The physical strength of marine snow and its implications for particle disaggregation in the ocean

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Abstract

Abiotic fragmentation of large, rapidly sinking aggregates into smaller, suspended particles by fluid shear has been suggested as an important process governing the particle size spectrum in the ocean and as one explanation for the exponential decrease of particulate flux with depth below the euphotic zone. We investigated this process by quantifying the small-scale energy dissipation rates required to disaggregate marine snow settling through a gradient of turbulent kinetic energy in a laboratory tank.

Aggregates of detrital debris, gelatinous houses of larvacean tunicates, and aggregates of living bacteria did not break apart even at energy dissipation rates >1 cm$^2$ s$^{-3}$. The rate of energy dissipation required to disaggregate fragile diatom floes up to 25 mm long ranged from $10^{-3}$ to >1 cm$^2$ s$^{-3}$ and increased exponentially with decreasing maximum aggregate diameter. Aged diatom aggregates were significantly stronger than otherwise identical but unaged particles. These results indicate that only the highest shears associated with storm events or flows in tidal channels would be able to fragment even the most fragile organic aggregates in the upper ocean. Biological processes of disaggregation, such as animal grazing, appear far more likely to mediate the size spectrum of aggregated particulate matter in the ocean than abiotic fragmentation due to fluid motion.

The magnitude of particulate flux to the ocean interior and the sea floor is largely determined by the abundance and sinking characteristics of particles in the larger size categories of the particle size spectrum (see Fowler and Knauer 1986). Particles in these larger size classes are primarily aggregates of smaller particles of algae, microorgan-

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isms, and detritus that have been repackaged into fecal pellets, mucous feeding webs, and animal biomass via animal grazing, or coagulated into aggregates by physical processes of particle collision and attachment. Once formed, aggregates are lost or become reduced in size by gravitational settlement, animal consumption, dissolution, microbial decomposition to dissolved species, or physical disaggregation by fluid motion. These competing processes of aggregate formation, breakup, and loss thus govern the characteristics and abundances of aggregated particulate matter in the ocean. They alter the oceanic size spectrum of particulate matter in ways that may significantly affect not only particulate flux but also the trophic structure, microbial activity, chemistry, and optical properties of the water column.

Although processes of particle aggregation occur predominantly in the surface ocean and nepheloid layer, processes of particle loss occur throughout the water column. Numerous recent studies with sediment traps have revealed a consistent exponential decrease in the vertical flux of particulate organic matter (POM) with depth below the euphotic zone in all types of oceanic regimes (Berger et al. 1988). This decrease indicates that rapidly sinking, large particles must be converted to smaller, suspended particles or to dissolved constituents as they descend. Consumption by animals, conversion of solubilized POM to suspended bacterial biomass (Cho and Azam 1988), or bacterial decomposition may contribute to this decrease, although Karl et al. (1988) concluded that microbial decomposition was unlikely to significantly decrease the flux of POM below the photic zone. They suggested a fourth alternative—abiotic fragmentation of fragile sinking aggregates by fluid shear—as a potentially significant physical process responsible for the apparent shift in the particle size spectrum with depth.

Aggregates of particulate organic matter >500 μm in diameter, known as marine snow, form a major component of particulate flux (Fowler and Knauer 1986). Moreover, they have been observed to break apart in water bottles and are generally considered to be quite fragile, lending support to the physical disaggregation hypothesis. Although indirect sampling and shipboard handling methods are vigorous and quite disruptive to marine snow (Alldredge and Silver 1988), we have noticed that aggregates subjected by divers to more natural levels of turbulence do not readily break apart. Certain types of aggregates appear to be considerably stronger than others. Moreover, since the minimal fluid shear required to fragment aggregates increases exponentially with decreasing aggregate size (Parker et al. 1972; Smith and Kitchener 1978), marine aggregates in size classes smaller than those of marine snow would be even stronger. These observations suggested that the hypothesis that abiotic fragmentation is a significant process affecting particle size in the water column needed testing. The variables affecting aggregate strength and the size and number of daughter particles produced at disaggregation may be essential to understand particle dynamics in the ocean.

In the following study we measured the physical strength of marine snow as a function of aggregate size and composition by determining the magnitude of the forces required to fragment, erode, or disrupt individual natural aggregates brought into the laboratory. We use these measurements to evaluate the possible significance of physical disaggregation by fluid motion as a process altering particle size distributions in the water column.

