
Sedimentation of principal phytoplankton species in Lake Constance

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Abstract. Sedimentation of nine phytoplankton species was studied in Lake Constance with the aid of sedimentation traps exposed at six different depths from 20 to 120 m. The study examines sedimentary fluxes at all depths, temporal variation of sinking velocities into the uppermost trap, annual averages of the sinking velocities at all depths and survival of algae during the sedimentation process. In spite of high intraspecific temporal variability of the sinking velocity there is a clear hierarchy from the pennate and the filamentous centric diatoms sinking the fastest to the Cryptomonads, nearly not at all affected by sedimentary losses. Temporal variability of the sinking velocity within species seems to be related to the 'physiological state', the highest velocities always occurring during stationary or decline phases of the population development. An analysis of the role of sedimentary losses in the population dynamics of *Asterionella formosa*, *Fragilaria crotonensis*, *Stephanodiscus binderanus*, *Melosira granulata* reveals positive correlations between the sedimentation rate and cell mortality.

Introduction

Recent developments in phytoplankton research have emphasized the importance of loss processes in the explanation of algal species succession (Kalff and Knoechel, 1978; Smayda, 1980; Reynolds *et al.*, 1982). One of the most prominent loss processes is sedimentation. Hutchinson (1967) postulated that 'much of the seasonal succession of the phytoplankton is due to ... inter-relation between turbulence and sinking speed'. Although it is obvious that sedimentation is the ultimate fate of any particle heavier than water, there is contradictory evidence as to whether sedimentation plays a controlling role in the succession of phytoplankton. There are well documented examples for diatom populations thriving during spring overturn, which are eliminated by sedimentation after the onset of stratification (Lund, 1971; Knoechel and Kalff, 1975; Reynolds, 1976a, 1976b). On the other hand, there is also evidence that mainly senescent populations are destined for high sedimentary losses (Eppley *et al.*, 1967; Smayda, 1970; Reynolds, 1973). In this case sedimentation is not a primary cause for elimination, but only accelerates replacement of a population handicapped by some other factor, e.g., nutrient limitation. Critical evaluation of these two interpretations is hampered by the difficulty in defining or measuring the 'physiological fitness' of a natural population. In this study it shall be attempted to use mortality and survival during the sedimentation process in a deep water column as indicators for 'physiological fitness'.

The DFG (Deutsche Forschungsgemeinschaft)-sponsored project 'carbon cycle in Lake Constance' (scientific leadership: M. Tilzer) offered the opportunity to study algal sedimentation in a deep, mesotrophic lake and to relate sedimentation

data to population density. Investigations were carried out at the deepest point of 'Überlinger See', the northwestern bight of Lake Constance, having a depth of 147 m. Sedimentation traps from 20 to 120 m depth allowed the fate of algae along a sinking distance of 100 m to be studied. Chemical analysis of sediments will be published by H.H. Stabel, whose leadership in planning, constructing and maintaining the sedimentation trap equipment is gratefully acknowledged. The present study encompasses the periods 25 June–6 November 1981 and 4 March–8 November 1982. In 1982 nearly the entire vegetation period was covered; in 1981 the spring bloom was omitted, a phase which is separated from the summer vegetation period by a clear-water phase of 3-week duration attributed to zooplankton grazing. Published information on the physico-chemical environment (Stabel and Tilzer, 1981) and phytoplankton succession (Sommer, 1981) is available for the years 1979 and 1980, but may be used for reference, since the seasonal periodicity of phytoplankton and of the most important physico-chemical variables has been fairly regular from 1979 to 1981.

Methods

An enormous variety of sediment traps is used both in freshwater and marine environments. The sediment traps should be constructed so that they provide realistic estimates of the sedimentary particle flux in the water column. Walsby and Reynolds (1980) doubt that the amount of material passing through the aperture of any trap is identical to the amount settling through an equivalent area of water. Conversely, several authors (Hargrave and Burns, 1979; Blomqvist and Håkanson, 1981) have deduced that cylindrical traps avoid both over- and under-trapping, if precautions are taken against the resuspension of material settled on the bottom of the traps. Bloesch and Burns (1980) recommend an aspect ratio (height: diameter) of 5 for calm and 10 for more turbulent lakes. Following these recommendations, simple cylindrical sediment traps 100 cm high and 10 cm in diameter made of transparent plexi-glass were used. Traps were exposed at 20, 40, 60, 80, 100 and 120 m depths. 20 m is the maximum extension of the euphotic zone in Lake Constance, and the 120 m trap is suspended 27 m above the bottom, a distance considered to be sufficient for avoiding the introduction of resuspended bottom material. The mooring system will be described elsewhere (H.-H. Stabel, personal communication). Exposure times were 2 weeks in spring and autumn 1982 and 1 week throughout 1981 and summer 1982. Subsamples for cell counts were fixed with Lugol's iodine solution. Samples for examining the concentration of algae in the free water zone were taken at 0, 1, 3, 4, 5, 6, 7, 8, 10, 12.5, 15, 17.5, 20, 25, 30, 40, 50, 70, 100 and 140 m with 9-l van Dorn bottles. Mixed samples were prepared, to represent the 0–5, 5–10, 10–15, 15–20 and 20–140 m sections of the water column.

