Planktonic primary production in the German Wadden Sea

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Abstract. By combining weekly data of irradiance, attenuation and chlorophyll a concentrations with photosynthesis (P) versus light intensity (E) curve characteristics, the annual cycle of planktonic primary production in the estuarine part of the Northfrisian Wadden Sea was computed for a 2 year period. Daily water column particulate gross production ranged from 5 to 2200 mg C m⁻² day⁻¹ and showed a seasonal pattern similar to chlorophyll a. Budget calculation yielded annual gross particulate primary productions of 124 and 176 g C m⁻² year⁻¹ in 1995 and 1996, respectively. Annual amounts of phytoplankton respiration, calculated according to a two-compartment model of Langdon [in Li, W. K. W. and Maestrini, S. Y. (eds), Measurement of Primary Production from the Molecular to the Global Scale. International Council for the Exploration of the Sea, Copenhagen, 1993, pp. 20–36], and dissolved production in 1996, were both in the range of 24–39 g C m⁻² year⁻¹. Annual total net production was thus very similar to particulate gross production (127 and 177 g C m⁻² year⁻¹ in 1995 and 1996, respectively). Phytoplankton growth was low or even negative in winter. In spring and summer, production/biomass (P/B) ratios varied from 0.2 up to 1.7. Phytoplankton growth during the growth season always surpassed average flushing time in the area, thus underlining the potential of local phytoplankton bloom development in this part of the Wadden Sea. The chlorophyll-specific maximum photosynthetic rate (P_Bmax) ranged from 0.8 to 9.9 mg C mg⁻¹ Chl h⁻¹ and was strongly correlated with water temperature (r² = 0.67). By contrast, there was no clear seasonal cycle in α₈, which ranged from 0.007 to 0.039 mg C mg⁻¹ Chl h⁻¹ (µmol photons m⁻² s⁻¹)⁻¹. Its variability was much less than P_Bmax and independent of temperature. The magnitude and part of the variability of P_Bmax and α₈ are presumably caused by changes in species composition, as evidenced from the range of these parameters found among 10 predominant diatom species isolated from the Wadden Sea. The ratio of average light conditions in the water column (Eₐv) to the light saturation parameter Eₛ indicates that primary production in the Wadden Sea region under study is predominantly controlled by light limitation and that nutrient limitation was likely to occur for a few hours per day only during 5 (dissolved inorganic nitrogen) to 10 (PO₄, Si) weeks in the 2 year period investigated.

Introduction
For the evaluation of the present role of the Wadden Sea as a sink or a source of organic matter, and also with respect to the ongoing discussion on eutrophication problem areas, it is of interest to obtain more detailed knowledge on the primary production capacity and its regulating factors in this shallow and turbid coastal region of the North Sea.

For the Dutch part of the Wadden Sea, there are several studies of the carbon budget, including estimates of planktonic and benthic primary production as well as estimates of the import of organic matter from rivers and open coastal waters [e.g. (Postma, 1954; van den Hoek et al., 1979; Cadée, 1980; E O N, 1988)]. However, considering the pronounced hydrographical and topographical differences in different parts of the Wadden Sea, results from one part are not directly assignable to other subregions of the Wadden Sea. For the German part of the Wadden Sea, only a few studies on primary production are available, exclusively performed in the Sylt/Rømø Bight, a small embayment with a rather narrow inlet, which is hardly influenced by continental run-off (A smus, 1982; A smus et al., 1998). By contrast, no information on primary production is available for the southern part of the Northfrisian Wadden Sea, which is a shallow, estuarine-like...
area characterized by its direct vicinity to the mouth of the River Elbe and the lack of protecting offshore islands.

The lack of information on primary production is due to the limited methodological possibilities for direct measurements for a thorough spatio-temporal resolution. An adequate tool to overcome these problems is the application of bio-optical productivity models, which are based on the functional relationship between photosynthesis (P) and light intensity (E). Hence, the magnitude and variability of P versus E parameters need to be known for a reliable model assessment of primary productivity. Whereas variations in assimilation number were initially hypothesized to be simply experimental errors (Ryther and Yentsch, 1958), it is now apparent that parameters of the P versus E curve may vary significantly according to environmental fluctuations (Sakshaug et al., 1997).

The present study is the first systematic approach to determining P versus E parameters and their seasonal variation in Northfrisian Wadden Sea phytoplankton communities. It presents annual budgets of primary production over a 2 year cycle and analyses the main regulating factors for its seasonal dynamics, such as temperature, irradiance, inorganic nutrients and species composition.

Method

In the period from March 1995 to December 1996, surface samples were taken at high tide at the permanent station Bümum-Mole, located on the coastline of the Northfrisian Wadden Sea south of the peninsula of Eiderstedt (Figure 1). Sampling frequency was weekly during the growth season from March to November and fortnightly in winter. Samples were processed within 15 min after sampling.

Seston dry weight (GF/C filters) was determined gravimetrically after drying at 70°C. Nutrient concentrations were determined according to Grashoff et al. (Grashoff et al., 1983).

