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[2.]

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Verzeichnis der zur kumulativen Habilitation eingereichten Schriften

1. Bodungen, B.v., K.v. Bröckel, V. Smetacek and B. Zeitzschel (1981): Growth and sedimentation of the phytoplankton spring bloom in the Bornholm Sea (Baltic Sea). Kieler Meeresforsch. Sonderh. 5, 49-60.

2. Bodungen, B.v., V. Smetacek, M. Tilzer and B. Zeitzschel (Ms.): Primary production and sedimentation during austral spring in the Antarctic peninsula region. Deep-Sea Res., (soll nach geringfügigen Änderungen angenommen werden).

3. Osterroht, C. and V. Smetacek (1980): Vertical transport of chlorinated hydrocarbons by sedimentation of particulate matter in Kiel Bight. Mar. Ecol. Prog. Ser. 2, 27-34.

4. Schnack, S.B., V. Smetacek, B.v. Bodungen, P. Stegmann (1985): Utilization of phytoplankton by copepods in Antarctic waters during spring. In: J.S. Gray and M.E. Christiansen (Eds.), Marine biology of polar regions and effects of stress on marine organisms. John Wiley & Sons, 65-81.

5. Smetacek, V. (1980a): Annual cycle of sedimentation in relation to plankton ecology in western Kiel Bight. Ophelia Suppl. 1, 65-76.

6. Smetacek, V. (1980b): Zooplankton standing stock, copepod faecal pellets and particulate detritus in Kiel Bight. Estuar. & Coast. Mar. Sci. 11, 477-490.

7. Smetacek, V. (1984a): Growth dynamics of a common Baltic protozooplankter: the ciliate genus Lohmanniella. Limnologica 15, 371-376.

. Smetacek, V. (1984b): The supply of food to the benthos. In: M.J.R. Fasham (Ed.), Flows of energy and materials in marine ecosystems: theory and practice. Plenum Press, 517-548.

. Smetacek, V. (1985a): Role of sinking in diatom life-history cycles: ecological, evolutionary and geological significance. Mar. Biol. 84, 239-251.

10. Smetacek, V. (1985b): The annual cycle of Kiel Bight plankton: a long-term analysis. Estuaries, 8, 145-157.

11. Smetacek, V. (in press): Plankton characteristics. In: H. Postma and J.J. Zijlstra (Eds.), Ecosystems of the world: Continental shelves. Elsevier, North Holland.

12. Smetacek, V., B.v. Bodungen, B. Knoppers, H. Neubert, F. Pollehne and B. Zeitzschel (1980): Shipboard experiments on the effect of vertical mixing on natural plankton populations in the Central Baltic Sea. Ophelia Suppl. 1, 77-98.

13. Smetacek, V., B.v. Bodungen, B. Knoppers, F. Pollehne and B. Zeitzschel (1982): The plankton tower. IV: Interaction between water column and sediment in enclosure experiments in Kiel Bight. In: G. D. Grice and M. R. Reeve (Eds.), Marine mesocosms. Springer Verlag 205-216.

14. Smetacek, V., B.v. Bodungen, B. Knoppers, R. Peinert, F. Pollehne, P. Stegmann and B. Zeitzschel (1984): Seasonal stages characterising the annual c cle of an inshore pelagic system. Rapp. P.-v. Reun. Cons. int. Explor. Mer 183, 126-135.

5. Smetacek, V., B.v. Bodungen, E.-M. Nöthig and U. Bathmann (Ms.): Sedimentation of planktonic diatoms in the Antarctic: evidence of a mechanism for accelerating sinking rates.

Kieler Meeresforsch., Sonderh. 5, 49 – 60. Kiel 1981

Growth and sedimentation of the phytoplankton spring bloom in the Bornholm Sea (Baltic Sea)*

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Abstract

Results obtained from short-term (8 h to 24 h intervals) measurements of physical, chemical and biological properties of the 70 m water column from an anchor station in the Bornholm Sea over a 10-day period are presented and discussed. Phytoplankton biomass concentration and production rates indicated that the spring bloom was in progress in this period. The onset of the spring bloom occurred prior to the advent of thermal stratification. Peak growth rates, accompanied by nutrient depletion and biomass accumulation in surface layers, were concomitant with calm weather and a cloudless sky after which a part of the population was observed to sink out of the water column unimpeded by the permanent halocline. Maximum sinking rates of the dominant species, *Skeletonema costatum*, ranged between 30 to 50 m per day during this event. The development of the spring bloom apparently takes place in a series of events during which periods of low production alternate with periods of high production and rapid sedimentation of parts of the population.

Introduction

In boreal regions, the spring bloom of phytoplankton is an outstanding event in the annual cycle of primary production. Increasing solar radiation in the spring is one of the major factors initiating commencement of the spring bloom which is eventually terminated by the exhaustion of available nutrients. The spring bloom thus represents the transition from light-controlled to nutrient-controlled phytoplankton production in the surface layers.

The development of the spring bloom is largely dependent on seasonal changes in physical factors of the environment, particularly light intensity in the water column and the depth of the mixed layer (SVERDRUP 1952). These gradual seasonal trends can be reversed for short periods by changing weather conditions (e.g. cloudiness, storms), which considerably affect the development of the spring bloom.

In this paper, data obtained over a 10-day period from an anchor station during spring bloom development is presented and discussed (Fig. 1). This investigation, carried out in the Bornholm Sea on board RV "Meteor", was part of the multidisciplinary exercise BALTIC 75.

The Bornholm Sea is one of a series of basins in the southern Baltic Sea with an average water depth of 80 m and sills of 45 m and 60 m depth to the west and east

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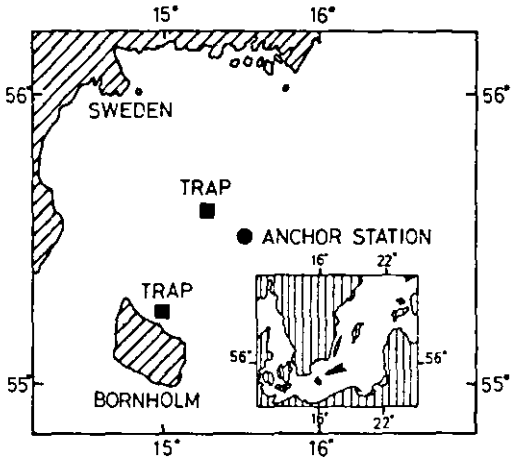

Figure 1

Location of the anchor station in the Bornholm Sea and position of the sediment traps of SMETACEK *et al.* (1978).

respectively. The water column is stratified by a permanent halocline at a depth of about 50 m (GRASSHOFF 1975). A seasonal thermocline develops at about 30 m in April/May.

Material and methods

Hydrographic profiles were obtained using a CTD-system (conductivity, temperature, depth) by Howaldt (Bathysonde). The data were made available to us by W. Horn.

Nutrient concentrations were measured by K. Grasshoff, H. Johannsen and A. Wenck using an autoanalyzer and the procedures described by GRASSHOFF (1976).

Samples for primary production were taken from 100, 50, 25, 10 and 1 % light depths. Production was estimated by the ^{14}C-method using the *in situ* simulated technique in collaboration with the International ^{14}C Agency, Denmark. Sets of samples were incubated from sunrise to noon, sunrise to sunset, noon to sunset. A fourth set was exposed to 70 % of surface light from sunrise to sunset and will be referred to as 'optimal production' in the following.

Discrete samples from 12 depths (including the light depths) down to 70 m were taken for chlorophyll a (Chl a), particulate organic carbon and nitrogen (POC and PON respectively) at 8 h intervals and for plankton counts at noon. Samples for Chl a were homogenized and then treated as recommended by UNESCO (1966). POC and PON were determined on precombusted Whatman GF/C filters using a CHN-Analyzer (Hewlett-Packard, 185B). Phytoplankton carbon (PPC) was derived by multiplying cell counts obtained with an inverted microscope with carbon conversion factors given by SMETACEK (1975).

Zooplankton was sampled by vertical bottom-to-surface hauls with a 100 µm Apstein net at noon each day.

Results

Hydrography

The water column was initially well mixed to the depth of the permanent halocline between 50 and 55 m with temperatures ranging from 3.9 to 4.2 °C in the mixed layer

(Fig. 2) and salinity between 7.95 and 8.05‰. In the subhalocline layer temperature and salinity ranged between 5.0 and 8.9 °C and 10.5 and 14.7‰ respectively. Daily average wind speeds (Fig. 2) varied from 6 to 14 kn, the range of actual values extended from 0 to 30 kn. A violent storm on the 14 and 15 April delayed commencement of the investigation and winds slackened with occasional interruptions up to 20 April. The calmest period was from 21 to 23 April which coincided with a cloudless sky, and a concomitant decrease in the depth of mixing was reflected in increasing temperatures in the surface layer (Fig. 2). Wind speed increased on 24 April and the depth of the mixed layer increased, as shown by the depression in the 4.5 °C isoline in Fig. 2. However, typical stable thermal stratification above the permanent halocline was not established before mid-May (KIELMANN, pers. comm.). Further aspects of the hydrography of the investigation area are given by SMETACEK et al. (1978). The authors state that neither the subhalocline water nor the water column of the mixed layer was exposed to sudden advection of water from distant areas throughout the investigation period.

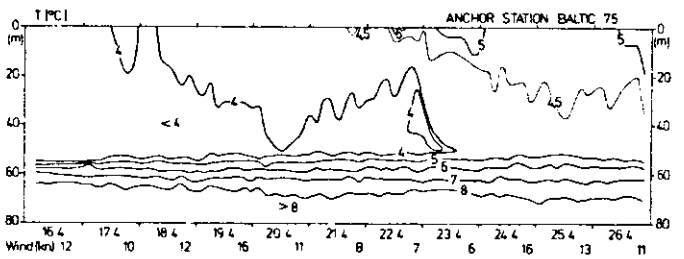

Figure 2

Isotherms during the investigation period. Average daily wind speeds in knots are given at the bottom of the figure.

The 1 % light depth, calculated from Secchi readings, was most commonly at 24 m and rose for 2 days to 20 m following an increase in phytoplankton biomass after 22 April (Fig. 4b).

Nutrients

Nutrient concentrations in the mixed layer during the first half of the investigation were approximately 1.5 µgat NO_3-N l^{-1} 0.4 µgat PO_4-P l^{-1} (Fig. 3a, b) and 15 µgat SiO_4-Si l^{-1}. These values are considerably lower than normal winter concentrations for the study area (GRASSHOFF 1975, SCHULZ et al. 1978), indicating that nutrient uptake due to phytoplankton growth had occurred before 17 April. A substantial decline in nutrient concentrations was observed after 20 April, and, by 21 April, nitrate values were below 0.1 µgat l^{-1}. Lowest recorded values for phosphate and silicate were 0.2 and 8.5 µgat l^{-1} respectively, indicating that neither of these elements played a role in limiting phytoplankton growth. Ammonia was not measured but, as this form of nitrogen is taken up more rapidly than nitrate, it can be safely assumed that little, if any, ammonia was avaiable and that nitrogen was indeed the limiting nutrient for phytoplankton growth during the period of investigation.

After 22 April, nutrient profiles in the mixed layer indicate a distinct alternation of nutrient depletion in the euphotic zone and upward mixing from the disphotic zone for all nutrients (Fig. 3a, b). Nutrient depletion and upward mixing corresponded with increasing phytoplankton growth and higher wind speeds respectively (Fig. 4a and 2).

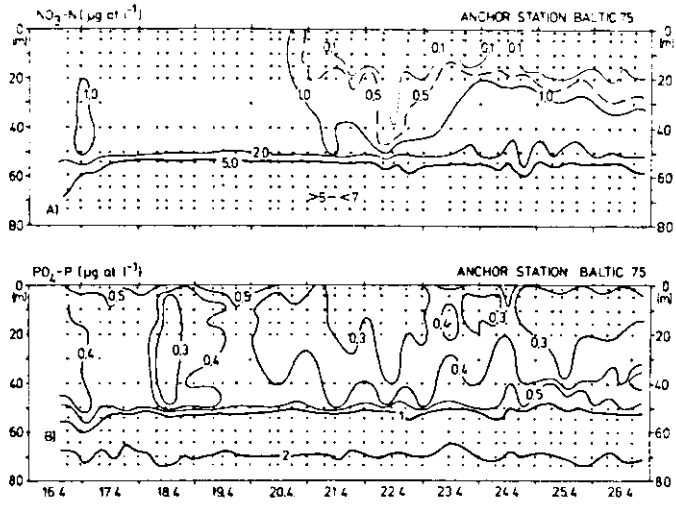

Figure 3
Nitrate (a) and phosphate (b) vertical distribution at the anchor station.

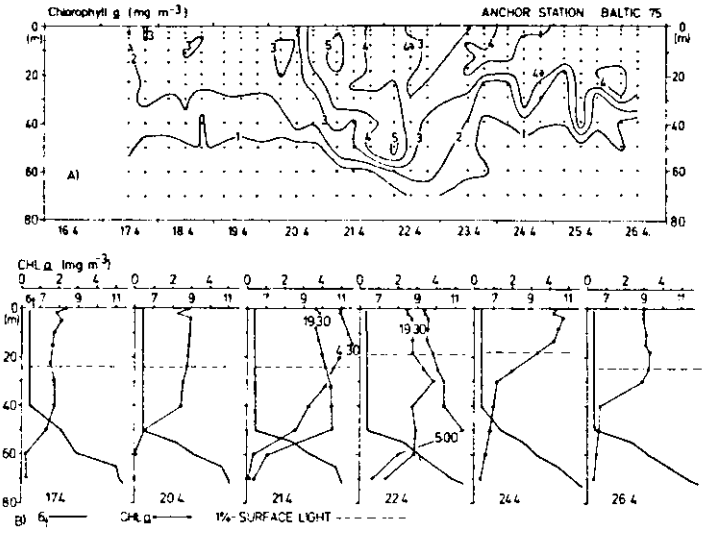

Figure 4
Chlorophyll distribution in the water column (a). Selected vertical profiles of density and chlorophyll (b). The dashed line indicates the 1 % light depth, the time of measurement is given in the profiles from 21 and 22 April.

Chlorophyll a

Before the beginning of the spring bloom, chlorophyll concentrations of less than 1 mg · m^{-3} are reported from the Bornholm Sea (KAISER and SCHULZ 1978). The higher concentrations of 2 to 3 mg·m^{-3} also indicated the commencement of phytoplankton growth before 17 April. From 17 to 20 April, the chlorophyll content was more or less evenly distributed throughout the mixed layer (Fig. 4a). A distinct accumulation of chlorophyll in the euphotic zone took place from 20 to 21 April, immediately followed by higher values in the disphotic and subhalocline layer on 21 and 22 April. Thereafter chlorophyll again accumulated in the euphotic zone.

More details of the chlorophyll distribution are given in the selected vertical profiles (Fig. 4b). For the first 4 days, the distribution in the mixed layer was homogeneous. By the morning of 21 April, the chlorophyll content in the water column had doubled to 233 mg·m^{-2}. In the night of the same day 230 mg·m^{-2} was measured, and the maximum recorded production of 2 gC m^{-2} was recorded on that day. The depth distribution of chlorophyll, however, changed markedly. Maximum levels were found within the euphotic zone at 4.30 hrs., but around the depth of the halocline at 19.30 hrs. The next day, 22 April, an even more distinct maximum was measured in the disphotic zone concomitant with increased levels below the halocline. By night more chlorophyll had sunk below the halocline and a general decrease in the entire water column was found. From 23 April onward the chlorophyll content below the euphotic zone declined sharply in the absence of any corresponding gradient in density.

Phytoplankton

Skeletonema costatum accounted for 40 % of the total phytoplankton carbon (PPC) in the initial period and for 60 % in the last days (Fig. 5a, b; Table 1). Another important contributor to PPC was the photoautotrophic ciliate *Mesodinium rubrum* (10 to 40 % of PPC). Other centric diatoms such as *Thalassiosira* sp. and *Chaetoceros danicus* accounted for most of the remainder. Initially PPC was 2 to 3 gC m^{-2}, during the maximum 7.8 gC m^{-2}, and in the last days 5 to 6 gC m^{-2}. The vertical PPC distribution basically followed that of the chlorophyll. After doubling of PPC in the euphotic zone on 21 April, rapidly increasing levels were recorded in the disphotic and subhalocline layer. Below the halocline 59 mg PPC m^{-3} was found on 24 April.

Table 1

Percentage contribution to total phytoplankton carbon by the dominant species *Skeletonema costatum* and *Mesodinium rubrum*. Other diatoms are grouped under the third column; flagellates, largely nanoflagellates, constituted the remainder.

Date	*S.costatum*	*M. rubrum*	other diatoms
17.4.75	49	27	12
18.4.75	33	39	17
19.475	43	28	19
20.4.75	47	39	10
21.4.75	64	13	9
22.4.75	61	10	12
23.4.75	64	19	7
24.4.75	47	29	8
25.4.75	62	19	7
26.4.75	64	19	9

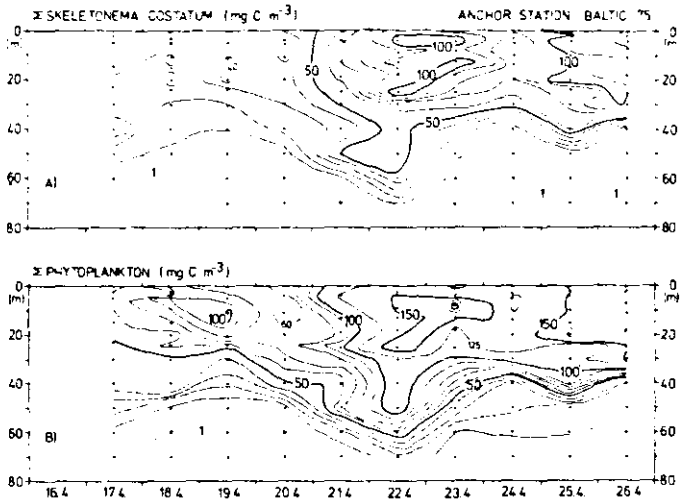

Figure 5
Vertical distribution of the dominant phytoplankton species *Skeletonema costatum* (a) and total phytoplankton biomass (b) in mgC m^{-3}.

Primary production

Primary production levels ranged between 0.65 and 0.99 gC $m^{-2}d^{-1}$ in the initial period. Similar values were recorded in spring blooms from the Baltic Sea (SCHULZ et al. 1978. RENK et al. 1975). Most of the production took place in the upper 6 m, as can be seen from Fig. 6a. Maximum production was measured on 21 April with 2.4 gC $m^{-2}d^{-1}$. After this, production declined but remained at a fairly high level of about 1 gC $m^{-2}d^{-1}$. In the last 2 days, production increased again to 1.9 gC $m^{-2}d^{-1}$ gC $m^{-2}d^{-1}$ as higher rates were recorded throughout the euphotic zone and even at the 1 % light level, 60 mgC $m^{-3}d^{-1}$ was measured. The total production over the 10 day period was 12.6 gC m^{-2}.

The results obtained from different incubation times have been compared in Fig. 6b, from which the following points of interest are evident: a. Production rates recorded during forenoon and afternoon of the same day are very similar with only 2 exceptions on 22 and 24 April; b. Some variation can be seen between results obtained from sunrise to sunset incubation (column 3) and those representing the sum of sunrise to noon and noon to sunset incubation (T-bars), although a consistent trend is absent; c. Optimal production rates are higher than simulated *in situ* rates up to 21 April, the discrepancy being much less or reversed thereafter.

Zooplankton

Zooplankton biomass was fairly constant throughout the investigation period and ranged between 0.40 and 0.45 gC m^{-2}. The main constituent was *Pseudocalanus elongatus* together with its young stages.

Discussion

It is apparent from the results that different stages of the spring bloom were encountered at the fixed station in this investigation. The observed changes in biomass and depth distribution of the phytoplankton point to a temporal sequence of

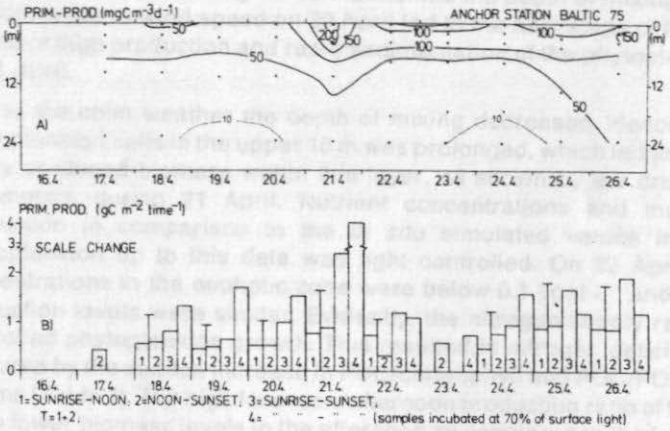

Figure 6

Vertical distribution of phytoplankton primary production (incubation from sunrise to sunset) from simulated *in situ* measurements (a). Histograms of daily production (gC m^{-2}) for different incubation times at simulated *in situ* and optimal light conditions (70 % of surface light) (b). Column 1: sunrise-noon incubation, column 2: noon-sunset incubation, column 3: sunrise to sunset incubation, column 4: optimal production from sunrise to sunset incubation. T-bars indicate the sum of 1 and 2).

events in bloom development governed by weather conditions. Before integrating the observations into a consistent picture of the growth and maturity of the bloom, it is important to consider the role of horizontal advection and the possible extent of spatial heterogeneity in determining the sequence of events.

The anchor station was situated in the middle of the Bornholm Sea which is a region of eddy formation generated by the interaction of wind stress and bottom topography (SMETACEK et al. 1978). SMETACEK et al. state that large scale addition of water masses from distant areas to the Bornholm Sea is a slow process because of its circulation patterns. Their arguments are based on data collected during BALTIC 75. Thus, because of the long residence time of water in the Bornholm Sea, one can assume that the water mass under observation during the 10 day period had experienced much the same irradiation and weather conditions. As plankton growth is most sensitive to the physical environment during this season, it is unlikely that spatial variations within such a homogeneous environment could account for the rapid changes in biomass and its depth distribution between 20 and 23 April. The fact that the observed changes in biological parameters of the water column could be attributed to the variations in local weather conditions proves that the results actually reflected a temporal sequence in spring bloom development that probably occurred in a wider area of the Bornholm Sea.

