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Long-term changes in spatiotemporal distribution of *Noctiluca scintillans* in the southern North Sea

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ABSTRACT

To assess the spatiotemporal evolution of the heterotrophic dinoflagellate *Noctiluca scintillans* in the North Sea, the Helgoland Roads time series and Continuous Plankton Recorder survey were analysed using generalized additive models. Over the last decades, blooms of *N. scintillans* have occurred more frequently and intensively in many regions. This harmful algal bloom forming species can alter food webs, reduce ecosystem productivity, and lead to economic losses while causing lower aquacultural yields. After the 1990s, *N. scintillans* abundances have significantly increased by 1.65-fold and a significant prolongation of the bloom window was found (from 27.5 to 98 days in recent decades) off the island of Helgoland, Germany. Significant correlations were found between bloom initiation and nutrients, as well as light availability since these factors lead to increased prey availability. Highest abundances of *N. scintillans* were associated with water temperatures around 17 °C and wind speed below 6 ms^{-1} causing dense surface accumulations. Solar radiation of more than 200 Wm^{-2} was identified as a main driver for post-bloom conditions as it can deteriorate the cells and lead to the decline of *N. scintillans* abundances. In the southern North Sea, *N. scintillans* occurrences have intensified and spread since the 1980s with hotspots identified as the coastal waters adjacent to the estuaries of the Elbe and Rhine rivers.

1. Introduction

Coastal ecosystems have been significantly altered by climate change and anthropogenic pressures during recent decades. Climate change has led to ocean warming and increased water stratification (Behrenfeld et al., 2006), while increasing anthropogenic development in coastal regions has increased nutrient inputs (Heisler et al., 2008). Physical and chemical conditions influence the taxonomic composition of plankton communities (Bouman et al., 2003; Hallegraeff, 1993), which is why plankton, that forms the base of marine life, is an indicator of ecosystem health. Altered plankton communities, spatiotemporal shifts, and changes in bloom size and duration were linked to recently changing environmental conditions (Ardyna and Arrigo, 2020; Atkinson et al., 2015; Bedford et al., 2020; van Oostende et al., 2023). Understanding these changes within plankton communities has become increasingly important, as several harmful algal bloom forming species (HABs) are rapidly expanding in the oceans (Berdalet et al., 2016; Gobler, 2020; Hallegraeff, 2010). This is of growing concern, since HABs have been associated to reduced plankton diversity, oxygen depletion, and altered nutrient and carbon cycles (Zingone and Enevoldsen, 2000).

Water temperature in the coastal shelf of the North Sea has increased significantly faster than at global level (Wiltshire et al., 2008). Since 1962, global ocean temperatures have risen by ~ 0.7 °C in 57 years, while average temperatures in the North Sea have increased by ~ 1.3 °C over the same period (Amorim et al., 2023). Available climate projections imply that the region will be subject to a variety of climate change impacts in the future, including further warming, sea level rise, and altered precipitation events. Freshwater discharge of large rivers such as the Elbe or Rhine, and the nutrient loads they carry to the coast, contribute to anthropogenic eutrophication, which is another factor that

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influences the coastal ecosystems of the southern North Sea and is affected by climate change (Quante and Colijn, 2016; Voynova et al., 2017). As important nutrient inputs enhance plankton growth (Groß et al., 2022), it can be expected that the plankton communities of the North Sea will exhibit substantial alterations over the coming decades.

Autotrophic and mixotrophic dinoflagellates decreased over the past decades in the North Sea (Di Pane et al., 2022). Interestingly, the blooms of the heterotrophic dinoflagellate *Noctiluca scintillans* (Macartney) Kofoid and Swezy, 1921 followed the opposite trend and have intensified, occurred more frequently and expanded geographically in the last decades in many regions including the Belgian part of the North Sea (Ollevier et al., 2021), the Australian (Hallegraeff et al., 2019) and Chinese coasts (Wang et al., 2023). Eutrophication and ocean warming were associated with these recent changes (Kordubel et al., 2024). *Noctiluca scintillans* is equipped with various competitive advantages including effective reproductive strategies leading to exponential growth, phagotrophic feeding allowing the ingestion of a wide range of prey types, and a high tolerance towards changing salinities and temperatures (Elbrächter and Qi, 1998).

This recent intensification of *N. scintillans* is alarming as dense proliferations can lead to significant ecosystem alterations. *Noctiluca scintillans* is non-toxic to human health but is considered one of the most common HAB forming species worldwide (Wang et al., 2023). The decay of dense accumulations of this organism can deteriorate water quality while depleting surface waters of oxygen (Zevenboom et al., 1991) and causing high ammonium (NH_4) concentrations (Hallegraeff et al., 2019). *Noctiluca scintillans* can act as vector for toxic *Dinophysis* sp. or *Gymnodinium catenatum* (Escalera et al., 2007; Yamamoto et al., 2004). These alterations can lead to reduced aquacultural yields (Escalera et al., 2007; Hallegraeff et al., 2019; Yan et al., 2002). This rapidly developing and voracious organism can outcompete and/or graze-down phytoplankton, and thus restructure the plankton community (Hansen et al., 2004; Zhang et al., 2021). This can alter the food webs and lead to lower ecosystem productivity. In the Black Sea for example, *N. scintillans* replaced diatoms and contributed to a shift towards jellyfish-dominated food webs leading to the collapse of fish stocks (Gomes et al., 2014; Oguz and Velikova, 2010). While affecting zooplankton through competition for food (Fonda Umani et al., 2004), and feeding on eggs and/or larvae considerably impacting the recruitment of copepod nauplii (Daro et al., 2006), *N. scintillans* directly impacts yet another trophic level. On the contrary, the regeneration of nutrients by *N. scintillans* can drastically increase the nitrogen and phosphorus concentrations in the upper water layers (Zhang et al., 2021), fuelling the growth of phytoplankton (Ara et al., 2013). Despite the recognized importance of dissolved inorganic nitrogen (DIN) and phosphate (DIP) for the growth of phytoplankton (Zhang et al., 2024), *N. scintillans* is not directly influenced by these nutrients. The heterotrophic dinoflagellate only indirectly relies on nutrients through increased prey availability (i.e. phytoplankton abundance) for growth (Dela-Cruz et al., 2002).

When considering the numerous effects of *N. scintillans* on coastal ecosystems, it is becoming increasingly evident that the understanding of the spatiotemporal distribution of this species under changing environmental conditions must be improved. In that aspect, long-term time series assessing plankton abundance combined with hydrological and meteorological conditions, are valuable. In combination with species distribution models (SDM), predictions in time and space can be obtained (Araújo and Rahbek, 2006; Elith and Leathwick, 2009). To assess the role of environmental variables on the distribution and abundance of different marine species, including various plankton species, SDM are widely applied (Barton et al., 2016; Jensen et al., 2017; Matus-Hernández et al., 2019).

Noctiluca scintillans is a common dinoflagellate in the North Sea (Uhlig and Sahling, 1990) and was thoroughly investigated during the 1990s and early 2000s in this area (Elbrächter and Qi, 1998; Fock and Greve, 2002; Kirchner et al., 1996; Uhlig and Sahling, 1990). Nevertheless, knowledge about its recent dynamics, involved drivers throughout a bloom, and associated impact on coastal ecosystems in the North Sea is still scarce (Ollevier et al., 2021). The availability of several unique datasets such as the Helgoland Roads time series (HR) (Wiltshire and Manly, 2004) and the Continuous Plankton Recorder survey (CPR) (Richardson et al., 2006) in the North Sea, provide a solid base for the investigation of long-term and recent trends. Both time series monitored plankton diversity and abundance over several decades. The comparison of a long-term dataset with high temporal resolution at HR and the spatial information provided by the CPR survey enables the thorough investigation of the temporal and geographical dynamics of *N. scintillans* in the North Sea.

Considering current and projected climate change scenarios for the North Sea, it can be expected that bloom frequency, duration, and intensity may increase in the future. Given the significant impact of *N. scintillans* on coastal ecosystems across multiple trophic levels, a potential increase in abundance may considerably influence the composition of local plankton communities and as a result, alter the associated food webs. Understanding *N. scintillans'* bloom dynamics, and its long-term and recent changes, is required to improve the predictive capacities for this species within the North Sea and potentially in changing costal ecosystems on a global scale. Experimental work has predicted the demise of *N. scintillans* under different future global change scenarios (Moreno et al., 2022), however, abundances of *N. scintillans* have tripled between 2014 and 2018 along the Belgian coast (Ollevier et al., 2021). This inconsistency in literature could be attributed to the short time frame analysed and to the high inter-annual variability of *N. scintillans* abundances (Uhlig and Sahling, 1990). This highlights the need of a large-scale analysis over a long time frame. Therefore, the aim of this study is to improve the understanding of *N. scintillans'* bloom dynamics and more specifically: (i) to describe the spatiotemporal expansion of *N. scintillans* in the North Sea over several decades, while delineating temporal patterns and pinpointing geographical hotspots, and (ii) to elucidate the environmental preferences of this dinoflagellate.

2. Material and methods

2.1. Study area

The North Sea is an enclosed shallow shelf sea reaching a maximum water depth of 750 m in the Skagerrak (De Haas et al., 1997), but most of the North Sea has depths shallower than 100 m. The deeper north is subject to North Atlantic water inflow and is stratified during the warmer months (Artioli et al., 2012), whereas water masses in the shallow south are generally well-mixed by winds and tides, with occasional stratified periods (van Leeuwen et al., 2015), and are significantly influenced by continental runoff (Bozec et al., 2005). Water masses are transported by an anticlockwise residual current system induced by the tidal motion and the dominantly westerly winds and influenced by the shape of the North Sea basin (De Haas et al., 1997). The North Sea is highly productive and intensively used for fishing, wind farms, oil platforms, and shipping (Quante and Colijn, 2016).

Helgoland is an island located in the German Bight about 60 km off the German coast. The waters surrounding the island are influenced by the Elbe River, as nutrient loads from the estuary plume can extend in the coastal region as far as Helgoland (Voynova et al., 2017). The maximum water depth around the island ranges from 20 to 60 m (Michaelis et al., 2019). Since 1962, the HR time series has monitored physicochemical and biological parameters including plankton on a daily basis (workdays) at Helgoland (54°11.3′N, 7°54.0′E) (Wiltshire et al., 2008)(https://deims.org/1e96ef9b-0915–4661–849f-b3a72f5aa9b1). In the North Sea and North Atlantic, the CPR, a mechanical plankton sampler, has been deployed to collect plankton samples since 1931 (Colebrook, 1960) (Fig. 1).

