The formation of large marine snow and its sustained residence in surface waters

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Abstract

The formation of large marine snow macroflocs and stringers was monitored at a fixed station in the southern North Sea. During an 18-month investigation, large marine snow flocs occurred in the water column on nine occasions for periods lasting between 5 and 16 d. Their formation coincided with both high phytoplankton biomass and low windspeeds. Retention of marine snow in the surface layer was related to slow sinking, neutral buoyancy, and rising of the large flocs. Applying a specially developed instrument showed buoyancy to be caused by gas bubbles incorporated in the flocs. Marine snow flotation coincided with periods of oxygen supersaturation in the water column, suggesting that oxygen production could be responsible for gas bubble formation within the flocs. Disappearance of the large marine snow flocs from the surface layer coincided with drastic increases in windspeed, indicating that enhanced wind-induced turbulent mixing in the surface layer could have resulted in the breakup of these flocs. Formation and disappearance of marine snow had a marked influence on the light regime in the water.

Formation of marine snow has been shown to result in the rapid transport of particulate material from the surface to the deep ocean (Fowler and Knauer 1986). Numerous measurements of marine snow sinking rates suggest that the aggregated particles sink rapidly at velocities ranging between 1 and 368 m d^{-1} (Alldredge and Silver 1988). On the basis of these measurements, the residence time of marine snow in the surface layer would only be on the order of hours (Shanks and Trent 1980). On the other hand, several studies have emphasized the importance of marine snow particles as sites of primary production (e.g. Knauer et al. 1982; Gotschalk and Alldredge 1989) and as microplankton habitats.

If we assume the short residence time of marine snow aggregates in the euphotic zone indicated by the sinking rate studies, the potential for marine snow-related primary production would be of little significance. Rather, the association of phytoplankton cells with marine snow would merely be a mechanism for their rapid removal from the euphotic zone, as hypothesized by Smetacek (1985). In recent investigations, however, large marine snow aggregates were observed to be retained in the surface layer for periods of several days (Stachowitsch et al. 1990; Riebesell 1991*a*). Under such conditions of sustained residence in the euphotic layer, marine snow aggregates could in fact function as highly effective, self-sufficient microhabitats. In these microcosms, the activities of autotrophic and heterotrophic organisms can be closely linked, thereby providing mutual benefit. For the duration of their residence in the euphotic zone, marine snow aggregates therefore represent an important and integral part of the planktonic system.

At any instant in time, the particle size distribution in the sea reflects the balance between continually occurring processes of aggregation on the one hand and those of disaggregation and loss on the other. A shift in the particle size distribution toward larger sizes occurs when the source for larger particles, i.e. particle aggregation, exceeds

the total sink of aggregates, which includes processes such as disaggregation, sedimentation, and grazing. Conversely, situations in which the sink is greater than the source will lead to a shift in the particle size distribution toward smaller aggregate sizes. Although the basic mechanisms responsible for particle aggregation were described theoretically by McCave (1984) and simulated for algal cells in a numerical model by Jackson (1990), the intrinsic conditions under which aggregate formation dominates over disaggregation and aggregate loss are not well understood.

Recent investigations of the particle size distribution in highly turbid and productive waters seem to demonstrate that marine snow is probably always present in such environments (Wells and Shanks 1987; Riebesell 1991*a*). Considerable variability is evident in both size and abundance of particle aggregates. In a study which documented the change in the aggregate size distribution during the course of a phytoplankton bloom (Riebesell 1991*a*), large macroflocs and stringers (as classified by Stachowitsch et al. 1990) were observed to occur during a limited period of several days following the peak of the bloom. The focus of this study is to identify the environmental conditions which promoted the formation and subsequent disappearance of these large marine snow aggregates and to determine the mechanism responsible for enhancing their residence time in the surface layer.

Methods

Theoretical considerations—For a particle settling through a fluid at a terminal velocity, the force of gravity pulling the particle downward is balanced by the retarding drag force of the fluid flowing around the particle. The force balance can be expressed in an equation of the form

$$(V_p\rho_p - V_p\rho_f)g = 0.5C_D A\rho_f U^2 \qquad (1)$$

where V_p is the volume of the particle, ρ_p the density of the particle, ρ_f the density of the fluid, g the acceleration due to gravity, C_D the drag coefficient, A the maximum cross-sectional area of the particle perpendicular to the direction of sinking, and U the settling velocity of the particle. In the

particular case that a particle is neutrally buoyant, the force of gravity $F_g = (V_p\rho_p - V_p\rho_f)g$ is equal to 0, i.e. the particle mass $m_p = V_p\rho_p$ must be equivalent to the mass of the fluid $m_f = V_p\rho_f$ it replaces. Natural aggregates consist of a heterogeneous mixture of many different components, each component having its own specific density ρ_p. Consequently, the mass balance for neutrally buoyant aggregates ($m_p - m_f = 0$) should have the form

$$\sum_{i=1}^{i_{max}} (V_{p_i}\rho_{p_i} - V_{p_i}\rho_f) = 0 \qquad (2)$$

where V_{p_i} is the volume of a component i within the aggregate with a density ρ_{p_i}, and ρ_f is the density of seawater (1.028 g cm^{-3}). Depending on its porosity, the interstitial water in an aggregate can be up to 99.9% of the total volume (Alldredge and Gotschalk 1988). Because the density of the interstitial water is roughly equivalent to that of the surrounding water, it can be neglected in this evaluation.

