

Spring seasonal pattern of primary production in the Gulf of Riga (Baltic Sea) after a mild winter

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Abstract

ABSTRACT: Spring phytoplankton production was estimated by a light and dark bottle oxygen technique in the southern part of the Gulf of Riga during spring 2014. The main study objective was to determine factors that define the spring primary productivity by analyzing the pattern of primary production and changes in succession of phytoplankton species along with environmental factors. The productivity was measured after an untypically mild winter without ice-cover on the Gulf of Riga and spring flooding, which resulted in large amounts of terrestrial nutrients retained in the catchment area. At that time precipitation played a major role in river-originated nutrient inflow in the study area. A vague diatom bloom was stretched throughout April, followed by increase in biomass of dinoflagellate *Peridiniella catenata* and autotrophic ciliate *Mesodinium rubrum*. The total amount of spring primary production (March–May) reached 116.3 to 127.2 g C m⁻² in the southern region of the Gulf of Riga. Our results suggest that diatoms contributed most to the “new” production and net primary production, whereas dinoflagellate *P. catenata* and autotrophic ciliate *M. rubrum* vernal production was mostly based on regenerated nutrients, although showing also the highest respiration rates.

Key words: eutrophication, Gulf of Riga, nutrients, phytoplankton, productivity, vernal succession.

Abbreviations: Chl, chlorophyll *a*; DIN, sum of nitrite, nitrate and ammonium; DIP, dissolved inorganic phosphate; DSi, dissolved silicate; GPP, gross primary production; *k*, attenuation coefficient; NPP, net primary production; PCA, principal component analysis; PSU, practical salinity units; R, planktonic community respiration; TN, total nitrogen; TP, total phosphorus.

Introduction

Baltic Sea is a shallow intra-continental brackish sea, affected by large nutrient inputs from densely populated drainage areas. The eutrophication status of nine of its seventeen sub-regions has been assessed as bad (Andersen et al. 2011), based on several environmental parameters, including winter concentrations of phosphorus and nitrogen, phytoplankton biomass and concentration of chlorophyll *a*. Although the amount of primary production is a good proxy of eutrophication, it is not included as indicator in eutrophication assessments due to lack of data in the Baltic Sea region (Wasmund et al. 2001). Even in the Baltic Sea Environmental Proceedings of Eutrophication (HELCOM 2009; HELCOM 2014), almost no long-term annual means of phytoplankton biomass and in situ primary production were reported.

In The Gulf of Riga is one of the Baltic Sea sub-regions marked with bad eutrophication status (Andersen et al. 2011; HELCOM 2014) and it has one of the longest phytoplankton time-series in the world, covering almost four decades (Jurgensone et al. 2011). Still, only two studies have been carried out to estimate primary production of the area (Olesen et al. 1999; Wassmann, Tamminen 1999; Wasmund et al. 2001) and both of them were carried out

almost 20 years ago, during a period when one of the lowest concentration of dissolved inorganic nitrogen was observed in the region (Jurgensone et al. 2011). Simulated annual primary productivity showed a slight decrease in 1990-ies as well, reaching up to 206 g C m⁻² (Müller-Karulis, Aigars 2011), consistent with the results of previously mentioned studies that estimated annual primary production in the range of 255 (Wasmund et al. 2001) to 350 g C m⁻² (Olesen et al. 1999). However, the concentration of nitrogen started to increase from early 2000-ies, and the concentration of phosphorus increased steadily at least until 2007 (Müller-Karulis, Aigars 2011), therefore we expect an increase in primary production as well.

The phytoplankton dynamics in the Gulf of Riga follows the classical scenario of boreal phytoplankton development (Yurkovskis et al. 1999; Jurgensone et al. 2011; Olli et al. 2011). Expressed spring blooms can be observed after ice melting, in April–May, which are usually dominated by diatoms *Achnanthes taeniata* and *Thalassiosira baltica*. Towards the end of the spring bloom, the diatom *Chaetoceros* spp. and dinoflagellate *Peridiniella catenata* become the dominating ones. The development of thermal stratification favours motile dinoflagellates, but promotes sinking of large-sized, non-motile diatoms. As a result, the majority of spring bloom production leaves the euphotic

zone and settles in sediments. In the second half of summer, a bloom of cyanobacteria (mainly *Aphanizomenon flos-aquae*) accompanied by chlorophytes and cryptophytes can occur, but succession of phytoplankton is terminated by the second bloom of diatoms in September-October, after the disruption of the thermocline (Yurkovskis et al. 1999; Jurgensone et al. 2011 and the references therein). As the bulk of annual primary production is produced during spring bloom and summer/autumn production contributes in a lesser way (e.g. Hällfors et al. 1981), the chosen study period was the spring season, covering the period from early March to the end of May. The main study objective was to determine factors that define the spring primary productivity by analyzing the pattern of primary production and changes in succession of phytoplankton species along with environmental factors in the southern part of the Gulf of Riga.

Materials and methods

Study area

The Gulf of Riga is situated at the north-eastern part of the Baltic Sea and covers an area of 16 330 km² with average depth of 26 m and maximal depth of approximately 60 meters. Its drainage basin (135 700 km²) covers more than eight times the surface area of the Gulf itself (Kotta et al. 2008), and 86% of the freshwater inflow comes from the southern part of the Gulf (Kļaviņš et al. 2002) resulting in a north-westward salinity gradient, from 0.5 – 2.0 practical salinity units (PSU) in surface layers of the southern regions to 7.0 PSU at the Irbe Strait. The mean salinity in the most parts of the Gulf of Riga is between 5.0 and 6.0 PSU. Surface water temperature varies seasonally from 0 to 20 °C.

