UNIVERSITY OF LATVIA

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THE INFLUENCE OF ENVIRONMENTAL FACTORS AND PHYTOPLANKTON FUNCTIONAL GROUPS ON THE SEASONAL DYNAMICS OF PRIMARY PRODUCTION IN THE GULF OF RIGA

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Summary of Doctoral Thesis

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Scientific supervisor:
Dr. biol. Ingrīda Andersone

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The studies for doctoral thesis were carried out at the University of Latvia, Faculty of Biology and Latvian Institute of Aquatic Ecology, Agency of Daugavpils University between October 2014 and October 2022.

The thesis contains the introduction, two chapters, conclusions, a reference list and four publications.
Form of the thesis: a collection of scientific publications in biology, hydrobiology.

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The thesis will be defended at the public session of the Doctoral Committee of Biology, the University of Latvia, at 14:00 on October 2, 2023. Riga, Jelgavas Street 1, Auditorium 545 of the Natural Sciences Academic Center.

The thesis is available at the Library of the University of Latvia, Raiņa blvd. 19, Riga.

Chairman of the Doctoral Committee: Prof. *Dr. biol.* Guntis Brūmelis
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SUMMARY

Primary production in an aquatic ecosystem depends on the process of photosynthesis carried out by autotrophic organisms such as phytoplankton, phytobenthos and macroalgae. This doctoral thesis focuses on a scarcely studied issue in the Gulf of Riga – the seasonal dynamics of primary production and its relationship to abiotic and biotic environmental factors. The obtained knowledge provides an opportunity for a more in-depth comprehension of the effects of eutrophication processes both locally and regionally. It also adds to the body of knowledge about the amount of energy available in the pelagic trophic food web and its impacting environmental factors, allowing for a more accurate assessment of the pelagic habitat and ecosystem. The main results indicate that the annual primary productivity in the Gulf of Riga reached 353–376 g C m^2. During the productive period (from April to October), the source of substances available to phytoplankton changes seasonally, thus primary production follows seasonal cycle. The highest net (NPP) and total (GPP) primary production were observed in the spring, while autumn was the least productive period during the growth season. Based on the isotopic signals, the spring measurements differed from the rest of the period implying greater influence from terrestrial and anthropogenic sources. Diatoms, dinoflagellates and the ciliate *Mesodinium rubrum* showed the strongest positive relation to isotopic changes in the Gulf of Riga, indicating their role in the creation of new production, supplementing the system with new energy. It should be emphasized that the mixotrophic ciliate *M. rubrum* dominated in all seasons, showing a significant correlation with increased productivity. On the other hand, diatoms were identified as the main producer of new production in spring, and diazotrophic cyanobacteria *Aphanizomenon flosaquae* – in summer, during the nutrient regenerating system. The main results of the doctoral thesis are published in four publications.

Key words: Primary production, *Mesodinium rubrum*, Baltic Sea, Gulf of Riga

CONTENTS

LIST OF ORIGINAL PUBLICATIONS

This doctoral thesis is based on the following published research papers, which are referred to in the text by Roman numerals:

I Labucis A., Purina I., Labuce A., Barda I., Strake S. **Spring seasonal pattern of primary production in the Gulf of Riga (Baltic Sea) after a mild winter.** *Environmental and Experimental Biology.* (2017) 15, 247–255.

II Purina I., Labucis A., Barda I., Jurgensone I., Aigars J. **Primary productivity in the Gulf of Riga (Baltic Sea) in relation to phytoplankton species and nutrient variability.** *Oceanologia.* (2018) 60, 544–552.

III Tunēns J., Aigars J., Poikāne R., Jurgensone I., Labucis A., Labuce A., Liepiņa-Leimane I., Buša L., Vīksna A. **Stable carbon and nitrogen isotope composition in suspended particulate matter reflects seasonal dynamics of phytoplankton assemblages in the Gulf of Riga, Baltic Sea.** *Estuaries and Coasts.* (2022) 45, 2112–2123.[1]

IV Labucis A., Labuce A., Jurgensone I., Barda I., Andersone I., Ikauniece A. **Seasonal variation in size structure and production of autotrophic plankton community in eutrophied, low-light environment: A focus on *Mesodinium rubrum*.** *Oceanologia* (2023) 65, 398–409.

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[1] A part of Publication III is included in this doctoral thesis – included are the results that describe the source (marine or terrestrial) of the phytoplankton assimilated biomass based on signals of stable carbon and nitrogen isotopes.

1 INTRODUCTION

Primary production in an aquatic ecosystem depends on the photosynthetic process carried out by autotrophic organisms, e.g. phytoplankton, phytobenthos, and macroalgae. Up to date, four approaches have been used widely to quantify the photosynthetic process over time: (a) changes in oxygen, (b) changes in carbon dioxide, (c) the formation of organic matter, and (d) the time-dependent changes in consumption of light (change in chlorophyll fluorescence) (Falkowski et al., 2003). Here, in this doctoral thesis, oxygen is used as a proxy for the synthesis of organic material by autotrophic phytoplankton (microalgae).

Phytoplankton are the main contributor to primary production in the pelagic habitat (Ask et al., 2016; Henriksen, 2009). It is comprised of a taxonomically diverse group of mainly single-celled and photosynthetic organisms (numerous mixotrophic and heterotrophic phytoplankton species also exist). Phytoplankton communities, thus predominant characteristics of phytoplankton, successively change throughout the productive season. The spring bloom period can be named as one example representing the contrasts between different phytoplankton communities and the impacts of environmental conditions. In the northern temperate and boreal seas, the spring bloom sustained by the nutrient winter pool lasts approximately one month but contributes up to 40–60% of the annual carbon fixation (Heiskanen, 1998). The rest of the productive season is lower in production efficiency.

Noteworthy that the majority of temperate and boreal spring primary production is new production (Falkowski et al., 2003). New production, in brief, is all primary production associated with newly available nitrogen (e.g., NO_3, NO_2, N_2). In a confined system such as the mixed productive layer of pelagic habitat, new production is a part of primary production formed from external nitrogen input (definition from Dugdale & Goering, 1967; Williams et al., 1989). Hence, new production is supported by physical and chemical processes, *inter alia*, water mixing, upwelling, riverine and atmospheric inputs. On the contrary, "regenerated production" is organic matter fueled by nutrients sustained within the confined system, e.g., ammonium (Berg et al., 2003).

The Baltic Sea is a continental inland sea with limited water exchange and a large-scale gradient from temperate marine to subarctic limnic ecosystems. Pelagic primary production in the Baltic Sea is variable (**Table 1**) between sub-basins and their trophic condition (mesotrophic to eutrophic) along the mentioned gradient due to differences in environmental and ecological factors. In the Baltic Proper (central Baltic) average gross primary production is estimated to be approximately 172 g C m^{-2} y^{-1} (Samuelsson et al., 2006).

The coastal areas and plumes, usually, are higher in primary production than open Baltic Sea waters. Although, in very turbid waters such as Klaipeda Strait (Secchi depth < 1 m) it can be lower due to limited light availability in surface waters.

