The Loss of Diatoms in the Spring Bloom

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Phil. Trans. R. Soc. Lond. B 1992 **335**, 237-246
doi: 10.1098/rstb.1992.0021

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SUMMARY

The sinking of diatoms towards the end of the spring bloom contributes to the loss of organic material below the mixer layer. Earlier work is reviewed. The study of Peinert *et al.* (*Neth. J. Sea Res.* **16,** 276 (1982)) in the Kieler Bucht was reworked assuming that the algal reproductive rate can be derived from the ratio of a radiocarbon measurement to stock in carbon. This method revealed a somewhat greater loss.

The material of Marshall & Orr (*J. mar. biol. Ass. U.K.* **16,** 853 (1930)) was reworked with an estimate of the diatom sinking rate. It was assumed that the difference between the algal reproductive rate and the grazing rate was constant in the shortest intervals of time and depth. A method was developed to estimate production, the quantity grazed and the quantity sunk. During the spring outburst, diatoms are lost, probably by detrainment, but at the end of the outburst there is a sudden loss. The quantity grazed may have been estimated somewhat more precisely.

1. INTRODUCTION

It has long been known, from the presence of diatomaceous ooze in the upwelling areas and in the Antarctic, that diatoms sink to the seabed. The proportion sinking has been estimated in model studies and the actual quantities that have sedimented have been measured in numerous and detailed trap observations both in shallow water and in the deep ocean. The physiology of sinking has long been investigated. In this short review, the sedimentation of diatoms from the spring outburst in temperate waters is examined. There are two reasons for the examination: (i) to understand the population processes; and (ii) to illuminate part of the processes that constitute the biological pump (for an account of the nature of the pump, see, for example, Volk & Hoffert (1985)).

2. THE SEDIMENTATION OF DIATOMS

Hart & Currie (1960) found diatomaceous ooze and anaerobic mud on the seabed in the Benguela upwelling. Deuser *et al.* (1980, 1981) studied the seasonal cycle of sedimentation in a trap at 1000 m above the seabed in a depth of 3200 m; they found a sedimentation rate of 3.5 g C m^{-2} in 60 days, of which about one fifth comprised organic carbon. Compared with the Menzel & Ryther (1960) estimate of primary production in the Sargasso Sea, the organic carbon in the trap amounts to about one hundredth of the primary production. However, Betzer *et al.* (1984) measured primary production and sedimentary flux at the same time at the equator and near it, and found that the flux amounted to about 10% of the primary production. Cronin & Morris (1982), Poutanen & Morris (1983) and Smith *et al.* (1983) found that the seabed off Namibia and Peru was rich in diatomaceous organic material, as indicated by fatty acid content and chlorophyll degradation products. In the same regions, Morris (1984) found the fatty acids characteristic of phytoplankton. Billet *et al.* (1983), Lampitt & Burnham (1983) and Lampitt (1985) with time-lapse cameras showed a seasonal cycle of phytodetritus on the seabed between 1000 m and 4000 m at stations in the northeast Atlantic. Barnett *et al.* (1984) confirmed the observations with a multiple corer. The increase started half-way through the month of June and continued into July; the aggregates were up to 12 mm in diameter. Rice *et al.* (1986) found high quantities of chloroplastic pigments, predominantly phaeophorbides. In one sample there was 12% of polyunsaturated acids, which suggests that the phytoplankton sank without being eaten; further, 12% of the cells were dividing. Takahashi (1986) studied the flux of diatoms to very deep sediment traps at Ocean Station Papa in the Alaska Gyral by periods of 11 to 16 days. At the time of the spring bloom, up to 4×10^{-7} cells m^{-2} d^{-1} sank into the traps. Their sinking speed, in aggregates, was up to 175 m d^{-1}.

Alldredge & Silver (1988) review the work on 'marine snow', first noticed by Rachel Carson (1951) and Gordon Riley (1963). The Japanese used the name 'marine snow' for the 'organic aggregates' of North American scientists. Trent *et al.* (1978) and Silver *et al.* (1978) made the first quantitative estimates by divers with hand-held rings; more traditional methods of sampling often destroyed the aggregates. Up to 489 aggregates per litre were recorded in near-surface waters and up to 7.5 per litre in deeper seas. They comprised chain-forming diatoms, appendicularian houses, faecal pellets and mucus. Intact cells of diatoms, dinoflagellates, coccolithophores and protozoa were observed. Mucus is generated by diatoms and the cosomatous pteropods. McCave (1984) described the physics of the aggregation of suspended particles. Fine material is aggregated by brownian motion, and larger pieces pick up particles

