Comparison of pelagic and nepheloid layer marine snow: implications for carbon cycling

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Abstract

Marine snow from upper and mid-water (i.e., pelagic) depths on the California margin is texturally and compositionally different from that traveling in the nepheloid layer. Transmission electron microscopy shows that pelagic marine snow consists primarily of bioclasts (e.g., diatom frustules, foram tests), organic matter, and microbes. These components are entrained as discrete particles or small aggregates (< 10 μm in diameter) in a loose network of exocellular, muco-polysaccharide material. Clays are infrequent but, when present, are constituents of comparatively compact organic-rich microaggregates. Microbes are abundant and appear to decrease in number with increasing water depth. In contrast, marine snow aggregates collected from just above the sea floor in the nepheloid layer are assemblages of clay particles, clay flocs, and relatively dense clay–organic-rich microaggregates in an exocellular organic matrix. Bioclasts and microorganisms occur only rarely. The prevalence of clay–organic-rich aggregates in the nepheloid layer suggests that, prior to final deposition and burial, marine snow from the pelagic zone is subject to disaggregation and recombination with terrigenous detrital material near or at the sea floor. Results have significant implications for the accumulation and burial rates of organic carbon on continental margins and the aging and bioavailability of sedimentary organic matter. Samples examined were collected offshore of northern and central California. © 1998 Elsevier Science B.V. All rights reserved.

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1. Introduction

Marine snow, the population of marine aggregates with diameters greater than 5 mm, is the primary means by which organic matter is transported down through the water column (Fowler and Knauer, 1986). In large part, marine snow research has focused on surface to mid-water column aggregate production and the rates and variability of organic carbon transport to the sea floor (see review in Alldredge and Silver, 1988). Recent research now suggests that marine snow aggregates may also play an important role in the development of sediment geotechnical properties (Svyitski, 1991) and the ultimate distribution of organic matter in continental margin sediments (Ransom et al., 1997). Below we present the results of a comparative study of the com-
ponents of marine snow from various water depths offshore California. Our objectives were to identify the components and textures of aggregates traveling in the nepheloid layer, improve our understanding of how processes and conditions in the nepheloid layer affect marine aggregates that originate in the upper water column (pelagic zone), and examine the possible impact these interactions may have on the distribution of organic matter in the sediment.

Marine snow is a complex assemblage of organisms, bioclasts (e.g., tests and frustules), organic matter, minerals, and fecal material entrained as discrete particles or small aggregates in a loose network of exocellular muco-polysaccharide slime and fibrils (e.g., Alldredge, 1989; Decho, 1990; Heissenberger et al., 1996). The composition of marine snow is a function of local particle abundance, particle encounter rates, and the ease with which different components can be incorporated into larger aggregates. Through aggregation and disaggregation, as well as grazing by bacterial and planktonic heterotrophs, the architecture, particle composition and organic matter in marine snow evolves through time (see review in Wakehan and Lee, 1993).

The direct observation of marine snow constituents and their textural relations requires use of a transmission electron microscope (TEM). To date, such studies have concentrated on fecal pellets and/or aggregates generated in surface waters and pelagic regions of the water column (e.g., Silver and Bruland, 1981; Gowing and Silver, 1983, 1985; Leppard et al., 1996). Only one study contains images of nepheloid aggregates (Ransom et al., 1997). The potential of this class of aggregates to influence sea floor sediment microfabric and the distribution and bioavailability of organic matter warrants further investigation.

