ORIGINAL RESEARCH ARTICLE

Primary productivity in the Gulf of Riga (Baltic Sea) in relation to phytoplankton species and nutrient variability

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Summary The seasonal patterns of primary production, phytoplankton biomass, chlorophyll *a*, and nutrients were investigated in the central part of the Gulf of Riga (Baltic Sea) during 2011 and 2012. Annual primary productivity in the gulf was in the range of 353.4—376.2 gC m^{-2}. Maximum carbon fixation rates occurred during the phytoplankton spring bloom from April to May when the winter nutrient pool was rapidly exhausted, suggesting the use of regenerated nutrients already in spring. The new production calculated on the draw-down of nitrates amounted to 51.80% of spring net community production. The production rates during summer were considerably lower owing to the availability of only regenerated nutrients and limited nitrogen fixation. Autumn was established as the least productive season. In autumn despite the elevated nutrient concentrations, the increasingly limited light hindered photosynthetic activity. Species governing the nutrient fluxes and the productivity of the Gulf of Riga are the diatom species responsible for new production in spring. The photosynthetic ciliate *Mesodinium rubrum* ((Lohmann) Hamburger & Buddenbrock 1911) prevailed in all seasons and significantly correlated with elevated productivity, while diazotrophic cyanobacteria *Aphanizomenon flosaquae* (Ralfs ex Bornet & Flahault 1886) contributed to new production in the summer nutrient regenerating system.

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1. Introduction

Primary production in an aquatic ecosystem depends on the photosynthetic process carried out by autotrophic organisms such as phytoplankton, phytobenthos, and macroalgae, where phytoplankton is the main primary producer. The taxonomical composition of the microalgae, the physiological and ecological characteristics of individual species, and the availability and optimal use of essential resources such as light and nutrients are the major factors controlling growth processes and phytoplankton production (Smayda and Reynolds, 2001).

The primary production in the Gulf of Riga, considered one of the most eutrophic areas of the Baltic Sea, thus far has only been measured from 1989 to 1997. Earlier researchers used the C^{14} method (Andrushaitis et al., 1992) but later, during the project investigating the Gulf of Riga ecosystem from 1993—1995, the oxygen method was used (Olesen et al., 1999; Wassman and Tamminen, 1999). Andrushaitis et al. (1992) calculated an annual production of 250 gC m^{-2}, while Olesen et al. (1999) suggested that annual production could exceed 350 gC m^{-2}. The discrepancy was attributed to an underestimation of the gross primary production by the C^{14} method in systems with high growth rates and respiratory losses (Olesen et al., 1999). Simultaneously, during a comparative assessment of the coastal and open areas of the south-eastern Baltic Sea from 1993 to 1997, Wasmund et al. (2001) concluded that annual primary productivity in the Gulf of Riga reaches 250—255 gC m^{-2}, attributing the eutrophic status to the Gulf of Riga. Boreal environment determines the scenario of phytoplankton development in the gulf (Jurgensone et al., 2011; Olli and Heiskanen, 1999; Yurkovskis et al., 1999). Diatoms *Pauliella taeniata* ((Grunow) F.E. Round & P. W. Basson 1997) and *Thalassiosira baltica* ((Grunow) Ostenfeld 1901) dominate the spring blooms after ice melt from April to May. *Chaetoceros* spp. becomes dominant towards the end of the bloom accompanied by dinoflagellates *Peridiniella catenata* ((Levander) Balech 1977), and ciliate *Mesodinium rubrum*. With the development of thermal stratification and the depletion of nutrients, the spring bloom phytoplankton species are sedimenting. Blooms of cyanobacteria can be observed in July—August with dominating species *Aphanizomenon flosaquae*. Chlorophytes and cryptophytes are often accompanying cyanobacterial blooms. The second bloom of diatoms terminates the phytoplankton succession in September—October after the disruption of the thermocline and convective mixing of water column (Jurgensone et al., 2011; Yurkovskis et al., 1999 and the references therein). In autumn and winter, wind-induced mixing of the water column brings up nutrients from the bottom to the surface, supporting the growth of phytoplankton (Rydberg et al., 1990). But the significant shortening of daylight and low light intensity (Vihma and Haapala, 2009) hinders photosynthetic activity.

Although the phytoplankton and nutrient dynamic is well described in the Gulf of Riga, the linkage between phytoplankton production and nutrients to date is insufficiently described. This, in turn, does not allow proper characterization of the eutrophication process in the Gulf of Riga. Even less attention was paid to phytoplankton species involved in the primary production. Therefore the aim of this study was to examine the seasonal variation of primary production with a focus on the controlling nutrient fluxes as well as the species composition involved in the production.