Since *N. scintillans* blooms exhibit exponential growth and sudden collapse (Dela-Cruz et al., 2002; Sathish et al., 2021), continuous monitoring at high temporal resolution is needed to accurately elucidate

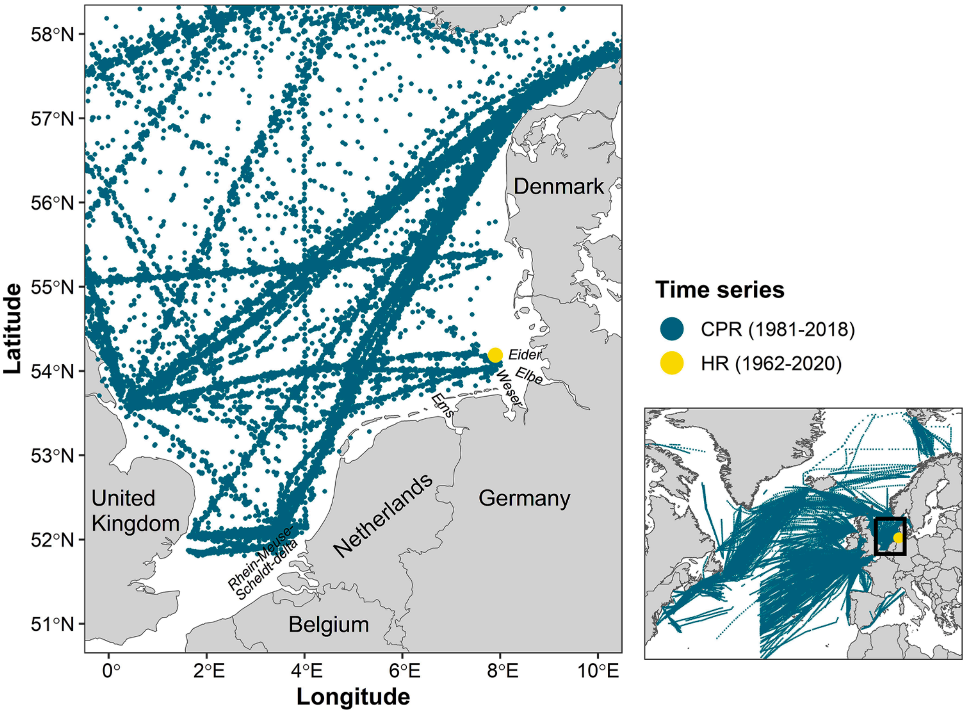

Fig. 1. Study area in the North Sea. The sampling effort of the Helgoland Roads (HR) and Continuous Plankton Recorder (CPR) time series are indicated by dots. Main rivers estuaries are indicated in italic.

the bloom dynamics of this organism. The HR time series has a uniquely high temporal resolution (work-daily sampling) but is restricted to one specific location (Wiltshire et al., 2008), and hence lacks a reliable spatial coverage. To adequately determine *N. scintillans'* geographical hotspots and a potential spatial spread of this organism, additional data with good horizontal coverage are required. The CPR survey has a lower temporal resolution (monthly sampling), but covers vast areas (Richardson et al., 2006) and therefore ideally complements data from HR. The different spatiotemporal resolution as well as the distinct sampling and plankton quantification methods that were applied for the HR and CPR time series, result in great differences particularly in terms of absolute abundances. Generally, abundance estimates from the CPR data are semi-quantitative and are most useful for assessing inter-annual or seasonal patterns rather than changes in absolute abundance (Richardson et al., 2006). Therefore, the two datasets were analysed separately to study distinct spatial and temporal patterns. This was done

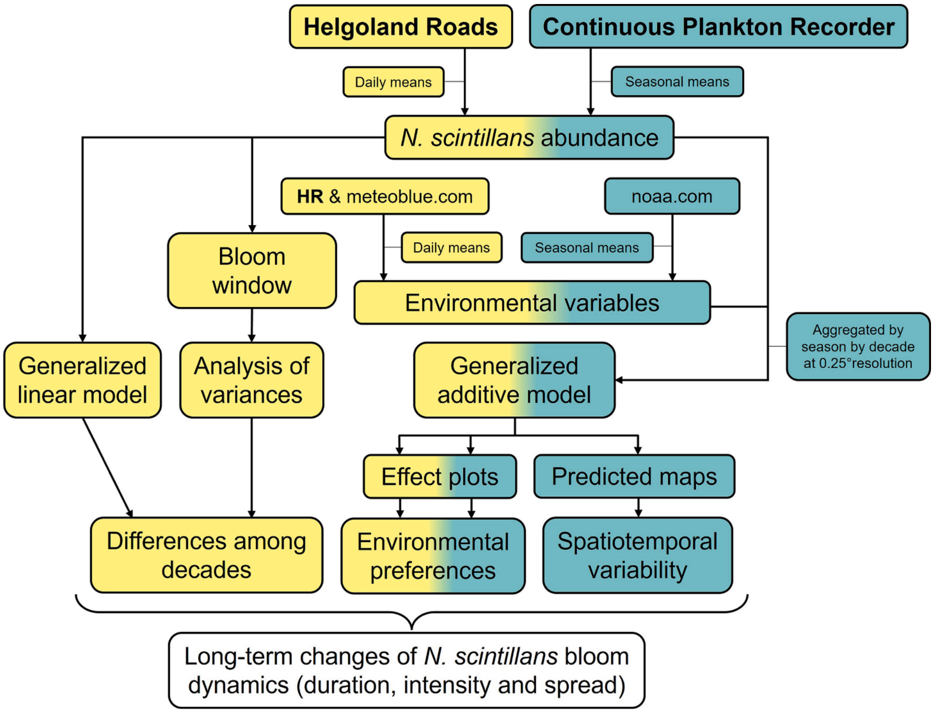

Fig. 2. Flowchart representing the methodological approach used in this study.

to assess the potential temporal increase of *N. scintillans* with the HR data and its spatial increase with the CPR data. A summary of the different methodological approaches applied in this study can be found in Fig. 2.

2.2. Helgoland roads time series

2.2.1. N. scintillans abundance data

For HR, surface water samples were collected daily from 1962 to 2020 with buckets lowered from a research vessel. Subsamples of 100 mL were obtained and preserved (final concentration 0.1 % Lugol) for plankton analysis (Dummermuth et al., 2023). Enumeration and identification, to species level when possible, were performed in the laboratory where subsamples were analysed using the Utermöhl method and an inverted microscope (Schlüter et al., 2008; Wiltshire et al., 2008).

2.2.2. Environmental data

Simultaneously, chemical, and physical parameters were also recorded along with the plankton samples since 1962. Surface water temperature was measured *in situ*, whereas for salinity and nutrient measurements, surface water samples were collected and analysed in the laboratory. For nutrients, subsamples were analysed by standard colorimetric methods (Grasshoff, 1976), whereas salinity was measured using a salinometer (Wiltshire et al., 2010). The data underlying this article are available in the Data Publisher for Earth & Environmental Science PANGAEA (https://doi.pangaea.de/10.1594/PANGAEA.960375) or will be made available on request. Solar radiation, wind speed and precipitation in Helgoland (54°25′N, 8°0′E) were downloaded at daily resolution from www.meteoblue.com for the period 1962–2020. The selection of variables was based on their mention in the literature as potentially important drivers influencing the dynamics of *N. scintillans* blooms (Kordubel et al., 2024). Specifically, sea surface temperature (SST), sea surface salinity (SSS), DIN, solar radiation (SR), wind speed (WS) and precipitation (Prec) were used. Dissolved inorganic nitrogen plays a major role in promoting the growth of a variety of phytoplankton species (Zhang et al., 2024), so this parameter was used rather than including the biomass of specific organisms due to the uncertainty of their importance for *N. scintillans*. A time lag of 30 days was used for DIN based on the temporal shift between the peak of DIN and the start of the exponential growth of *N. scintillans* from May to June (Fig. S-1), to account for *N. scintillans*' indirect response to changes in chemical variables because of its heterotrophy.

2.2.3. Statistical analyses

To assess the potential changes in *N. scintillans* densities over time, differences in *N. scintillans* abundances between different decades were tested for by using a generalized linear model (GLM) (Nelder et al., 1972). Since *N. scintillans* is most abundant from June to August, only abundances during these months were included in the GLM. The model was fitted with a Poisson distribution, given the integer nature of the data. This expresses the abundance of *N. scintillans* x as:

$$x \sim Poisson(\mu)$$

where μ represents the mean. The relationship between $\log(\mu)$ and the predictor is modelled as a linear function. Here,

$$\log(\mu) = \beta_0 + \beta_1 Decade$$

where β_0 represents the intercept term, and β_1 the coefficients for the factor Decade.

To test for differences in the length of the *N. scintillans* bloom window over time, a one-way analysis of variances (ANOVA) was used. This method was chosen for its statistical power, robustness and group mean estimations when compared with non-parametric tests which are based on ranks and could thus limit interpretations. This expresses the length of the bloom window y as:

$$y \sim Gaussian(\mu, \sigma^2)$$

where μ represents the mean and σ^2 the variance. The relationship between μ and the predictor is modelled as a linear function. Here,

$$\mu = \beta_0 + \beta_1 Decade$$

where β_0 represents the intercept term, and β_1 the coefficients for the factor Decade. A bloom was defined as a day or several consecutive days with abundances $\geq$ 500 cellsL^{-1}. This abundance was suggested as warning threshold for *N. scintillans* blooms in the Yellow Sea (Xue et al., 2020). The bloom window corresponds to the entire period during which *N. scintillans* blooms, e.g. all the days between the first and last measurements of abundance $\geq$ 500 cellsL^{-1}. Therefore, daily data was inspected, and the length of the bloom window was calculated for each year.

To describe the effect of environmental variables on the abundance of *N. scintillans*, generalized additive models (GAMs) were built using the "mgcv" package (Wood, 2017). Generalized additive models are semi-parametric extensions of GLMs describing complex relationships and allowing non-linear regressions to be fitted to the data (Wood, 2008). Here, the response variable was the daily abundance of *N. scintillans* (cellsL^{-1}) and the predictor variables the environmental factors listed in Table 1.

