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Variations in the elemental ratio of organic matter in the central Baltic Sea: Part I—Linking primary production to remineralization

Markus Kreis^{a,d,1}, Markus Schartau^{a,c,*}, Anja Engel^c, Monika Nausch^b, Maren Voss^b^a Institute of Coastal Research, Helmholtz-Zentrum Geesthacht GmbH, Germany^b Leibniz Institute for Baltic Sea Research Warnemünde, Germany^c GEOMAR Helmholtz Centre for Ocean Research Kiel, Germany^d Institute for Hydrobiology and Fisheries Science, University of Hamburg, Germany

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ABSTRACT

For most marine ecosystems the growth of diazotrophic cyanobacteria and the associated amount of nitrogen fixation are regulated by the availability of phosphorus. The intensity of summer blooms of nitrogen (N_2) fixing algae in the Baltic Sea is assumed to be determinable from a surplus of dissolved inorganic phosphorus (DIP) that remains after the spring bloom has ended. But this surplus DIP concentration is observed to continuously decrease at times when no appreciable nitrogen fixation is measured. This peculiarity is currently discussed and has afforded different model interpretations for the Baltic Sea. In our study we propose a dynamical model solution that explains these observations with variations of the elemental carbon-to-nitrogen-to-phosphorus (C:N:P) ratio during distinct periods of organic matter production and remineralization. The biogeochemical model resolves seasonal C, N and P fluxes with depth at the Baltic Sea monitoring site BY15, based on three assumptions: (1) DIP is utilized by algae though not needed for immediate growth, (2) the uptake of dissolved inorganic nitrogen (DIN) is hampered when the algae's phosphorus (P) quota is low, and (3) carbon assimilation continues at times of nutrient depletion. Model results describe observed temporal variations of DIN, DIP and chlorophyll-*a* concentrations along with partial pressure of carbon dioxide (pCO_2). In contrast to other model studies, our solution does not require N_2 fixation to occur shortly after the spring bloom to explain DIP drawdown and pCO_2 levels. Model estimates of annual N_2 fixation are 297 ± 24 mmol $N\ m^{-2}\ a^{-1}$. Estimates of total production are 14200 ± 700 mmol $C\ m^{-2}\ a^{-1}$, 1400 ± 70 mmol $N\ m^{-2}\ a^{-1}$, and 114 ± 5 mmol $P\ m^{-2}\ a^{-1}$ for the upper 50 m. The models C, N and P fluxes disclose preferential remineralization of P and of organic N that was introduced via N_2 fixation. Our results are in support of the idea that P uptake by phytoplankton during the spring bloom contributes to the consecutive availability of labile dissolved organic phosphorus (LDOP). The LDOP is retained within upper layers and its remineralization affects algal growth in summer, during periods of noticeable N_2 fixation.

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1. Introduction

The success of nitrogen-fixing cyanobacteria in the ocean is largely associated with the acquisition of phosphorus at times when the availability of inorganic nitrogen other than dinitrogen (N_2) is limited. Accordingly, estimates of N_2 fixation can be derived from the amount of residual phosphate that remains within the upper water column after all inorganic nitrogen has been

assimilated by the phytoplankton (Gruber and Sarmiento, 1997). For this approach the mean nutrient uptake by phytoplankton is typically assumed to happen with a constant elemental nitrogen-to-phosphorus ratio of N:P=16. The utilization of excess phosphate can then be directly used to approximate N_2 fixation, provided that no other factors limit diazotrophic growth. To date, the plausibility of assuming a constant mean Redfield ratio (N:P=16) for nutrient uptake by phytoplankton is challenged by the ever progressing compilation of field measurements (e.g., Martiny et al., 2013). Possible effects of variations of the elemental N:P ratio of organic matter on N_2 fixation are currently discussed in terms of a variable N:P nutrient uptake ratio of phytoplankton (Mills and Arrigo, 2010), or with respect to preferential remineralization of phosphorus (Monteiro and Follows, 2012). Also, a mechanistic description of nutrient N and P colimitation naturally

* Corresponding author. Current address: GEOMAR Helmholtz Centre for Ocean Research Kiel, Germany.

