Noctiluca scintillans: Dynamics, Size Measurements and Relationships With Small Soft-Bodied Plankton in the Belgian Part of the North Sea

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Climate driven changes and anthropogenic pressures on the marine environment have been shown to favor the increase in certain potentially harmful species. Among them, *Noctiluca scintillans,* a common dinoflagellate, often blooms during warm summers and is known to affect plankton communities. In this study, we assessed the dynamics in abundance and cell size of *N. scintillans* as well as the relationship between *N. scintillans* and small soft-bodied zooplankton in the Belgian part of the North Sea (BPNS), since negative correlations between these plankton groups have been previously reported for nearby regions. This study is the first to present consistently counted *N. scintillans* cell numbers and measured cell lengths, through the analysis of ZooScan images from samples taken monthly at stations throughout the coastal zone of the BPNS. The results show that *N. scintillans* demonstrated clear seasonal dynamics with both high densities and large cell sizes in spring/summer (May-July). The occurrence of *N. scintillans* in the analyzed plankton samples and the abundance of *N. scintillans* at the observed peak intensities nearly tripled over a period of 5 years. A zero-inflated model showed a correlation of *N. scintillans* abundance with temperature as well as with phosphate concentrations, suggesting that anthropogenic influences such as climate change and riverine nutrient inputs could affect the temporal dynamics of the species. The results, on the other hand, did not show any negative impact of *N. scintillans* on the soft-bodied plankton community.

Keywords: Noctiluca, ZooScan, gelatinous zooplankton, time-series, Belgian coast, plankton blooms

INTRODUCTION

Over the last decades, climate driven changes and anthropogenic pressures have increasingly influenced the marine environment. Nutrient inputs of anthropogenic origin have notably led to the eutrophication of marine systems, particularly in coastal areas. In the southern North Sea (Lancelot et al., 1998; Daro et al., 2006), major western European rivers like the Rhine, Meuse and Scheldt (Van Bennekom and Wetsteijn, 1990; Lacroix et al., 2004) have a dominant influence on the water nutrient balance and thus can greatly influence the spring algal bloom dynamics. Notable shifts from diatom to flagellate dominance such as flagellate dominance of *Noctiluca scintillans,* have been observed over the last decades in this zone (Vasas et al., 2007).

The blooms of certain flagellates and phytoplankton species can be associated with negative effects on the marine environment, human health and the economy (Granéli and Turner, 2006) and are hence referred to as "harmful algal blooms" (Glibert et al., 2005). *Noctiluca scintillans* is one of the most important and abundant red tide organisms and its blooms have been linked to increased fish and marine invertebrate mortality (Huang and Qi, 1997; Thangaraja et al., 2007), affecting yields in fisheries and aquaculture. The high accumulations of toxic ammonia during blooms, which assist in the buoyancy of the cells (Fonda Umani et al., 2004), possibly act as the killing agent for other organisms (Okaichi and Nishio, 1976; Faust and Gulledge, 2002). In addition, the large size (0.2–2 mm) and voracious feeding behavior of *N. scintillans* enables it to feed on a broad spectrum of organisms including fish eggs, phytoplankton, zooplankton, detritus and bacteria (Schaumann et al., 1988; Kirchner et al., 1996; Quevedo et al., 1999). Other species feeding on the same food sources as *N. scintillans* can be affected due to food competition (Enomoto, 1956; Quevedo et al., 1999) which might explain the negative correlations observed between various soft-bodied zooplankton species and *N. scintillans* (Heyen et al., 1998; Kovalev and Piontkovski, 1998; Fock and Greve, 2002). At present, no consensus has yet been found on the exact drivers of the dynamics or bloom formation of *N. scintillans*. However, many studies found a variety of factors that correlated with *N. scintillans* densities, including eutrophication (Polishchuk and Ghilarov, 1981; Boni, 1983; Porumb, 1992; Bologa et al., 1995), specific nutrients [more particularly phosphate (Degobbis et al., 1995)], chlorophyll *a* (Isinibilir et al., 2008), other plankton species presence [diatom spring blooms (Weston et al., 2008), zooplankton biomass (Cataletto et al., 1995; Fonda Umani et al., 2004; Yılmaz et al., 2005)], physical characteristics of the water column [winter sea surface temperature (Heyen et al., 1998), tides (Holligan, 1979), stratification (Boni, 1983)], and weather conditions [rainfall (Miyaguchi et al., 2006), wind direction (Yamamoto et al., 1997; Nakamura and Hirata, 2006)]. This shows that the dynamics of *N. scintillans* is complex and depends on many factors, which can differ among locations.

During bloom formation, *N. scintillans* can reach high densities and can often constitute a significant part of the plankton community. Because manually counting *N. scintillans* cells is too time consuming, the species is often excluded from microscopy counts (Nohe et al., 2020). Hence, little is known about its dynamics in the Belgian part of the North Sea (BPNS). However, novel imaging techniques such as the ZooScan allow for an accurate assessment of the densities and associated size measurements of such taxa. Due to the potential adverse effects of *N. scintillans* on the marine environment as well as its potential to increase in abundance as a result of climate change and ocean acidification (Moore et al., 2008), substantial research is needed to gain knowledge on the blooms, drivers and effects of *N. scintillans* in the BPNS. The ZooScan data series used in this research included data on soft-bodied species, for which time series are very scarce (Aubert et al., 2018). Because of the availability of this unique data series and also due to the significant negative correlations found between *N. scintillans* and small soft-bodied zooplankton in neighboring areas (Heyen et al., 1998; Fock and Greve, 2002), it was decided to focus on the potential impact of *N. scintillans* on small soft-bodied plankton in the BPNS. Based on the ZooScan data, this study explores the potential of ZooScan imaging for cell density and size estimates of species of interest such as *N. scintillans* and aims to unravel the population dynamics of *N. scintillans* in the BPNS, to determine the drivers of its dynamics, as well as to investigate the impact of the species on small soft-bodied zooplankton taxa.

MATERIALS AND METHODS

Study Area

The Belgian part of the North Sea (BPNS, ca. 3,600 km²) is located in the Southern Bight of the North Sea. It is a relatively shallow area with maximum depths of 40 meters. The strong tidal currents result in a well-mixed water column with very weak salinity and temperature stratification (Fettweis and Nechad, 2011). The BPNS is known as an eutrophicated ecosystem, due to anthropogenically induced nutrient inputs through the discharge of major West-European rivers such as the Ijzer, Scheldt, and Maas (Nihoul and Hecq, 1984; Lancelot et al., 1998; Daro et al., 2006; Goffin et al., 2015).