Phil. Trans. R. Soc. Lond. B (1992) **335,** 237–246
Printed in Great Britain

by shear-controlled coagulation; the shear depends on the turbulent energy in the water column. Organic material may provide a sticky substrate but cannot increase the frequency of collisions. Such aggregates sink at rates up to 368 m d^{-1}. Flocculation is the name given to this process. Kranck & Milligan (1980) showed that sedimentation increased in an inverted conical vessel in which turbulence was maintained and contact probably increased. Kranck & Milligan (1988), with cameras at fixed depths on four days during the spring bloom in the Bedford basin, showed that diatoms aggregated and sank. Fowler & Knauer (1986) review the question. Riebesell (1991*a*) showed that the number of aggregates followed the stock in the spring bloom, and that the size increased towards the end of the bloom. Riebesell (1991*b*) found that the proportion of aggregates by diatom species increased at the end of the bloom. The word 'flocculation' in its first definition means aggregation of wool-like substances, but there is a chemical connotation for which there is no evidence in this context. Gieskes & Elbrachter (1986) found that in the Southern Ocean there were many free chloroplasts because diatom frustules were broken during storms. Alldredge & Gotschalk (1989) found that intact diatoms in the aggregates were actively synthesizing. Flocculation occurred whether the wind was blowing or not. Further, nitrate and ammonium within the aggregates are high. Such is one of the major mechanisms by which organic material sinks to the seabed. It is of particular importance to the heavier cells such as diatoms and the calciferous organisms, such as radiolaria, foraminifera and coccolithophores.

Walsh and his colleagues, summarized in Walsh (1983), made several studies, each expressed in a simulation model, off Peru, in the Bering Sea, in the Gulf of Mexico and in the mid-Atlantic Bight (off New York). In general, they concluded that most of the primary production was not eaten, but sank as phytodetritus. Malone *et al.* (1983) made the case observationally. They showed that the flux of phaeophytin to the benthos was low (about 1%). They concluded that neither grazing nor the flux to the benthos could match the primary production in spring, and so the phytodetritus must be exported off the shelf to the slope. They admitted that the effect of the microzooplankton was not known. Further, the primary production was not partitioned by size of grazer. Walsh (1983) summarized the results of the models, off Peru, in the mid-Atlantic Bight in spring, in the Bering Sea in spring, and off the coast of Texas, the loss by grazing in all areas amounted to about 27% of the primary production.

As the copepods demand food particles greater than 5 μm in diameter (Bartram 1981; Harris 1982; Frost *et al.* 1983), the primary production used by them should be restricted to that size class and above. Rowe *et al.* (1986) disputed the export to the shelf; they pointed out that the pelagic microbial consumption was not taken into account, and that there is a lag between production and consumption. With traps on the slope bed they showed that the export to the slope was low. Further, their diagrams show that, through the year, consumption matched production and so there would not be much available for export.

A major attack on the problem was made in Walsh *et al.* (1988*b*) in the mid-Atlantic Bight on the Eastern Seaboard of the United States. Falkowski *et al.* (1988) found chlorophyll near the seabed forming a nepheloid layer but phaeophytin predominated. *In vivo* fluorescence near the seabed showed that some accumulation occurred near the shelf break front. If the nepheloid layer was 10 m thick, 25% of primary production sank in March and 51% in April, presumably because the front is convergent. Grazing, estimated by the gut clearance method (Smith & Lane 1988) accounted for about one third of the primary production, leaving about one quarter of the production unaccounted for. They found no export to the slope. Rowe *et al.* (1988), from a benthic study, found that about 25% of the primary production was used by the benthos, so the remainder must have gone to herbivores, either protozoa or copepods.

Jahnke *et al.* (1990) suggest that in the northeast Pacific half the organic input to the seabed occurs within 500 km of the slope. Walsh *et al.* (1988) made a simulation model of the spring bloom in the mid-Atlantic Bight to describe the possible export to the slope. The effect of wind stress on circulation is modelled in three dimensions between Cape Hatteras and Nantucket Island between the coast and a depth of 100 m. It was run daily between 28 February and 27 April 1979 at three depths, and was initiated by the chlorophyll distribution observed by satellite in that year. The maximal algal growth rate ranged from 0.234 d^{-1} to 0.390 d^{-1}, and the nutrient half saturation coefficient, $K_s = 0.1$ μg NO_3 N l^{-1}. The grazing formulation expresses an exponentially increasing grazing stress (doubling every ten days or so) as daylength increases. Fluorometers moored south of Long Island showed that the algae sank suddenly at 78–82 d into the middle layer, and in the bottom layer they increased steadily from 78 d to 90 d. The observation was simulated with a sinking rate of 20 m d^{-1} at all three levels for the whole period, which expresses the fact that diatoms sometimes sink more quickly than expected. Of primary production during the whole period, 66% was eaten at all three depths (and 21% was exported). From this considerable study, it appears that not only do the diatoms sink suddenly, but also may do so continuously.

3. STUDIES IN THE KIELER BUCHT AND OPEN BALTIC

Since the mid 1970s, extensive studies have been done in the western Baltic on the transfer of primary production to the benthos in rather shallow water. With the multi-depth sediment traps (Zeitschel *et al.* (1978)), Smetacek *et al.* (1978) described the accumulation of phytoplankton carbon and chlorophyll during the spring outburst in 1975 of the order of 0.1 to 0.3 g C m^{-2} d^{-1}; there were very few faecal pellets in the traps. Hargrave & Burns (1979) assessed the

