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Role of sinking in diatom life-history cycles: ecological, evolutionary and geological significance

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Abstract

Rapid mass sinking of cells following diatom blooms, observed in lakes and the sea, is argued here to represent the transition from a growing to a resting stage in the life histories of these algae. Mass sinking is of survival value in those bloom diatoms that retain viability over long periods in cold, dark water but not in warm, nutrient-depleted surface water. Mechanisms for accelerating sinking speed of populations entering a resting or "seeding" mode are proposed. Previously unexplained features of diatom form and behaviour take on a new meaning in this context of diatom seeding strategies. Diatoms have physiological control over buoyancy as declining growth is accompanied by increasing sinking rates, where the frustule acts as ballast. Increased mucous secretion in conjunction with the cell protuberances characteristic of bloom diatoms leads to entanglement and aggregate formation during sinking; the "sticky" aggregates scavenge mineral and other particles during descent which further accelerates the sinking rate. Such diatom flocs will have sinking rates of $\sim 100\ \mathrm{m\ d^{-1}}$ or more. This is corroborated by recent observations of mass phytoplankton sedimentation to the deep sea. This mechanism would explain the origin of marine snow flocs containing diatoms in high productivity areas and also the well-known presence of a viable deep sea flora. That mortality is high in such a seeding strategy is not surprising. A number of species-specific variables pertaining to size, morphology, physiology, spore formation and frustule dissolution rate will determine the sinking behaviour and thus control positioning of resting stages in the water column or on the bottom. It is argued that sinking behaviour patterns will be environmentally selected and that some baffling aspects of diatom form and distribution can be explained in this light. Rapid diatom sedimentation is currently believed to be mediated by zooplankton faecal pellets, particularly those of copepods. This view is not supported by recently published observations. I speculate that copepod grazing actually retards rather than accelerates vertical flux, because faecal pellets tend to be recycled within the surface layer by the common herbivorous copepods. Egestion of undigested food by copepods during blooms acts as a storage mechanism, as ungrazed cells are likely to initiate mass precipitation and depletion of the surface layer in essential elements. Unique features of diatoms are discussed in the light of their possible evolution from resting spores of other algae. An evolutionary ecology of pelagic bloom diatoms is deduced from behavioural and morphological characteristics of meroplanktonic and tychopelagic forms. Other shell-bearing protistan plankters share common features with diatoms. Similar life-history patterns are likely to be present in species from all these groups. The geological significance of mass diatom sinking in rapidly affecting transfer of biogenic and mineral particles to the sea floor is pointed out.

Introduction

Since the last decade, our concepts of vertical particle flux in aquatic systems have been undergoing profound changes. Seasonality in the particle flux even to the deep sea, corresponding to that of the surface plankton, has been demonstrated by sediment trap studies (Deuser *et al.*, 1981; Honjo, 1982) as well as by sequential photography of the sea bed (Billett *et al.*, 1983). Flux attains its annual maximum within days to weeks of the surface plankton bloom, indicating that large, rapidly sinking particles must constitute the bulk of this material. Intact faecal pellets of surface-feeding zooplankton are widely considered the major vehicles of this rapid flux (see Angel, 1984 for a review). However, evidence is now accumulating which shows that amorphous aggregates of small particles including phytoplankton cells ("marine snow") may well be equally or more important for rapid transfer (Honjo *et al.*, 1982; Billett *et al.*, 1983), although little is known about the various sources and modes of particle aggregation (Angel, 1984).

Rapid mass sedimentation of phytoplankton cells following surface blooms, without the agency of zooplankton, has been observed in lakes (Jewson *et al.*, 1981; Reynolds *et al.*, 1982), inshore marine waters (Smetacek, 1980a; Peinert *et al.*, 1982; Wassmann, 1983), the open Baltic and North Seas (Smetacek *et al.*, 1978; Davies and Payne, 1984), the Panama Basin (Honjo, 1982) and the NE Atlantic (Billett *et al.*, 1983). Walsh (1983) has provided evidence from a variety of sources showing that this process, particularly along continental margins, may well represent one of the major global sinks of carbon and nitrogen. However, the ecological and evolutionary significance of mass diatom sedimentation has hitherto received little attention as the widespread and recurring nature of this phenomenon is only just being realized. Further, mass sinking has been equated with mass mortality (Walsh, 1983), which is an incomplete explanation since there is considerable reason to believe that it has survival value for the diatom species concerned.

In this paper I propose that mass sinking of bloom diatoms is a crucial part of their survival strategy as it represents the transition from a surface-growing stage to a benthic or deep-water resting stage in their life-history cycles. The presence of such a survival strategy in some neritic diatoms has been known since the last century (Hensen, 1887), however, little is known about the behavioural mechanisms, other than spore formation, involved in such a strategy. I therefore attempt to bring together ideas and data scattered in the literature to argue that rapid mass sinking may well be of survival value even for oceanic bloom diatoms. Next, I examine the mechanisms of rapid sinking and go on to speculate on various life-history patterns of diatoms from different regions. This is followed by a consideration of the role of copepod faecal pellets in mass vertical flux. I return to the main issue by presenting some speculation on the evolutionary ecology of diatoms and the possible origin of the mechanisms affecting rapid sinking. The final section deals with some geological implications of this process.

This paper embraces a wide range of topics that are only dealt with here in relation to the central theme, viz. the significance of mass diatom sinking. As many of these topics have recently been reviewed individually, I have refrained from presenting the controversies and weighing the pros and cons of each issue except where I have felt them to be relevant to the theme of this paper. In many cases, I will be charged with oversimplification but the intention here is to provoke discussion rather than establish consensus, and I herewith acknowledge the bias running through the arguments.

Survival value of mass sinking in bloom diatoms

Most phytoplankton species exhibit a distinct seasonality of occurrence in the surface layer, i.e. they have life histories with an active growing phase. Garrison (1981) pointed out that the study of diatom ecology has focussed primarily on this phase, while survival strategies of the various species between growth phases have received much less consideration. The life histories of many shallow water plankters include benthic resting stages, often as resistant spores (Hensen, 1887; Dale, 1983; Hargraves and French, 1983; Sandgren, 1983). Hensen (1887) pointed out a century ago that such a strategy would ensure regional persistence wherever favourable growth conditions for the species recur seasonally. However, the importance of such benthic seed stocks in initiating red tides (Provasoli, 1979) and diatom blooms (Lund, 1971; Garrison, 1981) has only recently been demonstrated. Rapid mass sinking obviously has survival value in coastal environments, as it will minimize advective dispersal of the seed stock to unfavourable regions. With increasing water depth, the chances of a benthic spore's returning to the surface layer will diminish. The role of resting stages in oceanic diatom strategies has, therefore, received even less attention than in the case of their neritic counterparts.

