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Plankton Community Metabolism Variations in Two Temperate Coastal Waters of Contrasting Nutrient Richness

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Abstract Estuarine ecosystems play a crucial role in global carbon cycling. Understanding the factors controlling plankton metabolism in these regions is critical. This study investigates how contrasting nutrient conditions influence plankton metabolism and carbon flow in two Danish estuaries, Roskilde Fjord (RF) (eutrophic) and the Great Belt (GB) (less eutrophic). Despite higher nutrient concentrations in RF, chlorophyll *a* and biomass only showed a moderate increase compared to the GB. Interestingly, metabolic rates (photosynthesis and respiration) in RF displayed greater temperature sensitivity, suggesting potential nutrient limitation effects in the GB. While both stations exhibited similar annual net primary production, RF's higher net community production highlights the importance of nutrient availability for carbon accumulation within the system. Additionally, the study observed significant seasonal variations in plankton metabolism and its impact on the carbon cycle. Notably, the more dynamic hydrography in the GB weakened correlations between biological and environmental factors.

Plain Language Summary All seawater is full of microscopic organisms known as plankton. Plankton play a central role in controlling the global carbon cycle and phytoplankton is the marine counterpart to land-based plants. Phytoplankton harness sunlight and available nutrients from their environment, to take up carbon dioxide from the atmosphere and produce food and oxygen. Our study investigated how plankton change their activities over a year in two different coastal waters of Denmark in the Baltic Sea. We tried to understand how the differences in both the biological differences within the plankton, which are at the bottom of the food web, and the differences in their food sources affect their metabolism, both by conducting measurements in the sea and by applying experiments on the samples taken. Based on the available information, the Roskilde Fjord (RF), with a depth of 5 m, has slow water movement and is more exposed to fertilizers. This leads to more plankton and increased sensitivity to temperature changes compared to the Great Belt, an open sea with faster water flow. Areas with higher nutrient levels, like the RF, are expected to be more affected by rising sea temperatures due to climate change.

Key Points:

- Plankton metabolism responds rapidly and efficiently to biogeochemical and seasonal changes, making it vulnerable to anthropogenic effects
- Trophic dominancy in the community respiration varies with the quality and quantity of the carbon source
- The mixing zone of both stations was estimated to be net autotrophic, which provides carbon to upper trophic levels

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1. Introduction

Phytoplankton photosynthesis and plankton respiration are the main processes governing the cycling and turnover of nutrients and carbon in marine ecosystems (Behrenfeld et al., 2006; Jiao et al., 2024). Inorganic nutrients are essential for primary production, while photosynthetic and terrestrially derived organic carbon are required for plankton respiration. Since terrestrial inputs are the primary source of nutrients in seawater, estuaries and coastal waters play a key role in the functioning of metabolic processes by transporting organic matter to the open seas through currents (Giraud et al., 2008). One example is the organic matter from the Baltic Sea, which is transported by currents from the Danish Straits and Kattegat Sea through the North Sea and into the Atlantic Ocean, where it is transformed into biomass (Silva et al., 2021; Winther & Johannessen, 2006).

In the last century, the Baltic Sea, like other coastal systems, has been severely affected by anthropogenic activity and eutrophication peaked in the 1980s (Andersen et al., 2017). Increased primary production and plankton respiration may have adverse effects on shallow coastal systems with long regeneration times. It may cause excessive algal growth, reduced light transmission and decreased levels of dissolved oxygen leading to bottom anoxia (Andersen et al., 2019; Ferreira et al., 2011). Nowadays, Baltic countries have taken measures to restrict nutrient inputs to the sea which have caused improvements in some indicators of ecosystem health (e.g., nutrient

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concentrations and Chl *a*) (Ferreira et al., 2011; Riemann et al., 2016). However, despite having taken action to decrease nutrient concentrations, a mismatch still exists between the achieved reductions and the present water quality status (Murray et al., 2019; Savchuk, 2018). The main reason is accumulated nutrients in the sediment which may be released back into the water column through mixing (Jørgensen et al., 2013), thereby stimulating primary production and plankton respiration. Although primary production measurements have been carried out more extensively, respiration studies are few (Cloern & Jassby, 2010; Spilling et al., 2019). While the ^{14}C method (Steemann Nielsen, 1952) has allowed for increased sensitivity in primary production measurements, the lack of accompanying respiration data has hampered our understanding of net community production (NCP) and community respiration (CR), thus trophic status of the pelagic systems (Staehr et al., 2018). Globally, there are about a hundred times more ^{14}C primary production measurements than pelagic respiration measurements (Robinson & Williams, 2005). In order to understand the balance between the two processes, we need combined measurements of primary production and respiration in combination with empirical models that can predict CR from frequently monitored variables. To examine the effects of seasonal variations on plankton community metabolism in this study, primary production was measured using the ^{14}C method. Community and bacterial respiration (BR) were measured concurrently using O_2 optode technique. We then investigated the relationships between these measurements and various environmental variables.

Climate change has increased sea-surface temperatures globally (IPCC, 2023), and the ecological impact is likely to be potent in estuaries due to their shallow water and exposure to other anthropogenic pressures (Davies et al., 2016; Hansen & Bendtsen, 2013; Helcom, 2013). Since planktonic organisms are significant drivers of biogeochemical cycles (Falkowski, 1994), changes in constraining factors such as temperature and nutrients will affect cycling rates (López-Urrutia & Morán, 2007; Pomeroy & Wiebe, 2001). The metabolic theory of ecology (Brown et al., 2004) predicts exponential increases in metabolic rates with temperature. However, numerous studies (Hansen & Bendtsen, 2014; López-Urrutia et al., 2006; Vaquer-Sunyer & Duarte, 2013) demonstrate that plankton respiration exhibits greater temperature sensitivity compared to photosynthesis, reflected by higher respiration Q_{10} values. Consequently, warming is predicted to disproportionately accelerate heterotrophic respiration relative to primary production, potentially weakening ocean CO_2 sequestration (López-Urrutia et al., 2006). Such effects can be studied by controlled laboratory and mesocosm experiments (Hansen & Bendtsen, 2014; Lewandowska et al., 2014; Panigrahi et al., 2013; Sommer & Lengfellner, 2008; Vaquer-Sunyer & Duarte, 2013), and following changes in situ over the season (Lomas et al., 2002). This study investigated the effects of limiting factors, such as seasonally varying in situ temperature and nutrient concentrations, on primary production and CR. These processes play a critical role in determining the trophic balance within the ecosystem.

To achieve a comprehensive understanding of environmental influences on plankton metabolism, this study employed a year-round sampling campaign in two contrasting regions (Great Belt (GB) and Roskilde Fjord (RF)) of the Baltic Sea. These regions differ significantly in nutrient richness and hydrographic characteristics, allowing us to isolate and analyze the effects of these factors. Our specific objectives were.

- Quantify plankton community metabolism and identify the dominant trophic contributors based on environmental conditions.
- Determine the temperature sensitivity of plankton metabolic processes and develop an empirical model for CR.
- Estimate trophic status by calculating NCP in the pelagic zone of each site.
- Gain a nuanced understanding of the interplay between environmental factors and plankton processes, including dissolved organic matter dynamics, bacterioplankton community function, and nitrogen fixation rates (explored in parallel studies).
- By achieving these objectives, this study aims to contribute to a more comprehensive understanding of the biogeochemical effects of seasonal variations on carbon flow within coastal ecosystems.

2. Materials and Methods

2.1. Study Site and Sampling

Sampling was carried out at two contrasting coastal stations in the Baltic Sea (Bentzon-Tilia et al., 2015; Knudsen-Leerbeck et al., 2017; Traving et al., 2016) that have been monitored by The Danish National Aquatic Monitoring and Assessment Program (Conley et al., 2002) for decades. Water samples were collected monthly from January–December 2012 at two stations: One in the GB (bottom depth 35 m) and the other in RF (bottom

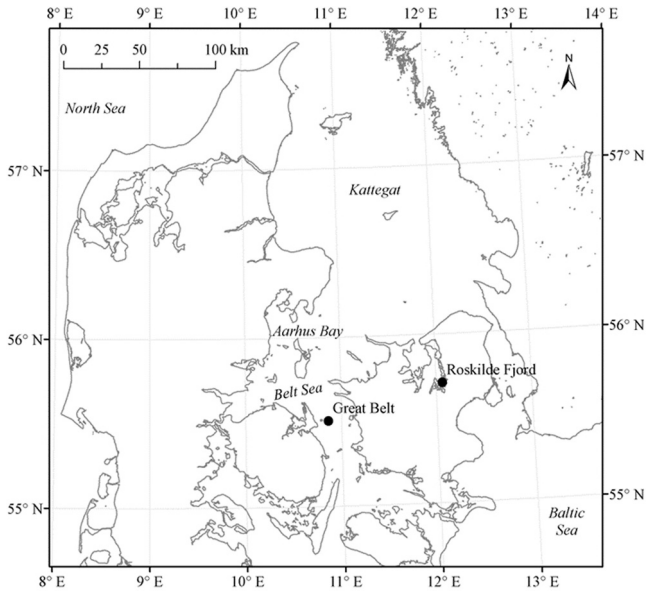


Figure 1. Map of Denmark with adjacent seas showing sampling stations in the Great Belt (55°30.27′N, 10°51.43′E) and Roskilde Fjord (55°42.00′N, 12°04.46′E).

depth 5 m; Figure 1). The GB is the primary connection between the Baltic Sea and the North Sea. Its water column is stratified with outflowing low-salinity Baltic Sea water at the surface and inflowing high-salinity bottom water from Skagerrak and the North Sea (Jørgensen et al., 2013). The GB is an important site for vertical mixing, leading to significant nutrient input to the surface layer, especially during high wind events (Bendtsen et al., 2009) which was also observed twice in 2012 (Figure 2). The GB is eutrophic with a production of organic matter of about 210–220 g C m^{-2} yr^{-1} (Lyngsgaard et al., 2017). The residence time is about 1 month during winter and about 2 months during summer (Bendtsen et al., 2009). RF is a 40 km long, narrow, shallow (mean depth of 3 m), and semi-enclosed estuary connected to the Kattegat via the Isefjord through a narrow opening in the north (Pedersen et al., 2014). The water residence time ranges between 90 and 720 days (Josefson & Rasmussen, 2000; Kamp-Nielsen, 1992). The phytoplankton community is monitored as part of the monitoring program mentioned above and time series for carbon biomass is available (Jakobsen et al., 2015). The GB is dominated by diatoms (Bendtsen et al., 2024), while RF exhibits dominance by cryptophytes, prasinophytes, and euglenophytes, with minimal contribution from diatoms (Haraguchi et al., 2022). Freshwater nutrient loadings have affected both sites for a century (Conley et al., 2000). With the Danish national nutrient reduction strategy from the early 1990s (Conley et al., 2002), nutrient concentrations and effects of eutrophication decreased significantly (Conley et al., 2007; Pedersen et al., 2014; Riemann et al., 2016; Staehr et al., 2017).