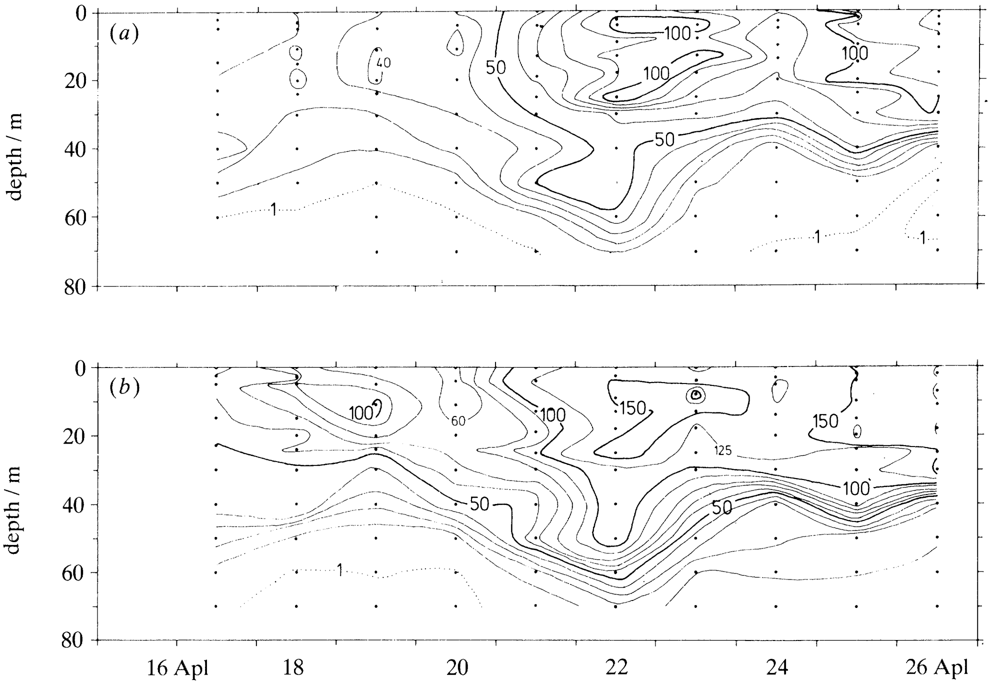

Figure 1. The downward movement below the compensation depth of the population of the diatom *Skeletonema costatum*, after the wind dropped in the western Baltic (von Bodungen *et al.* 1981). (*a*) *Skeletonema costatum* (mg C m^{-3}); (*b*) phytoplankton (mg C m^{-3}).

efficiency of sediment traps and showed that it depended on a high aspect ratio (height to diameter) in turbulent water. A very detailed study von Bodungen *et al.* (1981) was done each day at 11 depths for ten days in April. The 1% light level was at about 25 m. The wind dropped on 20 April, and between that date and 23 April the stock increased in the euphotic layer, but a sharp increase in stock occurred below the 1% light level and above the halocline (between 40 and 60 m), and this increment must have sunk. The cells of *Skeletonema costatum* were no longer being maintained in the euphotic layer. The proportion sunk into the halocline was perhaps a third of the stock on those three days and presumably a smaller fraction of production (figure 1). Peinert *et al.* (1982) linked primary production and sedimentation between February and June at a station in a depth of 25 m; the peak of algal stock occurred on 21 March (7.3 g C m^{-2}), and on 20 and 21 March there was a very sharp increment in sedimentation, probably because of resuspension from the seabed after a storm. The authors estimated that 10 g C m^{-2} sedimented during the period of the spring bloom. Smetacek *et al.* (1984) showed that in early spring the proportion of the bloom sedimenting is perhaps three times that going to larger herbivores, but in late spring that proportion is reversed. In general, it was believed that the spring bloom in the Kieler Bucht occurred before the herbivores grew very much in numbers.

The work of Peinert *et al.* (1982) may be examined in a little more detail. Let us assume that $\Delta P/P=\mu$, the algal reproductive rate, where ΔP is the increment of carbon estimated by the radiocarbon method, and P is the carbon content of the phytoplankton stock; the cells were counted by the Utermöhl method and sized. A small proportion of the radiocarbon measurement may have comprised picoplankton not counted by the Utermöhl method, so the estimate of algal reproductive rate might have been biased upward a little. Then the loss rate, $L=\mu-(1/t)\cdot\ln(P_1/P_0)$, where t is the time in days between observations, and P_0 and P_1 are the estimates of phytoplankton carbon at the beginning and end of the period between observations. Production, P_r, was estimated as follows: The rate of change of stock, P, is given by:

$$\mathrm{d}P(t)/\mathrm{d}t=(\mu-L)\cdot P \tag{1}$$

$$P(t)=P_0\cdot\exp(\mu-L)t. \tag{2}$$

Then production,

$$P_r=P_0\int_0^t \mu\cdot\exp(\mu-L)\cdot t\cdot\mathrm{d}t \tag{3}$$

$$=P_0\cdot\mu\int_0^t \exp(\mu-L)\cdot t\cdot\mathrm{d}t$$

$$=P_0\cdot\mu\cdot[\exp(\mu-L)\cdot t/(\mu-L)]_0^t \tag{4}$$

$$=\{\mu/(\mu-L)\}\cdot P_0\cdot\{\exp(\mu-L)t-1\} \tag{5}$$

$$=\{\mu/(\mu-L)\}\cdot(P_t-P_0). \tag{6}$$

Similarly, it can be shown that

$$L_t=\{L/(\mu-L)\cdot(P_t-P_0).$$

Figure 2 shows stock in g C m^{-2}, together with production and loss in g C m^{-2} d^{-1} for the whole period between February and June. A radiocarbon measurement was not made on 21 March, the date of the peak stock of the spring outburst; I have used the value observed on 28 March (when the stock was of the same order in g C m^{-2}). The loss is high just after