**Theoretical considerations**

The mechanisms by which aggregated particles are broken apart by physical processes depend upon the hydrodynamic regime, which in the ocean is generally turbulent. Eddies can be characterized by their velocity and scale of turbulence ($\lambda_e$), the distance across which the velocity of an eddy changes. Large-scale motions contain most of the energy and are responsible for distribution of the energy through the system. However, they do not dissipate energy or disrupt aggregates. The range of scales of turbulence that dissipate energy and have the potential to impact aggregates of the size range observed in the ocean (e.g. microns to centimeters) is called the universal equilibrium range. It has been separated into the
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Significant symbols

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>$C$</td>
<td>Floc strength coefficient</td>
</tr>
<tr>
<td>$d$</td>
<td>Floc diam, mm</td>
</tr>
<tr>
<td>$d_{\text{max}}$</td>
<td>Maximal stable floc diam, mm</td>
</tr>
<tr>
<td>$G$</td>
<td>Local velocity gradient or shear rate, s$^{-1}$</td>
</tr>
<tr>
<td>$p_d$</td>
<td>Pressure fluctuation across a floc of diam $d$, g cm$^{-1}$ s$^{-2}$</td>
</tr>
<tr>
<td>$\omega$</td>
<td>Oscillating frequency of grid, Hz</td>
</tr>
<tr>
<td>$z$</td>
<td>Vertical distance from the top stroke of the grid, cm</td>
</tr>
<tr>
<td>$\epsilon$</td>
<td>Energy dissipation rate, cm$^{3}$ s$^{-3}$</td>
</tr>
<tr>
<td>$\gamma$</td>
<td>Stable floc size exponent based on energy dissipation rate</td>
</tr>
<tr>
<td>$\gamma G$</td>
<td>Stable floc size exponent based on shear rate</td>
</tr>
<tr>
<td>$\lambda_v$</td>
<td>Scale of turbulence (the distance across which the velocity of an eddy changes), length</td>
</tr>
<tr>
<td>$\eta$</td>
<td>Kolmogorov microscale of turbulence, mm</td>
</tr>
<tr>
<td>$\tau_{\text{crit}}$</td>
<td>Limiting material strength due to the net attraction forces between primary component particles of an aggregate, g cm$^{-1}$ s$^{-2}$</td>
</tr>
<tr>
<td>$\nu$</td>
<td>Kinematic viscosity, cm$^{2}$ s$^{-1}$</td>
</tr>
</tbody>
</table>

Disaggregation is largely a result of fluid shear resulting from variations in fluid velocity across the length of the aggregate. The relationship between the local velocity gradient ($G$) and the more commonly measured energy dissipation rate is

$$G = (\epsilon/\nu)^{\gamma/3}.$$  

Several mechanisms of aggregate breakup have been developed theoretically in the literature. The three mechanisms of interest for marine snow are: surface erosion, where small subunits of the particle detach; instantaneous pressure fluctuations across the particle resulting in fragmentation; and filament fracture, where organic filaments joining subunits of the particle break.

**Erosion**—Argaman and Kaufman (1970) and Parker et al. (1972) suggested that surface erosion of primary particles from the surface layers of the aggregate by turbulent drag is a principal mode of disaggregation. Surface shear stresses exceeding the shear strength of the polymer bridges bonding primary particles to the aggregate surface are produced by eddies that partially entrain the floc and exist on a scale approximating the aggregate diameter. Eddies that are large enough to fully entrain the aggregate produce zero relative velocity and no surface shear. Likewise eddies much smaller than the aggregate result in little surface shear. Surface shearing increases with eddy scale and with aggregate diameter. Parker et al. (1972) derived expressions for the maximal stable floc diameter ($d_{\text{max}}$), above which floes were subject to disruption, for aggregates both smaller and larger than the Kolmogorov microscale. He assumed that aggregates smaller than the microscale were disrupted primarily by stresses in the viscous dissipation subrange, while those larger than the microscale were disrupted primarily by eddies in the inertial convection subrange. These expressions take the form

$$d_{\text{max}} = C \epsilon^{-\gamma}$$

where $C$ is the floc strength coefficient and $\gamma$ the stable floc size exponent. For erosion of aggregates larger than the Kolmogorov microscale, Parker et al. (1972) calculated that $\gamma = 1$; for erosion of floes smaller than $\eta$, $\gamma = 0.5$.

**Instantaneous pressure fluctuations across the aggregate**—Tomi and Bagster (1978) suggested that aggregate rupture resulted from instantaneous pressure differences produced by fluid motion on opposite sides of the floc. They defined the criterion for aggregate rupture as

$$p_d \propto \tau_{\text{crit}}$$

where $p_d$ is the instantaneous pressure fluctuation across a floc of size $d$ and $\tau_{\text{crit}}$ the limiting material strength due to attraction forces between primary particles of the aggregate. Although Tomi and Bagster assumed that $\tau_{\text{crit}}$ was a constant independent of aggregate size, they acknowledged that, in practice, it would decrease with increasing aggregate size due to structural nonuniformities.

For large aggregates where $\eta \ll d$ the force balance between aggregate strength and induced stress yields $d_{\text{max}} \propto \epsilon^{-1}$. Where $d \ll \eta$, $d_{\text{max}} \propto \epsilon^{-2}$. Tomi and Bagster also derived an expression for an intermediate zone
The value of the stable floc size exponent as predicted by theory for various mechanisms of aggregate breakup. Most of these studies determined aggregate size as a function of shear ($G$) rather than $\epsilon$. We have converted their stable floc size exponents with the relationship $y = 0.5 \sqrt{G}$ based on Eq. 2 in the text.