At both stations, we used 1.7 and 5 l Niskin bottles to collect >20 l of surface water (1 m depth) that we pre-screened through a 200 µm net to remove mesozooplankton before incubations. The sampled water was thoroughly mixed and transferred to the necessary containers for different analyses. The sampled water was kept dark in a cooler at as close to in situ temperature as possible during transport to the laboratory (a few hours). Vertical profiles of temperature, salinity, chlorophyll fluorescence, and photosynthetically active radiation (PAR) were collected twice a month. In the GB, the pycnocline depth was defined as the lowest depth with a density gradient over 1 kg m^{-4} (see Lyngsgaard et al., 2014), whereas stratification was not observed in RF. Due to sea ice, sampling in the GB started in February, and two samplings were conducted in March at 2-week intervals. RF was ice-covered in January, but sampling was conducted from a pier 1 km south of the station.

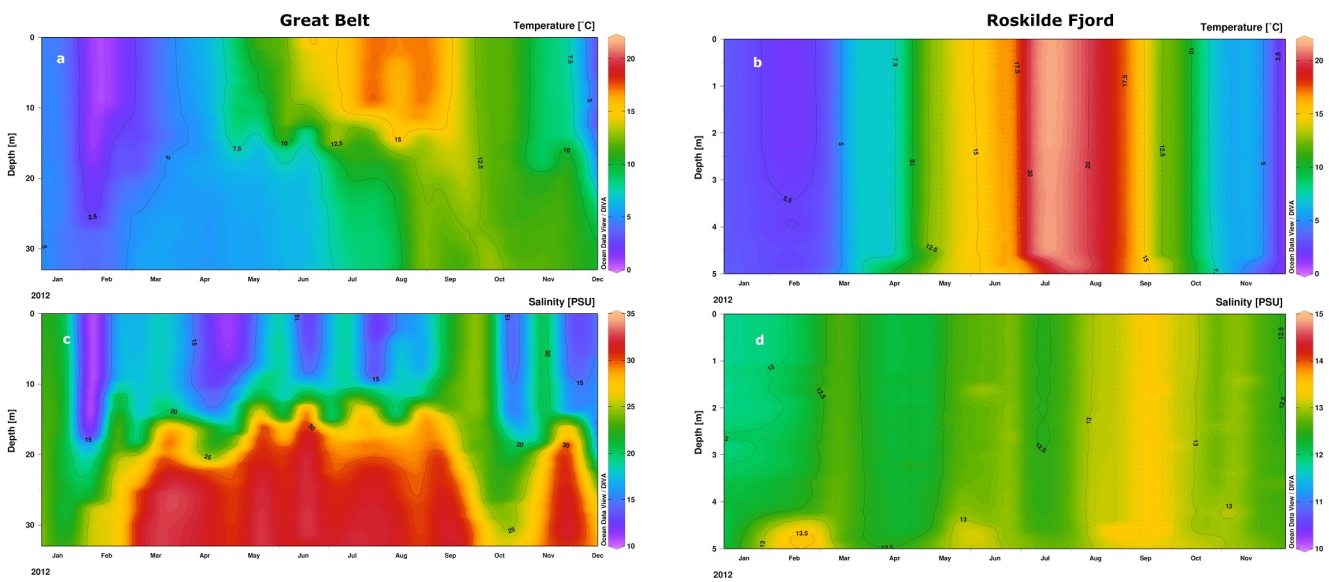


Figure 2. Contour plots of temperature and salinity for the two stations. Data from Bentzon-Tilia et al. (2015) and Traving et al. (2016).

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Table 1
Time-Weighted Annual Average Values of Environmental and Biological Variables for the Two Stations Where K Is the Ratio Roskilde Fjord:Great Belt Values

		Great Belt		Roskilde Fjord		
Type	Parameters	Mean	±SD	Mean	±SD	*K*
Physical	Temperature (°C)	9.5	5.2	10.0	6.4	1.1
	Salinity	16.4	3.0	12.6	0.4	0.8
Nutrients	DIN (μmol L^{-1})	2.7	1.8	15.4	14.9	5.6
	DIP (μmol L^{-1})	0.4	0.2	3.0	1.8	7.5
	DSi (μmol L^{-1})	10.4	6.4	50.0	20.8	4.8
	TN (μmol L^{-1})	19.6	5.6	56.1	14.3	2.9
	TP (μmol L^{-1})	0.8	0.2	4.0	1.9	5.3
Standing stocks	Chl *a* (μg L^{-1})	1.8	0.7	3.1	1.5	1.7
	BA (cell ml^{-1})	6×10^5	2×10^5	4×10^6	2×10^6	6.2
	POC (μmol L^{-1})	17.4	4.6	32.5	9.5	1.9
	PON (μmol L^{-1})	2.3	0.7	5.0	1.4	2.2
Volumetric rates	P_m (μmol C L^{-1} h^{-1})	0.40	0.31	1.05	0.86	2.6
	CR (μmol O_2 L^{-1} h^{-1})	0.12	0.06	0.31	0.21	2.6
	BR (μmol O_2 L^{-1} h^{-1})	0.10	0.04	0.10	0.05	1.1
	BP (μmol C L^{-1} d^{-1})	0.41	0.39	0.38	0.33	0.9
Biomass-specific rates and ratios	CR^B (mol O_2 g^{-1} Chl *a* h^{-1})	0.08	0.04	0.10	0.06	1.4
	$P^B{}_m$ (mol C g^{-1} Chl *a* h^{-1})	0.21	0.09	0.33	0.23	1.6
	α^B (g C g^{-1} Chl *a* mol^{-1} photons m^2)	17.8	8.5	17.6	7.3	1.0
	CR:P_m	0.30	0.20	0.29	0.24	1.0
	C:N (molar)	6.7	0.7	5.5	0.5	0.8

Note. CR, community respiration rate; CR^B, biomass-specific CR; BP, bacterial production; BA, bacterial abundance; BR, bacterial respiration rate; and CR:P_m: ratio of CR to P_m. Temperature data from Traving et al. (2016), nutrient and chlorophyll data from Bentzon-Tilia et al. (2015) and Knudsen-Leerbeck et al. (2017).

2.2. Biogeochemical Variables

Inorganic nutrient samples were frozen in 30 ml acid-washed plastic bottles and analyzed on a Scalar Continuous Flow Analyzer (San ++) as described previously (Grasshoff et al., 1983). Detection limits were 0.04, 0.1, 0.3, 0.06, and 0.2 μmol l^{-1} for nitrite (NO_2^-), nitrate (NO_3^-), ammonium (NH_4^+), ortophosphate (PO_4^{3-}), and dissolved silica (DSi), respectively. Samples for total nitrogen (TN) and total phosphorus (TP) measurements were collected in 30 ml brown glass bottles filled with Milli-Q water until just before sampling. Detection limits for TN and TP were 1.0 μmol Nl^{-1} and 0.1 μmol Pl^{-1}, respectively. Dissolved inorganic nitrogen (DIN) concentrations were calculated as the sum of NO_2^-, NO_3^-, and NH_4^+ concentrations.

Water samples of 100–500 ml for the analysis of Chlorophyll *a* (Chl *a*) were filtered in triplicate onto 25 mm Whatman glass microfiber filters (GF/F). Chl *a* was extracted in 10 ml 96% ethanol, stored at 4°C overnight (Jespersen & Christoffersen, 1987), and quantified fluorometrically with a Turner fluorometer calibrated against a Chl *a* standard. Water samples of 500–1,000 ml for particulate organic carbon (POC) and nitrogen (PON) were filtered in triplicate onto pre-combusted (3 hr, 450°C) 25 mm Whatman GF/F and stored at −20°C until analysis. Filters were dried for 24 hr at 40°C and analyzed on a Perkin Elmer 2400 CHNS analyzer. Time-weighted annual average values of environmental and biological variables in Table 1 were calculated by linear interpolation between data points. Data used in this study for TN, TP, DIN, dissolved inorganic phosphate (DIP), Chl *a*, temperature, and salinity are published in Bentzon-Tilia et al. (2015) and Knudsen-Leerbeck et al. (2017).