Temporal and spatial pattern of ice coverage and duration varies annually and the average ice-season lasts approximately 80 days (Kotta et al. 2008 and references therein). In the coldest season (November to April) water layers of the Gulf are mixed, such that the temperature, salinity and nutrient concentrations throughout the water column are similar (Stigebrandt 1996). From April to mid-October seasonal stratification restricts vertical water exchange and promotes oxygen depletion and nutrient accumulation in the bottom layer until the entire water column is mixed again in autumn (Yurkovskis 2004).

Sampling

Sampling was performed weekly in three stations (Fig. 1) during spring (March-May) 2014. Sampling was conducted using a Ferry Box Sampling Module (Ferry Box) installed aboard the Tallink passenger ferry “MS Romantika”, travelling between Riga and Stockholm. “MS Romantika” is 192.9 m long with draught of 6.5 m. The Ferry Box was used for the measurements and collection of water from 5 meter depth at the end of the ferry. Long term (1993-2012) mean depth of the vernal upper mixed layer of the

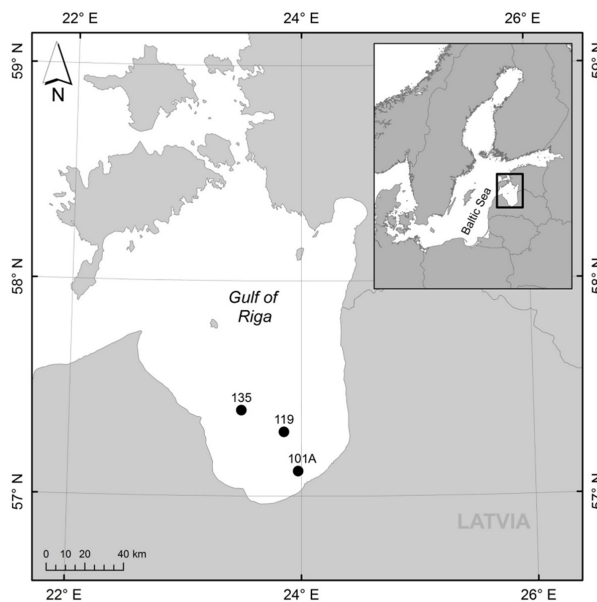


Fig. 1. The location of three sampling stations (black dots) in the Gulf of Riga.

Gulf of Riga is approximately 8 m deep with no evident trend over last twenty years (Skudra, Lips 2016), thus the assumption was made that samples collected from 5 m depth in general represents environmental conditions and planktonic community prevailing in upper mixed layer of studied locations.

Water samples for evaluating chemical parameters (nutrients), phytoplankton biomass and phytoplankton species composition, concentration of chlorophyll *a* (Chl) and community production/respiration were pumped via system of the Ferry Box as the ferry travelled. In a couple of hours samples were transported to laboratory for further execution. The data of water temperature and salinity were obtained from the system of the Ferry Box (PT-100 sensor). Meteorological data (maximal wind speed and dominating wind direction, precipitations and incident radiation) were obtained from the Latvian Environment, Geology and Meteorology Centre database for station located on building of University of Latvia in Riga (<https://www.meteo.lv>).

Analysis of field samples

The samples were treated for analysis of chemical parameters, phytoplankton biomass and concentration of Chl according to HELCOM COMBINE Manual (HELCOM 2015). Concentration of ammonium (NH₄) and phosphate (DIP) were measured by the indophenol blue and molybdenum blue methods (Grasshoff et al. 1983). The sum of nitrate and nitrite (NO₂₊₃) was determined by nitrite reaction with an azo dye after reduction of nitrate to nitrite in a copper coated cadmium column. The nitrite was determined by reaction with an azo dye and nitrate

was determined as difference between nitrite and sum of nitrate and nitrite. In further text, DIN refers to for the sum of nitrite, nitrate and ammonium. Concentration of dissolved silicate (DSi) was determined colorimetrically according to the procedure described by Grasshoff et al. (1983). Concentrations of total nitrogen (TN) and total phosphorus (TP) were analyzed as nitrate and phosphate after wet digestion with persulfate.

To Chl was collected on glass fiber filters (Whatmann GF/F), extracted in 96% ethanol for 24 h and further analyzed by a spectrophotometer (Cary 100 Conc UV-Visible Spectrophotometer). Phytoplankton samples (300 mL) were fixed with acid Lugol's solution. Subsamples of 10 and 25 mL of fixed samples were settled in a sedimentation chamber for 12 h and counted according to Uthermöl technique with an inverted microscope Leica DMI3000 at 200× and 400× magnification. The number of counted cells in all subsamples exceeded 500 (Utermöhl 1958; HELCOM 2015; Olenina et al. 2006). The cell volume for phytoplankton wet weight biomass determination was determined using geometrical formulae for various suitable geometrical shapes (Edler 1979).

Estimation of primary production

Light and dark bottle oxygen technique (Olesen et al. 1999) was used to evaluate net primary production (NPP) and planktonic community respiration (R). Oxygen concentrations were determined by the Winkler titration method. Water was filled in 15 glass bottles with volume of 100 mL. Winkler reagents (1 mL manganese chloride and 1 mL alkaline iodide) were added to three bottles immediately for estimation of initial oxygen concentration, and then they were stored in darkness at room temperature, while the others were divided in four groups with different transparency level and placed in an incubator for further analysis.

Specific light transmittance to each group was provided using GAM optical filters: no filter for 100% transparency, 1514 GAM optical filter for 66% transparency, 1516 GAM optical filter for 23% transparency and aluminum foil for 0% transparency. All the vials were fixed on a rotating device and were submerged in water to ensure the least

possible changes in ambient temperature during incubation that lasted for 24 h. After the incubation, 1 mL sulphuric acid was added to the samples. Sodium thiosulphate was added gradually during the titration in order to determine oxygen concentration.