Hensen (1887) suggested that the presence of resting spores in the life cycle of a species may serve as the criterion to distinguish neritic from oceanic forms. Hargraves and French (1983) showed that this criterion does not apply to diatoms and pointed out that their resting spores "as a whole ... function differently from similar stages in other algal classes". They suggested further that many diatoms are capable of forming resting cells, apparently without undergoing morphological change. Anderson (1975) demonstrated resting cell formation in a pennate diatom (*Amphora coffaeformis*) isolated from deep ocean water. Similar studies have not been conducted on other species; however, the prolonged survival time of non-growing vegetative cells of many diatoms (Smayda and Mitchell-Innes, 1974) is proof of the widespread existence of this type of resting stage. The alternative to a resting mode for prolonged dark existence is heterotrophy; however, such a faculty has not yet been demonstrated in "typically open-water, centric species" (Hellebust and Lewin, 1977). In the following, the term "resting stage" is used in a general sense and includes spores and resting cells.

Considerable evidence has accumulated showing that diatoms also have pelagic resting stages (Malone, 1980; Hargraves and French, 1983). There are numerous reports of viable diatoms occurring suspended at considerable depths in the ocean (see Guillard and Kilham, 1977; Platt *et al.*, 1983); Kimball *et al.* (1963), Berger (1976) and Fowler and Fisher (1983) have suggested that this deep-living flora might represent "waiting" or seeding populations. There are many reasons to support this view:

(1) Bloom diatoms are the characteristic flora of new environments, i.e. wherever and whenever nutrient-rich water from deeper layers is introduced to the surface and eventually stabilized. This occurs in spring at high latitudes following deep winter mixing, or in upwelling areas at low latitudes. The success of such pioneer species lies not only in their fast growth rates in nutrient-rich,

turbulent environments (Margalef, 1978), but also in effective seeding of the new environment by resting stages from a previous population (Malone, 1980). Thus, the environment will select for both growth and seeding performances of the various species. Seeding is effected by the sinking out of vegetative cells and resting spores from the nutrient-depleted surface layer to nutrient-richer deeper layers or the sediment surface.

(2) Diatom blooms are frequently terminated by nutrient depletion in the warming, stabilizing surface layer (Davis *et al.,* 1980). Such an environment precludes further growth of the population and hence it is advantageous to sink out of the surface layer as it must be replaced with nutrient-richer water in any case before a new diatom bloom can start.

(3) A nutrient-depleted, warm surface layer is actually a hostile environment for bloom diatoms. Non-growing diatom cells survive longer, the lower the temperature is (Smayda and Mitchell-Innes, 1974). This applies also to species that do not form spores, such as *Skeletonema costatum.* Cultures of this diatom kept at 2 °C survived for six months in the dark (Smayda and Mitchell-Innes, 1974). Further, darkness can prolong spore survival and strong light can actually be harmful to a nutrient-depleted population as it can prevent formation of resting stages (Anderson, 1975; Hargraves and French, 1983). Resting stages can, therefore, survive longest in the cold, dark conditions that prevail below the surface layer (Malone, 1980). Thus, bloom diatoms are physiologically adapted to grow rapidly in nutrient-rich, illuminated water and to maintain viability in cold, dark water or on the sediment surface in the course of their life histories. Formation of compact, resistant resting spores is not a prerequisite for this type of life cycle, although spore formation is more prevalent among bloom diatoms than in others (Hargraves and French, 1983).

(4) Grazing pressure of herbivorous zooplankton is greatest in the surface layer and prolonged residence here will increase the risk of being grazed, whereas dispersal in a deep-water column will lessen it. Vincent and Berger (1981) suggested that pelagic Foraminifera also sink to deeper levels in the course of their life history not only for reproduction but also to avoid predation. Hargraves and French (1983) showed that diatom spores survive gut passage better than vegetative cells. As grazing pressure on resting stages is likely to be greater at the sediment surface than in the deep-water column, the higher frequency of spore formation in neritic as compared to oceanic species may partly be explained by this selective mechanism.

(5) Several other holoplanktonic groups have deep-living resting stages of which copepods are the best known example. Hallberg and Hirche (1980) showed that these resting stages are in a state of diapause and totally immobile. Apparently, they must have buoyancy control mechanisms to maintain passive suspension at a specific depth. As discussed in a later section, diatoms also have considerable physiological control over buoyancy, a prerequisite for the positioning of suspended resting stages.

(6) Depending on the hydrographical regime, sinking from the surface layer can be of importance not only in affecting persistence in a given region (as in upwelling areas) but also in promoting dispersal to other, potentially more favourable localities. Diatoms face the choice of relatively rapid but hazardous transport by surface currents and slower but safer transport in deeper water. The latter "choice" has apparently been made by the several widely distributed oceanic species that also form resting spores.

The presence of a deep-sea flora has given rise to speculation as to their possible downward transportation, since sinking of individual cells from the surface layer would not seem rapid enough to serve as an explanation (Smayda, 1970, 1971; Bienfang, 1980). Zooplankton faecal pellets are generally regarded as the transport mechanism, whether following ingestion or by passive collection of suspended cells by sinking faecal material (Silver and Alldredge, 1981; Silver and Bruland, 1981; Platt *et al.,* 1983). Fowler and Fisher (1983) demonstrated viable gut passage of several diatom species including *Skeletonema costatum.* However, the diatom assemblage found at 1000-m depth by Platt *et al.* (1983) included species such as *Chaetoceros peruvianum, Corethron hystrix, Planktoniella sol, Rhizosolenia alata,* among others that were apparently intact on examination. Platt *et al.* (1983) calculated minimum sinking rates of 72 m d^{-1}. It is indeed difficult to visualize viable gut passage by any of these large fragile species, and their downward transport must have been effected without ingestion by zooplankton. Billett *et al.* (1983) estimated diatom sinking rates of 100 to 150 m d^{-1}, where transport within or in association with faecal pellets could be ruled out. Smetacek (1984) suggested aggregate formation of diatom cells at the pycnocline to account for field observations of *S. costatum* sinking rates of 40 m d^{-1} during a spring bloom (v. Bodungen *et al.,* 1981).

