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Chlorophyll in North Sea coastal and offshore waters does not reflect long term trends of phytoplankton biomass

Santiago Alvarez-Fernandez [a,b,*], Roel Riegman [a]

[a] Institute for Marine Resources & Ecosystem Studies (IMARES), Wageningen University & Research Centre, PO Box 167, 1797SZ 't Horntje, The Netherlands
[b] Department of Aquatic Ecology and Water Quality Management (AEW), Wageningen University & Research Centre, The Netherlands

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ABSTRACT

This study analyses long-term and seasonal changes of phytoplankton community Carbon: Chlorophyll a ratio (θ) during the period 1991 to 2010 in North Sea waters and its relationship to environmental drivers. Based on the data from the Dutch water monitoring programme covering 20 years, major trends in phytoplankton abundance, community structure and chlorophyll were identified. Overall C:Chla increased during the study period, particularly in coastal areas. This increase was related to an increase in average underwater photosynthetically active radiation (PAR) and a decrease in nutrient concentrations. A mismatch was detected between chlorophyll a and biomass carbon trends caused by both a decrease in chlorophyll a values and an increase in biomass. In coastal waters, physiological adaptation to higher light and lower nutrient levels may have enhanced the θ, increasing from yearly averages of 12 g C ∗ g Chl a^{-1} in 1990 to 69 g C ∗ g Chl a^{-1} in 2010. Offshore, the increased stratification coincided with a shift towards dinoflagellate dominance. This dominance of dinoflagellates co-occurred with an increased θ yearly averages from 62 g C ∗ g Chl a^{-1} in 1991 to 119 g C ∗ g Chl a^{-1} in 2010. Because of these changes detected in C:Chl a ratio of multispecies phytoplankton communities, we question the validity of chlorophyll a as a proxy for phytoplankton biomass and argue its possible misrepresentation of phytoplankton dynamics.

1. Introduction

Phytoplankton are the base of marine ecosystem. As primary producers of organic carbon, phytoplankton import carbon in the marine system making it available for secondary producers, sustaining the marine food webs. These primary producers are also very important for the regulation of biogeochemical cycles. Overall marine primary producers account for 50% of the planet's photosynthesis, extracting CO_2 from the atmosphere, and reducing its greenhouse effects (Falkowski, 1994).

Since the effects of nutrient enrichment in coastal waters due to anthropogenic land use have a clear impact on phytoplankton (Rabalais et al., 2009), monitoring programmes have been established in many coastal regions in which phytoplankton state was considered as a parameter of water quality. Since phytoplankton carbon is difficult to monitor (Llewellyn et al., 2005), optic methods have been developed to monitor the dynamics of primary producers. Detection of fluorescence, water colour and other methods have been used as proxies to infer the status of phytoplankton population. Chlorophyll has a centenary history as a phytoplankton biomass proxy (Buchanan, 1910; Harvey, 1934), and it is still the most common measure of phytoplankton in ecological studies (Boyce et al., 2010). Chlorophyll is often used as a proxy for phytoplankton biomass because it is both easy to measure in situ and from satellite measurements (Boyce et al., 2010). Furthermore, other proxies are related to chlorophyll to assess their validity as a representation of phytoplankton dynamics. As an example, the Phytoplankton Colour Index (PCI) calculated in the Continuous Plankton Recorder survey (CPR) is generally accepted as a representation of phytoplankton biomass and productivity, but as discussed by Batten et al. (2003) PCI can be thought of as analogous to remotely sensed chlorophyll estimates. Similarly to remote sensing and in situ chlorophyll measurements, it is only by comparisons between the PCI and the taxonomic structure that a shift in the phytoplankton community composition might be revealed.

Even though chlorophyll is widely used as a proxy, the relationship between chlorophyll and phytoplankton biomass is not straight forward. C:Chl a ratio (θ) has been shown to be highly variable within and between algal species. In laboratory studies, Geider (1987) showed how θ is dependent on light and nutrient availability and temperature; it increases linearly with an increased light level at a constant temperature and decreases exponentially with an increased temperature at a constant light level. Other studies using mesocosm experiments have also shown the interspecific differences of θ, with differences of one order of magnitude (Kruskopf and Flynn, 2006). Geider (1987) also

* Corresponding author at: Institute for Marine Resources & Ecosystem Studies (IMARES), Wageningen University & Research Centre, PO Box 167, 1797SZ 't Horntje, The Netherlands.
E-mail address: santiago.alvarezfernandez@wur.nl (S. Alvarez-Fernandez).

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showed how dinoflagellates have higher θ values than diatoms both in natural blooms and axenic cultures.

In nature the determination of θ responses to environmental factors is more difficult. Regarding the physiological responses of phytoplankton, light and temperature are generally correlated, and there is normally more than one growth rate limiting factor within multispecies communities. Moreover, depending on the species composition the overall community θ would change, as different phytoplankton species have different C:Chl a ratios. All these factors make the relationship between Chlorophyll and phytoplankton biomass theoretically variable, both seasonally and on an inter-annual basis. This raises the question of how well do chlorophyll measurements represent phytoplankton biomass.

For open ocean areas, Behrenfeld et al. (2005) already showed a mismatch between satellite estimations of phytoplankton carbon and chlorophyll, and advocated for carbon-based net primary production estimations. In a similar way, Lionard et al. (2008) showed how for a short term field study in 2002 chlorophyll was a good estimation of overall phytoplankton biomass when diatoms were clearly dominant, but the performance of this proxy was poor for other phytoplankton groups and did not perform well when phytoplankton biomass was low.