Oxygen consumption in the dark bottles (0% transparency) was used as a proxy of R, but the other three groups were used to evaluate NPP rates. R and NPP were transformed to carbon units. Daily produced carbon was calculated for each transparency group that was equalized to specific depths according to the attenuation coefficient (k). The attenuation coefficient was calculated based on the long-term average of Secchi depth in May for each sampling station. Then, a trapezoidal integration method was used to estimate daily NPP ($\text{g C m}^{-2} \text{d}^{-1}$) rates of the upper 10 m layer. Gross primary production (GPP) was calculated by summing NPP and R (expressed as positive values).

Statistical analysis

A Principal Component Analysis (PCA) based on correlation coefficients was applied to the primary production variables and the environmental parameters to identify the main sources of data variability and detect which factors responded similarly both spatially and temporally. Five of the environmental parameters (DIP, DIN, NH_4 , NO_{2+3} , DSi) were used as supplementary parameters in order to avoid creation of a non-essential third component, as these five variables did not show strong relation to any primary production variables, though showed strong inter-correlations. The analysis was performed using StatSoft® STATISTICA 7. Data were Box-Cox (Wessa 2015) transformed prior to analysis to ensure similar (normal) distribution for all variables.

Results

Meteorological conditions

The spring weather conditions were untypical for northern Europe in the year 2014. The winter was mild with little or no snow coverage on land (Table 1), and the Gulf of Riga was completely ice-free for the whole winter season. Accordingly, spring flooding did not occur. Wind conditions were moderate during spring 2014. The maximal wind speed was 5 m s^{-1} on average, and it exceeded 8 m s^{-1} only on several occasions (Fig. 2).

Due to absence of spring flooding, precipitation played the critical role in increasing river runoff and bringing fresh nutrient inputs to the Gulf of Riga. While riverine waters mainly affected the southern coastal regions of the Gulf, increased concentrations of nutrients were detected after rainfall in the farther station as well (e.g. station 135; see the next chapter). Regular precipitation occurred in the middle of March and beginning of May, but the heaviest rainfall occurred during the second week of April (Fig. 2).

Table 1. Meteorological observations during winter 2013/2014. Data were obtained from the Latvian Environment, Geology and Meteorology Centre database for station located on building of University of Latvia in Riga (<https://www.meteo.lv>)

Month	Average air temperature (°C)	Days below 0 °C (number)	Total precipitation (mm)
Dec 2013	2.7	5	57.4
Jan 2014	-5.5	20	33.7
Feb 2014	1.1	5	24.9

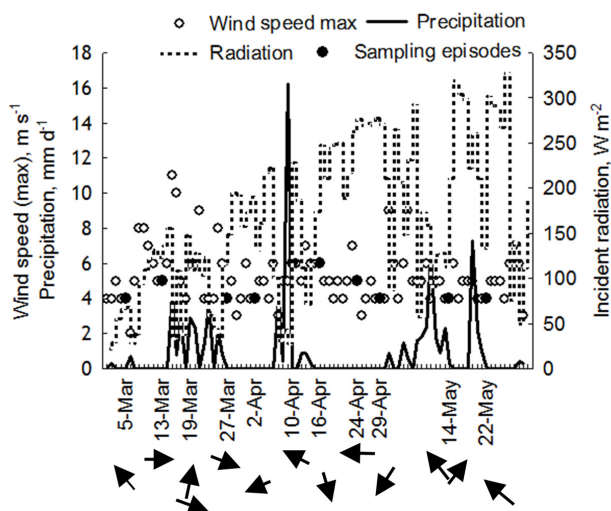


Fig. 2. Spring meteorological conditions (max. wind speed, dominating wind direction at sampling days, precipitations and incident irradiance) during spring 2014. Black arrows indicate the dominating wind direction during sampling day. Data obtained from the Latvian Environment, Geology and Meteorology Centre database for station located on the building of the University of Latvia in Riga.

Nutrients and hydrology

Initial spring concentrations of DIN, DIP and DSi were relatively low: 9.5, 0.6 and 17.8 $\mu\text{mol L}^{-1}$, respectively (Fig. 3). Despite the slow development of phytoplankton during March (Fig. 4), concentrations of nutrients were almost constant. Windy weather and convective mixing ensured instability of water column in this period, constantly supplying fresh nutrients to the upper water layer. Evidence of consumption of nutrients started in the beginning of April. The concentration of DIN began to decrease slightly in the farther stations (135 and 119), whereas the continuous supply of fresh DIN input from the River Daugava was observed in station 101A. The concentration of DIN doubled in this station after heavy rainfall on April 10, reaching 17.9 $\mu\text{mol L}^{-1}$. Subsequently it started to decrease in all stations, meeting the minimal value just slightly above 0.5 $\mu\text{mol L}^{-1}$ on May 15 (Fig. 3). However, a rainstorm on May 20 caused enrichment of DIN in two stations (101A and 119) closest to three large river plumes inflowing in the southern part of the Gulf.

