Significance of pelagic and benthic primary production in two shallow coastal lagoons of different degrees of eutrophication in the southern Baltic Sea

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ABSTRACT: Primary production by pelagic and benthic microalgae was measured in 2 shallow coastal lagoons in the southern Baltic Sea by *in situ* and laboratory incubations to quantify the significance of these 2 major groups of primary producers in absolute and relative terms. Pelagic primary production rates per volume at saturating light conditions were 7 to 12 times higher at the polytrophic location Kirr-Bucht (Darss-Zingst Bodden) than at the meso-/eutrophic location Rassower Strom (Nordrügensche Bodden). Chlorophyll *a* specific primary production rates, however, were in the same range at both locations, except for 1 situation in spring which is explicitly discussed. The pelagic chlorophyll *a* specific maximum light utilization coefficient (α^*) tended towards higher values in Kirr-Bucht samples, which can be interpreted as an adaptation to a lower supply of irradiance. Pelagic and benthic primary production varied seasonally, with highest rates occurring in June/July. A calculation of short-term variability due to cloud-modulated availability of irradiance revealed reductions of pelagic and benthic gross production (GP) rates on overcast days, compared to bright days, in the range of 26 to 69 % and 62 to 82 %, respectively. Net community production (NP) rates were more severely reduced than GP rates on overcast days. Benthic NP was generally reduced to below zero on overcast days, whereas it was mostly positive on bright days at both locations. To evaluate the significance of the different optical properties of both types of water (diffuse vertical attenuation coefficient, k = 3.3 to 3.7 and 0.5 to 0.7 m^{-1} at Kirr-Bucht and Rassower Strom, respectively) for primary production, the benthic and pelagic contributions at both sites were calculated regarding a water depth of 2 m, which is about the mean depth of the Bodden systems. This standardization revealed obvious differences in basic conditions for primary production which remained undetected when the comparison of the 2 sites was based on the water depths in which the *in situ* incubations had been carried out (0.6 and 3.4 m at Kirr-Bucht and Rassower Strom, respectively). In meso-/eutrophic Rassower Strom at a depth of 2 m, benthic GP would contribute about 30 to 45 % to the total GP of microalgae, depending on weather conditions and seasons. At the same depth in polytrophic Kirr-Bucht, the microalgae on the sediment surface would account for only 0.3 % or less of total GP. This demonstrates that optical properties of the water, which are closely related to the trophic state of the system, exert strong control on varying proportions of productivity, attributable to planktonic versus benthic microalgal communities. It can be concluded from the modeled data that the difference between both locations will be most prominent during periods of low supply of radiant energy, like on overcast days.

KEY WORDS: Primary production · Phytoplankton · Microphytobenthos · Irradiance · Eutrophication · Estuary · Baltic Sea

INTRODUCTION

The proportions of primary production attributable to benthic versus pelagic microalgal communities are highly variable among different types of aquatic systems. In deeper waters where the benthic zone is aphotic, pelagic primary production comprises 100 % of the system production and supports all of the heterotrophic activity of the benthos (Graf 1989, Trimmer et al. 1999, Ziegler & Benner 1999). Shallower systems like coastal lagoons may have a very different trophic status. Ziegler & Benner (1998) found that the water

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column in a seagrass-dominated lagoon was strongly net heterotrophic and largely dependent upon benthic primary production during most of the year. There is much evidence that the balance between benthic and pelagic primary production in shallow coastal water systems is heavily influenced by shifts in nutrient supply. Assemblages of primary producers found in estuarine waters often change if increased anthropogenic nutrient loads from coastal watersheds stimulate eutrophication (Fong et al. 1993, Kinney & Roman 1998, McClelland & Valiela 1998, Paerl et al. 1998). The general pattern of changes in benthic vegetation accompanying eutrophication is from rooted macrophytes at low nutrient availability to domination by epiphytic and water column algae (Frankovich & Fourqurean 1997). In particular in estuaries with a long residence time of water, phytoplankton may become dominant. Increased phytoplankton causes shading and can exclude benthic producers (Valiela et al. 1997).

While measurements of pelagic primary production are numerous and have a long tradition (e.g. Gessner 1940, Steemann Nielsen 1975, Talling 1984, Li & Maestrini 1993, Hübel et al. 1998), primary production of benthic microalgae inhabiting permanently submersed sediments has gained increasing interest during the past decades (Nienhuis & de Bree 1984, Wasmund 1984, Rizzo et al. 1992, Cahoon et al. 1993, MacIntyre et al. 1996). However, there remain few studies comparing the contribution of both benthic and pelagic microalgae to total primary production of non- or subtidal aquatic ecosystems (e.g. Grøntved 1960, Wasmund 1986, Schreiber & Pennock 1995, MacIntyre & Cullen 1996).

The present paper describes *in situ* and laboratory measurements of primary production of benthic and pelagic microalgae in 2 non-tidal shallow coastal inlets of the Baltic Sea exhibiting different degrees of eutrophication. The object of this study was to quantify the relative contributions of benthic and pelagic primary production to the total primary production of microalgae in these waters.

Eutrophication primarily acts on autotrophic communities by elevated nutrient supply, promoting fast-growing species with high uptake rates for nutrients (Pedersen & Borum 1997, Valiela et al. 1997). As a consequence of dense phytoplankton populations and subsequent detritus production, water transparency can be severely diminished. The attenuation of PAR depends on concentrations of particulate (phytoplankton, suspended matter) and dissolved (humic acids, 'Gelbstoff') substances in the water, and is closely related to the trophic state of the ecosystem. In productive waters, planktonic algae may be present in concentrations such that by self shading they limit their own growth (Kirk 1994). All the more, phytoplankton

can be a serious light-limiting factor for the development of benthic algae, even in very shallow waters. Since the attenuation of PAR in water, besides the presence of absorbing substances, depends very much on the length of the absorbing water column, water depth always has to be taken into account when relations between benthic and pelagic primary production are discussed. In the present paper, the problem of different water depths at the study sites was addressed by modeling primary production for equal water depths (standardized depth of 2 m), to achieve a comparability of the ratios of pelagic and benthic primary production at the study sites. Provided that variabilities in production due to differences in water depth are eliminated, the quantitative relation between pelagic and benthic primary production can contribute to a characterization of the ecological state of the aquatic system.

