

The unbalance of phytoplankton and copepods in the North Sea

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Estimates of phytoplankton and copepod standing stock and productivity are plotted against date to present seasonal production cycles in different areas of the North Sea. The data used were obtained during cruises in the Southern Bight and at the Oyster Ground and the Fladen Ground between 1971 and 1981. It is concluded that the delay between copepod production and primary production, which is most distinct in spring, excludes any possibility of all phytoplankton being directly eaten by copepods. At times much of the crop may sink to the bottom or be consumed directly by protozoa and bacteria. During the summer months copepod grazing matches primary production in all areas. Only during that period does a limitation of copepod growth by food scarcity and a high grazing pressure on phytoplankters seem to maintain a balance between phytoplankton and zooplankton. The unbalance between the phytoplankton and the herbivorous mesozooplankton in spring and autumn must lead to a loss of energy potentially available to the higher trophic levels. Either the copepod production (about $10 \text{ g C m}^{-2} \text{ yr}^{-1}$ in the south to at least $20 \text{ g C m}^{-2} \text{ yr}^{-1}$ in the north) is sufficient to sustain the fish production, or there is an important additional food chain to the top carnivores through herbivores and omnivores near or at the bottom.

Introduction

Pelagic copepods are considered to be important grazers of phytoplankton. In the North Sea they are the most abundant metazoans and they usually constitute more than 80 % of total zooplankton biomass (e.g. Evans, 1973; Steele, 1974; Fransz and van Arkel, 1980). The idea that the fate of marine algae is to be eaten by herbivorous copepods was introduced by Harvey (1945). It is still widely accepted by students of biological oceanography.

Recently, Williams (1981) made a plea for another view of the planktonic food web, presenting evidence that much, often most, of the organic matter produced through photosynthesis ('primary production') is channelled through microheterotrophs before it is mineralized. Secondary production by these microorganisms may well be equal to or even greater than the production by the larger zooplankton. We encountered a similar situation in the Southern Bight of the North Sea during the spring bloom of 1975. At that time the rapid increase in primary production of organic matter was matched by a similarly high consumption: between 1 February and 1 June total plant production was only 25 % higher than consumption of organic matter (Gieskes and Kraay, 1977a). Yet hardly any copepods were present in that period, let alone active enough (at temperatures below 8°C) to graze away the produced algal crop. The mismatch between spring primary pro-

duction and copepod production was apparently bridged by consumers other than copepods, as was also suggested by Joiris *et al.* (1979) and Lancelot (1982).

In this paper we present an analysis of production data collected in the southern, central, and northern North Sea between 1971 and 1981. We will show that in most areas of the North Sea the seasonal fluctuation in phytoplankton production is not reflected by the copepod production during most of the year. With respect to copepods this is in contrast to the assumption of Steemann Nielsen (1957) of a close relationship between the cycles of phytoplankton and zooplankton production, a coupling he considered necessary to maintain the 'balance' between growth and mortality of both phyto- and zooplankton.

Material and methods

The areas of the North Sea sampled by us are indicated in Figure 1. Primary production measurements were made with the ^{14}C method in 100-ml light and dark incubation bottles (Gieskes and Kraay, 1977a, 1980). During the "Tyro" cruises of 1981 this method was compared with the oxygen light-and-dark bottle technique; for this a new version of the Winkler method was used, involving photometric endpoint determination of the titration (Bryan *et al.*, 1976; Tijssen, 1980). This method was also used for measurements of com-