Considering that rapid sinking under certain conditions can well be of importance to bloom diatom survival, it is reasonable to expect that diatoms will have developed mechanisms to effect it. Hargraves and French (1983) suggest that resting spore formation might be a mechanism to accelerate sinking speed since spores have higher sinking rates than vegetative cells (Bienfang, 1981). However, spores tend to remain within the parental frustule or chain during sinking, and moreover, empty frustules, whole cells and chains sink out of the surface layer together (Smetacek, 1984). Apparently, there are mechanisms other than resting spore formation capable of inducing rapid sinking.

It might be pointed out here that mortality is the most likely fate of phytoplankton cells sinking out of the surface layer (Walsh, 1983), as only a small portion of the deep or benthic resting stages will later be returned to the surface layer. This does not, however, detract from the underlying function of this process, viz. to effect seeding. A terrestrial plant analogy will serve to illustrate the issue: the vast majority of wind-dispersed pollen or seeds are lost to the environment, nevertheless this strategy has been evolved by many successful and disparate groups, such as the conifers (pollen) and the Compositae and orchids (seeds). In biomass terms, the seeding unit in diatoms is equivalent to the vegetative cell; the environmental impact of the diatom seeding process will, therefore, in a relative context, be much more dramatic than in the case of terrestrial plants.

Sinking mechanisms in bloom diatoms

Sinking rates and growth rates are inversely correlated in the majority of planktonic diatoms (Eppley *et al.,* 1967; Smayda, 1970; Walsby and Reynolds, 1980). Vigorously growing cells can maintain themselves close to neutral buoyancy, but upon nutrient depletion, sinking rates can increase drastically. Rates can again decrease when the sinking cells encounter higher nutrient concentrations, for instance at greater depths (Bienfang *et al.,* 1983), indicating that buoyancy is physiologically controlled (Smayda, 1970; Bienfang, 1981). This is mediated in some species by the exchange of heavy ions for lighter ones (Anderson and Sweeney, 1978). The cell:vacuole volume ratio is important for this latter mechanism. Munk and Riley (1952) first pointed out that sinking would enhance the efficiency of nutrient uptake by moving the non-motile diatoms through the medium. Walsby and Reynolds (1980) suggested that the silica frustule is a sinking device, since it increases the rate of passive sinking. As a result of these properties, an ungrazed diatom bloom will eventually settle out after nutrient depletion of the surface layer.

The maximal *in-vitro* sinking rates of nutrient-depleted individual cells and chains of common bloom diatoms are well under $10\,\mathrm{m\,d^{-1}}$ (Smayda, 1970). This would not explain the accelerated rates observed in nature. However, sinking rate increases with particle size (McCave, 1975) and aggregates of interlocked chains sink faster than single cells or chains (Eppley *et al.*, 1967). Direct observations of material settling onto the sea bed (Billett et al., 1983) and of that collected in sediment traps (Malone, personal communication; Smetacek *et al.*, submitted) have shown that diatom chains were embedded in gelatinous aggregations. These also contained various other particles such as zooplankton faecal pellets. Flake-like aggregates ("marine snow") containing intact diatoms have also been observed in the bathypelagic zone (Silver and Alldredge, 1981). Alldredge (1979) and Shanks and Trent (1980) calculated sinking rates of these flakes to be approximately 50 to $100\,\mathrm{m\,d^{-1}}$. I suggest that such rapidly sinking aggregates can be formed by the diatoms themselves as elaborated upon below.

The mechanisms of aggregate formation can be deduced from consideration of certain features of diatom morphology and physiology. The majority of bloom diatoms are chain-forming, medium to small-sized cells adorned with protuberances such as silica spines, chitan microfibrils, and gelatinous threads. Microturbulence can cause these protuberances to turn and twist the cells through the medium, thereby increasing nutrient uptake efficiency (Smayda, 1970; Margalef, 1978; Walsby and Reynolds, 1980; Sournia, 1982). However, this movement also facilitates aggregation, and the protuberances, some of which are even barbed, greatly enhance the aggregation effect. If aggregation *per se* were detrimental to species survival, the widespread presence of protuberances would be hard to explain.

Mucous secretion increases in nutrient-depleted diatom populations (Degens and Ittekot, 1984) and flocculation of senescent cultures is a common observation (Eppley *et al.*, 1983). This is in contrast to absence of flocculation in vigorously growing populations at the same cell concentrations. It is a common observation that the surfaces of senescent cells are generally "stickier" than those of growing ones, as indicated by the presence or absence, respectively, of adhering particles. This stickiness is presumably multifunctional but its implications for aggregate formation following nutrient depletion are obvious.

Apparently, there are species-specific differences with regard to mucous production during senescence. Spontaneous aggregation has been observed in growing cultures of *Thalassiosira fluviatilis* at concentrations above 10^7 cells $\mathrm{l^{-1}}$ (Eppley *et al.*, 1967). Natural bloom concentrations are an order of magnitude less, but locally high cell concentrations may arise in the course of sinking. During calm periods, the uppermost cells are the first to suffer nutrient depletion and consequently initiate mass sinking (v. Bodungen *et al.*, 1981). These cells sweep lower layers in the course of their descent and may decelerate on encountering higher nutrient concentrations. The high cell concentrations in restricted layers, commonly recorded in declining diatom blooms (Platt and Subba Rao, 1970), reflect this process. Peak concentrations are invariably found at density discontinuity layers, where, as accumulation proceeds, aggregate formation eventually becomes unavoidable. The higher the phytoplankton biomass, the greater the likelihood of aggregate formation and the larger the percentage of bloom biomass that will sediment out of the surface layer. It is the ambient turbulence level and the physiological state of the bloom that will determine when aggregation begins. During descent, the sticky aggregates scavenge other particles which, if heavy, further accelerate sinking rates.

Summing up, one might conclude that sinking serves different purposes in the life-history cycles of diatoms. In the growing phase, it increases the "wash effect" of the cell surface, thus enhancing nutrient uptake efficiency. In senescent populations, however, rates can increase by an order of magnitude. This accelerated sinking, which is frequently accompanied by formation of resting stages, rapidly removes the population from an inhospitable environment and leads to establishment of a refuge population at depth or on the bottom. Thus, one of the functions in diatom life history is to increase the sinking speed of senescent populations. Previously unexplained features of diatom morphology and behaviour take on a new meaning in this light.

