S 1), we conducted an additional analysis to determine whether differences in time-series length affected the general spatial patterns in trend direction. We truncated all time-series to the period 2000 to 2019 and re-ran the Kendall trend test on the shortened time-series.

2.5. Cluster analysis of lifeform abundance trends

Spatially coherent patterns in long-term abundance trends across multiple lifeforms indicate possible changes occurring at the community level. To identify these patterns, a cluster analysis was conducted using K-means clustering on the Kendall's S-statistics for the 30 COMP4 assessment units and the 3 fixed-point stations that contained observations for all seven lifeforms (excluding gelatinous zooplankton due to limited data availability). Kendall's S-statistics were converted to matrix format with assessment unit and station names as rows and lifeform names as columns. Statistics for each lifeform (columns in the matrix) were normalised by subtracting their mean value and dividing by their standard deviation. To determine the optimal number of clusters to group the data, silhouette and within sum of squares (WSS) plots were generated from the matrix using the "factoextra" package for visualising multivariate data (Kassambara and Mundt, 2020) (see Supplemental methods: Determining the optimal number of clusters). Sensitivity analysis was performed to estimate the influence of the random starting assignments. K-means clustering was conducted with 100 random sets (nstart = 100) to ensure a more stable result.

2.6. Exploring variability within and among spatial clusters

Once assessment units and fixed-point stations were sorted into spatial clusters, boxplots were generated, and ANOVA was used to compare the distribution of Kendall's S-statistics among clusters for each lifeform. This step was intended to identify how trends in the abundance of plankton lifeforms varied among clusters. One-sample *t*-tests were conducted to determine whether abundance trend distributions within each spatial cluster were net increasing or decreasing. Shapiro-Wilk and Goldfeld-Quandt tests were also performed to test assumptions of normality and homoscedasticity, respectively.

To determine what contributed to similarities in lifeform abundance trends within clusters and differences among clusters, nonmetric multidimensional scaling (NMDS) was performed on the same matrix used for the K-means clustering. NMDS generates a nonmetric ordination based on

the distance or dissimilarity among samples. The 'metaMDS' function from the 'vegan' package for R was used to evaluate Bray-Curtis dissimilarity across the matrix (Oksanen et al., 2019). To use Bray-Curtis as the dissimilarity metric, negative Kendall statistics were eliminated from the matrix by adding the minimum value in the matrix to every value. This causes the smallest value to be zero and all other values to be positive. The results of the NMDS were plotted and overlaid with 95 % confidence ellipses for the distribution of points in each cluster.

The direction and magnitude of loading vectors generated using the 'envfit' function indicates the direction of increase in Kendall statistics for each lifeform relative to the axis of separation among clusters (Oksanen et al., 2019). To determine which lifeforms were important in driving the separation of data into clusters, the 'envfit' function was used to generate lifeform loadings as projected vectors on the NMDS ordination.

A similar approach was taken to project loading vectors generated from Kendall statistics at the lowest taxonomic level available in each dataset onto the same ordination to study the alignment of abundance trends in taxa with those of the lifeforms they comprised. This approach also indicates which taxa have experienced the greatest change in abundance. In some cases, this was conducted at a coarser taxonomic resolution than the species level (e.g. up to phylum level) since this was occasionally the highest level of classification recorded. Some datasets recorded a mixture of taxonomic classifications (e.g. *Calanus finmarchicus* and *Calanus* spp.). Where such cases existed, the higher order classification accounted for samples which could not be identified to species level. Gelatinous zooplankton and fish larvae/eggs were excluded from this component of the analysis due to lack of data, and poor taxonomic resolution, respectively. Therefore, only six lifeforms were considered for this component.

Finally, a matrix of per-taxa Kendall statistics was generated using the same combination of datasets to represent each assessment unit or fixed-point station. Due to differences in which taxa were observed and reported among datasets, only taxa with observations recorded in at least 80 % of assessment units and fixed-point stations used in the lifeforms analysis were retained. The remaining missing values were replaced with the mean Kendall statistic for each taxon before the columns were normalised. Loading vectors for taxa were generated in the same manner as for lifeforms. Finally, the top five taxon loading vectors by magnitude were projected onto the ordination for each lifeform.

3. Results

3.1. Lifeform abundance trends

Long-term trends (e.g. 1960 to 2019 for CPR; Fig. 3) indicate most plankton lifeforms, including diatoms, dinoflagellates, holoplankton, large copepods, and small copepods, have declined in abundance throughout beyond-shelf regions of the North-East Atlantic from 1960 to 2019. Considering all assessment units equally, Sen's slope estimates of the median rate of decrease in abundance per decade were 5 % for dinoflagellates, 7 % for holoplankton, 9 % for large copepods, and 8 % for small copepods. Diatom and fish larvae/egg abundance increased 0.1 % and 3 % per decade, respectively. Conversely, meroplankton demonstrated a very different pattern of increasing abundance or no change across most assessment units, with a median increase of 12 % per decade. Transitions from negative to positive abundance trends across adjacent assessment units generally occurred as gradients, such as for diatoms and small copepods. Patterns apparent from the widely distributed CPR data were largely reflected by the fixed-point stations from adjacent coastal areas, except for dinoflagellates and, in some cases, diatoms, which demonstrate increasing trends in coastal waters around Scotland and Northern Europe, and decreasing trends offshore.

Spatial patterns in the direction of change for both small and large copepods closely matched those of diatoms, with coastal areas of the English Channel and the North Sea often exhibiting abundance trends opposite to those from more offshore Atlantic assessment units. Due to the low availability of monitoring data, it was only possible to calculate trends in gelatinous zooplankton for three COMP4 assessment units and three fixed-point
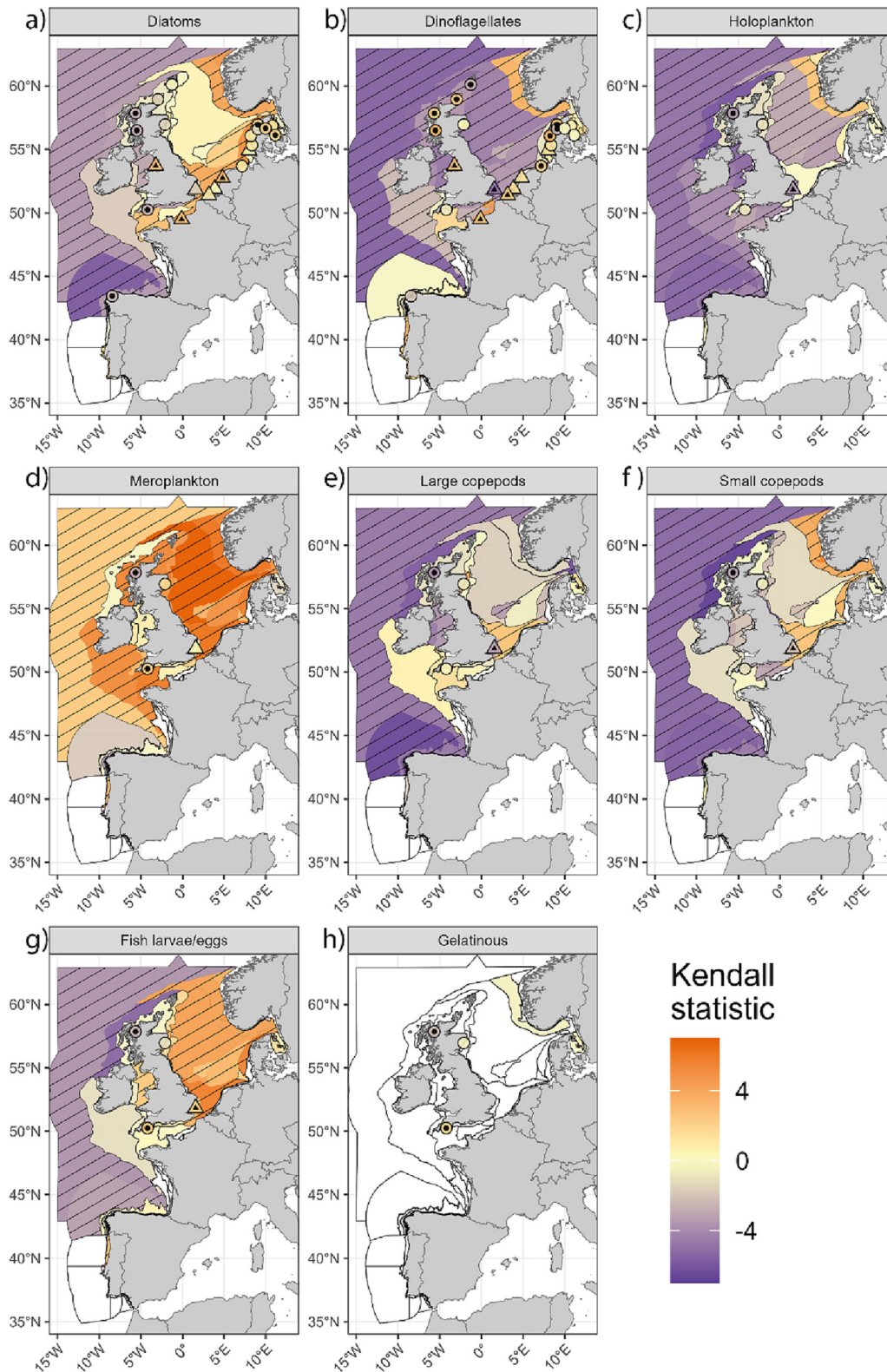
Fig. 3. Kendall statistics for eight plankton lifeforms displayed over COMP4 assessment units and fixed-point stations. River plumes are represented as triangles. Assessment units are coloured by the results of the Kendall trend test, indicating the magnitude of long-term increase (> 0) or decrease (< 0) in abundance over the duration of the time-series (1960–2019 for CPR and a shorter period for fixed-point stations; see Table S 1). Hatched assessment units, fixed-point stations, and river plumes with an internal black symbol indicate statistically significant change ($p \leq 0.05$). White areas indicate insufficient data to evaluate a trend.

stations. For fixed-point stations that collect data on this lifeform, one station in western Scotland indicated a declining trend (Loch Ewe) while another station in the English Channel indicated an increasing trend (L4). All other areas showed no trend.

