PRIMARY RESEARCH ARTICLE

Centennial decline in North Sea water clarity causes strong delay in phytoplankton bloom timing

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Abstract

With climate warming, a widespread expectation is that events in spring, such as flowering, bird migrations, and insect bursts, will occur earlier because of increasing temperature. At high latitudes, increased ocean temperature is suggested to advance the spring phytoplankton bloom due to earlier stabilization of the water column. However, climate warming is also expected to cause browning in lakes and rivers due to increases in terrestrial greening, ultimately reducing water clarity in coastal areas where freshwater drain. In shallow areas, decreased retention of sediments on the seabed will add to this effect. Both browning and resuspension of sediments imply a reduction of the euphotic zone and Sverdrup's critical depth leading to a delay in the spring bloom, counteracting the effect of increasing temperature. Here, we provide evidence that such a transparency reduction has already taken place in both the deep and shallow areas of the North Sea during the 20th century. A sensitivity analysis using a water column model suggests that the reduced transparency might have caused up to 3 weeks delay in the spring bloom over the last century. This delay stands in contrast to the earlier bloom onset expected from global warming, thus highlighting the importance of including changing water transparency in analyses of phytoplankton phenology and primary production. This appears to be of particular relevance for coastal waters, where increased concentrations of absorbing and scattering substances (sediments, dissolved organic matter) have been suggested to lead to coastal darkening.

KEYWORDS
CDOM, climate change, phenology, phytoplankton, Secchi disk, water clarity

1 | INTRODUCTION

High-latitude ecosystems are driven by seasonal dynamics, firmly structured around the spring onset. Increasing day length, light intensity, and temperatures trigger plant growth, budding, and flowering, which in turn influence phenological events throughout the trophic web (Fretwell, 1972). In both marine and terrestrial systems, several studies indicate that climate warming has caused an advance in spring phenology across multiple trophic levels (Parmesan & Yohe, 2003; Poloczanska et al., 2013; Walther

et al., 2002). The spring phenology in terrestrial plants is triggered directly by temperature and photoperiod (Koerner & Basler, 2010), whereas the timing of the phytoplankton spring bloom tends to be related to hydrographic properties (Lindemann & St. John, 2014; Nelson & Smith, 1991; Sverdrup, 1953). During high-latitude winters, incoming light intensity is low and vertical mixing is deep, causing phytoplankton cells to be mixed well below the photic zone, making them light limited rather than nutrient limited (Doney, 2006) although other limitations such as grazing are also involved (Behrenfeld, 2010; Behrenfeld & Boss, 2014). In spring, increasing surface light penetrates deeper in the water column, while at the same time, increasing temperatures and reduced winds stabilize the water column, driving the shoaling of the mixed layer. This eventually leads to an exponential increase in phytoplankton concentration, traditionally referred to as the spring bloom, where the vertically integrated gross primary production exceeds phytoplankton losses due to respiration, grazing, and sinking (Sverdrup, 1953). This classical view is strongly related to hydrographic properties, of which the stratification and water column light attenuation are central. More recent work modifies the simplified scheme of Sverdrup (1953) by highlighting the role of seasonally varying grazing pressure (Behrenfeld, 2010; Behrenfeld & Boss, 2014) and the difference between a "thoroughly mixed top layer" (Sverdrup, 1953) and a turbulent diffusivity rate-driven mixed layer (Franks, 2015; Huisman, Oostveen, & Weissing, 1999; Taylor & Ferrari, 2011). However, regardless of such modifications, under unaltered optical conditions, ocean warming will lead to earlier stratification and consequently to an earlier spring bloom (Behrenfeld et al., 2006; Doney, 2006). Here, we investigate to what extent this expectation might be modulated by increased light attenuation. In the North Sea and Baltic Sea, Secchi disk observations indicate increased light attenuation during the 20th century (Dupont & Aksnes, 2013; Fleming-Lehtinen & Laamanen, 2012; Sandén & Håkansson, 1996), causing a compressed euphotic zone (Dupont & Aksnes, 2013).

Together with resuspension of particulate matter (Capuzzo, Stephens, Silva, Barry, & Forster, 2015) and phytoplankton concentration (Fleming-Lehtinen & Laamanen, 2012), increased dissolved organic matter (DOM) of terrestrial origin (Painter et al., 2018) has been suggested to reduce the transparency of the Baltic Sea and the North Sea (Dupont & Aksnes, 2013). This reduction is in agreement with an observed increase in dissolved organic carbon (DOC) in many freshwater systems across northern latitudes (Clark et al., 2010; Haaland, Hongve, Laudon, Riise, & Vogt, 2010; Worrall, Burt, & Shedden, 2003), possibly due to rising temperatures increasing terrestrial plant growth (Jia, Epstein, & Walker, 2003; Larsen, Andersen, & Hessen, 2011; Myneni, Keeling, Tucker, Asrar, & Nemani, 1997).

Here, we have analyzed North Sea Secchi disk data in combination with chlorophyll *a* concentration estimates. Our results suggest that substances other than phytoplankton have been central to the reduced transparency of the North Sea. A sensitivity analysis using a water column model indicates that the transparency

loss may have caused up to 3 weeks delay in spring bloom over the last century.

2 | MATERIALS AND METHODS

Central to our analysis is the relationship between Secchi disk depth (*S*, m) and optical properties as recently described by Lee, Shang, Du, and Wei (2018) and Lee et al. (2015),

$$S = \frac{\Gamma}{K_S}, \tag{1}$$

where K_S, the attenuation coefficient of downwelling irradiance (m^{-1}) and Γ is a coupling constant found to be 1.48 (Lee et al., 2018). Thus, the reciprocal Secchi disk depth (*S*) is an optical property with unit/m, which enables the estimation of the composite attenuation, K_S. Equation (1) deviates from previous Secchi disk theory (Preisendorfer, 1986) in that the beam attenuation coefficient is not part of the denominator. Both theoretical and empirical evidence for Equation (1) are found in Lee et al. (2015, 2018).

