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2026-04-30

Changing *Pseudo-nitzschia* and *Dinophysis* distributions in the North Sea and Western Approaches (NE Atlantic) and their potential use in biodiversity assessments

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Recommended Citation

Holland, M., Bresnan, E., Edwards, M., Faith, M., Ostle, C., Stern, R., Tett, P., Widdicombe, C., Whyte, C., & McQuatters-Gollop, A. (2026) 'Changing *Pseudo-nitzschia* and *Dinophysis* distributions in the North Sea and Western Approaches (NE Atlantic) and their potential use in biodiversity assessments', *Harmful Algae*, 156. Available at: [10.1016/j.hal.2026.103113](https://doi.org/10.1016/j.hal.2026.103113)

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Published in:
Harmful Algae

DOI:
[10.1016/j.hal.2026.103113](https://doi.org/10.1016/j.hal.2026.103113)

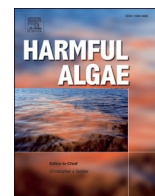
Publication date:
2026

Document version:
Publisher's PDF, also known as Version of record

Link:
[Link to publication in PEARL](#)

Citation for published version (APA):

Holland, M. M., Bresnan, E., Edwards, M., Faith, M., Ostle, C., Stern, R., Tett, P., Widdicombe, C., Whyte, C., & McQuatters-Gollop, A. (2026). Changing *Pseudo-nitzschia* and *Dinophysis* distributions in the North Sea and Western Approaches (NE Atlantic) and their potential use in biodiversity assessments. *Harmful Algae*, 156, Article 103113. <https://doi.org/10.1016/j.hal.2026.103113>



Changing *Pseudo-nitzschia* and *Dinophysis* distributions in the North Sea and Western Approaches (NE Atlantic) and their potential use in biodiversity assessments

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ARTICLE INFO

Keywords:

Climate change
Diatoms
Dinophysis
Dinoflagellates
Harmful algae
Phytoplankton
Plankton monitoring
Pseudo-nitzschia
Time-series

ABSTRACT

Pseudo-nitzschia and *Dinophysis* are two commonly occurring phytoplankton genera along Europe's Atlantic coast. Species within these genera can produce toxins that accumulate in shellfish and pose health risks if consumed. Sustained monitoring of shellfish growing waters has generated decades-long time-series for these two genera, which have been considered for use in statutory biodiversity assessments as proxies for diatoms and dinoflagellates. There is also evidence that distributions are shifting; It is important to document these changes to anticipate risks for shellfisheries, and higher trophic levels. We assessed whether *Pseudo-nitzschia* and *Dinophysis* data could support statutory biodiversity assessments and quantified distributional change through time. We compared seasonal and interannual variability in *Pseudo-nitzschia* and *Dinophysis* with total diatom and dinoflagellate abundance at two UK stations (L4, English Channel; Stonehaven, Scotland) and used Continuous Plankton Recorder data (1960–2020) to map decadal distributions. A notable spring increase in *Pseudo-nitzschia* occurred in the southern/eastern North Sea since ~2000, followed by a post-2010 reduction. *Dinophysis* remained largely summer-restricted and declined after 2000 in parts of the eastern North Sea. Station and CPR data were complementary, but not directly comparable, reflecting differences in spatial variability and capture efficiency. We found limited evidence, however, to support proxy potential for either genus. While there were some localised seasonal correlations, they were generally inconsistent or weak. Our results show that neither genus is suitable as a proxy for diatom or dinoflagellate lifeforms in statutory biodiversity assessment, but both are potentially valuable as evidence for HAB pressure when interpreted alongside toxin measurements.

1. Introduction

Phytoplankton communities in the North-East Atlantic have undergone substantial changes in recent decades (Bedford et al., 2020; Djeghri et al., 2023; Edwards et al., 2022; Holland et al., 2023b; Schmidt et al., 2020). Here, we define the North-East Atlantic to be inclusive of the North Sea, Celtic Seas, English Channel, Western Approaches, and adjacent oceanic waters directly west of this shelf (Fig. 1). Recent analyses based on plankton “lifeforms”, broad groups of taxa sharing common traits (McQuatters-Gollop et al., 2019a; Tett et al., 2008), have recorded declining diatom and dinoflagellate abundance across oceanic waters, contrasting with more stable diatom abundance in the coastal

North Sea (Edwards et al., 2022; Holland et al., 2023b). More localised studies support these regional patterns at specific coastal sites, reporting site-specific shifts in diatom and dinoflagellate abundance trends (Freund et al., 2012; Hernandez-Farinas et al., 2014; Kléparski et al., 2024). These observed changes have been linked to the effects of climate-driven warming and multidecadal variability in sea surface temperature (SST), altered wind regimes (Chivers et al., 2020; Edwards et al., 2022; Hinder et al., 2012), changing phenology of bloom formation (González Taboada and Anadón, 2014), and nutrient limitation associated with increasing summer stratification intensity (Edwards et al., 2022; Schmidt et al., 2020).

The plankton lifeform approach (Tett et al., 2008) is routinely

Graphical abstract

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<https://doi.org/10.1016/j.hal.2026.103113>

Received 1 September 2025; Received in revised form 26 March 2026; Accepted 30 March 2026

Available online 30 April 2026

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applied as a pelagic habitats (plankton) indicator to support biodiversity assessments for the Oslo-Paris Convention (OSPAR) (OSPAR Commission, 2023), which coordinates environmental protection of the North-East Atlantic (see Fig. 1 for a map of OSPAR regions relevant to this study) among 15 European countries (McQuatters-Gollop et al., 2019a, 2019b). Among the lifeforms assessed by OSPAR, diatoms and dinoflagellates have distinctive traits and play essential trophic and biogeochemical roles in the marine environment. As a lifeform, diatoms

are characterised by a coherent set of functional traits, including silica-based frustules, ability to bloom, and physiological adaptations to turbulent environments (Behrenfeld et al., 2021; Litchman, 2022), and by their role as major contributors to primary production, carbon sequestration, and silica cycling (Benoiston et al., 2017; Rousseaux and Gregg, 2013; Serodio and Lavaud, 2022). All pelagic diatoms are primarily phototrophic, although some have mixotrophic capabilities (Villanova and Spetea, 2021). Dinoflagellates, by contrast, encompass a

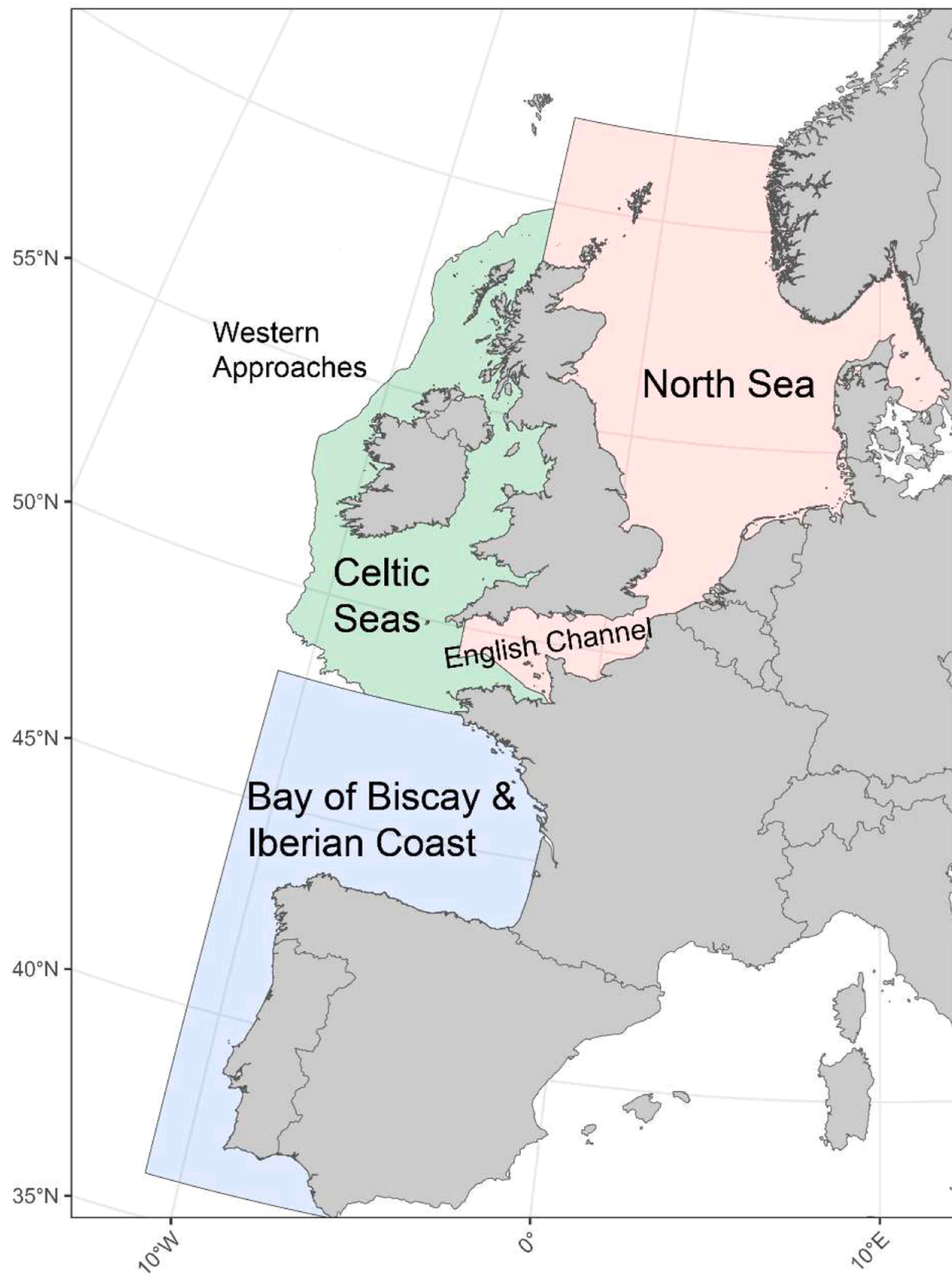


Fig. 1. Map of the study region, displaying the regional seas mentioned in this study, specifically with OSPAR regions relevant to this study coloured and indicated with larger text.

diverse group of planktonic protists that include phototrophic, heterotrophic, and mixotrophic species. Their mixotrophic members acquire energy both through photosynthesis and through predation on other cells (Mitra, 2024). Both diatoms and dinoflagellates include species capable of forming harmful algal blooms (HABs), though the specific traits associated with harmfulness and mechanism or concept of ‘harm’ vary across taxa. Currently there is no specific OSPAR indicator to assess the status of these HAB genera or their impacts, although an early theoretical framework to support decision making by managers and policy makers has been proposed (Sagarminaga et al., 2023).

A few diatom species of the genus *Pseudo-nitzschia* and dinoflagellate species of the genus *Dinophysis* have been responsible for enforced closures of shellfish harvesting areas in the UK on a near-annual basis. *Pseudo-nitzschia* spp. H. Peragallo in H. Peragallo and M. Peragallo (1897), are routinely detected in the waters around the British Isles (Bresnan et al., 2021, 2015b; Downes-Tettmar et al., 2013; Whyte et al., 2023). Species within this genus can be producers of the neurotoxin domoic acid (DA), which caused a number of human fatalities in Canada in the 1980s (Bates et al., 1988). To protect human health, the EU Shellfish Hygiene Directive (originally 79/923/EEC, now EU 2019/627) introduced statutory monitoring for DA in shellfish and for the causative organism, *Pseudo-nitzschia* spp. in shellfish growing waters since the early 1990s (European Commission, 1979, 2019). Since monitoring began, DA above regulatory levels has been responsible for significant closures of king scallop (*Pecten maximus*) harvesting and offshore fishing areas between 2000 and 2003 in UK waters (Bresnan et al., 2017; Gallacher et al., 2001; Rowland-Pilgrim et al., 2019). Closures of shellfish harvesting areas in Europe are enforced, particularly in countries influenced by Atlantic waters (Bresnan et al., 2021; Karlson et al., 2021). *P. australis* and *P. seriata* have been confirmed as DA producers in Scottish waters (Fehling et al., 2004), while *P. multiseriata* has been confirmed as a DA producer in the Southwest of England (Fehling et al., 2004; Percy et al., 2006; Percy, 2006).