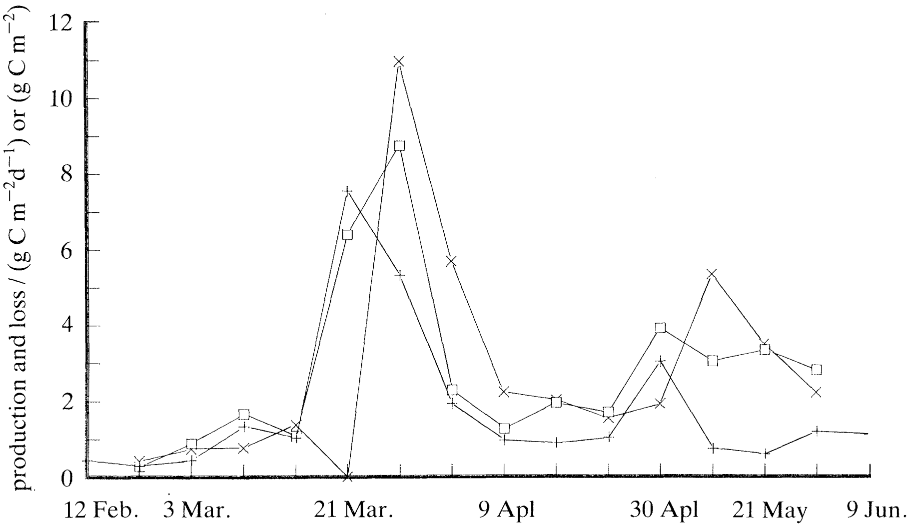

Figure 2. The algal stock (+), production (□) and loss (×) observed in winter, spring and early summer in the Kieler Bucht (after Peinert *et al.* 1982).

Table 1. *Production and loss in the Kieler Bucht in the first half of 1980 (after Peinert* et al. *1982)*

	Production (g C m^{-2} d^{-1})	Loss (g C m^{-2} d^{-1})
Winter	1.17	1.17
Spring	21.44	20.93
Summer	16.84	16.52

the peak of the spring outburst because the estimate of μ may have been a little low. The total production and loss for three periods, winter, spring and early summer, are summarized in table 1.

Peinert *et al.* (1982) suggested that the integral of radiocarbon measurements during the spring bloom amounted to 17.6 g C m^{-2} d^{-1}, not too far from the value of 21.4 g C m^{-2} d^{-1} in table 1. The quantity sedimented was approximately 10 g C m^{-2} d^{-1} during the spring bloom. The total loss as estimated in table 1 was perhaps twice as much.

The loss comprises algal cells which have both sunk and which have been eaten. The larger animals were not at all abundant during the spring bloom (Stegmann & Peinert 1984), but the protozooplankton reached a peak of 0.6 g C m^{-2} on 3 April. Perhaps a proportion of the algal cells were eaten. This question can only be resolved by analysing the processes a little more closely, as will be shown below in a brief study of the spring bloom in Loch Striven by Marshall and Orr (1929/30).

4. OTHER STUDIES ON SEDIMENTATION

The processes involved have been studied directly. Davies & Payne (1984) examined the sedimentation in depth during the spring bloom as part of the FLEX experiment on the Fladen ground in the North Sea in 1976. Before the spring bloom, 50 mg C m^{-2} d^{-1} settled into the traps; during the bloom itself the sedimentation amounted to 185 mg C m^{-2} d^{-1}. The primary production amounted to 1.9 g C m^{-2} d^{-1} (Weichart 1980; Gieskes & Kraay 1980), so about one-tenth of the primary production sank to the sea bed. Davies and Payne separated the sedimented material into faecal pellets, phytodetritus, diatoms, crustacean remains and sand grains. The important point is that the diatoms were whole cells which had presumably not been eaten. The quantity of faecal pellets was low (probably from euphausids).

A study by Forsskall *et al.* (1982) in the entrance to the Gulf of Finland found that about one quarter of the phytoplankton production reached the traps. With their siliceous cells, diatoms are relatively heavy (1020–1250 kg m^{-3}) but senescent cells sink three times as quickly as healthy ones (Reynolds 1984). Hargraves & French (1983) describe the heavily silicified resting spores which can survive for approximately a year in deep water, and which can sink at up to 16 m d^{-1}. Davis *et al.* (1980) found that resting spores of *Leptocylindrus danicus* appeared when the division rate stopped. Diatoms grow well in periods of weak or intermittent stratification. If they are not eaten before the wind slackens and the turbulence decreases, they tend to sink. So the problem is to estimate the rates of grazing, sinking and turbulence during the spring outburst.