The Gulf of Riga is a semi-isolated, shallow Baltic Sea sub-basin with high riverine input resulting in increased eutrophication compared to the Baltic Proper (Kotta et al., 2008). Also, the reported primary production values attribute it to eutrophic conditions (as defined in Wasmund et al., 2001). Surveys of primary production in the Gulf of Riga have been sporadic in recent decades (Andrushaitis et al., 1992, Wassmann, Tamminen, 1999; Olesen et al., 1999; Wasmund et al., 2001), mainly covering the period from 1989 to 1997. Overall, the estimated annual gross primary production in the Gulf of Riga is one of the highest for the Baltic Sea (**Table 1**). Its reported values vary between 250 and 350 g C m^{-2} y^{-1} which lies within the general range defined for coastal transitional water systems by Nixon (1982), i.e., 200-400 g C m^{-2} y^{-1}.

The knowledge base for the Gulf of Riga primary production dynamics and its driving factors show that plankton community production and respiration are predominantly limited by nutrient supply during spring and summer (Olesen et al., 1999), whereas the combination of low light levels and deep vertical mixing lead to light limitation during the autumn season. However, stabilizing (solar heating) and destabilizing (wind) forces strongly affect the Gulf of Riga pelagic habitat throughout the entire productive season due to its shallowness, and day-to-day primary production can vary by up to two times (Wassman, Tamminen, 1999). Variability is enhanced by local mixing events, such as upwelling, that usually result in a decreased primary production in the short term but an overall increase in the long term (Lehmann, Myrberg, 2008). Previous studies (Lundsgaard et al., 1999; Olesen et al., 1999; Olli, Heiskanen, 1999) point to high pelagic recycling efficiency in the Gulf of Riga and marks that new production is mostly limited to the southern part of the gulf and regenerated production predominate the system.

Still, the majority of previous studies were focused on abiotic factors affecting primary production and information about the linkages between ecological aspects and primary production is scarce for the Gulf of Riga and the Baltic Sea in general. It is known that pelagic primary production may respond to taxonomical composition, community structure, and physiological and ecological characteristics of phytoplankton (e.g., Chavez et al., 1990; Falkowski et al., 2003; Spilling et al., 2019; Barmejo et al., 2020).

Table 1. Primary production values reported for different Baltic Sea and North Atlantic areas

Area	Gross primary production, g C m^{-2} year^{-1}	Layer sampled	Period	Season	Reference
Baltic Sea					
Gulf of Riga	353–376	0–10 m	2011–2012	Apr–Oct	This study (**Paper II**)
coastal Gulf of Riga	350	1, 5, 10 m	1993–1995	May–Sep	Olesen et al., 1999
Gulf of Riga	290	NA	NA	Jan–Dec	Kotta et al., 2008
Gulf of Finland	74–111	NA	NA	Jan–Dec	Pitkänen, 2008
Bothnian Bay	18	0, 1, 2, 4, 8, 15, 20 m	2000	Jan–Dec	Samuelsson et al., 2006
Bothnian Sea	47	0, 1, 2, 4, 8, 15, 20 m	2000	Jan–Dec	Samuelsson et al., 2006
Baltic Proper	172	0, 1, 2, 4, 8, 15, 20 m	2000	Jan–Dec	Samuelsson et al., 2006
Gulf of Gdańsk	225	NA	1993–1997	Jan–Dec	Witek et al., 1999
Kattegat	135–165	2, 7, 15 and 22 m	1981–2000	Jan–Dec	Rydber et al., 2006
Belt Sea	185–220	2, 7, 15 and 22 m	1981–2000	Jan–Dec	Rydber et al., 2006
Other regions					
North Sea, German Wadden Sea	124–176	3 m	1995–1996	Jan–Dec	Tillmann et al., 2000
Chesapeake Bay, USA	300–500	from 0.5–1m	1995–2004	Jan–Dec	Harding et al., 2020
Atlantic Ocean	83.9	0-200	NA	Jan–Dec	Eppley, Peterson, 1979

The phytoplankton taxonomical composition and community structure in the Gulf of Riga follow the classical succession of boreal phytoplankton development (Yurkovskis et al., 1999; Jurgensone et al., 2011; Olli et al., 2011). Typically, diatoms *Pauliella taeniata* and *Thalassiosira baltica* dominate the vernal

period from April to May. Diatoms *Chaetoceros* spp. becomes prevalent towards the end of the spring bloom accompanied by dinoflagellates *Peridiniella catenata*, and mixotrophic ciliate *Mesodinium rubrum*. Summer blooms of cyanobacteria can be observed in July and August when *Aphanizomenon flosaquae* dominates. Chlorophytes and cryptophytes are often accompanying cyanobacterial blooms. The second bloom of diatoms completes the phytoplankton succession in September-October after the disruption of the thermocline due to convective mixing of the water column (Jurgensone et al., 2011; Yurkovskis et al., 1999). 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 in the following spring (Rydberg et al., 1990) that is hindered during winter time due to the significant shortening of daylight and windy conditions or ice sheet resulting in overall low light intensity (Vihma, Haapala, 2009).

Lastly, the role and impact of environmental factors vary regionally and, to an even higher extent, locally in the Baltic Sea (Snoeijs-Leijonmalm, Andrén, 2017). Therefore, the estimates of planktonic primary production and the identification of its main contributors are crucial to the comprehension of regional carbon flow dynamics and ecosystem functioning, both being relevant to ecosystem-based management. Moreover, the recently proposed mixotrophic-centric paradigm for marine ecology highlights the need for detailed ecological characterization of functional groups, especially mixotrophic organisms (Mitra et al., 2014, 2016), to provide sufficient data for their meaningful inclusion within regional food web models.

The main objective of the doctoral thesis was to examine the seasonal variation of planktonic primary production in the Gulf of Riga identifying the major impacting environmental factors and the most contributing phytoplankton groups.

The main tasks of the doctoral thesis were
- to identify the environmental factors impacting primary production and their effects;
- to estimate the amount of "new" and "regenerated" production;
- to determine the source of substances assimilated in primary production (land or marine environment);
- to pinpoint the important phytoplankton functional groups in the formation of primary production.

Scientific novelty and practical importance of the research

This doctoral thesis focuses on a scarcely studied issue in the Gulf of Riga – the seasonal dynamics of primary production and its relationship to abiotic and biotic environmental factors. The obtained knowledge provides an opportunity

for a more in-depth comprehension of the effects of eutrophication processes both locally and regionally. It also adds to the body of knowledge about the amount of energy available in the pelagic trophic food web and its impacting environmental factors, allowing for a more accurate assessment of the pelagic habitat and ecosystem. Moreover, this study is the first to estimate the new and regenerated primary production and identify the origin of substances assimilated in the biomass based on isotope signals. Hence, the results provide an analysis of the circulation of nutrients and their involvement in biological processes, which is essential information for a more complete understanding of biogeochemical cycling and food web processes – information that can be practically applied in environmental management, focusing on ecosystem-based approaches.