2. Material and method

2.1. Study area

The Gulf of Riga (Baltic Sea) is a shallow water body with an average depth of 26.2 m. Its surface area is 16,330 km^2, however, its drainage area covers 135,700 km^2. The south-eastern part of the gulf receives 86.0% of the total river runoff from the main rivers, the Daugava, Lielupe, Gauja, and Salaca (Yurkovskis et al., 1993). The salinity is low (5—7 PSU) due to weak water exchange with the Baltic Sea and the large freshwater impact (Berzinsh, 1995). During winter, the water column of the gulf is well-mixed to the bottom due to convective and wind-induced mixing. During the productive season the stratification restricts vertical water exchange and promotes nutrient accumulation in the bottom layer (Yurkovskis, 2004).

Nutrient limitation is the most important factor governing the phytoplankton community. Most of the earlier nutrient limitation studies in the Gulf of Riga showed that the spring phytoplankton blooms are mainly nitrogen-limited in the central part while the coastal areas can be phosphate-limited (Tamminen and Seppälä, 1999). In contrast, recent studies of long-term phytoplankton data indicated that the spring blooms are mainly phosphorus limited, but could shift to nitrogen or silicate limitation for diatoms in the later stages of the bloom due to the faster regeneration of phosphate relative to the other nutrients (Jurgensone et al., 2011). During the summer period, the system is nitrogen limited in terms of phytoplankton (Balode et al., 1998; Põder et al., 2003; Tamminen and Seppälä, 1999) when both DIN and DIP are depleted in the upper mixed layer, whereas silicates are always present excluding silica limitation as a structuring factor for the summer community.

2.2. Sampling

Sampling was performed by ships A-90 "Varonis" and r/v "Salme". Samples were collected at 5 regular monitoring stations in the central part of the Gulf of Riga (Fig. 1), 15 times each, over a period from April 2011 to October 2012 (Table 1) covering the full seasonal spectrum. Samples for the physical and chemical variables were taken simultaneously with biological variables. Water temperature and salinity was measured using a water probe (SBE 19plus SeaCat, USA). Water transparency was measured with Secchi disc. The water for physicochemical variables, phytoplankton, chlorophyll *a* concentrations, and primary production was sampled as an integrated sample from the euphotic upper layer (0—10 m).

2.3. Analytic analysis

Nutrient concentrations were determined according to Grasshoff et al. (1983), e.g. ammonium (NH$_4^+$) and phosphate (PO$_4^{3-}$) were measured by the indophenol blue and molybdenum blue methods, respectively. The sum of nitrate and
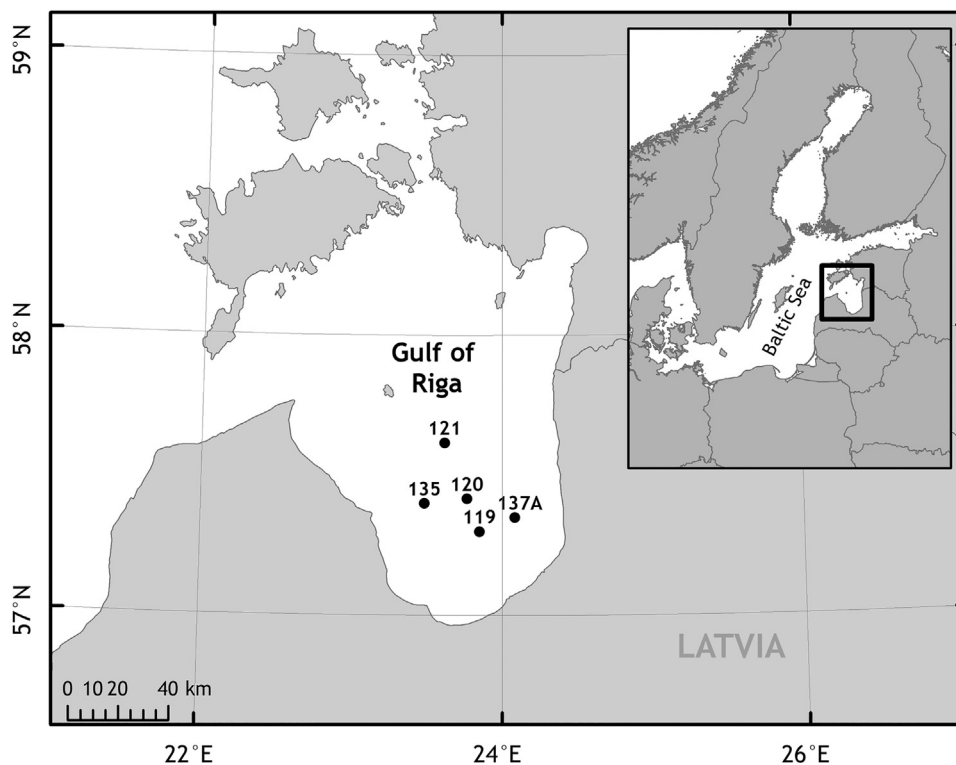
Figure 1 The location of the sampling stations in the Gulf of Riga.