Sinking and seeding strategies

The relationship between form and function has proved particularly elusive within the phytoplankton (Sournia, 1982; Elbrächter, 1984). This merely indicates that we know much less about function than about form and that performance in the surface layer is not the only "function" of phytoplankton. In this section, I speculate on the possible relationships between diatom form and life-history stages other than the active growing phase. I assume that environmental selection of life-history strategies may well be reflected to some extent in the geographical and seasonal distribution patterns of the various species or "races". In exploring such relationships, it is important to remember that a large number of independent factors are collectively involved in controlling species composition of phytoplankton assemblages (Smayda, 1980) and that the species comprising a given assemblage are likely to be following different, or even opposing, strategies; an explanation for the success of one species or strategy does not necessarily imply the failure of another, particularly in a diverse assemblage.

Further, the advantage conferred by effective seeding of the environment will not always be obvious. The very presence of a life-history strategy implies that the species will be entering and leaving the growth arena and not necessarily striving at all costs to maintain a maximum population presence there. As an example, it took many decades of study before the spectacular appearance and disappearance of red-tide dinoflagellates could be explained with a simple seeding strategy (Provasoli, 1979; Dale, 1983).

Field observations of seeding in diatoms are few and much of the evidence presented below is inferential. However, Malone *et al.* (1983) described how a portion of a diatom population that had sunk out of the surface layer following a coastal bloom was returned to the surface following mixing and upwelling events at the shelf break. Estrada and Blasco (1979) found that dinoflagellate or diatom dominance of the surface bloom off the California coast depended on the depth from which upwelled water originated: diatoms dominated when nutrient-richer water from greater depth reached the surface. I suggest that this indicates the presence of seeding populations positioned at the respective depths.

One might distinguish two extreme types of seeding strategies in species exhibiting drastic fluctuations in number over the year. In one type, seeding is effected by "fugitive cells" in the surface layer (Kilham and Kilham, 1980), presumably lurking below the herbivore grazing thresholds, and in the other, by deep-living refuge populations that have fled an inhospitable surface layer. Bloom diatoms are more likely to belong to the latter type, although both strategies can well be followed by the same species. Some cells are invariably "left behind" following mass sinking that can thus contribute to a fugitive population in the surface layer. However, in some species, resting spore viability can only be maintained under cold, dark conditions (Durbin, 1978). Such species (e.g. *Detonula confervacea, Thalassiosira nordenskiöldii*) are unlikely to have fugitive cells in warm surface water in contrast to species such as *Skeletonema costatum* that undoubtedly do (C. O. Davis, personal communication). The distribution of the former will hence be restricted to regions where refuge populations can endure or from where they can propagate.

The wide distribution of most diatom species in the oceans (Williams *et al.*, 1981) suggests that their dispersal mechanisms are indeed highly effective, whether by fugitive cells, refuge populations or both. Nevertheless, a quantitative evaluation of diatom spatial and temporal distribution in the sea does reveal characteristically recurring patterns of species occurrence (Smayda, 1980). The environmental conditions prevailing in regions with similar successional patterns can be so dissimilar (from region to region and also year to year) that it is hard to envision that species or genus appearance and disappearance will solely be governed by the immediate growth conditions in the surface layer (Sournia, 1982). Apparently, adaptation of a given species to a given region will also be geared to longer time scales than just those of the growth environment. Obviously, there will be species-specific differences in the time scales of response to the environment and in the following I shall consider to what extent these adaptations might be related to aspects of life-history strategies.

(1) Buoyancy and sinking. Regulating position in the water column is the primary means by which plankton organisms can effect regional persistence. In non-motile groups such as diatoms, radiolarians and foraminifers, this is apparently mediated by some form of buoyancy control in which the mineral shell functions as ballast. A given species will thus display a range of sinking speeds during its life history and it will be necessary to distinguish between an instantaneous sinking speed and a maximum potential speed for each species. The minimum sinking speed in the majority of diatoms appears to be well under 2 m d^{-1}, regardless of size or shell thickness (Smayda, 1970; Bienfang, 1980, 1981). Thus, even the large compact colonies of *Chaetoceros socialis* can have low sinking rates during growth (Bienfang, 1981). Similarly, the large aggregates of long smooth diatoms (*Rhizosolenia* spp.) of tropical "blue waters" (Alldredge and Silver, 1982), apparently also maintain suspension by active buoyancy control.

There appear to be considerable species-specific differences in sinking behaviour amongst common diatoms. Thus, Bienfang *et al.* (1982), in *in-vitro* studies, demonstrated that sinking of nutrient-depleted populations was related to the kind of nutrient depleted and varied among species. A similarly complicated picture was obtained by Bienfang (1981) in a study of enclosed natural populations. Malone *et al.* (1983), in a study of phytoplankton growth and sedimentation on the NW Atlantic shelf, found that *Skeletonema costatum* accumulated in their sediment traps in large numbers, whereas other diatoms (*Rhizosolenia* and *Nitzschia* spp.) remained in suspension in the surface layer. Such variability in response to environmental conditions could well be a reflection of differences in life-history strategies between species that could partly explain some features of seasonal successional patterns as suggested by Hutchinson (1967) and Smayda (1980).

Malone (1980) emphasized the role of cell size and sinking rate in growth and seeding strategies of the netplankton (including diatoms) versus nanoplankton. Even small-celled diatoms such as *Skeletonema costatum* attain high sinking rates (v. Bodungen *et al.*, 1981) by virtue of their chains and presumably their ability to form aggregates. The advantage conferred by small cell size is widely believed to be due to enhanced efficiency of nutrient uptake (Sournia, 1982). However, the characteristic species of high-nutrient environments – the bloom diatoms – tend to be small and spiny in contrast to diatoms of the nutrient-impoverished, mid-oceanic gyres that have many large, smooth-walled representatives. Large organisms have a lower surface area/volume (S/V) ratio than small ones, and, assuming that control over specific gravity by ion exchange in diatoms is a function of the S/V ratio, then large species will have a much wider range of sinking speeds than small ones. One might speculate that, given a large enough vacuole, some species might even achieve positive buoyancy. Such a capability would permit vertical migration in stratified water between nutrient-rich and illuminated layers, and large size would greatly increase the rate of sinking and also ascent.