Data Acquisition

Open-access time series data (2014–2018) from Flanders Marine Institute (VLIZ) (2019a,b) were used for this analysis. Zooplankton samples and associated water quality parameters were collected on a monthly basis since 2014 at nine stations in the BPNS (**Figure 1**). Zooplankton was sampled with a 200 μm WP2 net which was deployed vertically and equipped with a flowmeter. Zooplankton collected in the cod-end was then sedated by sodawater and fixated in 4% formalin. In the lab, the fixative was changed to 70% ethanol. All 404 samples were digitized by the ZooScan plankton imaging device and processed by ZooProcess and Plankton Identifier (PkID) in order to detect and classify the digitized objects (Grosjean et al., 2004; Gorsky et al., 2010). The associated water quality parameters (nutrients, pigments and suspended particulate matter) are based on water samples collected with Niskin bottles at 3 m depth. For pigments, seawater was filtered through Whatman GF/F glass fiber filters (47 mm). The filter was subsequently folded, dried and stored frozen. For nutrients, around 200 mL of water was filtered through a 47 mm, 0.2 μm cellulose-acetate filter for residual water. When the filter ran dry, 150mL of the filtered water was poured into a recipient and stored at −24°C. After filtration and processing on board, all samples were sent to specialized companies for further analysis. High Pressure Liquid Chromatography (HPLC) was used for the determination of pigments. Nutrient samples were analyzed by means of a SEAL QuAAtro analysis system or by means of discrete analysis system and spectrophotometric detection with a Skalar AutoAnalyser system. Information on the conductivity, temperature and depth of the water column was obtained by means of a CTD profile. The methodology of these two dataseries is fully described in Mortelmans et al. (2019a,b).
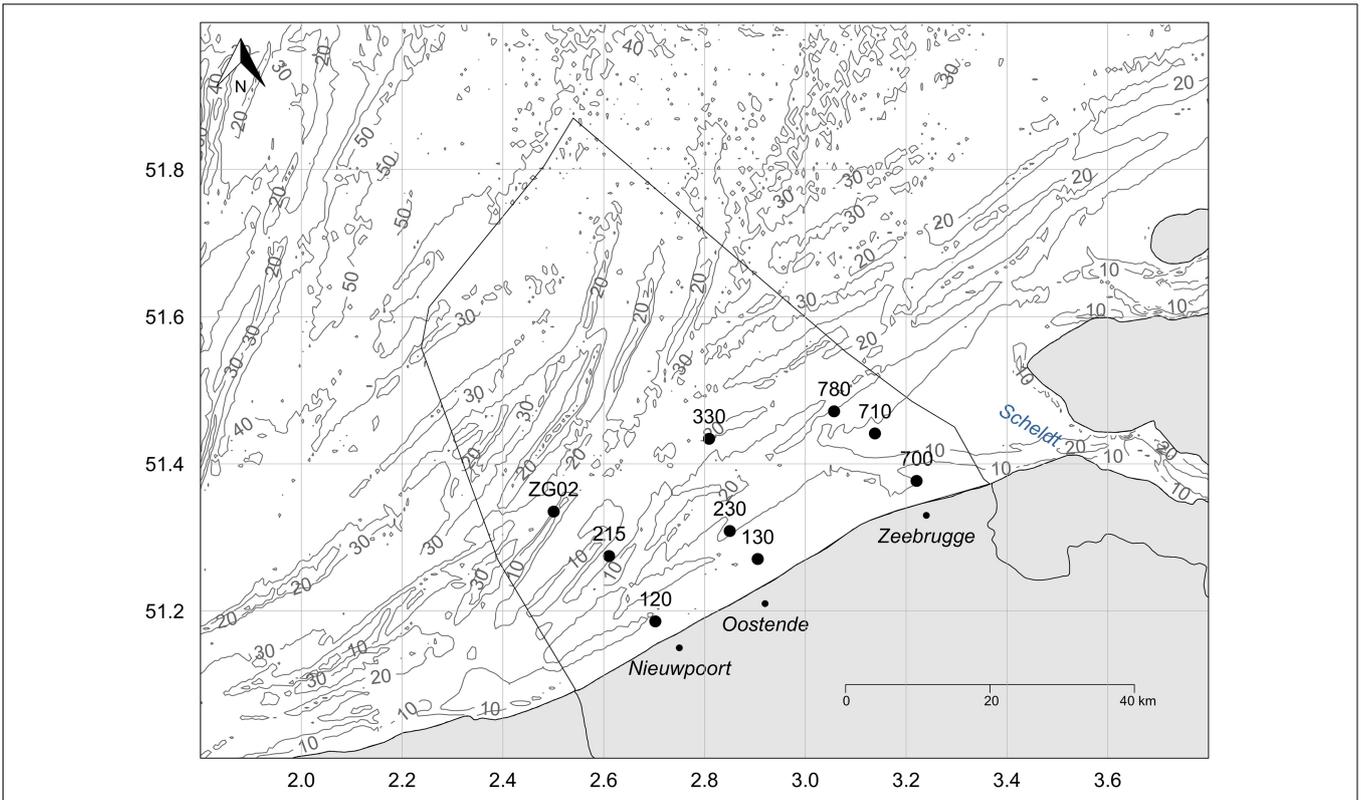
FIGURE 1 | Map of the Belgian part of the North Sea, outlined by the black line in the sea, with indication of the nine stations included in the analysis. The gray lines and numbers indicate the depth [m] of the water column.
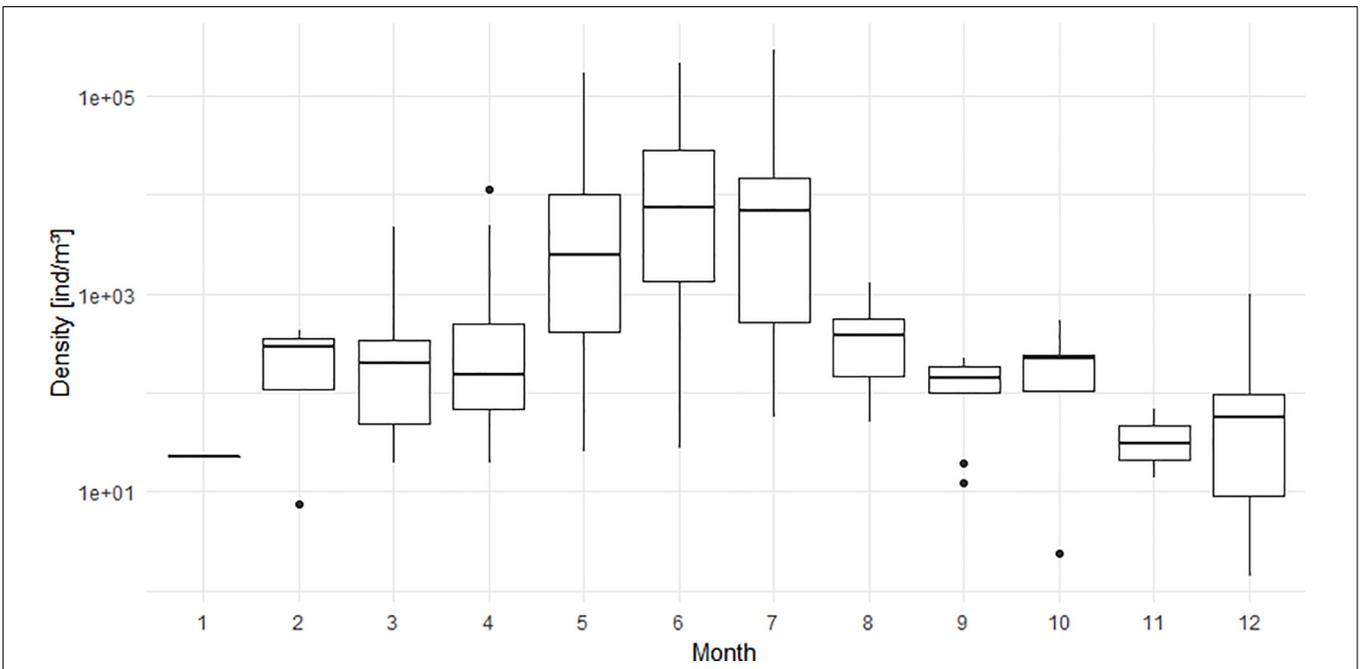

FIGURE 2 | Monthly variations shown as boxplots of abundances of *N. scintillans* [ind/m³] averaged for the period from 2014 to 2018 for all stations and including the sampled stations where *N. scintillans* was not encountered. *Y*-axis has a log10 scale.