Primary production samples (55 ml) were spiked with 1–4 µCi (depending on the time of year) of NaH14CO3 (= 3.7 × 10^4–14.8 × 10^4 Bq) and incubated immediately after sampling in a rotating incubator at in situ temperature. Different light regimes were achieved with a set of flasks with neutral-density filter coating (ZEMOKO, Middelburg, The Netherlands). Incubation time was 2 h, except in winter during low activity, when it was extended to 4 h. Incubation was stopped by gentle filtration through 0.45 µm nitrocellulose filters. Filters were washed with 10 ml of filtered sea water and dried at 30°C for 24 h. Analysis for radioactivity was carried out in a Packard scintillation counter (Model TR1-CAR 1900 TR) using FilterCount (Packard) as scintillation cocktail and the external standard method for quench correction. Dark bottle counts (30–100 d.p.m.) were sufficiently low so that filter treatment with fuming HCl was considered to be dispensable. Maximum incubation irradiance provided by cool white fluorescent tubes (Philips TL 33) ranged from 500 µmol photons m–2 s–1 applied in winter up to 900 µmol photons m–2 s–1 in spring and summer. Irradiance measurements were performed inside of the incubation flasks by means of a special 4-π microsensor (ZEMOKO, Middelburg, The Netherlands).
Dissolved inorganic carbon was calculated according to Strickland and Parsons (Strickland and Parsons, 1972). Rates of carbon fixation were corrected by subtraction of dark bottle values. Primary production was calculated using an isotope discrimination factor of 1.05.

Production measurements were normalized to chlorophyll (Chl) \( a \), which was measured spectrophotometrically after Lorenzen (Lorenzen, 1967). Photosynthesis-irradiance (\( P \) versus \( E \)) curves were fitted according to Platt et al. (Platt et al., 1980):

\[
P^B = a \left( 1 - e^{-bE} \right) e^{-cE}
\]

where \( E \) is the incubation irradiance (\( \mu \text{mol photons m}^{-2} \text{s}^{-1} \)) and \( a \), \( b \) and \( c \) are fit parameters. From that fit, \( P^B_{\text{max}} \left[ a \left( b/(b + c) \right) \left( c/(b + c)^{c/b} \right) \right] \), the maximal rate of photosynthesis (\( \text{mg C mg}^{-1} \text{ Chl h}^{-1} \)), \( \alpha^B \left( a \times b \right) \), the initial slope [\( \text{mg C mg}^{-1} \text{ Chl} \)....

**Fig. 1.** Study area.
h^{-1} (\mu mol photons m^{-2} s^{-1})^{-1} \) and \( E_k (P_{max}^B/\alpha^B) \), the light saturation parameter (\( \mu mol photons m^{-2} s^{-1} \)), were calculated.

In addition to the analysis of field samples, the species-specific variability of \( P \) versus \( E \) parameters was investigated for 10 diatom species isolated from the German Wadden Sea. Batch cultures [natural sea water enriched with f/2 (Guillard and Ryther, 1962)] were grown at 16°C and 100 \( \mu mol photons m^{-2} s^{-1} \) (light:dark cycle 16:8 h) and \( P \) versus \( E \) parameters of exponentially growing algae were measured as described for natural samples.

Daily water column production was estimated by combining values of irradiance and Chl a concentrations with \( P \) versus \( E \) curve characteristics. Surface irradiance was taken from global radiation measurements at the Deutsche Wetterdienst Station Sylt, assuming a conversion factor of \( 1 W m^{-2} = 4.17 \mu mol photons m^{-2} s^{-1} \) (Lalli and Parsons, 1995) and 45% photosynthetically active radiation (Kirk, 1994). Correction for light reflection at the water surface was performed according to Kirk (Kirk, 1994).

Attenuation coefficients \( [k (m^{-1})] \) were calculated from Secchi depth \( [S_d (m)] \) using the empirical relationship \( k = 0.191 + 1.242/S_d (r^2 = 0.853) \) determined from 61 simultaneous measurements of Secchi depth and vertical light profiles using a Licor spherical quantum sensor (LI-1935A). Production rates for sampling days in which no direct \( P \) versus \( E \) determination was carried out were calculated from measured irradiance, Chl a and light attenuation data, assuming that \( P \) versus \( E \) characteristics did not differ from the sampling date before.

Carbon turnover rates (\( Pr/B \) ratios) were calculated by dividing the daily column production (\( Pr \)) by the water column biomass (\( B \)) expressed as phytoplankton carbon. The latter was estimated from Utermöhl cell counts of Lugol-fixed samples, which were converted into carbon values according to Edler (Edler, 1979).

Total and dissolved production were measured on 13 sampling dates in 1996. For total production estimates, duplicate subsamples (10 ml) were removed from a transparent flask (which had achieved the maximum incubation irradiance), pipetted into a 20 ml scintillation vial and acidified with 0.3 ml of 1 N HCl. The remaining amount was filtered and duplicate subsamples of the filtrate were taken to measure dissolved production. Unfixed inorganic \( ^{14}C \) was removed by gentle shaking for at least 48 h. Duplicate subsamples of the dark bottle served as a control and were subtracted from light counts.

Respiration was modelled according to Langdon (Langdon, 1993). The respiration over the entire water column can be calculated as:

\[
R_{zt} = BZ[24R_0 + (24 - D) R_D P_{zt}^B + D R_D R_L P_{zt}^B]
\]

where \( B \) is the biomass (mg Chl m\(^{-3}\)), \( Z \) is the mixing depth (m), \( R_0 \) is the biomass-specific maintenance respiration (\( \mu mol O_2 \mu g^{-1} Chl \ h^{-1} \)), \( D \) is the daylength (h), \( R_D \) is the linear coefficient of the increase in biomass-specific dark respiration with gross photosynthesis (dimensionless), \( P_{zt}^B \) is \( P_{zt}/(D \ B \ Z) \), \( P_{zt} \) is the primary production in the water column (mmol \( O_2 \ m^{-2} \ day^{-1} \)) and \( R_L \) is the ratio of light to dark respiration (dimensionless).
Converting our production measurements from mg C to µmol O₂ with a PQ of 1.25 (mol O₂ mol⁻¹ C), respiration was calculated with parameter values typical for diatoms (Langdon, 1993), i.e. R₀ = 0.003 µmol O₂ µg⁻¹ Chl h⁻¹ and R_D = 0.064 and R_L = 2, and reconverted to carbon units.