2.3. Photosynthesis and Community Respiration Measurements

Photosynthesis rates as a function of irradiance were determined by the ^{14}C-technique (Steemann Nielsen, 1952) in a linear incubator (Markager et al., 1999). Samples were incubated in 62 ml Nunc cell culture flasks for 2 hr at 12 irradiances to describe the photosynthesis-irradiance (*P-E*) relationship. Two dark bottles were used to subtract dark fixation rates (Markager, 1998). A liquid scintillation analyzer (Perkin Elmer Tri-Carb 2910 TR) measured the ^{14}C radioactivity collected on Whatman GF/F filters. The inorganic carbon concentration was determined by titration from pH and alkalinity measurements. Photosynthetic parameters were calculated using a saturating exponential model (Webb et al., 1974) modified by including an offset (c) for $E = 0$:

$$P = P_{\text{est}} \times \left[1 - \exp^{(-\alpha \times E/P_{\text{est}})}\right] - c \quad (1)$$

where P is the photosynthesis rate, α is the initial slope, and E is irradiance. The light-saturated photosynthesis rate (P_m) is calculated as $P_{\text{est}} + c$. The offset (c) was incorporated to avoid the bias in the estimate of α, which can result when the curve is forced through the origin (Markager et al., 1999). Biomass-specific values for P_m, α, and c (P^B_m, α^B, c^B) were normalized using Chl *a* concentration as a proxy for phytoplankton biomass.

Community respiration was determined from O_2 consumption measured continuously with optodes (Fire$\text{sting}O_2$-PyroScience) in replicate 60 ml glass bottles, following the methodology described in Mantikci et al. (2017). Luminescence quenching by O_2 is highly temperature dependent (Tengberg et al., 2006). Therefore, temperature was controlled using a water circulator and monitored by temperature sensors (resolution ±0.02°C) immersed in each bottle. This resulted in a temperature variability of ±0.05°C during the experiments. O_2 concentration measurements were corrected for temperature using the Firesting software. Respiration rates were calculated by linear regression of O_2 concentration versus 12 hr incubation time. Data for the first 15 min after filling the bottles were omitted, as the signal was unstable.

Q_{10}-values for P_m and CR were calculated separately for each station. Rates were log-transformed and plotted against ambient temperature to reveal the exponential relationship with temperature. Q_{10} was calculated from the slope of linear regression using the following equation:

$$Q_{10} = \left(\gamma_2/\gamma_1\right)^{(10/t_2 - t_1)} \quad (2)$$

where γ_1 and γ_2 are the rates at the two different temperatures, 15°C (t_2) and 5°C (t_1).

2.4. Bacterial Measurements

BR was determined by optodes from O_2 consumption in Whatman GF/C filtered water previously described in Traving et al. (2016). The rate was sometimes higher during the first 24 hr than the following days but was constant between 24 and 72 hr. Filtration-induced cell damage may introduce available bacterial substrates and cause a higher initial respiration rate (Aranguren-Gassis et al., 2012; Hopkinson et al., 1989). To correct for such an effect, bacterial production (BP) was measured in both unfiltered and size-fractionated samples using [^{3}H]-thymidine incorporation (Fuhrman & Azam, 1982), modified for micro-centrifugation (D. C. Smith & Azam, 1992), with data for unfiltered samples from Bentzon-Tilia et al. (2015). Factor (f) was calculated as the ratio between raw sample BP and BP after filtration (BP_{raw} and BP_{filt}, respectively). Corrected BR (BR_{cor}) was then calculated using the following equation:

$$BR_{\text{cor}} = \frac{BR}{f} \times Q_{10}^{T_{\text{CR}} - T_{\text{BR}}/10} \quad (3)$$

where T_{CR} was the incubation temperature in the CR assay, T_{BR} was the incubation temperature in the BR assay, and a Q_{10} of three was assumed since this applies to a short-term temperature response (Hansen & Bendtsen, 2014). The respiratory quotient for converting moles of O_2 to moles of carbon was assumed to be one.

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2.5. Statistical Analysis

Separate statistical analyses were conducted using Sigma Plot version 12.3 to explore relationships between biogeochemical variables, standing stocks, and volumetric rates at each station. Spearman's rank correlation coefficient (rho) was employed due to the potential nonnormal distribution of some data. We considered p-values less than or equal to 0.05 (significant) and less than or equal to 0.001 (highly significant) to indicate statistically significant correlations. This approach allowed us to identify potential associations between various parameters within the plankton community and the surrounding environment. Additionally, Model II regression was employed to examine the relationship between CR, Chl *a*, and temperature with all observed data collected from both stations. A nonlinear regression model was fitted using the PROC NLIN procedure in SAS 9.4. The model, based on Model II regression, accounted for the potential covariation between the predictor variables. It specified a nonlinear relationship between CR, Chl *a*, and temperature, with parameters estimated to quantify these relationships.

2.6. Estimation of Depth-Integrated Primary Production, Respiration, and Net Community Production

The depth-integrated (areal-specific) net primary production (NPP) was calculated according to the procedure in Lyngsgaard et al. (2014). Rates were calculated for the entire water column for RF (station depth 5 m). For GB, rates were integrated from surface to pycnocline, as volume-specific rates in and below the pycnocline most likely differ from the surface layer. Chl *a*-specific photosynthetic parameters (P^B_m, α^B, c^B) were interpolated between sampling days (monthly), and volume-specific values were obtained by multiplying with profiles of Chl *a* concentrations from the CTD-fluorescence profile (measured twice a month) at 0.1 m intervals (Chl a^F) as in Lyngsgaard et al. (2014). The volume-specific carbon uptake at each depth was calculated from Equation 1, with irradiance obtained from half-hourly surface irradiance values and the attenuation coefficients for PAR (K_d) was calculated using PAR sensor attached to the CTD. Surface irradiances were obtained from a meteorological station in Copenhagen about 40 (RF) and 110 km (GB) from the sampling sites. Eventually, the rates were summed over the water column and over the day to obtain a daily rate in mg C m^{-2} d^{-1}. All rates were resolved in half-hourly and 0.1 m depth intervals over the year using all available measurements and linear interpolation in time and space when necessary.

To calculate depth-integrated gross primary production (GPP) and NCP, it is necessary to estimate phytoplankton respiration, a component of CR. In this study, CR was assumed to have autotrophic and heterotrophic compartments. Since only CR and BR were measured, PR was estimated assuming that BR_{cor} represents the heterotrophic compartment. The depth-integrated values of BR, PR, and CR were calculated assuming:

$$\mathrm{CR} = \mathrm{PR} + \mathrm{BR} \tag{4}$$

and by dividing by CR, we obtain:

$$1 = k_p + k_b \tag{5}$$

where k_p and k_b are the fractions of CR performed by phytoplankton and bacteria, respectively. In this way, respiration by all planktonic organisms, such as microzooplankton and nanoplankton, was included in the calculation, although they were not identified separately. Annual values of k_p and k_b were calculated for each station to find the ratio between BR and CR. PR was normalized to Chl *a* (PR^B), and BR was assumed constant over depth. Both rates were corrected with temperature profiles of the water column (measured twice a month) using the observed Q_{10} values. Then, PR^B and BR were linearly interpolated over time as *P-E* parameters. Thus, the daily depth-integrated pelagic CR (mg C m^{-2} d^{-1}) was estimated according to.

$$\mathrm{CR} = \int_{t=0}^{24} \int_{z=0}^{z_{\max}} \left(\mathrm{Chl}\, a^F(z)\, \mathrm{PR}^B(z)\right) + \mathrm{BR}(z)\, dz dt \tag{6}$$

It is assumed that the ^{14}C method measures NPP then daily GPP and NCP (mg C m^{-2} d^{-1}) were calculated using the following equations:

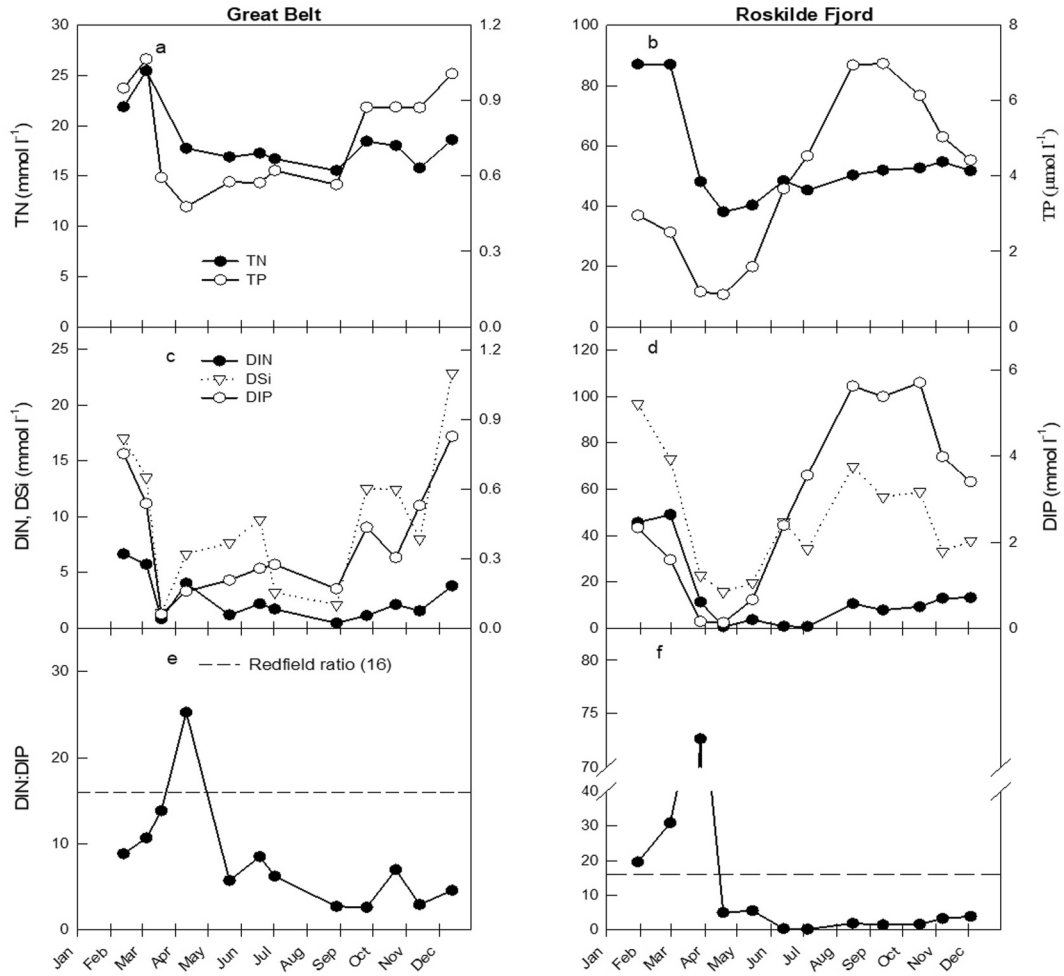


Figure 3. Seasonal variation in total nitrogen and total phosphorus (a and b), dissolved inorganic nitrogen (DIN), dissolved silica and dissolved inorganic phosphate (DIP) (c and d), the ratio of DIN to DIP (DIN:DIP) (e and f) at the two stations. Note the difference in scales between stations. Data from Bentzon-Tilia et al. (2015) and Knudsen-Leerbeck et al. (2017).

