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Phosphorus limitation during a phytoplankton spring bloom in the western Dutch Wadden Sea

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ABSTRACT

Like many aquatic ecosystems, the western Dutch Wadden Sea has undergone eutrophication. Due to changes in management policy, nutrient loads, especially phosphorus decreased after the mid-80s. It is still under debate, however, whether nutrients or light is limiting phytoplankton production in the western Wadden Sea, as studies using monitoring data delivered sometimes opposite conclusions and outcomes were related to years, seasons and approaches used. Clearly, the monitoring data alone were not sufficient. We therefore examined the limiting factors for the phytoplankton spring bloom using different experimental approaches. During the spring bloom in April 2010, we investigated several nutrient regimes on natural phytoplankton assemblages at a long term monitoring site, the NIOZ-Jetty sampling (Marsdiep, The Netherlands). Four bioassays, lasting 6 days each, were performed in controlled conditions. From changes in phytoplankton biomass, chlorophyll-*a* (Chl*a*), we could conclude that the phytoplankton in general was mainly P-limited during this period, whereas a Si–P-co-limitation was likely for the diatom populations, when present. These results were confirmed by changes in the photosynthetic efficiency (F_v/F_m), in the expression of alkaline phosphatase activity (APA) measured with the fluorescent probe ELF-97, and in the ^{13}C stable isotope incorporation in particulate organic carbon (POC). During our bioassay experiments, we observed a highly dynamic phytoplankton community with regard to species composition and growth rates. The considerable differences in net population growth rates, occurring under more or less similar environmental incubation conditions, suggest that phytoplankton species composition and grazing activity by small grazers were important structuring factors for net growth during this period.

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1. Introduction

The need for a better understanding of the impacts of eutrophication on freshwater, coastal and marine ecosystems has been one of the main reasons to explore relationships between primary producer communities and fluctuations of nutrient concentrations (Cloern, 2001). Apart from influencing productivity levels, changes in ambient nutrient concentrations can also affect phytoplankton species composition, grazer activity and the trophic transfer to higher trophic levels (Brett and Muller-Navarra, 1997; Finkel et al., 2010; Malzahn et al., 2007). Studies on the response of phytoplankton communities to changes in nutrient loads at various scales, ranging from small-scale laboratory techniques, via field mesocosms to lakes and estuaries (Beardall et al., 2001; Hecky and Kilham, 1988; Schindler, 2009), show that interpretation of the results obtained at small scales is sometimes difficult to extrapolate to field conditions.

The widely accepted paradigm on nutrient limitation assumes that nitrogen (N) is the limiting nutrient for primary production in marine ecosystems, whereas phosphorus (P) is the limiting nutrient for primary production in lakes (Hecky and Kilham, 1988; Howarth and Marino, 2006). In both marine and freshwater ecosystems, however, chlorophyll-*a* (Chl*a*) concentrations were found to be correlated with mean concentrations or loads of total nitrogen (TN) and total phosphorus (TP) (Heip et al., 1995; Smith et al., 2006). The study by Heip et al. (1995) also highlighted the importance of organic matter for primary production, whilst Monbet (1992) demonstrated the influence of the tidal regime on the relationship between N-availability and Chl*a* concentrations. In addition, a meta-analysis on nutrient enrichments in a suite of habitats by Elser et al. (2007) revealed that freshwater systems can be frequently limited by N, and marine habitats by P.

The Wadden Sea is one of the world's largest coastal marine ecosystems which is strongly affected by changes in anthropogenic nutrient loads (Cloern, 2001). In the western part of this area, the concentrations of dissolved inorganic phosphorus (DIP) and dissolved inorganic nitrogen (DIN) increased during the 1970s and decreased after the mid-1980s as the result of changing riverine loads (Cadée and Hegeman, 2002; Loebl et al., 2009; Philippart et al., 2007). Although the results here consider the Marsdiep basin of the western Dutch Wadden Sea, many coastal systems have seen a decrease in nutrient loading as a result of changes in policy measures to combat eutrophication, and for this reasons the results applied here can probably serve as an example for other temperate coastal system which underwent similar reductions in nutrient loadings. These changes in absolute and relative nutrient loads coincided with major changes in phytoplankton community structure during the late 1970s and the late 1980s (Philippart et al., 2000) and were accompanied by changes in community structures of macrozoobenthos, fish and estuarine birds (Philippart et al., 2007; Tulp et al., 2008).

Long-term trends in relative nutrient concentrations in the western Wadden Sea strongly suggest that phytoplankton production during the spring and summer blooms was P-limited in the 1970s, Si-limited (diatoms) or N-limited (flagellates) in the 1980s, and then P-limited again thereafter (Philippart et al., 2007). Light limitation appears to play a minor role during the blooms. Whilst previous analyses indicated co-limitation by light (Colijn and Cadée, 2003), more recent results using the same index (Cloern, 1999, 2001) suggested that nutrients were the main limiting resource during the growing season for phytoplankton in the Wadden Sea (Loebl et al., 2009). In addition, the turbidity of these waters was found to be highly variable during this period but did not exhibit the long-term trends (Philippart et al., 2013).

Previous results on the nature and strength of nutrient limitation in the western Wadden Sea were all based on ambient nutrient concentrations, which are only weak indices of nutrient limitation because no information on uptake and mineralization is taken into account (Dodd et al., 2003). To unambiguously determine the nature of the actual limiting nutrient, we performed nutrient enrichment experiments during the spring bloom in combination with several physiological measurements. To test the viability of historical statements on nutrient limitation in the western Wadden Sea, we performed bioassay experiments and physiological measurements and compare the results with conclusions drawn from ambient nutrient concentrations and ratios.

2. Material and methods

2.1. Sampling site and procedure

Water samples have been collected using a bucket at weekly intervals at high tide from the NIOZ-Jetty (53°00′06″ N; 4°47′21″ E) from 30th March to 30th April 2010 (Table 1). The NIOZ-Jetty is located in the Marsdiep basin near to the inlet between the North Sea and the Wadden Sea (Fig. 1). The average depth of the Marsdiep basin is approximately 4.5 m (Ridderinkhof, 1988). Comparison with ferry box observations as determined from a ferry sailing across the Marsdiep tidal inlet during 11 years showed that turbidity at the NIOZ-Jetty was correlated with total suspended matter concentrations in the Marsdiep tidal inlet (Philippart et al., 2013). This finding strongly suggests that information on trends derived from the NIOZ-Jetty samples is also indicative for trends in the western Wadden Sea.

In order to make sure that light availability did not influence our interpretation of the bioassays we estimated the underwater light climate in the Marsdiep basin during the period of our bioassay. Because the light attenuation coefficients (K_d; m^{-1}) were not measured during this period, we estimated K_d from Secchi depth measurements using the following empirical relationship:

$$K_d = a \cdot \sqrt{(\text{Secchi depth})} + b,$$

where $a = 5.377$ (m^{-1}) and $b = 2.07$ (m^{-1}) are fit constants obtained from a regression analysis ($r^2 = 0.71$; $n = 116$) of date obtained from the western part of the optically similar Oosterschelde estuary (Malkin and Kromkamp, unpublished results). These estimates of K_d varied

Table 1
Timing and start of the bioassays.

Bioassay	Start	End
B1	30th March 2010	5th April 2010
B2	10th April 2010	16th April 2010
B3	17thApril 2010	23rd April 2010
B4	24th April 2010	30th April 2010