The second focus of the present paper deals with the influence of variability in irradiance supply on pelagic and benthic primary production. The photon flux impinging on the water is a highly dynamic and variable factor affecting aquatic photosynthesis. The paper presents calculations of the effect of short-term changes due to cloud coverage on the relative significance of benthic and pelagic primary production. For this purpose, primary production rates of both components were modeled, taking into account conditions of irradiance during bright and overcast days. The importance of this ecological variable was pointed out earlier by Riegman & Colijn (1991), who found that variation in cloudiness could affect rates of pelagic primary production by a factor of up to 4.5.

MATERIALS AND METHODS

Study sites. The sampling locations Rassower Strom and Kirr-Bucht are part of 2 different systems of shallow estuarine basins, located in the southern coast of the Baltic Sea (Fig. 1). Rassower Strom is located in the outer part of the Nordrügensche Bodden, which cover an area of about 154 km^2 (Correns 1976). The gradient in salinity ranges from about 10 (PSU) at the outlet to the Baltic Sea to about 5 in the inner parts (Dahlke 1994). A steep gradient in inorganic nutrient concentrations, inverse to the gradient in salinity, causes a high degree of eutrophication in the inner parts of the Bodden while the outer parts are only moderately eutrophied (Köster et al. 1997, Hübel et al. 1998). Kirr-Bucht is a small shallow basin, located in the central part of the Darss-Zingst Bodden, which cover a total area of about 200 km^2. The salinity gradient ranges from 9 to 10 at the outlet to the Baltic Sea to <5 in the inner part, which receives a significant input of fresh water (Schlungbaum et al. 1994). Like the Nordrügen-
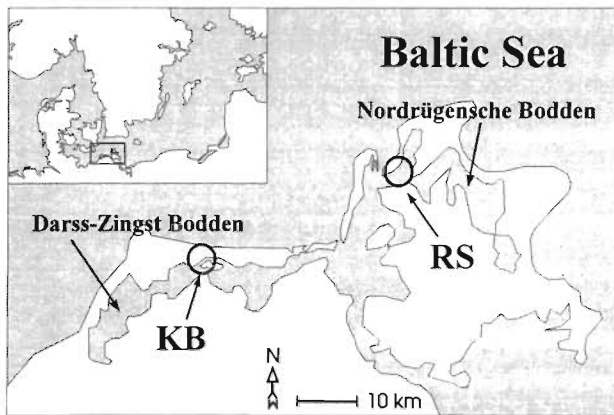
Fig. 1. Location of the study sites Kirr-Bucht (KB) and Rassower Strom (RS)

sche Bodden, the Darss-Zingst Bodden also show a gradual increase in trophic state from the outer towards the inner parts (Nausch & Schlungbaum 1991). Pigment excitation spectra (excitation at 400 to 630 nm, emission at 685 nm) of Kirr-Bucht samples showed no differences in pigment composition between water column and sediment samples, indicating that the sediment surface at Kirr-Bucht was mainly covered by sedimented planktonic algae (chlorophytes, cyanobacteria). Water and sediment samples from Rassower Strom, on the other hand, showed clear differences in excitation spectra, suggesting that at this site a typical microphytobenthos, dominated by diatoms and cyanobacteria, occurred (R. Schumann pers. comm.).

Sampling and *in situ* incubations. Sampling and incubations were carried out during spring, summer, and autumn at the dates indicated in Table 1. Sediment cores were incubated in plexiglass tubes ($\emptyset$ = 100 mm) *in situ* in a lowering frame that was deposited on the sea bottom (3 cores at ambient irradiance, 3 cores darkened). Additionally, 6 to 12 sediment cores were incubated in a laboratory incubator at defined irradi-

Table 1. Hydrographic conditions at the locations Kirr-Bucht and Rassower Strom during *in situ* incubations. Double values indicate a vertical gradient (surface/bottom); k = diffuse vertical attenuation coefficient

Date	Salinity (PSU)	Temperature (°C)	Oxygen saturation (%)	k (m^{-1})
Kirr-Bucht				
06 Apr 97	6.6	5.9	107	3.73
30 Jun 96	5.0	14.1	98	3.48
06 Oct 96	5.6	12.9	114	3.31
Rassower Strom				
07 May 96	7.8/9.0	9.8/9.2	99/102	0.50
07 Jul 96	8.2	16.9/16.6	99/104	0.57
28 Sep 96	8.2	12.2/12.1	95/101	0.73

ances to construct P-E curves. Preparation of sediment samples and incubation procedures were described in detail by Meyercordt & Meyer-Reil (1999). Water samples at Rassower Strom were taken with a 5 l water sampler ('Limnos', Turku, Finland) from water depths of about 3.4 and 2.0 m, and from the surface. At Kirr-Bucht a single water sample was sufficient due to the shallowness and intensive mixing at this site. Water was immediately filled into transparent glass bottles (100 ml 'Winkler-bottles'). Five bottles from each depth were taken to determine the O_2 concentrations at starting time. Additional bottles were exposed horizontally *in situ* at 20 cm below the surface, 20 cm above the bottom, and at the middle of the water column for periods of 4 to 8 h (4 light and 4 dark bottles at each depth; dark bottles wrapped in aluminium foil). During incubations, PAR above and under water was measured continuously using Li-Cor quantum sensors (LI-190SA and LI-193SA). Continuous records of atmospheric PAR were also carried out at the Institut für Ökologie by a permanently operating weather station (quantum sensor LI-190SA). The diffuse vertical attenuation coefficient (k) was calculated from irradiance measurements in 0.1 and 0.5 m depth intervals for the Kirr-Bucht and the Rassower Strom, respectively, using the equation: $k_{(z)} = -\ln (E_{(z)} \, E_{(0)}^{-1}) \, z^{-1}$; where z = depth, $E_{(z)}$ = irradiance at depth, and $E_{(0)}$ = surface irradiance. Salinity and temperature were measured with a conductivity meter (WTW LF 196 with TetraCon 96). Oxygen concentrations were determined by Winkler titration according to Grasshoff et al. (1983). The endpoint of titration was determined potentiometrically (Mettler DL 21 Titrator).