$$\text{GPP} = \text{NPP} + \text{PR}; \quad \text{NCP} = \text{GPP} - \text{CR} \tag{7}$$

3. Results

3.1. Environmental Parameters

Surface temperatures ranged from summer maxima of 17 and 21°C to winter minima of 0.4 and −0.6°C in GB and RF, respectively (Figures 2a and 2b). The water column in RF was always well mixed, whereas the GB was stratified, except in January (Figures 2c and 2d), with an average pycnocline depth of about 13 m ranging from 7 m in summer to 26 m due to alternating flow direction. Surface salinity values ranged from 10.8 to 23.7 in GB and from 11.9 to 13.3 in RF (Table 1 and Figures 2c and 2d). The average concentrations of TN, TP, DIN, DIP, and DSi were about three to eight times higher in RF compared to the GB (Table 1 and Figure 3). In GB, TN concentrations ranged from 15.55 to 25.46 µmol l^{-1}, TP from 0.48 to 1.07 µmol l^{-1}, DIN from 0.46 to 6.66 µmol l^{-1}, DIP from 0.06 to 0.83 µmol l^{-1}, and DSi from 1.41 to 22.86 µmol l^{-1}. In RF, TN ranged from 38.11 to 87.05 µmol l^{-1}, TP from 0.86 to 6.99 µmol l^{-1}, DIN from 0.64 to 49.05 µmol l^{-1}, DIP from 0.13 to 5.70 µmol l^{-1}, and DSi from 15.68 to 96.71 µmol l^{-1}. Both stations displayed a decline in dissolved inorganic nutrient concentrations (DIN, DIP, DSi) starting in March, reaching minima in spring. TN and TP exhibited a similar decreasing trend, initiating in March-April (Figures 3c and 3d). After reaching minima in spring,

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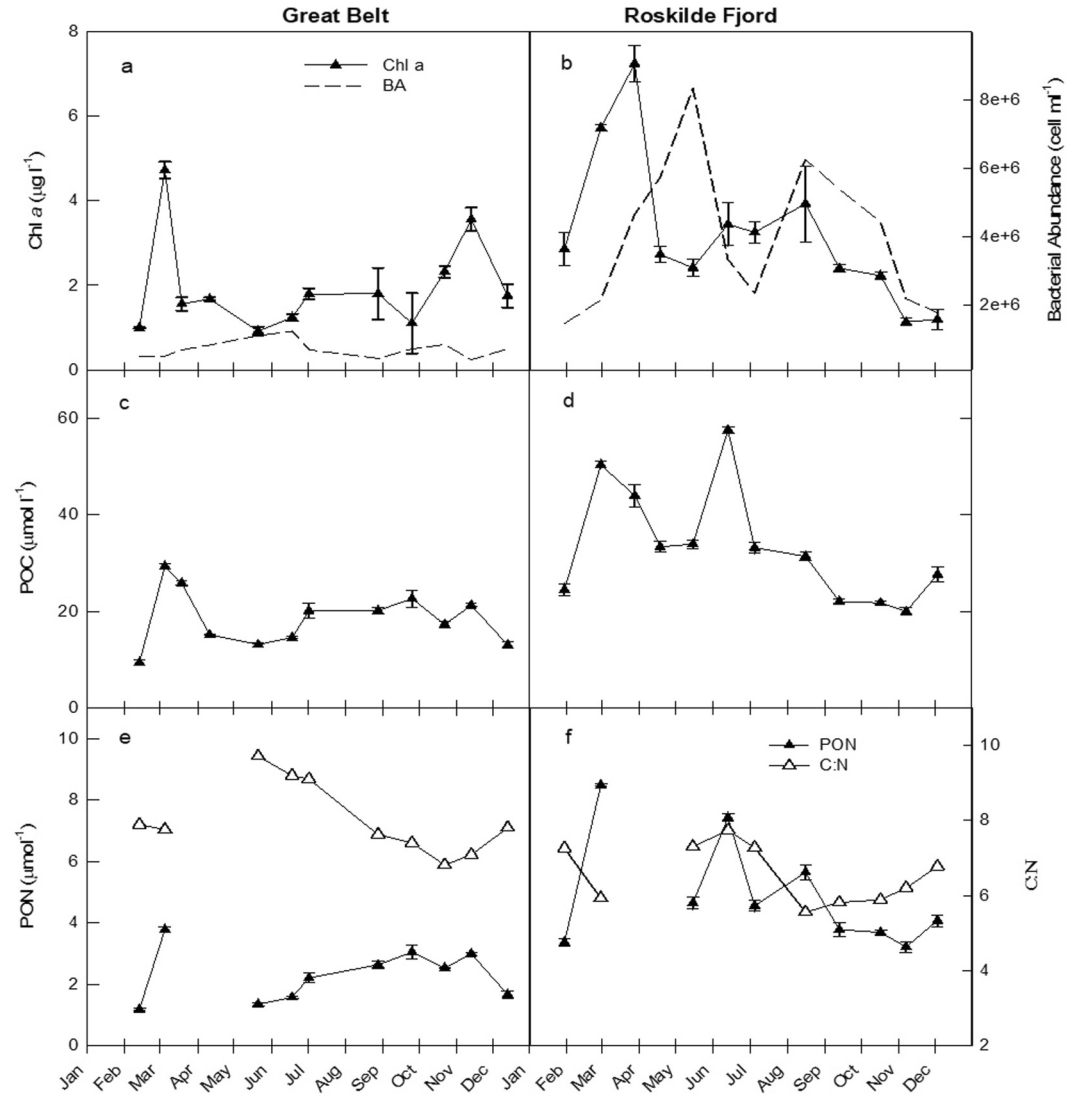


Figure 4. Seasonal variation in concentration of Chl *a* and bacterial abundance (BA) (a and b), particulate organic carbon (POC) (c and d), particulate organic nitrogen (PON), and the ratio of POC to PON (C:N) (e and f) at the two stations. Error bars show the standard deviation of replicates ($n = 3$). PON data for March and April were omitted due to measurement errors. BA plots from Bentzon-Tilia et al. (2015).

concentrations remained low until September in GB and increased toward the winter levels. DSi concentrations decreased from June to September and from November to December. In contrast, nutrient concentrations in RF increased over the summer to a maximum in September. However, DSi concentrations gradually decreased from August to November. DIN:DIP ratios ranged from 2.62 to 25.24 in GB and from 0.19 to 72.65 in RF (Figures 3e and 3f), where values were below 16 after a peak in spring.

Chl *a* concentrations varied from 0.92 to 4.7 µg l^{-1} in GB and from 1.13 to 7.2 µg l^{-1} in RF (Figures 4a and 4b). The average Chl *a* concentration in RF was 1.7 times higher than in the GB (Table 1). The first Chl *a* peaks were observed in early March for both stations, followed by a second peak in November in GB. In RF, Chl *a* concentrations were higher from June to August. Concentrations of POC ranged from 9.4 to 29.3 µmol C l^{-1} in GB and from 20 to 57.5 µmol C l^{-1} in RF (Figures 4c and 4d). POC concentration in GB was highest during March and then declined to about 15 µmol C l^{-1}. High POC concentrations (≥50 µmol C l^{-1}) were observed in RF on two occasions: at the end of February and again in June. PON concentrations varied from 1.2 to 3.8 µmol N l^{-1} in GB and from 3.2 to 8.5 µmol N l^{-1} in RF (Figures 4e and 4f), with peak concentrations similar to POC patterns. The C:N (molar) ratio of particulate organic matter varied from 6.8 to 9.7 in GB and from 4.8 to 6.6 in RF, with the

