Primary Productivity in the German Bight (1994–1996)

Hans J. Rick[1],*, Silke Rick[1], Urban Tillmann[2], Uwe Brockmann[3], Uwe Gärtner[4], Claus Dürselen[5], and Jürgen Sündermann[6]

[1] *University of Louisiana at Lafayette, Department of Biology, 300 East Saint Mary Boulevard, Lafayette, Louisiana 70504-2451*

[2] *Alfred Wegener Institute for Polar and Marine Research (AWI), Am Handelshafen 12, 27570 Bremerhaven, Germany*

[3] *University of Hamburg, Institute of Biogeochemistry and Marine Chemistry, Martin-Luther-King Platz 6, 20146 Hamburg, Germany*

[4] *Schulenburgstrasse 8, 26129 Oldenburg, Germany*

[5] *AquaEcology, Marie-Curie-Strasse 1, 26129 Oldenburg, Germany*

[6] *University of Hamburg, Zentrum für Meeres-und Klimaforschung, Bundesstrasse 53, 20146 Hamburg, Germany*

ABSTRACT: Within the KUSTOS program (Coastal Mass and Energy Fluxes–the Land-Sea Transition in the Southeastern North Sea) 28 to 36 German Bight stations were seasonally surveyed (summer 1994, spring 1995, winter 1995–1996) for light conditions, dissolved inorganic nutrient concentrations, chlorophyll *a* (chl *a*), and photosynthesis versus light intensity (P:E) parameters. Combining P:E curve characteristics with irradiance, attenuation, and chlorophyll data resulted in seasonal estimates of the spatial distribution of total primary production. These data were used for an annual estimate of the total primary production in the Bight. In winter 1996 the water throughout the German Bight was well mixed. Dissolved inorganic nutrient concentrations were relatively high (nitrogen [DIN], soluble reactive phosphorus [SRP], and silicate [Si]: 23, 1, and 10 μM, respectively). Chl *a* levels generally were low (< 2 μg l^{-1}) with higher concentrations (4–16 μg l^{-1}) in North Frisian coastal waters. Phytoplankton was limited by light. Total primary production averaged 0.2 g C m^{-2} d^{-1}. Two surveys in April and May 1995 captured the buildup of a strong seasonal thermocline accompanied by the development of a typical spring diatom bloom. High nutrient levels in the mixed layer during the first survey (DIN, SRP, and Si: 46, 0.45, and 11 μM, respectively) decreased towards the second survey (DIN, SRP, and Si: 30.5, 0.12, and 1.5 μM, respectively) and average nutrient ratios shifted further towards highly imbalanced values (DIN:SRP: 136 in survey 1, 580 in survey 2; DIN:Si: 13.5 in survey 1, 96 in survey 2). Chl *a* ranged from 2 to 16 μg l^{-1} for the first survey and rose to 12–50 μg l^{-1} in the second survey. Phytoplankton in nearshore areas continued to be light limited during the second survey, while data from the stratified regions in the open German Bight indicates SRP and Si limitation. Total primary production ranged from 4.0 to 6.3 g C m^{-2} d^{-1}. During summer 1994 a strong thermal stratification was present in the German Bight proper and shallow coastal areas showed unusually warm (up to 22°C), mixed waters. Chl *a* concentrations ranged from 2 to 18 μg l^{-1}. P:E characteristics were relatively high despite the low nutrient regime (DIN, SRP, and Si: 2, 0.2, and 1.5 μM, respectively), resulting in overall high total primary production values with an average of 7.7 g C m^{-2} d^{-1}. Based on the seasonal primary production estimates of the described surveys a budget calculation yielded a total annual production of 430 g C m^{-2} yr^{-1} for the German Bight.

Introduction

The fact that shelf seas have an important function in global change resulted in the establishment of the International Geosphere Biosphere Program core project LOICZ (Land–Ocean Interaction in the Coastal Zone), which focuses on the role of coastal waters in global cycles. The KUSTOS (Coastal Mass and Energy Fluxes—the Land-Sea Transition in the Southeastern North Sea) program was officially recognized as a German contribution to LOICZ (Sündermann et al. 1999). In order to

meet its objective of quantifying coastal mass and energy fluxes the central focus of KUSTOS was placed on systematic field experiments in the German Bight. This paper uses data from the seasonal grid surveys (summer 1994, spring 1995, and winter 1995–1996) to improve estimates of the primary productivity for the German Bight.

Primary production measurements are logistically difficult to perform and a time-consuming endeavor. The available temporal and spatial coverage of primary production data for the North Sea is rather low. In order to achieve optimum data coverage on spatial and temporal scales, Van Beusecom and Diel-Christiansen (1993) provided a compilation of primary production estimates available for the North Sea, subdivided into the standard (ICES)

* Corresponding author; tele: 337/482-6756; fax: 337/482-5834; e-mail: hansrick@louisiana.edu

boxes. Their attempt to summarize annual production estimates in the different areas clearly shows many areas where production data covering the complete annual cycle are not available. Even for well studied areas (e.g., the southern Bight), estimates of annual production are available only for a few years.

A comparison between different production data sets is difficult unless comparable methods have been used and statistical limits to the estimates are available. In the past, completely different methods of estimating primary production have been used, including changes in chlorophyll *a* (chl *a*) levels (Postma 1954), changes in pH and alkalinity (e.g., Weichart 1980, 1985), changes in nutrients (Weichart 1980), the oxygen method (Fransz and Gieskes 1984; Giekes and Kraay 1984), or the carbon-14 (^{14}C) method. Even the use of the ^{14}C method, which has been in use as a standard method for more than three decades, does not guarantee comparability of data sets, because ^{14}C-primary production may be estimated in situ, by means of deck incubators, or in incubators using constant light or a light gradient (Richardson and Heilmann 1995).

The lack of thorough spatial and temporal resolution of direct primary production measurements may be overcome by the application of biooptical productivity models, which are based on the functional relationship between photosynthesis and light. The magnitude and variability of photosynthesis versus light intensity (P:E) parameters need to be known for a reliable model assessment. Data on the P:E relationship from the open North Sea have only been reported by Peeters et al. (1993) and De Madariaga and Joint (1994). For the coastal area of the German Wadden Sea, a complete 2-yr annual cycle (1995–1996) of P:E parameters is provided by Tillmann et al. (2000).

Since the Tillmann et al. (2000) investigation area was adjacent to the KUSTOS area and both efforts had a 2-yr overlap in time, we adopted their method to estimate primary productivity in the German Bight. Depth dependent irradiance, attenuation, and chl *a* data were combined with P:E curve characteristics to estimate the spatial distribution of primary productivity during six seasonal surveys. These data were then used to describe short-term, spatial, and seasonal variability, as well as to calculate annual primary productivity in the German Bight. Interannual variability was assessed by a comparison with ZISCH data (Circulation and Contaminant Transfer in the North Sea: Aletsee et al. 1990; Heyer et al. 1994). Inorganic nutrient, light, and mixing data also were used to describe possible resource limitations of the phytoplankton in the different seasons. We used the high resolu-
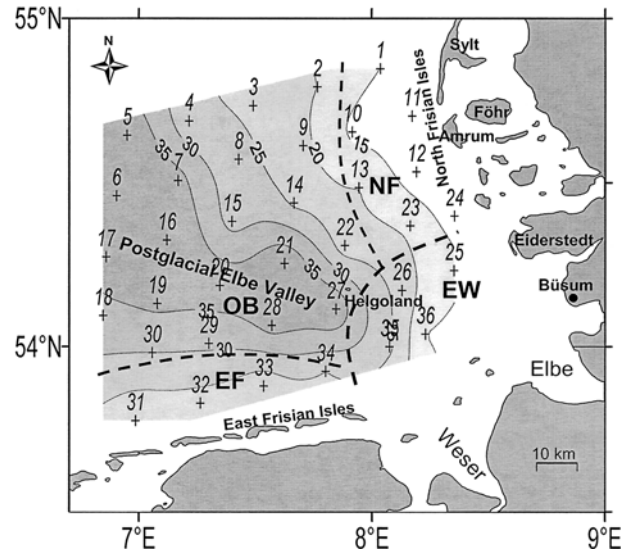

Fig. 1. Map of the German Bight including KUSTOS survey stations. Station numbers, depth contours (m), and sub regions (OB: open Bight, NF: North Frisian waters, EF: East Frisian waters, EW: Elbe-Weser waters) are displayed.

tion KUSTOS primary production data to optimize future sampling strategies.

Material and Methods

The overall research strategy of KUSTOS is described in detail elsewhere (Brockmann et al. 1999a,b; Sündermann et al. 1999). It is centered on three multiship cruises in the German Bight where a station grid (Fig. 1) was sampled quasisynoptically up to four times within 2–3 wk in summer 1994 (KUSTOS I, RV *Valdivia, Gauß, Atair*), spring 1995 (KUSTOS II, RV *Valdivia, Gauß, Atair*), and winter 1996 (KUSTOS III, RV *Valdivia, Heincke*, and sampling from a helicopter).

Total primary production (particulate and dissolved) measurements were performed using laboratory incubators. For the 1996 winter survey a rotating incubator, described in detail by Colijn et al. (1996) and Tillmann et al. (2000), was used; for the 1995 and 1994 surveys we used an incubator described by Baumann (1990). Different light regimes were achieved using a set of flasks with neutral-density filter coating (ZEMOKO, Middelburg, The Netherlands) or neutral-density glass filters.

Handling generally followed the recommendations given in UNESCO (1994). Triplicate samples (50 or 100 ml) from standard depths (0, 5, 10, and 20 m for 1994–1995, 1996 only surface samples) were spiked with 2–5 µCi 100 ml^{-1} (depending on the time of year) of NaH^{14}CO$_3$ (7.4×10^4 to 18.5×10^4 Bq), and incubated immediately after sampling.

TABLE 1. Photosynthetic parameters (P^B_{max}, α^B, E_k ± SD) based on P:E measurements in the German Bight during the KUSTOS program.

Period and grid	Maximal rate of photosynthesis P^B_{max} (mg C mg^{-1} chl h^{-1})	Initial slope α^B (mg C mg^{-1} chl h^{-1} (µmol photons m^{-2} s^{-1})$^{-1}$)	Light saturation E_k (P^B_{max}:α^B) (µE m^{-2} s^{-1})	n
Winter 1996, survey 1	2.6 (1.14)	0.0325 (0.0095)	80 (10)	12
Winter 1996, survey 2	3.1 (0.47)	0.0387 (0.0039)	81 (5)	8
Spring 1995, survey 1	6.5 (0.8)	0.054 (0.01)	122 (7)	21
Spring 1995, survey 2, surface	2.5 (0.63)	0.019 (0.0087)	132 (30)	10
Spring 1995, survey 2, bottom	6.9 (1.5)	0.051 (0.0075)	135 (10)	10
Summer 1994, surveys 1 and 2	7.8 (3.0)	0.033 (0.006)	235 (45)	26

In 1994 and 1995 the incubation took place on shipboard. Due to space restrictions on the RV *Valdivia* in 1996, surface samples had to be taken from a helicopter and were transferred within 2.5 h after actual sampling to the laboratory in Büsum for incubation. Incubation time was generally 2 h, except during low activity in winter, when incubation was extended to 4–5 h. Based on the short-term incubations in spring and summer it is assumed that measured rates of photosynthesis approximately equal gross rates of total primary production (Williams 1993), while the longer winter incubations should more equal net rates. In treating the results like this, one has to keep in mind that Williams et al. (1996) showed that even short incubations might not yield the daytime gross uptake.

Total production was measured according to Schindler et al. (1972). Samples (15 ml) were transferred from the incubation flask into a 20-ml scintillation vial and acidified with 0.3 ml of 1 N HCl. Nonfixed inorganic ^{14}C was removed by gently bubbling air through the samples for at least 24 h. Samples of the dark bottle served as a control and were subtracted from the light counts.

Analysis of radioactivity was carried out in a Packard scintillation counter (1996: Model TRI-CARB 1900 TR; 1994, 1995: Beckham LS 6000) using Instagel (Packard) as the scintillation cocktail and the external standard method for quench correction. Maximum incubation irradiance provided by cool white fluorescent tubes (Philips TL 33) was 600 µmol photons m^{-2} s^{-1}. Irradiance measurements were performed inside the incubation flasks by means of a 4-π microsensor (1996: ZEMOKO, Middelburg, The Netherlands; 1994 and 1995: Spherical Micro Quantum Sensor US-SQ S/Li).

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 chl *a*, which was measured spectrophotometrically. For the chloro-

phyll analysis, samples (0.5–2 l) were taken in duplicate from four standard depths (0, 5, 10, and 20 m), filtered through glass-fiber filters (Whatman GF/F) and frozen immediately on shipboard. They were processed within 3–4 wk after the respective survey in the Oldenburg laboratory using a spectrophotometric method from Lorenzen (1967). The fact that the percentage standard deviation (SD) of 155 duplicate samples from all three KUSTOS surveys was about 6.2% shows that this routine procedure had a relatively small analytical error.

P:E curves were fitted according to Platt et al. (1980): $P^B = a(1 - e^{-bE})e^{-cE}$, where E is the incubation irradiance (µmol photons m^{-2} s^{-1}) and a, b, and c are fit parameters. P^B_{max} [$a(b/(b + c))(c/(b + c)^{c/b})$], the maximal rate of photosynthesis (mg C mg^{-1} chl h^{-1}), α^B [$a \times b$], the initial slope (mg C mg^{-1} chl h^{-1} (µmol photons m^{-2} s^{-1})$^{-1}$), and E_k [P^B_{max}/α^B], the light saturation parameter (µmol photons m^{-2} s^{-1}), were calculated from that fit.

