

**OFFICE OF NAVAL RESEARCH
AGGREGATE DYNAMICS IN THE SEA
WORKSHOP REPORT**

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**Asilomar Conference Center
Pacific Grove, California
September 22-24, 1986**

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OFFICE OF NAVAL RESEARCH

AGGREGATE DYNAMICS IN THE SEA
WORKSHOP REPORT

ALICE L. ALLDREDGE

ERIC O. HARTWIG

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American Institute of Biological Sciences

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Cover: Aggregate of marine snow approximately 5 mm in diameter produced as a mucus feeding structure by the planktonic larvacean genus, *Oikopleura*. Photographer, James M. King, Marine Science Institute, University of California, Santa Barbara, photographed this aggregate and surrounding natural particles in situ with a macro lens and Nikon in an underwater housing.

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WORKSHOP ON AGGREGATE DYNAMICS IN THE SEA

SUMMARY

INTRODUCTION

Much of the suspended matter in the ocean exists as aggregates of organic detritus, living microorganisms and clay minerals. Historically, these aggregates have been categorized into the following two size classes: 1) marine snow, a general term describing amorphous suspended aggregates in the ocean larger than 500 μm in size; and 2) microaggregates which range from a few microns up to 500 μm in diameter. Both are primarily products of biological activity including mucus production, grazing, excretion, etc. In the open ocean, even those particles produced by physical/chemical coagulation processes (precipitation, particle collision, etc.) originate from largely biogenically derived component particles. Local loss terms include sinking, advection and decomposition which generally occur simultaneously with redistribution processes such as disaggregation, reingestion and defecation. Therefore, the dynamics of marine snow and microaggregates are functions of the actual aggregate properties, the biological processes and mechanisms which produce/redistribute them and physical/chemical processes.

Since aggregate production is largely a function of biological activity, aggregates are ubiquitous in the ocean, albeit at unknown abundances and presently with distributional statistics that are not yet quantified. Quantification of distributional patterns relies on obtaining in situ observations. To date, these have been accomplished by divers, submersibles and photography, all of which suffer from a small sampling base. The

properties and characteristics inherent to microaggregates and marine snow are also determined by those processes which form them. These properties and characteristics include shape, size, porosity, particle strength and rigidity, surface characteristics, chemical and biological composition, sinking rate, bioluminescence, and optical and chemical properties. However, none of these properties has been quantified either singly or in concert as unique identifiers of aggregated matter in a background environment of organisms and ocean water. A rapid advance in understanding in situ dynamics of marine snow and microaggregates, therefore, requires an advance in observational capability beyond present diver/submersible/photography technology.

PURPOSE

The purpose of the workshop was to specify and quantify, to the extent possible, the properties of marine snow and microaggregates which could be exploited to understand the abundance, distribution, dynamics and in situ characteristics and state (e.g., intact, dispersed, sinking rate, age, size, shape, source, etc.) of aggregated particles in the ocean.

The workshop participants were divided into 3 working groups: Aggregate Dynamics, In Situ Exploitable Optical Properties of Aggregates, and In Situ Exploitable Non-Optical Properties of Aggregates. The Aggregate Dynamics Working Group constructed a model of aggregate dynamics in the sea and prioritized its components as to which were most critical toward advancing our understanding. The In Situ Exploitable Properties working groups each identified crucial properties needed to understand aggregate dynamics and outlined existing or needed technologies necessary to quantify those properties.

The workshop took place in a very constructive and stimulating atmosphere which resulted from the cooperative spirit of the participants. We thank all of the attendees for their participation and input. Special thanks go to the working group rapporteurs, Nick McCave, Dave Mackas, Tim Stanton, Ken Carder, and Dick Eppley. Most of all, we thank Chris Lowe and Carol Loughney of the American Institute of Biological Sciences for organizing a most enjoyable and productive meeting.

MODEL OF AGGREGATE DYNAMICS

The building blocks of marine aggregates consist of four general classes of component particles: 1) microorganisms, especially phytoplankton and bacteria; 2) products of dissolved organic matter (DOM) to particulate organic matter (POM) conversions such as collapsed bubble coating; 3) inorganic particles of lithogenic (quartz, feldspar, clays) and biogenic (calcite, aragonite, opal, etc.) origin; and 4) the mucus produced by zooplankton as feeding structures. The model outlines the dynamics of aggregation/disaggregation of these component particles rather than their origin. The origins of these component particles are well studied in some cases (phytoplankton, bacteria, lithogenic) but are poorly known for others (DOM-POM conversions, zooplankton mucus).

For each of these classes of component particles we need to know size distribution, abundance, sinking rate, particle strength, and chemical and biological properties. We also need to know the numbers, sizes, locations, feeding and defecation rates, and feeding preferences of the major particle consumers in the sea. These data are needed so that we may make well informed estimates of the relative importance of particle aggregation mechanisms.

The major mechanisms bringing particles together are animal feeding and physical coagulation via Brownian, shear, and differential settling routes. These two mechanisms are sufficient to bring particles together, but not sufficient to make them stick. Different classes of particles have different sticking efficiencies which must be determined empirically. Fecal pellet formation may be the dominant mechanism by which particles are stuck together in some parts of the ocean. Once stuck together aggregates may be transported by mixing, sinking or lateral advection. They may be lost by deposition or mineralized via metabolic activities or they may be disaggregated by shear or animal feeding activities.

Certain portions of the model were singled out as being most important in advancing our knowledge of aggregate dynamics in the sea. These were:

- mechanisms which bring particles together (especially feeding and physical encounter mechanisms);
- mechanisms which stick particles together (especially defecation and the factors determining the sticking efficiency of various classes of aggregates);
- the abundances, properties and rates of formation of component particles.

RECOMMENDATIONS

The following recommendations were made by the three working groups with the goal of achieving a predictive understanding of aggregate dynamics in the sea.

1. Understanding of aggregate dynamics requires that we know the number concentration and size distribution of aggregates and component particles by class in situ, preferably in real time.

- develop an in situ, optical rapid survey instrument
 - develop an accessory survey platform for assisting the optical survey instrument in providing unambiguous identification of aggregates even where plankton is abundant
 - develop remote particle classification instruments
 - develop an in situ flow-through particle counter to characterize aggregates 0.5 mm in diameter
2. Investigation of aggregate properties requires the capture of aggregates in situ in a gentle, selective and non-disruptive manner.
- expand and improve existing in situ filtration systems, traps and water samplers
 - develop selective capture devices which can be effectively deployed by free-vehicles and submersibles
 - develop a sampler to collect aggregates at the water-sediment interface
 - refine present acoustic and optical instruments to guide efforts of in situ collection
3. In order to understand the relative importance of the various mechanisms which cause particles to bind together, to sink and to disaggregate we need information on the following particle properties:
- a. Settling velocity distribution as a function of particle class, size, shape
 - Conduct laboratory and field experiments to test theoretical/empirical relationships between settling speed, and aggregate size, shape, orientation, density, porosity and permeability etc.
 - b. Aggregate strength, rigidity, permeability
 - measure aggregate fracture strength, deformation and rates of break-up in the laboratory and on board ship
 - develop an in situ method to test laboratory data on deformation and settling behavior in situ
 - c. Surface and chemical characteristics
 - determine surface and chemical properties of each class of aggregates and component particles with laboratory/shipboard studies of freshly collected particles
 - determine how surface properties affect aggregation rates in situ

- d. Attractiveness to consumers
 - conduct lab/shipboard experiments to quantify how consumers detect and discriminate particles
 - Test concepts of particle selection in situ using instruments developed in recommendation #1.
- e. Age and origin
 - identify specific organisms (types of bacteria, protozoans, etc.), chemicals (pigments, organic compounds) or isotopic tracers (stable isotopes, radioisotopes, inorganic molecules) which are specific for particles of certain ages or sources.
 - Develop methods to use these markers on captured aggregates in conjunction with optical data.
- 4. Determine encounter rates in nature under various environmental conditions for various particle classes.
 - extend present efforts to model physical aggregation and natural encounter rates to include empirically determined sticking efficiencies and the physical complexities of a real ocean.
 - test these ideas in nature with a system for studying particle-particle interactions
- 5. Determine the numbers, sizes, locations, feeding and defecation rates, and particle preferences of major particle consumers.
- 6. Determine the rates and mechanisms of component particle formation, particularly DOM-POM conversions under varying environmental regimes. Develop models to predict the abundances of all component particles.
- 7. Accompany all field efforts to investigate aggregate dynamics with appropriate environmental data including physical, chemical and biological variables.

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INTRODUCTION

Working Group I was concerned with the processes by which changes in the sizes, abundances and characteristics of aggregates are brought about in the ocean. Our charge was two fold: first, to construct a model of the dynamics of aggregate formation, breakdown and loss in situ, and second, to prioritize the components of the model as to their importance in understanding aggregate dynamics. Our goal was to determine which avenues of research were most important in moving us toward a predictive, quantitative understanding of the spatial and temporal variations of marine snow and microaggregates in the sea.

Two major issues were identified as critical to understanding aggregate dynamics: production and fate. Quantitative knowledge of the mechanisms of aggregation, disaggregation and aggregate loss, the rates at which these processes occur, the factors governing those rates, and the properties of both aggregates and their component particles would allow prediction of the distribution, abundance, sizes and dynamics of marine aggregates. Additional information on processes of physical transport (lateral advection, mixing, etc.) would allow fine tuning of those predictions.

MODEL OF AGGREGATE DYNAMICS IN THE SEA

A conceptual model of aggregate dynamics in the ocean is presented in Figure 1. Aggregates are formed by the adhesion of smaller, component particles including living organisms, inorganic and organic particles and

zooplankton mucus. Aggregation involves two essential stages. Particles must be brought close enough together to interact and then they must stick. The two actions are unrelated in that sticking does not necessarily follow from close approach. Once formed, aggregates may undergo a variety of internal transformations which alter their size, composition and characteristics. Aggregates are typically broken apart by turbulent shear or by the activities of organisms. They may be transported by settling or lateral advection, and finally they are lost from the pelagic zone through deposition and remineralization. We will examine each of these steps in detail.

A. Origin of component particles

Marine aggregates arise from a diverse array of component particles. These particles fall into the following general classes:

(1) Microorganisms: The most abundant living particles in the sea are microorganisms, predominantly bacteria ($10^6/\text{ml}$) and phytoplankton (10^2 - $10^4/\text{ml}$). They are common components of naturally occurring particles. Factors controlling the distribution, growth rates, and abundance of phytoplankton and bacteria have been extensively studied by biological oceanographers and good predictions can be made regarding their availability for aggregation. Phytoplankton growth is usually controlled by light and nutrients. Bacterial growth is controlled by dissolved organic matter composition and supply and is generally correlated with phytoplankton standing stocks (chl a) and primary production. Phytoplankton production is (obviously) limited to the photic zone, while bacterial production occurs throughout the water column and in the sediments.

