

Annual dynamics of pelagic primary production and respiration in a shallow coastal basin

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Abstract

The Wadden Sea (North Sea, Europe) is a shallow coastal sea with high benthic and pelagic primary production rates. To date, no studies have been carried out in the Wadden Sea that were specifically designed to study the relation between pelagic respiration and production by comparable methods. Because previous studies have suggested that the import of primary-produced pelagic organic matter is important for benthic Wadden Sea carbon budgets, we hypothesised that on an annual average the northern Wadden Sea water column is autotrophic. To test this hypothesis, we studied annual dynamics of primary production and respiration at a pelagic station in a shallow tidal basin (List Tidal Basin, northern Wadden Sea). Since water depth strongly influences production estimates, we calculated primary production rates per unit area in two ways: on the basis of the mean water depth (2.7 m) and on the basis of 1 m depth intervals and their respective spatial extent in the List Tidal Basin. The latter more precise estimate yielded an annual primary production of $146 \text{ g C m}^{-2} \text{ y}^{-1}$. Estimates based on the mean water depth resulted in a ~40% higher annual rate of $204 \text{ g C m}^{-2} \text{ y}^{-1}$. The total annual pelagic respiration was $50 \text{ g C m}^{-2} \text{ y}^{-1}$. The P/R ratio varied between seasons: from February to October the water column was autotrophic, with the highest P/R ratio of ~4–5 during the diatom spring bloom in April/May. In autumn and winter the water column was heterotrophic. On an annual average, the water column of the List Tidal Basin was autotrophic (P/R ~3). We suggest that a large fraction of the pelagic produced organic matter was respired locally in the sediment.

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1. Introduction

Primary production and respiration are the two basic biological processes that control carbon and nutrient dynamics in marine ecosystems. In deep oceanic settings, most of the organic matter is produced and decomposed in the water column (Del Giorgio and Williams, 2005). With decreasing depth the relative importance of the sediment

for the overall respiration increases. In very shallow coastal seas, benthic and pelagic respiration and primary production may contribute equally to the overall carbon budget (Heip et al., 1995).

The Wadden Sea (North Sea, Europe) is a shallow coastal sea with a high benthic and pelagic primary production (Cadée and Hegeman, 1974, 2002; Asmus et al., 1998). It is characterised by the import of organic material from the adjacent North Sea (Postma, 1954, 1980). Fluxes of nutrients and organic material between the benthos and the pelagic are tightly coupled (e.g. Baird et al., 2004; Asmus et al., 1998). Suspended organic material is

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passed to the benthos by passive sedimentation, by particle trapping due to advective pore water exchange or by benthic filter feeders, and is rapidly remineralised (Dame and Dankers, 1988; Huettel et al., 1998; Crossland et al., 2005; De Beer et al., 2005). Strong wave action and tidal currents may resuspend benthic organic matter into the water column (Dijkema et al., 1980; De Jonge and Van Beusekom, 1995; Heip et al., 1995). High turbidity characterises the water column (Postma, 1954; Aarup, 2002) and the euphotic zone in the Wadden Sea is shallower than in the adjacent North Sea. Light is a major limiting factor for photosynthesis during most of the year, but nitrogen limitation may occur especially from May to September (Colijn and Cadée, 2003).

Pelagic primary production was best investigated in the Dutch Wadden Sea. Time series (Cadée and Hegeman, 1974, 2002) document an increase of up to $440 \text{ g C m}^{-2} \text{ y}^{-1}$ in primary production in the Marsdiep area until the mid 1990s, followed by a gradual decrease to $200\text{--}250 \text{ g C m}^{-2} \text{ y}^{-1}$ in 2000. Philippart et al. (2007) included actual daily irradiation in the estimation model for the Marsdiep, resulting in pelagic primary production values of $150\text{--}300 \text{ g C m}^{-2} \text{ y}^{-1}$ in the 1990s and values between 120 and $170 \text{ g C m}^{-2} \text{ y}^{-1}$ from 2000 to 2004. Colijn (1983) investigated primary production in the Ems estuary and found annual rates between $40 \text{ g C m}^{-2} \text{ y}^{-1}$ in the inner estuary and $500 \text{ g C m}^{-2} \text{ y}^{-1}$ in the outer estuary. Rates in the northern Wadden Sea are lower. In the Meldorfer Bucht, Tillmann et al. (2000) found values between ~ 120 and $180 \text{ g C m}^{-2} \text{ y}^{-1}$. Asmus et al. (1998) found values of $160 \text{ g C m}^{-2} \text{ y}^{-1}$ in the intertidal of the Sylt-Rømø Bight (=List Tidal Basin).

Compared to pelagic primary production, little is known about pelagic respiration and the ratio of pelagic primary production and respiration: Van Es (1982) reported an annual pelagic remineralisation of $260 \text{ g C m}^{-2} \text{ y}^{-1}$ for the Dollard including mineralisation from waste water discharge. Brussaard et al. (1996) investigated bacterial production rates in the Marsdiep area as a weekly time series and found rates of up to $90 \mu\text{g C L}^{-1} \text{ d}^{-1}$ during a *Phaeocystis* bloom. Poremba et al. (1999) suggested that the water column in the deeper tidal channels of the Wadden Sea is heterotrophic, whereas the shallow parts are autotrophic because of favourable light conditions. Available data range between near-balanced carbon budgets for the northern Wadden Sea (Asmus et al., 1998; Van Beusekom et al., 1999) to an autotrophic water column in the western Dutch Wadden Sea (e.g. Hoppema, 1991; Van Beusekom et al., 1999). Wadden Sea carbon budgets including both the water column and sediment report that total remineralisation (about $400 \text{ g C m}^{-2} \text{ y}^{-1}$) exceeds total primary production ($\sim 300 \text{ g C m}^{-2} \text{ y}^{-1}$) by about $100 \text{ g C m}^{-2} \text{ y}^{-1}$ (e.g. Hoppema, 1991; Van

Beusekom et al., 1999), indicating that the area is heterotrophic.

To date, no studies have been carried out in the Wadden Sea that were specifically designed to study the relation between pelagic respiration and production by comparable methods. In this study, we used oxygen production and oxygen consumption as a measure of primary production and remineralisation. Because previous studies suggest the importance of the import of pelagically produced organic material for intertidal carbon budgets (Baird et al., 2004) and for the Wadden Sea as a whole (Van Beusekom et al., 1999) we hypothesised that on an annual average the northern Wadden Sea water column is autotrophic. To test the hypothesis, we measured annual dynamics of pelagic primary production (P) and respiration (R) in a near-weekly time series in the List Tidal Basin and analysed the ratio (P/R) of the two processes. Since water depth strongly influences production estimates, we calculated primary production rates per unit area in two ways: on the basis of mean water depth (2.7 m), and on the basis of the spatial extent of each 1 m depth interval.

2. Methods

2.1. Study site

This study was conducted in the List Tidal Basin, a 405 km^2 semi-enclosed basin in the northern part of the Wadden Sea. The List Tidal Basin is enclosed by the islands of Sylt and Rømø and by the causeways connecting the two islands with the mainland. It is connected with the open North Sea by a single tidal inlet (Fig. 1). Salinity ranges between 27.5 (February) and 30.5 (August). The water column is homogeneously mixed. A detailed description of the area is given in Gätje and Reise (1998).