Table 1 Average temperature, Secchi depth, hydrological and hydrochemical data in the central part of the Gulf of Riga during 2011 and 2012.

		Temp. [°C]	PAR [mol photons $m^{-2} d^{-1}$]	Secchi depth [m]	Photic zone depth [m]	PO_4^{-3} [μmol l^{-1}]	P_{tot} [μmol l^{-1}]	SiO_4 [μmol l^{-1}]	NO_{2+3}^{-} [μmol l^{-1}]	NH_4^{+} [μmol l^{-1}]	N_{tot} [μmol l^{-1}]	DIN/DIP ratio
2011	Apr	2.27	50.29	2.3	6.10	0.28	1.25	25.83	20.05	0.47	53.38	76.26
	May	6.24	45.85	2.8	7.50	0.03	1.00	5.23	4.17	0.10	37.32	128.38
	Jun	17.99	56.37	2.5	6.80	0.08	0.95	2.75	0.22	0.00	39.50	2.97
	Aug	19.71	48.95	4.0	10.70	0.02	0.65	4.99	0.17	0.29	33.36	23.44
	Oct	14.30	9.39	5.1	13.80	0.04	0.53	10.04	1.22	1.31	31.80	68.63
	Nov	9.33	11.63	3.9	10.40	0.41	0.76	20.26	5.95	0.04	28.26	14.79
2012	Jan	3.57	15.54	3.0	8.10	1.10	1.56	31.34	12.77	0.09	36.91	11.69
	Mar	0.18	20.65	4.1	11.00	1.00	1.40	33.44	15.63	0.07	39.25	15.83
	Apr	1.00	39.92	3.5	9.40	0.97	1.46	30.51	15.30	0.07	39.16	16.32
	May	8.08	41.81	2.1	5.60	0.04	1.45	2.05	2.87	0.07	44.94	39.89
	Jun	10.61	51.69	3.2	8.50	0.04	0.76	2.72	0.69	0.41	31.72	27.08
	Jul	15.30	49.54	3.8	10.20	0.01	0.67	3.25	0.40	1.47	36.84	132.13
	Aug	19.02	58.44	3.3	8.80	0.04	0.66	6.10	0.09	0.64	33.15	22.60
	Sep	16.30	34.57	4.5	12.30	0.10	0.58	8.61	0.40	1.24	31.90	17.44
	Oct	12.95	10.77	4.3	11.70	0.26	0.69	13.69	2.59	1.49	28.10	16.23

nitrite (NO_{2+3}^{-}) was determined by nitrite reaction with an azo dye after the 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 the difference between nitrite and the sum of nitrate and nitrite. Dissolved silicate (SiO_4) was determined colorimetrically according to the procedure described by Grasshoff et al. (1983). The total nitrogen (N_{tot}) and total phosphorus (P_{tot}) were analyzed as nitrate and phosphate after wet digestion with persulfate. Dissolved inorganic nitrogen (DIN) is the sum of NO_{2+3}^{-} and NH_4^{+}. All laboratory analyses were performed in an accredited laboratory (ISO/IEC 17025).

2.4. Chlorophyll *a* and phytoplankton analysis

Concentrations of chlorophyll *a* (Chl *a*, mg m^3) were measured according to the standard method of the Manual for Marine Monitoring in the COMBINE Programme of HELCOM (HELCOM, 2006).

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 the Uthermöl technique with an inverted microscope at 200× and 400× magnification. The number of counted cells in all subsamples exceeded 500 (Edler, 1979; HELCOM, 2006; Olenina et al., 2006; Utermöhl, 1958). The biomass was expressed as mg m³ of wet weight. *M. rubrum* was included in phytoplankton counts as the only representative of division Ciliophora.