2. Sampling locations

Marine snow samples were collected with Martin-Knauer multi-collector (eight tubes per water depth) sediment traps (Knauer et al., 1979) from transects near Mendocino and San Luis Obispo on the California continental margin (Fig. 1) from June 13 to August 16, 1993. These samples form a companion data set to a high-resolution study of the sediment micro-

3. Methods

Samples were collected and prepared to ensure that aggregates represented the in-situ textures and particles present in the water column. Two of the eight collectors at each water depth were used to obtain samples for TEM study; the six others were used for an
investigation of organic carbon flux and spiked with formalin to kill planktonic scavengers. The TEM-designated collectors were filled with pH-buffered seawater containing 2 wt% glutaraldehyde. Sucrose was added to these to increase solution density to \( \sim 1.07 \) g cm\(^{-3}\) to minimize washout during trap recovery. Upon retrieval, liquid in the upper three quarters of the TEM collectors was slowly siphoned off. All but 50 ml of the remaining liquid was then slowly drained through the bottom of the collector. The resulting suspension, which contained marine snow, was gently decanted into a jar spiked with glutaraldehyde and osmium tetroxide and refrigerated. In the carbon flux collectors, fluid in each column was drained through the bottom and all entrained particulate matter was deposited on a tared filter paper.

Prior to processing the carbon flux material, planktonic scavengers were removed from the filter papers so as not to affect the mass of organic carbon corresponding to that of the water column particles. Filter papers were then dried and weighed to obtain the mass of marine aggregate material collected. The dried material was analyzed for total carbon using a Perkin Elmer CHN analyzer (precision = \( \pm 0.3\% \), based on repeated measurements of a cystine standard) and inorganic carbon using acid-dissolution coulometry (precision = \( \pm 0.5\% \), based on repeated analysis of a carbonate standard). Organic carbon was determined by difference. For further discussion of carbon analytical procedures and errors see Ransom et al. (1998).

In the laboratory, marine snow which was sus-
Fig. 2. Transmissometer plots from the Mendocino and San Luis Obispo sediment trap transects. The distinct gradient changes at the base of the surface and pelagic layers were used to distinguish boundaries between layers and shaded zones and indicate the relative extent of each layer.

...pended in the TEM-designated collectors was gently separated with forceps into pieces 1–3 mm in diameter in preparation for embedding. Aggregates were then quickly ethanol-exchanged (~10 min per fluid) and embedded in Spurr’s resin (Hayat, 1970). From these stubs, ultrathin-sections were cut and mounted on TEM grids and selectively post-block-stained with uranyl acetate and lead citrate (Hayat, 1970; Baerwald et al., 1991). Samples were imaged with a Hitachi H600 TEM at 100 kV. Approximately 80 grids were scanned with the TEM and hundreds of fields of view containing thousands of particles and hundreds of microaggregates were examined. Of these, photomicrographs of more than 300 representative fields of view were taken. Those that represent the best examples of the images obtained are shown in the plates below.

For the most part, aggregates examined by TEM contained four primary components: siliceous bio-
clastic particles (pieces of diatom frustules), clay minerals, organic matter, and microbes. Identification of specific components carries a number of caveats and the reliability of such determinations is a function of the operators’ expertise and experience with the materials and their familiarity with differences in appearance due to vagaries in particle orientation in the TEM section. For this study, our photomicrographs were examined by operators familiar with organic, biological, and mineralogical components of marine sediments using TEM. In general, bioclasts were identified on the basis of their geometric structures (e.g., smooth curves, polygonal shapes), repetitive structural appearance (e.g., evenly spaced protrusions or holes) and comparatively high electron density. Clay minerals, when oriented perpendicular to the section, were identified by their generally high electron density, commonly elongated or fibrous shapes with smooth upper and lower
boundaries and feathery lateral edges. When oriented parallel to the section, they were identified by their relatively low electron density equant shapes, generally with well defined boundaries. Amorphous organic matter was generally identified by its relatively low electron density, irregular size and shape, and patchy appearance. Cellular material was identified by its grainy appearance and the presence of organelles or vacuoles. Microbes were identified by their circular shape, size (0.2 to 1 μm in diameter), heavy take up of stain, and presence of internal cellular structures.