2.1.1. Analysis of bathymetrical data

The basis of the depth model of the List Tidal Basin is a dense grid of mostly equally distributed point data, where each point contains a depth value. The grid covers the entire basin. The depth data were collected in July 1994, stored in the KIS (coastal information system) data base and supplied by the Regional State Office for the Rural Areas in Husum/ Germany. The grid was put into the Geographic Information System ArcGIS 9.1, ArcMap and its coordinate system was converted to UTM 32 North, WGS 84. Thus, it was possible to check the accuracy of the grid of point data by a set of georeferenced aerial photographs which are in the same coordinate system. The aerial photographs were taken in October 2003. On the basis of these aerial

photographs the borders of the List Tidal Basin were digitised and saved as a shape-file. Only point data that had their position within these borders were taken into account for a Digital Elevation Model (DEM): 192956 points in an area of 405 km². These point data and the shape file were put into ArcGIS 9.1, ArcScene. In ArcScene, a Triangulated Irregular Network (TIN) within the borders of the List Tidal Basin was calculated and a DEM created. After the result was checked on the basis of existing marine charts, the DEM was improved by break lines. With this DEM the area and volume for each depth was calculated in ArcScene whereas 1 m intervals were determined for the List Tidal Basin. We chose intervals of 1 m because it was the most accurate that the raw data allowed. The interpolation in smaller intervals would have led to morphological structures that do not exist in real life and pretend a higher resolution than the raw data allowed.

2.2. Seawater sampling

Samples for nutrients, suspended matter, and chlorophyll-a analysis were taken twice a week as parts of the Sylt long-term time series. Seawater for primary production and respiration measurements were taken weekly, and in winter monthly. Surface seawater samples (1 m) were taken with a Niskin bottle at a routine station in the main channel of the

basin (Fig. 1). Water depth at this station was 10 m. Sampling took place between 8 am and 9 am irrespective of the tidal cycle. Water temperature was measured with a reverse thermometer fixed to the Niskin bottle.

2.3. Nutrients, suspended matter and chlorophyll-a concentration

Standard methods according to Grasshoff et al. (1983) were used for determining dissolved NO₃, NO₂, NH₄, PO₄, and Si. Volumetric suspended matter concentrations (SPM) were determined gravimetrically on a 0.47 µm pore-size Nucleopore filter. Phytoplankton biomass was determined as chlorophyll-a after Jeffrey and Humphrey (1975).

2.4. Light attenuation

Light attenuation in the water column was measured almost every week, using a LI-COR-Sensor (LI-COR; LI-193) attached to a CTD. The Sensor continuously measured irradiance in µmol photons s⁻¹ m⁻² and the CTD had a storage frequency of four data sets s⁻¹. Lowering speed of the CTD was approximately 10 cm s⁻¹. This provided at least four irradiance data per 10 cm depth interval. The vertical attenuation coefficient (k) in µmol photons m⁻² s⁻¹ follows Lambert's Law, (Eq. (1)): $I_z = I_0 \exp(-kz)$, where I_z is irradiance at a given depth (z) and I_0

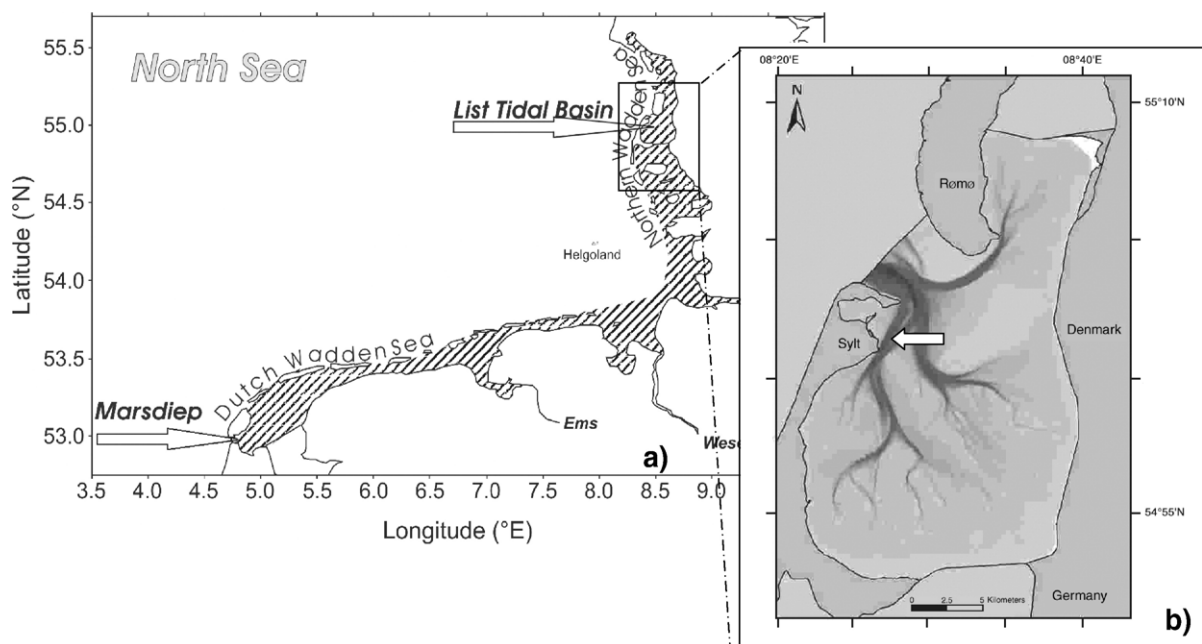


Fig. 1. a. Map of the south eastern North Sea and the List Tidal Basin, situated in the northern Wadden Sea. b. A bathymetrical map of the basin. Grey shadings depict water depth. The position of the sampling station (55°02' N, 8.27° E) is indicated by the arrow.

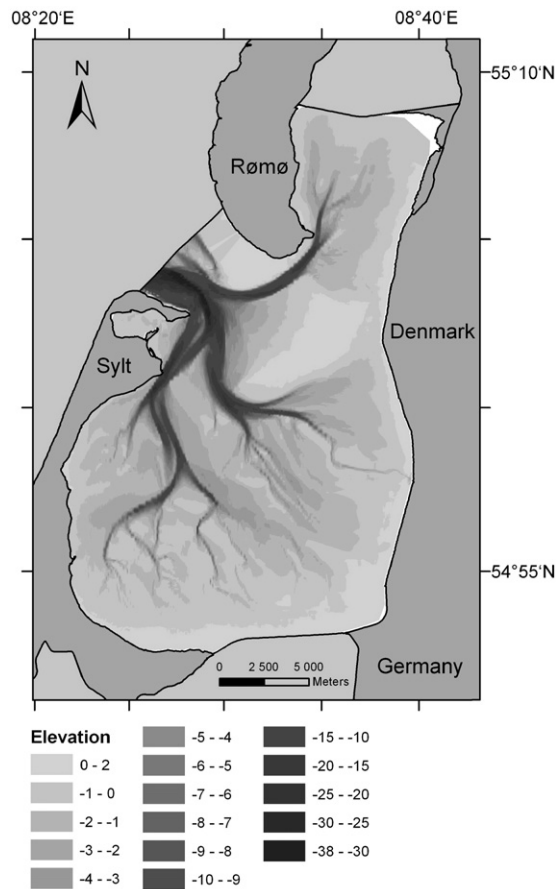


Fig. 1 (continued).

reflects surface irradiance. The relation between light attenuation and suspended matter (SPM) was determined by linear regression, Eq. (2): $k=y+x$ SPM.

