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Biological Consequences of Tidal Stirring Gradients in the North Sea [and Discussion]

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Biological consequences of tidal stirring gradients in the North Sea

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[Plate 1]

Tidal stirring gradients, interacting with seasonal variation in photosynthetically active radiation, sea-surface heating, and wind stirring, are proposed as the most important controls on plankton in the southern North Sea. The hypothesis, in the form of a numerical model, is tested against observations during 1988/89 of seasonal cycles and spatial variation in phyto- and zoo-plankton. The importance of the tidal mixing front, and the effects of residual circulation and nutrient-rich river discharges, are discussed, and estimates given of microplankton community production and its fate.

1. Introduction

The planktonic ecosystem in the North Sea is fuelled largely by local primary production, defined here as producer biomass multiplied by relative growth rate. Controls on biomass include nutrient availability, grazing pressure, and previous growth. Because plankton dynamics in the southern North Sea are dominated by transients (such as the spring bloom), we hypothesize that growth rate is the most important regulator of production, and that it is more constrained by light than by nutrients.

Light availability depends on (1) the mean photon flux density I_0 (μE m^{-2} s^{-1}) at the sea-surface of photosynthetically available radiation (PAR); (2) the thickness h_1 (m) of the layer through which algae are transported by vertical turbulence during an appropriate averaging period, here taken as 24 h; and (3) the turbidity of this layer, measured an appropriate diffuse attenuation coefficient λ (m^{-1}). The gist of our

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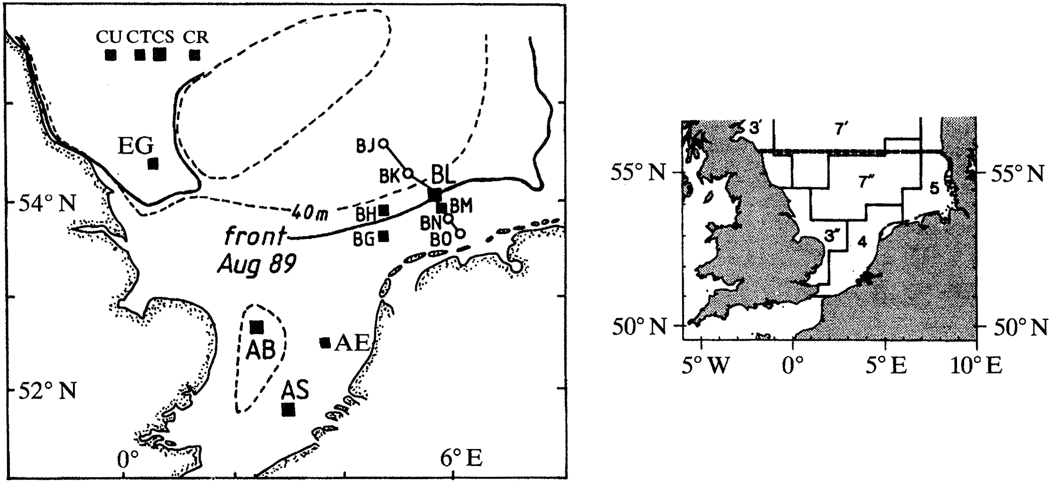

Figure 1. The southern North Sea. (*a*) Sites mentioned in the text, and the approximate position of the tidal mixing front as observed in early August 1989. (*b*) Subdivisions according to ICES (1983).

hypothesis is the sensitivity of primary production, and hence the food available to higher trophic levels, to regional and seasonal variations in λh_1, the 'mixed layer optical thickness'. In the southern North Sea, the main control on λh_1 is tidal flow. Tidal bottom stress resuspends sediments; injection of turbulent kinetic energy determines water column layering. Regional variation in tidal stirring determines the response in terms of stratification and turbidity to seasonally varying inputs of heating and wind stirring, and hence the seasonal cycles of plankton.

In contrast, 'eutrophication' hypotheses emphasize the stimulation of primary production by the plant nutrients in river discharges. Our hypothesis allows this to happen only where λh_1 is relatively small. Pingree *et al.* (1978) predict a maximum of phytoplankton production, as a result of an optimum combination of light and nutrient supply, at tidal mixing fronts in Summer. Such a front divides our study region into two (figure 1), and observations in the vicinity of this front provide critical tests of the 'eutrophication' and 'tidal stirring' hypotheses.

Many publications deal with the ecology of North Sea plankton. We have drawn especially from recent reviews by Adams (1987), Reid *et al.* (1990), Fransz *et al.* (1991) and Tett & Mills (1991). Survey methods are described by Howarth *et al.* (this symposium).

2. The physical controls

Implications of the 'tidal-stirring' hypothesis were explored by using a numerical model. The model (Tett 1990*a*; Huthnance *et al.*, this symposium) ignores horizontal transports and describes the water column in terms of surface and bottom boundary layers, separated, under stratified conditions, by an infinitely thin thermocline. Water, heat, dissolved nutrients, plankton and suspended particulate material (SPM) are transferred between layers by entrainment, and by sinking of particulates. Under stratified conditions, the surface layer is mixed by wind stirring and surface cooling. It is warmed, and its buoyancy increased, by sunshine. In the case of 'weather'-driven simulations, these exchanges were computed from daily means of solar irradiance, wind speed, and air dewpoint temperature, taken from Meteorological

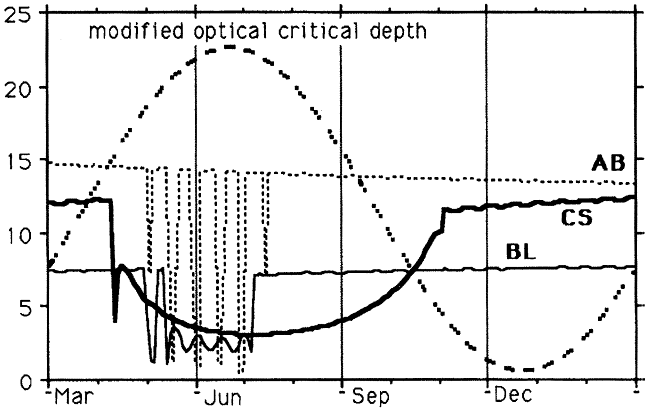

Figure 2. 'Climate' – forced simulations of the optical thickness of the surface mixed layer, including effects due to SPM, at three typical stations. Substantial production is possible only when λh_1 exceeds the modified optical critical depth $m_2 I_0 / I_c^*$.