Welschmeyer & Lorenzen (1984, 1985) used sediment traps at depth and just below the euphotic layer in Dabob Bay not far from Seattle and in the Central Pacific gyre. They estimated the loss of phaeophorbide by photodegradation, and the loss of phaeophorbide and chlorophyll by sedimentation; the cell sinking rate was estimated by the daily chlorophyll loss rate raised by the depth of the euphotic zone. The phaeopigment in the deep traps represents the quantity grazed by the macrozooplankton and that in the upper traps less the quantity degraded represents that grazed by the microzooplankton. Then grazing rates can be calculated and, from the differences in time of the quantities of chlorophyll, the division rates of the algae were

Table 2. *Loss rates in Dabob Bay and in the Central Pacific gyre*

	Phaeopigment loss (%)	Chlorophyll loss (%)	Cell sinking rate/(m d^{-1})
Dabob Bay	22.84	2.24	0.51
Pacific gyre	0.866	0.097	0.146

estimated. The major results of this work are shown in table 2.

The remainder of the loss is the result of grazing. The algal division rates in Dabob Bay ranged from 0.05 d^{-1} to 0.92 d^{-1}, which is reasonable for a tidally mixed area. In the Central gyre they were lower, 0.10 d^{-1} to 0.26 d^{-1}, which is an average for the whole euphotic zone including cells in the deep chlorophyll maximum. The same model was applied to a study of the spring bloom in Auke Bay, Alaska in about 80 m (Laws *et al.* 1988). They found that the estimate of division rate was well matched to that from the ratio of the radiocarbon increment of production to the phytoplankton stock. They concluded that about 40% d^{-1} of the production in Auke Bay sank, that 26% was taken by microbial grazing, and 32% by macrozooplankton grazing.

The most interesting point about this discussion is the sinking of the diatoms. They are heavy, and with rising temperature their photosynthesis per unit irradiance decreases (Harris 1978). They may produce spores or become senescent, and during periods of reduced turbulence they sink. The proportion that sinks must depend on the time of onset of grazing; in the Kieler Bucht in shallow water, production begins before the larger herbivores start to graze significantly. In deeper water where the development of production is intermittent the small diatoms may be eaten before they have a chance to sink. Cells can live at great depth and have been found with spores well below the euphotic zone (Smetacek 1985).

As noted above, Peinert *et al.* (1982) found that the diatom population sank when the wind stress dropped; they also recorded that sedimentation occurred at the end of the spring bloom on three occasions. Walsby & Reynolds (1980) showed that increments in lipids, polysaccharides or in gas vacuoles probably do not account for the sinking of the population. Reynolds (1976*a*, *b*) showed that *Fragilaria crotonensis* sank when the growth rate stopped, as indicated by silica uptake; more generally, the population starts to sink when the growth rate becomes less than the sinking rate. Reynolds *et al.* (1982) and Reynolds & Wiseman (1982) estimated sinking losses in Lund enclosures from growth rate (or silica uptake) less the net change in numbers.

Reynolds (1983) followed changes in a population of *Fragilaria crotonensis* in a Lund tube in Blelham Tarn in northwest England; approximately every two weeks the stability was broken with a heavy pump. Nutrients were maintained at a high level. After destabilization, numbers in the surface layers dropped considerably, but numbers in the traps (near the lake bed) did not change as much. In June and July the algal division rate was about 0.7 d^{-1} on average and the rate of sinking about 0.3 d^{-1}, so the production of the diatoms at the surface during these two months was greater than the quantity sunk by nearly two orders of magnitude. In August and September, a quiescent period, algal division rates rose to 0.1 d^{-1}, and the sedimentation rate rose to about 0.7 d^{-1}, so the greater proportion of the diatoms sank. Reynolds suggested that under calm conditions and in bright light (300–600 μE m^{-2} d^{-1}) the cells may suffer from photoinhibition; indeed he proposed that sinking was needed to recover from photoinhibition. *Fragilaria* is a summer diatom but the same mechanisms may prevail towards the end of spring.

From trap studies, sedimentation is much greater in spring blooms and in upwelling areas than in systems based on regenerated production (Smetacek *et al.* 1990). Indeed Peinert *et al.* (1989) name the two systems 'loss' and 'retention'. They are the two forms of ecosystem described by Cushing (1989) on quite different grounds. This implies that the main transfer to the seabed or to below the mixed layer occurs in 'loss' systems, in new production, spring blooms and in upwelling areas. In regenerated production, material is retained because the faecal pellets are eaten in the upper layers.

5. THE CONTINUOUS LOSS OF DIATOMS IN LOCH STRIVEN

Marshall & Orr (1930) studied the spring bloom in Loch Striven, a protected sea loch on the west coast of Scotland. They counted the cells from centrifuged water samples at six intervals of depth, and showed quite clearly that the diatoms (nearly all *Skeletonema costatum*) sank below the compensation depth towards the end of the spring bloom. Marshall & Orr's study may be examined in a little more detail. During much of the period of sampling, the water column was mixed; it became stratified in the first ten days of April, but was isothermal on 12 April, after which it stratified again. Table 3 shows the original material in numbers of cells per 20 ml (predominantly *Skeletonema costatum*). The sinking of the population is shown clearly on 16 and 26 April, but I have doubt about the data on 19 April.