For the purpose of simplification, a model aggregate consisting of only two components will be assumed. The first component is comprised of an equal volume of detrital-fecal material with a density $\rho = 1.23$ g cm^{-3} (Komar et al. 1981) and of living phytoplankton with a density $\rho = 1.178$ g cm^{-3}. The latter value is based on diatoms having a cell sap density of 1.020 g cm^{-3} and a density of the opaline cell wall, assumed to comprise 10% of the total cell volume, of 2.6 g cm^{-3}. The mean density of the combined first component $\rho_{p_1} = 1.204$. The second component with a volume V_{p_2} and density ρ_{p_2} should be adapted to balance Eq. 2. For this example, Eq. 2 can be rewritten in the form

$$V_{p_1}(\rho_{p_1} - \rho_f) + V_{p_2}(\rho_{p_2} - \rho_f) = 0 \qquad (3)$$

or

$$\frac{V_{p_2}}{V_{p_1}} = \frac{\rho_{p_1} - \rho_f}{\rho_f - \rho_{p_2}}. \qquad (4)$$

Because the density ρ_{p_1} of the first component is considerably higher than that of seawater, the second component has to be low-

er in density than seawater in order to satisfy Eq. 4. Only a few substances with densities less than seawater are likely to occur in aggregates in sufficiently large amounts to fulfill this requirement. If we assume that the density of the second component would be that of pure fat ($\rho = 0.95$ g cm^{-3}), $V_{p_2}/V_{p_1} \approx 2.26$—the volume of fat in the aggregate would have to be 2.26 times the volume of the rest of the aggregated material—a rather unrealistic assumption. On the other hand, if gas with a density $\rho_{p_2} = 1.29 \times 10^{-3}$ g cm^{-3} (air) would be entrapped in the aggregate, $V_{p_2}/V_{p_1} \approx 0.17$—the volume required to balance Eq. 4 would have to be less than a fifth of the total aggregate volume.
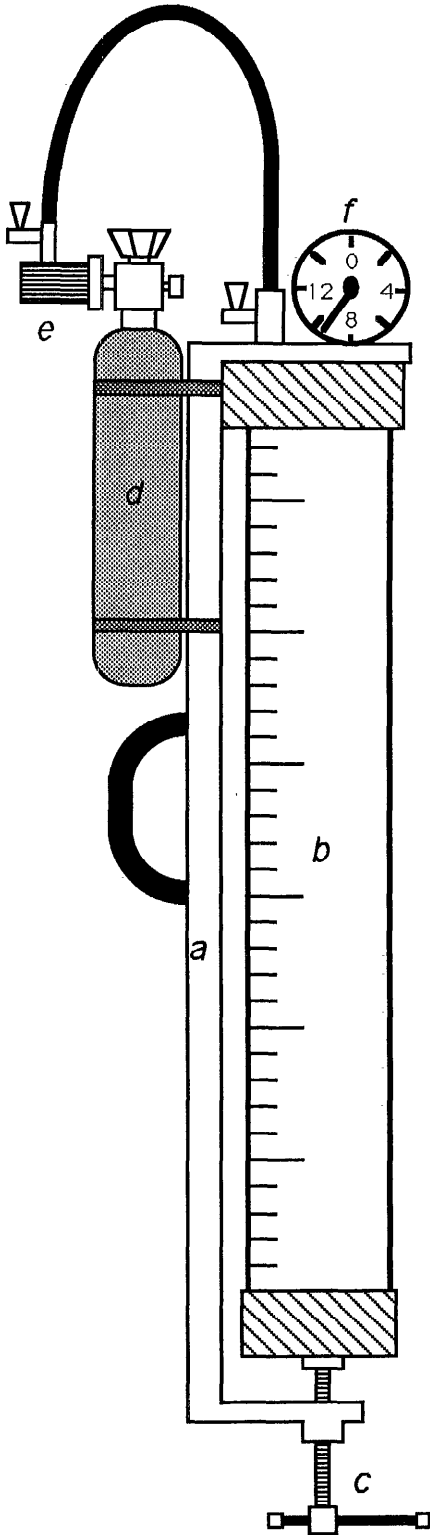
The outcome of this simple model led to the hypothesis that gas bubbles trapped in aggregates could be responsible for the observed neutral buoyancy of large aggregates. A test of this hypothesis can be based on the fact that the volume of any gas depends on the ambient pressure. If an aggregate is neutrally buoyant due to a given volume of gas enclosed in it, this aggregate will start to sink if the volume of the gas decreases as a result of an increase in hydrostatic pressure. With this in mind, an instrument was developed which allowed the in situ measurement of marine snow sinking velocity under both ambient hydrostatic and significantly increased pressure conditions.

Principle of the controlled-pressure settling chamber—The instrument (Fig. 1) consists of a 50-cm-long Plexiglas cylinder with an 8-cm i.d., which can be easily removed from and installed into an aluminum frame. When positioned in the frame, the cylinder can be closed with two PVC caps located at each end of the frame. The caps can be fastened by means of a screw fastener located at the bottom of the frame. Rubber pads fixed to the inside of each cap ensure complete sealing of the cylinder. A 500-cm^3 steel tank containing compressed air at 200 bars is attached to the outside of the frame. The pressure tank is equipped with a pressure reduction valve, which reduces the air pressure to a constant value of 9.5 bars. A pressure tube connects the tank unit with the upper cap and opens into the Plexiglas cylinder. Three-way valves positioned at each end of the pressure tube

allow pressure release out of the cylinder and out of the tube to occur independently. The tube is filled with seawater before each measurement to prevent air from entering the cylinder. A pressure gauge connected to the upper cap measures the actual pressure inside the cylinder.

The settling tube is operated in situ by SCUBA divers. The open Plexiglas cylinder is carefully lowered over an individual marine snow aggregate. The frame is then placed adjacent to the cylinder with the two caps in position to close the cylinder. The caps are slowly closed over the cylinder ends by turning the screw fastener. At this stage, the three-way valves are open to avoid buildup of pressure inside the settling tube. Marine snow movements (sinking-ascending) were recorded over distances of 15–35 cm by measuring the time needed to pass 5-cm intervals marked on the Plexiglas cylinder. After the initial measurement at ambient pressure, the pressure inside the cylinder is increased to 9.5 bars and the sinking rate of the same aggregate is measured again. If gas bubbles are entrapped in the aggregate, the sinking rate at increased pressure should be significantly greater than that recorded in the initial measurement.