Table 1. *Comparison of typical sites*

(All data are 1988/89 observations, from BODC, unless otherwise stated.)

site...	CS	BL	AB	BO
	moor. A	incl. BM	moor. E	
position...	55° 30′ N	54° 03′ N	52° 42′ N	53° 40′ N
	0° 55′ E	5° 40′ E	2° 25′ E	6° 10′ E
description...	stratified	frontal	mixed	mixed
stirring data				
h, sea-bed depth/m	80	35	45	27
$u = m_2$ tidal amplitude[1]/(m s^{-1})	0.28	0.40	0.85	0.45
tidal stirring $= u^3/h$/(dm^2 s^{-3})	0.3	1.8	13.6	3.4
spring-neap amplitude,[2] s_2/m_2	0.3	0.2	0.3	0.2
(min. tide)/(max. wind) stirring[3]	0.03	0.11	0.73	0.16
(max. tide)/(min. wind) stirring[3]	1.0	2.4	29.2	3.4
chemical, SPM and optical data				
winter (January/February)				
near-surface nitrate/(mmol m^{-3})	5	10	12	31
near-surface total SPM[4]/(g m^{-3})	0.3	3.1	5.7	2.8
λ, min. diffuse PAR att.[5]/m	0.08	0.32	0.59	0.38
λh, optical depth, SML[6]	6	11	27	10
summer (July/August)				
near-surface nitrate/(mmol m^{-3})	0.2	0.7	0.4	2.5
near-surface total SPM/(g m^{-3})	0.5	1.7	2.9	0.28
λ, min. diffuse PAR att.[5]/m	0.11	0.24	0.36	0.29
h_1, depth of SML[6]/m	27	12	~ 45	~ 27
λh_1, optical depth, SML	3	3	< 16	< 8

[1] Tidal amplitude from literature.

[2] Spring/neap tide ratios (s_2/m_2) from literature.

[3] Ratios of kinetic energy (J/m_2) from each source, calculated as (m_2 amplitude $\pm s_2$ amplitude) divided by (wind mean $\pm$ wind amplitude); wind parameters (mean = 7.1, amplitude = 2.1, m s^{-1}) from 365 day sine wave fitted to Meteorological Office 1989 data.

[4] SPM is all particulates retained on GF filter.

[5] Min. diffuse attenuation from various sources, including PAR profiles, converted red beam attenuation, and optical model.

[6] Depth of surface mixed layer (SML) from summer temperature profiles; ~ indicates some weak stratification; full mixing assumed in winter.

Office data for 1989. 'Climate'-driven simulations were forced by sine waves, of period one year, fitted to these data. The bottom layer is mixed by tidal stirring, computed from m_2 and s_2 tidal amplitudes. When turbulent inputs exceeded accumulated buoyancy the two layers merge.

The model was used, under 'climate' drive, to predict the mixed layer optical thicknesses shown in figure 2 for three sites (figure 1) differing (table 1) in depth, tidal stirring, and supply of fine inorganic sediment, and each characteristic of a different part of the study region. Calculation of h_1 used algorithms by Clarke (1986), which embody the energy-conserving mixed-layer model of Kraus & Turner (1967) as adapted by Simpson & Bowers (1984) to include tidal stirring. λ_1 included the effects of particulate material resuspended when the bottom stress, due to tidal and wind-wave motions, exceeded a critical stress. The 'modified optical critical depth' in figure 2 is $m_2 I_0/(I_c^*)$, where $m_2 = 0.37$ allows for hyper-exponential decay of irradiance near the sea surface (Tett 1990*b*). I_c^* is a modified compensation irradiance, being the 24 h mean PAR allowing the producers to grow at a rate exceeding typical losses by grazing and sinking during the spring bloom. The value of 7.2 μE m^{-2} s^{-1} was taken from the biological model.

At each site, the daily inputs of turbulent kinetic energy from wind and tidal stirring, and convective mixing, opposed by buoyancy inputs due to solar heating, change throughout the year. The balance amongst these factors controls thermal layering. The weakly stirred northern site CS shows well-developed seasonal stratification, the frontal site BL displays a few months of weak stratification, and the strongly stirred southern site AB remains mixed except during some neap tides. Survey cruise observations support these predictions.

Significant plant production can occur only when the modified critical depth exceeds the mixed layer thickness. Thus, at CS, the productive season should roughly coincide with stratification. At BL it should last longer. The season should be short at AB. These distinctions result not only from the direct impact of depth and tidal stirring on summer stratification, but also from the indirect effect mediated by SPM. Thus, AB is optically deeper than CS, because of greater SPM as well as stronger mixing in summer.

3. Calibrating the biological model

The main features of the biological model are (*a*) the marriage of phytoplankton and associated microheterotrophs in a *microplankton* compartment, with growth described by cell-quota, threshold-limitation kinetics (Droop, 1983) with nitrogen as the limiting nutrient, and (*b*) a detrital compartment for longer-lived particulate organic material subject to microbial (oxic) remineralization in the water-column and sediment. *Microplankton production* was estimated by summing μB to a specified depth, where μ is relative microplankton growth rate (d^{-1}), and B is microplankton biomass (μM C). Under light-limiting conditions,

$$\mu = (k\chi\alpha I_h - r)\,\mathrm{d}^{-1}, \tag{1}$$

where k is 86400 s d^{-1}. I_h is 24 h mean PAR over the layers included in the integration. It is given, for a deep surface mixed layer, by $m_2 I_0/(\lambda_1 h_1)$. The other parameters refer to the microplankton: χ is the ratio of chlorophyll to carbon (mg mmol^{-1}), a function of cellular nutrient content; α is (maximum) photosynthetic 'efficiency' (nmol C (mg chl)$^{-1}$ (μE m^{-2})$^{-1}$); r is respiration rate (d^{-1}), a function of growth rate.

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Table 2. *Process studies during Challenger cruise 50*

	mean	(s.d.)
fixed station near EG, weak stratification, 14–16 April 1989		($n = 3$)
photosynthetic efficiency/(nmol C (mg chl)$^{-1}$ (μE m^{-2})$^{-1}$)	0.8	(model)
daily mean sub-surface PAR/(μE m^{-2} s^{-1})	212	(194)
mixed-layer thickness/m	22	(16)
(minimum) diffuse attenuation/m^{-1}	0.12	(0.03)
mixed-layer mean chlorophyll/(mg chl m^{-3})	1.7	(0.2)
mixed-layer ^{14}C production/(mg C m^{-2} d^{-1})	344	(277)
model mixed-layer microplankton prod. (mg C m^{-2} d^{-1})	668	(856)
tracked *Phaeocystis* bloom, mixed water near AE, 21–24 April 1989		($n = 3$)
photosynthetic efficiency/(nmol C (mg chl)$^{-1}$ (μE m^{-2})$^{-1}$)	1.3	(0.3)
daily mean sub-surface PAR/(μE m^{-2} s^{-1})	235	(86)
water-column depth/m	32	(3.2)
(minimum) diffuse attenuation/m^{-1}	0.31	(0.01)
column mean chlorophyll/(mg chl m^{-3})	6.9	(1.4)
col. microplankton production by O_2/(mg C m^{-2} d^{-1})	1573	(323)
column ^{14}C production/(mg C m^{-2} d^{-1})	1578	(407)
model column microplankton prod./(mg C m^{-2} d^{-1})	1459	(314)
col. microplankton respir. by O_2/(mg C m^{-2} d^{-1})	760	(302)
model column microplankton respir./(mg C m^{-2} d^{-1})	758	(154)