Consider samples of diatoms at intervals of time, t, and of depth, z. P_0 and P_1 are the initial and final numbers in that interval of time at the same depth.

Let $$P_1 = P_0 \cdot \exp(\mu - g - s_1)t, \qquad (7)$$

where P_0 is the initial number of cells ml^{-1} of *Skeletonema costatum* at z_1, P_1 is the final number at the same depth, μ is the instantaneous diatom division rate, g is the instantaneous rate of mortality resulting from grazing, and s_1 is the instantaneous rate of loss resulting from sinking.

$$P_1' = P_0 \cdot \exp(\mu - g + (s_1 - s_2))t, \qquad (8)$$

where P_1' is the final number of cells at the depth z_2 ($> z_1$) at the end of the interval of time.

Table 3. *Numbers of Skeletonema costatum per 20 ml by depth and in time in Loch Striven in 1928*

Depth/m	14 March 1928	19 March 1928	22 March 1928	26 March 1928	29 March 1928	2 April 1928	4 April 1928	6 April 1928	9 April 1928	12 April 1928	16 April 1928	19 April 1928	26 April 1928
0	2182	8100	7600	9 000	64 000	73 000	180 000	128 000	90 000	225 000	14 200	1120	101
2	2246	7300	8300	11 300	68 000	61 000	248 000	199 000	106 000	220 000	99 000	2015	138
5	2191	7300	7800	13 500	57 000	133 000	60 000	510 000	176 000	169 000	24 000	1400	3 072
10	2607	7600	6800	2 900	41 000	8 000	2 100	56 000	152 000	83 000	13 000	306	18 400
20	579	1900	3400	1 800	2 000	1 200	1 250	3 100	77 000	10 000	10 900	400	17 800
30	—	—	—	1 500	1 050	115	890	1 280	3 500	2 400	4 700	1008	19 600
Mean	1961	6440	6780	6 667	38 842	46 053	81 873	149 563	100 750	118 233	27 767	1042	9 852

It is assumed that the effects of turbulence are common to these intervals of depth and time and that $(\mu - g)$ is constant in the same intervals.

As $(1/t)\cdot\ln(P_1/P_0) = \mu - g - s_1$,

and $(1/t)\cdot\ln(P_1'/P_0) = \mu - g + s_1 - s_2$,

and $\mu - g - s_1 - \mu + g - s_1 + s_2 = 2s_1 - s_2$, (9)

then $(1/t)\cdot\ln(P_1'/P_0) - (1/t)\cdot\ln(P_1/P_0) = 2s_1 - s_2$, an index of sinking.

The sinking indices were averaged for all depths. Then the average index is

$$(2s_1 - s_2 + 2s_2 - s_3 + 2s_3 - s_4 + 2s_4 - s_5 + 2s_5 - s_6)/6, \text{ or}$$

$$(2s_1 + s_2 + s_3 + s_4 + s_5 - s_6)/6. \qquad (10)$$

Figure 3 shows the quantity sunk (see below for estimation) for a period of about six weeks during the spring bloom; it is initially very low and rises during the spring bloom, but in the later stages the loss rate at the lowest level predominates (see table 3, 26 April). The figure also shows the history of the stock in numbers of cells per 20 ml. The quantity sunk was highest during the peak period of the spring bloom, a result also noted in the work of Peinert *et al* (1982). There is a positive relation between the quantity sunk and the stock of algae ($r^2 = 0.56$; $p = 0.01$).

Woods & Onken (1982) describe the development of the spring bloom in the ocean as a function of irradiance and the physics of the mixed layer, described in a Lagrangian model. They show, as a consequence of the diurnal variation in the depth of the mixed layer, that cells can become irrevocably lost below that layer. If the daily maximum depth of the mixed layer does not increase faster than the sinking rate, many cells are lost; indeed, all would be eventually lost if the depth of the mixed layer was decreasing fast enough; it decreases in spring, but the cells are also eaten. This process depends on changes in the physical conditions.

Given the discussion of physiological effects by Walsby & Reynolds (1982), the Woods & Onken mechanism could be all that is needed to describe the continuous process which appears to have taken place in Loch Striven. But the cells form spores, become senescent and may no longer have silica to sustain

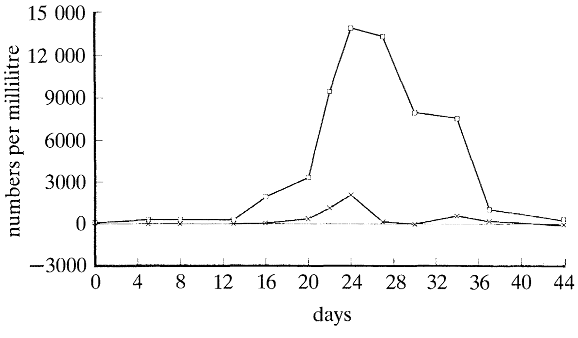

Figure 3. The loss of diatoms, *Skeletonema costatum*, during the spring outburst in 1928; both the algal stock (□) and the quantity sunk (×) are shown (after Marshall & Orr 1930) in cells per millilitre. Peak date of stock was 6 April 1928 at 24 days.

them, and so may sink more quickly. The peremptory loss at the end of the spring bloom is shown quite clearly in table 2 on 26 April.