Consumption of DIP started on April 2, but in contrast to DIN it did not vary with river runoff. Concentration of DIP reached a minimum that neared the analytical detection limit (0.1 $\mu\text{mol L}^{-1}$) on April 24 (Fig. 3) in farther stations 135 and 119. At the same time a rapid increase in values of Chl were detected (Fig. 4). Mean concentration of DSi was 17.9 $\mu\text{mol L}^{-1}$ when the diatom bloom started, and it never became depleted in any of sampled sites. In coastal station 101A, the River Daugava ensured fresh supply of DSi with runoff, which was especially evident after rainfalls (Fig. 3). Concentrations of TN and TP did

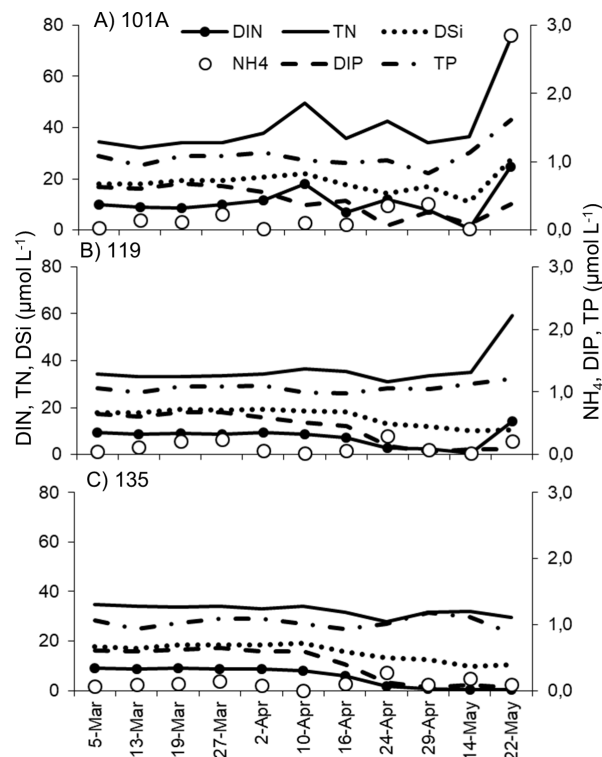


Fig. 3. Concentrations of nutrients in the Gulf of Riga during spring 2014 at three sampling sites. DIN, dissolved inorganic nutrient; TN, total nitrogen; DSi, dissolved inorganic silica; DIP, dissolved inorganic phosphorus; TP, total phosphorus.

not vary noticeably until May, when they started to increase rapidly, reaching the highest values.

Changes in water temperature showed dynamics of typical spring warming (Fig. 4) closely following increasing solar radiation (Fig. 2). Water temperature gradually rose from 1.6 to 14.6 °C during the study period (Fig. 4), reaching the point of maximal water density (salinity 5.5; 2.7 °C) on April 2 and triggering the onset of thermal stratification at this point.

Phytoplankton biomass and production

Diatoms, dinoflagellates and autotrophic ciliate *Mesodinium rubrum* were analyzed during present study, as they are the dominating groups in the vernal phytoplankton community (Jurgensone et al. 2011). The succession of phytoplankton spring bloom in the Gulf of Riga followed the pattern for temperate coastal waters. The phytoplankton development was divided in three phases: pre-bloom period, growth-peak phase and declining phase. In the pre-bloom period, which lasted all March, diatoms comprised more than 80% of phytoplankton biomass (Fig. 4). Diatom *Thalassiosira baltica* dominated during this phase, and relatively small amount of biomass was composed by *Achnanthes taeniata*. The growth-peak phase started on April 2 and lasted until April 24, when increase of diatoms *Chaetoceros holsaticus* and *Chaetoceros wighamii* was detected. They gradually

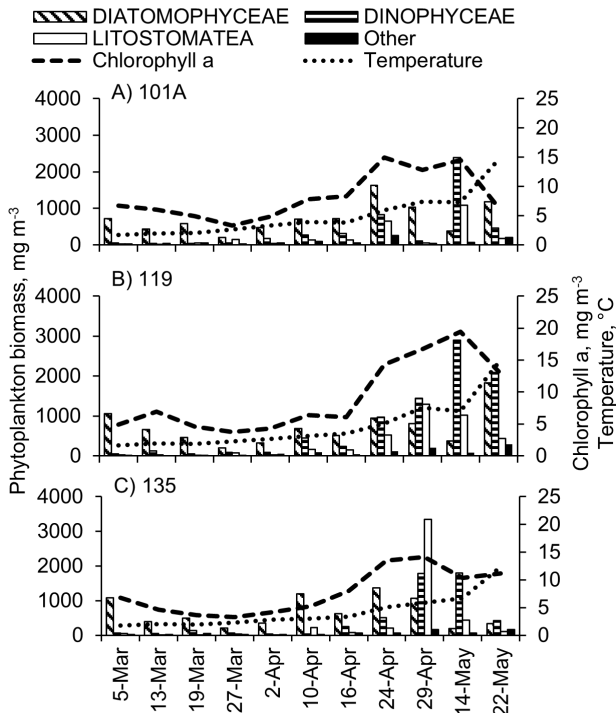


Fig. 4. Succession of dominating phytoplankton groups, chlorophyll a concentration and water temperature in the Gulf of Riga during spring 2014

took over previously prevailing *T. baltica* and *A. taeniata*. Although biomass of diatoms rose till April 24, a clear peak of the spring bloom was not observed.

Phytoplankton biomass increased until late April-early May, when a rapid increase in dinoflagellates, mainly *Peridiniella catenata*, and ciliate *M. rubrum* (Litostomeata) was observed. At this time, total phytoplankton biomass was 3785 mg m^{-3} and reached the highest values during the study period. Chl concentration, mirroring phytoplankton biomass, was low during March and early April and did not exceed 8 mg m^{-3} . After a rapid increase in Chl concentration, starting from the middle of April, the highest values were reached at different times in relation to the location of the station, and the maximal concentration of Chl, almost reaching 20 mg m^{-3} , was observed in station 119 on May 14 (Fig. 4).