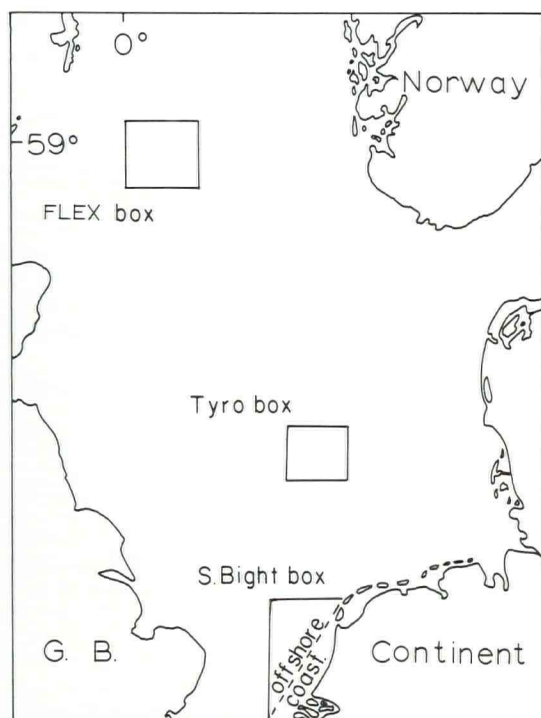


Figure 1. Areas of the North Sea that were sampled. The "Tyro" box was visited in 1981; the FLEX box in 1976; the Southern Bight during numerous cruises between 1971 and 1979.

munity respiration by monitoring oxygen changes in 20-litre seawater samples. Comparisons made between the ^{14}C and the oxygen light-and-dark bottle methods have shown that during the intercalibration exercise in the central North Sea the ^{14}C results were neatly in between gross and net production (Fig. 2), at least when a photosynthetic quotient of 1.2 at all depths was used for converting the oxygen evolution into carbon fixation (cf. Williams *et al.*, 1979). This agreement between the ^{14}C and the oxygen methods of measuring primary production also indicates that particulate ^{14}C production was close to total production. The spring bloom data of the Southern Bight do include production of dissolved organic matter because they were obtained by Schindler's (1971) version of the ^{14}C method.

Most chlorophyll *a* measurements were made with the fluorimetric method of Holm-Hansen *et al.* (1965). Continuous chlorophyll registrations were obtained with a Turner III fluorimeter and with a VarioSens®. Algal cells in Lugol-preserved samples were counted and categorized by size with a Zeiss inverted microscope. The data were used for the calculations of algal biomass following formulas of Hagmeier (pers. comm.). For diatoms: $\log C (\text{picogram}) = -0.864 + 0.857 \log V (\mu\text{m}^3)$; for flagellates: $C (\text{picogram}) = 0.075 \text{ volume } (\mu\text{m}^3)$. These conversions apply to Helgoland plankton data. The relationships resemble those given by Mullin

et al. (1966) and Strathmann (1967). The 'biomass' of *Phaeocystis* colonies was measured with the Carbon Analyzer of Oceanography International (ampoule method).

The zooplankton were sampled with a multiple high-speed sampler with 300 μm and 50 μm mesh nets and counted per species and length class (Fransz, 1976; Fransz and van Arkel, 1980). The whole water column was sampled, either in one double oblique haul, or in different depth layers in stratified areas. In the Southern Bight the number and position of sampling stations varied from year to year, but were always sufficient to represent the mean conditions in a coastal region within 30 km from the shore, and a more offshore region. At the Fladen Ground, samples were taken at a central station in the FLEX box (Fig. 1), and in the central North Sea near subsurface drifters which were supposed to mark a fixed water mass.

Total copepod ash-free dry weight was determined from densities of length classes and length-weight relationships established per species (Fransz and van Arkel, 1980; Klein Breteler *et al.*, 1982). The carbon content of the small neritic species was determined by wet oxidation with potassium peroxodisulphate. The mean value of the four common species (copepodites) was 32 % of ash-free dry weight. Most authors (e.g. Williams and Lindley, 1980) apply a higher value for *Calanus finmarchicus*. We assumed 40 % for this species in our Fladen Ground data (Fransz and van Arkel, 1980). The numbers of *Calanus finmarchicus* stages per m^2 during the whole Fladen Ground Experiment were obtained from Krause (pers. comm.) and averaged per three consecutive days (Fransz, 1980). The original densities are given by Krause and Radach (1980). They were converted to carbon biomass by adding 10 % for nauplii and other species and applying adequate weights of stages and carbon content.