The dinoflagellate genus, *Dinophysis* Ehrenberg (1841), is a common component of the summer dinoflagellate community in the North Sea, Atlantic coast of the UK, Irish Sea, and English Channel (Bresnan et al., 2021; Karlson et al., 2021). Species within this genus can produce diarrhetic shellfish toxins (DSTs), including okadaic acid (OA) and dinophysistoxins (DTXs), as well as pectenotoxins (PTXs), of which the latter are not considered harmful to humans. Intoxication of wild and farmed shellfish is widespread along the Atlantic margin of Europe during the summer months (Bresnan et al., 2021; Karlson et al., 2021). In the UK, the main toxin producing *Dinophysis* species are members of the *D. acuminata* complex and *D. acuta* (Bresnan et al., 2021, 2005; Davidson and Bresnan, 2009; Whyte et al., 2014). *D. acuminata* complex is responsible for widespread closures of shellfish harvesting areas in Scotland on an annual basis (Whyte et al., 2023) and sporadic closures in Northern Ireland and the South west coast of England (Bresnan et al., 2021). In contrast, impacts from *D. acuta* are more sporadic in Scotland (Swan et al., 2018), and less frequent along the south coast of England (Brown et al., 2022).

Phytoplankton populations respond to environmental changes by altering distribution, phenology, and abundance, thus it is important we understand these changes so that we can anticipate potential impacts from harmful taxa on higher trophic levels, coastal industries, and communities. Several recent studies have investigated alterations in physical and chemical conditions of the North-East Atlantic over the past 15 to 20 years (Beaugrand, 2009; Capuzzo et al., 2018; Schmidt et al., 2020). Sea surface temperature has increased significantly in North-East Atlantic over recent decades (Bedford et al., 2020). The northern North Sea shows long-term declining nutrients and salinity alterations alongside a long-term decline in silicate (Hátún et al., 2021). The Western English Channel has experienced increasing summer stratification in surface waters due to increasing SST, reducing nutrient exchange with otherwise productive surface waters. Increasing stratification and declining silicate are likely to have a negative impact of diatom growth,

and indeed the abundance of diatoms has declined in the Channel (Atkinson et al., 2021, 2024; Holland et al., 2023b). This region has also experienced a decline in eukaryotic plankton relative to smaller bacterioplankton (Atkinson et al., 2021, 2024; Schmidt et al., 2020). While the conventional thought is that stratification may benefit dinoflagellates, in reality they are showing long-term declining abundance, both offshore and coastal (Atkinson et al., 2021, 2024; Holland et al., 2023b).

In the UK, monitoring of shellfish growing waters for the presence of toxin producing species, including *Pseudo-nitzschia* and *Dinophysis* spp., commenced in the late 1990s in response to the EU Shellfish Hygiene Directive (79/923/EEC) (Bresnan et al., 2021; Brown et al., 2022). Previous studies using data from the Continuous Plankton Recorder (CPR) Survey (Richardson et al., 2006), a large scale plankton monitoring programme, have shown how changes in environmental/climatic conditions have influenced the distribution of these two genera in the North-East Atlantic. Edwards et al. (2006) showed how the distribution of high abundances of *Dinophysis* had shifted in the North Sea between the 1970s and early 2000s from the east coast of the UK to the Norwegian coast due to regional climate-driven hydrographic changes, specifically warming, increased freshwater influence, combined with basin-scale impacts of the North Atlantic Oscillation (NAO). Hinder et al. (2012) showed *Pseudo-nitzschia* abundance had increased in the North Sea since the 1990s, linked to increases in sea surface temperature and wind velocity.

Currently, the long-term full community taxonomic phytoplankton time-series needed for statutory biodiversity assessment of the marine environment in the North-East Atlantic (i.e., to support OSPAR and national assessments) are often scarce, or restricted to a few data-rich coastal locations (Holland et al., 2025). While all Contracting Parties of the OSPAR Convention are obligated to monitor phytoplankton biodiversity in support of Marine Strategy Framework Directive (MSFD) descriptor D1C6, not all currently provide suitable biodiversity time-series. In such cases, some have submitted shellfish hygiene monitoring time-series for *Pseudo-nitzschia* and *Dinophysis* to OSPAR for use as raw inputs to lifeform-based indicator assessments. As an example, for the OSPAR Quality Status Report 2023 (QSR2023; OSPAR Commission, 2023), where suitable phytoplankton biodiversity data were unavailable for the Portuguese coast (within OSPAR Region IV: Bay of Biscay & Iberian Coast; Fig. 1), monitoring data for *Pseudo-nitzschia* and *Dinophysis* (from 2002 to 2020) were provided as proxies for total diatoms and dinoflagellates to support statutory indicator assessment (Holland et al., 2023a).

Portugal and northwest Spain's Atlantic coast form the northern limit of the Canary/Iberia Current Upwelling System (CCUS) (Kämpf and Chapman, 2016). Along this coastal margin, wind-driven upwelling pulses and relaxations control seasonal production and species succession, with *Pseudo-nitzschia* spp. often responding rapidly to upwelling and can dominate after the initial bloom of centric diatoms, whereas *Dinophysis* spp. typically peak during later, stratified periods or are advected along the shelf (Díaz et al., 2019, 2014; Escalera et al., 2010; Torres Palenzuela et al., 2019). Considering this regional heterogeneity, any use of genus-level counts as proxies for whole lifeforms requires an understanding of how these groups covary with their broader lifeforms, and site-specific justification, reflecting the local hydrodynamic and nutrient regimes (Ferreira Cordeiro et al., 2022). It was therefore our intention to test this proxy assumption formally across different sites and habitats by comparing *Pseudo-nitzschia* and *Dinophysis* time-series with total diatom and total dinoflagellate lifeforms at fixed-point stations and in adjacent offshore CPR data.

Coastal and open water communities are impacted by different hydrographic conditions, the former by direct anthropogenic input from river output and coastal erosion or disturbance, whilst open waters are affected by Atlantic currents carrying salinity, heat, and nutrients. Yet, both are connected by wind driven advection or transport on phytoplankton, including HAB species (Gillibrand et al., 2016; Whyte et al.,

2014). The abiotic drivers directly impact biological communities in different ways at coastal and open water habitats. Thus, our aims are to use data from two fixed-point monitoring stations in UK waters, as well as data from the Continuous Plankton Recorder (CPR) Survey, to: 1) assess how *Pseudo-nitzschia* and *Dinophysis* data can be used to support statutory biodiversity assessments; 2) assess how *Pseudo-nitzschia* and *Dinophysis* abundance data from the CPR Survey compares with data from fixed-point monitoring stations; and 3) examine regional variability in *Pseudo-nitzschia* and *Dinophysis* abundance across the North-East Atlantic, and assess how their distributions have shifted over time.

2. Methods

2.1. Monitoring data

Phytoplankton abundance data used for this analysis, primarily focused on UK waters of the Greater North Sea (OSPAR Region II) (Fig. 1), were obtained from three sources (Fig. 2):

1. Plymouth Marine Laboratory (PML) phytoplankton data from the L4 monitoring station in the western English Channel (1992–2021) (1225 samples)
2. Marine Directorate of the Scottish Government Scottish Coastal Observatory (SCOs) phytoplankton data from the Stonehaven monitoring station on the east coast of Scotland (2000–2021) (938 samples)
3. Marine Biological Association (MBA) Continuous Plankton Recorder (CPR) Survey phytoplankton data from the North-East Atlantic (1960–2021) (Bounding box: W = -18° , S = 32° , E = 14° , N = 66°) (122,122 samples)

2.2. Site description and monitoring methods

2.2.1. Plymouth Marine Laboratory (PML) – L4 station

The L4 station is located about 16 km southwest of Plymouth, England, in the western English Channel at approximately 50 m depth. L4

is a dynamic coastal site influenced by tidal mixing and occasional riverine input (Smyth et al., 2010). The site develops seasonal stratification during summer with a weak thermocline ($2-3^{\circ}\text{C}$ difference) and nutrient depletion in surface waters; the mixed layer depth (MLD) during this period is typically confined to 10–20 m (Atkinson et al., 2025). Sampling is conducted weekly, weather permitting, from a depth of 10 m, using a 10 or 20 L Niskin bottle attached to the CTD. This depth is chosen as being representative of the surface mixed layer. A 200 mL sample is immediately preserved in acid Lugol's iodine at a final concentration of 2% and stored in cool, dark conditions until analysis using the Utermöhl technique (Widdicombe et al., 2010). A full suite of physical and chemical samples is collected concurrent with phytoplankton sampling and can be downloaded from: <https://doi.org/10.17031/645110fb81749> (McEvoy et al., 2023).

2.2.2. Marine Directorate Scottish Coastal Observatory (SCOs) – Stonehaven station

The SCOs Stonehaven site lies about 5 km offshore on Scotland's east coast, 15 miles south of Aberdeen, in the North Sea. It is also roughly 50 m deep and highly exposed, with strong tidal mixing that keeps the water column well mixed for most of the year. Samples are collected weekly, weather permitting (Bresnan et al., 2016). Phytoplankton samples are collected using a 10 m integrated tube sampler and 1 L subsample returned to the laboratory. Samples are preserved in 0.5% acidic Lugol's iodine and analysed using the Utermöhl technique (Bresnan et al., 2016). A full suite of physical and chemical samples collected and can be downloaded from: <https://data.marine.gov.scot/dataset/scottish-coastal-observatory-stonehaven-site>. More detailed descriptions of the site and methodologies used can be found in Bresnan et al. (2016).

2.2.3. Marine biological association Continuous Plankton Recorder (CPR) survey

Phytoplankton abundance data were obtained from the Continuous Plankton Recorder (CPR) Survey monitoring programme. This spatially extensive open water survey programme represents the longest running, most geographically extensive marine ecological survey in world, and

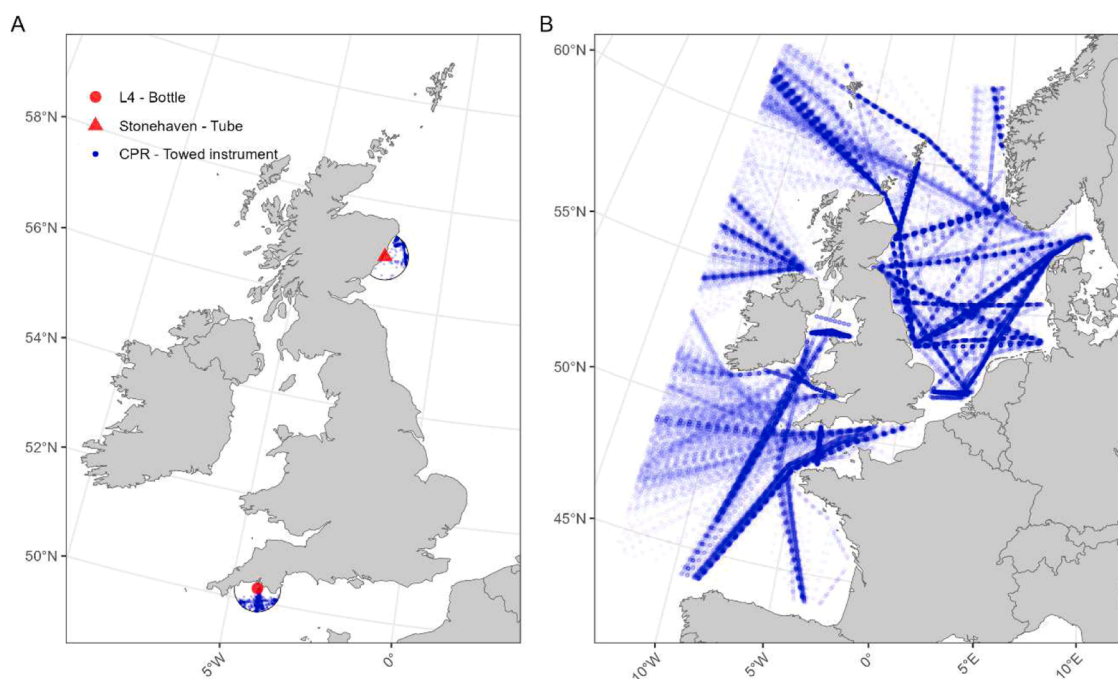


Fig. 2. Locations for the CPR samples (blue), and the L4 and Stonehaven monitoring stations (red) used for the comparisons of station and CPR data (A), and locations of CPR samples used to assess long-term changes in *Pseudo-nitzschia* and *Dinophysis* distribution (B). The buffer (black radius) around each station in A represents the 50 km radius which was used to extract intersecting data from the CPR for comparison with station data.