To identify highly correlated predictor variables which can lead to collinearity issues, Pearson's correlation coefficients (Pearson, 1920) were estimated for all predictors (Table 2, Table S-2, and Table S-3). Variables with coefficients higher than 0.6 or lower than −0.6 were considered collinear and removed (Dormann et al., 2013). Since the response variable is integer and positive, the Poisson family of error distribution and logarithm as link function was used. The general model can be expressed as follows:

$$\log(z) = a + f_1(SST) + f_2(SSS) + f_3(DIN) + f_4(Year) + f_5(Month) + f_6(Prec) + f_7(WS) + f_8(SR)$$

where z is the daily abundance of *N. scintillans, a* is the intercept and f_n are the smooth functions (thin plate regression splines). A backward stepwise procedure was used to select the minimal adequate model (best-fit model). This consisted of building a full model (including all predictor variables), then removing a single variable, and evaluating the significance of its removal for the new model with Akaike's Information Criterion (AIC) (Sakamoto et al., 1986). If the AIC of a model was significantly lower (at least by 2 units) than the previous model, then this model was retained as the best-fit one (Sakamoto et al., 1986). The best-fit GAM was used to describe the effects of the environmental variables on the estimated abundance of *N. scintillans* using the effect plots.

The high temporal resolution of the HR data allowed not only to identify suitable drivers leading to abundance peaks of *N. scintillans* (e.g. bloom conditions), but also of different *N. scintillans* bloom phases. Therefore, the daily HR data were additionally subdivided into pre-bloom and post-bloom phases (Fig. S-4). Considering the fast development and break-down of *N. scintillans* blooms, the pre-bloom phase represents the two weeks before an abundance of $\geq$ 500 cellsL^{-1} was measured, and the post-bloom phase represents the two weeks after the last abundance of $\geq$ 500 cellsL^{-1} was measured. These time frames were chosen following Sathish et al. (2021), who observed distinct reproductive strategies in those specific time frames and established these guidelines as indicators for the different *N. scintillans* bloom phases . For both pre- and post-bloom phases, GAMs were built (Table S-5).

2.3. Continuous plankton recorder

2.3.1. N. scintillans abundance data

Samples were collected at monthly intervals by using a CPR, a

Table 1
Environmental data used in the GAMs for the HR and the CPR time series.

	Variable	Units	Range (min. – max.)	Average	Source/method	Temporal resolution	Temporal range
HR	SST	°C	−1.6 – 20.5	10.5	*In situ*	Work-daily	1962–2020
	SSS	–	22.8 – 36.1	32.2	Laboratory		
	DIN	$\mu molL^{-1}$	0.0 – 143.9	18.2			
	SR	Wm^{-2}	2.4 – 335.8	128.7	meteoblue.com	Daily	
	WS	ms^{-1}	1.2 – 18.1	7.7			
	Prec	mm	0.0 – 43.5	2.2			
CPR	SST	°C	4.1 – 18.5	10.5	noaa.com	Seasonal	1985–1994
	SSS	–	29.6 – 35.3	34.1			1995–2004
							2005–2017
	MLD	m	5.2 – 81.4	23.8			1981–2010
							2011–2017

Table 2
Correlation matrices for the predictor variables for HR. On the lower diagonal are Pearson's correlation coefficients; on the upper diagonal are *p*-values. * indicate significant *p*-values (<0.05).

	SST	SSS	DIN	Prec	WS	SR
SST	–	*	*	*	*	*
SSS	−0.12	–	*	*	*	*
DIN	−0.41	−0.23	–	*	*	*
Prec	0.09	0.07	−0.09	–	*	*
WS	−0.15	0.16	−0.06	0.31	–	*
SR	0.40	−0.32	0.11	−0.23	−0.36	–

Table 3
Correlation matrices for the predictor variables for the CPR survey. On the lower diagonal are Pearson's correlation coefficients; on the upper diagonal are *p*-values. * indicate significant *p*-values (<0.05).

	SST	SSS	MLD
SST	–	*	*
SSS	−0.04	–	*
MLD	−0.16	−0.54	–

filtering mechanism housed in an external body, towed repeatedly within the year by ships-of-opportunity on regular routes (Fig. 1) at an average speed of 10 nautical miles per hour and at a fixed depth of 7–10 m (Warner and Hays, 1994). Planktonic organisms were continuously filtered upon a silk band moving in the housing at a rate of approximately 10 cm per 10 nautical miles, and preserved in 4 % formaldehyde (Warner and Hays, 1994). One sample represents approximately 3 m^3 of seawater taken over 10 nautical miles. After each tow, samples were analysed in the laboratory, for identification and counting of organisms (counts $3m^{-3}$) following the methodology described in Batten et al., 2003. *Noctiluca scintillans* is usually identified by its striated ventral tentacle in the CPR samples (Kraberg et al., 2010; Richardson et al., 2006). In this study, *N. scintillans* abundances collected with the CPR for nearly 4 decades (1981–2018) in the North Sea (51°0′–58°0′N, 0°0′–10°0′E) were used (Johns, 2020).

2.3.2. Environmental data

For the CPR data, environmental variables were downloaded from the World Ocean Atlas 2018 (https://www.ncei.noaa.gov/data/oceans/woa/WOA18/DATA/). Seasonal means (winter = January-March, spring = April-June, summer = July-September, autumn = October-December) of SST, SSS, and mixed layer depth (MLD) were obtained (Table 1). For modelling, environmental variables and abundance data were aggregated by season and decade over an area of 0.25°

2.3.3. Statistical analyses

For the CPR data, collinearity was checked (Table 3) before building GAMs to describe the effects of the environmental (SST, MLD, and SSS), spatial (longitude and latitude as interaction term), and temporal (season and decade) variables (predictor variables) on the abundance of *N. scintillans* (response variable). Because the response variable was continuous, positive, and had large overdispersion, the negative binomial family of distribution and logarithm as a link function was used in the GAMs. The general equation can be written as follows:

$$\log(z) = a + f_1(SST) + f_2(SSS) + f_3(MLD) + f_4(Lon,\ Lat) + f_5(Season) + f_6(Decade)$$

with z as the abundance of *N. scintillans, a* as the intercept and f_n as the smooth functions.

The minimal adequate model was selected as described above. The best-fit GAM was used to describe the effects of environmental variables on the estimated abundance of *N. scintillans* using effect plots, whereas the spatiotemporal variability of *N. scintillans* was described with predicted maps by decade and by season. All data analyses were realized using the R programming software version 4.2.1 (R Core Team, 2023).

3. Results

3.1. Main drivers of N. scintillans in the North Sea

The best-fit model with the highest explained deviance (55.54 %) and lowest AIC for the HR time series included all predictor variables (Table 4). The results of the GAMs revealed that SST and wind speed are most influential for peak abundances of *N. scintillans* (Table S-5). Variables contributing least were precipitation, DIN concentrations, and SSS. The visualisations of the model for the HR time series (Fig. 3) show that maximum abundances of *N. scintillans* are more likely to occur at water temperatures around 17 °C (Fig. 3A) and at salinities around 30 (Fig. 3B). Moreover, highest densities are expected in waters with DIN around 30 $\mu molL^{-1}$ (Fig. 3C). Favourable conditions for abundant *N. scintillans* also include solar radiation below 75 Wm^{-2} (Fig. 3D), local precipitation around 7.5 mm (Fig. 3E), and wind speed below 6 ms^{-1} (Fig. 3F). Years in which conditions for *N. scintillans* were most suitable were between 1980 and 1990, and after 2010 (Fig. 3G). The months with highest cell densities are expected to be June and July (Fig. 3H).

Table 4
Statistical summary of the best-fit GAMs for the HR and the CPR time series.

Time series	Model	Explained Deviance	Adjusted R^2
HR	$y = a + f_1(SST) + f_2(SSS) + f_3(DIN) + f_4(Year) + f_5(Month) + f_6(Prec) + f_7(WS) + f_8(SR)$	55.54 %	0.16
CPR	$y = a + f_1(SST) + f_2(SSS) + f_3(MLD) + f_4(Lon, Lat) + f_5(Season)$	29.45 %	0.05

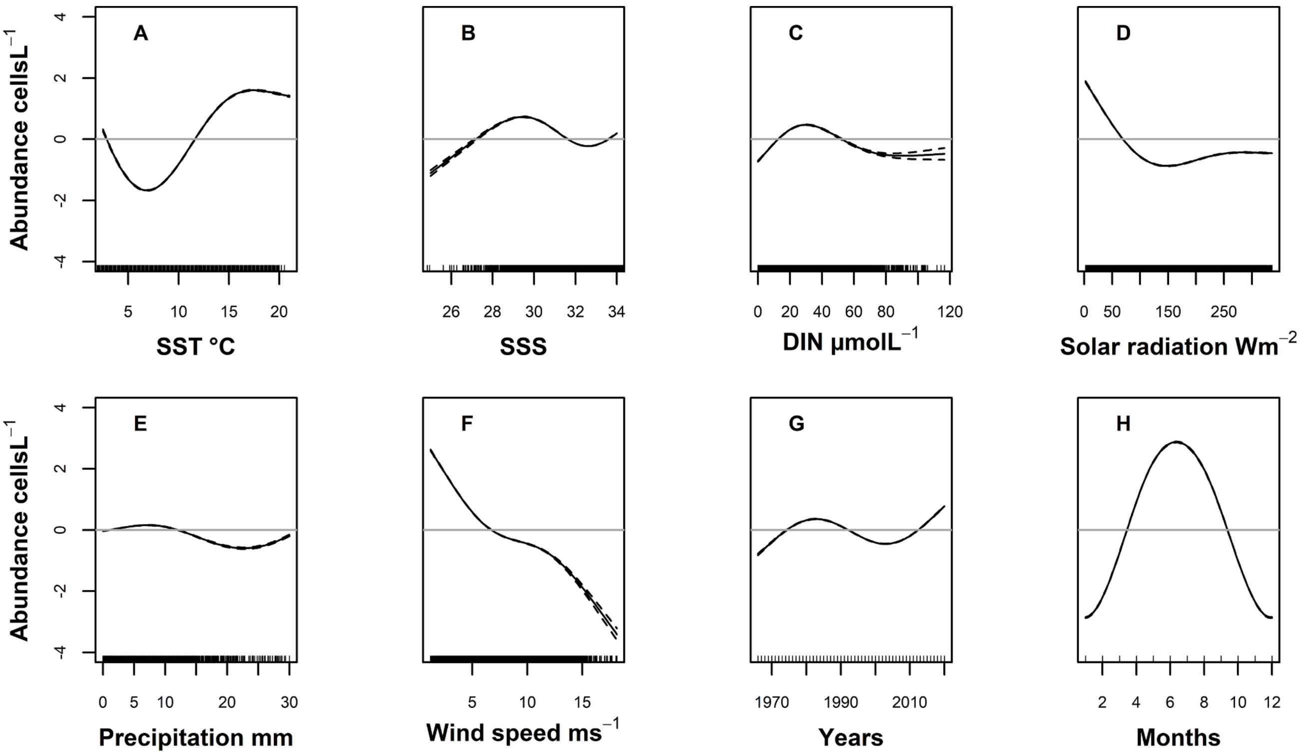

Fig. 3. Effect plots of the best-fitted GAM for the HR time series. Dashed lines represent two standard errors above and below the estimate of the smooth curve represented by the solid line. Y-axes are on the scale of the predictor variable, e.g. *N. scintillans* abundance (cellsL^{-1}). The rug plots at the bottom of the x-axes indicate observations of the predictor variable.