FIGURE 3 | Monthly abundances [ind/m³] of *N. scintillans* per station for the period from 2014 to 2018 for each sampled station in the BPNS.
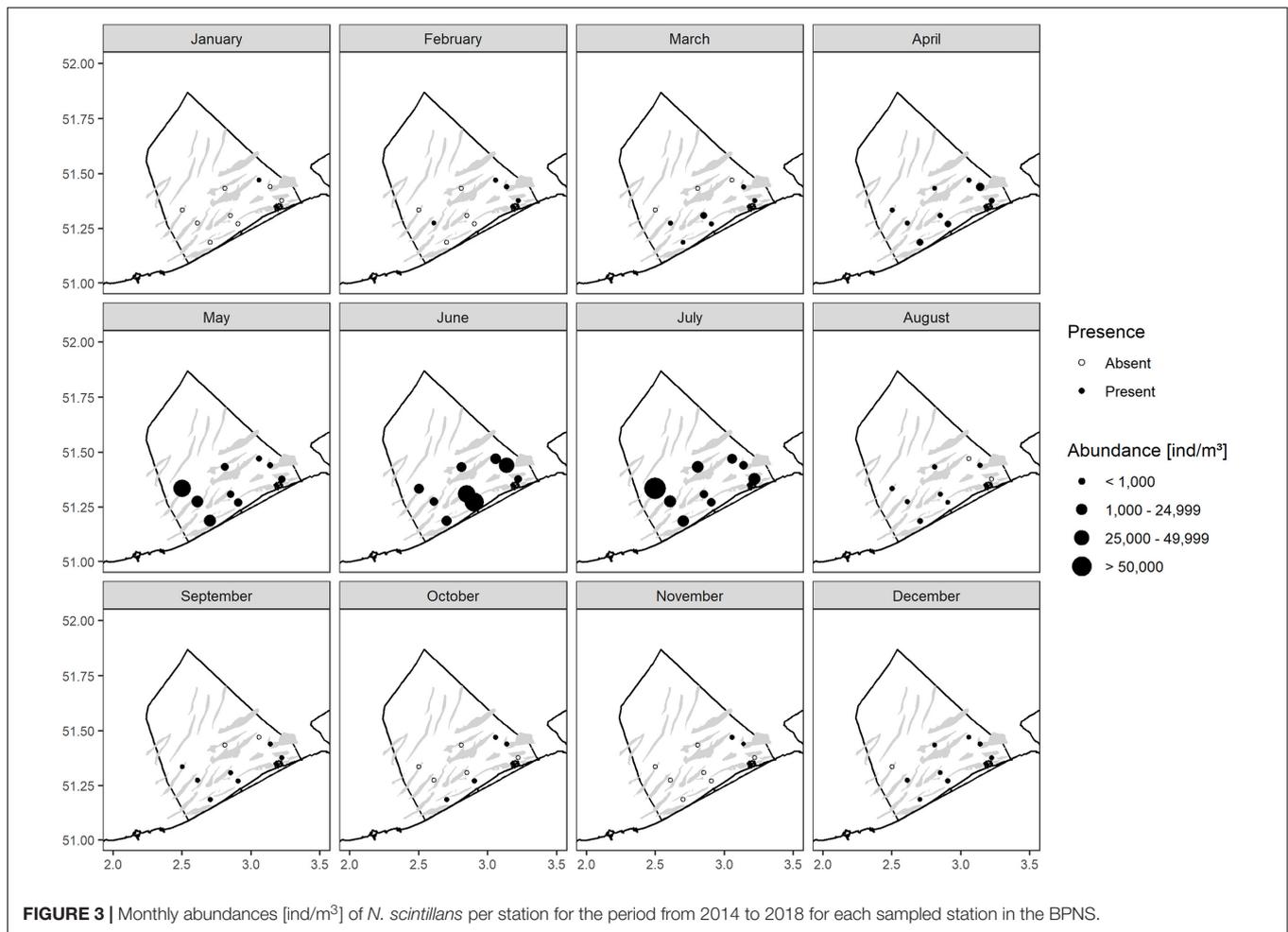
Size estimations of *N. scintillans* were based on the dataset "Flanders Marine Institute (VLIZ) (2019a)," according to the calculations given in Gorsky et al. (2010). These size estimations were performed on regions of interest (ROI's), a portion of an image presenting a certain particle or organism of interest. Because some ROI's had overlap between the actual organism of interest and other particles on the scanning bed, size estimations were overestimated in these particular ROI's. In PkID, a new category called "Noctiluca_unsuitable" was created to store ROI's containing overlapping particles, ROI's where the *N. scintillans* cells are not fully in view and ROI's of damaged or reproducing *N. scintillans* cells. After revalidation of the entire dataset, the original category, "Noctiluca," only held the ROI's with one *N. scintillans* cell. About half of the images were transferred to the "Noctiluca_unsuitable" folder, which came down to 33,624 of the 66,142 images. The size estimations were only based on the "Noctiluca" category in the further analysis, whereas density measurements were based on all ROI's, including the images with overlapping particles. The diameter of a *N. scintillans* cell was calculated as the mean of the major and minor axis of the ROI [mm]. It should be noted that fixation in formaldehyde affects the *N. scintillans* cells, as they shrink and can get damaged (Yang et al., 2016). Living *N. scintillans* cells are thus larger

than the size measurements used in this study, and real size can be recalculated as: volume of live cell = volume of intact fixed cell/0.61 (Yang et al., 2016). However, it was decided to work with the length measurements as measured by the ZooScan and not with the recalculated cell measurements, as a matter of comparability with most other studies which used length measurements of formaldehyde fixed cells (e.g., Dela-Cruz et al., 2003; Miyaguchi et al., 2006).

Data Analysis

Before analysis, samples from stations where *N. scintillans* was not encountered were added to the dataset. Environmental variables provided through the dataset "Flanders Marine Institute (VLIZ) (2019b)" were selected based on literature (Harrison et al., 2011) and availability in the dataset: conductivity, salinity, temperature, ammonia (NH4), phosphate (PO4), and chlorophyll a were taken into the analysis. Conductivity and salinity were collinear, and as salinity was available for fewer samples compared to conductivity, it was removed from further analysis. Samples missing one of the selected environmental variables were not included in the analysis, leading to a total of 311 samples considered over a period of 5 years in the present analysis.

TABLE 1 | Summary of the sampling effort in terms of number of samples per year and indication of the number and percentage of samples containing *N. scintillans*.

Year	Number of samples	Number of samples with *N. scintillans*	Presence of *N. scintillans* in samples [%]
2014	79	16	20
2015	84	26	31
2016	100	39	39
2017	64	33	52
2018	77	43	56

The data was subsequently explored (Zuur et al., 2010) and graphically represented per year, month or station.