<table>
<thead>
<tr>
<th>Breakup mechanisms</th>
<th>Inertial range</th>
<th>Intermediate range</th>
<th>Viscous range</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Erosion</td>
<td>1</td>
<td></td>
<td>0.5</td>
<td>Parker et al. 1972</td>
</tr>
<tr>
<td>Filament fracture</td>
<td>0.25</td>
<td></td>
<td>0.25</td>
<td>Parker et al. 1972</td>
</tr>
<tr>
<td>Pressure fluctuations</td>
<td>$&gt;0.5$</td>
<td>0.25-0.5</td>
<td>$&lt;0.5$</td>
<td>Tomi and Bagster 1978</td>
</tr>
<tr>
<td></td>
<td>0.4-0.5</td>
<td></td>
<td>0.33-0.38</td>
<td>Tambo and Hozumi 1979</td>
</tr>
</tbody>
</table>

where $d \approx \eta$ and where both viscous and inertial effects might be significant. The value of $\gamma$ derived for this region at the critical condition where $p_d = \tau_{\text{crit}}$ was $\gamma = 0.5$ yielding $d_{\text{max}} \propto \epsilon^{-0.5}$.

**Fragmentation due to filament fracture**—Although most investigations of floc breakup have considered inorganic chemical flocs with relatively homogeneous interparticle bonding, Parker et al. (1972) considered the disaggregation of large biological flocs of activated sludge. They predicted that maximal aggregate size would be limited by the tensile strength of the bacterial filament network binding the components of the aggregate together. For this filament network to fail, two eddies must act on the floc, simultaneously entraining and propelling the clusters in different directions. Parker et al. predicted that the stable floc size exponent ($\gamma$) would be 0.25 in both the inertial convection and viscous dissipation subranges.

Additional theoretical and empirical studies (Table 1) support the relationship between energy dissipation and floc size described by Eq. 3. The value of $\gamma$ indicates the breakup mechanism which dominates. In many cases floc erosion and floc fragmentation occur simultaneously which dominates. Glasgow and Luecke (1980). Other complex expressions have been developed for calculating $C$ as well (Parker et al. 1972; Tambo and Hozumi 1979).

**Materials and methods**

**Aggregate collection**—Intact natural aggregates of marine snow were collected individually in 6-ml polypropylene cylinders by SCUBA divers at depths of 10–15 m in the Santa Barbara Channel, California (34°20'N, 119°49'W), between February and June 1989. Samples were stored undisturbed in their collecting cylinders at ambient seawater temperature (15°C–18°C) and, except for the sample set collected 9 June, their strength was determined within 18–40 h of collection. The effects of aging on aggregate strength were determined for marine snow collected on 9 June. The strength of half of these samples was measured within 30 h of collection, while the strength of the other half was determined after they had been rotated within their collecting cylinders end over end at 2 rpm for 5 d in an environmental chamber at 15°C. Aggregates remained suspended in their slowly rotating cylinders, simulating natural settlement in the water column (Gotschalk and Alldredge 1989).

Almost all of the aggregates collected at any one station were of the same type and composition. Fifteen aggregates from each collecting date were examined microscopically and identified as to origin based on their morphology, the presence of filtering nets, and on the identity of the dominant component particles forming them (e.g. diatoms, fecal pellets, and unidentifiable debris).

We also compared the strength of marine snow with that of aggregates of *Zoogloea ramigera*, representative of the slime-forming bacteria associated with activated sludge flocculating processes. Pure cultures of *Z. ramigera* were grown in nutrient broth at 23°C until they aggregated.

**Aggregate strength**—Aggregate strength was determined by videorecording the fate of individual aggregates as they settled through a gradient of gradually increasing turbulent kinetic energy in the laboratory. Turbulence was generated by a stainless steel grid oscillating vertically about a mean depth.
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of 22.5 cm within a square Plexiglas tank (Fig. 1). The tank (62 x 62 x 76 cm) was filled with artificial seawater (Fig. 1). The grid was made of 24 stainless steel tubes (1-cm o.d. x 61 cm long) spot-welded together at right angles with 5-cm separation midpoint to midpoint (Fig. 1). This system approximates a homogeneous, isotropic turbulent field horizontally with turbulence intensity decreasing exponentially with increasing distance from the grid vertically (Fig. 2). Various turbulent flow conditions could be created by adjusting the oscillation frequency and amplitude of the grid. Generally we used frequencies from 2.4 to 4.9 Hz. Stroke length (grid amplitude) was held constant at 6 cm.

