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Lifeform indicators reveal large-scale shifts in plankton across the North-West European shelf

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Abstract

Increasing direct human pressures on the marine environment, coupled with climate-driven changes, is a concern to marine ecosystems globally. This requires the development and monitoring of ecosystem indicators for effective management and adaptation planning. Plankton lifeforms (broad functional groups) are sensitive indicators of marine environmental change and can provide a simplified view of plankton biodiversity, building an understanding of change in lower trophic levels. Here, we visualize regional-scale multi-decadal trends in six key plankton lifeforms as well as their correlative relationships with sea surface temperature (SST). For the first time, we collate trends across multiple disparate surveys, comparing the spatially and temporally extensive Continuous Plankton Recorder (CPR) survey (offshore) with multiple long-term fixed station-based time-series (inshore) from around the UK coastline. These analyses of plankton lifeforms showed profound long-term changes, which were coherent across large spatial scales. For example, 'diatom' and 'meroplankton' lifeforms showed strong alignment between surveys and coherent regional-scale trends, with the 1998–2017 decadal average abundance of meroplankton being 2.3 times that of 1958–1967 for CPR samples in the North Sea. This major, shelf-wide increase in meroplankton correlated with increasing SSTs, and contrasted with a general decrease in holoplankton (dominated by small copepods), indicating a changing balance of benthic and pelagic fauna. Likewise, inshore-offshore gradients in dinoflagellate trends, with contemporary increases inshore contrasting with multi-decadal decreases offshore (approx. 75% lower decadal mean abundance), urgently require the identification of causal mechanisms. Our lifeform approach allows the collation of many different data types and time-series across the NW European shelf, providing a crucial evidence base for informing ecosystem-based management, and the development of regional adaptation plans.

KEYWORDS
climate change, food webs, functional groups, indicators, pelagic, time-series

1 | INTRODUCTION

Plankton provide primary and secondary productivity that fuel marine food webs. Plankton communities therefore form a key part of marine natural capital, supporting globally important ecosystem services that include fish production and carbon sequestration (Beaugrand, Brander, Lindley, Souissi, & Reid, 2003; Canu et al., 2015). As such, the importance of plankton as ecosystem state indicators is increasingly being recognized by national and international marine policy mechanisms (Chiba et al., 2018; McQuatters-Gollop et al., 2015; Tweddle, Gubbins, & Scott, 2018). Their sensitivity to environmental change (Richardson, 2008) means that shifts in plankton can provide information on a range of anthropogenic pressures affecting marine biodiversity, including eutrophication and climate change. Indicators revealing changes in the plankton can therefore contribute to an ecosystem approach to management, and the development of plans to support adaptation to climate change (McQuatters-Gollop et al., 2009; Racault et al., 2014; Richardson, 2008).

In response to the multiple policy drivers for an ecosystem approach to management (Apitz, Elliott, Fountain, & Galloway, 2006), a concerted effort has been undertaken to develop plankton indicators for reporting on status and trends. An indicator based on change in the balance of 'plankton lifeforms' is used to assess lower trophic levels in the North-East Atlantic and monitor progress towards environmental targets (McQuatters-Gollop et al., 2019). Plankton lifeforms are groupings of plankton taxa based on shared functional traits (e.g. size class, feeding mode). Monitoring changes in the absolute and relative abundance of key plankton lifeforms can be used to detect changes in community functioning, in turn informing on changes to ecosystem services.

To maximize the utility of the plankton lifeform approach for informing the management of marine ecosystems, changes in the abundance of lifeforms need to be attributed to drivers of change. These drivers may include 'directly manageable' anthropogenic pressures (such as eutrophication caused by nutrient loading) as well as larger-scale and longer-term changes in climate and oceanography (Bedford, Johns, Greenstreet, & McQuatters-Gollop, 2018). Ecological time-series are critical for understanding the drivers of change, especially of climatic factors such as changing thermal regimes (Edwards, Beaugrand, Hays, Koslow, & Richardson, 2010; Giron-Nava et al., 2017).

Globally, multi-decadal plankton time-series are still few in number (O'Brien, Lorenzoni, Isensee, & Valdés, 2017). In the UK and North-West Shelf however, a number of datasets initially established for different monitoring purposes exist. These have the potential to form a novel integrated plankton-monitoring network that can powerfully capture changes in the plankton community in inshore, coastal and offshore environments. Regional-scale offshore plankton monitoring is provided by the Continuous Plankton Recorder (CPR) survey, which has used ships of opportunity to collect a consistent plankton time-series since 1958. Plankton in coastal areas are monitored through a variety single station-based surveys. These provide high temporal frequency data with large taxonomic coverage, but have shorter time-spans than the CPR survey. Combining all of these data across inshore and offshore areas permits the understanding of whether indicators are displaying spatially coherent trends and responses to climate variables (in a similar pattern over the region), or spatially variable dynamics. Spatially variable dynamics may reveal range shifts, with taxa showing different trends towards the colder and warmer limits of their ranges. Spatially variable dynamics and responses to climate variables may also reveal the impacts of more localized direct pressures, for example anthropogenic nutrient loading causing eutrophication of coastal areas (Devlin, Best, Bresnan, Scanlan, & Baptie, 2007; Greenwood et al., 2019; McQuatters-Gollop & Vermaat, 2011).

Crucially, our lifeform approach also allows comparison of shorter time-series with longer multi-decadal datasets. Given the inherent variability of ecosystems, climate change effects, such as the response to signals of increasing sea surface temperatures (SSTs), are often only clearly and statistically demonstrable using multi-decadal time-series datasets (Giron-Nava et al., 2017; Henson et al., 2010). Comparison between surveys therefore can highlight synergies between long- and short-term datasets, and increase the robustness of the attribution of drivers of change in shorter time-series. Furthermore, this temporal comparison builds understanding as to whether the direction of shorter-term coastal trends are part of a longer-term, multi-decadal signal, or whether they are deviating from the long-term trend in abundance, reflecting the influence of local drivers.

Here, we collate a unique regional scale, multi-decadal dataset to provide an analysis of trends in six ecologically important plankton lifeforms across the North-West European shelf. The lifeform indicator approach enables trends across multiple disparate surveys to be analysed, comparing both offshore time-series from the CPR with coastal station-based time-series and inshore sampling programmes. We also correlate lifeforms with SST, to provide a broad overview of correlative responses of the plankton lifeforms to fluctuations in the thermal regime, a key aspect of climate change (Beaugrand et al., 2019). By understanding lifeform indicator dynamics over both large temporal and spatial scales, we provide a holistic overview of trends in the plankton assemblage. As plankton occupy the base of the food web, this information is critical for informing effective policy decisions and climate change adaptation measures into the future.

2 | MATERIALS AND METHODS

2.1 | Plankton lifeforms

This study focuses on three pairs of key lifeforms—diatoms and dinoflagellates (representing the phytoplankton community), large and small copepods, and holoplankton and meroplankton (representing the zooplankton community). Here we map the dynamics of each lifeform individually, but when interpreted in pairs, the absolute and relative abundances of the lifeform pair can indicate change in key aspects of ecosystem function (McQuatters-Gollop et al., 2019). These lifeforms are well sampled, and their associated functional traits can be unambiguously applied to the individual taxa identified during sample analysis.