Algae were counted according to Utermöhl's inverted microscope technique. Whenever possible, 400 cells or colonies of each species were counted. According to Lund *et al.* (1958) this gives a counting precision of $\pm 10\%$ if particles are randomly distributed. Usually this requirement was fulfilled for the plankton samples. Counting precision of the sediment samples was $< 10\%$ because of the optical disturbance caused by detrital particles. A test with 30 identical sub-

samples gave a coefficient of variation of $\pm 20\%$ for *Asterionella formosa*. Empty diatom thecae were counted separately.

Results

Sedimentary flux

Sedimentation of all species under study had a distinct seasonality which was related to their periodicity in the lake plankton (Sommer, 1981). Euplanktonic species were not found in the sediment traps out of season, whereas irregular recoveries of tychoplanktonic and littoral species (*Melosira varians*, *Surirella ovalis*, *Diatoma vulgare* and *Spirogyra* spp.) were quite common, even if these algae had not been detected before in the plankton samples. They possibly originated from the periphyton on the buoy. Hence, their occurrence in the sediment traps is considered at least partly to be an artifact and was not studied in further detail. The only algal species not included in the analysis that was common in the traps was *Phacotus lenticularis*. Because of rareness in the plankton samples planktonic cell numbers were statistically unreliable. Although very abundant in the plankton Cryptophyceae were nearly not at all recovered from the traps. Among several 100 000 cells counted only five *Rhodomonas minuta*, three *Cryptomonas ovata* and no *Rhodomonas lens* cells were seen. Compared to their importance in the plankton, diatoms were over-represented in the sediment traps. The summer and autumn maxima of pennate and filamentous centric diatoms were followed by corresponding maxima in the sedimentary flux (Figure 1). In 1981 *Fragilaria crotonensis* produced two maxima (July/August and September) that were followed by flux rates of $>2 \times 10^9$ cells $m^{-2} d^{-1}$ (summer) and 3×10^9 cells $m^{-2} d^{-1}$ (autumn). In 1982 the summer maximum of the sedimentary flux was 3×10^9 cells $m^{-2} d^{-1}$, whereas the far less pronounced autumn maximum resulted in a sedimentary flux one order of magnitude smaller. The periodicity of *Asterionella formosa* differs from *F. crotonensis* in that the former has an additional, though small, maximum in spring, reflected in moderate sedimentary fluxes up to 1.5×10^7 cells $m^{-2} d^{-1}$. More than 10^9 cells $m^{-2} d^{-1}$ were observed only during the summer maximum. The development of the filamentous diatoms *Stephanodiscus binderanus* and *Melosira granulata* was considerably different in the two years. In 1981 *M. granulata* was too rare to obtain statistically reliable counts. Conversely *S. binderanus* had a very pronounced summer maximum in 1981 that resulted in a sedimentary flux up to 7×10^9 cells $m^{-2} d^{-1}$. The sedimentation maxima into the 20 m trap of these four diatom species followed the maxima of planktonic abundance with a slight time shift. The time shift between the sedimentation maxima at the different depths was small, if not undetectable. Even between the 20 m and the 120 m trap it never exceeded two weeks. The magnitude of sedimentary flux maxima was hardly reduced with depth, the reduction from 20 to 120 m never exceeding 30%.

The sedimentation pattern of *Stephanodiscus hantzschii* differed from that of the other much larger diatoms. This small alga (cell volume $50 \mu m^3$) is an important contributor to the vernal bloom in May and develops further short-time maxima throughout the whole year. Only the sedimentation maxima in May and July