The laboratory turbulence system used for the present study was originally designed to study the effects of water turbulence on gas transfer across an air–water interface by Hartman (1983), Dickey et al. (1984), and Isenogle (1985). They used a motion analysis technique (Dickey and Mellon 1980) which established that turbulent characteristics of flow in a tank can be determined using small passive particles to follow the smallest scales of turbulent motion. They used this technique to calculate turbulent kinetic energy and integral length scales produced in the tank and to compute energy dissipation rates at 5, 7, 9, 11, and 13 cm above the stroke of the grid for frequencies of 0.50, 2.0, 3.5, and 4.5 Hz. Energy dissipation rates for our experiments were determined with the empirical function

$$\epsilon(z, \omega) = 10 \times \exp(0.57 - 0.23z + 0.20z \log \omega)$$

where $z$ is the distance from the grid in centimeters (cm) and $\omega$ the grid frequency in hertz (Hz) (Hartman 1983; Isenogle 1985). Equation 5 regressed against the data of Hartman (1983) and Isenogle (1985) accounted for >95% of the variance of energy dissipation at any given frequency at distances between 5 and 13 cm above the grid.

Salinity in the grid-turbulence tank was monitored with a YSI model 33 salinity-conductivity-temperature meter and adjusted to match ambient seawater salinity around the aggregates by addition of NaCl or dilution with freshwater. The tank and

Fig. 1. Diagram of the oscillating grid system used to produce a vertical gradient of turbulent kinetic energy in the laboratory. $x = 62$ cm; $y = 62$ cm; $z = 76$ cm. Aggregates were magnified by a 55-mm macro lens so as to fill ~5–10% of each frame and tracked as they moved throughout the viewing area. A second camera remained focused on a ruler, yielding vertical distance above the top stroke of the grid.

Fig. 2. Example of the decay of turbulence with distance from the grid at a grid oscillation frequency of 4.50 Hz as predicted by Eq. 5. Curve fitted by least-squares.
aggregate samples were equilibrated to room temperature (21°C–24°C). Each individual aggregate was then released 4–5 cm below the surface at a point in the center of the tank by gently immersing and inverting the seawater-filled cylinder in which it had been collected and allowing the aggregate to exit slowly via gravitational settling (Fig. 1). This method limited manipulation and disturbance of the aggregates. The strength of *Zoogloea* aggregates was also determined in seawater.

The behavior of each aggregate was videorecorded from the point of its initial release in the tank until it disaggregated or passed through the oscillating grid. Each aggregate was followed and kept in focus manually with a 55-mm, F3.5 Nikon macro lens attached to a Panasonic video camera (model WV-1550) on a tripod. The vertical distance of the particle above the maximal upward stroke position of the oscillating grid was measured with a second video camera positioned below the first. This camera was also affixed to the vertically adjustable tripod and remained focused on a ruler showing the position to the nearest millimeter of the particle above the grid (Fig. 1). The images from both cameras were merged with a screen splitter and recorded simultaneously on 0.5-inch (1.27 cm) VHS videotape.

**Data analysis** — Video tapes were analyzed on a MegaVision 1024 XM image processing system. Aggregate areas and maximal diameters were determined by averaging measurements from three different orientations of each aggregate immediately after it had settled out of the collecting cylinder. Measurements were scaled with the diameter of the collecting cylinder as a reference. Equivalent spherical volume was calculated from average area assuming the area to be a circle. The distance above the grid and the numbers and relative sizes of the daughter particles produced when the aggregate fragmented, eroded, or disintegrated were also recorded. Absolute fragment sizes were not measured directly because the distance of the floc from the camera (along the *y*-axis) was unknown at the point of aggregate rupture (see Fig. 1). Fragment areas were calculated by measuring the area of the parent floc immediately before rupture and then determining the proportion of the parent floc area represented by each fragment immediately after rupture. This proportion was then multiplied by the calibrated parent floc volume determined when the floc was first introduced into the tank in order to obtain absolute fragment sizes. Length measurements were recalculated immediately before disaggregation in the small number of trials (~5%) where the aggregates deformed appreciably (>20% change in apparent volume) as they sank. A component particle within the floc whose shape and size did not change was used as a size reference in these cases. Trials where the aggregate disintegrated upon release, encountered wall effects, or otherwise exhibited aberrant behavior were discarded before image processing and are not included in our analysis.