The Kendall trend test analysis on the truncated time-series (i.e. 2000 to 2019; Fig. S 4) revealed similar spatial patterns in trend direction when compared to the full time-series (Fig. 3). Due to the variation in the lengths of time-series analysed in this study, we encourage readers to

refer to Fig. S 4 to aid interpretation of more recent trends in plankton lifeform abundance relative to the longer-term trends displayed in Fig. 3. Trend direction was mostly maintained with the shortened time-series, although there were fewer statistically significant trends, likely due to the reduced statistical power associated with smaller sample size (Yue et al., 2002). The difference in trend direction for dinoflagellates between COMP4 areas and fixed-point stations in Scotland and Northern Europe was also still apparent with the truncated time-series.

3.2. Cluster analysis of lifeform abundance trends

The silhouette plot (Fig. S 1(a)) indicated that the optimal number of clusters was two, resulting in an average silhouette width of 0.33. The point of inflexion on the WSS plot (Fig. S 1(b)) also indicated two or three clusters as optimal. There was a clear spatial separation of the two clusters, primarily delineating the North-East Atlantic (cluster: NEA) from the Greater North Sea (cluster: GNS) (Fig. 4). One COMP4 assessment unit on the east coast of England (East Coast (permanently mixed) 2) one off the coast of Portugal (Intermediate Waters AI (D5)), and one fixed-point station (Loch Ewe) diverged from this general spatial pattern, while the English Channel stood out as a likely area of transition between

clusters. The outer Celtic Seas (Atlantic Seasonally Stratified) and Bay of Biscay shelf also appeared as a transition between GNS (including the English Channel) and NEA waters. Inconsistencies in the clustering may have been caused by differences in sampling period, or possibly through contaminating the east-west gradient with spatially interpolated data from the adjacent region.

3.3. Exploring variability within and among clusters

When the distributions of Kendall statistics for each lifeform were compared between the two clusters it is apparent that the division of assessment units was driven by a difference in the strength and direction of abundance trends between the NEA and GNS clusters (Fig. 5).

Shapiro-Wilk tests showed that distributions were not significantly different from normal, with the one exception being meroplankton. Goldfeld–Quandt tests also showed no evidence of heteroscedasticity. The results of the ANOVAs comparing the distribution of Kendall statistics for the two clusters indicated significant differences for all other lifeforms examined (Fig. 6).

One sample t-tests determine whether a Kendall statistic distribution significantly differs from 0. The results of one-sample tests indicate that
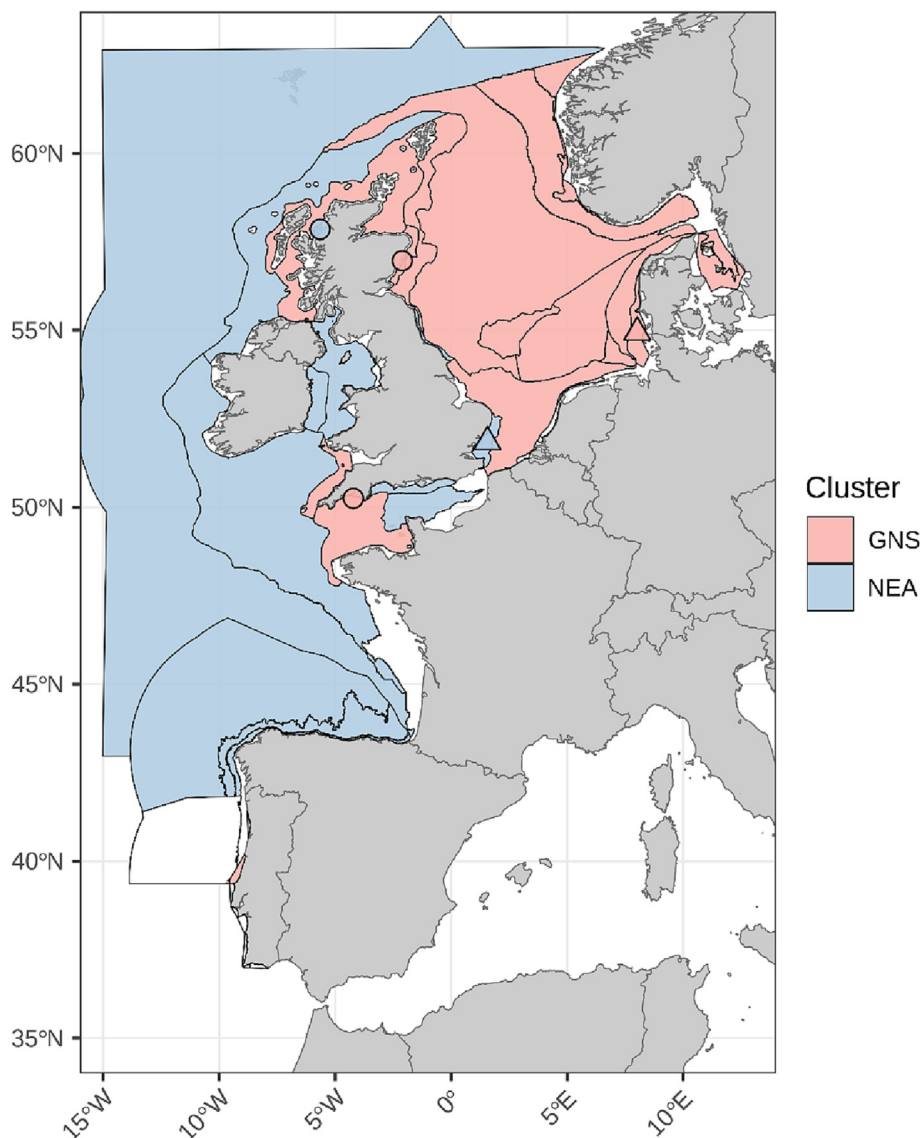