According to Klein Breteler *et al.* (1982) the potential weight-specific growth rate of subadult copepodites of the four neritic species at 15°C with ample food is on average 29.4 % per day. Usually, more than 60 % of the copepod biomass is formed by subadult copepodites. Therefore, their growth rate was multiplied by total copepod biomass to estimate the potential daily production in the Southern Bight. The influence of temperature was taken into account by applying the Bělehrádek relationship (McLaren, 1963, 1966, 1978):

$$g_t = [(t + 12)/(15 + 12)]^{2.05} \times g_{15}$$

where t is the actual temperature in °C and g_t is the weight-specific growth rate at this temperature. This relationship also fits the temperature dependence found by Landry (1975) and Vidal (1980) and seems sufficiently accurate to estimate a seasonal production curve, the temperature during the summer peak of production approaching 15°C. Klein Breteler *et al.* (1982)

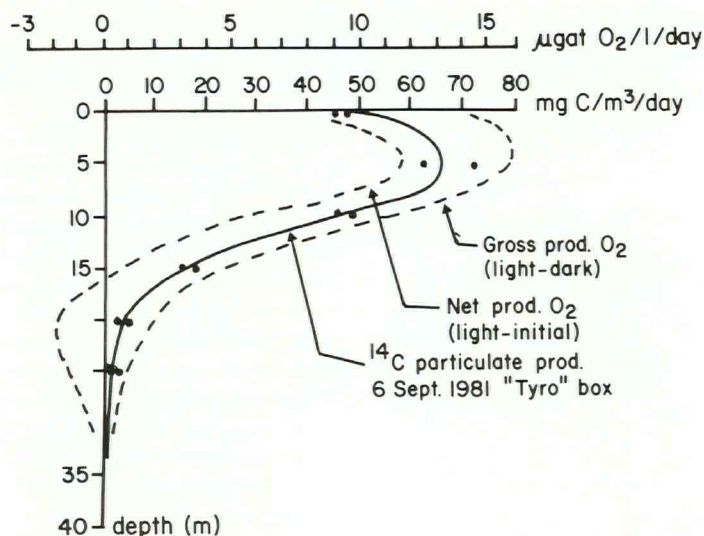


Figure 2. Primary production in the central North Sea, 6 September 1981, measured with the light-and-dark bottle oxygen method and with the ^{14}C method (in 100-ml bottles). ^{14}C filtrate values were less than 15 % of ^{14}C filter values; dark ^{14}C bottle values less than 5 % of light ^{14}C bottle values. A series of short incubations gave values similar to those obtained with a day-long incubation, both for ^{14}C and O_2 methods.

also established that in the Southern Bight the potential growth will probably not be reached owing to food scarcity, particularly during the summer months. They measured a more or less constant minimal growth of about 14 % near the coast and 7 % offshore. These values were applied to estimate minimum values.

Fransz (1980) determined the mean growth of *Calanus* subadult copepodites during the Fladen Ground Experiment as 17 % per day. Assuming a rather constant mean temperature experienced by the animals, which migrated to greater depths at the end of the period, this constant value was applied to estimate copepod production at the Fladen Ground.

To obtain smooth seasonal production curves, the products of growth and biomass were plotted against time for all years and progressive mean regression was applied per three consecutive points.

Results

Data on phytoplankton and copepod biomass are shown, for the three areas studied, in Figure 3. Figure 4

and Tables 1 and 2 give estimates of primary production and copepod production for the same seasons and areas. A seasonal production cycle of copepods for the central North Sea cannot be derived from the available information. The estimated stock indicates that the annual copepod production here was of the same order as in the Southern Bight.

Much of the biomass of phytoplankton was clearly formed during periods when the standing stock of copepods was low. For example, the spring and autumn blooms in the Southern Bight, and the spring bloom in the FLEX box, waxed and waned in the near-absence of copepods. Only during summer did we register co-occurrence of phytoplankton and copepods (Figs. 3 and 4). However, even during these months the algal crop was not necessarily eaten: e.g., in 1977 a *Leptocylindrus danicus* bloom was present for several weeks in the Southern Bight, senescing during that time as evidenced by the gradual loss of chlorophyll from the cells (Table 3).