2.5. Primary production

2.5.1. Photosynthesis versus Irradiance (P/E)

P/E curves were determined weekly (during winter monthly) from January to November 2004, using the light and dark bottle oxygen method under controlled laboratory conditions. Incubation bottles (~120 ml) were filled bubble-free through a silicon tube immediately after sampling with a Niskin bottle. The initial seawater oxygen content was measured in triplicate. In the laboratory, eight bottles were wrapped each with different neutral density light filters and two bottles were wrapped in aluminium foil. The bottles were attached to a rotating wheel in a water bath kept at in situ temperature. Incubation irradiance was provided by a cool light fluorescent emitter (Norka). Irradiance was measured inside the incubation bottles and re-adjusted before each experiment using a spherical mini

light sensor (LIC-COR). Incubation irradiance was between 70 and 780 $\mu\text{mol photons s}^{-1} \text{ m}^{-2}$ (~70, 130, 170, 225, 320, 460, 550, 780 $\mu\text{mol photons s}^{-1} \text{ m}^{-2}$). The incubation time was determined in pre-experimental studies before the time series started and was then adapted to the increase in oxygen measured during the experiments the week before. This was done to provide a measurable oxygen increase on the one hand and on the other to keep bottle artefacts caused by too long incubation times at a minimum. The incubation time ranged between four hours in spring and seven hours in winter. Oxygen was measured with the Winkler-technique (Grasshoff et al., 1983) using an automatic titration apparatus (Metrohm Multi-Dosimat 645). With this method an accuracy of $\pm 0.45 \mu\text{mol O}_2 \text{ L}^{-1}$ can be reached. Results were converted from mg O_2 into mg C assuming a PQ of 1.3 from oxygen to carbon (Asmus et al., 1998). P/E curves were fitted following the formula of Platt et al. (1980) as shown in Eq. (3): $P_N = P_{\text{max}} ((1 - \exp(-\alpha I_d / P_{\text{max}})) (\exp(\beta I_d / P_{\text{max}})))$. Primary production (P_N) was standardised to chlorophyll-a ($\mu\text{g L}^{-1}$). From that fit, the maximum rate of photosynthesis P_{max} (mg C mg $\text{Chl}^{-1} \text{ h}^{-1}$), the initial slope of the curve α (mg C mg $\text{Chl}^{-1} \text{ h}^{-1} (\mu\text{mol photons m}^{-2} \text{ s}^{-1})^{-1}$) and the saturation parameter $E_k (P_{\text{max}}/\alpha)$ were calculated.

Table 1
Spatial extent of depth intervals in the List Tidal Basin

	Area [km ²]	water covered area in %	water volume [km ³]
total area	405		
Sandbanks	49		
Water covered	356	100	946
Depth intervals			
0–1	128.2	36.03	295.5
1–2	113.5	31.90	166.2
2–3	46.7	13.12	87.8
3–4	18.1	5.08	56.8
4–5	7.5	2.12	45.2
5–6	4.6	1.30	39.4
6–7	3.7	1.05	35.3
7–8	3.5	0.98	31.7
8–9	3.3	0.92	28.3
9–10	3.1	0.87	25.2
10–11	3.1	0.87	22.1
11–12	2.8	0.79	19.1
12–13	2.7	0.75	16.4
13–14	2.8	0.78	13.7
14–15	2.6	0.74	10.9
15–16	2.0	0.57	8.6
16–17	1.4	0.39	6.9
17–18	0.9	0.24	5.8
18–19	0.8	0.23	5.0
19–37	3.9	1.1	21.5

2.5.2. Depth-integrated primary production

Surface irradiance was based on hourly global radiation measurements by the Deutsche Wetterdienst Station List/Sylt, assuming a conversion factor of $1 \text{ W m}^{-2} = 4.17 \mu\text{M photons m}^{-2} \text{ s}^{-1}$ (Tillmann et al., 2000). Since primary production is not linear to irradiance, we used hourly light data and interpolated P/E-parameters, chlorophyll-a and suspended matter concentrations to hourly values. Since

SPM concentrations were measured more regularly than the attenuation coefficients, we recalculated light attenuation from suspended matter values using the linear regression established during this study. The annual primary production (P_a) was calculated following Eq. (4): $P_a = \int_1^Y \int_s^z \text{chl}a P_N$, where the hourly primary production is integrated over water depth (s =surface, z =water depth) and over time from 1 to y ($y=8760 \text{ h y}^{-1}$). Areal primary

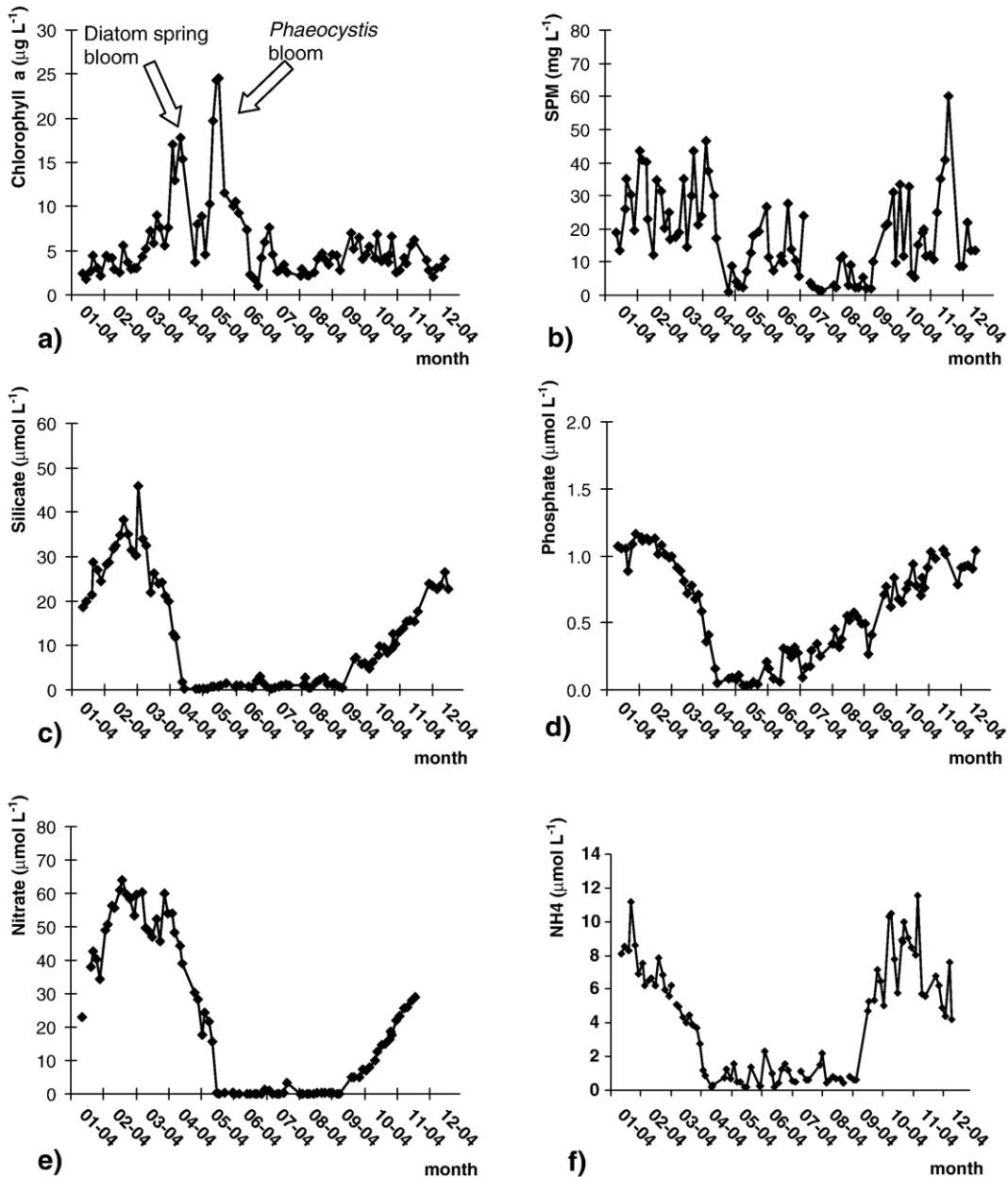


Fig. 2. Annual dynamics of (a) chlorophyll-a, (b) suspended matter (SPM), (c) silicate, (d) phosphate, (e) nitrate, (f) ammonium in the List Tidal Basin.