Determination of chlorophyll *a* (chl *a*) and phaeopigment concentrations. At the end of incubations, the top 5 mm of sediment cores were removed and thoroughly mixed; 5 subsamples of 0.5 cm^3 were taken from the slurry with a cut-off syringe, and stored deep frozen (−18°C) in polyethylene centrifuge tubes. Phytoplankton was concentrated on Whatman GF/C filters (5 parallels) by filtration of 100 to 1000 ml of water (depending on chlorophyll concentration) and immediately deep frozen. Pigment analyses were done in accordance with the guidelines of HELCOM (1988), including extraction with 96 % ethanol, followed by spectrophotometric readings at 665 nm before and after acidification with HCl for the measurement of phaeopigment concentrations (Perkin Elmer UV/VIS Spectrometer Lambda 2).

Calculations of primary production. The calculation of benthic primary production was described by Meyercordt & Meyer-Reil (1999). Pelagic net production and respiration rates were derived from changes in dissolved O_2 concentrations over time in light and dark bottles, compared to initial O_2 concentrations. The standard error (SE) of the mean of parallel measurements

of the O_2 concentration was taken for a calculation of the propagated error, resulting after subtraction of initial O_2 concentrations (SE_{ini}) from O_2 concentrations after light or dark incubations (SE_{inc}). The propagated error (z) was calculated according to $z = \sqrt{SE_{ini}^2 + SE_{inc}^2}$, and is reported in Table 2 as analytical error (AE). The measurements reflect the O_2 turnover of the entire system, including photoautotrophic and heterotrophic activities. Therefore, respiration expresses community respiration. Since it is extremely difficult operationally to obtain a figure for 'net primary production', the term 'net community production' (NP) is more appropriate. NP is already corrected for the metabolism of the entire pelagic community (Platt & Sathyendranath 1993, Williams 1993). Gross production (GP) was calculated as the sum of respiration and NP. O_2 production rates have been converted to CO_2 fixation rates using a photosynthetic quotient of 1.2 (Mills & Wilkinson 1986, Oviatt et al. 1986). This quotient was also used to convert O_2 data from the literature to C-values.

The relationship between photosynthesis and irradiance is described by the equation of Webb et al. (1974), as rewritten by Jassby & Platt (1976):

$$P = P_m [1 - \exp(-\alpha E/P_m)]$$

Production (P) is dependent on irradiance (E) and the parameters α and P_m. The parameter α (maximum light utilization coefficient; Sakshaug et al. 1997) characterizes the slope of the light-saturation curve at low light levels, when photosynthesis is assumed to be proportional to photon flux density. P_m is the photosynthetic rate at optimal illumination, also called maximum photosynthetic rate or photosynthetic capacity. The influences of factors such as temperature, nutrients, and adaptation are represented mathematically through their effect on α and P_m (Jassby & Platt 1976). A simultaneous fit of α and P_m to the data was obtained by using a nonlinear curve-fitting procedure of the programm 'Fig.P® for Windows™'.

RESULTS

Hydrographic conditions during the *in situ* incubations are summarized in Table 1. Salinity of Kirr-Bucht waters was in the lower β-mesohaline range (cf. Caspers 1959), and salinity of Rassower Strom waters in the medium to upper β-mesohaline range. A rather clear vertical salinity gradient existed on 7 May 1996 in Rassower Strom, indicating inflow of water from the Baltic Sea. Optical properties of the water were very different at both sampling sites, with diffuse vertical attenuation coefficients (k) of 0.5 to 0.7 m^{-1} at Rassower Strom compared to k values of 3.3 to 3.7 m^{-1} at

Table 2. Volume specific and chlorophyll a specific rates of pelagic net production (NP), respiration (R), and gross production (GP) in different water depths (AE = Analytical Error)

Date	Depth (m)	PAR in water (µmol m^{-2} s^{-1})	Chl a (µg l^{-1})	Phaeo. (µg l^{-1})	NP	AE	Volume specific rates R (µmol O_2 l^{-1} h^{-1})	AE	GP	AE	Chl a specific rates NP [mg C (mg chl a)$^{-1}$ h^{-1}]	R	GP
Kirr-Bucht													
06 Apr 97	0.20	497	13.32	21.00	5.15	0.37	−1.72	0.92	6.42	0.69	3.87	−1.29	4.82
	0.65	93	13.32	21.00	4.94	0.39	−0.85	0.55	6.22	0.57	3.71	−0.64	4.67
	1.10	17	13.32	21.00	1.88	0.73	−1.25	0.27	3.15	0.78	1.41	−0.94	2.37
30 Jun 96	0.20[a]	281	32.90	12.90	14.19	0.29	−1.41	0.35	15.61	0.45	4.31	−0.43	4.74
	0.60[a]	70	32.90	12.90	6.10	1.08	−1.42	0.34	7.51	1.16	1.85	−0.43	2.28
	0.20[b]	392	32.90	12.90	14.33	0.53	−2.04	0.53	16.36	0.79	4.36	−0.62	4.97
	0.60[b]	97	32.90	12.90	5.69	1.03	−2.02	0.63	7.72	1.25	1.73	−0.61	2.35
06 Oct 96	0.20	385	29.60	24.90	13.15	0.82	−1.12	0.11	14.49	0.83	4.44	−0.38	4.90
	0.45	168	29.60	24.90	11.05	0.56	−1.38	0.18	12.39	0.69	3.73	−0.47	4.19
	0.70	74	29.60	24.90	8.07	0.93	−1.54	0.13	9.41	1.07	2.73	−0.52	3.18
Rassower Strom													
07 May 96	0.20	1298	0.49	1.66	0.43	0.82	−0.54	0.87	0.94	1.16	8.80	−10.93	17.83
	1.60	644	0.59	1.63	0.32	0.67	−0.88	0.52	0.82	0.94	5.34	−14.96	14.37
	3.20	290	0.79	1.29	0.28	0.96	−0.10	1.06	0.79	1.13	3.58	−1.20	12.61
07 Jul 96	0.20	1164	4.21	0.97	2.04	0.39	−0.40	0.39	2.38	0.55	4.85	−0.95	5.61
	2.20	372	4.47	0.89	2.14	0.42	−0.20	0.36	2.49	0.56	4.80	−0.46	5.55
	4.20	119	4.87	0.91	1.04	0.33	−0.42	0.40	1.38	0.50	2.13	−0.86	2.89
28 Sep 96	0.20	611	3.49	2.62	1.36	0.79	−0.54	0.78	1.92	1.14	3.91	−1.53	5.23
	1.70	204	4.38	0.57	0.84	0.82	−0.35	0.82	1.39	1.01	1.92	−0.79	3.23
	3.20	68	4.74	0.59	0.24	0.86	−0.77	0.86	0.79	0.94	0.50	−1.63	1.82

[a]Incubation from 10:00 to 18:00 h
[b]Incubation from 10:00 to 14:30 h

Kirr-Bucht. This difference can be explained by high numbers of phytoplankton cells in Kirr-Bucht. Concentrations of chl *a* and phaeopigment at this location were about 1 order of magnitude higher than at Rassower Strom (Table 2).