Growth of the spring bloom had commenced before 17 April, prior to the development of stable thermal stratification in the mixed layer. Apparently, the critical depth had receded below the halocline level as a result of the seasonal increase in irradiation. The diatom population was fairly evenly distributed in the 50 m of the mixed layer. Up to 20 April, biomass build up was relatively slow and occurred in the entire mixed layer. This is because significant production was restricted to the upper 10 m. The entire population, however, was continuously dispersed in the 50 m water column down to

the halocline as the strong winds maintained the depth of mixing down to that depth. The decrease in wind speed on 20 April led to the next stage of this spring bloom – a period of high production and rapid sedimentation of the phytoplankton that lasted up to 23 April.

Due to the calm weather the depth of mixing decreased. Hence, residence time of phytoplankton cells in the upper 10 m was prolonged, which led to accumulation of the newly produced biomass within this layer, as shown by the dramatic change in all parameters during 21 April. Nutrient concentrations and much higher optimal production in comparison to the *in situ* simulated values indicate clearly that phytoplankton up to this date was light controlled. On 22 April, however, nitrate concentrations in the euphotic zone were below 0.1 μgat·l^{-1} and *in situ* and optimal production levels were similar. Evidently, the nitrogen supply rather than light now controlled phytoplankton growth. This resulted in nitrogen deficiency of the cells as indicated by the sudden increase in POC/chlorophyll and POC/PON ratios in the water column (Table 2). The high forenoon/afternoon production ratio of this day is due to the much lower biomass levels in the afternoon as compared to the forenoon. This is also indicated by comparatively low variation in assimilation numbers during this period (Table 2).

Table 2

Temporal changes in growth dynamics and composition of particulate material expressed as ratios of different parameters (POC, PON: particulate organic carbon and nitrogen; PPC : phytoplankton carbon; Chl a : chlorophyll a; assimilation number : mg C/mg Chl a m^{-2} h^{-1}. Ratios are calculated from integrated values for the euphotic zone).

Date	POC/PON	PPC/Chl a	Assimilation number	Daily Production/ Optimal Production	Forenoon/ Afternoon Production
17. 4. 75	7.5	29	1.6	–	–
18. 4. 75	6.5	25	1.3	0.6	0.95
19. 4. 75	7.4	32	0.8	0.4	0.91
20. 4. 75	6.4	25	1.1	0.6	1.00
21. 4. 75	6.9	23	1.6	0.6	0.88
22. 4. 75	8.5	46	1.5	1.1	2.30
23. 4. 75	6.4	38	1.5	0.8	–
24. 4. 75	6.8	33	1.0	0.7	0.62
25. 4. 75	6.9	41	1.9	1.4	0.93
26. 4. 75	7.7	53	1.8	1.6	1.03

The biomass that had accumulated in the upper layers during 21 April dispersed in the water column and a new accumulation appeared at the halocline level on 22 April. Nutrients declined concomitantly. We attribute this vertical movement to a sinking out of a part of the population rather than to downward mixing for the following reasons:

a. The sea surface was very calm on 22 and 23 Arpil and a temperature gradient in the near surface region appeared for the first time on these days.

b. The population apparently continued its descent through the halocline as a considerable amount of phytoplankton cells suddenly appeared in this stagnating layer of water. There is no explanation other than sinking to account for the presence of such large numbers of cells below the halocline.

c. Both decreasing turbulence levels and nutrient deficiency are known to greatly increase sinking rates of diatom cells (TITMAN and KILHAM 1976, ANDERSON and SWEENEY 1978, MARGALEF 1978). Such nutrient-deficient cells take up dissolved nutrients from the environment even in the dark (YENTSCH et al. 1977), which would explain why nutrients decreased in the entire water column above the halocline.

Apparently, the phytoplankton cells of the population that suffered most from nutrient deficiency were the ones that settled out. It is reasonable to assume that these were mainly the cells that divided on 22 April, i.e. cells from the euphotic zone rather than from deeper layers. This would give sinking rates for *Skeletonema costatum* cells in the order of 30 to 50 m per day which is well above the maximum sinking rates of 8 m per day reported by SMAYDA and BOLEYN (1966). SMAYDA (1970) gives maximum rates for living phytoplankton of 30 m per day but suggests that, under certain circumstances, much higher sinking rates are possible. Our data show that these higher sinking rates do indeed occur for short periods of time. If this is true, it will necessitate a reassessment of the possible role of sedimentation in eliminating phytoplankton cells from the euphotic zone. That cells did indeed settle through the subhalocline layer after rapid passage of the density barrier posed by the halocline itself was proven beyond doubt by the large quantity of 'fresh' phytoplankton cells collected in traps deployed in the subhalocline water during BALTIC 75 (SMETACEK et al. 1978).

A rough estimate of the quantity of phytoplankton that sedimented during this period can be gained by subtracting the integrated biomass value recorded in the water column between compensation depth and bottom (30 to 70 m) after the sedimentation event i.e. 23 April, from the maximum recorded on 22 April. This gives a figure of 2 g PPC m^{-2} and 105 mg Chl a m^{-2} input to the bottom. The PPC/Chl a ratio of this material was 52 which is approximately double the average values of suspended cells before the event. Higher PPC/Chl a levels are a sign of increasing nutrient deficiency (SMETACEK and HENDRIKSON 1979) and this observation would substantiate the arguments on nutrient deficiency having precipitated the sedimentation event. Another estimate of the quantity of organic carbon that settled out on 22 April can be derived from a comparison of biomass and production rates of 21 and 22 April. This figure of 1.6 gC m^{-2} is in reasonable agreement with the first estimate.

The chlorophyll values in the subhalocline water returned to their original low levels. Although the weather remained calm on 23 April, no additional sinking was observed and production was low on this day.

Increasing wind speeds on 24 April led to renewed homogenisation in the upper layers evidenced by the downward transport of heat and the upward transport of nutrients. Production levels increased and the nutrient input again was reflected in the higher optimal production values in comparison to values from *in situ* simulated conditions. Nitrate, after this, was again depleted in the upper 20 m and increasing biomass levels were observed during the last 2 days of the investigation period. It is likely that renewed nutrient depletion led to a new sedimentation event after 26 April, as the C/N and PPC/Chl a ratios had risen to similar levels as observed on 22 April when the first rapid sedimentation occurred. This assumption is also supported by sediment trap results from the vicinity where large quantities of phytoplankton cells were collected in subhalocline water as late as the second week of May (SMETACEK et al. 1978).

The above interpretation of the results leads to some interesting implications regarding the dynamics of spring phytoplankton growth that should be of some general importance. For one thing, the decisive influence of weather in shaping day to day events is clearly demonstrated. The depth of mixing apparently changes with wind speed in the unstratified upper layer as indicated by the phytoplankton distribution in the water column. RYTHER and HULBURT (1960) have shown that the vertical distribution of phytoplankton can be independent of density and dissolved properties in the same water column. Such vertical inhomogeneity can be the result of growth in surface layers and downward mixing of the daily increment to a depth depending on the daily variations of physical factors. Processes such as sinking and vertical migration of motile organisms can also determine the position of plankton in the water column within a certain range of vertical mixing intensity. The distribution of the ciliate, *Mesodinium rubrum*, which is known to be a motile organism (LINDHOLM 1981) was much more restricted to the upper 10 m than the diatoms. LÄNNERGREN (1979) has shown that even diatoms can achieve positive buoyancy during spring bloom growth. This would enable them to maintain a desired depth, again within a certain turbulence range. One can conclude that phytoplankton cells, because of the great variation in sinking rates of at least a factor of 4 (TITMAN and KILHAM 1976) exercise control over their position in the water column to an extent greater than widely appreciated at present.

If phytoplankton cells are indeed constantly being mixed downward indefinitely in the absence of stratification, which is a basic assumption of the Sverdrup model, some sort of a stratification will be necessary before the spring bloom can start. If, however, mixing only occurs to a certain depth such as the bottom in shallow areas or to a shallow permanent halocline, the advent of the spring bloom will be determined by the seasonal increase in irradiation independent of any thermal stabilisation of the mixed layer. In the 20 m Kiel Bight for instance, the spring bloom occurs in March and stormy weather can delay it up to early April, but not later (SMETACEK and HENDRIKSON 1979). In this shallow region, growth and sedimentation of the bloom takes place rapidly, and as little as 10 days sometimes separate the advent and the disappearence of the bloom. Nutrients are totally stripped from the water column during this process and sedimentation is one short intense event (SMETACEK 1980, PEINERT 1981, POLLEHNE 1981).

Growth and sedimentation of the spring bloom becomes increasingly complex with progressively greater depth of mixing. Thus, in the Bornholm Sea, which is in the same latitude as Kiel Bight, the spring bloom starts in mid-April and lasts well into May. KAISER and SCHULZ (1978) state that thermal stratification in the Bornholm Sea is essential for the commencement of the spring bloom. Our results do not corroborate their statement and show instead that the depth of the mixed layer varies with atmospheric conditions even in unstratified water bodies. It can extend to the pycnocline or to the bottom during convective mixing, but is more restricted when the mixing is wind-induced. Thus, even in deeper areas, it would seem that increasing solar radiation and the concomitant deepening of the critical depth combined with increasing day length is a more decisive factor in initiating phytoplankton biomass build up than a lessening of wind-induced vertical mixing.

Intermittent vertical mixing due to changes in wind speed apparently leads to successive stages of biomass accumulation and dispersal with sedimentation events following calm periods during the later stages. The upward transport of nutrients into surface layers during this process leads to utilization of nutrients from a much greater water column than merely the euphotic zone. The spring bloom is ultimately terminated

by the development of thermal stratification (which occurred in the Bornholm Sea in mid-May) and the resultant barrier to upward transport of dissolved nutrients. One can presume that year to year variation in biomass production will depend not only on the initial nutrient concentrations but also on the pattern of thermocline development, i.e. the number and the intensity of mixing events between the start of biomass build up and eventual establishment of the thermocline. Sedimentation rates and their temporal sequence will also be determined by the same process and this in turn can be expected to affect the benthos. During the investigation period, zooplankton biomass was generally less than 10 % of phytoplankton biomass. The role of metazooplankton in influencing the course of the spring bloom is apparently a minor one in the Bornholm Sea as biomass of this pelagic component was low and not influenced by phytoplankton biomass build up.

Conclusions

1. In the Bornholm Sea the advent and development of the spring bloom is independent of the presence of a thermocline.
2. Development of the spring bloom takes place in a series of events whereby periods of low growth alternate with periods of enhanced growth and sedimentation.
3. Sedimentation of phytoplankton does not occur as a steady loss but rather as distinct events where a part of the population rapidly sediments out *en masse*. An appreciable portion of biomass produced by the spring bloom is eventually utilised by the benthos or accumulates on the bottom in anaerobic areas such as the Bornholm Basin.
4. The establishment of the thermocline eventually terminates the spring bloom by cutting off nutrient input in the euphotic zone via vertical mixing.

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References

ANDERSON, L. W. J. and B. M. SWEENEY, 1978. Role of inorganic ions in controlling sedimentation rate of a marine centric diatom *Ditylum brightwelli*. J. Phycol. **14**, 204–214.

GRASSHOFF, K., 1975. The hydrochemistry of landlocked basins and fjords. In: J. P. RILEY and G. SKIRROW (eds.), Chemical Oceanography **2**, 455–597. Academic Press.

GRASSHOFF, K., 1976. Methods of seawater analysis. Verlag Chemie, Weinheim, New York,317 pp.

KAISER W. and S. SCHULZ, 1978. On the causes for the differences in space and time of the commencement of the phytoplankton bloom in the Baltic. Kieler Meeresforsch., Sonderheft **4**, 161–170.

LÄNNERGREEN, C., 1979. Buoyancy of natural populations of marine phytoplankton. Mar. Biol., **54**, 1–10.

LINDHOLM, T., 1981. On the ecology of *Mesodinium rubrum*. Proc. 15th Europ. Mar. Biol. Symp., Kieler Meeresforsch., Sonderh. **5**, 117–123.

MARGALEF, R., 1978. Life-forms of phytoplankton as survival alternatives in an unstable environment. Oceanol. Acta **1**, 493–509.

PEINERT, R., 1981. Die Sedimentation von Plankton und Detritus unter verschiedenen Umweltbedingungen. Diplomarbeit Universität Kiel 70 pp.

POLLEHNE, F., 1981. Die Sedimentation organischer Substanz, Remineralisation und Nährsalzrückführung in einem marinen Flachwasserökosystem. Dissertation Universität Kiel. 149 pp.

RENK, H., H. TORBICKI and S. OCHOKI, 1975. Primary production in the Gdansk Deep. Merentutkimuslait. Julk./Havsforskningsinst. Skr. **239**, 45–48.

RYTHER, J. H. and E. M. HULBURT, 1960. On winter mixing and the vertical distribution of phytoplankton. Limnol. Oceanogr. **5**, 337–338.

SCHULZ, S., W. KAISER and G. BREUEL, 1978. The annual course of some biological and chemical parameters in the Arkona and Bornholm Sea in 1975 and 1976. Kieler Meeresforsch., Sonderheft **4**, 154–160.

SMAYDA, T. J., 1970. The suspension and sinking of phytoplankton in the sea. Oceanogr. Mar. Biol. A. Rev. **8**, 353–414.

SMAYDA, T. J. and B. J. BOLEYN, 1966. Experimental observations on the flotation of marine diatoms. II. *Skeletonema costatum* and *Rhizosolenia setigera*. Limnol. Oceanogr. **11**, 18–34.

SMETACEK, V., 1975. Die Sukzession des Phytoplanktons in der westlichen Kieler Bucht. Dissertation Universität Kiel. 151 pp.

SMETACEK, V., 1980. Annual cycle of sedimentation in relation to plankton ecology in Western Kiel Bight. Ophelia, Suppl. **1**, 65–76.

SMETACEK, V., K. v. BRÖCKEL, B. ZEITZSCHEL and W. ZENK, 1978. Sedimentation of particulate matter during a phytoplankton spring bloom in relation to the hydrographical regime. Mar. Biol. **47**, 211–226.

SMETACEK, V. and P. HENDRIKSON, 1979. Composition of particulate organic matter in Kiel Bight in relation to phytoplankton succession. Oceanol. Acta **2**, 287–298.

TITMAN, D. and P. KILHAM, 1976. Sinking in freshwater phytoplankton: some ecological implications of cell nutrient status and physical mixing processes. Limnol. Oceanogr. **21**, 409–417.

SVERDRUP, H. U., 1952. On the conditions for the vernal blooming of phytoplankton. J. Cons. Int. Explor. Mer **18**, 287–295.

UNESCO, 1966. Determination of photosynthetic pigments in seawater. Monogr. oceanogr. Methodol. (UNESCO) **1**, 1–66.

YENTSCH, C. M., CH. S. YENTSCH and L. R. STRUBE, 1977. Variations in ammonium enhancement, an indication of nitrogen deficiency in New England coastal phytoplankton populations. J. mar. Res. **35**, 537–555.

Primary production and sedimentation during austral spring in the Antarctic peninsula region.

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Running title: Production and sedimentation of Antarctic blooms

ABSTRACT

Phytoplankton biomass and composition, primary productivity (in-situ simulated and in vitro incubations) and sedimentation rates (measured with free-drifting sediment traps) were recorded in the Bransfield Strait area of the Antarctic peninsula during November/December 1980. Three distinct and persistent zones were encountered: low biomass comprising flagellates and diatoms in the Drake Passage and Scotia Sea (Zone I); high to moderate biomass of Phaeocystis and diatoms in the northern and central Bransfield Strait (Zone II); moderate biomass (Thalassiosira spp. in the process of forming resting spores) in the vertically homogeneous water on the northern Antarctic peninsula shelf (Zone III). Nutrient concentrations were high throughout; zooplankton

grazing relative to phytoplankton biomass and production was heavy in Zone I but negligible in the other 2 zones. Rates of primary production in the Zones I, II, and III averaged 230, 1660 and 830 mg C m^{-2} d^{-1} respectively. Assimilation numbers were low throughout (< 1 mg C (mg Chl.a)$^{-1}$ h^{-1}) and growth physiology of the zonal phytoplankton assemblages was basically similar.

Sedimentation rates recorded by 2 traps in Zone II were low (97 and 138 mg C m^{-2} d^{-1}) and higher (546 mg C m^{-2} d^{-1}) in a third trap which collected mostly euphausiid faeces. Sedimentation was heaviest in Zone III (450 - 1400 mg C m^{-2} d^{-1}) where collections of the 3 traps deployed were dominated by intact diatom frustules(Thalassiosira spp.) in chains and clumps. Spore formation and heavy sedimentation of diatoms thus also occurs at the end of Antarctic blooms in spite of high ambient nutrients. As approximately 2/3 of the diatoms in traps were resting spores, we suggest that sinking out of cells represents a seeding strategy which ensures regional persistence of neritic assemblages. Species-specific differences in seeding strategies may well be important in determining spatial and temporal patterns of Antarctic phytoplankton abundance. This aspect of phytoplankton biology is likely to have far-reaching implications, not previously considered, for the structure of Antarctic food webs.

INTRODUCTION

The growth period of Antarctic phytoplankton is generally restricted to a few months; HART (1934; 1942) showed that, even in this short period, seasonal changes in biomass and species composition occurred that were characteristic of different regions. For the region of the Bransfield Strait he reported a spring biomass maximum - comprising mainly neritic species - followed by a biomass decline and a shift in species composition into the summer. HART (1934) considered water column stability to

be the controlling factor for phytoplankton biomass build-up and speculated that zooplankton grazing was the most likely reason for its decline thereafter. Nutrients were not considered to play a decisive role in shaping plankton annual cycles as they were always present in excess of phytoplankton demand.

The questions pertaining to seasonality posed and speculatively answered by HART (1942) have rarely been addressed since then as most recent work on Antarctic phytoplankton has been carried out, for technical reasons, along long transects during the summer months (FOGG, 1977; SAKSHAUG and HOLM-HANSEN 1984). Large phytoplankton stocks of bloom dimensions have been encountered particularly in coastal waters (see FOGG, 1977; EL-SAYED, 1984 for reviews); however, little is known about the growth dynamics of Antarctic blooms and the fate of their biomass has not been specifically investigated yet. Thus, the factors controlling seasonal changes during the growth period in the Antarctic are not well documented (SAKSHAUG and HOLM-HANSEN 1984).

The aim of the present investigation, carried out in the Antarctic peninsula region during austral spring, was to locate a phytoplankton bloom and then to study its growth dynamics and the fate of its biomass, both by grazing and sinking, over a period of several weeks. We assumed that phytoplankton blooms were most likely to occur close to the retreating ice-edge as indicated by HART's (1934) observations as well as those of other authors (EL-SAYED, 1984), and also by studies from the Arctic (SAKSHAUG and HOLM-HANSEN, 1984).

In this paper, data on phytoplankton production and sedimentation are presented and discussed. The light:photosynthesis relationship studied during this cruise has been published elsewhere (TILZER, v. BODUNGEN and SMETACEK, 1985) as also the role of zooplankton grazing (SCHNACK, SMETACEK, v. BODUNGEN and STEGMANN, 1984) and distribution of bacterial biomass and activity (BÖLTER and DAWSON, 1982).

MATERIAL AND METHODS

The data presented here were obtained from 20 November - 14 December 1980 during cruise no.56/2 of RV METEOR. The complicated cruise track has not been included in Fig. 1 but station numbers indicate temporal sequence of sampling in the investigation area.

On our arrival in the investigation area, the pack-ice had retreated to the southern Bransfield Strait and still covered large areas of the shelf north of Joinville Island; the South Shetland Islands were free of pack-ice but large ice fields were still adrift in the area between Elephant and Joinville Islands. A pack-ice border per se was not present and the fluctuating ice conditions encountered by us prevented the ship from occupying a given position in the vicinity of ice for a longer period. Sediment trap deployments were also not possible for the same reason. Besides, phytoplankton abundance was independent of the ice cover. We accordingly modified our plans and conducted investigations both in the central Bransfield Strait as well as at the "ice-edge" on the southern shelf.

Temperature, salinity and in-vivo fluorescence of surface water was monitored continuously and 82 vertical profiles of these parameters and light attenuation were recorded down to 200 m depth with a combined probe (HAARDT and MAASSEN, 1983). In addition, detailed measurements of water column properties were carried out at 25 stations in the following order: the above-mentioned probe profiles, vertical light gradient with a spectroradiometer (HAARDT and MAASSEN, 1983) followed by discrete water bottle sampling from 12 depths and vertical zooplankton net hauls. Furthermore, 22 horizontal midwater-trawl hauls of various extent for sampling of krill and other macrozooplankton were carried out during the night.

The discrete sampling depths were fixed after evaluation of probe profiles. Five to eight samples were taken from the euphotic zone,

i.e. down to the 0.1% light level as determined with the spectroradiometer. The remaining 4 - 7 bottles taken from below the euphotic zone were spaced according to fluorescence profiles and water depth. The following parameters were measured: oxygen (Winkler titration), pH and alkalinity (after acidification), the nutrients ammonia, nitrite, nitrate, phosphate and silicate (according to GRASSHOFF, 1976). Suspended particles were filtered onto Whatman GF/C glass fibre filters and the following properties measured: dry weight (LENZ, 1971); organic carbon (POC) and nitrogen (PON) with a Hewlett Packard CHN-Analyser, Model 185B; total particulate phosphorous (TPP) according to GRASSHOFF (1976); chlorophyll a (Chl. a) spectrophotometrically using trichromatic equations (UNESCO, 1966); The chlorophyll data have not been corrected for phaeopigments.