For wavelengths available for photosynthesis (photosynthetically active radiation [PAR], 400–700 nm), we considered the composite light attenuation to be a quasi-inherent optical property that to a first-order approximation is:

$$K_S = K_W + K_{PHY} + K_{NON-PHY}, \tag{2}$$

where K_W, K_{PHY}, and $K_{NON-PHY}$ are contributions from clear water, phytoplankton, and other substances (such as suspended particulate inorganic matter and dissolved organic matter), respectively. Given estimates for K_S, K_W, and $K_{PHY,}$ the contribution from non-phytoplankton substances, $K_{NON-PHY}$ can be approximated by use of Equation (2).

2.1 | Secchi disk data

The majority (~93%, *n* = 9,546) of the Secchi disk measurements in the North Sea (1903–1998, 51°N–61°N, 3.5°W–11°E) were compiled by Aarup (2002) and are available from ICES (https://www.ices.dk/ocean/project/secchi). In addition, we utilized Secchi disk measurements recorded in the World Ocean Database (~4%, *n* = 400) (https://www.nodc.noaa.gov/OC5/WOD/secchi-data-format.html) and those collected by Capuzzo et al (~3%, *n* = 306; Capuzzo & Stephens, 2017; Capuzzo et al., 2015), available from the Cefas database (https://doi.org/10.14466/CefasDataHub.47). This gave a total of 10,252 Secchi disk measurements in the North Sea in the period 1903–1998. The ICES Secchi disk data were also used in the study by Dupont and Aksnes (2013), and we followed their approach in separating the North Sea into a shallow (bottom depth <100 m) and a deep (bottom depth >100 m) area. In addition, we corrected for the bias originating from systematic change in locations of Secchi disk measurements over time. This bias arose from the fact that certain time periods are sampled at relatively confined and/or different areas compared to other time periods. For example, all Secchi depth measurements

for the shallow North Sea between 1931 and 1949 were sampled along the east coast of England, while all those recorded in the deep areas in 1903 are from two single stations in the Norwegian trench. In addition, it has been shown that the later Secchi disk observations were taken on average closer to the coasts and at shallower bottom depths (Dupont & Aksnes, 2013). Consequently, for each of the two areas, we used a generalized additive model (GAM) to construct a time series of annual mean Secchi depth (S_t) for two hypothetical locations (one deep and one shallow) in January throughout the time period (t, 1903–1998). The locations were defined as the point of highest sampling density for the shallow (LAT_{loc} = 54.5°N, LON_{loc} = 7°E) and deep (LAT_{loc} = 58°N, LON_{loc} = 8.5°E) areas of the North Sea. After this, a linear regression model was fitted to describe annual Secchi disk depth (S_t) as a function of time ($S_t \sim a + m \times t$). See Supporting Information for a detailed methodology description.

2.2 | Phytoplankton and the effect on composite light attenuation

To estimate light attenuation from phytoplankton, we derived chlorophyll a concentrations (mg/m^3) in the North Sea (51°N–61°N, 3.5°W–11°E) from three different sources: (a) the *ICES-dataset* with chlorophyll a concentration measurements (1961–1998) from >6,000 unique stations (>30,000 bottle samples) available from the ICES Oceanography database (http://ocean.ices.dk/HydChem); (b) the *PCI-dataset* (Johns, 2019) with phytoplankton color indices (PCI) sampled by continuous plankton recorders (Batten, Clark, et al., 2003) and converted to chlorophyll a concentrations following the approach by McQuatters-Gollop et al. (2007). Due to the relatively low accuracy of the PCI to predict chlorophyll a concentrations (Batten, Walne, Edwards, & Groom, 2003), these data were only used when <50 stations from the *ICES-dataset* were available; and (c) the *CellCount-dataset*, which are chlorophyll a concentrations derived from individual cell counts in 1948 and 1912, and consist of >100 stations (>650 samples; Braarud, Gaarder, & Grøntved, 1953; Gran, 1915). Estimation of the overall annual mean chlorophyll a concentration (CHL_t, mg/m^3) was done the same way as for Secchi disk depth, using a GAM model, but including also a variable for sampling methodology. Having constructed a time series of the annual mean chlorophyll a concentration (CHL_t), a linear regression model was fitted to describe chlorophyll a concentration as a function of time ($CHL_t \sim a + m \times t$, t = 1912–1998), and extrapolated back to 1903. Due to the lack of chlorophyll a concentration estimates prior to 1912, and between 1912 and 1946, the regression confidence intervals were adjusted by setting the α-value very low (α = 1E-9) to ensure that the earliest datapoint in 1912 is within the uncertainty borders. By including this early near-zero chlorophyll a concentration, we captured the largest possible change in chlorophyll a concentration in the first half of the 20th century. See Supporting Information for a detailed methodology description.