Biological parameters were initially estimated from the literature (Tett & Droop 1988; Tett 1990*a*, *b*). Site-specific seasonally varying, grazing pressures were derived from observed copepod abundances (figure 5). Parameters for photosynthesis and respiration were improved by comparing model predictions with observations during Challenger cruise 50 in April 1989 (table 2; Daneri 1992; Iriarte *et al.* 1991), under conditions presumed to have been light-limiting. Photosynthetic ‘efficiency’ was deduced from rates of oxygen evolution by water samples in a light-gradient incubator. Water column production was estimated from simulated *in situ* light & dark bottle oxygen incubations, and *in situ* ^{14}C measurements (Joint & Pomroy 1983). Model photosynthetic ‘efficiency’ was set to that measured, and respiration parameters adjusted to fit model predictions to *in situ* observations. Thus we had three semi-independent estimates of ‘net microplankton community production’ (Williams *et al.* 1979), the rate of photosynthetic production of organic material, less respiration by phytoplankton and microheterotrophs, between the surface and a defined depth. It is the production available to mesozooplankton and the benthos.

Two sites were studied. Production rate was computed to the observed depth of 1% surface irradiance. In the case of the vertically mixed water mass tracked by a drogue near AE, and dominated by *Phaeocystis*, there was good agreement amongst the three estimates of production, given only the assumption of 1.5 mol O_2 (mol C)$^{-1}$ for the photosynthetic quotient (Q_p). Agreement between model and observations was less good at the weakly stratified fixed station EG, where diatoms are likely to have dominated, perhaps because of the difficulty of evaluating mixed layer depth under these early spring conditions.

Best-fit respiratory parameters did not differ significantly between sites. Although photosynthetic ‘efficiency’ could be lower (better to fit the observations at EG) than the 0.8 nmol C (mg chl)$^{-1}$ (μE m^{-2})$^{-1}$ estimated for EG, or higher (given Q_p less than 1.5) than 1.3 nmol C (mg chl)$^{-1}$ (μE m^{-2})$^{-1}$ near AE, there seems little doubt that ‘efficiency’ was higher in the mixed than in the stratified water. This might imply

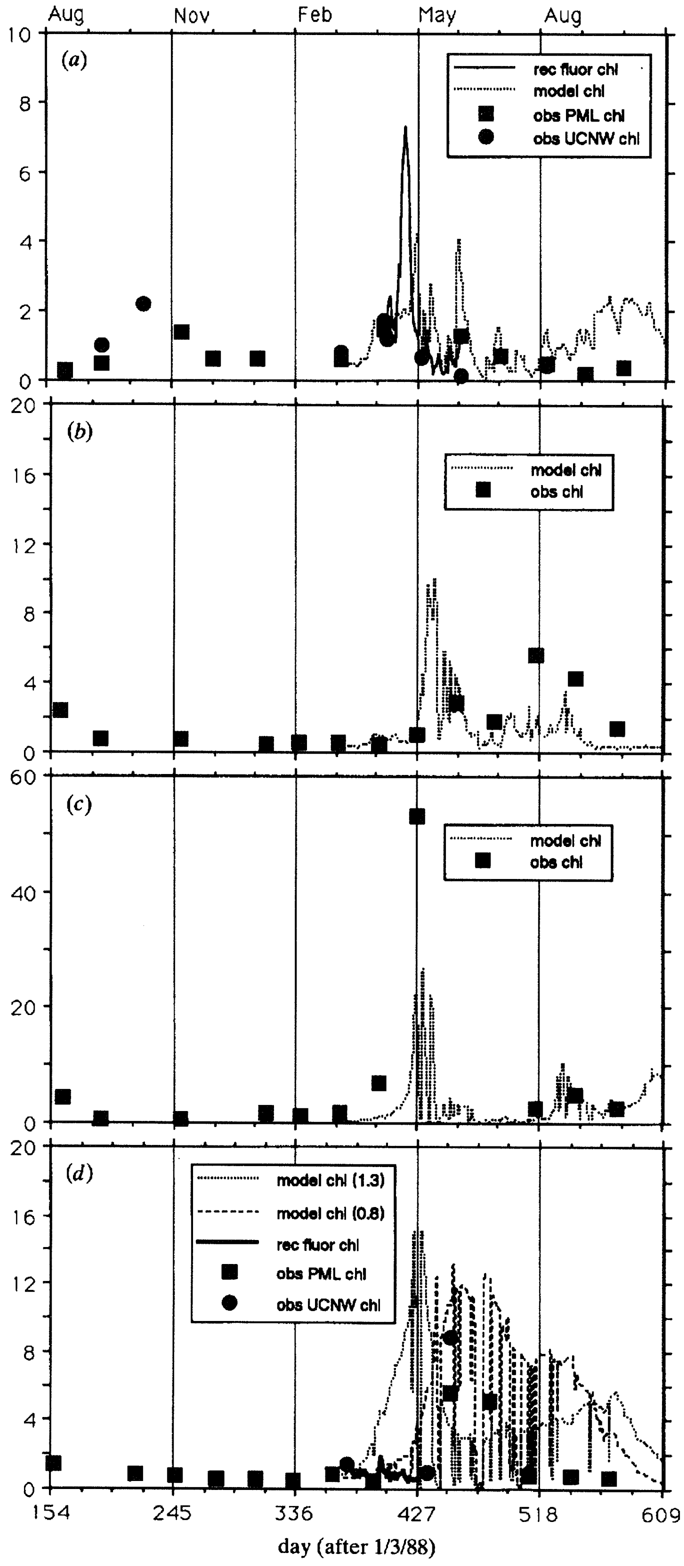

Figure 3. For description see opposite.

adaptation by the algae, and especially *Phaeocystis*, to the more turbid conditions encountered in these well-stirred waters. Finally, microscopic analysis showed colonial *Phaeocystis* increasing more quickly than other algae at EG, in accord with the idea that the colonies resist grazing.

4. Seasonal cycles of phytoplankton

Figure 3 shows seasonal cycles of surface-layer chlorophyll concentration at typical sites. Large symbols show pigment measured spectrophotometrically at the Plymouth Marine Laboratory (PML) or fluorometrically at Bangor (UCNW) after filtration of phytoplankton from CTD-bottle-sampled water. The intervals of about a month between ship visits were long in relation to characteristic timescales of about a week shown by the continuous record of *in situ* chlorophyll fluorescence made during Spring at site CS. The record was made by a prototype battery-powered fluorometer logging to a solid-state memory, and moored at 18 m below the surface (Mills & Tett 1990). A second instrument was deployed at AB.