E-mail addresses: markus.kreis@zmaw.de (M. Kreis), mschartau@geomar.de (M. Schartau).

¹ Current address: Institute for Hydrobiology and Fisheries Science, University of Hamburg, Germany.

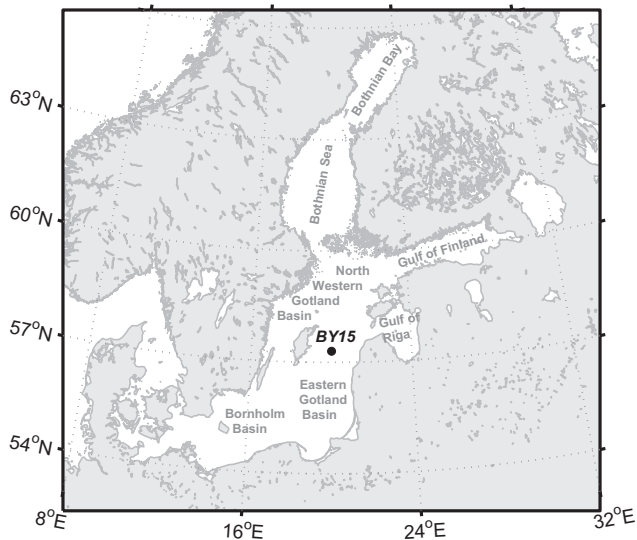


Fig. 1. Map of the Baltic Sea and subregions, highlighting the position of the monitoring station BY15 located in the eastern Gotland Basin.

involve variable carbon-to-nitrogen-to-phosphorus (C:N:P) uptake rates of phytoplankton. For example, variable C:N:P uptake ratios are inevitable when resolving the effect of P quota on N acquisition while N quota regulate C uptake, which has been described as a chain model in Pahlow and Oschlies (2009).

Variations in the availability of inorganic N and P in space and time is one of the most pronounced biogeochemical characteristics in the Baltic Sea, which thrives adaptation and the emergence of specific ecological niches, like for diazotrophic cyanobacteria to cope with conditions of severe N limitation. In the Baltic Proper, that is the Baltic Sea excluding the Bothnian Sea, the Gulf of Finland and the Gulf of Riga (Fig. 1), the annual phytoplankton development is characterized by the formation of a spring bloom of diatoms and/or dinoflagellates, followed by a cyanobacteria bloom in summer and again a diatom bloom in fall. Winter mixing introduces dissolved inorganic nitrogen (DIN) and phosphorus (DIP) to the surface layers, causing a ratio of about only DIN:DIP \approx 8. This low DIN:DIP ratio in winter is responsible for a termination of the spring bloom due to N limitation of the algae. The spring bloom is typically followed by a period of reduced primary production in May, with concentrations of $\approx 2 \text{ mg m}^{-3}$ of chlorophyll-*a* (Chl-*a*). The cyanobacteria start to grow and build up biomass when the stratification of the water column is strong enough to prevent mixing below the euphotic zone. In general, cyanobacteria blooms are observed from June to July. They remain abundant depending upon the availability of P and the bloom usually ends when N:P ratios of the biomass pool exceed values that are 2–3 times the 16:1 ratio (Walve and Larsson, 2010).

Field measurements (Fig. 2) suggest that the initial decline of DIN and DIP concentrations during the early spring bloom period is based on an algal nutrient assimilation ratio of N:P ≈ 10 (Nausch et al., 2008; Wan et al., 2011). When nitrate becomes depleted, about 0.3–0.4 mmol m^{-3} of phosphate remain in the water column, which is continuously drawn down until mid of June. Thereafter, nutrient levels of both nitrogen and phosphorus are kept low until autumn. Thus, the fate of DIP during spring (March–May) and the development of cyanobacteria, especially the onset of summer bloom (June–July), are not directly correlated. A similar finding was reported by Larsson et al. (2001), based on data for the Landsort Deep (North Western Gotland Basin).