An increase of diatom biomass was detected in stations 101A and 119 at the end of May. Apparently, prolonged precipitation in the middle of May resulted in increased runoff from adjacent rivers, providing better conditions compared to station 135, where no increase was observed. Although it would be expected that majority of diatom population originated from riverine freshwater inflow, analysis showed the opposite results: more than 75% were composed by *T. baltica* and *Chaetoceros* spp., and only 15% were freshwater species (*Diatoma tenuis*, *Aulacoseira granulata*, *Synedra ulna*, *Asterionella formosa*). This indicates ability of more efficient assimilation of nitrogen

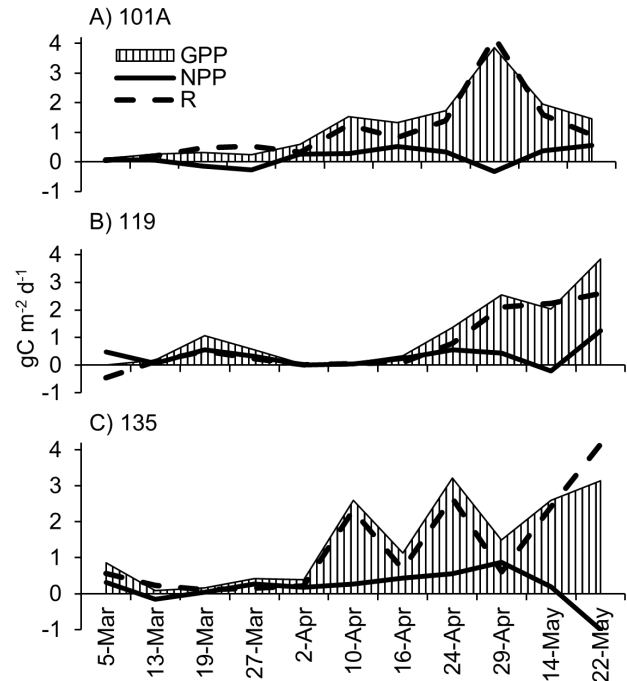


Fig. 5. Spring pattern of changes in primary productivity parameters (GPP, gross primary production; NPP, net primary production and R, planktonic community respiration) in the southern part of the Gulf of Riga during spring 2014.

for *T. baltica* and *Chaetoceros* spp. than other spring phytoplankton taxa. At the same time, biomass of other phytoplankton groups declined (Fig. 4).

GPP showed an increasing trend throughout the study period (Fig. 5) mirroring the typical spring increase in solar radiation, thus also water temperature and growth of phytoplankton biomass, which according to the PCA results was PO_4 limited (Fig. 6, PCA analysis). The role of DIN might have been evaluated as non-significant as it was affected by several episodes of precipitation, however the importance of DIN could be possible, as biomass of diatoms followed its variation.

GPP was lowest during the pre-bloom period, never exceeding $1 \text{ g C m}^{-2} \text{ day}^{-1}$. It started to rise steadily during April, reaching maximum at the end of the bloom, exceeding $3 \text{ g C m}^{-2} \text{ day}^{-1}$ in all stations. Similar dynamics was observed in community respiration (R). Net primary production (NPP) did not vary much, yet the positive values throughout the growth-peak phase implied strong relation to biomass of diatoms (Fig. 5), which was confirmed by PCA (Fig. 6).

Discussion

Phytoplankton primary production is the most important biological energy source in the ecosystem (Elmgren 1984), while the annual spring bloom represents the most significant production phase (Klais et al. 2011). Spring

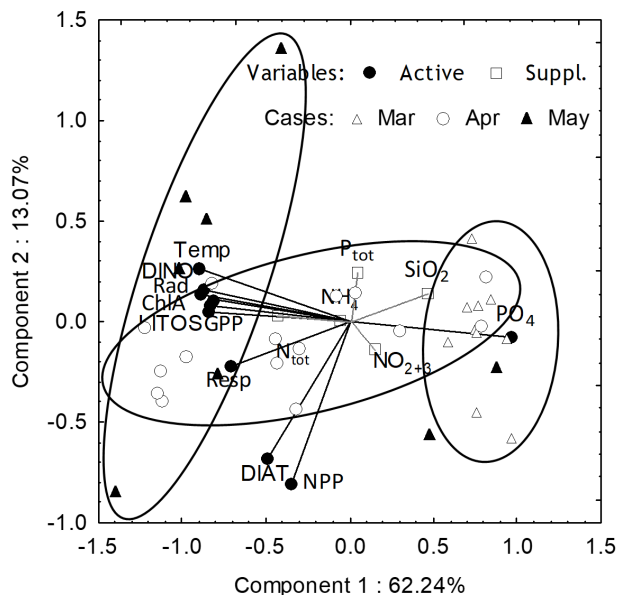


Fig. 6. Results of PCA analysis. Plot for environmental variables of Principal component 1 and Principal component 2. Temp, temperature; Rad, Solar radiation, ChlA, chlorophyll *a*; DINO, dinoflagellates; LITOS, Litostomatea (*Mesodinium rubrum*); DIAT, diatoms; GPP, gross primary production; NPP, net primary production; Resp, community respiration; Nutrients (Ntot, Ptot, NH_4 , NO_{2+3} , PO_4 , SiO_2). Each ellipse compiles majority of cases from the same month (March, April, May), starting from the right side.

bloom termination and sedimentation of the biomass, within a period of approximately two weeks, accounts for half of the annual organic matter input to the benthos in the northern Baltic Sea. Moreover, it can account for 30 to 65% of annual primary production, depending on the dominant species (Heiskanen, Kononen 1994). Diatoms sink rapidly as intact cell aggregates, whereas the bulk of dinoflagellates disintegrate in the water column and sink slowly as refractory phytodetritus or in forms of resistant resting cysts (Heiskanen, Kononen 1994). Also zooplankters profit from spring bloom, as it is one of the triggers for their reproduction (Peinert et al. 1982).