All calculations were based on a water depth of 3 m, which is the mean depth in the Meldorf Bight (Figure 1), an area covering 275.4 km² with a water volume at mid-tide of 0.896 km³ (S.Dick, personal communication).

### Results

#### Euphotic depth

The Secchi depth ranged from 0.2 m in winter up to occasional values of 2.5 m in summer 1996 (Figure 2a). Accordingly, attenuation coefficients varied between >7 m⁻¹ to a minimum of 0.8 m⁻¹. Regression analysis revealed that 84% of this variation could be explained by varying seston concentrations.

CTD profiles showed that the water column was always well mixed down to the bottom. The ratio of Z_mix (total water depth, taken to be 3 m; see Method) to Z_eu, calculated as depth with 1% surface light, is shown in Figure 2b. In summer, this ratio may be below one, i.e. the entire water column of 3 m is located within the euphotic zone. This ratio never exceeded five, which may represent an upper limit for net primary production and bloom initiation (Cole and Cloern, 1984; Grobbelaar, 1985; Aipine and Cloern, 1988).

#### Chlorophyll a and primary production

There were pronounced Chl a maxima in spring and summer, peaking to 70 mg m⁻³ during the spring bloom in April 1996 (Figure 3a). Daily water column primary production ranged from 5 to 2200 mg C m⁻² day⁻¹ and showed a similar seasonal pattern as Chl a, but with the highest values in summer (Figure 3b), which is in keeping with enhanced temperature. Defining the growth season arbitrarily by threshold values for Chl a and primary production of 5 mg Chl m⁻³ and 200 mg C m⁻² day⁻¹, respectively, rapid growth of phytoplankton was restricted to 18 weeks from May to August in 1995. In 1996, the spring bloom started in mid-March and the growth season lasted for 23 weeks.

The Chl-specific maximum photosynthetic rate (P_B max) ranged from 0.8 to 9.9 mg C mg⁻¹ Chl h⁻¹, exhibiting the highest values in summer (Figure 4a). P_B max was strongly correlated with water temperature (r² = 0.67). The best fit was achieved with an exponential model (Figure 5), resulting in a Q₁₀ of 1.93, which is close to a typical Q₁₀ of ~2 (e.g. Davison, 1991). Analysis of residuals of the exponential model showed that deviations from predictions based only on temperature were significantly positively correlated to P_B max itself (P < 0.05), to the slope α_B (P < 0.0001) and to seston concentrations (P < 0.01), whereas significant negative correlations were found with phytoplankton parameters (Chl a: P < 0.05; total biomass: P < 0.005; biomass of diatoms: P < 0.05; biomass of nanoflagellates: P < 0.05).

A large part of the P_B max variation at one temperature is certainly due to differences in species composition, as evidenced by the wide range of different
$P_{\text{max}}$ values found among 10 predominant Wadden Sea diatom species, ranging from 2.9 ($\text{Plagiogrammopsis vanheurckii}$) to 7.7 mg C mg$^{-1}$ Chl h$^{-1}$ ($\text{Thalassiosira minima}$) (Figure 5).

In contrast to $P_{\text{max}}$, there was no clear seasonal cycle in the slope of the $P$ versus $E$ curves ($\alpha_B$) (Figure 4b). It ranged from 0.007 to 0.039 mg C mg$^{-1}$ Chl h$^{-1}$ (µmol photons m$^{-2}$ s$^{-1}$)$^{-1}$, and was much less variable than $P_{\text{max}}$, and independent of temperature (Figure 5). From the diatom culture experiments, it could be traced that variability of $\alpha_B$, too, is species related, exhibiting values between 0.012 ($\text{Ditylum brightwellii}$) and 0.022 mg C mg$^{-1}$ Chl h$^{-1}$ (µmol photons m$^{-2}$ s$^{-1}$)$^{-1}$ ($\text{Atteya longicornis}$) (Figure 5). In keeping with this, correlation analysis of the

Fig. 2. Annual cycle of (a) Secchi depth and (b) the ratio of mixing depth ($Z_{\text{mix}}$) to euphotic depth ($Z_{\text{eu}}$) at the permanent station Büsum Mole in 1995/1996.

1258
field data set showed that $\alpha^B$ is significantly correlated to the biomass of different algal groups (nanoflagellates: $P < 0.05$; diatoms: $P < 0.05$; Phaeocystis: $P < 0.001$), whereas no significant correlation was found with abiotic parameters.

$E_k$ values were relatively high throughout the year (Figure 4c), indicating acclimation to strong light. They ranged from 67 to 538 $\mu$mol photons m$^{-2}$ s$^{-1}$ and, as for $P^B_{\text{max}}$, varied strongly with the seasonal cycle. Within the 2 years of observation, no marked photoinhibition could be observed at incubation irradiances up to 900 $\mu$mol photons m$^{-2}$ s$^{-1}$.