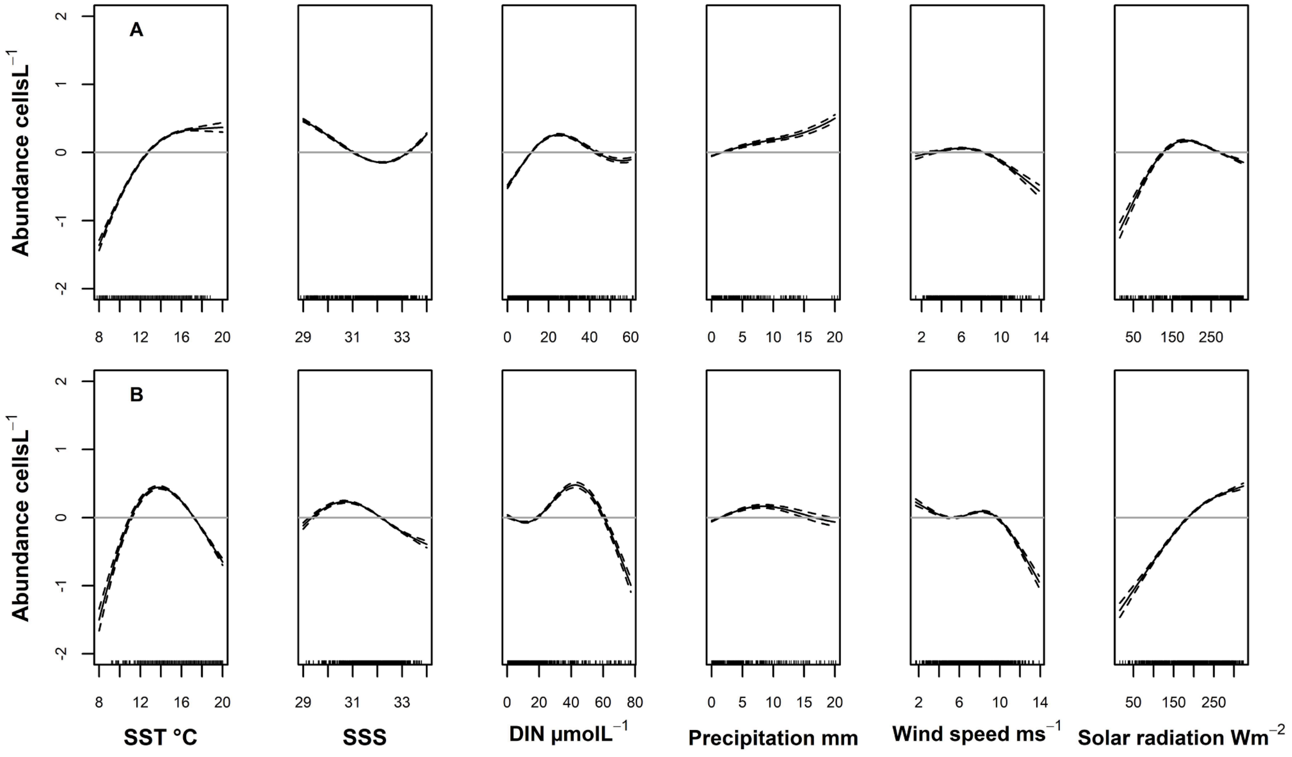

Fig. 4. Effect plots of GAMs for A) Pre-bloom phase; B) Post-bloom phase from the Helgoland Roads time series. All values are on the scale of the linear predictor. Dashed lines represent two standard errors above and below the estimate of the smooth curve. Numbers after the predictor variable name denotes the effective degrees of freedom of the smooth curve. Rug plot (at the foot of each plot) shows observations of predictor variables.

Table 5
Summary of drivers associated with different bloom phases (see Fig. 5, Fig. 6, and Table S-5).

	Pre-bloom	Bloom	Post-bloom
SST °C	> 12	~ 17	~ 13
SSS	> 34	29–31	~ 30.5
DIN µmolL^{-1}	20–30	~ 30	~ 45
SR Wm^{-2}	~ 175	< 75	> 200
Prec mm	> 5	~ 7.5	~ 7.5
WS ms^{-1}	~ 6	< 6	< 10

The results of the GAMs showed that the most influential drivers for the pre-bloom phase were SST, SSS, and DIN (Fig. 4A, Table S-5), whereas for the post-bloom phase SST, solar radiation and DIN were most relevant (Fig. 4B, Table S-5). The environmental factors at which the different bloom phases of *N. scintillans* are most likely to occur are summarized in Table 5.

For the CPR data, the highest deviance explained (29.45 %) and lowest AIC was obtained for the model including all factors except decade (Table 4). The results of the GAMs applied to the CPR time series, indicated that position (longitude and latitude), MLD, and Season were most important for *N. scintillans* in the North Sea. Variables contributing least were SSS and SST (Table S-6). Highest densities of *N. scintillans* in the North Sea can be expected to occur in waters with a MLD of < 20 m (Fig. 5A), salinity > 34 (Fig. 5B) and temperature above 11 °C (Fig. 5C). High abundances of *N. scintillans* are more likely to occur in coastal environments and particularly near river outflows such as the Elbe Estuary. Densities of *N. scintillans* are expected to decrease with distance from the coast and lowest abundances are expected to occur in the open sea (Fig. 5D). Lastly, highest abundances are more likely to occur in summer (Fig. 5E).

3.2. Temporal trends

Noctiluca scintillans was present in over 2600 from nearly 13,000 samples collected for the HR time series between 1962 and 2020, with yearly maximum abundances ranging from 80 to 22,500 cellsL^{-1} (in 1965 and 1984, respectively). Over time, occurrences and blooms of *N. scintillans* increased, particularly after the 1990s (Table 6). In comparison with the 1990s, the organism was encountered more than twice as often in the samples in the 2020s (14 % and 34 %, respectively). Similarly, the number of blooms sampled in this period showed a positive trend between the 1990s and the 2020s (1.5 % and 2.0 %, respectively).

Abundances of *N. scintillans* displayed a strong seasonal pattern at HR with lowest abundances measured in winter, increasing in spring, reaching a peak in summer, and decreasing again in autumn (Fig. 6). Highest mean densities of *N. scintillans* were recorded in the 1970s in summer with 280.8 cellsL^{-1}. Results from the GLM indicated that *N. scintillans*' summer mean abundances decreased significantly between the 1970s and the 1990s by nearly a factor of 2 ($p < 0.05$). After the 1990s, a 1.65-fold increase in *N. scintillans* abundance occurred ($p < 0.05$) (Table S-7).