2.1.1 | Diatoms and dinoflagellates

Diatoms and dinoflagellates are key primary producers. These two phytoplankton lifeforms have fundamentally different traits, including differences in motility, silicification and extent of heterotrophy (Armbrust, 2009; Jeong et al., 2010; Sherr & Sherr, 2007). These different traits affect their biogeochemical and food web roles, meaning diatoms and dinoflagellates are not functionally equivalent, likely supporting different trophic pathways (Legendre & Rassoulzadegan, 1995; Parsons, 1979). For example, the differences in seasonality and motility may mean that diatom dominance indicates enhanced energy flow to the benthos at certain times of the year as they can dominate the phytoplankton community and have more rapid sinking rates. In comparison, dinoflagellate dominance may indicate that energy is kept for longer in the pelagic component of the food web (Wasmund et al., 2017). Differences in water column preference, silicification and nutrient requirements may mean changes in diatoms and dinoflagellates indicate changes in the stability of the water column, as well as changing nutrient balances because of eutrophication or imbalanced nutrient reductions resulting from management measures. In the North Sea, for example, the managed reduction of phosphate from sewage has been more effective than that of nitrate from agriculture. This has led to increasing nitrate:phosphate loading ratios (Burson, Stomp, Akil, Brussaard, & Huisman, 2016; McQuatters-Gollop et al., 2007; Officer & Ryther, 1980; Tett, Hydes, & Sanders, 2003). Increasing temperature can also affect both diatoms and dinoflagellates, with diatoms exhibiting higher niche plasticity than dinoflagellates; dinoflagellates track the movement of isotherms more closely than diatoms in order to conserve their niche (Chivers, Walne, & Hays, 2017; Kemp & Villareal, 2018). These different functional traits and responses to environmental drivers mean that these two lifeforms are often compared when monitoring changes in phytoplankton community functioning (Hinder et al., 2012).

2.1.2 | Holoplankton and meroplankton

Holoplankton are plankton that spend their whole lifecycle in the pelagic environment, and include copepods, euphausiids, appendicularians and chaetognaths. Meroplankton, on the other hand, are plankton that only spend part of their lives in the pelagic environment. Meroplankton are a highly diverse taxonomic group with representatives of polychaetes, molluscs, cirripedes, decapods, echinoderms, bryozoans and others; here the eggs and larvae of fish are not included in the lifeform. The relative abundance of holoplankton and meroplankton therefore reflect energy partitioning between the pelagic and benthic environments (Kirby, Beaugrand, & Lindley, 2008). Furthermore, meroplankton stages exist for commercially important taxa such as lobster, brown crab, scallops and other bivalves. Climate change and ocean acidification may impact the reproduction and recruitment of benthic invertebrates, affecting meroplankton abundance (Birchenough et al., 2015).

2.1.3 | Large and small copepods

Here we define 'large' copepods as over 2 mm in length as adults, and 'small' copepods as those smaller than 2 mm as adults. Large, cold-water copepods often accumulate energy-rich lipids (Record et al., 2018), and small copepods such as *Pseudocalanus* spp. tend to dominate the zooplankton in terms of abundance and so are key trophic links in marine food webs, for example by being prey for larval fish (Robert, Murphy, Jenkins, & Fortier, 2013; Turner, 2004).

Ecological theory and observations suggest that climate warming is expected to favour small copepods over large copepods (Daufresne, Lengfellner, & Sommer, 2009; Garzke, Ismar, & Sommer, 2015). The species-shift hypothesis outlined by Daufresne et al. builds on Bergmann's rule that warm regions tend to be inhabited by small species, to suggest that an increase in temperature should result in an increase in the proportion of smaller-sized species in a community. The replacement of large copepods with small ones has also been a documented effect of eutrophication (Uye, 1994). The species composition of large copepods has been linked to climate change, with a decrease in the abundance of *Calanus finmarchicus* in the North Sea and a corresponding increase in *Calanus helgolandicus*, a more temperate species with a more southerly distributed range (Beaugrand, Luczak, & Edwards, 2009; Helaouët & Beaugrand, 2007).

2.2 | Plankton lifeform time-series

Plankton monitoring around the UK consists of continuous, offshore sampling along transects via the CPR survey, coastal station-based surveys and inshore sampling programmes (within 1 nautical mile of the shore; Figure 1). CPRs consist of a filtering mechanism housed in an external body that is towed behind ships, of opportunity, at an average speed of ~11–15 knots (Jonas, 2004), and at a depth of ~7–10 m. Each sample represents approximately 10 nautical miles (18.5 km) of tow, and approximately 3 m^3 of seawater (Batten et al., 2003). Coastal station-based time-series and inshore (up to 1 nautical mile from the shore) sampling programmes use a variety of sampling methods (Table 1), with analysis of phytoplankton mainly done using the Utermöhl method (Edler & Elbrächter, 2010).

Each individual time-series was first screened to include taxa reliably and consistently sampled throughout the full extent of the time-series. This often included aggregation of taxa in the instances where taxonomic resolution improved over time. To ensure consistency in the trends, taxa were removed from each time-series if they were not consistently 'looked for' from its start. From these screened data, we then used a database of phytoplankton and zooplankton lifeform traits (McQuatters-Gollop et al., 2019) to aggregate raw taxonomic data into lifeforms. During the assembling of this database, each taxon was assigned traits describing, where possible, plankton functional type, feeding mechanism, size and habitat. Following methodology developed and outlined in Ostle et al. (2017), here queries were used to extract the constituent species for each lifeform group, based on specific combinations of
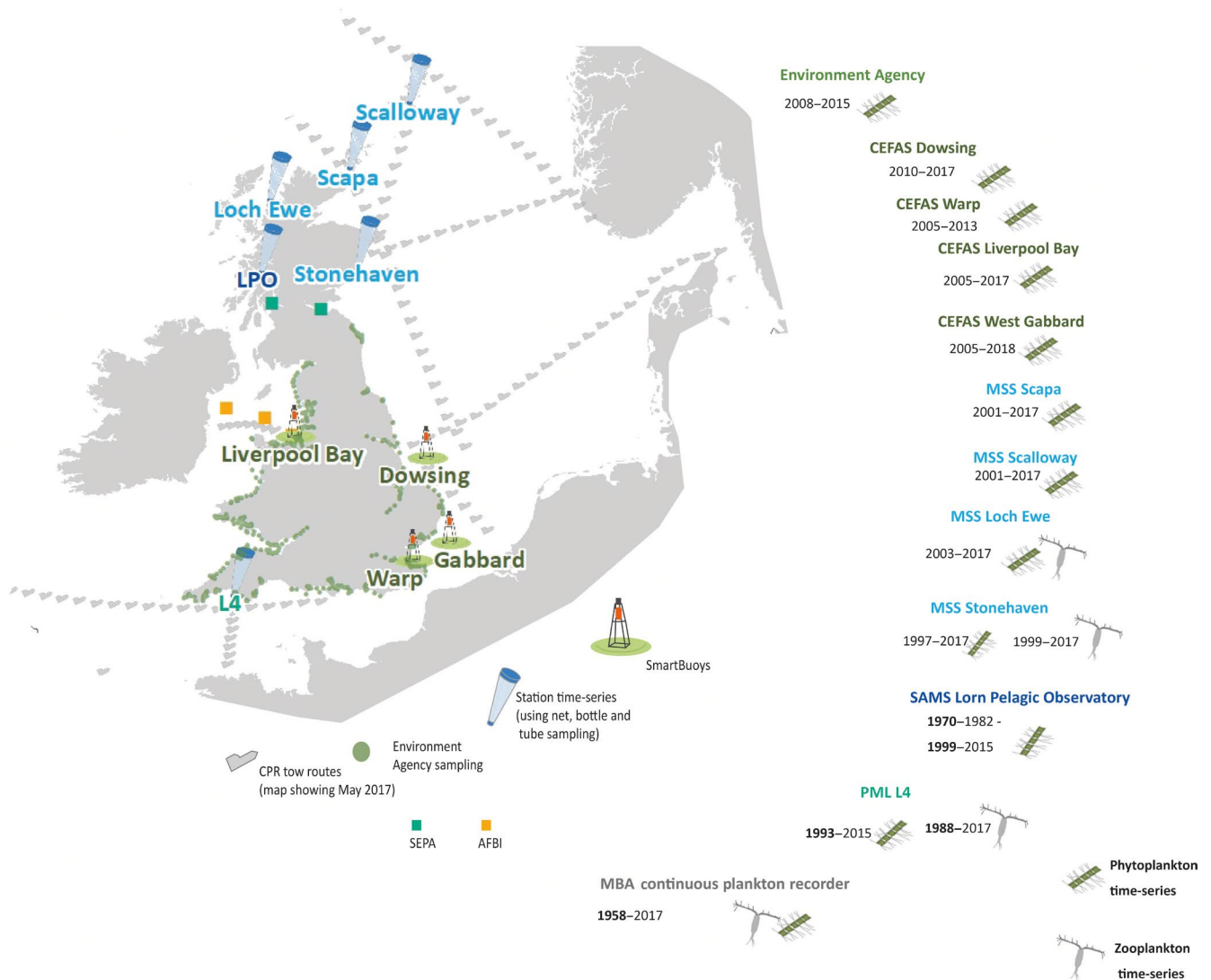
FIGURE 1 Plankton surveys contributing to the UK plankton biodiversity-monitoring network, along with the length of each time-series used to calculate trends is annual mean lifeforms. The network includes coastal stations sampled by Plymouth Marine Laboratory (PML), Marine Scotland Science (MSS), the Scottish Association for Marine Science (SAMS) and the Centre for Environment, Fisheries and Aquaculture Science (Cefas), as well as the Environment Agency (EA) inshore water quality sampling. Scottish Environmental Protection Agency (SEPA) and Agri-Food and Biosciences Institute (AFBI) are part of the UK plankton-monitoring network, but do not yet have long enough time-series to examine trends for the current study. Continuous Plankton Recorder (CPR) tow routes are displayed for May 2017 for visualization purposes, but wider offshore spatial coverage is provided when looking at the full survey