Phyto- and protozooplankton were analysed qualitatively and quantitatively in water samples preserved individually with buffered formalin and Lugol's solution under an inverted microscope. Phytoplankton biomass was calculated from cell counts using appropriate factors (EDLER, 1979). Comparison with the chlorophyll and POC measurements indicate underestimation of biomass by this method by a factor of approximately 2.

Primary production was measured by the carbon-14-technique applying *in-situ* simulated incubation at ambient temperature; *in-vitro* incubation was carried out on the same samples at 0.5 ± 0.5 C and photosynthetic available irradiance of 40 $W\ m^{-2}$. Incubation generally began at 13.30 hrs ± 1h and lasted for 6 and 4 hrs for the *in-situ* simulated and the *in-vitro* incubations respectively. Samples were spiked with 10 µCi of radioactive bicarbonate and, immediately after incubation, filtered onto 0.45 µm Membrane filters, which were rinsed with acidified filtered seawater (pH 3-4). Filters were dissolved in a Dioxan scintillation fluid and radioactivity was counted in a Beckman LS 100C

counter. Daily production was calculated by multiplying the value for the incubation time by the ratio of daily incident light to incident light during incubation. Incident light was measured with a Pyrrheliometer on ship deck. More details of the primary production measurements are given by TILZER et al. (1985).

A free-drifting sediment trap was deployed on 6 successive occasions for periods of 7 - 30 hrs. Individual deployments are referred to as Trap 1 - 6. Trap locations are indicated in Fig. 1. The trap consisted of two "Kiel-funnels" (ZEITZSCHEL, DIEKMANN and UHLMANN, 1978) each with a single collection glass. No preservative was used. Traps were suspended at 100m water depth and at 75 m at Sta. 116. After recovery, material of each collection glass was gently removed, examined under a microscope and photographed. Thereafter, the contents of each glass (glasses of traps 1 and 2 were not processed separately) were suspended in filtered sea water after gently washing the material through a 300 µm gauze. Large firm particles such as zooplankton carcasses were retained by the gauze and later discarded but loose aggregates and fragile zooplankton faeces were dispersed by this treatment. Aliquots of the suspension were filtered over Whatman GF/C filters and a portion was preserved with formalin for later quantitative microscope evaluation. Dry weight, POC, PON, TPP and Chl. a was measured on the filters as described above.

Three polyethylene tanks (1 m^3) were filled with untreated surface water and growth of the plankton population at ambient temperature observed over 1 - 3 weeks on shipboard. One tank was filled at each of stations 28, 33 and 97 (Fig. 1). Water in the tanks was stirred only once a day prior to sampling. Light supply was aproximately 40% of incident light. Nutrient uptake, dry weight, POC, PON, TPP, Chl. a and phytoplankton biomass and composition were monitored at 1 - 2 day intervals.

The weather was unusually calm throughout the investigation period, by Antarctic standards, although storm activity was reported from the area prior to our arrival. Surface registrations and vertical probe profiles revealed the presence of hydrographically distinct and persistent zones in the investigation area that differed in terms of total plankton biomass and species composition, as well as its vertical distribution. Nutrient concentrations were high throughout. A detailed presentation of phytoplankton distribution in relation to hydrography will be given elsewhere. Here, we shall briefly describe the chief characteristics of the zones outlined in Fig. 1. Water column properties are summarized in Table 1 and Figs. 2, 3.

Zonation of phytoplankton biomass and composition

The ice-free waters of the Drake Passage and Scotia Sea comprised Zone I. Phytoplankton biomass was low (< 1 mg Chl *a* m^{-3}) and homogeneously mixed down to the pycnocline at 70 - 100 m depth. The dominant phytoplankters were flagellates (*Distephanus* and nanoflagellates) and diatoms (*Corethron* and small pennates) were of lesser importance. Zooplankton grazing pressure was high relative to biomass and production rate of the phytoplankton (SCHNACK et al., 1984).

Zone II extended from the shelf of the South Shetland Islands, across the Bransfield Strait to the edge of the shelf north of Joinville Island. The zone was sharply separated from Zone I to the North and bounded to the south-east by drifting ice fields. This Zone was hydrographically complex and will be distinguished for convenience into 2 sub-zones on the basis of density structure and also biomass which was dominated by *Phaeocystis* and the diatoms *Thalassiosira* and *Corethron*. Zone IIa was characterized by 2 weak pycnoclines - one at 20 - 40 m and the other at 60 - 120 m depth. Biomass in the surface layer was

higher (5-10 mg Chl.a m^{-3}) than in the deeper layer (2 - 5 mg Chl.a m^{-3}).

The plankton-rich surface layer of Zone IIa was separated by a prominent front in the central Bransfield Strait from a somewhat poorer Zone IIb to the South. Phaeocystis was of lesser importance here, and the degree of variability was greatest in this sub-zone (Fig. 3). As a rule, only one pycnocline, located at 50 -70 m depth was present. The differences between the sub-zones were most evident in the fluorescence profiles but less so in the discrete measurements (Fig. 2). Vertical fluorescence distribution was always correlated with that of temperature and/or salinity, indicating that biomass distribution was primarily related to that of the water masses and as such reflected their respective past histories. Zooplankton biomass was lower than in Zone I and accordingly grazing pressure on the large phytoplankton stock was negligible. A few krill were collected by trawling in Zone IIb.

To the South, Zone IIb merged into Zone III, located on the broad shelf ($<$ 200 m deep) off Joinville Island but separated from it by a narrow, deep canyon. The phytoplankton of Zone III consisted almost entirely of diatoms (chiefly Thalassiosira but also Biddulphia and Chaetoceros). The depth of vertical homogeneity increased landwards and was most prominent in the southernmost stations. Chlorophyll concentrations, more or less homogeneously distributed to the bottom, ranged between 2 - 6 mg Chl.a m^{-3}; the easterly stations of Zone III tended to have the lower biomass levels. At Sta. 96, situated over a canyon, vertical homogeneity in all properties including phytoplankton biomass extended down to 300 m depth. Thus, biomass stocks in this Zone rivalled, on a m^{2} basis, those of Zone IIa where much higher concentrations were found, albeit restricted to the shallow surface layer. Water column homogeneity was maintained throughout the study period, and was not a result of continuous storm activity as, on occasion, we experienced periods of flat calm in this Zone. The Thalassiosira population was undergoing resting spore formation. Zooplankton biomass and grazing

pressure were also very low here and no krill was found.

Primary production

Primary production was more or less a function of light and biomass (Figs. 2 and 3). Maximum values at stations in Zones I, IIa, IIb, and III ranged between 0.19-0.53, 4.88-10.35, 1.54-4.05 and 1.24-4.63 mg $C\ m^{-3}\ h^{-1}$ respectively. Maximum production rates occurred at depths with 30 to 10 % of incident light, corresponding to a photosynthetically available radiation between 100 and 20 $W.m^{-2}$. Light inhibition appeared to occur above the depth of maximum production as indicated by the depressed photosynthetic rates at the surface. This effect is possibly an incubation artifact, since phytoplankton is exposed for longer time periods to surface light intensities in the bottles than it presumably would be in the well mixed euphotic layer (LEWIS, CULLEN and PLATT, 1984). Thus, primary production rates on an areal basis were probably underestimated by this method. Serious light stress of surface phytoplankton was not evident from the photosynthetic rates obtained from in-vitro measurements (Fig. 3).

The mean maximum photosynthetic rates derived from the in-situ measurements were 0.49±0.25, 0.74±0.30, 0.87±0.39 and 0.71±0.26 mgC (mg Chl.a)$^{-1}$ h^{-1} and from the in-vitro measurements 0.81±0.25, 0.80±0.15, 0.94±0.40 and 0.64±0.14 mg C (mg Chl a)$^{-1}$ h^{-1} for Zones I, IIa, IIb and III respectively. These numbers and a comparison of the profiles in Fig. 3 indicate that there were no basic differences in photosynthetic capacity between the plankton populations of the 3 zones. In a more detailed analysis of the light-photosynthesis relationship, TILZER et al.(1985) found that variability within each zone and even within a given water column was often in the same range as that between zones.

The similarity in growth characteristics of phytoplankton from different assemblages was also reflected in specific growth rates

calculated from primary production and POC data from depths of maximum production. Only stations with C:Chl *a* ratios below 100 were considered, i.e. only from Zones II and III. Average rates and ranges, as doublings per day calculated from the expression given by EPPLEY (1972), were 0.32 (0.17 - 0.75) and 0.32 (0.13 - 0.81) for Zones II and III respectively. These values are underestimates as the POC at all stations comprised some detrital material. The maximum values lie well within the range calculated for low temperatures from thermodynamic models (EPPLEY, 1972), and further indicate that, for the given temperature regime, the phytoplankton in these zones was in reasonably "good" physiological condition. This is also substantiated by the low C:N and C:P ratios of the suspended material from surface layers of all zones (Tables 1, 2).

Similar growth performance was recorded from the tank populations (collected from Zone III), maintained at ambient temperatures. Primary production rates in the tanks were not estimated by the carbon-14 method but from POC increments. In all tanks, the enclosed population grew, until nitrate depletion, at rates within the same range as maximum rates recorded in the water column. The maximum biomass (measured as POC) attained was 3.29, 2.69 and 2.78 g C m^{-3} for tanks 1 - 3 respectively. Photosynthetic rates, averaged over five days of exponential growth, were 1.28, 0.60 and 1.72 mg C (mg Chl.*a*)$^{-1}$ h^{-1} and specific growth rates during the same period were 0.70, 0.41 and 1.07 d^{-1} for tanks 1, 2 and 3 respectively. The tank populations grew under optimal light conditions (40 % of surface light) and the above values can well be regarded as maxima for the assemblage.

Trap collections

When interpreting trap data, it is important to bear in mind that the collection efficiency of a trap depends on several independent factors pertaining to its configuration, degree of turbulence at its mouth and

the sinking rates of particles entering the traps (SMETACEK, v. BRÖCKEL, ZEITZSCHEL and ZENK, 1978; GARDNER, 1980). The traps employed by us have been specially designed to reduce turbulence at the mouth and their collection efficiency under field conditions has been shown to compare favourably with that of cylinders with a height to diameter ratio of >4:1 (SAURE, 1981), which are reported to provide the most realistic estimates of vertical flux (BLOESCH and BURNS, 1980). Further, the efficiency of sediment traps is improved if they are free-drifting rather than moored, as this reduces turbulence around the mouth of the trap (STARESINIC, ROWE, SHAUGHNESSY and WILLIAMS, 1978). Variation in data from individual funnels within the same trap array was always less than 10%, hence, only the mean value for the two funnels are presented here. The composition of material collected in the traps of Zone II (Traps 1 - 3) varied considerably whereas the traps in Zone III (Traps 4 - 6) collected essentially similar material. Zooplankton faeces dominated collections in Zone II but were scarce in Zone III. Only krill faeces (long, thread-like, fragile and fluffy-looking) and calanoid faecal pellets (sausage-shaped, compact, with one tapering end) could be identified. The former dominated collections in Traps 2 and particularly 3. Copepod faecal pellets were a minor constituent despite the fact that copepods vastly dominated zooplankton biomass (Schnack et al, 1984). The foraminifer Globoquadrina pachyderma was present in large numbers in Trap 1 (26,000 individuals $m^{-2}\ d^{-1}$), but was of lesser importance in Traps 2 and 3 and totally absent in Traps 4 - 6 of Zone III. Intact and apparently viable diatom cells dominated the sedimented material of Zone III but also contributed significantly to Traps 1 and 2. The percentage contribution of biomass of intact phytoplankton cells to trapped POC is given in Table 2. As mentioned in the method section, these figures are underestimates. The large amounts of phytoplankton collected by the traps in Zone III

cannot be simply attributed to the high phytoplankton concentrations in the vicinity of the traps. Studies from other localities (SMETACEK, 1980; PEINERT, SAURE, STEGMANN, STIENEN, HAARDT and SMETACEK, 1982) have shown that when traps are suspended within the mixed layer, phytoplankton cells do not accumulate in them as long as the population is growing. The increase in cell sinking rate that accompanies the cessation of growth (SMETACEK, 1985), however, results in mass collection of cells.

Thalassiosira spp. dominated the phytoplankton in all trap collections and settled out in 3 forms: a) extraordinarily long chains of up to 150 cells, b) short chains and single cells and, c) compact gelationous clumps tightly packed with 50-150 frustules. The latter are apparently formed autonomously from open chains as reported by SMETACEK, v.BODUNGEN, NÖTHIG and BATHMANN (in prep.). The majority of cells in chains and clumps contained resting spores ($\sim$65%). Long chains were collected only in Zone III but clumps were found in all traps, particularly in Trap 2, where their relative contribution to total particles was greatest. However, the largest numbers of clumps occurred in the collections of Zone III.

The lowest sedimentation rates were recorded with Traps 1 and 2 and the highest with Trap 6 (Table 2) which is also true when sediment trap yield is expressed as percentage of standing stock and primary production of the 100 m water column (Table 3). Elemental composition of the material differed significantly between Traps 1 - 3 but was basically similar in Traps 4 - 6. The high inorganic contribution in Trap 1 can be attributed to foram shells and in Traps 4 and 6 to 50-100 µm sand grains of various shape and colour. The fact that these traps, suspended 50 - 100 m above the bottom, collected sand grains is an indication of the intensity of vertical mixing in the water column of Zone III. Surprisingly, the POC:Chl a ratios in material of all traps were essentially similar and significantly lower than in material suspended

in the water column (Table 2). This is further proof that traps did not merely accumulate material from their surroundings but rather collected particles selectively, presumably on the basis of sinking rates. The high chlorophyll content of resting spores is also indicated by these results. The low POC:Chl a ratios from Trap 3, where krill faeces dominated, is particularly surprising. It is most likely that chlorophyll was present as phaeopigments in the faeces which would mean that the actual pigment content, including chlorophyll break-down products, was even higher as the latter were underestimated by the method employed by us. The fairly high C:N and C:P ratios indicate that some of the material at least was indeed digested.

DISCUSSION

The factors controlling primary productivity and phytoplankton abundance in Antarctic waters have been discussed frequently (HART, 1934, 1942; FOGG, 1977; TRANTER, 1982; EL-SAYED, 1984; SAKSHAUG and HOLM-HANSEN, 1984). In this connection it is important to distinguish between factors such as light, temperature and nutrients that control cell growth rates and others such as water column stability, grazing and sinking that control the accumulation rate of cells in the euphotic zone and hence growth of the population (WHITAKER, 1982). In the following, we shall discuss the possible role of each of these factors in shaping the distinct zonal distribution of phytoplankton encountered by us.

Factors influencing specific growth rates

Light: The zones were spatially too small and the biomass differences too sharply delineated to have been affected by such a global factor. Ice cover was also not of direct importance: Zone I, with the smallest population had been ice-free longest and Zone III, the only zone still

with some degree of ice-cover, had already developed a large standing stock. Further, the photosynthesis:light relationship in phytoplankton of the three zones was basically similar and varied as much within zones as between them (TILZER, et al., 1985). No evidence of specific adaptation to low light levels in the assemblages encountered were found.

Temperature: The distinct albeit slight temperature differences between zones were not reflected in the basically similar growth characteristics of the 3 phytoplankton assemblages. Assimilation numbers and calculated specific growth rates were in the same range in all zones and also in the tank populations. HOLM-HANSEN, EL-SAYED, FRANCESCHINI and CUHEL (1977) also reported values in the same range as ours from Antarctic waters. NEORI and HOLM-HANSEN (1982) conclude that the low rate of photosynthesis in Antarctic waters is a result of temperature limitation. Surprisingly, the maximum rates were found at stations 23-25 in Zone IIb where temperatures were amongst the lowest recorded.

Macronutrients: Production rates were not controlled by macronutrients as they were at high concentrations throughout.

Micronutrients: The possible role of micronutrients in controlling phytoplankton abundance in the Antarctic has been suggested for a long time and most recently by CARLUCCI and CUHEL (1977) and JAQUES, DESCOLAS-GROS, GRALL and SOURNIA (1979). However, HAYES, WHITAKER and FOGG (1984) detected no significant effect of micronutrient enrichment on Antarctic phytoplankton. We take the basic similarity in growth physiology of surface phytoplankton populations in the widely differing water masses comprising the 3 zones and from the tank populations as an indication that they were not rate-limited by any micronutrient such as vitamins or trace elements.

We conclude that the interzonal differences in phytoplankton abundance were not due to corresponding differences in specific growth rates of

the various assemblages. Thus, factors controlling the accumulation rate of cells in the euphotic zone are most likely to have been responsible for the zonal differences encountered by us.

Factors influencing accumulation rates

Water column stability: The zonal pattern of phytoplankton distribution clearly reflected the hydrography of the investigation area as described by CLOWES (1934), PATTERSON and SIEVERS (1980) and STEIN and RAKUSA-SUSCZEWSKI (1984). On the basis of a large-scale survey of surface phytoplankton distribution in the Antarctic, HAYES et al. (1984) concluded that "phytoplankton distribution is strongly influenced by features of hydrography and bottom topography". PATTERSON and SIEVERS (1980) have commented on the complex relationship between hydrography and topography of this area as a result of which small-scale patchiness in phytoplankton distribution can be expected. We shall consider the complicated situation encountered by us in greater detail elsewhere; here we shall dwell shortly on the possible relationships between past history and phytoplankton populations of the water masses comprising the various zones.

Zone I had the longest growth history as indicated by the well developed zooplankton population and the high POC:Chl.a ratios brought about by accumulation of organic detritus (probably the result of zooplankton grazing) in the surface layer. The deep mixed layer prevented optimal utilization of light, thus suppressing biomass build-up. SAKSHAUG and HOLM-HANSEN (1984) speculate that 50 m is the maximum depth of the mixed layer in which Antarctic blooms can develop; they observed high chlorophyll concentrations (>2 mg m^{-3}) only at stations where the pycnocline was above 40 m depth. The large phytoplankton population in the shallow surface layer of Zone IIa confirms their observations. In the deeper mixed layer of Zone IIb, phytoplankton concentrations were accordingly lower. However, the large standing

stocks in the well-mixed waters of Zone III would seem to contradict the presence of such a relationship; this large standing stock could not possibly have been built-up under the conditions encountered by us. Rather, we assume that in Zone III, deep mixing commenced after a massive Thalassiosira bloom had accumulated in a previously stratified water body. Such stratification could have been present under a more extensive pack ice cover earlier in the year. The presence of resting spores in this population also suggests that the bloom had passed its peak. The fact that in-vitro photosynthesis rates and the C:Chl.a ratios had not declined does not contradict this view: such behaviour can be expected only if bloom development is terminated by nutrient depletion which was evidently not the case here. Furthermore, as diatom resting spores contain chlorophyll and are capable of photosynthesis (FRENCH and HARGRAVES, 1980), their formation would not necessarily result in significant change in short-term growth performance of the population. The situation in Zone II was more complicated and not the result of deep vertical mixing; apparently, the complex vertical stratification of density and biomass, most apparent in Zone IIa, reflected recent overlayering of different water masses with differing past histories.

Grazing: Copepods were the most important grazers in the 3 zones. Their grazing pressure in Zone I was equivalent to approximately 50 % of daily primary production, whereas it was less than 1 % in zones II and III (SCHNACK et al., 1984). The low biomass of Zone I can be partly but not entirely attributed to heavy grazing pressure: the bulk of zooplankton biomass here was contributed by copepodids indicating that grazing pressure had increased well after the start of the phytoplankton growth season. Protozooplankton biomass was negligible throughout and krill was only collected in noteworthy numbers by mid-water trawling in Zone I, and occasionally in small numbers in Zone II. However, the presence of scattered swarms in Zone II - presumably

juvenile forms because of the relatively small faeces ($\lesssim$ 100 um diameter) - was clearly indicated by trap collections. Organic carbon loss from the water column above Trap 3 was equivalent to a day's primary production and 8 % of the standing stock. Mid-water trawling in the vicinity of the trap failed to collect krill which we take as an indication that only a small swarm must have passed over the trap during its deployment. Krill distribution is known to be highly patchy (HAMNER, HAMNER, STRAND and GILMER, 1983). Our results suggest that arrays of sediment traps located at a few hundred meters' depth may well prove useful in monitoring krill distribution and feeding activity. Thus, krill grazing pressure is likely to have been patchy and locally intense but certainly not of importance in controlling phytoplankton biomass build-up. HARDY and GUNTHER (1935), BIGGS (1982) and WITEK, PASTUSZAK and GRELOWSKI (1984) also reported low grazing pressure in Antarctic blooms encountered by them.

Sinking: Antarctic diatoms tend to be larger and, because of the abundance of silica, also have more robust frustules than those from silicate-poorer waters. Accordingly, one would expect the former to exhibit higher sinking rates than the latter. However, it is a well-known fact that the sinking rate of live diatoms is a function of their physiological condition as well as size and specific gravity: healthy, growing cells have lower, and senescent cells and resting spores from the same population have higher sinking rates (SMAYDA, 1970; SMETACEK, 1985). The trap collections clearly show that this rule also applies in the Antarctic. Loss due to sinking out of vegetative cells from the vigorously growing population of Zone II was low and even in the light-depleted population of Zone III, a far greater proportion of resting spores as compared to vegetative cells was collected by the traps. The fact that phytoplankton vertical distributions in all zones closely matched those of density indicates that selective movement of cells due

to sinking was not of importance prior to and during the investigation period. Thus, sinking does not pose a greater problem to growing Antarctic phytoplankton populations than it does to populations from other regions. The important role of sinking in non-growing populations is, however, another matter and will be discussed in the next section.