The results of the phytoplankton bottle incubations are compiled in Table 2. NP rates showed a strong vertical gradient, as could be expected from the concomitant gradient in light availability. Volume-specific NP rates were generally much lower in samples from Rassower Strom and often were just as high or even lower than the AE. This was evident in particular for the samples from 7 May 1996, where the AE exceeded the measured oxygen exchange rates. Fig. 2 shows plots of volume-specific NP rates against irradiance. Differences of 1 order of magnitude in maximal production per volume occurred between samples of Kirr-Bucht and Rassower Strom (high and low rates, respectively). Differences between single incubation dates were

smaller, but nevertheless obvious. At both locations, lower volume-specific NP rates were found during the spring incubations than in summer and autumn. The photosynthesis model of Webb et al. (1974) did fit the data very well. The parameters of the regression lines are summarized in Table 3.

Volume-specific respiration rates were about 3 times higher at Kirr-Bucht than at Rassower Strom. The difference between the 2 locations, however, was less prominent than in the case of NP rates, which were 7 to 12 times higher at Kirr-Bucht. There was no obvious dependency of the respiration rates on water depth, and its variability may have been in part due to analytical uncertainties. Therefore, the calculation of GP rates, as given in Table 2, was based on depth-averaged respiration rates.

Chl *a* specific rates were converted from O_2 to C to facilitate comparsion with data of other investigations. It was remarkable that chl *a* specific NP rates at both sampling sites were similar. The spring incubation in Rassower Strom led to an exception; both chl *a* specific NP rates and respiration rates were comparatively high, resulting in prominent chl *a* specific GP rates (Fig. 3). The regression of chl *a* specific GP rates against irradiance, which revealed coefficients of determination of >0.98, provided information about the photosynthetic capacity of the algae (P^*_m) and about the proportionality of photosynthesis and irradiance in the low irradiance range (α^*). The parameters α^* and P^*_m of the regression curves (Fig. 3) are summarized in Table 3. P^*_m had similar values of about 5 mg C (mg chl a)$^{-1}$ h^{-1} for both Kirr-Bucht and Rassower Strom samples at all investigated times, except the abovementioned incubation on 7 May 1996 in Rassower Strom. The α^* values, conversely, showed differences between sampling dates and sampling sites, with the lower values tending to occur during incubations of samples from Rassower Strom.

In addition to *in situ* incubations of pelagic samples, sediment cores taken from the sampling stations were incubated *in situ* (Meyercordt & Meyer-Reil 1999) to measure primary production rates, performed by benthic microalgae. Duration of the sediment incubations, mean photon flux densities at the water surface during incubation periods and the water depth in which sediment incubations were carried out are given in Table 4. Benthic GP rates (Table 4) ranged from 4.2 to 30 mg C m^{-2} h^{-1}. Due to differences in water depth, attenuation, and irradiance, it is not recommended to compare dates and sites in view of benthic primary production. A comparison of benthic GP with the related pelagic GP, however, gives an initial idea of the relative significance of both benthic and pelagic production for total microalgal primary production. For this purpose, pelagic GP has been calculated to meet with the individual periods of
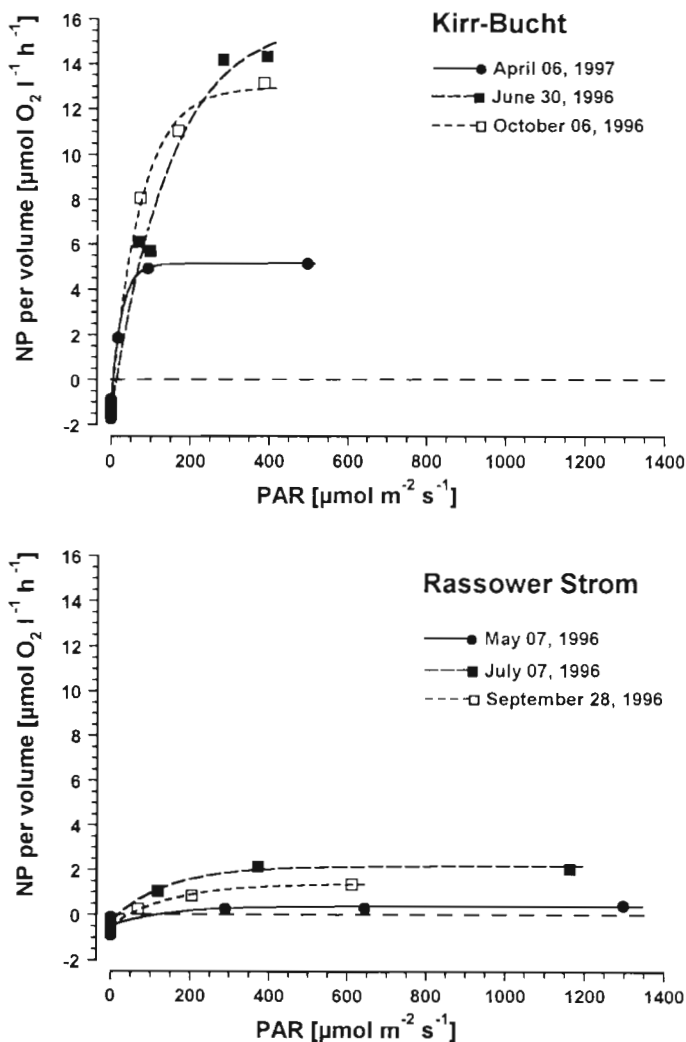

Fig. 2. Pelagic net production rates (NP) as related to volume

Table 3. Parameters α, $\alpha^\bullet$, P_m, $P^\bullet_m$ and respiration of the P-E function as derived from *in situ* bottle incubations in the pelagial; the coefficient of determination (R^2) indicates how well the regression model describes the data