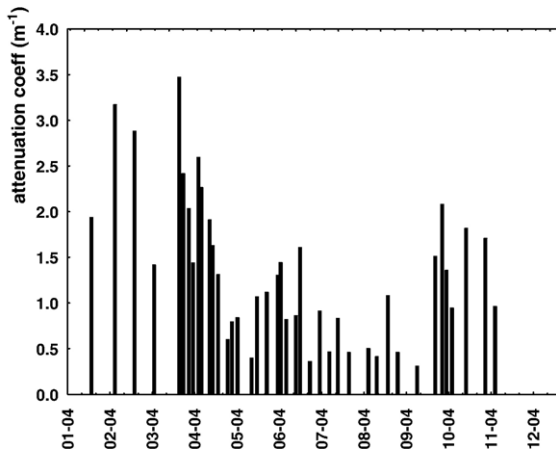


Fig. 3. Annual dynamics of light attenuation coefficients (k) in the List Tidal Basin.

production was estimated in two ways: For the first estimate, data were integrated using the mean water depth of the List Tidal Basin, ($z=2.7$). For the second estimate primary production was integrated for each depth interval ($i=1-37$) and summed up according to the areal share of each depth interval (see Table 1) and divided by the total surface. The mean water depth within each depth interval was assigned to the mid of the interval (e.g. the mean depth of the depth interval 2–3 m is 2.5 m).

2.6. Respiration

Respiration was measured weekly (during winter monthly) over the period of one year. Seawater was sampled with a Niskin-bottle and six incubation bottles (~ 120 ml) were filled bubble-free through a silicon tube immediately after sampling. In three bottles, the initial seawater oxygen content was fixed by adding Winkler-chemicals. Three bottles were wrapped in aluminium foil and incubated in the dark at controlled in situ temperature for 24 h. Oxygen content was measured with the Winkler-technique (Grasshoff et al., 1983) and oxygen consumption rates were converted into carbon respiration rates ($\mu\text{g C L}^{-1} \text{ h}^{-1}$) as described above. For the calculation of areal respiration rates ($\text{mg C m}^{-2} \text{ d}^{-1}$) we assumed a homogeneous water column (no depth gradient in respiration).

2.7. The ratio of pelagic primary production (P) and respiration (R)

We calculated P/R ratios from primary production and respiration rates per surface area on an annual scale, for each month, and also for the diatom spring bloom,

and the *Phaeocystis* bloom. We subdivided both blooms in periods before and after their peak. Moreover, we determined the P/R ratios for the depth intervals of the List Tidal Basin.

3. Results

3.1. Analysis of bathymetrical data

At mean sea level (msl) the List Tidal Basin covers an area of 405 km^2 (Fig. 1). Approximately 49 km^2 of this area are sandbanks not covered by water at mean high tide. The maximum water depth was 37 m. Table 1 shows the areal share of each depth interval (i). The water volume at mean tide is $\sim 0.960 \text{ km}^3$. The mean water depth (at msl) is 2.7 m (excluding sandbank areas). Approximately 36% of the area is intertidal (depth < 1 m; mean low water = 1 m below msl) and 50% of the area is shallow subtidal (< 4 m). The latter level of 4 m is about equal to the annual mean euphotic zone of 3.2 m (see below). The maximum depth of 37 m covers 0.01% of the area.

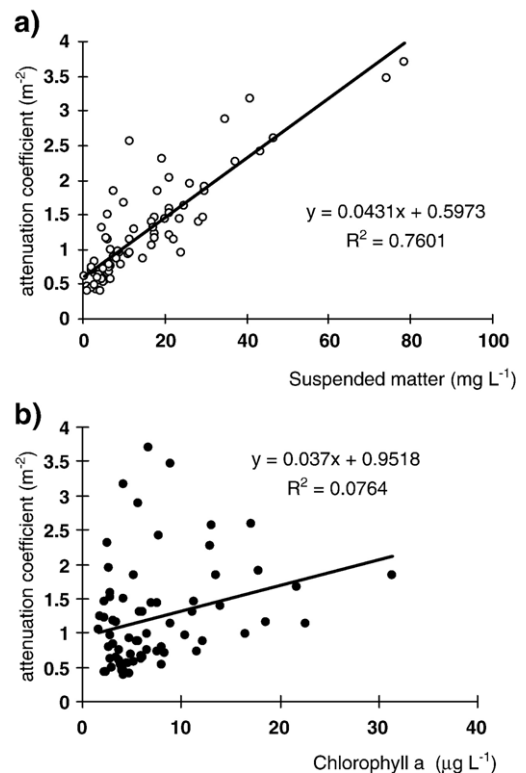


Fig. 4. Linear regression of (a) light attenuation coefficients and suspended matter concentrations, (b) light attenuation coefficients and chlorophyll-a concentrations.

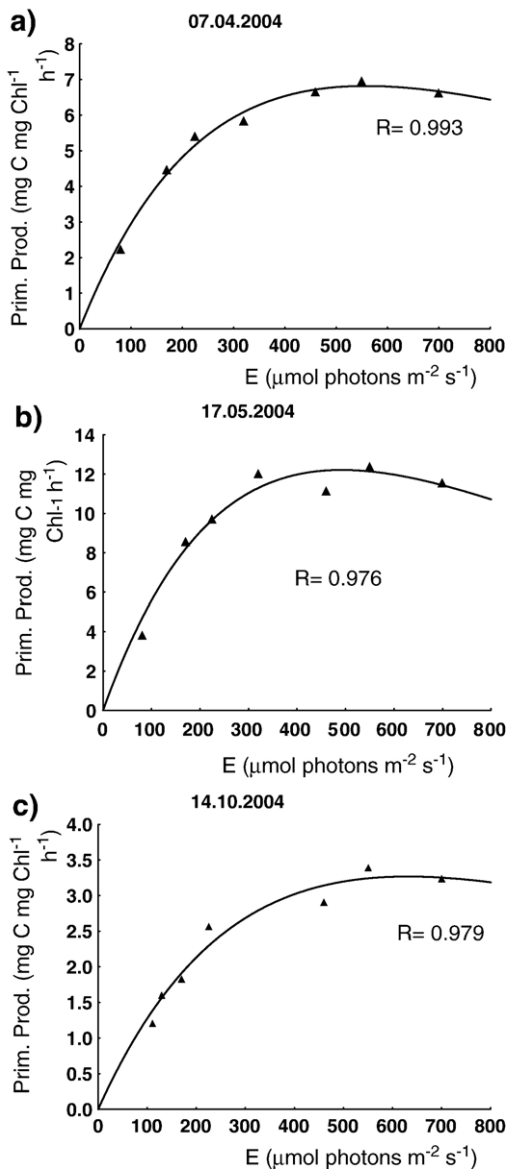


Fig. 5. Examples of P/E curves, measured (a) during the diatom spring bloom, (b) during the *Phaeocystis* bloom, (c) in autumn. Curves were fitted to the formula of Platt et al. (1980).