We conclude that the interaction between hydrography and topography is the single most important factor influencing build-up of phytoplankton blooms in the area and we join HART (1942), FOGG (1977), TRANTER (1982) EL-SAYED (1984) and SAKSHAUG and HOLM-HANSEN (1984) in suggesting that this applies to Antarctic waters in general. The Bransfield Strait area is known to be more productive than the adjoining waters of the Drake Passage (FOGG, 1977). However, this distinction applies only to the spring period as much lower biomass levels appear to be the rule in later months (v. BRÖCKEL, 1981; EL-SAYED, 1984). This marked seasonal difference in biomass and hence productivity was commented on by HART (1934) and more recently by WITEK et al. (1983). Investigations carried out by SCHNEIDER (1983) in the same area in the following summer (January/February 1981) during leg 4 of RV METEOR cruise no. 56 also revealed low levels of biomass (< 1 mg Chl. $\underline{a}$ m^{-3}). The question then arising is: what is the eventual fate of the large spring bloom biomass? WHITAKER (1982) also posed this question but could not provide a definitive answer. SAKSHAUG and HOLM-HANSEN (1984) suggest that stability erosion combined with heavy grazing are the most likely reasons for termination of Antarctic blooms. However, observations supporting this view are lacking. The data at our disposal do not provide direct evidence but nevertheless permit the formulation of some tentative conclusions. The disappearance of a large phytoplankton stock can be brought about by any of 4 factors: 1) dispersal by horizontal and/or deep vertical mixing, 2) zooplankton grazing, 3) natural mortality and plasma breakdown within the surface layer, and 4) sinking of

living or dead cells to deeper water layers or the bottom. The possible role of each of these factors is discussed below.

Fate of bloom biomass

Dispersal by mixing and advection: In one year, but not in 2 others, WHITAKER (1982) found a major rapid decline in production in inshore water off Signy Island following mixing by a severe storm. Such storm events can well serve to rapidly disperse a spatially restricted inshore bloom; however, the extensive blooms found by us could hardly be dispersed by mixing within a few weeks as a dilution factor of 1:10 would be necessary to reduce chlorophyll concentrations to the low values found subsequently by SCHNEIDER (1983). The other possibility, viz. large-scale horizontal advection, is also an unlikely explanation for two reasons: a) The residence time of water in the investigation area is prolonged by the presence of a series of cyclonic gyres that retard the general eastward flow through the Bransfield Strait (GRELOWSKI and PASTUSZAK, 1983). The situation encountered by us, for instance, persisted for over 3 weeks. b) We found that large phytoplankton stocks extended at least to the southwestern opening of the Bransfield Strait; this water would then have replaced that of the northeastern opening in the event of strong horizontal advection. In short, the large phytoplankton stocks of such an extensive area could not possibly have been dispersed by vertical or horizontal water movement within two months.

Zooplankton grazing: In the weeks following our observations, grazing pressure on the blooms might well have increased drastically. HART (1942) speculated that grazing was the cause for the decline of the spring maximum. However, he mentioned that neritic species such as Thalassiosira vanished much more rapidly than oceanic ones such as Corethron. SCHNEIDER (1983) also found that Thalassiosira spp. were rare in the Bransfield Strait in summer. Selective grazing by zoo-

plankton such as copepods might be responsible but we feel this to be a tenuous explanation in the present context. Krill abundance in the investigation area was much higher later on in the season (STEIN and RAKUSA-SUSZCZEWSKI, 1984) but the swarms were too patchily distributed to have made significant inroads into the large phytoplankton stocks. WITEK et al. (1983) studied net-phytoplankton and zooplankton distribution and abundance in the Bransfield Strait area over several months. They report that spring bloom biomass decreased before that of zooplankton increased. Further, on the basis of rough calculations, they showed that zooplankton including krill biomass build-up during the entire season was much too low to account for the decline in spring bloom biomass observed by them.

Natural mortality and breakdown within the surface layer: Although the importance of this process cannot be dismissed, we have little evidence that it can account for the phytoplakton biomass decline from spring to summer. Plasmolysed cells were frequently observed by KARSTEN (1905) and also by us. However, the significance of these observations is not yet apparent.

Sinking: Rapid, mass sedimentation of diatom cells is an important process in eliminating bloom biomass from surface layers of many coastal and shelf localities (WALSH, 1983; SMETACEK, 1984, 1985); although direct evidence is lacking, our observations and those of other authors (KARSTEN, 1905; HARDY and GUNTHER, 1935; WHITAKER; 1982) as well as considerable circumstantial evidence strongly suggest that this can well be an important process in the Antarctic as well. Thus, none of the factors dealt with above, singly or in combination, provide a satisfactory explanation for the well-documented decline of Antarctic spring blooms. In the following, we shall present arguments supporting our hypothesis that mass sinking of phytoplankton blooms is of major importance in the Antarctic and then discuss some of the implications of this process for the ecosystem.

Role and significance of mass sinking

Factors triggering mass sedimentation: In other localities, mass sedimentation of diatom blooms is triggered by nutrient depletion (SMETACEK, 1985) which does not occur in the Antarctic. However, the same applies to resting spore formation by diatoms which is reported to be triggered only by nitrogen depletion (HARGRAVES and FRENCH, 1983); if this were the only triggering mechanism, then resting spores would be rare in Antarctic phytoplankton. Nevertheless, KARSTEN (1905), HART (1934, 1942) and DOUCETTE and FRYXELL (1983), reported resting spore formation in various Antarctic diatoms and our results confirm their observations. Thus, factors other than nitrogen depletion must trigger resting spore formation and it seems reasonable to assume that the same will apply to the initiation of mass sedimentation as the two processes tend to occur concomitantly (SMETACEK, 1985). DOUCETTE and FRYXELL (1983) have argued that deterioration of the growth environment - other than nutrient depletion - must trigger resting spore formation in Antarctic phytoplankton. They suggest that reduction in light supply might be such a triggering factor. Although not supported by culture experiments (ELBRÄCHTER, pers. comm.) our observations support this hypothesis: both the obviously light-depleted population of Zone III and portions of the Zone II population - below the upper pycnocline - were engaged in forming resting spores. Light reduction in this case was not related to seasonal but to hydrographical factors. Further, in Kiel Bight, spore formation and mass sedimentation of autumn diatom blooms (in November) have been observed in the presence of high nitrogen concentrations (GRAF, SCHULZ, PEINERT and MEYER-REIL, 1983; CZYTRICH, EVERSBERG, NOJI and PASSOW, unpubl. data). The triggering factor here appeared to be seasonally induced reduction in light supply in conjunction with increased storm activity. The relationship between spore formation and light deprival due to deep mixing will be more

complex than in the case of nutrient depletion which is experienced by the entire population simultaneously. More work on this important aspect of phytoplankton ecology is called for.

Evidence from sediment traps: We have argued above that trap collections provide a measure of the potential sinking behaviour of a given population. Thus, the large collections of phytoplankton cells and particularly resting spores in the traps of Zone III indicate that at least a portion of the population had high sinking rates. The many small sand grains collected by the traps suspended 50 to 100 m above the bottom indicate that turbulence at the sea bed was high; it was thus unlikely that material equivalent to that collected in the traps was also accumulating on the sea bed at the time. However, the intense mixing in progress during the investigation period must have been a transient phenomenon as it was apparently not present during the preceding growth phase of the bloom. Presumably, slight horizontal advection of the water mass or a change in mesoscale hydrography following further retreat of the ice cover could well have resulted in decreasing turbulence. Under such conditions, rapid mass sinking of a significant portion of the phytoplankton population can be expected, all the more so, since, by then, an even greater proportion of the population would have formed resting spores and clumps. A similar fate can be construed for the Zone II population as the shallow mixed layer here can also be regarded as having been a transient phenomenon. Summer mixed layer depths in the area are, as a rule, much deeper than those recorded by us (PATTERSON and SIEVERS, 1980; SCHNEIDER, 1983).

Evidence from the sediments: The sediments of the area are extremely rich in organic matter even at great depths indicating this to be a region of heavy pelagic sedimentation. Vertical particle flux in the sea is generally thought to be dominated by zooplankton faeces (ANGEL, 1984) which implies that sedimentation rates will be a function of grazing. As indicated above, zooplankton grazing can only account for a

portion of the phytoplankton biomass produced in the area. Further, our trap collections and those of SCHNACK (subm.) indicate that only krill faeces (and possibly those of other macrozooplankters such as salps) but not those of copepods can be of importance to vertical flux. SMETACEK (1985) has argued that this is a general phenomenon. On the basis of results from sediment traps moored at depths of 300, 500, 1000 and 1400 m, GERSONDE and WEFER (1984) conclude that krill faeces tend to disintegrate within the upper 1000 m water column during descent. The contents of krill faeces are finely shredded (FOWLER and SMALL, 1972; our observations) and subsequent sinking of this fine material following faeces disintegration will be significantly retarded. GERSONDE and WEFER argue that the large amounts of intact frustules in the sediments indicate that direct sedimentation of frustules rather than their prior incorporation into krill faeces is the process dominating vertical flux to the deep sediments. Their conclusions are substantiated by the detailed observations of surface sediments in the Antarctic peninsula region by NEAVERSON (1934) who found that intact frustules of phytoplanktonic diatoms, often in loose aggregates and sometimes still containing plasma, were prominent in surface sediments of many stations along various transects in the Bransfield Strait. Water depths where large quantities of intact diatom frustules were found ranged between 100 and 4000 m depth.

Evidence from phytoplankton species succession: The role of sinking in planktonic diatom life history cycles has been discussed at length by SMETACEK (1985) who suggests that the mass sinking characteristic of bloom diatoms represents the transition from an active surface-growing stage to a resting stage positioned in deep water or on the sediment surface. The resting stages have higher sinking rates than vegetative cells. These refuge populations then provide seed cells for the next growth season. Different species are likely to differ with regard to

seeding and hence sinking behaviour and the significance of such seeding strategies in determining spatial and temporal patterns of occurrence of different species, first suggested by KARSTEN (1905), has been discussed by SMETACEK (1985). Their role is likely to be even more important in the Antarctic than elsewhere for reasons discussed below. Antarctic phytoplankton must withstand a prolonged period of highly unfavourable growth conditions. Thus, overwintering stages will have to be dormant and positioning of these stages will be of considerable survival value for the species concerned (KARSTEN, 1905). HART (1934, 1942) classified Antarctic diatoms according to patterns of spatial and seasonal distribution. He distinguished the diatom genera contributing most to the spring biomass maximum into two groups: those that do not decline rapidly after attainment of the peak (e.g. Corethron) and those that do (e.g. Thalassiosira). The former tend to be oceanic and the latter neritic or associated with pack-ice in their distributional characteristics. Phaeocystis is also considered to be neritic (KARSTEN, 1905) and JONES and HAQ (1963) suggested that it has a benthic resting stage. HART (1942) pointed out that species that formed resting spores belonged to the latter group which he termed "meroplanktonic". Thus, HART (1942) clearly implied that sinking of the resting spores to the sea bottom following the spring maximum would be an important feature in the life histories of these species. WITEK et al. (1983) also commented on the marked paucity of net-phytoplankton on the shelves following the spring maximum in contrast to the more oceanic areas. The conclusion here is that loss rates of coastal and shelf plankton are greater than in the case of their open ocean counterparts and that this difference is related to species-specific differences in behavioural response to the advent of unfavourable growth conditions. Thus, genera such as Thalassiosira will have mechanisms for increasing sinking rates concomitant with deterioration of the growth environment. Other genera such as Corethron will tend to retain seed cells within the water

column (KARSTEN, 1905). The latter strategy will enable wide dispersion within the extensive circumpolar current system whereas transient appearance in the water column will permit regional persistence in shallower areas. Some species with pelagic resting stages might even exploit deep counter-currents to maintain regional persistence as suggested by KARSTEN (1905) and HARDY and GUNTHER (1935).

Environmental selection of seeding strategies will be manifested in the mechanisms by which seeding stages are retained in the region during the winter and returned to surface layers at the onset of the growth season. Although the mechanisms are not yet quite clear, turbulent mixing and upward entrainment of seeding cells is likely to be important in shallow areas. WHITAKER (1982) observed massive Thalassiosira blooms in the (~20 m) shallow Borges Bay of Signy Island in 3 successive years. The convoluted coast-line and broad shelf of the Antarctic peninsula region provides many similarly suitable locations for deposition of seed beds. The interaction between topography and hydrography thus not only determines biomass build-up but can also influence the species composition of the phytoplankton. Conversely, as more information on details of phytoplankton biology accumulates, their species composition might well provide useful information on the past history of Antarctic water masses. One interesting aspect is the role of sea ice as a seed bed and transport medium for "meroplanktonic" species that was also suggested by HART (1934). However, the mechanisms by which seeding cells are incorporated into the ice, which forms at a time when such species are rare in the water column, have not been studied. HEMPEL (pers. comm.) suggests that ice which forms on the shelf sea bed and then rises with its sediment load to the surface, might represent such a mechanism. Other possible mechanisms have been discussed by TRANTER (1982).

Ecological implications of phytoplankton seeding strategies

Phytoplankton seeding strategies can have considerable effect on the ecosystem, not only in terms of transfer of biomass from pelagic to benthic subsystems but also with regard to the absolute amount of biomass available to pelagic and benthic heterotrophs. Thus, macro-nutrients do not control the size of the bloom biomass peak as they tend to do in most oceans where nutrient depletion limits further growth of phytoplankton blooms. This is because stratification is either deep or transient in the Antarctic. Assuming that there are indeed no fundamental differences in growth rates amongst Antarctic diatoms, then the size attained by a given bloom population will be determined by its history of light supply and the size of the initial seed population. The larger the latter, the larger the eventual size of the bloom prior to outbreak of unfavourable conditions.

It is obvious that phytoplankton seeding strategies will be accompanied by high mortality as only a small portion of the resting cells sinking out of the water column will succeed in colonizing a suitable area and benthic grazers will still further reduce the number of potential seed cells. The large benthic stocks of the Antarctic shelves (DELL, 1972) can be partly explained by the presence of this rich food supply. If sedimentation of phytoplankton is indeed an important process in shelf environments, it follows that the sea bed here will be a richer source of food over a longer period of the year than the water column. Interestingly, krill, which is generally considered to live and feed entirely in the water column (KILS, 1978) has recently been observed on the sea bed (HUNTLEY, pers. comm.) and has also been found in the stomachs of demersal fish (PERMITIN, 1970). HAMNER et al. (1983) observed krill feeding on the under-surface of ice in a mode which differed strikingly from that employed in collection of suspended particles in the water column. Possibly, this feeding mode could also be effective on the sediment surface which would provide an additional

explanation for the apparent lack of dormancy in krill, viz. that they feed on the sediment surface when food supplies in the water column or ice are scarce. Thus more knowledge on the biology of Antarctic organisms is likely to yield interesting information on seasonal changes in the structure of Antarctic food webs.

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LITERATURE REFERENCES

ANGEL M.V. (1984) Detrital organic fluxes through pelagic ecosystems. In: Flows of energy and materials in marine ecosystems: theory and practice, M.J.R. FASHAM, editor, Plenum Press, pp. 475-516.

BIGGS D.C. (1982) Zooplankton excretion and NH_3-cycling in near surface waters of the Southern Ocean. I. Ross-Sea, austral summer 1977-1978. Polar Biology 1, 55-67.

BODUNGEN B.v., K.v. BRÖCKEL, V. SMETACEK and B. ZEITZSCHEL (1981) Growth and sedimentation of the phytoplankton spring bloom in the Bornholm Sea, (Baltic Sea). Kieler Meeresforschungen, Sonderheft 5, 49-60.

BLOESCH J. and N.M. BURNS (1980) A critical review of sedimentation trap technique. Schweizerische Zeitschrift für Hydrologie, 42, 15-55.

BÖLTER; M. and R.DAWSON (1982) Heterotrophic utilisation of biochemical compounds in Antarctic waters.Netherlands Journal of Sea Research, 16, 315-332.

BRÖCKEL K.v.(1981) The importance of nanoplankton within the Antarctic ecosystem. Kieler Meeresforschungen, Sonderheft 5, 61-67.

CARLUCCI A.F. and R.L. CUHEL (1977) Vitamins in the South Polar Seas: Distribution and significance of dissolved and particulate vitamin B_{12}, thiamine and biotin in the southern Indian Ocean. In: Adaptations within Antarctic ecosystems, G.A. LLANO, editor, Smithsonian Institution, pp. 11-50.

CLOWES A.J. (1934) Hydrology of the Bransfield Strait. Discovery Reports 9, 1-164.

DELL R.K. (1972) Antarctic benthos. In: Advances in Marine Biology, 10, F. RUSSEL and C.M. YOUNGE; editors, Academic Press pp. 1-216.

DOUCETTE G.J. and G.A. FRYXELL (1983) Thalassiosira antarctica: vegetative and resting stage composition of an ice-related marine diatom. Marine Biology, 78, 1-6.

EDLER L., editor (1979) Recommendations on methods for marine biological studies in the Baltic Sea. Baltic Marine Biologists, **5**, 1-38.

EL-SAYED S.Z. (1984) Productivity of the Antarctic waters - A reappraisal. In: Marine phytoplankton and productivity, O. HOLM-HANSEN, L. BOLIS and R. GILLES, editors, Springer-Verlag, pp.19-34.

EPPLEY R.W. (1972) Temperature and phytoplankton growth in the sea. Fisheries Bulletin, **70**, 1063-1085.

FOGG G.E. (1977) Aquatic primary production in the Antarctic. Philosophical Transactions of the Royal Society, London B, **279**, 27-38.

FOWLER S.W. and L.F. SMALL (1972) Sinking rates of euphausiid fecal pellets. Limnology and Oceanography, **17**, 293-296.

FRENCH F.W. and P.E. HARGRAVES (1980) Physiological characteristics of plankton diatom resting spores. Marine Biological Letters, **1**, 185-195.

GARDNER W.D. (1980) Field assessment of sediment traps. Journal of Marine Research, **38**, 41-52.

GERSONDE R. and G. WEFER (1984) Diatoms and foraminifera in sediment trap material from Drake Passage and Bransfield Strait. Abstract, 1984 meeting of the Geological Society of America, Reno.

GRAF G., R. SCHULZ, R. PEINERT and L.-A. MEYER-REIL (1983) Benthic response to sedimentation events during autumn to spring at a shallow-water station in the Western Kiel Bight. Marine Biology, **77**, 235-246.

GRASSHOFF K., editor, (1976) Methods of seawater analysis. Verlag Chemie, 317 pp.

GRELOWSKI A. and M. PASTUSZAK (1983) Preliminary determination of the occurrence and movement of water masses in the regions of South Georgia Island, the Scotia Sea and the Antarctic Peninsula. Oceanologia, **14**, 87-111.

HAARDT H. and R. MAASSEN (1983) CTD and optical data from the Antarctic-

METEOR 56, ANT I. Part I: CTD and chlorophyll profiles. Report No. 61 Sonderforschungsbereich 95, Kiel University, 183 pp.

HAMNER W.M., P.P. HAMNER, S.W. STRAND and R.W. GILMER (1983) Behavior of Antarctic krill, Euphausia superba: chemoreception, feeding, schooling, and molting. Science, 220, 433-435.

HARDY, A.C. and E.R. GUNTHER (1935) The plankton of the South Georgia whaling grounds and adjacent waters, 1926-27. Discovery Reports, 11, 1-486.

HARGRAVES P.E. and F.W. FRENCH (1983) Diatom resting spores: significance and strategies. In: Survival strategies of the algae, G.A. FRYXELL, editor, Cambridge University Press, pp. 49-68.

HART, T.J. (1934) On the phytoplankton of the South-West Atlantic and the Bellingshausen Sea, 1929-31. Discovery Reports 8, 1-268.

HART T.J. (1942) Phytoplankton periodicity in Antarctic surface waters. Discovery Reports, 21, 261-356.

HAYES P.K., T.M. WHITAKER and G.E. FOGG (1984) The distribution and nutrient status of phytoplankton in the Southern Ocean between 20° and 70° W. Polar Biology, 3, 153-165.

HOLM-HANSEN O., S.Z. EL-SAYED, G.A. FRANCESCHINI and R.I. CUHEL (1977) Primary production and the factors controlling phytoplankton growth in the Southern Ocean. In: Adaptations within Antarctic ecosystems, G.A. LLANO, editor, Smithsonian Institution, Washington D.C. pp 11-50.

JAQUES G., C. DESCOLAS-GROS, J.R. GRALL and A. SOURNIA (1979) Distribution du phytoplancton dans la partie Antarctique de l'Ocean Indien en fin d'ete. Internationale Revue der gesamten Hydrobiologie, 64, 609-628.

JONES P.G.W. and S.M. HAQ (1963) The distribution of Phaeocystis in the eastern Irish Sea. Journal du Conseil. Conseil permanent international pour l'exploration de la mer, 28, 8-20.

KARSTEN G. (1905) Das Phytoplankton des antarktischen Meeres nach dem

Material der deutschen Tiefsee-Expedition 1898-1899. Wissenschaftliche Ergebnisse der deutschen Tiefsee-Expedition, **2**, 1-136.

KILS U. (1979) Performance of Antarctic krill, Euphausia superba at different levels of oxygen saturation. Meeresforschung, **27**, 35-48.

LENZ J. (1971) Zur Methode der Sestonbestimmung. Kieler Meeresforschung, 27, 180-193.

LEWIS M.R., J.J. CULLEN and T. PLATT (1984) Relationships between vertical mixing and photoadaptation of phytoplankton: similarity criteria. Marine Ecology Progress Series, 15, 141-149.

NEAVERSON E. (1934) The sea floor deposits. I. General characteristics and distribution. Discovery Reports, 9, 295-350.

NEORI A. and O. HOLM-HANSEN (1982) Effect of temperature on rate of photosynthesis in Antarctic phytoplankton. Polar Biology, 1, 33-38

PATTERSON S.L. and H.A. SIEVERS (1980) The Weddell-Scotia-Confluence. Journal of Physical Oceanography, 10, 1584-1610.

PEINERT R., A. SAURE, P. STEGMANN, C. STIENEN, H. HAARDT and V. SMETACEK (1982) Dynamics of primary production and sedimentation in a coastal ecosystem. Netherlands Journal of Sea Research, **16**, 276-289.

PERMITIN Yu. (1970) The consumption of krill by Antarctic fishes. In: Antarctic ecology, M.W. HOLDGATE, editor, Academic Press, pp.177-182.

RAYMONT J.E.G. (1980) Plankton and productivity in the oceans. Pergamon Press, 489 pp.