Of great importance to the aggregation potential of plankton are their

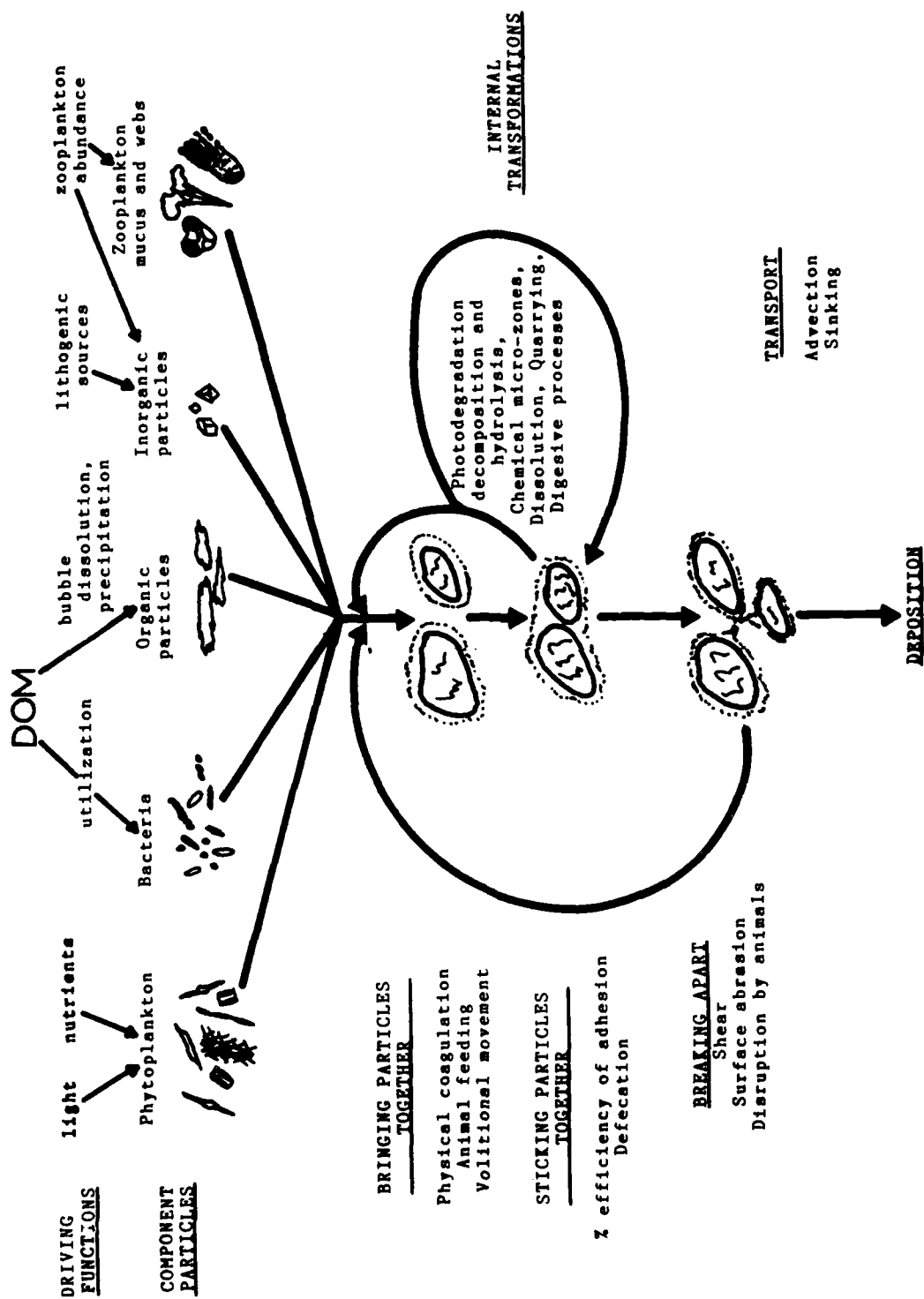


FIGURE 1: MODEL OUTLINING THE MAJOR PROCESSES DETERMINING THE PRODUCTION AND FATE OF AGGREGATES IN THE SEA

cell surface properties. These properties have been relatively little studied by ocean scientists, but it is likely that cell surfaces change with the physiological condition of the cell. Nutrient limitation leads to the production of sticky material by phytoplankton, while the production of capsular polysaccharides by bacteria may enhance aggregation. Models of aggregation thus require information regarding the physiological state, cell surface properties and exudate production rates of these microorganisms.

(2) Organic particles: Organic detrital particles are very abundant in all ocean regions, but their origins are still speculative. Various mechanisms have been suggested to account for their origins. One mechanism involves dissolved organic matter (DOM) to particulate organic matter (POM) conversions. Mechanisms of this conversion include adsorption to dissolving bubbles, de novo formation of particles via precipitation of organic and inorganic molecules, and utilization of DOM by bacteria. The rates of these processes are governed by: a) size and composition of the DOM and inorganic pools; b) abundance of bacteria; and c) sea-surface mixing. While considerable information exists regarding the rates at which bacteria in the sea convert DOM to POM, almost no quantitative information exists on the importance of bubble dissolution or precipitation (see Alldredge overview in this volume for detailed discussion). Other organic particles include crustacean moults, body parts, and carcasses which are relatively rare and are probably not major contributors to the particle pool.

(3) Inorganic particles: Inorganic particles are derived from external sources, primarily rivers and atmospheric inputs, and from the shells and tests of organisms. The importance of these non-living sources to bulk

particulate concentrations in surface ocean waters is probably relatively small, with the important exception of coastal ocean regions. The lower 500 to 1000 m of the water column in ocean basins is dominated by resuspended terrigenous particles comprising the bottom nepheloid layer.

(4) Mucus: Mucus produced by pelagic plants and animals is a significant nucleus for particle formation. Important animal sources include the filtering structures of larvaceans (houses) and pteropods (webs), and slimes produced by a variety of gelatinous zooplankton (ctenophores, salps, siphonophores). Likewise, phytoplankton produce mucus to form colonies (some *Thalassiosira*, *Phaeocystis*, etc.) and when they senesce or prepare for resting stages during poor growth conditions. Depending on its source, mucus likely differs chemically as does its ease of degradation, and physical properties (stickiness, rheological properties). The production rates of mucus by these sources are best known for larvaceans, where a typical individual produces 4-6 houses per day. The production rates for other zooplankton and phytoplankton sources are not so well known and require further study before models can quantitatively assess the importance of these materials for the aggregation process. Mucus production is primarily a function of producer abundance but may also be affected by the producing organism's physiological state and the quality and quantity of food available.

While models exist for the origin of many classes of these component particles, i.e., primary production models, the characteristics, abundances and sources of others are poorly understood quantitatively (e.g., bubble dissolution, chemical precipitation, etc.). Furthermore, while quantities of component particles may be a major factor governing aggregation rates physical coagulation or by feeding, particle qualities such as the sticking efficiency,

nutritional value, chemical composition, and tastiness may be more significant in certain environments. For instance, particles may be so rare in the oligotrophic ocean that biological mechanisms of aggregation substantially dominate over physical processes. In the open ocean, particle quality may thus be much more important than particle quantity in determining aggregation rates. In coastal oceans where particles including senescent diatoms and lithogenic material can be very abundant, physical aggregation processes may dominate. These hypotheses require testing.

B. Bringing particles together

In order for particles to aggregate, the component parts must first be brought together. This is accomplished by two major mechanisms.

(1) Physical coagulation: Physical aggregation occurs a) through Brownian action mainly involving small ($d < 5 \mu\text{m}$) particles because the Brownian diffusivity ($D = kT/3\pi \mu d$) is large for small particles; b) through turbulent shear at a rate related to the shear rate and the cube of the collision radius given by the sum of the radii of the two colliding particles; and c) due to the differential movement of particles, often vertically under gravitational settling but also along other trajectories in the case of self-propelled or turbulently mixed particles. The removal rate of particles is proportional to the square of the number concentration of particles and is also affected by the fraction of particle collisions that result in coalescence. Clearly, to make a start on predictions of aggregation rates we need to know the volume (or size) distribution function, $n(v) = dN/dv$, of component particles and aggregates for different locations and depths in the ocean, the settling velocity distribution of particles, and the shear rate. Some of these data are available for a few ocean areas, but the data are very fragmentary and limited to a narrow particle size range.

At present, our knowledge of the relative importance of particle aggregation rates due to physical mechanisms is rudimentary. Calculations suggest that Brownian motion is most important for particles smaller than about 5 μm . However, only simple models which do not take retardation into account have been used for Brownian and shear coagulation and it is not clear whether shear or differential settling is more important for large particles. Certainly McCave's (1984) calculations, which suggest extremely low particle scavenging rates by aggregates, run counter to Honjo's (1982) observations in the Panama Basin which suggest appreciable removal of fine lithogenic particles by sinking palmelloid coccoliths. In fact, the models of collision efficiency for sinking particles have not been tested experimentally.

Estimates of coagulation rate have been based on monodisperse or two-component size distributions. A modelling effort involving realistic size distributions and the full range of oceanic turbulence needs to be undertaken. Only in that way can we properly examine the capacity of physical mechanisms to produce aggregates at the rates which are known to exist in nature. Laboratory experiments to test differential settling and particle coagulation mechanisms should be conducted as well.

(2) Feeding: McCave (1984) concluded that physical aggregation mechanisms were inadequate to explain aggregation rates in the ocean. Aggregation rates of particles above submicron sizes appear to be biologically determined. Consumption by animals is the major biological pathway by which particles are brought together in the open ocean and is probably the best studied and

understood. Dispersed particles including phytoplankton, bacteria, and aggregates are consumed by animals and repackaged into larger, aggregated particles as fecal pellets. The rate at which food particles are brought together is a function of the concentration of the food particles, the abundance of the consumers, and the types of consumers present. Consumer species composition is critical to both the rate of production and to the characteristics of the pellets produced. Large-bodied, gelatinous zooplankton such as salps, larvaceans and doliolids are capable of consuming particles at rates an order of magnitude higher than copepods.

In general, rates of particle aggregation by zooplankton feeding are a linear function of food concentration up to a species-dependent particle concentration threshold. Beyond this threshold, feeding rates level off and aggregation is determined by the rate of digestive processes. Additional factors which affect feeding include temperature, time of day (many organisms feed in surface waters at night), size, taste, shape, species composition of food particles, and the size and age of the consumers.