**Results**

We determined the strength of 337 individual aggregates representing four types of natural marine snow and one bacterial floc type not found in marine systems. One type of aggregate, collected on both 16 March and 9 June, was dominated primarily by chains, spines, and frustules of the setose centric diatom genus *Chaetoceros*, especially *Chaetoceros debilis*, *Chaetoceros peruvianus*, *Chaetoceros socialis*, and *Chaetoceros radicans*. Diatoms of the genera *Nitzschia*, *Eucampia*, and *Rhizosolenia* also occurred in low abundance. A second type of marine snow, composed predominantly of the pennate, chain-forming diatom genus *Nitzschia*, especially *Nitzschia delicatissima* and *Nitzschia pacifica*, was collected on 19 May. Other species of diatoms were rare in these floes. Both types of diatom aggregates also contained abundant unidentifiable debris, mucus, and occasional fecal pellets. The third type of aggregate investigated was composed predominantly of the pennate, chain-forming diatom genus *Nitzschia*, especially *Nitzschia delicatissima* and *Nitzschia pacifica*, was collected on 19 May. Other species of diatoms were rare in these floes. Both types of diatom aggregates also contained abundant unidentifiable debris, mucus, and occasional fecal pellets. The third type of aggregate investigated was composed primarily of miscellaneous, unidentifiable debris and bacteria embedded in a mucous medium. These aggregates were small, contained a few fecal pellets or identifiable algal cells, and were typical of aggregates we have commonly observed in oligotrophic, open-ocean regimes. The fourth type of marine snow was not formed by coagulation. These aggregates were the
Table 2. Summary of the sizes and disaggregation outcomes of the aggregates investigated in this study. The table shows the proportion of the total number of aggregates of each type (n) that went through the grid without disaggregating or disaggregated at rates of energy dissipation (e) < 1 cm² s⁻³. The sizes of aggregates disaggregating at energy dissipation rates both higher and lower than 1 cm² s⁻³ are also compared. Some of those disaggregating at rates >1 cm² s⁻³ broke apart within 5 cm of the grid where the turbulence was not homogeneous and could not be quantified accurately.

<table>
<thead>
<tr>
<th>Snow type</th>
<th>% disagg. at e &lt; 1</th>
<th>Through grid (%)</th>
<th>Max diam (mm)</th>
<th>Volume (mm³)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>n</td>
<td></td>
<td>e &lt; 1</td>
<td>e &gt; 1</td>
</tr>
<tr>
<td><strong>Diatoms</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Chaetoceros</td>
<td>16 Mar 91</td>
<td>50</td>
<td>25</td>
<td>5.7±2.2</td>
</tr>
<tr>
<td></td>
<td>9 Jun 75</td>
<td>84</td>
<td>7</td>
<td>7.4±3.5</td>
</tr>
<tr>
<td></td>
<td>13 Jun 62</td>
<td>53</td>
<td>44</td>
<td>7.3±3.5</td>
</tr>
<tr>
<td>Nitzschia</td>
<td>19 May 65</td>
<td>86</td>
<td>3</td>
<td>7.6±5.6</td>
</tr>
<tr>
<td>Misc. debris</td>
<td>3 Nov 30</td>
<td>0</td>
<td>100</td>
<td>—</td>
</tr>
<tr>
<td>Larvacean houses</td>
<td>7 Feb 14</td>
<td>0</td>
<td>100</td>
<td>—</td>
</tr>
<tr>
<td>Zoogloea floes</td>
<td>7 Feb 10</td>
<td>0</td>
<td>100</td>
<td>—</td>
</tr>
</tbody>
</table>

spherical, discarded, gelatinous feeding structures, or houses, of the planktonic larvacean tunicates Oikopleura dioica and Oikopleura longicauda. They contained numerous fecal pellets, algae, and debris in their filters. We also studied a fifth type of biological aggregate formed by the sewage bacterium Z. ramigera. These floes were small and bound together by numerous internal fibrils.

The sizes of the five types of aggregates ranged from 1.8 to 25.0 mm in maximum diameter and 0.8 to 198 mm³ in volume (Table 2). We have expressed aggregate size as maximal diameter since this is the largest dimension over which eddy motion can encounter each particle. This choice is consistent with most previous studies of aggregate strength (Table 3). Aggregates of miscellaneous debris, larvacean houses, and Zoogloea floes were so strong that they could not be disaggregated at the highest calibrated energy dissipation rates within the tank (Table 2). All passed through the grid openings and ruptured only if struck directly by a grid bar. Many of these aggregates were captured by circular flows and accelerated around the grid bars before sinking intact to the bottom of the tank. Larvacean houses fragmented only when struck repeatedly by the grid bars.

The highest measurable energy dissipa-
Fig. 3. The rate of energy dissipation required to disaggregate marine snow composed predominantly of aggregated *Chaetoceros* spp. as a function of maximal aggregate diameter. Dashed lines—Kolmogorov microscale. A. Size at disaggregation of individual aggregates collected on three sampling dates. B. Mean size at disaggregation of the aggregates in panel A grouped by ascending energy dissipation into 13 bins of 0.25 log ε units each. Linear regression coefficient ($r = 0.86$; $P < 0.001$). The regression in panel A was similar and also significant ($P < 0.001$).