All analyses were performed with RStudio (version 1.4.1106; RStudio Team, 2020). Kruskal-Wallis test was performed to analyze the spatio-temporal dynamics of *N. scintillans* abundance and a Wilcoxon test was executed to see which stations, months or years differed significantly from each other. To investigate which environmental variables influenced the dynamics of *N. scintillans,* generalized linear models (GLMs) were first tested but they did not predict the absence of *N. scintillans* well. Zero-inflated (ZI) models (Zuur and Ieno, 2016) were subsequently applied as the data contained a significant amount of zero values (e.g., 58% of the *N. scintillans* abundance data). Akaike information criterion (AIC) scores of different models showed that a ZI model with negative binomial distribution (ZINB) revealed to be the best suited for the overdispersed dataset. The Vuong test supported this and showed that a ZINB model was a significant improvement over a GLM with negative binomial distribution. In our dataset, the densities of the organisms were essentially count data converted to a fixed volume. As ZI models ("pscl" package) can only deal with the dependent variable being a natural number, the densities were rounded. Upwards rounding was, however, chosen to not change the low abundance values (low presence) to zero (absence). Based on AIC scores it was determined which variables were included in the count (abundance) and binary (presence/absence) part of the ZINB. The model with the lowest AIC score of which all included variables were significant, was selected as the final model. The same approach was used to define the models for the soft-bodied taxa: Appendicularia, Chaetognatha, Cnidaria, and Ctenophora. Autocorrelation patterns were analyzed with the autocorrelation function (ACF) in RStudio. A Redundancy Data Analysis (RDA) was performed to complement the modeling approach by investigating and visualizing the relationship between plankton taxa and environmental predictors. For this, plankton data was log(x+1) transformed to stabilize variance and to reduce the influence of dominant variables on the arrangement.

RESULTS

Seasonal and Inter-Annual Variations of *Noctiluca scintillans* Abundances

Abundances of *N. scintillans* displayed a clear seasonal pattern (**Figure 2**) in the BPNS over the 5-year period. Densities started to increase in spring up to a peak in late spring/early summer (May to July). The peak was subsequently followed by a density decrease starting in August. The distribution of the species (**Figure 3**) showed that it was the most widespread during the end of spring/summer peak (May to July) with high densities at all stations. From August to March, some stations did not observe the species. The lowest observation frequency corresponded to the month January for which *N. scintillans* was found at only one station.

What strikes for the period from 2014 to 2018, is the strong increase in prevalence (**Table 1**) and abundance (**Figure 4A**) of *N. scintillans*. In a period of 5 years, we observed that the species was encountered approximately three times more often in the samples, and that peaks during late spring/summer became more numerous per year within the season and became more important in terms of density. The highest density was observed in July 2018 at station ZG02 with a peak density of 290,181 ind/m^3. The Kruskal-Wallis test (**Supplementary Material 1**) showed that the abundance of *N. scintillans* significantly differed among years ($p < 0.001$) and months ($p < 0.001$), but not among stations. A Wilcoxon test demonstrated that 2014 significantly differed from the years 2016 up to 2018 included, and that 2015 differed from 2017 and 2018. December was the month that showed significant differences with all the other months at the exception of March, October and September. Furthermore, January, February and March each significantly differed from the months of April to July. April additionally also differed significantly from June, July, September, October and November. The months May, June and July differed as well from all the months comprised between August and November.

After evaluating models with the five selected variables (conductivity, temperature, ammonia, phosphate and chlorophyll a), a ZINB model (**Supplementary Material 2**) with the following variables best explained the dynamics of *N. scintillans*:

$$N.\ scintillans \sim Temperature\ |\ Temperature + PO4\ (M1)$$

The first part of this model proposed temperature ($p < 0.001$) as the main variable driving the abundance of *N. scintillans*. With higher temperatures, higher *N. scintillans* abundances will be observed. The second part of the model proposed that the presence or absence of *N. scintillans* was determined by both temperature ($p < 0.01$) and phosphate ($p < 0.05$). The model predicts that the chance for *N. scintillans* to be present is significantly larger in high temperatures and in low phosphate concentrations compared to low temperatures and high phosphate concentrations. This matches with the *in situ* seasonal patterns of temperature and phosphate concentrations (**Figures 4B,C**). The dispersion statistic of the model was 1.21, indicating some overdispersion. This means that significant results may not always appear significant in the model and that other variables can also potentially influence the seasonality of *N. scintillans*. A clear autocorrelation trend could be discerned for temperature, and correlations for small lags for *N. scintillans* abundance and PO4 were detected by the ACF, possible indicating time correlation. However, these were not

FIGURE 4 | Time series of **(A)** *N. scintillans* densities [ind/m³] on a log10 scale; **(B)** temperature [°C] and **(C)** phosphate concentrations [µmol/L] for the period 2014–2018.

taken into account in M1. The RDA ordination matched with the correlations found in M2 and indicate that *N. scintillans* was negatively correlated with phosphate concentrations and strongly positively correlated with temperature, which was visually represented in the RDA analysis bi-plot (**Figure 5**). It also showed a seasonal effect with a separation of e.g., the winter and summer season. The percentage of explained variance and the correlation coefficients with environmental factors are given in **Supplementary Material 3**.

Seasonal and Inter-Annual Variations of *Noctiluca scintillans* Cell Size
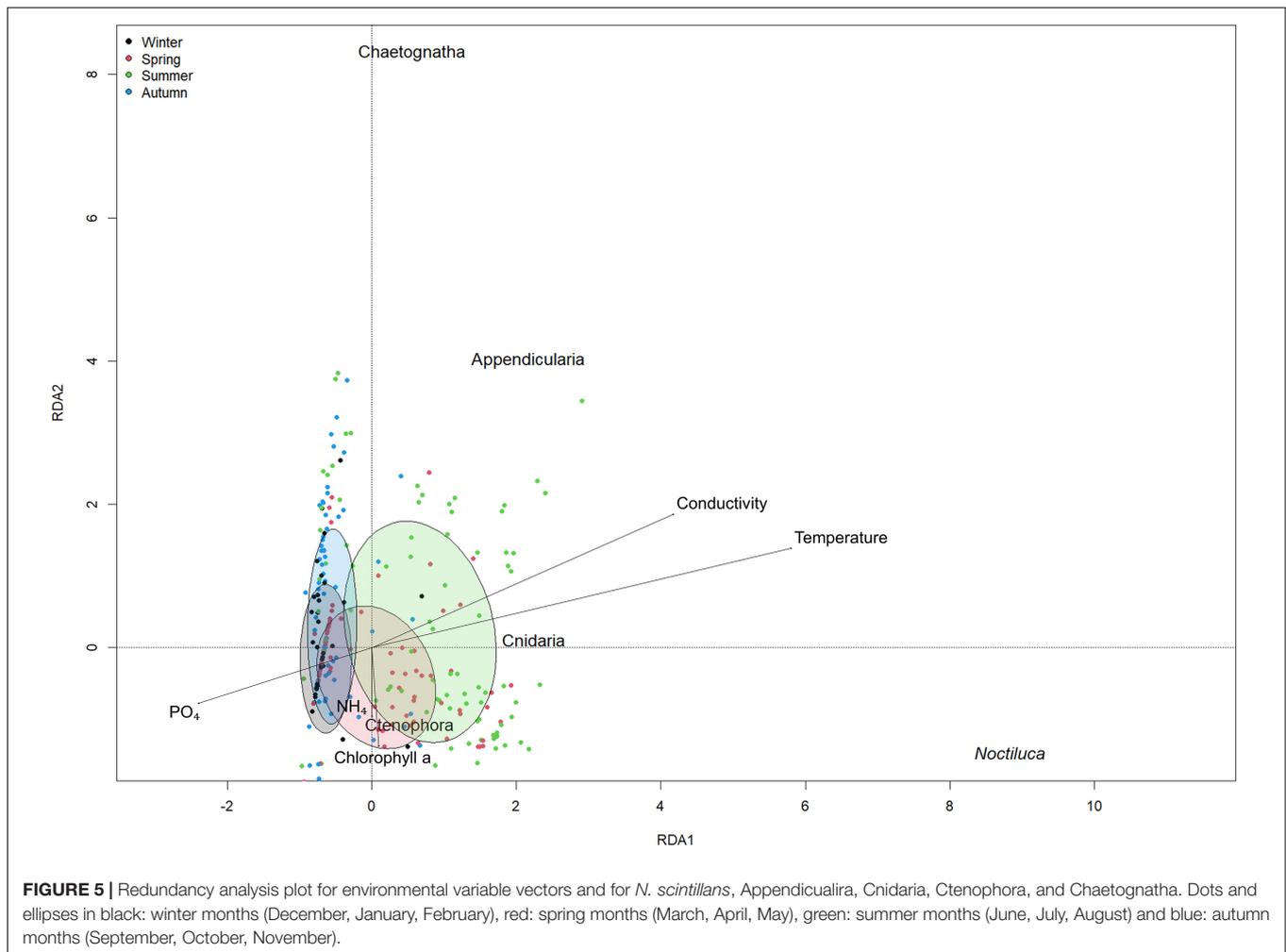
The cell size of *N. scintillans* ranged between 261 and 1,121 µm over the study period from 2014 to 2018, with smaller mean cell sizes in December and larger ones in May and June (**Figure 6**). The averaged monthly cell size variation for the 5-year period depicted an increase in mean cell size during the spring season, from 443 µm in January to 475 µm in April, which was subsequently followed by a peak during late spring/early summer (571 and 555 µm in May and June, respectively). At the end of summer and autumn (July–November) the mean cell size ranged between 419 and 480 µm. In December, a decrease of the mean