The results were presented at three national and three international **conferences:**

1. 73rd scientific conference of the University of Latvia. February 2–6, 2015. Section "Research and protection of Latvian water environment", Department of Hydrobiology, Faculty of Biology. Oral presentation: **Development of limit values of phytoplankton ecological quality element indicator classes for the coast of Latvia.** *Atis Labucis, Ieva Barda, Iveta Jurgensone.*
2. 74th scientific conference of the University of Latvia. February 1, 2016. Section "Research and protection of the Latvian water environment". Oral presentation: **Seasonal dynamics of phytoplankton primary production in the Gulf of Riga in 2015.** *Atis Labucis, Iveta Jurgensone, Anda Ikauniece.*
3. ICES Annual Science Conference. September 19–23, 2016, in Riga. Oral presentation: **Phytoplankton community and controlling factors of primary production in the Gulf of Riga (Baltic Sea).** *Atis Labucis, Iveta Jurgensone, Anda Ikauniece.*
4. ICES/PICES Early Career Scientist Conference in Busan, Republic of Korea. May 30 – June 2, 2017. Oral report: **Phytoplankton community and controlling factors of primary production in the Gulf of Riga (Baltic Sea).** *Atis Labucis, Iveta Jurgensone, Ieva Barda, Anda Ikauniece.*
5. 3rd scientific conference of the National Research Program EVIDEnT. November 24, 2017, in Riga. Oral presentation: **Dynamics of primary production in the Gulf of Riga.** *Atis Labucis, Iveta Jurgensone, Ieva Barda, Lelde Ozoliņa.*
6. European Space Agency's 2019 Living Planet Symposium. May 13–17, 2019, in Milan, Italy. Poster Presentation: **Sentinel-3 Ocean and Land Colour Instrument data comparison with in situ chlorophyll a.** *Atis Labucis.*

The doctoral thesis includes results obtained in the following projects:

- European Union LIFE+ Nature & Biodiversity programme project "Innovative approaches for marine biodiversity monitoring and assessment of conservation status of nature values in the Baltic Sea (MARMONI)";
- project "Development of a mechanistic model of the Gulf of Riga ecosystem in support of efficient national policy to ensure the protection of the Baltic Sea and to promote the sustainable use of its ecosystem (LIMOD)" funded by the European Regional Development Fund;
- National Research Programme "The value and dynamic of Latvia's ecosystems under changing climate (EVIDEnT)" funded by the Latvian state research programme for 2014–2017.

2 MATERIALS AND METHODS

2.1 Study area

The Gulf of Riga is situated in the north-eastern part of the Baltic Sea and covers an area of 16 330 km² with an average depth of 26 m and a maximum depth of approximately 60 m. 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 (henceforth: PSU) in surface layers of the southern regions to 7.0 PSU at the Irbe Strait. The mean salinity in 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 patterns of ice coverage and duration vary annually, and the average ice season lasts approximately 80 days (Kotta et al., 2008). 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).

2.2 Sample collection and analysis

Samples were collected at national monitoring stations in the open and coastal Gulf of Riga (**Figure 1**) between 2011 and 2017 (**Table 2**). At each sampling occasion, physical, chemical and biological parameters were surveyed and collected following the recommendations of the HELCOM COMBINE Manual (HELCOM, 2017), except for the study described in **Publication I**, where water samples were collected by Ferry box installed on passenger ferry *Tallink MS Romantika* (pumping water from 5 m depth).

Nutrient concentrations were determined according to Grasshoff et al. (1983). All laboratory analyses were performed in an accredited laboratory of the Latvian Institute of Aquatic Ecology (ISO/IEC 17205). Chlorophyll a and phytoplankton taxonomical composition and biomass were analyzed according to the standard method of the Manual for Marine Monitoring in the HELCOM COMBINE Program (HELCOM, 2017). Stable isotope analysis was conducted in the Laboratory of Analytical Chemistry at the Faculty of Chemistry, University of Latvia.

The light and dark bottle oxygen technique (see Olesen et al., 1999 for details) was used to estimate the primary production of the study area. Initial and post-incubation oxygen concentrations were determined by titration with sodium thiosulfate according to ISO 5813:1983. Photosynthetically active radiation (PAR) was measured on board using the LI-1400 Data Logger and the LI-190 Quantum Sensor during experimental incubation.

New production was calculated using the nutrient depletion approach (see Wasmund et al., 2005 for details) for the year 2012. April was considered the starting month of the spring bloom. Deposition of nitrogen from air was considered in the calculations; 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, the rate at which nitrogen deposits from air was assumed to be 0.12 mmol m^{-2} day^{-1}. PO$_4^{3-}$ excess production as described by Rahm et al. (2000) was assumed irrelevant for the calculations.

Size-fractionation (**Publication IV**) was conducted immediately after sampling prior to the analysis of the samples. The phytoplankton samples were divided by reverse fractionation: passed through a sieve with a mesh size of 56 μm (henceforth: <56-fractionated). The 56 μm sieve was chosen for fractionation based on the observed distribution of *M. rubrum* size classes in the long-term data collected at Station 101A (see database https://latmare.lhei.lv/).

2.3 Statistical methods

Multivariate techniques (i.e., principal component analysis, and partial least squares regression) were applied to analyse relationships between environmental factors and primary production variables. Before the analysis, phytoplankton biomass was normalized and all variables were centred and scaled to unit variance. The analysis was performed using StatSoft© STATISTICA 7 (**Publication I**) and R software v.3.6.1 (R Core Team 2019) (**Publications III and IV**). A comparison of NPP between the unfractionated community and <56-fractionated community was conducted by the Wilcoxon signed-rank test.
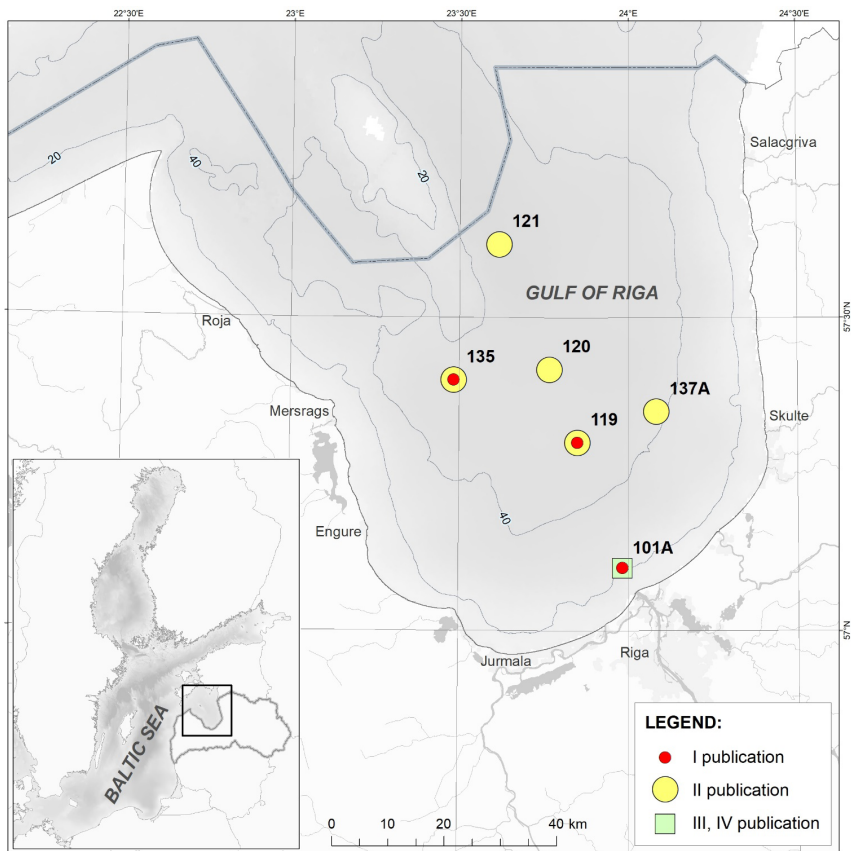
Figure 1. Study sites in the Gulf of Riga