In spite of the disconnection of the phytoplankton and copepod seasonal cycles, consumption of organic matter was found to be high even at times when the

Table 1. Estimates of primary production ($\text{mg C m}^{-2} \text{ day}^{-1}$) in different seasons based on measurements between 1971 and 1981 in the North Sea.

	Jan-Feb	Mar-May	Jun-Sep	Oct-Dec	Annual estimate ($\text{g C m}^{-2} \text{ yr}^{-1}$)
Southern Bight, coast	100	1 000	1 000	100	200
Southern Bight, offshore	100	1 200	700	500	250
Central North Sea, 1981	100	1 000	800	400	200-250
Northern North Sea (FLEX)	300	1 000	—	—	>>100

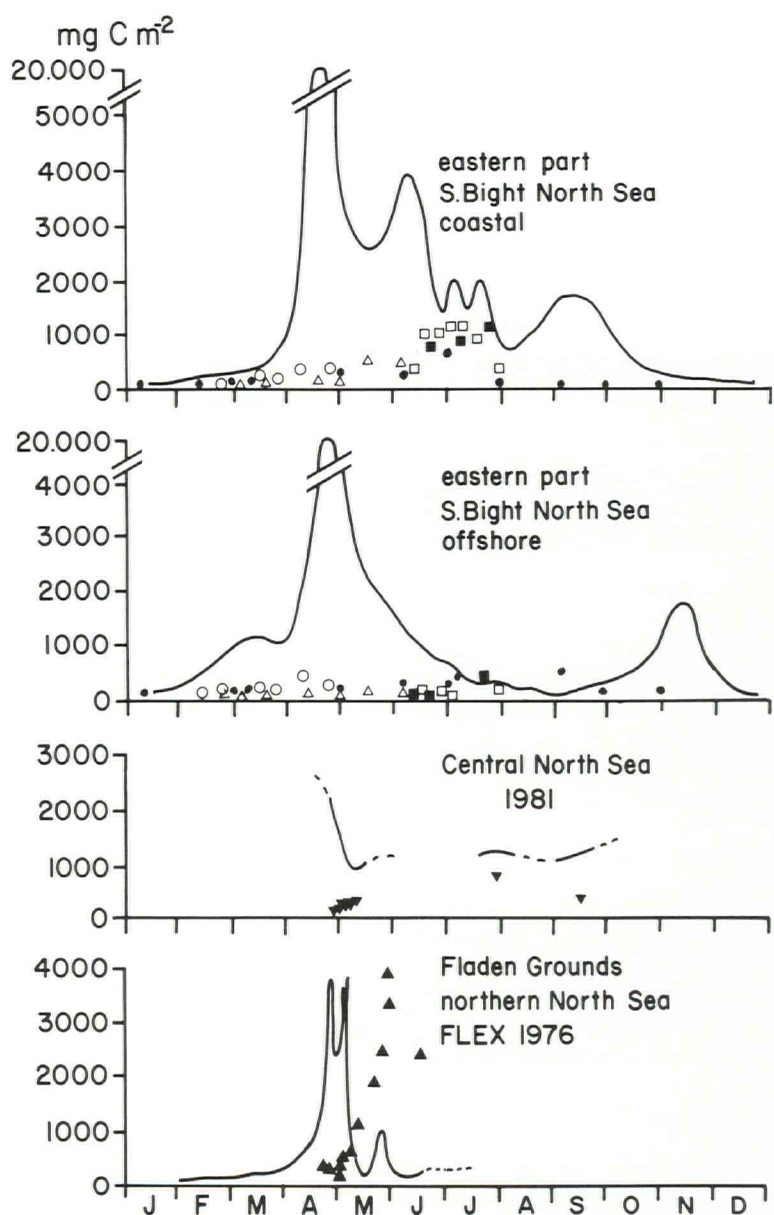


Figure 3. Biomass of phytoplankton and copepods (in mg C m^{-2}) in different areas of the North Sea (see Fig. 1 for location). Solid lines: mean biomass of phytoplankton between 1971 and 1979 (dotted lines for estimates). Symbols: copepod biomass in 1973 (dots), 1974 (open circles), 1975 (open triangles), 1977 (solid squares), and 1979 (open squares). Data for the Fladen Ground are derived from the FLEX Atlas (which includes own observations at end of April/beginning of May and in mid-June 1976).