Daily production rates for standard depths (g C m^{-3} d^{-1}) were calculated by combining chlorophyll concentrations with averaged P:E curve characteristics from the respective survey (Table 1) and mean irradiance values from three time intervals of light hours. The time intervals of the seasonally different light hours (winter: 10.6 h, spring: 15.2 h, summer 15.7 h) were chosen as 25% morning, 50% midday, and 25% evening of respective light hours. Daily water column production (P_{WC}, g C m^{-2} d^{-1}) was estimated by depth integration of the standard depth production rates (surface, 5, 10, and 20 m) as $P_{WC} = P_{surface} \times 2.5 + P_{5\,m} \times 5 + P_{10\,m} \times 7.5 + P_{20\,m} \times 5$. Spatial variation in productivity fields was derived from differences in biomass and light fields and not from horizontal differences in P:E parameters.

For estimates of net primary production, respiration loss also has to be taken into account. Tillmann et al. (2000) assessed total water column respiration according to Langdon (1993) for particulate production data from Büsum Mole. They found a relatively constant relationship between particulate production and phytoplankton respiration with a mean of 21 ± 4%. Since this paper focuses on

total production values phytoplankton respiration was generally accounted for by subtracting 15% from the total modeled production rate.

Light profiles were derived from vertical measurements using a LI-COR 193SB 4π quantameter sensor, which was attached to the CTD. At stations where these data were not available we calculated attenuation coefficients k_d (m^{-1}) from turbidity (660 nm) readings using the empirical relationship $k_d = 0.1546e^{0.0506 \times \text{turb (\%)}}$ ($R^2 = 0.9522$) determined from 21 simultaneous turbidity measurements and vertical light profiles from the LI-COR 193SB. Light conditions at standard depths, as well as the depth of the euphotic zone (Z_{eu}: 1% surface [PAR]) were calculated using k_d information and continuous surface PAR data from a LI-COR QSR-240 installed on the accompanying RV *Atair*. Correction for light reflection at the water surface was performed according to Kirk (1994).

Mixing depth, Z_{mix} (m), was assessed based on the stratification intensity parameter ($\Delta\rho{:}\Delta z$, kg m^{-4}; Druon et al. 2004). $\Delta\rho/\Delta z$ was calculated in 1-m increments throughout the water column. The shallowest depth with a threshold level of 0.1 kg m^{-4} or higher was regarded as the mixing depth.

During KUSTOS I and II (summer 1994 and spring 1995) several simulated in situ production measurements (incubation time 2 h) were performed exposing samples from standard depths (5, 10, and 20 m) to natural temperature ($\pm 0.2°C$) and light conditions close to the actual light recorded from the respective sampling depth using a laboratory incubator described by Baumann (1990). To assess the reliability of the model these simulated in situ measurements were compared to model production values based on exactly the same light used in the laboratory incubator, chlorophyll, and P:E information.

Samples for dissolved inorganic nutrient (DIN: nitrite, nitrate, ammonia, SRP: soluble reactive phosphorus, Si: silicate) measurements were obtained from rosette samplers attached to the CTD probe. The samples were filtered immediately (vacuum 0.2 atm) using precombusted glass-fiber filters (Whatman GF/C). These filters have a nominal retention size of 1.2 µm, but retain particles down to 0.4 µm diameter (Hickel 1984). Nutrients were analyzed using the Technicon AutoAnalyzer methods according to Murphy and Riley (1962), Armstrong et al. (1967), Koroleff (1969), and Grasshoff et al. (1983) modified by Eberlein and Kattner (1987). Samples were directly analyzed in 1996 aboard the RV *Valdivia*, while in 1994 and 1995 the RV Gauss samples were fixed with mercury chloride (0.01% w:v) and stored at 4–10°C until analysis in the Hamburg laboratory. Fixed samples

were processed generally within 1.5 mo after the respective survey.

Results

Table 1 shows the overall data from the P:E measurements carried out during the three seasonal KUSTOS surveys with standard deviations. At the high end light irradiances (summer and spring: 600, winter: 200 µmol m^{-2} s^{-1}) P:E curves suggest that photoinhibition did not occur in the incubated samples. E_k values generally increased from winter through spring and summer. P^B_{max} was relatively high during spring 1995 and summer 1994, while significantly lower rates were measured in winter 1996. This is in accordance with the 1995–1996 Büsum Mole data (Tillmann et al. 2000), which demonstrated that P^B_{max} values were strongly correlated to temperature. α^B was not correlated to the ambient temperature with the highest values in spring and lower numbers both during winter and summer. Modeled and measured primary production values were in good agreement. The significantly lowered P^B_{max} and α^B values in the surface mixed layer during the second survey in spring 1995 was possibly related to Si depletion in the course of the developing spring bloom (compare Fig. 4 lower panel).

WINTER 1996 SURVEYS

The unusually strong 1995–1996 winter ranked 14th in severity for the last 100 yr (Strübing 1996). Horizontal temperature gradients weakened over the 2-wk campaign due to continuous, modest warming ($-1.5°C$ to $-0.5°C$) at nearshore stations accompanied by unchanged temperature conditions in the German Bight proper (Becker et al. 1999). Low freshwater runoff kept salinity in a narrow range (32–34 psu). Most areas of the Bight were well mixed, and only during the second survey did a few stations (26, 27, 35 in Fig. 1) show weak stratification. Due to the unusually low speeds (6.5 ± 3.4 [SD] m s^{-1}: climatological mean February-March: 8 m s^{-1}; Dünsing and Zöllner 1978), the wind effect was small (Becker et al. 1999).

From the first (February 24–26) to the second (March 1–3) survey average surface PAR for the light phase (10.6 h) rose from 70 to 180 µmol m^{-2} s^{-1}. Light penetration through the water column was extremely limited during the whole campaign along the North Frisian coast, but was relatively high (Z_{eu}: 16 m) in all other parts of the Bight (Fig. 2). Results from nutrient measurements are published elsewhere (Brockmann et al. 1999a). Overall the dissolved inorganic nutrient levels were very high. DIN ranged from 12 to 40 µM, SRP from 0.75 to 1 µM, and Si from 5 to 39 µM, resulting in
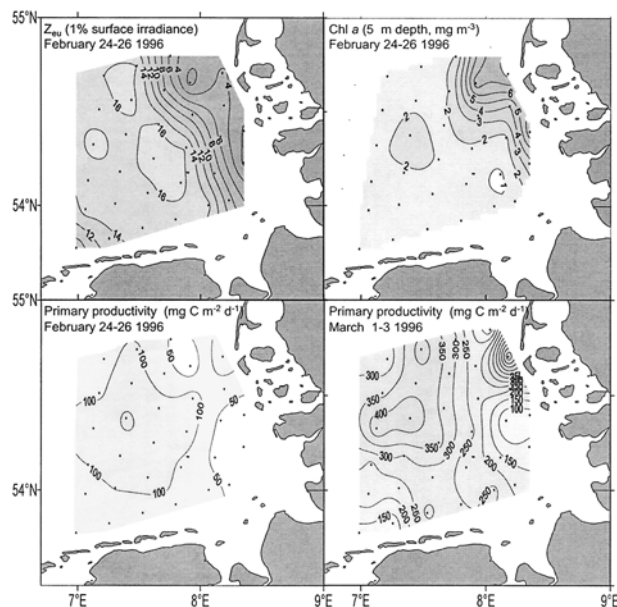
Fig. 2. KUSTOS winter surveys 1996: Contour charts of depth (m) of the euphotic zone (Z_{eu}: 1% surface irradiance, Li-Cor 4π sensor), Chl a, and primary productivity. For stations sampled at nighttime Z_{eu} was estimated applying a correlation between light attenuation and turbidity measurements. Stations used to produce the contour plots are shown in Fig. 1.

relatively balanced dissolved DIN:SRP and DIN:Si ratios (15–30 and 3–4, respectively) throughout the Bight. The nutrient situation almost remained the same from the first to the second survey for most of the Bight. Due to the enhanced diatom development west off the Islands of Sylt and Amrum during the second survey the Si levels dropped in the affected areas.

During both surveys most areas of the German Bight were characterized by low surface chlorophyll values ($< 2 \, \mu g \, l^{-1}$), while elevated chlorophyll concentrations up to 8 (first survey) and 20 $\mu g \, l^{-1}$ (second survey) prevailed only to the west of the North Frisian Islands (Fig. 2). In these high chlorophyll regions the diatom *Odontella aurita* (Lynbye) C.A. Agardh dominated the phytoplankton community. Bottom water chlorophyll generally resembled the distribution at the surface, indicating almost total mixing of the water column.

Estimated total primary productivity was extremely low in February ranging from < 50 to 150 mg C $m^{-2} \, d^{-1}$. Highest values were estimated for the German Bight proper: > 100 mg C $m^{-2} \, d^{-1}$ (Fig. 2). Very low production rates were prevalent in the most turbid areas (River Elbe plume and off the North Frisian Islands). During the second survey total production ranged from 100 to almost 400 mg $m^{-2} \, d^{-1}$, with the highest numbers still located in the German Bight proper and at station

11 to the west of the North Frisian Islands. The lowest rates were found in the turbid Elbe plume (< 100 mg $m^{-2} \, d^{-1}$) and in the outermost southwestern part of the Bight (< 150 mg $m^{-2} \, d^{-1}$).

SPRING 1995 SURVEYS

From May 11 to April 22 surface temperatures warmed by 2–3°C resulting in the development of a typical seasonal thermocline. Despite the prevailing heavy winds (6 $\pm$ 2.7, maximum 15.5 m s^{-1}), a strong thermal stratification built up with up to 1.8°C m^{-1} at depths around 10 m. The low salinity plume of the River Elbe extended in the surface layer along the North Frisian coast and all the way to Helgoland. Resulting strong vertical salinity gradients supported the development of the thermocline (Becker et al. 1999). Mean surface PAR values for the light phase (15.2 h) ranged from 1,170 to 1,240 $\mu mol \, m^{-2} \, s^{-1}$ for the entire spring campaign. During the first survey (April 24–27), the euphotic zone (Z_{eu}) was as shallow as 8 m in a wide band stretching from the mouth of the River Elbe northward along the North Frisian Islands. Low values (8–10 m) also were recorded to the north of the western East Frisian coast. In the German Bight proper the transparency gradually improved reaching values > 18 m in its central region (Fig. 3). The second survey (May 9–11) displayed an almost identical pattern, with some reduced transparency (12–14 m) in the open German Bight.

Mixed layer nutrient data are published elsewhere (Brockmann et al. 1999a; Rick 1999). During the first survey Si concentrations were elevated in the Elbe plume with maximum values exceeding 30 μM. Along the western coastline of the North Frisian Islands Si levels were as low as 2 μM; the lowest concentrations ($< 1 \, \mu M$) were measured in the southwest. DIN and SRP, as well as DIN:Si and DIN:SRP, resembled the Si pattern. The Elbe plume was characterized by DIN:SRP ratios around 100 and DIN:Si ratios < 5 (Fig. 4). The southwestern low nutrient region and the area west of the North Frisian Islands showed elevated DIN:SRP values > 200 and DIN:Si levels > 20. These high ratios hint at possible SRP limitation of the phytoplankton accompanied by a Si colimitation for diatoms.

During the second survey mixed layer Si concentrations had decreased almost by an order of magnitude. Within the River Elbe plume Si ranged from 0.3 to 2 μM, while the German Bight proper showed higher levels (1–5 μM). A band of very low Si stretched from the southwestern Bight towards the North Frisian coastline (0.1–0.5 μM). While DIN concentrations remained very high throughout the German Bight (4–60 μM), the outermost southwestern part showed the lowest numbers (4–10 μM). In most areas, SRP concentrations were
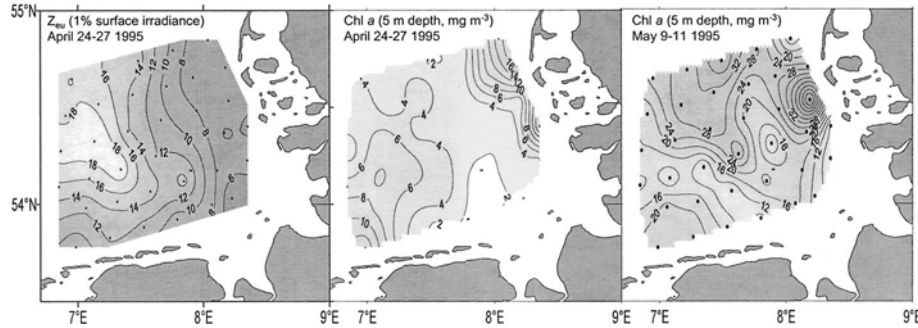
Fig. 3. KUSTOS spring surveys 1995: Contour charts of depth (m) of the euphotic zone (Z_{eu}: 1% surface irradiance, Li-Cor 4π sensor), and Chl *a*. For stations sampled at nighttime Z_{eu} was estimated applying a correlation between light attenuation and turbidity measurements.

close to the limit of detection (< 0.1 μM). Low SRP and Si levels accompanied by still elevated DIN values gave rise to extremely high DIN:SRP and DIN:Si ratios (Fig. 4) in the surface mixed layer. DIN:SRP at all stations was > 500, with high spots $> 2,000$ north west off Amrum and north of Helgoland and in the northwestern part. DIN:Si at most stations was > 20 with the highest values (> 200) southwest off Amrum.

Chlorophyll in the first survey (Fig. 3) ranged from 2 to 16 μg l^{-1} in the surface layer with high values in the Southwest and along the North Frisian coastline (> 10 μg l^{-1}), while lower numbers were found throughout the Elbe plume (< 4 μg l^{-1}). During the second survey chlorophyll concentrations were very high throughout the German Bight

Fig. 4. KUSTOS spring surveys 1995: Contour charts of primary productivity, and molar DIN/Si ratios in the surface layer (5 m).

ranging from 10 to 40 μg l^{-1} with maximum values in the northeast, to the west of the North Frisian Islands (40 μg l^{-1}), the central Bight (20–30 μg l^{-1}), as well as in its southwestern part (20–25 μg l^{-1}). The spatial distribution of bottom chlorophyll during both surveys almost mirrored the surface pattern of the first survey with elevated levels in the southwest and northeast and lowest values in the area of River Elbe postglacial valley.