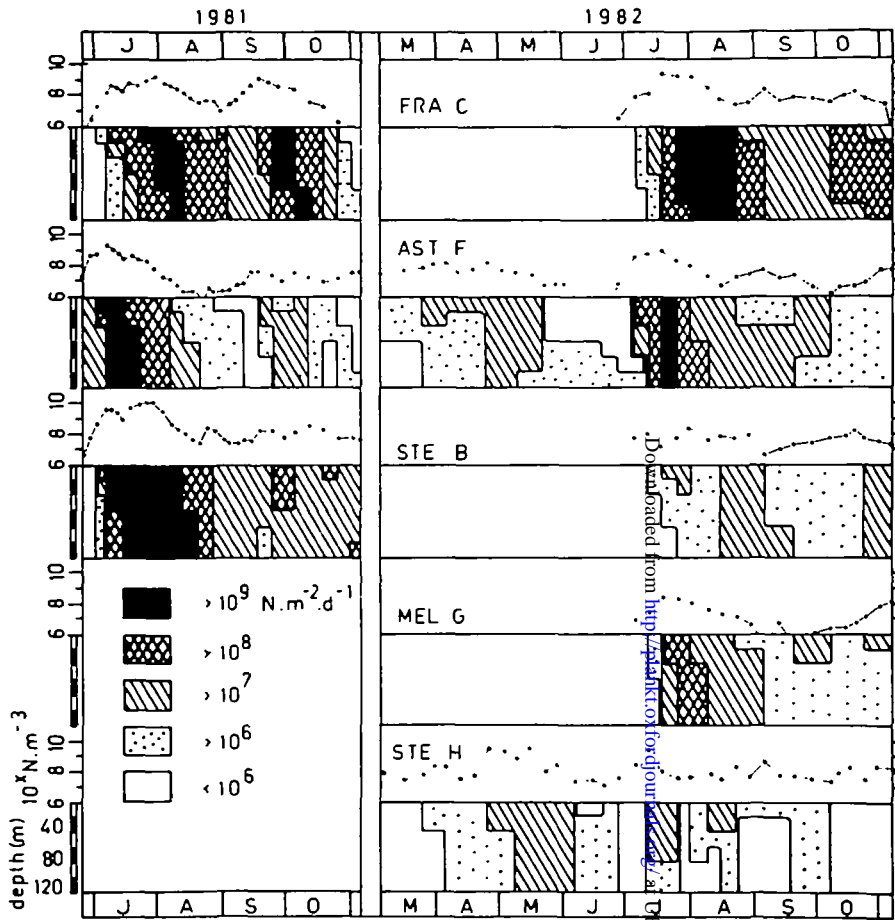


Fig. 1. Population density (log-scale; cells m^{-3} , average from 0–20 m) and depth time diagrams of sedimentary flux of diatoms in Lake Constance. FRA C: *Fragilaria crotonensis*; AST F: *Asterionella formosa*; STE B: *Stephanodiscus binderanus*; MEL G: *Melosira granulata*; STE H: *Stephanodiscus hantzschii*.

could clearly be connected with preceding maxima of abundance in the pelagial. Although population density maxima were in the same order of magnitude as of the other diatoms sedimentary fluxes for live cells never exceeded 8×10^7 cells $m^{-2} d^{-1}$ at 20 m and 2×10^7 cells $m^{-2} d^{-1}$ at 120 m. The non-diatom species (Figure 2) included in this study had both lower abundance and smaller sedimentary fluxes than the diatoms. The colonial flagellate *Pandorina morum* had its typical early summer maximum in both years and an additional autumnal growth phase in 1982. High sedimentary fluxes were only recorded in connection with the summer maximum: 2×10^7 colonies $m^{-2} d^{-1}$ in July 1981 and 9×10^6 in July 1982 at 20 m depth, while at 120 m depth sedimentation maxima were more than one order of magnitude smaller. Sedimentation maxima fell into the decline phase of the mass developments. *Mougeotia thylespora* had an extended late summer and

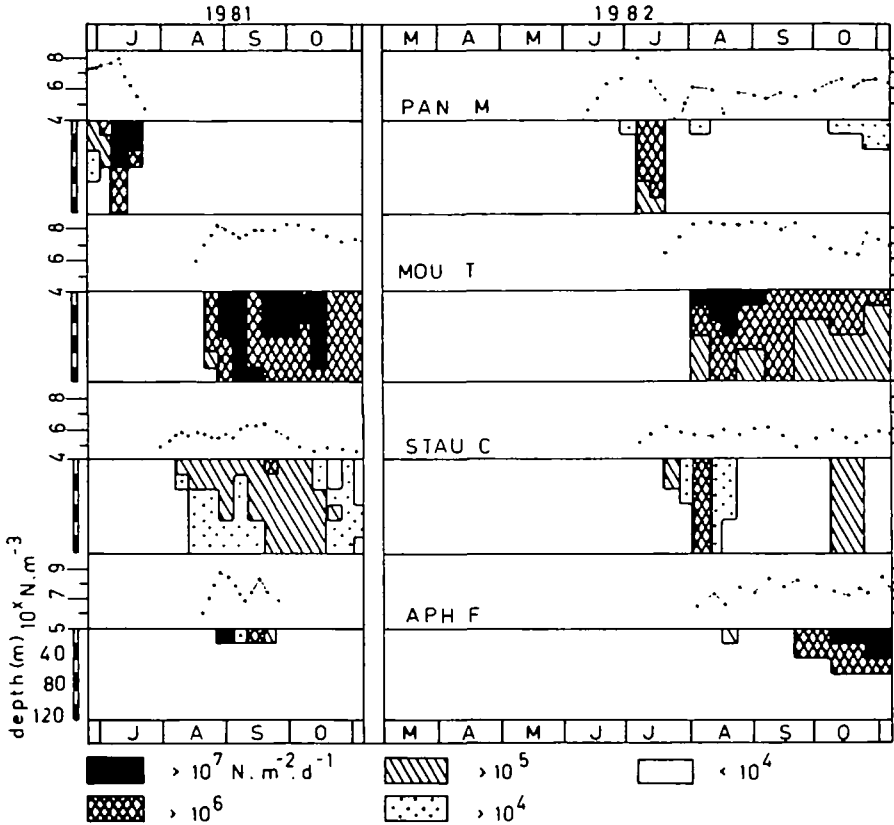


Fig. 2. Population density and sedimentary flux of non-diatom species. Symbols as in Figure 1, but note the difference in scale. PAN M: *Pandorina morum* (here colonies instead of cells); MOU T: *Mougeotia thylespora*; STAU C: *Staurastrum cingulum*; APH F: *Aphanizomenon flos-aquae*.