3.2. Annual cycles of chlorophyll-a, nutrients, suspended matter and light attenuation

Chlorophyll-a showed a seasonal pattern (Fig. 2a): from January to March chlorophyll-a concentrations remained between 2 and 8 $\mu\text{g L}^{-1}$. During the diatom spring bloom in early April, chlorophyll-a increased to 18 $\mu\text{g L}^{-1}$. After the diatom spring bloom, *Phaeocystis globosa* bloomed from the beginning of May to mid June, with chlorophyll-a concentrations of up to 24 μg

L^{-1} . In summer and autumn, chlorophyll-a values were again between 2 and 8 $\mu\text{g L}^{-1}$.

3.2.1. Suspended matter concentrations

Suspended matter concentrations ranged between 1 and 60 mg L^{-1} (Fig. 2b). The annual mean ($\pm\text{SD}$) was

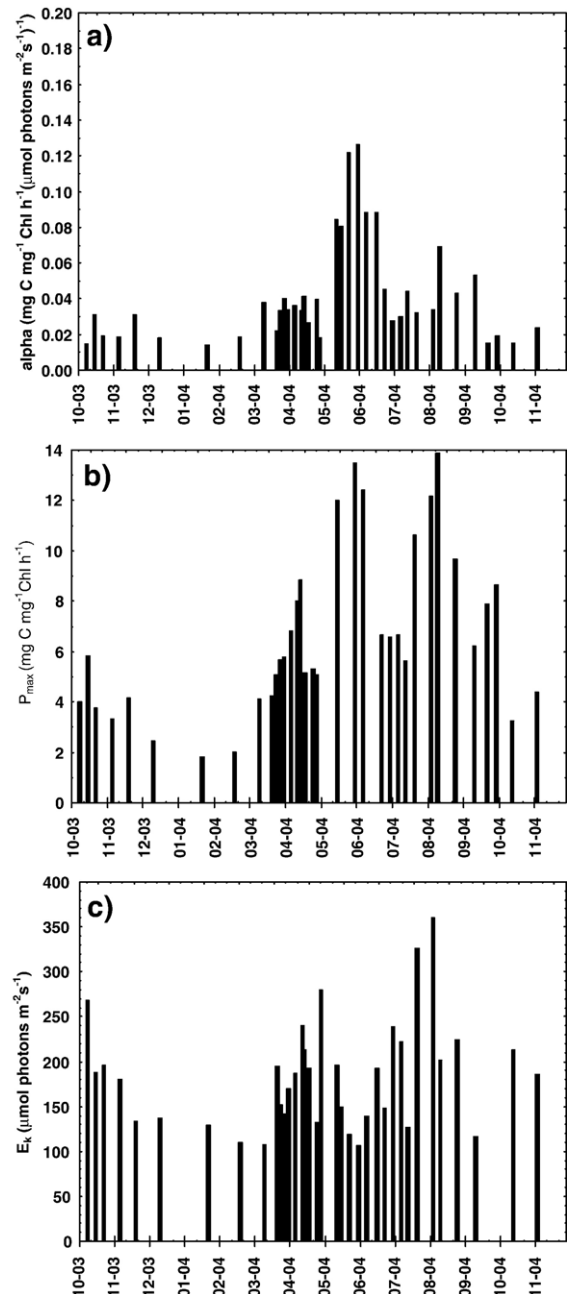


Fig. 6. Annual dynamics of parameters describing P/E-curves, calculated following Platt et al. (1980). (a) Alpha reflects the initial slope of the linear part of the P/I-curve; (b) P_{max} is the maximum of production; (c) E_k is the light intensity at which photosynthesis becomes saturated.

Table 2

Pelagic primary production, pelagic respiration, and the ratio P/R

depth interval [i]	water depth [z]	respiration [g C m ² y ⁻¹]	prim. prod. [g C m ² y ⁻¹]	P/R
Mean	2.7	50	204	4.1
1–37		50	146	2.9
0–1	0.5	9.3	28	8.3
1–2	1.5	28	50	5.8
2–3	2.5	47	27	4.3
3–4	3.5	65	11	3.3
4–5	4.5	84	4.7	2.6
5–6	5.5	103	2.9	2.2
6–7	6.5	121	2.4	1.9
7–8	7.5	140	2.2	1.6
8–9	8.5	159	2.1	1.4
9–10	9.5	177	2.0	1.3
19–20	19.5	364	0.5	0.6
36–37	36.5	681	0.02	0.3

Results are shown for the mean water depth of 2.7 m and the different depth intervals.

18.4±14.3 mg L⁻¹. Between April and August, concentrations ranged between 1 and 27 mg L⁻¹; in autumn and winter, between 6 and 60 mg L⁻¹.

3.2.2. Nutrient seasonal cycles

Nutrient seasonal cycles are presented in Fig. 2 c–f. During winter, high concentrations prevailed (NO₃ up to 60 μmol L⁻¹, NH₄ up to 11 μmol L⁻¹, PO₄ ~ 1.1 μmol L⁻¹ and Si up to 40 μmol L⁻¹). During the diatom spring bloom, Si dropped to below 1 μmol L⁻¹, PO₄ to below 0.1 μM and NH₄ to below 0.5 μmol L⁻¹. NO₃ went down to values below 1 μmol L⁻¹ one month later during the peak of the *Phaeocystis* bloom. Phosphorus slightly increased directly after reaching its minimum in April and reached its winter maximum in November. Silicate, nitrate and ammonium remained low until the beginning of September, then increased again and reached their maximum during autumn (ammonium) or reached their winter maximum in January the following year (silicate and nitrate).

3.2.3. Light attenuation in relation to suspended matter and chlorophyll-a

The light attenuation coefficient in the List Tidal Basin ranged between 0.3 and 3.5 m⁻¹ (Fig. 3). The annual mean attenuation coefficient was 1.44 m⁻¹. From November to March the attenuation coefficient was usually higher than 1 m⁻². From April to September most observations showed values below 1 m⁻¹. Light attenuation showed a strong linear correlation with suspended matter ($r^2=0.76$, $p=0.00$, Fig. 4a) and low but significant correlation with chlorophyll-a ($r^2=0.076$, $p=0.02$; Fig. 4b). Multiple regression between light attenuation and suspended matter

plus chlorophyll-a concentrations gave a slightly better fit ($r^2=0.80$; $p=0.00$). Whereas chlorophyll had a significant effect, it contributed little to the overall regression (beta Chl-a=0.17; beta SPM=0.86). The annual mean euphotic zone, defined as 1% surface irradiance, was ~3.2 m and ranged between ~7.5 and 1.2 m, depending on the light attenuation.

3.3. Primary production

3.3.1. Annual dynamics of photosynthesis versus irradiance (P/E)

P/E curves were determined weekly (during winter monthly) for one year. We used 34 P/E curves in total for this study. Fig. 5 shows three examples of P/E curves: during the diatom spring bloom, during the *Phaeocystis* bloom and during autumn. Parameters describing the P/E curves (P_{max} , E_k , alpha) represent physiological light adaptations of the phytoplankton community. The initial slope of P/E curves (alpha) ranged between 0.014 and 0.13 mg C mg Chl⁻¹ h⁻¹ (μmol photons m⁻² s⁻¹) (Fig. 6a). The chlorophyll-specific maximum photosynthetic rate P_{max} ranged from 1.8 to 14 mg C mg Chl⁻¹ h⁻¹

Table 3

Monthly mean values of pelagic respiration (R), primary production (P), and their ratio P/R

Month/ Period	R [mg C m ⁻² d ⁻¹]	P [mg C m ⁻² d ⁻¹]	P/R
2004			
January	17	5	0.3
February	40	30	0.7
March	32	132	4.1
April	115	500	4.4
May	393	1996	5.1
June	491	867	1.8
July	157	433	2.8
August	176	494	2.8
September	118	229	1.9
October	48	53	1.1
November	36	22	0.6
December	33	10	0.3

diatom spring bloom

before peak (29 March – 13 April)	81	426	5.3
after peak (~14 April – 6 May)	152	595	3.9

Phaeocystis bloom

before peak (~7 May – 19 May)	401	1857	4.6
after peak (~20 May – 17 June)	580	1779	3.0

Values are also given for the periods before and after the peak of the diatom spring bloom and the *Phaeocystis* bloom.