Although aggregation of particles by consumption occurs in the deep sea, most of the animal biomass occurs in the upper 1,000 meters and a substantial proportion of those animals migrate into surface waters and feed at night. Phytoplankton concentrations are also highest in the euphotic zone. Thus, particle aggregation via consumption is likely to be most significant in the upper layers of the ocean. At great depths both the numbers of consumers and the concentration of particles is much lower indicating much slower particle aggregation rates. We do not know whether feeding activity dominates over physical coagulation in the production of aggregates at these depths.

(3) Active movement by organisms: Many marine organisms, including sub-micron-sized bacteria and micro-flagellates, heterotrophs, and still larger dinoflagellates and metazoans, have the capacity for active movement. Colonization of particles by organisms is one mechanism bringing particles together. However, due to the size of the organisms, relatively little biomass is involved in this process of aggregation and it is likely to be relatively insignificant in comparison with the other processes.

C. Sticking Particles Together

Once particles have been brought together, two major mechanisms cause them to stick together.

(1) Adhesion: Sticking efficiency or attachment probability is an essential component of all coagulation processes. Some determinations of sticking efficiencies have been made for clays and sediment particles, involving measurement of the rate of change in particle number in a suspension and comparison with theoretical predictions. Results indicate sticking efficiencies of 10 to 20%, but these are based on theoretical contact modes that do not include hydrodynamic retardation and therefore overestimate probable contact rates. It is possible that the sticking probability of particles in sea water is 100%. Mucus produced by phytoplankton may enhance sticking efficiency and bacterial mucus is known to greatly enhance aggregation rate. Moreover, organisms produce spines and colloidal projections which may increase the effective particle size and tendency to entangle. The role of cellular excretions and biogenic "glue" needs much further investigation.

When particles are not "sticky" in sea water, their stability may be ascribed to electrostatic and steric effects. Diffuse layers in sea water are small, on the order of angstroms in thickness, and electrostatic stabilization may be unimportant in the ocean. It is possible that oceanic particles are sterically stabilized by natural organic agents, possibly of low molecular weight. Larger organic molecules can destabilize particles. The role of organic matter on the stability and instability of particles in the ocean should be examined.

Present methods of measuring sticking efficiency should be extended to living particles and related to the physiological state of the organisms. The possibility of making optical experimental measurements of contact rates, thus eliminating the dependency of attachment probabilities on contact models should be pursued.

(2) Defecation: Feeding animals collect particles and stick them together through the process of fecal pellet formation and defecation. In parts of the ocean where component particles are scarce (such as the oligotrophic ocean) defecation may be the major mechanism by which particles are aggregated. Fecal pellet production depends primarily on animal population concentrations, on feeding rates, on ambient particle concentration and size spectra, and on digestion efficiencies. Digestion efficiencies are about 70%, and if we assume that all new production is consumed, then as much as 30% of primary production can become aggregated in fecal pellets. Digestion efficiencies decrease with increasing food concentration and thus more feces will be produced where both food and consumer populations are high.

Fecal pellet formation and repackaging appears quantitatively most important in the upper water column organisms typically

produce 10-100 pellets/day over a broad range of sizes and densities. Despite the broad range of settling velocities measured for many species, it appears that even large, relatively dense feces may remain in the upper water column for periods of at least days, allowing for interactions with other particles, and chemical and biological diagenesis. For many feces coprophagy is a common fate, indicating that component particles in feces may be stuck together several times via defecation processes before they are lost from the pelagic system. During settling, larger feces are believed to adsorb luminescent bacteria which may render them more visible to coprophagous organisms, and thus enhance their rate of reingestion.

The production of feces by many marine zooplankton groups (pteropods, amphipods, pelagic polychaetes, ctenophores, siphonophores) is poorly known. Variations in fecal composition and production rates with organism age, size and food supply, the role of coprophagous organisms and the importance of fecal pellet bioluminescence have also received very little study.

D. Internal Transformations

Once formed, particle sizes and properties may be altered by internal transformations. These include:

(1) Aggregate food webs: The size and characteristics of aggregates as well as the nature and extent of the biological glue helping hold them together will be altered by the growth, feeding, and interactions of the complex detrital communities which inhabit them. These activities will result in utilization of much of the labile organic matter and conversion of the particles to a more refractory state.

(2) Chemical microzones: Because of their high concentrations of organisms and their semienclosed physical structure, macroaggregates may serve as chemically altered microenvironments. The high metabolic activity of microorganisms leads to high concentrations of metabolic end products and inorganic molecules. These unique microzones may enhance particle degradation or colonization.

(3) Alteration of aggregate quality by microbial colonization:

Aggregates, particularly those of low nutrient value (and poor "taste"), may become more attractive to animal consumers if the aggregate becomes colonized by bacteria (and protozoa). This paradigm is well established in trophic interactions in detrital food webs, microbial growth being responsible for enriching detritus with respect to N and P. Aggregate disruption (breakup) could be increased by increased attractiveness of colonized aggregates to animals.

(4) Photodegradation: DOM, primarily fulvic and humic acids, is important in coating particles and determining their surface characteristics. Photochemical transformation of marine fulvic acids has recently been shown to occur and to closely resemble photo-induced cross-linking of polyunsaturated fatty acids, which are important components of phytoplankton, especially diatoms. Such photochemical transformations would enhance particle aggregation. By contrast, polysaccharide linkages are expected to photodegrade and particle disaggregation may occur if polysaccharides are important in aggregate binding. Photodegradation is poorly understood and its impact on particle dynamics needs investigation.

E. Aggregate Breakup

Aggregates may be broken apart into smaller aggregates or into their component particles via shear or the activities of organisms.

(1) Shear breaking: Aggregates can break up in a shear field. Important factors include turbulence intensity and scale, particle size and strength, breakup mode (surface erosion or aggregate splitting) and the time of exposure of the particle to the turbulent shear.

Perhaps the largest fluid shears in the ocean interior (away from surfaces) occur in turbulent regions which result from breaking internal waves, or in the wake of larger passing bodies (fish or zooplankton) or along the boundary between differentially moving stratified layers. The parameter which characterizes the shear forces within the turbulence is the turbulent energy dissipation rate, commonly denoted as ϵ . Typical oceanic values of ϵ are 10^{-5} to 10^{-3} cm^2/sec^3 . The larger values are typically found in isolated "patches". Still larger values of ϵ can be found in the ocean's upper mixed layer and in the benthic boundary layer. Different relationships for floc disaggregation have been proposed which depend on the floc composition and the floc size relative to the smallest turbulent scale, l_k . $l_k = 5$ mm at $\epsilon = 10^{-5}$ cm^2/sec^3 and $l_k = 1$ mm at $\epsilon = 10^{-3}$ cm^2/sec^3 . If floc fracture does occur, such as for clay-aluminum flocs, the maximum remaining size is very nearly equal to l_k using the numbers from McCave (1984). Basically, particles larger than l_k can be broken whereas those smaller than l_k live in a "laminar world". Such calculations do not account for the strength of the aggregated material, information which is presently unavailable.

It is useful to develop models for the breakup of oceanic aggregates by turbulence, but the development of a useful theory can be expected to be

difficult and so requires some time. In the meantime, experiments to measure breakup of a variety of types of aggregates under turbulent conditions of interest in the ocean (e.g. mid-depth, the benthic boundary layer, breaking internal waves) should be made.

(2) Activities of organisms: Animals break apart aggregates during feeding. Many zooplankton are highly selective feeders capable of grasping, tasting, shredding and discarding unsatisfactory food particles. Some quarry or scrape away the aggregate surface, others consume entire particles. Bacterial decomposition on the particle surfaces may also weaken aggregates structurally, potentially leading to particle fragmentation. The role of animals in breaking apart particles is poorly understood.

F. Aggregate Transport

Both aggregates and component particles may be transported either vertically via sinking and mixing or laterally via advection.

(1) Sinking: Measured or calculated sinking rates for marine snow range from 1 to 150 m/day. The rate at which an aggregate settles through the water column is dependent on the density difference between the floc and the surrounding water, and the drag on the particle. Drag is strongly dependent on shape. Marine snow comes in a large variety of complex shapes. Due to this complexity, drag will have to be determined empirically.

(2) Mixing: Various researchers have speculated on the importance of turbulence and mixing in retarding the sinking of aggregates. This has not as yet been adequately demonstrated, but it may occur in situations where sinking rates are slow relative to mixing rates.

(3) Lateral advection: The abundance of marine snow within a water parcel is dependent on the rates of aggregate formation

and destruction, the vertical flux of aggregates through the water parcel, and the exchange of aggregate populations with adjacent water parcels. However, the distribution of marine snow within a water column may also be affected by lateral advection of parcels of water bearing flocs from distant sources. The amount of horizontal advection is probably dependent on sinking rate of the aggregates (greater for slower sinking flocs), the current velocity (greater at higher current speeds), and the vertical extent of the current (greater for thicker currents). Situations where advection may be particularly important are near the continental slope, around submarine ridges, and where aggregates are "trapped" on density interfaces (i.e., aggregates which have become neutrally buoyant or nearly so at a density interface).

G. Aggregate Loss

Aggregates are ultimately lost from the pelagic zone through deposition to the sea floor, by conversion to DOM or by mineralization (conversion to CO_2 , NO_2 , PO_4 etc.) through the metabolic activities of organisms.

(1) Deposition: Part of the rain of aggregates survives as the sediment of the sea bed. The behavior of particles in the benthic boundary layer is principally controlled by the boundary shear stress. Deposition of most classes of suspended particles can occur when the shear velocity (U) is less than 0.5 cm/sec. However, close to the bed, in the lowermost centimeter or so, the shear may be intermittently very high, at least two orders of magnitude higher than that found above a meter away from the bed. This is likely to prove highly disruptive to some classes of aggregates. The resuspension of material may inject it back into the water column in a more finely divided form than that in which it arrived. As a part of the bottom

layer this material may be transported for long distances while reaggregating. Many cycles of deposition, breakup, resuspension and reaggregation during transport may occur.

(2) Metabolism by organisms: Bacteria and protozoa may play a major role in the degradation of aggregates. Only limited information is available regarding microbial colonization, hydrolysis, and metabolism of the organic components of macroaggregates. Microbial activity can cause rapid degradation of POM, some of which is remineralized via respiration and some of which re-enters the DOM pool. Aggregates consumed by animals are partially mineralized via metabolism and respiration, producing an as yet poorly quantified loss of particulate matter with each reconsumption.