represents the longest continuous phytoplankton time-series in UK waters (Guinness World Records, 2023; McQuatters-Gollop et al., 2015; Richardson et al., 2006). CPR samples are collected offshore and in the open ocean in transects using ships-of-opportunity. Samples are collected at a mean depth of ~10 m with a mesh size of 270 µm and divided into samples of ~10 nmi. Due to the vessel’s propellers, the CPR instrument samples a mixed vertical profile of between 15 - 30 m within the surface layer (Nylund et al., 2023). Laboratory processing and counting protocols for the CPR Survey have been maintained as a standardised procedure since 1958 (Reid et al., 2003), explicitly to enable direct comparison of samples across decades and regions. CPR Survey data are best analysed at a monthly time scale, as was the case for our analyses, due to high variability (Richardson et al., 2006).

Plankton specimens contained in samples are identified and counted using light microscopy, with different counting methods for large zooplankton (> 2 mm), microzooplankton (< 2 mm), and phytoplankton (Richardson et al., 2006). A standardised subsample of each CPR filtering silk is analysed for phytoplankton; phytoplankton abundance is therefore semi-quantitatively estimated from the frequency of taxa observed across multiple fields of view (Richardson et al., 2006). While the majority of phytoplankton are < 200 µm diameter, many of these cells are consistently retained in CPR samples despite the larger mesh size, due to partial clogging by other plankton reducing the mesh size (Batten et al., 2003).

Despite the different sampling and counting methods between these three datasets, they often show the same trends in abundance over a multidecadal scale (John et al., 2001; Stern et al., 2023). The two data types are complementary, each revealing different aspects of spatial and temporal variability across the plankton community. CPR Survey data can be particularly useful for examining the direction and magnitude of changes occurring across large offshore pelagic habitats, revealing regional patterns of change (Bedford et al., 2020). Fixed-point station time-series provide complementary information at a higher sampling frequency for a larger fraction of the plankton size spectrum, including fragile and very small species that are poorly retained in CPR nets due to the harsh sampling method and relatively large mesh size. Additionally, fixed-point monitoring stations provide valuable data for more near-shore habitats that are particularly valuable for studying anthropogenic pressures such as eutrophication (McQuatters-Gollop et al., 2019a) and pollution (Serranito et al., 2016).

2.3. Spatial, temporal, and taxonomic aggregation

Due to differences in sampling, analysis, and enumeration methods, all datasets were analysed separately, using an identical set of data processing and statistical methods. To ensure datasets were comparable, CPR abundance values were transformed to units of cells litre⁻¹ by dividing abundance by 3000, since an average CPR sample filters ~3 m³ of seawater (Richardson et al., 2006). All data analysis for this study was conducted using R-programming language (Version 4.5.1; R Core Team, 2025).

Pseudo-nitzschia cells cannot be identified to species level using routine light microscopy and are often divided into size categories, e.g., ‘*P. delicatissima* group’ (width < 3 µm), ‘*P. seriata* group’, and ‘*P. pungens* group’ (> 3 µm), with the L4 time-series making a further separation of the ‘*P. seriata* group’ and ‘*P. pungens* group’ based on morphological features (Downes-Tettmar et al., 2013). Practicably, when analysing samples using 200x magnification for L4 and Stonehaven, this means plus or minus one division (equivalent to ~ 5 µm) in the eyepiece graticule. CPR samples are analysed at 500x magnification, where one division in the eyepiece graticule is ~2 µm diameter. To calculate total *Pseudo-nitzschia* abundance for each plankton sample from the PML L4 station data, we summed the abundances of ‘*P. delicatissima* group’, ‘*P. pungens* group’, and ‘*P. seriata* group’ (Table 1). For Stonehaven data, *Pseudo-nitzschia* have not been consistently sized since the commencement of the time-series in 1997, so for our study *Pseudo-nitzschia* cells

Table 1
List of recorded names counted as *Pseudo-nitzschia* groups and *Dinophysis* species for each of the three plankton monitoring programmes used in this analysis. Genus level Aphia ID is used for all *Pseudo-nitzschia* categories due to the diversity of species potentially contained within these groups.

Pseudo-nitzschia categories counted					
L4 (PML)		Stonehaven (SCObs)		CPR Survey	
Aphia ID	Record name in institute species list	Aphia ID	Record name in institute species list	Aphia ID	Record name in institute species list
149151	<i>Pseudo-nitzschia delicatissima</i>	149151	<i>Pseudo-nitzschia</i>	149151	<i>Pseudo-nitzschia delicatissima</i>
	<i>Pseudo-nitzschia pungens</i>				<i>Pseudo-nitzschia seriata</i>
	<i>Pseudo-nitzschia seriata</i>				<i>Nitzschia/Pseudo-nitzschia</i> spp. (unidentified)
Dinophysis categories counted					
L4 (PML)		Stonehaven (SCObs)		CPR Survey	
Aphia ID	Record name in institute species list	Aphia ID	Record name in institute species list	Aphia ID	Record name in institute species list
109462	<i>Dinophysis</i>	109462	<i>Dinophysis</i>	109462	<i>Dinophysis</i>
109603	<i>Dinophysis acuminata</i>	109603	<i>Dinophysis acuminata</i>		
109604	<i>Dinophysis acuta</i>	109604	<i>Dinophysis acuta</i>		
232496	<i>Dinophysis nasuta</i>	109616	<i>Dinophysis dens</i>		
232261	<i>Dinophysis sacculus</i>				
109662	<i>Dinophysis tripos</i>				

were considered as a single category and no summing was necessary. For CPR data, the ‘*P. seriata* group’ is defined as *Pseudo-nitzschia* cells > 3 µm in width, whereas the ‘*P. delicatissima* group’ are < 3 µm in width. CPR data also includes a ‘*Nitzschia/Pseudo-nitzschia* spp. (unidentified)’ category, which applies to cells which do not fit clearly into the *P. delicatissima* or *P. seriata* size ranges. For our analysis of CPR data, we summed the abundance of ‘*P. delicatissima* group’, ‘*P. seriata* group’, and ‘*Nitzschia/Pseudo-nitzschia* spp. (unidentified)’ cells.

To calculate total *Dinophysis* abundance for each plankton sample from the PML L4 station data, we summed the abundances of five counted species, as well as genus level *Dinophysis* abundances (Table 1), while for Stonehaven data *Dinophysis* abundance was summed from three taxa and genus level *Dinophysis* abundances. For the CPR data, *Dinophysis* cells were only counted as a single category to genus level without speciation, so no summing was necessary.

To investigate how the abundance of *Pseudo-nitzschia* and *Dinophysis* cells relate to the wider diatom and dinoflagellate communities, respectively, we also calculated per sample total diatom and dinoflagellate abundance, using the UK and OSPAR Masterlist of plankton trait information (available from <https://www.dassh.ac.uk/lifeforms/>; Ostle et al., 2021), to identify matching records by World Register of Marine Species (WoRMS) Aphia ID (Vandepitte et al., 2015). Per sample total *Pseudo-nitzschia* and *Dinophysis* abundance were then subtracted from total diatom and total dinoflagellate abundance to generate the categories ‘other diatoms’ and ‘other dinoflagellates’, respectively, to ensure these groups remained independent.

To support the comparison of station data with CPR data, station and CPR sample coordinates were projected to the ETRS89-extended / LAEA Europe planar coordinate system and a 50 km radius buffer was generated around each of the two stations. The size of radius was selected to ensure it would intersect samples from the CPR A- (Aberdeen

to Shetland) and LR-routes (Hull to Aberdeen) which pass close to the Stonehaven station. This radius was also suitable for capturing the CPR PR- (Plymouth to Roscoff) and B-routes (Portsmouth to Caribbean) that run close to the L4 site. The two buffers were intersected with CPR sample coordinates to extract all CPR samples falling within each radius and corresponding range of dates, resulting in a match of 794 CPR samples for L4, and 601 for Stonehaven (Fig. 2).

Station data and CPR samples intersecting each buffer were then aggregated by month to generate monthly mean abundance time-series for *Pseudo-nitzschia* and *Dinophysis*, for station and adjacent CPR data to generate four data subsets (i.e. Station data: PML data at L4, SCObS data at Stonehaven; CPR data: CPR data around L4, CPR data around Stonehaven).

2.4. Seasonal component of the phytoplankton community

To assess how well *Pseudo-nitzschia* and *Dinophysis* represent changes occurring their respective diatom and dinoflagellate communities, and whether this varies regionally and seasonally, we divided the L4 and Stonehaven station data into four seasons (Spring: March to May, Summer: June to August, Autumn: September to November, and Winter: December to February) and conducted Pearson correlation tests between z-score normalised abundances (i.e., $y = (x - \text{mean}(x)) / \text{sd}(x)$) for “total *Pseudo-nitzschia*” and “other diatoms”, and for “total *Dinophysis*” and “other dinoflagellate” for each subset.

We subsequently assessed the full monthly abundance time-series for each group and calculated the mean annual abundance cycle for the four data subsets across a shared period (1992–2021). Finally, we used linear regression to assess synchronisation in the seasonality of the annual peak in abundance by comparing the month when peak abundance occurred (1–12) for each year to assess how well annual cycles in *Pseudo-nitzschia* and *Dinophysis* abundance reflect annual cycles of the overall diatom and dinoflagellate communities.

2.5. Trend analysis of station time-series

To examine and compare long-term abundance trends in *Pseudo-nitzschia* and *Dinophysis* with those of the ‘other diatoms’ and ‘other dinoflagellates’, we applied the Kendall trend test (Millard, 2013) separately for each time-series. The Kendall trend test was also used to identify any long-term trends in the annual mean values for the five environmental variables monitored in common between the two stations, namely temperature, chlorophyll-a, total oxidised nitrogen, phosphate, and silicate. For any significant trends, Sen’s slope was used to estimate the rate of change in environmental variables. Prior to calculating trends, annual mean values were calculated to smooth out the seasonal variation typical of plankton time-series. The sign of the test statistic reveals the direction of the trend, and the magnitude is proportional to the consistency in the trend, ranging between –1 and 1. A benefit of this nonparametric test is that it yields identical results irrespective of the data transformation method and is not sensitive to either gaps in data or to non-linear or irregular trends.

2.6. Examining changes in distribution

To calculate changes in the distribution of *Pseudo-nitzschia* and *Dinophysis* over the last six decades, CPR Survey data was used exclusively, due to its broad offshore coverage across the North-East Atlantic (Fig. 2B), with abundances calculated as described in Section 2.3. Separate distribution maps were also generated for *P. delicatissima* and *P. seriata* groups to understand how variation in the distribution of the genus is influenced by variation in these two size categories. For *Dinophysis*, the aggregation to genus level step was unnecessary since *Dinophysis* is only counted at genus level in the CPR Survey dataset, thus it was not possible to study how individual *Dinophysis* species contributed to the overall distribution of the genus.