Positive buoyancy has only occasionally been reported in pelagic diatoms (Smayda, 1970; Lännergren, 1979). However, planktonic foraminifers may serve as a useful analogy as they can maintain their position in the water column and have stages in their life history in which they sink out of the surface layer and later return to it (Vincent and Berger, 1981).

Buoyancy can also be regulated by discarding ballast, i.e. by escape from and/or dissolution of the frustule. Bloom diatoms tend to have thin frustules that dissolve fairly rapidly and they are thus poorly represented in the sedimentary record in contrast to those diatoms more typical of stratified water (Berger, 1976). Silica availability is certainly not responsible for this difference, as bloom diatoms grow at high silica concentrations. I suggest that interspecific variation in frustule dissolution rate (Hurd *et al.*, 1979) that has not yet been satisfactorily explained, might well be of adaptive significance in the positioning of resting stages. This can be achieved by jettisoning or retaining ballast following resting stage formation. Breakup of aggregates and release of resting spores would be mediated by frustule dissolution. Rapid dissolution following spore formation would hence be advantageous in such species. Mucous secretion and its ultimate removal, presumably by heterotrophs, will considerably influence the frustule dissolution rate. Thus, the role of mucus will also have to be re-examined in this light.

(2) Resting stage positioning. If voluntary ascent is not possible, then positioning of resting stages at the pycnocline will ensure restoration of cells to the surface layer by restricted mixing events (Hargraves and French, 1983). Bienfang *et al.* (1983) reported that some bloom diatoms reduce sinking speed on encountering higher nutrient concentrations and lower light levels at the pycnocline and can thus contribute to the subsurface chlorophyll maxima characteristic of summer stratified waters of temperate zones. These cells might be regarded as "semi-dormant" resting stages that multiply vigorously when entrained upwards, since nutrient uptake and storage in the dark permit several cell divisions on illumination (Malone, 1980; Walsby and Reynolds, 1980). This strategy has been observed in lakes, (Walsby and Reynolds, 1980) and might well explain the sudden appearance of large diatom populations in the Sargasso Sea following limited vertical mixing (Kilham and Kilham, 1980). Large biomass build-up will be detrimental to this strategy as high particle concentrations at the pycnocline will lead to aggregation and fall out of seeding cells. Billett *et al.* (1983) reported that "detrital material collecting at the thermocline has been seen to peel off and sink in strings up to 15 cm long" by divers in the Sargasso Sea. Such a process would explain the rapid transfer of particulate material produced in the surface layer during bloom phases to the deep sea floor of even impoverished oceans.

The success of the relatively small-celled bloom diatoms is controlled to a much greater extent by water movement than in the case of warm water species. As mortality will be higher in the former case, it will be advantageous for bloom diatoms to invest seeding biomass in a large number of small cells rather than fewer larger ones, an interpretation that conforms well with the *r* and *K* strategy classification of Kilham and Kilham (1980).

Some small-celled bloom diatoms form large, firm colonies (up to several mm) in the vegetative stage that are gelatinous (*Thalassiosira subtilis, Chaetoceros socialis*) or entangled (*T. partheneia*). These colonial species are characteristic of high-nutrient, high-turbulence environments (Margalef, 1978) and tend to disintegrate into individual cells or chains during sinking and senescence (Elbrächter and Boje, 1978), which would slow further descent. Such reverse behaviour can be advantageous in upwelling areas. The potentially greater sinking rate of colonies might enable them to remain close to the centre of upwelling during growth (Malone, 1980). However, colony disintegration and dispersal of the many small individual cells during the seeding process will ensure that the "seeds" are scattered over a wide depth range in nutrient-rich subsurface layers which increases the chances of some being transported back to the surface in the course of further upwelling.

Senescent diatom populations have rarely been studied under natural conditions and little information is available on species-specific differences in behaviour. However, factors triggering resting spore formation have received some attention. Hargraves and French (1983) reported that nitrogen depletion is the primary factor in species studied by them, although the proportion of vegetative cells that formed spores varied widely between species and even between clones of the same species. Durbin (1978) demonstrated temperature dependence of this process in two boreal species. Doucette and Fryxell (1983) observed spore formation in *Thalassiosira antarctica* at high ambient nitrate concentrations; they suggested that nitrogen depletion is a triggering factor only in temperate but not in polar species. However, mass sedimentation in autumnal diatom blooms – also at high nitrogen concentrations – have been observed in Kiel Bight (Graf *et al.,* 1983). Further, Anderson (1975) triggered resting cell formation in *Amphora coffaeformis* by transferring exponentially growing cells to cold, dark conditions.

Similarly, species-specific differences in mucous production and thus in size, shape and consistency of diatom aggregates can be expected. Nöthig (1984) reported aggregation in two *Thalassiosira* spp. but disintegration of chains in *Skeletonema costatum* and *Detonula confervacea.* However, her observations were carried out on natural populations maintained in containers that were stirred vigorously daily. In the field, long chains of both species have been collected in sediment traps below the surface layer (Smetacek *et al.,* 1978; Malone *et al.,* 1983), indicating that chain disintegration is preceded by rapid sinking. These species will presumably form loose, fragile aggregates such as those described by Emery *et al.* (1984) from the east Asian shelf.

Some *Thalassiosira* spp. appear to form firm aggregates or clumps on occasion. Thus, Hustedt (1930) observed that "pelagic diatoms normally occurring in loose chains appear to have the capability of forming irregular gelatinous thalloids (Gallertthalloide) under certain conditions". He cited *T. nordenskiöldii* as a specific example and suggested that this capability is related to auxospore formation. Compact gelatinous clumps containing over 100 cells and with high sinking rates have been found in a normally chain-bearing Antarctic *Thalassiosira* sp. (Smetacek *et al.,* submitted). Similar clumps have been observed elsewhere in various open-chained *Thalassiosira* spp. and in the pennate diatom *Achnanthes taeniata.* The authors suggested that such clumps represent seeding stages that are either overlooked or regarded as faecal pellets during routine counting. They would then represent a sinking counterpart to the floating gelatinous colonies of other species.