APPLICATION OF THE MODEL TO THE OCEAN

We may think of the open ocean as comprising three zones, the upper mixed layer (UML), <200 m deep, the interior down to about 500 m above the sea floor and the bottom nepheloid layer (BNL) in the lowermost 500 m. Different proportions of primary components and filter feeding animals are expected in each zone.

The UML contains the region of production of the majority of new material entering the ocean. It also has the highest concentration of biological particles. Some fraction of the aggregates produced in this region pass out of it by sinking into the interior, where concentrations of all particle classes are much lower. Physical coagulation rates will also be lower. It is not clear for any of these regions whether physical or biological aggregation is dominant, though the latter seems most likely in the interior and any which

form anew sink into the BNL. The BNL is a region of higher physical stress and the active supply of lithogenic material from resuspension may produce dominance of physical mechanisms.

A fourth zone is the continental shelf region. Both lithogenic and biogenic particles are abundant here and the relative significance of biological and physical aggregation processes is unclear. This case is particularly important for understanding the fate of particulate matter in the coastal zone.

PRIORITIZATION OF MODEL COMPONENTS

Certain portions of the model were singled out as being especially important for our understanding of aggregate dynamics in the sea.

Top Priority

- Mechanisms of particle aggregation: Both physical aggregation and feeding are of central importance to particle dynamics.
- Mechanisms of particle sticking: Understanding the % sticking efficiency of various classes of particles and the defecation and reconsumption rates of organisms are central to understanding particle dynamics.
- Abundance, properties, and rates of formation of component particles: While the rates of formation for some component particles are well known (phytoplankton), others have not been quantified. Abundances and properties are largely unknown for several classes of component particles.

Lesser Priority

- Internal transformations: Although important, these processes were considered less important in explaining particle sizes and abundances.

- Breakup: Particles appear to be lost primarily through sinking and reconsumption. Particles may not break up, once formed, in any significant quantities.
- Transport and loss: Deposition and sinking have been the subject of numerous large-scale studies which have already provided considerable information. The significance of transport processes can only be evaluated with information on formation processes.

RECOMMENDATIONS

Our goal is to achieve a predictive understanding of aggregate dynamics in the sea. Although not an exclusive list, the working group identified the following recommendations as top priorities toward achieving that goal.

(1) Understanding of aggregate dynamics requires that we know the number, concentration and size distribution of aggregates and component particles, where possible, by particle class. We recommend development of instrumentation which could provide this information, preferably in real time, over a variety of temporal and spatial scales.

(2) In order to understand the relative importance of the mechanisms which bring and stick particles together we need additional information for each class of aggregates or component particles on the following properties:

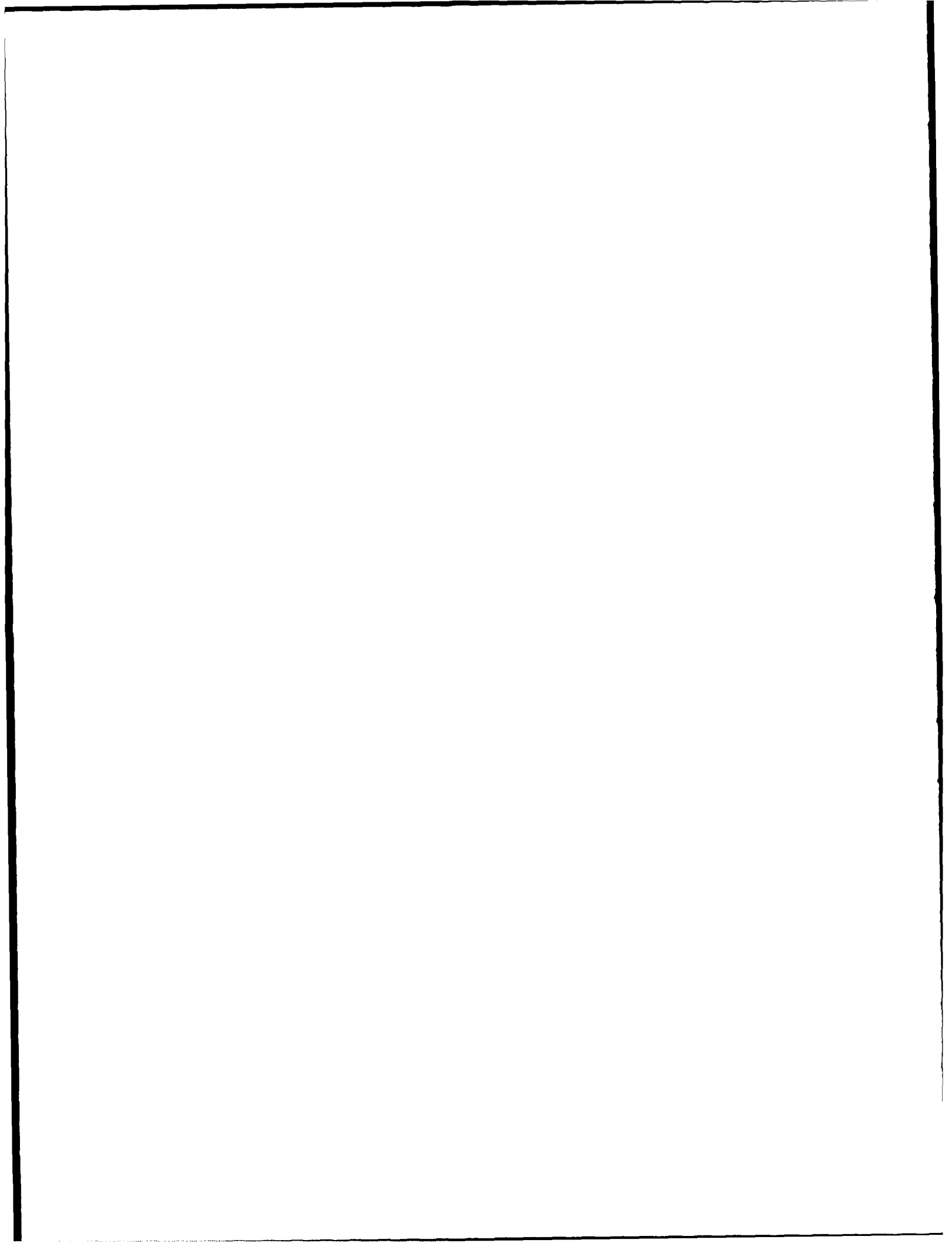
- a. settling velocity distribution as a function of size, shape, source, porosity, etc;
- b. strength or rigidity;
- c. surface characteristics, % sticking efficiency, and significance of biogenic "glues";
- d. attractiveness to consumers, including nutritional value, tastiness, bioluminescence, age.

(3) We need to determine the numbers, sizes, locations, feeding and defecation rates, and the particle size and composition preferences of major particle consumers. The prevalence of coprophagous species and rates of fecal pellet consumption require particular attention.

(4) We need to determine the encounter rates of particles in nature and the effects of physical processes, particularly short duration, high energy events such as internal waves, storms, etc., and biological factors such as phytoplankton buoyancy changes on those rates. A theoretical modeling approach taking these kinds of factors into account might be an appropriate first step toward predicting if and when physical coagulation mechanisms are significant in particle formation.

(5) The rates and mechanisms of component particle formation, particularly DOM-POM conversions, must be determined under varying environmental regimes. The factors driving production of component particles must be quantified in order to predict abundances of component particles.

(6) The abundances, aggregate class composition, and the rates of aggregation and disaggregation for each class of aggregates needs to be determined for contrasting oceanic environments in order to quantify the relative significance of the various mechanisms of aggregate formation and loss in these systems. A good start would be a comparison of the oligotrophic open ocean with a coastal or upwelling zone.



WORKING GROUP II: IN SITU EXPLOITABLE PROPERTIES OF AGGREGATES: OPTICS

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A. Introduction

There is little information on the large scale distributions of marine aggregates; automatic aggregate identification and classification methodologies remain to be developed. Present optical classification schemes for aggregates require human attention: an objective observer to view high resolution particle images.

Acquiring particle size frequency data is feasible in the survey mode at present, and we propose the development of a Marine Aggregate Survey Camera (MASC) designed to collect size frequency data for particles from about 25 μm to 5 cm diameter as an important first step for quantifying marine aggregates.

Concurrent with the MASC development and deployment, we need to acquire improved optical methods to discriminate aggregates from living organisms by laboratory and shipboard methods. The knowledge gained can then be exploited either to improve the discrimination of MASC or to develop an additional survey instrument suite to identify, size and enumerate aggregates in the euphotic zone.

B. Aggregate Classification Methods

In order to understand the optical characteristics of marine particles well enough to develop an automatic method to accurately classify them as aggregates, an extensive suite of laboratory measurements on fresh and aged aggregates is required. Biologists typically classify aggregates microscopically. Instrumental image analysis of aggregate shape, size and texture (e.g. heterogeneity and patchiness of scattering centers) should accompany other optical measurements of aggregates until a classification scheme is fully verified.

An example of a classification strategy is to discriminate marine snow from zooplankton by the forward volume scattering function. Aggregates are clusters of smaller scattering centers, and small scatterers do not scatter light as predominantly in the forward direction as do large particles of low refractive index such as zooplankton or phytoplankton. The near-forward rate of change in scattering with angle should provide a much larger negative value for zooplankton than for marine snow of the same cross-sectional area. Tests of other hypotheses for automatic aggregate identification should be part of this laboratory effort.

Some of the optical measurements to be considered are volume scattering functions, absorbance, index of refraction, polarization, fluorescent properties, luminescent characteristics, and heterogeneous or amorphous qualities of aggregates.

Four of these exploitable optical properties of aggregates, refractive index, absorbance, bioluminescence and fluorescence, may provide aggregate age discrimination. For aggregates containing significant polysaccharide exudates which may serve as a cohesion mechanism, the exudate can be easily observed due to phase lag in light passing through it. This is due to a slight

slight increase in its refractive index relative to seawater. Schlieren or holographic interferometric techniques can be used to visualize such aggregates. If these exudates are degraded over time, the phase contrast may disappear, providing a possible aggregate age discriminator.

Marine snow may emit bioluminescent light. The characteristics of that light are indicative of its component organisms, and therefore, may be an exploitable optical property in determining the life histories and ages of the macroaggregates.

Eukaryotic luminous organisms such as dinoflagellates and radiolarians emit pulses of light which are mechanically (or acoustically) stimuable. Luminous bacteria, however, emit only a steady glow. Since the presence of bacteria in concentrations high enough to luminesce can occur only on older aggregates, the properties of emitted light may be an indication of age.