2.5. Primary production measurements

The light and dark bottle oxygen technique (Olesen et al., 1999) was used in order to evaluate the productivity of the study area. Water was filled in 15 transparent, calibrated glass bottles for oxygen measurements. Bottles were divided into 5 groups (with 3 replicates in each group) to imitate the light conditions at specific depths of the euphotic layer: Start, 100%, 66%, 23% and 0% light transmittance. Specific light transmittance to each group was provided by wrapping the bottles in the plastic optical filters produced by GAM-PRODUCTS, Inc.: no filter for 100% transparency, 1514 GAM for 66% transparency, 1516 GAM for 23% transparency and aluminium folium for 0% transparency. Initial oxygen concentrations were fixed with Winkler reagents (1 ml manganese chloride and 1 ml alkaline iodide) before incubation. All vials were mounted on a rotating wheel and submerged in the onboard incubator with a continuous flow of outboard seawater to ensure ambient water temperature and *in situ* illumination during the 24 h incubation. Photosynthetically active radiation (PAR) was measured on board using the LI-1400 Data Logger and the LI-190 Quantum Sensor during experimental incubation. At the end of incubation, samples were fixed with Winkler reagents. Oxygen concentrations were determined by titration with sodium thiosulphate.

Oxygen consumption in the dark bottles was used as a proxy for community respiration (CR), while the other three groups were used to evaluate daily, water column, primary production rates. Measured oxygen concentrations were converted to carbon units according to the stoichiometry of photosynthesis equation. The approximate attenuation coefficient (k) was calculated for each sampling from the simultaneously measured Secchi depth according to the equation $k = 1.7/D_s$, where D_s is Secchi depth. The depth of specific light conditions (z) was calculated from $z = -\ln I_z/I_o/k$, where I_z is light intensity at a specific depth (66% or 23%) and I_o is the light intensity below the surface (100%). Daily water column net community production (NCP, gC m^{-2} d^{-1}) rates were estimated by trapezoidal integration of the data from various light conditions. Gross primary production (GPP, gC m^{-2} d^{-1}) was calculated summing up the NCP and CR. GPP, NCP, and CR values from 5 stations were averaged to get the monthly average. Annual primary production was calculated as the GPP monthly averages multiplied by the number of days and summed up for 365 days.

2.6. New production calculation from nutrient concentrations

Since primary production rates have low representativeness in time and space, there have been attempts to use other parameters to calculate them, such as nutrient depletion (Rahm et al., 2000; Wasmund et al., 2005), increase in particulate organic carbon (Wasmund et al., 2005), and changes in CO_2 concentrations (Schneider et al., 2003). In our study, we applied the nutrient depletion method described in detail by Wasmund et al. (2005). We used data obtained during 2012, because the sampling frequency was higher this year, and calculated primary production, assuming that carbon, nitrogen, and phosphorus are assimilated in a stable molar ratio of 106:16:1 (Redfield et al., 1963). In April, what we consider the starting month of the spring bloom, the DIN:DIP ratio was 16.3 (Table 1), we assumed that the PO_4^{3-} excess production as described by Rahm et al. (2000) was not relevant for our calculations. The nutrient concentration decrease pattern suggests that the new production period lasts until June. We used concentration change (ΔDIN) in the upper mixed layer (0—20 m) to calculate new production for the period from April to May (1st period, 37 days) and for the period from May to June (2nd period, 23 days). We also considered air depositions of nitrogen in our calculations. Since there was no published information on air deposition for 2012, values calculated for 2010 were used instead. The air deposition over the whole surface area of the Gulf of Riga was 9973 t of nitrogen in 2010 (HELCOM, 2013). Averaging the deposited amount over the surface area of the Gulf of Riga (16,330 km²), we estimated that nitrogen air deposition is 0.12 mmol m^{-2} day^{-1}. Since the Gulf of Riga is much more significantly impacted by river runoff than air deposition, we also considered the amount of DIN delivered by the four largest rivers, the Daugava, Gauja, Lielupe, and Salaca, which constitute close to 90% of freshwater input to the Gulf of Riga (Yurkovskis et al., 1993), over the respective period. The monitoring frequency was not sufficient for our purposes, so we used the linear regression method (Hirsch et al., 2010) to estimate missing values. The method employs the use of weighted regressions of concentrations on time, discharge, and season. This weighting results in a set of weights on every observation in the dataset, based on the selected values of time and discharge. So, we used known values of specific time and discharge to estimate the expected value of concentration. Data from national monitoring (e.g., flowrate and nutrient concentrations), stored in the database of Latvian Environment, Geology and Meteorology Centre, were used as input data. Estimated nitrogen loads were averaged over the whole area of the Gulf of Riga. Furthermore, from April to May, depletion of DIN could be observed in water layer 20—30 m. We used this concentration change to calculate an additional primary production for the 1st period.

Diatom biomass production was estimated from the silicate consumption by using N:Si = 1.25 mol mol^{-1} constant conversion factor (Sarthou et al., 2005). The nitrogen units thereafter were converted into carbon units by the Redfield ratio of C:N = 6.625 (Redfield et al., 1963).

3. Results

3.1. Environmental factors

The seasonal variation in water temperature, Secchi depth, PAR and nutrient concentrations are summarized in Table 1.