In both surveys the spatial distribution of primary productivity (Fig. 4) resembled the surface chlorophyll distribution. During the first survey low values (< 2 g C m^{-2} d^{-1}) were prevalent in the inner plume area, while elevated production was found along the North Frisian coastline (up to 6 g C m^{-2} d^{-1}). Highest values (up to 9 g C m^{-2} d^{-1}) occurred in the southwestern part of the German Bight characterized by high light penetration and elevated chlorophyll concentrations. The second survey showed highest levels in the central German Bight (7–12 g C m^{-2} d^{-1}). Other hot spots were located southwest off Amrum (6–8 g C m^{-2} d^{-1}) and in the southwestern part of the German Bight (6–9 g C m^{-2} d^{-1}). Lowest numbers < 1 g C m^{-2} d^{-1} were detected in the inner Elbe plume.

P:E parameters from the second survey show striking differences between surface and bottom layers (Table 1). While the average light saturation (E_k) stayed the same in the whole water column, P^B_{max} and α values from surface and bottom samples differed remarkably. Surface P^B_{max} values dropped by more than a factor of 2 between the first and second surveys, while the values from the deeper layer remained constant, hinting at a developing nutrient limitation for the phytoplankton in the surface mixed layer.

SUMMER 1994 SURVEYS

Calm weather with high solar heating before the surveys generated an extremely stable thermal
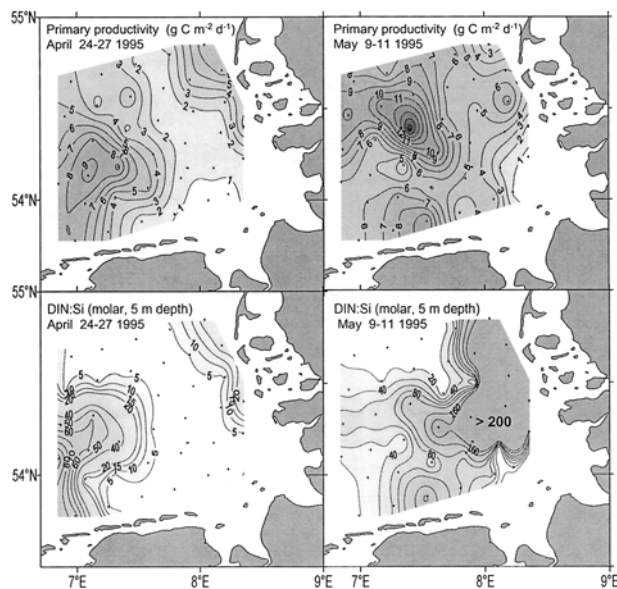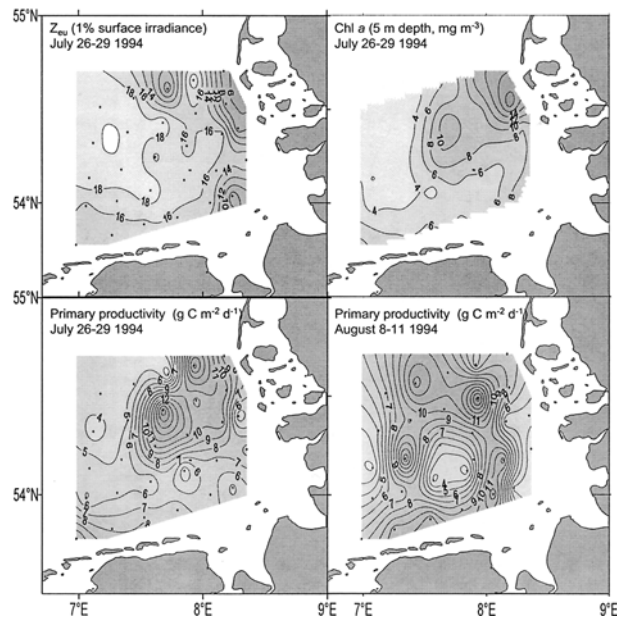
Fig. 5. KUSTOS summer surveys 1994: Contour charts of depth (m) of the euphotic zone (Z_{eu}: 1% surface irradiance, Li-Cor 4π sensor), Chl a, and primary productivity. For stations sampled at nighttime Z_{eu} was estimated applying a correlation between light attenuation and turbidity measurements.

Fig. 6. KUSTOS summer surveys 1994: Contour charts of DIN concentrations (µM) and molar DIN/SRP ratios in the surface layer (5 m).

summer stratification with temperature differences up to $6.7°C$ between surface and bottom layers and surface temperatures up to $20°C$ in the German Bight proper. Mixed, shallow coastal waters were unusually warm too, exceeding monthly means ($16.5°C$ for July, $17.5°C$ for August; Damm 1989) by $6°C$. Winds ($5–6$ m s^{-1}) slightly below mean conditions (Dünsing and Zöllner 1978), which were predominant for almost the whole campaign, did not disturb the vertical density structure (Becker et al. 1999). For both surveys (July 26–29 and August 8–11) mean surface PAR values for the light phase (15.7 h) were about 1,200 µmol m^{-2} s^{-1}. During the first survey, Z_{eu} (Fig. 5) was high in the German Bight proper including the outermost northwestern part (> 16–19 m) and along the East Frisian coast (15–18 m). Decreased transparency was recorded from the Elbe plume (10–12 m) and the area west of the North Frisian Wadden Sea (6–8 m). The second survey showed an identical spatial pattern with overall slightly decreased transparencies (average Z_{eu}: 15.4 and 14.1 m for the first and second surveys, respectively).

Nutrient data for the summer campaign are published in part elsewhere (Brockmann et al. 1999a). Over the whole campaign Si and SRP concentrations were generally extremely low in most of the Bight but slightly elevated values were recorded during the second survey (first: < 0.5–3;
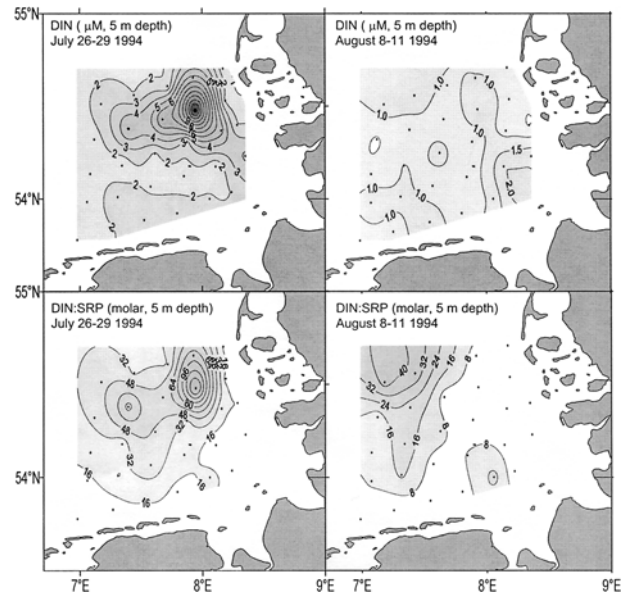
second: 1–5 µM Si; first: < 0.1–0.3; second: < 0.1–1 µM SRP). Compared to winter and spring DIN levels were also down, but concentrations dropped considerably between the first and second survey (first: < 2–12 µM; second: < 1–2 µM, Fig. 6).

Molar DIN:Si ratios from the first survey ranged from 1 to 10 in the whole Bight. Balanced levels from 1 to 3 were recorded from most of the eastern part, while the western part showed slightly unbalanced numbers ranging from 4 to 10. DIN:Si ratios (range < 0.5–2) were more balanced during the second survey.

DIN:SRP molar ratios (Fig. 6) appeared fairly balanced over huge areas in the German Bight (8–32). The Redfield isoline of 16 was located slightly offshore the Wadden areas. Elevated ratios (48–112) were recorded from the central Bight and offshore the North Frisian Islands. DIN:SRP shifted considerably towards the second survey. The Redfield isoline, located close to the shore during the first survey, moved into the northwestern area of the Bight exposing huge areas (central Bight, North and East Frisian waters, Elbe plume) to a possible nitrogen deficiency with DIN:SRP ratios < 8.

Surface chlorophyll values (first survey, Fig. 5) spanned from < 4 to 18 µg l^{-1} with highest values west of Amrum (10–18 µg l^{-1}) and the German Bight proper (6–10 µg l^{-1}). Low chlorophyll concentrations were found throughout the western part of the German Bight (< 4 µg l^{-1}). Values recorded during the second survey were slightly lower (< 2 to 12 µg l^{-1}) with highest values in the most northern

part (8–12 µg l^{-1}) and north of the East Frisian Islands (8–10 µg l^{-1}). A large band of lower chlorophyll stretched from the Elbe River plume to the east (6 to < 2 µg l^{-1}). Bottom chlorophyll distribution for both surveys mirrored the surface chlorophyll pattern of the first survey. Lowest values (< 4 µg l^{-1}) were recorded again from the deep River Elbe postglacial valley.

Total production (Fig. 5) mirrored the surface chlorophyll distribution in both surveys. Overall the estimated values were very high (first: 4–14 g C m^{-2} d^{-1}; second: 4–16 g C m^{-2} d^{-1}). The first survey showed the lowest but still high values (4–6 g C m^{-2} d^{-1}) in the Elbe plume, at station 24 offshore the Isle of Süderogsand, and in the entire western Bight with exception of an area off the East Frisian Islands, which had fairly high rates ranging from 6 to 9 g C m^{-2} d^{-1}. The German Bight proper and the northeastern part offshore the Island of Amrum showed highest production levels (8–14 g C m^{-2} d^{-1}). Total production appeared relatively patchy in the second survey. Overall the estimated values were still very high (4–16 g C m^{-2} d^{-1}). The lowest values of 4–7 g C m^{-2} d^{-1} were found stretching from the Elbe plume northward along the North Frisian Wadden Sea, in a huge area west of Helgoland, and on the western border of the Bight.

Discussion

CRITICAL EVALUATION OF THE PRIMARY PRODUCTION ESTIMATE

Although in use as a standard method for more than three decades, determination of primary production using the ^{14}C method is still a theme of intense debates. The determination is based on a complex protocol involving several steps, each with its own source of error. These steps include sampling (e.g., metal sampler might be toxic), incubation (e.g., volume of incubation flask, incubation time, in situ or simulated in situ incubation, type of incubator, incubation irradiance), sample preparation (e.g., filtration, filter type, filtration pressure), and sample counting (scintillation cocktail, quenching; e.g., Peterson 1980; Gieskes and Kraay 1984). Although reproducibility within replicate samples performed by one lab might be quite good (about 10%; Anonymous 1983), multiple sources of methodological errors make it difficult to compare results from different investigators (Anonymous 1990; Richardson 1991).

Beside all the methodological handling problems, it is still theoretically not clear to what extent net or gross production is estimated by this method (Peterson 1980; Dring and Jewson 1982; Richardson et al. 1984; Williams and Lefevre 1996; Williams et

al. 1996). Some authors regard incubation length as important to assess this problem (Williams 1993). For our estimate we assumed for the short-term incubations (2 h) in spring and summer that measured rates approximately equaled gross rates of total primary production while the longer (4–6 h) winter incubations more likely resemble net rates. A possible source of error in the presented estimate is the fact that even short incubations sometimes might not yield the daytime gross uptake (Williams et al. 1996).

Photoinhibition is more likely to occur in samples incubated at high fixed irradiances (e.g., P:E incubator) than in natural phytoplankton populations exposed to the rapidly changing light conditions in the upper mixed layer. Our P:E curves gave no indication of photoinhibition in the high irradiances (200–600 µmol m^{-2} s^{-1}) used. Gallegos and Platt (1982) showed that P:E relationships measured at fixed levels of irradiance might be used to calculate primary production if photoinhibition is low.

During the KUSTOS campaigns the German Bight was characterized by strong vertical irradiance gradients and mixing processes. During the winter 1996 campaign the water column at all stations was totally mixed except for the stations in the outer Elbe estuary (Becker et al. 1999). In summer 1994 mixing depth for stratified areas was 15.4 ± 5.3 m during the first survey and 16.4 ± 4.4 m during the second survey. Spring 1995 showed values of 12.8 ± 7.6 (first survey) and 11.8 ± 6.1 m (second survey). These data underline that it is least unlikely that photoinhibition occurred over an extended time during the KUSTOS campaigns. The use of the simple P:E production model calculating primary production seems to be appropriate.

While daily variation of surface irradiance was included in our estimate, the quasisynoptical sampling strategy unfortunately prohibited consideration of daily variation of other important parameters (chl *a*, P:E parameters, attenuation in the water column). Daily variations in chlorophyll, photosynthetic parameters, and turbidity are well documented (e.g., Postma 1954; Harding et al. 1982; MacIntyre and Cullen 1996). If we assume a systematic daily variation of these parameters the effects should be largely balanced in the overall estimate since the quasisynoptical sampling took place evenly distributed over the whole day.

Since only information from standard depths (surface, 5, 10, and 20 m) was available, the presented estimates may not account for chlorophyll heterogeneities occurring between these fixed sampling depths. The importance of subsurface phytoplankton blooms for the primary productivity in the North Sea is well documented (Richardson

and Peterson 1998; Richardson et al. 2000). This might be a source of error in estimates of primary productivity in the strongly stratified German Bight proper during the summer campaign. In fact continuous fluorescence profiles from the KUSTOS summer campaign show some chlorophyll heterogeneities, which were not properly accounted for by the standard depth sampling (e.g., survey 1: stations 8, 15, 21, 23).