Fig. 4. As Fig. 3, but of *Nitzschia* spp. A. Size at disaggregation of individual aggregates collected on 19 May. B. Mean size at disaggregation of the aggregates in panel A grouped into 8 bins of 0.20 log ε units each by ascending energy dissipation rate ($r = 0.96$; $P < 0.001$). The regression in panel A was similar and also significant ($P < 0.05$).

cm$^2$ s$^{-3}$. Nonetheless, 7–44% passed through the grid, indicating that many were strong enough to withstand energy dissipation rates potentially of much greater magnitude (Table 2). Only 2% of all *Nitzschia* flocs and 10% of all *Chaetoceros* flocs investigated disaggregated at energy dissipation rates $<10^{-2}$ cm$^2$ s$^{-3}$. The rate of energy dissipation required to fracture *Chaetoceros* aggregates increased with decreasing maximal aggregate diameter (Fig. 3A). Disaggregation occurred well within the inertial convection subrange. Marine snow is fractal in its geometry (Logan and Wilkinson 1990), resulting in length dimensions that vary by ±20% depending on the plane in which the fractal aggregate is viewed (Meakin 1988). This uncertainty in size along with nonuniformity of floc composition introduced con-

The majority of both types of diatom flocs disaggregated at energy dissipation rates $<1$
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Fig. 5. Comparison of the mean energy dissipation required to disaggregate 1- and 5-d-old Chaetoceros aggregates as a function of size. Points represent mean size at disaggregation of data from Fig. 3A grouped into bins of 0.20 log energy dissipation units each ($r = 0.87; P < 0.001$).

siderable scatter in our plots. In order to ascertain more clearly the relationship between energy dissipation rate and aggregate size we grouped the data by the independent variable—energy dissipation rate—into 13 bins of 0.25 log $\varepsilon$ units each. There was a significant exponential relationship (Fig. 3B) between energy dissipation rate and maximal particle length ($P < 0.001$), and a stable floc size exponent ($\gamma$) of 0.11, which approximates the 0.25 predicted by Parker et al. (1972) for biological flocs breaking via filament fracture. Visible filaments occasionally separated fragments of dissociating diatom snow and were observed to stretch and snap.

The energy dissipation rate required to fragment diatom aggregates, composed predominantly of Nitzschia, was also a significant exponential function of maximal aggregate diameter ($P < 0.001$, Fig. 4B). The $\gamma$ of these flocs was 0.29, indicating that Nitzschia aggregates had lower internal strength than similarly sized aggregates of Chaetoceros (Fig. 4A,B).

No significant difference in the relationship between maximal diameter and energy dissipation rate at disaggregation was observed between 1- and 5-d-old Chaetoceros flocs for either unbinned (Fig. 3A) or binned data (Fig. 5). The two populations were not significantly different in length or volume (Student's $t$-test; Table 2). A significantly higher proportion of aged aggregates (44 vs. 7%) was able to pass through the grid without disaggregating ($P < 0.001$, test for the equality of two percentages for unequal sample sizes, Sokal and Rohlf 1969), however, and a significantly smaller fraction of aged aggregates (53 vs. 84%) fragmented at energy dissipation rates < 1 cm$^2$ s$^{-3}$ ($P < 0.001$), indicating that short-term aging increases the strength of some aggregates appreciably (Table 2).

Seventy-one percent of disaggregating

Fig. 6. Frequency distribution of the number of fragments produced in all trials resulting in disaggregation.

Fig. 7. Number of fragments vs. parent aggregate size produced by all trials resulting in disaggregation. Dots represent mean mean maximal diameter; horizontal bars are $\pm$ 1 SD.
particles broke into two fragments, while about 11% broke into more than 10 (Fig. 6). The number of fragments produced increased with increasing parent floc size (Fig. 7), although the number of fragments produced was highly variable among aggregates of similar size. In order to test the significance of this trend we compared the mean size at breakup of the population of aggregates breaking into two fragments with that breaking into more than 10 with a Student's t-test. The trend was significant at $P < 0.001$, partially due to our large sample size ($n = 198$).

The relative fragment volume (RFV) for those trials which resulted in two fragments was calculated at

$$RFV = \frac{\text{volume of the smaller fragment}}{\text{volume of the larger fragment}}.$$  

(6)

Aggregates with relative fragment volumes near 1 broke into two equally sized fragments while those with RFV nearer to 0 broke into fragments highly dissimilar in size. Although the RFV was highly variable, larger flocs tended to disaggregate into more equally sized fragments than smaller flocs (Fig. 8). While this trend was significant at $P < 0.01$, no significant relationship was found between relative fragment size and the rate of energy dissipation at disaggregation.

Discussion

Strength of marine snow—The approach used in this study departs considerably from that used in previous investigations of aggregate strength. Although we directly observed individual natural aggregates disaggregating, previous studies have examined the average maximal size attainable by large populations of uniform aggregates subjected to varying levels of quantified shear generated in laboratory reaction vessels (see Table 3). This approach gives statistically valid average floc strengths but obscures variability among particles. It is more appropriate for aggregates that are uniform and homogeneous in structure, while an approach such as the one used here is probably more appropriate for heterogeneous, non-uniform, natural aggregates.