All samples were intersected with a $1^\circ \times 1^\circ$ square grid to calculate monthly mean abundance values for each grid cell and regularise the data across the grid. Abundance values were then $\log_{10}(x + 1)$ transformed and interpolated across the grid using inverse distance weighted interpolation with a minimum number of neighbours of 3, following methods described in Edwards et al. (2021) and Beaugrand (2024), which used a maximum search radius of 250 km to interpolate 1° gridded CPR data. Finally, to fill additional gaps in the CPR time-series all gaps of three months or less were filled via linear interpolation independently for each grid cell (Bedford et al., 2020; Holland et al., 2024, 2023b). To assess the performance and reliability of the interpolation results, we plotted interpolated values against raw monthly mean values from corresponding grid cells and used linear regression to assess how the comparison varied from the expected 1:1 relationship.

From the interpolated gridded abundance data, maps displaying mean patterns of *Pseudo-nitzschia* and *Dinophysis* distribution were generated for the four seasons so that changes in distribution could be studied through time. Because each grid cell represents decadal seasonal averages, any gaps previously filled by interpolation were likely further smoothed by incorporating data from other years without gaps. Decadal anomaly maps were also generated to show the percentage difference in *Pseudo-nitzschia* and *Dinophysis* abundance for each grid cell relative to mean values recorded for the same cell in the first decade of the time-series (i.e., 1960 – 1970).

3. Results

3.1. Overall abundance trends in station and CPR survey monitoring

3.1.1. *Pseudo-nitzschia*

The seasonal cycle of *Pseudo-nitzschia* at the L4 site over the course of the time-series shows the ‘*P. delicatissima* group’ to be more abundant, while the CPR data shows the ‘*P. seriata* group’ to be the dominant group. Total *Pseudo-nitzschia* cells were more abundant in the L4 and corresponding CPR time-series, relative to the corresponding data from Stonehaven (Fig. 3A). At L4, the CPR dataset showed earlier appearance and more mixed *Pseudo-nitzschia* groups relative to the corresponding station data, which predominantly detected the ‘*P. delicatissima* group’. CPR data also shows increasing *Pseudo-nitzschia* abundance between July and October, contrasting with the L4 dataset.

3.1.2. *Dinophysis*

CPR and L4 station data show similar *Dinophysis* seasonal abundance profiles. Both CPR and fixed-point station abundance cycles from L4 and Stonehaven, respectively show that *Dinophysis* spp. are more abundant at Stonehaven than in the English Channel, and dominated by two species, *D. acuminata* complex and *D. acuta* at both sites, with the former more abundant with an earlier peak abundance. Further, SCObS data for Stonehaven recorded earlier seasonal bloom start and peak abundances versus data from the CPR Survey (Fig. 3B). In the English Channel, CPR and L4 *Dinophysis* spp. seasonal profiles were similar, mostly between May and September, although the maximum abundance at L4 was a month earlier for the CPR data, versus the station data. Similar to Stonehaven, *D. acuminata* was more abundant than *D. acuta* at L4 and peaked earlier in the summer.

3.2. Seasonal abundance in the wider phytoplankton community

Fig. 4 presents how the seasonal abundances of *Pseudo-nitzschia* spp. relate to the ‘other diatom’ component of the community and how *Dinophysis* seasonal abundance relates to ‘other dinoflagellates’. All datasets revealed only short discrete periods where peak abundance of both *Pseudo-nitzschia* and *Dinophysis* at L4 and Stonehaven co-occurred with ‘other diatoms’, and with ‘other dinoflagellates’, respectively. The period of high abundance for ‘other diatoms’ spanned roughly from March to October, whereas the main peak in *Pseudo-nitzschia* abundance

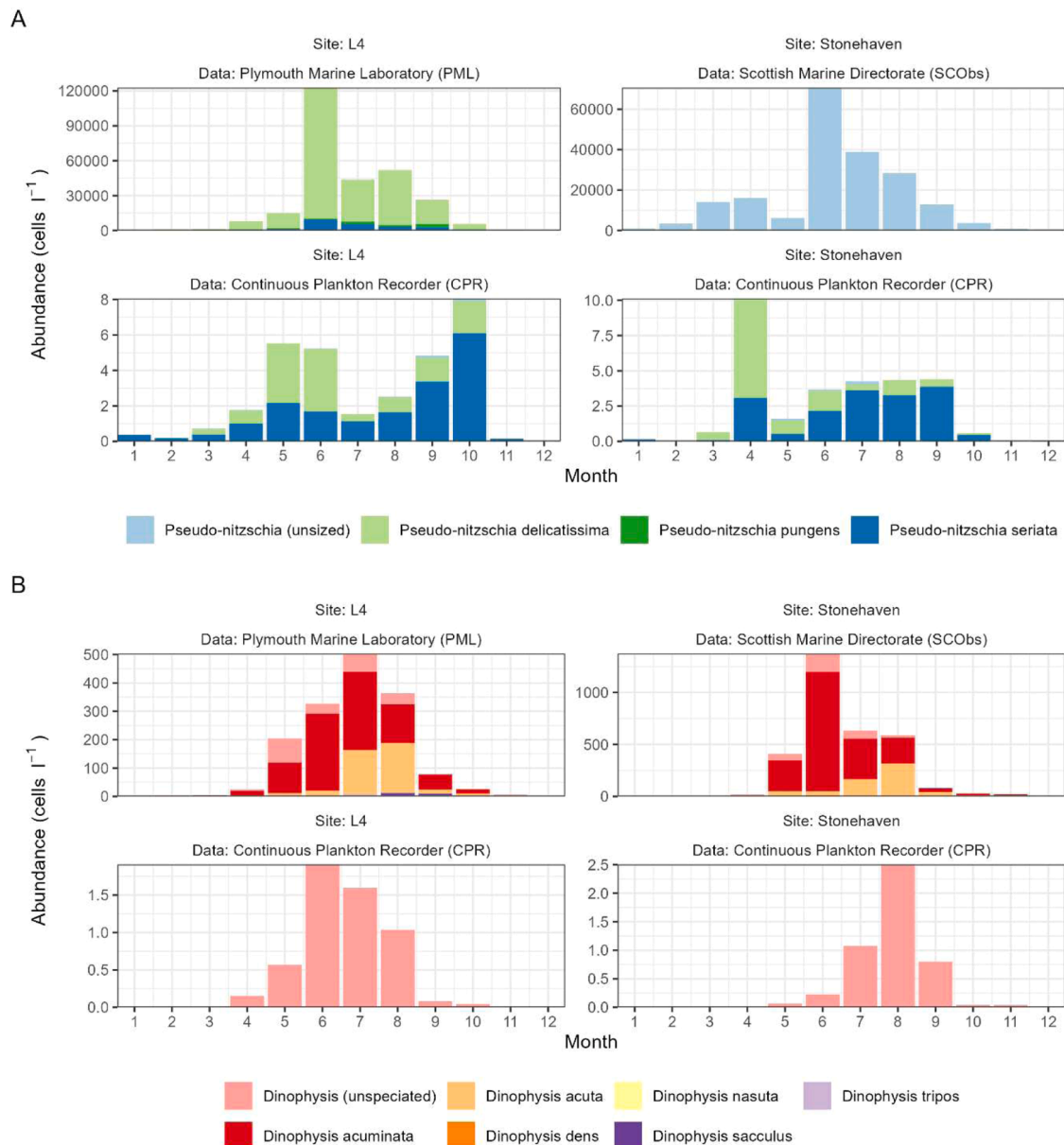


Fig. 3. The mean annual abundance cycle for *Pseudo-nitzschia* (A) and *Dinophysis* (B) species at the L4 (left panels) and Stonehaven (right panels) sites, calculated from CPR and station datasets. Note that each subplot has a unique y-axis scale.

lasted for a shorter period, from May to September. At both stations the annual abundance cycle for *Pseudo-nitzschia* demonstrated two peaks per year, with the first peak typically occurring in spring, between April and June, and the second peak occurring between June and September. The seasonal timing of peak *Pseudo-nitzschia* abundance (Figure S 2) coincided with the periods of strongest (albeit still weak) correlation between *Pseudo-nitzschia* and 'other diatoms' abundance in spring and autumn (Figure S 1). However, *Pseudo-nitzschia* spp. seasonality was much weaker at station L4 compared to that of Stonehaven. Both *Dinophysis* and 'other dinoflagellates' demonstrated only one abundance peak in their mean annual cycles. The mean seasonal peak in *Dinophysis* spp. abundance mainly occurred earlier than that of 'other dinoflagellates'. At site L4, *Dinophysis* peaked in July, while 'other dinoflagellates' peaked August to September. At Stonehaven, SCOBS data showed that *Dinophysis* peaked in June and 'other dinoflagellates' peaked in July, while for CPR data both peaked in August.

Regression analysis, performed to compare the timing of annual abundance peaks in *Pseudo-nitzschia* with 'other diatoms', indicated

some similarity in their timing. However, the comparison was only statistically significant for station data at Stonehaven and CPR data at L4 (Figure S 1). For *Dinophysis* and 'other dinoflagellates', the only statistically significant pairing was for CPR data at Stonehaven, indicating high variability in the timing of annual peaks in abundance. In all cases except for *Dinophysis* from CPR data at Stonehaven, regression coefficients were below 1, indicating a tendency for *Pseudo-nitzschia* and *Dinophysis* to peak in abundance earlier than 'other diatoms' and 'other dinoflagellates', respectively.

The proportion of total diatom abundance contributed by *Pseudo-nitzschia* varied throughout the annual cycle (Figure S 3). At L4, PML data showed that *Pseudo-nitzschia* abundance, relative to the rest of the diatom community, was 12% on average and peaked throughout the summer, between June and September, during which time it comprised on average 22% of all diatoms present in samples. At Stonehaven, SCOBS data revealed the relative abundance of *Pseudo-nitzschia* was on average 16% and peaked in February at 24%, prior to the spring diatom bloom, with a second peak in July at 26% of total diatom abundance. *Dinophysis*