As aggregates age, they are degraded by marine bacteria. This process changes the color and chemical composition of the marine snow. Some of the constituent chemicals such as fulvic and humic acids may fluoresce. These properties, too, might be exploited in determining the age of marine snow by optical observations.

Spectral absorbance, while admittedly a formidable measurement on single particles, could provide extremely valuable data. The opacity of fecal pellets is quite high relative to that of phytoplankton and zooplankton, and its spectral character probably includes effects of degradation products. Ratios of the beam attenuation coefficient to near-forward, scattered light will increase with absorption and are easily measurable on an individual particle basis. Thus indirect methods of observing opacity effects are available for possible use as fecal pellet discriminators. Also, fluorescent

properties of fecal pellets may be useful as they should contain more products of pigment degradation such as phaeophytin, than do those of phytoplankton. This additional measurable should be considered for pellet discrimination.

C. Devices and Studies

C1. Marine Aggregate Survey Camera (MASC)

The abundance and size frequency distribution of aggregates may be determined by analyzing in situ video images of an illuminated volume of water. This volume is defined by a linear collimated light "slice" extending normal to the axis of a video camera. In the interests of great economies in costs, development time, and other resources, it is proposed that the instrument initially utilize commercially available TV cameras, recorders, and displays, with currently available resolutions and TV formats. As higher resolution systems reach the commercial market, it would be a simple matter to upgrade the cameras without altering the rest of the system.

The low resolution of commercially available TV systems, compared to either the highest pixel count charge-coupled detector (CCD) arrays of photographic systems, and the need to count and/or size aggregates over very large size ranges requires that more than one camera should be used, each with a different focal length and field-of-view.

As the system is towed through the water, aggregates entering the illuminated volume scatter light into the camera. The images produced represent the integral of all illumination received at each pixel so that a continuous volume of water is imaged as the system moves through the water. The dimensions of the illumination and imaging system are determined by the expected sizes of the aggregates and the resolution of currently available CCD imaging chips. For example, a 400 x 300 pixel chip yields an ultimate

resolution of 500 μm per pixel for a 20 x 15 cm illuminated area in the water. This primary image is designed to assess the abundance of macro-aggregates and is supplemented by a second camera with a 2 cm field width and 50 μm resolution, aimed at assessing the abundance of micro-aggregates. A photographic camera in this mode would provide resolution to less than 10 μm if needed.

The system is mounted on a towed fish configured to cycle between the surface and the maximum depth of interest at speeds up to 5 knots. Data are transmitted up the tow cable for realtime viewing and storage on a magnetic medium. Alternatively, the images could be analyzed in real time and the numbers and size frequency distributions of aggregates determined by pattern recognition algorithms. Displays could include size histograms or continuous two-dimensional contour plots of abundance.

Important surveying parameters for the MASC involve sample volume and volume sampling rate, both of which are simple to calculate. The sample volume, VS, interrogated by each frame is simply:

$$VS = \frac{h \times w \times (\text{ship velocity})}{\text{sampling rate}}$$

$$h = 15 \text{ cm}$$

$$w = 20 \text{ cm}$$

$$\text{sampling rate} = 30 \text{ Hz}$$

A ship speed of 1 knot results in a sample volume of 0.5 liters per frame. The flow-through rate, RV, of this surveying instrument is the above

volume times the sampling rate and is 15 liters/second or 54,000 liters/hour. For 5 knot ship speed this became 2.5 liters for VS and 270,000 liters/hour for RV. Towing speed would be determined by the maximum speed of the towed fish and the sample concentration.

For the design suggested, in which the high-resolution camera has 10 times the resolution of the other, the higher resolution camera would experience a flow rate and sample volume 1/100 of the above.

Background light may be a problem in surface waters during daylight if the radiance of the particles in the sample sheet beam is less than the radiance of the background as seen by the camera. This problem can be minimized if the camera is stopped down until it barely sees the background illumination (correspondingly increasing the depth-of-focus), and if the aggregates still scatter enough light to be seen against the dark background. Correspondingly, the effects of any bioluminescence stimulated by the aggregate's passage through the sheet can be minimized if the intensity of the sheet beam can be made as bright as possible.

It is clear that the effective depth-of-field of such a camera system will be determined either by the thickness of the sheet beams, or the optical depth-of-focus of the camera system, whichever is less. The narrow field-of-view camera may require a correspondingly narrow sheet-beam thickness to reach the maximum achievable resolution. These trade-offs must be studied during early engineering design studies.

C2. Laboratory Studies of Optical Properties of Aggregates

It is recommended that a variety of optical measurements of aggregates be

made based upon a generalized multiangle configuration. This structure could be comprised of a laser source, an array of detector positions from very small scattering angles ($<10^\circ$) to large angles ($<170^\circ$). Near-forward scattering can be measured by focusing a collimated laser beam onto a small stop ($<10\text{ }\mu\text{m}$ diameter) on an area array detector. Non-parallel scattered light will fall beyond the stops and can be measured in great detail. Measurement of scattering at larger angles is straightforward.

Although extant instruments have most of these features, the measurement of scattering at very small angles, together with larger angle scattering in the same instrument must be achieved. While such design modifications are being pursued, a variety of preliminary measurements using separate, existing small-angle and large-angle devices should be undertaken. In this manner, aggregates of various compositions may be examined for the purpose of characterizing optical observables. Integrating these scattering data over all scattering angles, realistic extinction coefficients for aggregates of various classes could be estimated for those structures whose theoretical values cannot be calculated.

Among the types of light scattering measurements that may yield meaningful observables are:

- 1) Intensity values versus angle: These measurements could form the basis for comparison of the measured values of the extinction and volume scattering coefficients with those theoretically derived or predicted.
- 2) Fluorescent properties: Laser stimulation with this device will also permit spectral observations of fluorescence for discrimination of many pigments and their degradation products.

- 3) Depolarization measurements as a function of θ and ϕ : The degree of depolarization of scattered light for a fixed incident polarization state provides an excellent measure of the scatterer's asphericity, birefringence, optical activity, refractivity, and/or intrinsic multiple-scattering properties. Aggregates of particulates having any of these properties will produce varying degrees of depolarization whose measurement may prove a particularly attractive means for classification.
- 4) Settling and dynamic measurements: Settling rates and tumbling characteristics for selected structures may be measured based on the temporal recording of their light scattering properties during their motion through an inhomogeneous laser source. Simultaneous sequential images will provide particle size, shape, dynamics and identification. Such measurements will provide important information concerning aggregate density and mass distributions that could aid further in their classification.

The light absorption characteristics of marine snow and aggregates are important for the classification of these particles. Specifically, through the use of either a reflecting tube, or integrating sphere-based absorption meter the quantitative measurement of the absorption coefficient can be made on a "per aggregate" basis. By performing these measurements for visible wavelengths the absorption of the particulate components, including photosynthetic pigments will be determined. Because of the potential significance of non-particulate exudates and pigment degradation products in the composition of aggregates, it would be of value to measure total absorption at shorter wavelengths as well, perhaps even in the ultraviolet.

Fluorometry is an essential technique for laboratory-based aggregate particle classification. An effort should be made to define the optimal excitation and emission bandwidths for aggregate analysis. Spectrofluorometric techniques should be used to assess the chlorophyll and pheopigment composition of the aggregates. Additionally, an emphasis on ultraviolet excitation may be important for measurement of pore water-dissolved organic matter. Lab measurements must be intensive enough to define the optimal wavelengths for eventual use of in situ fluorometry in aggregate classification. The use of fluorometry is also suggested as a means of assessing internal aggregate flushing or perfusion rates. The fluorescence history of an aggregate as it falls through (and past) a discrete layer of fluorescent dye should provide some measure of the rate of exchange of water in the aggregate in a quiescent environment.

During the course of this program, large numbers of images of various types will be collected for subsequent analysis and as permanent records. These images can be manipulated to recover information not readily apparent, to increase signal-to-noise rates, to increase contrast, etc. Image analysis can be used to recover information on aggregates such as size, shape, orientation, area, circumference and texture or homogeneity. A search for image characteristics unique to certain classes of aggregates is a very high priority in order to automate the identification and analysis of aggregates from imagery.

C3. Holographic/Photographic Camera System for Use in Sediment Traps

Aggregate fall velocity can be determined in situ in damped sediment traps by acquiring sequential holograms (Carder et al, 1982) or photographs. The

advantage of holography is magnification without loss of depth of field. Other settling techniques, such as time of flight of particles settling through narrow light beams, can also be exploited.

The porosity and permeability of aggregates affect their fall velocity and dynamic density (inversion of Stokes' equation). Methods for assessing these characteristics can be determined holographically by observing aggregates settling through density interfaces and measuring the volume of low density, low refractive index fluid flushed from the aggregate pores into the denser, more refractive layer (Carder, Steward, and Costello, this report).

Organic-rich aggregates in a density gradient will continue to settle to a depth with density equal to that of the average of the non-fluid structural components of the aggregate. This structural density value together with the dynamic density of the aggregate provides a measure of its porosity.

Isotonic solutions as dense as 1.4 g/ml can be developed using heavy water-saline metrizamide solutions. Denser, inorganic-rich aggregates may be buoyed by denser solutions such as Maxidens (density = 1.9 g/ml).

C4. In situ, Lagrangian Observations of Particle Interactions

To observe the fate over prolonged time of marine snow particles which are suspended in the water column we propose the following system:

- 1) an optical system, called a Spatially Filtered Camera (SFC), similar to the one used in Strickler (1977, 1982, 1985) which will allow the observation of suspended particles in situ and in real time in a sample volume of typically 2 ml with a resolution of better than 10 μ m.

- 2) an interface between the optical system and its transport system, e.g. videocable if the transport system is a submarine, targeting sights and in situ TV monitors for divers. With such an SFC it will be possible to observe:

- a) the formation and "life" of a particle over a time period of up to 5 hours;
- b) any interaction this particle may have with other particles and/or live animals during the observation time;
- c) the desirability of capturing the particle for subsequent in vitro analyses.

The SFC would consist of two units, the laser and collimating unit and the imaging unit with the imaging lens and the TV camera. The second unit would contain also a mini-VCR and a mini-TV monitor if the transport system is a diver.

A first prototype of a SFC with divers as transport system is at the moment under construction and the first results have shown that it will produce data which are comparable in resolution and information content to results from laboratory experiments. The interface between the SFC and a submarine (e.g. Sea-Link of the Harbor Branch Oceanographic Institution) may include a digital transmitter of the video signals to facilitate using light fibers as a link.