cell size could be observed with a mean cell size of 379 µm. These monthly differences in cell size can also be clearly observed from the ZooScan images of *N. scintillans* in **Figures 7A,B**.

A Kruskal-Wallis test (**Supplementary Material 4**) showed that the cell diameter was highly variable between years ($p < 0.05$) and months ($p < 0.001$), but also between stations ($p < 0.05$). Year 2014 significantly differed from 2017 and 2018; and 2016 differed from 2015 and 2017. May and June significantly differed from February, March, July, August, September and December; and the month December differed from April. Station 330 significantly differed from station 130, 230, and 700.

Seasonal Variations of *Noctiluca scintillans* and Soft-Bodied Plankton

A majority of the soft-bodied taxa considered in this study exhibited a distinguishable seasonal trend (**Figure 8**) with low abundances in winter, which increased at the end of spring/early summer, although subtle differences were observable among taxa. Ctenophora tended to peak before *N. scintillans*, whereas Chaetognatha experienced a later peak. For Cnidaria it was unclear when its peak occurred. The seasonal trend of Appendicularia appeared as the most similar to the one

FIGURE 5 | Redundancy analysis plot for environmental variable vectors and for *N. scintillans*, Appendicualira, Cnidaria, Ctenophora, and Chaetognatha. Dots and ellipses in black: winter months (December, January, February), red: spring months (March, April, May), green: summer months (June, July, August) and blue: autumn months (September, October, November).

of *N. scintillans* with Appendicularia peaking at the end of spring and beginning of summer, just before the *N. scintillans* peaks. A ZINB model was drawn up for each taxon, and only Appendicularia covaried significantly with *N. scintillans* abundances (**Supplementary Material 5**). The best-fitted model found for Appendicularia was the following:

$$\text{Appendicularia} \sim N.\ scintillans + \text{PO4} \mid 1\ (\text{M2})$$
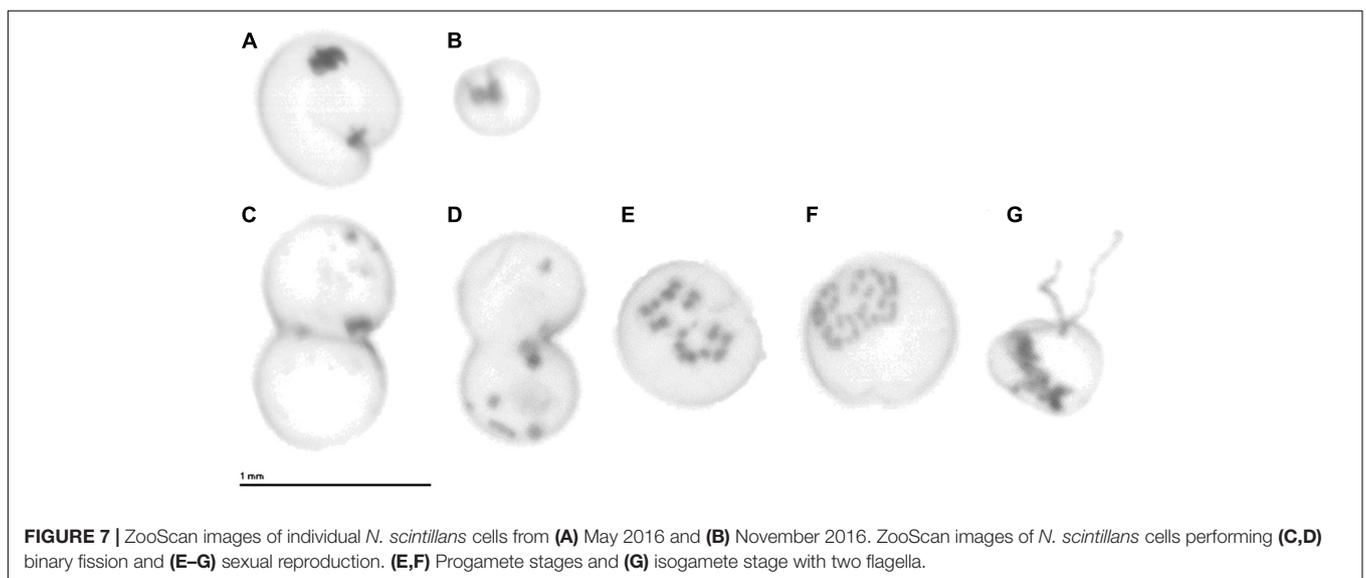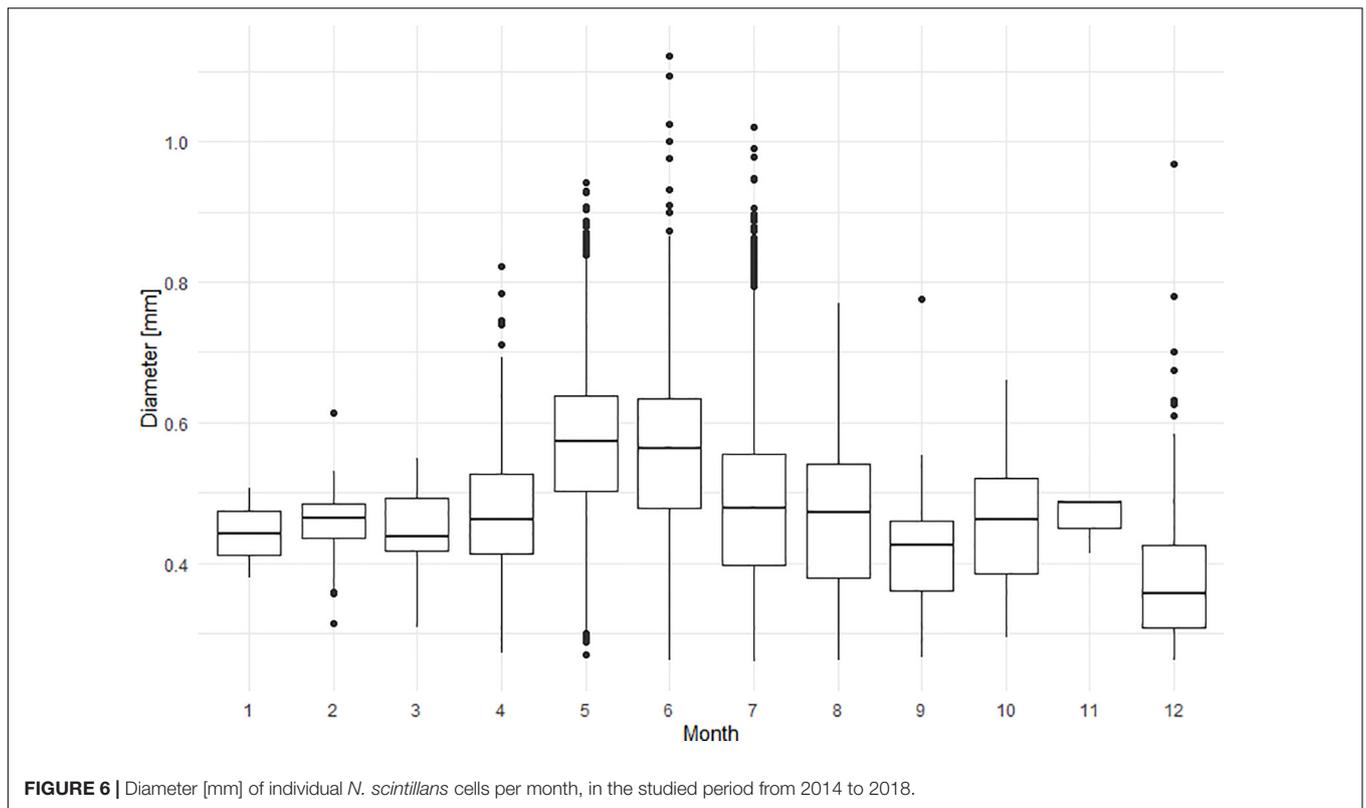
The model reports that the abundances of Appendicularia positively covariated with *N. scintillans* abundances ($p < 0.001$) and negatively with phosphate concentrations ($p < 0.001$) and that both covariations were highly significant. The dispersion statistic for the model was 1.24, indicating overdispersion. Similarly to M1, correlations for small lags for *N. scintillans* abundance, Appendicualria abundance and PO4 were detected by the ACF. The RDA ordination shows the negative correlation of Appendicularia with phosphate concentrations and positive correlation with *N. scintillans* abundances (**Figure 5** and **Supplementary Material 2**). The other soft-bodies species are represented as well on the RDA analysis bi-plot, which showed that NH4 and chlorophyll a concentrations were positively related to Ctenophora and negatively to Chaetognatha. Cnidaria