The short-term P:E technique was chosen because of certain constraints superimposed by the KUSTOS sampling strategy. This technique was an ideal choice to achieve a thorough spatiotemporal resolution of primary productivity during the grid surveys. Since the ships were moving almost constantly, direct (in situ) measurements of primary production were not possible, and space restrictions in the laboratory incubators prohibited performing simulated in situ measurements with the necessary temporal resolution.

Chlorophyll Values and P:E Parameters

The seasonally ascertained chlorophyll data from the three KUSTOS campaigns are generally in good agreement with chlorophyll values published for different seasons in the German Bight and adjacent estuarine and Wadden areas (Hickel et al. 1971; Weigel and Hagmeier 1976: Helgoland Roads; Gieskes and Kraay 1975; Lancelot and Billen 1984; van Haren and Joordens 1990; Mills et al. 1994; Boon et al. 1998: southern North Sea; Eberlein et al. 1985; Gerdes 1985; Weichard 1985; Schaumann et al. 1988; and Hesse et al. 1989a,b, 1992: German Bight; Veldhuis et al. 1987: Dutch coastal waters; Cadee and Hegeman 1993; Bot and Colijn 1996; and Philippart et al. 2000: Marsdiep; Tillmann et al. 2000: German Wadden Sea).

Pennock and Sharp (1986), Keller (1988), and van Spaendonk et al. (1993) provide extensive compilations of P^B_{max} values for coastal phytoplankton assemblages. P^B_{max} ranges measured during KUSTOS (winter: 1.5–3.5; spring: 1.8–8.5; summer: 4–11 mg C mg^{-1} chl h^{-1}) fit well into these data sets, although they generally do not reach published maximum P^B_{max} values. This finding is supported by Tillmann et al. (2000), who performed a comparable study at Büsum Mole, North Frisian Wadden Sea. In most cases P^B_{max} values exceeding 10 are published for high temperature conditions ($> 20°C$) only. As already stated in the result section, P^B_{max} values were positively correlated with water temperature, so low temperatures during the winter and spring surveys might have prevented higher numbers. On the other hand, high-end P^B_{max} values were lacking during the extreme 1994 summer with surface temperatures above the monthly climatological mean ($> 20°C$ in almost the whole German Bight;

Becker et al. 1999). Low SRP and Si concentrations, which were at most summer stations way below the published half saturation constants for nutrient uptake of natural phytoplankton populations (Fig. 8; Fisher et al. 1988), might have contributed to this finding. There is ongoing discussion as to what extent P^B_{max} is related to nutrient limitation (e.g., Tillmann et al. 2000). Species composition might also have contributed to the lack of high P^B_{max} numbers. Diatoms, which were most abundant during the spring and winter surveys, generally show higher chlorophyll contents compared to nanoflagellates, dinoflagellates, or Prymnesiophytes and have lower values in photosynthetic parameters (Mandelli et al. 1970; Verity et al. 1991; Johnsen et al. 1992). Tillmann et al. (2000) isolated 10 diatom species from the North Frisian Wadden Sea and conducted P:E measurements using batch cultures (16°C, 100 µmol quanta m^{-2} s^{-1}). They reported P^B_{max} values ranging from 3.9 to 7.8 almost matching our overall field data for winter and spring.

Photosynthetic efficiencies (α^B) and light saturation values (E_k; Table 1) measured during all three KUSTOS surveys fit almost perfectly with the compilation for coastal marine ecosystems given by Keller (1988). Averaged α^B were well above, while E_K values were below the Büsum Mole data reported by Tillmann et al. (2000). This is in line with the overall lower turbidity in open German Bight compared to North Frisian Wadden Sea waters. Low α^B combined with elevated E_k values during growth season also were reported from the turbid Hudson River estuary (Cole et al. 1992).

Factors Limiting Primary Productivity in the German Bight

Few studies focusing on factors limiting primary production and growth and biomass development in North Sea phytoplankton communities are available. A detailed data set on limiting factors in coastal and central North Sea regions is given by Peeters et al. (1993) who used several indicators of nutrient and light limitation, such as nutrient concentrations and ratios, nutrient enrichment bioassays, nutrient uptake kinetics, and P:E measurements. Their results showed that the development of winter phytoplankton in the North Sea is limited by light (e.g., Peeters et al. 1991, 1993), while during the growth season, nutrient limitation becomes more important. SRP (and Si for diatoms) tends to be the first potentially limiting nutrient(s) in spring and DIN follows in summer. In the further offshore areas nitrogen is regarded more often potentially limiting compared to in the coastal zone. A variety of different methods were used in other studies to assess factors limiting North Sea phyto-
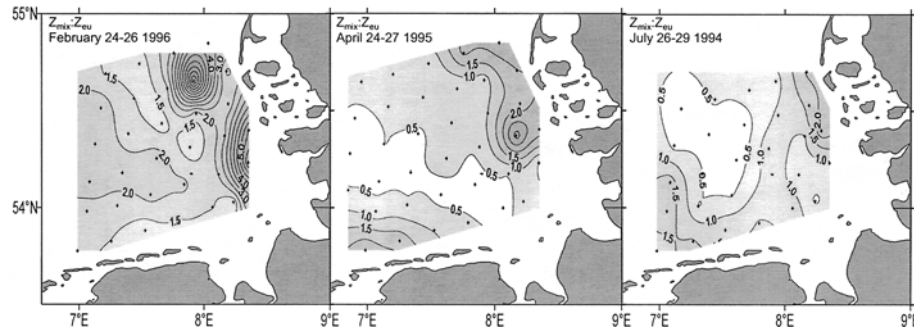
Fig. 7.   Contour plots of the ratio between mixing depth (Z_{mix}) and euphotic depth (Z_{eu}) for winter 1996, spring 1995, and summer 1994.

plankton. Veldhuis et al. (1987), using alkaline phosphatase activity as an indicator, identified SRP limitation of a *Phaeocystis* bloom along the Dutch coastline. Based on nutrient concentrations and nutrient ratios, Bauerfeind et al. (1990) considered SRP and Si as potentially limiting nutrients during the spring bloom in coastal waters of the southeastern North Sea, whereas they considered nitrogen as the potentially limiting element in more offshore areas. The same conclusion, i.e., potential SRP and Si limitation in coastal waters and potential DIN limitation in the open North Sea, was drawn by Peeters and Peperzak (1990) based on differential nutrient enrichment bioassays. A close relationship between low carbon fixation rates and low dissolved nitrate concentrations was regarded as evidence for DIN limitation of *Phaeocystis* along the Belgian coast (Lancelot et al. 1986), and Owens et al. (1990) used the same method to prove DIN limitation for summer phytoplankton in the North Sea. Riegman et al. (1990) used nutrient uptake kinetics, a method based on the physiological adaptation of the nutrient uptake system due to nutrient limitation, as a tool for identification of nutrient limited growth of summer phytoplankton in the North Sea. Their results show that nutrient limitation of summer phytoplankton in the open North Sea was severe, with DIN limitation dominating especially around the Dogger Bank. At the Dogger Bank SRP, not DIN, was limiting.

The German Bight is primarily affected by the nutrient rich freshwater discharge of the River Elbe (Rick 1999). With regard to efforts to reduce nutrients in the Elbe, it is of critical importance to assess to what extent primary production in this region is limited by nutrients or by light. Tillmann et al. (2000) already addressed this question for the adjacent North Frisian Wadden Sea based on their Büsum Mole data set from 1995–1996. They assumed limiting nutrient conditions when the concentration of the respective nutrient was below half-saturation constants for uptake by natural phytoplankton populations (Fisher et al. 1988). Light limitation was assumed if the $E_{av}:E_k$ was below 1 (Peeters et al. 1991), where E_{av} is the mean irradiance in the water column and E_k is the light saturation of the P:E curve. Using this approach Tillmann et al. (2000) demonstrated that the phytoplankton in the North Frisian Wadden Sea was primarily limited by light over the whole time series, which seems to be a common feature for turbid coastal systems (Cloern 1996). For the 2-yr period, only two sampling dates in April 1996 showed indications of SRP and Si limitation for phytoplankton.

For comparability reasons we adopted the Tillman et al. (2000) approach to describe nutrient limitation but had to modify the characterization of light-limiting conditions. Since only a relatively small number of E_k values were available (Table 1) we used instead of $E_{av}:E_k$ the ratio of mixing depth and euphotic depth ($Z_{mix}:Z_{eu}$). The first onset of light limitation was assumed at a ratio of 1, while a ratio of 5 represents the upper limit of net primary production and bloom initiation (Cole and Cloern 1984; Alpine and Cloern 1988).

Figure 7 shows the spatial distribution of $Z_{mix}:Z_{eu}$ for the first survey late in February 1996. The second survey in March showed an almost identical pattern, but overall the values decreased. Most numbers are > 1.5–2 with extreme high values (up to 9) along the North Frisian coast, representing a moderate light limitation for the phytoplankton in the open German Bight and along the East Frisian coast. Light limitation was severe, sometimes even exceeding the critical value of 5 in the eastern part of the Bight. In this region the phytoplankton experienced even lower light conditions than inside the Wadden Sea at Büsum Mole ($Z_{mix}:Z_{eu}$), which simply reflects the effect of greater depth and total water column mixing at comparable turbidity. Highest chlorophyll values were found in the areas of intense light limitation (Fig. 2). This chlorophyll possibly originated from the less light-limited
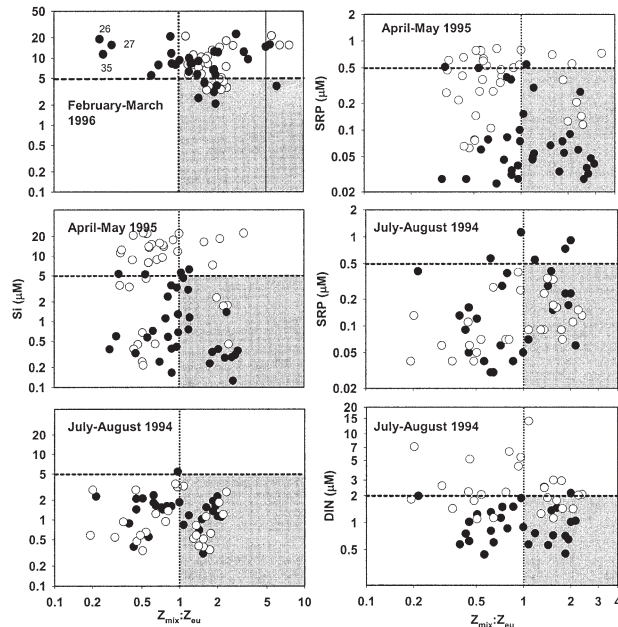
Fig. 8. Plots of Z_{mix}:Z_{eu} versus mixed surface layer inorganic nutrient concentrations—Si , SRP , DIN—for the KUSTOS surveys in winter 1996 (February 24–26 and March 1–3), spring 1995 (April 24–27 and May 9–11), and summer 1994 [July 26–29 and August 8–11). Mixing depth (Z_{mix}) and euphotic depth (Z_{eu}) were derived from shipboard density and light measurements. Open circles refer to 1st and filled circles to 2nd survey stations of the respective survey. Dotted lines mark Z_{mix}:Z_{eu} =1, continuous lines show Z_{mix}:Z_{eu} = 5 (Alpine and Cloern 1988). Dashed lines mark half-saturation constants for nutrient uptake by natural phytoplankton assemblages (Fisher et al. 1988). The shaded area defines the region for which Z_{mix}:Z_{eu} is > 1 and nutrient concentrations are below published half-saturation constants for nutrient uptake of natural phytoplankton.

Wadden Sea and was tidally mixed into the offshore coastal waters. In the open German Bight Z_{mix}:Z_{eu} was close to the values reported from inside the Wadden Sea (Tillmann et al. 2000) and some chlorophyll buildup was evident in this region.

Figure 8 displays dissolved nutrient and light availabilities for all stations sampled during the winter campaign. It is evident from Fig. 8 that light is the main limiting resource for the phytoplankton at least for the February survey. Results from March show that some of the open Bight and North Frisian stations experienced more favorable light conditions. DIN and SRP concentrations (data not shown) are in most cases well above half-saturation concentrations for their uptake, while at several stations Si concentrations are well below that limit. This does not necessarily impose a Si limitation since all low Si stations also show a slight (Z_{mix}:Z_{eu}: 1–2) to severe (station 24, second grid, Z_{mix}:Z_{eu}: > 6) light limitation. Nutrient ratios are in most cases well above the published optima (DIN:SRP = 16; Redfield 1934, 1958; DIN:Si ratio = 1, Levasseur

and Therriault 1987; Sommer 1994), reflecting the imbalanced nutrient influx (extremely high DIN relative to SRP and Si; Brockmann et al. 1999a; Rick 1999) from the River Elbe.

The first spring survey showed improved light conditions for the whole German Bight compared to winter Z_{mix}:Z_{eu} values (Fig. 7). In the German Bight proper light conditions were far from limiting values. In North Frisian coastal waters, the situation also improved with Z_{mix}:Z_{eu} in the range from 1.5 to 3. The second spring survey revealed less optimal light conditions (Fig. 8) mainly due to the rising turbidity from the developing spring bloom. Z_{mix}:Z_{eu} data from Büsum Mole (Tillmann et al. 2000) gathered over the time of the KUSTOS spring surveys were in the same, but still marginally light limiting, range given for the North Frisian coastal waters.

For spring 1995, Si as well as SRP concentrations were below limiting values at many stations, while DIN values (data not shown) were still extremely high. At most stations of the second survey the phytoplankton might have been limited by these two nutrients. Nutrient ratios were generally very high (Fig. 4, DIN:Si) underlining this possible Si and SRP limitation in the surface layer for the second survey, which is supported by the P:E data (Table 1).