Fig. 4. COMP4 assessment units and fixed-point stations are coloured according to the two clusters (NEA: North-East Atlantic, GNS: Greater North Sea). Triangle symbols are overlaid on top of COMP4 polygons representing river plumes and round symbols indicate locations of fixed-point time-series used in the cluster analysis.
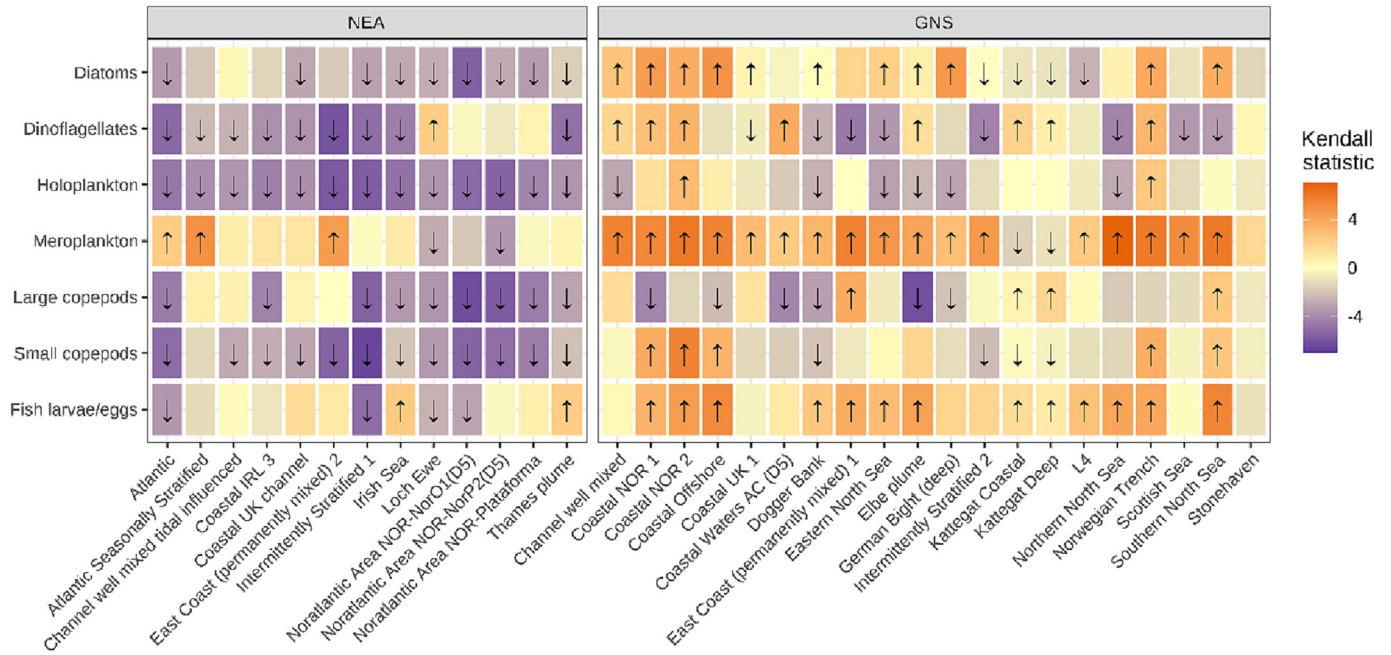
Fig. 5. Heat maps displaying the distribution of Kendall statistics for the 30 COMP4 assessment units and 3 fixed-point stations for each lifeform, categorised according to cluster. Arrow symbols indicate whether a lifeform abundance time-series was significantly ($p \leq 0.05$) increasing (↑) or decreasing (↓).
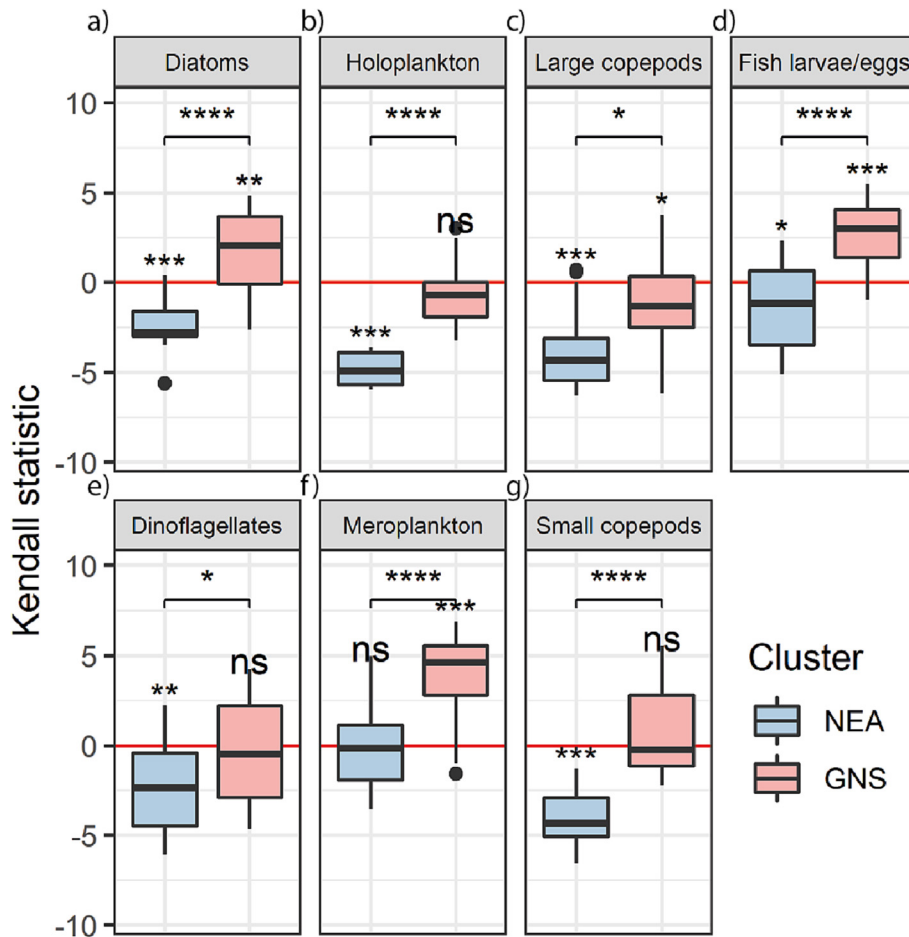

Fig. 6. Boxplots displaying the distribution of Kendall statistics for the 30 COMP4 assessment units and 3 fixed-point stations for each lifeform, categorised according to cluster. The red line indicates the point where abundance is neither increasing nor decreasing. The central dark line in each boxplot indicates the median value, while lower and upper hinges indicate 25th and 75th percentiles, respectively. The significance level of a one-sample *t*-test (difference from zero change) is indicated above each boxplot. The significance level of *t*-tests for each pairwise comparison of clusters is indicated above. Significance level is displayed as follows; ns: $p > 0.05$, *: $p \leq 0.05$, **: $p \leq 0.01$, ***: $p \leq 0.001$, ****: $p \leq 0.0001$.

diatoms and fish larvae/eggs had opposing abundance trends between the two clusters (they increased in GNS, whereas a clear decreasing trend is evident in NEA). Large copepods exhibited decreasing abundance trends across both clusters, while dinoflagellates, small copepods, and holoplankton only decreased in NEA. Copepod taxa were largely responsible for driving changes in holoplankton. Finally, meroplankton increased in GNS, but not in NEA.

For the NMDS ordination (stress = 0.0907; Fig. 7), gelatinous zooplankton and fish larvae/eggs were not analysed due to poor data availability and taxonomic resolution, respectively. The NMDS indicates a much broader separation for assessment units in the NEA, while the GNS cluster was bunched more tightly, indicating more similar trends in the GNS versus the NEA. Two points representing assessment units in the NEA cluster fell outside the ellipse (Atlantic, Intermittently Stratified 1). Both showed strong decreasing trends across the same six lifeforms (Fig. 5), possibly contributing to this separation.

The results of the ANOVA were supported by the lifeform loading vectors, which were aligned along the axis separating the two clusters and oriented in the direction of the GNS cluster (Fig. 7). This orientation indicated a trend of increasing Kendall statistics along a transition from the NEA to the GNS. The difference in abundance trends between clusters was most prevalent for diatoms, small copepods and holoplankton, since these loading vectors demonstrated greater alignment with the axis separating clusters.

Loading vectors for taxa were all lesser magnitude than their respective lifeform vectors, indicating stronger abundance trends in lifeforms relative to taxa. Taxa loading vectors aligned closely with the lifeform loading vector for dinoflagellates and diatoms, indicating a high degree of cohesion in trends among taxa comprising phytoplankton lifeforms. For dinoflagellates, taxa in the thecate genus *Ceratium* (renamed Tripos, Gómez, 2013) likely drove the overall pattern in trends. For zooplankton lifeforms there was less cohesion among trends within lifeforms, as the spread of vectors was typically much wider than for diatoms and dinoflagellates.

Across all six lifeforms, none of the top five strongest loading vectors were oriented in the direction of the North-East Atlantic cluster, indicating that any abundance trends opposing this broad spatial pattern were likely weak. The only exception to this was *Calanus finmarchicus*, which had a loading vector oriented opposite to that for the large copepod lifeform.

4. Discussion

Our study represents the most comprehensive time-series compilation achieved for the North-East Atlantic to-date, charting the regionality of long-term change in key plankton lifeforms, from diatoms up to fish larvae. Our comparison of lifeform trends allows integration of diverse data sets, such as those from the CPR and water-bottle samples, which are difficult to combine directly. This large-scale, long-term integrative approach has identified widespread and serious declines in most of the assessed lifeforms over much of the North-East Atlantic, contrasting with less change or even increases across the North Sea (Fig. 6). This contrast is unexpected and counter-intuitive, because it is the North Sea that is the exemplar of a suite of major and well-documented pressure changes over the past 50 years. These include very rapid rates of warming, a regime shift at the end of the 1980s, major reduction in nutrient inputs from rivers and very large changes in fishing activity. Here, we review a series of candidate explanations for the differential changes and examine consequences for marine ecosystems and their services.