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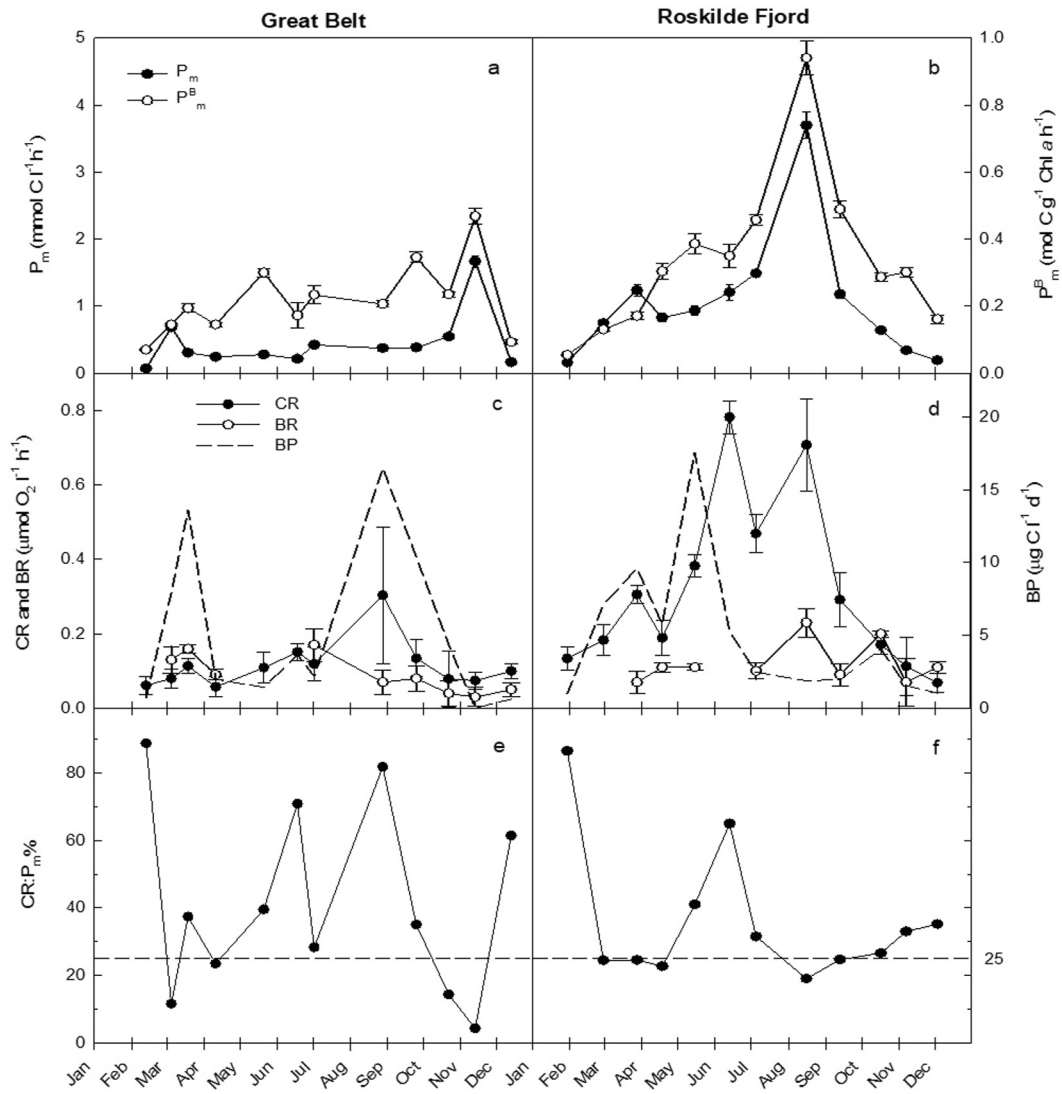


Figure 5. Seasonal variation in maximum photosynthesis (P_m) and Chl *a* normalized maximum photosynthesis rate (P^B_m) (a and b), community respiration (CR), bacterial respiration (BR, data from Traving et al. (2016)) and bacterial production (BP, data from Bentzon-Tilia et al. (2015)) (c and d), and the ratio of CR to P_m (CR:P_m%) (e and f) at the two stations. Error bars are standard error in panels (a and b) (often within the symbol) and standard deviation ($n = 6$) in panels (c and d). Dashed lines indicates CR:P_m% of 25 (e and f).

highest values in May-June at both stations (Figures 4e and 4f). The annual average was higher in GB (6.7) than in RF (5.5, Table 1).

In the GB, spring blooms occurred in March-April with a second bloom in autumn (October–November). RF, however, displayed blooms in late February-March and August, with the latter event potentially corresponding to an autumn bloom (Figure 3).

3.2. Photosynthetic Performance and Respiration Rates

The maximum photosynthetic rate, P_m, varied from 0.07 to 1.67 and from 0.15 to 3.70 µmol C l^{-1} h^{-1} in GB and RF, respectively, with the annual average being 2.6 fold higher in RF (Figures 5a and 5b and Table 1). Minor peaks in P_m were recorded at both stations in March, but the highest rates occurred in late summer-autumn (Figures 5a and 5b). Thus, a clear peak in the spring was absent. P_m exhibited contrasting seasonal patterns between the two sites. In GB, P_m remained relatively constant during summer, with the highest rates recorded in November. Conversely, in RF, P_m displayed a gradual increase, peaking in late summer. P_m values showed a

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Table 2
Bacterial Respiration (BR) and the BR to Community Respiration (CR) Ratio at the Two Stations

		μmol O_2 l^{-1} h^{-1}				
Station	Date	BR	BR_{cor}	BR_{cor}:CR %	f	ΔT(°C)
Great Belt	05/03/2012	0.13	0.13	163	1.0	0.3
	19/03/2012	0.15	0.16	142	1.0	−0.7
	11/04/2012	0.09	0.09	163	1.0	−0.9
	02/07/2012	0.40	0.17	143	1.9	1.9
	28/08/2012	0.09	0.07	24	1.0	1.7
	25/09/2012	0.07	0.08	62	1.0	−1.7
	22/10/2012	0.04	0.04	48	1.0	−0.1
	13/11/2012	0.03	0.03	36	1.0	0.6
	13/12/2012	0.08	0.05	54	1.6	−1.0
			Median	62		
			Mean	93		
Roskilde Fjord	28/03/2012	0.07	0.07	28	1.0	−1.6
	18/04/2012	0.18	0.11	68	1.4	−0.1
	15/05/2012	0.22	0.11	42	1.4	0.0
	05/07/2012	0.14	0.10	18	1.8	−0.9
	16/08/2012	0.15	0.23	5	7.5	−5.0
	13/09/2012	0.15	0.09	6	8.2	0.2
	17/10/2012	0.31	0.20	160	1.0	1.1
	07/11/2012	0.09	0.07	24	3.8	−0.7
	03/12/2012	0.18	0.11	169	1.6	0.2
			Median	28		
			Mean	58		

Note. ΔT is the difference in incubation temperature between CR and BR measurements, where negative values indicate that BR incubations were colder than CR incubations, and f is the ratio of bacterial production before and after filtration. BR_{cor} is the corrected BP rate according to Equation 3.

positive correlation ($p < 0.05$) with Chl *a* at both stations (Table A1). Additionally, P_m values correlated positively ($p < 0.001$) with in situ temperature and negatively ($p < 0.05$) with TN, but only in RF (Table A1). The seasonal pattern of $P^B{}_m$ showed many of the same features as P_m. $P^B{}_m$ showed an overall increase in GB from February to November but was relatively stable from May to October. The annual average $P^B{}_m$ and its variability were lower in GB (Figures 5a and 5b, Table 1). In RF, $P^B{}_m$ values followed the temperature with a pronounced peak of 0.94 mol C g^{-1} Chl *a* h^{-1} in August.

Values of volumetric CR varied from 0.06 to 0.30 μmol O_2 l^{-1} h^{-1} in GB and from 0.07 to 0.78 μmol O_2 l^{-1} h^{-1} in RF (Figures 5c and 5d). The annual average CR was 2.6 times lower in GB (Table 1) and was relatively stable over the year except for a peak in late August. In contrast, CR in RF showed a clear seasonal pattern with a winter minimum and summer maximum and a small peak in March coinciding with Chl *a* maxima. CR values exhibited a positive correlation ($p < 0.05$) with in situ temperature at both stations (Table A1). Additionally, CR values showed significant positive correlations ($p < 0.05$) with biomass-related variables (Chl *a*, POC, PON, and BA) (Table A1). Furthermore, a strong positive correlation ($p < 0.001$) was observed between CR and P_m values in RF. CR values also correlated with DIN and TN in RF, but only with DIN in GB (Table A1).

BR values varied without a clear pattern during the study, ranging from 0.03 to 0.17 in GB and from 0.07 to 0.23 μmol O_2 l^{-1} h^{-1} in RF (Figures 5c and 5d, Table 2). BR exceeded CR on four occasions in GB and twice in RF. BR values exhibited no significant correlations with other variables at either station. BR in percent of CR (BR_{cor}: CR%) ranged from 24% to 163% with a median of 62% in GB (Table 2) and from 5% to 169% with a median of 28% in RF. The CR to P_m (CR: P_m) ratio was highly variable during the year, without a clear seasonal