Empirically determined values of the stable floc size exponent, $\gamma$, of a variety of organic and inorganic aggregates investigated in laboratory reactors fall within the range of 0–1 predicted by theory (Table 3). The stable floc size exponents of *Chaetoceros* and *Nitzschia* aggregates of 0.11 and 0.29 are near the 0.25 predicted by Parker et al. (1972) for aggregates breaking via filament fracture—a special case of fragmentation. Pressure fluctuation in the intermediate range ($\eta \approx d$), where Tomi and Bagster (1978) predicted $\gamma = 0.25$–0.5, may also be an important mechanism of disaggregation. The $\gamma \ll 1$ for both types of diatom flocs indicates that erosion was an uncommon mode of disaggregation. Smaller aggregates were more likely to fragment into disparately sized fragments, however, suggesting that they were affected by smaller eddies acting more as agents of particle erosion.

Rupture into a few large fragments is consistent with the fractal geometry of marine snow (Logan and Wilkinson 1990). This geometry indicates that aggregates have been formed primarily via collisions of clusters of particles rather than by attachment of primary particles to the aggregate surface one at a time (Meakin 1988). Cluster–cluster collisions result in an inhomogeneous floc structure and increase the potential for fragmentation between adjoining clusters.
We observed high variability in the turbulence required to disrupt individual aggregates of the same type and size. Each particle may not have experienced the exact same fluid motion within the tank. Aggregates also vary in composition. Although marine snow from any one sampling station is composed of similar types of primary particles (Alldredge and Gotschalk 1990), the proportions of these components vary according to the previous history of the aggregate and the nature of its attached microbial community. Algal and microbial exopolymers and capsular material, which are significant binding agents (Alldredge and Silver 1988), vary among aggregates. Entwining setae may make *Chaetoceros* floes stronger than *Nitzschia* floes since *Nitzschia* is a nonsetose genus.

A larger proportion of aged diatom aggregates than unaged flocs could withstand higher rates of shear without disaggregating. Because the physical properties of the aggregates remained unchanged over the aging period, biological and related chemical changes associated with aging are likely to be responsible. The growth of microbial populations inhabiting marine snow occurs rapidly in the first 72–96 h after aggregate formation (Alldredge and Silver 1988). These growing microbial populations produce microbial exudates and capsular material that may increase aggregate strength with age. Attached bacteria also produce fimbriae and fibrils that form a network of intertwining strands that potentially strengthen aggregates (Alldredge and Silver 1988). Bacterial filament networks of this sort are responsible for the high strength of activated sludge flocs (Parker et al. 1972). Activated sludge flocs and diatom aggregates have very similar stable floc size exponents (Table 3).

The nearly identical relationship between maximal length and energy dissipation rate of aged and unaged *Chaetoceros* flocs suggests that collection and handling did not alter aggregate strength appreciably. Aged flocs were rotated and handled considerably more than unaged flocs, with little change. Thus, our data on laboratory-manipulated aggregates probably accurately reflect aggregate strengths in nature.

Particle composition was a major factor determining aggregate strength. Larvacean houses, aggregates formed of amorphous debris, and aggregates of *Z. ramigera* did not disaggregate at the highest grid oscillation frequencies. Larvacean houses are composed of mucopolysaccharides secreted by the epithelial cells of the animal's trunk. This gelatinous framework maintains the integrity of the house for many days (Alldredge and Silver 1988), suggesting that these aggregates are unlikely to fragment from fluid shear unless considerably decomposed. The strength of aggregates formed of amorphous, unidentifiable debris may result from their abundant bacterial communities (Alldredge and Gotschalk 1990) as well as their small size.

Although we have not investigated all types of marine snow—most notably aggregates composed primarily of fecal material or of other types of algae (Alldredge and Silver 1988)—our previous observations of marine snow in situ indicate that diatom flocs are among the most fragile. Overall, our results indicate that most types of natural aggregates of marine snow, including a significant fraction of diatom snow (14–50% depending on sampling date), fragment at energy dissipation rates $> 1 \text{ cm}^2 \text{s}^{-3}$.

**Implications for particle disaggregation in situ**—Available estimates of energy dissipation rates in the ocean indicate that $\epsilon$ varies considerably on both vertical and horizontal spatial scales as well as on temporal scales of hours or longer (Gregg 1987). Available measurements suggest that $\epsilon$ is too low in much of the ocean most of the time, however, to disaggregate even the most fragile marine snow. Energy dissipation rates in the upper mixed layer and thermocline under low winds range from $10^{-2}$ to $10^{-6} \text{ cm}^2 \text{s}^{-3}$ (Dillon and Caldwell 1980; Lueck and Reid 1984). Even under high wind conditions of 15 m s$^{-1}$, $\epsilon$ ranges only from $10^{-2}$ to $10^{-4} \text{ cm}^2 \text{s}^{-3}$ in the upper 10–20 m of the water column (Dillon and Caldwell 1980; Oakey and Elliott 1982). Energy dissipation rates in the wave zone in the upper 10 m of the water column, especially under storm conditions, are not known. However, these rates could be high enough to disrupt dia-
tom aggregates in the immediate surface layer.