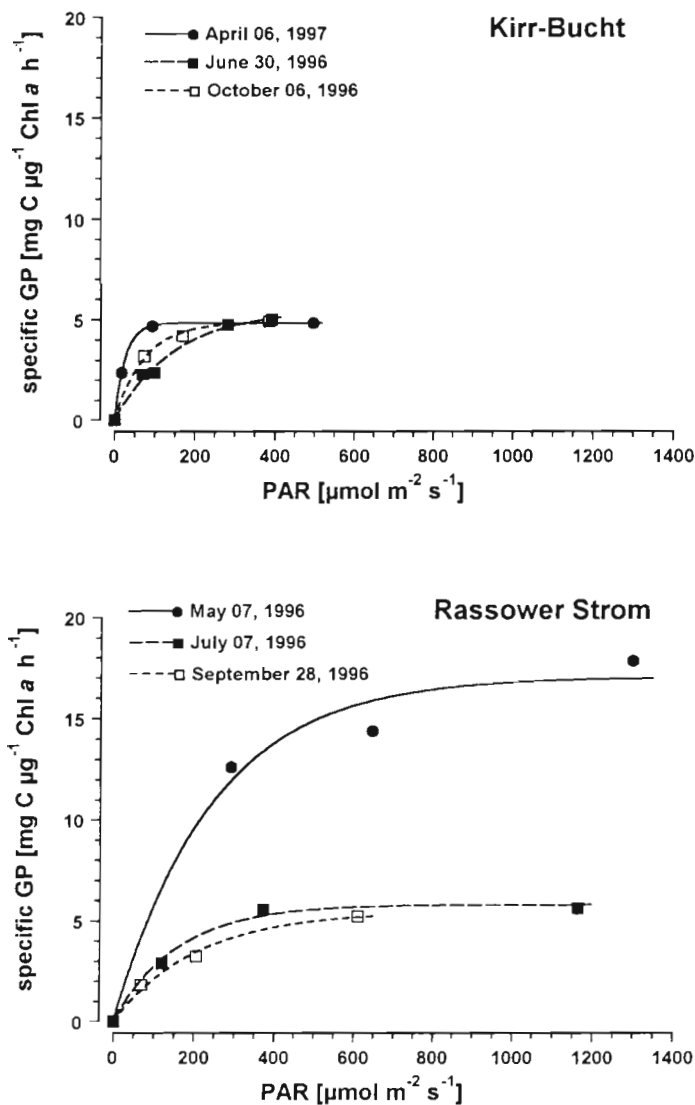| | Volume specific net production | | | | chl *a* specific GP | | |
	α [µmol O_2 l^{-1} h^{-1} (µmol m^{-2} s^{-1})$^{-1}$]	P_m (µmol O_2 l^{-1} h^{-1})	Resp. (µmol O_2 l^{-1} h^{-1})	R^2	$\alpha^\bullet$ [mg C (mg chl *a*)$^{-1}$ h^{-1} (µmol m^{-2} s^{-1})$^{-1}$]	$P^\bullet_m$ [mg C (mg chl *a*)$^{-1}$ h^{-1}]	R^2
Kirr-Bucht							
06 Apr 97	0.250	5.13	−1.27	0.992	0.188	4.81	>0.999
30 Jun 96	0.122	15.95	−1.71	0.989	0.037	5.43	0.994
06 Oct 96	0.197	12.95	−1.33	0.998	0.067	4.83	0.997
Rassower Strom							
07 May 96	0.006	0.38	−0.50	0.773	0.071	17.01	0.981
07 Jul 96	0.018	2.15	−0.35	0.991	0.037	5.79	0.993
28 Sep 96	0.013	1.37	−0.54	0.972	0.026	5.46	0.993

Fig. 3. Pelagic gross production rates (GP) as related to chlorophyll *a*

sediment-core incubations, taking into account water depth, duration of the incubations, and light availability during these periods. Resulting pelagic GP rates ranged from 27 to 96 mg C m^{-2} h^{-1} (Table 4). The relative proportion of pelagic production in these specific examples varied between 58 and 90% of the total microalgal primary production of the system, indicating the significance of both groups of primary producers. It has to be pointed out that these results were valid only for a minor part of the day (periods of 4 to 8 h), and only for incidental water depths and solar irradiations.

Therefore, further calculations have been performed to support more generalized statements on the primary production at the study sites. A better comparability of both sites could be achieved by modeling production rates, based on the same water depth and the same regimes of irradiance. For this purpose, day-to-day fluctuations of irradiance during periods of 4 wk, including the dates of the *in situ* incubations, were examined (Fig. 4). The *in situ* incubation dates mostly represented more or less bright days with high solar irradiance (also the *in situ* incubation at Kirr-Bucht on 6 April 1997; graph not shown). Under natural conditions, rapid changes from bright to overcast conditions and vice versa often occur. Therefore, an example of a bright and an overcast day were chosen in each period to calculate pelagic and benthic primary production for 24 h days, taking into account respective PAR courses (see Fig. 4). The functional parameters of the P-E relationship for the benthic photoautotrophs, which were necessary for these calculations, have been obtained from laboratory incubations of sediment cores under varied irradiances (Meyercordt & Meyer-Reil 1999). Since water depth was significantly different at the particular spots where the *in situ* incubations were carried out at Kirr-Bucht (0.6 m) and Rassower Strom (3.4 m), a standardized depth of 2 m, representing more or less the mean depth of the Bodden waters, was used for comparative calculations.

Table 4. Pelagic and benthic gross production rates during the *in situ* incubations; pelagic gross production rates were adjusted to time-intervals and water depth of the sediment incubations by application of the P-E function and the mean irradiance level of the respective period. Data of benthic GP were taken from Meyercordt & Meyer-Reil (1999)

Date	Time (CET)	Mean PAR at surface (μmol m^{-2} s^{-1})	Depth (m)	Gross production Pelagic (mg C m^{-2} h^{-1})	Benthic	Pelagic (% of total)
Kirr-Bucht						
06 Apr 97	10:50 – 17:10 h	1089	0.65	41.5	30.0	58
30 Jun 96	09:30 – 14:20 h	816	0.60	87.1	14.8	85
30 Jun 96	14:20 – 17:30 h	344	0.60	60.9	10.6	85
06 Oct 96	09:20 – 13:30 h	924	0.45	63.5	27.4	70
06 Oct 96	13:30 – 17:40 h	416	0.45	58.2	15.4	79
Rassower Strom						
07 May 96	10:00 – 12:40 h	1617	3.20	27.8	16.8	62
07 May 96	12:40 – 16:40 h	1261	3.20	27.3	16.2	63
07 Jul 96	09:10 – 13:30 h	1543	4.20	95.9	17.6	84
28 Sep 96	09:20 – 13:20 h	988	3.20	50.6	10.8	82
28 Sep 96	13:20 – 17:20 h	407	3.20	35.9	4.2	90