3.2. Phytoplankton and chlorophyll a

The highest phytoplankton biomass and Chl a were observed in spring — April 2011 and May 2012 (5715, 5411 mg m^{-3} and 18.5, 29.1 mg m^{-3}, respectively) (Fig. 2). However, the typical spring bloom of phytoplankton with high biomass and more than 90.0% dominance of diatoms, consisting mainly of P. taeniata, Chaetoceros wighamii (Brightwell 1856), and T. baltica, was observed only in April 2011. The succession of phytoplankton in May 2011 and 2012 was formed mainly from three taxonomical groups where single species composed up to 72.2—93.4% of the corresponding phytoplankton group — diatoms (T. baltica), dinoflagellates (P. catenata), and ciliophora (M. rubrum).

The summer (June—September) phytoplankton was characterized by relatively low Chl a and total phytoplankton biomass (Fig. 2). In this period, cyanobacteria (mostly N_2-fixing A. flosaquae) in both years constituted 15.2—57.8% of total phytoplankton biomass with the highest value in July 2012. The dominance of photosynthetic ciliate M. rubrum (56.3% of total biomass) was recorded in June 2012 (Fig. 2).

The autumn (October, November) phytoplankton consisted of cyanobacteria, diatoms, and M. rubrum (28.2%, 18.4% and 19.8%, respectively) in 2011, whereas in 2012 autumn was dominated by diatoms (>50.3%). The Chl a values were slightly higher in 2011 than in 2012 (Fig. 2). In the winter, total phytoplankton biomass (143.6—268.5 mg m^{-3}), as well as Chl a concentrations (1.62—1.71 mg m^{-3}), were low. The relative abundance of M. rubrum in the phytoplankton community increased during winter, reaching 34.2% of the total biomass in January. The next two most abundant groups, cyanobacteria (mainly A. flosaquae) and diatoms, composed 23.3 and 17.4%, respectively. The beginning of the increase in phytoplankton biomass was detected in March when M. rubrum composed, on average, 48.4% of total biomass.

3.3. Primary production and respiration

The data of primary production obtained from 5 stations were averaged for each month due to low variability in hydrological and hydrochemical conditions at the individual stations. Therefore, the patchiness of biological communities is the main source of measurement uncertainties. On average, the GPP was highest during the spring. Thereafter, it gradually decreased over summer and reached minimum values during the autumn—winter period (Fig. 3). Multiple regression analyses with dominant species as explanatory values showed the significant importance of P. catenata and M. rubrum in the formation of GPP in springtime in both years (r^2 = 0.59, p = 0.009, n = 9). The carbon biomass variance of both species explains 59.2% of GPP variance in spring. However, during summer, when similar dominance of M. rubrum and A. flosaquae was observed, no significant correlation could be established.

Plankton CR varied between 0.01—3.12 gC m^{-2} d^{-1} (average 1.01 gC m^{-2} d^{-1} of both years), accounting to 40.4% of GPP in 2011 and 68.5% in 2012. The rate of respiration mostly followed the pattern of GPP (Fig. 3), except in April 2012 when respiration exceeded GPP. NCP is also highest during the spring bloom and decreased over summer, except for in April 2012, when negative values of NCP were observed.

3.4. New production calculation from nutrient concentrations

The change of DIN concentrations in water from 15.3 μmol l^{-1} to 2.87 μmol l^{-1} (ΔDIN = 12.4 μmol l^{-1}) in the upper mixed layer (0—20 m) amounted to the new production of 1647 mmol C m^{-2} for the period from April to May (1st period) and ΔDIN = 2.18 μmol l^{-1} resulted in new production of 289 mmol C m^{-2} for the period from May to June (2nd period). The depletion of DIN from April to May in water layer 20—30 m (ΔDIN = 5.04 μmol l^{-1}) amounted to an additional primary production of 331 mmol C m^{-2} in the 1st period. The new production, estimated from average nitrogen air deposition rate (0.12 mmol m^{-2} day^{-1}), was 29.0 and 18.0 mmol C m^{-2} for the 1st and 2nd periods, respectively. The calculated average supply of riverine DIN was 289 t day^{-1} in April, 87 t day^{-1} in May and 38 t day^{-1} in June. Averaging received nitrogen over the area of the Gulf of Riga, we estimated an additional supply of 31.2 and 6.45 mmol N m^{-2} in the 1st and 2nd periods, respectively. This resulted in the new production of 205 and 40.1 mmol C m^{-2} in the 1st and 2nd periods, respectively.