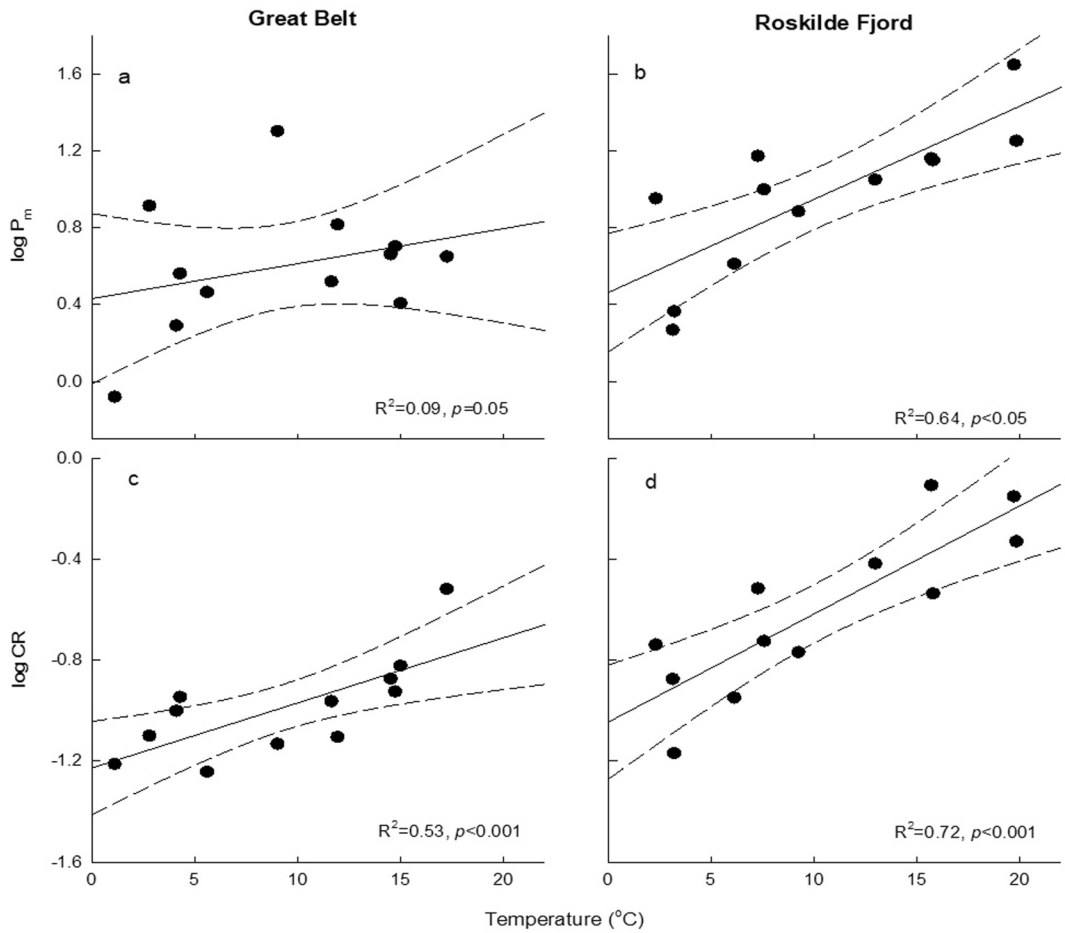


Figure 6. Log-transformed values for light-saturated photosynthesis rate (P_m) (a and b) and community respiration rate (CR) (c and d) versus temperature at the two stations. Dashed lines show 95% confidence intervals for the linear regression.

pattern at either station (Figures 5e and 5f). However, the lowest values (<25%) were observed during spring and autumn blooms at both stations. Annual averages were similar at the two stations (Table 1).

Temperature responses for the two rates, CR and P_m, were variable within and between the stations (Figure 6). In GB, Q_{10} values were 1.8 and 1.5 for CR and P_m, respectively, in RF these values were 2.7 and 3.0, respectively. In addition, p-values were lower for CR ($p < 0.001$) than for P_m ($p < 0.05$) for both stations (Table A1).

Community respiration rate has been shown to correlate with Chl *a* concentrations (Agusti et al., 2004; Satta et al., 1996) and temperature (Lomas et al., 2002; E. M. Smith & Kemp, 1995) in estuarine and coastal waters, and a model predicting the rates from Chl *a* and temperature was presented by (López-Urrutia & Morán, 2007). In this study, CR at the two stations could be predicted from the Chl *a* concentration and temperature (T) (Figure 7), by the equation:

$$CR = Chl\,a \times (0.0254) \times \exp^{(T \times (0.101))} \quad (8)$$

The R^2 for the model was 0.90 ($n = 24$). The residuals did not correlate with any of the other variables ($p > 0.05$).

3.3. Depth-Integrated Primary Production, Respiration, and Net Community Production

NPP was 143 g C m^{-2} y^{-1} for the mixed layer in GB and 145 g C m^{-2} y^{-1} for the entire RF water column (Table 3). In GB, a spring bloom in March followed low productivity in April (Figure 8a) and a gradual increase

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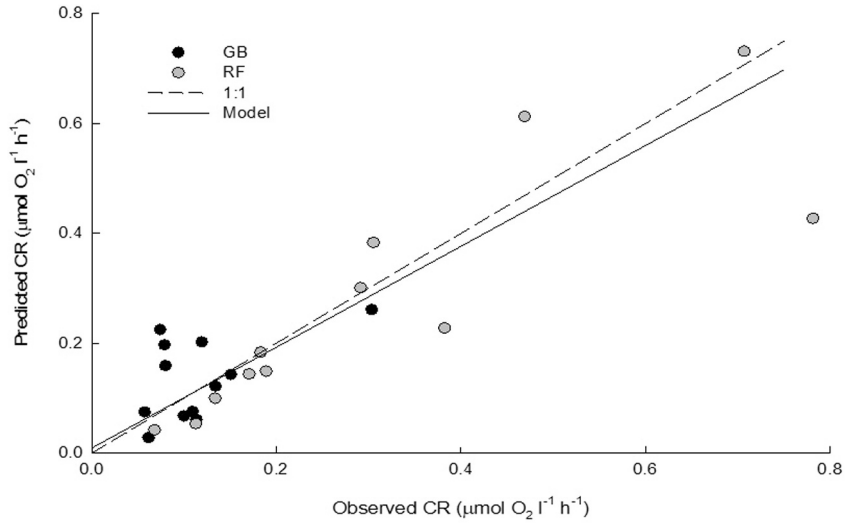


Figure 7. Comparison of predicted (from Equation 8) and observed community respiration rate (CR) in the Great Belt and Roskilde Fjord. The model slope is 0.918, intercept −0.009, and $R^2 = 0.90$.

with three peaks in August, October, and November. There was a gradual increase in RF until September, but with several large oscillations. The spring bloom was only present with a small peak in late March. Overall, primary production in RF followed the annual variation in surface irradiance and temperature, with a peak in August (Figure 8b). The depth-integrated CR exceeded NPP in the mixed layer of GB and was roughly equal to it over the entire water column in RF, with values of 165 and 147 g C m^{-2} y^{-1}, respectively (Table 3). The seasonal pattern in CR largely mirrored the production. However, deviations could be seen, for example, during spring blooms and during the November production peak in GB (Figures 8a and 8b), where CR was low despite a high NPP, resulting in periods with a positive NCP. The depth-integrated annual estimated NCP (Equation 7) was positive (net autotrophic) at both stations: 45 and 99 g C m^{-2} y^{-1} in GB and RF, respectively (Table 3). Seasonal pattern in NCP mirrored GPP. NCP was negative (net heterotrophy) from January until the spring bloom in March and December, as respiration exceeded NPP in both stations (Figure 8). NCP was consistently estimated positive in summer and the rest of the year. Although NPP was similar in the two systems, the differences in GPP and CR seemed to have affected the NCP in the pelagic system (Table 3). GPP was slightly higher while CR was marginally lower, in the more eutrophic RF.

Table 3
The Annual Depth-Integrated Net Primary Production (NPP), Community Respiration (CR), Phytoplankton Respiration (PR), Bacterial Respiration (BR), Gross Primary Production (GPP), and Net Community Production (NCP) for the Great Belt and Roskilde Fjord

	g C m^{-2} y^{-1}	
	Great Belt	Roskilde Fjord
GPP	210	245
NPP	143	145
CR	165	147
PR	67	101
BR	98	46
NCP	45	99

4. Discussion

4.1. Seasonal Dynamics of Nutrients

Both the GB and RF, located within the Baltic Sea system, exhibit seasonal phytoplankton blooms with differing timing and nutrient dynamics (Wan et al., 2011). The GB displayed low DIN:DIP ratios during the spring and autumn blooms, even below a N:P ratio of 16:1, suggesting potential N limitation. This aligns with ratios as low as 6:1 observed in the Baltic Proper during spring blooms (Wan et al., 2011). In contrast, RF exhibited a DIN:DIP ratio exceeding 30 during the spring bloom, indicative of N excess. However, by August, the DIN:DIP ratio dropped below two, despite a relatively high DIP, suggesting co-limitation. Post-bloom oscillation of DSi suggests an importance of diatoms in both sites (Conley et al., 2000), though potentially less pronounced in RF (Bendtsen et al., 2024; Haraguchi et al., 2022; Henriksen, 2009). Notably, vertical mixing likely fuels the GB's autumn bloom by transporting sediment nutrients upwards (Bendtsen et al., 2024).

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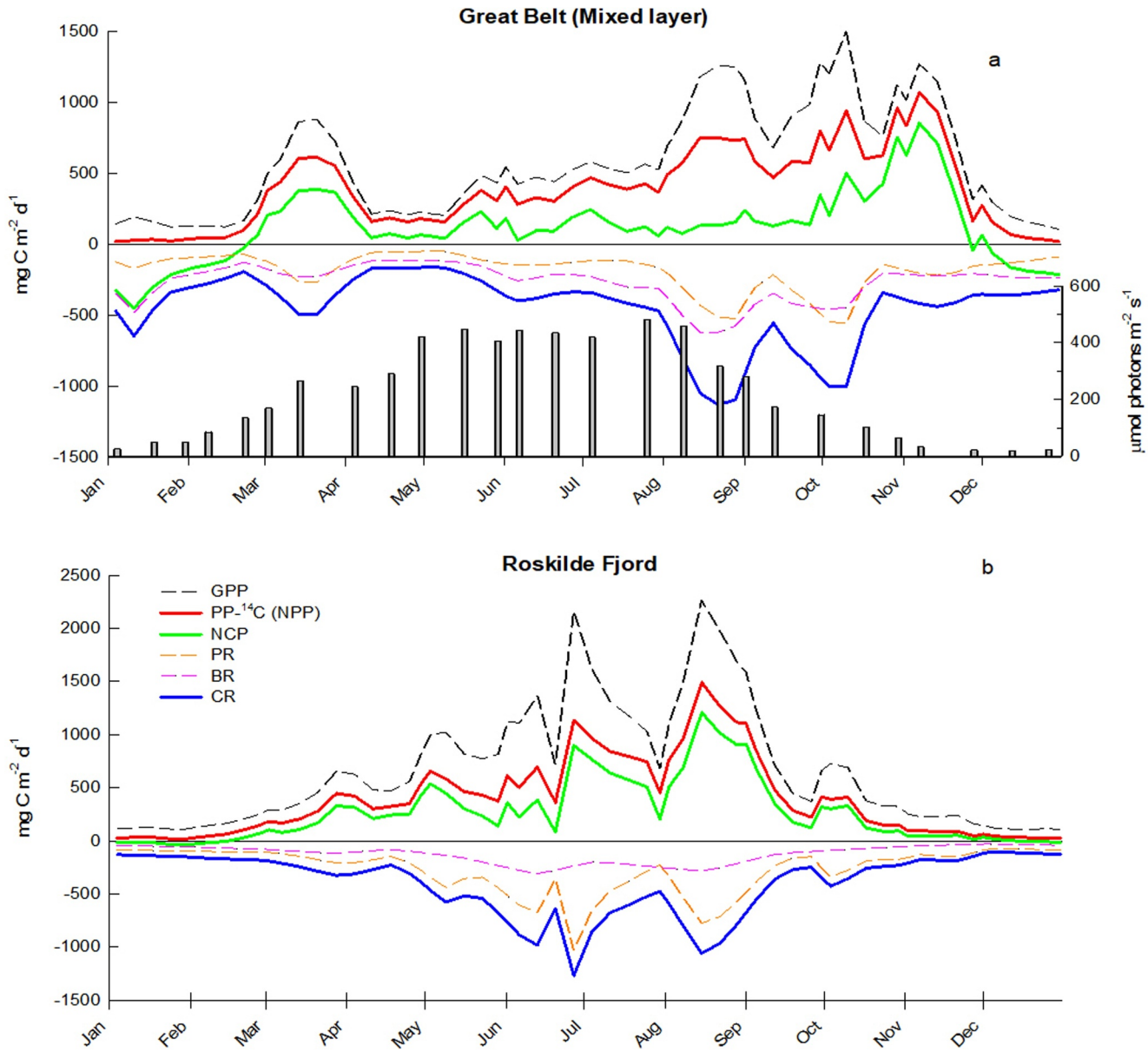