traits (McQuatters-Gollop et al., 2019). As each survey uses different sampling methods, and quantifies plankton abundance in different ways, data were not combined between surveys. Instead, non-parametric tests were used to calculate trends and compare between surveys, and correlations between abundance and SST were calculated separately for each time-series before being compared across surveys.

2.3 | Trend and correlation mapping

Continuous Plankton Recorder samples were extracted for the North-West European shelf. Raw taxonomic data for each CPR sample were then summed to lifeform totals (counts/3 m^3), before being

log transformed ($\log_{10} (x + 1)$). To visualize spatial variation in trends, CPR samples were then interpolated onto a 2° × 2° grid covering the OSPAR (the regional seas convention for the North-East Atlantic) Region II Greater North Sea and Region III Celtic Sea areas (Figure 2) using inverse squared distance interpolation (Planque & Batten, 2000; Vezzulli & Reid, 2003). The raw sample size for each 2° grid square between 1958 and 2017 is shown in Figure 2. Interpolated maps for each lifeform were created for each month in each year (12 × 60) using a search radius of 250 nautical miles, a minimum sample size of 5, and a maximum sample size of 15 as the interpolation parameters (Beaugrand, Reid, Ibanez, Lindley, & Edwards, 2002). Years with fewer than 10 months of interpolated data were then removed from each grid square's time-series; no more than 10% of years needed to be removed for any given grid square. For the remaining time-series

TABLE 1 Sampling and analysis methodology for the plankton surveys included in this analyses. Some surveys in Figure 1 were omitted due to short time-series length

Survey	Sampling method	Net mesh size	Analysis method	Units of abundance	Key references
CPR survey	CPR. Routes towed monthly	270 μm	Phytoplankton and zooplankton preserved in formalin and analysed by light microscopy	Phytoplankton and small copepods: semi-quantitative counts/3 m³ Large copepods: quantitative counts/3 m³	Batten et al. (2003), Richardson et al. (2006)
PML L4	Phytoplankton: 10 m depth water bottles. Sampled weekly Zooplankton: replicate 0–50 m WP2 nets. Sampled weekly	N/A 200 μm	Phytoplankton: preserved in Lugol's and analysed by light microscopy Zooplankton: preserved in formalin and analysed by light microscopy	Phytoplankton: cells/L Zooplankton: individuals/m³	Atkinson et al. (2015), Widdicombe, Eloire, Harbour, Harris, and Somerfield (2010)
Environment Agency (inshore)	Phytoplankton: 1 m depth water bottles. Water bodies sampled monthly at multiple sites	N/A	Phytoplankton: preserved in Lugol's and analysed by light microscopy	Cells/L	Devlin, Best, Bresnan, Scanlan, and Baptie (2012)
Cefas Smartbuoys	Water samplers mounted 1m below the surface: 150 ml into bag pre-spiked with Lugol's. Sampled weekly	N/A	Phytoplankton: preserved in Lugol's, analysed by light microscopy	Cells/L	Weston, Greenwood, Fernand, Pearce, and Sivyer (2008)
SAMS Lorn Pelagic Observatory (LPO)	0–10 m water bottles. Sampled monthly, more frequently in some years	N/A	Phytoplankton: preserved in Lugol's, analysed by light microscopy	Cells/L	Tett (1987), Whyte et al. (2017)
MSS Scottish Coastal Observatory (SCObs)	Phytoplankton: 10 m integrated tube. Sampled weekly Zooplankton: vertical haul (45 m Stonehaven, 35 m Loch Ewe) with 40 cm diameter Bongo net. Sampled weekly	N/A 200 μm	Phytoplankton: preserved in Lugol's, analysed by light microscopy Zooplankton: preserved in formalin and analysed by light microscopy	Cells/L Zooplankton: individuals/m³	Bresnan et al. (2016)

Abbreviation: CPR, Continuous Plankton Recorder; MSS, Marine Scotland Science.

in each grid square, any remaining gaps in the monthly time-series were filled through linear interpolation, before the annual mean for each grid square calculated. To avoid misinterpreting trends in areas not accessed by CPR sampling, grid squares with fewer than 250 samples were not displayed on the maps.

After the data were interpolated, trends and correlations were calculated to visualize spatial variation. Methodology set out by the International Group for Marine Ecological Time-series for reporting trends was adapted (O'Brien et al., 2017). First, the Mann–Kendall test was applied to the annual mean time-series for each grid square to test for significant monotonic upward or downward trend over time. This non-parametric method was selected because it is not affected by any transformation of the annual data values, and it is flexible for time-series with missing data points (Desmit et al., 2020). Under this method, each value in the time-series is compared to each of the values preceding it, giving a total of $n(n − 1)/2$ pairs of data. If the later time point in each pairwise comparison is higher

than the earlier time point, the comparison is given a score of 1, and if it is lower it is given a score of −1, with no difference given a score of 0. These scores are then summed to calculate Kendall's S statistic (S; i.e. the number of increases − the number of decreases). Next, the variance of S is calculated according to Millard (2013) and used to standardize S in to a 'Z-score'. The Z-score test statistic has an approximate normal distribution, and it is used to assign a significance level to the presence of a trend. High positive Z-scores and high negative Z-scores indicate clear increasing and decreasing monotonic trends, respectively, with statistically significant trends suggesting that the null hypothesis (no monotonic trend) can be rejected.

Next, in order to evaluate SST change at the scale of the CPR sampling, monthly gridded SST data were downloaded for the Greater North Sea and Celtic Seas OSPAR regions from the International Comprehensive Ocean Atmosphere Dataset (ICOADS) at a 2° resolution, available at https://www.esrl.noaa.gov/psd/. These data were then overlaid onto the same 2° × 2° grid