autumn vegetation period. Temporal variability of both planktonic abundance and of sedimentation was small compared to the other species, the maxima being 4×10^7 cells $m^{-2} d^{-1}$ in both years at 20 m depth. *Staurastrum cingulum* is rare in terms of cell numbers, but, because of its cell size ($16\,000 \mu m^3$), at times an important contributor to total phytoplankton biomass (up to 20% in early autumn). Temporal variation of sedimentary fluxes was slightly irregular, with a tendency towards maxima occurring after population density maxima. In both years maximum sedimentary fluxes were 2×10^6 cells $m^{-2} d^{-1}$. The vegetation period of *Aphanizomenon flos-aquae* was restricted to September in 1981 but extended from August to the end of October in 1982. In 1981 *A. flos-aquae* was only found in the 20 m trap, whereas in 1982 sedimentation reached down to 60 m. Below that depth no filaments were recovered from the traps.

Sinking velocity

Sinking velocity (v) was calculated according to Hargrave and Burns (1979) by

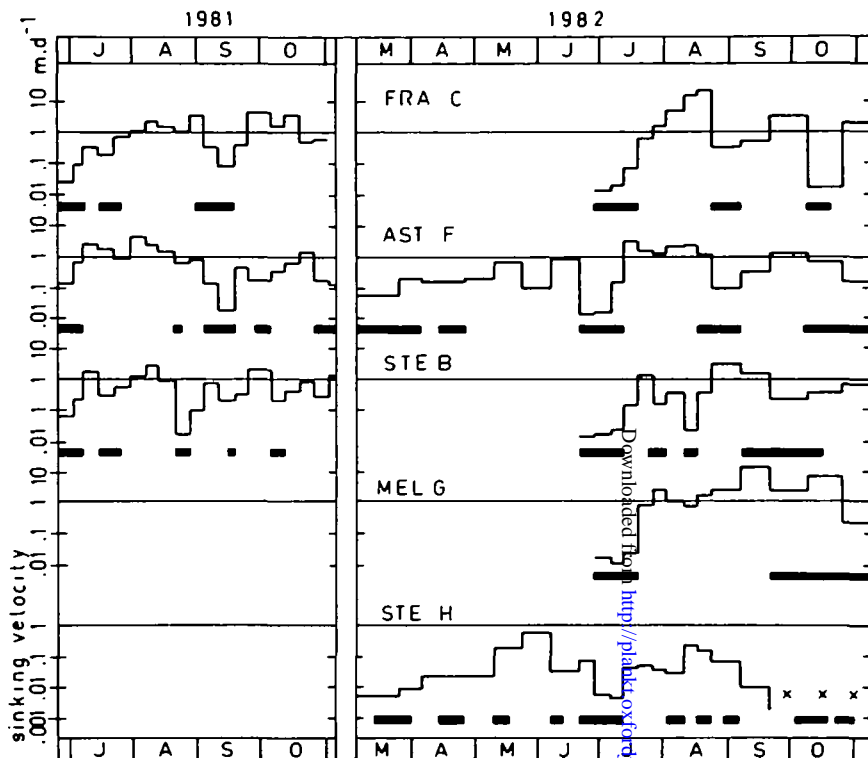


Fig. 3. Sedimentation velocity at 20 m depth for diatoms in Lake Constance (log-scale; m d^{-1}). Horizontal bars mark periods of exponential growth; x marks periods when too few cells were present in sediment samples to give reliable counts, sedimentation velocity certainly $<0.01 \text{ m d}^{-1}$. Abbreviations as in Figure 1.

dividing the sedimentary flux (F ; cells or colonies $\text{m}^{-2} \text{d}^{-1}$) by the concentration of settling particles above the trap (C ; cells or colonies m^{-3}).

$$v = FC^{-1} \tag{1}$$

Both F and C change with time. While F gives the real average over the exposure time, the average of C has to be calculated. The data presented here are based on the assumption that the change of C between samples is exponential. Linear interpolation would have yielded numerically different values, but none of the conclusions here would have been made invalid by these differences. Exponential interpolation was also used if plankton samples could not be taken on the same day as sediment traps were exchanged. For v into the 20 m trap C referred to the 0–20 m water column. For the deeper traps only a total annual average was calculated, since C was only available for the entire 20–140 m water column and temporal resolution of v was beyond the scope of this study. Equation (1) assumes that particles are evenly distributed above the trap, which was only the case in autumn.