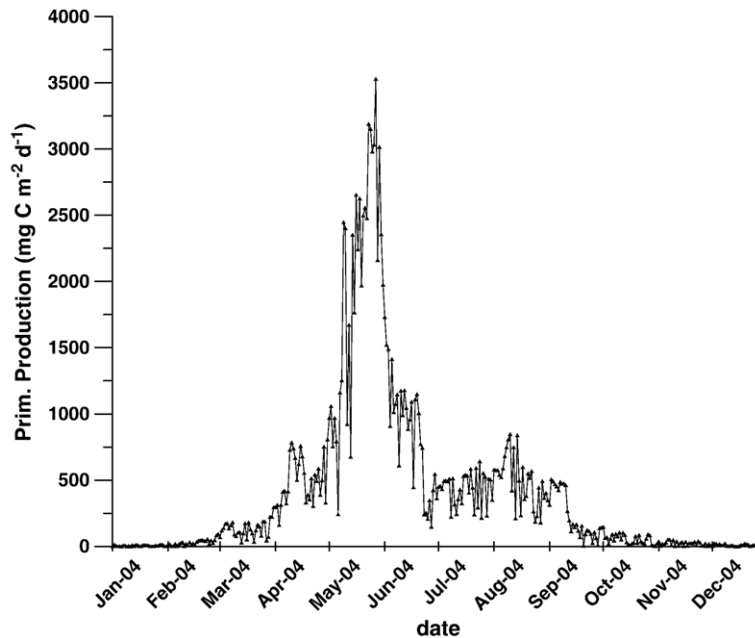


Fig. 7. Annual dynamics of primary production in 2004. The plot shows daily values ($\text{mg C m}^{-2} \text{d}^{-1}$), resulting from calculations based on the areal share of different water depths in the List Tidal Basin.

(Fig. 6b). The highest values were observed during a *Phaeocystis* bloom in May and June, lowest values in December and in January. E_k ranged between 107 and $360 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ (Fig. 6c).

3.3.2. Depth-integrated annual primary production

The mean annual primary production was $146 \text{ g C m}^{-2} \text{y}^{-1}$. The estimate was based on calculations with the spatial extent of the depth intervals (Table 2). Table 3 shows monthly means. Primary production rates ranged from $0.1 \text{ mg C m}^{-2} \text{d}^{-1}$ in winter to $\sim 3500 \text{ mg C m}^{-2} \text{d}^{-1}$

at the end of May during the *Phaeocystis* bloom peak (Fig. 7). More than 50% of the annual production occurred during the *Phaeocystis* bloom. Highest rates during the diatom spring bloom were $\sim 800 \text{ mg C m}^{-2} \text{d}^{-1}$. Approximately 75% of the overall pelagic production occurred within the first 3 m (Table 2). The total annual production calculated for the mean water depth of 2.7 m gave higher results of $204 \text{ g C m}^{-2} \text{y}^{-1}$. Fig. 8 shows the dependence of annual primary production estimates per unit surface area in the List Tidal Basin on water depth.

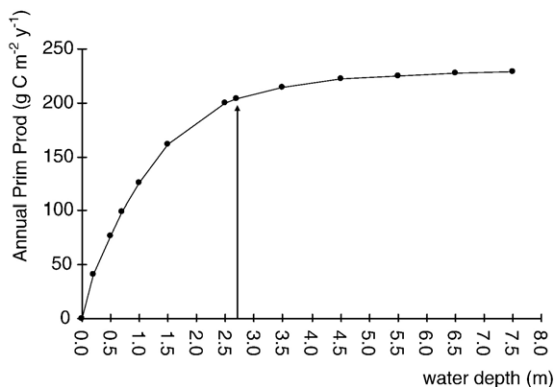


Fig. 8. Dependence of annual primary production ($\text{gC m}^{-2} \text{y}^{-1}$) on water depth in the List Tidal Basin. The arrow indicates the annual primary production for the mean water depth of 2.7 m.

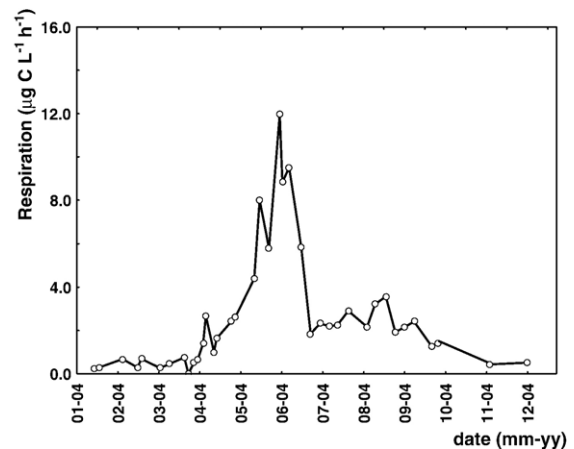


Fig. 9. Annual dynamics of pelagic respiration in the List Tidal Basin.

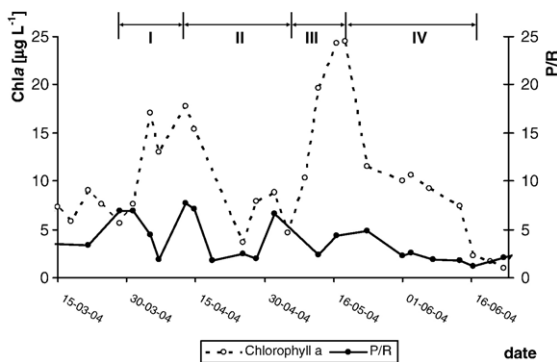


Fig. 10. Chlorophyll-a (left axis) concentrations and P/R ratios (right axis) from mid March until the end of June. The numbers I–IV indicate the different bloom periods. I: spring bloom before peak; II: spring bloom after peak; III: *Phaeocystis* bloom before peak; IV: *Phaeocystis* bloom after peak. See also Table 3.

3.4. Pelagic respiration

Respiration was measured weekly (during winter monthly) and determined as $\mu\text{g C L}^{-1} \text{ h}^{-1}$. Total annual pelagic respiration was $50 \text{ g C m}^{-2} \text{ y}^{-1}$ (in volumetric units: $18.6 \text{ g C m}^{-3} \text{ y}^{-1}$) and based on 42 measurements. Respiration ranged between 0.1 and $12 \mu\text{g C L}^{-1} \text{ h}^{-1}$ (Fig. 9). During winter, respiration was low ($<1 \mu\text{g C L}^{-1} \text{ h}^{-1}$) and increased slightly to $\sim 2.7 \mu\text{g C L}^{-1} \text{ h}^{-1}$ in April during the diatom spring bloom. Highest respiration rates of up to $\sim 12.0 \mu\text{g C L}^{-1} \text{ h}^{-1}$ were measured about two weeks after the *Phaeocystis* bloom in May and June. During this period (May to mid June) approximately 50% of the total annual pelagic respiration occurred. In summer, respiration reached values between 2 and $4 \mu\text{g C L}^{-1} \text{ h}^{-1}$. Table 3 shows monthly mean values.