Such continuous records were, however, not available for other times of the year or other sites. Instead, model predictions, forced by 1989 'weather', supplement observations. There were some obvious differences between predictions and observations. Simulations for CS included, in the surface layer in summer, chlorophyll that was in fact mostly in the thermocline (figure 7). The higher value of photosynthetic 'efficiency' estimated from Challenger 50 data predicted an early bloom at AB. Predictions with lower efficiency better matched the spring bloom observations, including those made with the recording fluorometer, but substantially overestimated summer chlorophyll. Nevertheless, interpreted cautiously, the combination of ship sampling, moored instruments, and model predictions, allows the main features of the seasonal cycle to be compared between sites.

The contrast between the seasonally stratified CS and the almost-always mixed AB is clear. The spring bloom at CS coincided with the development of stratification, which substantially reduced the optical thickness of the mixed layer from an initial value of 8. Chlorophyll concentrations continued low for another month at AB where the optical thickness exceeded 13, although increasing in late April at the Challenger 50 site AE where the optical thickness was about 10. Surface water at CS showed the classical 'twin-peaked' seasonal cycle with spring and autumn blooms, whereas AB showed only one peak.

At the frontal site BL, the model predicted that chlorophyll concentrations would peak in May with the onset of seasonal stratification, when mixed layer optical thickness fell to less than 4. The two peaks of the seasonal cycle were less clearly separated than at CS.

Figure 3 includes site BO, in shallow, nutrient-rich continental coastal water. Here simulation with the higher value of photosynthetic 'efficiency' provided a good fit to

Figure 3. Seasonal cycles of surface-layer chlorophyll (mg m^{-3}) at (*a*) CS, (*b*) BL, (*c*) BO and (*d*) AB. Large symbols are from samples taken during regular survey cruises. Data for CS and AB include chlorophyll estimated by moored fluorometry, and additional chlorophyll samples measured at UCNW, corrected to PML standard used in survey. The broken lines, commencing 1/3/89, are simulations driven by 'weather' and properly phased tides, commencing 1/3/88 and with microplankton biomass, alone, re-initialized on 1/3/89. Standard photosynthetic efficiency was 0.8 nmol C (mg chl)$^{-1}$ (μE m^{-2})$^{-1}$ for CS and BL, and 1.3 nmol C (mg chl)$^{-1}$ (μE m^{-2})$^{-1}$ for AB and BO. AB results include those of a simulation with a lower photosynthetic efficiency.

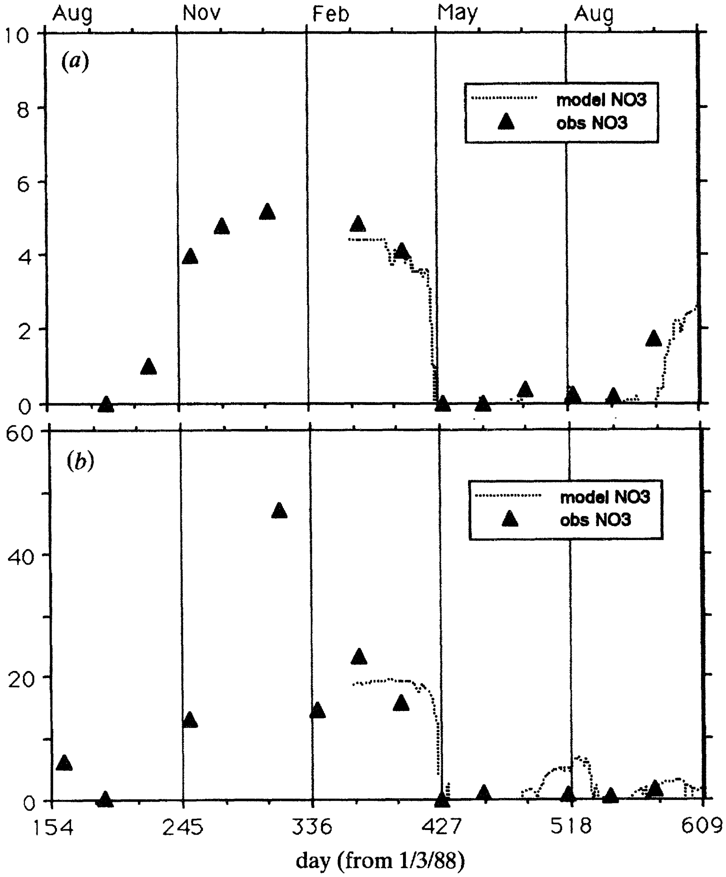

Figure 4. Seasonal changes in surface-layer nitrate (μM) at (*a*) CS and (*b*) BO. Large symbols are from samples taken during regular survey cruises. Broken lines are results of simulations, as described for figure 3.

observations. The large amplitude of the spring bloom is explained as the result of the conversion of high late-winter nutrient concentrations into *biomass*. However, the period when nutrient supply might have been controlling *growth rate* can be equated with the time when dissolved inorganic nitrogen (DIN) concentration was less than the half-saturation constant for uptake, taken as 0.5 μM (Tett & Droop 1988). The concentrations were regularly measured at most survey sites by auto-analysis of water-bottle samples. The most interesting comparison was between BO and CS (figure 4), amongst, respectively, the most and least nutrient-rich sites. Over all observations between May 1 and September 15, mean surface layer nitrate concentration was 0.14 μM at CS and 2.5 μM at BO. Only two out of six observations at BO were less than 0.5 μM, whereas no CS observation exceeded this value.

5. Mesozooplankton seasonal cycles

Mesozooplankton samples were taken by hauling a 200 μm mesh net vertically through the water column. Biovolume between 0.2 and 2 mm diameter, mostly contributed by copepods, was determined by electronic particle counting of preserved samples. Results, averaged over ICES regions, are shown by month in figure 5, and