Study location, field and laboratory measurements—During an 18-month investigation (April 1989–September 1990), measurements were conducted at a station between Helgoland Island and the dune to the east of the island in the North Sea (54°11.3′N, 7°54.0′E). This station with a water depth of 16 m is identical with the Helgoland Roads station of the Biologische Anstalt Helgoland (BAH), where a routine sampling program has been carried out daily by the BAH since 1962 (Radach et al. 1990). Dissolved inorganic nutrient concentrations and phytoplankton cell counts (converted to phytoplankton carbon) at the sea surface, as well as Secchi depth, were measured 5 times a week by the BAH and the data provided to me. Windspeed measurements recorded at a weather station on Helgoland Island 10 m asl at 10-min intervals were made available by the Deutscher Wetterdienst. Both presence or absence and approximate size of the large marine snow (macroflocs and stringers, 1–10 cm in lon-

gest dimension; *see* Stachowitsch et al. 1990 for classification of marine snow types) in the study area were continuously monitored by divers of the BAH diving group, who carry out routine dives around Helgoland Island several times a week year-round.

During periods of marine snow occurrence, intensive measurements of both water column and marine snow properties were carried out. Temperature and salinity profiles were taken with a WTW LF 191 conductometer. Oxygen profiles were recorded with an Orbisphere model 27141 oxygen detector equipped with a 2112 sensor holder. Parallel measurements on selected samples with the Winkler titration method revealed deviations between the two methods of <5% over a wide range of oxygen concentrations. Aggregate size and abundance were determined from underwater photographs taken at a 6–8-m water depth with a Nikonos-V underwater camera system as described by Riebesell (1991*a*). The original system was modified with a 1:3 extension tube to account for the larger sizes of marine snow encountered in this study. During each dive, 30 exposures were taken randomly, each photograph representing a volume of ~0.7 dm^3 (8 cm high × 12.5 cm wide × 7-cm depth-of-focus). Visual inspection of marine snow size over the entire water column provided an approximate estimate of the vertical distribution of macroflocs and stringers.

Sinking velocities of 57 marine snow aggregates were measured at ambient and increased pressure in the controlled-pressure settling chamber during nine dives. Sinking rate measurements were started following a time lag of 3 to 4 min after closure of the settling tube in order to allow convective water movement inside the tube to cease. Only those flocs were used for velocity measurements which, based on continuous visual inspection, remained unaffected during

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Fig. 1. Outline of the controlled-pressure settling chamber: a—aluminum frame with handle; b—Plexiglas cylinder with length scale; c—screw fastener for tight closure of the cylinder; d—steel tank containing compressed air at 200 bars; e—reduction valve regulating released pressure at 9.5 bars; f—pressure gauge.

Table 1. Occurrences and characterization of large marine snow aggregates (SD in parentheses, $n = 10$). Not determined—ND.

Period	Day measured	Length (cm)	Width (cm)	Abundance (No. dm^{-3})	Mean Chl a content (μg aggr.$^{-1}$)	Mean pheop. content (μg aggr.$^{-1}$)	Dominant phytoplankton
16–20 May 89	19 May	3–5	0.3–2.2	4.9	0.170(0.156)	0.057(0.042)	Diatoms
18–22 Jun 89	20 Jun	4–8	0.4–2.5	2.0	0.782(0.530)	0.342(0.222)	Diatoms
21–30 Jul 89	23 Jul	3–8	ND	ND	ND	ND	ND
16–22 Aug 89	21 Aug	2–6	ND	ND	ND	ND	ND
1–8 Sep 89	5 Sep	3–5	ND	ND	ND	ND	ND
9–16 May 90	9 May	6–16	0.6–3.5	3.8	1.198(0.392)	0.196(0.059)	Diatoms
31 Jul–15 Aug 90	1 Aug	3–4	0.3–1.0	2.6	0.063(0.028)	0.058(0.032)	Flagellates
	15 Aug	2–3	0.3–0.6	0.2	0.013(0.003)	0.056(0.021)	Flagellates
31 Aug–3 Sep 90	31 Aug	3–4	ND	ND	ND	ND	ND
11–17 Sep 90	14 Sep	3–10	0.4–3.2	0.7	0.153(0.057)	0.307(0.152)	Flagellates

the entire closure and measurement procedure, i.e. no alteration of floc orientation, shape, and macrostructure occurred. The sinking velocity of each undisturbed floc was measured twice, first under in situ hydrostatic pressure at 6–8-m water depth and then again under 9.5 bars of additional pressure.

Individual flocs were collected by SCUBA divers at a depth of 6–8 m as described by Riebesell (1991*b*). Both Chl *a* and pheopigment content were determined on 10 flocs from each dive. Individual flocs were filtered onto 25-mm Whatman GF/C glass-fiber filters. After extraction in 90% acetone (filters were homogenized with glass beads), the Chl *a* and pheopigment content was measured with standard fluorometric methods. Determination of the dominant phytoplankton groups in marine snow was achieved by microscopic analysis of 5–8 intact flocs under the inverted microscope.

Results

Over the period of investigation from April 1989 until September 1990, large marine snow aggregates were observed during nine intervals, each lasting for at least 4–5 and up to 16 d (Table 1). Marine snow aggregates were generally evenly distributed throughout the upper mixed layer; below this layer, marine snow abundances were generally lower, although in a few situations high abundances were recorded throughout the entire water column (e.g. 14 September 1990). Largest sizes of the predominantly elongated, comet-shaped aggregates (string-ers) were between 2–3 cm and 6–16 cm in longest dimension. Although slightly smaller marine snow sizes occurred in the immediate 1–2-m surface layer, no visible size difference with depth was recorded below that layer. Living phytoplankton cells were a major component of marine snow at all times. The largest fraction generally consisted of detrital material and, in some cases, fecal pellets. The dominance of particular phytoplankton groups was always identical in the water column and in aggregates.