Table 2. Station coordinates, depths and studied periods

Station	N latitude	E longitude	Depth, m	Data period
101A	57.1000	23.9833	22	Mar–May 2014 (**I**), Mar–Nov 2017 (**III**, **IV**)
119	57.3000	23.8500	44	Mar–May 2014 (**I**), Apr 2011 – Oct 2012 (**II**)
120	57.4167	23.7667	45	Apr 2011 – Oct 2012 (**II**)
121	57.6167	23.6167	56	Apr 2011 – Oct 2012 (**II**)
137A	57.3500	24.0833	42	Apr 2011 – Oct 2012 (**II**)
135	57.4000	23.4833	44	Mar–May 2014 (**I**), Apr 2011 – Oct 2012 (**II**)

3 RESULTS AND DISCUSSION

3.1 Gross primary production

The estimated annual GPP of the Gulf of Riga was relatively high (353–376 g C m^{-2} y^{-1}; **Publication II**) compared to other Baltic Sea regions (**Table 1**). For the period 1993–1995, the annual GPP was estimated to range between 250–255 g C m^{-2} y^{-1} (Andrushaitis et al., 1992; Wasmund et al., 2001). However, this estimate was based on measurements that did not include the most productive period of phytoplankton succession, i.e., from the end of March until the end of April. Olesen et al. (1999), on the other hand, approximated that annual primary production in the Gulf of Riga can exceed 350 g C m^{-2}, impending to the values obtained in this study (**Publication II**). Noteworthy, that despite the maintained eutrophication and high P and N inputs (HELCOM, 2018), primary production has not changed notably since the early 90'ties (Andrushaitis et al., 1992; Wasmund et al., 2001) in the Gulf of Riga.

Overall, GPP in the Gulf of Riga mirrored phytoplankton biomass with the highest values (from 4.53 to 3.45 g C m^{-2} d^{-1}) in the spring period and the lowest values during the autumn-winter time (**Publication II**), which is consistent with the boreal seasonal succession. A rapid increase in GPP during early spring (typically March – early April; **Figure 2**) is directly linked to increasing solar irradiance and high nutrient concentrations after the winter convection period, also spring flooding and heavy precipitation events sustain nutrient enrichment supporting high GPP (**Publication I**, **II**). Moreover, the dynamics of stable carbon and nitrogen isotopes in suspended particulate matter (SPM) (**Publication III**) did not eliminate sources of terrestrial or anthropogenic origin during winter and early spring (i.e., March). All through the remaining productive period (April–October), however, the main drivers of δ^{13}C and δ^{15}N variability were established to be the succession of phytoplankton species, marking limited impact from terrestrial or anthropogenic sources on primary production. Diatoms, dinoflagellates and mixotrophic ciliate *Mesodinium rubrum* showed the strongest positive relation to isotopic changes in the Gulf of Riga, whereas the diazotrophic cyanobacteria had an evident but statistically insignificant negative effect on δ^{15}N values.
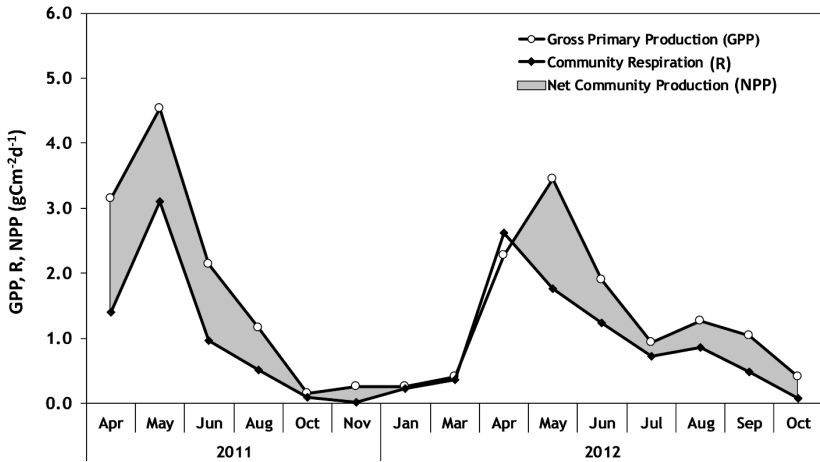
Figure 2. Average daily production rates (GPP, NPP and R) in the central part of the Gulf of Riga (depth > 30 m) during 2011 and 2012. Figure from **Publication II**

The annual GPP in coastal waters was 8.5–14.1% lower (i.e., 323 g C m^{-2}; **Publication IV**) than estimated for the euphotic layer of the central part of the Gulf of Riga (**Publication II**). This spatial difference most likely is a result of lowered water transparency due to coastal water turbidity and a direct impact of opaque freshwater discharge at the coastal study site. Indeed, Secchi depth varied between 2.3 and 5.1 m in the central part of the Gulf of Riga (**Publication II**), whereas it did not exceed 2.5 m in studied southern coastal area (station 101A; **Publication IV**). Based on National monitoring data (see database https:// latmare.lhei.lv/) the euphotic layer depth differed notably between coastal and open areas; during period 2011–2014, on average it was 5.9 m and 9.7 m for coastal (101A) and open waters (119), respectively. In contrast to this observation, a 20% higher primary production was observed in the Daugava plume compared to the open Gulf of Riga during 1994–1997 (Wasmund et al., 2001; Olesen et al., 1999). However, differences in the approaches of sampling and calculations between this study (**Publication II, IV**) and the previous studies (Wasmund et al., 2001; Olesen et al., 1999) have to be noted. The most important difference is that the plankton community of the upper mixed layer was sampled and used for the oxygen metabolism incubations by Olesen et al. (1999) and Wasmund et al. (2001), hence the layer depth compared between open and coastal waters differed (ranging from 15–25 m for station 119 and 10 m for the coastal station 101A). In this doctoral thesis, plankton community from euphotic layer (assumed to be 10 m) was sampled and used in the dark-and-light-bottle incubations (**Publication II, IV**). The difference in the sampling approach, when including also non-euphotic layer where naturally is lower

autotrophic organism biomass (Andersson, Rudehäll, 1993; Lugioyo et al., 2007), potentially has resulted in more diluted integrated samples. Subsequently, incubations by Olesen et al. (1999) and Wasmund et al. (2001) resulted in lower gross primary production values in open water stations compared to coastal waters where only euphotic layer was sampled, thus limiting direct comparison of the studies considering open waters and spatial differences; the results from the coastal areas, though, are directly comparable.