Using manned submarines as transport systems will limit the range for deployment. In a later stage, it may become mandatory to observe the fate of particles over longer time periods and/or in greater depths. Unmanned remote controlled vehicles could then be used to transport the SFC, especially when the interface facilitates a real time link between the SFC/vehicle and the observer/driver of the vehicle.

D. Recommendations: Optics Working Group

1. Develop a marine aggregate survey instrument, MASC;
2. Develop laboratory instruments for shipboard use to determine the optical characteristics of aggregates and living organisms in order to develop aggregate discrimination strategies;
3. Use and improve existing sediment trap mounted holographic and photographic systems to measure aggregate size, shape, orientation, settling speed, density, porosity, and permeability;
4. Develop in situ Schlieren camera (the SFC) for studying particle interactions over time (hours).
5. Develop accessory instruments, based upon studies under 2 (above), to provide certain identification of aggregates, even in waters high in plankton. This approach should provide accurate size frequency information for aggregates even in waters of complex particle characterization.

Rationale for the Recommendations

There is an immediate need for survey instruments for assessing aggregate size-frequency distributions and for studies of the distribution and abundance of these ubiquitous marine particles.

The MASC instrument will be most effective below the surface waters where aggregates dominate the particle field. Optical studies of aggregates are needed to determine how best to discriminate between aggregates and plankton in surface waters. While these problems are being solved, work should proceed with available instruments in order to characterize aggregate dynamics,

including animal-particle interactions. The instruments that can do this are 1) the holographic/photographic camera system for use in sediment traps (see section C.3) and 2) the Spatially Filtered Camera (C.4), respectively.

Developing instruments that can remotely identify, size and enumerate aggregates is an important goal of this program. Laboratory studies are expected to lead to design criteria for robust aggregate discrimination.

WORKING GROUP III: IN SITU EXPLOITABLE PROPERTIES
OF AGGREGATES: OTHER PROPERTIES

Rapporteurs: D. L. Mackas, T. K. Stanton

Members: R. Bidigare, J. Bishop, J. Brooks, K. Bruland, C. Lee,
K. Stolzenbach, M. Tyler, N. Welschmeyer, M. Youngbluth

1. Introduction

Our working group was asked to evaluate the methods (other than optical) which would be most useful for improving understanding of non-living organic particles in the ocean. We identified three major categories of desirable observations and techniques. The first includes measurements relating to the distribution and classification of aggregate populations in the ocean. These provide information on the demography of the particle population. What kinds of particles are present? What is the size spectrum of each class? What are their spatial and temporal concentration fields? We also included under this heading methods for collection of samples from natural particle populations.

A second group of observations relate to the production, persistence and eventual fate of the particles in each class identified above. These measurements should describe and quantify the expected "life history" of particles. They provide information on the type and rate of the dynamic processes that create and modify the observed demographic distributions.

A third group of observations is needed to characterize the local oceanographic environment in which the particles reside. Both the distribution and dynamics of non-living aggregates are likely to vary with spatial and temporal changes in environmental properties and conditions, especially those affecting the frequency and effectiveness of encounters between particles (both living and non-living).

We recommend application and (where necessary) development of the instruments and analytical methods described in the remainder of the report. For logical convenience, we consider the methods and approaches in the sequential order listed above. Our ratings of relative importance and feasibility are given in the body of the text.

2. Detection, Classification, Census, and Capture Methods.

Detection and location may involve the optical techniques discussed by the optics working group, or the sonar, particle counting, and visual observation techniques outlined in this section. Because the occurrence of marine snow is so wide-spread in the ocean, it is important that the detection and location techniques be rapid enough that the temporal and spatial variability may be measured. The measurements may often give some information on particle properties. For example, visual detection (by divers or camera) could describe size and shape of at least the larger particles. However, measurements of most important particle characteristics (e.g., their chemical and biotic composition) will require prior concentration and separation steps to allow collection of sufficient material and analysis by sophisticated laboratory techniques. Because details of the concentration field will often be of interest, it is essential that sampling methods be able to resolve local patches and layers. Because not all of the desired measurements can be made in situ, samples of the aggregate population will need to be captured for laboratory analysis and experimentation. Some aggregates are very fragile and porous, hence the capture methods should be gentle and non-disruptive to avoid altering important particle properties. Because the size, composition and origin of the aggregates are so diversified (even at a single location), the capture techniques must be selective so that analyses may be performed on targeted subsets of the total particle population.

Because of the large volumes of water that sonar systems can scan in a short period of time (order $10^7 \text{ m}^3 \text{ hour}^{-1}$), it would probably be desirable to employ this technique in at least a preliminary survey mode. Acoustics could be used in two ways. The first is direct detection of the marine snow to determine its location and perhaps abundance. Marine snow aggregates may have such a small scattering cross section that they are not detectable on an individual basis. However, when occurring at sufficiently high densities it is possible that they can be "seen" acoustically when their collective echo is received. A second approach involves indirectly locating the snow by directly detecting other scatterers such as marine biota. Many organisms will have a scattering cross section much larger than that of marine snow and hence will be more readily detectable. However, their distribution may be linked to that of the non-living aggregates. Thus, scanning a large area and locating these detectable objects may give a clue as to the location of the marine snow.

Flow-through particle counters (optical and resistive) may also be useful as survey tools. A major limitation for these is the probability of particle breakup when larger aggregates are drawn through the sensor orifice. For porous aggregates, the two particle sensing methods will give very different estimates of particle size. Optical counters detect a cross-sectional area (the size of the "shaded" area as the particle passes through the sensor). Interstitial pore space will typically be included in this estimate. Resistive counters record the volume of the non-conductive particle. The interstitial water in a porous aggregate will be conductive, hence the volume estimate will be of only the particulate phase. If problems with particle breakup can be minimized, it may be possible to combine these different types of data in a useful way. By knowing the "shadow" area, the total occupied volume (including interstitial water) can be estimated for

simple external particle geometries. The ratio of particulate volume to the total volume would then provide an estimate of aggregate porosity.

Aggregates have been physically collected with bottles, in situ pumping systems, and traps. These devices can be tethered on wires, deployed on free vehicles, operated by divers, and attached to submersibles. Future use of these collectors to sample aggregates (such as marine snow particles and fecal material) should incorporate video (or photographic) and environmental data logging (depth, temperature, conductivity, fluorescence and transmittance) instruments into a sampling package in order to provide useful information about the natural state of the aggregates and the conditions under which aggregates were collected.

The selection of a particular sampler for aggregates should take into account: (1) the degree to which aggregates are likely to be physically altered, (2) the sample size and replication required for analysis, (3) the scales of sampling needed (spatial, temporal, and regional), and (4) the need to separate aggregates into different type classes and from organisms not associated with the aggregates. Present collection methods, when used in conjunction with visual observation by divers or from submersibles, allow both gentle and selective sampling of the larger aggregates (roughly 1 mm and larger). The smaller aggregates are probably less vulnerable to mechanical disruption, but non-selectivity of sampling is a major limitation.

Two modes of particle collection are envisioned: (1) profile studies of the water column over large spatial scales (km to 100's of km) and (2) localized studies of aggregates over scales of tens of meters. The profile studies provide information on large scale patchiness and the relationship between aggregate distributions and the physical and biotic characteristics of the water column. Local sampling can be guided by the aggregate and environmental profiles and by visual observations to give an expanded view of

particular areas of interest. For example, scientists could use a submersible or oceanographic information such as pycnocline depth to select a target area for study. An in situ filtration system fitted with several filter channels, each permitting the collection of several mgs of materials, could be activated to sample specific classes of aggregates as determined by high resolution video information. The filtration rate should be both high enough to capture the desired aggregate, and low enough to minimize the disruption of the collected materials.

Profile sampling with a multiple unit large volume in situ filtration system can collect milligram quantities of size-fractionated samples of aggregates from the water column. The slow filtration rate of the system (approximately 1 cm sec^{-1}) enables the collection of aggregates ranging from delicate gelatinous diatom colonies to robust fecal pellets. More fragile aggregates can be sampled by reducing the filtration rates.

At least two new capture devices should be developed: (1) a sampler to collect fluff at the water/sediment interface and (2) an in situ flow cytometer to characterize small ($<0.5 \text{ mm}$) aggregates.

3. Measurement of Particle Properties Relating to Source, Persistence, and Fate

3.1 Mechanical Properties

3.1.1 Size and Shape

Because of their flexibility and fragility, the size and shape of marine snow aggregates should, if possible, be determined in situ using non-intrusive techniques. A combination of different optical methods (imaging, shadowgraphs, etc.) is the most likely method for this determination.

Specifications of size and shape for a complex form such as a marine snow aggregate must be done jointly and in terms appropriate for the process of interest. For example, the size measure (cross-sectional area) most

related to interception of smaller particles is not the same as the size measure (surface area) determining viscous drag (and thus velocity). If the aggregate is porous, in the sense of having an appreciable exchange of the internal fluid, the internal structure will be an important component of the shape and size parameterization.

3.1.2 Fragility and Flexibility

Marine snow aggregates are complex materials being at the same time viscous, elastic and compressible. The flexibility of the aggregates may be a factor in determining changes in the physical structure over time (e.g., compaction leading to higher densities) and in mediating biological and chemical interactions within the aggregate (how "well-stirred" is an aggregate?). Fragility will be important if it sets an upper limit on the size and thus the "age" of the aggregate and if aggregate breakup is a significant source of smaller particles in the water column. It is crucial to know if the physical process of aggregate breakup is a significant source of smaller particles in the water column (of comparable magnitude to chemical and biological degradation).

Marine snow aggregates may be deformed and possibly broken up by the action of local fluid motion. In the interior of the oceanic water column, marine snow particles are smaller than the turbulent microscale and will thus experience a viscous shearing regime. However, within bottom boundary layers, at pycnoclines in the presence of internal waves, and at the water surface, marine snow may be exposed to more complex turbulent fluid motions.

No generally applicable model exists for either the rate of deformation or the fracture strength of composite materials such as marine snow. Thus, aggregate behavior in the presence of fluid shear must be determined empirically by experiments on actual aggregates and the results correlated with other observable properties to the extent possible. These experiments

should provide a fluid environment with a controlled rate of shear and should enable observations of threshold shear for breakup and the rate and mode of breakup (surface erosion vs. ripping in half vs. shattering into many pieces).

3.1.3 Settling Velocity

The settling of aggregates promotes collisions with smaller particles and may determine the residence time of the aggregates in the water column. Settling velocity is determined by the aggregate size, shape, and density. Of these, the effective density is the most difficult to determine because of the complexity and fragility of the aggregates. Thus, it is likely that settling velocity will have to be determined directly by observation, and correlated with size and shape (including perhaps porosity). Settling velocity determinations are probably best done in situ using optical (unaided or otherwise) methods.