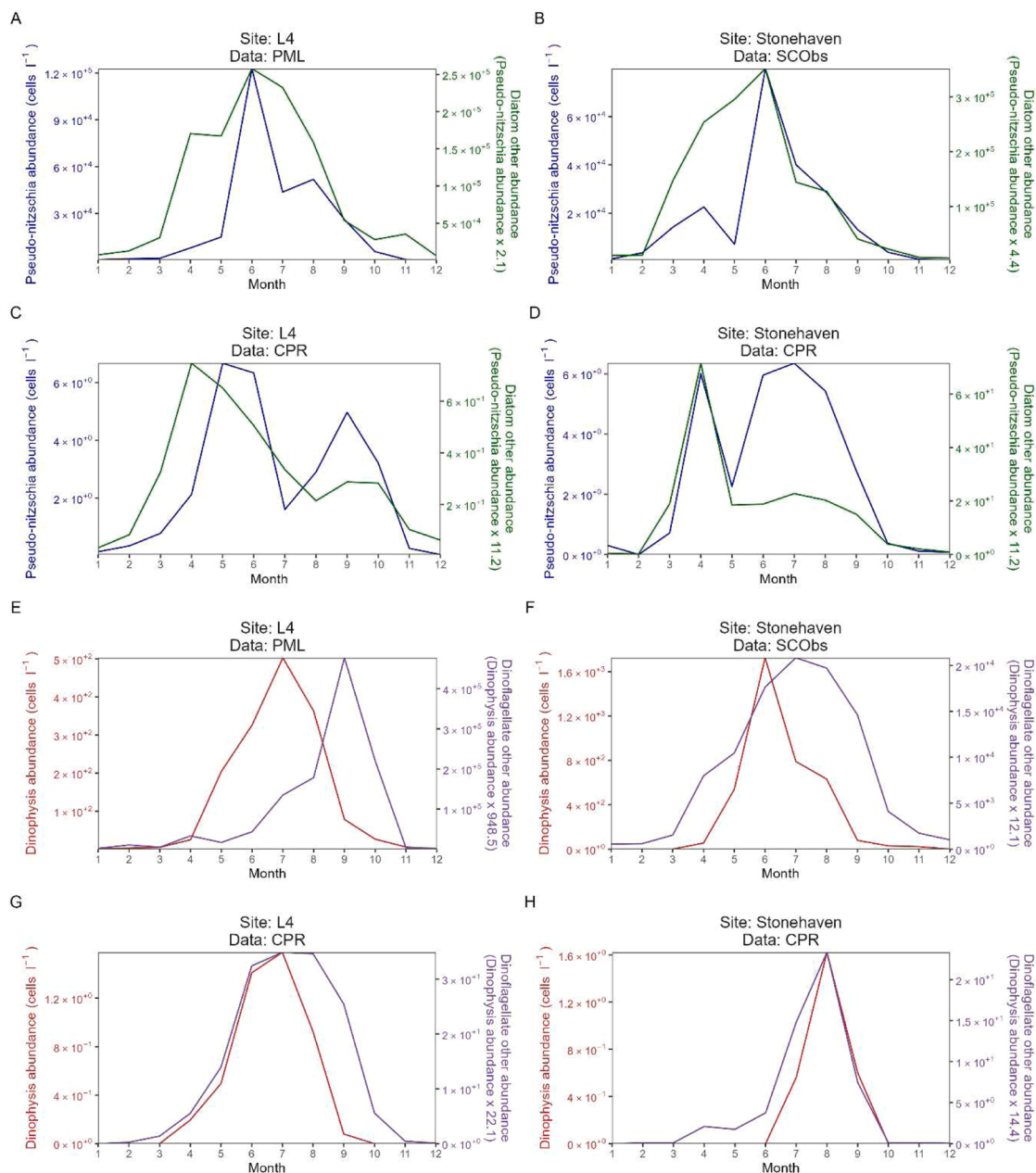


Fig. 4. The mean annual cycle of *Pseudo-nitzschia* (blue) and 'other diatom' (green) abundance for station L4 using the PML data (A) and using CPR data (C), and for Stonehaven using SCObS data (B) and using CPR data (D), as well as the mean annual cycle of *Dinophysis* (red) and 'other dinoflagellates' (purple) abundance for station L4 using the PML data (E) and using CPR data (G), and for Stonehaven using SCObS data (F) and using CPR data (H). Note that the second y-axis on all plots has been transformed to allow for both time-series to be resolved on the same plots.

made up only a small proportion of the dinoflagellate community, on average 0.4% at L4 and 2.5% at Stonehaven. At L4, the proportion of dinoflagellates belonging to *Dinophysis* peaked at 1.5% in May, while at Stonehaven they peaked in June at 9.5%.

3.3. Trend analysis of station time-series

Long-term abundance trends in *Pseudo-nitzschia* and 'other diatoms' were most similar for PML data at L4, with near-identical results of the Kendall trend test ($z = -0.22$, $p = 0.10$ for both groups; **Figure S 4**). However, the only statistically significant trend observed was an increasing trend at L4 from CPR data, indicating only limited evidence of long-term change within the surveyed period at the two stations. For *Dinophysis*, long-term abundance trends demonstrated a similarly low level of similarity. The negative trend in 'other dinoflagellate'

abundance at L4 was the only statistically significant trend observed. Despite lack of evidence for persistent long-term trends in abundance, the timing of peaks and troughs in annual mean abundance showed some synchronisation, particularly for dinoflagellates and *Dinophysis* at Stonehaven. This synchronisation in the timing of annual peaks was also reflected in the direct comparison of annual abundance peak month of occurrence (**Figure S 2**).

At the L4 station, temperature has increased at a rate of $0.028\text{ }^{\circ}\text{C year}^{-1}$, chlorophyll-a has decreased at a rate of $0.025\text{ }\mu\text{g L}^{-1}\text{ year}^{-1}$, and silicate has decreased at a rate of $0.042\text{ }\mu\text{M year}^{-1}$ (**Fig. 5**). Extrapolating over the time-series, temperature has increased $0.8\text{ }^{\circ}\text{C}$ and chlorophyll-a has decreased $0.73\text{ }\mu\text{g L}^{-1}$ since 1992, while silicate has decreased $0.88\text{ }\mu\text{M}$ since 2000. At Stonehaven, the only statistically significant change in monitored environmental variables was a $0.05\text{ }\mu\text{M year}^{-1}$ decrease in silicate. Over the course of environmental monitoring at Stonehaven,

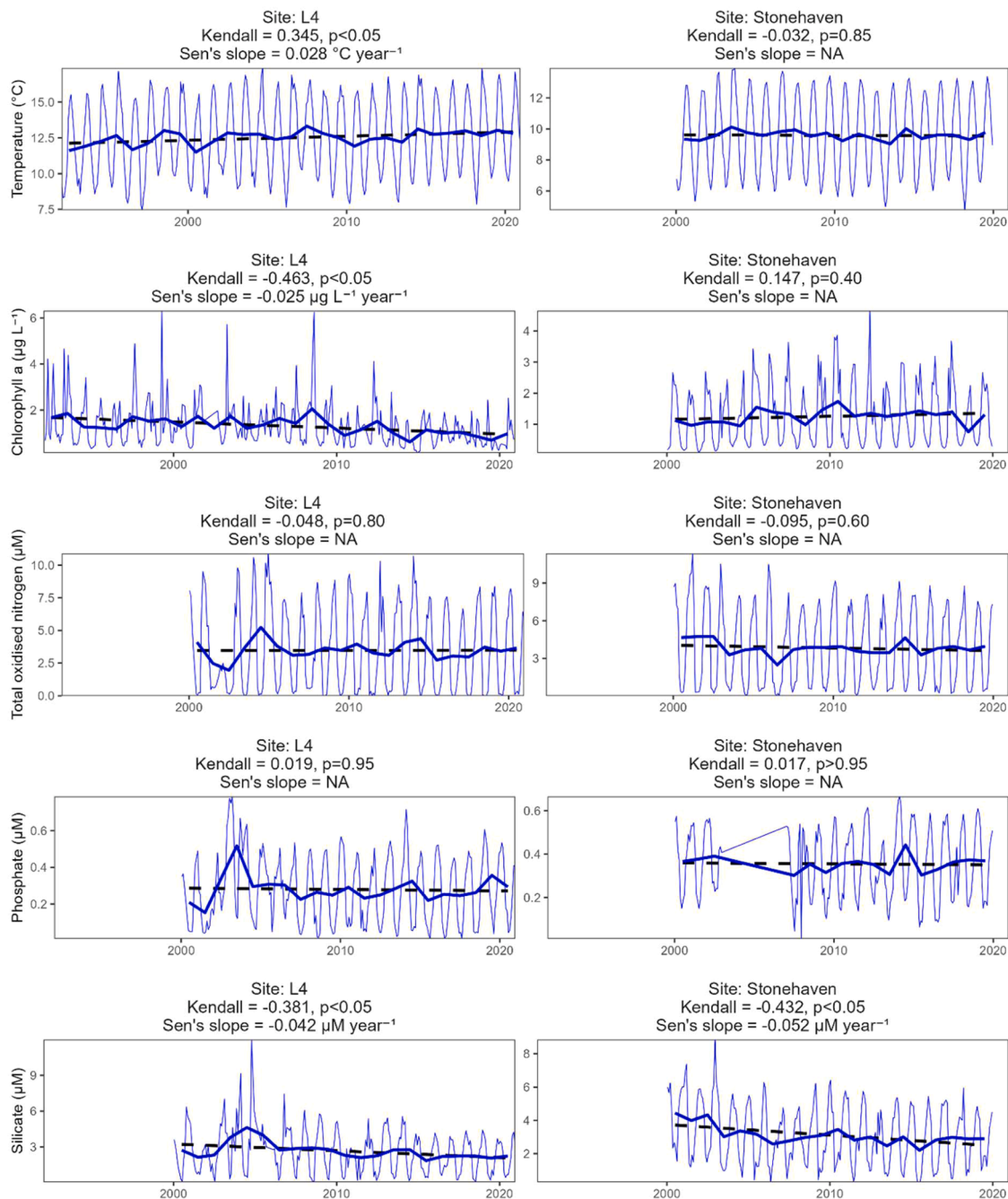


Fig. 5. Time-series for in situ environmental variables monitored at each of the two study sites. Blue lines display monthly variability (thinner line), and annual mean (thicker line) values. Dashed black lines indicate linear trend lines in annual mean values without any inference on statistical significance. The Kendall trend test is used to infer significance of trends, and Sen's slope provides an estimate of rate of change for statistically significant trends, with results displayed above each subplot.

there has been a reduction in mean silicate concentration of 1.04 µM since 2000. There was a gap in phosphate monitoring at Stonehaven between 2002 and 2007 which may have influenced trend results for this variable.

3.4. Examining changes in spatial distribution

3.4.1. *Pseudo-nitzschia*

Spatially interpolated abundances of *Pseudo-nitzschia* from CPR data revealed a reasonable degree of correlation between the raw and interpolated values, with R^2 of 0.62 (Figure S 5). It was much more common to observe zero abundance counts in the raw data than in the

interpolated data, which contributed to the smaller linear coefficient of 0.55. Despite the small coefficient, R^2 of 0.62 was still reasonable, indicating that while reported abundance values in the interpolated plots are likely underestimated, the general spatial patterns were likely to be a reliable approximation of *Pseudo-nitzschia* distribution across the period examined.

Seasonal distribution patterns of *Pseudo-nitzschia* abundance have been highly dynamic over the past six decades (Figure S 6). In the North Sea, abundances rose from the 1970s through the 2000s, with a decadal maximum in 2000–2010 and a subsequent decline in 2010–2020. While springtime areas of high abundance were largely restricted to the north of Ireland and west of Scotland, their abundance was relatively low in

the North Sea until 2000. Between 2000 and 2010 there has been a large increase in springtime *Pseudo-nitzschia* abundance along the Flemish coast and extending to the eastern Channel and southeast England. In summer, abundances declined, while an area of high cell density formed off the northeast of Scotland, extending as far as Shetland. Autumn distributions between 2000 and 2010 also indicate an increase along the eastern North Sea extending into the Kattegat. Decadal anomaly maps (Figure S 7). also indicate the largest increases in abundance along the Flemish coast and the northern North Sea, peaking between 2000 and 2010, and subsiding between 2010 and 2020.

Separate distribution maps for '*P. delicatissima* group' (Fig. 6) and '*P. seriata* group' (Fig. 7) reveal that the large increase in springtime abundance off the Flemish coast was attributed mainly to '*P. delicatissima* group' cells, while the high summertime abundances off northeast Scotland and autumn high abundances in the eastern North Sea and Kattegat were primarily driven by '*P. seriata* group'. These group-specific patterns, together with the reduction after 2010 may explain why a simple monotonic trend was not detectable from our trend analyses.

3.4.2. *Dinophysis*

Spatially interpolated abundances of *Dinophysis* (Fig. 8) also revealed a reasonable degree of correlation between the raw and interpolated values, with R^2 of 0.61 (Figure S 5). Like the *Pseudo-nitzschia* example, zero abundance counts were more commonly observed in the raw data than in the interpolated data, contributing to the smaller linear coefficient of 0.53.

Seasonal distribution patterns of *Dinophysis* abundance have been less variable than those for *Pseudo-nitzschia* over the past six decades.