3.5. The ratio of pelagic primary production and pelagic respiration (P/R)

The annual mean P/R ratio was $146/50=2.9$, indicating that the water column in the List Tidal Basin was autotrophic. Monthly P/R values ranged between 0.3 in winter and 5.1 in May (Table 3). From November to February, P/R was <1 (0.3–0.7), indicating heterotrophic conditions in winter. In spring, the P/R ratio increased to maximum values of 4.4 in April and 5.1 in May. The diatom spring bloom showed higher P/R values than the *Phaeocystis* bloom. Fig. 10 shows chlorophyll-a concentrations and P/R ratios from mid March to mid June: the P/R ratio was 5.3 during the build-up of the diatom spring bloom until its peak (~ 29 March – 13 April 2004). After the peak (~ 14 April – 6 May 2004) the P/R ratio was 3.9 (Table 3). The P/R ratio was 4.6 from the

beginning of the *Phaeocystis* bloom until its peak (7 May – 19 May 2004). The P/R dropped to 3.0 after the peak (~ 20 May – 17 June 2004). The ratio of pelagic primary production and respiration decreases with increasing water depth (Table 2). The water column remains autotrophic to a depth of ~ 12 m, suggesting that in about 95% of the area the water column is autotrophic.

4. Discussion

In aquatic ecosystems less attention has been given to pelagic respiration than to primary production (Del Giorgio and Williams, 2005). This paper presents for the first time parallel measurements of pelagic primary production, respiration and light attenuation data, covering an entire annual cycle in the Wadden Sea. As production and respiration measurements were based on oxygen dynamics, both processes can be compared directly. On an annual scale, pelagic primary production (based on the areal share of different water depths) exceeded respiration by a factor of 3, implying that the water column was autotrophic. A clear seasonal pattern in P/R ratios was observed with heterotrophic conditions during late autumn and winter (P/R ~ 0.3 –0.7), maximum values during the spring bloom (P/R ~ 4 –5), and intermediate values during summer (P/R ~ 2 –3).

In the following we compare our results with other Wadden Sea areas and discuss the ecological implications of an autotrophic water column. The importance of estimating the areal primary production based on the spatial extent of each depth interval will be stressed.

4.1. The impact of water depth on production estimates

Pelagic primary production is usually reported per unit surface by integrating production rates over water depth. Using the mean water depth may overestimate areal primary production in very shallow systems (where water depth varies within the euphotic zone) as shown for the List Tidal Basin (see Fig. 8).

We compared two ways of areal primary production estimates based (1) on the mean water depth, and (2) on the areal share of each depth interval. Calculations on the basis of the mean water depth ($=204 \text{ g C m}^{-2} \text{ y}^{-1}$) overestimated pelagic productivity by approximately 40% compared to estimates based on the areal share ($=146 \text{ g C m}^{-2} \text{ y}^{-1}$) (Table 2). Since the latter was the more precise estimate, the following discussion is based on the lower production estimate of $146 \text{ g C m}^{-2} \text{ y}^{-1}$. Differences between the results of the two estimation methods can be explained by turbidity (depth of the

euphotic zone) and local bathymetry; therefore our value of 40% cannot be transferred to other systems.

4.2. Primary production in the List Tidal Basin compared to other Wadden Sea areas

The total annual primary production of $146 \text{ g C m}^{-2} \text{ y}^{-1}$ in 2004 was in the same range as other estimates for the northern Wadden Sea. Asmus et al. (1998) reported $160 \text{ g C m}^{-2} \text{ y}^{-1}$ based on samples taken at the low water line in the List Tidal Basin during 1990–1995. Tillmann et al. (2000), using the ^{14}C -technique, estimated primary production in the Meldorfer Bucht (northern Wadden Sea) to be 124 and $176 \text{ g C m}^{-2} \text{ y}^{-1}$ in 1995 and 1996, respectively. The light attenuation coefficient (k) in the Meldorfer Bucht ranged between 0.8 and 7 m^{-1} , indicating that the water column is more turbid than in the List Tidal Basin ($k=0.3\text{--}3.7 \text{ m}^{-1}$). Compared to those of the Dutch Wadden Sea, the observed primary production values are low. For the Marsdiep area, Cadée and Hegeman (2002) reported low values of about $150 \text{ g C m}^{-2} \text{ y}^{-1}$ from 1964–1975, increasing to $440 \text{ g C m}^{-2} \text{ y}^{-1}$ in 1994, and then a decreasing trend to values between 200 and $250 \text{ g C m}^{-2} \text{ y}^{-1}$ in 2000. Philippart et al. (2007) included actual daily irradiation in the estimation model for the Marsdiep giving lower pelagic primary production values of $150\text{--}300 \text{ g C m}^{-2} \text{ y}^{-1}$ in the 1990s and values between 120 and $170 \text{ g C m}^{-2} \text{ y}^{-1}$ from 2000 to 2004. The decreasing trend observed in the western Dutch Wadden Sea is not evident from the data available for the northern Wadden Sea (Loebl, 2006). The generally higher primary production levels in the southern Wadden Sea as compared to the northern Wadden Sea are in line with lower chlorophyll levels and a less intense cycling of nitrogen compound in the northern Wadden Sea (Van Beusekom, 2006).

Only little information on P/E-parameters (P_{max} , α , E_k) is available for the northern Wadden Sea. Primary production measurements by Asmus et al. (1998) in the List Tidal Basin were field incubations. Tillmann et al. (2000) showed P/E-parameters in the Meldorfer Bucht for a two-year period in 1995/96. They used the ^{14}C -technique, but nevertheless P/E-parameters are in a similar range as in our study using the O_2 -technique. In summer, some measurements of the present study show higher values of P_{max} and α . Different species composition between years as well as different photo-acclimations of the phytoplankton community on a modified light field and the ambient temperature may modify P/E-parameters and productivity (Coté and Platt, 1983; Macedo et al., 2002). *Phaeocystis globosa*, in

particular, is known to have higher P_{max} values than diatoms (Verity et al., 1991), which is in line with our observations.