4.1. Changes at the species level

A key finding of this study was the spatial coherence in abundance trends for planktonic lifeforms between adjacent COMP4 assessment units (Fig. 4). This finding supports (Bedford et al., 2020b), who found high spatial consistency in the way that diatom and dinoflagellate lifeforms responded to increasing sea surface temperatures. Similar coherence was
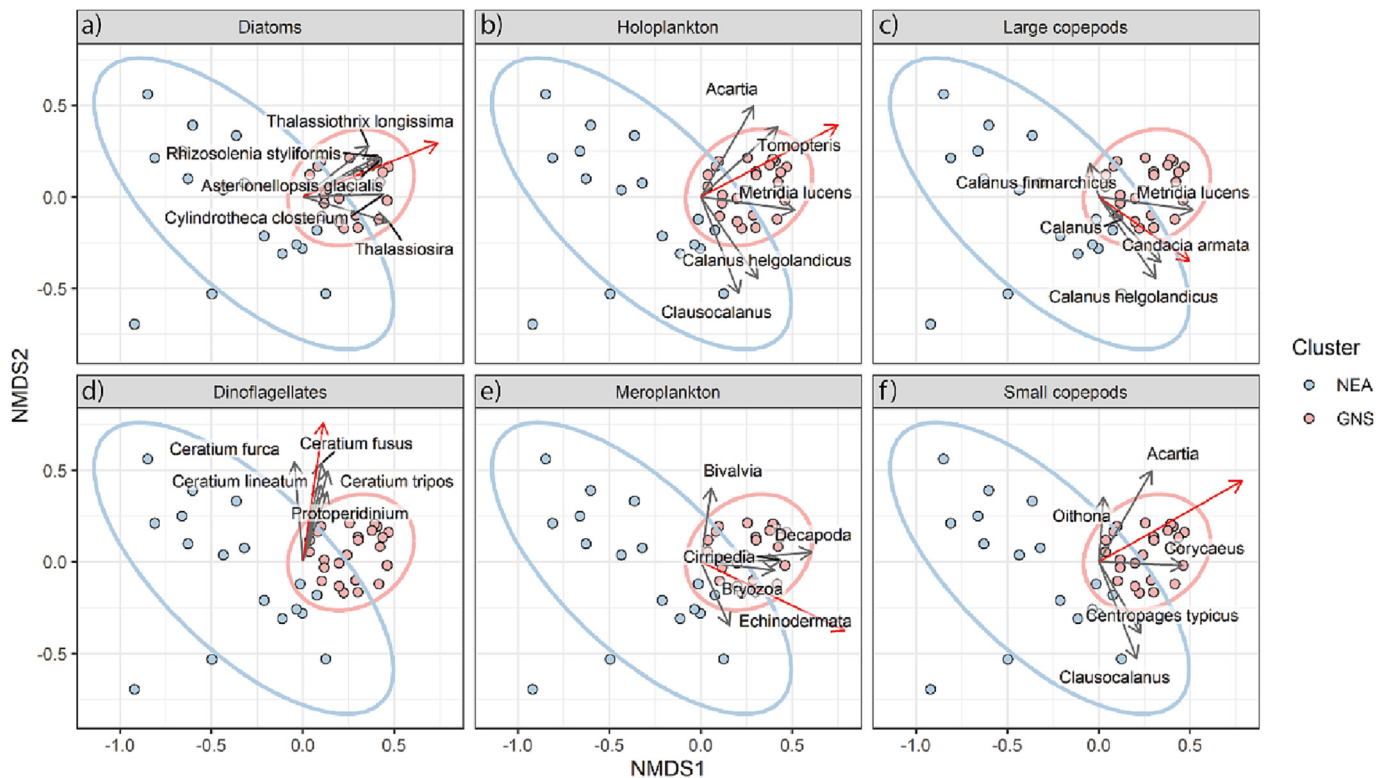

Fig. 7. Nonmetric multidimensional scaling (NMDS) ordination for the 30 COMP4 assessment units and 3 fixed-point stations for each lifeform (stress = 0.0907). Points are coloured according to cluster membership and ellipses represent 95 % confidence intervals for each cluster. Overlaid vectors represent the direction and magnitude of separation in taxon and lifeform abundance trends. Lifeform loading vectors in each subplot are indicated in red, while the five taxon loading vectors with the greatest magnitude for each lifeform are shown in grey.

found for phytoplankton, with trends in the individual taxa comprising the diatom and dinoflagellate lifeforms (Fig. 7); suggesting a common response to drivers of change (Bedford et al., 2020a).The distribution of trends in the abundance of dinoflagellates differed on the scale of the COMP4 areas from those exhibited by other lifeforms. Dinoflagellates showed decreasing trends across most offshore areas and increasing trends at coastal fixed-point stations and river plumes. The fact that this pattern was still present when time-series were truncated to the most recent 20-year period suggests that this discrepancy may be due to the undersampling of athecate dinoflagellates, such as *Gyrodinium,* by the CPR (CPR Survey Team, 2004), whereas these organisms are better preserved with bucket, bottle, or hose sampling methods and Lugol's iodine preservative routinely used for inshore samples. By contrast, zooplankton lifeforms exhibited a greater degree of variation in abundance trends among taxa (Fig. 7), indicating that the taxa comprising phytoplankton lifeforms are more cohesive in their response to environmental drivers of change (Bedford et al., 2020a).

There were several other important observations for zooplankton at the taxon level. The ordination (Fig. 7) showed that taxon loading vectors for *C. helgolandicus* and *C. finmarchicus* had opposite orientations. This is likely due to *C. finmarchicus* being a cold-water species that is experiencing a range shift towards higher latitudes, while *C. helgolandicus* is tolerant of warmer temperatures and is expanding into the range where *C. finmarchicus* was previously dominant (Bonnet et al., 2005). The ordination also revealed echinoderms, decapods, and cirripedes were driving the increase in meroplankton, while bivalve larvae conversely experienced decreasing abundance. These findings are supported by Kirby et al. (2007) which concluded that increased temperature was driving an increase in reproductive output for decapods and echinoderms in the North Sea, and by Kirby et al. (2008), which concluded that increased decapod abundance was suppressing bivalves through an increase in predation pressure from decapod recruits.

4.2. Contrasting changes in North-East Atlantic and North Sea: potential explanations

Changes in biotic communities, such as those of plankton, typically result from internal ecological dynamics (Okubo, 1988), environmental change (Beaugrand, 2004), and population exchanges across spatial boundaries or along gradients (Chivers et al., 2017). Internal ecological dynamics include predator-prey (Reid et al., 2000) and disease-host interactions (Vezzulli et al., 2016). While these can result in changes at the species level not only within annual cycles, but also year-on-year, such dynamics alone would not be expected to cause large-scale, long-term trends at the level of lifeforms. It is assumed that such trends originate from persistent environmental change, although links through food webs might be complex and difficult to disentangle.

Numerous studies have used long-term CPR datasets from the Northeast Atlantic and fringing seas to correlate changes in plankton with climate and environmental changes. Beaugrand et al. (2002) related northwards shifts in copepod assemblages to increasing Northern Hemisphere Temperature (NHT). Alvarez-Fernandez et al. (2012) explained major changes in phytoplankton and zooplankton abundance and seasonality as associated with three ecological regime shifts in the North Sea, driven by changes in air temperature, wind speed and inflow of North Atlantic water. Hinder et al. (2012) ascribed a marked increase in the relative abundance of diatoms versus dinoflagellates to increasing sea surface temperatures combined with more windy conditions in summer. Similarly, our study revealed increasing diatom abundance within coastal areas where dinoflagellate abundance has decreased. Recently, Edwards et al. (2022) related long-term trends in diatom abundance to the Atlantic Multidecadal Oscillation (AMO) index and NHT anomalies.

Models provide another method for identifying causal links, albeit subject to correct formulation of these links within the model. Several studies have investigated energy flows through North Sea food webs with 'end-to-end' models (Heath and Lough, 2007; Thorpe et al., 2022), calculation schemes constrained by observations (Frederiksen et al., 2006;

Greenstreet et al., 1997; Heath, 2005a; Heath, 2005b), or ECOPATH software (Lynam and Mackinson, 2015). Most concluded that fish production depended on phytoplankton production, channelled through zooplankton in a 'bottom-up' fashion. Findings that planktivorous fish (Maar et al., 2014) or their young (Heath and Lough, 2007) consumed a substantial portion of zooplankton production might suggest that fisheries-related stock changes could reduce zooplankton abundance, as we observed in the North-East Atlantic; but Heath (2005a) concluded that the planktivore niche might be rapidly refilled by other species. Thorpe et al. (2022) found that simulated warming raised primary productivity; but also increased metabolic rates of omnivorous zooplankton and reduced their abundance.

In summary, these studies suggest that long-term trends showing forced changes in plankton might be ascribed with most confidence to: (1) direct effects of climate change on SST and stratification; (2) indirect effects of climate change by way of run-off and oceanic circulation; and (3) in some coastal areas by changes in inputs of anthropogenic N and P. Effects of changes in fisheries might be harder to identify, and natural inter-annual and semi-cyclical variability in plankton, as well as in climate features such as the NAO, can mask long-term trends and lead to false conclusions about causality. There is a need for wide-area analyses of multi-decadal and multi-source datasets, such as we have reported here.