Dinophysis spp. were only abundant in summer months. In the 2010s, summertime abundance declined in more coastal areas relative to what was observed between the 1970s and 1990s. *Dinophysis* spp. were consistently abundant through the decades between the Shetland and Orkney Islands off northern Scotland, as well as in the eastern North Sea. Between the 1970s and 1990s, high abundance was observed along the north-east coast of England in autumn, however, this has not been observed since 2000. Decadal anomaly maps (Figure S 6) also indicate that these large areas of high concentration along the eastern North Sea and Scotland have largely declined since 2000, however, elevated concentrations in the English Channel and Shetland persisted between 2010 and 2020.

Overall, *Pseudo-nitzschia* spp. have undergone a significant altered spatial distribution, with peak abundances generally shifting towards higher latitudes over six decades. Less variability was observed for *Dinophysis* showing little spatial variation, but a temporal peak between the 1980s and 2000s over the same period, with a subsequent decline since 2000.

4. Discussion

4.1. *Pseudo-nitzschia* and *Dinophysis* as proxies for diatom and dinoflagellate lifeforms

A proxy is a measurement of one physical quantity that is used to indicate the value of another such quantity. In this study we assessed the performance of *Pseudo-nitzschia* and *Dinophysis* as indicators of higher-level taxa (i.e., lifeforms), which are routinely used to indicate the quality status or health of pelagic habitats. Despite uncertainties in the

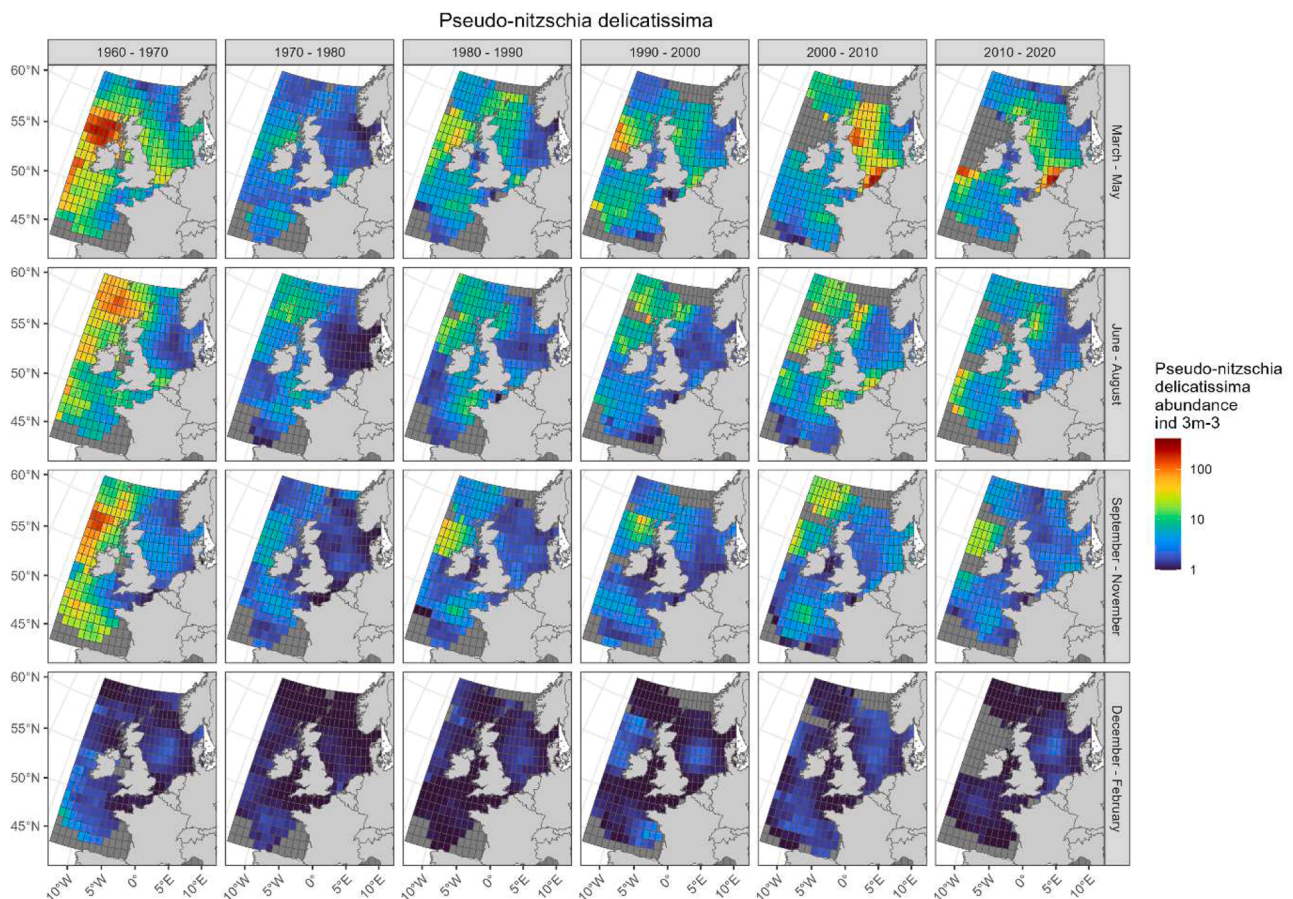


Fig. 6. Mean spatial distribution of total *Pseudo-nitzschia delicatissima* across the North-West European shelf for March to May (top row), June to August (second row), for September to November (third row) and for December to February (bottom row) separately for each decade, from 1960 to 2020. All subplots use the same logarithmic colour scale to represent abundance.

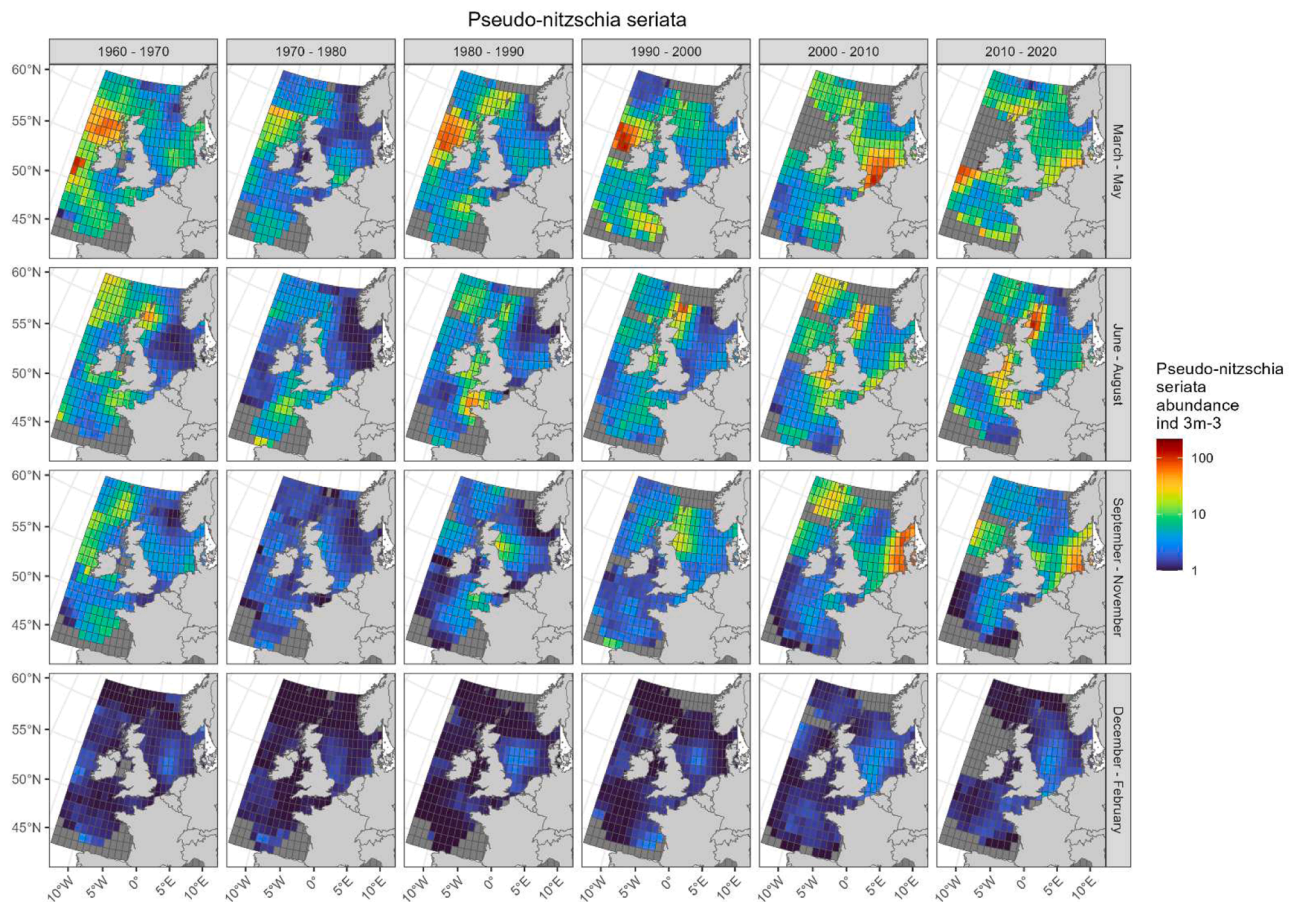


Fig. 7. Mean spatial distribution of total *Pseudo-nitzschia seriata* across the North-West European shelf for March to May (top row), June to August (second row), for September to November (third row) and for December to February (bottom row) separately for each decade, from 1960 to 2020. All subplots use the same logarithmic colour scale to represent abundance.

current taxonomy of diatoms, phylogenomics (Alverson et al., 2025; Theriot et al., 2010) maintains the distinction between centric and pennate diatoms, seeing the pennates as mainly benthic organisms that have evolved from the originally pelagic centrals. Although made up of several clades (Alverson et al., 2025) the pelagic centric diatoms are not only a monotypic group but also a distinctive lifeform characterised by silicification, adaption to turbulent environments, blooming ability, and roles in trophic transfer and carbon cycling (Behrenfeld et al., 2021; Benoiston et al., 2017; Litchman, 2022; Serôdio and Lavaud, 2022). *Pseudo-nitzschia* spp. belong to a group of araphid pennate diatoms that have (in the past 50 million years) re-adapted to pelagic life (Alverson et al., 2025). As a result of this re-adaption, the physiological traits and ecological roles of some *Pseudo-nitzschia* species can overlap with those of centric diatoms, except for interactions in which toxicity plays a part. Thus, we wanted to formally assess the extent to which *Pseudo-nitzschia* could be used as a representative proxy, if at all.

The results show this theory not to hold. *Pseudo-nitzschia* abundance showed low correlation with the abundance of 'other diatoms', and their mean seasonal cycles were largely inconsistent. This result is not surprising, as the spring bloom at both Stonehaven (Bresnan et al., 2015a) and L4 (Widdicombe et al., 2010) is frequently dominated by centric diatoms (e.g., *Skeletonema* spp., *Thalassiosira* spp., and *Chaetoceros* spp.). The proportion of the diatom community made up by *Pseudo-nitzschia* also varies throughout the seasonal cycle, typically peaking in summer, but with inconsistent dynamics between the two study sites. Similar differences were also observed in a comparison between the Stonehaven and Alfred Wegner Institute's Helgoland Roads time-series (Bresnan et al., 2015b).

Nevertheless, *Pseudo-nitzschia* spp. often comprise substantial proportion of the diatom community, in our case up to 26% of numerical abundance. The individual species have a broad range of ecological niches within the 'macro-niche' of the pelagic diatom lifeform, and it may be that other methods for matching patterns and trends might find the expected relationship. For example, Macintyre et al. (2011), applying multi-variate analysis to observations in the Gulf of Mexico, found that *Pseudo-nitzschia* grouped with other bloom-forming pelagic diatoms including *Skeletonema* and *Chaetoceros*.