Estimating net production

Considering the short-term incubation period (2 h) and the filtration method used, it is assumed that measured rates of photosynthesis rather equal gross rates
of particulate primary production (Williams, 1993), although even short incubations may fail in yielding the daytime gross uptake rate (Williams et al., 1996). For estimates of net primary production, both respiration loss and surplus dissolved production have to be taken into account.

Respiration estimates ranged from 0.3 to 442 mg C m\(^{-2}\) day\(^{-1}\) (Figure 6a) with a mean of 188 mg C m\(^{-2}\) day\(^{-1}\) during the growth season. The ratio of phytoplankton respiration to gross particulate production (\(R_{zt}/P_{zt}\)) of the water column showed large seasonal variation with maxima of 1.5 in winter (Figure 6b). During the growth season, this ratio was fairly constant with a mean of 0.21 ± 0.04.

Phytoplankton \(P_r/B\) ratios were low or negative in winter. In spring and summer, they showed large variations from 0.2 to ~1.7 (Figure 7).

A quantitative estimation of dissolved production was taken from measurements carried out in 1996 (Table I). The ratio of dissolved to particulate production was highly variable, ranging from 0.03 to 2.78. High amounts of dissolved organic carbon (>50% of total production) were produced when blooms of

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**Fig. 4.** Annual cycle of P versus E parameters at the permanent station Büsum Mole in 1995/1996. (a) Maximal rate of Chl-specific photosynthesis \(P^\text{max}\); (b) slope \(\alpha\); (c) light saturation parameter \(E_k\).
Fig. 5. Relationship between temperature and $P^\text{B}_{\text{max}}$ and $\alpha^\text{B}$. In the lower panel, $P^\text{B}_{\text{max}}$ and $\alpha^\text{B}$ for 10 diatom species isolated from the Wadden Sea are given.

Table I. Measurements of total and dissolved production (mg C m$^{-3}$ h$^{-1}$) and corresponding ratios of dissolved/particulate production. In addition, the contribution of Phaeocystis carbon to total phytoplankton carbon (PPC) is given.

<table>
<thead>
<tr>
<th>Date</th>
<th>Total production</th>
<th>Dissolved production</th>
<th>Particulate production (total – dissolved)</th>
<th>Dissolved/particulate</th>
<th>Phaeocystis (% of PPC)</th>
</tr>
</thead>
<tbody>
<tr>
<td>5 June 1996</td>
<td>37.2</td>
<td>6.0</td>
<td>31.1</td>
<td>0.19</td>
<td>0.1</td>
</tr>
<tr>
<td>19 June 1996</td>
<td>339.9</td>
<td>250.0</td>
<td>89.9</td>
<td>2.78</td>
<td>92.0</td>
</tr>
<tr>
<td>26 June 1996</td>
<td>186.0</td>
<td>109.5</td>
<td>76.5</td>
<td>1.43</td>
<td>89.5</td>
</tr>
<tr>
<td>12 July 1996</td>
<td>81.0</td>
<td>12.2</td>
<td>68.8</td>
<td>0.18</td>
<td>13.7</td>
</tr>
<tr>
<td>17 July 1996</td>
<td>104.2</td>
<td>3.3</td>
<td>100.9</td>
<td>0.03</td>
<td>11.4</td>
</tr>
<tr>
<td>24 July 1996</td>
<td>66.9</td>
<td>5.5</td>
<td>61.4</td>
<td>0.09</td>
<td>48.2</td>
</tr>
<tr>
<td>31 July 1996</td>
<td>436.7</td>
<td>275.6</td>
<td>161.1</td>
<td>1.71</td>
<td>79.0</td>
</tr>
<tr>
<td>21 August 1996</td>
<td>38.5</td>
<td>4.4</td>
<td>34.1</td>
<td>0.13</td>
<td>0</td>
</tr>
<tr>
<td>9 October 1996</td>
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<td>0.8</td>
<td>5.1</td>
<td>0.16</td>
<td>0</td>
</tr>
<tr>
<td>23 October 1996</td>
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<td>1.2</td>
<td>5.4</td>
<td>0.22</td>
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</tr>
<tr>
<td>13 November 1996</td>
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<td>1.5</td>
<td>6.1</td>
<td>0.25</td>
<td>0</td>
</tr>
<tr>
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<td>4.4</td>
<td>0.50</td>
<td>0</td>
</tr>
<tr>
<td>11 December 1996</td>
<td>5.5</td>
<td>1.9</td>
<td>3.6</td>
<td>0.52</td>
<td>0</td>
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</tbody>
</table>
Phaeocystis made up >75% of the standing stock. For samples with a lower share of Phaeocystis abundance, the mean ratio of dissolved to particulate production was 0.22 ± 0.15.

Based on the production estimates above, the annual gross particulate production for the Wadden Sea region under study was calculated to be 124 and 176 g C m\(^{-2}\) year\(^{-1}\) in 1995 and 1996, respectively (Table II). Given the calculated respiration losses, annual net particulate production was 100 and 138 g C m\(^{-2}\) in 1995 and 1996, respectively. With a mean ratio of dissolved/particulate production of...
0.22, total net production was 127 and 177 g C m\(^{-2}\) year\(^{-1}\) in 1995 and 1996, respectively, which is very close to the gross particulate production.

**Discussion**

Critical evaluation of production estimates

In the present study, incubation was carried out in an artificial irradiance gradient, because this procedure is less time consuming and delivers more physiological information than in situ incubations, which, in addition, are usually hampered by the strong currents prevailing in the Wadden Sea.