The light attenuation from phytoplankton (K_{PHY}) was approximated from the empirical relationship between K_{PAR} and chlorophyll a concentration according to Morel (1988);

$$K_{PHY}(PAR) = 0.121 \times CHL^{0.428}, \tag{3}$$

where CHL is the chlorophyll a concentration (mg/m^3). To represent light attenuation of pure water (K_W), we used observations from Morel
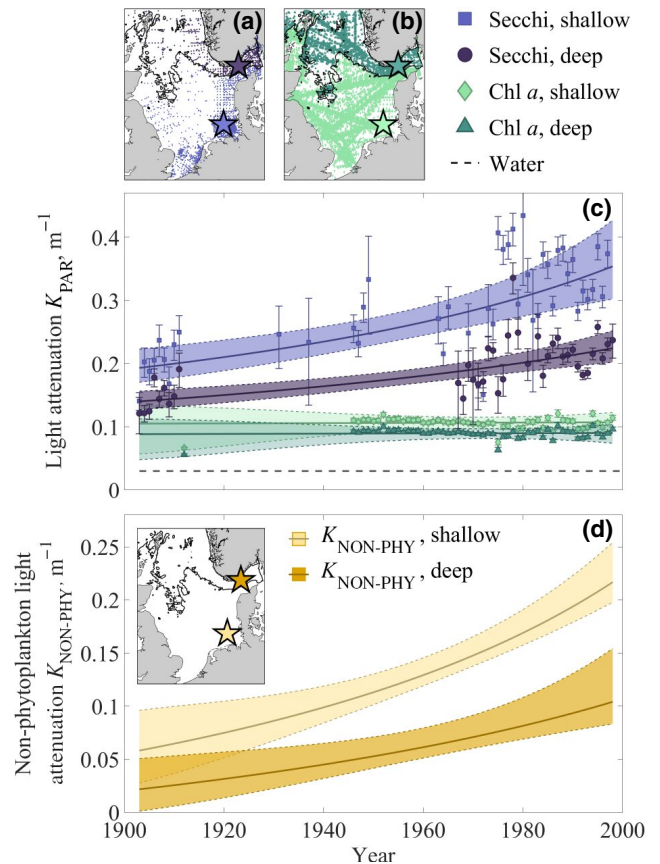

FIGURE 1 Composite light attenuation in the North Sea. Panels a and b show the geographical locations of the shallow (light blue squares) and deep (dark blue circles) Secchi disk measurements (a), and the corresponding shallow (light green diamonds) and deep (dark green triangles) chlorophyll a sampling stations (b). The stars denote the shallow and deep location at which annual mean Secchi disk depth and chlorophyll a concentrations have been statistically estimated (see Section 2). Panel c shows light attenuation estimated from Secchi disk depth measurements (K_S) and chlorophyll a concentrations (K_{PHY}) at shallow and deep locations (marked with stars in top panels). In addition, light attenuation from water itself (K_W) is shown as a black dotted line. Error bars denote the standard error of the mean, while blue and green lines and shading indicate mean and confidence intervals of the linear models of Secchi disk depth and chlorophyll a concentrations. Note that CI for chlorophyll a concentration is expanded to include the chlorophyll a concentration in 1912 (see text), and thereby capturing the uncertainty associated with the lack of data between 1903 and 1946. Panel d denotes the corresponding non-phytoplankton light attenuation ($K_{NON-PHY}$) for same the deep (dark brown) and shallow (light brown) locations (shown in map insert)

et al. (2007), who found mean K_{PAR} to be 0.0352 m^{-1} (±0.00025) for the clearest ocean waters.

2.3 | Water column model

To estimate the effect of reduction in transparency on phytoplankton bloom dynamics, we applied a water column model of phytoplankton growth previously applied by Huisman, Thi, Karl, and Sommeijer (2006) and Urtizberea, Dupont, Rosland, and Aksnes (2013). The model was used to simulate the annual bloom timing dynamics for an area representing the deep location in the North Sea (Figure 1; Figure S3) between 1903 and 1998.

The model was set up similar to that of Huisman et al. (2006), where change in phytoplankton concentration (P, µmol N/m^3) and nitrate concentration (N, µmol N/m^3) over time (t) is described by the following two equations,

$$\frac{\partial P}{\partial t} = \mu(N, I)P - mP - \nu\frac{\partial P}{\partial z} + \kappa\frac{\partial^2 P}{\partial z^2}, \tag{4}$$

$$\frac{\partial N}{\partial t} = \mu(N, I)P + \varepsilon mP + \kappa\frac{\partial^2 N}{\partial z^2}, \tag{5}$$

where $\mu(N, I)$ is the nitrate- (N, µmol N/m^3) and light- (I, µmol photons m^{-2} s^{-1}) dependent phytoplankton growth rate (day^{-1}), m is the loss rate (day^{-1}), ν is the cell sinking speed (m/s), κ is the vertical turbulent diffusivity (m^2/s), and ε is the fraction of nitrate that is recycled from lost phytoplankton (Table 1).

The specific phytoplankton growth rate is determined by the most limiting resource, such that

$$\mu(N, I) = \mu_{max} \min\left(\frac{N}{H_N + N}, \frac{I}{H_I + I}\right), \tag{6}$$

where μ_{max} is the maximum specific growth rate, and H_N and H_I are the half saturation constants for nitrate- and light-limited growth, respectively.

Light intensity in the water column (I_z) at depth (z) is described by

$$I_z = I_0 e^{-Kz}, \tag{7}$$

where I_0 is the incoming light (µmol photons m^{-2} s^{-1}) provided hourly from the Hybrid Coordinate Ocean Model (HYCOM; Bleck, 2002) for the North Sea and K (m^{-1}) is the background light attenuation ($K_{NON-PHY} + K_W$) as derived from Equations (1)–(3).