An anticipated relationship between *Dinophysis* spp. and other pelagic dinoflagellates was less likely, as the latter are not a coherent functional group, while species within *Dinophysis* occupy a specialised niche. The observed relationship between *Dinophysis* and 'other dinoflagellate' abundance was even more tenuous than that for *Pseudo-nitzschia* and diatoms, with lower correlation coefficients at the seasonal level. *Dinophysis* usually forms low biomass blooms and are rarely the dominant dinoflagellate in a sample, in our case never more than 13% of dinoflagellate abundance.

Smayda and Reynolds (2001) partitioned the pelagic dinoflagellate 'macro-niche' into nine types corresponding to distinct pelagic habitats, with *Dinophysoids* the sole occupants of 'Type VII'. *Dinophysis* spp. have a complex feeding strategy, performing kleptoplasty and incorporating plastids from its ciliate prey, *Mesodinium* (Hansen et al., 2016), which has previously fed on and stolen plastids from cryptophytes belonging to the *Teleaulax/Gemingeria* clade (Park et al., 2006; Reguera et al., 2024). This ability to combine heterotrophy and phototrophy, often in thin layers at depth, means that our observed lack of correlation between *Dinophysis* and 'other dinoflagellates' is not surprising. The very specific

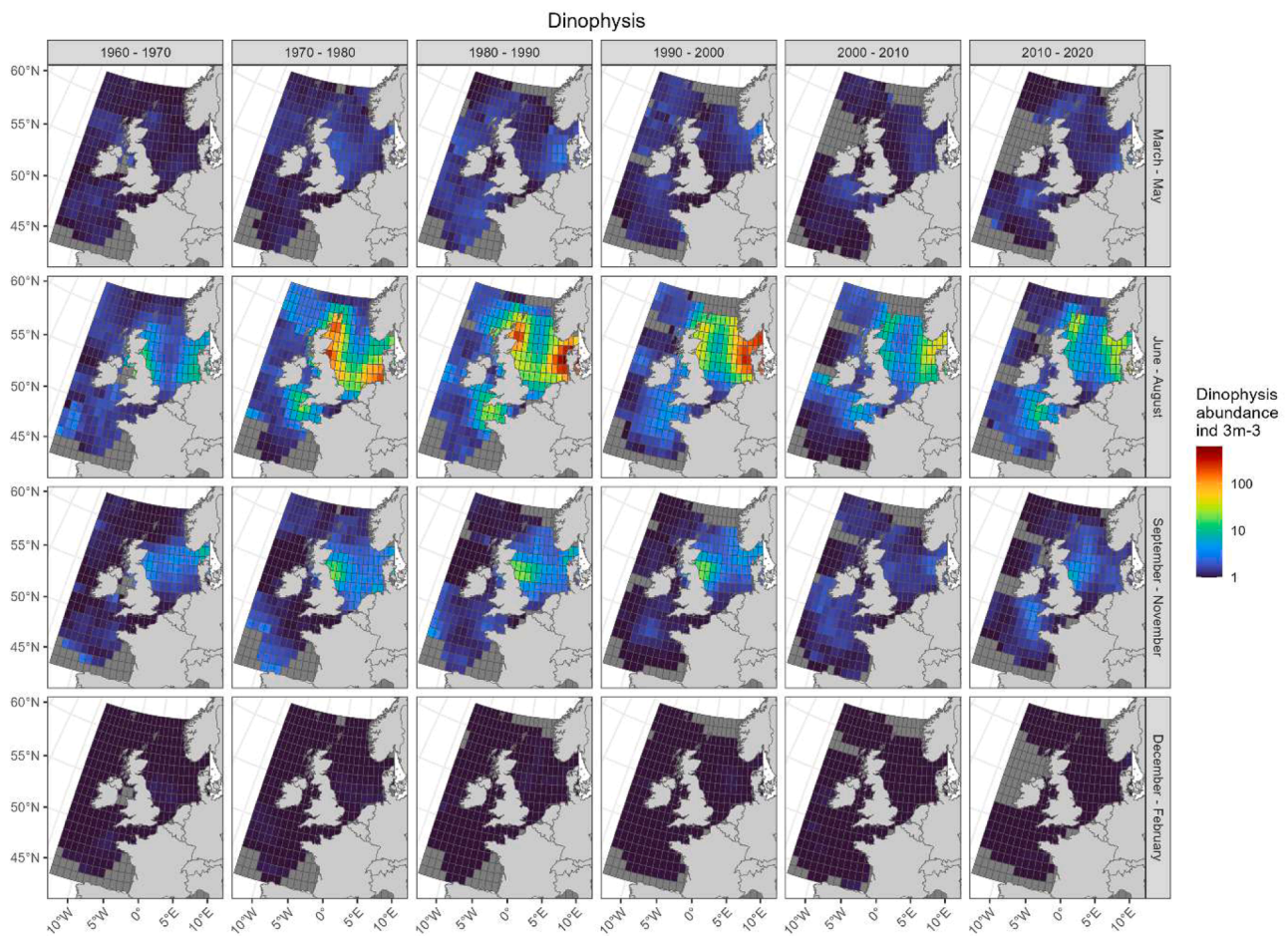


Fig. 8. Mean spatial distribution of total *Dinophysis* cells across the North-West European shelf for March to May (top row), June to August (second row), for September to November (third row) and for December to February (bottom row) separately for each decade, from 1960 to 2020. All subplots use the same logarithmic colour scale to represent abundance.

niche occupied by *Dinophysis* is not representative of most of the species that are included in the dinoflagellate ‘lifeform’ used for statutory assessment. Thus, results from our study formally demonstrate that *Pseudo-nitzschia* and *Dinophysis* cannot act as proxies for the total diatom and total dinoflagellate lifeforms.

4.2. Comparability of station and CPR data

Significant discrepancies exist between station-based and CPR data for both genera possibly arising from difference in capture or preservation between station and CPR methods, very high spatial variability within the 50 km radius, and high temporal variability within each month.

The CPR Survey instrument is biased in terms of what can be captured in its 270 μm silk mesh; it tends to capture larger, more robust phytoplankton cells, but also captures the smaller size classes (down to $\sim 5 \mu\text{m}$) semi-quantitatively, due to the weave of the silk and clogging, depending on the abundance and composition of ‘other’ plankton trapped on the net (Rivero-Calle et al., 2015; Vezzulli et al., 2022). The smaller size of ‘*P. delicatissima* group’ ($< 3 \mu\text{m}$), relative to ‘*P. seriata* group’ ($> 3 \mu\text{m}$), would also suggest biases in capture efficiency between these two groups, although considering the much larger size of the net mesh this difference is likely to be minor. A comparative study using the CPR Survey and bottle samples from the L4 station found differences in the seasonal range and species composition captured: the CPR showed a bias toward the *P. seriata* group, while L4 bottle samples were dominated by the *P. delicatissima* group. However, despite these differences, the

P. delicatissima group displayed similar temporal trends across all datasets (Stern et al., 2023).

The CPR samples within each radius were also more restricted to the open ocean, with Fig. 2A demonstrating the spatial differences between the fixed-point stations and CPR data within highly dynamic waters. The identification of distinct coastal and oceanic species groups of *Pseudo-nitzschia* in the North-East Atlantic can be complex, hindered by the discrete sampling on offshore cruises. For example, a study of phytoplankton along a transect in Scottish coastal waters and off the shelf in the Rockall Trough in 2001 showed ‘*P. seriata* type’ cells to be present in coastal waters, while high abundances of ‘*P. delicatissima* type’ cells were observed off the shelf edge (Fehling et al., 2012). In contrast, data from the National Monitoring Programme in Ireland found blooms of ‘*P. delicatissima* type’ cells in coastal waters, while ‘*P. seriata* type’ cells formed thin layers in offshore waters (Cembella et al., 2023).

Both *Dinophysis* (Escalera et al., 2012; Moita et al., 2006) and *Pseudo-nitzschia* (Rines et al., 2002; Trainer et al., 2012; Velo-Suarez et al., 2008), can be distributed in layers ($< 5 \text{ m}$ thick in midwater) when the water column is stratified. While such layers can be sampled adequately by integrated tube sampling if formed above 10 m (e.g., at Stonehaven), they could potentially be missed by discrete bottle sampling (e.g., at L4), potentially resulting in differences between one and two orders of magnitude, and deeper layers could be missed or diluted by the CPR Survey instrument, which samples a mixed vertical profile of between 15 - 30 m within the surface layer (Nylund et al., 2023).

The differences we have documented here are partially a reflection of these biases among sampling methods. However, our comparisons of

fixed-point station data with CPR Survey data primarily concerned community composition, seasonality, and trend direction, which should be internally comparable when sampling methods have been applied consistently over time. Awareness of these differences is important because, in regions with little or no coastal monitoring, CPR data are often used as a substitute.

4.3. Changes in distribution of *Pseudo-nitzschia* and *Dinophysis* through time

4.3.1. *Pseudo-nitzschia*

Multiple recent studies have found that diatoms are increasing in the North Sea but declining in oceanic waters of the North-East Atlantic (Bedford et al., 2020; Edwards et al., 2022; Holland et al., 2023b; Kléparski et al., 2023). Focused studies on changes in abundance in *Pseudo-nitzschia* are scarce. Hinder et al. (2012) found an increase in abundance in *Pseudo-nitzschia* linked to a $\sim 1^\circ\text{C}$ rise in SST since 1960, concurrent with a $\sim 1\text{ m s}^{-1}$ increase in wind speed during summer. Consistent with this, our study has documented a similar increase in *Pseudo-nitzschia* in the North Sea, with less definitive evidence of change in oceanic waters. These changes in *Pseudo-nitzschia* distribution within the North Sea began in the 1970s, peaking between 2000 and 2010, and declining between 2010 and 2020. Since 2000, higher abundances have been recorded in the southern and eastern parts of the North Sea in spring, as well as northeast of Scotland, and along the Faroe-Shetland Channel in summer (Figure S 6). While we found limited evidence of long-term monotonic trends across the full time-series for *Pseudo-nitzschia* abundance at either fixed term site, this may be attributed to a mismatch of temporal scales. Variation in *Pseudo-nitzschia* abundance at L4 appeared to be more cyclical, following a cycle of ~ 5 years (Figure S 4). It is quite possible that periodic changes occurred over shorter time scales which were undetectable with our employed methods.

At L4 we observed sustained warming ($0.02^\circ\text{C yr}^{-1}$) alongside declining chlorophyll-*a* and silicate. A decline in silicate has also been observed in other regional seas (Rey, 2012). Offshore oceanographic processes associated with the dynamics of the subpolar gyre can influence levels of silicate in the North Atlantic (Hátún et al., 2017; Rey, 2012). The extent of this silicate decline has yet to be fully investigated in UK waters.

The seasonal variation in dominance of ‘*P. delicatissima* group’ versus ‘*P. seriata* group’ has been documented in multiple studies in UK waters (Bresnan et al., 2017, 2015b; Downes-Tettmar et al., 2013; Fehling et al., 2006; Rowland-Pilgrim et al., 2019; Stern et al., 2023; Whyte et al., 2023). The temporal and regional species diversity within the *Pseudo-nitzschia* genus in UK waters (Bresnan et al., 2015b) and range of ecologies makes identification of relevant environmental drivers for these different size groups difficult. Species recorded in UK waters using electron microscopy include: *P. americana*, *P. australis*, *P. cacciantha*, *P. calliantha*, *P. cuspidata*, *P. delicatissima*, *P. decipiens*, *P. fraudulenta*, *P. multiseries*, *P. cf. plurisecta*, *P. cf. pseudodelicatissima*, *P. pungens*, *P. seriata*, and *P. subpacifica* (Bresnan et al., 2021, and references therein). More recently, molecular methods have been employed to improve species-level information available from routine light microscopy (e.g., Stern et al., 2023). An investigation on environmental drivers on the seasonality of *Pseudo-nitzschia* at a coastal site on the west of Scotland showed that the variables measured explained on 31% of abundance (Fehling et al., 2006). The southern North Sea has also experienced considerable reductions in nutrient input since the late 1980s, resulting in altered nutrient ratios (Skogen et al., 2004; van Beusekom et al., 2009) and a decline in phytoplankton biomass in this region has been observed (Capuzzo et al., 2018). This is in contrast to an observed increase in *Pseudo-nitzschia* abundance between 2000 - 2018 (Brandenburg et al., 2025), although no management actions associated with DA have been enforced in this area (Karlson et al., 2021).