showed a positive correlation with temperature and conductivity, and a negative one with phosphate concentrations.

DISCUSSION

Seasonal and Interannual Dynamics of *Noctiluca scintillans*

N. scintillans has a worldwide distribution with, in general, a density peak in spring or summer and in some cases an additional lower peak in another season (Harrison et al., 2011). In the German Bight in the North Sea, *N. scintillans* was reported to usually peak in spring (March to late June), after which its abundances decrease significantly in August. In winter, a small population remains (Uhlig and Sahling, 1990). Similar seasonal patterns have been observed in the Dutch North Sea (Kat, 1979; Zevenboom et al., 1991) and in areas near Helgoland in the North Sea (Uhlig and Sahling, 1985). The seasonal dynamics of *N. scintillans* in the BPNS was consistent with the seasonal dynamics found in other parts of the North Sea and other parts of the world: a large peak at the end of spring/early summer (June-July) and a small winter population in December. Additionally,

FIGURE 6 | Diameter [mm] of individual *N. scintillans* cells per month, in the studied period from 2014 to 2018.

FIGURE 7 | ZooScan images of individual *N. scintillans* cells from **(A)** May 2016 and **(B)** November 2016. ZooScan images of *N. scintillans* cells performing **(C,D)** binary fission and **(E–G)** sexual reproduction. **(E,F)** Progamete stages and **(G)** isogamete stage with two flagella.

the important abundance decrease in August after the peak was concurrent with the findings of Uhlig and Sahling (1990) and Miyaguchi et al. (2006).

In the BPNS, *N. scintillans* cell size demonstrated a seasonal pattern characterized by larger sizes in May-June (555–571 μm) and smaller ones in December (379 μm). The concurrence of the largest cell sizes and abundance peak in spring/summer contradicts the findings of Miyaguchi et al. (2006) who noted an

increase in *N. scintillans* abundance concurrent with a decrease in cell volume during the spring period. Miyaguchi et al. (2006) hypothesized that the small volume and large abundances of *N. scintillans* might be an indication that cells actively conduct binary fission during bloom formation. The ZooScan recorded images of *N. scintillans* performing both binary fission and sexual reproduction (**Figure 7**) in May, June, and July of the covered sampling period, despite the relative large size of the cells during
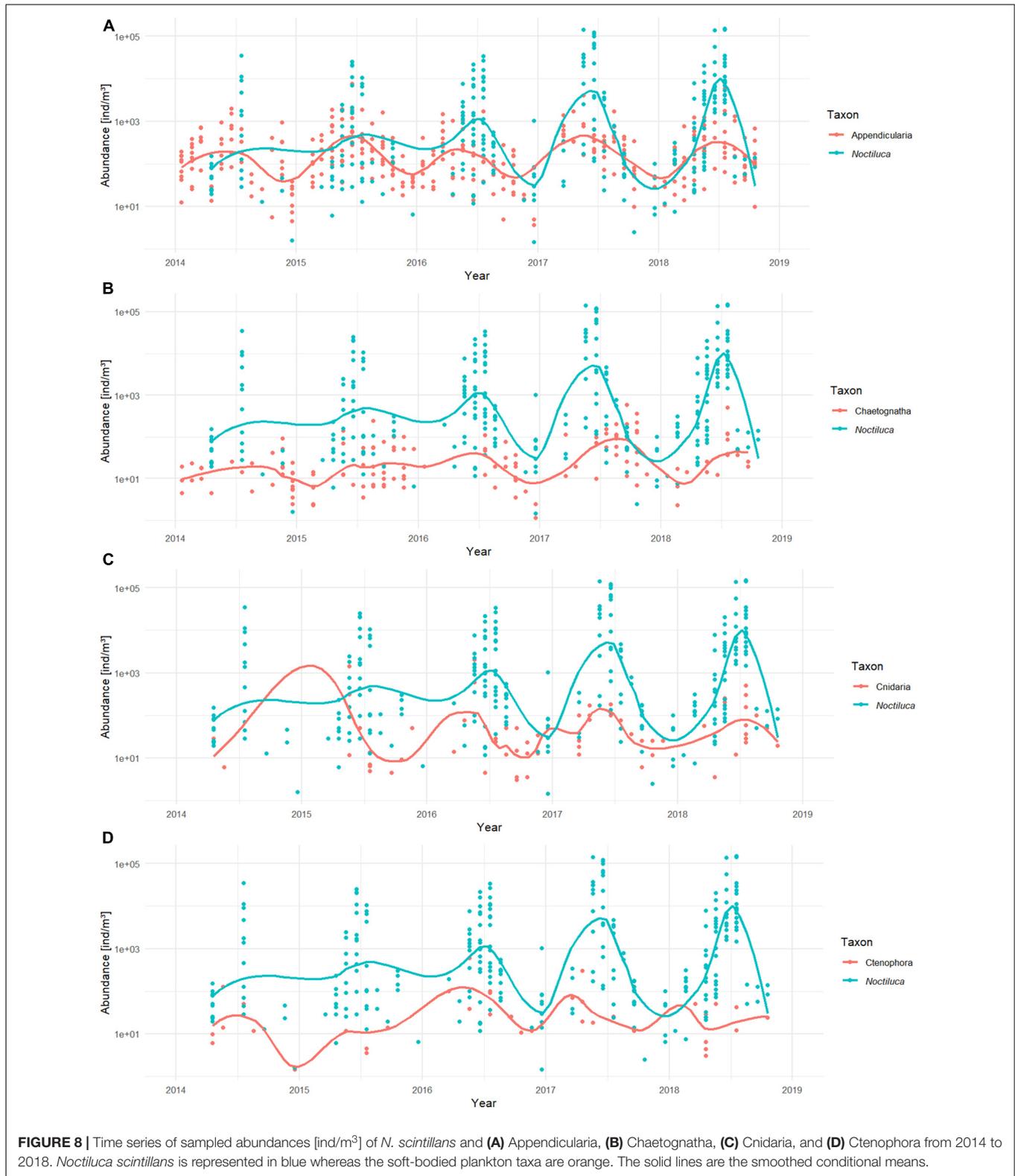
FIGURE 8 | Time series of sampled abundances [ind/m³] of *N. scintillans* and **(A)** Appendicularia, **(B)** Chaetognatha, **(C)** Cnidaria, and **(D)** Ctenophora from 2014 to 2018. *Noctiluca scintillans* is represented in blue whereas the soft-bodied plankton taxa are orange. The solid lines are the smoothed conditional means.