3.2 Planktonic community metabolism

Plankton community respiration varied between 0.01 and 3.12 g C m^{-2} d^{-1} (on average 1.01 g C m^{-2} d^{-1}) and accounted for a vast portion (40.4% to 68.5%; **Figure 2**) of GPP. Size-fractionation exposed unfractionated communities as inefficient net producers due to their high respiration rates (**Figure 3**). Hence, unsurprisingly, the amount of both NPP and GPP of the unfractionated community was not significantly different from the amount produced by the <56-fractionated community (for NPP $V_{Wilcoxon}$ = 205.00, p = 0.488, n = 19; for GPP $V_{Wilcoxon}$ = 194.00, p = 0.708, n = 19). Moreover, the results of this doctoral thesis demonstrate strong covariation between NPP and <56-fractionated community taxa, particularly the small-sized (16-33 μm) *M. rubrum* biomass (**Figure 4**). This implies that the majority of NPP stems from the lower end of the size spectrum.

Notably, the respiration of the unfractionated community was high because it also included heterotrophic protozoans (e.g., tintinnids) and metazoans (e.g., rotifers and Copepoda nauplii). In general, respiration of microzooplankton is estimated to reach 35–43% on average of daily primary production (Calbet, Landry, 2004), whereas Witek et al. (1997) calculated zooplankton respiration to contribute 1% of the total respiration during winter and 20% (on average) in the remaining period. Anyhow, due to the size overlap, it was impossible to filter out zooplankton before incubation without removing diatoms, cyanobacteria filaments, and dinoflagellates. Hence, the results of respiration (and GPP) should be interpreted with caution if compared to estimates obtained by a different method (i.e., other than the light-dark bottle oxygen technique).

The productive layer of the central Gulf of Riga was net heterotrophic (NPP < respiration) during winter and early spring (**Figure 2**), whereas coastal plankton communities were more dynamic and shifted from net autotrophic to net heterotrophic throughout the year (**Figure 3A**). An increase in planktonic community respiration towards river mouths has been also observed in, e.g., the Gulf of Gdańsk (Witek et al., 1997). In transitional water systems, a high rate of allochthonous matter boosts bacterial activity increasing the planktonic community respiration (Alongi, 1998; Smith, 1993; Hopkinson, 1985), and, consequently, causes the shifts in community metabolism (varying between net autotrophic and net heterotrophic).
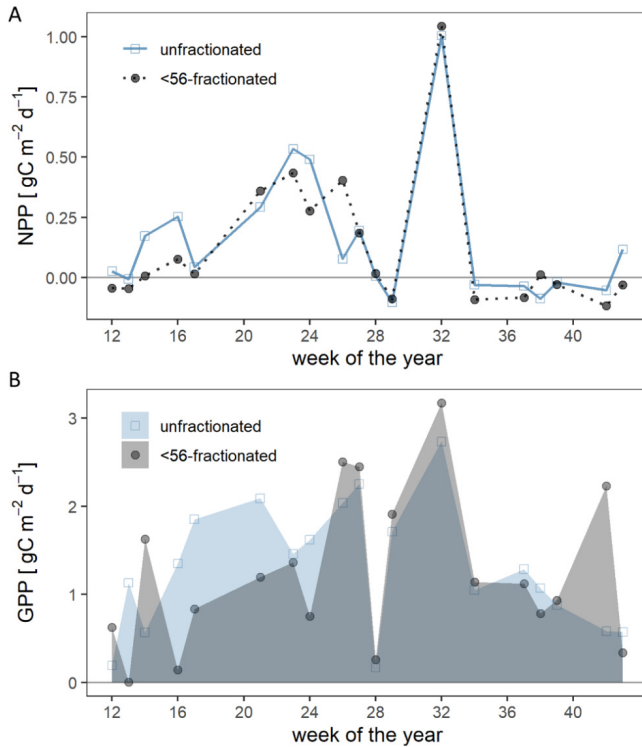
Figure 3. Average daily A) net primary production (NPP) and B) gross primary production (GPP) of unfractionated and <56-fractionated autotrophic communities from the top 10 m layer in the coastal Gulf of Riga (Station 101A). Figure from **Publication IV**

The observed dynamics of pelagic habitat metabolism are in contrast to the study by Olesen et al. (1999) which identified mid-to-late spring (April–May) as the only period when the productive layer of the Gulf of Riga was net autotrophic. Albeit, the study by Olesen et al. (1999) denoted respiration measurements as hampered for the summer season; the community respiration was overestimated in their study resulting in an underestimation of summer NPP, hence net autotrophic periods throughout the rest of the productive season might have been left unidentified. Also, studied layers differ between this study and study by Olesen et al. (1999). Here, planktonic communities from 0–10 m are described whereas in Olesen et al. (1999) sampling was conducted from the upper mixed layer (varying from 10 to 25 m depth). The differences between sampled communities could be the reason for the discrepancies.

All things considered, the euphotic layer of the Gulf of Riga, most likely, is net autotrophic during spring and early summer and in many instances during the rest of the year depending on environmental factors and autotrophic biomass. Multivariate analysis showed that the NPP was influenced by fewer environmental factors than the GPP (**Figure 4**) in the Gulf of Riga. The partial least squares regression analysis identified small-sized *M. rubrum* and PAR as the most important influencing parameters for NPP in both unfractionated and <56-fractionated communities (**Figure 4A, C**), whereas for GPP, besides small-sized *M. rubrum* and PAR, also nutrients, temperature, and carbon mass of diatoms were identified as significant factors (**Figure 4B, D**).
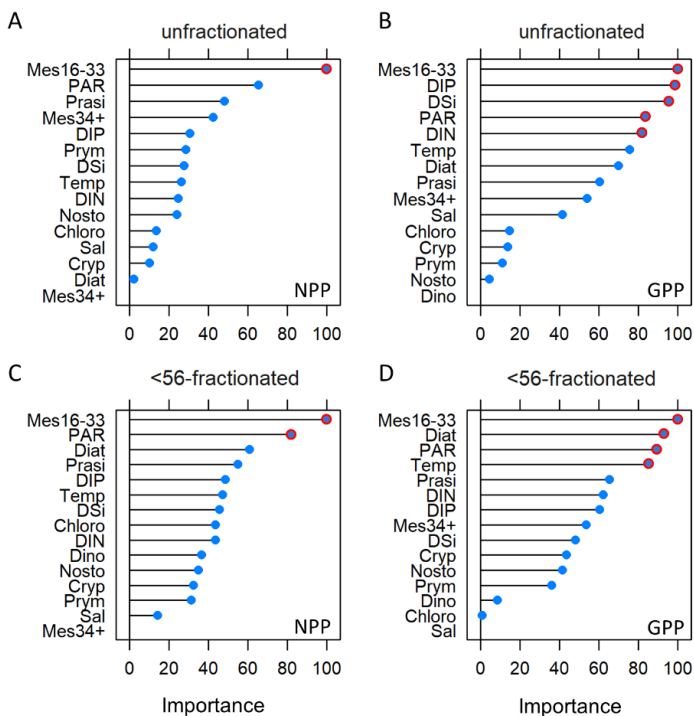

Figure 4. Variable Importance for the projection (VIPs) for explanatory variables of partial least squares regression (PLSR) model. A) VIPs of NPP of unfractionated community, B) VIPs of GPP of unfractionated community, C) VIPs of NPP of <56-fractionated community, and D) VIPs of GPP of <56-fractionated community. The most influential variables (VIPs > 80%) are marked with a red circle. Figure from **Publication IV**