4.3. Respiration in the Wadden Sea

The total annual pelagic respiration in the List Tidal Basin was $50 \text{ g C m}^{-2} \text{ y}^{-1}$ ($18.6 \text{ g C m}^{-2} \text{ d}^{-1}$). Respiration was low in winter ($\sim 17\text{--}40 \text{ mg C m}^{-2} \text{ d}^{-1}$), increased slightly during the diatom spring blooms ($\sim 115\text{--}160 \text{ mg C m}^{-2} \text{ d}^{-1}$) and then peaked during the *Phaeocystis globosa* bloom, when highest levels ($750 \text{ mg C m}^{-2} \text{ d}^{-1}$) were reached. After the peak of the diatom spring bloom, phytoplankton standing stock rapidly decreased. Zooplankton grazing rates (Loebl, 2006) and respiration rates remained low, suggesting that most of the organic matter was transferred to the sediment. An export of part of the organic matter cannot be excluded on the basis of our observations. But on average the Wadden Sea is an accumulation area (e.g. Postma, 1980; Van Beusekom et al., 1999) and most of the accumulation in the Wadden Sea seems to take place during April – June (Cadée, 1980). Low remineralisation rates have also been observed during and after the diatom spring bloom in other parts of the Wadden Sea. Van Boekel et al. (1992) showed for the Marsdiep that at the end of a diatom spring bloom the cell lysis rate did not increase. Bacterial production showed only a slight increase during a diatom spring bloom (Brussaard et al., 1995). During the *Phaeocystis* bloom more than 50% of the total annual pelagic respiration occurred. During this period daily volumetric respiration rates (up to $280 \mu\text{g C L}^{-1} \text{ d}^{-1}$) were about three times higher than the bacterial production rates of $90 \mu\text{g C L}^{-1} \text{ d}^{-1}$ reported by Brussaard et al. (1996) for the Marsdiep area. Zooplankton grazing pressure was high during the *Phaeocystis* bloom in 2004 (Loebl, 2006) and may be one factor explaining the difference in respiration rates between the two blooms. After the *Phaeocystis* bloom respiration remained on a higher level than before the bloom. This is in accordance with the observations of Brussaard et al. (1996), who also observed higher bacterial production rates after the collapse of the *Phaeocystis* bloom. Van Boekel et al. (1992) suggested that the microbial food web is carbon limited during the diatom spring bloom and that release of dissolved organic carbon through lysis at the end of the *Phaeocystis* bloom supports the microbial food web. Stelfox-Widdicombe et al. (2004) reported that during a *Phaeocystis* bloom in near-shore waters of the southern North Sea, the phytoplankton production was largely recycled within the water column. Together this indicates that also in the List Tidal Basin a significant

fraction of the *Phaeocystis* biomass remained in the water column due to grazing and fast bacterial degradation, thereby supporting the pelagic food web.

We measured an annual pelagic volumetric respiration of $18.6 \text{ g C m}^{-3} \text{ y}^{-1}$, which is much lower than the $110 \text{ g C m}^{-3} \text{ y}^{-1}$ previously estimated for the same area by Van Beusekom et al. (1999). This may be explained by different sampling sites: the value estimated by Van Beusekom et al. (1999) was based on field measurements with water taken at a shallow intertidal station during low tide (Asmus et al., 1998, their Fig. 2). Resuspension (De Jonge and Van Beusekom, 1995) and pore water seepage (Billerbeck et al., 2006) may have contributed to the high respiration rates.

Only few pelagic respiration data are available for the Wadden Sea. The present value of $18.6 \text{ g C m}^{-3} \text{ y}^{-1}$ is in closer agreement with estimates from the Dutch part. Van Duyl and Kop (1988) estimated annual respiration rates of $165\text{--}205 \text{ g C m}^{-2} \text{ y}^{-1}$ ($\sim 56 \text{ g C m}^{-3} \text{ y}^{-1}$) in the western Dutch Wadden Sea during the 1980s. The higher value is in accordance with a higher eutrophication level of the western Wadden Sea compared to the northern Wadden Sea (Van Beusekom, 2006) and with a higher eutrophication level during the 1980s (e.g. Cadée and Hegeman, 2002). Robinson and Williams (2005) reported a mean daily pelagic respiration in coastal areas of $3.5 \text{ O}_2 \text{ mmol m}^{-3} \text{ d}^{-1}$ (calculated from 323 observations of a global data base). Mean daily respiration rates of $4.25 \text{ mmol O}_2 \text{ m}^{-3} \text{ d}^{-1}$ as observed in the List Tidal Basin are well within this range.

4.4. The ratio of pelagic primary production and respiration

On an annual average, the water column of the List Tidal Basin was autotrophic (P/R ~ 3). The P/R ratio varied seasonally: from February to October the water column was autotrophic, from November to February slightly heterotrophic. The largest autotrophy (P/R $\sim 4\text{--}5$) was observed during the diatom spring bloom in April, whereas pelagic respiration remained low. A large fraction of the spring bloom biomass produced in April was not respired in the water column and transported to the sediment (see above). Shortly after the *Phaeocystis* bloom peak, the P/R-ratio dropped to 2.8 as a result of high pelagic respiration rates. We suggest that the diatom bloom mainly boosts benthic food webs, but that the *Phaeocystis* bloom supports both the pelagic and the benthic food web.

In conclusion, the annual mean P/R of ~ 3 indicates that on an annual scale a large fraction of pelagic primary production was remineralised in the benthos.

This is in accordance with high respiration rates in intertidal sediments in the List Tidal Basin (De Beer et al., 2005). Their study specifically addressed the influence of permeability on the turnover of organic matter in intertidal sands. Sand dominates $\sim 95\%$ of the sediment in this part of the Wadden Sea. The aerobic respiration rates measured by De Beer et al. (2005) were much higher than previously reported (e.g. Kristensen et al., 1997). The authors estimated that benthic primary production could not account for the observed respiration rates and suggested that most of the remineralised organic matter was derived from the water column. An annual net export of biomass from the List Tidal Basin to the adjacent North Sea is not very likely, since the Wadden Sea is an accumulative import area for organic material (Postma, 1954, 1980; Van Beusekom et al., 1999). Baird et al. (2004), who carried out a food web analysis for the intertidal of the List Tidal Basin, concluded that organic matter is imported from the subtidal parts of the Basin or from the North Sea to the intertidal. Available carbon budgets indicate that the Wadden Sea (sediments plus water column) is heterotrophic (e.g. Postma, 1954; De Jonge and Postma, 1974; Hoppema, 1991; Van Beusekom et al., 1999). The surplus organic matter is largely imported from the North Sea (e.g. Postma, 1954; Cadée, 1980; Van Beusekom and De Jonge, 2002) suggesting an autotrophic coastal zone outside of the Wadden Sea. Annual primary production rates in the adjacent German Bight are about $430 \text{ g C m}^{-2} \text{ y}^{-1}$ (Rick et al., 2006), almost three times higher than in the northern Wadden Sea. It is interesting to note that also within the Wadden Sea the water column is autotrophic. On the basis of annual budgets for the western Dutch Wadden Sea, Van Duyl and Kop (1988) also concluded that pelagic primary production exceeded remineralisation rates. The P/R ratio in their study was 1.4 (253/186). Both import of dissolved or suspended organic matter from the IJsselmeer and the large and long-lasting *Phaeocystis* blooms that prevailed in this area during the 1980s (e.g. Cadée and Hegeman, 2002) may have contributed to a lower P/R ratio. A further factor that influences the P/R ratio is water depth, as respiration rates per surface area increase linearly with water depth but primary production rates per surface area depend on light penetration. The List Tidal Basin is shallower than the western Dutch Wadden Sea and the mean water depth lies well within the euphotic zone, increasing the P/R-ratio. But also the filtering activity of sandy sediments and of benthic filter feeders may remove organic material faster from the shallow water column in the List Tidal Basin than in the deeper western Dutch Wadden Sea. Poremba et al.

(1999) suggested that in deep tidal channels heterotrophic conditions prevail whereas the shallow parts are autotrophic because of favourable light conditions. Our study showed that in the List Tidal Basin, autotrophic conditions prevail down to a depth of approximately 12 m, i.e. in about 95% of the area.

The P/R-ratio shown for 2004 may vary from year to year. In the present study, the diatom spring bloom contributed more to the water column autotrophy than the *Phaeocystis* bloom, even though primary production rates were much higher during the latter bloom. In the List Tidal Basin diatom blooms as well as *Phaeocystis* blooms vary in onset, quantity, and duration (Martens, 2001; Van Beusekom, unpubl. data). This affects the water column autotrophy. In years with large diatom spring blooms and low *Phaeocystis* blooms, the water column autotrophy is presumably higher than in years with low diatom spring blooms and long-lasting *Phaeocystis* blooms.

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