Marine snow sinking velocities at ambient hydrostatic pressure ranged between -184 m d^{-1} (i.e. ascending) and $+295$ m d^{-1} (i.e. sinking). About half of the aggregates measured were neutrally buoyant. With the exception of three aggregates, sinking velocities were significantly higher at the additional pressure of 9.5 bars (Fig. 2). The mean sinking velocity of 46.2 m d^{-1} measured at ambient hydrostatic pressure increased to 307.7 under increased pressure conditions. This observation strongly supports the hypothesis that gas bubbles entrapped in the aggregates were responsible for the observed neutral or positive buoyancy of marine snow. In a few cases, minute gas bubbles caught in the matrix of large aggregates were observed in situ by the naked eye.

Each occurrence of large marine snow recorded during the study period was associated with a phytoplankton bloom (Fig. 3). Marine snow formation occurred either during or shortly after the bloom. However, the inverse was not true, i.e. not every phy-
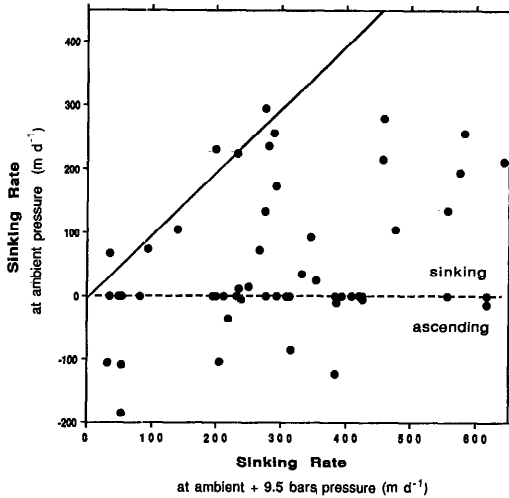
Fig. 2. Sinking (ascending) rates of a total of 57 marine snow aggregates measured in the controlled-pressure settling chamber under ambient hydrostatic pressure vs. sinking rates of the same aggregates under hydrostatic plus 9.5 bars of additional pressure. Dashed line indicates the level of neutral buoyancy under ambient pressure conditions; data points above this line represent sinking aggregates and below it, ascending aggregates. Solid line indicates level of equivalent sinking rate under ambient and increased pressure conditions; data points to the upper left of this line represent aggregates that sink faster under ambient conditions and those to the lower right aggregates that sink faster under increased pressure conditions.

toplankton bloom also led to marine snow formation (e.g. June 1990). No obvious relationship was found between marine snow formation and the concentrations of any of the macronutrients (Fig. 3). With the exception of silicate depletion following the diatom spring blooms, nutrient concentrations were never sufficiently depleted to limit phytoplankton growth. The presence of large marine snow evidently coincided with periods of both relatively low windspeeds and high Secchi depth readings. In fact, days with large marine snow were characterized by significantly lower windspeeds (two-sample t-test, $P < 0.001$) and significantly higher Secchi depths ($P < 0.001$) than days when macroflocs and stringers were absent. Temperature-salinity and oxygen concentration profiles (Fig. 4) obtained during periods of marine snow indicate density stratification and oxygen supersaturation throughout the water column (1 August, 15 August, decreasing with depth), in the upper

mixed layer (5 May), and below the surface layer (14 September).

In seven of nine cases, the abrupt disappearance of marine snow coincided with a sudden drastic increase in windspeed (>8–10 m s^{-1}, Fig. 3), which suggests that enhanced mixing of the water column may have resulted in the breakup of macroflocs and stringers or may have transported them to greater depth. Measurements immediately before (15 August 1990) and after the end of a marine snow period (17 August 1990) show that wind-induced mixing of the water column, due to windspeeds >10 m s^{-1}, caused the density stratification to become disrupted and the oxygen concentration to decrease from supersaturation to a level slightly below saturation (Fig. 4). Disappearance of the large marine snow flocs generally coincided with marked decreases in Secchi depth (Fig. 3), indicating that marine snow retained in the surface layer was likely to have been subject to breakup. The observed increase in turbidity could thus be explained by dispersion of the aggregated material into fine suspended particulates.

Discussion

Marine snow retention in the surface layer—Aggregation of particulate material generally increases particle sinking rate (Fowler and Knauer 1986). Marine snow aggregates were shown to sink at mean rates of ~50–100 m d^{-1} (Alldredge and Silver 1988). In contrast, the large marine snow aggregates discussed here were characterized by relatively slow sinking rates, neutral buoyancy, or slow ascending rates. Although the high sinking rates generally recorded for marine snow appear to be the rule under most conditions, marine snow buoyancy as observed in this study was related to very specific environmental conditions. As suggested by both theoretical considerations and sinking rate measurements, buoyancy of the large marine snow flocs was related to gas bubble formation within the flocs. For the development of gas bubbles in marine snow, at least three conditions must be met: gas generation by biological processes such as primary production (O_2 formation) or degradation of organic material (CH_4 formation) within marine snow; partitioning of marine

snow aggregates in areas of primary production and degradation or a net imbalance between the two processes for the aggregate as a whole; and a lower rate of diffusive exchange between marine snow and the surrounding water compared to the rate of gas production.

A possible mechanism by which gas production in marine snow can be achieved was indicated by both the composition of the flocs (Table 1) and the recorded oxygen profiles (Fig. 4). Living algal cells were always a major component of marine snow, so algal growth was a likely source of O_2 formation in them. In addition, the occurrence of neutrally buoyant marine snow coincided with oxygen supersaturation in the upper mixed layer (Fig. 4)—a result of high primary production during phytoplankton blooms. Supersaturation in the surface layer, combined with a high rate of O_2 production in marine snow flocs and a reduced oxygen diffusion rate due to the low concentration gradient between marine snow and the surrounding water, could therefore have resulted in formation of bubbles in the flocs. Supersaturation in the water would also prevent dissolution of oxygen bubbles entrapped in the flocs at night when O_2 production ceases.