A further source of error lies in the fact that C is affected by phytoplankton patchiness, whereas F as an average over at least one week integrates out small

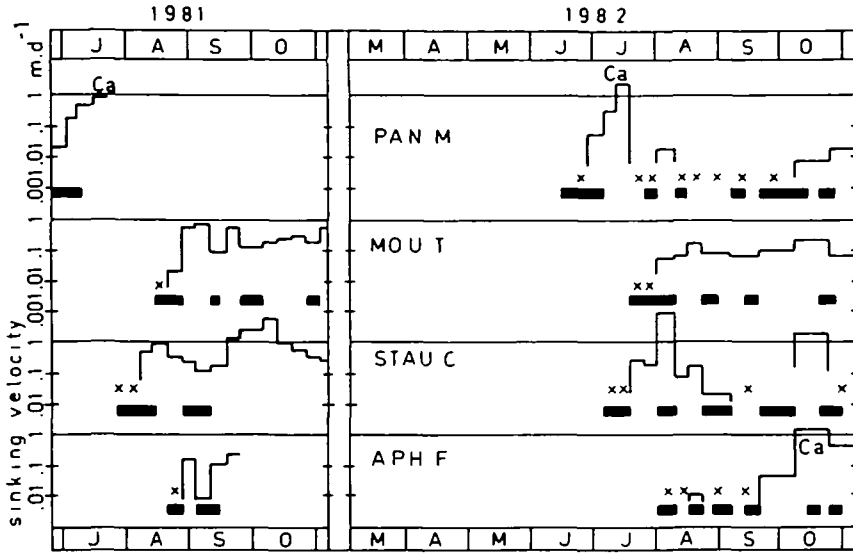


Fig. 4. Sedimentation velocities of non-diatom species. Symbols as in Figure 3, abbreviations as in Figure 2. Ca marks periods where sedimented cells were encrusted with calcite.

scale patchiness and may only be affected by long distance heterogeneities and lateral advection. Therefore it might have been preferable to calculate v by the time shift of maxima of F at the different depths, but the frequency of trap collections was not sufficient to resolve time shifts of <1 week. Although numerical values of v should be regarded with caution, observed trends are considered to be real, since both interspecific differences and temporal variation within species exceeded several orders of magnitude (Figures 3 and 4). Interspecific differences can best be demonstrated by annual averages as in Table I. There is a clear hierarchy of the sinking velocity, the large diatoms sinking the fastest, the desmid *Staurastrum cingulum* being nearly in the same range, and the small *Stephanodiscus hantzschii* along with *Mougeotia thylespora* and *Pandorina morum* sinking with low velocities. The lowest sinking velocities were calculated for *Aphanizomenon flos-aquae*. Zero sinking velocities have to be concluded for *Rhodomonas* spp. and *Cryptomonas* spp., which is in agreement with Livingstone and Reynolds (1981) and Reynolds and Wiseman (1982), who also failed to find Cryptophyceae in their traps. The increase of sinking velocities from the 0–20 m to the 20–120 m water column can easily be explained by reduced turbulence. Temporal variability within species was as pronounced as interspecific differences. If changes in the hydrographic regime were the sole or predominant source of temporal variation, sinking velocities of the different species should have paralleled each other. This is obviously not the case. Sinking velocities seem more to be correlated with the developmental cycle of the respective populations. With the exception of *Stephanodiscus hantzschii* there is a clear tendency towards increasing sinking velocities during stationary or declining phases, whereas

Table I. Annual average of the sinking velocity of algae in Lake Constance (m d^{-1}).

Species	1981		1982	
	0–20 m	20–120 m	0–20 m	20–120 m
<i>Fragilaria crotonensis</i>	1.3	16.6	1.46	7.0
<i>Asterionella formosa</i>	1.6	8.1	0.78	7.6
<i>Stephanodiscus binderanus</i>	0.8	6.6	0.48	11.0
<i>Melosira granulata</i>	–	–	0.87	8.0
<i>Stephanodiscus hantzschii</i>	–	–	0.033	3.8
<i>Staurastrum cingulum</i>	0.38	4.7	0.38	4.5
<i>Pandorina morum</i>	0.05	0.50	0.10	0.70
<i>Mougeotia thylespora</i>	0.15	2.1	0.06	1.8
<i>Aphanizomenon flos-aquae</i>	0.04	0	0.034	0.03

phases of rapid increase are associated with small sinking velocities. The highest sinking velocities of *Pandorina morum* and *Aphanizomenon flos-aquae* were found when these algae were encrusted with calcite crystals. The maximum values for the 0–20 m sinking velocity and most of the values for the hypolimnetic sinking velocity by far exceeded expectation. If we assume a specific weight of water of $1 \times 10^3 \text{ kg m}^{-3}$, a viscosity of $1 \times 10^{-3} \text{ kg m}^{-1} \text{ s}^{-1}$ and a specific weight of diatoms of $1.2 \times 10^3 \text{ kg m}^{-3}$ (Einsele and Grim, 1938) the terminal sinking velocity according to Stoke's law (v_s) for a sphere of $11 \mu\text{m}$ diameter – the spherical equivalent of an *Asterionella* cell ($700 \mu\text{m}^3$) – should be 1.13 m d^{-1} . For a real *Asterionella* cell it should be less because of bigger form resistance. An increase of the apparent sinking velocity over v_s can be explained by aggregation with other colonies and detrital particles. In fact, such aggregates with sizes up to a few mm are often seen in fresh samples from deep water. When fixed with Lugol's iodine solution and mixed before counting, these particles break apart. It might well be possible, that increased tendency towards flocculation accounts for the increased sinking velocities during stationary and declining phases of the population cycle.