The total value of spring GPP varied between stations from 116 to 127 g C m^{-2} in the present study. However, the majority of GPP was produced in May (72 to 88 g C m^{-2}) when dinoflagellates and autotrophic ciliate *Mesodinium rubrum* dominated. Consequently, only one third of spring production composed of diatoms could be effectively sedimented, while the remaining part of production regenerated in the water column, resulting in a considerably lower sedimentation rate and different nutritional value for benthic organisms.

There has been continuous discussions over increasing evidence of dinoflagellate dominance over diatoms. Kononen and Niemi (1984) suggested that diatom-dominated spring blooms tended to follow cold winters

with long-lasting ice cover, but mild ice-free winters or early ice breakup in spring favoured dominance of dinoflagellates during the spring bloom in the northern Baltic Sea. Klais et al. (2011) hypothesized that a specific sequence of seasonal events, involving wintertime mixing and resuspension of benthic cysts, followed by proliferation in stratified thin layers under melting ice, favoured successful seeding and accumulation of dense dinoflagellate populations over diatoms in coastal areas. In our study, the spring bloom began with the dominance of diatoms in the phytoplankton (Fig. 4), even after a mild winter. Thus, our study presents a possibility to test the classical theories of phytoplankton spring bloom development. The sampling of phytoplankton started at the beginning of March after a week of sunny weather (Fig. 2), when the early bloom of diatoms could be expected. The biomass of phytoplankton was low and 80% was composed by diatoms; however dinoflagellates and *M. rubrum* were already present in small quantities. At later sampling time environmental conditions favoured to growth of diatoms.

The mixing of water masses was promoted by stormy weather prevailing in March (Fig. 2). Vertical mixing of the water column is tolerated mainly by diatoms (Cushing 1989), mostly heavy diatom cells like *Thalassiosira baltica* and chain-forming *Achnantes taeniata*. Although turbulence decreases average light intensity, it favours non-motile cells by retaining them in euphotic layer (Kjørboe 1993). However, the biomass and gross primary production was low (Fig. 3, 4) during the turbulent period, as the phytoplankton cells, presumably, were often forced out of the shallow euphotic layer. However, community respiration of plankton was also low compared to that in later phases of the bloom. PCA suggested relation of lower respiration rate and relatively higher NPP values to diatom dominance (Fig. 6). According to Falkowski and Owens (1978) and Spilling and Markager (2008), diatoms have a lower respiration rate and higher growth rates under light limitation than dinoflagellates.

The onset of stratification might have triggered the spring diatom bloom. Unfortunately, no vertical profiles were examined during the present study, yet in theory during low winter temperatures (e.g. 1.6 °C in the present study) the seasonal warming is causing vertical mixing of water column until the maximum density point is reached (2.7 °C at the salinity of 5.5 prevailing in the Gulf of Riga). After that thermal stratification begins. In present study the maximum density point was reached on April 2. but the following increasing temperatures, presumably, stabilized the stratification. Constant increase of phytoplankton biomass was observed after the maximum density point was reached and thus we argue that onset of stratification triggered the diatom spring bloom. Although the conventional peak of diatoms was not observed, a rise in *Chaetoceros* spp. biomass was detected. *Chaetoceros* spp. is characteristic during the peak of the spring bloom in the

Gulf of Riga (Yurkovskis 1999; Jurgensone et al. 2011). During the growth-peak phase, increased consumption of nutrients from the upper water layer, which previously was hindered by vertical mixing, began.

While the initial spring nutrient concentrations were relatively low (Fig. 3) and the DIN:DIP ratio indicated nitrogen limitation according to the conventional Redfield ratio (Redfield 1963), PCA analysis recognized only DIP as a significant factor (Fig. 6) for phytoplankton development in the Gulf of Riga during spring 2014. Riverine runoff caused by precipitation played a major role supplementing fresh DIN (mainly in the form of NO_3) to surface waters, but did not contribute to concentration of DIP. Accordingly, throughout the study period the DIN:DIP ratio increased from 14 up to more than 70, when the exhaustion of phosphates occurred due to biological uptake processes. Arrigo (2005) attributed diatoms to “bloomers” that invest energy in reproduction under low DIN:DIP ratios, as more phosphorus is required for synthesis of ribosomal RNA used for cell divisions, allowing diatoms to grow exponentially. Indeed, an increasing trend of diatom biomass was observed until April 24, when DIP decreased to its lowest values, resulting in an increased DIN:DIP ratio, despite a concurrent slight reduction in DIN.

The biomass of dinoflagellates *Peridiniella catenata* and autotrophic ciliates *Mesodinium rubrum* increased as the bloom of diatoms gradually ceased at the end of April. However the diatoms never completely disappeared from the phytoplankton community, even if the composition of species showed decline of the bloom. As the DIN and DIP concentrations were depleted after the end of the diatom bloom, particularly, in stations distant from riverine influence, the production of dinoflagellates and autotrophic ciliates could be based only on regenerated nutrients. In station 101A, fresh nitrate supply was observed, especially after rainy periods (May 22), obviously explaining the persistent existence of diatoms in this station. This indicates ability of more efficient assimilation of nitrates for *T. baltica* and *Chaetoceros* spp. than other spring phytoplankton taxa. Consequently, we deduce that spring diatoms contributed to the “new production”, whereas dinoflagellates *P. catenata* and autotrophic ciliates *M. rubrum* reincorporated the excreted nutrients and contributed mainly to “regenerated production”. Furthermore, the diatom associated nitrate uptake in the Gulf of Riga has been proved also experimentally (Berg et al, 2003).