After the 1990s, a positive trend was also found for the length of the

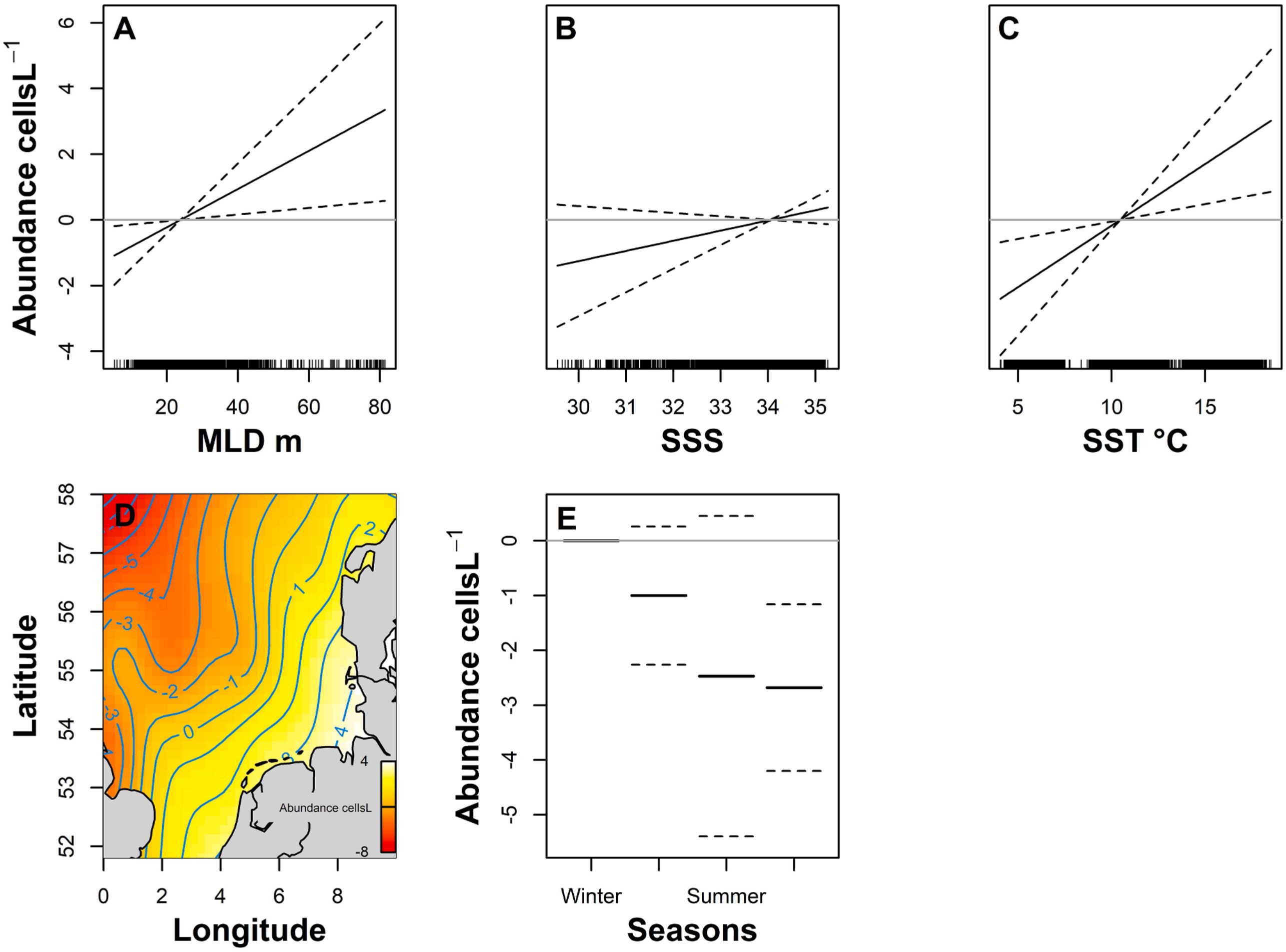

Fig. 5. Effect plots of the best-fitted GAM for the CPR survey. Dashed lines represent two standard errors above and below the estimate of the smooth curve, represented by the solid line. Y-axes are on the scale of the predictor variable, e.g. *N. scintillans* abundance (cellsL^{-1}). The rug plots at the bottom of the x-axes indicate observations of the predictor variable.

Table 6
Summary of the decadal sampling effort at HR including number and percentage of analysed samples containing *N. scintillans*, as well as number and percentage of sampled *N. scintillans* blooms ($\geq$ 500 cellsL^{-1}).

Decades	Total samples	Samples with *N. scintillans*	*N. scintillans* occurrence (%)	Sampled *N. scintillans* blooms	*N. scintillans* blooms (%)
1960s	1111	178	16.0	24	2.2
1970s	1914	340	17.7	48	2.5
1980s	2445	464	19.0	60	2.5
1990s	2393	331	13.8	37	1.5
2000s	2442	566	23.2	42	1.7
2010s	2373	670	28.2	43	1.8
2020s	250	84	33.6	5	2.0

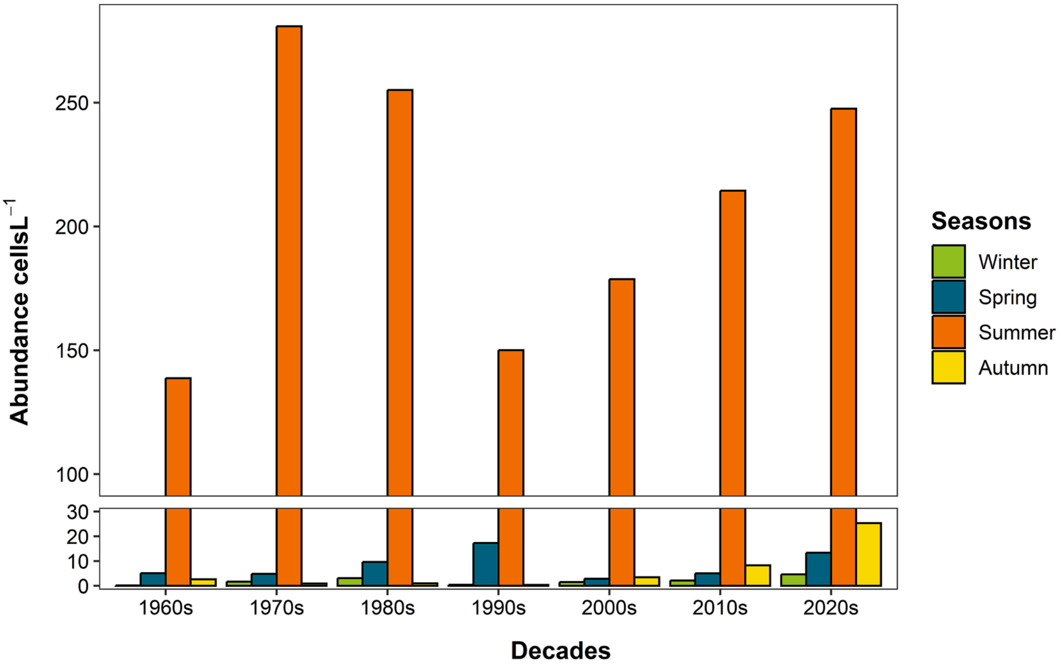

Fig. 6. Decadal variations of mean seasonal abundance of *N. scintillans* at HR for the period 1962–2020.

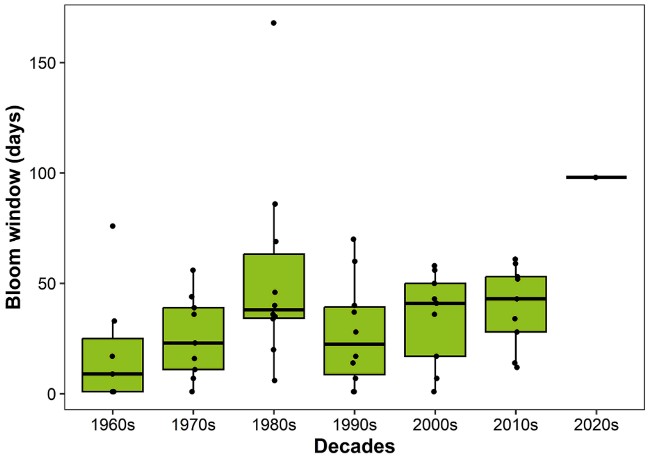

Fig. 7. Decadal variations of the *N. scintillans* bloom window duration at HR shown as boxplots for the period 1962–2020. The bloom window corresponds to the yearly timeframe between the first and last measurement of *N. scintillans* abundances $\geq$ 500 cellsL^{-1}. The exclusion of the extreme value from the 1980s results in non-significant differences between the 1970s and 1980s (See Table S-8). The boxes extend from the 25th to the 75th percentile where the solid line indicates the median. Observations are indicated by dots.

bloom window of *N. scintillans* for HR, increasing 3.6-fold between the 1990s and 2020s (Fig. 7). The shortest bloom window occurred in the 1960s with 19.7 days, whereas the longest bloom window was recorded for the 2020s and lasted 98 days (Fig. 7, Table S-8). The analysis of variances showed a significant increase between the 1970s and 1980s, and between the 2010s and 2020s ($F_{6,48}$=2.26, $p < 0.05$). Nevertheless, after the removal of the extreme value (i.e. *N. scintillans* bloom recorded in January 1989), there were no significant differences in the length of the bloom window between the 1970s and 1980s (Table S-9).

Abundances of *N. scintillans* also displayed a strong seasonal pattern in the entire North Sea with lowest abundance in autumn and winter, increasing in spring, and peaking in summer (Fig. 8). Highest abundances were observed in summer between 2005 and 2017. Over time, an increasing trend in *N. scintillans* abundance was observed mainly for summer, but a positive trend was also present during winter and spring. Densities in autumn remained rather constant over time.

3.3. Spatial trends

The spatiotemporal predictions of *N. scintillans* in the North Sea are represented in Fig. 9. The distribution of this dinoflagellate is restricted to the coastal regions of the southern North Sea and highest values are predicted for summer. Over time, the distribution of *N. scintillans* underwent a geographical spread and an intensification especially in areas near major estuaries outflows. Between 1985 and 1994, abundances were very low in winter (Fig. 9A) and autumn (Fig. 9D), with highest

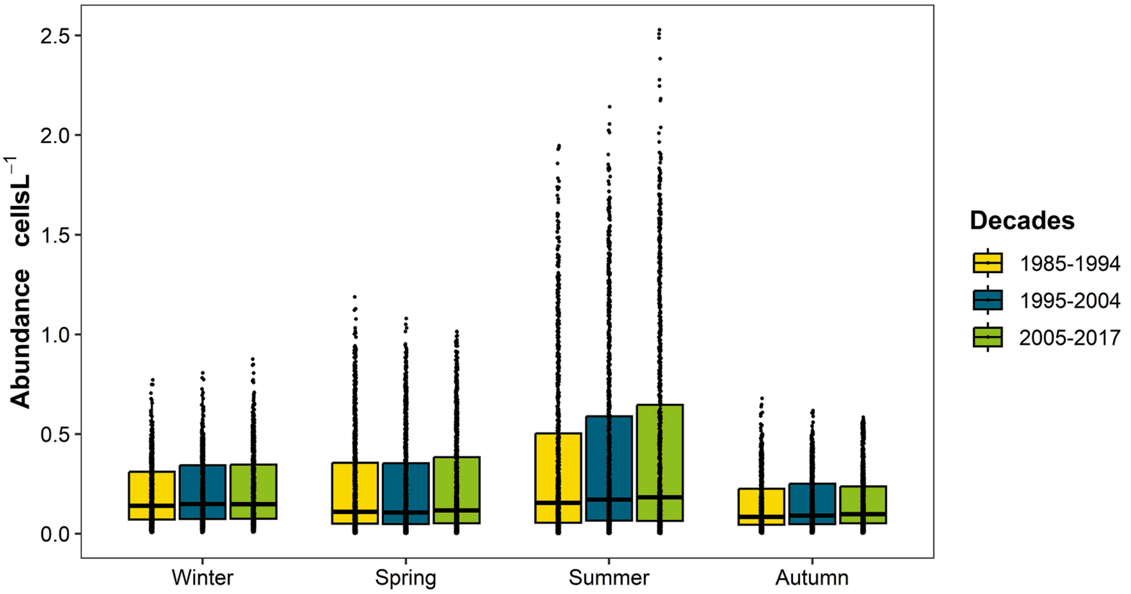

Fig. 8. Seasonal variations of predicted *N. scintillans* abundance (cellsL^{-1}) by decade (square root-transformed) shown as boxplots for the period 1985–2017 (CPR). The boxes extend from the 25th to the 75th percentile where the solid line indicates the median. Observations are indicated by dots.