In this study the long term trends of C:Chl ratio, taxonomic structure of phytoplankton and environmental factors are inspected in order to assess the validity of chlorophyll as a representation of phytoplankton biomass in the southern North Sea. To our knowledge this is the first study that addresses this issue based on long term field measurements (two decades) inspecting the C:Chl a behaviour both in the long term and seasonal scale. The inclusion of both coastal and offshore areas adds another important aspect to the analysis of performance of chlorophyll a as phytoplankton biomass proxy, as their intrinsic differences in limiting factors and physico-chemical parameters could be important for the C:Chl ratio.

2. Materials and methods

2.1. Study area

Dutch marine waters lie in the southern North Sea, a shallow shelf sea in the European continental shelf (Fig. 1). The water circulation in the North Sea is tidally driven, generally counter-clockwise, with water from the North Atlantic entering from the north-west, and flowing southward in the direction of the English channel, to flow from there together with Channel water along the Belgian and Dutch coast northward, leaving the North Sea with the Norwegian coastal current (Baretta-Bekker et al., 2009; Gieskes and Kraay, 1975).

2.2. Monitoring stations

Ten stations from two transects running perpendicular to the Dutch coast were selected for the study (Fig. 1). The Noordwijk transect is located off the west coast of The Netherlands, with four stations at 2, 10, 20 (coastal) and 70 km (offshore) from the coast. Waters covered by this transect do not present a consistent thermo-haline stratification during the summer. The Terschelling transect lies north of The Netherlands, in front of the Wadden islands. In this study 6 stations were selected, at 4 and 10 (coastal) and at 100, 135, 175 and 235 km off the coast (offshore). The offshore stations present thermal stratification during the summer (Baretta-Bekker et al., 2009).

2.3. Data

Phytoplankton data from the selected stations were used for the analyses. Water samples were collected at 1 m below the water surface. One litre of phytoplankton samples was preserved with 4 ml acid Lugol's iodine and stored in brown glass bottles at 4 °C. Phytoplankton

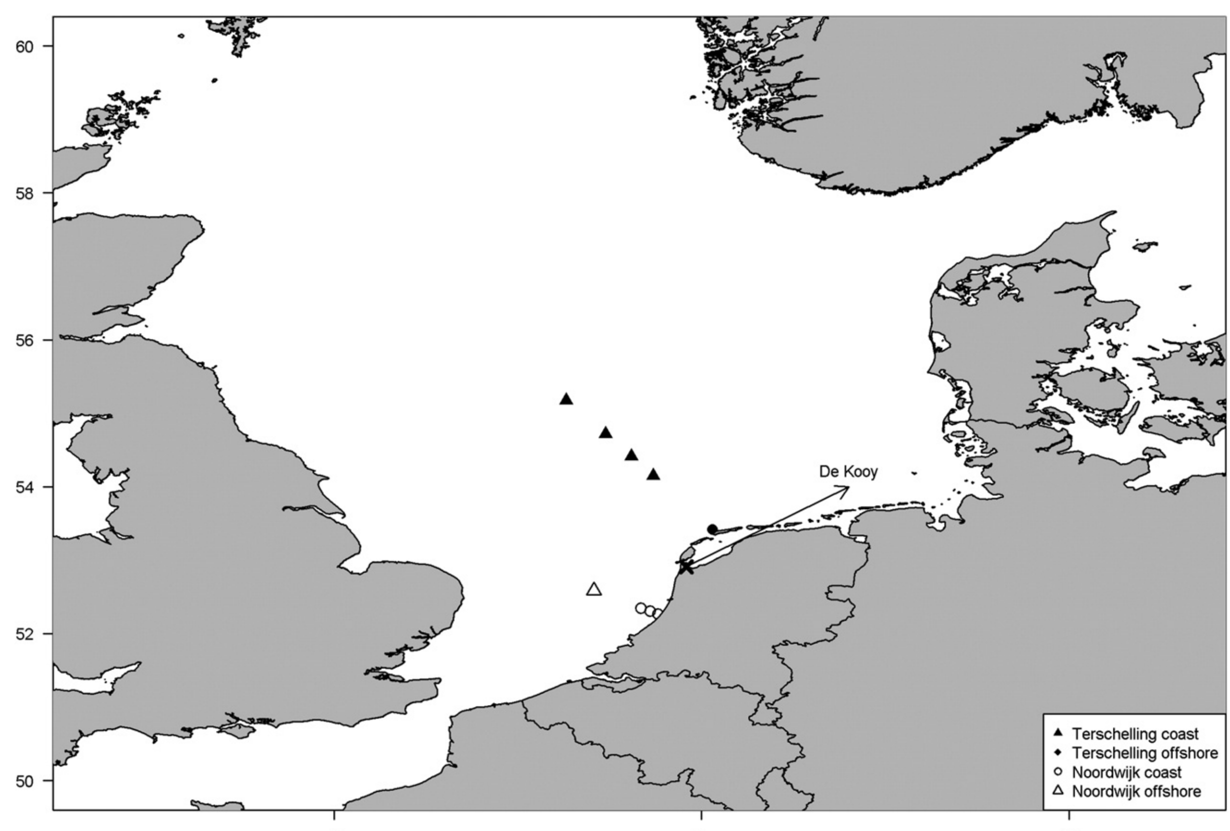

Fig. 1. Area of study. Four different areas are distinguished: Noordwijk offshore (open triangle), Noordwijk coast (open circle), Terschelling offshore (filled triangle), and Terschelling coast (filled circle).