A simulation was performed to represent the deep location (Figure 2a) in the North Sea in 1998. The simulation model was initialized with observed depth-resolved chlorophyll a concentrations and nutrient concentrations in January that were averaged for the period 1990–2010. The model was calibrated (Table 1) to replicate the observed seasonal bloom dynamics (January–December) averaged for the same period (1990–2010), and in the same area. The sensitivity of bloom dynamics to alterations in the non-phytoplankton

TABLE 1 Variables and parameter values used in the water column model

Variables and parameters	Symbol	Unit	Value	Reference/comment
Phytoplankton concentration	P	µmol N/m^3		
Nutrient concentration	N	µmol N/m^3		
Surface light	I_0	µmol photons m^{-2} s^{-1}	0–1200	Bleck (2002)
Maximum growth rate	μ_{max}	day^{-1}	1.20	*Fitted* (this study)
Loss rate	m	day^{-1}	0.19	*Fitted* (this study)
Half saturation constant for light-limited growth	H_I	µmol photons m^{-2} s^{-1}	20	Huisman et al. (2006)
Half saturation constant for nutrient-limited growth	H_N	µmol N/m^3	0.025	Huisman et al. (2006)
Cell sinking speed	ν	m/s	1.2 × 10^{-5}	Huisman et al. (2006)
Vertical turbulent diffusivity	κ	m^2/s	8.4 × 10^{-4}	*Fitted* (this study)
Nutrient recycling rate	ε		0.5	Huisman et al. (2006)
Nutrient concentration at bottom	N_B	µmol N/m^3	13	North Sea (this study)
Initial phytoplankton concentration (0–300 m)	P_0	µmol N/m^3	0.36–0	North Sea (this study)
Initial nutrient concentration (0–300 m)	N_0	µmol N/m^3	7.5–13	North Sea (this study)
Non-phytoplankton light attenuation	$K_{NON-PHY}$	m^{-1}	0.02, 0.10	1905, 1998 (this study)
Carbon to nitrogen ratio	CN		6.6	Redfield ratio in µmol
Carbon to chlorophyll a	CChl	µmol C/mg chl a	50	Sarmiento and Gruber (2006)

Parameters denoted *Fitted* were used to calibrate the model to observed average (1990–2010) North Sea phytoplankton bloom dynamics.
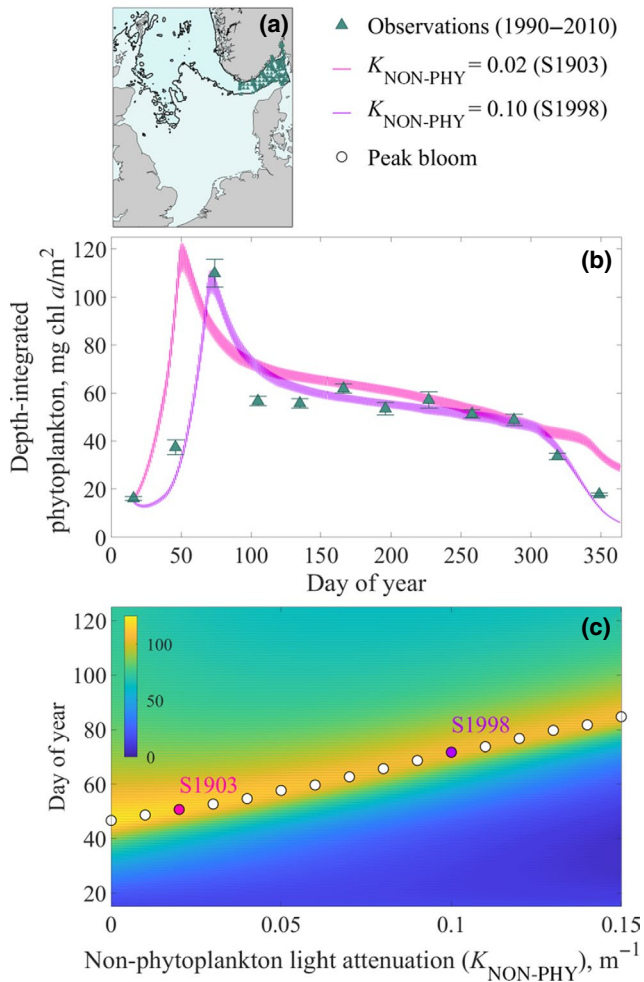
FIGURE 2 Observed and simulated bloom dynamics and their sensitivity to changing non-phytoplankton light attenuation. The top panel (a) shows the geographical locations of the 3,500 stations (1990–2010, green triangles) for which the seasonal bloom dynamics has been estimated. The mean seasonal bloom dynamics (b) are calculated based on monthly mean depth-integrated phytoplankton concentration over the period 1990–2010 (green triangles), with the standard error of the mean denoted by error bars. The purple line indicates the model simulation scenario S1998 ($K_{NON-PHY}$ = 0.10), fitted to the observed bloom dynamics. The pink line indicates the corresponding bloom dynamics when changing $K_{NON-PHY}$ to the estimated 1903 level (S1903, $K_{NON-PHY}$ = 0.02). The bottom panel (c) illustrates how the modeled bloom dynamics change as a function of changing $K_{NON-PHY}$. Color shading indicates the depth-integrated phytoplankton concentration (mg/m^2), and white circles denote the respective peak bloom for different values of $K_{NON-PHY}$. Peak blooms for the simulation scenarios S1903 and S1998 shown in panel b are marked with pink and purple color, respectively

attenuation, $K_{NON-PHY}$, was mapped by running the model with different values of $K_{NON-PHY}$. To check for spatiotemporal differences in the bloom dynamics of the deep areas of the North Sea, we compared in situ bloom dynamics to surface bloom dynamics derived from monthly satellite imaging (SeaWiFS) for the entire deep North Sea (see Supporting Information and Figure S3).

3 | RESULTS

Composite light attenuation, K_S, estimated by the Secchi disk depth observations according to Equation (1) is shown in Figure 1c. It is evident that K_S, through all years, is greater than the sum of the calculated K_W and K_{PHY} and that this discrepancy ($K_{NON-PHY}$) has increased across the 20th century for both the shallow and deep areas of the North Sea (Figure 1d). These findings suggest that there are other drivers for the observed reduction in transparency than increased phytoplankton concentrations.