4. Results and discussion

There is a large difference in size between marine snow (> 5 mm in diameter) and its constituent particles (~10 to 0.1 μm in size). In the present study, we focused on the textures and compositions of the building blocks of marine snow, i.e., microaggregates, those aggregates ≤10 μm in diameter, non-organic particles, and organic matter. Representative photomicrographs of marine snow components from pelagic and nepheloid layer sediment traps are shown in Figs. 3 and 4. It should be noted that each piece of marine snow embedded for our study acted as a loose, yet coherent mass when suspended in solution. This coherency indicated that the constituent particles were all interlinked in some manner. This interlinking is provided by exocellular organic material, similar in character to the polysaccharide fibrils and slime imaged by Leppard et al. (1996). In marine studies such material is commonly referred to as transparent exopolymer particles or TEP (Alldredge et al., 1993; Schuster and Herndl, 1995). These extensive slime and fibril networks originate from a variety of sources, including the linking together of bacterial mucus secretions (Decho, 1990), and aggregation of colloids and mucus secretions by diatoms (e.g., Logan et al., 1995). In general, we did not directly observe TEP in our samples because the non-specific organic staining protocol we adopted was best suited for our overall objectives, while optimal resolution of TEP requires a polysaccharide-specific stain such as Ruthenium Red (Leppard et al., 1996). Nevertheless, on occasion, TEP was detected and, when present, occurred as a thin, low electron density, web-like material. TEP and its effect on marine snow textures have been described in the literature (e.g., Passow and Alldredge, 1994; Dam and Drapeau, 1995; Heissenberger et al., 1996) and the features noted therein are consistent with those we observed.

4.1. Pelagic aggregates

Aggregates from three depths in the pelagic layer over the California continental slope were examined. Representative images of samples from the three water depths (150 m in San Luis Obispo; 250 and 750 m in Mendocino) are shown in Fig. 3. Aggregates from both locations and all three depths are strikingly similar in their relatively open architecture and overall composition. It is well known that physical conditions and water column biology control, in large part, the types and compositions of aggregates that form. The similarity in composition and structure of aggregates from the two deployment sites can be accorded to their similar oceanographic characteristics (Huyer, 1983; Huyer et al., 1991; Strub et al., 1991) and surface water biological communities (Rau et al., 1982; Sancetta et al., 1992).

Pelagic aggregates from both sampling sites and the water depths sampled are dominated by siliceous bioclasts (pieces of diatom frustules) and amorphous organic matter, with the textural relations of components of typical microaggregates being emphasized in Fig. 3. Within the larger aggregated masses, microaggregates (≤ 10 μm) are common (e.g., Fig. 3A). These tend to be comprised of particles that are more closely associated with one another than with those in the surrounding aggregate. Not all particles in the pelagic aggregates are found in microaggregates. Individual bioclasts, caught up in the TEP network of the larger aggregates, are also prevalent (e.g., Fig. 3A,D). Organic matter on the whole appears to be amorphous in character although, on occasion, large pieces of disrupted cellular material are evident (Fig. 3C). Microbes in pelagic aggregates occur as both individuals (Fig. 3A) as well as components of microaggregates (Fig. 3B); their abundance appears to decrease with water depth (compare Fig. 3A,B with Fig. 3E,F).

Overall, clay minerals are a minor component of the pelagic aggregates caught in our traps.
When present, clays occur primarily as components of clay–organic-rich microaggregates or flocs (Fig. 3D). Only infrequently do dispersed clay particles occur inside the bioclast-rich pelagic aggregates (Fig. 3C,F). It should be noted that bioclasts are rarely present inside clay-dominated microaggregates. Because the composition of marine aggregates is a function of particle abundance, it is probable that the clay-rich microaggregates formed prior to entering an area of high marine productivity. Thus, these aggregates probably formed near shore as the result of the flocculation of clay minerals suspended in river plumes during the mixing of salt and fresh water. After formation, these clay-rich microaggregates must have been advected out over the continental slope into the area of high biological productivity where they could be incorporated into bioclast-dominated marine snow aggregates. The relative paucity of clay in our pelagic layer aggregates indicates that during the time our traps were deployed, the impact of cross-shelf processes on aggregate development was minimal.