In recent years, interest in the formation, function and fate of organic aggregates – "marine snow" – has increased rapidly. Riley (1963) studied aggregate occurrence over an annual cycle and did not consider zooplankton as an important agency in their formation. Several types of aggregates occur from the surface to bathypelagic layers (Silver *et al.,* 1978; Silver and Alldredge, 1981; Angel, 1984). Some are clearly produced by gelatinous zooplankton, some appear to be the remains of disintegrating faeces and others were of unknown origin (Silver and Alldredge, 1981). However, as shown above, diatoms also certainly contribute to aggregate formation in the pelagial. The mode of formation and transfer to depth of some types can now be explained in terms of phytoplankton seeding strategies. Aggregates will be considerably modified with age because of protozoan and bacterial activity (Angel, 1984). Further, dissolution of silica frustules will reduce sinking rates and also release diatom spores commonly found in marine snow (Hargraves and French, 1983) from the frustules. So far, few quantitative studies of marine snow have been done but they have shown aggregates to be of considerable importance (Riley, 1963; Silver and Alldredge, 1981; Angel, 1984). Following a diatom bloom, the downward flux of flakes is likely to be at its thickest. "Marine blizzard" might be an appropriate term to describe this phenomenon.

(3) Regional aspects. Diatom blooms generally progress from the coast to the open ocean, and where lateral seaward advection of surface layers occurs, neritic species will be transported offshore. These species tend to have benthic resting stages and will be primarily responsible for offshore and even open ocean mass sedimentation. Therefore, regional and seasonal patterns in cross shelf water transport might greatly affect species distribution and hence sedimentation patterns (Malone, 1980; Malone *et al.* 1983; Walsh, 1983).

Diatom geographical distribution and temporal patterns of species succession in a given region can thus be partly explained by the degree of concurrence between species life-history patterns on the one hand and seasonality and hydrography/topography of that region on the other. One might conclude that many diatoms have a greater affinity for nutrients than for light, growing when introduced to the euphotic zone but settling out again into deeper regions after depletion of nutrients in surface layers. Their morphological features can no longer be regarded solely as flotation aids in the surface layer, as previously assumed and still suggested (Walsby and Reynolds, 1980), but rather as devices to facilitate aggregation and thus accelerate the sinking rate of senescent populations.

Zooplankton grazing and bloom diatom sedimentation

Calanoid copepods are the dominant herbivores grazing diatom blooms. The longstanding view that zooplankton utilize most of the phytoplankton within the surface layer has led to the implicit assumption that copepod faeces comprise the bulk of sinking particles (Steele, 1974). Rapid diatom sedimentation has accordingly been attributed to the mass packaging of diatoms into compact, rapidly sinking faecal pellets as a consequence of heavy copepod grazing (Smayda, 1970; Schrader, 1971). The conclusion is that copepod grazing will enhance vertical particle flux. There is, however, little field evidence to support this view.

Knauer *et al.* (1979), Rowe and Gardner (1979) and Urrere and Knauer (1981) found, in sediment trap studies, that all classes of zooplankton pellets combined contributed < 25%, often only a few percent, to total flux. Faecal pellets of zooplankton other than copepods (salps, euphausiids) have dominated mass flux in some collections (Dunbar and Berger, 1981; Iseki, 1981; Smetacek *et al.* submitted), but in all these studies, copepod faecal pellets were of only minor importance. Smetacek (1980a, b) found that in shallow (20 m) Kiel Bight, the annual minimum sedimentation rate coincided with the copepod maximum. Wassmann (1983) and Lutter (1984) also found only a negligible contribution of copepod pellets to vertical flux in an enclosed and an open Norwegian fjord respectively. Krause (1981) studied vertical distribution of *Calanus* spp. faecal pellets in the water column in the North Sea at short intervals over many weeks during a spring bloom. His data indicate that copepod pellets tend to accumulate and remain in suspension in the upper layer. Honjo *et al.* (1982) stated: "Fecal pellets account for only a small fraction of the total organic flux to deep water". They conceded that pellet disintegration in the traps might have biased their observations but add that "microscopic examination of the matrix strongly suggests that many particles had never been so pelletized". It appears that the role of faecal pellets in general and copepod pellets in particular in the sedimentation process has been over-emphasized in the last decade.

Although more field observations of annual cycles are called for, it appears that direct diatom sedimentation is a quantitatively more important process than their transportation in copepod faecal pellets in many regions experiencing diatom blooms. Budgetary analyses of phytoplankton blooms from many different areas have shown that rapid loss of biogenic elements from the surface layers can occur over time scales (days) too short to be explained by zooplankton grazing and the associated sinking out of faecal material (Eppley *et al.*, 1983).

We are now faced with a paradox: why can diatoms sink out in greater quantities than copepod faecal pellets? Invoking aggregation of diatoms helps only insofar as it puts both particle categories, i.e. aggregates and copepod pellets, within the same range of sinking rates (50 to 300 m d^{-1}). Therefore, there must be other explanations for this paradox. Mass diatom sedimentation is a highly episodic event (Smetacek *et al.* 1978; Smetacek, 1980a; Peinert *et al.*, 1982; Billett *et al.*, 1983; Davies and Payne, 1984); this is also why it has generally been overlooked before. Within a short period of time (days to weeks), a large number of particles traverse the water column, well in excess of the utilization capacity of pelagic heterotroph standing stocks. Further, the mucilaginous aggregates might deter feeding by some herbivores as shown in the case of large colony-forming diatoms such as *Thalassiosira partheneia* (Schnack, 1983). In contrast, copepod faecal pellets are produced at a slowly increasing rate over a much longer period, concomitant with growth of the copepod population. Thus, surface and bathypelagic coprophagous organisms will be better able to adjust their feeding pressure to this food source. Copepod pellets are also much easier to "handle" than mucilaginous diatom aggregates. Paffenhöfer and Knowles (1979) showed that coprophagy within the surface copepod population can be sufficiently intense as to reduce losses by sinking of pellets to only a few percent of the pellet production rate.

Bacterial decomposition in the water column is another mechanism that could prevent sinking of pellets. Gowing and Silver (1983) showed that zooplankton faecal pellets are egested with internal bacteria. They suggested that microbial decomposition is initiated in the sea from inside the pellets. This would result in more rapid disintegration than if decomposition proceeded only from outside as observed by Honjo and Roman (1978) in *in-vitro* studies. Further, Gowing and Silver (1983) pointed out that bacterial growth chemistry within an organic matrix is likely to differ considerably from that on the outside. Krause (1981) even speculated that formation of gas vacuoles within the pellets by bacterial decomposition might function as a suspension mechanism, which would explain why copepod pellets are so neatly packed and sealed in contrast, for example, to the long, friable "strings" produced by euphausiids. Bacterial growth within the pellets would also improve nutritive value (Johannes and Satomi, 1966) and reingestion of pellets by copepods would make considerable ecological "sense".