The spatial distribution of Z_{mix}:Z_{eu} for both summer 1994 surveys is very similar (Fig. 7, first survey). During both surveys phytoplankton experienced almost no light limitation in most of the German Bight, while the coastal areas showed slightly elevated levels of 1.5–2. Nutrient concentrations were generally lowest compared to the winter and spring data. During both surveys Si concentrations were generally below half-saturation constants for uptake (Fig. 8); the second survey showed the same for DIN (Figs. 6 and 8), and the first survey for SRP concentrations (Fig. 8). Nutrient ratios were more balanced compared to the winter and spring values (Fig. 6).

Despite low concentrations of dissolved inorganic nutrients, P^B_{max} values and resulting primary productivity estimates were still high during both summer surveys (Table 1, Fig. 5). It might be possible that the thresholds used to assess nutrient limitation, which were in the upper range of half-saturation constants for coastal plankton communities published by Fisher et al. (1988), did not match this extreme summer situation for the German Bight. Due to the calm and sunny weather prevailing during the survey (Becker et al. 1999), an unusually stable thermocline had built up in the German Bight proper. This gave rise to a planktonic community adapted to lower nutrient levels and capable of instantaneous nutrient recycling with

TABLE 2.   Time series (1986–1996) of primary production in the German Bight based on NERC, ZISCH, and KUSTOS data. Values are given as monthly means m^{-2}. KUSTOS data are total primary production (particulate + dissolved) values. All other listed studies refer to particulate primary production.

Date	Sample size	Primary production (g C m^{-2} mo^{-1})	Program	Reference
May 1986	3	18	ZISCH	Rick (1990)
June 1986	3	36	ZISCH	Rick (1990)
February 1987	8	3	ZISCH	Rick (1990)
January 1989	4	3	NERC	Joint and Pomroy (1993)
January 1989	13	10	ZISCH	Heyer et al. (1994); Aletsee et al. (1990)
February 1989	4	5	NERC	Joint and Pomroy (1993)
February 1989	12	9	ZISCH	Heyer et al. (1994); Aletsee et al. (1990)
March 1989	4	14	NERC	Joint and Pomroy (1993)
March 1989	4	15	ZISCH	Heyer et al. (1994); Aletsee et al. (1990)
April 1989	4	33	NERC	Joint and Pomroy (1993)
April 1989	16	29	ZISCH	Heyer et al. (1994); Aletsee et al. (1990)
May 1989	4	47	NERC	Joint and Pomroy (1993)
May 1989	19	174	ZISCH	Aletsee et al. (1990)
May 1989	8	152	ZISCH	(only range overlap with NERC 1992)
June 1989	4	25	NERC	Joint and Pomroy (1993)
July 1989	4	40	NERC	Joint and Pomroy (1993)
July 1994	28	236	KUSTOS	This study
August 1994	28	239	KUSTOS	This study
April 1995	36	120	KUSTOS	This study
May 1995	36	189	KUSTOS	This study
February 1996	31	2.7	KUSTOS	This study
March 1996	32	9.3	KUSTOS	This study

high biomasses of dinoflagellates, nanoplankton, protozooplankton, and bacteria (Fehner 1996; Gärtner 1996; Rieling 1996). Instantaneous recycling of phosphorus and nitrogen compounds, as well as the use of dissolved organic nitrogen (DON) and phosphorus (DOP), was not considered in the limitation assessment shown above. Since DON accounted for 50% to > 70% of the total nitrogen and DOP for 25% to > 50% of the total phosphorus in the surface layer during the summer surveys (Brockmann et al. 1999a), it is very likely that dissolved organic nutrients contributed to the high photosynthetic performance of the phytoplankton.

It is still discussed as to what extent P$^B_{max}$ values are coupled to nutrient limitation (e.g., Tillmann et al. 2000). Often no distinct drop in the primary production potential was evident with decreasing nutrient concentrations (e.g., Takahashi et al. 1973). Results from continuous cultures sometimes showed P$^B_{max}$ as independent from nutrient-limited growth, while in batch cultures P$^B_{max}$ declined with increasing nutrient starvation (Cullen et al. 1992). Both laboratory models might be applicable for certain situations in the German Bight encountered during KUSTOS. While the batch model best resembled the development of the spring bloom, with P$^B_{max}$ depending on nutrient limitation (Table 1, Figs. 3, 4, and 8), the 1994 summer situation reflected more the continuous model where P$^B_{max}$ is almost independent of nutrient-limiting growth conditions (Table 1, Figs. 5, 6, and 8).

VARIABILITY OF PRIMARY PRODUCTIVITY IN THE GERMAN BIGHT

Few studies exist on primary productivity in the German Bight (Aletsee et al. 1990; Rick 1990; Heyer et al. 1994), while the data coverage for adjacent waters is slightly better (Gieskes and Kraay 1975, 1977; Joint and Pomroy 1993; De Madariga and Joint 1994; and Howarth et al. 1994: southern North Sea; Cadee and Hegeman 1993; Bot and Colijn 1996: Marsdiep; Tillmann et al. 2000: German Wadden Sea). A comprehensive paper about seasonal changes (August 1988–October 1989) in primary production in the southern North Sea is given by Joint and Pomroy (1993). Their data were obtained during monthly sampling campaigns in the frame of the British North Sea Community Research Project (NERC 1992).

Table 2 compiles a primary production time series (1986–1996) based on seasonally gathered data from the NERC, ZISCH 1 (Circulation and Contaminant Cycling in the North Sea), ZISCH 2 (Circulation and Contaminant Cycling in the German Bight), and KUSTOS programs.

Similarities, as well as sharp differences, between the data sets are evident. The differences between NERC (January 1989–July 1989) and ZISCH 2 (January 1989–May 1989) are especially striking, since both programs had an overlap in time and range. These discrepancies might be caused by different methodology, sampling density in the area of overlap, and patchy phytoplankton distribution, as well as slightly different sampling times. During

ZISCH 2 generally a 13–19 station grid was sampled (exception March: 6 stations), while NERC sampling overlapped with the ZISCH area by only 4 stations, generally missing the highly productive nearshore regions. April 1989 values are strikingly parallel in both programs, while ZISCH 2 February data are 1.8 times and May data are 3.7 times higher. Considering only the regional overlap of both programs, ZISCH 2 data remain 3.2 times elevated. Sampling the rapid pulse of the ''nutrient-limited spring production peak'' (Longhurst 1995, p. 100–101) during ZISCH 2 and a slightly different date of sampling in both programs might have caused the observed discrepancies.

An interannual comparison of the summer season also shows great differences. KUSTOS (August 1994) estimated extremely high values > 200 g C m^{-2} mo^{-1}, while NERC and ZISCH 1 values are significantly lower but in a comparable range of 25–40 g C m^{-2} mo^{-1}. The KUSTOS survey in summer 1994 encountered an extreme situation with extraordinarily high temperature, intense light, and a strong stratification (Becker et al. 1999). This gave rise to a highly regenerating plankton community, characterized by high abundances of nanoplankton and unicellular zooplankton, as well as bacteria (Fehner 1996; Gärtner 1996; Rieling 1996). NERC and ZISCH 1 sampled rather more average summer conditions with low production capacities.

The spatial resolution (24–36 stations per survey) of the KUSTOS primary productivity data is not matched by any other German Bight study. Even the ZISCH 2 program (Aletsee et al. 1990; Heyer et al. 1994) had only half of this resolution. Data from both programs were used to analyze the spatial variability within single surveys, the short-term variability by comparing two surveys in the identical season, as well as the seasonal and interannual variability (Fig. 9) of primary productivity in the German Bight. The bar charts in Fig. 9 show total primary production expressed as average values for the whole German Bight, as well as for four of its subregions (compare Fig. 1) with standard deviations. Subregions generally follow depth contours and were additionally refined based on previous work by Goedecke (1936) and Hesse (1988).

KUSTOS winter data (Fig. 9) show relatively low variability in the first survey, while both the value and variability are higher in the second survey. This pattern holds for all subregions. Open German Bight and North Frisian stations were most productive. The Elbe-Weser water showed lowest productivity.

Both spring surveys showed high primary productivity, which is relatively variable, in the whole German Bight as well as in all the subregions. The general increase in productivity from the first to the second survey was accompanied by a rise in variability occurring in all subregions. Open German Bight and the East Frisian waters were most productive and again the Elbe-Weser waters showed the lowest values.

The summer surveys displayed almost identical high production values with a slight rise of variability in the second survey. Overall the variability was in the same range as during the second spring survey. In both surveys the East Frisian stations showed the lowest variability. Contrary to the winter and spring campaigns the open German Bight had the lowest productivity levels, while the highest numbers were measured in the North and East Frisian waters.

KUSTOS and ZISCH 2 had only two periods of seasonal overlap (early March 1996–late February 1989, May 1995–1989) that could be used to assess the interannual variability of primary production in the Bight (Fig. 9). For this comparison the ZISCH 2 particulate production data were converted to total production values by applying a factor of 1.18 from Tillmann et al. (2000). The overall averages, as well as the variability, were strikingly matched for the compared seasons in both years. Some subregions also showed production values that were in a very close range for 1989 and 1995 (e.g., open German Bight and North Frisian waters for winter surveys, North Frisian and Elbe-Weser waters for May surveys), while East Frisian waters displayed very different production levels for both assessed seasons in KUSTOS and ZISCH 2.

ESTIMATE OF ANNUAL TOTAL PRIMARY PRODUCTIVITY IN THE GERMAN BIGHT

Longhurst (1995) developed a conceptual model for the development of canonical spring-autumn blooms on continental shelves based mainly on publications by Harvey (1955) for the English Channel and Riley (1947) and Davies (1987) for the Georges Bank. The annual development is considered to consist of three main phases. First, a short, rapid pulse of increased productivity and chlorophyll is induced by early water column stability and fuelled by accumulated winter nutrients. The following summer stratification of the water column is associated with relatively low productivity, principally driven by regenerated nutrients. In a third phase a progressive breakdown of the stratification in autumn induces renewed production fuelled by nutrients accumulated below the summer pycnocline.

Smetacek et al. (1984) presented an extended concept with five phases of plankton development for inshore pelagic systems. This concept was extended to eight phases to meet the conditions in the German Bight. One of the most striking
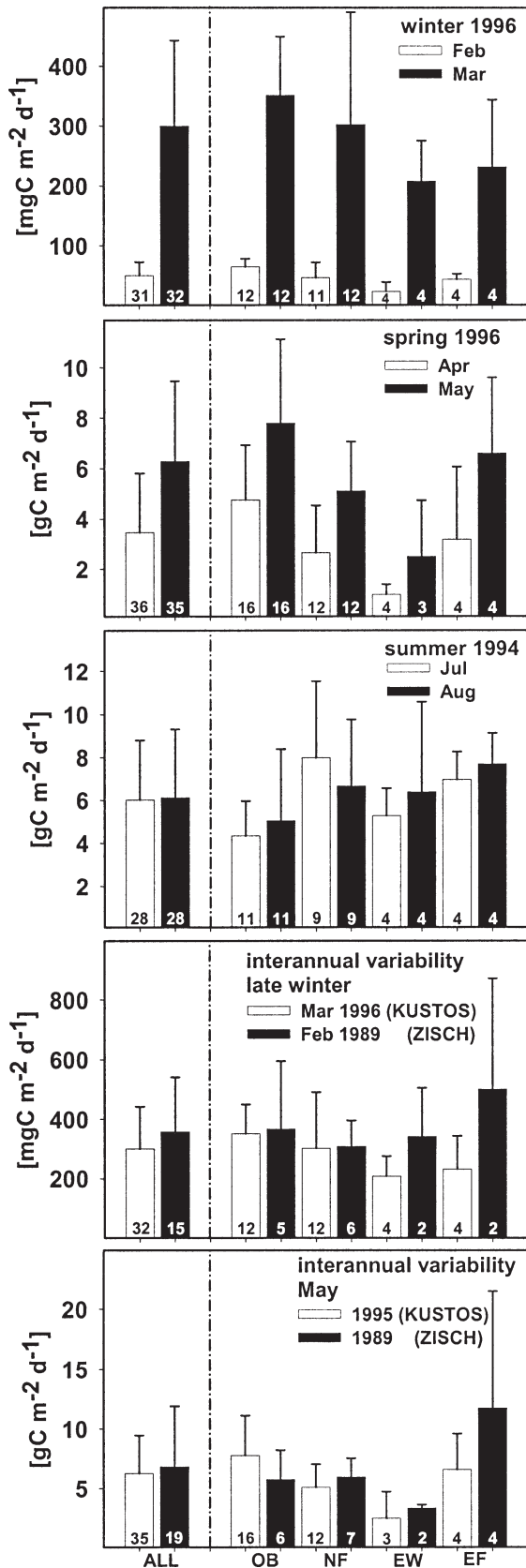
problems in estimating annual production based on the data in Table 2, is weighing the different seasonal measurements over the annual cycle. The duration, as well as the overall occurrence of seasonal plankton phases, is strongly affected by meteorological features, light conditions, mixing or stratification, nutrient concentrations, recycling, and fuelling, and by trophic interactions. For the annual primary production estimate the duration of the phases was chosen as shown in Table 3.

Daily total primary production rates and average production values for the eight phases are given. Primarily data from the KUSTOS surveys were used for this estimate. For seasons not covered during KUSTOS particulate primary production data from NERC and ZISCH adjusted to total production values were used (Tillmann et al. 2000). This approach yielded an annual total primary production for the German Bight of about 430 g C m^{-2} yr^{-1}.