these months. This confirms that cells do indeed conduct binary fission during abundance maxima, but more importantly, our results highlight that this does not exclusively occur when cell size

is small or decreasing. In general, cell size has been considered as a valuable indicator of the condition of *N. scintillans* population. When small, the cell is considered in a good nutritional status

and capable of population growth, while a large cell has been considered as in a poor condition (Murray and Suthers, 1999; Dela-Cruz et al., 2003). The size of what is defined "small" or "large" ranges between 340 and 525 μm and 400 and 1,200 μm, respectively, depending on the study. Dela-Cruz et al. (2003) designated the cutoff boundary at 525 μm, based on the modal cell-size class determined by the total number of cells measured in their study. Although cell size was larger in spring/summer in our study, a considerable part of the *N. scintillans* cells in the BPNS were still smaller than this cutoff value. Therefore, a large part of the *N. scintillans* population were most likely healthy and capable of population growth, allowing for a high spring/summer bloom as it was observed.

In a timespan of only 5 years, the occurrence of *N. scintillans* in the samples nearly tripled, which could not be attributed to the sampling effort (**Table 1**). High abundance peaks also increased in cell concentration values over the covered period (**Figure 4A**). This increasing trend differs from the 3-year interval oscillations observed over 20 years in the German Bight (Uhlig and Sahling, 1990), whereby a year with a relatively high abundance was followed by 2 years of relatively low abundances. In the BPNS, both 2017 and 2018 were characterized by high *N. scintillans* abundances. The highest abundance peak was observed in July 2018 with densities rising up to 290,181 ind/m^3. The peak densities of *N. scintillans* found in spring/summer in the present dataset were higher than previous peak densities reported in the BPNS: Van Ginderdeuren et al. (2014) observed a maximum of 39,800 ind/m^3 in July–August between 2009 and 2010, and Daro et al. (2006) reported peak maxima of 16,000 ind/m^3 in the period from 1988 to 2004. It should be noted, however, that these authors used a different methodology, which hampers direct comparisons of peak densities with our measurements. Annual maximum densities can differ strongly among methodologies, but also among years as shown by the high inter-annual variability in *N. scintillans* reported by Uhlig and Sahling (1990). Thus, while our observations suggest an increasing trend in *N. scintillans* over the years, further observations to evaluate and confirm this trend are necessary. The present peak density values in the end of spring/summer were 30–300 times lower than densities reported in the German Bight from 1968 to 1988 ($\sim$10^7–10^8 ind/m^3; Uhlig and Sahling, 1990). Such a difference could partly be attributed to the fact that *N. scintillans* in the German Bight was sampled with bottle samplers near the water surface (0.5 and 5 m depth), where it has been shown to accumulate due to its positive buoyancy (Omori and Hamner, 1982; Uhlig and Sahling, 1985). *Noctiluca scintillans* cells normally are positively buoyant due to their large cell vacuoles filled with ammonium ions (Elbrachter and Qi, 1998). They only tend to sink to the bottom if they are well fed, where they remain until digestion and defecation have taken place (Omori and Hamner, 1982). Observations made during VLIZ sampling campaigns support the accumulation in the surface layer, where *N. scintillans* aggregated in the top layer of water samples. Additionally, data collected in May 2020 with a Video Plankton Recorder in the BPNS showed that while *N. scintillans* was present in the whole water column, its

densities were 4.5 times higher in the upper layers (personal observations). The magnitude of the difference is still too large to be attributed to sampling depth alone, and it is likely that regional and temporal factors also contributed to this difference (Uhlig and Sahling, 1990).

Biotic and Abiotic Factors Driving the Dynamics of *Noctiluca scintillans*

Temperature and phosphate concentrations are potential factors shaping the dynamics of *N. scintillans*, as suggested by the present results. Temperature is known to play an important role in the reproduction and lifecycle of many plankton species (Richardson, 2008) and the presence of *N. scintillans* has been correlated to temperature in previous studies (Tada et al., 2004; Jang et al., 2010). *Noctiluca scintillans* has been reported to occur over large temperature ranges from temperatures below 0–30°C. The maximum growth rate measured was found at 23–24°C in laboratory settings (Uhlig and Sahling, 1985; Lee and Hirayama, 1992). Higher temperatures, above 25°C (Nakamura, 1998; Liu and Wong, 2006), 28°C (Jang et al., 2010), and 30°C (Qi et al., 2004), were shown to decrease the growth rate of the species and were referred to as the cause of the decline or disappearance of the species. In the BPNS, water temperatures above 25°C have been rarely observed and therefore, a decline of *N. scintillans* abundance due to temperature increase is unlikely to occur. The maximum observed temperature in the dataset was 22.32°C in July 2018. It actually shows that summer temperatures in the BPNS are in line with the optimal growth conditions for *N. scintillans* populations.

In the BPNS, high nutrient concentrations are generally observed in winter, while in spring (April–May), phosphate concentrations are low (Van der Zee et al., 2007). Our results for the period 2014–2018 match the typical seasonal dynamics in phosphate concentrations. The ZINB model highlighted that phosphate negatively correlated with *N. scintillans* abundance, which is concurrent with the findings of Mohamed and Mesaad (2007) in the Red Sea. *Noctiluca scintillans* abundance was potentially indirectly linked to phosphate concentrations through food availability. Usually, low phosphate concentrations in spring are an indication of phytoplankton uptake as the bloom develops which, in turn, forms an abundant food source for *N. scintillans* (Sahayak et al., 2005). This is in accordance with other parts of the world where *N. scintillans* has been shown to often bloom after eutrophication-induced phytoplankton blooms (Painting et al., 1993; Hayward et al., 1995; Mohamed and Mesaad, 2007).