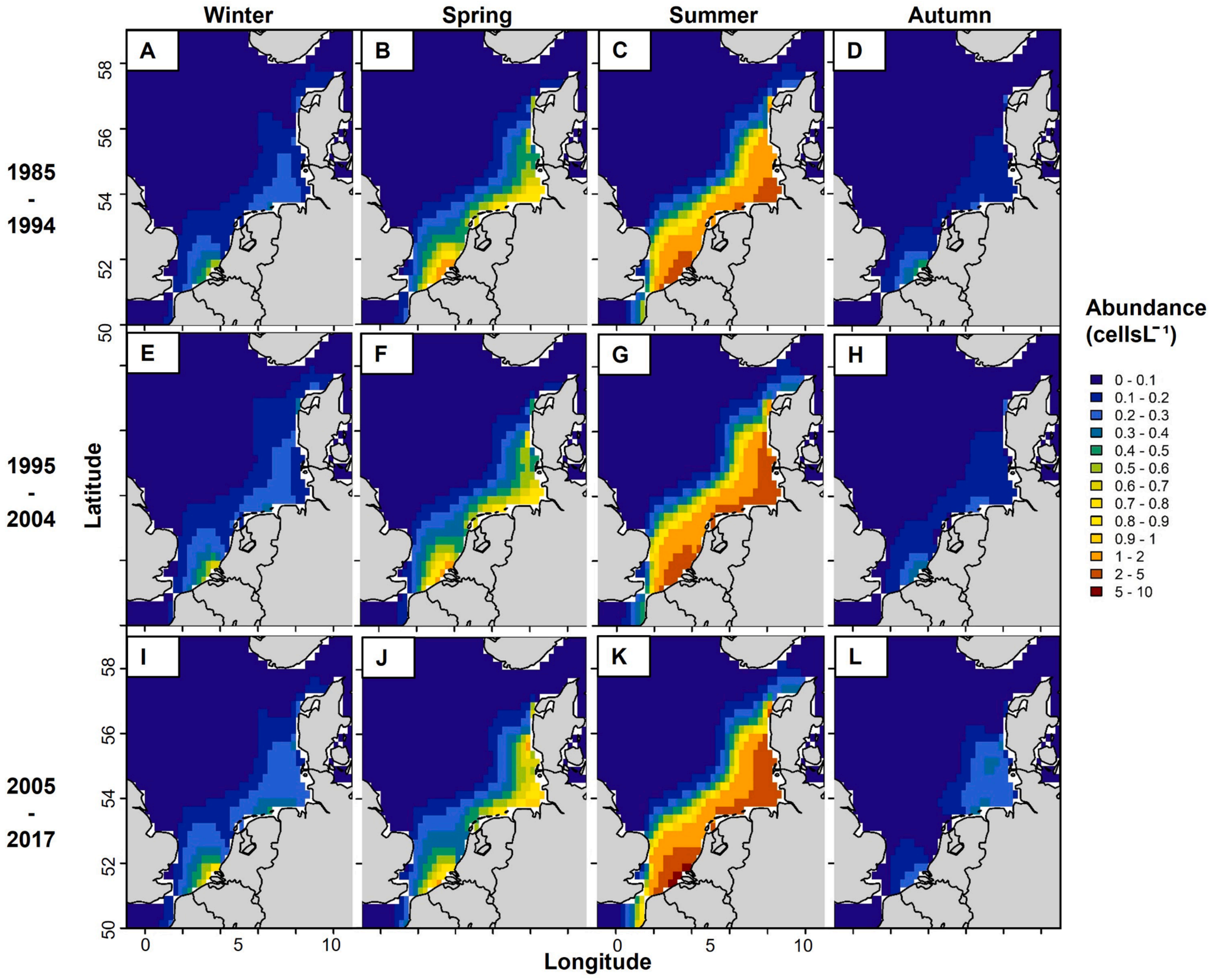

Fig. 9. Seasonal predictions of *N. scintillans* abundance (cellsL^{-1}) by the best-fitted GAM for the CPR time series in the North Sea (1985–2017).

densities (0.6–0.7 cellsL^{-1}) predicted off the coast of Zeeland, Netherlands. Abundances in spring (Fig. 9B) were highest in the Rhine-Meuse-Scheldt delta (1–2 cellsL^{-1}). In summer, highest concentrations of *N. scintillans* (2–5 cellsL^{-1}) were expected near the main river plumes (Meuse, Rhine, Ems, Weser, Elbe) (Fig. 9C). Between 1995 and 2004, the distribution of *N. scintillans* followed similar patterns during winter (Fig. 9E), spring (Fig. 9F), and autumn (Fig. 9H) compared to previous decades. During summer, the region with higher *N. scintillans* concentrations (2–5 cellsL^{-1}) spread from the Elbe Estuary to the East Frisian Islands and northwards along the Danish coast (Fig. 9G). From 2005 to 2017, results suggested a slight widening of the area of occurrence of low *N. scintillans* densities (0.2–0.3 cellsL^{-1}) in winter when compared to previous decades (Fig. 9I). The distribution of *N. scintillans* in spring follows a similar pattern than in previous decades, with a slight intensification at regional level such as the southern Danish coast (Fig. 9J). In summer, abundances were predicted to increase in the Rhine-Meuse-Scheldt delta, reaching maximum abundances of 5–10 cellsL^{-1}, corresponding to more than double the abundances measured in the previous periods (2–5 cellsL^{-1} between 1995 and 2004) (Fig. 9K). The area in which low abundances (0.2–0.3 cellsL^{-1}) of *N. scintillans* are expected in autumn, widened when compared to the previous decade, extending from the Ems to the Elbe estuary and up to the Danish coast (Fig. 9L).

4. Discussion

4.1. Drivers throughout N. scintillans blooms

In this study, the spatiotemporal distribution of the dinoflagellate *N. scintillans* in the North Sea was described, along with its associated drivers, while using data from two different long-term time series. It was established that the abundance of *N. scintillans* intensified since the 2000s and that the distribution of this species expanded throughout the southern North Sea over the last decades. Moreover, it was determined that dense *N. scintillans* occurrences are influenced by several factors combined, including warm waters, low wind speed, and light intensity below 75 Wm^{-2}. Lastly, hotspots for this species were identified within near-shore waters and particularly near the outflow from river estuaries.

The best-fit models for both analysed time series indicated that the abundances of *N. scintillans* are driven by multiple predictor variables. For HR, temperature and wind speed were identified as main factors driving *N. scintillans* abundances, with peak densities predicted for waters around 17 °C. This corresponds to the highest range of temperatures measured around Helgoland and coincides with results obtained with cultured *N. scintillans*, reporting highest growth rates at water temperatures between 19 and 25 °C (Harrison et al., 2011; Uhlig et al., 1995).

Calm wind conditions (wind speed < 6 ms^{-1}) have been identified as a significant factor contributing to high concentrations of *N. scintillans* around Helgoland (Lin et al., 2024; Nakamura, 1998; Uhlig and Sahling, 1990; Zhang et al., 2021). This is consistent with the buoyant nature of *N. scintillans*, leading to the formation of dense surface patches when wind or tidal mixing fails to resuspend the cells in the water column. Enhanced stratification often results in nutrient-depleted environments, and, hence, to lower phytoplankton biomass (Lewandowska et al., 2014). Buoyant *N. scintillans* cells feed while rising through the water column, intercepting prey on their ascent (Kiørboe and Titelman, 1998). With low prey availability, the cells remain empty and accumulate in dense patches at the surface (Uhlig and Sahling, 1990). This may explain the significance of stratification for the abundance peaks of *N. scintillans*.

Peak abundances of *N. scintillans* have been predicted to occur at SSS between 27 and 30 near Helgoland, encompassing nearly the entire range of salinities recorded within the study area. This underscores the tolerance of *N. scintillans* to a wide range of salinities, as evidenced by earlier investigations (Hallegraeff et al., 2019; Wang et al., 2023). Results showed that high abundances o are expected at solar radiation below 75 Wm^{-2}. High light intensity has the potential to damage *N. scintillans* cells, and with peak abundances often associated with surface accumulation, high light intensity would be detrimental and could cause a bloom collapse (Uhlig and Sahling, 1990).

Pre-bloom conditions included DIN concentrations and solar radiation above average (20–30 $\mu molL^{-1}$ and ~ 175 Wm^{-2}, respectively). As phytoplankton relies on nutrients and light to grow, it can be expected that *N. scintillans* can start developing when light and nutrients are available, and prey is abundant. These findings suggest that prey availability is the main requirement for the growth of *N. scintillans* (Kiørboe and Titelman, 1998; Kopuz et al., 2014; Zhang et al., 2020). Consistent with this, the analysis predicted peak abundances of *N. scintillans* in June and July, following the spring bloom in the North Sea. Pre-bloom conditions were associated with temperatures above 12 °C. Together with DIN concentration (Fig. S-10D) and solar radiation (Fig. S-10I), the SST associated with the pre-bloom phase corresponds to the environmental conditions between April and May (Fig. S-10A), during the temporal range of the annual spring bloom. Uhlig and Sahling (1990) observed first *N. scintillans* cells already dividing in March at SST between 5 and 6 °C. This observation suggests that *N. scintillans* initiates its development in early spring but attains pre-bloom conditions only in April-May due to insufficient prey.

Post-bloom conditions were characterized by SST around 13 °C, DIN around 45 $\mu molL^{-1}$, and solar radiation above average ($>$ 200 Wm^{-2}). The temperatures associated with the post-bloom phase fall within the suitable temperature range for *N. scintillans* and the DIN concentration is above average. Therefore, the bloom termination is most likely attributed to the limited prey availability and increased light intensity. During dense *N. scintillans* blooms, cells heavily graze on phytoplankton and can cause the end of other phytoplankton blooms (Kitatsuji et al., 2019). It can be expected that after the bloom peak of *N. scintillans*, prey availability drastically drops due to intense predation, which would in turn contribute to the accumulation of cells at the surface. Since *N. scintillans* cells in surface waters which are exposed to elevated light suffer from irreversible deterioration, elevated solar radiation could accelerate the bloom decay. The higher DIN concentrations associated with the post-bloom phase might be partially influenced by the excretion of NH_4 by *N. scintillans* upon cell lysis (Ara et al., 2013; Zhang et al., 2021). Highest concentrations of NH_4 were measured in late summer in Helgoland (Fig. S-10F), following the decline of *N. scintillans* abundances.