4.2. Nepheloid aggregates

Representative TEM images of aggregates collected about 20 m above the sea floor inside the nepheloid layer in the Mendocino area are shown in Fig. 4. As for our pelagic study, the textural relations and components of microaggregates representative of those comprising the larger aggregates are emphasized. Comparison of images in Figs. 3 and 4 shows that nepheloid aggregates differ significantly, both texturally and compositionally, from those in the overlying water column. Unlike the pelagic aggregates, those from the nepheloid layer are comparatively more dense and composed dominantly of clay minerals and organic matter. The large bioclasts that dominate pelagic macroaggregates are infrequent, and when present commonly occur as single entities or as isolated particles (e.g., Fig. 4A,C). On occasion, a bioclast-dominated microaggregate, which displays textures and compositions identical to those in the overlying column, appears to be included, with little or no modification, as part of a larger nepheloid aggregate. Such behavior is predicted by studies of aggregate strength (Alldredge et al., 1990). In such studies, resistance to disaggregation is closely related to aggregate size, with resistance increasing as aggregate diameter decreases.

Organic matter in our nepheloid aggregates is primarily amorphous in character. For the most part it is closely associated with the clays (e.g., Fig. 4E,F). In some instances, degrading organic matter forms a nucleus around which clays accumulate (Fig. 4D). Overall, however, the proportion of organic matter in nepheloid aggregates appears to be significantly less than that in pelagic aggregates. This observation is supported by the organic carbon content of pelagic and nepheloid layer marine snow caught in our traps (Table 1). These data show a more than fourfold decrease in the wt% organic carbon in material collected in the nepheloid layer, compared to that retrieved from the upper part of the water column. Although a qualitative assessment, nepheloid organic matter appears, overall, to be slightly more electron dense under the beam, suggesting that it may be more highly polymerized (i.e., degraded) than that in pelagic aggregates.

Another notable feature of our nepheloid aggregates is the apparent near absence of microbes. While this could be an artifact of sampling or di-
Table 1

<table>
<thead>
<tr>
<th>Water depth (m)</th>
<th>Mass (g)</th>
<th>C_{org} a (wt%)</th>
<th>C_{inorg} a (wt%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>250 (pelagic)</td>
<td>0.161</td>
<td>13.33</td>
<td>1.28</td>
</tr>
<tr>
<td>750 (pelagic)</td>
<td>0.124</td>
<td>9.13</td>
<td>1.66</td>
</tr>
<tr>
<td>930 (nepheloid)</td>
<td>0.920</td>
<td>3.77</td>
<td>0.85</td>
</tr>
</tbody>
</table>

Note. Collection surface area for samples from each water depth was 48.7 cm².

a C_{org} and C_{inorg} denote organic and inorganic carbon, respectively.

olution due to increased amounts of inorganic detritus in suspension in the nepheloid layer (Table 1), this appears to represent the continuation of the trend observed in the pelagic aggregates, i.e., decreasing bacterial colonization of aggregates with increasing water depth.

The textural arrangement of the clays in the nepheloid aggregates collected in our study was also examined. These arrangements commonly consisted of random domains and chains of clay particles (e.g., Fig. 4C,D,F). Upon closer inspection, sub-units in the chains and domains consist of parallel and sub-parallel arrangements of clay minerals (see Fig. 4A,C). Such sub-units may represent small microaggregates that were later incorporated into larger microaggregates. A class of microaggregates commonly observed was one with clays arranged tangentially along the boundary (e.g., Fig. 4E; also see Ransom et al., 1997). These latter aggregates resemble fecal pellets in morphology, but their size, compactness, and the absence of a discernible pelllicle leaves their origin in doubt. Similar marine aggregates, labeled mini-pellets and attributed to fecal material of protozoa and planktonic larva have been described (Gowing and Silver, 1985). There is, however, a substantial degree of uncertainty associated with positive identification of these aggregates as mini-fecal pellets (M. Silver, pers. commun.). The possibility that some nepheloid microaggregates may have originated as mini-fecal pellets cannot be overlooked. Nevertheless, in the case of understanding aggregate deposition and origin, the process of aggregation is less important than its location of origin. With the exception of omnivorous protozoans that might preferentially feed on clay particles in the generally clay-poor pelagic layer aggregates in the upper water column, the origin of the nepheloid pellet-like microaggregates we have observed must be either within the clay-rich nepheloid layer or in underlying surface sediments that have been resuspended.