Lower growth rates, as well as higher photosynthetic capacity at higher irradiance and higher respiration rates (Spilling, Markager 2008) allows dinoflagellates to thrive at lower nutrient concentrations, effectively using regenerated nutrients. Also, dinoflagellates, in contrast to diatoms, prefer high water column stability and are negatively affected by turbulence and mixing (Margalef 1978; Klais et al. 2013). At the declining phase of diatom bloom, an increase in biomass of all phytoplankton groups was observed, resulting in the highest values of total phytoplankton biomass at the end

of April and beginning of May. With the development of dinoflagellates and ciliates, also an increase in GPP was observed; however, 78 to 90% of the GPP were lost via community respiration (Fig. 5). The increased NPP at the end of May could be attributed to a secondary increase of diatoms in the near-shore stations (101A and 119), presumably supported by rise of river-originated DIN.

Conclusions

The present study described untypical spring conditions after mild winter. However with climate changes, mild winters might become typical, as there is evidence that winter conditions in the study area have become milder over the last twenty years, and duration as well as coverage of ice in the Gulf of Riga has declined. The present study showed that the most important factors triggering the spring diatom bloom were onset of stratification, high concentrations of nitrates and also phosphates, as increased uptake of DIP was associated with diatoms. The diatoms are more rapidly growing and produce the larger part of NPP, which potentially sediments delivering high quality food for benthic organisms.

The nutrients remaining in the water column after the spring diatom bloom are regenerated by dinoflagellates and autotrophic ciliates *Mesodinium rubrum*, which produce the bulk of vernal GPP in the Gulf of Riga. However, most of the fixed carbon associated with regenerated production is lost via planktonic metabolic processes and only a minor part of it might reach the sediments, thus increasing the pelagic production in general. Lack of snow and spring flooding retains a lot of terrestrial nutrients in the catchment area, strengthening the importance of spring precipitation that creates pulse-like inflows of nutrients in the Gulf of Riga. As the diatom bloom is triggered by environmental conditions, which are not favourable for other phytoplankton groups, the bloom intensity will depend on the concentration of inorganic nutrients in the area. It might be speculated that in the future, small scale diatom blooms will be observed in the vicinity of river mouths over prolonged time periods and that the majority of phytoplankton assemblage in the spring might be composed of dinoflagellates and ciliates.