With the observed possibilities of marine snow vertical motion including ascension, neutral buoyancy, and sinking (Fig. 2), a hypothetical scenario can be developed to account for the documented retention and accumulation of large flocs in the surface layer. In a wind-mixed water column, the energy dissipation rate decreases with depth (Oakey and Elliott 1982). Marine snow rising toward the surface would therefore be exposed to continuously increasing turbulent mixing and eventually be subjected to breakup. As a result, entrapped gas bubbles would be released and the marine snow fragments would begin to sink. In encountering lower levels of turbulence with depth, the particles would collide and become attached to other particle aggregates, predominantly those moving upward or remaining neutrally buoyant. This process, in addition to vertical mixing of the water column, could explain both the relatively uniform distribution and the retention of marine snow in the upper mixed layer.

Sustained residence of macrocrustacean fecal pellets in surface waters off southern California was attributed mainly to vertical mixing processes (Alldredge et al. 1987). In this study, sustained residence of marine snow was observed during periods of low windspeeds and therefore conditions of low wind-induced mixing of the water column. The process of marine snow retention by gas bubble formation appears to be strongly dependent on the depth of the upper mixed layer and the intensity of vertical mixing in this layer. In the case of a deep mixed layer, marine snow flocs would be subject to large vertical displacements and would thereby encounter large differences in ambient pressure. Under these conditions, gas bubbles are likely to either dissolve when ambient pressure is high or become too large and detach from the aggregate when ambient pressure is low. Thus, strong vertical stratification of the water seems to be prerequisite for the retention of marine snow due to gas bubble formation.

Sustained residence of copepod fecal pellets in surface waters of the North Sea was hypothesized to be caused by gas bubbles generated in the pellets by bacterial degradation (Krause 1981). However, Krause (1981) recorded highest accumulations of fecal pellets during periods of high phytoplankton biomass, so fecal pellet retention may have been related to the simultaneous retention of marine snow aggregates. Such an interpretation is supported by the large number of fecal pellets found incorporated in marine snow in the present study. Furthermore, the observed disappearance of surface-layer accumulations of fecal pellets during a storm (Krause 1981) parallels the disappearance of marine snow during strong wind periods, as reported here, and may similarly have been a result of breakup.