Table 5. Pelagic and benthic production rates calculated for the locations Kirr-Bucht and Rassower Strom, comparing the effect of the irradiance regime of a bright day with the one of an overcast day in May, June/July, and October (see Fig. 4); water depth was standardized to 2 m

24 h rates (g C m^{-2} d^{-1})	Kirr-Bucht Bright day May 05/07	Jun/Jul 07/07	Oct 10/06	Overcast day May 05/04	Jun/Jul 06/29	Oct 10/01	Rassower Strom Bright day May 05/07	Jun/Jul 07/07	Oct 10/06	Overcast day May 05/04	Jun/Jul 06/29	Oct 10/01
Pelagic												
GP	1.02	1.63	1.16	0.55	0.89	0.43	0.23	0.64	0.31	0.12	0.45	0.11
NP	0.40	0.81	0.53	−0.06	0.07	−0.21	−0.01	0.47	0.05	−0.12	0.29	−0.15
Benthic												
GP	0.003	0.003	0.001	0.000	0.001	0.000	0.19	0.30	0.13	0.07	0.15	0.04
NP	−0.10	−0.25	−0.20	−0.10	−0.26	−0.20	0.06	0.12	−0.09	−0.06	−0.03	−0.18
Portion of total production												
Pelagic gross production (%)	99.7	99.8	99.9	99.9	99.9	99.9	55.0	67.9	70.5	61.8	75.1	71.5
Benthic gross production (%)	0.3	0.2	0.1	0.1	0.1	0.1	45.0	32.1	29.5	38.2	24.9	28.5

Data calculated for the standardized water depth, which also consider the influence of different cloud coverage, are presented in Table 5. The increase of water depth from 0.6 to 2.0 m had a dramatic effect on benthic GP at Kirr-Bucht, which declined to zero, causing a negative oxygen balance of the benthic system. Considering the same water depth for Rassower Strom, benthic GP would profit by 46% on bright days and by 106% on overcast days, relative to a depth of 3.4 m. Focusing on the relative contribution of benthic GP to total primary production of the benthic-pelagic system at a water depth of 2.0 m revealed a portion of about 30 to 45% for Rassower Strom, depending on weather conditions and seasons, whereas in Kirr-Bucht only 0.3% or less would be contributed by benthic microalgae.

DISCUSSION

Kirr-Bucht is part of a coastal inlet that not only receives considerable nutrient input from terrestrial runoff, but also contains a large storage of nutrients in its sediments. The eutrophic condition of Kirr-Bucht waters was evident from its considerable concentrations of chl *a*, sustaining a high primary production per volume, which was about 7 times higher than in Rassower Strom. The latter benefits from a rather frequent water exchange with the Baltic Sea, which keeps nutrient concentrations and phytoplankton abundance on a markedly lower level compared to Kirr-Bucht. Respiration of the pelagic community at Kirr-Bucht was 2 to 3 times higher than at nearshore sampling locations in the Gulf of Gdansk, southern Baltic Sea (Witek et al.
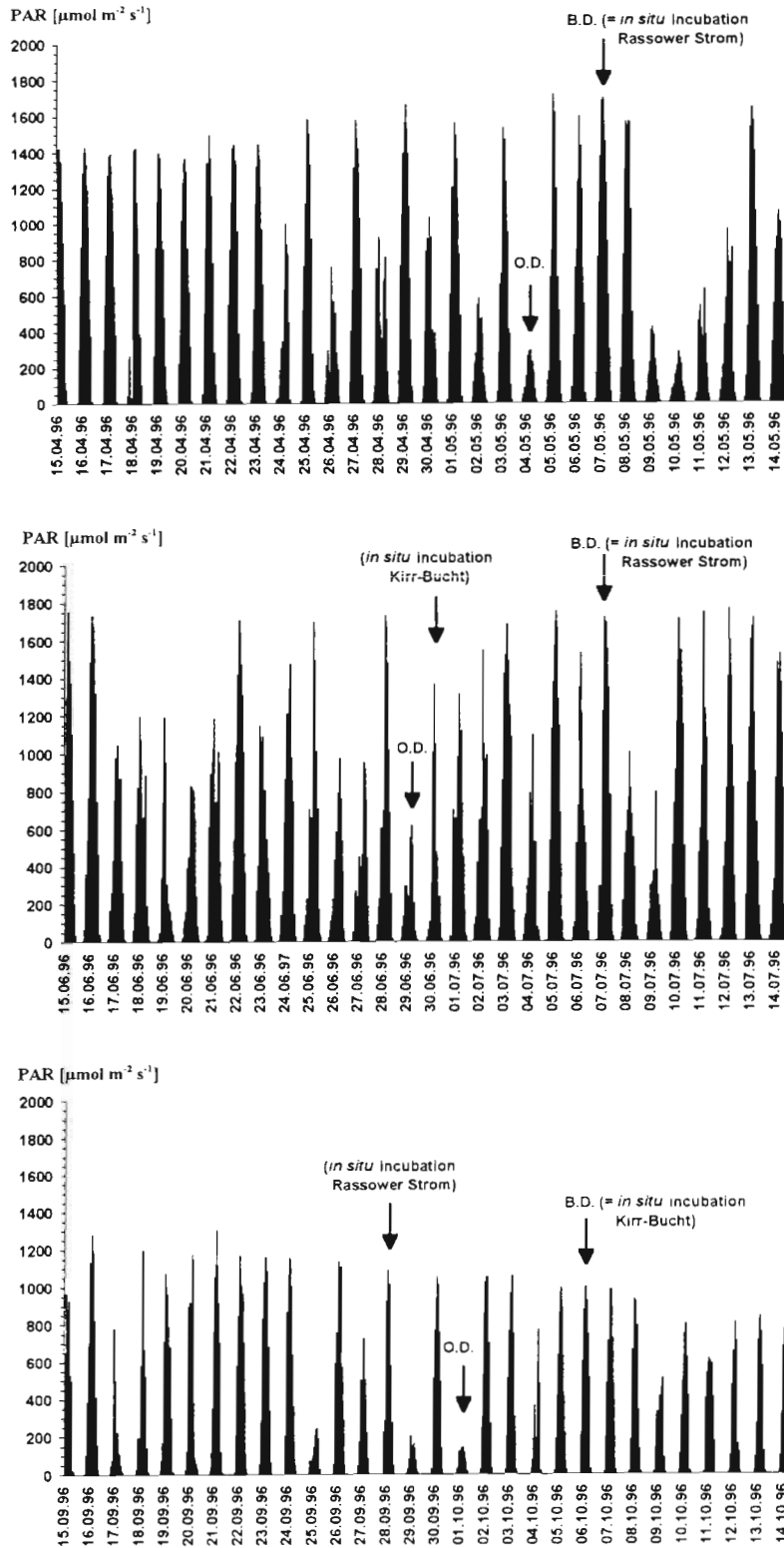
PAR [μmol m⁻² s⁻¹]