The next step is to estimate production, the quantity grazed and the quantity sunk. Following Fasham *et al.* (1990), the maximal algal division rate, $\mu_{\max}$, was taken from Eppley (1972) as function of temperature, T, in °C: $\log \mu_{\max} = 0.0275\ T - 0.07$. The maximal division rate at temperature T is probably that of the smallest cells and so applies well to *S. costatum*. In irradiance, the maximal division rate was assumed to occur at 300 μ E $\mathrm{m}^{-2}\ \mathrm{d}^{-1}$ (see Platt & Jassby (1976) for coastal marine phytoplankton; Reynolds (1984) for spring phytoplankton in Crose Mere). Marshall & Orr measured the compensation depth, D_c, frequently during the period of observation. At D_c, $I_o = \exp - kz = 0.01$, where k is the attenuation coefficient and z is the depth of water in m and I_o the irradiance at the surface. This is unknown, and I have assumed that $I_o = 300$ μ E $\mathrm{m}^{-2}\ \mathrm{d}^{-1}$; it is much less than the irradiance under a clear sky at mid-day. Marshall & Orr give the hours of sunshine, low until the end of March, but up to 5 h in the first ten days of April. The effects of photoinhibition are unknown, but the low surface irradiance may express them. The irradiance at depth z, $I_z = 300 \exp - kz$ in μ E $\mathrm{m}^{-2}\ \mathrm{d}^{-1}$. Again, following Fasham *et al.* (1990), the division rate at depth μ_z was estimated with the Smith (1936) equation:

$$\mu_z = (\mu_{\max} \cdot a \cdot I_z)/(\mu_{\max}{}^2 + a^2 \cdot I_z{}^2)^{1/2},$$

where a is the slope of the photosynthesis–irradiance curve at the origin ($= 0.025$ [W m^{-2}] d^{-1}). With this method, μ_z was established at intervals of depth of 1 m from the surface to D_c and were averaged for the euphotic layer. Then the daily average, $\mu' = 0.7 \cdot \mu_z$ (0.63–0.77 (Vollenweider 1965)). The depth of mixing, D_m, was taken as the depth of water or the depth of the thermocline, z_t. If $D_c > z_t$, μ' was averaged to z_t; if $D_c < z_t$, μ' was averaged to D_c. Then μ was reduced by the appropriate fraction at the time of observation.

Marshall & Orr estimated phosphorus as the pentoxide; the quantities were raised by 1.35 to correct for salt error (Cooper 1938) and converted to mM m^{-3}. Eppley *et al.* (1969) found a half-saturation coefficient of 0.4 mM N (0.025 mM P) for *S. costatum*. The simple Michaelis Menten relation was used because there was no information on cell quota or ammonia regenerated (but this is a direct function of the quantity grazed, and the grazers were not recorded). Silica limitation is unlikely because its use during the period was less than the winter maximum for these waters. The maximum algal division rate at temperature T (for each depth and date of observation) was reduced by phosphorus limitation and by self shading, expressed in the dependence of attenuation coefficient on stock. The grazing rate is given by $\ln(P_1/P_0) - (\mu - s) \cdot t$, where s is the average sinking rate. Then, for each interval between observations for t_0 and t_1, with the methods described above, production, P_r, quantity grazed, Q_g, and the quantity sunk, Q_s, were estimated, i.e

$$P_r = [\mu/(\mu - g - s)] \cdot (P_1\text{-}P_0),$$

$$Q_g = [g/(\mu - g - s)] \cdot (P_1 - P_0),$$

and $Q_s = [s/(\mu - g - s)] \cdot (P_1 - P_0)$.