Survival of cells during the sedimentation process

Visual inspection of iodine-fixed cells can at best yield a very rough estimate concerning the state of the cells. Knoechel and Kalff (1978) used autoradiography to show that cells with at least one optically distinguishable chloroplast were able to fix carbon. Consequently, these were counted as live cells, and cells with no visible chloroplast or empty cell walls were considered to be dead. Figure 5 gives the survival rates at the different depths expressed as percent of the total annual catch in the 20 m trap, which is considered to be almost identical with the number of cells lost from the euphotic zone by sinking. Seventy to 90% of the large diatoms reach the 120 m trap, whereas no intact cells of *Aphanizomenon flos-aquae* were found in this trap. The green algae and *Stephanodiscus hantzschii*

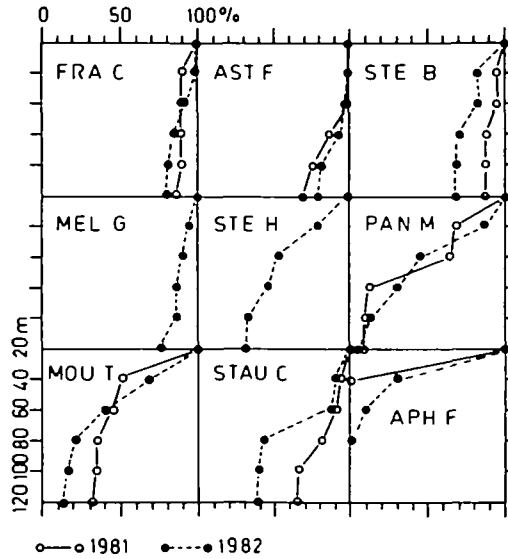


Fig. 5. Survival rate (in % of total annual catch in the 20 m trap) of algae during the sedimentation process. Abbreviations as in Figures 1 and 2.

stayed at an intermediate position. Algae with high sinking velocities had high survival rates. Regression analysis between the survival rate in 120 m (SR; %) and the mean annual hypolimnetic sinking velocity (see Table I; v_H ; $m\ d^{-1}$) gave equation (2).

$$SR = -0.3 + 9.2 v_H; r = 0.82; F = 28.4; n = 16; \quad (2)$$

significant at $p < 0.001$.

This close correlation indicates that taxonomic differences in an alga's ability to survive in the dark play only a minor role in comparison to the sinking velocity. From the regression equation a half-life of 18 ± 4.5 (95% confidence limits) days can be derived. This does not necessarily indicate poor survival abilities in the dark. It seems probable, that cells in a deteriorated physiological state are overrepresented in the settling material.

The impact of sedimentation on population dynamics

Since the cell division rate has not been investigated here only an indirect approach to estimate the potential growth rate (μ) via estimates of the losses is possible. This method is only applicable to algae which have a 'skeleton' remaining recognizable for counting purposes for at least one sampling interval after cell death. This requirement is fulfilled by the diatoms. Unfortunately no data for grazing, one of the major loss factors, are available. Therefore the analysis shall be restricted to the four large diatoms. *Fragilaria crotonensis* was reported as nearly inedible and *Asterionella formosa* as badly edible for *Daphnia hyalina* by Reynolds and Wiseman (1982). Together with *D. galeata*, *D. hyalina* is also the dominant grazer in Lake Constance. Grazing experiments with Lake Constance

phytoplankton confirmed the near zero filtration rate of *Daphnia* on *F. crotonensis* and low filterability of *A. formosa*, *Stephanodiscus binderanus* and *Melosira granulata* (Wegener and Geller, in preparation).

In a strict sense grazing effects may only be disregarded in the case of *F. crotonensis*; however, the consequences for the further discussion are minor, if μ of the other three species is slightly underestimated by omission of grazing. Excreted frustules should in any case appear either in the plankton samples or in the sediment traps. Thus the calculated death rate covers part of the grazing losses. The derivation of the equations used to calculate the growth and loss rates will be published elsewhere (Sommer, 1983b) and shall therefore not be repeated in detail here. Let k be the net rate of growth, μ the potential growth rate, δ the death rate, σ the sedimentation rate and γ the grazing rate, then:

$$k = \mu - \gamma - \delta - \sigma \quad \text{or} \quad \mu = k + \delta + \gamma + \sigma \quad (3)$$

under omission of γ :

$$\mu^* = k + \delta + \sigma \quad (4)$$

k can easily be calculated from the apparent increase or decrease during the exposure time:

$$k = \frac{\ln N_2 - \ln N_1}{t_2 - t_1} \quad (5)$$

where N is the number of living cells m^{-2} surface area integrated from 0–20 m depth. Let N_S be the number of cells m^{-2} accumulated in the 20 m sediment trap from t_1 to t_2 , then:

$$N_S = \int_{t_1}^{t_2} \sigma N_1 e^{k(t_2 - t)} dt \quad (6)$$

if sedimentation is assumed to be proportional to population density.