Although more field observations are required, it is nevertheless tempting to speculate that copepod faecal pellets actually represent a mechanism to retain essential elements within the surface layer countering the downward "pull" of the diatoms. An ungrazed diatom bloom will tend to sink out of the surface layer and deplete it of essential elements. In the North Atlantic, the spring copepod maximum is attained well after the passing of the diatom bloom (Heinrich 1962; Colebrook, 1983; Fransz and Gieskes, 1984). Thus, the first herbivore generation, spawned by the overwintering individuals, generally commences breeding during the subsequent sparse period dominated by flagellates and must also be adapted to these conditions (Krause, 1981). Loss of the bulk of faecal material produced at this stage in the upper layer and the resulting depletion of essential elements would hence pose a serious problem to breeding success of the next generation (Krause, 1981).

When food supply is plentiful, such as during a bloom, herbivorous copepods feed in excess of their metabolic demands and much undigested food and even whole cells are egested (Turner and Ferrante, 1979; Angel, 1984). Assuming that most of the pellets do not sink out, this behaviour could be interpreted as a storage mechanism whereby the overwintering population of a species maximizes the food supply for its next generation.

Admittedly, the mechanisms maintaining suspension are yet to be proven and *in-vitro* measurements do indicate that copepod pellets can possess high sinking rates (Angel, 1984), although Small *et al.* (1979), in a detailed *in-vitro* study, showed that only the larger copepod pellets can be of importance to vertical flux. Apparently, as discussed above, sinking of even these larger pellets appears more the exception than the rule. However, the still larger faeces of euphausiids, salps, pteropods and clupeids can indeed contribute substantially to mass flux as reported from sediment trap studies (Lutter, 1984; Dunbar and Berger, 1981; Iseki, 1981; Staresinic *et al.*, 1983); the sinking rates of pellets in this size class are sufficiently high to result in mass sedimentation. These larger animals tend to occur in swarms and many, such as euphausiids and fish, can easily change their feeding grounds (Hamner *et al.*, 1983). They would therefore not necessarily profit from the retention and recycling of their faecal material within the surface layer. Recycling of salp faeces within upper layers was reported by Pomeroy and Deibel (1980), whereas Iseki (1981) and Madin (1982) found that they sink out rapidly.

Such conflicting observations call for much more attention to this recycling aspect of zooplankton feeding behaviour, particularly since existing ecosystem models indicate that the zooplankton must suffer from a food shortage (Platt *et al.*, 1981). Incorporation of large-scale phytoplankton sedimentation into these models would further aggravate the problem. As a rule, of course, zooplankton at large are not starving, which merely emphasizes the still serious gaps in our knowledge of zooplankton feeding strategies (Omori and Hamner, 1982). Pelagic copepods and diatoms appear to have evolved together (Parsons, 1979). The hypotheses presented above would provide one explanation for the dominant role of copepods as grazers of diatom blooms in the sea.

Evolutionary considerations

Pelagic systems progress from relatively simply structured diatom blooms in turbulent nutrient-rich water to complex, recycling, flagellate communities at much lower biomass levels in stratified, nutrient-depleted water (Margalef, 1978; Davis, 1982). Progression from the bloom to the recycling community occurs within a few weeks to months and is driven by the loss of essential elements sinking out of the surface layer (Margalef, 1978). Thus, the sinking behaviour of the pioneer population will have a decisive impact on the structure of succeeding communities and the success of planktonic bloom diatoms evidently lies in their displacement of earlier flagellated pioneer species.

Diatoms have been suggested to have evolved from resting spores of chrysophyte flagellates, because they are non-motile, diploid and have a silicified exoskeleton (e.g. Drebes, 1974). Vegetative diatom cells – with their mineral shells armed with spines and bristles or coated in mucus – are themselves reminiscent of resting spores of other organisms. The physiological capability of many species to switch back and forth between growing and resting stages without undergoing morphological change is further support for this hypothesis. However, the presence of large vacuoles suggests that vegetative diatom cells represent germinating stages of resting spores that have retained their original ability to sink rapidly and maintain a resting mode. The aberrant nature of diatom-resting spores amongst the algae also suggests a resting spore origin of diatoms. Thus, French and Hargraves (1980) showed that diatom-resting spores can well be functionally active and are capable of photosynthesizing when exposed to light. However, they cannot undergo cell division without germinating. Further, a high degree of variability within genera and even within some species is present with respect to resting spore formation (Hargraves and French, 1983), indicating differences in life-history strategies between closely related taxa. All these unique features of diatoms indicate that their evolutionary success lies at least partly in their versatile response to the environment: enduring for long periods under adverse conditions and growing rapidly when conditions improve (Anderson, 1975).

Progressively decreasing cell size from division to division, another striking feature of many bloom diatoms, may also be a useful seeding strategy because biomass is invested in a greater (factor of 10 to 100) number of units. Decreasing size will result in a lower maximal sinking rate of individuals but incorporation into aggregates will overcome this effect, unless of course the small cells are destined to become fugitive cells. Further, buoyancy control is also hampered by the relative decrease in cell to vacuole volume ratios. Formation and eventual germination of auxospores restores original cell size and thus a more favourable ratio for improving buoyancy control. Positive buoyancy has been reported from growing diatom populations (Lännergren, 1978). Possibly, the bladder-like germinating auxospore of many species (Drebes, 1974) represents a flotation device that aids in returning cells to the surface. However, upward displacement by mixing will be of greater importance in many cases (Malone, 1980), particularly because reactivation of resting cells and excystment of spores is reported to require environmental change, i.e. increased light or nutrients (Hargraves and French, 1983). It is likely that species-specific differences with regard to this behaviour are present.

