Journal of Marine Systems 178 (2018) 75–85

Contents lists available at ScienceDirect

Journal of Marine Systems

journal homepage: www.elsevier.com/locate/jmarsys

The role of life cycle processes on phytoplankton spring bloom composition: a modelling study applied to the Gulf of Finland

Soonmi Lee[a,b,*], Richard Hofmeister[a,c], Inga Hense[a]

[a] *Institute of Hydrobiology and Fisheries Science, Center for Earth System Research and Sustainability, University of Hamburg, Germany*
[b] *Ecological Networks and Global Change Group, Theoretical and Experimental Ecology Station, CNRS and Paul Sabatier University, Moulis, France*
[c] *Institute of Coastal Research, Helmholtz-Zentrum Geesthacht, Geesthacht, Germany*

ARTICLE INFO

Keywords:
Baltic Sea
Life cycle
Cold-water dinoflagellates
Diatoms
Resting stages
Seed pool
Spring bloom

ABSTRACT

Diatoms are typical representatives of the spring bloom worldwide. In several parts of the Baltic Sea, however, cold-water dinoflagellates such as *Biecheleria baltica* have become dominant during the past decades. We have investigated the mechanisms behind this trend by using an ecosystem model which includes the life cycles of three main phytoplankton groups (diatoms, dinoflagellates and cyanobacteria). Coupled to a water column model we have applied the model system for the period 1981–2010 to the Gulf of Finland. In agreement with observations, the model results show an increasing trend in the proportion of dinoflagellates in the Gulf of Finland. Temperature and life cycle-related processes explain the relative increase of dinoflagellates and corresponding decrease of diatoms. Warming over the 30 years has enabled a head start of dinoflagellates by reducing the time lag between germination and growth of vegetative cells. Although diatoms have a much higher growth rate, they cannot compete with the high dinoflagellate concentrations that result from the inoculum. Diatoms will only dominate in years when the inoculum concentrations of dinoflagellates or the temperatures are low. Overall, the model results suggest that consideration of life cycle dynamics of competing phytoplankton groups may be crucial to understand trends and shifts in community composition.

1. Introduction

In most temperate waters spring blooms are dominated by diatoms (Smayda, 1980; Smayda and Reynolds, 2003). This is not the case in the Baltic Sea, where large (20–30 µm radius/diameter) cold-water dinoflagellates often compete successfully with diatoms (Niemi, 1975; Kononen and Niemi, 1984; Heiskanen, 1993; Heiskanen and Kononen, 1994; Heiskanen, 1998; Kremp and Heiskanen, 1999; Olli and Heiskanen, 1999; Jaanus et al., 2006; Spilling, 2007b). In recent decades, an increasing trend in the spring bloom proportion of cold-water dinoflagellates has been observed in several parts of the Baltic Sea, including the Gulf of Finland (Wasmund and Uhlig, 2003; Alheit et al., 2005; Jaanus et al., 2006; Klais et al., 2011; Wasmund et al., 2011; Klais et al., 2013). The causes behind this trend, however, are unclear.

Generally, dinoflagellates are considered to be less competitive compared to diatoms. Spring bloom dinoflagellates from the Baltic Sea for example have a lower maximum light utilization coefficient (Spilling, 2007b; Spilling and Markager, 2008), a narrower temperature window (Kremp et al., 2005) and a lower maximum growth rate (Spilling, 2007b; Spilling and Markager, 2008) than diatoms. Given these competitive disadvantages, the apparent paradox (low maximum specific growth rate but sudden bloom formation of dinoflagellates) may be related to life cycle aspects (see, e.g., Hense and Burchard, 2010).

Individual life cycle strategies seem to be important in regulating dinoflagellate blooms (Anderson and Rengefors, 2006; Bravo et al., 2010; Kremp, 2013; Wyatt and Zingone, 2014). For example, *Biecheleria baltica* (sensu Moestrup et al., 2009 = *Woloszynskia halophile* sensu Kremp et al. (2005)), one of the dominant spring bloom dinoflagellate species in the Gulf of Finland, forms numerous resting cysts at the end of the bloom period (Olli and Trunov, 2010); the accumulation of cysts in the sediment leads to the formation of seed banks. Enhanced encystment and the spreading of cyst beds are assumed to increase the abundance of this species in the water column (Olli and Trunov, 2010; Klais et al., 2011). Kremp et al. (2008) have emphasized that the size of the inoculum regulates bloom formation and the dominance of the cold-water dinoflagellates over diatoms. In their mesocosm experiments, nutrient concentrations and elemental ratios have played a minor role in influencing the competition between dinoflagellates and diatoms.