The total new production estimated from DIN consumption summed to 2212 and 347 mmol C m^{-2} (26.6 and
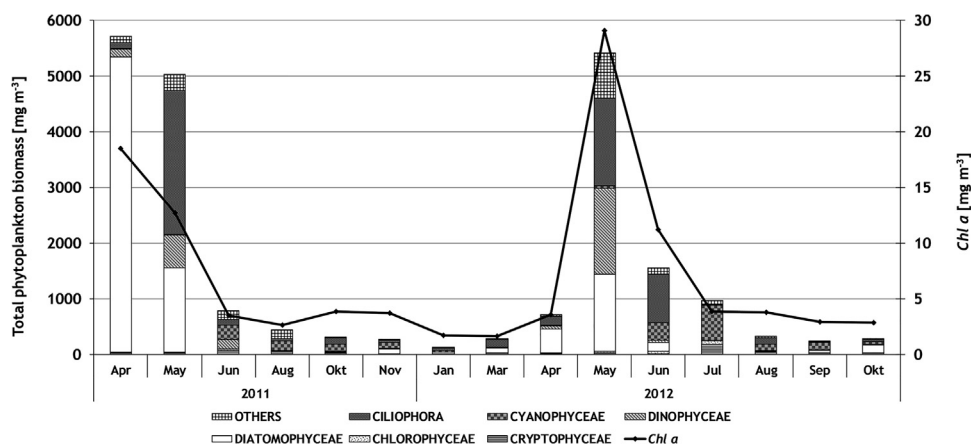

Figure 2 Total phytoplankton biomass and Chl a concentrations in the central part of the Gulf of Riga during 2011 and 2012.
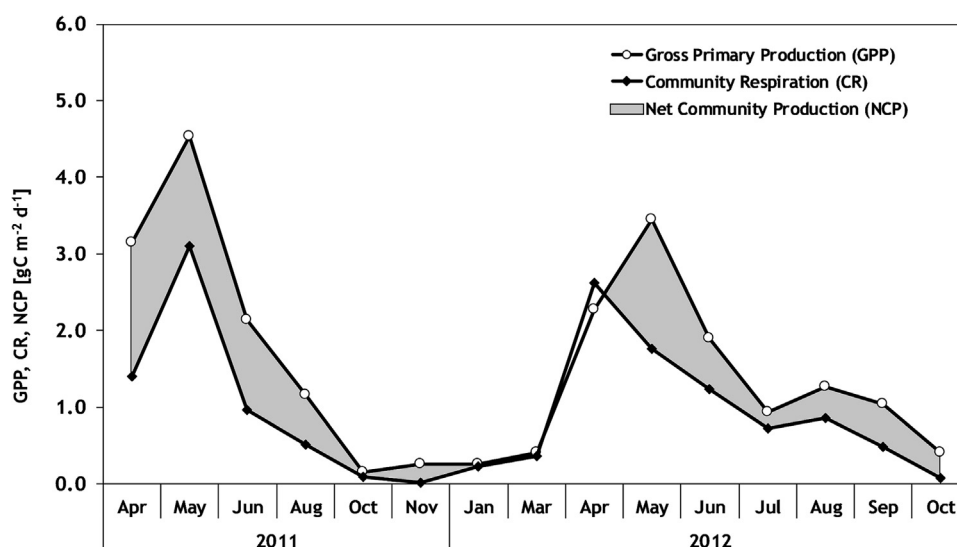
Figure 3   Average daily production (GPP and NCP) and CR in the central part of the Gulf of Riga during 2011 and 2012.

4.23 gC m^{-2}) for the 1st and 2nd period, respectively. The average new primary production rates estimated from the available DIN pool in the upper mixed layer and loads from atmosphere and rivers are 0.72 and 0.17 gC m^{-2} d^{-1} in May and June, respectively.

The change of silicate concentration in the upper mixed layer from April to May 2012 (Table 1) gave an estimate of ΔSi = 569 mmol m^{-2} for the 1st period. The concentration changes from 30.5 μmol l^{-1} to 15.3 μmol l^{-1} in the 20—30 m water layer, which gives an additional 155 mmol m^{-2} of silicate accessible for diatom growth. By applying conversion factors we estimated that new production of diatoms was 5997 mmol C m^{-2} in the 1st period, corresponding to a new production rate of 1.95 gC m^{-2} d^{-1}.