The larger number of benthic species than purely pelagic ones indicates that diatoms as a group have evolved a number of ecological strategies in which an affinity for the sea bed is prominent. In this respect they are not unique amongst aquatic organisms. In diatoms, however, all the intermediate stages between the holoplanktonic and holobenthic mode of existence are present, and there are many genera or groups of related genera that include oceanic, neritic, meroplanktonic, tychopelagic and benthic species (Drebes, 1974). The distinction between these types depends on their life-history patterns and, in the neritic, meroplanktonic and tychopelagic types, on the degree of turbulence necessary to maintain vegetative stages in suspension, i.e. on sinking behaviour relative to other environmental conditions such as nutrient or light supply. It appears likely that if diatoms originated evolutionarily from benthic resting spores, their invasion of the pelagic environment must have occurred as the ability of some species to remain afloat increased in the face of diminishing turbulence. Thus, both the ability to remain in suspension as well as to sink out rapidly are of equal importance in the diatoms as a group.

Tychopelagic forms can give some indication of the mechanisms involved in transition of diatoms from a benthic to a pelagic mode of life. Thus, the tychopelagic species *Thalassiosira decipiens* and *T. levanderi* are invariably covered with sediment particles adhering to the chains when found suspended in the water column (Drebes, 1974). Adherence to the sediment particles is apparently effected by gelatinous microfibrils; on turbulent resuspension, mineral particles can act as ballast and thus ensure rapid resettling of the chains.

As pointed out in a previous section, most bloom diatoms secrete mucus only on senescence, i.e. in conjunction with rapid sinking. These mucous flocs will scavenge other particles from the water column in the course of sinking. The ecological significance would be to increase aggregate sinking rates and also the depth of light penetration by reducing the suspended load. The latter effect would be particularly important in turbid shallow water of mud flats where non-motile centric diatoms also flourish on the sediment surface alongside motile pennate diatoms (Drebes, 1974). Evidently, both groups are well equipped to avoid both dispersal as well as burial in this physically unstable environment. The importance of mucous secretion and buoyancy regulation as potential adaptive features subject to environmental selection is apparent. Morphological features such as shape, cell protuberances and chain formation do not necessarily appear to be adaptations *per se* to a particular environment as they can well be encountered in both planktonic as well as tychopelagic or even benthic forms. Thus, the peculiar surf zone diatom *Chaetoceros armatum* resembles planktonic *Chaetoceros* spp. superficially except for its unique, tightly cemented coat of clay particles (Lewin *et al.*, 1980). The *Thalassiosira* spp. mentioned above do not differ morphologically from planktonic species other than in the degree of mucous production. One might conclude that environmental selection of morphological features is best understood in conjunction with behavioural characteristics such as buoyancy/sinking control, mucous secretion or control over frustule dissolution rates within the framework of life-history strategies.

In this connection, similarities with other shell-bearing planktonic protists appear to be present. Coccolithophorids, for example, have pelagic bloom-forming and benthic species and some planktonic forms have benthic resting stages (Berger, 1976). In some pelagic coccolithophorids, motile and non-motile stages are present and, significantly, it is the carbonate shells of the non-motile stages that are more robust and accumulate preferentially in the sediments (Berger, 1976). Apparently, the shell here also functions as a sinking device. Formation of rapidly sinking palmelloid stages with thousands of individuals enclosed in a gelatinous matrix was reported in *Cyclococcolithus fragilis* (Bernard, 1963). Mass sedimentation of another species (*Umbellicosphaera sibogae*) to the deep sea was recorded by Honjo (1982) who observed that the individual cells appeared to be embedded in mucus. Various biogenic and mineral particles adhered to the mucous aggregates which apparently increased their sinking speed. Coccolithophorid cultures, on cessation of logarithmic growth, have been observed to form mucous agglomerations that sank to the bottom of the culture vessel (Honjo, personal communication). The striking similarity of this behaviour with that of bloom diatoms strongly suggests similar life-history patterns amongst species in both groups. Foraminifera also have benthic and pelagic species and the sedimentary record clearly shows that benthic forms were the precursors in this group (Berger, 1976). As mentioned above, the foram shell also apparently serves as a sinking device in the life-history cycles of pelagic forms. Very little is known about the life history of Radiolaria but some parallels with those of diatoms can be expected, particularly with respect to depth positioning.

Geological implications of bloom diatom sedimentation

The global importance of diatoms as contributors to aquatic sediments is well documented (Berger, 1976). Further, the strategy of mass sinking presented above has geological implications other than vertical transfer of opal and biogenic material. Thus, major input of non-marine mineral particles to the sea bed coincides with the annual maximum input of pelagic particles (Honjo *et al.*, 1982; Deuser *et al.*, 1983). Apparently, many of the small, slowly sinking mineral particles are scavenged by sinking phytoplankton aggregates and precipitated out in a matter of weeks. Mutual flocculation of fresh water algae and clay has also been observed to enhance sedimentation (Avnimelech *et al.*, 1982). The various forms of interaction between algal mucopolysaccharides and clay minerals have recently been discussed by Degens and Ittekot (1984), who suggested that diatoms will be of significance in the formation of certain types of marine sediments such as mud, even if the frustules are dissolved in the process.

The geochemical implications of sinking diatoms discussed at length by Walsh (1983) take on a new dimension as a precipitation agent of smaller mineral particles. The water column will be most effectively "swept" during bloom sedimentation (the pelagic "spring cleaning") and the removal rate of dissolved substances such as trace elements will also be enhanced (Reynolds *et al.*, 1982). Downward transport of naturally occurring zinc from the surface layer by a sinking diatom bloom was observed in an enclosure experiment (Imber *et al.*, submitted). It appeared that zinc was complexed to diatom cell surfaces during growth and prior to sedimentation.

Before the advent of diatoms, marine phytoplankton was dominated by flagellates (Parsons, 1979). One might speculate that earlier pelagic annual cycles were less subject to the present drastic change from a massive bloom state to a sparse regenerating community. Thus, with the evolution of bloom diatoms, sedimentation patterns in the sea may have been fundamentally modified because of diatom sinking behaviour, with greater deposition of organic and inorganic material occurring closer to the sites of new production. The periodicity of diatom bloom sedimentation is of considerable significance for benthos ecology (Graf *et al.,* 1982, 1983; Smetacek, 1984). Moreover, the higher the sedimentation rate, the greater the proportion of organic matter that is eventually buried in the sediments (Müller and Suess, 1979). The impact of diatom sinking on the benthic ommunity and on the formation of pelagic sediments will, therefore, be greater than currently appreciated.

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