FIGURE 2 Numbers of Continuous Plankton Recorder (CPR) samples collected within each 2° grid square from 1958 to 2017. Yellow line denotes the OSPAR Greater North Sea and Celtic Seas boundary. Samples are highest along the core CPR tow routes, for example in the Western Channel, but lower in the most northerly areas of the North Sea. These less well-sampled areas are therefore most heavily interpolated, and have the lowest confidence associated with any trends and correlations found. Blacked out squares show areas not covered by CPR sampling (<250 samples), including the West of Scotland, as well as the area between the Eastern Channel and the Southern North Sea. These squares are omitted from the interpolated lifeform trend maps (blacked out squares)
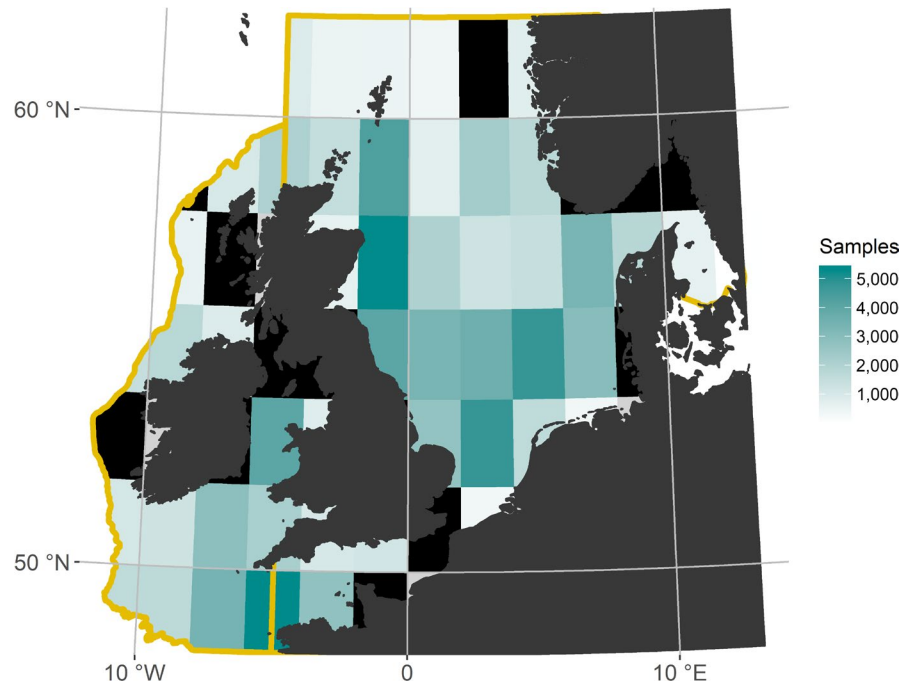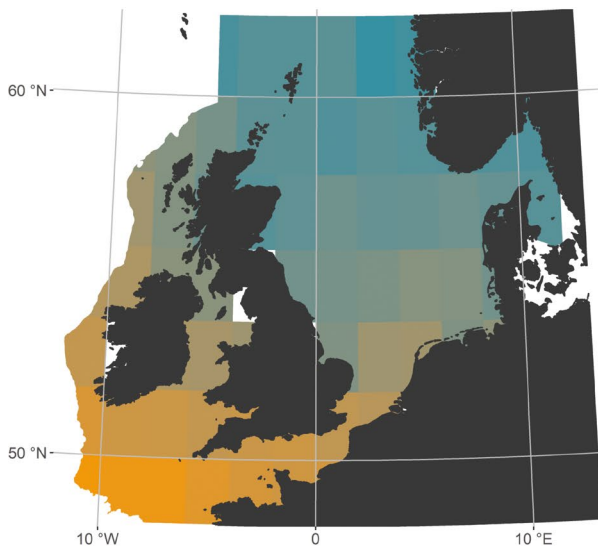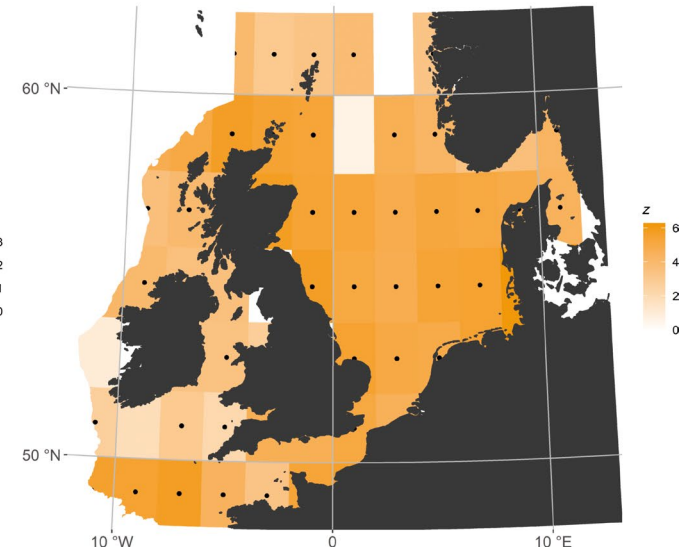

FIGURE 3 (a) Sea surface temperature (SST) climatology between 1958 and 2017 (based on the average annual mean SST over the time period). (b) The Mann–Kendall trend score (z) for International Comprehensive Ocean Atmosphere Dataset SST in the study area. Orange shade represents strength of increasing trend, with points representing statistically significant trends

as the plankton data, before annual means were calculated. This overlaying allowed a comparison between annual mean lifeform abundance and annual mean SST for each grid square. Missing SST values in each grid square were temporally interpolated using linear interpolation. Climatology for the study area and Mann–Kendall trends in the SST data are shown in Figure 3.

The Pearson's correlation coefficient between annual mean SST and annual mean lifeform abundance was then calculated for each grid square. In order to account for temporal autocorrelation, the 'modified Chelton' method (Pyper & Peterman, 1998) was used to

adjust the *df*s according to the level of autocorrelation, and a second *p* value calculated.

In addition to the interpolated maps, Mann–Kendall trends and Pearson's correlation coefficients with SST were calculated on non-interpolated CPR data (i.e. raw samples), averaged into annual means for the Greater North Sea and Celtic Sea OSPAR regions. To illustrate the magnitude of change in abundance as well as the direction of trend, the difference in abundance between the first (1958–1967) and last decade (2008–2017) of the CPR time-series in each region was calculated. The annual means from each decade

were further aggregated into decadal means. These values were then back-transformed to obtain the geometric decadal mean abundance per sample of each lifeform for both decades. The last decade was then expressed as a proportion of the first decade.

For all station-based time-series, sample totals of each lifeform were calculated, before being $\log_{10} (x + 1)$ transformed and monthly averages calculated. Data gaps in the monthly time-series were interpolated as appropriate before calculating annual means. Environment Agency inshore samples were also ($\log_{10} (x + 1)$) transformed before calculating monthly then annual means, with missing months interpolated as appropriate. To divide up the inshore Environment Agency sampling, the coastline was divided into five regions based on the UK Charting Progress 2 assessments: Northern North Sea, Southern North Sea, Eastern Channel, Western English Channel and Celtic Sea and Irish Sea (UK Marine Monitoring Assessment Strategy Community, 2010). For each time-series, the Mann–Kendall test for trend and the correlation with SST were calculated. For station-based surveys, SST is often measured at the same time as taking a plankton sample. Correlations with SST calculated at stations therefore were based on these in-situ temperature readings. SST data from the nearest ICOADS grid square were used for the Lorne Pelagic Observatory (LPO) due to missing in-situ data, where Colville (2019) has shown that the ICOADS data correlate well with local CTD observations. These Mann–Kendall trend scores and correlation coefficients with SST were then superimposed onto the CPR interpolated maps.

3 | RESULTS

3.1 | Diatoms and dinoflagellates

Diatoms and dinoflagellates were sampled by all surveys included in the study. Data from Cefas SmartBuoys were excluded from the analysis of annual means, however, due to too many missing months for confident calculation of annual means. Maps of trends and correlations with SST for diatoms and dinoflagellates are shown in Figure 4. At a broad spatial scale, diatoms show an increasing trend in the Greater North Sea, and a decreasing trend in the Celtic Sea (Table 2). Trends from station samples show strong alignment with the CPR trends, suggesting spatial coherence in diatom dynamics between different survey areas, and that the shorter-term coastal trends are aligned with the longer-term multi-decadal offshore signal. For example, the L4 diatom time-series in the Western Channel shows a weak, non-significant increasing trend, which is aligned with the wider diatom trend for the Channel shown by the CPR. Similarly, while there is no significant increasing trend in diatoms in the Marine Scotland Science (MSS) Stonehaven time-series, this is aligned with CPR trends when moving offshore, where diatoms also seem to be stable. Further north however, the MSS Scapa time-series in Orkney shows a significant increasing trend in diatoms ($z = 3.485$, $p < .01$), aligned with the CPR trends in the northern North Sea offshore areas.

Although increasing, there is a weak, non-significant trend in diatoms at the MSS Scalloway site in the Shetland Isles, despite a strong increase at the multi-decadal scale in the surrounding most northerly latitudes of the North Sea. As well as the result of local environmental influences, the lack of trend alignment at this site may be a result of different temporal scales. For comparison purposes, trend maps for all lifeforms were repeated with CPR data over a reduced time period of 2000–2017, and are included as Supporting Information. When only looking at 2000–2017, so a similar temporal scale to the MSS time-series, the diatom trends at these most northerly latitudes are also weak and non-significant, suggesting that the increases in diatoms in this area occurred before 2000.