Solution of equation (6) gives:

$$\sigma = \frac{N_S k}{N_1 (e^{k(t_2 - t_1)} - 1)} \quad (6)$$

An analogous procedure is possible for the death rate, but N_D does not only cover the number of dead cells in the trap but also the increase of dead cells in the pelagial ($N_{D2} - N_{D1}$). (It is also assumed that the number of dead cells is proportional to population density.)

$$\delta = \frac{N_D k}{N_1 (e^{k(t_2 + t_1)} - 1)} \quad (8)$$

Figure 6 gives the values for k , σ , δ , μ^* calculated by these equations. Periods for which μ^* was negative are marked. In at least four cases for *Stephanodiscus binderanus* the negative values of μ^* must be taken as significant and are probably a consequence of neglected grazing. Sedimentation rates of all species were low during the first two weeks of the July diatom increase. Both σ and δ were negligible in comparison to μ^* . The following decline of the potential growth rate

was accompanied by an increase of σ and δ . Later in the year there were only few occasions where growth was not restricted by losses: in September 1981 for *A. formosa* and *F. crotonensis* and September/October 1982 for *M. granulata*. The highest potential growth rates (*Fragilaria* in October 1981, August 1982, *Melosira* at the end of September 1982) were observed when loss rates were also extremely high. In August 1982 *F. crotonensis* achieved nearly two doublings per day, which is close to the maximum growth rate observed in culture (Sommer, 1983a). These extreme values are considered to be reliable because very similar results were obtained for two successive periods. Nevertheless these high growth rates could not balance the combined losses due to sedimentation and mortality. Obviously the sedimentation rate is neither positively nor negatively correlated with μ . Both vigorously growing population and stagnant populations might be affected by great sedimentary losses. On the other hand, high sedimentation rates never occurred when the death rate was low (with the single exception of *Stephanodiscus binderanus* from 12 to 19 October 1981). Regression analysis showed a weak, but in the majority of cases, significant positive correlation between the death rate and the sedimentation rate (Table II).

Discussion

The results presented here might have been influenced by horizontal heterogeneities in the distribution of phytoplankton. However, temporal variation of population densities far exceeded possible spatial variation in such an exposed lake like Lake Constance. Potentially necessary correction of the data presented here does not invalidate the essential conclusions. Both temporal and interspecific variations of sedimentary fluxes are discussed at the level of orders

Table II. Correlation between death rates and sedimentation rates of diatoms. Levels of significance.

Species		1981	1982	1981 + 1982
<i>Asterionella formosa</i>	N	19	21	40
	r	0.39	0.63	0.51
	F	3.09 ^b	12.5 ^c	13.1 ^c
<i>Fragilaria crotonensis</i>	N	18	14	21
	r	0.64	0.62	0.48
	F	10.6 ^d	7.35 ^d	9.15 ^c
<i>Stephanodiscus binderanus</i>	N	18	13	31
	r	0.47	0.19	0.22
	F	3.63 ^c	0.40 ^a	1.49 ^a
<i>Melosira granulata</i>	N		13	
	r		0.51	
	F		3.80 ^b	

^aUnsignificant, ^b $p < 0.1$, ^c $p < 0.05$, ^d $p < 0.01$, ^e $p < 0.001$.

of magnitude. Survival rates are derived from annual averages, which certainly integrate out patchiness. In the calculation of growth and loss rates numerical error is dampened by logarithmic transformation of the population density data. Although the exact values for μ^* , k , σ , δ shall not be taken for warranted, there is no doubt about the general trends; e.g., minimum loss rates during July increase of diatoms, correlation between δ and σ .

A more serious limitation of the results lies in the fact that settled material was not fixed in the traps. This was necessary in order to avoid trapping of vertically migrating zooplankton (H.-H. Stabel and J. Bloesch, personal communication). Thus, cell death might have occurred in the sediment traps and led to an overestimate of δ and an underestimate of the sedimentary flux, the sinking velocity and σ . This effect has at least to be considered for the two week exposures. The error is smaller when in growing populations comparatively higher proportions of cells reach the trap towards the end of the exposure time and vice versa. Usually about half of the dead cells that accounted for the calculation of δ were still found in the plankton samples. Given the proportionality between δ and N_D (equation 8) a downward correction of 25% of δ would be necessary, if half of the dead cells recovered from the trap were due to death in the trap. Cell division of cells caught in the traps, which would have had the opposite effect as a source of error, is less probable, because for most of the time of the investigation 20 m was beyond the euphotic zone. It seems probable that even after the necessary downward correction of δ and upward correction of σ , the positive correlations between δ and σ would hold, though with a changed slope of the regression.