In the following sections we examine in turn changes in the physical environment, nutrients, and fisheries as potential explanations for regional difference in lifeform abundance trends. Because the clustering of COMP4 assessment units in Fig. 4 resulted in a complex pattern in the MSFD 'Celtic Seas' sub-region (OSPAR Region III; i.e. the waters over the continental shelves to the west of the island of Britain), we focus here on the MSFD 'Greater North Sea' subregion (OSPAR Region II) within our GNS cluster and the oceanic main part (OSPAR Region V) of the NEA cluster.

4.3. Changes in the physical environment

The North Sea is a largely enclosed shelf sea, deepening towards the north (~120 m) and strongly influenced by tidal flows and river discharges in its shallow south. Despite a variety of hydrodynamic regimes (van Leeuwen et al., 2015), the water column is almost completely mixed during winter. The main exceptions lie off the west coasts of Sweden and Norway, where the Norwegian Trench (~700 m) extends towards the Skagerak and is overlain by a northward flowing reduced salinity coastal current.

Although the mean flushing time of the North Sea is approximately one year (Rodhe et al., 2006), the annual heating-cooling cycle is largely locally controlled. Huthnance et al. (2016) reported an upwards trend of observed SST in the North Sea, with models suggesting increased duration of summer stratification in offshore waters, which might explain why increasing lifeform abundance trajectories in the North Sea were mainly restricted to coastal areas. Salinity variability, however, did not appear related to climate trends, and changes in oceanic inflow correlated with changes in the North Atlantic Oscillation (NAO) rather than long-term trends. Temperature and/or stratification trends may be the main drivers of the plankton changes we have reported from the North Sea. Increased stratification, however, might be expected to induce a decrease in diatom abundance, the opposite of what we have found in the North Sea (Edwards et al., 2022).

To the west of the NW European shelf-break, the NEA cluster region includes oceanic waters of moderate depth that are shared between the major circulatory features of the Sub-Polar Gyre (SPG) and the Sub-Tropical Gyre (STG). They exhibit a permanent thermocline that is reached but not eroded by autumn and winter convective mixing responsible for creating the winter mixed layer, within which warming during spring and summer creates a seasonal thermocline. Burmeister et al. (2022) investigated the present state (1980–2019) of the Atlantic Ocean combining observations and output from high-resolution ocean models. Their area 02 (47 to 60° N) corresponds well with the oceanic portion of our NEA cluster, although not extending to waters west of Iberia: the dominant upper water mass was Eastern North Atlantic Central Water (EANCW), its exact properties depending on the proportion of ENACW entering area 02 from the south

versus the water mass entering from the west (Johnson et al., 2013). The defining feature of observational time-series was a cooling and freshening event after 2010, ascribed by Holliday et al. (2020) to unusual winter wind patterns driving major changes in ocean circulation. In contrast to these changes, however, models predict long-term warming and salinity increase into the future (Burmeister et al., 2022), continuing trends observed between 1975 and 2010 in the Rockall Trough (Jones and Holliday, 2020). The cooling event might relate to the plankton changes we have observed more as an indicator of changes in water mass than through a direct impact on metabolism.

4.4. Changes in nutrients

The North Sea is a nutrient sink (Rodhe et al., 2006), supplied from the north by oceanic exchange and in the south by anthropogenically enriched rivers. Lowest winter nutrient concentrations occur in the central part, where we typically observed a contrast in lifeform abundance trends in comparison to adjacent coastal areas. As the result of management measures, nutrient loads from river discharge into the North Sea have been reduced considerably since 1988 (Desmit et al., 2020). Reduction objectives have mostly been achieved for phosphate, but nitrate has been more difficult to mitigate (McQuatters-Gollop et al., 2007; Riemann et al., 2016). Nitrate loads have declined much more slowly, particularly for UK rivers entering the North Sea (Desmit et al., 2020), leading to phosphate limitation (Breton et al., 2022).

Edwards et al. (2022) concluded in southern areas warming has led to nutrient limitation from increased stratification, driving a decline in diatom abundance. In contrast, in more northern areas and the North Sea, which exhibit less nutrient limitation, warming has elevated metabolic rates leading to greater diatom biomass in the spring bloom. In the case of our study, there was some evidence of this latitudinal gradient in diatom abundance trends, however, it may have been partially obscured by the limited latitudinal resolution of the COMP4 assessment areas.

Surface warming and a reduction in nutrient inputs from rivers also contribute to declining primary production across the North Sea (Capuzzo et al., 2018). Primary production and eutrophication events have been reduced in the coastal zone, which may be associated with a shift from dinoflagellate to diatom dominance (Spilling et al., 2018; Xiao et al., 2018). Our results provide evidence for such a shift in dominance throughout coastal and shelf areas of the North Sea. The decline in the abundance of micro-

phytoplankton, including diatoms and dinoflagellates, has been associated with an increasing proportion of biomass from the pico- and nano-phytoplankton size fraction across our entire study region (Schmidt et al., 2020). A major contributor to this shift is the cyanobacteria *Synechococcus*, which flourishes under low-nutrient conditions during summer stratification (Schmidt et al., 2020). However, its small size and low nutrient content make it a poor primary producer to sustain shelf food webs. This shift in dominance, combined with the earlier occurrence of the spring bloom, has resulted in suboptimal feeding conditions for copepods during summer, and may contribute to the declines in copepod abundance documented here.

The NEA oceanic cluster in Fig. 4 spans a north-south gradient of silicate concentrations in the late-winter mixed layer (LWML), with highest values in Atlantic Water (AtW) to the north-west of Britain and Ireland (BI), and lowest values in Subtropical Water (StW) to the SW (Hátún et al., 2017). During the last 25 years there has been a marked decrease in AtW LWML silicate, described by Hátún et al. (2017) as the down-phase of a longer cycle involving changes not only in the depth of winter convection (which entrains nutrients from deeper water) but also in the balance between the Sub-Tropical Gyre (and StW) and the Sub-Polar Gyre (and AtW). Johnson et al. (2013) had earlier associated the weakening of the Sub-Polar Gyre (SPG) with decreased LWML nitrate and phosphate to the north-west of BI. Such decreases in nutrients, and especially in silicate, would be expected to result in lower spring bloom diatom abundance over the northern part of our NEA cluster, which may contribute to the downwards trend in annual mean diatom abundance we observed for that region. Although these changes may have been cyclical in the past (Hátún et al., 2017; Hátún et al., 2009), the down-phase may continue in future due to global warming and the long-term weakening of the SPG.

4.5. Changes in fisheries

Due to its proximity to major ports and human population centres, fishing pressure in the North Sea has historically been much greater than in the North-East Atlantic. Most relevant to our focus on plankton is the harvesting of wholly or partially planktivorous "forage fish", particularly herring, Norway pout, sprat, and sand eel. Until 1970 herring made up most landings. Since 1980 landings have been dominated by sand eel (Engelhard et al., 2014). Greatest biomass was extracted between 1970 and 2000; subsequent years have decreasing landings, although the exact temporal pattern varies by North Sea region (Fig. 8).
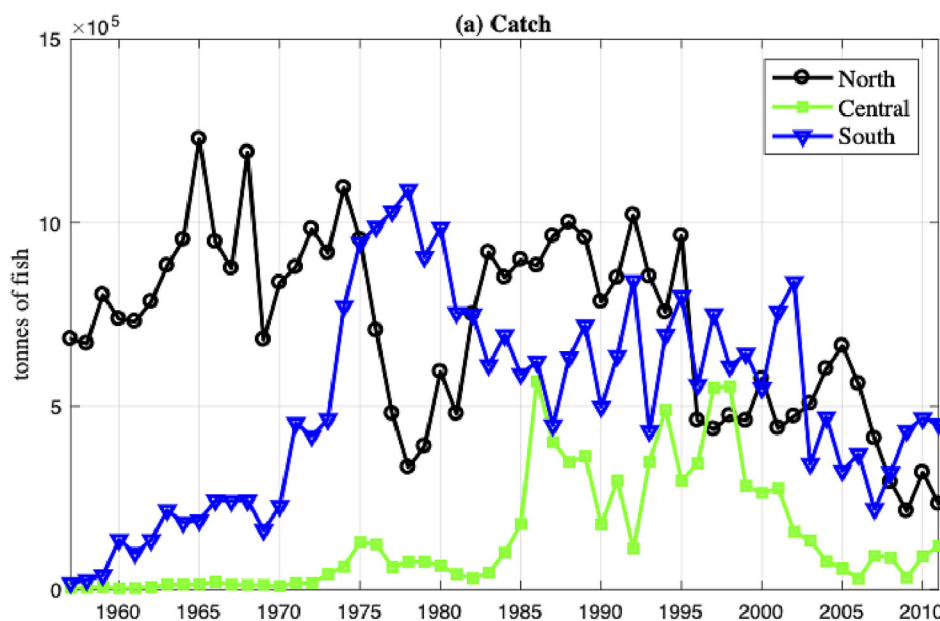

Fig. 8. Catches of forage fish in three North Sea regions. Unpublished manuscript, Tett, Englehard & Painting (2019), based on Engelhard et al. (2014) and ICES data: 'ICES Historical Nominal Catches 1950-2010' from www.ices.dk/marine-data/Documents/CatchStats/HistoricalLandings1950-2010.zip.