Although the correlations with temperature show a general alignment with the trend scores for diatoms, very few correlations are statistically significant, for either the CPR survey or the station-based surveys. This lack of significance suggests that SST may be contributing to the observed changes in diatoms, but other factors are likely to be influencing diatom abundance, especially in inshore and coastal areas where trends and correlations often do not align with offshore CPR data. This spatial difference is to be expected, as it is likely that many environmental drivers, for example, wind speed/direction, grazing pressure and other offshore influences, may be exerting an effect on diatoms. The Environment Agency sampling programme, which is the closest inshore sampling programme included in this study, shows a significant increasing trend for diatoms in the Southern North Sea region, as well as the Western Channel and Celtic sea regions, but these trends are not significantly correlated with SST.

Dinoflagellates broadly show a decreasing trend across both the North Sea and Celtic Seas (Table 2), and are largely negatively correlated with SST, although this decreasing trend is less clear in the Western Channel. Unlike trends for diatoms, however, dinoflagellate trends in CPR data differ from those reported by inshore and coastal surveys. This disparity could be the result of a number of factors including different drivers and pressures between the coast and the open sea. For example, in the Western Channel, there is a significant increase in dinoflagellates from the inshore sampling, but no significant trends when moving further out to the coastal L4 station time-series, and then further to the wider Channel region sampled by the CPR. These trend disparities may highlight a pressure affecting coastal phytoplankton communities that is not extending offshore.

The trend disparities in dinoflagellates (Figure 4) could also highlight different trends manifesting at different temporal scales. When only looking at 2000–2017, the offshore dinoflagellate trends are weak suggesting that the major changes in dinoflagellates observed occurred before 2000. When comparing with the station-based surveys at this shorter temporal scale, the direction of dinoflagellate trends is more closely aligned with the station-based surveys (Figure 5a), although the trends are largely non-significant. This stronger alignment suggests the short-term trends in coastal areas may be divergent from the longer-term multi-decadal trend.
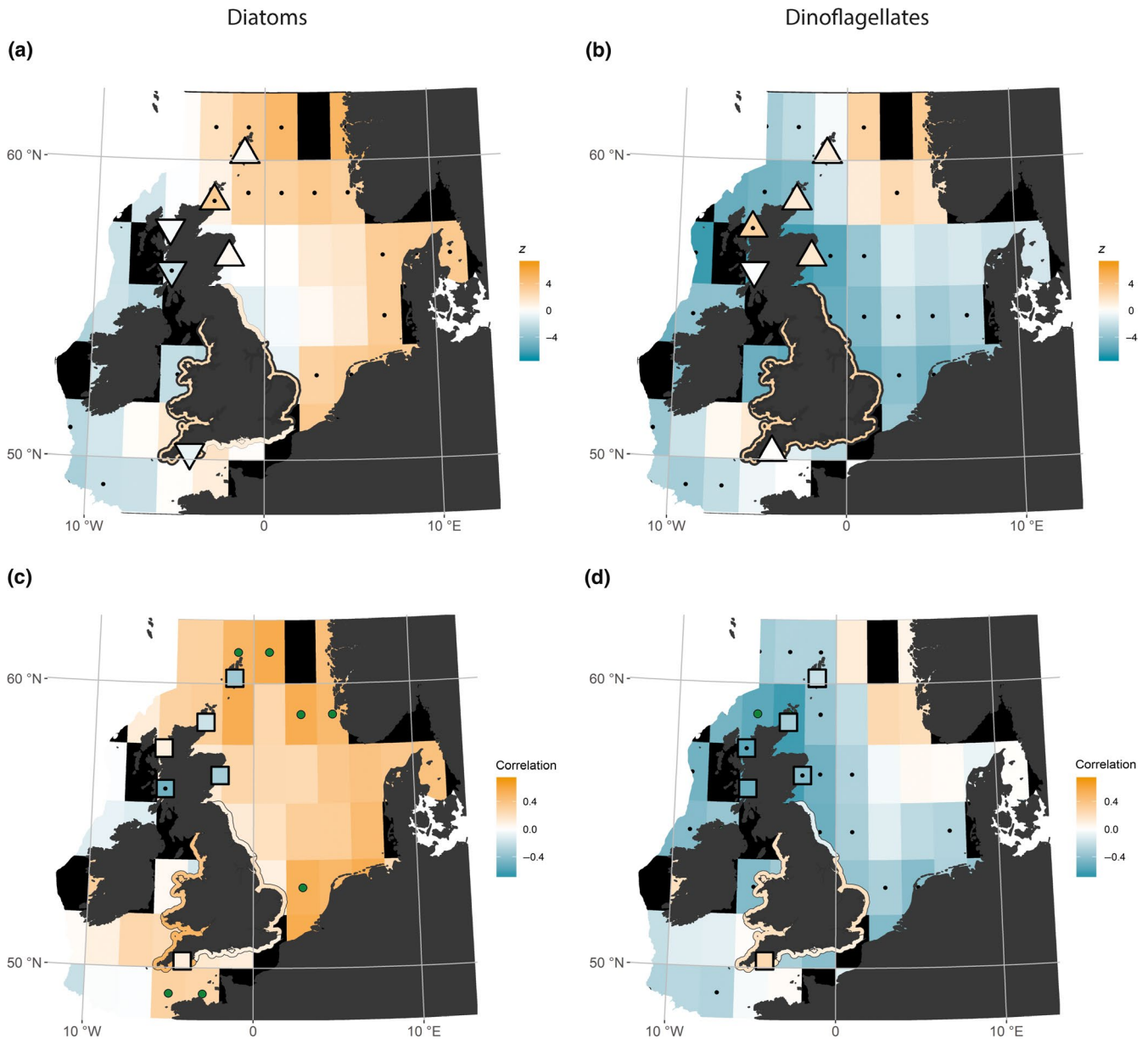
FIGURE 4 (a) Diatom Mann–Kendall trend scores and (b) dinoflagellate Mann–Kendall trend scores. (c) Diatom correlations with sea surface temperature (SST) and (d) dinoflagellate correlations with SST. Orange indicates increasing monotonic trend/positive correlation, and blue indicates decreasing monotonic trend/negative correlation, with points representing statistically significant trends/correlations. Large green dots indicate significant modified Chelton *p* values for correlation with SST. Blacked out squares have fewer than 250 Continuous Plankton Recorder samples over the time-series. Triangles show coastal stations and the direction of trend; squares show coastal station correlations with in-situ SST. The Environment Agency aggregation regions are shown as a narrow strip along the coasts of England and Wales, with significance indicated with a bold border

Another factor explaining the trend disparity, however, may be differences in sampling methods between the different surveys. The coarse nature of the CPR sampling mesh results in sampling of mainly large, armoured dinoflagellates, such as those from the genus *Ceratium* (now called *Tripos* by Gómez, 2013). Station-based and in-shore programmes, on the other hand, sample more of the smaller members of the dinoflagellate community in addition to the large taxa. This sampling difference may in part explain disparity in trends observed. For example, the Loch Ewe time-series on the west coast of Scotland showed a significant increasing trend in dinoflagellates

(Mann–Kendall *z* = 3.06, *p* < .01). However, there was no such trend when only *Ceratium* spp. data were analysed (Figure 5b; Mann–Kendall *z* = −0.09, *p* = .93), although a period of low abundance could be identified. Furthermore, the dinoflagellate lifeform at LPO similarly consists predominantly of large, armoured dinoflagellates, and the LPO time-series showed a decreasing trend in dinoflagellates, consistent with the offshore CPR area. These patterns suggest that the increasing trends in dinoflagellates found in the other station-based time-series, as well as the inshore sampling, may be from taxa that are not sampled in high abundance by the CPR survey.