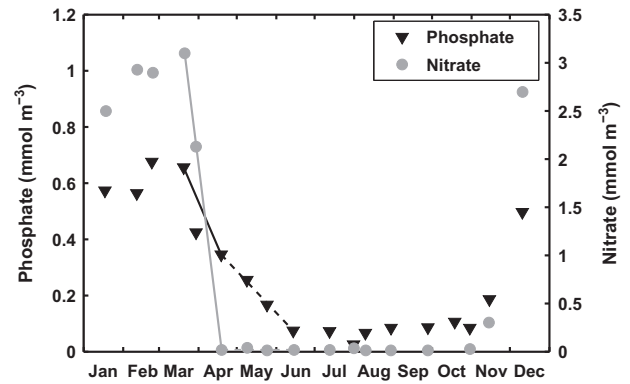


Fig. 2. Annual phosphate- and nitrate cycle in the surface layer (0–10 m) of the eastern Gotland Sea (station BY15) for 2007. Figure redrawn from Nausch et al. (2008, Fig. 24).

Most ecosystem models developed for the Baltic Sea and subareas relate diazotrophic cyanobacteria growth to DIP still available after all DIN has been utilized by the phytoplankton community. The winter mixing then determines the amount of excess DIP after the spring phytoplankton bloom in May (Janssen et al., 2004). Model simulations assuming a constant N:P assimilation ratio for the entire season show a strong mismatch between observed and simulated DIP concentrations in late spring (April–May) (Neumann et al., 2002; Wan et al., 2011; Kuznetsov et al., 2011). In consequence, as growth is formulated with respect to phosphorus availability, development of cyanobacteria is poorly constrained, if modeled DIP concentrations at the onset of the cyanobacteria bloom are far too high. On the other hand, modeling the intensity of blooms during spring and summer months is critical for simulating the partial pressure of carbon dioxide ($p\text{CO}_2$) in surface waters. The latter determines the air–sea CO_2 flux and is important in regard to the potential for carbon sequestration.

In a study from Schneider et al. (2009), the characteristic drawdown of excess phosphate along with continuous carbon fixation has been attributed to some latent nitrogen (N_2) fixation to occur in spite of low temperature conditions; therefore referred to as “cold fixation”. This idea stimulated Kuznetsov et al. (2011) to introduce an additional diazotrophic plankton group of “cold N_2 -fixing” cyanobacteria to their model, so the utilization of phosphate and carbon from late April throughout May can be better reproduced. According to their model results, approximately 74 mmol N m^{-2} must be assigned to cold N_2 fixation during the respective period.

Besides the continuous DIP and $p\text{CO}_2$ drawdown after the spring bloom, another peculiarity is that the estimation of N_2 fixation from post-spring bloom DIP residues yields lower rates than those inferred from direct measurements (Rahm et al., 2000). Additional mechanisms are discussed to explain this discrepancy. One idea is that the period of P limitation is mitigated by upwelling events (Vahtera et al., 2005; Nausch et al., 2009; Lass et al., 2010). Another mechanism considers an effective and fast utilization of dissolved organic phosphorus (DOP) (Nausch and Nausch, 2007). In fact, the combination of both mechanisms, upwelling and an effective DOP utilization, corresponds with more recent findings where intracellular phosphorus (P quota) and nitrogen (N quota) of algae yield N:P ratios that are well below 16, in particular during short-term upwelling events in spring (Nausch et al., 2009).

To date, no dynamical model study has addressed variability in utilization and turnover of nitrogen and phosphorus along with carbon fixation in the Baltic Sea. In this study we provide a dynamical model solution that considers variations in

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