Table 2. Estimates of total copepod production and its percentage of primary production in different areas and periods between 1971 and 1981 in the North Sea.

	Period	g C m^{-2}	%
Southern Bight, coast	Year	12–23	6–11
Southern Bight, offshore . .	Year	5–15	2– 6
Central North Sea, 1981 . .	Year	10	5
Northern North Sea (FLEX)	20 Apr–3 Jun	12	28

discrepancy between production of algae and copepods was greatest. The consumption of the spring phytoplankton bloom of 1975 in the Southern Bight has been ascribed to microbial activity (Gieskes and Kraay, 1977a). Recent observations on Lugol-preserved samples taken in the central North Sea (Tyro box, Fig. 1) in May 1981, revealed an abundance of ciliates (50 000/litre) and other protozoa (*Strombidium* up to 250/litre, tintinnids up to 500/litre). Community respiration measurements in surface samples taken in this region in

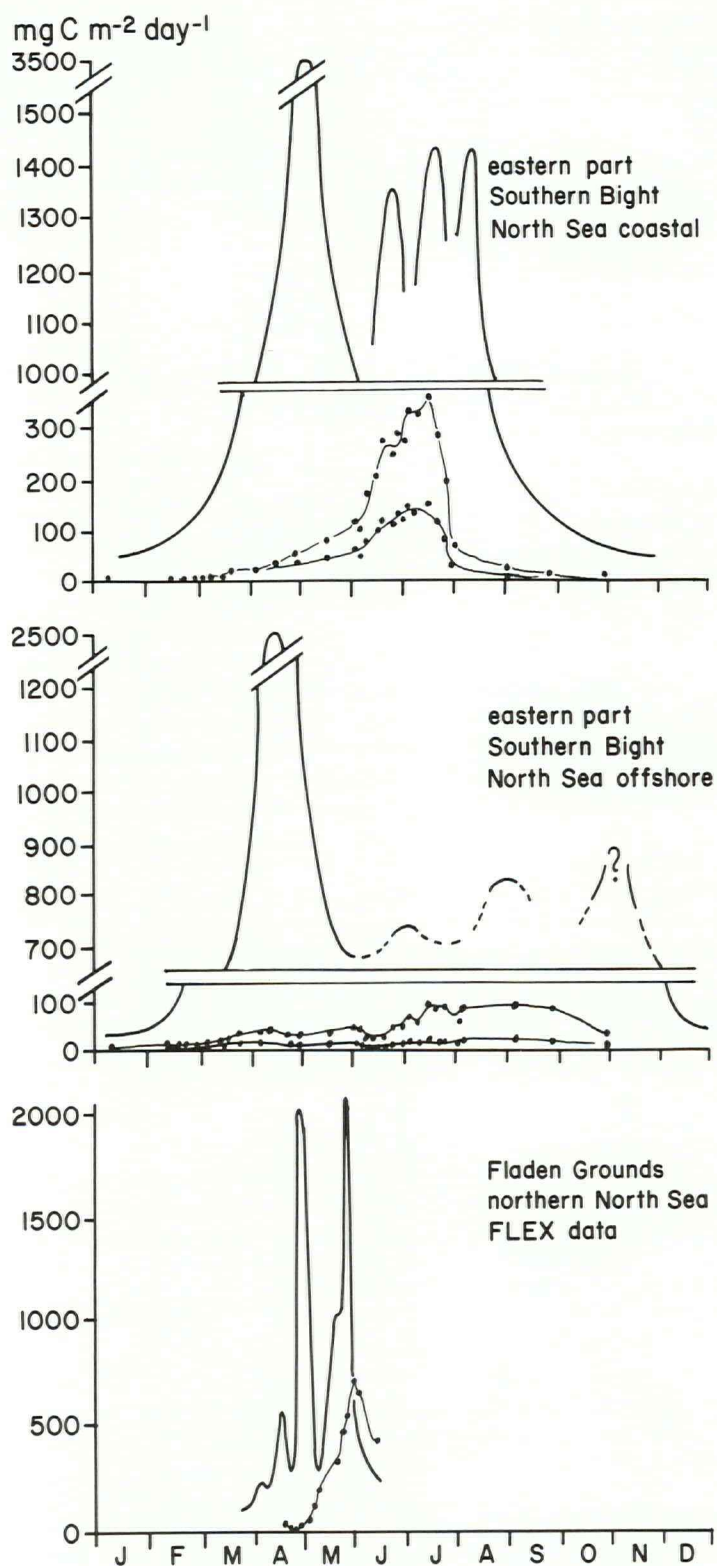


Figure 4. Solid lines: primary production (dotted lines for estimates). Thin lines connecting dots: copepod production. (For copepod production two values are given: potential production and lowest estimate.) Production data for the Fladen Ground are derived from the FLEX Atlas (which includes own observations at end of April/beginning of May and in mid-June 1976).

Table 3. Variation of chlorophyll *a* per cell of *Leptocylindrus danicus* during four consecutive weekly cruises in the Southern Bight in June/July 1977. Number of cells in analysed samples between 20 000 and 1 000 000 per litre seawater.

	Chlorophyll <i>a</i> per cell (μg)
13–14 Jun	1.00–1.90 ($\times 10^{-5}$)
20–21 Jun	0.58–1.00 ($\times 10^{-5}$)
27–28 Jun	0.50–1.00 ($\times 10^{-5}$)
4– 5 Jul	0.20–0.50 ($\times 10^{-5}$)

September 1981 showed that all of the nightly decrease of oxygen was due to organisms smaller than 50 μm (Table 4).