Floating macroaggregates were reported from early investigations in the North Sea (Savage and Wimpenny 1936; Grøntved 1952) and the Adriatic Sea (Cori 1906; Oltmanns 1923). Savage and Wimpenny (1936, p. 3) described "masses of floating particles . . . and short strings hanging vertically in the water" during periods when "the weather has been a dead calm for some days." In a recent study in the Adriatic Sea, Stacho-
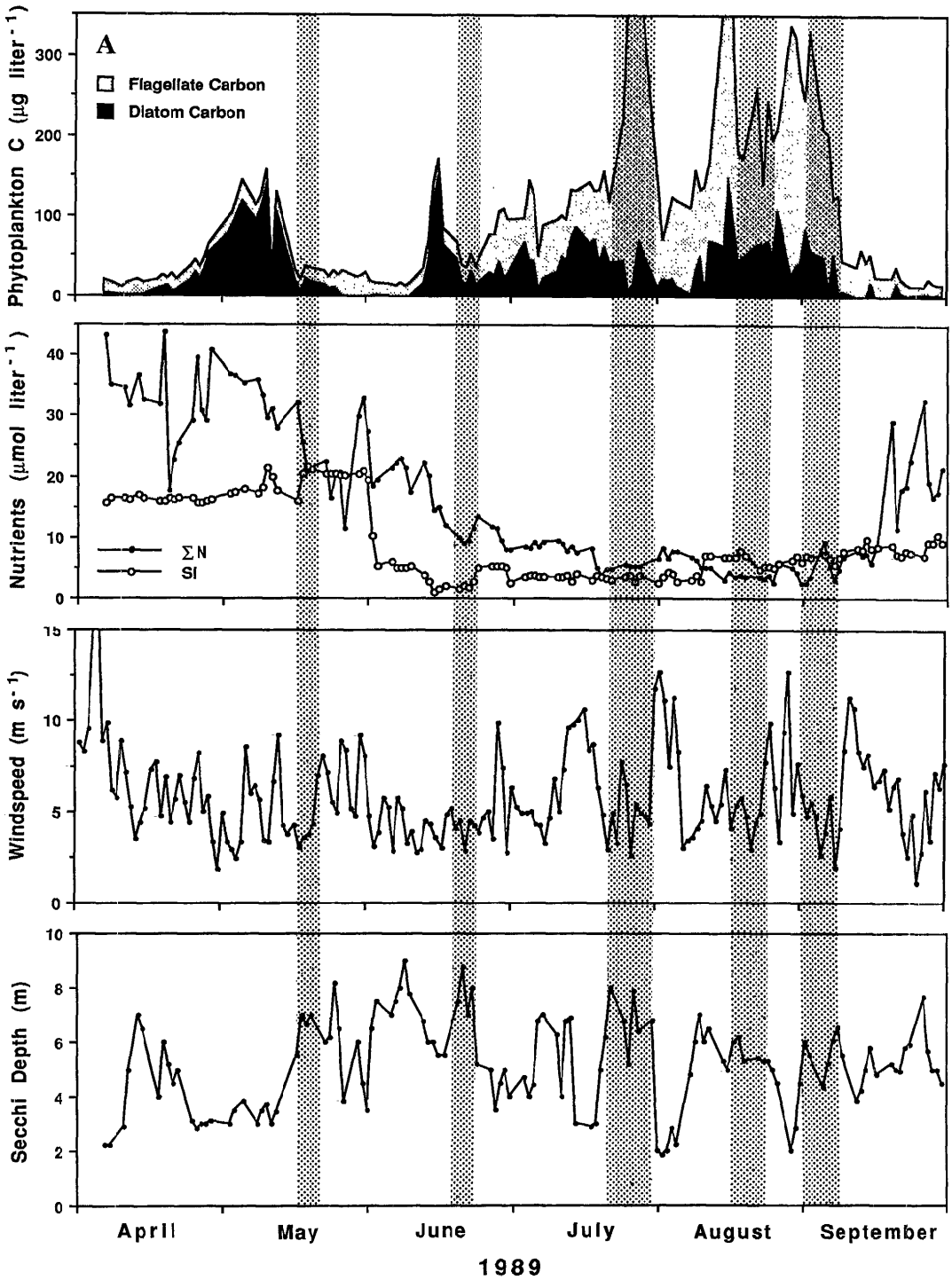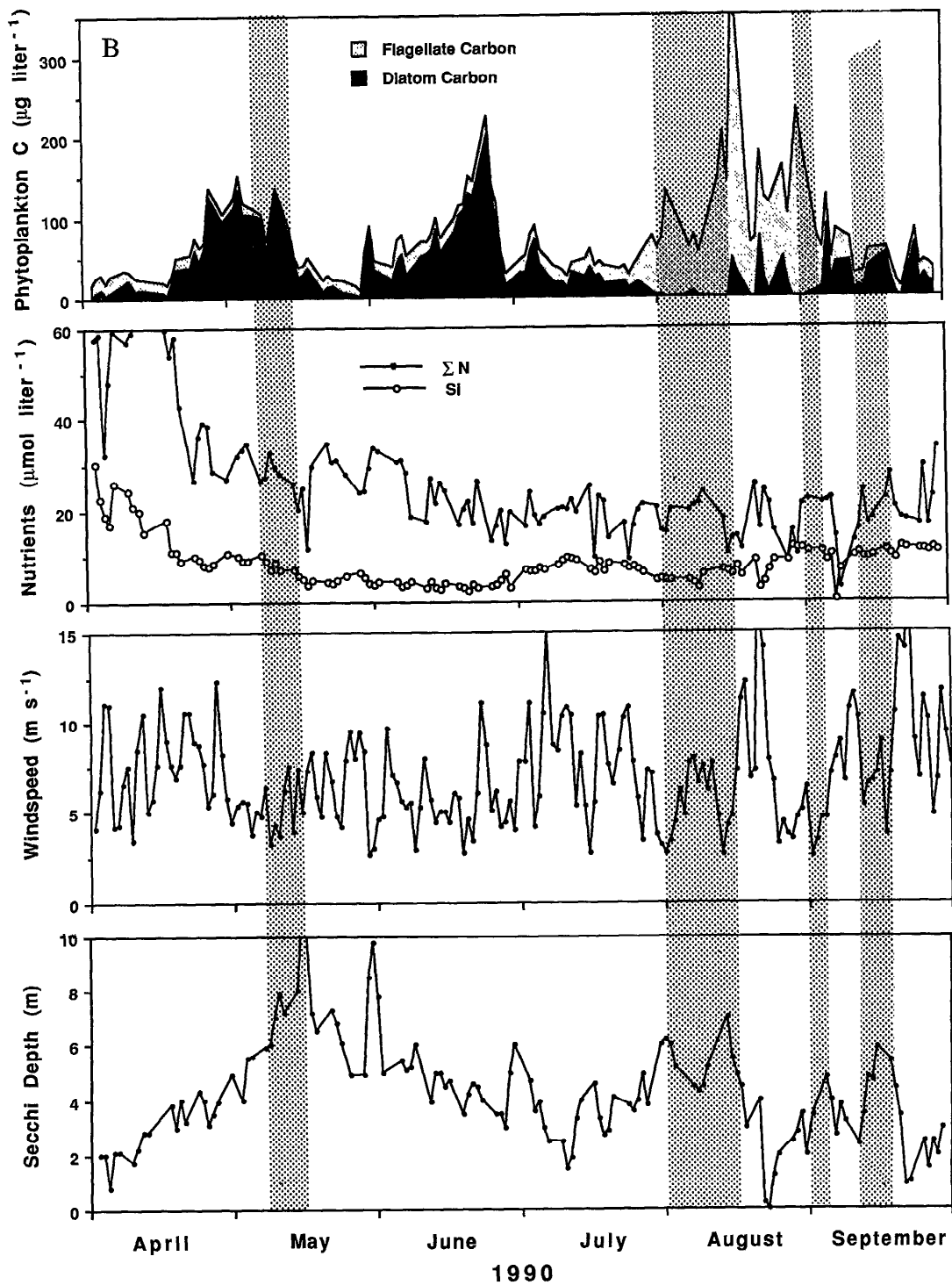
Fig. 3. Phytoplankton biomass concentration (cumulative plotting), $NO_3^- + NO_2^- + NH_4^+$ (ΣN) and silicate concentrations, Secchi depth, and windspeed measurements from April until September for 1989 and 1990. Stippled areas indicate periods of marine snow.

Density (σt)

Oxygen Saturation (%)

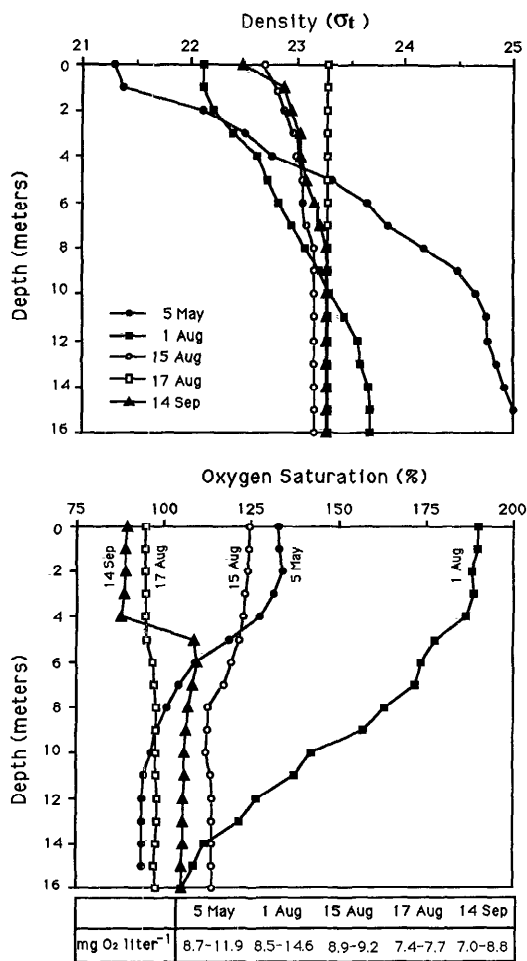| mg O₂ liter⁻¹	5 May	1 Aug	15 Aug	17 Aug	14 Sep
	8.7–11.9	8.5–14.6	8.9–9.2	7.4–7.7	7.0–8.8