Within the changing distribution of this genus, there could also be an undetected shift in the dominant species present. Time-series of *Pseudo-*

nitzschia species are scarce, due to the effort involved in electron microscopy to make this species-level identifications. Hasle et al. (1996) recorded *P. multiseries* as abundant in the late 1960s in the Skagerrak, but not present in the early 1990s, potentially due to temperature effects on growth during mild winters in the 1990s. Lundholm et al. (2010) used sediment cores from the Mariager Fjord in Denmark to construct a *Pseudo-nitzschia* time-series from 1905 to 2001, and observed shift in the dominant species while the relative abundance of *Pseudo-nitzschia* cells remained unchanged. *P. multiseries* was dominant until 1947, with a subsequent shift towards dominance by *P. pungens*, thought to be driven by increasing nutrient inputs and warming temperatures. *P. seriata* and *P. americana* also increased in relative abundance during this period.

The decadal variability we have documented is largely consistent with basin scale climate variability and its effects on stratification and mixed layer depth. Northeast Atlantic phytoplankton exhibit multi-decadal fluctuations that co-vary with the Atlantic Multidecadal Oscillation (AMO) and North Atlantic Oscillation (NAO) and long term trends in warming and stratification documented in CPR and satellite studies (e.g., Barton et al., 2003; Edwards et al., 2022; Head and Sameoto, 2007; Head and Pepin, 2010; Henson et al., 2009; McQuatters-Gollop et al., 2015). While we did not explicitly test for the influence of AMO/NAO, the peak in abundance observed in the 2000s followed by the decline after 2010 is may be attributable to these low frequency cyclical processes, operating via changes in mixing, light, nutrient balance, and seasonal stratification.

In UK waters, *P. australis* and *P. seriata* are the dominant toxin producers associated with closures of shellfish harvesting areas (Fehling et al., 2004; Rowland-Pilgrim et al., 2019). While *P. seriata* is a cold water species (Hasle et al., 1996) elsewhere in the world, blooms of *Pseudo-nitzschia australis* can be associated with upwelling systems (Díaz et al., 2014; Pitcher et al., 2020; Ryan et al., 2017), as well as transport via physical process or wind into coastal areas (Cusack et al., 2015; Whyte et al., 2014).

4.3.2. *Dinophysis*

Edwards et al. (2006) first documented changes in the distribution of *Dinophysis* in the North Sea between 1960 and 2000, with a shift in abundance from west to east, and with peak abundances along the Norwegian coast and the Skagerrak. The seasonal and decadal anomaly distribution maps we generated indicated that elevated abundances Edwards et al. (2006) observed in the eastern North Sea have largely declined between 2000 and 2020, and overall abundance of *Dinophysis* has declined over this period.

At L4 and Stonehaven stations, *Dinophysis* contributed only a small fraction of total dinoflagellates with *D. acuminata* blooming in early summer and *D. acuta*, when it occurred, blooming during late summer when warm, stratified conditions were likely to occur. It is no surprise that in this study, we cannot make inferences about environmental drivers of *Dinophysis* abundance from the physical and chemical parameters measured at the fixed-point sites due to the role of large-scale physical drivers and transport on *Dinophysis* blooms as well as the complexity of their ecology.

Studies from the Iberian Peninsula have shown the onset of *D. acuminata* complex blooms associated with the beginning of upwelling in spring, while *D. acuta* blooms are associated with the relaxation of upwelling at the end of summer and can be transported northwards from Portugal to the Galician Rias (Díaz et al., 2019; Escalera et al., 2010; Moita et al., 2006). While these upwellings will not be such a driver in the waters around the UK or the North Sea, they highlight the influence of physical processes on the development of blooms.

Observations from the west coast of Scotland and Shetland indicate that *Dinophysis* spp. growth is strongly seasonal and exhibits regional variability (Gianella et al., 2021). Whyte et al. (2014) proposed that much of the observed biomass for the genus *Dinophysis* spp. originates along the North-East Atlantic shelf edge and is subsequently advected shoreward across the shelf. This supports earlier suggestions by Smayda

and Reynolds (2001), who argued that *Dinophysis* blooms are more likely driven by advection processes rather than local in situ growth. Furthermore, Swan et al. (2018) demonstrated that seasonal water column stratification and the formation of local frontal systems play a critical role in regulating *Dinophysis* bloom dynamics. A complementary analysis by Raine et al. (2010) showed that *Dinophysis* and *Karenia* populations can aggregate in tidal fronts and be transported by coastal jets along the Irish coast, highlighting the importance of physical transport mechanisms in bloom development and dispersal.

Gobler et al. (2017) modelled an increase in *Dinophysis* spp. abundance and an extension of its growing season under future climate scenarios. An analysis by Dees et al. (2017), using CPR data, found no evidence of an increase, and that *Dinophysis* has declined in the North Sea since 2000. Previous studies (e.g., Belgrano et al., 1999; Edwards et al., 2006; Naustvoll et al., 2012) flag the influence of climatic indices such as the North Atlantic Oscillation (NAO) on *Dinophysis* in Norwegian waters. No relationship between the NAO and *Dinophysis acuta* was observed in the Galician Rias (Díaz et al., 2016).

4.4. *Pseudo-nitzschia* and *Dinophysis* in North-East Atlantic marine biodiversity assessments

This study has shown that *Pseudo-nitzschia* and *Dinophysis* are likely poor indicators for assessing the state of pelagic habitats in the Greater North Sea (OSPAR Region II) and, by extension, other OSPAR regions (Fig. 1), however, they could still provide valuable evidence for assessing the societal impacts of changes to pelagic biodiversity (e.g., 'ecosystem hazards'; Faith et al., 2025). The recent OSPAR QSR2023 assessment reported that pelagic habitats across the North-East Atlantic are in a 'not good' environmental state, with likely consequences for food-web functioning and human wellbeing (OSPAR Commission, 2023).

Harmful algal blooms can have wider ecosystem impacts which can accumulate across marine food webs, resulting in morbidity and mortality of marine animals, including seabirds and seals (Gibble and Hoover, 2018; Hall et al., 2024). The impact of shellfish toxins on marine mammals and seabirds in the North-East Atlantic has been poorly studied, however, several studies suggest that they can present a 'pressure' on higher trophic levels (Ben-Gigirey et al., 2021; Jensen et al., 2015). Harðardóttir et al. (2018) showed that the escape response of two copepods was impacted after feeding on DA producing *P. seriata*. A small study investigating the presence of DA in copepods at Stonehaven recorded DA in every sample analysed, suggesting that algal toxins are readily passed through the food web (Cook et al., 2022). These results lend support to an *ad hoc* study of algal toxins in fish from Scottish waters, which detected OA, DA, as well as paralytic shellfish toxins in fish, including areas such as Orkney and the east coast of Scotland where there is little shellfish toxin monitoring (Kershaw et al., 2021). Pilot studies have shown the presence of DA in the urine, faeces, and amniotic fluid of harbour seals in Scottish waters (Hall and Frame, 2010; Jensen et al., 2015). A recent modelling study also showed the potential for DA in fish prey to represent a risk to harbour seals in Scotland (Hall et al., 2024).

In this context, rather than for supporting biodiversity assessments of pelagic habitat state, monitoring data for these two genera, along with shellfish or other toxicity data (e.g., as from passive environmental sampling; Lane et al., 2010), may be more useful for assessing impacts of pelagic habitat state changes on higher trophic levels such as seabirds and marine mammals. Changes in the diversity and distribution of toxin producing genera may represent a change in chronic toxin exposure with an impact on breeding success and survival.

5. Conclusion

Data from fixed point stations and CPR data showed differences in seasonality and diversity which is important to consider when using CPR

data in areas with little coastal monitoring. Distribution maps of *Pseudo-nitzschia* and *Dinophysis* using CPR data have been updated since 2012 and 2006, respectively. These updated distribution maps highlight that since 2000 there has been a notable increase in spring *Pseudo-nitzschia* spp. abundance in the southern North Sea in spring and eastern North Sea in summer, followed by a post-2010 reduction; whereas *Dinophysis* spp. have remained largely summer-restricted and declined after 2000 in parts of the eastern North Sea.

Our findings present the formal evidence that monitoring *Pseudo-nitzschia* spp. and *Dinophysis* spp. alone does not provide sufficient information to identify changes in pelagic habitat biodiversity, however it may support full community phytoplankton monitoring during high biomass bloom events. While *Pseudo-nitzschia* and *Dinophysis* cannot directly support pelagic habitat diversity assessments, information on toxin loading in the marine ecosystem can provide 'pressure' data to support assessments of reduction and abundance of higher trophic levels such as seabirds and marine mammals.

CRedit authorship contribution statement

Matthew M Holland: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Eileen Bresnan:** Writing – review & editing, Writing – original draft, Methodology, Conceptualization. **Martin Edwards:** Writing – review & editing, Writing – original draft, Methodology. **Matthew Faith:** Writing – review & editing, Writing – original draft. **Clare Ostle:** Writing – review & editing, Writing – original draft, Methodology. **Rowena Stern:** Writing – review & editing, Writing – original draft, Methodology. **Paul Tett:** Writing – review & editing, Writing – original draft. **Claire Widdicombe:** Writing – review & editing, Writing – original draft, Methodology. **Callum Whyte:** Writing – review & editing, Writing – original draft, Methodology. **Abigail McQuatters-Gollop:** Writing – review & editing, Writing – original draft, Supervision, Project administration, Funding acquisition.

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.

Acknowledgements

We are grateful for the funding received from the UK Department for Environment, Food & Rural Affairs (Defra) through the marine arm of their Natural Capital and Ecosystem Assessment (NCEA) programme (NC34 Pelagic program-“PelCap”). The marine NCEA programme delivered evidence, tools and guidance to integrate natural capital approaches into decision making for the marine environment. Find out more at <https://www.gov.uk/government/publications/natural-capital-and-ecosystem-assessment-programme>. AMG would like to thank the United Kingdom National Environmental Research Council (UKRI-NERC) for support through the NERC Knowledge Exchange Fellowship Scheme (NE/R002738/1). MF acknowledges funding from Defra, the University of Plymouth, and The Alan Turing Institute's Enrichment Scheme. Current funding that supports data collection by the CPR survey in the North Atlantic includes: the UK Natural Environment Research Council; Atlantic Climate and Environment Strategic Science (AtlantiS) NE/Y005589/1, Department for Environment Food and Rural Affairs UK ECM_64770, National Science Foundation USA A101666/83643000, NERACOOS N21A01303, Fisheries and Oceans Canada F521A-210734/001/HAL, Horizon 2020: 862428 Atlantic Mission and AtlantECO 862923, IMR Norway and Ireland Marine Institute SERV-22-FEAS-090. L4 plankton data were provided by the Plymouth Marine Laboratory's (PML) Western Channel Observatory (<https://www.westernchannelobservatory.org.uk>), which was funded as part of the UK's Natural

Environmental Research Council's National Capability Single Centre Science Programme, grant number NE/R015953/1. Marine Directorate Scottish Coastal Observatory data was collected under ADP#703. The Marine Directorate Scottish Coastal Observatory Stonehaven site is funded as part of ADP#703.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.hal.2026.103113.

Data availability

Data will be made available on request.

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