3.1.4 Permeability

Many aggregates are known to be structurally "open"; they contain interstitial water that can exchange with the surrounding fluid. The rate of this exchange is important to many aspects of particle dynamics. Flow at and near the particle "boundary" will vary with the extent to which streamlines can intersect this boundary. The extent to which the particle interior represents a chemical environment different from the outside world depends on the balance between chemical reaction rates and the rate of diffusion of dissolved reactants and products into and out of the particle. The rate of leakage of chemical attractants (and their stability in the outside environment) will determine their concentration field in the vicinity of aggregates and will thus strongly affect the rates of "volitional" encounters with living particles that use these chemical cues to guide their swimming pattern. For a permeable particle, the time history of internal concentrations of natural or artificial dissolved tracers will tend to follow

(with bond smoothing and time lag) the history of concentration in the surrounding fluid; the extent of smoothing and the length of the lag will covary inversely with the permeability of the particle. Laboratory measurements of the rate of gain or loss of dissolved tracers from particles sinking through a tracer gradient or "spike" thus provide one possible methodological approach for measurement of permeability.

3.1.5 Acoustic Estimation of Density

The density (mass per unit volume) of the marine snow is an important quantity as it dictates in part the settling rate of the particles and also gives an indication of its origin and composition. There are many techniques to measure the density of objects; however, they typically require removing the object from its natural environment. Because marine aggregates are fragile and porous, measurements of density outside the natural environment may not be representative of the true in situ value. An in situ non-invasive technique would therefore be desirable. In general, acoustic techniques are attractive both because they are non-destructive and because they can be applied in situ at many or all of the depths at which marine snow is found.

The acoustical scattering cross section depends on the size, shape, and specific density and compressibility of the scattering particle. It is possible under appropriate experimental conditions that the specific density of the scatterer can be isolated, hence allowing in situ measurement of density. Many or all of the aggregates of interest may have very small acoustic cross sections (they may be nearly "transparent" to sound). If this is the case, the result of the measurement would not be specific density, but rather an upper bound on density. Either way, the acoustically derived information is useful, especially if interpreted in conjunction with density measurements by other techniques.

3.2 Glue, Stickiness and Charge

Very little is known about the forces which cause marine aggregates to coalesce. The "stickiness" of a particle or the likelihood of aggregation is dependent on factors like electrostatic charge and the rate and strength of covalent bond formation. Charge is dependent upon the particular organic or inorganic functional groups present in the aggregate. For example, clay minerals are charged bodies whose natural repulsion can be reduced by organic coatings. We recommend laboratory and field studies of the relationship between coagulation efficiency (fraction of particle collisions which result in aggregation) and chemical composition of the colliding particles. Chemical composition of the dissolved organic matter in the surrounding fluid may also need to be considered.

3.3 Compositional Tracers of Age and Origin

The working group was very enthusiastic about the potential interpretive value of measurements describing the age and source of particles at different places in the water column. A number of investigators have used microscopy to examine the compositional makeup of organic aggregates; our present understanding of particle origin is based largely on these measurements. Chemical, biochemical, and isotopic tracers offer additional opportunities to study aggregates. So far, their use has been restricted to suspended and sediment trap particles. There is enough known at this time to strongly suggest their usefulness to studies on marine aggregates; however, this application will require rigorous evaluation of each approach. Studies of natural environments in which the aggregate population is transient (for example inlets from which the ambient population is removed by episodic flushing events) may be of particular value in developing and evaluating these tracer methods.

3.3.1 Microscopic Identification of Aggregate Components

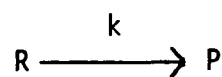
There are a number of properties of marine aggregates that can be identified by means of microscopic techniques which may provide information as to the origin and age of the particle. Most of the existing classification of aggregates is based on this type of information. In many cases observation of bulk structures may give information as to its origin, i.e., intact larvacean houses, zooplankton feeding webs. In other cases, direct microscopic observation can define the nucleus of the particle, i.e., dinoflagellate cyst, diatom spore, fecal pellet. If the snow is degraded, chemical means of identification may be employed as well. Classification of organisms inhabiting (consuming) the particle is possible. Techniques such as fluorescence microscopy can easily distinguish non-pigmented from pigment containing organisms. Techniques such as Nomarski interference microscopy can give information about mucilage structure. Polarization microscopy can use birefringent characteristics to classify mineral matter. Vital cellular stains can distinguish living from non-living components. SEM and TEM may provide information as to the origin of broken or degraded attached particles (i.e., diatom frustule, coccolith) as well as indicate internal structure related to the "health" of intact particles. Epifluorescence microscopy is capable of enumerating and distinguishing bacteria from eukaryotes. Immunofluorescent properties can measure the activity of living components of the aggregate as well as provide a tag for origins of individual subparticles.

Once the components are identified, diversity of the biotic community present on and within the particle might be used to indicate age. For example, newly formed aggregates may be inhabited only by a few bacteria. Their number and activity may help define the length of time the particle has been in the water column. As the particle becomes bacteria laden, it provides prime feeding sites for higher trophic level consumers such as heterotrophic

flagellates and ciliates. The types of organisms inhabiting the particle may give clues to the site of particle formation. For example, some species are indicators of shallow water or benthic environment. Their presence in the snow would indicate that the particle reached its present location by resuspension from the seabed and subsequent lateral transport rather than by vertical flux from pelagic surface waters.

3.3.2 Specific Organic Compounds

Organic compounds in particle aggregates reflect the age and source of those particles. By measuring the composition and quantities of certain individual compounds, we can estimate the age and source of an aggregate. Age can be determined by taking advantage of the basic kinetic properties of chemical reactions of biogenic organic compounds. Compounds have given stabilities on particles and are decomposed or transformed at rates which depend on the nature of the compound and on the environment in which it exists. The compounds decompose or are transformed according to the following simplified scheme:



where R is the reactant,

P is the product, and

k is the assumed first-order rate constant

By measuring concentrations of R and P in a particle, and using an experimentally determined k, we can calculate the length of time R has been present on a particle. If we calculate ages for several classes of compounds produced during formation of the particles, we can estimate an average age for

the aggregate. Choosing compounds which react at different rates, e.g., minutes versus days, we can estimate ages for particles with different life spans.

As an example, the dating technique which has been used most frequently by organic geochemists exploits a chemical reaction, the racemization of amino acids. With time, the L-enantiomers racemize, eventually reaching equilibrium with the corresponding D-amino acids. The ratio of D/L amino acid and the racemization rate constant, k , can be used to calculate the time elapsed since all the amino acids were in the L-form. Theoretically, any organic compound which undergoes a decomposition or transformation reaction can be used in this manner. For dating particles, compounds which are chemically unstable on a time scale of hours to days may be most useful, e.g., carotenoids and other pigments. For example, diadinoxanthin, a carotenoid found in diatoms, dinoflagellates and prymnesiophytes, quickly undergoes a light-induced, reversible de-epoxidation reaction to form diatoxanthin. It also may be possible to determine k values for biological consumption of organic compounds on particles and use biological rate constants in a similar way.

In addition to the kinetic approach, organic biomarkers can be used to estimate particle history. For example, an aggregate that is composed of senescent diatoms would have significant concentrations of chlorophyllide a (chlorophyll minus the phytol side chain) as a result of the chlorophyllase that is released when cells lyse. However, an aggregate composed of diatoms that have been grazed would be composed predominantly of phaeophorbide a (chlorophyll minus phytol and Mg) due to the chemical environment in a zooplankton gut. This type of marker provides important information on the history of a particle to supplement the kinetic approach to aggregate dating.

Individual organic compounds reflect the source as well as the age of a particle. Certain compounds are found only in a taxonomically restricted set of organisms. This specifically can be used to determine the source of particles within an aggregate. For example, chlorophyll a can be used as a general index of phytoplankton biomass, while specific accessory pigments can be used as diagnostic tags for identifying the source of the algal material. Chlorophyll b, fucoxanthin, peridinin, phycoerythrin, and hexanoyloxyfucoxanthin are characteristic biomarkers of green algae, diatoms, dinoflagellates, cyanobacteria, and prymnesiophytes, respectively. Fucoxanthinol and fucoxanthin 5'-dehydrate are specifically produced as the result of heterotrophic and microbial metabolism, respectively. Steroidal alcohols such as dinosterol, diatomsterol, brassicasterol, etc. are specific source indicators. There are potentially hundreds of organic molecules that may be specific to particular taxonomic groups.

Molecular markers have been used to differentiate more broadly between terrestrial and marine organic matter. Such markers include sterols (terrestrial sterols are enriched in 8-sitosterol), hydrocarbons (terrestrial hydrocarbons are enriched in odd number *n*-alkanes between C_{23} and C_{31}), lignins, fatty acids, selected polynuclear aromatic hydrocarbons, etc. These terrestrial/marine source markers could be used to determine whether the source of organic matter in an aggregate was from water column primary production or from material transported from a terrestrial source.

3.3.3 Isotopic and Inorganic Tracers of Source and Age

Isotopic and inorganic tracers provide powerful constraints for determining both the source and age of marine aggregates. These tracers can be used on either the bulk aggregates or on particular components of the aggregates and so provide information of very different kinds. Stable isotopic composition can yield information on environments of formation and

transformation pathways. Radioactive isotopes serve as time clocks for transport and reaction, yielding information unavailable from other techniques. Further information on the source and age of aggregates may be determined from other inorganic compositional information such as the clay mineral composition.

The fractionation between the stable isotopes of carbon, nitrogen, oxygen, hydrogen and sulfur is determined by the source of material in the aggregates and by the transformation pathways of this material. For example, oxygen isotopic measurements of material (in particular, foraminifera) reaching deep moored sediment traps have monitored seasonal events in the upper water column as reflected in sinking particulate matter reaching the traps. The depths and time of origin of material can be estimated from its isotopic composition. The offset between the times of origin and arrival in the sediment traps gives an unambiguous determination of settling rates.