SAKSHAUG E. and O. HOLM-HANSEN (1984) Factors governing pelagic production in polar oceans. in: Marine phytoplankton and productivity, O. HOLM-HANSEN, L. BOLIS and R. GILLES, editors, Springer-Verlag, pp. 1-18.

SAURE A. (1981) Die Zufuhr von organiscer Substanz zum Sediment und ihre Bedeutung für das Ökosystem Kieler Bucht. Diplom thesis, Kiel University, 104 pp.

SCHNACK S.B. (subm.) A note on the sedimentation of particulate matter in Antarctic waters during summer. Polar Biology

SCHNACK S.B., V. SMETACEK, B.v.BODUNGEN and P. STEGMANN (1984) Utilisation of phytoplankton by copepods in Antarctic waters during spring. In: Proceedings of the 18th European Marine Biology Symposium, J. GRAY and M.E. CHRISTENSEN, editors, John Wiley & Son, pp.

SCHNEIDER A. (1983) Verbreitung und Ökologie des Phytoplanktons im atlantischen Sektor der Antarktis. PhD-Thesis, Kiel University, 125 pp.

SMAYDA T.J. (1970) The suspension and sinking of phytoplankton in the sea. Oceanographic and marine Biological Annual Review **8**, 353-414.

SMETACEK V. (1980) Annual cycle of sedimentation in relation to plankton ecology in Western Kiel Bight. Ophelia, Supplement 1, 65-76.

SMETACEK V. (1984) The supply of food to the benthos. In: Flows of energy and materials in marine ecosystems: theory and practice. M.J.R. FASHAM, editor, Plenum Press, pp. 517-548.

SMETACEK V. (1985) Role of sinking in diatom life-history cycles: ecological, evolutionary and geological significance. Marine Biology 84, 239-251.

SMETACEK V., K.v. BRÖCKEL, B. ZEITZSCHEL and W. ZENK (1978) Sedimentation of particulate matter during a phytoplankton spring bloom in relation to the hydrographical regime. Marine Biology, 47, 211-226.

SMETACEK V., B.v. BODUNGEN, E.-M. NÖTHIG and U. BATHMANN (in prep.) Sedimentation of planktonic diatoms in the Antarctic: evidence of a mechanism for accelerating sinking rates.

STARESINIC N., G.T. ROWE, D. SHAUGHNESSY and A.J. WILLIAMS III (1978) Measurement of the vertical flux of particulate organic matter with a free-drifting sediment trap. Limnology and Oceanography, **23**, 559-561.

STEIN M. and S. RAKUSA-SUSZCZEWSKI (1984) Meso-scale structure of water

masses and bottom topography as the basis for krill distribution in the SE Bransfield Strait February-March 1981. Meeresforschung, 30, 73-81.

TILZER M.M., B.v. BODUNGEN and V. SMETACEK (1985) Light dependence of phytoplankton photosynthesis in the Antarctic Ocean: Implications for regulating productivity. In: Antarctic nutrient cycles and food webs, R. SIEGFRIED, CONDY and LAWS, editors, Springer Verlag, pp. 60-69.

TRANTER D. (1982) Interlinking of physical and biological processes in the Antarctic Ocean. Oceanographical and Marine Biological Annual Review, 20, 11-35.

UNESCO (1966) Determination of photosynthetic pigments in seawater. Monographs on oceanographical Methodology, The UNESCO-Press 1, 66 pp.

WALSH J.J. (1983) Death in the sea: enigmatic phytoplankton losses. Progress in Oceanography, 12, 1-86.

WHITAKER T.M. (1982) Primary production of phytoplankton off Signy Island, South Orkneys, the Antarctic. Proceedings of the Royal Society, London, B, 214, 169-189.

WITEK Z., M. PASTUSZAK and A. GRELOWSKI (1982) Net-phytoplankton abundance in western Antarctic and its relation to environmental conditions. Meeresforschung, 29, 166-180.

ZEITZSCHEL B., P. DIEKMANN and L. UHLMANN (1978) A new multisample sediment trap. Marine Biology 45, 285-288.

Table 1. Euphotic zone (down to 0.1% of surface light depth) properties from Zones I, IIa, IIb and III as averages with standard deviations. Depth is 0.1% light depth; temp. range is temperature range; Prim. prod. is primary production rate; POC and Chl. a is standing stock of organic carbon and chlorophyll a integrated for euphotic zone respectively; C:N and C:P are averages of carbon to nitrogen and phosphorous ratios (by atoms) respectively from the euphotic zone; n is the number of stations occupied in each zone.

Zone	n	depth m	temp. range ^{o}C	Prim. prod. mg m^{-2} d^{-1}	POC g m^{-2}	Chl. a mg m^{-2}	C:N	C:P
I	4	94 ± 9	0.66 – -0.30	233 ± 101	12.7 ± 5.0	49 ± 10	8.6 ± 1.2	130 ± 24
IIa	4	22 ± 3	-0.31 – -1.29	1663 ± 514	13.5 ± 0.5	209 ± 30	6.4 ± 0.7	102 ± 12
IIb	7	47 ± 6	-0.80 – -1.52	803 ± 339	9.5 ± 2.0	128 ± 18	7.7 ± 0.9	138 ± 47
III	10	55 ± 7	-1.40 – -1.79	834 ± 421	12.2 ± 1.3	217 ± 30	8.1 ± 0.5	116 ± 21

Table 1

Table 2. Amounts and composition of material collected by sediment traps. Values in parentheses represent averages of suspended material from the 100 m water column. Exp.t. is exposure time in hours; Stn. nr. is number of the corresponding station; POC is particulate organic carbon collected by traps calculated for m^2 and day; C%/DW is carbon percentage of dry weight (seston); C/Chl*a* is carbon to chlorophyll ratio (not corrected for phaeopigmants); PPC%/POC is phytoplankton carbon (calculated from cell counts) percentage of POC; C:N and C:P is carbon to nitrogen and phosphorous ratios (by atoms) respectively.

Trap nr.	Exp.t. (hrs)	Stn. nr.	POC (mg m^{-2} d^{-1})	C%/DW	C/Chl*a*	PPC%/POC	C:N	C:P
1	8	73	97	8(14)	-(73)	18	9.6(8.6)	- (102)
2	30	92	138	15(27)	34(54)	23	8.4(6.4)	191(103)
3	17	123	546	22(19)	36(87)	4	11.1(7.5)	296(133)
4	24	102	569	7(18)	28(54)	47	7.4(7.8)	97(93)
5	7	107	459	15(20)	32(54)	60	8.9(7.7)	120(95)
6	10	116	1404	10(17)	48(38)	48	8.0(7.7)	106(96)

Table 3. Trap collections expressed as percentage losses of suspended particulate material from the respective 100 m water columns per m^2 and day. Legends as in Tables 1 and 2.

Trap nr.	Stn. nr.	Prim. prod.	DW	POC	PON	TPP	Chl*a*
1	73	19	1.2	0.7	0.6	-	-
2	92	15	0.7	0.4	0.3	0.2	0.6
3	123	94	2.9	3.2	2.2	1.5	7.8
4	102	77	8.0	3.0	3.1	2.9	5.8
5	107	122	2.8	2.1	1.8	1.6	3.6
6	116	189	12.4	6.8	6.5	6.1	5.2

FIGURE CAPTIONS

Fig. 1. Map of the investigation area showing location (inset) and posiiton of zones, some selected stations (dots and small numbers) and free-drifting sediment traps (inverted triangles and large numbers). Trap positions are identical with those of respective adjacent stations.

Fig. 2. Water column properties at stations from trap positions, Zone II (upper panel) and Zone III (lower panel). Stations 73, 92 and 123 correspond to traps 1, 2 and 3 respectively and stations 102, 107, 116 to traps 4, 5 and 6. : density; NO_3 : nitrate concentrations; Chl. a: chlorophyll a; PRIM. PROD.: primary production; C:Chl., C:N and C:P ratios of particulate organic carbon to chlorophyll a, particulate nitrogen (by atoms) and phosphorous (by atoms) respectively.

Fig. 3. Photosynthetic rates (P^B) estimated by in-situ simulated (upper panel) and in-vitro (middle panel) methods and chlorophyll concentrations (lower panel) from Zones I, IIa, IIb and III; horizontal bars represent standard deviations. For comparative purposes, depths are given as percentage of surface light ("light depths"): for true depths see text and Table 1.

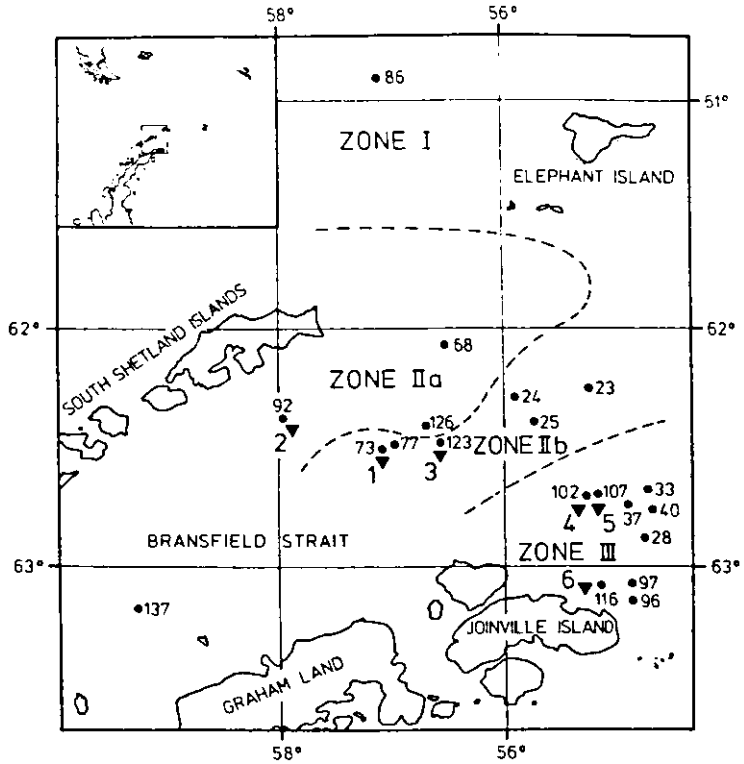
58°
56°
51°
62°
63°
ZONE I
ELEPHANT ISLAND
SOUTH SHETLAND ISLANDS
ZONE IIa
ZONE IIb
ZONE III
BRANSFIELD STRAIT
JOINVILLE ISLAND
GRAHAM LAND
86
68
24
23
92
126
25
73
77
123
102
107
33
37
40
28
97
116
96
137
1
2
3
4
5
6

Fig. 1

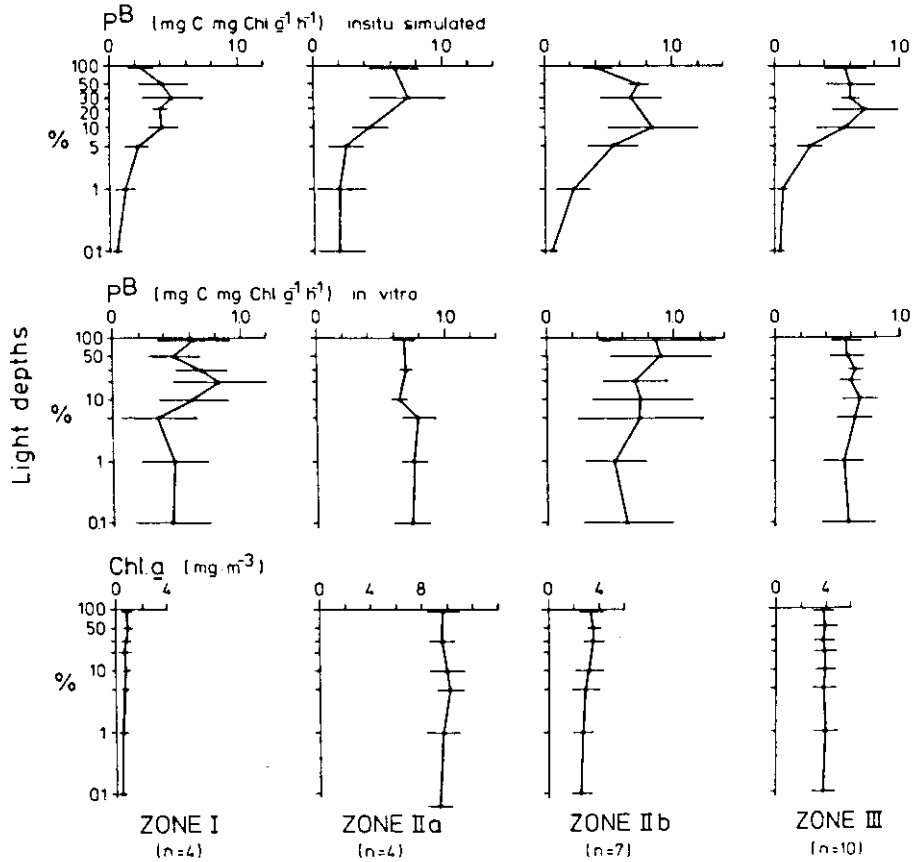
PB (mg C mg Chl g⁻¹ h⁻¹) insitu simulated
PB (mg C mg Chl g⁻¹ h⁻¹) in vitro
Chl.a (mg m⁻³)
Light depths
%
ZONE I
(n=4)
ZONE IIa
(n=4)
ZONE IIb
(n=7)
ZONE III
(n=10)

Fig. 3

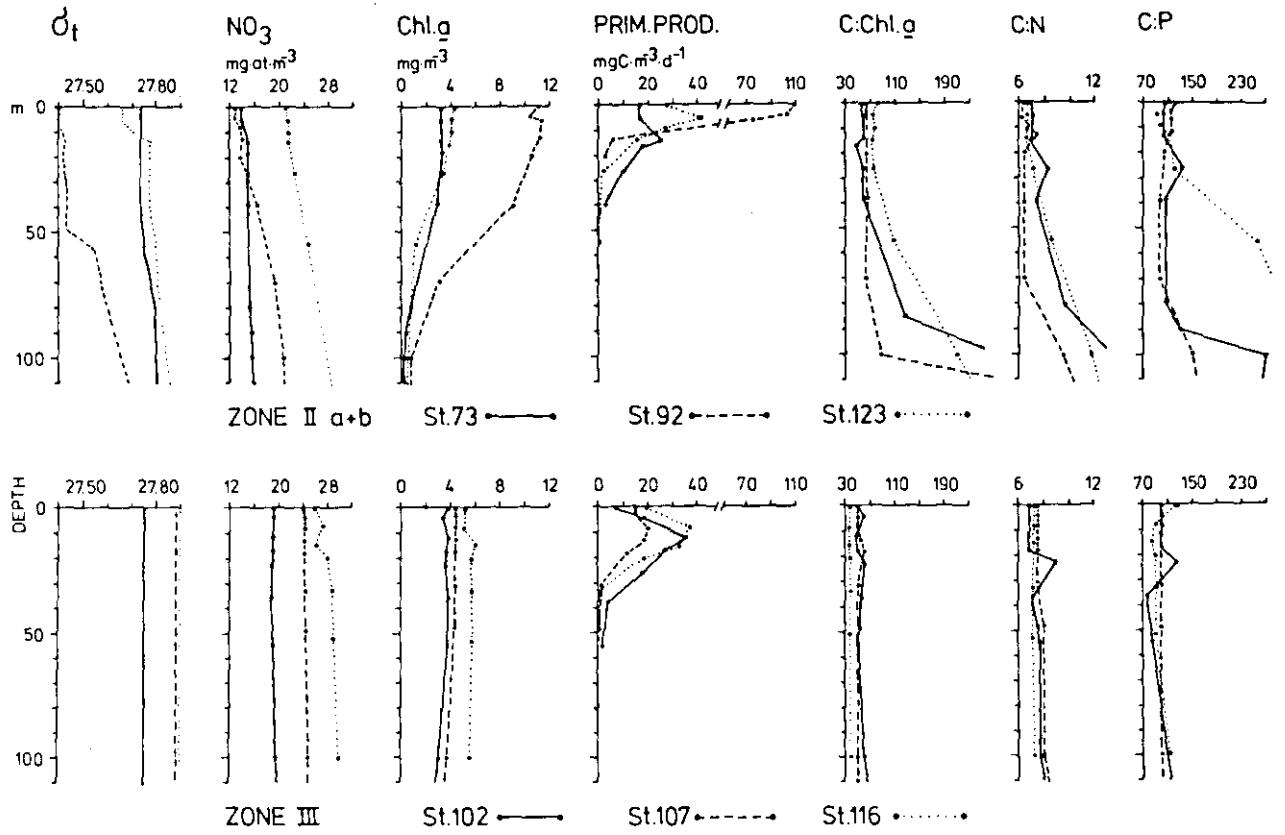

Fig. 2

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Vertical Transport of Chlorinated Hydrocarbons by Sedimentation of Particulate Matter in Kiel Bight*

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ABSTRACT: Particulate matter settling out of the water column was collected continuously over a two-year period by means of multisample sediment traps in the coastal waters of the Western Baltic Sea. The content of PCBs and organochlorine pesticides of this matter was determined and compared with its dry weight, and with its organic carbon, nitrogen, and plant pigment content. The pesticide content of this material was highly variable and a marked decline in absolute concentrations was present from 1975–1977; in most samples from 1977, pesticide content was below detection limit. For PCBs, a distinct annual cycle was observed which was inversely related to the rates of sedimentation of seston; highest absolute values for PCBs in each year were recorded during the summer. The input rates of PCBs to the sediments ranged between 112.10^3 and 24.10^3 ng $m^{-2}y^{-1}$.

INTRODUCTION

Chlorinated hydrocarbons enter the surface layers of the sea through atmosphere, land drainage and shipping. Sources and fate of these pollutants in the sea have been discussed by several authors (Holden, 1970; Walsh, 1972; Harvey et al., 1973; Dawson and Riley, 1977). The removal of these compounds from the surface layer and introduction to deeper layers and/or sediments is effected by various agencies such as migrating organisms, vertical mixing processes and adsorption onto sedimenting particulate matter. The latter process is a major transport pathway in the sea, and life below the euphotic zone is dependent for its energy requirements on material derived in this way. The sedimenting particles may be living organisms (plankton), dead organic matter (organic detritus) as well as inorganic particles (inorganic seston). As a result of adsorption, it is possible for any of these categories of particulate matter to contain chlorinated hydrocarbons (Weil et al., 1973; Derenbach et al., 1978). Thus, sedimentation is bound to be an important mechanism by which pollutants introduced into the surface layer will be dissipated throughout the marine ecosystem.

Quantity and composition of the particulate matter depends on both hydrographic regime and seasonal cycle of plankton (Smetacek et al., 1978). Therefore, it can be assumed that the quantity of chlorinated hydrocarbons transported vertically will vary seasonally, depending not only on input rate to the sea surface, but also on quantity and composition of the material sinking out of this layer.

The aim of the present investigation was to assess the amount of chlorinated hydrocarbons reaching the sediments in sinking organic matter during the course of two years, and to ascertain the presence of seasonal trends, possibly linked to factors controlling the sedimentation process. This investigation was carried out within the framework of the Special Research Project 95 (SFB 95) at Kiel University, investigating the interaction between sea and sediments in the South-Western Baltic Sea, and DFG project Eh 39/17. Sediment traps were employed to collect the material analyzed in the investigation. The investigation site – the 'Hausgarten' of the SFB 95 project – was situated at the entrance of a shallow fjord, about a nautical mile from the coast. Land run-off into Kiel Bight is minimal as the watershed in Schleswig-Holstein lies close to the eastern coast. Much of the land area surrounding Kiel Bight is under cultivation and no major industrial centers are present in the region.

The hydrography of Kiel Bight is fairly well-known (e. g. Bodungen, 1975; Lenz, 1977). It is characterized

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by influxes of low salinity water from the Baltic Sea proper and of higher salinity water from the Kattegat. The SW corner of Kiel Bight, where the 'Hausgarten' is situated, is well away from the major pathway of water exchange and the residence time of water here is longer than elsewhere in the region. The water column is generally homogeneous during winter and strongly stratified during summer, with a halocline at a depth of 8–14 m. Plankton ecology in relation to seasonal cycles of suspended particulates and sedimentation rates at the investigation site and elsewhere in Kiel Bight has been the subject of many papers (e. g. Krey, 1961; Zeitzschel, 1965; Lenz, 1974; Bodungen et al., 1975; Smetacek and Hendrikson, 1979).

MATERIAL AND METHODS

Sedimenting material was collected at the 'Hausgarten' by means of multisample sediment traps that enable a short-term resolution of sedimentation rates to be made (Zeitzschel et al., 1978). Two traps were suspended, one at 2 m and the other at 5 m above the bottom at water depth of 20 m. The 2-m trap was deployed from November 1975 to December 1977; the 5-m trap from March 1976 to December 1977. Until December 1976, collections of sedimenting material were made at 2-d intervals; 4-d intervals were used thereafter.

The material collected in each of the glasses of the traps was strained through a 300 μm gauze to remove larger zooplankton and then suspended in a known volume of filtered sea water. Subsamples for analysis were pipetted from this suspension, kept homogeneous by agitation.

The dry weight (DW) of particles < 300 μm was determined on precombusted Whatman GF/C filters as described by Lenz (1977).

Particulate organic carbon (POC) and nitrogen (PON) on the filters were measured with a CHN-Analyzer (Hewlett Packard, 185 B) after pre-treatment in the sample boats with diluted HCl to remove carbonate.

Chlorophyll *a* and phaeopigment analyses were carried out as recommended by UNESCO (1966), using a cell mill to homogenize the samples (Derenbach, 1969). Spectrophotometric equations given by Lorenzen (1967) were used for evaluating chlorophylls and phaeopigments. As chlorophyll degradation to phaeopigment occurred in the collecting glasses, both values were added together and are referred to as chlorophyll-*a*-equivalents (chl.-*a*-equiv.) below. Total carotenoids were estimated from the absorption at 480 nm as suggested by Strickland and Parsons (1972).