Apart from algal consumption by heterotrophs in the upper part of the water column, phytoplankton populations grown in the euphotic zone may of course also reach the bottom, either through sinking or through physical mixing processes. Abundance of non-active diatoms near the bottom has been observed in Kiel Bight, where the total crop sank to the bottom in a few weeks (Smetacek *et al.*, 1984). An example from our research area is given in Figure 5a.

Discussion

The methods by which both phytoplankton production and phytoplankton biomass were measured may of course be distrusted. In a recent review Peterson (1980) discussed the value of the ^{14}C method for productivity

Table 4. Two examples of nightly decrease in oxygen ($\mu\text{gat litre}^{-1}$) in 20-litre samples of surface seawater of the central North Sea, September 1981. 'Filtered' samples were passed through a 50- μm net before the experiment.

	9 Sep, 20.30 h	10 Sep, 06.45 h	Decrease
Unfiltered	557.11 \pm 0.54	546.54 \pm 0.52	10.67
Filtered	546.74 \pm 0.34	536.00 \pm 0.75	10.75

	10 Sep, 21.15 h	11 Sep, 08.30 h	Decrease
Unfiltered	542.16 \pm 0.55	530.40 \pm 0.57	11.76
Filtered	533.52 \pm 0.45	521.95 \pm 1.18	11.57

estimates; and the method of calculating phytoplankton carbon from cell volume conversions (see Material and methods section) may lead to underestimates of algal standing crop because delicate algal cells are more often than not overlooked when preserved samples are examined by microscope. Moreover, it may be argued that one can hardly present data on algal biomass and production in the summarizing format of a mean seasonal variation over a number of years when the data originate from discrete measurements, even when the number of measurements is considerable. The main cause of this difficulty is the patchiness of the plankton in space and time, and the variation in algal crop between years. Examples of the latter have been given by Gieskes and Kraay (1977b). An example of the former is given in Figure 6, where strong weekly changes in the chlorophyll isopleth pattern are shown – the rule rather than the exception in the southern North Sea. In the