Table 4 summarizes annual phytoplankton primary production estimates of the North Sea, European coastal, and estuarine areas. Our 1994–1996 estimate for the German Bight is higher than other annual production estimates for all regions of the North Sea and it exceeds the NERC calculation (261 g C m^{-2} yr^{-1}; Joint and Pomroy 1993) by almost a factor of 1.6. In comparing these estimates, one has to keep in mind that the presented annual value for the German Bight is based on total production, while most published estimates used particulate production. Dissolved and particulate production data from Büsum Mole for the period June–December 1996 show dissolved:particulate ratios ranging from 0.13 to 2.78. The high-end ratios were generally caused by high abundances of the Prymnesiophyte *Phaeocystis globosa*, a species not encountered in high numbers during the KUSTOS surveys. Omitting values based on high *Phaeocystis* abundance, dissolved production averaged about 18% of the total production (Tillmann et al. 2000).

$\leftarrow$

Fig. 9. Variability of primary productivity in the German Bight. Spatial, short term, and seasonal variability based on the KUSTOS data are given in the upper three panels. The first two bars (all) compare all data from two consecutive surveys (first–open, second–filled bars) during different seasons (winter, spring, summer) and allow to access overall short-term and seasonal variability. The bars on the right from the hatched line (unfilled: survey 1, filled: survey 2) add spatial information based on data from sub regions (see Fig. 1: open Bight [OB], North Frisian waters [NF], Elbe-Weser water [EW], and East Frisian waters [EF]). Interannual variability is assessed in the lower two panels. KUSTOS data (unfilled: 3/96, 5/95) are compared with ZISCH 2 data (filled: 2/89, 5/89) for the whole Bight (first two bars) and sub regions. Error bars show standard deviations and numbers at the bottom of each bar give respective sample sizes.

TABLE 3.   Estimates of the annual total primary production in the German Bight.

No	Plankton phase	Phase duration		Production	
		Months	Days	g C m^{-2} d^{-1}	g C m^{-2} phase^{-1}
1	Winter conditions	5	152	0.1	15.2
2	Winter-spring transition	0.5	15	0.3	4.5
3	Spring bloom	0.75	25	4.0	100
4	Spring bloom decay	0.25	8	6.3	50.4
5	Spring-summer transition[1]	1.5	45	0.7	31.5
6	Summer high production	0.5	15	7.7	115.5
7	Summer stagnation[2] low production	2	60	1.2	72
8	Autumn conditions[1]	1.5	45	0.9	40.5
Annual primary production estimate (g C m^{-2} yr^{-1})					ca. 430
Without summer high production					ca. 330

[1] NERC, ICES Box 5 (Joint and Pomroy 1993).
[2] ZISCH May 1986 (Rick 1990). NERC and ZISCH data were converted from particulate to total production applying a factor of 1.18 derived from Tillmann et al. (2000).

TABLE 4.   Annual phytoplankton primary production estimates of the North Sea, European coastal, and estuarine areas.

System	Primary production (g C m^{-2} yr^{-1})	Reference
Open North Sea		
Entire North Sea	45–110	Steele (1956a)
	190–290	Rick (1990)
Fladenground	54–82	Steele (1956b)
	160	Horwood (1982)
Northern North Sea	100	Horwood (1982)
	150–200	Reid et al. (1990)
Central North Sea	250	Gieskes and Kraay (1984)
	250	Reid et al. (1990)
Central North Sea (ICES box 7)	119	Joint and Pomroy (1993)
Coastal North Sea		
Denmark coast	74	Steemann-Nielsen (1952)
England northeast coast	40	Horwood (1982)
England northeast coast (ICES box 3)	79	Joint and Pomroy (1993)
Southern North Sea	200	Reid et al. (1990)
Southern North Sea (ICES box 4)	199	Joint and Pomroy (1993)
German Bight (ICES box 5)	261	Joint and Pomroy (1993)
German Bight	430	This study
North Sea estuarine and Wadden Sea areas		
Western Wadden Sea	100	Cadee and Hegeman (1974)
	146	Boynton et al. (1983)
Eastern Wadden Sea	120	Cadee and Hegeman (1974)
	114	Boynton et al. (1983)
Dutch Wadden Sea	335	Hoppema (1991)
Ems (1972–1973)	240	Cadee and Hegeman (1979)
Ems Dollard (1976–1980)	70–283	Colijn (1983)
Marsdiep area (1963–1965)	170	Postma and Rommets (1970)
1986	303	Veldhuis et al (1988)
1960–early 1970s	150–200	Cadee and Hegeman (1993)
1981–1982	250–390	Cadee and Hegeman (1993)
Osterschelde	180–500	Kromkamp and Peene (1995)
Westerschelde	100–300	Wetsteyn and Kromkamp (1994)
Sylt-Rømø Bight	160	Asmus et al. (1998)
Büsum Wadden Sea	152	Tillmann et al. (2000)
Adjacent coastal waters		
Kattegat	85	Bertelsen and Hansen (1969)
	130	Aertebjerk et al. (1981)
	190	Heilman et al. (1994)
Southampton water	144	Collins (1978)
Outer Bristol Channel	165	Joint and Pomroy (1981)
Bay of Morlaix	314	Wafar et al. (1983)

TABLE 5. Average primary production (SD) for six seasonal surveys (W: winter, SP: spring, SU: summer, 1: first survey, 2: second survey) in the German Bight (KUSTOS data). (A) displays values (av_{all}, SD_{all}) based on complete data sets from the 10-nm grid (Fig. 1). Data sets split in half (20 nm distance between stations, n = 14–18) were used to calculate averages (PP_{20}) and standard deviations (SD_{20}) given as percentages of av_{all} and SD_{all} in (B). For (C) only every 4th station of the original grid (40 nm distance, n = 7–9) was included in the calculation. Four nonoverlapping data sets were analyzed and the range of lowest and highest percentages (PP_{40}, SD_{40}) is displayed. Including only every 8th station (80 nm distance, n = 3–5, 8 nonoverlapping data sets) resulted in the values (PP_{80}, SD_{80}) given in (D). The maximum range of results from 8 calculations is shown.

	A (10 nm)			B (20 nm)			C (40 nm)			D (80 nm)		
	mg C m⁻² d⁻¹			PP_{20}	SD_{20}		PP_{40}	SD_{40}		PP_{80}	SD_{80}	
	av_{all}	SD_{all}	n	$\%av_{all}$	$\%SD_{all}$	n	$\%av_{all}$	$\%SD_{all}$	n	$\%av_{all}$	$\%SD_{all}$	n
W1	49.4	22.9	31	93.6 (106.8)	99.7 (101.5)	15 (16)	85 (119.3)	68.9 (126.8)	7 (8)	84.6 (147.4)	34.5 (154)	4
W2	300	143	32	95.7 (104.3)	74.5 (122.2)	16	83.4 (121.5)	71.5 (143.6)	8	73.9 (126.5)	32.6 (190.1)	4
	g C m⁻² d⁻¹											
SP1	3.46	2.35	36	92 (108)	98.4 (102)	18	86.8 (125)	66 (122.8)	9	82.8 (145.4)	43.6 (144.1)	4 (5)
SP2	6.28	3.17	35	90.3 (109.2)	78.5 (116.1)	17 (18)	88.6 (116)	75 (126.6)	8 (9)	71.3 (149.2)	42 (173.2)	4 (5)
SU1	6.02	2.78	28	97.3 (102.7)	76.4 (121.9)	14	92.8 (112.5)	66.7 (153.6)	7	66.5 (138.5)	24 (183.4)	3 (4)
SU2	6.13	3.18	28	97.2 (102.8)	95.3 (107.8)	14	90.7 (110.7)	70.1 (141)	7	80 (126.9)	36.3 (164.6)	3 (4)

Applying this percentage to our German Bight data adjusts the annual estimate to 352 g C m⁻² yr⁻¹. Estimates for the adjacent North Frisian Wadden areas (Sylt-Rømø Bight: Asmus et al. 1998; Büsum Wadden Sea: Tillmann et al. 2000) are 2.2 times lower. This striking difference is supported by a compilation by Cloern (1987), who demonstrated that pelagic primary production in open coastal waters generally is higher compared to adjacent estuaries.

Our high-end estimates have to be interpreted with care since they might not reflect average annual conditions for the Bight. There is only limited evidence that the chosen lengths of the eight phases (Table 3) are perfectly correct for the years 1994–1996. Shifts in phase lengths will influence the overall annual estimate profoundly. It is also strongly influenced by the extreme spring bloom of 1995 and the unusual hot and calm summer of 1994 with its high regenerated production. Both events contribute about 60% to the annual total. Omitting the probably most unusual summer high production phase and filling in instead the possibly more likely summer stagnation phase brings the estimates down to about 332 (total) or 272 (particulate production) g C m⁻² yr⁻¹. These numbers fit better into the compilation given in Table 4. Globally, our estimates are also in the higher range and equal values given for the eutrophicated areas like Narragansett and Chesapeake Bays (Nixon and Pilson 1984; Marshall and Nesius 1996) or Georgia coastal waters (Hopkinson 1985).

The German Bight is characterized by a high variability of its physicochemical environment (Kalle 1956; Krause et al. 1986; Brockmann et al. 1990). This is mirrored in turn by the distribution and primary productivity of the phytoplankton (Fig. 9).

The high-resolution KUSTOS production data were used to develop a more efficient sampling strategy without sacrificing lot of precision. Based on complete and reduced (50%, 25%, and 12.5% of the original size) data sets, Table 5 gives a compilation of primary production averages with standard deviations for the seasonal studies in the German Bight. The sampling of 16–18 instead of 36 stations still results in an average production value ranging ± 6% from the comparative figure (av_{all}), while the variability will only be captured by ± 13% of SD_{all} (column B in Table 5). Sampling every fourth station (n = 7–9) of the original grid results in an average of ± 15% of av_{all} but the variability information with ± 33% of SD_{all} becomes very vague (column C). A further reduction in sample size (n = 3–5) results in relatively unreliable data (column D, average: ± 33% of av_{all}, variability: ± 67% of SD_{all}).

Sampling a 10-station grid covering the KUSTOS area (1 Elbe-Weser waters, 2 East Frisian waters, 3 North Frisian waters, 4 open German Bight) would give a decent insight into the primary production capacity of the Bight with an average in the ± 10–15% and variability in the ± 25–30% range of comparative figures based on the evaluation of 24–36 stations. It is strongly recommended to apply station-specific P:E characteristics for the production estimates instead of averaged values used in this study.

In order to cover the annual development most efficiently, focus should lie on the higher productive period from late March to early October, omitting the period of extremely low production in winter. At least 4–5 surveys should be carried out during this period and should cover the most productive times (e.g., spring bloom, summer high production). Timing of the respective surveys as well

as the weighting of the phases (compare Table 3) can be accomplished by applying seasonal meteorological, hydrographical, and remote sensing information.

LITERATURE CITED

AETREBJERK, G., T. JACOBSON, E. GARGAS, AND E. BUCH. 1981. The Belt Project. Evaluation of the Physical, Chemical, and Biological Measurements. National Agency of Environmental Protection, Copenhagen, Denmark.

ALETSEE, L., H.-J. RICK, V. BECKER, AND C.-D. DÜRSELEN. 1990. Zirkulation und Schadstoffumsatz in der Nordsee (ZISCH). Teilprojekt B2: Einfluss des Phytoplanktons auf die Schadstoffverteilung und den Schadstoffumsatz in der Deutschen Bucht. Data report, RWTH Aachen, Insitut für Biologie 1, Abteilung für Systematik und Geobotanik, Worringerweg 1, 5100 Aachen, Germany.

ALPINE, A. E. AND J. E. CLOERN. 1988. Phytoplankton growth rates in a light-limited environment, San Francisco Bay. *Marine Ecology Progress Series* 44:167–173.

ANONYMOUS. 1983. Second Biological Intercalibration workshop. Proceedings Baltic Sea Environment, 9, Helsinki Baltic Marine Environmental Protection Commission, Helsinki, Finland.

ANONYMOUS. 1990. ICES ^{14}C Primary Production Intercomparison Exercise Report. International Council for the Explanation of the Sea, Copenhagen, Denmark.

ARMSTRONG, F. A. J., C. R. STEARNS, AND J. D. H. STRICKLAND. 1967. The measurement of upwelling and subsequent biological processes by means of the Technicon Autoanalyzer and associated equipment. *Deep Sea Research* 14:381–389.

ASMUS, R., M. H. JENSEN, D. MURPHY, AND R. DOERFFER. 1998. Primary production of microphytobenthos, phytoplankton and the annual yield of macrophytic biomass in the Sylt-Rømø Wadden Sea, p. 367–391. *In* C. Gätje and K. Reise (eds.), Ökosystem Wattenmeer. Springer, Berlin, Germany.

BAUERFEIND, E., W. HICKEL, U. NIERMANN, AND H. VON WESTERNHAGEN. 1990. Phytoplankton biomass and potential nutrient limitation of phytoplankton development in the southeastern North Sea in spring 1985 and 1986. *Netherlands Journal of Sea Research* 25:131–142.

BAUMANN, M. E. M. 1990. Untersuchung zur Primärproduktion und Verteilung des Phytoplanktons der Grönlandsee mit Kulturexperimenten zum Einfluss des Lichtes und der Temperatur auf das Wachstum und Photosyntheseleistung arktischer Diatomeen. Ph.D. Dissertation, Rheinisch-Westfälische Technische Hochschule (RWTH) Aachen, Germany.

BECKER, G. A., H. GIESE, K. ISERT, P. KÖNIG, H. LANGENBERG, T. POHLMANN, AND C. SCHRUM. 1999. Mesoscale structures, fluxes and the water mass variability of the German Bight as exemplified in the KUSTOS-experiments and numerical models. *German Journal of Hydrography* 51:155–180.

BERTELSEN, E. AND P. M. HANSEN. 1969. Fiskeriundersogelser 1969 Danmark, Färöarne og Grönland. *Skrifter Danmarks Fiskeri og Havundersogelser* 30:1–101.