Fig. 4. Density profiles calculated from temperature and salinity measurements and oxygen profiles (% saturation) on five selected days in 1990. Also indicated is the range of absolute oxygen concentrations corresponding to the respective profiles.

witsch et al. (1990) noted mucus aggregates rising to the surface and observed gas bubbles entrapped in these aggregates. They argued that gas bubble formation, in addition to other mechanisms such as turbulence, density gradients, and mucus production, may delay settlement and prolong the residence of aggregates in the surface layer. The presence of slowly sinking and nonsinking large aggregates even in deeper waters was documented by Asper (1987) in a study with a camera-equipped sediment trap positioned at 3,800-m depth. He observed that large aggregates (4–5 mm) had average sink-

ing rates of 1 m d^{-1}—a value much lower than the 36 m d^{-1} measured for small aggregates (1–2.5 mm). Asper attributed these results to a predominance of nonsinking aggregates in the large size class. These measurements were conducted in the deep ocean, so the low sinking rates were likely to have been produced by a mechanism other than gas bubble formation.

The potential for sustained residence of marine snow in the surface layer, as observed in this study, requires a broader interpretation of the role of large aggregates with respect to the fate of aggregated material. In addition to the well-documented enhancement in vertical transport of particulate material by marine snow formation (e.g. Fowler and Knauer 1986), large aggregates can apparently also retard sedimentation of particulate material. The possibility for retention of particles in the form of large aggregates in the surface layer should be considered when assessing the vertical flux of particulate material in the ocean.

Marine snow formation and disappearance—High phytoplankton biomass seems to be prerequisite for the formation of large marine snow aggregates. Under conditions of high algal cell concentrations, floc formation occurred regardless of whether the phytoplankton community was dominated by diatoms or flagellates. Jackson (1990) showed that algal cell concentration is a critical variable in the process of physical coagulation. The rate of aggregation increases exponentially with increasing particle concentration. Because formation of the large marine snow in this study was restricted to periods of high cell concentrations, physical coagulation of the algal cells appears to be the dominant process leading to floc formation. However, not every phytoplankton bloom resulted in the formation of macroflocs and stringers (*see June 1990*), indicating that additional factors were important.

Smetacek (1985) hypothesized that nutrient stress triggers phytoplankton flocculation. A difference of two orders of magnitude in cell stickiness between nutrient-replete and nutrient-depleted cells was found for the diatom *Thalassiosira pseudonana* (Kiørboe et al. 1990). Sticking efficiency is in fact an important, biologically

controlled parameter strongly affecting the rate of algal aggregation (Jackson 1990). In this study, however, mass flocculation of the phytoplankton was apparently not induced by an increase in algal stickiness due to nutrient depletion. Large marine snow flocs generally formed under conditions of high nutrient concentrations (Fig. 3). Similarly, Alldredge and Gotschalk (1989) observed marine snow formation when inorganic nutrients were replete. Thus, mass flocculation must have been triggered by factors other than nutrient depletion. Alternative factors include amorphous mucus formation due to increasing concentrations of dissolved organic carbon during phytoplankton blooms (Degens and Ittekkot 1984), enhanced physical aggregation due to increasing effective cell size caused by growth of colonial and chain-forming algae over the course of the bloom (Riebesell 1991*b*), and enhanced biological aggregation due to an increase in the activity of heterotrophic organisms during and after the bloom.

Another factor that seems to be important in forming large marine snow is indicated by coincidence of the large flocs with periods of low windspeed (Fig. 3). Similarly, large mucus aggregates floating in the surface layer during periods of low wind were reported from the North Sea by Savage and Wimpenny (1936), indicating that accumulation of large amounts of marine snow flocs in the surface layer can only occur under conditions of low turbulent mixing of the water. The absence of macroflocs and stringers during periods of increased wind-induced mixing could be caused by two different mechanisms. First, increased mixing could reduce the residence time of large marine snow flocs and thus prevent their accumulation in the surface layer. A short residence time may be because a high level of wind-induced mixing prevents formation of gas bubbles within the flocs, thus resulting in high sinking rates. At sinking rates on the order of tens of meters, as generally observed for marine snow aggregates (Alldredge and Silver 1988), the large flocs would be subject to rapid sedimentation out of the surface layer. Second, the formation of macroflocs and stringers could be prevented directly by disaggregation of "growing" ma-

rine snow due to turbulent water motion in the surface layer. Either mechanism could explain why large marine snow was not observed during a diatom bloom in June 1990—a period characterized by intermittent high windspeeds.

In seven of the nine large marine snow events, the sudden disappearance of macroflocs and stringers coincided with increased windspeeds >8–10 m s^{-1}. A rise in windstress enhances turbulent mixing of the water and can result in deepening of the upper mixed layer. Hence, the abrupt end of the marine snow events could have resulted either from vertical mixing of the macroflocs and stringers to greater depth or their disaggregation. The decrease in Secchi depth observed concomitant to the disappearance of large marine snow suggests that at least part of this material was retained in the surface layer where it was subject to breakup. The dispersion of the aggregated material into fine suspended particulates is a likely explanation for the observed increase in turbidity.