TABLE 2 Trend and correlation results for non-interpolated CPR samples averaged over the Greater North Sea and Celtic Seas regions. Significant trend and correlation (p < .05) are shown in bold, 'mod' is the modified Chelton p value accounting for autocorrelation. Change in abundance is indicated as the geometric decadal mean lifeform abundance for 1998–2017, expressed as a proportion of the geometric decadal mean lifeform abundance for 1958–1967 (last/first decadal mean)

Lifeform	Greater North Sea					Celtic Seas				
	Trend		Correlation		Last/first decadal mean	Trend		Correlation		Last/first decadal mean
	Z	p	Corr	p		Z	p	Corr	p	
Diatoms	**2.53**	**.011**	.43	.001 mod = .069	1.13	−1.53	.124	.06	.63	0.21
Dinoflagellates	**−3.89**	**<.01**	−.241	.068	0.25	**−4.80**	**<.01**	**−.503**	**<.01 mod = .03**	0.29
Holoplankton	**−4.1**	**<.01**	−.076	.58	0.49	**−4.97**	**<.01**	−.27	.036 mod = .224	0.21
Meroplankton	**6.18**	**<.01**	**.587**	**<.01 mod = .024**	2.3	**2.799**	**<.01**	.216	.103	1.14
Large copepods	**−5.08**	**<.01**	−.36	**<.01 mod = .084**	0.48	**−3.16**	**<.01**	−.23	.091 mod = .235	0.41
Small copepods	−0.33	.73	.127	.341	0.79	**−2.51**	**.012**	−.197	.138	0.36

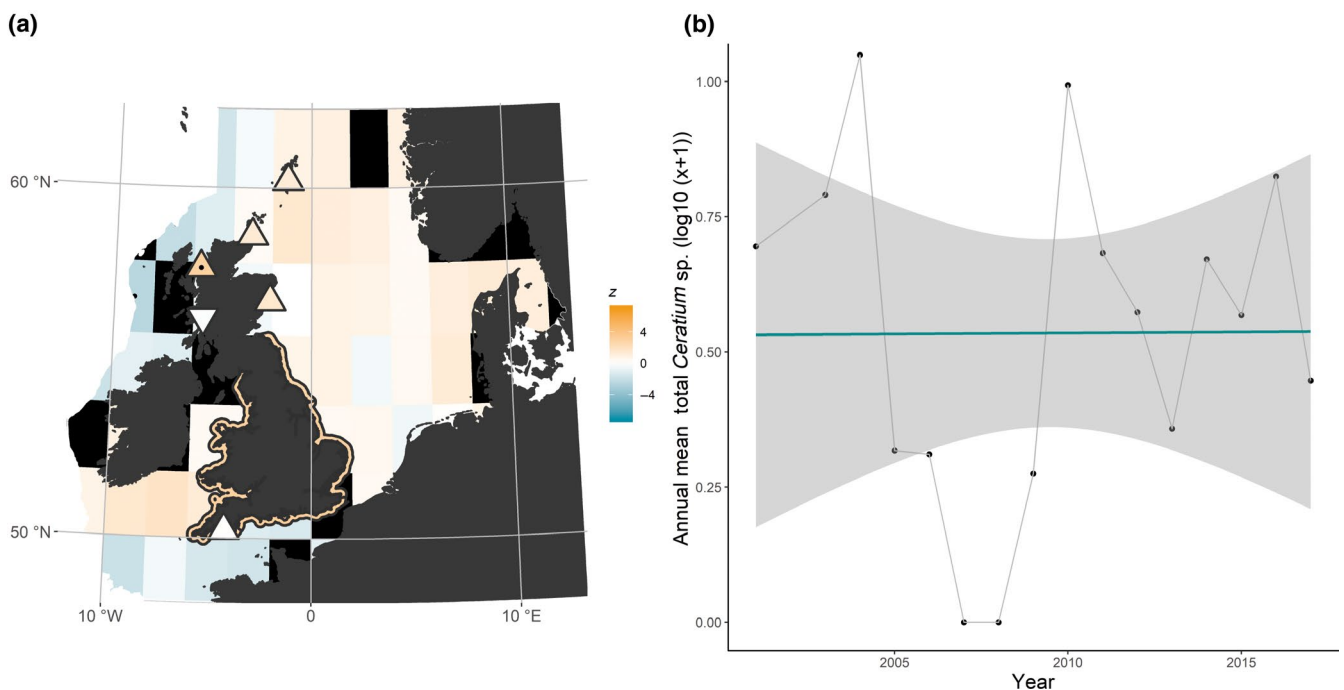Abbreviation: CPR, Continuous Plankton Recorder.

FIGURE 5 (a) Dinoflagellate trend map repeated with Continuous Plankton Recorder data post-2000. (b) Annual mean abundance of 'total *Ceratium* spp.' (cells/L) from the Loch Ewe station time-series. Applying the Mann–Kendall test reveals no monotonic trend is present, contrasting to the significant increasing trend found in the Loch Ewe broader dinoflagellate lifeform

3.2 | Holoplankton and meroplankton

Trends and correlations with SST for holoplankton and meroplankton are shown in Figure 6. It should be noted that trends for holoplankton and meroplankton for the CPR do not include gelatinous zooplankton due to the sampling method, although gelatinous zooplankton are

included in the data from the station-based surveys. There is a general decline in the mean annual abundance of holoplankton, reflected in both CPR data and station-based time-series data, although only the Loch Ewe out of the station surveys shows a significant decline (z = −3.56, p < .001). The correlations between holoplankton and SST, however, from both the CPR and station-based time-series, are largely
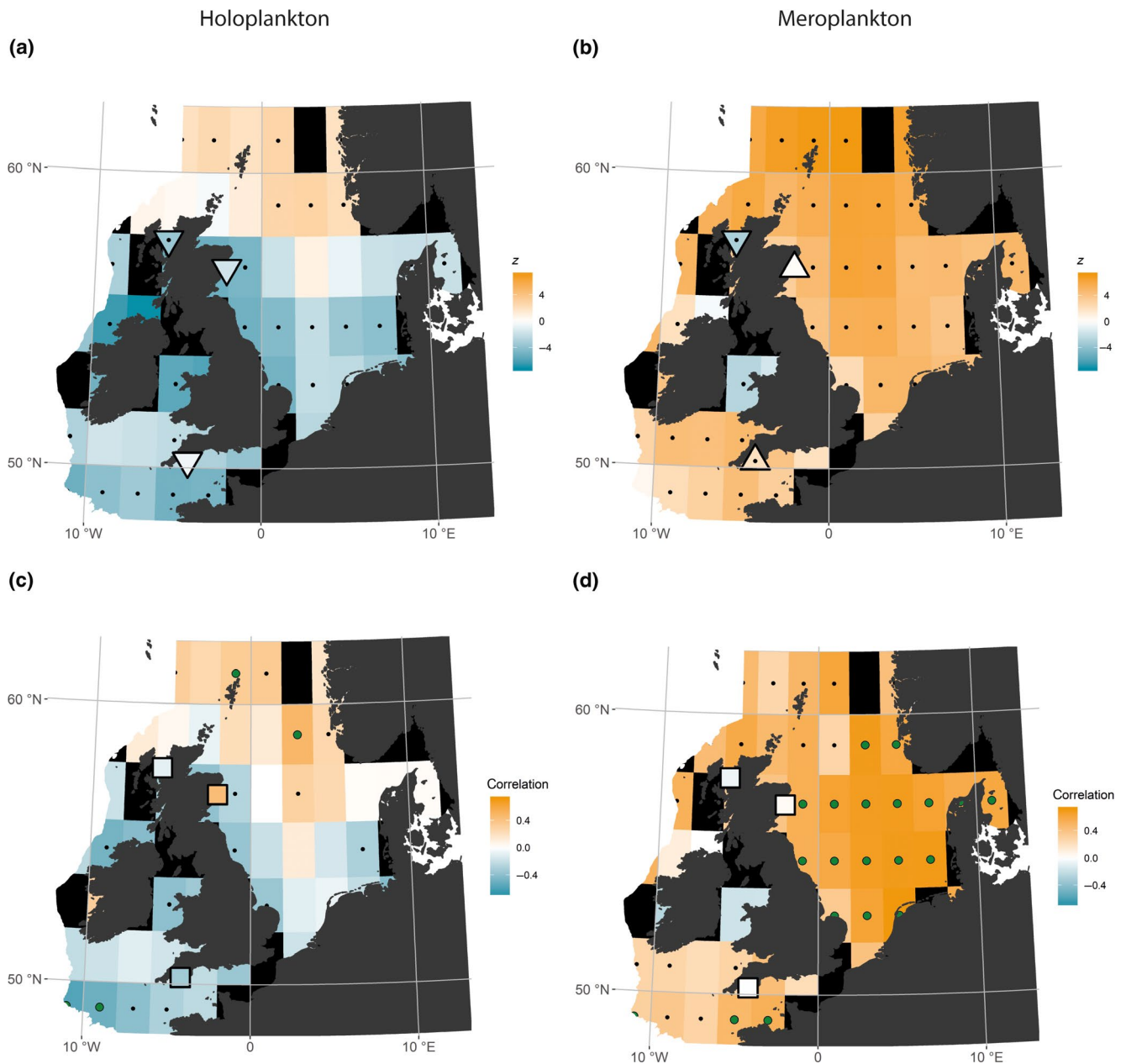
Holoplankton