Based on the chlorophyll *a* concentration observations in the deep areas of the North Sea in the period 1990–2010 (Figure 2a, green triangles), an average seasonal signal of depth-integrated chlorophyll *a* concentration (mg/m^2) was estimated (Figure 2b, green triangles). Similarly, the $K_{NON-PHY}$ for the deep areas of the North Sea (Figure 1c, dark line and shading) was found to increase from 0.02 m^{-1} (95% CI: 0–0.05 m^{-1}) to 0.10 m^{-1} (95% CI: 0.08–0.15 m^{-1}) between 1903 and 1998.

To simulate a phytoplankton bloom in the deep areas of the North Sea in 1998 (S1998), the water column model was initially fitted to the corresponding observed bloom dynamics (Figure 2b; Table 1) and non-chlorophyll light attenuation ($K_{NON-PHY}$ = 0.10 m^{-1}; Figure 2a, purple line). The model (S1998) fit is significant (R^2 = 0.93, *p*-value < .001) with an average monthly error in chlorophyll *a* concentration of 5.1 mg/m^2 (*SE* = 1.2 mg/m^2) corresponding to an average monthly error of ca. 9% (*SE* = 2%). In a sensitivity analysis, the model was run for a series of $K_{NON-PHY}$ values ranging from 0 to 0.15 m^{-1} (Figure 2c). It is evident that the peak bloom day occurs later in the year as $K_{NON-PHY}$ increase, and that we see a shift in peak bloom by 22 days from early (day 51) to late March (day 73) between scenarios S1903 and S1998 (Figure 2b,c).

4 | DISCUSSION

Our results suggest that the centennial reduction in water clarity in the North Sea, as observed through Secchi disk measurements, is unlikely to be explained by changes in phytoplankton concentration. This indicates an increase in other light-attenuating substances such as suspended particulate matter and/or DOM. We estimate a centennial increase in non-phytoplankton light attenuation ($K_{NON-PHY}$) from 0.02 m^{-1} in 1903 to 0.10 m^{-1} in 1998 in the deep areas of the North Sea, which suggest a delay in peak spring bloom by 22 days according to the idealized water column model. This finding suggests that reduced water clarity shifts bloom timing in a direction opposite to that expected from increased stratification (Behrenfeld et al., 2006; Doney, 2006), which for the North Sea appears to have been unchanged (van Leeuwen, Tett, Mills, & Molen, 2015; Figure 3).

Several data sources were used to estimate annual chlorophyll *a* concentrations, with particular uncertainty related to the estimates derived from PCI and phytoplankton cell counts. There are also uncertainties in microscopy cell counts, species/taxa-specific cell size assumptions, and volume to carbon ratios. For PCI-derived chlorophyll *a* concentration, we know from direct comparisons with chlorophyll *a*
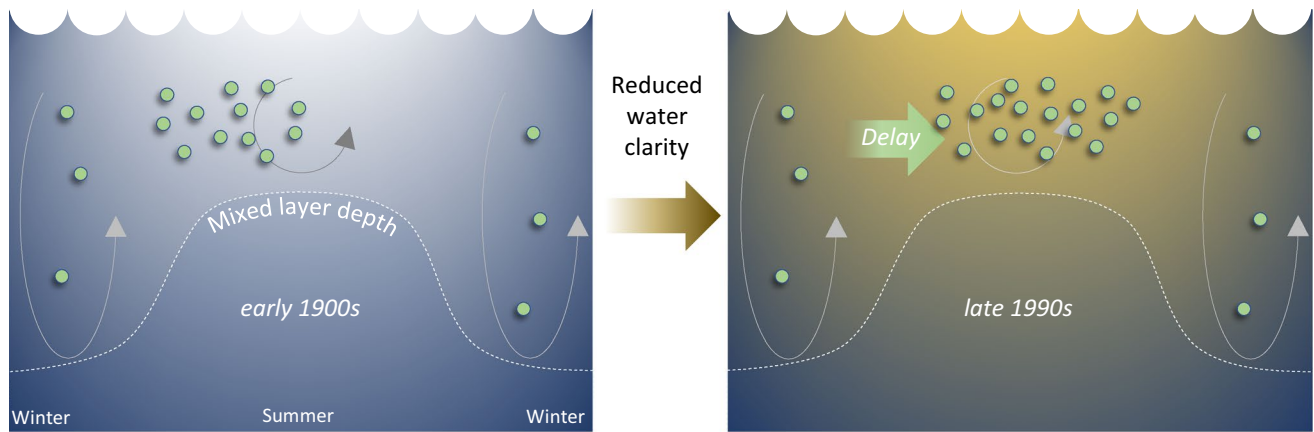
FIGURE 3 Predicted phytoplankton response to increased non-chlorophyll light attenuation. In this study, we present evidence suggesting a centennial increase in non-chlorophyll light-attenuating substances in the North Sea. This implies a reduction of the euphotic zone, leading to a delayed, intensified, and prolonged spring bloom. While climate warming is suggested to advance the spring bloom due to earlier shoaling of the mixed layer, it also causes browning in lakes and rivers due to increases in terrestrial greening, ultimately reducing water clarity in downstream coastal areas. These contrasting responses highlight the importance of including water transparency in analyses of phytoplankton phenology and primary production

measurements that the PCI is a coarse and inaccurate proxy for chlorophyll *a* concentrations (Batten, Walne, et al., 2003). Moreover, the conversion factor as suggested by McQuatters-Gollop et al. (2007) is likely to yield too high, considering-PCI values of zero are converted to chlorophyll *a* concentrations of ca. 2 mg/m^3. However, this bias has explicitly been accounted for in the GAM model. Regarding the net-collected phytoplankton cells in 1912 (the only datapoint prior to 1946), this is likely an underestimate as smaller phytoplankton cells would slip through the mesh. To account for the uncertainty prior to 1946, the confidence intervals for the linear regression were expanded, by setting α = 1E-9, to place the low chlorophyll *a* concentration in 1912 within the uncertainty boundaries. In this way, the resulting uncertainty envelope essentially represents all possible chlorophyll *a* concentrations in the period 1903–1946 (Figure S2). This adds confidence to our conclusion that factors other than phytoplankton have contributed to the reduction in water clarity in the North Sea. Although this study is not designed to derive an exact change in K_{NON_PHY}, we believe that the direction in which $K_{NON-PHY}$ has changed is correct, and thus also the direction in which the spring bloom likely has shifted during the 1900s.