In general, however, changes in nutrient conditions as well as

---

[*] *Corresponding author at: Institute of Hydrobiology and Fisheries Science, Center for Earth System Research and Sustainability, University of Hamburg, Germany.
E-mail address: soonmi.lee@sete.cnrs.fr (S. Lee).

http://dx.doi.org/10.1016/j.jmarsys.2017.10.010
Received 10 April 2017; Received in revised form 20 October 2017; Accepted 24 October 2017

elemental ratios as a result of eutrophication are often made responsible for ecosystem changes in the Baltic Sea. In particular, high nitrogen and phosphorus loading over decades (see e.g. Elmgren, 2001) but a decrease in the land-sea flux of silica (Humborg et al., 2006) suggest that conditions for diatom growth have deteriorated in the Baltic Sea. However, the silica:nitrogen ratio, specifically in the Gulf of Finland, is quite high (2.0, Papush and Danielsson, 2006) and field studies in the entire Baltic Sea have shown that the spring bloom is limited by nitrogen (Tamminen and Anderson, 2007). Thus, although nutrient concentrations definitely control the total biomass concentrations, it seems unlikely that they can explain the observed long-term trends and neither do the corresponding nutrient ratios.

Other explanations regarding the increasing trend in the spring bloom proportion of dinoflagellates have been put forward, such as decadal climate oscillations (Wasmund et al., 1998; Alheit et al., 2005) or the decrease in ice cover (Klais et al., 2011, 2013). Both seem plausible, as they are consistent with a stronger stratification in winter and spring: since dinoflagellates prefer such stratified conditions, they may have a competitive advantage over diatoms, who do not. The same argument may be used to attribute the trend in species composition to global warming. However, rising temperatures have also more direct effects on growth and life cycle processes of phytoplankton. And some of these effects, e.g., the temperature-dependence of growth, or the life cycle transition regulation and germination control of dinoflagellates (Kremp and Anderson, 2000; Anderson and Rengefors, 2006), may or may not favor dinoflagellate species. In summary, existing observational evidence alone does not easily lead to an explanation of the positive trend in the proportion of dinoflagellates.

Ecosystem models may be a useful tool to address some of the open questions regarding the observed trend. As the inoculum and thus life cycle aspects seem to be important, such an ecosystem model needs to consider life cycle processes of both diatoms and dinoflagellates. So far, there are only few model studies that take these processes into account. Eilertsen and Wyatt (2000) have shown that the consideration of the seed stock better explains spring bloom dynamics in high latitudes. Warns (2013) has coupled a complex dinoflagellate life cycle model (Warns et al., 2013a, 2013b) with a simple diatom life cycle model and found that the alternating patterns between diatoms' and dinoflagellates' dominance can be explained by the abundance of the resting stages and the temperature gradient in spring. Neither of these studies, however, has addressed the observed increasing trend of the spring bloom proportion of dinoflagellates in the Baltic Sea.

By using an ecosystem model that resolves the life cycle of both dinoflagellates and diatoms, we specifically want to understand the underlying mechanisms leading to the increasing trend found in the spring bloom proportion of dinoflagellates in the Gulf of Finland for the period 1981–2010. Our ecosystem model is coupled to a water column model and considers the life cycle processes of three main Baltic Sea phytoplankton groups (diatoms, dinoflagellates and cyanobacteria). We are particularly interested in answering the following questions: (1) is the model able to reproduce the observed trend? If so, (2) what are the underlying mechanisms leading to it?

2. Observations

We will compare our model results with observations from the Gulf of Finland (longitude 24.8°E, latitude 54.8°N). Specifically, we use the Helsinki Commission (HELCOM) monitoring data for nutrients from the International Council for the Exploration of the Seas (ICES) database (ICES, 2016) and the phytoplankton monitoring datasets which are provided by national monitoring agencies (Klais et al., 2011). Although the phytoplankton data set covers all seasons and includes various taxonomic groups, we only consider data of diatoms and dinoflagellates in spring (March–June) from the upper 10 m of the water column.