Increasing abundance of larval fish and eggs we observed in the North Sea likely relate to recovery of historically overfished populations (Auber et al., 2022). Alternatively, this increase could be limited to small bodied species experiencing reduced mortality due to the removal of their predators (Daan et al., 2005). However, since most zooplankton datasets do not identify larval fish to species level, it was not possible to conclude whether the increasing abundance trends in the North Sea extended to commercially exploited species.

In the NEA oceanic and outer shelf waters, Hátún et al. (2009) related the increase (1995–2005) in the fishery of the pelagic planktivore blue whiting (*Micromesistius poutassou*) to richer zooplankton environments, as sampled by the CPR (Hátún et al., 2009). However, using different time-series, a longer time-period, a larger area of study, and different numerical approaches, our analysis detected decreasing zooplankton abundance in the NEA cluster; this points to a general problem both in making temporal comparisons and in generalising/extrapolating conclusions.

4.6. Differences between GNS and NEA drivers and plankton trends

Studies often fail to agree on trends and causes of trends in the environment of the North-East Atlantic and adjoining continental shelf seas, partly because of the different areas and periods in time across studies, and because of the complexity and medium-term variability of this environment. Such high variability overwhelms, for example, the long-term trends of increasing temperature in the upper waters of the sea and the large-scale circulatory changes that are expected to follow warming of the Arctic Ocean (Jungclaus et al., 2005). Nevertheless, there would seem to be at least moderate confidence in the following potential environmental differences between North Sea and the North-East Atlantic oceanic waters:

1. The long-term warming trend is more evident in the North Sea than in the North-East Atlantic Ocean (Beaugrand, 2009).
2. Loading of the southern North Sea with anthropogenic P and (to a lesser extent) N has been decreasing since 1988 (Breton et al., 2022), without changing Si inputs, whereas reductions in winter mixing in the North-East Atlantic Ocean has decreased Si along with N and P (Edwards et al., 2022).
3. Pelagic fisheries have significantly impacted North Sea stocks of planktivorous fish since the 1950s; this impact has reduced since about 2000. In contrast, oceanic fisheries did not start until the mid-1970s and peaked more recently than in the North Sea (Engelhard et al., 2014).

The strongest evidence and most parsimonious logic support classical bottom-up food web effects. Thus, large diatoms and dinoflagellates have declined strongly in the oceanic area, in turn related to declines in the dependent food chain, including copepods and fish larvae. By contrasts this decline was not so marked in the North Sea, with more stable or increasing links in this simplified food chain. Nutrient changes might also favour diatoms in the North Sea and constrain them in the North-East Atlantic. However, the warming trend (and associated extended seasonal stratification) may further decrease diatom and large copepod abundances in the North Sea relative to the North-East Atlantic.

Finally, while we aimed to conduct a comprehensive assessment of the plankton community, there were of course important components, or lifeforms, which were poorly represented or absent from our datasets, including gelatinous zooplankton and small size taxa, pico- to micro- plankton. Until recently gelatinous zooplankton were largely considered a trophic dead end (Richardson et al., 2009), however, there is growing evidence that this group is an important vector for the transfer of energy from pico-plankton to higher trophic levels, including fish (Aubert et al., 2022; Jaspers et al., 2015; Lamb et al., 2017). Similarly, pico- and nano-plankton, along with micro-zooplankton, are difficult size categories to measure routinely and are thus absent from most datasets. However, they also make up a significant proportion of plankton biomass, diversity, and trophic roles (De Vargas et al., 2015) relevant to marine food webs and

carbon export (Leblanc et al., 2018). Adoption of improved sampling methods and new technology (Aubert et al., 2018) will be necessary to improve holistic understanding of the plankton community.

5. Conclusions

Even without fully understanding the pressures acting on plankton lifeforms, it is possible to draw some conclusions about the consequences of sustained declines in their abundance. Declining abundance of important planktonic lifeforms is a cause for concern for the future of productive herbivory-driven pelagic food webs supported by diatoms and dinoflagellates (Lynam et al., 2017) and may indicate a shift towards a less productive food web state, with a greater proportion of production fuelled by microorganisms (Schmidt et al., 2020; Trombetta et al., 2020). This could lead to a restructuring or regime shift, impacting fisheries and biogeochemical cycling (Cheung et al., 2011). Conversely, increasing abundances of fish larvae and meroplankton throughout the North Sea could indicate an improved ecological state for a highly disturbed and historically overexploited marine system. Increasing the abundance of both lifeforms could benefit fisheries yields, but only if recruitment increases with larval abundance and the increasing taxa are exploitable.

CRediT authorship contribution statement

Matthew M. Holland: Conceptualization, Methodology, Software, Formal analysis, Writing – original draft, Visualization. **Arnaud Louchart:** Conceptualization, Writing – review & editing. **Luis Felipe Artigas:** Conceptualization, Writing – review & editing. **Clare Ostle:** Methodology, Writing – review & editing. **Angus Atkinson:** Writing – review & editing. **Isabelle Rombouts:** Writing – review & editing. **Carolyn A. Graves:** Writing – review & editing. **Michelle Devlin:** Writing – review & editing. **Birgit Heyden:** Writing – review & editing. **Margarita Machairopoulou:** Writing – review & editing. **Eileen Bresnan:** Writing – review & editing. **Jos Schilder:** Writing – review & editing. **Hans H. Jakobsen:** Writing – review & editing. **Hannah Llody-Hartley:** Writing – review & editing. **Paul Tett:** Methodology, Writing – original draft, Writing – review & editing. **Mike Best:** Writing – review & editing. **Eric Goberville:** Methodology, Writing – review & editing. **Abigail McQuatters-Gollop:** Writing – review & editing, Supervision, Funding acquisition.

Data availability

As described in the article, all data have been made publicly available from https://www.dassh.ac.uk/lifeforms/.

Declaration of competing interest

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

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2023.165505.

References

Alvarez-Fernandez, S., Lindeboom, H., Meesters, E., 2012. Temporal changes in plankton of the North Sea: community shifts and environmental drivers. Mar. Ecol. Prog. Ser. 462, 21–38.

Auber, A., Waldock, C., Maire, A., Goberville, E., Albouy, C., Algar, A.C., et al., 2022. A functional vulnerability framework for biodiversity conservation. Nat. Commun. 13, 1–13.

Aubert, A., Rombouts, I., Artigas, L.F., Budria, A., Ostle, C., Padegimas, B., et al., 2017. Combining methods and data for a more holistic assessment of the plankton community. EcApRHA deliverable WP 1.

Aubert, A., Antajan, E., Lynam, C., Pitois, S., Pliru, A., Vaz, S., et al., 2018. No more reason for ignoring gelatinous zooplankton in ecosystem assessment and marine management: concrete cost-effective methodology during routine fishery trawl surveys. Mar. Policy 89, 100–108.

Aubert, A., Beauchard, O., De Blok, R., Artigas, L.F., Sabbe, K., Vyverman, W., et al., 2022. From bacteria to zooplankton: an integrative approach revealing regional spatial patterns during the spring phytoplankton bloom in the Southern Bight of the North Sea. Frontiers in Marine. Science 9.

Beaugrand, G., 2004. The North Sea regime shift: evidence, causes, mechanisms and consequences. Prog. Oceanogr. 60, 245–262.

Beaugrand, G., 2009. Decadal changes in climate and ecosystems in the North Atlantic Ocean and adjacent seas. Deep-Sea Res. II Top. Stud. Oceanogr. 56, 656–673.

Beaugrand, G., Reid, P.C., Ibanez, F., Lindley, J.A., Edwards, M., 2002. Reorganization of North Atlantic marine copepod biodiversity and climate. Science 296, 1692–1694.

Beaugrand, G., Brander, K.M., Alistair Lindley, J., Souissi, S., Reid, P.C., 2003. Plankton effect on cod recruitment in the North Sea. Nature 426, 661–664.

Beaugrand, G., Edwards, M., Legendre, L., 2010. Marine biodiversity, ecosystem functioning, and carbon cycles. Proc. Natl. Acad. Sci. 107, 10120–10124.

Bedford, J., Johns, D.G., McQuatters-Gollop, A., 2020a. Implications of taxon-level variation in climate change response for interpreting plankton lifeform biodiversity indicators. ICES J. Mar. Sci. 77, 3006–3015.

Bedford, J., Ostle, C., Johns, D.G., Atkinson, A., Best, M., Bresnan, E., et al., 2020b. Lifeform indicators reveal large-scale shifts in plankton across the North-West European shelf. Glob. Chang. Biol. 26, 3482–3497.

Behrenfeld, M.J., O'Malley, R.T., Siegel, D.A., McClain, C.R., Sarmiento, J.L., Feldman, G.C., et al., 2006. Climate-driven trends in contemporary ocean productivity. Nature 444, 752–755.