3.3 New and regenerated primary production

Primary production in the euphotic layer can be viewed as dependent on two different sources of nitrogen supply. One is the dissolved nitrogen compounds derived from the metabolism of heterotrophic organisms, e.g., ammonia, urea and to a lesser extent amino acids. The primary production resulting from this recycled nitrogen is called "regenerated" production. In a theoretical balanced steady-state system, the recycling of nutrients can continue indefinitely. However, in real ecosystems, there are losses such as the flux of sinking material, migration and extraction of organisms (fishing) and most importantly, denitrification. The losses have to be replaced by external inputs of nutrients to avoid a decline in the productivity of the system. Nutrient replenishing is a natural process occurring during convective mixing – a period when nutrients accumulated in deeper layers are brought upwards to the euphotic layer. Although this is the dominant process of nitrate renewal, other processes of external nitrogen inputs exist, e.g., N_2 fixation by diazotrophs and inputs of terrestrial and anthropogenic origin. The primary production based on external nitrogen input in the form of N_2 or oxidized nitrogen forms is called "new" production (Eppley, Peterson, 1979).

The nutrient concentration decrease pattern suggested that the new production period in the Gulf of Riga lasts until June and shifts to the predomination of regenerated production afterwards. That coincides with the previous studies (Lundsgaard et al., 1999; Olesen et al., 1999; Olli, Heiskanen, 1999) which revealed high pelagic recycling efficiency in the Gulf of Riga during the productive period, especially summer. The average new production, calculated from the nutrient consumption, was equivalent to 51.8% of NPP during the studied period. Still, it varied together with phytoplankton succession. New production exceeded 75.0% of NPP during diatom bloom, whereas during the dinoflagellate dominance period, it was approximately 50% (**Publication II**). If new production is calculated from the consumption of SiO_4 (following Wasmund et al., 2013), it gives an average estimate of 1.95 g C m^{-2} d^{-1} for the diatom bloom period (April–May). This implies the significant role of diatoms in primary production during the spring bloom period. Also, the results of **Publication III** indirectly support the importance of diatoms during the spring bloom, but no direct linkage between diatoms and primary production rates was identified in other studies of this doctoral thesis (**Publication I, II, IV**).

In the summer nutrient-regenerating system, diazotrophic cyanobacteria are well known for bloom formation in the Baltic Sea (Kahru et al., 1994; Eigemann et al., 2019; Liepina-Leimane et al., 2022) despite the low concentrations of inorganic nutrients. Ploug et al. (2010) showed that cyanobacteria *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. This suggests that the population of *A. flosaquae* sustains the observed high

biomass values in the Gulf of Riga (**Publication II**) by rapid recirculation of phosphorus upon the death of phytoplankton cells and the assimilation of nitrogen via N_2 fixation. This is supported also by the isotopic signals (**Publication III**) that displayed a negative effect (although, insignificant) of diazotrophic cyanobacteria on $\delta^{15}N$ values during the summer period. Dugdale and Goering (1967) noted that nutrient recycling is almost non-measurable due to its continuous and fast nature that prevents the detection of changes in concentrations of nutrients and makes causal linkages ambiguous.

3.4 Importance of phytoplankton community on primary production

SPM is a dynamic pool of both living and non-living particles that can have a role in the functioning of food webs, nutrient and contaminant cycling, and system productivity, especially in coastal and estuarine environments (Cresson et al., 2012; Golubkov et al., 2017; Jędruch et al., 2017; Xu et al., 2019). The amount and composition of SPM in such environments are affected by various external sources like riverine inflows, coastal erosion, and atmospheric deposition, as well as internal processes like primary production and mineralization of organic matter.

In the Baltic Sea surface layer, SPM isotopic content is generally controlled by the presence or absence of phytoplankton that incorporates dissolved nutrients into SPM (Winogradow et al., 2019; **Publication III**). As dissolved nutrient concentrations in the water column decrease, autotrophic organisms, i.e., phytoplankton, exhibit less discrimination to absorbing isotopically enriched and energetically more consuming dissolved carbon compounds, e.g., bicarbonate or atmospheric CO_2 (Golubkov et al., 2017). Detailed examination of phytoplankton species along with primary production rates revealed key species governing the nutrient fluxes and the productivity of the Gulf of Riga. The mixotrophic ciliate *M. rubrum* prevails in all seasons and significantly correlates with elevated GPP, while diazotrophic cyanobacteria *A. flosaquae* contributes to new production in the summer nutrient-regenerating system (**Publication II, III**).

As mentioned previously, the dynamics of stable carbon and nitrogen isotopes in SPM (**Publication III**) strongly indicate that the cause of the variability in carbon and nitrogen isotope fractionation is biological processes. The co-variation of $\delta^{13}C$ and $\delta^{15}N$ with seasonally changing abiotic factors, e.g., temperature and nutrient concentrations, establishes the seasonal nature of $\delta^{13}C$ and $\delta^{15}N$ values (as observed in Savoye et al., 2003), reflecting the seasonal succession of phytoplankton species (**Publication III**). It defines carbon and nitrogen isotopic ratios of SPM during the spring bloom and substantially affects isotope ratios until mid-autumn. Diatoms, dinoflagellates, and *M. rubrum* show

the strongest positive relation to isotopic changes in the Gulf of Riga, meaning that their growth enriches ^{13}C and ^{15}N implying new production (hence, coinciding with the results of **Publication II**). Whereas the lower values of δ^{15}N during summer can be explained by isotopically depleted atmospheric nitrogen (δ^{15}N = 0‰) fixation by diazotrophic cyanobacteria. However, the negative correlation between cyanobacterial biomass and δ^{15}N values is not evident in summer (**Publication III**), plausibly, because the cyanobacteria were never the main and only dominating taxa during the non-vernal phytoplankton community.

By the end of the spring bloom, in April, δ^{15}N values barely exceeded the range of values that are typical for deep ocean inorganic nitrogen (Jędruch et al., 2017; Pantoja et al., 2002) or Baltic Proper surface SPM δ^{15}N values (Winogradow et al., 2019) suggesting a limited impact of the riverine inflows, which delivers inorganic nitrogen of terrestrial and anthropogenic origin. Presumably, in the absence of a significant external nitrogen pool by the end of spring bloom, the δ^{15}N value in SPM would be determined by the recycling of an already assimilated nitrogen pool. Contrary to this assumption, the highest δ^{15}N value was observed in May when no further phytoplankton carbon biomass increase could be detected. Most likely, the shift in phytoplankton species composition, e.g., successive diatom replacement by actively migrating ciliate *M. rubrum* in May, was an important factor. It is highly possible that the vertical migration ability of this ciliate causes δ^{15}N value increase from utilizing the bottom layer nitrogen pool (Lips, Lips, 2017). Additionally, it is possible that unfiltered water, as sampled in the study, contains other taxa, e.g., small-sized zooplankton that could increase the overall δ^{15}N values of bulk SPM as shown by Rolff (2000).