To convert wet weight biomass ($\mu g\ l^{-1}$) into carbon concentration ($mg\ C\ m^{-3}$), we use the proposed conversion factors (5.0% of the wet weight for diatoms: *Thalassiosira baltica* and *Chaetoceros wighamii*, 12.5% of the wet weight for dinoflagellates: *B. baltica*) based on the volume-to-carbon ratio proposed by Menden-Deuer and Lessard (2000). Carbon concentrations ($mg\ C\ m^{-3}$) are converted to nitrogen concentrations ($mmol\ N\ m^{-3}$, the model unit) by using the Redfield ratio (nitrogen:carbon = 16:106) and the unit conversion factor from g into mol (1/12). Outliers are removed by using John Tukey's method of leveraging the Interquartile Range (Tukey, 1949); they result from error or skew results in ways that are inaccurate or misleading.

In addition, to compare our simulated seed pool - defined here as the total amount of viable resting cysts that germinate - with observations, we use sediment data from Olli and Trunov (2010) who have investigated the abundance of benthic cysts in the sediments of the Gulf of Finland in late May 2004. We calculate the seed pool from observed cyst amounts of *B. baltica* within ± 0.25° of station LL7 of HELCOM by considering a germination potential (40%) according to Kremp (2000) and a fixed nitrogen content of cysts ($1.7 \times 10\ pmol\ N\ cyst^{-1}$), following Warns et al. (2013a).

3. Model description

Our model is based on a Baltic Sea ecosystem model, the Ecological ReGional Ocean Model, (ERGOM, Neumann, 2000; Neumann et al., 2002), with an improved description of the phytoplankton groups: we now consider the life cycles of diatoms (Warns, 2013), dinoflagellates (Warns et al., 2013a, 2013b) and cyanobacteria (Hense and Beckmann, 2006; Hense and Burchard, 2010). All other ecosystem variables and processes of ERGOM (related to zooplankton, the three nutrients (nitrate, ammonium and phosphorus), the nutrient based detritus pools and the oxygen compartment, as well as the fluffy layer) are not modified, except minor changes in the rates to adjust the model results to observations (see Appendix A).

Phytoplankton growth processes are assumed to depend on photosynthetically available radiation (PAR), nutrients and temperature. Dissolved inorganic nitrogen (DIN) is taken up by all phytoplankton except the nitrogen fixing cyanobacterial life cycle stage. Phyto- and zooplankton mortality represents a nitrogen flux into the detritus pool and the nitrogen based detritus is remineralized into ammonium which is nitrified to nitrate depending on oxygen conditions. The phosphorus cycle is coupled to the nitrogen cycle, assuming a constant stoichiometric ratio (phosphorus:nitrogen = 1:16). The external input of nutrients is driven by atmospheric deposition at the sea surface. The fluffy layer at the bottom affects the exchange process between sediment and water column processes.

The life cycles of the three phytoplankton groups are represented by compartments for different life cycle stages (Fig. 1). For diatoms we do not consider the Size-Reduction-Restitution Cycle (SRRC, Hense and Beckmann, 2015), but only two stages: growing vegetative cells (Dia_{veg}) and resting spores (Dia_{res}), following Warns (2013). The transfer from vegetative cells into resting spores is determined by the actual growth conditions. The life cycle of dinoflagellates is divided into four life cycle stages: germinating cells (Din_{ger}), vegetative cells (Din_{veg}), gametes (Din_{gam}) and resting cysts (Din_{res}), following Warns et al. (2013a) and Warns et al. (2013b). The transition between individual life cycle stages of dinoflagellates depends on temperature or PAR. The cyanobacteria are also described by four life cycle stages: recruiting cells (Cya_{rec}), vegetative cells (Cya_{veg}), nitrogen fixing heterocysts (Cya_{het}), and akinetes (Cya_{aki}) which are characterized by their internal nitrogen and energy quota (Hense and Beckmann, 2006). The transitions between life cycle stages are due to the changes in their internal quota. Diatoms and dinoflagellates are both grazed by zooplankton, cyanobacteria however are assumed to be non-grazeable because of their ability to produce toxins.

To provide the physical environment, the ecosystem model is coupled to the one-dimensional water column model, General Ocean Turbulence Model (GOTM, Umlauf et al., 2005) using the infrastructure