The use of \(P\) versus \(E\) relationships measured at fixed irradiance levels to calculate primary production is justified if effects of photoinhibition are small (Gallegos and Platt, 1982). In the Wadden Sea, vertical mixing and steep irradiance gradients make it unlikely that photoinhibition will ever occur (Colijn, 1983). Thus, simple production models using \(P\) versus \(E\) relationship are
appropriate for tidal mixed waters (Uncles and Joint, 1983). Colijn compared in situ measurements with values calculated from P versus E relationships and found a reasonably good agreement with a mean difference of only 5% (Colijn, 1983).

However, calculating daily production on the basis of one single measurement per day implies constant conditions of the main parameters, i.e. Chl, attenuation and P versus E parameters, in the water column over the whole day. Daily variations in the photosynthetic parameters of coastal marine phytoplankton are well documented (Harding et al., 1982), ranging between 15 and 49% for \( P_{\text{max}} \) and \( \alpha \) in a turbid estuary (MacIntyre and Cullen, 1996). In the present study, P versus E parameters were always determined at high tide, irrespective of time of day. Hence, over the annual cycle, times of sampling are evenly distributed over the day. If systematic variation in P versus E parameters during the day occurs, this effect should largely be balanced in calculating annual production.

Daily variation in incoming light is easy to measure and can thus be incorporated in the model calculations. Time-dependent variations in underwater light conditions are more complicated to address since turbidity changes according to the tidal cycle. A part from tidal advection, the magnitude of tidal stirring affects the degree of turbidity, typically showing lowest values at the turn of the tide and maximum values at mid-tidal current velocity amplitudes (Postma, 1954). Calculations of daily production presented above are based on single turbidity measurements conducted at high tide, thus leading to some overestimation of the daily underwater light availability and, consequently, of production. In order to get an idea of the degree of overestimation, we used a simple model assuming the attenuation coefficient \( k \) to vary in a cosine function with the amplitude of \((k_{\text{max}} - k_{\text{min}})\) and a frequency of 3 h [equation (1)], thereby implying a linear relationship of turbidity to current velocity.

\[
k(t) = k_{\text{min}} + ((k_{\text{max}} - k_{\text{min}})/2) + ((k_{\text{max}} - k_{\text{min}})/2 \times \cos (\pi \times (t - (t_{\text{HW}} - 3))/3))
\]

where \( t \) is time of day (h), \( t_{\text{HW}} \) is time of high water, and \( k_{\text{max}} \) and \( k_{\text{min}} \) are attenuation coefficients at midwater and slack tide.

With the results of this model, we recalculated daily primary production in time steps of 0.1 h, assuming an idealized daily light curve \([E(t) = E_{\text{max}} \times \sin (\pi \times (t - t_{\text{sunrise}})/n_{\text{light-hours}})]\), where \( E_{\text{max}} = 1000 \mu\text{mol photons m}^{-2}\text{s}^{-1}, t_{\text{sunrise}} = 6.00 \text{h} \) and \( n_{\text{light-hours}} = 16 \), high water at noon, and constant values of \( P_{\text{max}} \) (5.5 mg C mg\(^{-1}\text{Chl}\) h\(^{-1}\)), \( \alpha \) (0.025 mg C mg\(^{-1}\text{Chl}\) (\( \mu\text{mol photons m}^{-2}\text{s}^{-1})^{-1} \)) and \( B \) (1 mg Chl m\(^{-3}\)). The results of the computation with varying amplitudes of \((k_{\text{min}} - k_{\text{max}})\) are presented in Figure 8. For example, a doubling of \( k \) at midwater compared to high-water conditions results in a reduction of daily primary production of ~25%, whereas variation in \( k_{\text{min}} \) has a rather low impact. It is of note that a phase displacement between time of sunrise and time of high water was found to be only of minor importance to the modelled daily production values (<3%) since minima and maxima of attenuation are more or less evenly distributed over the light hours.

As a usually minor component of total suspended particulates in the northern German Wadden Sea, phytoplankton biomass and composition may also change over the tidal cycle (S.Dick et al., accepted). If algal biomass increases at mid-tide
due to resuspension of benthic diatoms and sedimented algae (Baillie and Welsh, 1980; Shaffer and Sullivan, 1988; Cloern et al., 1989), this effect may counterbalance the negative impact of a tidally increased turbidity on daily water column production (Maclentyre and Cullen, 1996). If, however, changes are dominated by tidal advection, an increased turbidity may coincide with low biomass concentrations and the cumulative effect may exert a profound influence on daily production estimates based on single measurements. A true and regionally valid magnitude of tidal variation in attenuation is difficult to define since resuspension and sedimentation processes as main causes for turbidity variations are a joint effect of tidal friction, sediment composition and stochastic events, such as wind-induced turbulence.

As for temporal variability, spatial variability of water depth is high in the Wadden Sea. The area does not exhibit a clear bathymetric land/sea gradient, but is rather composed by a mesoscale assemblage of rather narrow channels with quasi-fractal embraunchments, banks and shallow tidal flats. Calculations of daily production in this study are based on a fixed, average water depth of 3 m, which represents the ratio of total area and total volume at mid-tide. Calculation of gross primary production per square metre is relatively insensitive to water depth since production is restricted to a narrow upper layer. However, water depth has a large impact on $Z_{\text{mix}}/Z_{\text{eu}}$ ratios, and hence on respiration estimates and the related net production as well as on $P_r/B$ ratios. In order to get an impression of the impact, mean values of production parameters in the 1995 growth season (defined as the period with Chl $>$5 mg m$^{-3}$; see Results) were calculated as a function of water depth (Figure 9). As in the Wadden Sea the whole water column is mixed, the mean $Z_{\text{mix}}/Z_{\text{eu}}$ ratio is linearly related to water depth (Figure 9a). The critical ratio of five, which may be an upper limit for net primary production and bloom initiation (Cole and Cloern, 1984; Grobbelaar, 1985; Alpine and Cloern, 1988), is achieved at a depth of $\sim$13 m. The mean ratio of water column phytoplankton respiration to gross production ($R_{zt}/P_{zt}$) decreases in 1995 from 0.35 at 20 m depth to a minimum of $<$0.2 at 3 m, but increases slightly again at smaller water depth due to the progressive spatial limitation of the euphotic zone by the