Mesodinium rubrum is a mixotrophic Litostomatea ciliate that possesses plastids preying upon cryptophyte algae (Johnson et al., 2016; Fenchel, Juel Hansen, 2006). It is highly productive in turbid waters and at low light irradiance (Crawford, 1989; Herfort et al., 2012; Johnson, Stoecker, 2005; Moeller et al., 2011). *Mesodinium rubrum* is often abundant in estuarine-coastal waters (Cloern et al., 1994; Leles et al., 2017; Sanders, 1995), including the brackish Baltic Sea (Lips, Lips, 2017; Rychert, 2004). The next section delves into *M.rubrum*'s behaviours and strategies that allow it to dominate in the Gulf of Riga and beyond.

3.5 Mixotrophic ciliate *Mesodinium rubrum* – an efficient key player

Mesodinium rubrum has been identified as an important contributor to the primary production of the Gulf of Riga in **Publications I**, **II**, and **III** of this doctoral thesis. Hence, its role was investigated more closely in **Publication IV** by assessing the production of size-fractionated autotrophic communities,

including small-sized (length of 16–33 μm) and large-sized *M. rubrum* (length ≥ 34 μm). *Mesodinium rubrum* displays a wide size distribution (from 15 to 70 μm; **Figure 5**); therefore, size distinction is introduced in numerous studies on *M. rubrum* (e.g., Johansson, 2004; Johnson et al., 2016; Montagnes et al., 2008), revealing different ecological responses to environmental changes between size classes.
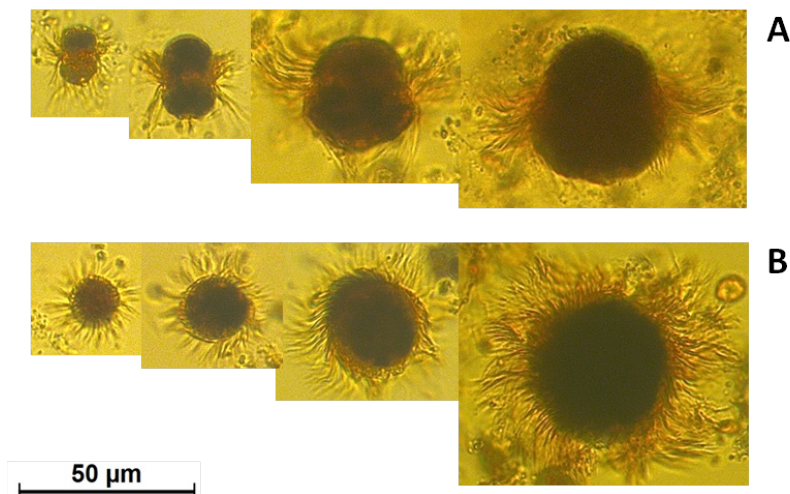

Figure 5. A) Lateral and B) superior view of *Mesodinium rubrum* cell demonstrating its wide size distribution

Mesodinium rubrum showed significant covariation to primary production rates in both open and coastal areas (**Publication I, II, IV**; **Figure 4**) despite the different underwater light conditions, expressing its flexible nature. Additionally, in several other Baltic sub-basins, *M. rubrum* has been stated as a significant contributor to primary production (Höglander et al., 2004; Johansson, 2004; Lips, Lips, 2017; Nielsen, Kiørboe, 1994), implying its essential role as one of the main producers in the Baltic Sea and beyond as it has been noted as highly productive organisms in various turbid waters and, especially, at low light irradiance (Crawford, 1989; Herfort et al., 2012; Johnson, Stoecker, 2005; Moeller et al., 2011). Hence, *M. rubrum* is often abundant in estuarine-coastal waters (Cloern et al., 1994; Leles et al., 2017; Sanders, 1995) and under certain conditions, it forms blooms (red tides) (Taylor et al., 1971), yet *M. rubrum*-induced red tides are not reported from the temperate Baltic Sea region – the research area of the present study.

Notably, *M. rubrum* has been recently recognised as a species complex consisting of at least two described and accepted species – *M. rubrum* and

Mesodinium major (cf. Garcia-Cuetos et al., 2012; Johnson et al., 2016). Both have similar morphology and they possess plastids of the same origin (red plastid cryptophytes), but they show differences in cell length and ecology. However, as molecular methods were not utilised in this doctoral thesis all *M. rubrum*-like ciliates are referred to as *M. rubrum*. However, studies on the genetic diversity of *M. rubrum* should follow to continue expanding the understanding of the processes, including primary production in the Gulf of Riga and the Baltic Sea in general.

Mesodinium rubrum is known to have migration behaviour based on the response of phototaxis (Crawford, Lindholm, 1997) and has wide temperature, salinity and light tolerances (Lindholm, Mörk, 1990; Olli et al., 1996). It can migrate vertically over tens of meters per day (Hajdu et al., 2007), exploiting the nutrient-rich lower layers. *Mesodinium rubrum* benefits from this behaviour under stratified conditions in the shallow Baltic Sea (Lips, Lips, 2017). Due to the focus on the surface layer in the present study, subsurface accumulations of motile phytoplankton are most likely missed, potentially resulting in an underestimate of the overall abundance and biomass of *M. rubrum*. However, the efficient production of *M. rubrum* is attributed to mixotrophy and photosynthetic machinery of cryptophyte-originated chloroplasts that are well adapted to dim light (Daneri et al., 1992; Herfort et al., 2012) rather than the ability of vertical migration. In general, mixotrophy is an advantage under nutrient-limited conditions (Mitra et al., 2014), and it is an important feeding strategy during the decline of spring blooms and during summer or other periods when the system shifts from net autotrophy to net heterotrophy (Haraguchi et al., 2018). However, the ecological flexibility of *M. rubrum* and its implications for its phototrophic production remain poorly understood and require further in-depth research.

The photosynthetic activity of *M. rubrum* increases with the availability of cryptophytes, although with a 7-day lag (Gustafson et al., 2000). Cryptophytes are common in the Gulf of Riga during summer (**Publication IV**). Hence, the acquisition of chloroplasts does not limit the growth of *M. rubrum*, allowing it to reach the highest efficiency in photosynthetic activity without notable limitations. Although no direct linkage between cryptophytes and primary production rates was detected in this study, cryptophytes are known to prevail in biomass and contribute significantly to production in the polar regions, especially in the upper mixed layer under stratified conditions (e.g., Moline et al., 2004; Mendes et al., 2018). Polar regions are not the main distribution area of *M. rubrum*, hence under low predation pressure cryptophytes thrive there (Anschütz et al., 2022).

Cryptophytes affect various aspects of the performance of *M. rubrum*. In addition to the aforementioned physiological components, the availability of *Teleaulax* cryptophytes results in a reduction of the average size and volume of *M. rubrum* cells, as the high prevalence of cryptophytes promotes cell division

(Gustafson et al., 2000). This is a potential explanation for a shift to small-sized *M. rubrum* during summer in the Gulf of Riga as cryptophytes were the most abundant in the period between weeks 26 and 32. A shift from larger to smaller *M. rubrum* during summer has also been observed in other Baltic Sea regions. This is, however, explained by increased grazing pressure (Johansson, 2004; Rychert, 2004; Witek, 1998), higher temperature (Garcia-Cuetos et al., 2012; Haraguchi et al., 2018), and low DIN values (Haraguchi et al., 2018) during the summer.