(a)

(c)

Meroplankton

(b)

(d)

FIGURE 6 (a) Holoplankton Mann–Kendall trend scores and (b) meroplankton Mann–Kendall trend scores. (c) Holoplankton correlations with sea surface temperature (SST) and (d) meroplankton correlations with SST. Orange indicates increasing monotonic trend/positive correlation, and blue indicates decreasing monotonic trend/negative correlation, with points representing statistically significant trends/ correlations. Large green dots indicate significant modified Chelton p values for correlation with SST. Blacked out squares have fewer than 250 Continuous Plankton Recorder samples over the time-series. Triangles show coastal stations and the direction of trend; squares show coastal station correlations with in-situ SST

non-significant, likely reflecting variability caused by the high number of taxa, and broad taxonomic groups, that this lifeform encompasses.

Meroplankton, by contrast, show a clear and significant increasing trend coherent across most of the Greater North Sea and Celtic Sea, with the decadal mean abundance per sample in the Greater North Sea more than doubling between the start and end of the CPR time-series (Table 2). This increase in meroplankton is highly correlated with increases in SST, largely remaining significant when adjusting for temporal autocorrelation. The L4 time-series in the Western Channel also shows a significant increasing trend (z = 2.00,

p = .044), highlighting coherence between coastal and offshore areas in the Western Channel. The Stonehaven site showed an increasing direction of trend, but this was not statistically significant. In contrast, the Loch Ewe site shows a significant decreasing trend in meroplankton (z = −2.97, p < .01), which goes against the overall increasing trend observed elsewhere, highlighting potential localized drivers in this coastal area. The positive correlations with SST are weaker at the station-based time-series than with the CPR survey and are non-significant. This could be a result of the difference in length between the station-based time-series and the CPR survey.

3.3 | Large and small copepods

Trends and correlations with SST for large and small copepods are shown in Figure 7. There is a broad trend for a decline in small copepods in the Greater North Sea and Celtic Seas OSPAR regions, with the strongest declines in the Channel and the western areas of the North Sea. There is a latitudinal divide in the direction of trend in the North Sea, with small copepods declining in the southern regions, and increasing in the most northerly regions of the North Sea, potentially indicating distributional shifts. Where there is a trend

present in the interpolated CPR data, trends are frequently correlated with SST, although often do not remain significant when adjusting for autocorrelation. The declining trend is also reflected in the station-based sampling, although only the Loch Ewe site shows a statistically significant decline ($z = −2.97$, $p < .01$). A significant negative correlation between small copepods and SST is found in the Western Channel with the L4 time-series, even though the correlation is weak in the CPR data in the surrounding Channel area. Comparing with the spatial patterns of holoplankton trends visualized in Figure 6, it is likely that the trends in holoplankton are largely
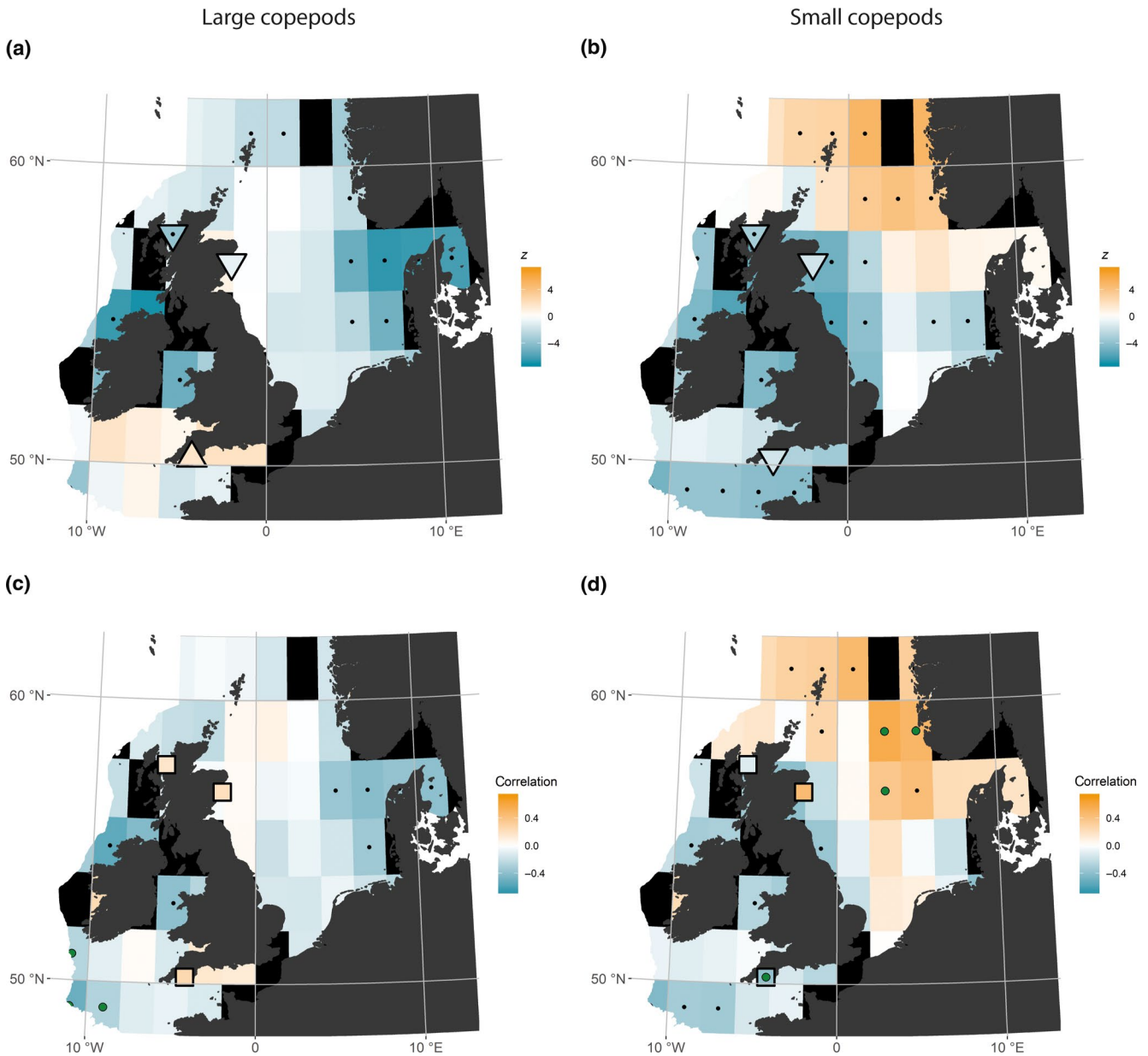

FIGURE 7 (a) Large copepods Mann–Kendall trend scores and (b) small copepods Mann–Kendall trend scores. (c) Large copepod correlations with sea surface temperature (SST) and (d) small copepod correlations with SST. Orange indicates increasing monotonic trend/ positive correlation, and blue indicates decreasing monotonic trend/negative correlation, with points representing statistically significant trends/correlations. Large green dots indicate significant modified Chelton p values for correlation with SST. Blacked out squares have fewer than 250 Continuous Plankton Recorder samples over the time-series. Triangles show coastal stations and the direction of trend; squares show coastal station correlations with in-situ SST

driven by trends in small copepods. Small copepods make up a large proportion of holoplankton abundance across all datasets. For instance, at the L4 station in the Western Channel, small copepods comprise a median of 85% of the total holoplankton (based on 1,316 individual time points).