Chlorinated hydrocarbon levels present in 2-d samples were below detection limit; therefore, a number of samples (the number depending on the dry weight content) had to be pooled for each analysis. Five pooled samples were analyzed for each year. The filters were extracted with a mixture of acetone-water (3 : 2 by volume) in a Soxhlet apparatus for 6 h. The extracts were concentrated in a rotary evaporator until most of the acetone had been evaporated, and the remaining aqueous solution was extracted three times with small amounts of hexane. The combined hexane phases were successively shaken with distilled water, concentrated sulfuric acid, distilled water again, reduced to a small volume (200–300 μl) and fractionated by liquid-liquid chromatography. The latter was performed on a column of 3.5 % deactivated silicagel (0.04–0.63 mm grain size) by elution with hexane followed by hexane-ether (9 + 1) to give two fractions: the first containing the PCBs and pp'-DDE, and the second the rest of the organochlorine pesticides. Both fractions were evaporated to $^1/_{10}$ of their volume to give an appropriate concentration for the linear range of the EC-detector, when injecting a 10 μl aliquot into the GC. For details see Osterroht (1977).

Surface sediments from the vicinity of sediment traps were sampled with a bottom corer. After freezing, the upper 1 cm sediment layer was sliced off and desiccated in a drying chamber at 80 °C for 3 h. After weighing, the dried sediments were extracted by the same procedure described above.

Gas chromatographic conditions: Chromosorb W AW-DMCS was deactivated with 6 % Carbowax according to the method of Aue (Aue et al. 1973, 1974) and coated separately with both 2 % OV 101 and 2 % QF-1 as stationary phases. The two packings were mixed in equal portions and packed into micropack-columns (i. d. 0.8 mm, 1.50 m length). The 5730A Hewlett-Packard GC was equipped with a pulsed ECD and connected to a 3380 A integrator. Quantitative evaluation was achieved with the aid of an external standard (Clophen A60). Five of the major peaks arising from the PCBs were measured.

All data were calculated on the basis of results from aliquots for the whole sediment traps per day, corresponding to the fallout from one square meter of surface per day to make them comparable to the other parameters.

RESULTS

Data for sedimentation rates of organochlorine compounds from the two traps are given in Table 1. There is a striking decline in the amounts of pesticides settling out of the water column during the course of the

Table 1. Input rates of PCBs and organochlorine pesticides into sediment traps in ng m^{-2} d^{-1}. Values at 2 m and 5 m are from traps suspended 2 m or 5 m above the bottom. – no data

Period	PCBs	Lindane	Dieldrin	DDE	DDD	DDT
2 m						
5. XI.–16. XII. 75	844.6	1986.7	546.3	–	–	–
9. I.–29. II. 76	459.3	571.8	100.0	–	–	–
1. III.–29. IV. 76	–	150.7	8.0	–	1.8	–
29. IV.–10. VIII. 76	318.2	85.9	216.7	65.0	154.7	112.1
10. VIII.–22. IX. 76	758.3	–	–	243.3	–	–
5. X.–23. XI. 76	457.8	146.7	101.2	–	96.1	10.1
28. XII. 76–28. II. 77	–	–	–	–	–	–
28. II.–30. IV. 77	67.5	–	–	–	–	–
8. V.–29. VIII. 77	124.3	–	–	–	–	–
30. VIII.–17. X. 77	168.4	–	–	–	–	–
17. X.–22. XII. 77	–	–	–	–	–	–
5 m						
1. III.–22. IV. 76	550.8	137.7	7.3	–	1.8	–
29. IV.–10. VIII. 76	175.4	–	–	17.8	–	–
10. VIII.–22. IX. 76	363.6	–	–	86.2	–	–
22. IX.–23. XI. 76	196.4	–	10.1	–	10.1	–
23. XI.–28. XII. 76	–	–	–	–	–	–
28. XII. 76–28. II. 77	–	–	–	–	–	–
28. II.–4. V. 77	68.5	–	9.1	–	9.1	–
8. V.–1. VIII. 77	137.7	–	–	–	–	–
2. VIII.–23. IX. 77	254.4	–	–	–	–	–
23. IX.–10. XII. 77	78.3	–	–	–	–	–

Table 2. Sedimentation rates of seston (dry weight), particulate organic carbon (POC) and nitrogen (PON), chlorophyll *a* equivalents (chl.-*a*-equiv.) and total carotenoids (carot.) in mg m^{-2} d^{-1}. Values at 2 m and 5 m are from traps suspended 2 m or 5 m above the bottom

Period	Seston	POC	PON	Chl.-*a* equiv.	Carot.
2 m					
5. XI.–16. XII. 75	5584	362	41	2.4	1.0
9. I.–29. II. 76	16476	707	93	5.4	2.8
1. III.–29. IV. 76	4050	257	32	4.4	1.5
29. IV.–10. VIII. 76	797	92	10	0.6	0.3
10. VIII.–22. IX. 76	3960	311	41	2.7	1.8
5. X.–23. XI. 76	6188	411	41	2.4	2.0
28. XII. 76–28. II. 77	5436	223	28	1.5	0.9
28. II.–30. IV. 77	2051	147	15	2.8	1.1
8. V.–29. VIII. 77	376	41	5	0.4	0.2
30. VIII.–17. X. 77	1658	154	16	3.8	1.5
17. X.–22. XII. 77	8419	371	39	2.2	1.2
5 m					
1. III.–29. IV. 76	3083	226	27	3.1	1.0
29. IV.–10. VIII. 76	495	65	7	0.7	0.2
10. VIII.–22. IX. 76	2787	282	33	3.9	2.5
22. IX.–23. XI. 76	3413	190	27	2.1	1.3
23. XI.–28. XII. 76	4974	178	25	2.9	1.5
28. XII. 76–28. II. 77	2830	118	15	0.8	0.4
28. II.–4. V. 77	2648	159	18	3.5	1.4
8. V.–1. VIII. 77	556	71	9	0.9	0.4
2. VIII.–23. IX. 77	375	49	6	0.8	0.2
23. IX.–10. XII. 77	1848	177	22	1.6	0.9

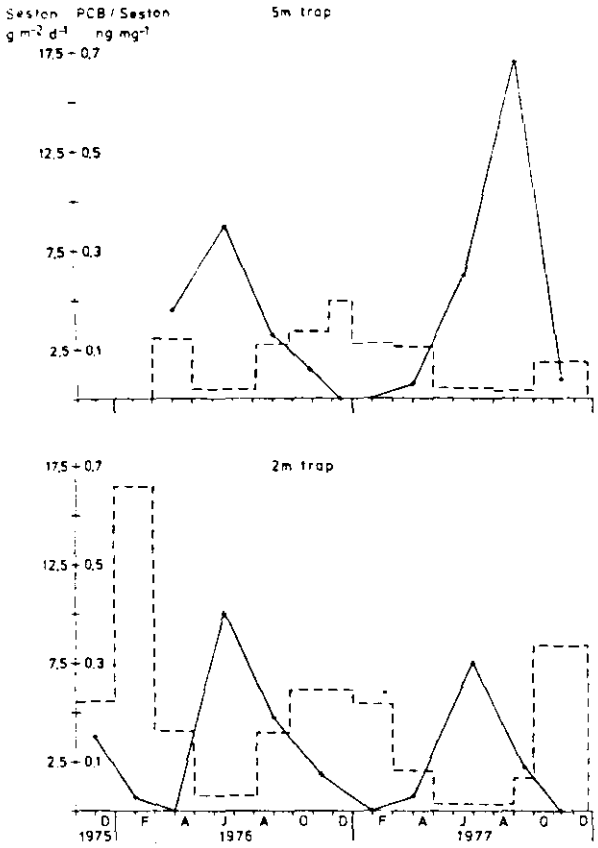

Fig. 1. Histograms: sedimentation rates of seston dry weight (g m^{-2} d^{-1}) averaged for periods when samples were pooled for analysis of PCBs. Curves: ratios of PCBs per dry weight (ng : mg). 2 m and 5 m: results from traps 2 m or 5 m above the bottom

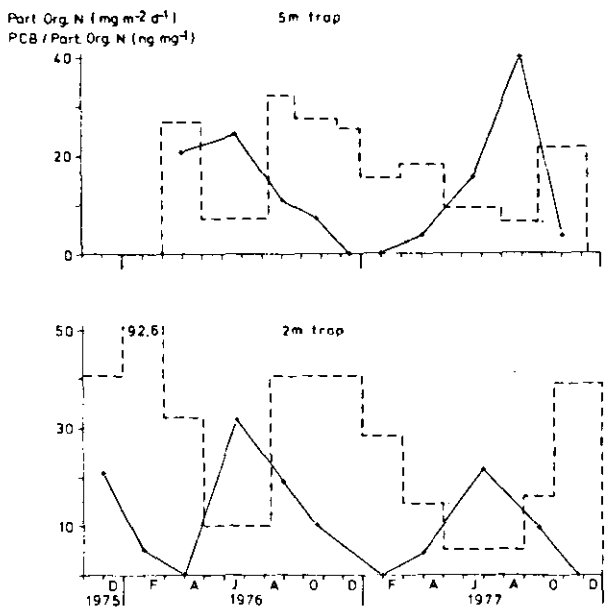

Fig. 3. Sedimentation rates of particulate organic nitrogen (PON mg m^{-2} d^{-1}) and ratios PCB : PON (ng : mg) in histograms and curves, respectively. Further details as in Figure 1

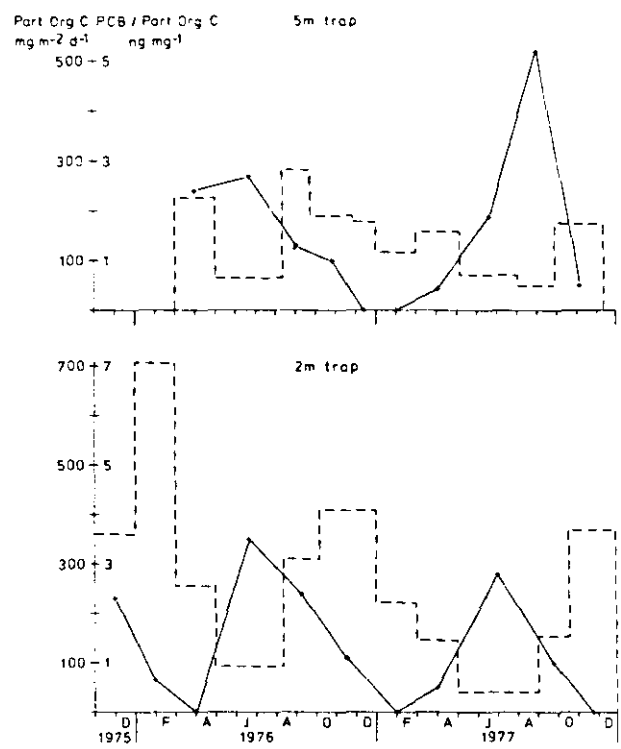

Fig. 2. Sedimentation rates of particulate organic carbon (POC mg m^{-2} d^{-1}) and ratios PCB : POC (ng : mg) in histograms and curves, respectively. Further details as in Figure 1

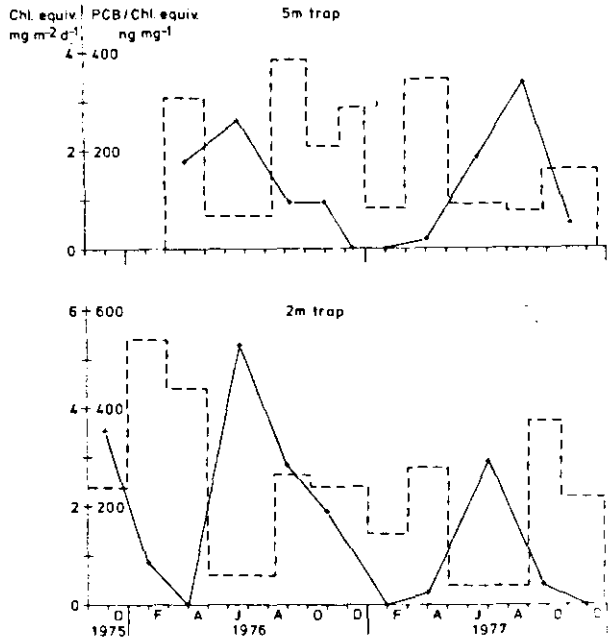

Fig. 4. Sedimentation rates of chlorophyll *a* equivalents (mg m^{-2} d^{-1}) and ratios PCB : chl.-*a*-equiv. in histograms and curves, respectively. Further details as in Figure 1

investigation period, with practically zero values recorded during 1977 from both traps. The position is different for the PCBs where substantial amounts were recorded in 1977 although these values are generally lower than those of 1976.

Sedimentation rates of the particulate matter and its various components recorded by the two traps for the period investigated are given in Table 2 and shown in histogram form in Figures 1–4. Highest and lowest annual rates were found for both traps during winter and summer, respectively, with intermediate values in spring and autumn. No relationship between sedimentation rates of pesticides and particulate matter is present, but for PCBs an inverse relationship between particulate matter and its content of PCBs is apparent. This has been shown in the curves depicting the ratios of the dry weight of particulate matter as well as its various components to the content of PCBs also given in Figures 1–4. A very striking cycle is present in these curves which is common to traps from both depths, apart from a slight phase shift in the summer of 1977. This cycle appears to be seasonal and, in general, it can be stated that maxima are present in summer and minima in winter. However, there are temporal shifts in this pattern from one year to the next: the first minimum is in February/March, the other two in mid-winter; the 1976 and 1977 peaks are in June/July and July/September, respectively. From Table 1 it can be seen that the absolute amounts of PCBs in summer were higher, concomitant with lower rates of sedimentation of particulate matter (Table 2), than during the rest of the year. The presence of this distinct seasonal cycle may be related either to the rates of input of PCBs into the system or to ecological factors associated with the seasonal cycle of sedimentation in Kiel Bight.

PCBs entering Kiel Bight may originate from several sources, all of which are difficult to quantify, as Kiel Bight receives water from the Baltic Sea as well as the North Sea.

The seasonal cycle in the quantity and composition of the particulate matter and its relationship to the plankton ecology and hydrography of Kiel Bight is described in greater detail elsewhere (Smetacek, in press); only a brief description is given here. Data on plankton ecology have been taken from Bodungen (1975), Smetacek (1975) and Smetacek and Hendrikson (1979).

During the winter months primary production is at its lowest although the sedimentation rates are the highest of the year. These high sedimentation rates are evidently the result of resuspension of surface sediment as the hydrographical conditions (homogeneous water column) and meteorological (prolonged stormy weather) factors combine to produce higher turbulence levels in the water column in winter than at other times of the year. This resuspension is also reflected in the greater amounts collected by the lower trap during winter. When resuspension is not of importance, amounts collected by the two traps are much more similar.

Much of the biomass produced by the spring phytoplankton bloom in March/April sediments out of the water column and is clearly recognizable in sediment trap material by increases in the proportions of carbon, nitrogen and pigments relative to the dry weight. Sedimentation rates in summer are generally low, although production rates and plankton biomass levels are comparatively high throughout this period. Organic matter in the water column is apparently turned over more rapidly than it can sediment, the former process being aided not only by higher temperatures but also by the large zooplankton stocks present in the summer months. In autumn, Kiel Bight plankton is characterized by a large population of dinoflagellates (various *Ceratium* spp.) to which zooplankton do not appear to be partial. Organic carbon present in this population sediments out in a fashion similar to the spring bloom. Thereafter, the winter situation prevails. Because of lumping of data, this pattern is not so evident from the histograms given in Figures 1–4, but the trend can be discerned.

The annual cycle described above was found both in 1976 and 1977, although the absolute amounts of sedimented matter differed considerably from year to year. Thus, during 1976, a total of 61 g C m^{-2} was collected by the lower trap during the growth season of plankton (March–October), whereas in 1977 only 22 g C m^{-2} was recorded for the same period.

Table 3. Amounts of PCBs and organochlorine pesticides in two surface sediment samples from April 1978, expressed as ng g^{-1} dry weight of sediment

PCBs	8.4	10.8
Lindane	2.4	3.2
Dieldrin	0.9	1.3
DDE	1.3	0.47
DDD	–	–
DDT	1.1	1.5

Concentrations of chlorinated hydrocarbon in surface sediments are shown in Table 3. The PCB content of the sediment on a dry weight basis is much lower than that of the particulate material collected by the traps from the water column during summer, but similar to values recorded during winter. This is further proof that winter sedimenting matter is indeed resuspended sediment.

DISCUSSION

Material collected by sediment traps is equivalent to information integrated over time; hence the time scale of each measurement carried out on such material is much larger than when discrete samples are collected from the water column (Soutar et al., 1977). Thus, although the number of data presented here is only 5 per annum, these values can be regarded as representative of the whole year, which would certainly not be the case if the water column itself had been monitored the same number of times. However, since the results determined with traps depend on trap shape and current speed around the orifice, they do not necessarily give a correct picture of the actual sedimentation flux (Gardner, 1977). The performance of the traps used in this study has been discussed by Smetacek et al. (1978) who have shown that they tend to underestimate the actual sedimentation rate, and that the greater amounts collected by lower traps is not only due to resuspension but is also related to trap efficiency. The lower trap (2 m above bottom) generally collected more material, even during periods when resuspension was low; it is believed, therefore, that these results are more representative of the actual flux than those from the upper trap. Suprisingly, lesser amounts of chlorinated hydrocarbons were collected by the upper traps during 1976, but in 1977 the situation was reversed although discrepancies in the amounts collected by the two traps were less in 1977 than in 1976.

For all pesticides, the decline in input to the sediments from 1976 through 1977 is noteworthy. During 1977, less sedimenting material was collected by the traps than in 1976, and, although this could serve as a possible explanation for the accompanying decline in PCBs, the almost total absence of other organochlorine compounds from the 1977 material is in all probability due to other factors. The ban on the use of DDT and the restrictions on the use of other chlorinated hydrocarbon pesticides imposed by the states bordering the Baltic Sea during the past few years could possibly explain the decline in these compounds. The sporadic appearance of pesticides in particulate matter during 1976 is more likely related to input rates into the sea than to the autochthonous processes of particle formation and sedimentation within the water column. High concentrations of pesticides were recorded both during summer and winter when sedimentation regimes differ drastically.

Surface sediments contained measurable amounts of all the organochlorine compounds sought except DDD, and the ratios of these compounds to each other differed widely from those found in matter settling down the water column. Whether the fact that the PCBs content of sediments is relatively lower than that of the pesticides is due to differences in breakdown rates, or whether pesticide inputs in the past were higher than those during the period of investigation, is a matter of conjecture. The former effect seems more probable as the input of PCBs to the sediments was on average 0.19 ng PCBs mg^{-1} of sedimenting matter during the two years of the investigation, and even if the upper 1 cm of sediment were mixed, the average content of PCBs in this 1 cm layer should be higher than the measured 0.0096 ng PCBs mg^{-1} sediment (dry weight). Thus, in winter when sediment trap material consists largely of resuspended sediment, its content of PCBs is low to not detectable.

Not much information is present on the content of PCBs in the water column of Kiel Bight. The only data available were recorded in October in both 1974 and 1975 (Stadler and Ziebarth, 1976; Stadler, 1977). The content of PCBs averaged for both years was 3.1 ± 2.7 ng dm^{-3} ($n = 12$) equivalent to 62×10^3 ng m^{-2} for the 20-m water column, which is the mean depth of the Bight. The PCBs present in the water column can be in various states ranging from dissolved to particulate (Dawson and Riley, 1977) and without knowledge of input rates, one can only speculate on residence times of the pollutants in the water column. However, annual rates of input of PCBs to the sediments as recorded by the 2-m and 5-m traps were 112×10^3 and 79×10^3 ng m^{-2} y^{-1}, respectively, in 1976; corresponding figures in 1977 were 24×10^3 and 33×10^3 ng m^{-2} y^{-1}. Thus, approximately twice to only a third of the content of PCBs in the water column settles out each year.

The seasonality of the rate of input to PCBs to the sediments is remarkable and is presumably due to the seasonality in input to the sea surface as well as to the annual cycle of sedimentation. There are several pathways by which PCBs are introduced into the sea, of these the paint of ships (Jensen et al., 1972) is likely to be of importance in the Kiel Bight as it is situated on a major international shipping route. During the summer, the number of vessels increases considerably, as the Bight is a popular water sport resort. Although this source is difficult to quantify, it is possible that this seasonality in the recreation industry is one of the factors influencing the input of PCBs to the sediments.

It is well known that organisms concentrate chlorinated hydrocarbons and progressively accumulate them in their body tissue up the food chain (Olsson et al., 1973; Södergren, 1973; Parsons et al., 1977). The marked seasonality of PCB input to sediments can thus be attributed to the much higher activity of organisms during the summer. Most of the organic matter produced by phytoplankton spring and autumn blooms (March/April and October, respectively) enters the

benthic food web as a result of mass sedimentation of cells. PCB input rates to sediments were low during these periods in both years. The pelagic food web develops during late spring and reaches its greatest complexity in late summer. The combination of high production and low rates of sedimentation in the intermediate period indicates that the organic matter is utilized mainly within the water column. The large number of filter feeders and the frequency with which organic matter is recycled within the pelagic food web (Smetacek, in preparation) would lead to the concentration of persistent chlorinated hydrocarbons in particulate residues of the food web. This is a further possible explanation for the seasonality of the PCBs : dry weight ratios of the sedimenting material.

This seasonality in PCB input to the sediments of Kiel Bight, whether related to the recreation industry, or to cumulatory effects of the pelagic web in summer, is likely to have an impact on the benthos because its biomass reaches its maximum in summer (Arntz, 1971). Thus, during the period of greatest food demand, the concentration of PCBs per unit food is the highest for the year.