When framing our observations in a broader context of general dinoflagellate dynamics over the past decades in the North Sea, similarities can be seen regarding trends and drivers. Nohe et al. (2020) stated that in the BPNS the total abundance and biovolume of dinoflagellates significantly increased from 1970s to the 2000s and that dinoflagellates increased year-round, although more specifically in summer. Climate warming was identified as one of the possible drivers for the overall increase of dinoflagellates in summer in the 2000s, as dinoflagellates

are generally associated with warmer conditions (Baretta-Bekker et al., 2009). The capacity of many dinoflagellates for mixotrophic growth, and more specifically their ability to access alternative phosphorous sources, may have also contributed to their dominance during summer when nutrient levels were at their lowest (Burson et al., 2016). Our results, despite covering a shorter time series of 5 years, are thus in line with the trends and potential drivers proposed by Nohe et al. (2020). Although *N. scintillans* in the BPNS is not considered mixotrophic, it predates on a wide spectrum of particles and organisms, from several µm to 600–800 µm (Nikishina et al., 2011), and is therefore not dependent on one food source (Schaumann et al., 1988; Kirchner et al., 1996; Quevedo et al., 1999). Diatoms, *Phaeocystis* aggregates, copepod eggs and molts, fecal pellets and various protists such as dinoflagellates, ciliates and suctorians were reported in the food vacuoles of *N. scintillans* in the BPNS (Daro et al., 2006). The positive trend in abundance and peak intensity of *N. scintillans* over the studied period is most likely the result of a combination of factors: the ability of the species to predate on a wide food range leading to a competitive food advantage over many other zooplankton species, its optimum growth rate concordant with warmer temperatures in the BPNS in summer, as well as its ability to multiply quickly rendering it highly competitive and most likely explain its positive trend in abundance and peak intensity over the studied period.

Noctiluca scintillans in Relation to Soft-Bodied Plankton

The dynamics of *N. scintillans* has previously been correlated to the dynamics of other zooplankton species. Several studies observed inverse relationships with copepod abundance and the biomass of the overall zooplankton community, most likely due to the predation of *N. scintillans* on zooplankton itself and on their eggs as well as due to the competition for similar food sources (Fonda Umani et al., 2004; Yılmaz et al., 2005; Isinibilir et al., 2008). Negative interactions were also suggested between *N. scintillans* and small soft-bodied plankton species, such as *Pleurobrachia pileus* (Ctenophora), *Pleurobrachia bachei* (Ctenophora), chaetognaths (Chaetognatha), *Rathkea octopunctata* (Cnidaria) and *Lizzia blondina* (Cnidaria) (Heyen et al., 1998; Kovalev and Piontkovski, 1998; Fock and Greve, 2002). In the Black Sea, significant negative inter-annual correlations between *N. scintillans* and *Pleurobrachia bachei* were found (Kovalev and Piontkovski, 1998), whereas Fock and Greve (2002) found a strong indication that interactions occurred between *N. scintillans*, *Pleurobrachia pileus*, chaetognaths, and hydromedusae. Heyen et al. (1998) observed that a late timing or high abundances of *P. pileus* led to late timing and low abundances of *N. scintillans*. They concluded that the timing of *N. scintillans* not only depends on sea surface temperature, but also on the timing and abundance of *P. pileus*. Such a conclusion could not be supported by our results, as *N. scintillans* did not correlate with Ctenophora, nor with Chaetognatha or Cnidaria. In case the plankton groups used in this study contained plankton species with very different dynamics, then

it might be possible that species-specific relationships of soft-bodied species with *N. scintillans* were not detected due to the inability of the ZooScan to identify organisms to species level. On the other hand, the ZINB model indicated that appendicularians were significantly positively correlated with *N. scintillans,* contrary to what was expected. It is most likely that the dynamics of Appendicularia is governed by similar factors as *N. scintillans* dynamics, rather than *N. scintillans* having a direct positive effect on the species, especially considering that *N. scintillans* peaks later than Appendicularia. Studies found that certain phytoplankton blooms (of e.g., Coccolithophores or *Phaeocystis*) had a strong positive effect on the nutrition of both *N. scintillans* and Appendicularia (Lancelot et al., 2002; Amelina et al., 2017). Beside the raptorial feeding habit, *N. scintillans* is also capable of producing mucoid strands that bind suspended particles, small diatoms and other algae in a non-selective manner (Kiφrboe and Titelman, 1998). Appendicularia on the other hand feed within a mucous house that processes large volumes of water and concentrates small particles inside the house prior to feeding (Deibel, 1986). These two taxa are both considered fine particle feeders (Amelina et al., 2017) and their similar trends in dynamics might be linked to their ability for non-selective food uptake.

CONCLUSION

This study is the first one to provide consistent counts of *N. scintillans* cell concentrations as well as measured cell lengths for the region of the BPNS, which demonstrates that imaging methods such as the ZooScan are a powerful tool to monitor and study the *N. scintillans* population. Although *N. scintillans* occurred more frequently and in higher abundances in the most recent years of our time series, no negative impact of this species was observed on the small soft-bodied plankton community. The results of this study show that temperature and phosphate concentrations are potential drivers of the dynamics of *N. scintillans* in the BPNS, factors which can be influenced by anthropogenic pressures. The presence and density of *N. scintillans* are likely to increase in the future, notably due to global warming with warmer water temperatures (IPCC, 2021) forming the ideal growth condition for the species. The potential of *N. scintillans* to negatively influence other plankton in addition to its increasing prominent role in the plankton community, underlines the importance of further studying its role and impact on marine food webs. While there is still a large number of knowledge gaps related to the poorly studied gelatinous organisms (Aubert et al., 2018), especially when it comes to their inter-relationships, the new era of advanced optical techniques can bring more insight. Imaging techniques such as the Video Plankton Recorder (Davis et al., 2004) or the Continuous Particle Imaging and Classification System (Gallager, 2016) enable to register and quantify the gelatinous plankton community more effectively than techniques based on net sampling, as fragile gelatinous species can be observed *in situ* without being damaged (Remsen et al., 2004). The use of *in situ* optical methods should be

thus encouraged for poorly studied gelatinous species as it could bring a major contribution to future research into the dynamics, distribution and impact of species such as *N. scintillans*.

DATA AVAILABILITY STATEMENT

Publicly available datasets were analyzed in this study. The datasets used in this study are: Flanders Marine Institute (VLIZ), Belgium (2019a): LifeWatch observatory data: zooplankton observations in the Belgian part of the North Sea (https://doi.org/10.14284/329) and Flanders Marine Institute (VLIZ), Belgium (2019b): LifeWatch observatory data: nutrient, pigment, suspended matter and secchi measurements in the Belgian part of the North Sea (https://doi.org/10.14284/328).

AUTHOR CONTRIBUTIONS

AO: processing of the data, statistical analyses, and writing. JM: processing of the data, project supervision, and reviewing. AA: reviewing. KD: project supervision. MV: project supervision and reviewing. All authors contributed to the article and approved the submitted version.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2021.777999/full#supplementary-material

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