The findings demonstrated that *N. scintillans* is not solely driven by individual variables but rather by several factors acting together (Fig. 10). The models indicated that the month was important for *N. scintillans*, accounting for a combination of environmental conditions. High temperatures, low wind speed, and moderate light intensity collectively contributed to favorable conditions for dense *N. scintillans* blooms during June and July.

Results from the CPR analysis showed that highest *N. scintillans* abundance in the North Sea were associated with water temperatures around 11 °C, differing from the results near Helgoland. This difference could imply either that the optimal temperature range for *N. scintillans* varies with the study area, indicating potential adaptability of this dinoflagellate to its local environment, or that SST only partially drives *N. scintillans.*

A deep mixed-layer depth ($<$ 20 m) positively influenced *N. scintillans*, contradicting the findings in Helgoland, where increased stratification promoted peak densities. With the sampling depth of the CPR usually occurring between 7 and 10 m, dense surface patches are likely to be missed. If surface accumulations are not accounted for, it is logical that a deep MLD corresponding to well-mixed waters, favours high *N. scintillans* abundance. Highest *N. scintillans* abundances within the water column were associated with well-mixed, nutrient-rich waters benefitting the growth of phytoplankton (Dela-Cruz et al., 2008). In the eastern Atlantic, stronger spring blooms occurred when a deep MLD and strong winds occurred (Martinez et al., 2011). This might promote the growth of *N. scintillans* through increased prey availability. A deep MLD may limit light availability which was associated with shifts from autotrophic to heterotrophic organisms (Monier et al., 2015), thereby

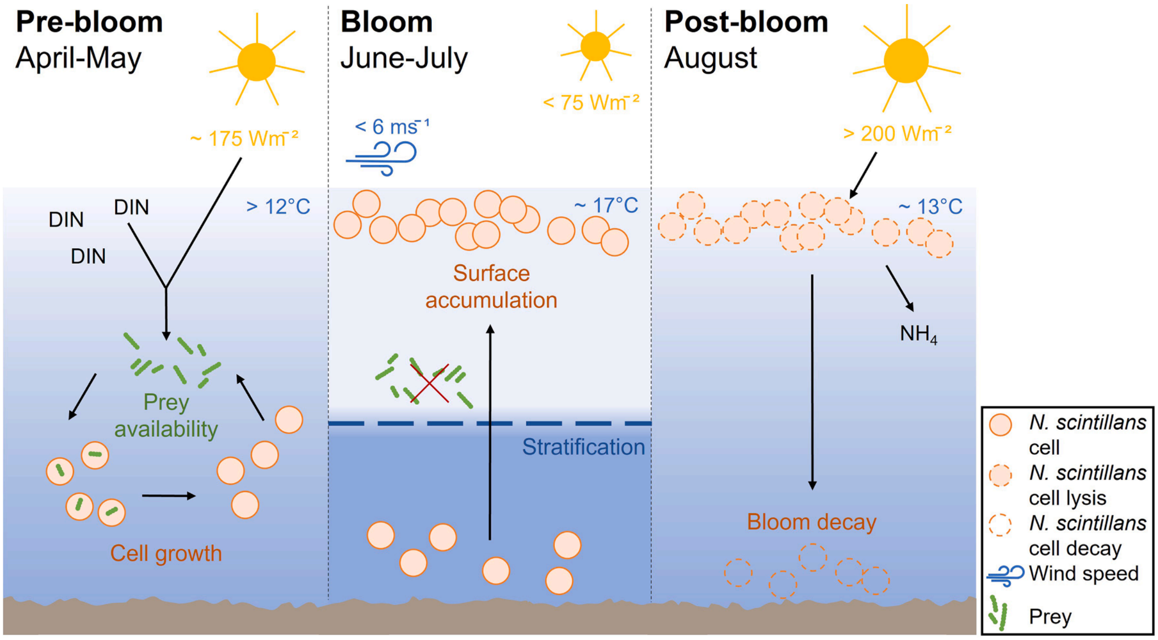

Fig. 10. Schematic representation of the environmental preferences of *N. scintillans* during different bloom phases (including pre-bloom, bloom, and post-bloom). Suitable pre-bloom conditions for the growth of *N. scintillans* include high DIN and light availability, leading to phytoplankton growth and, thus, to high prey availability for *N. scintillans.* The bloom phase with peak abundances occurs in June-July, once calm conditions (including low wind speed and stratification) prevail, leading to nutrient depleted surface waters, thus, low prey availability. With no prey encounter, *N. scintillans* cells accumulate at the surface. Post-bloom conditions correspond to higher solar radiation, damaging the cells accumulated at the surface, hence, inducing the bloom collapse.

potentially benefitting *N. scintillans.*

4.2. Temporal increase

Noctiluca scintillans abundances continuously increased after the 1990s and a significant elongation of the bloom window at HR was observed, with a 3.6-fold increase between the 1990s and 2020s. Temperature is widely acknowledged as important environmental factor shaping the marine ecosystems and the abundance and community composition of phytoplankton (Richardson, 2008). Ocean warming affects plankton either indirectly through increased stratification limiting the nutrient supply and directly through increased plankton metabolic rates (Lewandowska et al., 2014). The results suggested that SST is one of the factors driving the bloom dynamics of *N. scintillans* in the North Sea, where temperatures increased faster than the global average (~ 1.3 °C/57 years and ~ 0.7 °C/57, respectively). The waters around Helgoland are experiencing an even more accelerated warming, evidenced by an increase of 1.86 °C/57 years (Amorim et al., 2023). Considering that *N. scintillans* reaches highest densities in warm waters, the warming of the North Sea results in more frequent conditions favourable for population growth and for longer bloom periods. At HR, the occurrence of warm months with water temperatures between 17 and 18 °C shifted from 2.3 % to 12.4 % since 1991, whereas the cold months with temperatures below 2–3 °C have significantly decreased (Amorim et al., 2023). Since *N. scintillans* can engage cell division at low SST (Uhlig and Sahling, 1990), nearly year-round the temperatures around Helgoland could fall within the suitable range for *N. scintillans* and small populations are maintained. Regional occurrences of *N. scintillans* in the southern North Sea in winter and autumn suggested that suitable temperatures occur even during the colder months. A significant correlation between *N. scintillans* abundance and winter SST was established for waters around Helgoland, indicating that when higher SST occurs in winter, higher abundances of *N. scintillans* can be expected in the following summer (Heyen et al., 1999). This could explain the increasing trend in *N. scintillans* abundances, and the elongation of the bloom window. Climate change has also caused a significant increase of marine heatwaves (Oliver et al., 2018). During the heatwave in the German Bight in 2018, rapid changes in temperatures reduced nutrient loads to coastal waters and increased water column stratification (Kaiser et al., 2023). This might affect bloom timings and phytoplankton community composition, shifting from less resilient species towards more tolerant and rapidly developing species (Remy et al., 2017), such as *N. scintillans.*

The alterations in the bloom timing of different phytoplankton groups were associated with the warming of the North Sea. Diatoms reached their peak abundance 22 days earlier in the early 2000s than in the late 1950s, whereas dinoflagellates peaked 23 days earlier (Richardson, 2008). *Noctiluca scintillans* effectively feeds on various prey types, including diatoms and dinoflagellates (Fonda Umani et al., 2004; Zhang et al., 2015). Since heterotrophic *N. scintillans* requires high prey availability to bloom, the earlier blooms of its most common prey types have certainly contributed to the earlier start of *N. scintillans* blooms evidenced here.

The findings suggested that *N. scintillans* did not follow a constant increase between the 1960s and 2020s at HR. Abundances fluctuated with a significant decrease of *N. scintillans'* summer mean abundance between the 1970s and 1990s and an intensification after the 1990s. The southern North Sea is highly affected by eutrophication. Measures implemented in the late 20th century reduced nutrient inputs in the North Sea by 50 % by the late 2000s (Howarth and Paerl, 2008; Rewrie et al., 2023). Accordingly, the analysis of abiotic factors between 1962 and 2001 around Helgoland, revealed a major decrease in phosphorus since the mid-1970s (Wiltshire et al., 2008). The high DNA-content of dinoflagellates implies a high demand for phosphorus (Rizzo, 2003). This link has been established in earlier investigations observing dense *N. scintillans* blooms when phosphorus concentrations were high (Ollevier et al., 2021; Zhang et al., 2021). Reductions of phosphorus inputs have limited *N. scintillans* proliferations (Fonda Umani et al., 2004; Oguz and Velikova, 2010), suggesting that the steep decline in abundance between the 1970s and 1990s may be linked to the decreasing phosphorus concentrations during this period. Diatoms followed a decreasing trend between the 1960s and 1990s in the North Sea

(Leterme et al., 2006). Since diatoms are common prey of *N. scintillans* (Dela-Cruz et al., 2002), this could provide another explanation for the decrease in *N. scintillans* abundances after the 1970s. Similar results were obtained in mesocosm experiments, where the abundance of *N. scintillans* significantly decreased with lower proportions of diatoms within the phytoplankton community (Moreno et al., 2022).

The decrease in abundance between the 1970s and 1990s coincided with a significant increase in the bloom window length. This can be attributed to the unusual occurrence of a *N. scintillans* bloom in January 1989, which substantially elongated the bloom window for that year and influenced the bloom window length for the 1980s. Another possible explanation is the increase in "strong wind events" in the North Sea during the 1980s (Siegismund and Schrum, 2001). Findings revealed that the daily mean wind speed during the 1980s more frequently surpassed 10 ms^{-1} during the *N. scintillans* bloom windows compared to other decades (Table S-11). This could have affected abundances, as cells could be more easily resuspended in the water and less likely to accumulate densely at the surface. Additionally, as well-mixed conditions benefit the development of *N. scintillans*, more windy days might cause favourable bloom conditions over longer periods, thereby increasing the bloom window length.