Increased sedimentary losses of moribund populations seem to be independent of the particular cause of mortality. Two potential factors which might partially explain the high death rates could be diagnosed as chytrid parasitism (marked in Figure 6) and silicon shortage. The latter probably explains the relatively high death rates of *Asterionella formosa* during the second half of July and during August. There is both field (Lund, 1950) and experimental (Moed, 1973) evidence that silicon limitation can lead to increased mortality of *A. formosa*.

From a study in the years 1979 and 1980, when environmental conditions and phytoplankton species composition were comparable to the present study, it is known that *Fragilaria crotonensis* and *Stephanodiscus hinderanus* are less sensitive to silicon limitation than *Asterionella* (Sommer and Stabel, 1983).

For the species investigated in this study, it can be concluded, that sedimentation plays only a secondary role in the elimination of populations. If the 'physiological fitness' of a population deteriorates, as indicated by increased death rates, then sedimentation rates rise to a level which has marked influence on population dynamics. There was no occasion when non-senescent populations were eliminated by sedimentation.

It should be emphasized that this conclusion probably only applies to large and wind-exposed lakes, like Lake Constance. For smaller lakes there is plenty of evidence to the contrary. Reynolds et al. (1982) concluded, that the removal of the vernal population of *A. formosa* in their Lund enclosures was due mainly to sedimentation. It is a commonly observed phenomenon that, with the onset of thermal stratification, the heavy diatoms are replaced by buoyant or motile algae

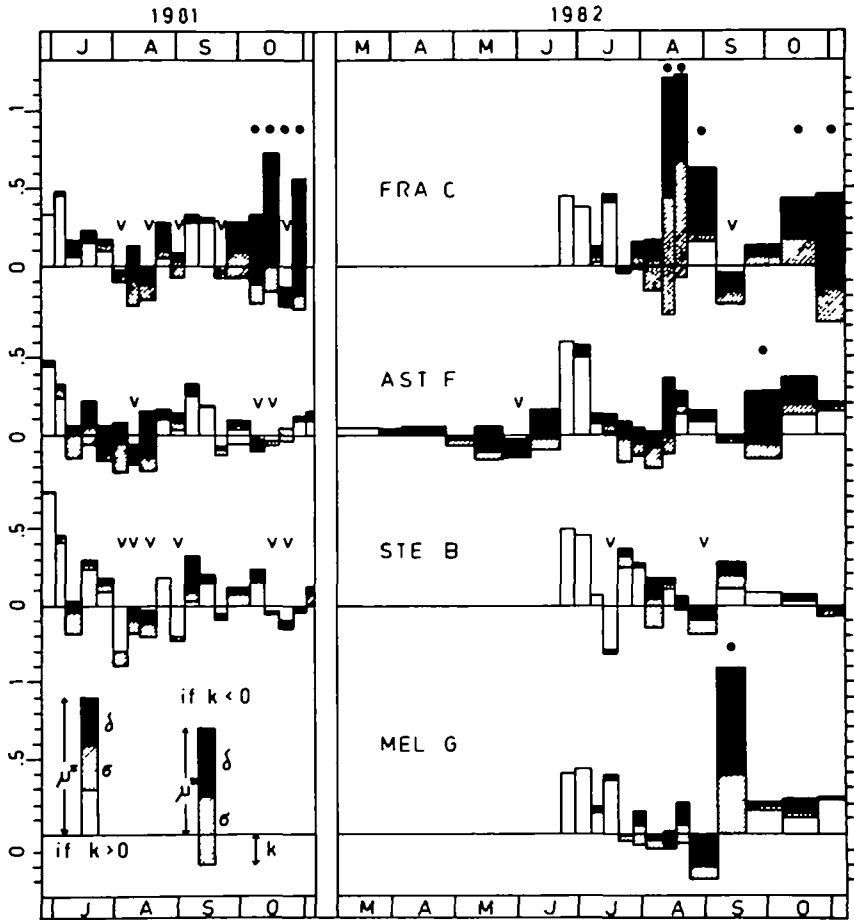


Fig. 6. Population dynamics of diatoms in Lake Constance. Upper limit of bars: μ^* , black area: δ , hatched area: σ , lower limit of signatures: k ; V: periods where $\mu^* < 0$; ●: periods where δ is probably caused by fungal parasitism. Abbreviations as in Figure 1.

(Knoechel and Kalff, 1975; Reynolds, 1976a, 1976b). In Lake Constance no marked increase of the sedimentation rate of *A. formosa* could be found following the onset of thermal stratification in April. The regularly occurring July dominance of diatoms in Lake Constance phytoplankton contradicts the classical assumption that a deep mixed water layer is a prerequisite for successful diatom growth. The mixing depth during that phase is usually < 3 m, sometimes a temperature gradient starts directly from the surface. Only the autumnal diatom maxima fall into a period of deep mixing (15–30 m mixing depth). There are two additional species, *Diatoma elongatum* and *Stephanodiscus astraea*, which are restricted to this period. These two species might also in Lake Constance be dependent on deep mixing.

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