![Fig. 8. Percent reduction of depth-integrated daily production as a function of the tidal variation of attenuation coefficient ($k$) as derived from simple model calculations (for details, see the text).](https://academic.oup.com/plankt/article-abstract/22/7/1253/1519339)
sea bottom (Figure 9b). The average \( P_r/B \) ratio during the growth season in 1995 is close to 1 for the mean depth of 3 m in the study area, but would rise to a value of 2 for a 1.5 m depth or decline down to 0.5 for a 6 m water column (Figure 9c). Light saturation, defined as a mean \( E_{av}/E_k \) ratio of at least one, would be reached at a water depth of ~1.5 m (Figure 9d).

**P versus E parameters of the Wadden Sea phytoplankton**

A main goal of the study is to classify the photosynthetic characteristics of the typical Wadden Sea phytoplankton assemblages in order to determine the production of the system and the decisive factors for its seasonal dynamics. \( P_{B_{max}} \) values of the Wadden Sea phytoplankton assemblages, with a mean value of 4.5, are well within the range of mean \( P_{B_{max}} \) reported for phytoplankton populations from many different coastal areas [e.g. tabulations in Pennock and Sharp (Pennock and Sharp, 1986), Keller (Keller, 1988) and van Spaendonk et al. (van Spaendonk et al., 1993)]. However, the maximum \( P_{B_{max}} \) of 9.9 found in the present study is substantially lower than maximum values reported from some other coastal seas. These intense assimilation activities are usually associated with high water temperature (>20°C). The lack of \( P_{B_{max}} > 10 \) in the present study may thus reflect the comparably low maximum water temperature of the Wadden Sea.
(<20°C). This assumption is supported by the fact that temperature was the main factor explaining 67% of the $P_{B_{\text{max}}}$ variability in the Wadden Sea phytoplankton communities. This correlation is not self-evident when considering the succession in natural phytoplankton communities with a selection of species exhibiting intrinsically different photosynthetic properties. Especially dinoflagellates, prymnesiophytes (such as $Phaeocystis$) and many other nanoflagellates are lower in Chl than diatoms and may thus have higher values for Chl-normalized photosynthetic parameters (Mandelli et al., 1970; Verity et al., 1991; Johnsen et al., 1992). However, dinoflagellates only play a very subordinate role in the Wadden Sea, and during the limited period of $Phaeocystis$ dominance $P_{B_{\text{max}}}$ did not increase substantially, which might be due to the fact that dissolved production was not considered in the calculation. To conclude, both the moderate $P_{B_{\text{max}}}$ values and their strong exponential dependence on temperature reflect the typical composition of the phytoplankton community in the area, which is characterized by the dominance of large diatoms with a high proportion of tychopelagic forms the whole year round (Hesse et al., 1995).

Averaged photosynthetic efficiencies, which accounted for 0.02 mg C mg$^{-1}$ Chl h$^{-1}$ (µmol photons m$^{-2}$ s$^{-1}$)$^{-1}$, are in the low end of the range when compared to mean coastal marine ecosystems as reviewed by Keller (Keller, 1988). However, for the tidal estuary of the Hudson river, which has a turbidity comparable to the region under study, Cole et al. found even lower mean values of $\alpha$ during the growth season (Cole et al., 1992). The relatively low photosynthetic efficiencies in the Wadden Sea phytoplankton are consistent with relatively high values of $E_{k}$, exhibiting an annual mean of 216 µmol photons m$^{-2}$ s$^{-1}$, which reflects a rather elevated level of light saturation when compared to phytoplankton communities in the low-light environment of deeper waters of the open sea (Maranon and Holligan, 1999). Comparably high values of $E_{k}$ throughout the year were also found in other temperate tidal estuaries (Fisher et al., 1982; Pennock and Sharp, 1986; Cole et al., 1991). $E_{k}$ has been used extensively as an indicator of light acclimated state (Harris, 1978; Sakshaug et al., 1997). The high $E_{k}$ values found for the Wadden Sea phytoplankton suggest acclimation of the community to high light intensities, in spite of the mean low irradiance levels prevailing in the turbid water column. However, there is sound evidence that, with moderate mixing, photosynthetic parameters of phytoplankton are uniformly adapted to near-surface conditions (Gallegos and Platt, 1985; Mallin and Paerl, 1992), while shade adaptation occurs only when low light conditions are stable.