Particles sinking through current boundaries or intrusions will also generally encounter low shear. For example, $\epsilon$ ranged from $10^{-4}$ to $10^{-3}$ cm$^2$ s$^{-3}$ in the intrusion region between the California Current and the California Undercurrent (Yamazaki and Lueck 1987) and from $10^{-2}$ to $10^{-3}$ cm$^2$ s$^{-3}$ in the highly energetic Equatorial Undercurrent (Crawford and Osborn 1979). Bottom stresses in many parts of the ocean may also be too low to disaggregate marine snow sinking through the benthic boundary layer. Energy dissipation rates of $10^{-4}$ to $10^{-3}$ cm$^2$ s$^{-3}$ are reported at 15 cm above the bottom in some coastal regions (Dewey and Crawford 1988).

The highest rates of energy dissipation reported for the ocean are adequate to disaggregate diatom aggregates. Storm events with winds $>20$ m s$^{-1}$ produce energy dissipation rates ranging from $10^{-1}$ to $10^{-2}$ cm$^2$ s$^{-3}$ in the upper 25 m of the water column—rates sufficient to disaggregate about 78% of Chaetoceros snow and about 94% of Nitzschia floes, assuming that they were similar to those investigated here. Energy dissipation rates in tidal channels of $10^{-4}$ to $10^{-3}$ cm$^2$ s$^{-3}$ (Grant et al. 1962) would disaggregate most diatom snow. Marine snow sinking through the bottom boundary layer of some tidal currents could experience energy dissipation rates as high as $10^{-1}$ cm$^2$ s$^{-3}$ within 1 m of the bottom (Gross and Nowell 1985), resulting in fragmentation. The other types of marine snow we investigated are sufficiently strong, however, to withstand even these high rates of fluid shear.

Implications for oceanic fluxes and particle size spectra—Much of the particulate organic matter (POM) reaching the ocean interior and the sea floor does so in the form of large, rapidly sinking particles, primarily of marine snow and fecal pellets (Fowler and Knauer 1986; Alldredge and Silver 1988). These larger particle classes mediate the exchange of POM between the surface and the deep ocean while the smaller, suspended size classes dominate the standing stock of particulate organic matter in the water column. The downward vertical flux of particulate matter decreases exponentially with depth below the mixed layer (Berger et al. 1988). Greater than 75% of the net loss of POM occurs in the upper 500 m of the water column. This decrease indicates that large, rapidly sinking particles must be converted either to small suspended particles, including organisms, or to dissolved constituents as they descend.

Abiotic fragmentation due to fluid shear is one possible mechanism by which large particles may be converted to small, suspended forms (Karl et al. 1988). Our data indicate, however, that this process is unlikely to be significant in the upper ocean at most times. Physical disaggregation may affect the particle size spectra if the turbulent kinetic energy of the system increases, for example during episodic storms, but then only if the particles present are of algal origin and in the uppermost surface layers. The size-to-strength relationships measured here suggest that aggregates smaller than marine snow would be even less likely to disaggregate. Moreover, large disaggregating floes produce fragments which, because of their relatively small size, are sufficiently strong to withstand further disaggregation. Although smaller than their parent floes, such fragments would still be sufficiently large to sink relatively rapidly and contribute significantly to the vertical flux of POM.

The strength of aggregates reaching the deep sea remains unknown. Although aggregate strength can increase with short-term aging, aggregates sinking on the order of 100 m d$^{-1}$ might require a month or more to traverse the ocean interior. During this time microbial exudates and binding material may decompose sufficiently to weaken the attraction between attached clusters within the aggregates. Further research on effects of long-term aging on the strength of marine snow is required before its disaggregation behavior in the deep sea can be predicted.

Several other alternative processes may explain the reduction in POM flux with depth. Microbial decomposition by abundant and metabolically active microorganisms attached to sinking particles has been suggested as one pathway, although large, rapidly sinking particles in deep water appear to be relatively poor habitats for bac-
terial growth and are unlikely sites for active remineralization of organic matter (Karl et al. 1988). The conversion of sinking particles to dissolved constituents via bacterial solubilization may also control the net loss of particulate organic matter from the upper regions of the ocean. POM solubilized by bacteria attached to rapidly sinking particles is converted into biomass by the growth of free-living bacteria around the particles and by the release of offspring into the surrounding water by the attached forms. This process results in production of fine suspended particles at the expense of large, rapidly sinking ones (Cho and Azam 1988). A third alternative is that large particles are consumed by animal grazers, both vertically migrating and nonmigrating forms, and converted into smaller fecal particles, animal biomass, CO₂, and dissolved excretory by-products. Our laboratory results suggest that these biological processes are far more likely to mediate the size spectrum of aggregated particulate matter in the ocean than are physical processes of particle disaggregation due to fluid motion.

References


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