The intensification of *N. scintillans* after the 1990s could partly be related to the increase in oceanic water inflow into the North Sea during the late 1980s (Drinkwater et al., 2003), leading to warmer SST, previously identified as beneficial for *N. scintillans*. Moreover, diatom abundances have been increasing in the North Sea since the 1990s (Hinder et al., 2012). The increased prey availability might have positively influenced *N. scintillans* and contributed to the observed increase.

The trends identified here, differ from the 3-year interval oscillations in *N. scintillans* abundance observed by Uhlig and Sahling (1990) in the German Bight. Maximum abundances every third year could not be clearly identified, as abundances remained high over several consecutive years (Figure S-12). Similarly, results from a time series analysis carried out between 2014 and 2018 in the Belgian Part of the North Sea, revealed an increase of *N. scintillans* over time rather than 3-year oscillations (Ollevier et al., 2021).

Increasing trends in the intensity, duration, and frequency of *N. scintillans* occurrences in the southern North Sea were identified. It is important to note that while the data for the 2020s exhibited comparable patterns to the trends observed in the preceding decades, this decade is represented solely by data from the year 2020. Consequently, definite conclusions about very recent trends at HR may be skewed and might solely be considered as indicators of potential recent trends.

4.3. Spatial increase

The models revealed that the sampling location had a strong influence on densities of *N. scintillans* and that highest abundances of this dinoflagellate can be expected during summer in coastal waters close to the outflow of rivers mouths and estuaries. Similarly, Tasmanian coastal waters showed elevated concentrations of *N. scintillans*, whereas lower concentrations were observed offshore (Hallegraeff et al., 2019). Interestingly, in autumn and winter *N. scintillans* exclusively occurred in estuaries in the North Sea. Overwintering populations of *N. scintillans* were also found in estuaries near Sydney, where conditions for stable but low standing stocks of the dinoflagellate (e.g. warmer waters and higher nutrients) are maintained throughout the colder season (Dela-Cruz et al., 2003). The ability of *N. scintillans* to survive in estuarine environments can undoubtedly be attributed to its euryhaline characteristics. Hallegraeff et al. (2019) found that the tolerance of *N. scintillans* to a wide range of salinities is a fundamental asset during transport and range extension. Additionally, *N. scintillans* benefits from several temperature ecotypes, allowing it to grow at a wide range of temperatures from near 0 °C (Elbrächter and Qi, 1998) up to 30 °C (Qi *et al.*, 2004), another asset in coastal environments where conditions rapidly change.

Over time, the distribution of *N. scintillans* expanded, initially concentrating near the main estuaries in the late 1980s and spreading along the coasts of the southern North Sea until 2017. The main intensification of this dinoflagellate was observed in summer between 2005 and 2017 within the river plume of the Rhine, where abundances doubled between the late 1990s/early 2000s and the late 2000s/2010s. Supporting these results, geographical hotspots for *N. scintillans* were identified at the East Frisian islands in the late 1980s (Uhlig and Sahling, 1990). Together with estuaries, these shallow, well-mixed and nutrient-rich areas offered ideal conditions for the initiation of *N. scintillans* population growth and were identified as main reproduction areas for this organism in the southern North Sea (Uhlig and Sahling, 1995). Since the mid-1990s, the area in which *N. scintillans* occurred spread northwards up to the central Danish coast, and westwards up to the West Frisian Islands in summer. Within the North Sea, the German Bight showed the highest warming trend in recent decades and particularly since the 1980s (Wiltshire et al., 2008). The nutrient input through the main rivers and the rising SST have certainly played an important role in the observed spatial spread of *N. scintillans* over time. Projections indicate increasing occurrences of westerly winds in the North Sea throughout the 21st century (Gaslikova et al., 2013). Given that *N. scintillans* hotspots are located around the West and East Frisian Islands, and that populations commonly drift from coastal to more offshore environments (Uhlig and Sahling, 1990), these changes in wind direction could have further contributed to the spread of this dinoflagellate along the coasts of the southern North Sea.

Noctiluca scintillans has bloomed more intensively, frequently and longer in various regions worldwide over the last decades (Kordubel et al., 2024). The geographical expansion, the rising abundance and elongation of the bloom duration identified here show that *N. scintillans* underwent similar changes within the North Sea. When considering the many competitive advantages of *N. scintillans* including its tolerance to changing environmental conditions, and the foreseen climate change scenarios predicting further increasing SST, decreasing salinities, and potentially increasing river nutrient loads caused by increased runoff in the North Sea (Quante and Colijn, 2016), it can be expected that the identified trends might follow similar patterns in the future. Dense *N. scintillans* blooms are associated with many negative impacts on coastal ecosystems and food webs. Further increases and broader areas of occurrence of *N. scintillans* could have major repercussions on ecosystem productivity and can lead to substantial economic losses. Therefore, the monitoring of this species needs to be further improved to minimize ecological and economic damage.

4.4. Limitations of the methodological approach

The analysis of two technically different time series has been effective in defining main drivers and long-term spatiotemporal dynamics of *N. scintillans* in the North Sea. Nevertheless, the heterotrophic nature of *N. scintillans* implies that the models might have performed better if prey abundance would have been included as potential driver. The identification of main prey types for *N. scintillans* in the field is crucial to improve predictions of the bloom dynamics of this species. This calls for methods allowing continuous *in situ* observation of *N. scintillans'* feeding behaviour such as cabled underwater cameras (Fischer et al., 2020). Similarly, the different bloom phases of *N. scintillans* were determined solely by abundances. However, it has been previously demonstrated that the precise determination of the different *N. scintillans* bloom stages requires information about its reproductive behaviour such as binary fission leading to the exponential growth during pre-bloom and bloom phase (Sathish et al., 2021).

The high temporal resolution of the HR time series allowed us to assess the bloom dynamics of this organism, whereas the duration of the dataset and consistency of the sampling method provided an insight in the long-term trends of *N. scintillans*. Nevertheless, the gelatinous constitution of *N. scintillans* and fragility of its agglomerations can lead to deteriorated cells and disrupted colonies when sampled with traditional methods including nets or bottles (Omori and Hamner, 1982). Moreover, species such as *N. scintillans* form patchy and filamentous bloom structures of only several meters width (Astoreca et al., 2005), and sampling carried out in one single location implies that patchy bloom structures can easily be missed. This patchiness could lead to over- or underestimated *N. scintillans* abundances.

In that aspect, the CPR ensures a wider geographical coverage. Despite the numerous modifications applied to the original sampling mechanism over time (Batten et al., 2003), data from the CPR are robust, providing multi-decadal information of marine plankton dynamics at high horizontal resolution (Richardson et al., 2006). It was shown here that for *N. scintillans,* reliable estimates of long-term trends over large spatial scales could be made. The main constraint associated with the CPR survey, particularly for coastal species like *N. scintillans*, is that sample collection generally starts approximatively 10 km offshore. Consequently, the accurate identification of hotspots near the immediate coastline can be limited. When comparing the densities of *N. scintillans* between the two time series, abundances measured with the CPR were substantially lower. Similarly, the comparison of two time series (i.e. CPR and Longhurst-Hardy Plankton Recorder) revealed underestimations of abundance by the CPR of a factor up to 40 (Richardson et al., 2004). Underestimated abundances have been linked to the clogging of the CPR mesh by *N. scintillans*, reducing the filtering efficiency of the CPR (McLeod et al., 2012). Physical damage to the organisms leading to the deterioration of morphological key features (i.e. striated flagellum of *N. scintillans*), can additionally impact counts. Another factor that could mislead abundance estimates is the sampling depth carried out at 7 to 10 m. Since the vertical distribution of *N. scintillans* is highly variable, with peak abundances observed at the surface as well as deep in the water column, *N. scintillans* blooms might be missed (Omori and Hamner, 1982). Nevertheless, the water masses in the shallow southern North Sea are generally well mixed (Quante and Colijn, 2016), which means that surface samples are representative of the entire water column. Despite the high horizontal resolution of the CPR, patchy *N. scintillans* proliferations increase the probability of under-sampling. The determination of precise spatial distribution patterns is limited and requires data at higher spatial resolution such as remote sensing. With satellites such as Sentinel-2 or Landsat, large-scale observations of surface waters down to 10 m resolution can be obtained. Novel methodologies and feature recognition allow a systematic identification of *N. scintillans* (Detoni et al., 2023; Gernez et al., 2023; Liu et al., 2024), greatly improving the monitoring of this species in the coming years. Nevertheless, here similar patterns in two significantly different time series were identified, suggesting that *N. scintillans*' abundance, as well as its spatial and temporal distribution in the North Sea is changing.

5. Conclusion

This study represents a systematic approach to assess main drivers for different bloom phases of *N. scintillans* and to determine spatiotemporal changes of this species in the North Sea. For the first time, two long-term time series of *N. scintillans* abundance in the North Sea were analysed, revealing essential information about this organism, on the rise in many regions around the globe. Results indicated that frequency of occurrence, abundance, and length of the bloom window of *N. scintillans* have significantly increased after the 1990s around Helgoland, Germany. Furthermore, findings indicated that occurrences of *N. scintillans* have geographically spread along the coast of the southern North Sea over the last decades. Regional intensifications such as in the Rhine-Meuse-Scheldt delta, where abundances doubled within a decade, were also identified. These trends were associated with increasing temperatures, fluctuations in nutrient discharges, and changes in phytoplankton community composition. The results highlight the need of continuous monitoring of *N. scintillans,* while applying traditional observation methods in combination with novel techniques such as underwater cameras and remote sensing. This could increase the ecological understanding of this organism and will ensure that occurrences of *N. scintillans* can be accurately predicted, limiting potential ecological and economic damages in the future.

CRediT authorship contribution statement

Katharina Kordubel: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Conceptualization. **Raúl O. Martínez-Rincón:** Conceptualization, Formal analysis, Visualization, Writing – review & editing. **Burkard Baschek:** Writing – review & editing, Supervision, Conceptualization. **Maarten Boersma:** Writing – review & editing, Conceptualization. **Martin Hieronymi:** Writing – review & editing, Conceptualization. **David G. Johns:** Writing – review & editing, Conceptualization. **Inga V. Kirstein:** Writing – review & editing, Conceptualization. **Yoana G. Voynova:** Writing – review & editing, Conceptualization. **Klas O. Möller:** Writing – review & editing, Supervision, Conceptualization.

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.

Data availability

Data will be made available on request.

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Supplementary materials

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