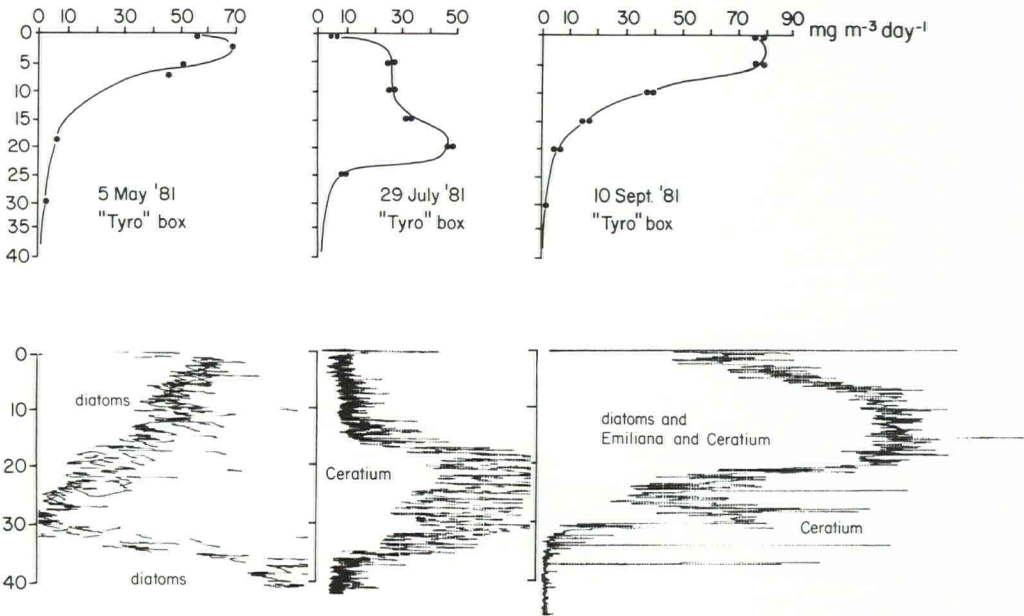


Figure 5. Primary production and chlorophyll measured by VarioSens® in the central North Sea. Bottom at 45 metres.

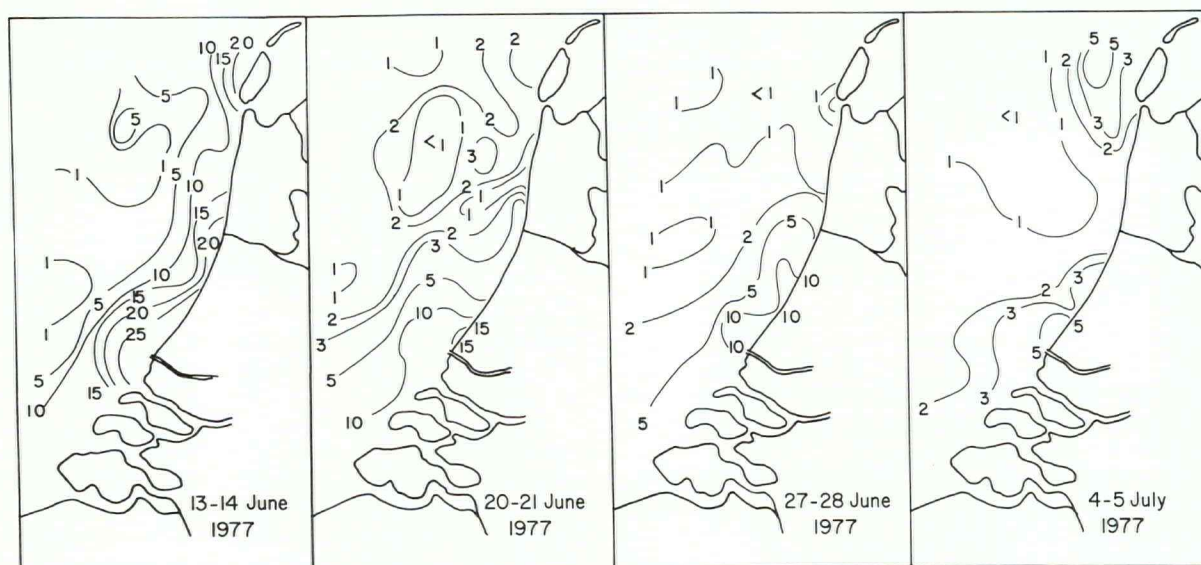


Figure 6. Isopleths of chlorophyll *a* near the surface (mg m^{-3}) during four consecutive weekly cruises in the summer of 1977. Surface values are representative for the water column because of complete vertical mixing due to tidal movements, wind, and waves.