4.3. Aggregate evolution and implications for organic carbon distribution and burial

The change in composition between pelagic and nepheloid layer marine snow we have observed can be explained in terms of aggregation theory. For a particle to be incorporated into an aggregate, it must come in contact with the aggregate and stick upon contact. These two conditions are referred to as contact rate and contact efficiency (Hill, 1992; Alldredge and Jackson, 1995). Contact rate depends on particle and aggregate size, concentration, sinking rate, and on the amount of energy in the system. Contact efficiency is a measure of how many contacts result in the incorporation of a particle and is a function of the ‘stickiness’ of the colliding particles/aggregates. The abundance of a given type of particle in a population of aggregates is an indication of its concentration in the water column and the energy of the system at the time of aggregation. As can be seen in Figs. 3 and

Fig. 4. Representative TEM photomicrographs of nepheloid layer particles and aggregates about 20 m above the sea floor in 950 m of water on the California continental slope near Mendocino. Scale bars = 2 µm. (A) Partial view of typical nepheloid macroaggregate containing clay minerals (c), amorphous organic matter (o), and occasional dispersed large bioclasts (bc). Dark lines indicated by AR are artifacts resulting from wrinkling of the section and h represents a hole in the section. (B) Typical nepheloid microaggregate dominated by clays and amorphous organic matter. (C) Clay-dominated microaggregate containing clay and rare large bioclastic pieces. A single large bioclast caught in the marine snow is located just below the microaggregate. (D) Clay–organic-matter-dominated microaggregate with a core of organic matter around which clays have accumulated. (E) Clay–organic-rich microaggregate showing parallel alignment and chaining of clays internally and around the exterior of the aggregate. Note the presence of stacked clay domains within some of the clay particles. (F) Clay–organic-matter-dominated microaggregate with a few large bioclasts associated on its boundary and nearby. Note arrangement of stacked clay domains.
4, the inorganic particulate species that predominate in pelagic and nepheloid systems are different. From the bioclast-rich, clay-poor character of the pelagic aggregates we imaged, it is apparent that primary productivity in the surface layer controls aggregate composition in much of the water column in our study area (i.e., the surface and pelagic regions). The dramatic change in aggregate character that occurs near the sea floor must therefore be attributed to a significant change in both particle composition and water column energetics.

The nepheloid layer is a dynamic and ubiquitous phenomenon that occurs on continental slopes. Its presence, however, can be temporally and spatially variable (see review in Gorsline, 1984). Suspended particle concentrations in this layer are generated and maintained by a variety of processes that bring in new detritus and/or resuspend and laterally advect previously deposited clastic material (Biscaye et al., 1988; Chassefiere, 1990; Sherwood et al., 1994). The change in character with increasing water depth in the marine snow we examined indicates that when pelagic marine snow intersects the nepheloid layer, it encounters a zone of comparatively high shear and terrigenous particle concentration. At times of high pelagic particle flux, such as plankton blooms, pelagic macroaggregates falling to the sea floor may scavenge fine detritus moving laterally in the nepheloid layer and arrive at the sea floor virtually intact (Hill and Nowell, 1990). However at the flux rates that more commonly prevail, the higher-energy regime near the sea floor and the subsequent changes in density distribution that pelagic macroaggregates in our study area must experience, as they are exposed to shear, seem to destabilize their structure and cause disaggregation. This releases pelagic aggregate components (i.e., microaggregates, TEP, cellular material, etc.) into the siliclastic-rich nepheloid system where they are assimilated by nepheloid aggregates. It would, therefore, appear that nepheloid processes redistribute organic matter descending from the overlying water column and disperse this material down and across the California continental slope. Similar conclusions regarding the offshore transport of organic carbon at other sites have been drawn on the basis of changes in sediment bulk properties (e.g., Walsh et al., 1981; Grant et al., 1987; Walsh, 1989). These studies, however, were unable to specify the exact mechanism by which the transfer occurred. Conclusions drawn on the basis of our observations would provide such a mechanism.