There is also an overall decline in large copepods in the Greater North Sea (Table 2), but when mapping trends very few grid squares show a statistically significant trend, suggesting this overall decrease is driven largely by eastern and northern areas. There are similarly weak, non-significant trends in large copepods at all stations apart from Loch Ewe, and no significant correlations with SST in any station time-series. In comparison with small copepods therefore, large copepods appear more stable in interannual abundance, and have less latitudinal variation in trend direction.

4 | DISCUSSION

Plankton lifeforms reveal multi-decadal, whole-region-scale change over the North-West European shelf indicating shifts in the functional balance of plankton communities. For example, CPR data revealed a significant increasing trend in meroplankton in the Greater North Sea, with the last decadal mean ~2.3× higher than the beginning of the time-series. Holoplankton, on the other hand, showed a significant decreasing trend, with the last decadal mean approximately half that of the beginning of the time-series. Similarly, the dinoflagellate decadal mean abundance was ~one-quarter of that of the start of the time-series.

Mapping these trends across the two OSPAR regions, as well as comparing CPR data with that from coastal stations, revealed that many lifeforms show evidence of coherent changes across wide spatial scales. For example, diatoms broadly show an increase in the North Sea and a decreasing trend in the Celtic Sea. Alignment in diatom trends also suggests similar drivers affecting the coast and the open sea in some areas. In contrast to diatoms, dinoflagellates show a broad-scale declining trend offshore in both the Greater North Sea and Celtic Sea regions. These dinoflagellate trends, however, are not so strongly aligned with inshore sampling and coastal station-based time-series as the diatom trends. Although this could indicate different pressures affecting the coast and the open sea, it is likely that differences in sampling methods also influence these trends. Although the CPR dinoflagellate trend may not represent all dinoflagellates, the consistent sampling over time means that a trend in CPR dinoflagellates still indicates a change in the pelagic food web.

Links to SST change are inconsistent for diatoms and dinoflagellates. Offshore, there are similar spatial patterns between direction and strength of trends, and direction and strength of correlations with SST. In particular, the offshore decline in dinoflagellates correlates with increasing temperatures. Hinder et al. (2012) stress, however, that SST is not the sole driver of declines in dinoflagellates after finding interactions between SST and wind speed, which both affect levels of mixing. Towards the coast, the influence of SST is less clear. Only the Lorn Pelagic Observatory time-series showed a significant correlation with SST for diatoms. Furthermore, at the Loch Ewe site off the west coast of Scotland, although the abundance of dinoflagellates was negatively correlated with SST, there was a significant increasing trend. Further work is therefore needed to understand fine-scale drivers of phytoplankton lifeforms near the coast, including understanding influences of trophic interactions, parasites and direct anthropogenic pressures. The significant increasing trend in dinoflagellates in the Loch Ewe time-series, for example, may be linked to the declining trends in all the zooplankton lifeforms also found at this site, causing a release of grazing pressure on dinoflagellates and allowing an increase in abundance. This research gap is particularly apparent for inshore dinoflagellates. In the Western Channel, the area sampled through the inshore sampling showed a significant increasing trend in dinoflagellates which was not correlated with SST, and which did not extend out to the site of the L4 time-series, nor was there a multi-decadal signal in the surrounding offshore area sampled by the CPR. Further investigation as to whether these inshore dinoflagellate increases are a result of anthropogenic nutrient inputs is therefore warranted.

Other lifeforms show a consistent and clear link to the signal of SST change. For example, the increasing trend in the absolute abundance of meroplankton, and therefore their abundance relative to holoplankton, is consistent throughout the North Sea and most of the Celtic Seas offshore areas as well as the L4 time-series in the western channel, highlighting that different sampling methods detect the same trend. Furthermore, this increase at a large spatial scale, along with the strong correlations with SST, provides strong evidence that the increase in meroplankton is driven by climatic and oceanographic change (Kirby et al., 2008), rather than impacts of more localized direct pressures on seafloor integrity, such as trawling and dredging. Over smaller spatial scales, the strong increasing trend in meroplankton in CPR data has previously been documented (Kirby et al., 2007) and identified to be largely driven by an increase in echinoderm and decapod larvae. Bivalve larvae, on the other hand, have been shown to be decreasing (Kirby et al., 2008). Mechanistic links to SST have also been hypothesized including increased reproductive output and larval survival under higher temperatures (Kirby et al., 2007). In contrast to meroplankton, comparing trend directions across both CPR and station-based surveys here illustrates an overall decline in holoplankton, suggesting a shift from pelagic to benthic productivity in the plankton community across the whole North-West European shelf.

Such large-scale trends in plankton lifeforms have implications for the functioning of food webs and the provision of ecosystem services. For example, small copepods are important prey items for larval fish, and are therefore important to monitor for understanding and managing the dynamics of higher trophic levels. The decline in holoplankton, which is being replaced by meroplankton, is largely driven by these small copepods. There is a broad spatial trend showing a decline in small copepods in the Celtic Sea and the central and southern areas of the Greater North Sea, while the most northern areas of

the North Sea showed an increasing trend. The declining direction of trend was also reflected in station-based time-series, although only Loch Ewe's was statistically significant. Evidence for a relationship with temperature was inconsistent, with few significant correlations, a notable exception being the L4 time-series, which showed a significant negative correlation between small copepods and SST. This latitudinal difference in the direction of trend in small copepods was documented by Pitois and Fox (2006), and later Capuzzo et al. (2018) found evidence for a link between declining small copepods since 1990 and declining primary productivity, suggesting an overall bottom-up control of food web structure in the North Sea.

The abundance of large copepods is more stable. Although the decrease in offshore decadal mean abundance between the first and last decade was greater for large than for small copepods, mapping trends revealed this decline was concentrated in the eastern areas of the North Sea, and may also be explained by the lack of latitudinal gradient in the direction of trend compared with small copepods. Instead, the maps revealed weak, largely non-significant declines across the majority of the study region. The ecology of large copepods is comparatively more intensively studied than that of small copepods, with well-documented changes in relative dominance of the two species that numerically dominate the large copepod fraction, namely *C. finmarchicus* and *C. helgolandicus* (Beaugrand, Mackas, & Goberville, 2013). It seems, therefore, that the taxonomic composition of the large copepod lifeform, rather than the total abundance of large copepods, is the variable affected by climate change. Further research is needed to understand the drivers of change in small copepods; as yet a robust mechanistic explanation is lacking because the trends are not explained solely by temperature-size-based ecological theories (Daufresne et al., 2009).

5 | CONCLUSIONS

We have used a plankton lifeform indicator approach to demonstrate changes in the state of pelagic habitats across the North-West European shelf. As a result of mapping trends, and correlating them with SST, we have identified significant changes in plankton lifeforms. Increase in meroplankton was the most dominant change and aligned well with SST while others (e.g. increases in diatoms) were restricted to more northern parts of the North Sea and the drivers of change appear more complex. Comparison of lifeform trends in offshore and coastal areas, and including both short and multi-decadal time-series, distinguished local from large-scale signals, both of which have been identified. Through this process, knowledge gaps in the assessment of plankton communities have become evident. For example, a more in-depth understanding of the drivers of change in inshore dinoflagellate communities is needed, especially given the potential sensitivity of the diatom and dinoflagellate lifeform pair to anthropogenic pressures. Furthermore, an understanding of the drivers and implications of the shift in the holoplankton and meroplankton lifeform pair on foodweb functioning is needed, given the large spatial scale and magnitude of the shift. Even though knowledge gaps exist in both the levels of directly manageable anthropogenic influence and the ecological consequences of indicator change, these signals in plankton communities form the foundations of our understanding of environmental change in the marine environment. Any change in plankton communities has the potential for negative consequences for the marine ecosystem and the services it provides. It will only be through continued integrated monitoring that these knowledge gaps can be filled, to fulfil the growing requirement for adaptive management of marine ecosystems in the context of a changing climate.

DATA AVAILABILITY STATEMENT
Data are available upon request from the authors.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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