Fig. 4. Course of daily irradiation during the periods of *in situ* incubations. Arrows indicate dates of *in situ* incubations and of those individual days that were taken as examples for modeling primary production under conditions of different cloud coverage (B.D. = bright day, O.D. = overcast day)

1997). The height of pelagic community oxygen consumption was in accordance with the eutrophic conditions of Kirr-Bucht waters, which supported considerable heterotrophic activity. Pelagic respiration rates in Rassower Strom were markedly lower, compared not only to Kirr-Bucht, but even to the Gulf of Gdansk (Witek et al. 1997), indicating a relatively low state of eutrophication in Rassower Strom, owing to a fairly good water exchange with the Baltic Sea. Gieskes & Kraay (1984) reported planktonic community oxygen consumption rates from the central North Sea which were at about the same level or somewhat lower than the respiration rates from Rassower Strom.

Pelagic GP, as related to chl *a*, showed interesting features. Maximal production under saturating light conditions (P^{*}_{m}) was very similar for both sampling stations and all investigated dates, except during spring in Rassower Strom (see below), indicating that the photosynthetic capacity of the phytoplankton was similar. Under conditions of limited light, the response to increasing irradiance seemed to be more pronounced in spring than in summer and autumn (Table 3; α^{*}). Compared to Rassower Strom, Kirr-Bucht phytoplankton showed a higher α^{*} in spring and autumn. This may indicate more severe light limitation early in the year and, additionally, under conditions of turbid water as present in Kirr-Bucht. The spring incubation (7 May 1996) in Rassower Strom produced some striking results. Volume specific primary production was very low (Fig. 2), while chl *a* specific GP was very high (Fig. 3). Respiration rates showed high variability in the vertical distribution (with lowest rates at the bottom; Table 2). It was the only situation with a prominent vertical salinity gradient, evidence for inflow of saline Baltic Sea water (Table 1). Unfortunately, the relative AE was very high (Table 2). If the production rates obtained are a true reflection of the photosynthetic activity of the phytoplankton, it can be postulated that a very distinct phytoplankton coenosis, adapted to high-irradiance conditions, was present in Rassower Strom on 5 May 1996, probably originating from the Baltic Sea. The high AE shows that, in relatively unproductive waters, the limits of detection of the oxygen method were encountered.

The $\alpha^\bullet$- and $P^\bullet_m$-values determined for phytoplankton of Kirr-Bucht and Rassower Strom were comparable with data from other aquatic systems (Table 6). Daily rates of pelagic GP per unit of area were determined in the range of 0.14 to 1.17 g C m^{-2} d^{-1}. We assessed these findings in relation to production rates of other estuaries, focusing on earlier investigations of coastal inlets in the southern Baltic Sea. MacIntyre & Cullen (1996) reported daily rates of pelagic primary production from 0.1 to 2.5 g C m^{-2} d^{-1} for a shallow (<2 m) turbid estuary in Texas; their maximum values exeeded our maximum (1.17 g C m^{-2} d^{-1}) by a factor of 2. Hübel (1972) made early measurements of pelagic primary production along a gradient, reaching from the most eutrophied parts of the Darss-Zingst Bodden waters to the open Baltic Sea. He found summertime peaks in production ranging from 7.3 g C m^{-2} d^{-1} in Saaler Bodden, which is the innermost Bodden, to 3.2 g C m^{-2} d^{-1} in Barther Bodden (situated close to Kirr-Bucht) and to only 0.45 g C m^{-2} d^{-1} in the Baltic Sea. In Barther Bodden, Hübel (1973) found a seasonal course of pelagic production with lowest rates in December (0.26 g C m^{-2} d^{-1}) and highest rates in July (3.2; May/June: 0.66, October: 1.06). The reported rates exceeded the values of the present investigation at Kirr-Bucht by a factor of 1.2 to 2.7. Börner & Kell (1981) measured pelagic production rates on 'sunny days' in Zingster Strom (directly adjacent to Kirr Bucht), which differed from our production rates by a factor of 0.9 to 2.2. Overall, production rates reported by these authors were mostly higher than rates measured during our study. These findings are in accordance with the supposition that the degree of eutrophication in the waters under investigation reached its maximum in the 1970s and has since been declining.

Pelagic production rates reported for Rassower Strom by Hübel (1968), on the other hand, differed from our corresponding Rassower Strom data only by a factor of 1.1 to 0.7. That means the production rates determined in the 1960s were about the same or slightly lower than our rates from 1996. The transitional position of Rassower Strom between the Baltic Sea and the inner Bodden waters causes a considerable variability in water column properties due to a frequent exchange of water. Because of this high natural varability, it should be more difficult to detect long-term trends in primary production rates. Our findings, anyhow, do not show a decline in primary production rates at Rassower Strom compared with the data of Hübel (1968).

While the previous discussion focused exclusively on aspects of pelagic primary production, the ensuing part will place emphasis on the relation between pelagic and benthic production in the Bodden waters. A detailed discussion focusing on benthic primary production in these waters was given in a paper by Meyercordt & Meyer-Reil (1999). As previously pointed out, the particular spots at the 2 study sites where sediment samples were taken and in situ incubations were carried out differed considerably in water depth. Conditions for primary production in terms of irradiance supply at the bottom of both waters were very similar due to the fact that at the Kirr-Bucht spot a shallow, but highly eutrophied and turbid water was investigated, while at the Rassower Strom spot the water was deeper but less eutrophied and therefore clearer. To evaluate the general influence of the optical properties of the 2 different types of water on primary production, we used a standardized water depth of 2 m, which is about the mean depth of the Bodden systems, for comparative calculations. This standardization revealed obvious differences in basic conditions for benthic and pelagic primary production which otherwise remained undetected.