Figure 8. Seasonal variation in weekly average estimated rates of depth-integrated production and respiration (negative values) in the Great Belt's upper mixed layer (a) and Roskilde Fjord's entire water column (b). Biweekly average surface irradiances (photosynthetically active radiation) during the study area (a). Note the difference in scale between stations.

4.2. Plankton Metabolism

Seasonal variations in physical and biochemical characteristics significantly impacted plankton community metabolism within both RF and the GB. However, the magnitude and timing of these effects displayed distinct spatial heterogeneity. In RF, characterized by eutrophic conditions, lower water renewal rates, shallower depth, and a lack of stratification, the variability in plankton metabolism was more pronounced compared to the GB. As expected, disparities in nutrient richness between the stations were reflected in standing biomasses. RF exhibited approximately twice the levels observed in GB, highlighting the role of nutrients in shaping biomass. However, this finding underscores the multifaceted nature of factors influencing biomass. Additional environmental variables such as grazing pressure, light availability, and turbulence likely exert significant influence on the final measured biomass at a given time point. Similarly, a complex interplay of factors is likely responsible for shaping metabolic process rates.

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In both sites a clear link between nutrient dynamics and metabolic activity was observed. The changes in nutrients and standing biomasses coincided with increased CR during the spring bloom, supporting established findings on the positive relationship between blooms and CR (e.g., Iriarte et al., 1991; Md Amin et al., 2012). The negative significant relationship between DIN and CR can be further explained by the fact that DIN is readily utilized by phytoplankton during production, leading to increased CR as labile organic matter becomes available both for heterotrophs and autothrophs (Mantikci et al., 2017, 2020; Sadro et al., 2011, 2014). The observed discrepancies in biomass-specific rates and ratios suggest the influence of additional factors beyond nutrient availability on CR. These factors may include the trophic dominance of the plankton community (autotroph-vs. heterotroph-dominated) and the availability of different sources of organic matter, both produced within the system (autochthonous) and derived from external sources (allochthonous).

The CR values reported here are in good agreement with previous values from the same areas and other estuaries (Hopkinson & Smith, 2005; Kruse & Rasmussen, 1995). While our CR values in RF appear lower than earlier findings (Jensen et al., 1990) the difference is likely resolved when considering biomass-normalized respiration rates. RF experienced a threefold reduction in Chl *a* concentration after local loadings decreased by 81% for phosphorus and 57% for nitrogen since the mid-1980s (Pedersen et al., 2014). Staehr et al. (2017) found a significant decrease in water column respiration and sediment O_2 uptake since 1997. Our findings suggest that differences in eutrophic status significantly affect both photosynthetic and respiratory processes in these coastal regions. RF, characterized by its eutrophic conditions, showed strong relationships between photosynthetic rates, CR, and other variables, with biomass-specific metabolic rates notably higher compared to GB. These observations suggest distinct metabolic strategies within the plankton communities. In RF, the higher P^B_m values indicate that phytoplankton might be more adept at carbon assimilation. This could be due to factors like species composition optimized for nutrient utilization in eutrophic conditions or environmental factors like temperature. In addition, higher CR^B values in RF, compared to GB, further support this notion. The elevated respiration rates suggest a more active heterotrophic compartment in RF, likely fueled by the higher primary production and potentially a different microbial community structure adapted to decompose organic matter efficiently.

BR is often assumed to comprise 30%–50% of CR in marine surface waters (Aranguren-Gassis et al., 2012; Hopkinson & Smith, 2005). BR showed indications of increasing biomass-specific rates (k_b, Equation 5) with decreasing phytoplankton biomass. The lower BR in RF compared to GB aligns with findings by Jensen et al. (1990) and Sand-Jensen et al. (1990) that noted reduced BR relative to CR in areas with higher phytoplankton biomass. Besides, Pringault et al. (2009) and Hitchcock et al. (2010) found that heterotrophs dominate CR when phytoplankton biomass is low. The seasonal pattern observed in our study supports this, as low values in both sites, equal to high net production, were observed during phytoplankton blooms. Although the yearly average values were the same for the two stations, low values were observed more often in RF than in GB, suggesting a higher contribution of respiration by autotrophs (Iriarte et al., 1991) in RF.

Several factors may contribute to the observed differences in plankton dominance and CR between the two regions. One reason might be a shift in the carbon source fueling BR. In both sites, the yearly average of BP was similar and significantly correlated with POC. However, RF exhibited higher nutrient concentrations associated with increased BA. Bacterioplankton enzymatic activities were higher in RF (Traving et al., 2016), likely reflecting a preference for fresher, phytoplankton-derived dissolved organic matter compared to the aged and photodegraded organic material in the GB. However, (Asmala et al., 2018) suggest a more complex interaction, where nutrient richness in RF stimulates phytoplankton extracellular release of dissolved organic matter, further fueling bacterial consumption. Furthermore, while more heterotrophic species, such as re-suspended sediment bacteria, predominate in RF, communities such as cyanobacteria adverted from the central Baltic Sea dominated in GB (Bentzon-Tilia et al., 2015). Differences in phytoplankton species composition in both sites may also affect both phytoplankton derived organic matter and heterotrophic respiration. For example, RF is known to be dominated by small flagellates (Haraguchi et al., 2022), whereas the GB is dominated by diatoms (Bendtsen et al., 2024). Given that small-celled phytoplankton enhance P^B_m (Edwards et al., 2015), the higher production observed in RF can likely be attributed to this dominance. This increased production may further influence the interactions within the microbial loop, affecting bacteria feeding on dissolved organic matter and microzooplankton grazing on phytoplankton. Consequently, these altered interactions could lead to distinct microbial loop patterns in the carbon cycle, ultimately impacting CR. A study using mesocosm experiments in a Norwegian fjord showed that during the spring bloom, microzooplankton and nanoplankton have carbon requirements equivalent to more than half of primary production, while bacterioplankton are intermediate and variable (Md

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Amin et al., 2012). Perhaps because of this, the role of other heterotrophs in CR outweighs that of the bacterial compartment, which may explain why we were unable to detect significant seasonal differences. In addition, advection and mixing of water masses and, thereby, mixing of different organic matter sources (Asmala et al., 2018) may uncouple BR, BP, and BA in coastal systems (del Giorgio & Cole, 1998). Importantly, both our findings and those of previous studies (Griffith et al., 1990; Iriarte et al., 1991) highlight the variability of bacterial contribution to CR. This contribution can range from as low as 10% during phytoplankton blooms to over 80% during winter or bloom collapse (Iriarte et al., 1991).

4.3. Effect of Temperature on Metabolism and Predicting Community Respiration

Seasonal variations in water temperature significantly impact planktonic metabolism as indicated by the regulation of metabolic rates across diverse marine systems (Hansen & Bendtsen, 2014; Sampou & Kemp, 1994). The Q_{10} values measured in our study are consistent with earlier reports from similar coastal environments (Lomas et al., 2002; Robinson & Williams, 1993). Higher nutrient and organic matter concentrations and bioavailability in RF (Knudsen-Leerbeck et al., 2017) caused a more pronounced temperature sensitivity of the metabolic rates, seen as high Q_{10} values (López-Urrutia & Morán, 2007; Marañón et al., 2014). Lower Q_{10} values for GB compared to RF suggest lower internal enzyme concentrations within GB phytoplankton cells. This difference could reflect the higher degree of nutrient limitation experienced in GB, as enzyme production is often energy-intensive (Markager et al., 1999). Traving et al. (2016) showed that extracellular enzyme rates were higher in RF compared to the GB. Thus, over the season, the observed effect of higher temperatures during summer may be counteracted by more pronounced nutrient limitation, which constrains the metabolic process rates. This mechanism is probably more pronounced in GB than in RF. A general consequence is that Q_{10} values calculated from relationships between community process rates and seasonal temperature will likely be lower than such values observed under nutrient-replete conditions. This agrees with previous studies (López-Urrutia & Morán, 2007; Marañón et al., 2014; Pomeroy & Wiebe, 2001) where resource limitations played a significant role in controlling both phytoplanktonic and bacterial processes. Therefore, Q_{10} values derived from seasonal studies under nutrient limitation should be considered minimum estimates. Coastal systems are inherently more sensitive to temperature increases due to their shallowness. They may therefore respond differently to warming compared to deeper oligotrophic oceans, with their trophic status further influencing the responses (Gattuso et al., 1998; Giraud et al., 2008).