4. Discussion

4.1. Annual and seasonal primary productivity

In the northern temperate and boreal seas, including the Baltic Sea, the spring bloom, sustained by the nutrient winter pool, lasts approximately one month, but typically dominates the annual phytoplankton productivity cycle, contributing 40.0—60.0% of the annual carbon fixation (Heiskanen, 1998). The autumn bloom, sustained by the delivery of nutrients from deeper water layers upon the breakdown of seasonal stratification, is considered second most important period for annual phytoplankton productivity cycle. The summer production and biomass are considered to be low in comparison to the spring bloom period, while winter production is usually neglected as important. This has been somewhat challenged in the past (Platt et al., 1989; Stigebrandt and Djurfeldt, 1996) especially in the case of summer productivity (Sahlsten et al., 1988). In our study, the spring bloom (April—May) comprised 46.3% while summer productivity made another 44.5% of annual productivity. The autumn-winter productivity (October—March) comprised the remaining 10.2% of the annual productivity. Moreover, in our study we established that the least productive period is during October—November

despite the water temperature still remaining rather high (13.4°C) and nutrient concentrations substantially increasing due to the breakdown of thermal stratification and resuspension of re-mineralized nutrients from deeper layers. The autumn is characterized by strong, westerly winds that bring mild and moist Atlantic air to northern Europe (Vihma and Haapala, 2009), resulting in dense cloud cover and frequent rain. At the same time the shortening of daylight hours (from 10 h 50 min in October to 6 h 40 min in December) can be observed. Therefore, we can hypothesize, that meteorological conditions in autumn lead to strong light limitation of GPP despite rather good water transparency conditions measured as Secchi depth (Table 1). Later, the onset of colder winter air temperatures results in clear skies and higher light intensity. As a result, relatively low but still comparable primary production was also measured during winter months that previously were considered unproductive.

The annual primary productivity in the Gulf of Riga reached values as high as 353—376 gC m^{-2} in our study, while in the previous studies (Andrushaitis et al., 1992; Wasmund et al., 2001) the estimated annual primary productivity of the Gulf was only 250—255 gC m^{-2} for the period of 1993—1995. However, this estimate was based on measurements that had not included the most productive period of phytoplankton succession from the end of March until the end of April when the biomass of spring diatoms can reach even 20.3 g m^{-3} (Yurkovskis et al., 1999). This allowed the Olesen et al. (1999) to hypothesize that primary productivity in the Gulf of Riga can exceed 350 gC m^{-2}. So, our values of annual production were similar to estimations of Olesen et al. (1999). At the same time, we cannot exclude the possibility that the productivity values in our study were still underestimated since sampling frequency was still too low to fully capture spring phytoplankton bloom development. For example, phytoplankton biomass and composition from April to May 2012 could not explain the depleted pool of SiO$_4$, suggesting that diatom bloom between these sampling events was unregistered by our study at least at the level of that observed in April 2011.

4.2. New production

The values of new production calculated from nutrient concentrations (0.70 and 0.17 gC m^{-2} d^{-1}, in May and June, respectively) were substantially lower than measured NCP rates, e.g., 1.68 and 0.72 gC m^{-2} d^{-1}, in May and June, respectively. The total new production, calculated from the nitrate consumption, was equivalent to 51.8% of spring NCP. Smetacek et al. (1984) divided the spring bloom into two stages. Stage 1 was characterized by a rapid bloom of diatoms exhausting the winter-accumulated nutrient pool where production is strictly "new" in the sense of Dugdale and Goering (1967). Stage 2 was characterized by the dominance of dinoflagellates and an increase of protozooplankton. Loss rates of this planktonic system were amongst the lowest of the year, indicating a great retention capacity (Smetacek et al., 1984). The new production during stage 1 was >75.0% of NCP, but during stage 2 it was approximately 50%. These data were consistent with our calculations where new production, based on nutrient consumption, composed 51.8% of NCP during both stages of spring bloom. At steady state, there should be a balance between the input of nitrogen and the export of carbon, implying that on a longer time scale, sedimentary loss from the pelagic system approaches new production (Eppley et al., 1983). This could be the case in the Gulf of Riga as the bloom of diatoms, that used most of nitrates and predominantly contributed to the new production and sedimentation fluxes, was largely unobserved in 2012. However, if new production is calculated from the consumption of SiO$_4$ according to Wasmund et al. (2013), it alone gives an average estimate of 1.95 gC m^{-2} d^{-1} for the first period. As no other algae, except diatoms, can use SiO$_4$, the bloom maxima of diatoms should be assumed between the sampling occasions in April and May 2012 followed by rapid sedimentation as diatoms composed only 25.2% of total phytoplankton biomass in May. The excess consumption of silica can be explained either by different silicification of diatom species (Olli et al., 2008) or by diatom resting spore formation as this process requires plenty of silicate. It has been reported that the resting spores generally have higher sinking rates than vegetative cells (Alldredge et al., 1995). The spore formation in the deeper water layers could explain the SiO$_4$ consumption in the 20—30 m (data not shown) layer of the Gulf of Riga.