Several studies have concluded that water clarity in the North Sea and Baltic Sea has declined throughout the 1900s (Dupont & Aksnes, 2013; Fleming-Lehtinen & Laamanen, 2012; Sandén & Håkansson, 1996). While phytoplankton concentration (Fleming-Lehtinen & Laamanen, 2012), resuspension of particles (Capuzzo et al., 2015), and dissolved organic matter (Harvey, Walve, Andersson, Karlson, & Kratzer, 2019; Kowalczuk, Stedmon, & Markager, 2006; Stedmon, Markager, & Kaas, 2000) are all considered important for light attenuation in these areas, quantifying centennial change has been challenging.

Most of the North Sea has a bottom depth less than 100 m. In fact, the average bottom depth for all Secchi disk measurements in the shallow North Sea is 28 m, while being closer to 300 m in the deep areas. Thus, water clarity in the shallow North Sea is more likely to be influenced by resuspension of bottom sediments than that of the deep areas. This is somewhat corroborated by Capuzzo et al. (2015) who in a study of the shallow North Sea suggested that an observed increase in suspended particulate matter in the period 1988–2011 was driving a simultaneous reduction in Secchi disk depth. However, in the deep North Sea, where the distance between the bottom and the submerged Secchi disk can be several hundred meters, resuspension of bottom sediments is less likely to influence Secchi disk depth. Thus, dissolved organic matter may play a relatively larger role in driving water clarity changes in the deep North Sea.

Increased concentrations of DOC in freshwater lakes and rivers draining to the North Sea and Baltic Sea have been found on both decadal (Evans, Monteith, & Cooper, 2005; Monteith et al., 2007) and centennial (Kritzberg, 2017; Meyer-Jacob, Tolu, Bigler, Yang, & Bindler, 2015) time scales. In addition, climate warming is predicted to increase terrestrial vegetation coverage, causing DOC concentrations in lakes and rivers to increase also in the future (Larsen et al., 2011).

In the Baltic Sea, river runoff is expected to increase by 15% in the next century (Graham, 2004), thus suggesting a positive correlation between higher temperatures and transport of DOC to coastal waters. In the Norwegian coastal current, evidence for such freshening, which implies coastal water darkening, has been given by Aksnes et al. (2009).

Spatial variation in light absorption is known to be strongly associated with DOM concentrations (Højerslev, Holt, & Aarup, 1996; Kowalczuk, Olszewski, Darecki, & Kaczmarek, 2005; Stedmon et al., 2000), and potential temporal increases in terrestrial DOM load will likely decrease the North Sea transparency, particularly in the deep areas, suggesting increased light attenuation and delayed spring bloom.

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REFERENCES

Aarup, T. (2002). Transparency of the North Sea and Baltic Sea – A Secchi depth data mining study. *Oceanologia*, *44*, 323–337.

Aksnes, D. L., Dupont, N., Staby, A., Fiksen, O., Kaartvedt, S., & Aure, J. (2009). Coastal water darkening and implications for mesopelagic regime shifts in Norwegian fjords. *Marine Ecology Progress Series*, *387*, 39–49. https://doi.org/10.3354/meps08120

Batten, S. D., Clark, R., Flinkman, J., Hays, G., John, E., John, A., ... Walne, A. (2003). CPR sampling: The technical background, materials and methods, consistency and comparability. *Progress in Oceanography*, *58*, 193–215. https://doi.org/10.1016/j.pocean.2003.08.004

Batten, S. D., Walne, A. W., Edwards, M., & Groom, S. B. (2003). Phytoplankton biomass from continuous plankton recorder data: An assessment of the phytoplankton colour index. *Journal of Plankton Research*, *25*, 697–702. https://doi.org/10.1093/plankt/25.7.697

Behrenfeld, M. J. (2010). Abandoning Sverdrup's Critical Depth Hypothesis on phytoplankton blooms. *Ecology*, *91*, 977–989. https://doi.org/10.1890/09-1207.1

Behrenfeld, M. J., & Boss, E. S. (2014). Resurrecting the ecological underpinnings of ocean plankton blooms. In C. A. Carlson & S. J. Giovannoni (Eds.), *Annual review of marine science* (Vol. *6*, pp. 167–194). Boca Raton, FL: CRC Press.

Behrenfeld, M. J., O'Malley, R. T., Siegel, D. A., McClain, C. R., Sarmiento, J. L., Feldman, G. C., ... Boss, E. S. (2006). Climate-driven trends in contemporary ocean productivity. *Nature*, *444*, 752–755. https://doi.org/10.1038/nature05317

Bleck, R. (2002). An oceanic general circulation model framed in hybrid isopycnic-Cartesian coordinates. *Ocean Modelling*, *4*, 55–88. https://doi.org/10.1016/S1463-5003(01)00012-9

Braarud, T., Gaarder, K. R., & Grøntved, J. (1953). The phytoplankton of the North Sea and adjacent waters in May 1948. *Rapports et procès-verbaux des Réunions*, *133*, 5–89.