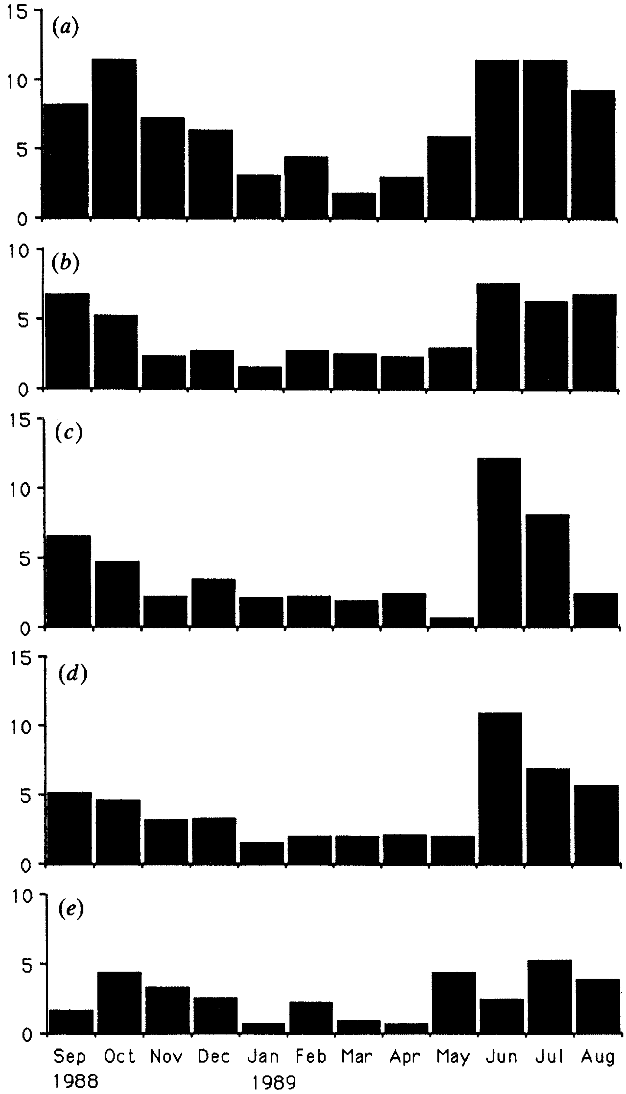

Figure 5. Seasonal changes in the biovolume (in $\mathrm{cm^3\ m^{-2}}$) of mesozooplankton (0.2–2 mm diameter) in ICES regions. Typical standard error is $1.1\ \mathrm{cm^3\ m^{-2}}$. Regions: (*a*) $3'+7'$, (*b*) $7''$, (*c*) 5, (*d*) 4, (*e*) $3''$.

table 3 includes annual means. Greatest biovolumes occurred in the western seasonally stratified waters of ICES regions $3'+7'$, and least in the south-western mixed waters of region $3''$. Peak biovolume occurred in June in most regions, with a second peak in October in $3'+7'$. It seems that mesozooplankton followed phytoplankton with a lag of 1–2 months.

6. Regional variability in flora and fauna

Compared with the electronic measurement of temperature or chlorophyll fluorescence, the taxonomic analysis of preserved plankton samples was labour-consuming. Phytoplankton data, based on sedimented, Lugol-preserved material, are restricted to samples from the surface mixed layer, and we have most information

Table 3. *Production and mesozooplankton biovolume estimates for southern North Sea during 1988/89*

Adams (1987) region (or other descriptor)	ICES region	Joint & Pomroy ^{14}C prod. to 1 % I_0	Klein & van Buuren ^{14}C prod.	model site
		gC m^{-2} a^{-1}	gC m^{-2} a^{-1}	
N. British coastal	3′	75	—	—
(summer stratified)	3′+7′	—	—	—
offshore central	7′	100	82	CS
offshore southern	7″	119	120	BI, BK, BJ
(frontal)	4/7″	—	—	BL, BM
continental coastal	5	261	—	BO, BN
continental coastal	4	199	254	—
S. British coastal	3″	79	—	AB

Adams (1987) region (or other descriptor)	model microplankton production (over column)			mesozooplankton biovolume
	g C m^{-2} a^{-1}	% to zoo.	% to sed.	cm^{3} m^{-3}
N. British coastal	—	—	—	—
(summer stratified)	—	—	—	6.9
offshore central	60	70	12	—
offshore southern	79	63	24	4.1
(frontal)	82	72	15	—
continental coastal	202	48	35	4.0
continental coastal	—	—	—	4.1
S. British coastal	149	45	13	2.7

for continental coastal waters. Mesozooplankton abundances are water-column totals.

Figure 6 analyses abundances of selected plankters by ICES regions. Numbers of diatoms, the characteristic phytoplankton of the North Sea, are shown for spring and autumn maxima. The data for copepods are means of surveys in August 1988 and August 1989. *Temora longicornis* is used as an exemplar of the group of small copepods that typify the southern North Sea. Other members include *Acartia clausii*, *Pseudocalanus elongatus* and *Centropages* spp. *Calanus* spp. are *finmarchicus* and *helgolandicus*.

Calanus were most abundant in the western, summer-stratified, waters included in ICES regions 3′+7′. At CS, the abundance of adult *Calanus* peaked in July, whereas the small copepods did not reach a maximum until the Autumn. The lesser abundance of *Calanus* in the eastern waters of region 7″ suggests, as did the time-series for CS, that the anti-clockwise residual circulation may be importing *Calanus* from deeper waters in the northern North Sea where continuous plankton recorder (CPR) data (Colebrook 1982) show it to be abundant relative to small copepods. The proportion of small copepods increased in clockwise progression around the southern North Sea, through regions 3′+7′, 7″, 5 and 4 of increasing tidal stirring, with the greatest absolute abundances in the continental coastal waters of region 4. *Temora* itself was most abundant in frontal waters (region 4/7″). Figure 6 shows *Calanus* more abundant in region 3″ than in continental coastal waters. At AB and adjacent

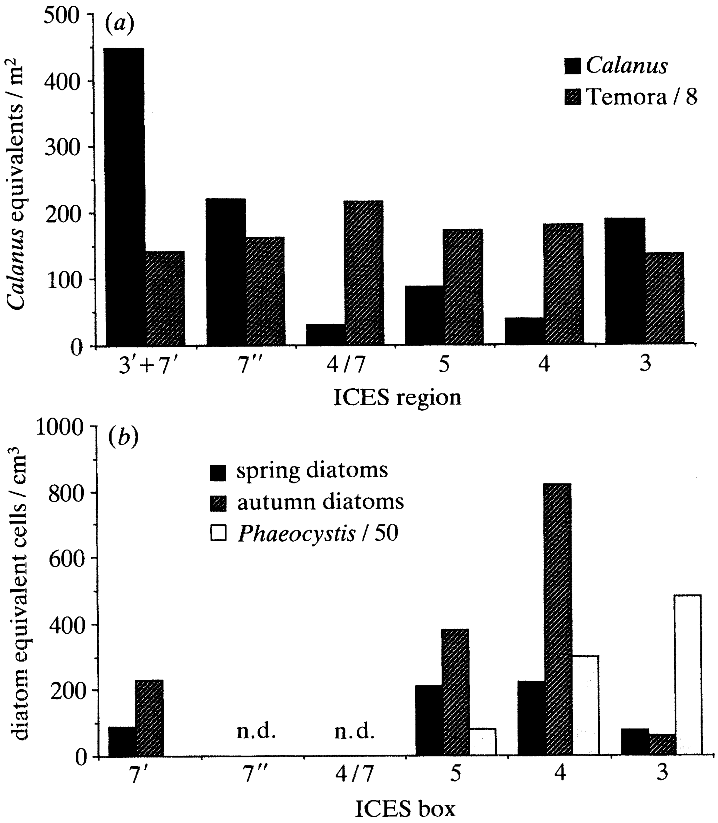

Figure 6. Regional differences in abundance of important plankters, scaled to allow approximate comparison of biomasses. ‘ICES region 4/7′ refers to the tidal mixing front north of the Friesian islands. (*a*) Copepods in August; (*b*) phytoplankton during maximum abundance.

well-stirred sites, however, *Calanus* was scarce; the impression of abundance arises because region 3″ includes sites of greater abundance of *Calanus* on the Flamborough Head front.