BOON, A. R., G. C. A. DUINEVELD, E. M. BERGHUIS, AND J. A. VAN DER WEELE. 1998. Relationships between benthic activity and the annual phytopigment cycle in near-bottom water and sediments in the southern North Sea. *Estuarine and Coastal Shelf Science* 46:1–13.

BOT, P. V. M. AND F. COLIJN. 1996. A method for estimating primary production from chlorophyll concentrations with results showing trends in the Irish Sea and the Dutch coastal zone. *ICES Journal of Marine Sciences* 53:945–950.

BOYNTON, W. R., C. A. S. HALL, P. G. FALKOWSKI, C. W. KEEFE, AND W. M. KEMP. 1983. Phytoplankton Productivity in Aquatic Ecosystems, *Encyclopedia of Plant Pysiology* 12D:305–327.

BROCKMANN, U. H., R. W. LAANE, AND H. POSTMA. 1990. Cycling of nutrient elements in the North Sea. *Netherlands Journal of Sea Research* 26:239–264.

BROCKMANN, U., T. RAABE, K. HESSE, K. VIEHWEGER, S. RICK, A. STARKE, B. FABISZISKY, D. TOPÇU, AND R. HELLER. 1999a. Seasonal budgets of the nutrient elements N and P at the surface of the German Bight during winter 1996, spring 1995, and summer 1994. *German Journal of Hydrography* 51:267–292.

BROCKMANN, U., K. VIEHWEGER, T. RAABE, S. RICK, H.-J. RICK, AND R. HELLER. 1999b. Conversion of nutrients in the Elbe River plume during drift experiments in the German Bight during spring 1995 and summer 1994. *German Journal of Hydrography* 51:293–312.

CADEE, G. C. AND J. HEGEMAN. 1974. Primary production of phytoplankton in the Dutch Wadden Sea. *Netherlands Journal of Sea Research* 8:240–259.

CADEE, G. C. AND J. HEGEMAN. 1979. Phytoplankton primary production, chlorophyll and consumption in an inlet of the Western Wadden Sea (Marsdiep). *Netherlands Journal of Sea Research* 13:224–241.

CADEE, G. C. AND J. HEGEMAN. 1993. Persisting high levels of primary production at declining phosphate concentration in the Dutch coastal area (Marsdiep). *Netherlands Journal of Sea Research* 31:147–152.

CLOERN, J. E. 1987. Turbidity as a control on phytoplankton biomass and productivity in estuaries. *Continental Shelf Research* 7:1367–1381.

CLOERN, J. E. 1996. Phytoplankton bloom dynamics in coastal ecosystems: A review with some general lessons from sustained investigation of San Francisco Bay, California. *Reviews of Geophysics* 34:127–168.

COLE, J. J., N. F. CARADO, AND B. L. PEIERLS. 1992. Can phytoplankton maintain a positive carbon balance in a turbid, freshwater, tidal estuary? *Limnology and Oceanography* 37: 1608–1617.

COLE, B. E. AND J. E. CLOERN. 1984. Significance of biomass and light availability to phytoplankton productivity in San Francisco Bay. *Marine Ecology Progress Series* 17:15–24.

COLIJN, F. 1983. Primary production in the Ems Dollard estuary. Ph.D. Dissertation, State University Groningen, Groningen, The Netherlands.

COLIJN, F., G. W. KRAAY, R. N. M. DUIN, U. TILLMANN, AND M. J. W. VELDHUIS. 1996. Design and test of a novel P_{max} incubator to be used for measuring the primary production in ICES monitoring studies. *International Council for the Exploration of the Sea* ICES CM 1996/L3.

COLLINS, K. J. 1978. Fluxes of organic carbon and nutrients in Southampton water. Ph.D. Dissertation, University of Southampton, Southampton, U.K.

CULLEN, J. J., X. YANG, AND H. L. MACINTYRE. 1992. Nutrient limitation of marine photosynthesis, p. 69–88. *In* P. G. Falkowski and A. D. Woodhead (eds.), Primary Productivity and Biogeochemical Cycles in the Sea, 1st edition. Plenum Press, New York.

DAMM, P. E. 1989. Klimatologischer Atlas des Salzgehaltes, der Temperatur und der Dichte in der Nordsee, 1968–1985. Technical Reports, Institut für Meereskunde, No. 89-6, Hamburg, Germany.

DAVIES, C. S. 1987. Components of the zooplankton production cycle in the temperate ocean. *Journal of Marine Research* 45:947–983.

DE MADARIAGA, I. AND I. JOINT. 1994. Photosynthesis and carbon metabolism by size-fractionated phytoplankton in the southern North Sea in early summer. *Continental Shelf Research* 14:295–311.

DRING, M. J. AND D. H. JEWSON. 1982. What does the ^{14}C uptake by phytoplankton really measure? A theoretical modeling approach. *Proceedings of the Royal Society of London, Series B* 214:351–368.

DRUON, J.-N., W. SCHRIMPF, S. DOBRICIC, AND A. STIPS. 2004. Comparative assessment of large-scale marine eutrophication: North Sea area and Adriatic Sea as case studies. *Marine Ecology Progress Series* 272:1–23.

DÜNSING, G. AND R. ZÖLLNER. 1978. Die Windverhältnisse in der Bundesrepublik Deutschland im Hinblick auf die Nutzung der Windkraft. Teil II: Küstenvorfeld. *Berichte des Deutschen Wetterdienstes* 147:76–82.

EBERLEIN, K. AND G. KATTNER. 1987. Automatic method for the determination of ortho-phosphate and total dissolved phosphorus in the marine environment. *Fresenius Journal of Analytical Chemistry* 326:354–357.

EBERLEIN, K., M. T. LEAL, K. D. HAMMER, AND W. HICKEL. 1985. Dissolved organic substances during a *Phaeocystis pouchetii* bloom in the German Bight (North Sea). *Marine Biology* 89:311–316.

FEHNER, U. 1996. Untersuchungen zur Verteilung des Protozooplanktons im Bereich der Flussfahnenfronten der Elbe. M.S. Thesis, University of Oldenburg, Oldenburg, Germany.

FISHER, T. R., L. W. J. HARDING, D. W. STANLEY, AND L. G. WARD. 1988. Phytoplankton, nutrients and turbidity in the Chesapeake, Delaware and Hudson estuaries. *Estuarine and Coastal Shelf Science* 27:61–93.

FRANSZ, H. G. AND W. W. C. GIESKES. 1984. The unbalance of phytoplankton and copepods in the North Sea. *Rapports et Proces-Verbaux Reunions Conseil International Exploration Mer* 183:218–225.

GALLEGOS, C. L. AND T. PLATT. 1982. Phytoplankton production and water motion in surface mixed layers. *Deep-Sea Research* 29:65–76.

GÄRTNER, U. 1996. Bakterioplanktonverteilung in der deutschen Bucht während einer Sommersituation. M.S. Thesis, University of Oldenburg, Oldenburg, Germany.

GERDES, D. 1985. Zusammensetzung und Verteilung von Zooplankton sowie Chlorophyll- und Sestongehalte in verschiedenen Wassermassen der Deutschen Bucht in den Jahren 1982/83. *Veröffentlichungen des Institutes für Meeresforschung Bremerhaven* 20:119–139.

GIESKES, W. W. C. AND G. W. KRAAY. 1975. The phytoplankton spring bloom in Dutch coastal waters of the North Sea. *Netherlands Journal of Sea Research* 9:166–196.

GIESKES, W. W. C. AND G. W. KRAAY. 1977. Primary production and consumption of organic matter in the southern North Sea during the spring bloom of 1975. *Netherlands Journal of Sea Research* 11:146–167.

GIESKES, W. W. C. AND G. W. KRAAY. 1984. Phytoplankton, its pigments, and primary production at a central North Sea station in May, July and September 1981. *Netherlands Journal of Sea Research* 18:51–70.

GOEDECKE, E. 1936. Der Kalkgehalt in Oberflächenwasser der Unterelbe und der Deutschen Bucht. *Archiv der Deutschen Seewarte* 55:1–37.

GRASSHOFF, K, M. EHRHARDT, AND K. KREMLING. 1983. Methods of Seawater Analysis, 2nd edition. Verlag, Chemie, Weinheim.

HARDING, L. W., B. B. PREZELIN, B. M. SWEENEY, AND J. L. COX. 1982. Diel oscillations of the photosynthesis-irradiance (PI) relationship in natural assemblages of phytoplankton. *Marine Biology* 67:167–178.

HARVEY, H. W. 1955. The Chemistry and Fertility of Seawaters, 1st edition. Cambridge University Press, Cambridge, Massachusetts.

HEILMANN, J. P., K. RICHARDSON, AND G. AERTEBJERG. 1994. Annual distribution and activity of phytoplankton in the Skagerrak/Kattegat frontal region. *Marine Ecology Progress Series* 112:213–223.

HESSE, K.-J. 1988. Zur Ökologie des Phytoplanktons in Fronten und Wassermassen der Deutschen Bucht. Ph.D. Dissertation, Christian-Albrechts-Universität, Kiel, Germany.

HESSE, K.-J., D. GERDES, AND K. SCHAUMANN. 1989a. A winter study of plankton distribution across a coastal salinity front in the German Bight. *Meeresforschung* 32:177–191.

HESSE, K.-J., U. HENTSCHKE, AND U. BROCKMANN. 1992. A synoptic study of nutrient and phytoplankton characteristics in the German Wadden Sea with respect to coastal eutrophication, p. 5–53. *In* G. Colombo, V. Ferrari, U. Ceccherelli, and R. Rossi (eds.), Marine Eutrophication and Population Dynamics. Olsen and Olsen, Fredensborg, Denmark.

HESSE, K.-J., Z. L. LIU, AND K. SCHAUMANN. 1989b. Phytoplankton and fronts in the German Bight. *Scientia Marina* 53:187–196.

HEYER, K., M. ENGEL, U. H. BROCKMANN, H.-J. RICK, C.-D. DÜRSELEN, H. HÜHNERFUSS, U. KAMMANN, M. STEINHART, W. KIENZ, L. KARBE, A. FAUBEL, AND S. REGIER. 1994. Local studies in the German Bight during winter/spring 1988/89, p. 190–249. *In* J. Sündermann (ed.), Circulation and Contaminant Fluxes in the North Sea, 1st edition. Springer, Berlin, Germany.

HICKEL, W. 1984. Seston retention by Whatman GF/C glass fiber filters. *Marine Ecology Progress Series* 16:185–191.

HICKEL, W., E. HAGMEIER, AND G. DREBES. 1971. *Gymnodinium* blooms in the Helgoland Bight (North Sea) during August 1968. *Helgoländer Wissenschaftliche Meeresuntersuchungen* 22:401–416.

HOPKINSON, C. S. 1985. Shallow-water benthic and pelagic metabolism: Evidence for heterotrophy in the nearshore Georgia Bight. *Marine Biology* 87:19–32.

HOPPEMA, J. M. J. 1991. The oxygen budget of the western Dutch Wadden Sea, the Netherlands. *Estuarine Coastal and Shelf Science* 32:483–502.

HORWOOD, J. 1982. Algal production in the west-central North Sea. *Journal of Plankton Research* 4:103–124.

HOWARTH, M. J., K. R. DYER, I. R. JOINT, D. J. HYDES, D. A. PURDIE, H. EDMUNDS, J. E. JONES, R. K. LOWRY, T. J. MOFFAT, A. J. POMROY, AND R. PROCTER. 1994. Seasonal cycles and their spatial variability, p. 5–25. *In* H. Charnock, K. R. Dyer, J. M. Huthnance, P. S. Liss, J. H. Simpson, and P. B. Tett (eds.), Understanding the North Sea System, The Royal Society, 1st edition. Chapman and Hall, London, U.K.

JOHNSEN, G., E. SAKSHAUG, AND M. VERNET. 1992. Pigment composition, spectral characterization and photosynthetic parameters in *Chrysochromulina polylepis*. *Marine Ecology Progress Series* 83:241–249.

JOINT, I. R. AND A. POMROY. 1981. Primary production in a turbid estuary. *Estuarine Coastal Shelf Science* 13:303–316.

JOINT, I. R. AND A. POMROY. 1993. Phytoplankton biomass and production in the southern North Sea. *Marine Ecology Progress Series* 99:179–182.

KALLE, K. 1956. Chemisch-hydrographische Untersuchungen in der inneren Deutschen Bucht. *Deutsche Hydrographische Zeitschrift* 9:55–65.

KELLER, A. A. 1988. An empirical model of primary production (^{14}C) using mesocosm data along a nutrient gradient. *Journal of Plankton Research* 10:813–834.

KIRK, J. T. O. 1994. Light and Photosynthesis in Aquatic Ecosystems, 2nd edition. Cambridge University Press, Cambridge, Massachusetts.

KOROLEFF, F. 1969. Direct determination of ammonia in natural waters as indophenol blue. *International Council for the Exploration of the Sea* C.M.- ICES/C:9.

KRAUSE, G., G. BUDEUS, D. GERDES, K. SCHAUMANN, AND K.-J. HESSE. 1986. Frontal systems in the German Bight and their physical and biological effects. *Elsevier Oceanography Series* 42:119–140.

KROMKAMP, J. AND J. PEENE. 1995. Possibility of net phytoplankton primary production in the turbid Schelde Estuary (SW Netherlands). *Marine Ecology Progress Series* 121:249–259.

LANCELOT, C. AND G. BILLEN. 1984. Activity of heterotrophic bacteria and its coupling to primary production during the spring phytoplankton bloom in the southern bight of the North Sea. *Limnology and Oceanography* 29:721–730.

LANCELOT, C., S. MATHOD, AND N. J. P. OWENS. 1986. Modeling protein synthesis, a step to an accurate estimate of net primary production *Phaeocystis pouchetii* colonies in Belgian coastal waters. *Marine Ecology Progress Series* 32:193–202.