3.6 Primary production under changing environmental factors

Primary production is a fundamental process in any ecosystem as it provides energy for the entire food web. Therefore, it is critically important to understand and quantify the regulatory effects that environmental factors have on rates of important biogeochemical processes such as primary production. Realistic biogeochemical rates are fundamental for properly calibrating coupled hydrodynamic-biogeochemical models (Kuliński et al., 2022) which are the foundation of successful ecosystem-based management implementation.

New production, in theory, is directly dependent on mixing and vertical advective processes. Gross primary production, on the other hand, in a long term depends on new production to replace the lost material due to sinking, extraction or other processes. Thus, climate change can have an impact on the primary productivity of shelf seas by affecting meteorological and thermohaline situations in the systems. In line with future global projections, climate change scenarios for the Gulf of Riga region foresee a continuation of already occurring air temperature and precipitation increases. A consequent drop in frost and ice days will follow (BACC II, 2015). Overall, the winters will become milder and sea-ice cover will decrease, but the summers will become more pronounced. The changes, most likely, will promote stratification and inorganic nutrient (especially nitrogen) limitation in the surface layer, as well as potentially decrease the light availability even further (Skudra, Lips, 2017; Sommer et al., 2012; Winder, Schindler, 2004). From an ecological perspective, organisms with coping mechanisms to nutrient deficiency in the euphotic layer (e.g., motile *M. rubrum*, diazotrophic cyanobacteria) will outperform others under such conditions (Griffiths et al., 2016; Spilling, Markager, 2008; Wasmund, Uhlig, 2003). Moreover, future climate conditions appear non-detrimental to cryptophytes (Gaillard et al., 2020), thus predicting the continuous availability of cryptophyte-originated chloroplasts ensuring autotrophy of mixotrophic ciliate *M. rubrum*. Several studies have revealed that *M. rubrum* is able to remain photosynthetic and survive for months at low irradiance (Johnson, Stoecker, 2005) considering its efficient inorganic nutrient uptake rates (Stoecker et al., 1991; Tong et al., 2015; Wilkerson, Grunseich, 1990). Therefore, an increase in

the prevalence of *M. rubrum*, along with a consequent rise in its contribution to primary production, can be expected in the region, especially during the summer period. However, shifts in communities at the first trophic level, plausibly, will affect the following food chains – a topic that requires further studies.

Projected climate change (BACC II, 2015) is likely to exacerbate eutrophication effects in the Baltic Sea due to (i) increased runoff that will consequently increase external nutrient loads and (ii) water temperature rise that will reduce oxygen flux from the atmosphere and intensify internal nutrient cycling (e.g., Meier et al., 2011, 2012a; Neumann et al., 2012; Omstedt et al., 2012; Meier et al., 2018). In the Baltic Proper, phytoplankton growth and consequent primary production will likely increase as a result of the projected intensification of nutrient cycling in the euphotic zone. Also, bacterial activity will rise (e.g., Wulff et al., 2001) and enhance nutrient flow from the sediments (Meier et al., 2012b) amplifying the effects. On the other hand, in the northern Baltic Sea, primary production may be reduced due to increased land runoff of allochthonous organic matter that will favor heterotrophic bacteria (Andersson et al., 2015). The potential changes in the primary production of the Gulf of Riga have not yet been the focus of the modelling studies, hence it requires more attention in future research disentangling the effects from eutrophication and brownification (decrease of water transparency due to increased optically-active allochthonous material, e.g., dissolved humic compounds). However, a recent study revealed that brownification affects phytoplankton community composition shifting from larger to smaller organisms but it did not affect primary productivity in eutrophic coastal waters (Spilling et al., 2022).

Another environmental aspect that unavoidably is changing in global oceans, including the Baltic Sea, is ocean acidification (decrease in pH) due to increased CO_2 concentration in the atmosphere. Ocean acidification is known to have both direct and indirect impacts on pelagic species, communities and entire ecosystems. Noteworthy that the responses of Baltic phytoplankton to acidification are highly variable and species-specific (Havenhand et al., 2019). Cyanobacterial species display positive, negative or no response (western Baltic, Bergen et al., 2016; Gulf of Finland, Hornick et al., 2017), *M. rubrum* also seem tolerant (Nielsen et al., 2010), whereas diatoms increased under acidification treatment in experimental studies (Kremp et al., 2012). Additionally, mesocosm studies revealed that ocean acidification can influence phytoplankton community structure, but overall phytoplankton productivity tends to increase under acidification treatment, although with seasonal variation in the response (Skagerrak, Eberlein et al., 2017).

In conclusion, primary production fuel the pelagic food web, and, consequently, climate-driven shifts in primary production will have major impacts on carbon cycling and the structure and functioning of the entire marine biome. Understanding the underlying processes and drivers will help

to improve the conceptual understanding of the complex marine system and its functioning. The results of this doctoral thesis identified phytoplankton functional groups (i.e., small-sized *M. rubrum* and diatoms) that play a key role in primary productivity in the Gulf of Riga. Hence studies focusing on their responses to climate change and their specific interactions with other trophic guilds (e.g., competition or predator-prey relationships) are required to understand the Gulf of Riga food web dynamics and ecosystem as a whole.

CONCLUSIONS

- The annual primary production in the Gulf of Riga was 353–376 g C m^{-2} in our study. It showed no evident increase in productivity compared to the period 1993-1995.

- The highest net (NPP) and total (GPP) primary production can be observed in the spring, while autumn was the least productive during the growth season. New production prevailed during spring, accounting for 51.80% of spring NPP.

- During the productive period in the Gulf of Riga, the source of substances available to phytoplankton changes seasonally. Based on the isotopic signals, the spring measurements differed from the rest of the period, implying greater influence from terrestrial and anthropogenic sources.

- Diatoms, dinoflagellates, and *Mesodinium rubrum* show the strongest positive relation to isotopic changes in the Gulf of Riga, implying their contribution to new production.

- Mixotrophic ciliate *Mesodinium rubrum* prevailed in all seasons and significantly correlated with elevated productivity. Whereas diatoms were identified as the main contributors to new production in spring and diazotrophic cyanobacteria *Aphanizomenon flosaquae* – in a nutrient-regenerating system of the summer.

- *Mesodinium rubrum* is identified as a significant contributor to primary production in the Gulf of Riga. A close covariation between small-sized (16–33 μm) *M. rubrum* and NPP was detected in the coastal waters of the Gulf of Riga.

- The primary production dynamics of both the unfractionated and <56-fractionated plankton community in the Gulf of Riga is directly influenced by the biomass of *Mesodinium rubrum* small-sized (16–33 μm) cells and the amount of available light, while the primary productivity of the <56-fractionated plankton is also affected by temperature and diatom biomass.

THESIS FOR DEFENCE

- The amount of primary production has decreased in the Gulf of Riga compared to the period 1993–1995 due to the changed management of the Gulf of Riga (due to decreased P and N loads).

- Phytoplankton taxonomical composition, size structure and biomass affect primary production dynamics.

- The new production in the Gulf of Riga is formed by diatoms in spring and diazotrophic cyanobacteria – in summer.

- The ciliate *Mesodinium rubrum* is an important contributor to net primary production of the Gulf of Riga.

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