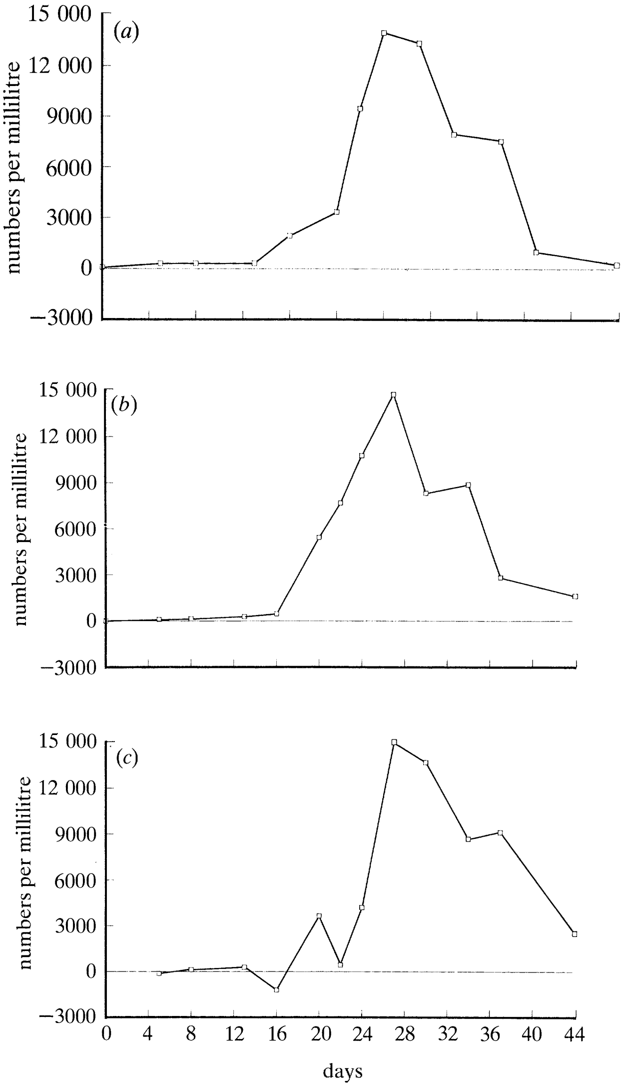

Figure 4. Stock, production and losses in Loch Striven in 1928 in cells per ml; (*a*) the stock of diatoms, predominantly, *Skeletonema costatum*; (*b*) the production of diatoms; (*c*) the quantity grazed. Peak date of stock was 6 April 1928 at 24 days.

Figure 4 shows (*a*) standing stock, (*b*) production, and (*c*) quantity grazed. The stock builds up in three stages to a peak after 24 days on the 6 April, after which it declines. During the first eight days the surface layer was slightly warmer (about 0.07 °C), but D_c was deep, 13 m, and on days 13 and 16 the water column was mixed. The thermocline between 2 m and 5 m appeared on day 20 and was probably responsible for the sudden increment in stock between day 20 and day 24; the increment until day 20 must have been a function of irradiance.

Production follows a similar course, but the peak occurs later. The quantity grazed remains low until day 20 and reaches a peak by day 27, after which it declines as stock is eaten. The quantity sunk is less by about an order of magnitude (see figure 3). During the period, 64 000 cells ml^{-1} were produced, 59 000 cells ml^{-1} were eaten, and 5000 cells ml^{-1} were sunk in a continuous manner. But 2790 cells ml^{-1} sank during the peremptory loss at the end of the bloom. It is instructive to compare the quantities grazed and sunk with the stock. The greatest quantity sunk appears at peak stock as noted above. But there is a lag of four days between the development of the peak stock and that of the quantity grazed. The grazers were probably *Calanus*, but their numbers are not known.

Self shading was of some importance. When the attenuation coefficients were plotted on the stock, there was an inverse relation ($r^2 = 0.46$; $p = 0.05$–0.01). With a quadratic fit, $r^2 = 0.51$ ($p = 0.05$–0.01). The data are somewhat variable, but the effect of self shading starts at between 3000 and 6000 cells ml^{-1}, and so operates for much of the spring bloom. The effective division rate was reduced by self shading from about 0.34 to about 0.27, a reduction to 79%. As control of this spring outburst, self shading was more effective than the nutrient lack, which reduced division rate to 88% (but the regeneration of ammonium as a result of grazing was not taken into account).

6. DISCUSSION

The sedimentation of diatoms from the spring bloom in temperate waters and from upwelling areas in subtropical seas is an important problem for two reasons (as suggested in § 1), first, to understand the dynamics of the population processes, and secondly, the loss of material from the upper mixed layer needs to be assessed as part of the biological pump.

Diatoms sink rapidly in large aggregates to the deep seabed and, indeed, they appear there soon after the spring outburst in temperate waters. The extensive work by Walsh and his colleagues raised the question of how much of the diatom production sinks and how much is eaten. Then the work of Smetacek and his colleagues showed how much of the spring bloom ended in the sediment traps in the Kieler Bucht. From several studies it now appears that the quantity grazed is often, but not always, greater than the quantity lost by sinking. I have limited this study to the sinking of diatoms in the temperate spring bloom, but analogous methods could be used to study the sinking of coccolithophorids and radiolarians.

From the analysis of Marshall & Orr's detailed study, diatoms sink continuously during the spring outburst, and the quantity sunk is linked to the stock rather than production or the quantity grazed. The Woods & Onken mechanism is probably responsible. In this example the quantity grazed is greater than that sunk by about an order of magnitude. But the ratio might be less with larger cells which sink more quickly. Further, the variability of the physical processes may alter the rates by which cells become detrained below the mixed layer.

The self shading mechanism is density dependent. There are three possible controls of the spring bloom in temperate waters (and, by extension, of upwelling areas in subtropical seas), self shading, grazing and nutrient lack. An investigation of these potential controls under different physical conditions would be most desirable. Part of this development would be the fact that the mortality caused by grazing can now be estimated if the loss rate by sinking is known. But Paffenhofer (1988) has noted that most experimental estimates are defective in some way. Further, Nicholls and Thompson (1991) have found that the numbers of small copepods have not been well sampled, reiterating a conclusion by Saville (1959). It is necessary to tie the mortality caused by grazing during the spring bloom to the numbers and sizes of grazers and their behaviour.

I am grateful to Dr Alan Longhurst, Dr Colin Reynolds, Professor Louis Legendre, Dr M. J. R. Fasham and Dr Rolf Peinert for their comments on earlier drafts.

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Received 2 July 1991; accepted 29 August 1991