Phytoplankton were most abundant in region 4. Diatoms were widespread, but the colonial alga *Phaeocystis* was common only south of the tidal mixing front. Its relative abundance was greatest in East Anglian coastal waters at AB (the main site of analysed samples from ICES region 3″), in contrast with CPR data showing (Gieskes & Kraay 1977) maximum abundance in continental coastal waters.

Autotrophic dinoflagellates, notably *Ceratium* spp., were abundant in waters showing thermal (ICES regions 3′ and 7′) and thermohaline (ICES region 5) during summer and early autumn. It is likely that they contributed a substantial amount of the midwater chlorophyll maxima sometimes observed in these regions (figure 7). Small, possibly heterotrophic, gymnodinioid dinoflagellates were common during much of the phytoplankton growth season at a variety of sites. They could have been grazing on smaller diatoms. Naked oligotroph ciliates were typical of continental coastal waters in summer, with numbers increasing from ICES region 3″ through 4 to 5. The observation of decreasing numbers of *Phaeocystis* along this gradient agrees with the hypothesis that ciliates are important grazers of unicellular *Phaeocystis* (Admiraal & Venekamp 1986). Novarino (1991) describes cyptomonads taken by the Survey, and Mills *et al.* (1993) detail spring bloom microplankton at CS and AB.

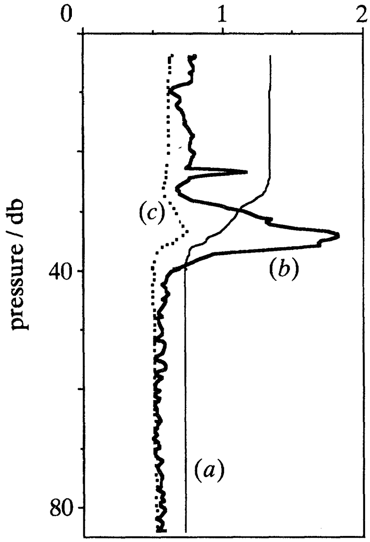

Figure 7. Profiles of (*a*) temperature (°C × 10), (*b*) chlorophyll (from fluorescence) (mg m^{-3}) and (*c*) beam attenuance (m^{-1}) at CS, 1 July 1989, showing thermocline maxima in the optical properties. Bottom-layer chlorophyll concentration was overestimated by the fluorometer, and was shown by water-bottle samples to be 0.2 mg m^{-3}.

7. Biological consequences of the tidal mixing front

The 1988/89 Survey included a line from BO to BJ (figure 1), crossing the tidal mixing front to the north of the Friesian islands. The physical sections showed a complex thermohaline structure, and the corresponding biological distributions were difficult to interpret (Mills & Tett 1991). Instead, figure 8 presents average values for Summer months at sites along this frontal transect.

Tidal stirring, predicted by u^3/d, increases onshore. The consequences for stratification were confirmed by observed temperature differences between surface and bottom waters. Mixed layer optical thickness increased towards the shore, as a result of increasing layer depth and slightly greater turbidity. Although there were more nutrients inshore, in summer as well as in winter, column chlorophyll peaked (significantly) at frontal station BM. Zooplankton numbers (and biovolumes) also suggested frontal enhancement, but differences were not significant. Summer DIN concentrations at BN and BO exceeded 1 μM, suggesting that nitrogen uptake was not limiting phytoplankton here.

8. Primary production and its fate

Table 3 includes three sets of estimates, by subregion, of annual microplankton production for 1988/89. Estimates from the North Sea survey (Joint & Pomroy 1993) were obtained in two stages. First, results from simulated *in situ* ^{14}C incubations were used to relate carbon-fixation to chlorophyll, integrated to the depth of 1% of surface light. Second, chlorophyll data were used to compute production in each month in each ICES region. Dutch ^{14}C data are those tabulated by Klein & van Buuren (1992) for sites on two lines normal to the coast of the Netherlands. Model predictions for characteristic sites summed μBh to the sea-bed and over a year. Because of extra respiratory losses below the depth of 1% of surface