Boero, F., Bouillon, J., Gravili, C., Miglietta, M.P., Parsons, T., Piraino, S., 2008. Gelatinous plankton: irregularities rule the world (sometimes). Mar. Ecol. Prog. Ser. 356, 299–310.

Bonnet, D., Richardson, A., Harris, R., Hirst, A., Beaugrand, G., Edwards, M., et al., 2005. An overview of Calanus helgolandicus ecology in European waters. Prog. Oceanogr. 65, 1–53.

Brander, K., Dickson, R., Edwards, M., 2003. Use of continuous plankton recorder information in support of marine management: applications in fisheries, environmental protection, and in the study of ecosystem response to environmental change. Prog. Oceanogr. 58, 175–191.

Breton, E., Goberville, E., Sautour, B., Ouadi, A., Skouroliakou, D.-I., Seuront, L., et al., 2022. Multiple phytoplankton community responses to environmental change in a temperate coastal system: a trait-based approach. Front. Mar. Sci. 9.

Burmeister, K., Johnson, C., Jones, S., Inall, M., Cunningham, S., Biastoch, A., et al., 2022. Ecosystem relevant variation & oceanographic trends from present day to 2070. iAtlantic (D1.2: 95, internal EDC review).

Capuzzo, E., Lynam, C.P., Barry, J., Stephens, D., Forster, R.M., Greenwood, N., et al., 2018. A decline in primary production in the North Sea over 25 years, associated with reductions in zooplankton abundance and fish stock recruitment. Glob. Chang. Biol. 24, e352–e364.

Cheung, W.W., Dunne, J., Sarmiento, J.L., Pauly, D., 2011. Integrating ecophysiology and plankton dynamics into projected maximum fisheries catch potential under climate change in the Northeast Atlantic. ICES J. Mar. Sci. 68, 1008–1018.

Chivers, W.J., Walne, A.W., Hays, G.C., 2017. Mismatch between marine plankton range movements and the velocity of climate change. Nat. Commun. 8, 1–8.

CPR Survey Team, 2004. Continuous plankton records: plankton atlas of the North Atlantic Ocean (1958–1999). II. Biogeographical charts. Mar. Ecol. Prog. Ser. 11–75.

Daan, N., Gislason, H., Pope J, G., Rice J, C., 2005. Changes in the North Sea fish community: evidence of indirect effects of fishing? ICES J. Mar. Sci. 62, 177–188.

De Vargas, C., Audic, S., Henry, N., Decelle, J., Mahé, F., Logares, R., et al., 2015. Eukaryotic plankton diversity in the sunlit ocean. Science 348, 1261605.

Desmit, X., Nohe, A., Borges, A.V., Prins, T., De Cauwer, K., Lagring, R., et al., 2020. Changes in chlorophyll concentration and phenology in the North Sea in relation to de-eutrophication and sea surface warming. Limnol. Oceanogr. 65, 828–847.

Durkin, C.A., Van Mooy, B.A., Dyhrman, S.T., Buesseler, K.O., 2016. Sinking phytoplankton associated with carbon flux in the Atlantic Ocean. Limnol. Oceanogr. 61, 1172–1187.

Edwards, M., Beaugrand, G., Reid, P.C., Rowden, A.A., Jones, M.B., 2002. Ocean climate anomalies and the ecology of the North Sea. Mar. Ecol. Prog. Ser. 239, 1–10.

Edwards, M., Beaugrand, G., Kléparski, L., Hélaouët, P., Reid, P.C., 2022. Climate variability and multi-decadal diatom abundance in the Northeast Atlantic. Commun. Earth Environ. 3, 1–8.

Emeis, K.-C., van Beusekom, J., Callies, U., Ebinghaus, R., Kannen, A., Kraus, G., et al., 2015. The North Sea—a shelf sea in the anthropocene. J. Mar. Syst. 141, 18–33.

Engelhard, G.H., Peck, M.A., Rindorf, A., Smout S, C., van Deurs, M., Raab, K., et al., 2014. Forage fish, their fisheries, and their predators: who drives whom? ICES J. Mar. Sci. 71, 90–104.

Enserink, L., Blauw, A., van der Zande, D., Markager, S., 2019. Summary Report of the EU Project 'Joint Monitoring Programme of the Eutrophication of the North Sea with Satellite Data' (Ref: DG ENV/MSFD Second Cycle/2016). p. 21.

Frederiksen, M., Edwards, M., Richardson, A.J., Halliday, N.C., Wanless, S., 2006. From plankton to top predators: bottom-up control of a marine food web across four trophic levels. J. Anim. Ecol. 75, 1259–1268.

Gómez, F., 2013. Reinstatement of the dinoflagellate genus Tripos to replace Neoceratium, marine species of Ceratium (Dinophyceae, Alveolata). Cicimar Oceánides 28, 1–22.

Greenstreet, S.P., Bryant, A.D., Broekhuizen, N., Hall, S.J., Heath, M.R., 1997. Seasonal variation in the consumption of food by fish in the North Sea and implications for food web dynamics. ICES J. Mar. Sci. 54, 243–266.

Guidi, L., Chaffron, S., Bittner, L., Eveillard, D., Larhlimi, A., Roux, S., et al., 2016. Plankton networks driving carbon export in the oligotrophic ocean. Nature 532, 465–470.

Hátún, H., Payne, M., Beaugrand, G., Reid, P., Sandø, A., Drange, H., et al., 2009. Large biogeographical shifts in the north-eastern Atlantic Ocean: from the subpolar gyre, via plankton, to blue whiting and pilot whales. Prog. Oceanogr. 80, 149–162.

Hátún, H., Azetsu-Scott, K., Somavilla, R., Rey, F., Johnson, C., Mathis, M., et al., 2017. The subpolar gyre regulates silicate concentrations in the North Atlantic. Sci. Rep. 7, 1–9.

Hays, G.C., Richardson, A.J., Robinson, C., 2005. Climate change and marine plankton. Trends Ecol. Evol. 20, 337–344.

Heath, M.R., 2005a. Changes in the structure and function of the North Sea fish foodweb, 1973–2000, and the impacts of fishing and climate. ICES J. Mar. Sci. 62, 847–868.

Heath, M.R., 2005b. Regional variability in the trophic requirements of shelf sea fisheries in the Northeast Atlantic, 1973–2000. ICES J. Mar. Sci. 62, 1233–1244.

Heath, M., Lough, R., 2007. A synthesis of large-scale patterns in the planktonic prey of larval and juvenile cod (Gadus morhua). Fish. Oceanogr. 16, 169–185.

Hinder, S.L., Manning, J.E., Gravenor, M.B., Edwards, M., Walne, A.W., Burkill, P.H., et al., 2012. Long-term changes in abundance and distribution of microzooplankton in the NE Atlantic and North Sea. J. Plankton Res. 34, 83–91.

Holliday, N.P., Bersch, M., Berx, B., Chafik, L., Cunningham, S., Florindo-López, C., et al., 2020. Ocean circulation causes the largest freshening event for 120 years in eastern subpolar North Atlantic. Nat. Commun. 11, 1–15.

Huthnance, J., Weisse, R., Wahl, T., Thomas, H., Pietrzak, J., Souza, A.J., et al., 2016. Recent change—North Sea. North Sea Region Climate Change Assessment. Springer, pp. 85–136.

Ives, A.R., 2015. For testing the significance of regression coefficients, go ahead and log-transform count data. Methods Ecol. Evol. 6, 828–835.

Jaspers, C., Acuña, J.L., Brodeur, R.D., 2015. Interactions of Gelatinous Zooplankton within Marine Food Webs. 37. Oxford University Press, pp. 985–988.

Johnson, C., Inall, M., Häkkinen, S., 2013. Declining nutrient concentrations in the northeast Atlantic as a result of a weakening Subpolar Gyre. Deep-Sea Res. I Oceanogr. Res. Pap. 82, 95–107.

Jones, S., Holliday, N.P., 2020. 4.13 Rockall Trough. In: Gonzalez-Pola, C., KMH, Larsen, Fratantoni, P., Beszczynska-Möller, A. (Eds.), ICES Report on Ocean Climate 2019. ICES Cooperative Research Reports (CRR).

Jungclaus, J.H., Haak, H., Latif, M., Mikolajewicz, U., 2005. Arctic–North Atlantic interactions and multidecadal variability of the meridional overturning circulation. J. Clim. 18, 4013–4031.

Kassambara, A., Mundt, F., 2020. Extrac and Visualize the Results of Multivariate Data Analyses. R Package Version 1.0. 3. R Package Version.

Kirby, R.R., Beaugrand, G., Lindley, J.A., Richardson, A.J., Edwards, M., Reid, P.C., 2007. Climate effects and benthic–pelagic coupling in the North Sea. Mar. Ecol. Prog. Ser. 330, 31–38.

Kirby, R.R., Beaugrand, G., Lindley, J.A., 2008. Climate-induced effects on the meroplankton and the benthic-pelagic ecology of the North Sea. Limnol. Oceanogr. 53, 1805–1815.