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References

- Andersen J.H., Axe P., Backer H., Carstensen J., Clausen U., Fleming-Lehtinen V., Järvinen M., Kaartokallio H., Knuuttila S., Korpinen S., Kubiliute A., Laamanen M., Lysiak-Pastuszek E., Martin G., Murray C., Møhlenberg F., Nausch G., Norkko A., Villnäs A. 2011. Getting the measure of eutrophication in the Baltic Sea: towards improved assessment principles and methods. *Biogeochemistry* 106: 137–156.
- Arrigo K.R. 2005. Marine microorganisms and global nutrient cycles. *Nature* 437: 15–21.
- Berg P., Roy H., Janssen F., Meyer V., Jørgensen B.B., Huettel M., Beer D. 2003. Oxygen uptake by aquatic sediments measured with a novel non-invasive eddy correlation technique. *Mar. Ecol. Prog. Ser.* 261: 75–83.
- BIM 2014. Baltic Sea Icebreaking Report 2013-2014. p. 27. Available at: <http://baltice.org/app/static/pdf/BIM%20Report%2013-14.pdf> /Accessed on 28 March 2016/
- Cushing D.H. 1989. A difference in structure between ecosystems in strongly stratified waters and those that are only weakly stratified. *J. Plankton Res.* 1: 1–13.
- Dugdale R.C., Georing J.J. 1967. Uptake of new and regenerated forms on nitrogen in primary productivity. *Limnol. Oceanogr.* 2: 196–206.
- Edler L. 1979. Recommendations on methods for marine biological studies in the Baltic Sea. Phytoplankton and chlorophyll. *Baltic Marine Biologist Publication* 5: 38.
- Elmgren R. 1984. Trophic dynamics in the enclosed, brackish Baltic Sea. *Rapp. P.V. Reun. Cons. Int. Explor. Mer* 183: 152–169.
- Falkowski P.G., Owens T.G. 1978. Effects of light intensity on photosynthesis and dark respiration in six species of marine phytoplankton. *Mar. Biol.* 45: 289–295.
- Grasshoff K., Ehrhardt K., and Kremling K. 1983. *Methods of Seawater Analysis*. 3rd Ed. Verlag Chemie. P. 226.
- Hällfors G., Niemi Å., Ackefors H., Lassig J., Leppäkoski E. 1981. Biological Oceanography. In: Voipio A. (ed) *The Baltic Sea*. Elsevier Oceanography, pp. 219–274.
- HELCOM 2009. Eutrophication in the Baltic Sea — an integrated thematic assessment of the effects of nutrient enrichment and eutrophication in the Baltic Sea region. *Baltic Sea Environment Proceedings* No. 115B, pp. 148.
- HELCOM 2014. Eutrophication status of the Baltic Sea 2007-2011 – A concise thematic assessment. *Baltic Sea Environment Proceedings* No. 143, pp. 7–36.
- HELCOM 2015. Manual of Marine Monitoring Programme in the COMBINE programme of HELCOM. Programme of HELCOM. p. 416.
- Heiskanen A.S., Kononen K. 1994. Sedimentation of vernal and late summer phytoplankton communities in the coastal Baltic Sea. *Arch. Hydrobiol.* 131: 175–198.
- Jurgensone I., Carstensen J., Ikauniece A., Kalveka B. 2011. Long-term changes and controlling factors of phytoplankton community in the Gulf of Riga (Baltic Sea). *Estuaries Coasts* 34: 1205–1219.
- Kjørboe T. 1993. Turbulence, Phytoplankton cell size and the structure of pelagic food webs. *Adv. Mar. Biol.* 29: 1–72.
- Klais R., Tamminen T., Kremp A., Spilling K., Olli K. 2011. Decadal-scale changes of dinoflagellates and diatoms in the anomalous Baltic Sea spring bloom. *PLoS ONE* 6: e21567.
- Klais R., Tamminen T., Kremp A., Spilling K., Woong An B., Ajdu S., Olli K. 2013. Spring phytoplankton communities shaped by interannual weather variability and dispersal limitations: Mechanisms of climate change effects on key coastal primary producers. *Limnol. Oceanogr.* 58: 753–762.
- Kļaviņš M., Rodinovs V., Kokorite I. 2002. *Chemistry of Surface Waters in Latvia*. University of Latvia, Riga.
- Kononen K., Niemi A. 1984. Long-term variation of the phytoplankton composition at entrance to the Gulf of Finland. *Ophelia Suppl.* 3: 101–110.
- Kotta J., Lauringson V., Martin G., Simm M., Kotta I., Herkül K., Ojaveer H. 2008. Gulf of Riga and Pärnu Bay. In: Schiewer U. (ed) *Ecology of Baltic Coastal Waters*. Springer-Verlag Berlin Heidelberg. pp. 217–243.
- Lundsgaard C., Olesen M., Reigstad M., Olli K. 1999. Sources of settling material: Aggregation and zooplankton mediated fluxes in the Gulf of Riga. *J. Marine Syst.* 23: 197–210.
- Margalef, R. 1978. Life-forms of phytoplankton as survival alternatives in an unstable environment. *Oceanol. Acta* 1: 493–509.
- Müller-Karulis B., Aigars J. 2011. Modelling the long-term dynamics of nutrients and phytoplankton in the Gulf of Riga. *J. Mar. Syst.* 87: 161–176.
- Olenina, I., Hajdu S., Andersson A., Edler L., Wasmund N., Busch S., Göbel J., Gromisz S., Huseby S., Jaanus A., Kokkonen P., Ledaine I., Niemkiewicz E. 2006. Biovolumes and size-classes of phytoplankton in the Baltic Sea. *Baltic Sea Environment Proceedings* 106: 1-144.
- Olli K., Klais R., Tamminen T., Ptacnik R., Andersen T. 2011. Long term changes in Baltic Sea phytoplankton community. *Boreal Environ. Res.* 16: 3–14.
- Olesen M., Lundsgaard C., Andrushaitis A. 1999. Influence of nutrients and mixing on the primary production and community respiration in the Gulf of Riga. *J. Mar. Syst.* 23: 127–143.
- Peinert R., Saure A., Stegmann P., Stienen C., Haardt H., Smetacek V. 1982. Dynamics of primary production and sedimentation in a coastal ecosystem. *Neth. J. Sea Res.* 16: 276–289.
- Redfield A.C., Ketchum B.H., Richards F.A. 1963. The influence of organisms on the composition of sea-water. In: Hill M.N. (ed) *The Sea: Ideas and Observations on Progress in the Study of the Seas*. Vol. 2. Interscience Publishers, New York, pp. 26–77.
- Skudra M., Lips U. 2016. Characteristics and inter-annual changes in temperature, salinity and density distribution in the Gulf of Riga. *Oceanologia* 59: 37–48.
- Spilling K., Markager S. 2008. Ecophysiological growth characteristics and modelling of the onset of the spring bloom in the Baltic Sea. *J. Mar. Syst.* 73: 323–337.
- Stigebrandt A., Djurfeldt L. 1996. Control of production of organic matter in the ocean on short and long terms by stratification and remineralisation. *Deep Sea Res. II Top. Stud. Oceanogr.* 43: 23–35.
- Tamminen T., Seppälä J. 1999. Nutrient pools, transformations, ratios, and limitation in the Gulf of Riga, the Baltic Sea, during four successional stages. *J. Mar. Syst.* 23: 83–106.
- Utermöhl, H. 1958. Zur Vervollkommnung der quantitativen Phytoplankton-Methodik. *Mitt. Int. Verein. Theor. Angew. Limnol.* 9: 1–38.
- Wessa P. 2015. Box-Cox Normality Plot (v1.1.11) in Free Statistics Software (v1.1.23-r7). Office for Research Development and Education. Available at: http://www.wessa.net/rwasp_boxcoxnorm.wasp/ /Accessed on 28 March 2016/
- Wasmund N., Andrushaitis A., Lysiak-Pastuszek E., Müller-Karulis B., Nausch G., Neumann T., Ojaveer H., Olenina I., Postel L., and Witek Z. 2001. Trophic status of the South-Eastern Baltic

- Sea: a comparison of coastal and open areas. *Est. Coastal Shelf Sci.* 56: 1–16.
- Wassman P., Tamminen T. 1999. Pelagic eutrophication and sedimentation in the Gulf of Riga: a synthesis. *J. Mar. Syst.* 23: 269–283.
- Yurkovskis A. 2004. Long-term land-based and internal forcing of the nutrient state of the Gulf of Riga (Baltic Sea). *J. Mar. Syst.* 50: 181–197.
- Yurkovskis A., Kostrichina E., Ikauniece A. 1999. Seasonal succession and growth in the plankton communities of the Gulf of Riga in relation to long-term nutrient dynamics. *Hydrobiologia* 393: 83–94.