4.3. Influence of dominant species on the nutrient fluxes and productivity

The species which exert a dominant role in the planktonic ecosystem are often those that govern the fluxes of organic matter and nutrients in the pelagic system (Heiskanen, 1998). To understand the functioning of the aquatic ecosystem it is necessary to understand the role, regulation, and species-specific properties of the "key" species (Verity and Smetacek, 1996).

The main "key" planktonic species dominating almost all seasons was photosynthetic ciliate M. rubrum. Leppänen and Bruun (1986) reported that M. rubrum contributed about 10.0% of the primary production during spring in the open northern Baltic. Similar values of 6.00—9.00% of phytoplankton biomass and production have also been shown for

M. rubrum in the Gdańsk Basin of the southern Baltic Sea (Witek, 1998). It appears that in the Gulf of Riga, M. rubrum plays an even more important role in the primary production than in other regions of the Baltic Sea, since its biomass composed 18.2—73.9% of the total phytoplankton biomass during the spring bloom period in May, 6.22—41.4% during summer, 14.9—22.2% during autumn, and 40.1—61.3% during winter. Significant positive correlation was detected between the biomass of M. rubrum and GPP ($r = 0.650$, $p > 0.001$, $n = 42$). The importance of M. rubrum in the Gulf of Riga was observed during periods when nutrient recycling was the most important (spring—summer) as well as during periods when nutrients were freely available, but the light limited the phytoplankton development (autumn—winter). It has been observed that M. rubrum demonstrates an ability to accumulate near the sea surface and to photosynthesize at high light intensities (Esteban et al., 2010). At the same time, it has been noted that M. rubrum can also tolerate the low-light conditions, composing the main phytoplankton biomass also during winter period (Moeller et al., 2011). In addition, its rapid swimming behaviour appears to reduce its susceptibility to grazing (Jonsson and Tiselius, 1990) and may increase its ability to utilize nutrient micropatches (Stoecker et al., 1991). Our study confirms that the M. rubrum is a highly competitive and opportunistic specie that substantially contributes to the productivity of the Gulf of Riga.

Another "key" species substantially contributing to productivity and internal nutrient fluxes of the Gulf of Riga is A. flosaquae. Filamentous, N$_2$-fixing cyanobacteria are well known for bloom formation during August—September in the Baltic Sea (Kahru et al., 1994). In our study, the relative dominance of A. flosaquae (18.7—37.4% of total phytoplankton biomass) begun in June when inorganic nutrients (both, N and P) were exhausted, reached a maximum in July (59.4—65.2%) and continued until September (21.3—42.1%). The blooms of A. flosaquae are usually associated with calm weather, high surface temperatures, availability of phosphates, and a low DIN:DIP ratio (Kononen et al., 1996). However, according to the results of this study, the phosphates were exhausted already during the spring bloom creating the apparent phosphorus limitation in May (Table 1). This suggested that N$_2$ fixation was not likely to occur during the summer. Furthermore, the increase of A. flosaquae biomass from 309 mg m^{-3} (in June 2012) to 543 mg m^{-3} (in July 2012) was observed simultaneously with the fast increase of the DIN:DIP ratio as well as increase of total N (Table 1). The river runoff and atmospheric deposition was of the secondary importance, since both these nutrient pathways are relatively small during the summer and unlikely to sustain, or let alone increase, the observed population. At the same time, Ploug et al. (2010) showed that A. flosaquae was highly productive in the Baltic Sea with high rates of C and N assimilation and the capacity to release a large fraction (35.5%) of newly assimilated N to the surrounding water. This allowed us to create a hypothesis that the population of A. flosaquae sustains the observed population level by rapid recirculation of phosphorus upon the death of phytoplankton cells and the assimilation of nitrogen via N$_2$ fixation to compensate nitrogen loss in the sedimentation pathway.

The importance of M. rubrum and A. flosaquae was also observed during the autumn and winter seasons. However, more observations were needed to understand their roles

during those seasons as well as regulatory factors of these species under conditions of limited light and replenished nutrients.

5. Conclusions

The annual primary productivity in the Gulf of Riga reached values 353—376 gC m^{-2} in our study. It showed no significant increase of productivity since 1992—1998. Spring bloom (April—May) comprised 46.2% of annual production with maximal carbon fixation rates and draw-down of winter nutrient pool. The new production calculated from consumption of nitrates amounted to 51.8% of spring NCP. Detailed examination of phytoplankton species along with measurements of productivity revealed key species governing the nutrient fluxes and the productivity of the Gulf of Riga. The autotrophic ciliate *M. rubrum* prevailed in all seasons and significantly correlated with elevated productivity, while diazotrophic cyanobacteria *A. flosaquae* contributed to "new production" in the summer nutrient-regenerating system.

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