**Annual production**

Our estimate of primary production in the northern German Wadden Sea of 150 g C m$^{-2}$ year$^{-1}$ is close to the 190 g C m$^{-2}$ year$^{-1}$ estimated as a worldwide mean of 45 estuarine systems, as reviewed by Boynton et al. (Boynton et al., 1982). Besides this excellent data set, there are only few comparative studies on the phytoplankton production capacity of European estuaries and coastal seas. A compilation of these data is given in Table III. It can be traced that the annual primary production of the Wadden Sea area under investigation is well in the
middle range between the lowest estimates for the inner parts of North Sea estuaries (Ems Dollard, Bristol Channel) and the highest values observed in the Oosterschelde or Marsdiep area. For the northernmost part of the Northfrisian Wadden Sea (Sylt/Rømø Bight), annual phytoplankton production accounts for 160 g C m⁻² year⁻¹ (Asmus et al., 1998), which almost equals the amount obtained in the present investigation, in spite of pronounced differences in freshwater load (Hickel, 1980). It can thus be speculated that annual primary production does not differ much within the coastal stretch of the northern Wadden Sea and that the massive nutrient discharge deriving from the River Elbe does not play a significant role in regulating primary production in the Wadden Sea region under study.

A completely different situation prevails in the adjacent coastal water of the

<table>
<thead>
<tr>
<th>Area</th>
<th>Annual production (C m⁻² year⁻¹)</th>
<th>Method</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Inner</td>
<td>70</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Middle</td>
<td>91</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Outer</td>
<td>283</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bay of Morlaix (mean 1979–1980)</td>
<td>314</td>
<td>¹⁴C particulate production</td>
<td>Wafar et al. (1983)</td>
</tr>
<tr>
<td>Inner</td>
<td>7</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Middle</td>
<td>49</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Outer</td>
<td>165</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Westerschelde 1989</td>
<td></td>
<td>¹⁴C particulate production</td>
<td>van Spaendonk et al. (1993)</td>
</tr>
<tr>
<td>Inner</td>
<td>122</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Middle</td>
<td>197</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Outer</td>
<td>212</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Western part</td>
<td>150–300</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Eastern part</td>
<td>100</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1972–73</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Western Wadden Sea</td>
<td>100</td>
<td>¹⁴C particulate production</td>
<td>Cadée and Hegeman (1974)</td>
</tr>
<tr>
<td>Eastern Wadden Sea</td>
<td>120</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ems estuary</td>
<td>55</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dollard</td>
<td>13</td>
<td></td>
<td></td>
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<tr>
<td>Northern IJsselmeer</td>
<td>400</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean of a 12 year time series Interannual variability</td>
<td>241</td>
<td>¹⁴C particulate production</td>
<td>Lindahl et al. (1998)</td>
</tr>
<tr>
<td>German Bight 1994–1996</td>
<td>420</td>
<td>¹⁴C total production</td>
<td>H.-J. Rick et al. (submitted)</td>
</tr>
<tr>
<td>Büsum Wadden Sea 1995–1996</td>
<td>152</td>
<td>¹⁴C net total production</td>
<td>This study</td>
</tr>
</tbody>
</table>
German Bight. In these less turbid and deeper waters, annual primary production, as calculated from data for a comparable period (1994–1996), accounted for more than twice as much as that of the Wadden Sea (H.-J. Rick et al., submitted). This corroborates with the compilation of Cloern, who showed that primary production in estuaries generally does not keep up with that of the adjacent open coastal zone (Cloern, 1987).

However, these comparisons do not take benthic primary production into account, which is usually most elevated in the shallow near-shore area. Moreover, it should be kept in mind that the calculations mentioned above are exclusively based on water column production data. A similar comparison, but calculated on a volume basis, may result in a completely different rating even if only the upper mixed layer is considered. The proper choice has to be made according to the specific trophic relationships addressed.

Limitation of primary production

The Northfrisian Wadden Sea is directly influenced by freshwater discharge deriving from the River Elbe and the as yet unresolved question—to what extent nutrients or light are limiting primary production in the Wadden Sea—is also of some practical importance with respect to the ongoing efforts on nutrient reduction. Limiting nutrient conditions may be suggested when the in situ concentration of the limiting nutrient is below the half-saturation constant for uptake by phytoplankton (Fisher et al., 1988). However, a nutrient can only limit primary production when there is no light limitation. According to Peeters et al., light limitation may be defined by the $E_{av}/E_k$ ratio (Peeters et al., 1991). $E_{av}$ is the mean irradiance in the water column and is defined as $E_0 (k z)^{-1} (1 - e^{-kz})$, where $E_0$ is the average surface irradiance during light hours. Assuming a linear scale of vertical turbulence and an exponential decrease of light with depth, cells spend only 31% of time at light intensities higher than $E_k$ when the $E_{av}/E_k$ ratio is one. This may be an appropriate threshold value for light limitation (Figure 10). Owing to high turbidity, the $E_{av}/E_k$ ratio is ~0.2 during winter months and somewhat higher during the growth season. $E_{av}/E_k$ ratios > 1 only occurred once in 1995 (7 June 1995) and twice in 1996 (12–19 April 1996) (Figure 10a).

However, $E_{av}/E_k$ ratios calculated on the basis of average values of daylight irradiance are not suited to characterizing restricted periods of light availability in the course of the day, as high light intensities at midday are counterbalanced by low light at dawn and dusk. In order to identify times of day of light saturation, we computed separately for each day the number of hours for which $E_{av}/E_k > 1$ (Figure 10b). From this calculation, it turned out that intermediate periods of saturating light conditions (arbitrarily defined as $E_{av}/E_k > 1$ for at least 5 h per day) occurred within the Wadden Sea water at 5 and 12 weeks in 1995 and 1996, respectively.