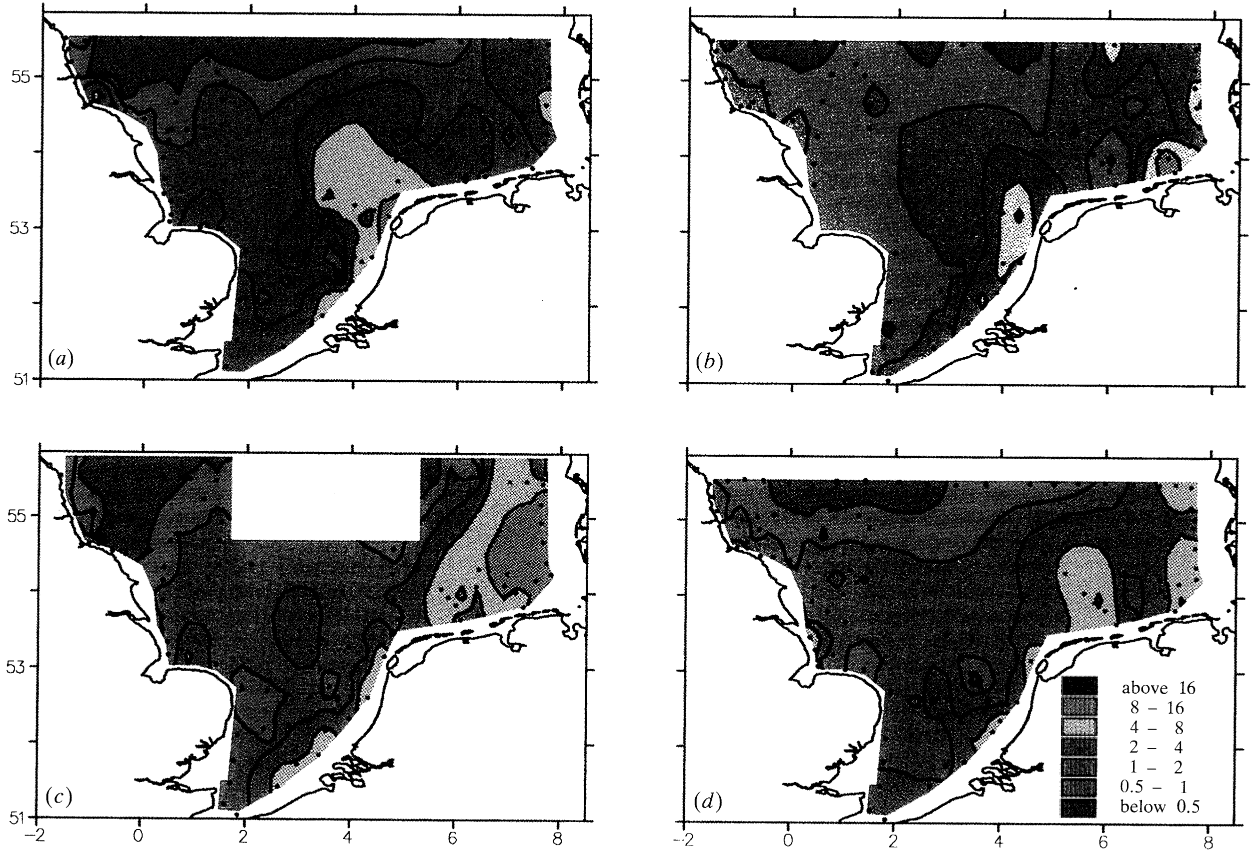

Figure 9. Surface-layer chlorophyll concentrations (mg m^{-3}) during Summer 1988 ((*a*) 4–18 August and (*b*) 3–14 September) and 1989 ((*c*) 24 July to 5 August and (*d*) 23 August to 3 September).

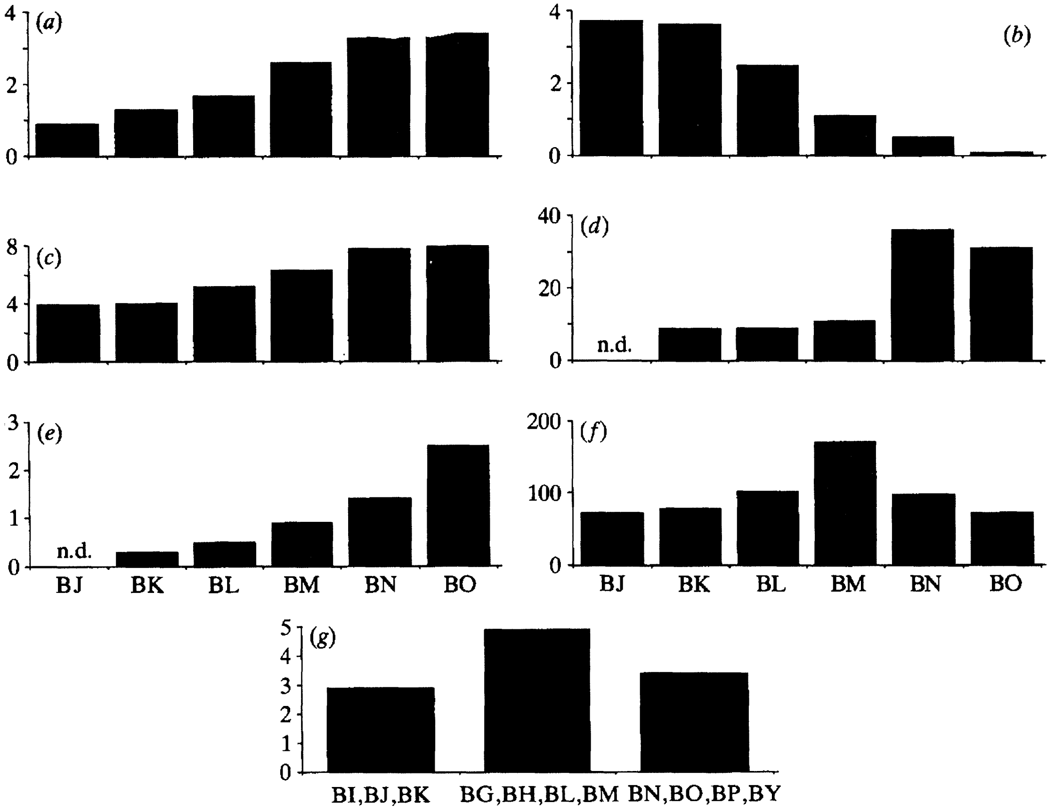

Figure 8. Mean properties on a section through the tidal mixing front north of the Friesian islands. The zooplankton numbers are totals of all adult copepods. (*a*) $u^3/d \times 10^3$ ($\mathrm{m^3\,s^{-2}}$), (*b*) summer surface–bottom temperature difference (°C), (*c*) optical thickness of surface mixed layer in summer, (*d*) winter DIN (μM), (*e*) summer DIN (μM), (*f*) summer column chlorophyll ($\mathrm{mg\,m^{-3}}$), (*g*) adult copepods in summer ($10^4\,\mathrm{m^{-2}}$).

light, model values should be less than production deduced from ^{14}C data. Excepting results from AB, the predictions can be considered as satisfactory, and can thus be used to discuss the fate of production.

Continental coastal waters had the greatest annual production, and the greatest proportion of production reaching the sea-bed. At the deep site CS most simulated production was mineralized before reaching the sea-bed. At AB, strong tidal stirring prevented deposition, so that, here too, most mineralization occurred in the water column. Predicted transfers to mesozooplankton were most effective in seasonally stratified waters, as also concluded by Fransz & Gieskes (1984).

9. Discussion

The repeated cruises of the 1988/89 survey provided a series of maps of the concentration of chlorophyll in the surface layer. Examples are shown for spring in Howarth *et al.* (1993), and in figure 9, plate 1, for summer. At first sight these maps support the eutrophication hypothesis by showing the greatest amounts of phytoplankton in waters near the continental coast. However, the high concentrations of chlorophyll did not occur continuously at any site, and the frontal transect suggests that mean summer chlorophyll was highest at sites of intermediate mixing and not at sites of greatest nutrient availability. The data for BO suggest that, although the nutrient enrichment of these inshore waters allow a large spring bloom, this takes place only under favourable illumination conditions in May and June. Growth of the bloom may be aided by the high photosynthetic 'efficiency', and perhaps also the resistance to grazing, of colonies of *Phaeocystis*. In these respects this alga might be especially adapted to life in mixed, turbid, waters.

Overall, the results presented in this paper support the predictions of the tidal stirring hypothesis with regard to phytoplankton *growth*, while showing that nutrient availability helps to control peak *biomass*. Since production is determined by both effects, it is unsurprising that continental coastal waters have higher production than waters north of the front. Nevertheless, observations at AB demonstrate the overriding importance of light limitation. Although winter nitrate concentrations were about twice those in region 7′ (characteristic site CS), annual production was less. Difficulties in simulating the seasonal cycle at AB emphasize the importance of understanding the control of photosynthetic 'efficiency' and algal and micro-heterotroph respiration, in these turbid, strongly stirred, waters.