LANGDON, C. 1993. The significance of respiration in production measurements based on oxygen, p. 69–78. *In* W. K. W. Li and S. Y. Maestrini (eds.), Measurement of Primary Production from the Molecular to the Global Scale, Volume 197. ICES Marine Science Symposium, International Council for the Exploration of the Sea, Copenhagen, Denmark.

LEVASSEUR, M. E. AND J. C. THERRIAULT. 1987. Phytoplankton biomass and nutrient dynamics in a tidally induced upwelling: The role of the NO_3:SiO_4 ratio. *Marine Ecology Progress Series* 39:87–97.

LONGHURST, A. 1995. Seasonal cycles of pelagic production and consumption. *Progress in Oceanography* 36:77–165.

LORENZEN, C. Y. 1967. Determination of chlorophyll and phaeopigments: Spectrophotometric equations. *Limnology and Oceanography* 12:343–346.

MACINTYRE, H. L. AND J. J. CULLEN. 1996. Primary production by suspended and benthic microalgae in a turbid estuary: Timescales of variability in San Antonio Bay, Texas. *Marine Ecology Progress Series* 145:245–268.

MANDELLI, E. F., P. R. BURKHOLDER, T. E. DOHENY, AND R. BRODY. 1970. Studies of primary productivity in coastal waters in southern Long Island, New York. *Marine Biology* 7:153–160.

MARSHALL, H. G. AND K. K. NESIUS. 1996. Phytoplankton composition in relation to primary production in Chesapeake Bay. *Marine Biology* 125:611–617.

MILLS, D. K., P. B. TETT, AND G. NOVARINO. 1994. The spring bloom in the southwestern North Sea in 1989. *Netherlands Journal of Sea Research* 33:65–80.

MURPHY, J. AND J. P. RILEY. 1962. A modified single solution method for the determination of phosphate in natural waters. *Analytica Chimica Acta* 27:31–36.

Natural Environment Research Council (NERC). 1992. North Sea Project CD-ROM. British Oceanographic Data Base, Proudman Oceanographic Laboratory, Bidston Observatory, L43 7RA, Birkenhead, U.K.

NIXON, S. W. AND M. E. Q. PILSON. 1984. Estuarine total system metabolism and organic exchange calculated from nutrient ratios: An example from Narragansett Bay, p. 261–290. *In* V. S. Kennedy (ed.), The Estuary as a Filter. Academic Press, San Diego, California.

OWENS, N. J. P., E. M. S. WOODWARD, J. AIKEN, I. E. BELLAN, AND A. P. REES. 1990. Primary production and nitrogen assimilation in the North Sea during July 1987. *Netherlands Journal of Sea Research* 25:143–154.

PEETERS, J. C. H., H. A. HAAS, L. PEPERZAK, AND I. VRIES DE. 1993. Nutrients and light as factors controlling phytoplankton biomass on the Dutch continental shelf (North Sea) in 1988–1990. Report DGW-93.004: Dutch Ministry Transport, Public Works and Water Management, The Hague, The Netherlands.

PEETERS, J. C. H., H. A. HAAS, L. PEPERZAK, AND L. P. M. J. WETSTEYN. 1991. Limiting factors for phytoplankton in the North Sea. *Water Science and Technology* 24:261–267.

PEETERS, J. C. H. AND L. PEPERZAK. 1990. Nutrient limitation in the North Sea: A bioassay approach. *Netherlands Journal of Sea Research* 26:61–73.

PENNOCK, J. R. AND J. H. SHARP. 1986. Phytoplankton production in the Delaware Estuary: Temporal and spatial variability. *Marine Ecology Progress Series* 34:143–155.

PETERSON, B. J. 1980. Aquatic primary production and the ^{14}C-CO_2 method: A history of the productivity problem. *Annual Review of Ecology and Systematics* 11:359–385.

PHILIPPART, C. J. M., G. C. CADEE, W. VAN RAAPHORST, AND R. RIEGMAN. 2000. Long-term phytoplankton-nutrient interactions in a shallow coastal sea: Algal community structure, nutrient budgets, and denitrification potential. *Limnology and Oceanography* 45:131–144.

PLATT, T., C. L. GALLEGOS, AND W. G. HARRISON. 1980. Photoinhibition of photosynthesis in natural assemblages of marine phytoplankton. *Journal of Marine Research* 38:687–701.

POSTMA, H. 1954. Hydrography of the Dutch Wadden Sea. *Archives Neerlandaises de Zoologie* 10:405–511.

POSTMA, H. AND J. W. ROMMETS. 1970. Primary production in the Wadden Sea. *Netherlands Journal of Sea Research* 4:470–493.

REDFIELD, A. C. 1934. On the proportions of organic derivatives in seawater and their relation to the composition of plankton, p. 176–192. *In* R. J. Daniel (ed.), James Johnstone Memorial. Liverpool University Press, Liverpool, U.K.

REDFIELD, A. C. 1958. The biological control of chemical factors in the environment. *American Scientist* 46:205–221.

REID, P. C., C. LANCELOT, W. W. C. GIESKES, E. HAGMEIER, AND G. WEICHART. 1990. Phytoplankton of the North Sea and its dynamics. *Netherlands Journal of Sea Research* 26:295–331.

RICHARDSON, K. 1991. Comparison of ^{14}C primary production determinations made by different laboratories. *Marine Ecology Progress Series* 72:189–201.

RICHARDSON, K. AND J. P. HEILMANN. 1995. Primary production in the Kattegat: Past and present. *Ophelia* 41:317–328.

RICHARDSON, K. AND F. B. PEDERSEN. 1998. Estimation of new production in the North Sea: Consequences for temporal and spatial variability of phytoplankton. *ICES Journal of Marine Sciences* 55:574–580.

RICHARDSON, K., G. SAMUELSSON, AND J. E. HALLGREN. 1984. The relationship between photosynthesis measured by ^{14}C incorporation and by uptake of inorganic carbon in unicellular algae. *Journal of Experimental Marine Biology and Ecology* 81:241–250.

RICHARDSON, K., A. W. VISSER, AND F. B. PEDERSEN. 2000. Subsurface phytoplankton blooms fuel pelagic production in the North Sea. *Journal of Plankton Research* 22:1663–1671.

RICK, J. J. 1990. Ein Beitrag zur Abschätzung der Wechselbeziehungen zwischen planktischen Primärproduzenten des Nordseegebietes und den Schwermetallen Kupfer, Zink, Cadmium und Blei auf Grundlage von Untersuchungen an natürlichen Planktongemeinschaften und Laborexperimenten mit bestandsbildenden Arten. Ph.D. Dissertation, Rheinisch-Westfälische Technische Hochschule, Aachen, Germany.

RICK, S. 1999. The spring bloom in the German Bight: Effects of high inorganic N:P ratios on the phytoplankton development. *Berichte aus dem Institut für Meereskunde* 305:1–142.

RIEGMAN, R., F. COLIJN, J. F. P. MALSCHAERT, H. T. KLOOSTERHUIS, AND G. C. CADEE. 1990. Assessment of growth rate limiting nutrients in the North Sea by the use of nutrient-uptake kinetics. *Netherlands Journal of Sea Research* 26:53–60.

RIELING, T. 1996. Bestand und Leistung des Phytoplanktons während einer typischen Sommersituation in der Deutschen Bucht. M.S. Thesis, University of Oldenburg, Oldenburg, Germany.

RILEY, G. A. 1947. Seasonal fluctuations of the phytoplankton population in New England waters. *Journal of Marine Research* 6:114–125.

SCHAUMANN, K., D. GERDES, AND K.-J. HESSE. 1988. Hydrographic and biological characteristics of a *Noctiluca scintillans* red tide in the German Bight. *Meeresforschung* 32:77–91.

SCHINDLER, D. W., R. V. SCHMIDT, AND R. A. REID. 1972. Acidification and bubbling as an alternative to filtration in

determining phytoplankton production by the ^{14}C method. *Bulletin of the Fisheries Research Board of Canada* 29:1627–1631.

SMETACEK, V., B. VON BODUNGEN, B. KNOPPERS, R. PEINERT, F. POLLEHNE, P. STEGMANN, AND B. ZEITZSCHEL. 1984. Seasonal stages characterizing the annual cycle of an inshore pelagic system. *Rapport et Proces-verbaux des Reunions Conseil Permanent International pour l'Exploration de la Mer* 183:126–135.

SOMMER, U. 1994. Are marine diatoms favored by high Si:N ratios? *Marine Ecology Progress Series* 115:309–315.

STEELE, J. H. 1956a. Plant production in the northern North Sea. Her Majesty's Stationary Office, Edinburgh, Scottish Home Department, *Marine Research* 7:3–36.

STEELE, J. H. 1956b. Plant production on the Fladen Ground. *Journal of the Marine Biological Association of the United Kingdom* 35:1–33.

STEEMANN NIELSEN, E. 1952. The use of radioactive carbon (^{14}C) for measuring organic production in the sea. *Journal Conseil International pour l'Exploration de la Mer* 18:117–140.

STRICKLAND, J. D. H. AND T. R. PARSONS. 1972. A practical handbook of seawater analysis. *Bulletin of the Fisheries Research Board of Canada* 167:1–310.

STRÜBING, K. 1996. The ice winter of 1995/96 on the German Coasts between Ems and Oder, with a survey of the entire Baltic Sea. *German Journal of Hydrography* 48:73–87.

SÜNDERMANN, J., K.-J. HESSE, AND S. BEDDIG. 1999. Coastal mass and energy fluxes in the southeastern North Sea. *German Journal of Hydrography* 51:113–132.

TAKAHASHI, M., K. FUJII, AND T. R. PARSONS. 1973. Simulation study of phytoplankton photosynthesis and growth in the Fraser River estuary. *Marine Biology* 19:102–116.

TILLMANN, U., K.-J. HESSE, AND F. COLIJN. 2000. Planktonic primary production in the German Wadden Sea. *Journal of Plankton Research* 22:1253–1276.

UNITED NATIONS EDUCATIONAL, SCIENTIFIC AND CULTURAL ORGANIZATION (UNESCO). 1994. Intergovernmental Oceanographic Commission, Scientific Committee on Oceanographic Research: Protocols for the joint global ocean flux study (JGOFS) core measurements. http://www/uib.no/jgofs/Publications/Report_Series/JGOFS_19.pdf.

VAN BEUSEKOM, J. AND S. DIEL-CHRISTIANSEN. 1993. A Synthesis of Phyto- and Zooplankton Dynamics in the North Sea Environment. World Wildlife Fund, Hamburg, Germany.

VAN HAREN, J. J. M. AND J. C. A. JOORDENS. 1990. Observations of physical and biological parameters at the transition between the southern and central North Sea. *Netherlands Journal of Sea Research* 25:351–364.

VAN SPAENDONK, J. C. M., J. C. KROMKAMP, AND P. R. M. DE VISSCHER. 1993. Primary production of phytoplankton in a turbid coastal plain estuary, the Westerschelde (the Netherlands). *Netherlands Journal of Sea Research* 31:267–279.

VELDHUIS, M. J. W., F. COLIJN, L. A. H. VENEKAMP, AND L. VILLERIUS. 1988. Phytoplankton primary production and biomass in the western Wadden Sea (The Netherlands): A comparison with an ecosystem model. *Netherlands Journal of Sea Research* 22:37–49.

VELDHUIS, M. J. W., L. A. H. VENEKAMP, AND T. IETSWAART. 1987. Availability of phosphorus sources for blooms *Phaeocystis pouchetii* (Haptophyceae) in the North Sea: Impact of the river Rhine. *Netherlands Journal of Sea Research* 21:219–229.

VERITY, P. G., T. J. SMAYDA, AND E. SAKSHAUG. 1991. Photosynthesis, excretion and growth rates of *Phaeocystis* colonies and solitary cells. *Polar Research* 10:117–128.

WAFAR, M. V. M., P. LECORRE, AND J. L. BIRRIEN. 1983. Nutrients and primary production in permanently well-mixed temperate coastal waters. *Estuarine Coastal Shelf Science* 17:431–446.

WEICHART, G. 1980. Chemical changes and primary production in the Fladen Ground area (North Sea) during the first phase of a spring phytoplankton bloom. *Meteor Forschungs Ergebnisse Reihe A* 22:79–86.

WEICHART, G. 1985. High pH values in the German Bight as an indicator of intensive primary production. *Deutsche Hydrographische Zeitung* 38:93–117.

WEIGEL, H.-P. AND E. HAGMEIER. 1976. Chlorophyll, phytoplankton carbon, and nutrients off Helgoland. *Annales of Biology Copenhagen* 33:72–73.

WETSTEYN, L. P. M. J. AND J. C. KROMKAMP. 1994. Turbidity, nutrients and phytoplankton primary production in the Oosterschelde (The Netherlands) before, during and after a large-scale coastal engineering project (1980–1990). *Hydrobiologia* 282/283:61–78.

WILLIAMS, P. J. LEB. 1993. Chemical and tracer methods of measuring plankton production, p. 20–36. *In* W. K. W. Li and S. Y. Maestrini (eds.), Measurements of Primary Production from the Molecular to the Global Scale. Volume 197. ICES Marine Science Symposia, International Council for Exploration of the Sea, Copenhagen, Denmark.

WILLIAMS, P. J. L. AND D. LEFÉVRE. 1996. Algal ^{14}C and total carbon metabolisms. 1. Models to account for the physiological processes of respiration and recycling. *Journal of Plankton Research* 18:1941–1959.

WILLIAMS, P. J. LEB., C. ROBINSON, M. SONDERGAARD, A. M. JESPERSEN, T. L. BENTLEY, D. LEFÉVRE, K. RICHARDSON, AND B. RIEMANN. 1996. Algal ^{14}C and total carbon metabolisms. 2. Experimental observations with the diatom *Skeletonema costatum*. *Journal of Plankton Research* 18:1961–1974.