central and northern North Sea there is an extra dimension to patchiness, namely the variability of phytoplankton density in a *vertical* direction, caused by the hydrographic inhomogeneity in the water column between late spring and early autumn (Fig. 5). Because of all these variations it is evident that the phytoplankton biomass and production curves presented in Figures 3 and 4 and the data in Table 1 are at best rough approximations of mean conditions. Patchiness and differences in the vertical distribution were of less importance in determining copepod biomass, as the sampling method tends to integrate in spatial dimensions.

Most of the particles suitable as copepod food are probably produced in spring and autumn, when the copepod ingestion seems to be insignificant. If the daily ingestion can be estimated as about 3–5 times the daily production (e.g. Paffenhöfer, 1976), the amount eaten during the spring season (before June) in the Southern Bight is at most 25 g C m^{-2} , and during the short diatom bloom at the Fladen Ground from 20 April to 5 May about 9 g C m^{-2} . The high copepod production immediately following the diatom increase at the Fladen Ground suggests that *Calanus* is able to harvest the crop after all, but it is not clear how this is achieved.

The situation is quite different during the peak of the copepod density in summer. In the coastal area of the Southern Bight at least 40 g C m^{-2} is consumed in June and July, which matches the primary production. At the Fladen Ground a potential consumption of 70 g C m^{-2} between the middle of May and the middle of June can be assumed, although the animals looked very inactive at the end of this period (Fransz and van Arkel, 1980). Prerequisites for copepod growth are a sufficiently high concentration of algae, at least about 150 mg C per m^3

(Adams and Steele, 1966), adequate particle size, and edibility. Low growth rates (Klein Breteler *et al.*, 1982) seem to indicate that these conditions do not prevail in the Southern Bight during the summer months. At the Fladen Ground copepod growth and production will be severely reduced during the summer months. The sustained growth of *Calanus* after the diatom spring increase may be attributed to feeding on detrital remains of the bloom (Radach, pers. comm.) or to switching to animal food (Landry, 1981). In the northern North Sea production of eggs and faecal pellets by *Calanus* was mainly observed during the diatom peak (Fransz and van Arkel, 1980; Krause, 1981).

Conclusions

- 1) The delay between the copepod production and the primary production, which is most distinct in spring in all areas investigated, makes it unlikely that all phytoplankton is directly eaten by the copepods. This applies to about 75 % of the annual primary production in the Southern Bight.
- 2) During the summer months copepod grazing matches primary production in all areas. Only during that period does a limitation of copepod growth by food scarcity and a high grazing pressure on phytoplankters seem to maintain a balance of phytoplankton and zooplankton.
- 3) The fate of phytoplankton is not necessarily ingestion by copepods. At times much of the crop may be channelled through the 'small food web' of protozoa and bacteria, either after natural mortality following nutrient depletion or by grazing by protozooplankton.

4) The low consumption rate of the herbivorous mesozooplankton during periods of high phytoplankton density must lead to a loss of energy potentially available to the higher trophic levels. This loss clearly does not prevent high fish production in the North Sea ($0.85 \text{ g C m}^{-2} \text{ yr}^{-1}$ according to Steele, 1974). Either the copepod production (about $10 \text{ g C m}^{-2} \text{ yr}^{-1}$ in the south to at least $20 \text{ g C m}^{-2} \text{ yr}^{-1}$ in the north) is sufficient to sustain this fish yield, or there is an additional food chain to the top carnivores through herbivores and detritivores living near the bottom.

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