Capuzzo, E., & Stephens, D. (2017). Cefas historic Secchi depth measurements. Cefas, UK. V1. https://doi.org/10.14466/CefasDataHub.47

Capuzzo, E., Stephens, D., Silva, T., Barry, J., & Forster, R. M. (2015). Decrease in water clarity of the southern and central North Sea during the 20th century. *Global Change Biology*, *21*, 2206–2214. https://doi.org/10.1111/gcb.12854

Clark, J. M., Bottrell, S. H., Evans, C. D., Monteith, D. T., Bartlett, R., Rose, R., ... Chapman, P. J. (2010). The importance of the relationship between scale and process in understanding long-term DOC dynamics. *Science of the Total Environment*, *408*, 2768–2775. https://doi.org/10.1016/j.scitotenv.2010.02.046

Doney, S. C. (2006). Oceanography – Plankton in a warmer world. *Nature*, *444*, 695–696. https://doi.org/10.1038/444695a

Dupont, N., & Aksnes, D. L. (2013). Centennial changes in water clarity of the Baltic Sea and the North Sea. *Estuarine Coastal and Shelf Science*, *131*, 282–289. https://doi.org/10.1016/j.ecss.2013.08.010

Evans, C. D., Monteith, D. T., & Cooper, D. M. (2005). Long-term increases in surface water dissolved organic carbon: Observations, possible causes and environmental impacts. *Environmental Pollution*, *137*, 55–71. https://doi.org/10.1016/j.envpol.2004.12.031

Fleming-Lehtinen, V., & Laamanen, M. (2012). Long-term changes in Secchi depth and the role of phytoplankton in explaining light attenuation in the Baltic Sea. *Estuarine Coastal and Shelf Science*, *102*, 1–10. https://doi.org/10.1016/j.ecss.2012.02.015

Franks, P. J. S. (2015). Has Sverdrup's critical depth hypothesis been tested? Mixed layers vs. turbulent layers. *Ices Journal of Marine Science*, *72*, 1897–1907. https://doi.org/10.1093/icesjms/fsu175

Fretwell, S. D. (1972). Populations in a seasonal environment. *Monographs in Population Biology*, *5*, 1–217.

Graham, L. P. (2004). Climate change effects on river flow to the Baltic Sea. *Ambio*, *33*, 235–241. https://doi.org/10.1579/0044-7447-33.4.235

Gran, H. H. (1915). The plankton production of the North European waters in the spring of 1912. Bulletin planktonique pour l'anée 1912. *Conseil Permanent International pour L'exploration de la Mer*, *7*, 1–142.

Haaland, S., Hongve, D., Laudon, H., Riise, G., & Vogt, R. D. (2010). Quantifying the drivers of the increasing colored organic matter in boreal surface waters. *Environmental Science & Technology*, *44*, 2975–2980. https://doi.org/10.1021/es903179j

Harvey, E. T., Walve, J., Andersson, A., Karlson, B., & Kratzer, S. (2019). The effect of optical properties on secchi depth and implications for eutrophication management. *Frontiers in Marine Science*, *5*, 496. https://doi.org/10.3389/fmars.2018.00496

Højerslev, N. K., Holt, N., & Aarup, T. (1996). Optical measurements in the North Sea-Baltic Sea transition zone 1. On the origin of the deep water in the Kattegat. *Continental Shelf Research*, *16*, 1329–1342. https://doi.org/10.1016/0278-4343(95)00075-5

Huisman, J., Thi, N. N. P., Karl, D. M., & Sommeijer, B. (2006). Reduced mixing generates oscillations and chaos in the oceanic deep chlorophyll maximum. *Nature*, *439*, 322–325. https://doi.org/10.1038/nature04245

Huisman, J., Van Oostveen, P., & Weissing, F. J. (1999). Critical depth and critical turbulence: Two different mechanisms for the development of phytoplankton blooms. *Limnology and Oceanography*, *44*, 1781–1787. https://doi.org/10.4319/lo.1999.44.7.1781

Jia, G. S. J., Epstein, H. E., & Walker, D. A. (2003). Greening of arctic Alaska, 1981–2001. *Geophysical Research Letters*, *30*(20). https://doi.org/10.1029/2003GL018268

Johns, D. (2019) *Phytoplankton colour index (51–61N, -3.5-11E) 1946–2017 as recorded by the Continuous Plankton Recorder*. Plymouth, UK: Sir Alister Hardy Foundation for Ocean Science.

Koerner, C., & Basler, D. (2010). Phenology under global warming. *Science*, *327*, 1461–1462. https://doi.org/10.1126/science.1186473

Kowalczuk, P., Olszewski, J., Darecki, M., & Kaczmarek, S. (2005). Empirical relationships between coloured dissolved organic matter (CDOM) absorption and apparent optical properties in Baltic Sea waters. *International Journal of Remote Sensing*, *26*, 345–370. https://doi.org/10.1080/01431160410001720270

Kowalczuk, P., Stedmon, C. A., & Markager, S. (2006). Modeling absorption by CDOM in the Baltic Sea from season, salinity and chlorophyll. *Marine Chemistry*, *101*, 1–11. https://doi.org/10.1016/j.marchem.2005.12.005

Kritzberg, E. S. (2017). Centennial-long trends of lake browning show major effect of afforestation. *Limnology and Oceanography*, *2*(4), 105–112. https://doi.org/10.1002/lol2.10041

Larsen, S., Andersen, T., & Hessen, D. O. (2011). Climate change predicted to cause severe increase of organic carbon in lakes. *Global Change Biology*, *17*, 1186–1192. https://doi.org/10.1111/j.1365-2486.2010.02257.x

Lee, Z. P., Shang, S. L., Du, K. P., & Wei, J. W. (2018). Resolving the long-standing puzzles about the observed Secchi depth relationships. *Limnology and Oceanography*, *63*, 2321–2336. https://doi.org/10.1002/lno.10940