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LITERATURE CITED

Arntz, W. (1971): Biomasse und Produktion des Makrobenthos in den tieferen Teilen der Kieler Bucht im Jahre 1968. Kieler Meeresforsch. 27: 36–72

Aue, W. A., Hastings, C. R., Gerhardt, K. O. (1974). Gas chromatography on modified supports. J. Chromat. 99: 45–49

Aue, W. A., Hastings, C. R., Kapila, S., Augl, J. M. (1973). Non-extractable polymer coatings (modified supports) for chromatography. J. Chromat. 87: 49–55

Bodungen, B. von (1975). Der Jahresgang der Nährsalze und der Primärproduktion des Planktons in der Kieler Bucht unter Berücksichtigung der Hydrographie. Dissertation, Universität Kiel

Bodungen, B. von, Bröckel, K. von, Smetacek, V., Zeitzschel, B. (1975). Ecological studies on the plankton in Kiel Bight. I. Phytoplankton. Merentutkimuslait. Julk./Havsforsk-Ingsinst. Skr., Helsingfors 239: 179–186

Dawson, R., Riley, J. P. (1977). Chlorine-containing pesticides and polychlorinated biphenyls in British coastal waters. Estuar. & Coast. Mar. Sci. 4: 55–69

Derenbach, J. (1969). Zur Homogenisation des Phytoplanktons für die Chlorophyllbestimmung. Kieler Meeesforsch. 25: 166–171

Derenbach, J., Ehrhardt, M., Osterroht, C., Petrick, G. (1978). Sampling of dissolved organic material from seawater with reversedphase techniques. Mar. Chem. 6: 351–363

Gardner, W. D. (1977). Fluxes, dynamics and chemistry of particulates in the ocean. Ph. D. thesis, M. I. T./Woods Hole Oceanographic Institution, Joint Program in Oceanography

Harvey, G. R., Steinhauer, W. G., Teal, J. M. (1973). Polychlorobiphenyls in North Atlantic Ocean water. Science, N. Y. 180: 643–644

Holden, A. V. (1970). Source of polychlorinated biphenyl contamination in the marine environment. Nature, Lond. 228: 1220–1221

Jensen, S., Renberg, L., Olsson, M. (1972). PCB contamination from boat bottom paint and levels of PCB in plankton outside a polluted area. Nature, Lond. 240: 358–360

Krey, J. (1961). Beobachtungen über den Gehalt an Mikrobiomasse und Detritus in der Kieler Bucht 1958–1960. Kieler Meeresforsch. 17: 163–175

Lenz, J. (1974). Untersuchung zum Nahrungsgefüge im Pelagial der Kieler Bucht. Der Gehalt an Phytoplankton, Zooplankton und organischem Detritus in Abhängigkeit von Wasserschichtung, Tiefe und Jahreszeit. Habilitationsschrift, Universität Kiel

Lenz, J. (1977). Hydrographic conditions. In: Rheinheimer, G. (ed.) Ecol. Stud. 25. Microbial ecology of a brackish water environment. Springer-Verlag, Berlin, pp. 12–25

Lorenzen, C. J. (1967). Determination of chlorophyll and phaeopigments: spectrophotometric equations. Limnol. Oceanogr. 12: 343–346

Olsson, M., Jensen, J. S., Renberg, L. (1973). PCBs in coastal areas of the Baltic. Reprint from PCB Conference II, National Swedish Environmental Protection Board Publications: 4E

Osterroht, C. (1977). Dissolved PCB's and chlorinated hydrocarbon insecticides in the Baltic, determined by two different sampling procedures. Mar. Chem. 5: 113–121

Parsons, T. R., Takahashi, M., Hargrave, B. (1977). Biological oceanographic processes, 2nd ed., Pergamon Press, Oxford

Smetacek, V. (1975). Die Sukzession des Phytoplanktons in der westlichen Kieler Bucht. Dissertation, Universität Kiel

Smetacek, V. (in press). Annual cycle of sedimentation in relation to plankton ecology in western Kiel Bight. Ophelia

Smetacek, V. Zooplankton standing stock, copepod faecal pellets and particulate detritus in Kiel Bight. Estuar. & Coast. Mar. Sci. (submitted)

Smetacek, V., Bröckel, K. von, Zeitzschel, B., Zenk, W. (1978). Sedimentation of particulate matter during a phytoplankton spring bloom in relation to the hydrographical regime. Mar. Biol. 47: 211–226

Smetacek, V., Hendrikson, P. (1979). Composition of particulate organic matter in Kiel Bight in relation to phytoplankton succession. Oceanol. Acta 2: 287–298

Södergren, A. (1973). Transport, distribution and degradation of chlorinated hydrocarbon residues in aquatic model ecosystems. Oikos 23: 30–41

Soutar, A., Kling, S. A., Crill, P. A., Duffrin, E., Bruland, K. W. (1977). Monitoring the marine environment through sedimentation. Nature, Lond. 266: 136–139

Stadler, D. (1977). Chlorinated hydrocarbons in the seawater of the German Bight and the Western Baltic in 1975. Dt. hydrogr. Z. 30: 189–215

Stadler, D., Ziebarth, U. (1976). pp'DDT, Dieldrin and polychlorierte Biphenyle (PCB) im Oberflächenwasser der westlichen Ostsee 1974. Dt. hydrogr. Z. 29: 25–31

Strickland, J. D. H., Parsons, T. R. (1972). A practical handbook of sea-water analysis, 2nd ed., Bull. Fish. Res. Bd Can. 167: 1–310

UNESCO (1966). Determination of photosynthetic pigments in sea water. Monogr. oceanogr. Methodol. (UNESCO) 1: 1–66

Walsh, G. E. (1972). Insecticides, herbicides and polychlorinated biphenyls in estuaries. J. Wash. Acad. Sci. 62: 122–139

Weil, L., Duré, G., Quentin, K. E. (1973). Adsorption von chlorierten Kohlenwasserstoffen an organischen Wassertrübstoffen und an Böden. Wasser-, Abwasserforsch. 4: 107–112

Zeitzschel, B. (1965). Zur Sedimentation von Seston, eine produktionsbiologische Untersuchung von Sinkstoffen und Sedimenten der westlichen und mittleren Ostsee. Kieler Meeresforsch. 21: 55–80

Zeitzschel, B., Diekmann, P., Uhlmann, L. (1978). A new multisample sediment trap. Mar. Biol. 45: 285–288

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Marine Biology of Polar Regions and Effects of Stress on Marine Organisms
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UTILIZATION OF PHYTOPLANKTON BY COPEPODS IN ANTARCTIC WATERS DURING SPRING

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ABSTRACT

Copepod biomass, species composition and feeding have been compared with the standing stock and production of phytoplankton in the upper 100 m from 3 stations in the region of the Antarctic Peninsula. The 3 stations, representative for the 3 ecological zones encountered in this region in November/December 1980, differed considerably in biomass and composition of phytoplankton and zooplankton. In the open waters of the Drake Passage, phytoplankton biomass was low ($\sim$1-2 g C m^{-2}) and that of the copepods high (0.77 g C m^{-2}). Copepod ingestion was approximately 50% of daily primary production (0.14 g C m^{-2} d^{-1}). In the region of the ice edge adjoining Joinville Island, phytoplankton biomass ($\sim$10 g C m^{-2}) and production (1.1 g C m^{-2} d^{-1}) was high and biomass of zooplankton (0.02 g C m^{-2}) low. Daily ingestion was only 0.6% of primary production. Feeding activity of individual copepods at this station was much higher than in the Drake Passage and small copepods dominated community ingestion in contrast to large copepods in the open water region. Diatoms dominated phytoplankton in both these regions. In the Bransfield Strait *Phaeocystis* dominated phytoplankton and its biomass and production levels were similar to those of the ice edge. The copepod biomass (0.07 g C m^{-2}) and feeding activity were low, possibly due to the unsuitability of *Phaeocystis* as copepod food. In the regions of high phytoplankton biomass, sinking of cells accounted for greater loss from the surface zone than grazing by copepods, which is similar to findings reported from spring blooms in shelf areas of the northern hemisphere.

INTRODUCTION

Phytoplankton in the sea are often grazed down by zooplankton (Cushing, 1958; Menzel and Ryther, 1961; Hargrave and Geen, 1970; Frost *et al.*, 1983) but, particularly during diatom blooms in shallower regions, sedimentation can cause a greater loss of phytoplankton cells from the surface than grazing by zooplankton

(Smetacek et al., 1978; Dagg et al., 1982; Walsh, 1983; Conover and Mayzaud, in press; Smetacek, in press; Fransz and Gieskes, in press). This has not yet been reported from the Southern Ocean although Biggs (1982) has suggested that utilization of phytoplankton by zooplankton can be negligible during blooms in Antarctic waters.

In this paper we present data on the phytoplankton/copepod relationships from the upper 100 m obtained during the cruise of RV "Meteor" to the Antarctic Peninsula in November/December 1980. Phytoplankton biomass, composition and production, copepod standing stock and feeding behaviour were studied on board at three stations.

MATERIALS AND METHODS

The three stations chosen for this study were fairly typical of the three ecological zones found during the cruise (Fig. 1). Details of

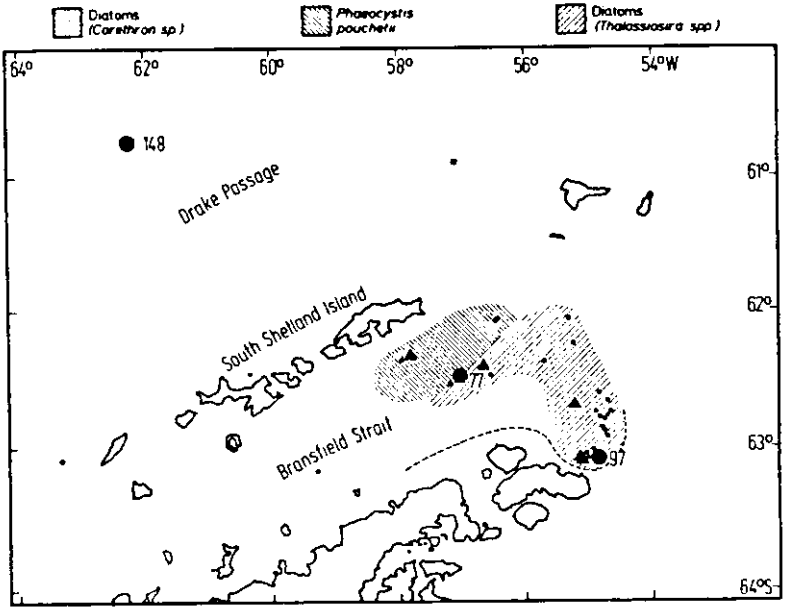

Fig. 1. The Antarctic Peninsula region with the area covered by RV "Meteor". The locations, water depths and sampling dates of the three stations are as follows:
St. 77: 62°30'S, 57°03'W, 910 m, 1.12.1980.
97: 63°04'S, 54°53'W, 355 m, 6.12.1980.
148: 60°44'S, 62°16'W, 3774 m, 14.12.1980.
Zones with similar phytoplankton composition and biomass are indicated. Sediment trap deployments are marked with triangles. The approximate border of the ice edge is denoted by the dashed line.

the cruise together with a preliminary report of the results have been summarized by Zeitzschel and Zenk (1981).

Water samples were collected with Niskin bottles from 6 light depths within the euphotic zone down to 0.1% of incident light determined with an in situ radiometer (Haardt and Maassen, 1981) and from 6 further depths below. Chlorophyll a and particulate organic carbon (POC) were measured on GF/C filters spectrophotometrically and with a CHN Analyzer (Hewlett Packard 185B) respectively. In addition, vertical profiles of chlorophyll fluorescence were recorded with an in situ fluorometer (Haardt and Maassen, 1981). Simulated in situ incubation (4 h, under natural light conditions) was employed for primary production measurements (14C-method). Phytoplankton species composition was quantitatively analysed under an inverted microscope. Free-drifting sediment traps (Kiel funnel (Zeitzschel et al., 1978)) were deployed at 100 m depth on 6 occasions within the Bransfield Strait (Fig. 1) to assess vertical flux of settling particles.

Zooplankton was sampled by vertical hauls with a Nansen closing net (mesh size 200 µm) and preserved with buffered formalin (end concentration 4%). Copepods for feeding experiments were collected only from the upper 100 m and the animals sorted into species, sexes and stages immediately. Experiments were carried out with the following categories: adult females and copepodite stage V of the large copepods according to species; copepodite stages I-IV of large species combined; adults and copepodite stages IV-V of small copepods.

For the feeding experiments, seawater was collected in the upper 100 m with Niskin bottles, screened through 200 µm to remove mesozooplankton and thoroughly mixed in a 50 l polyethylene carboy. The natural phytoplankton suspension was transferred from the carboy into experimental 5 l bottles to which copepods were added. Densities ranged between 33 and 150 copepods per bottle depending on their size. One bottle per experiment served as control (i.e. without copepods). All bottles were stoppered with a silicon plug and the water within the bottles was circulated with a peristaltic pump at 200 ml hr^{-1}. Pump inlets and outlets were protected with a 200 µm mesh sieve. The experiments were run at 0°C in dim light for 8 to 9.5 hours.

For phytoplankton identification and counts, initial and final subsamples of 200 ml were taken and preserved with Lugol's solution. The phytoplankton, including the nanoflagellates, was counted under an inverted microscope (Utermöhl, 1958). Cell size and volume were measured and converted to carbon according to Strathmann (1967). Mean cell concentration, filtration and ingestion rates were calculated after Frost (1972). After the experiments, the contents of the experimental bottles were concentrated with a 55 µm sieve. Copepods and faecal pellets were picked out by pipette. The faecal pellets and half the copepods were immediately deep-frozen for determination of dry weight and carbon. The remaining half was preserved with formalin for later species verification. Assimilation efficiency was estimated from the ratio of dry weight to ash-free dry weight in food and faecal pellets (Conover, 1966).

Copepod respiration was measured by the Winkler method in 100 ml

bottles. Five to ten large copepods or 10 to 20 small copepods were pipetted into a 1 l bottle containing filtered (0.2 µm) and oxygen saturated seawater. One bottle without copepods served as control. All bottles were kept at 0°C for 3-4 hours. The respiration rates were calculated from the difference between dissolved oxygen in the control and in the experimental bottles measured at the beginning and at the end of each experiment. For converting oxygen consumption to carbon utilization, a respiratory quotient of 0.9 was assumed (Dagg et al., 1982).

Growth can be expressed as

$$G = AR - T,$$

where A is the assimilation efficiency of food, R the food consumed and T the food used for metabolism, i.e. growth is assumed to be the difference between carbon assimilated and the amount of carbon respired. Estimations of copepod community feeding are based on the results obtained for each copepod species or group studied, multiplied by their observed density.

RESULTS

Three distinct ecological zones, characterized by biomass and species composition of the phytoplankton, were encountered during this cruise. In the open waters of the Drake Passage, biomass and production were low and the diatom genera Corethron and Chaetoceros dominated the crop although nanoflagellates were also of importance. Station 148 is fairly typical for this zone. Phytoplankton biomass was much higher within the Bransfield Strait, and in the central region, large gelatinous colonies of Phaeocystis dominated, particularly in the upper 20 m. Individual swarmers of Phaeocystis were also important. Mixed diatoms, chiefly represented by the genus Thalassiosira, also contributed substantially to biomass. It was not possible to quantitatively collect zooplankton in the middle of this zone because of Phaeocystis clogging the net. Further, the copepods separated from such net collections could not be used for feeding experiments because of Phaeocystis fragments adhering to their appendages. Station 77, situated on the southern border of this zone, was therefore selected, as the Phaeocystis concentration here was less than in the middle of the Bransfield Strait. The third zone, represented by station 97 located at the ice edge in the region of Joinville Island, also had high phytoplankton concentrations and high production. Severeal species of the diatom genus Thalassiosira contributed the bulk of the phytoplankton crop there.

Chlorophyll a concentration and primary production differed greatly between station 148 and the other two stations (Fig. 2). The much higher POC/chlorophyll a ratio at station 148 than at the other two, suggested that a proportionally greater percentage of POC consisted of detritus at this station. This was confirmed by microscopic examination. The depth distribution of POC and chlorophyll at the 3 stations is fairly homogeneous. At all stations, assimilation numbers (mg C m^{-3}.mg Chl a m^{-3} h^{-1}) were

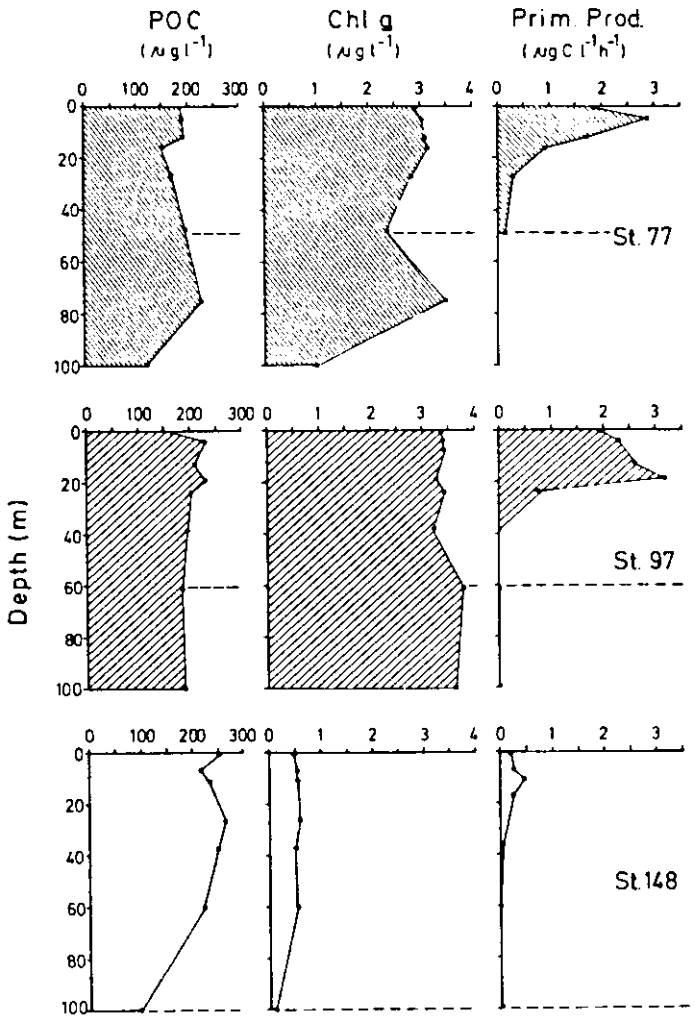

Fig. 2. Vertical distribution of particulate organic carbon (POC), chlorophyll a (chl. a) and primary production in the upper 100 m on the 3 stations. (Dashed line represents euphotic zone).

fairly low (<1). Nutrient concentrations were very high at all stations.

At stations 77 and 97, standing stocks of copepods in the upper 100 m were very low in contrast to station 148 (Table 1). With a few minor exceptions, the biomass of adults and copepodids was highest

TABLE 1. Standing stock of the major copepods at the 3 stations in the upper 100 m (mg C m^{-2}) listed under 3 groups: small copepods, copepodite stages I-IV and large adult females plus copepodite stage V.

	Stat. 77	Stat. 97	Stat. 148
I Small copepods			
Microcalanus	0.15	-	16.41
Ctenocalanus	0.10	1.47	21.75
Stephus	0.10	0.86	-
Subtotal I	0.35	2.33	38.16
II Copepodite stages I-IV			
M. gerlachei	7.89	4.69	-
C. acutus	-	1.77	313.44
R. gigas	-	-	27.26
Subtotal II	7.89	6.46	340.70
III Large adult females and copepodite stage V			
C. acutus	1.37	0.75	175.10
M. gerlachei	36.71	6.57	6.20
C. propinquus	0.92	2.97	7.04
R. gigas	14.29	0.92	199.75
Subtotal III	53.29	11.21	388.09
Grand total I+II+III	61.53	20.00	766.95

at station 148, with Calanoides acutus adults and copepodids as well as adult Rhincalanus gigas contributing the bulk of biomass. Metridia gerlachei was the dominant species at station 77 and 97 in contrast to station 148 where its biomass was insignificant compared to the other copepods. Of interest is the larger contribution of copepodids to total biomass at station 148 (44%) in comparison to stations 77 and 97 (13% and 32% respectively). In the following, small copepods and their copepodids have not been further differentiated.

Copepods greatly dominated zooplankton biomass in the net hauls, while various other zooplankton groups were also present (Table 2). Meroplanktonic larvae were most common at station 97, closest to the coast. Adult Euphausia superba (sampled with a Rectangular Midwater Trawl net) were only recorded in small numbers in the vicinity of station 77 although naupliar stages were found at station 77 and 97 and calyptopis stages of Thysanoessa at station 148. Large numbers of euphausiid faeces were occasionally collected in the sediment traps deployed in the Bransfield Strait indicating the presence of small scattered swarms there.

TABLE 2. Relative occurrence of other zooplankters (xxx common, xx uncommon, x seldom, - absent).

	Stat. 77	Stat. 97	Stat. 148
echinoderm larvae	-	xx	x
barnacle larvae	x	xxx	-
polychaete larvae	xx	xxx	xx
ascidian larvae	-	xx	-
juvenile euphausiids	xx	xx	xxx
adult Euphausia superba	x	-	-
pteropods	x	x	xx
ostracods	xxx	x	x
amphipods	x	-	x
appendicularians	x	x	-
small salps	x	x	-
small medusae	x	x	-
small siphonophores	xx	-	xxx
chaetognaths	xxx	x	xxx
fish larvae	-	x	-
isopods	x	-	-

The similarity between stations in terms of dry weight, carbon content, C/N ratio and cephalothorax length of the copepods used in the experiments is striking (Table 3).

The results of the feeding and respiration experiments have been summarized in Table 4. At station 77, Phaeocystis colonies were removed by pipette from the culture vessels and the proffered food consisted of centric diatoms Thalassiosira spp. (50%), μ-flagellates, mainly Phaeocystis swarmers (36%) and the diatoms Biddulphia and Corethron (5% and 4% respectively) in terms of cell carbon. Correlations between filtration rates and mean concentrations of individual food items (Frost, 1972) were positively significant at the 1% level in C. acutus, copepodids and small copepods, at the 5% level in M. gerlachei and R. gigas, but not significant in Calanus propinquus (Spearman rank correlation, Table 5).