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Discussion

M. J. HOWARTH (*Proudman Oceanographic Laboratory, U.K.*). Can Dr Tett explain the observed fourfold difference in primary productivity between the waters of the German Bight (more productive) and those off the English coast, described in Dr Howarth's paper?

P. TETT. The higher production is associated with higher chlorophyll and nutrient concentrations in the German Bight. The region has tidal stirring intermediate between the mixed waters of the Southern Bight and the seasonally stratified waters near the Northumbrian coast. Stratification is aided by freshwater, and the concentration of inorganic particulates is lower than in the Southern Bight. Thus optical conditions are more favourable than in East Anglian waters. Some phytoplankton in the German Bight, especially *Phaeocystis* and dinoflagellates, may resist grazing, and mesozooplankton biovolumes (and deduced grazing pressures) are on average lower than in Northumbrian waters. So I suggest that the German Bight is the most favourable of the southern North Sea regions for phytoplankton growth for a variety of reasons, of which anthropogenic nutrient enrichment is only one.

R. Lankester (*North Sea Work Group, East Anglia, U.K.*). The conclusion that phytoplankton blooms in the Wadden Sea are light dependent rather than nutrient dependent is clearly contrary to the previously held scientific view. What is equally interesting is the fact that phytoplankton blooms off the East Anglian coast of the U.K. are a quarter of that in the Wadden Sea.

However, I believe that sea bed sand and gravel extraction may be a significant contribution to these events. Disturbance to the sea bed as a result of this activity is considerable and no doubt assists in the resuspension of nutrients in the water column where they become available to phytoplankton. One wonders whether the eastward current takes this nutrient across to the Wadden Sea area, increasing the available nutrients to the point where light is indeed the controlling factor. Therefore, if the available nutrient was less, a different balance with light would be struck and consequently nutrient becomes the governing factor.

Furthermore, sand and gravel extraction must also increase substantially the turbidity of the sea off East Anglia with the result that light penetration is reduced with a consequential diminishing of the phytoplankton bloom, allowing a greater reservoir of nutrient to remain in the water column for dispersal to other parts of the North Sea.

Has this anthropogenic influence has been considered? Dr Radach, in his paper, indicated that phytoplankton blooms could be extended throughout the summer if storms, or perhaps other disturbing factors, cause appropriate distribution of nutrients.

P. Tett. The North Sea survey did not sample the Wadden Sea itself. Our closest station was BO, about 20 km north of the Friesian islands. My conclusions for this station were that (*a*) low light levels, due to vertical mixing and SPM attenuation, restricted summer phytoplankton growth in comparison with that at the frontal site BM, but (*b*) the magnitude of the spring bloom was the result of nutrient enrichment. The evidence I have seen suggests that rivers are the main source of this enrichment. Numerical simulations show that whereas storms in stratified waters in summer augment production by entrainment of deep water nutrients into the surface layer, they reduce production in mixed waters, such as those at BO, by increasing SPM.

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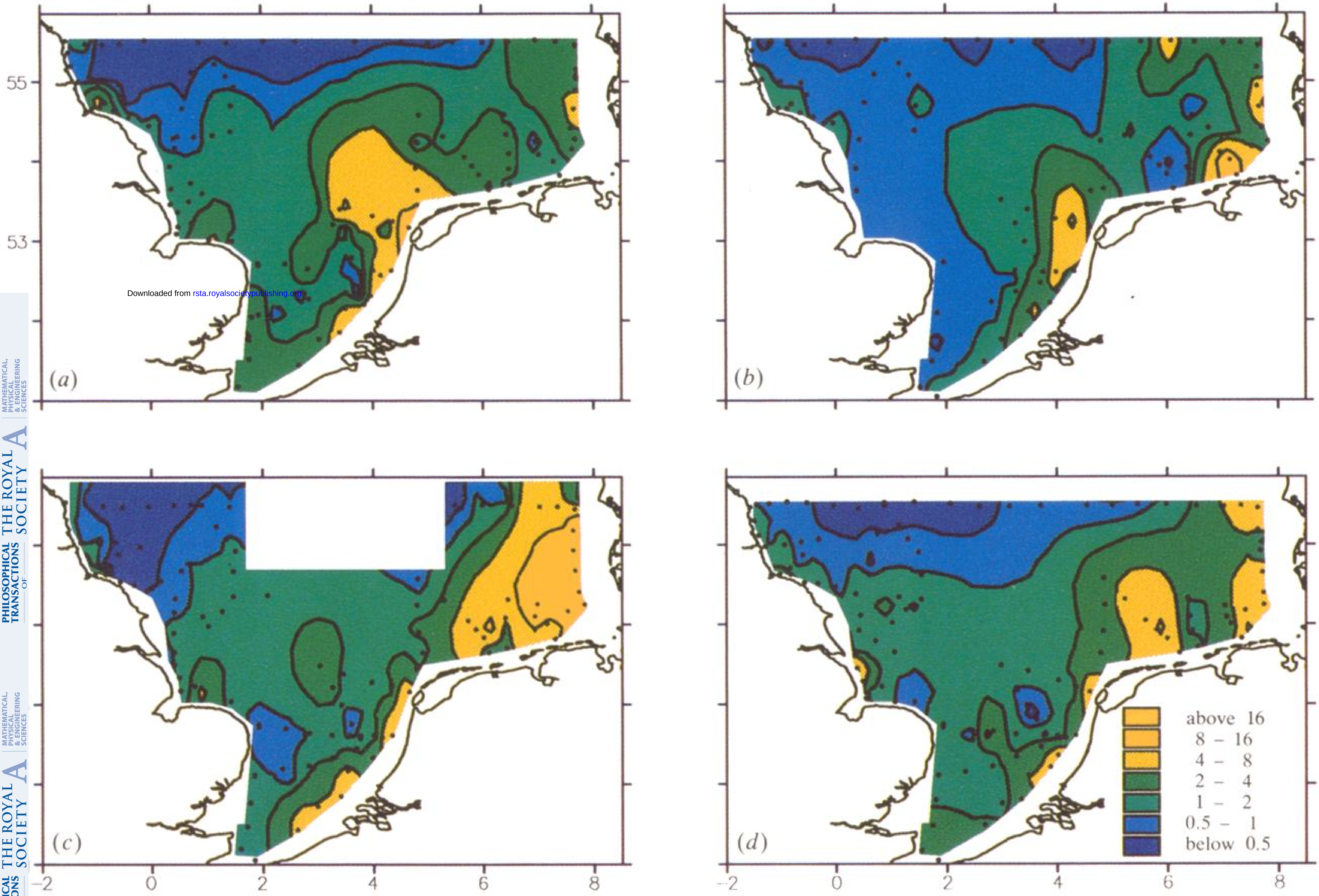

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