In a next step, $E_{av}/E_k$ ratios were compared to the ambient nutrient concentrations in order to detect periods of possible nutrient limitation defined as concentrations below the limits given in Figure 11. Assuming that light and nutrients are exclusive resources (see above) and using daily average light intensities,
nutrient limitation on a daily basis was likely to occur only on two sampling days for \( \text{PO}_4 \) and \( \text{Si} \) (Figure 11a) in April 1996. However, taking the intermediate periods of light saturation lasting at least 5 h per day (see above) into consideration, dissolved inorganic nitrogen limitation may be effective on 5 (3 August, 1995, 15 May, 21 May, 26 June, 31 July 1996), dissolved phosphate limitation on 10 (in April/May 1995/1996) and silicate limitation on 10 (28 June, 3 August 1995; April/May 1996) of the weekly sampling days during the 2 year period investigated (Figure 11b). It can thus be concluded that light limitation is of major importance for planktonic primary production in the Wadden Sea and that nutrient limitation only plays a minor role in annual phytoplankton production in the area.
Fig. 11. (a) Plot of $E_{av}/E_k$ (derived from daily average light conditions) with ambient nutrient concentrations. The dotted area defines the region for which $E_{av}/E_k > 1$ ('light saturation') and nutrient concentrations are below published half-saturation constants for nutrient uptake of natural phytoplankton populations. (b) The same plot, but hours per day for which $E_{av}/E_k > 1$ are given.
This conclusion, however, is derived from the comparison of actual inorganic nutrient concentrations with threshold values derived from published half-saturation constants. The thresholds were set at the upper range of half-saturation constants given by Fisher et al. for coastal phytoplankton species (Fisher et al., 1988). On the one hand, the impact of nutrients may be underestimated by this procedure since Wadden Sea phytoplankton species may be adapted to the overall high nutrient concentrations prevailing most of the year and probably need higher nutrient concentrations to sustain maximum growth rates. On the other hand, dissolved organic nitrogen and phosphorus, which in spring and summer account for 20-50% of total nitrogen and 10-20% of total phosphorus concentrations in the area (U.Brockmann et al., accepted), as well as instantaneous nutrient recycling are not considered. The latter is supposed to be quite intense in the Wadden Sea due to the large amount of heterotrophs both in the water column (Tillmann and Hesse, 1998) and the sediments (Beukema, 1983).

Additional evidence for the subordinate role of nutrients may be derived from the fact that seasonal variability of \( P_{\text{Bmax}} \) values was mainly determined by temperature, since temperature effects on the annual cycle of \( P_{\text{Bmax}} \) are not likely to occur if serious nutrient limitation occurs [e.g. (Takahashi et al., 1973)]. Even at times of low nutrient concentrations in the water column, no distinct depression of the production potential was observed. However, it is still an open question to what extent the maximum rate of photosynthesis is related to nutrient limitation. Under starving nutrient conditions, cells may accumulate storage products and may regulate their cellular carbon/Chl ratio, resulting in unchanged Chl-specific production rates. Several continuous culture experiments indicate that \( P_{\text{Bmax}} \) is largely independent of nutrient-limited growth rates. By contrast, in batch cultures, a strong decline in \( P_{\text{Bmax}} \) was observed when nutrient starvation sets in (Cullen et al., 1992). Hence, for the interpretation of our results, it is important to consider which laboratory model is most suited to reflect the situation in the Wadden Sea. With its strong gradients, currents and intense turbulence, environmental conditions in this region are far from being stable and thus do not allow much for physiological regulation at the cellular level. Therefore, it seems likely that the measured \( P \) versus \( E \) parameters reflect the nutrient status of the phytoplankton community and that the ratio \( E_{\text{av}}/E_{k} \) is a suitable indicator for the evaluation of light limitation of phytoplankton.

The predominance of light limitation seems to be a common feature for turbid coastal systems (Cloern, 1996). Cole and Cloern showed that in several temperate estuaries variability of in situ estimates of daily primary production can largely be attributed to variation in phytoplankton biomass and light availability (Cole and Cloern, 1984, 1987). The same is likely to be the case for the Wadden Sea. This relationship constitutes a promising simplification for future monitoring strategies, especially with regard to assessment of eutrophication.

In spite of the moderate light availability, the Wadden Sea is at times subjected to massive phytoplankton blooms, especially of \( \text{Phaeocystis} \) spp. and different diatom species (Hesse et al., 1995). Local blooms may originate from autochthonous growth processes or advection from the adjacent coastal waters. With respect to the potential of autochthonous bloom formation in the Wadden Sea,
local growth rates must exceed the losses due to mortality (including sedimentation) and dispersion of cells by flushing. The mean turnover time of the region under study, as calculated according to Ridderinkhof et al. (Ridderinkhof et al., 1990), is in the range of 5 days (S. Dick, personal communication). The average phytoplankton-specific growth rates of 1 with maxima up to 1.7 per day in spring and summer thus clearly exceed the loss due to dispersion. A utochthonous growth is fast enough to build up the observed high algal standing stocks during the growth season and to provide a significant amount of organic material for the Wadden Sea heterotrophs. However, first budget calculations reveal that planktonic primary production in the area is just sufficient to match the pelagic respiration per year and that estimates of benthic primary production do not cope with benthic respiration. This net heterotrophic system metabolism seems to be balanced by the import of a considerable amount of organic matter deriving from the adjacent North Sea. From recent studies in the Northfrisian Wadden Sea, it turned out that this additional import of organic carbon is in the order of magnitude of phytoplankton production in the Wadden Sea itself (S. Dick et al., accepted).

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Planktonic primary production in German Wadden Sea


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