At station 97, Thalassiosira spp. with cell diameters ranging between 20 and 60 μm with a mean at 40 μm constituted 80% of the proffered food. The remainder consisted of nanoflagellates (11%) and pennate diatoms (type Nitzschia) (7%). A positive significant correlation between filtration rates and food concentration was found at the 0.1% level in R. gigas, at the 1% level for the other copepod species and groups excluding small copepods, where the relationship was not significant (Table 5).

At station 148, the diatoms Corethron (42%) and Chaetoceros (26%) constituted the bulk of the food supply. Small flagellates and pennate diatoms (type Nitzschia) followed with 15% and 9% respectively. The relationship between food concentration and filtration rates was significant in all cases at the 1% level except in M. gerlachei and R. gigas, where a 0.1% significance level was found.

TABLE 3. Mean dry weight (DW), carbon content (C), carbon/nitrogen ratio (by weight) and the cephalothorax length (mm) and standard deviation of the copepods at the 3 stations.

	DW (µg)	C (µg)	C/N	Cephalo-thorax length (mm)
Stat. 77				
Small copepods	15± 2.5	7± 1.6	4.1±0.5	0.7±0.07
Copepodids	160±25.8	82±19.0	3.7±0.5	2.3±0.4
C. acutus	288±10.6	133± 6.1	4.9±0.19	3.5±0.12
M. gerlachei	362±12.1	162±11.0	4.0±0.1	2.5±0.18
C. propinquus	457±24.1	230±22.7	4.3±0.23	4.5±0.27
R. gigas	1097±27.0	503±12.6	4.1±0.35	6.0±0.15
Stat. 97				
Small copepods	13± 2.1	6± 1.2	4.3±0.4	0.6±0.13
Copepodids	204± 9.4	99± 9.0	4.7±0.2	2.4±0.16
C. acutus	304±12.6	141± 3.2	4.9±0.31	3.4±0.16
M. gerlachei	341±15.7	161±13.0	4.0±0.08	2.5±0.19
C. propinquus	444±24.1	209±14.9	4.3±0.17	4.6±0.12
R. gigas	1112±65.3	511±19.0	4.0±0.39	6.1±0.14
Stat. 148				
Small copepods	17± 1.4	8± 1.0	4.4±0.2	0.9±0.1
Copepodids	148± 8.2	69± 5.0	4.9±0.13	2.2±0.09
C. acutus	293±11.6	135± 6.0	5.0±0.14	3.6±0.1
M. gerlachei	340±34.2	159±20.3	4.1±0.18	2.6±0.19
C. propinquus	439±14.6	220±19.2	4.5±0.16	4.6±0.14
R. gigas	1084±15.2	492±13.3	4.2±0.22	6.0±0.3

The copepod population at station 97 was much more active than at the other stations (Table 4), as they had the highest filtration, ingestion, assimilation, respiration as well as growth rates. This applied to all species and groups. At all stations, highest respiration rates were found in the largest species, R. gigas, although feeding and assimilation rates were in the same range as for the other copepods. The exceptionally high growth efficiencies in small copepods are difficult to explain.

The total amounts ingested by the copepod population (for 100 m depth) at stations 77 and 97 (5.46 and 6.44 mg C $m^{-2}d^{-1}$) were lower by an order of magnitude than at station 148 (77.2 mg C $m^{-2}d^{-1}$) (Table 6). At station 77, M. gerlachei accounted for 72% of community ingestion, whereas small copepods were the main feeders in

TABLE 4. Results of the feeding and respiration experiments per copepod and day.

	Filtration rate (ml $cop^{-1}d^{-1}$)	Ingestion rate (R) ($\mu gCcop^{-1}d^{-1}$)	Assimilation rate (A) (%)	Assimilated food (AR) ($\mu gCcop^{-1}d^{-1}$)	Respiration rate ($\mu l O_2 cop^{-1}d^{-1}$)	Respiration rate ($\mu gCcop^{-1}d^{-1}$)	Growth rate ($\mu gCcop^{-1}d^{-1}$)
Stat. 77							
Small copepods	74	5.9	65.4	3.9	0.8	0.4	3.5
Copepodids	101	7.8	91.9	7.2	9.2	4.4	2.8
C. acutus	68	6.7	54.1	3.6	6.5	3.1	0.5
M. gerlachei	261	17.3	78.1	13.5	8.9	4.3	9.2
C. propinquus	281	18.7	61.7	11.5	10.7	5.2	6.3
R. gigas	134	12.2	53.3	6.5	12.5	6.0	0.5
Stat. 97							
Small copepodids	214	9.9	70.1	6.9	0.9	0.4	6.5
Copepodids	338	14.8	85.9	12.7	10.4	5.0	7.7
C. acutus	538	22.4	61.7	13.8	16.4	7.9	5.9
M. gerlachei	718	25.9	92.6	24.0	19.8	9.5	14.5
C. propinquus	744	27.6	78.2	21.6	20.7	10.0	11.6
R. gigas	663	28.6	62.1	17.8	27.9	13.5	4.3
Stat. 148							
Small copepods	95	4.5	50.5	2.3	1.6	0.8	1.5
Copepodids	167	7.5	56.1	4.2	7.8	3.8	0.4
C. acutus	221	9.5	56.1	5.3	10.0	4.8	0.5
M. gerlachei	267	10.2	71.1	7.3	8.8	4.2	3.1
C. propinquus	273	11.6	68.7	8.0	10.4	5.0	3.0
R. gigas	302	13.8	58.0	8.0	16.0	7.7	0.3

TABLE 5. Rank-Correlation coefficient (r^*_s) between filtration rates and food concentrations.

	Small Cops	Copepodids	C. acutus	M. gerlachei	C. propinquus	R. gigas
Station 77	0.752**	0.785**	0.733**	0.576*	0.382	0.564*
Station 97	0.657	0.886**	0.943**	0.886**	0.886**	0.990***
Station 148	0.738**	0.833**	0.883**	0.967***	0.833**	0.9 ***

*, **, *** significance levels 5%, 1% and 0.1% respectively.

TABLE 6. Amounts ingested ($mgCm^{-2}d^{-1}$) by the various species and groups in the 100 m water column and their percentage contribution to total ingestion and contribution of species or group to total copepod biomass in percent.

	Stat. 77			Stat. 97			Stat. 148		
	Amount ingested ($mgCm^{-2}d^{-1}$)	% of total ingestion	% of total biomass	Amount ingested ($mgCm^{-2}d^{-1}$)	% of total ingestion	% of total biomass	Amount ingested ($mgCm^{-2}d^{-1}$)	% of total ingestion	% of total biomass
Small copepods	0.30	5.5	0.6	3.85	59.8	11.6	21.47	27.8	5.0
Copepodids	0.75	13.7	12.8	0.97	15.1	32.3	37.04	48.0	44.4
C. acutus	0.07	1.3	2.2	0.12	1.9	3.7	12.32	16.0	22.8
M. gerlachei	3.92	71.8	59.7	1.06	16.4	32.9	0.40	0.5	0.8
C. propinquus	0.07	1.3	1.5	0.39	6.1	14.8	0.37	0.5	0.9
R. gigas	0.35	6.4	23.2	0.05	0.8	4.6	5.60	7.2	26.0

TABLE 7. Potential food concentration (chlorophyll *a* = Chl *a*), particulate organic carbon (POC), primary production (Pr.Pr.), copepod biomass (CB), ingestion rate (IR) and copepod production (CP) integrated for the 100 m water column.

Station	Chl *a* mg m^{-2}	POC g m^{-2}	Pr.Pr. mgC $m^{-2}d^{-1}$	CB mgC m^{-2}	IR mgC $m^{-2}d^{-1}$	CP
77	284	18.5	550	62	5.5	3.1
97	355	19.8	1120	20	6.4	4.0
148	44	21.1	140	767	77.2	15.3

station 97 (60%); the latter figure is surprising, as small copepods contributed only 12% to total biomass. At station 148, copepodids accounted for 48% of community ingestion. At all stations, *R. gigas* contributed substantially less to community ingestion than to community biomass.

In Tables 7 and 8 copepod biomass, ingestion, production, and P/B ratios have been lumped together in order to demonstrate the relationship between potential food (detritus has not been considered) and copepod grazing pressure. As no direct estimates of phytoplankton biomass are available, these have been roughly calculated from chlorophyll concentrations. A phytoplankton carbon/chlorophyll ratio of 30 - obtained from diatom populations growing under nutrient-rich but light-poor conditions (Smetacek and Hendrikson, 1979) - has been employed to gain a rough estimate of biomass. The differences between phytoplankton/copepod biomass ratios, percentage ingestion of primary production and daily copepod production/biomass ratios from stations 77 and 97 as compared to station 148 are striking (Table 8). Their percentage of primary production lost by sinking from the 100 m water column has been calculated from the mean of 6 sediment trap deployments and 13 measurements of primary production in the region of stations 77 and 97. A mean of 0.54 g C $m^{-2}d^{-1}$ (range 0.01-1.4 g C $m^{-2}d^{-1}$) was collected by the traps and mean primary production for the region was 0.83±0.43 g C $m^{-2}d^{-1}$ (n=13). The material collected by the traps

TABLE 8. Ratios of phytoplankton/copepod biomass (PP/CB), percentage ingestion of primary production (% IR of Pr.Pr.), daily copepod production/biomass (Cop. P/B) ratios and percentage sedimentation of primary production (% sed. of Pr.Pr.) of the 100 m water column.

Station	PP/CB	% IR of Pr.Pr.	Cop. P/B	% sed. of Pr.Pr.
77	137:1	1.1%	0.05	64%
97	533:1	0.6%	0.20	64%
148	1.7:1	55.0%	0.02	-

consisted either of Thalassiosira chains with resting spores or euphausiid faecal pellets. Amorphous detritus and large unidentified pellets were also significant but whole copepod pellets were rare. This average value for the Bransfield Strait and ice edge indicates that sinking out of organic carbon from the upper 100 m is several orders of magnitude higher than copepod ingestion. Unfortunately, no comparable sedimentation data are available from the region of station 148.

DISCUSSION

Large, comparatively ungrazed spring blooms have been described from many inshore and coastal areas in the northern hemisphere (Taguchi and Fukushi, 1975; Conover and Mayzaud, in press; Fransz and Gieskes, in press). Sediment trap deployments in the Baltic Sea have shown that a significant portion of the ungrazed phytoplankton sinks out of the surface layer (Smetacek et al., 1978; Smetacek, 1980) and Fransz and Gieskes (in press) provide evidence to show that the same also occurs in the North Sea. Dagg et al. (1982) found that a large portion of the spring bloom sank out in the coastal and mid shelf region of the Bering Sea.

Alexander and Niebauer (1981) reported a similar fate for the spring phytoplankton bloom in the Bering Sea ice edge. Walsh (1983) has postulated that sedimentation is the usual fate of diatom blooms on the continental shelves, whether related to upwelling or spring blooms. Our observations suggest that this also applies to the phytoplankton of the Antarctic continental shelf. However, more information will be required before this suggestion can be confirmed.

In the deeper waters of the outer shelf region of the Bering Sea and in the open North Pacific, however, zooplankton grazing has been reported to be the primary factor regulating phytoplankton biomass (Dagg et al., 1982; Frost et al., 1983). Copepod grazing at station 148 in the open, deep water of the Drake Passage accounted for 55% of daily primary production. Unfortunately, sedimentation was not recorded here and further, it is not known whether this is the usual situation in this region.

There appears to be a relationship between water depth and zooplankton grazing pressure on the spring bloom, presumably a function of the size of the overwintering copepod population that commences feeding during bloom development. Thus, the persistently low phytoplankton biomass and high nutrient content of the open temperate and sub-arctic North Pacific has been attributed to heavy grazing by the large overwintering populations of the large copepods Neocalanus cristatus and N. plumchrus, which prevents the rapid build-up of diatom biomass characteristic of the spring blooms of all shallow temperate and sub-arctic regions and the North Atlantic in general (Parsons et al., 1967; Frost et al., 1983).

The poor utilization of the North Atlantic spring bloom by zooplankton (Colebrook, 1982) in contrast to that of the North Pacific, is possibly due to the fundamentally differing circulation patterns of the two oceans. The North Pacific overwintering populations are retained in the same region and are hence more likely to be in balance with their potential food supply in contrast

to their North Atlantic counterparts. Circulation in the Antarctic is dominated by circumpolar currents; the productive regions (Antarctic Peninsula, Ross Sea area) constitute patches within this generally oligotrophic environment. The overwintering strategies of Antarctic copepods relative to regional hydrography and their patchy food supply are not well known.

At station 77 a large population (2.5 g C m^{-2}) of Metridia gerlachei was present below 100 m with its maximum between 150-500 m. These copepods were actively feeding as evident by presence of food - mostly diatoms - in their guts. Further, most males had developed spermatophores. We do not know whether the animals had left the surface to avoid the gelatinous Phaeocystis colonies and were feeding at depth on sinking diatom cells, or whether they were actively migrating between surface and deeper layers. The genus Metridia is known to be an active vertical migrator (Hardy and Gunther, 1935). However, at station 97 there was no similar maximum at depth and the sparce copepod population down to 300 m. The deeper living copepods, in striking contrast to those in the upper 100 m, were lethargic in their movements and might well have represented an overwintering population. In contrast, the copepod maximum at station 148 was located in the upper layer with a very small population between 150-400 m.

The larger Antarctic copepods have low feeding rates similar to those of the large copepods (N. cristatus, N. plumchrus) of the North Pacific (Ikeda, 1971; Taguchi and Ishii, 1972). Thus, Rhincalanus gigas (0.5 mg C/ind.) ingested 2-6% of body carbon per day and N. cristatus (0.7 mg C/ind.) was found to ingest 5-8.4%; the range for intermediate Antarctic species (Calanus acutus, M. gerlachei, C. propinquus: 0.1-0.2 mg C/ind.) was between 5 and 16% whereas N. plumchrus (0.1 mg C/ind.) of the North Pacific ingested 6-7% of body carbon. However, the North Atlantic C. finmarchicus (0.1 mg C/ind.) has been found to have much higher ingestion rates (35-40%, Gamble, 1978). To what extent these differences in feeding behaviour reflect differences in developmental stages in the animals is undecided. The much higher feeding activity of all copepods at station 97 in comparison to the other stations demonstrates the variability in activity, although the similarity in size and weight of the copepods at all stations is indeed striking and differences in behaviour difficult to explain in this light.

Food quality might be another explanation for regional differences in feeding activity. Thus, the large spiny Corethron and Chaetoceros characteristic of station 148 are reported not to be relished by copepods (Parsons et al., 1967; Hargrave and Geen, 1970) although Marshall and Orr (1955) and Schnack (1979) reported heavy feeding on Chaetoceros. Similarly, Dagg et al. (1982) and Schnack (1983) reported poor feeding of copepods on Phaeocystis in the Bering Sea and the Antarctic respectively, whereas Weisse (1983) found reasonable feeding on this alga by small copepods in the North Sea. We feel that the heavy feeding at station 97 was related to the high concentration and suitability of Thalassiosira as copepod food. The ten times higher P/B ratio at this station indicates that an initial phase of heavy feeding was in progress here. The large Phaeocystis population at station 77 probably inhibited feeding by the copepods there. At station 148, feeding rate of the copepods was

possibly geared to the low food concentration ensuring optimum utilization of the available crop. The comparatively high detritus levels at this station together with the large copepodid population indicate that growth had progressed for several weeks prior to the sampling date and that balance between phytoplankton growth and copepod feeding had been achieved here in contrast to the stations closer to the ice edge.

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REFERENCES

Alexander, V., and Niebauer, H.T., 1981. Oceanography of the eastern Bering Sea ice-edge in spring. Limnol. Oceanogr., 26, 1111-1125.

Biggs, D.C., 1982. Zooplankton excretion and NH_4^+ cycling in near-surface waters of the Southern Ocean. I. Ross Sea, Austral summer 1977-1978. Polar Biol., 1, 55-67.

Colebrook, J.M., 1982. Continuous plankton research: seasonal variations in the distribution and abundance of plankton in the North Atlantic Ocean and the North Sea. J. Plankton Res., 4, 435-462.

Conover, R.J., 1966. Assimilation of organic matter by zooplankton. Limnol. Oceanogr., 11, 338-345.

Conover, R.J., and Mayzaud, P. Utilization of phytoplankton by zooplankton during spring bloom in a Nova Scotia Inlet. Canadian J. Fish. Aquat. Sci. (In press.)

Cushing, D.H., 1958. The effect of grazing in reducing the primary production: a review. Rapp. P.-v. Réun. Cons. perm. int. Explor. Mer, 144, 149-154.

Dagg, M.J., Vidal, J., Whitledge, T.E., Iverson, R.L., and Goering, J.J., 1982. The feeding, respiration, and excretion of zooplankton in the Bering Sea during a spring bloom. Deep Sea Res., 29, 45-63.

Fransz, H.G., and Gieskes, W.W.C. The imbalance of phytoplankton and copepods in the North Sea. Rapp. P.-v. Réun. Cons. perm. int. Explor. Mer. (In press.)

Frost, B.W., 1972. Effects of size and concentration of food particles on the feeding behaviour of the marine planktonic copepod Calanus pacificus. Limnol. Oceanogr., 17, 805-815.

Frost, B.W., Landry, M.R., and Hassett, R.P., 1983. Feeding behaviour of large calanoid copepods Neocalanus cristatus and N. plumchrus from the subarctic Pacific Ocean. Deep Sea Res., 30, 1-13.

Gamble, J.C., 1978. Copepod grazing during a declining spring phytoplankton bloom in the northern North Sea. Mar. Biol., 49,

303-315.

Haardt, H., and Maassen, R., 1981. Optische Beobachtungen, in Beobachtungen und erste Ergebnisse der "Meteor"-Reise 56 aus der Scotia-See und der Bransfield-Strasse im November/Dezember 1980 (ANT I): ein nautischer und wissenschaftlicher Bericht (Eds. B. Zeitzschel and W. Zenk). Ber. Inst. Meeresk., 80, 21-27.

Hardy, A.C., and Gunther, M.A., 1935. The plankton of the South Georgia whaling grounds and adjacent waters, 1926-1927. 'Discovery' Rep., 11, 1-456.

Hargrave, B.T., and Geen, G.H., 1970. Effects of copepod grazing on two natural phytoplankton populations. J. Fish. Res. Bd. Can., 27, 1395-1403.

Ikeda, T., 1971. Preliminary shipboard culture experiments on the feeding and respiration of an oceanic copepod, Calanus cristatus, in the Bering Sea. Bull. Plankton Soc. Japan, 18, 5-14.

Marshall, S.M., and Orr, A.P., 1955. On the biology of Calanus finmarchicus: Food uptake, assimilation and excretion in adult and stage V. J. mar. biol. Ass. U.K., 34, 495-529.

Menzel, D.W., and Ryther, J.H., 1961. Zooplankton in the Sargasso Sea off Bermuda and its relation to organic production. J. Cons. perm. int. Explor. Mer, 26, 250-258.

Parsons, T.R., LeBrasseur, R.J., and Fulton, J.D., 1967. Some observations on the dependence of zooplankton grazing on the cell size and concentration of phytoplankton blooms. J. oceanogr. Soc. Japan, 23, 10-17.

Schnack, S.B., 1979. Feeding of Calanus helgolandicus on phytoplankton mixtures. Mar. Ecol. Prog. Ser., 1, 41-47.

Schnack, S.B., 1983. On the feeding of copepods on Thalassiosira partheneia from the Northwest African upwelling area. Mar. Ecol. Prog. Ser., 11, 49-53.

Smetacek, V., 1980. Annual cycle of sedimentation in relation to plankton ecology in western Kiel Bight. Ophelia, Suppl. 1, 65-76.

Smetacek, V. The supply of food to the benthos, in Flows of matter and energy in marine ecosystems: theory and practice (Ed. M.J. Fasham). Plenum Press, New York. (In press.)

Smetacek, V., and Hendrikson, P., 1979. Composition of particulate organic matter in Kiel Bight in relation to phytoplankton succession. Oceanol. Acta, 2, 287-298.

Smetacek, V., von Bröckel, K., Zeitzschel, B., and Zenk, W., 1978. Sedimentation of particulate matter during a phytoplankton spring bloom in relation to the hydrographical regime. Mar. Biol., 47, 211-226.

Strathmann, R.R., 1967. Estimating the organic carbon content of phytoplankton from cell volume or plasma volume. Limnol. Oceanogr., 12, 411-418.

Taguchi, S., and Fukuchi, M., 1975. Filtration rate of zooplankton community during spring bloom in Akkeshi Bay. J. exp. mar. Biol. Ecol., 19, 145-164.

Taguchi, S., and Ishii, H., 1972. Shipboard experiments on respiration, excretion, and grazing of Calanus cristatus and C. plumchrus (Copepoda) in the northern North Pacific. Biol. Ocean. Northern North-Pacific Ocean, 419-431.

Utermöhl, H., 1958. Zur Vervollkommnung der quantitativen Phytoplanktonmethodik. Int. Ver. theor. angew. Limnol., 9, 1-38.

Walsh, T.T., 1983. Death in the sea: Enigmatic phytoplankton losses. Prog. Oceanogr., 12, 1-86.

Weisse, T., 1983. Feeding of calanoid copepods in relation to Phaeocystis pouchetii blooms in the German Wadden Sea area off Sylt. Mar. Biol., 74, 87-94.

Zeitzschel, B., and Zenk, W., 1981. Beobachtungen und erste Ergebnisse der "Meteor"-Reise 56 aus der Scotia-See und der Bransfield-Strasse im November/Dezember 1980 (ANT I): ein nautischer und wissenschaftlicher Bericht. Ber. Inst. Meeresk., 80, 1-73.

Zeitzschel, B., Diekmann, P., and Uhlmann, L., 1978. A new multisample sediment trap. Mar. Biol., 45, 285-288.