Lee, Z. P., Shang, S., Hu, C., Du, K., Weidemann, A., Hou, W., ... Lin, G. (2015). Secchi disk depth: A new theory and mechanistic model for underwater visibility. *Remote Sensing of Environment*, *169*, 139–149. https://doi.org/10.1016/j.rse.2015.08.002

Lindemann, C., & St. John M. A. (2014). A seasonal diary of phytoplankton in the North Atlantic. *Frontiers in Marine Science*, *1*. https://doi.org/10.3389/fmars.2014.00037

Mcquatters-Gollop, A., Raitsos, D. E., Edwards, M., Pradhan, Y., Mee, L. D., Lavender, S. J., & Attrill, M. J. (2007). A long-term chlorophyll dataset reveals regime shift in North Sea phytoplankton biomass unconnected to nutrient levels. *Limnology and Oceanography*, *52*, 635–648. https://doi.org/10.4319/lo.2007.52.2.0635

Meyer-Jacob, C., Tolu, J., Bigler, C., Yang, H., & Bindler, R. (2015). Early land use and centennial scale changes in lake-water organic carbon prior to contemporary monitoring. *Proceedings of the National Academy of Sciences of the United States of America*, *112*, 6579–6584. https://doi.org/10.1073/pnas.1501505112

Monteith, D. T., Stoddard, J. L., Evans, C. D., de Wit, H. A., Forsius, M., Høgåsen, T., ... Vesely, J. (2007). Dissolved organic carbon trends resulting from changes in atmospheric deposition chemistry. *Nature*, *450*, 537–540. https://doi.org/10.1038/nature06316

Morel, A. (1988). Optical modeling of the upper ocean in relation to its biogenous matter content (case-I waters). *Journal of Geophysical Research-Oceans*, *93*, 10749–10768. https://doi.org/10.1029/JC093iC09p10749

Morel, A., Gentili, B., Claustre, H., Babin, M., Bricaud, A., Ras, J., & Tieche, F. (2007). Optical properties of the "clearest" natural waters. *Limnology and Oceanography*, *52*, 217–229. https://doi.org/10.4319/lo.2007.52.1.0217

Myneni, R. B., Keeling, C. D., Tucker, C. J., Asrar, G., & Nemani, R. R. (1997). Increased plant growth in the northern high latitudes from 1981 to 1991. *Nature*, *386*, 698–702. https://doi.org/10.1038/386698a0

Nelson, D. M., & Smith, W. O. (1991). Sverdrup revisited – Critical depths, maximum chlorophyll levels, and the control of southern-ocean productivity by the irradiance-mixing regime. *Limnology and Oceanography*, *36*, 1650–1661. https://doi.org/10.4319/lo.1991.36.8.1650

Painter, S. C., Lapworth, D. J., Woodward, E. M. S., Kroeger, S., Evans, C. D., Mayor, D. J., & Sanders, R. J. (2018). Terrestrial dissolved organic matter distribution in the North Sea. *Science of the Total Environment*, *630*, 630–647. https://doi.org/10.1016/j.scitotenv.2018.02.237

Parmesan, C., & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, *421*, 37–42. https://doi.org/10.1038/nature01286

Poloczanska, E. S., Brown, C. J., Sydeman, W. J., Kiessling, W., Schoeman, D. S., Moore, P. J., ... Richardson, A. J. (2013). Global imprint of climate change on marine life. *Nature Climate Change*, *3*, 919–925. https://doi.org/10.1038/nclimate1958

Preisendorfer, R. W. (1986). Secchi disk science – Visual optics of natural-waters. *Limnology and Oceanography*, *31*, 909–926. https://doi.org/10.4319/lo.1986.31.5.0909

Sandén, P., & Håkansson, B. (1996). Long-term trends in Secchi depth in the Baltic Sea. *Limnology and Oceanography*, *41*, 346–351. https://doi.org/10.4319/lo.1996.41.2.0346

Sarmiento, J. L., & Gruber, N. (2006). *Ocean biogeochemical dynamics*. Princeton, NJ: Princeton University Press.

Stedmon, C. A., Markager, S., & Kaas, H. (2000). Optical properties and signatures of chromophoric dissolved organic matter (CDOM) in Danish coastal waters. *Estuarine Coastal and Shelf Science*, *51*, 267–278. https://doi.org/10.1006/ecss.2000.0645

Sverdrup, H. U. (1953). On conditions for the vernal blooming of phytoplankton. *Journal de Conseil*, *18*, 287–295. https://doi.org/10.1093/icesjms/18.3.287

Taylor, J. R., & Ferrari, R. (2011). Shutdown of turbulent convection as a new criterion for the onset of spring phytoplankton blooms. *Limnology and Oceanography*, *56*, 2293–2307. https://doi.org/10.4319/lo.2011.56.6.2293

Urtizberea, A., Dupont, N., Rosland, R., & Aksnes, D. L. (2013). Sensitivity of euphotic zone properties to CDOM variations in marine ecosystem models. *Ecological Modelling*, *256*, 16–22. https://doi.org/10.1016/j.ecolmodel.2013.02.010

Van Leeuwen, S., Tett, P., Mills, D., & Van Der Molen, J. (2015). Stratified and nonstratified areas in the North Sea: Long-term variability and biological and policy implications. *Journal of Geophysical Research-Oceans*, *120*, 4670–4686. https://doi.org/10.1002/2014JC010485

Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T. J. C., ... Bairlein, F. (2002). Ecological responses to recent climate change. *Nature*, *416*, 389–395. https://doi.org/10.1038/416389a

Worrall, F., Burt, T., & Shedden, R. (2003). Long term records of riverine dissolved organic matter. *Biogeochemistry*, *64*, 165–178.

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