If in fact an increase in turbulent mixing during periods of high windspeed resulted in the breakup of the large marine snow flocs, this raises the question of the physical strength of the flocs. The physical strength of marine snow was recently tested in laboratory experiments by Alldredge et al. (1990). They found that fragile diatom flocs up to 25 mm long required energy dissipation rates on the order of 10^{-7} to $>10^{-4}$ m^{-2} s^{-3} in order to disaggregate. An approximate estimate of the energy dissipation rate prevalent in situ during the present study can be calculated with the windspeed measurements. The energy generated in the water due to the passage of wind over the sea surface, termed friction velocity u^*, can be calculated as:

$$u^* = (C_{DA}\rho_a/\rho_w)^{1/2}W_{10} \qquad (5)$$

where $C_{DA} = 1.25 \times 10^{-3}$ is the drag coefficient, $\rho_a = 1.29$ kg m^{-3} the density of air, $\rho_w = 1,028$ kg m^{-3} the density of seawater, and W_{10} (m s^{-1}) the windspeed at 10 m. A relationship between friction velocity and turbulent energy in the upper mixed layer was formulated by van Aken (1984):

$$\epsilon = 53.5u*^2f \exp[z/(0.068u*/f)] \quad (6)$$

where ϵ (m² s⁻³) is the turbulent energy dissipation rate, f (s⁻¹) the Coriolis parameter with $f = 2 \times 7.29 \times 10^{-5} \times \sin\wp$ ($\wp$ = latitude), and z (m) the water depth. At 54°11′N, the approximate latitude of the sampling station, $f = 1.18 \times 10^{-4}$ s⁻¹. From Eq. 5 and 6 the energy dissipation rate ϵ generated by a windspeed of 10 m s⁻¹—a value which seems to have been a threshold for the breakup of the large marine snow— is calculated as $\epsilon = 7.2 \times 10^{-7}$ m² s⁻³ at 1-m depth and $\epsilon = 4.1 \times 0^{-8}$ m² s⁻³ at 10-m depth. Integrating over the upper 10 m of the water column gives a mean energy dissipation rate $\epsilon = 6.9 \times 10^{-7}$ m² s⁻³ in this layer.

These estimates of ϵ are in the lower range of the values required to break up fragile diatom flocs in the laboratory ($\epsilon = 10^{-7}$ to $>10^{-4}$ m⁻² s⁻³) as measured by Alldredge et al. (1990), which indicates that the physical strength of the large marine snow aggregates encountered in situ during this study is comparable to the strength of the most fragile diatom flocs tested in the laboratory. As the size of the diatom flocs studied by Alldredge et al. (1990) ranged between 1.8 and 25 mm in diameter, they were considerably smaller than the macroflocs and stringers (ranging to 100 mm long) encountered in this study. The physical strength of marine snow decreases with increasing size (Alldredge et al. 1990). Hence, the apparently low physical strength estimated for the marine snow aggregates in this study may have resulted from their comparatively large sizes. On the other hand, the physical strength of marine snow measured in the laboratory may be somewhat overestimated due to unavoidable compaction during handling of the aggregates.

Based on their experimental results, Alldredge et al. (1990) concluded that abiotic fragmentation of marine snow due to fluid motion is probably of minor importance in the ocean. Their estimates of the energy dissipation rates required for marine snow disaggregation were far greater than values normally measured in the sea surface layer. Results from this study indicate that under certain conditions, marine snow disaggre-

gation due to turbulent water motion may be significant, which can be the case in a situation such as that encountered in this study. Here a period of calm weather, during which extremely large marine snow flocs formed and accumulated in the surface layer, was followed by a sudden, drastic increase in wind-induced mixing. The presence of comparatively small marine snow aggregates (up to a few millimeters in size) at most times, on the other hand, could indicate that the physical strength of these flocs was sufficient to withstand even strong turbulent mixing during periods of high windspeeds.

The effect of aggregation on light penetration—Significantly higher readings of Secchi depth were recorded during periods of large marine snow occurrence than at times when large flocs were absent (Fig. 3). The occurrence of macroflocs and stringers coincided with periods of high phytoplankton biomass concentrations, so this latter variable in turn coincided with high values of Secchi depth. This positive relationship between Secchi depth and biomass concentration appears paradoxical because high biomass would intuitively be expected to result in low, rather than the observed high, Secchi depths. The apparent contradiction can be resolved by taking into account that light attenuation by suspended particles is a function of the total particulate cross-sectional area perpendicular to the direction of light (Williams 1970). Aggregation of particles results in a decrease in cross-sectional area and thus in an increase in light penetration through the water column. Because living phytoplankton plays a key role in aggregate formation, high phytoplankton biomass concentrations can promote particle aggregation, a process which also results in binding large amounts of lithogenic and biogenic detrital material (Alldredge and Silver 1988). Under these conditions, a coincidence of high concentrations of phytoplankton biomass and high Secchi depth readings becomes plausible.

A change in the light climate of the water due to aggregate formation could be of significance to phytoplankton growth. Increased light penetration following aggregation could enhance depth-integrated

primary production. Aggregate formation would obviously improve the light climate for algae that remain dispersed or are attached to the periphery of the floating marine snow flocs. The negative effect of self-shading on those algae incorporated within aggregates remains to be examined. If aggregate formation is associated with rapid sedimentation of the aggregated material, an increase in light penetration would be of benefit only to that portion of the phytoplankton community that remains dispersed. On the other hand, if aggregate formation results in retention of the aggregated phytoplankton in the surface layer, as reported here, this process may be of potential advantage to the entire planktonic community. For the duration of their sustained residence in the euphotic zone, marine snow flocs can act as "metabolic hotspots" in which, due to the close cycling of energy and nutrients, autotrophic and heterotrophic activities can be significantly enhanced (Knauer et al. 1982; Gotschalk and Alldredge 1989). Under these conditions, marine snow aggregates represent highly effective, self-sufficient microcosms that can constitute an important and integral part of the planktonic system.

Conclusions

From the results of this study it appears that the formation of large, floating marine snow flocs and their accumulation in the surface layer occur only under specific environmental conditions. Prerequisites for the formation of large macroflocs and stringers are high phytoplankton cell concentrations and low wind-induced mixing of the water column. Similarly, sustained residence and accumulation of the flocs in the surface layer as a result of gas bubble formation requires high primary production and shallow mixed-layer depths. Thus, formation of large marine snow flocs and their subsequent retention in the surface layer is likely to be confined to highly productive areas with temporary strong and shallow stratification of the water.

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