Kvaavik, C., Óskarsson, G.J., Daníelsdóttir, A.K., Marteinsdóttir, G., 2019. Diet and feeding strategy of Northeast Atlantic mackerel (Scombrus scomber) in Icelandic waters. PLoS One 14, e0225552.

Lamb, P.D., Hunter, E., Pinnegar, J.K., Creer, S., Davies, R.G., Taylor, M.I., 2017. Jellyfish on the menu: mtDNA assay reveals scyphozoan predation in the Irish Sea. R. Soc. Open Sci. 4, 171421.

Leblanc, K., Queguiner, B., Diaz, F., Cornet, V., Michel-Rodriguez, M., Durrieu de Madron, X., et al., 2018. Nanoplanktonic diatoms are globally overlooked but play a role in spring blooms and carbon export. Nat. Commun. 9, 1–12.

van Leeuwen, S., Tett, P., Mills, D., van der Molen, J., 2015. Stratified and nonstratified areas in the N orth S ea: long-term variability and biological and policy implications. J. Geophys. Res. Oceans 120, 4670–4686.

Lynam, C.P., Mackinson, S., 2015. How will fisheries management measures contribute towards the attainment of Good Environmental Status for the North Sea ecosystem? Glob. Ecol. Conserv. 4, 160–175.

Lynam, C.P., Llope, M., Möllmann, C., Helaouët, P., Bayliss-Brown, G.A., Stenseth, N.C., 2017. Interaction between top-down and bottom-up control in marine food webs. Proc. Natl. Acad. Sci. 114, 1952–1957.

Maar, M., Rindorf, A., Møller, E.F., Christensen, A., Madsen, K.S., van Deurs, M., 2014. Zooplankton mortality in 3D ecosystem modelling considering variable spatial–temporal fish consumptions in the North Sea. Prog. Oceanogr. 124, 78–91.

Margalef, R., 1978. Life-forms of phytoplankton as survival alternatives in an unstable environment. Oceanol. Acta 1, 493–509.

McQuatters-Gollop, A., Raitsos, D.E., Edwards, M., Attrill, M.J., 2007. Spatial patterns of diatom and dinoflagellate seasonal cycles in the NE Atlantic Ocean. Mar. Ecol. Prog. Ser. 339, 301–306.

McQuatters-Gollop, A., Edwards, M., Helaouët, P., Johns, D.G., Owens, N.J., Raitsos, D.E., et al., 2015. The continuous plankton recorder survey: how can long-term phytoplankton datasets contribute to the assessment of good environmental status? Estuar. Coast. Shelf Sci. 162, 88–97.

McQuatters-Gollop, A., Atkinson, A., Aubert, A., Bedford, J., Best, M., Bresnan, E., et al., 2019. Plankton lifeforms as a biodiversity indicator for regional-scale assessment of pelagic habitats for policy. Ecol. Indic. 101, 913–925.

McQuatters-Gollop, A., Guérin, L., Arroyo, N.L., Aubert, A., Artigas, L.F., Bedford, J., et al., 2022. Assessing the state of marine biodiversity in the Northeast Atlantic. Ecol. Indic. 141, 109148.

Murgier, J., McLean, M., Maire, A., Mouillot, D., Loiseau, N., Munoz, F., et al., 2021. Rebound in functional distinctiveness following warming and reduced fishing in the North Sea. Proc. R. Soc. B 288, 20201600.

Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., et al., 2019. Vegan: Community Ecology Package. R package version 2.5-6. Community Ecology Package, Version.

Okubo, A., 1988. Biological-physical interactions in the sea: marine ecodynamics. Ecodynamics. Springer, pp. 102–112.

Olin, A.B., Banas, N.S., Johns, D.G., Heath, M.R., Wright, P.J., Nager, R.G., 2022. Spatiotemporal variation in the zooplankton prey of lesser sandeels: species and community trait patterns from the Continuous Plankton Recorder. ICES J. Mar. Sci. 79, 1649–1661.

Ostle, C., Paxman, K., Graves, C.A., Arnold, M., Artigas, L.F., Atkinson, A., et al., 2021. The plankton lifeform extraction tool: a digital tool to increase the discoverability and usability of plankton time-series data. Earth Syst. Sci. Data 13, 5617–5642.

Platt, T., Fuentes-Yaco, C., Frank, K.T., 2003. Spring algal bloom and larval fish survival. Nature 423, 398–399.

R Core Team, 2020. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Raven, J., Waite, A., 2004. The evolution of silicification in diatoms: inescapable sinking and sinking as escape? New Phytol. 162, 45–61.

Reid, P., Battle, E., Batten, S., Brander, K., 2000. Impacts of fisheries on plankton community structure. ICES J. Mar. Sci. 57, 495–502.

Richardson, A.J., Bakun, A., Hays, G.C., Gibbons, M.J., 2009. The jellyfish joyride: causes, consequences and management responses to a more gelatinous future. Trends Ecol. Evol. 24, 312–322.

Riemann, B., Carstensen, J., Dahl, K., Fossing, H., Hansen, J.W., Jakobsen, H.H., et al., 2016. Recovery of Danish coastal ecosystems after reductions in nutrient loading: a holistic ecosystem approach. Estuar. Coasts 39, 82–97.

Rodhe, J., Tett, P., Wulff, F., 2006. The Baltic and North Seas: A Regional Review of some Important Physical-Chemical-Biological Interaction Processes. 20, S.

Rombouts, I., Simon, N., Aubert, A., Cariou, T., Feunteun, E., Guérin, L., et al., 2019. Changes in marine phytoplankton diversity: assessment under the marine strategy framework directive. Ecol. Indic. 102, 265–277.

Ross, O.N., Sharples, J., 2007. Phytoplankton motility and the competition for nutrients in the thermocline. Mar. Ecol. Prog. Ser. 347, 21–38.

Sarker, S., Yadav, A.K., Akter, M., Hossain, M.S., Chowdhury, S.R., Kabir, M.A., et al., 2020. Rising temperature and marine plankton community dynamics: is warming bad? Ecol. Complex. 43, 100857.

Schmidt, K., Birchill, A.J., Atkinson, A., Brewin, R.J., Clark, J.R., Hickman, A.E., et al., 2020. Increasing picocyanobacteria success in shelf waters contributes to long-term food web degradation. Glob. Chang. Biol. 26, 5574–5587.

Serranito, B., Aubert, A., Stemmann, L., Rossi, N., Jamet, J.-L., 2016. Proposition of indicators of anthropogenic pressure in the Bay of Toulon (Mediterranean Sea) based on zooplankton time-series. Cont. Shelf Res. 121, 3–12.

Sherr, E.B., Sherr, B.F., 2007. Heterotrophic dinoflagellates: a significant component of microzooplankton biomass and major grazers of diatoms in the sea. Mar. Ecol. Prog. Ser. 352, 187–197.

Smayda, T.J., Reynolds, C.S., 2003. Strategies of marine dinoflagellate survival and some rules of assembly. J. Sea Res. 49, 95–106.

Spilling, K., Olli, K., Lehtoranta, J., Kremp, A., Tedesco, L., Tamelander, T., et al., 2018. Shifting diatom—dinoflagellate dominance during spring bloom in the Baltic Sea and its potential effects on biogeochemical cycling. Front. Mar. Sci. 5, 327.

Tett, P., Carreira, C., Mills, D.K., van Leeuwen, S., Foden, J., Bresnan, E., et al., 2008. Use of a phytoplankton community index to assess the health of coastal waters. ICES J. Mar. Sci. 65, 1475–1482.

Thorpe, R.B., Arroyo, N.L., Safi, G., Niquil, N., Heath, M., Pace, M.C., et al., 2022. The response of North Sea ecosystem functional groups to warming and changes in fishing. Front. Mar. Sci. 9.

Trombetta, T., Vidussi, F., Roques, C., Scotti, M., Mostajir, B., 2020. Marine microbial food web networks during phytoplankton bloom and non-bloom periods: warming favors smaller organism interactions and intensifies trophic cascade. Front. Microbiol. 11, 502336.

Turner, J.T., 2004. The importance of small planktonic copepods and their roles in pelagic marine food webs. Zool. Stud. 43, 255–266.

Vezzulli, L., Grande, C., Reid, P.C., Hélaouët, P., Edwards, M., Höfle, M.G., et al., 2016. Climate influence on Vibrio and associated human diseases during the past half-century in the coastal North Atlantic. Proc. Natl. Acad. Sci. 113, E5062–E5071.

Xiao, W., Liu, X., Irwin, A.J., Laws, E.A., Wang, L., Chen, B., et al., 2018. Warming and eutrophication combine to restructure diatoms and dinoflagellates. Water Res. 128, 206–216.

Yue, S., Pilon, P., Cavadias, G., 2002. Power of the Mann–Kendall and Spearman's rho tests for detecting monotonic trends in hydrological series. J. Hydrol. 259, 254–271.