As can be deduced from composition, the pelagic aggregates examined in our study were formed near the sea surface. Once greater than about 5 mm in diameter, such aggregates would have attained sufficient size and mass to sink through the water column. In general, as marine snow passes through the less turbid (i.e., less aggregate-rich) pelagic layer, remineralization of incorporated organic matter occurs (e.g., Alldredge et al., 1986). Consequently, aggregates reaching the nepheloid layer contain less organic matter, as well as that which is less labile than that of its counterparts in the overlying water column. Indeed, this has been documented by organic geochemical studies of sediment trap material from the Santa Monica Basin just a few tens of kilometers south of our San Luis Obispo sampling site (Venkatesan and Kaplan, 1992). It is therefore likely that the clay-dominated nepheloid aggregates we examined contain organic matter that is more refractory than that in their upper water column pelagic counterparts.

The release of insecurely bound, possibly aged, pelagic organic matter into the nepheloid layer and its role in nepheloid aggregation provides a mechanism by which clay particles and organic matter can become closely associated to produce the nepheloid aggregates observed in our study. Similar textural relations between clays and organic matter have been observed in sediments deposited on the sea floor (Lavoie et al., 1996; Ransom et al., 1997). This suggests that the association of organic matter with terrigenous clastic material in continental margin sediments and the distribution of a potentially significant percentage of the organic matter in such sediments happens prior to its permanent deposition and burial. The redistribution of pelagic organic matter among terrigenous clays in the nepheloid layer provides a mechanism that explains the recently observed correlation between sediment organic carbon content, specific surface area, and clay content (Mayer, 1994; Keil et al., 1994; Ransom et al., 1998) and may shed light on the controversy surrounding the controlling mechanisms of organic carbon preservation on continental margins. A further possible consequence of the periodic resuspension and deposition
that can occur as a result of nepheloid layer–surface sediment interactions is a considerable increase in organic matter residence time at, or near the sea floor in oxic or suboxic aerobic conditions. It would seem that such an increase in exposure could substantially increase the degradation of organic matter prior to its final incorporation and burial in the sediment, affecting significantly its bioavailability to local benthic fauna.

5. Conclusions

Marine aggregates in the upper water column are significantly different in texture and composition from those that occur in the nepheloid layer. Because marine snow is the dominant means by which organic matter is transported to the sea floor, our study provides insights into processes that ultimately control the organic carbon contents of surface sediments and the preservation and bioavailability of sedimentary organic matter. Our investigation suggests that pelagic marine snow aggregates undergo repeated episodes of disaggregation, aggregation, and mixing with terrigenous detritus in the nepheloid layer near and at the sea floor, such that the components, textural relations, and distribution of organic matter in the resulting macroaggregates bear little resemblance to those in the overlying water column. It is these strongly modified bottom-water aggregates and their included organic matter that provide the baseline for understanding the preservation of organic carbon in continental margin sediments and the evolution and in-situ distribution of sedimentary organic matter. Our study indicates that for oxic and suboxic continental margins, models of organic carbon deposition should include provisions for lateral transport of organic matter and its possible extended residence time in near-sea-floor, oxygenated, aerobic environments. During such intervals, organic matter would be repeatedly cycled between surface sediments and the overlying bottom water, being moved down slope from its initial point of impact with the sea floor to its site of ultimate burial and removal from the carbon cycle. It seems likely that such a process would increase significantly the refractory character of the organic matter, thus reducing its bioavailability to benthic fauna.

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