Table 6. P-E parameters of planktonic communities in different waters

$\alpha^\bullet$ [mg C (mg chl a)$^{-1}$ h^{-1} (µmol m^{-2} s^{-1})$^{-1}$]	$P^\bullet_m$ [mg C (mg chl a)$^{-1}$ h^{-1}]	Site	Source
0.027 – 0.188	4.81 – 17.01	Bodden Waters, Baltic Sea	This study
0.04 – 0.24	2 – 26	Massachusetts Bay, USA	Kelly & Doering (1997)
0.008 – 0.009	0.64 – 0.98	Scott Inlet, Canadian Arctic	Platt et al. (1980)
0.014 – 0.206	0.90 – 15.2	Coastal water, Peru	Platt et al. (1980)
0.013 – 0.142	1.22 – 11.22	North Atlantic	Kyewalyanga et al. (1997)
	1.5 – 10	Gulf of Gdansk	Witek et al. (1997)
	3.0 – 24.4	Turbid estuary, Texas, USA[a]	MacIntyre & Cullen (1996)
	0.09 – 2.39	Iroise Sea, France	Compiled by Baines et al. (1994)
	0.25 – 5.67	North Pacific, Hawaii	Compiled by Baines et al. (1994)
	3.69 – 14.9	Westland, New Zealand	Compiled by Baines et al. (1994)
	5.00 – 9.63	North Pacific gyre	Compiled by Baines et al. (1994)

[a]Suspended benthic microalgae

While water transparency at 2 m at Rassower Strom would allow benthic microalgae a contribution of 30 to 45% to total microalgal primary production, this proportion at the turbid Kirr-Bucht would be only 0.3% or less, depending on weather conditions and seasons. This difference between both locations demonstrated the profound alteration of the conditions for benthic primary production by diminishing water transparency, going along with the process of eutrophication in shallow waters. According to our calculations, this difference was more prominent during periods of low supply of solar radiation, like on overcast days, compared to bright days. A study of the photosynthetic response of benthic microalgae along a depth profile (0.5 to 4.5 m) in Rassower Strom revealed no significant differences in P-E characteristics along the gradient (unpubl. data). This result supported the suitability of calculating benthic primary production for a standardized water depth.

The conditions for primary production in the tideless Bodden systems are totally different from conditions in tidal estuaries. On tidal flats in the estuary of the River Elbe (northern Germany), the microphytobenthos only held about one-sixth of the biomass of the phytoplankton, but it accounted for some 80% of the total primary production. This was due to the fact that the benthic algae received full light intensity for distinct periods of time, whereas the productivity of the phytoplankton was strictly limited by high turbidity in the estuary (Fast 1993; cf. also Pinckney & Zingmark 1991, Barranguet et al. 1998).

Finally attention is drawn to the question whether the total utilization of PAR by the benthic-pelagic system depended on water depth. If the utilization of irradiance were independent of the length of the water column, the sum of benthic and integral pelagic GP should be equal for 0.6 and 2.0 m depths in Kirr-Bucht. It should also be equal for 3.4 and 2.0 m depths in Rassower Strom. A lower pelagic primary production in the shallower water should be compensated by a rise in benthic primary production, due to higher photon fluxes reaching the sediment surface. Total GP rates modeled for the deeper water exceeded those for the shallower water by 21% (bright days) and 8% (overcast days) for Rassower Strom, and by 21 and 12% for Kirr-Bucht, respectively. The following conclusion can be drawn from these findings: If a great portion of the PAR supply is absorbed and utilized in the water (i.e. deep water) and only a minor part reaches the sediment surface, the efficiency of PAR utilization is higher than in shallower water, where more of the irradiance reaches the bottom. The lower PAR utilization can be explained by the fact that benthic microalgae live in a medium that strongly absorbs light. This is particularly true for sediments with a high content of organic car-

bon (Epping 1996, MacIntyre et al. 1996). Therefore, within sediments a greater portion of radiation is not available for photosynthesis compared to the pelagial, because it is strongly absorbed by high concentrations of non-photosynthesizing components. On overcast days, the low irradiance is almost completely absorbed in the upper part of the water column, and the contribution of benthic microalgae to total primary production is of minor importance. Therefore our modeled results showed a smaller difference between the shallower and deeper waters for overcast (about 10%) than for bright weather situations (21%).

Our results showed that in the inner part of the Bodden waters, there is some indication of a reduction in primary production rates during the last decades, which may be due to a reduced nutrient load to the system. Such a developement could not be shown for the outer part of the Bodden waters, probably because of high natural variability due to frequent water exchange with the Baltic Sea. The relative significance of pelagic and benthic primary production in the Bodden waters is supposed to be highly variable on short time scales due to fast changing light conditions, as calculations based on P-E parameters have shown. It also depends very much on the combined effects of water quality and water depth on the supply of irradiance, the major driving force for photosynthesis. Water quality in terms of optical properties is closely related to eutrophication, since eutrophication favours phytoplankton development and the formation of particles in the water column. In eutrophied shallow waters, only a small part of these particles, mainly consisting of dead and living phytoplankton cells, exopolymers and inorganic constituents, is utilized by pelagic food webs. The major part settles down and serves as a food source for benthic heterotrophs or contributes to mud formation. The sedimented particles can also be easily resuspended, thus intensifying light attenuation in the water. Particle formation, settling and resuspension are processes which are closely related to the trophic state, and which reduce the significance of benthic primary production in absolute terms as well as relative to pelagic primary production. It seems worth considering in further investigations to what extent the relative contribution of benthic and pelagic photoautotrophs to total primary production may serve as a meaningful parameter for the ecological characterization of a coastal shallow-water system.

tem Boddengewässer — Organismen und Stoffhaushalt ÖKO-BOD' (ecosystem Bodden — organisms and nutrient balance), financed by the Bundesministerium für Bildung, Wissenschaft, Forschung und Technologie (BMBF).

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