Plankton respiration is measured much less frequently than primary production (Robinson & Williams, 2005). Therefore, predicting CR from models using more frequently measured parameters is convenient. Temperature regulates metabolic rates (Lomas et al., 2002) and is a good predictor of pelagic respiration rates (Hansen & Bendtsen, 2014). Studies have shown a significant correlation between Chl *a* and respiration rate (Agusti et al., 2004; Satta et al., 1996), but this alone may not be sufficient to explain respiration rate variability in estuaries and marine waters (del Giorgio & Williams, 2005). Phytoplankton can contribute substantially to CR (Iriarte et al., 1991), as discussed above. However, the relative importance of phytoplankton versus heterotrophic respiration can vary depending on ecosystem characteristics, such as difference in the supply of organic matter (Mantikci et al., 2017, 2020; Sadro et al., 2011, 2014). High phytoplankton biomass, as estimated from Chl *a*, suggests a greater supply of labile organic matter from phytoplankton cells or exudates (Thornton, 2014). This organic matter input can fuel both heterothrophic and autotrophic respiration. Our model (Equation 8, Figure 7) can describe CR across the two study sites, even though CR is not significantly correlated to Chl *a* in GB. Deviations from the model could be explained by the variation in BR_{cor}:CR and CR:P_m ratios mentioned above. The highest respiration rate in this study was underestimated by our model. An explanation could be that the BR was enhanced by the high concentration of POC relative to Chl *a*, which could also be seen from the high value of CR:P_m in the sample. Four observations from the GB which clustered above the 1:1 line (CR lower than expected) are all from days with low CR:P_m values, suggesting a healthy, growing phytoplankton community, and that CR was dominated by phytoplankton (Iriarte et al., 1991). Another potential explanation, as previously mentioned, is that CR^B was lower in GB. This could be due to variations in phytoplankton diversity and their carbon source utilization patterns. Comparing measurements across different seas might allow for a more comprehensive understanding of how plankton diversity influences respiration processes. Consequently, this approach should lead to more accurate estimations of CR.

4.4. Depth-Integrated Metabolic Rates in the Mixed Layer

In RF, the two-fold higher NCP compared to GB can be attributed to a deeper mixed layer affecting light penetration and consequently, both production and respiration rates. This sensitivity of NCP to even minor changes in process rates is particularly seen during seasonal blooms, when primary production exceeds CR. These findings align with those of Staehr et al. (2018), who documented similar metabolic dynamics in RF. Conversely, in the GB, reduced nitrogen loading has led to lower NPP compared to previous years, underscoring the crucial role of nitrogen in regulating primary production (Lyngsgaard et al., 2014). Nidzieko's (2018) modeling study suggests that pelagic metabolism in coastal waters is influenced by ecosystem size and residence time, with nutrient limitations leading to shifts toward autotrophy and altered metabolic rates. Our results in RF support this model, showing higher NCP in a smaller, shallower environment with extended nutrient residence times, indicative of a system skewed toward net autotrophy influenced by high nutrient and organic carbon availability.

The methodological differences in these measurements and calculations may also significantly impact the results. For example, in this study, only surface sampling was used to extrapolate the mixing zone metabolism with certain assumptions, and the contribution of the benthic ecosystem to the NCP could not be taken into account, especially in the very shallow RF, considering the effect of the benthic metabolism on the whole net ecosystem production (Staehr et al., 2018). On the other hand, we believe it is a general phenomenon in coastal seas and estuaries that the estimated primary production in pelagic systems is insufficient to account for the estimated carbon sinks (Sandberg et al., 2004; Serret et al., 1999). Besides, we employed a 2 hr incubation period for the ^{14}C measurements. While this falls within the range of "short-term" incubations, previous studies suggest that short incubations might not always accurately reflect NPP (Halsey et al., 2013; Milligan et al., 2015). We acknowledge this limitation and its potential to lead to an overestimation of NPP in our results, particularly for phytoplankton communities with a high abundance of respiring species.

5. Conclusion

Biogeochemical differences in the two coastal systems directly affected the volumetric primary production and respiration rates but had less effect on biomass-specific rates. Nutrient availability significantly affected community activity with temperature, as seen in RF. Therefore, we were able to estimate CR using Chl *a* and temperature. Bacterial contribution to CR varied over the season and stations mainly due to varying carbon sources and plankton diversity. While the decoupling between BR, BP, and BA made it difficult to precisely quantify the trophic balance within CR, our methods did reveal the presence of both autotrophic and heterotrophic dominance at different times. The biogeochemical changes caused by the seasons in both sites and especially the effects of phytoplankton blooms on plankton metabolism and production in the pelagic mixed zone were shown. Studying plankton metabolism only in surface water has likely introduced errors in the estimation of the entire water column. Therefore, the results should be interpreted with this limitation in mind. It is recommended for future studies that studies of plankton metabolism and ecosystem net production should be conducted temporally, regionally, and with high-frequency sampling to cover the entire study area. These findings highlight the complex interplay between nutrients, plankton communities, and carbon cycling in coastal ecosystems. This knowledge is crucial for informing sustainable management practices that maintain healthy marine environments in a changing climate.

Appendix A

This appendix provides additional details and results of the statistical analyses performed as described in the Methods section of the manuscript (Table A1). Analyses were conducted using SigmaPlot version 12.3 to assess relationships between biogeochemical variables, standing stocks, and volumetric rates across various stations. Spearman's rank correlation coefficient (rho) was used to determine the correlations due to the non-parametric nature of some of the data sets, which potentially deviate from a normal distribution. This non-parametric method is suitable for ordinal data or continuous data that do not meet the assumptions required for parametric tests.

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Table A1
Spearman Rank Correlation Coefficients for the Correlations Among Variables for the Two Stations

Great Belt															
	P_m	BR	BP	BA	Chl *a*	POC	PON	C:N	TN	TP	DIN	DIP	DSi	CR:P_m	*T*
CR	0.02	0.32	0.61*	0.14	−0.15	0.25	0.10	0.27	−0.38	−0.31	−0.65*	−0.32	−0.34	0.41	0.73*
P_m		−0.20	0.25	−0.32	0.72*	0.77*	0.79*	−0.60	−0.26	0.18	−0.32	0.03	−0.20	−0.80**	0.22
BR			0.38	0.02	−0.33	0.33	0.14	0.71	0.21	−0.25	0.05	−0.45	−0.38	0.18	−0.07
BP				0.01	0.11	0.62*	0.49	−0.24	−0.01	−0.22	−0.50	−0.50	−0.41	0.08	0.41
BA					−0.46	−0.38	−0.36	0.41	0.12	−0.26	0.09	−0.27	0.07	0.07	0.29
Chl *a*						0.52	0.72*	−0.62*	−0.10	0.27	0.06	0.20	−0.03	−0.64*	0.01
POC							0.95**	−0.53	−0.15	0.06	−0.43	−0.21	−0.34	−0.57*	0.11
PON								−0.70*	−0.02	0.20	−0.31	0.08	−0.05	−0.66*	0.10
C:N									0.03	−0.29	0.21	−0.24	−0.12	0.48	0.03
TN										0.76*	0.72*	0.65*	0.87**	0.01	−0.71*
TP											0.45	0.87**	0.79**	−0.20	−0.59*
DIN												0.55	0.66*	−0.06	−0.61*
DIP													0.90**	−0.06	−0.46
DSi														0.05	−0.48
CR:P_m															0.11

Roskilde Fjord															
	P_m	BR	BP	BA	Chl *a*	POC	PON	C:N	TN	TP	DIN	DIP	DSi	CR:P_m	*T*
CR	0.91**	0.19	0.47	0.61*	0.62*	0.59*	0.67*	0.18	−0.59*	−0.01	−0.62*	−0.05	−0.13	−0.18	0.80**
P_m		0.06	0.41	0.63*	0.60*	0.46	0.61	−0.08	−0.60*	0.11	−0.55	0.06	−0.20	−0.45	0.85**
BR			−0.02	0.37	0.07	−0.03	0.58	−0.25	−0.16	0.17	−0.18	0.34	0.43	−0.19	0.22
BP				0.55	0.45	0.71*	0.65*	0.25	−0.55	−0.59*	−0.37	−0.56	−0.46	−0.28	0.18
BA					0.13	0.18	0.27	−0.19	−0.67*	−0.02	−0.63*	−0.05	−0.45	−0.46	0.63*
Chl *a*						0.76*	0.81*	0.04	−0.18	−0.38	0.03	−0.39	0.20	−0.36	0.15
POC							0.92**	0.52	−0.48	−0.66*	−0.20	−0.67*	−0.19	−0.09	0.08
PON								0.15	−0.44	−0.36	−0.16	−0.38	0.10	−0.27	0.27
C:N									−0.42	−0.71*	−0.39	−0.69*	−0.47	0.83**	−0.07
TN										0.40	0.80**	0.41	0.78*	0.19	−0.54
TP											0.05	0.97**	0.46	−0.05	0.46
DIN												0.06	0.57	0.08	−0.71*
DIP													0.48	−0.04	0.41
DSi														0.04	−0.17
CR:P_m															−0.21

Note. See Table 1 and text for abbreviations and units. *$p < 0.05$, **$p < 0.001$.

Data Availability Statement

The observation and experimental data used for plankton metabolism and environmental conditions in the study are available at Zenodo with Creative Commons Attribution 4.0 International license (CC-BY-4.0) (Mantikci, 2015; https://zenodo.org/doi/10.5281/zenodo.10178777).

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Erratum

The originally published version of this article contained typographical errors in Equation 8. The numbers 384 and 385 should be deleted from the equation. The errors have been corrected, and this may be considered the authoritative version of record.

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