Radioisotopes such as carbon-14, beryllium-7, and isotopes of the uranium- and thorium-decay series are natural chronometers of events because their decay occurs at a fixed rate for each isotope (generally expressed as a half-life for decay). The isotopes of thorium have proven particularly useful for studies of transformation and aging. Thorium has strong hydrolysis characteristics and thus rapidly adsorbs to solids. The decay rates of the various thorium isotopes range over six orders of magnitude, from thorium-234 (half-life of 24 days) to thorium-230 (half-life of eighty thousand years). Studies of thorium-234, 228 and 230, each with identical chemical behavior but differing decay rates, have yielded important information on particle residence times and transformation rates in both the deep sea and in surface waters. Another promising measure of particle residence times in the water column involves the use of beryllium-7, produced in the stratosphere and with a short (53 day) half-life. It is delivered to the surface waters from the

atmosphere and its presence in particles in the deep sea is indicative of relatively rapid vertical transport from the surface layers.

Inorganic tags such as clay mineral assemblages have proven to be extremely useful in tracing both the source and movement of particulates in the ocean. Clay minerals may be particularly useful for distinguishing sediment resuspension and lateral transport from atmospheric input to the surface layers coupled with vertical transport.

The condition of the biogenic hard parts (opal, calcite and aragonite, and celestite) is indicative of the environments to which they have been exposed and the duration of exposure. For example, the extent of dissolution and fragmentation provides information on the age of these components and the physical and chemical processes to which they have been exposed.

Isotopic and inorganic tracers, in conjunction with the specific organic and microscopic approaches, can add valuable source and age information to studies of the distribution and dynamics of marine aggregates.

4. Supporting Oceanographic Measurements

Field measurements of aggregate distribution and dynamics will need to be supported by a suite of oceanographic measurements. Information about the local physical environment is needed to interpret aggregate movement and dispersal as well as the physical controlled subset of aggregate formation and disruption mechanisms. Chemical information is needed to interpret rates of dissolution and decomposition, and to describe ambient concentrations of selected isotopic and chemical tracers. Biological measurements are needed to estimate the importance of organisms producing or repackaging non-living organic matter, to establish local biotic tracers, and to establish correlations (or lack of correlation) with the amount and seasonality of biological productivity. The potential shopping list is very long; we have tried to highlight some of the most important variables.

4.1 Physical Measurements

These should at minimum include the following:

Vertical profiles of temperature and salinity allow calculation of density and viscosity profiles of prediction of settling velocities. It is possible, however, that in some environments the viscosity may be modified by the amount and composition of dissolved organic matter. The density field also largely controls the vertical distribution of velocity shear (discussed next).

Small scale shear (over scales of a few mm to cm, typically measured as the rate of kinetic energy dissipation) affects the encounter rates of particles (production of larger particles by accretion), and will also determine the importance of mechanical disruption as a loss mechanism for portions of the overall size spectrum (by conversion of large particles into smaller units).

Kinetic energy inputs at seabed and sea-surface interfaces control the rates of resuspension of bottom sediment and bubble injection. They will also (over greater time and space scales) control the amount and distribution of velocity shear within the water column, e.g., by determining the sharpness of internal density gradients.

Mean velocity profiles and sections are valuable for estimating the rate of lateral transport of slowly sinking particulates. This may not be needed for all studies; however, it will be extremely important where inputs are spatially localized, e.g., resuspension of sediment from continental margins by high energy boundary currents and subsequent transport into the deep sea.

Incident light and water-column attenuation properties determine the potential for photochemical transformation processes.

4.2 Biological and Chemical Environmental Variables

The formation and fate of marine micro-aggregates is closely related to the composition and activity of planktonic organisms (auto- and heterotrophs), and to non-living substances that serve as nuclei and agglutinating agents. The latter include both particulate and dissolved substances. In order to develop an understanding of micro-aggregate dynamics, the biological and chemical characteristics of the water column must obviously be known. These characteristics can be broadly divided into three groups: 1) standing stocks; 2) activities; and 3) food web structure. Appropriate variables within these groups are listed below:

1. Standing stocks
 - a. nutrients
 - b. dissolved organic matter
 - c. non-living particulate matter (other than aggregates)
 - d. algal crop
 - e. bacterial crop
 - f. microheterotrophs
 - g. zooplankton
2. Biological activity
 - a. primary production, including DOC leakage
 - b. heterotrophic bacterial production
 - c. zooplankton grazing (micro- and macro-) and rate of fecal pellet production
3. Food Web Structure
 - a. phytoplankton composition (algal groups; or species in those cases where aggregate-formers are obvious, i.e., *Phaeocystis* sp.)
 - b. relative abundances of micro- and macro-zooplankton
 - c. relative abundances of crustaceans and gelatinous zooplankton, and absolute abundance of known aggregate producers such as larvaceans and pteropods.

Aggregate formation is expected to be related strongly to biological/chemical conditions in the upper ocean (euphotic zone), but repackaging and transformations will continue throughout the water column. For these reasons, chemical and biological measurements must be made over relatively large space scales, especially in those cases where migrating organisms could influence formation or loss of aggregates. Some of the

variables listed above are of major importance, but are problematic from a methodological standpoint (especially for large scale survey sampling). Dissolved organic matter, for example, is difficult to characterize and quantify, due to its complex chemical nature. Many of the gelatinous zooplankton, although major mucus producers, are fragile and difficult to census by standard methods. New methodologies may be appropriate here.

CHARACTERISTICS AND DISTRIBUTIONS OF MARINE AGGREGATES

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"When I think of the floor of the deep sea, the single, overwhelming fact that possesses my imagination is the accumulation of sediments. I see always the steady, unremitting, downward drift of materials from above, flake upon flake, layer upon layer - a drift that has continued for hundreds of millions of years, that will go on as long as there are seas and continents. . . . For the sediments are the materials of the most stupendous snowfall the earth has ever seen. . . ." Rachael Carson, The Sea Around Us

INTRODUCTION

Early interest in non-living particulates was stirred by direct observations of large, amorphous flocs in coastal and deep waters. Most of the subsequent oceanographic research on particles, however, concerned itself with smaller, more numerically abundant and generally refractive particles. Only recently has attention returned to the visible, rarer flocs of detritus. The purpose of this brief review is to summarize discoveries regarding some of the biologically significant features and behavior of these large suspended flocs. The review will highlight discoveries about the particles that have been called marine snow, because these are hypothesized to be particularly important as centers of microbial activity in the water and to play central roles in geochemical cycles as they settle into the deep sea.

CHARACTERISTICS OF PARTICLES

Aggregates and Marine Snow

Historically, studies on naturally occurring particulates in seawater developed simultaneously in two distinctive schools. One is based on a tradition of in situ observations of particles, and was exemplified by the reports of a number of Japanese researchers. Early in the 1940s and 1950s these workers called attention to the large, fragile, readily visible flocs of material that occurred particularly in shallow coastal seas but also in deeper waters. Japanese researchers named these "marine snow" (Suzuki and Kato, 1953) after the "long snowfall" of sedimentary material described by Rachael Carson (1951). Particles were photographed underwater (Suzuki and Kato, 1953; Nishizawa et al., 1954), gently collected by hand and good descriptions of them published, including information on the associated organisms and detritus (Tsujita, 1952). Even sinking rates of submersible collected flocs were measured (Kajihara, 1971) and their origins and importance discussed as unique microenvironments in the pelagic zone (Suzuki and Kato, 1953; Nishizawa, 1966: see review in Trent, 1985).

The second tradition of studies on particulates, carried out primarily by North American scientists, studied particles obtained from water bottles. These researchers examined cleared filter preparations, which were dominated by the small, refractory, and numerically abundant size classes. Careful study of these preparations in the 1960s and 1970s led to descriptions of at least three particle classes: "organic aggregates", flakes,

and debris from organisms (Riley, 1963; Riley 1970; Gordon, 1970; Wiebe and Pomeroy, 1972). The term "organic aggregate" was chosen by Riley (1963) to describe a variable class of flocculant, often fragile-appearing conglomerates of smaller particles, materials whose origin was unknown. The aggregates commonly fell in the size range of 25-50 μm (though they exhibited a large size spectrum), stained dominantly with carbohydrate reagents, were occasionally organism-rich, reached sizes up to a mm or more, and were common only in near surface waters. Some of these aggregates may have included remnants of the larger, fragile marine snow, likely broken apart during bottle collection and sample preparation. Flake-like particles were more abundant than aggregates, but were so transparent they were easily missed, unless stained. Flakes tended to be more uniform in size, small (rarely $>50 \mu\text{m}$), thin and scale-like, stained mostly with protein stains, and their abundances changed little with depth. The third class of particles consisted of the fragments or remains of once living organisms, including animal and plant residues.

In the late 1970s and 1980s the two traditions of studying particulates were combined in a series of investigations on the large flocs known to divers and submersible users. Researchers made in situ observations on particle abundances in shallow water, hand-collected the fragile particles, and made quantitative measurements on their contents, extrapolating these observations to indicate the importance of the large particles to the total suspended pool (e.g. Trent et al., 1978; Silver et al., 1978). They retained the term "marine snow", using it to

describe the >0.5 mm particles, which were clearly aggregates of many different types of materials. These studies also were augmented by observations using other methods, including work on particles obtained from large volume pumps and sediment traps, which collect large aggregates or disrupted fragments of them (Bishop et al., 1977; Honjo et al., 1982).

Abundance of marine snow

Most of the records of marine snow abundance have been obtained by divers using a now-standard approach (Trent et al., 1978): divers count the number of particles passing through a hand-held ring, as they swim a horizontal transect whose length is recorded by an attached current meter. With such counting methods, some variability in counts can be expected depending on the ability of the diver to see the particles (related to ambient light, diver's visual acuity, size and color of the aggregates, etc.). Furthermore, there will be some error in sizing the particles, and divers may differ in ability to correctly assess particles as >0.5 mm. Alternative methods of in situ counting involve the monitoring of fragile, larger particles by cameras (Carder et al. 1982; Honjo et al. 1984), with such methods allowing both sizing and counting of particles.

Measurements of marine snow are now available from a variety of near-surface locations, usually in neritic environments. Numbers of particles per liter vary from none to a maximum of 35, with common neritic values being 1-10/l (Table 1) within the normal SCUBA diver range of 0-30m. Even at one site, there is considerable variability in the numbers and sizes of marine snow

over time (e.g. Monterey Bay values, Table 1). Volumes of individual snow aggregates in surface waters have been shown to range between .001 ml and 1 ml with the particles occupying between .006 and .3% of the total water volume (Table 2). Larger mucus flocs are known to occur (Johannes, 1967; Alldredge et al., 1986), though they are probably uncommon. The measurements of marine snow abundances in surface waters, it should be remembered, are usually made at sites known to be good study areas for marine snow (e.g. Monterey Bay), and thus may not be representative of the range of neritic, and certainly not of oceanic, environments.

TABLE 1

Abundances of Flocculent Marine Snow

#S/liter	location	reference
<i>Nearsurface (upper 30 m)</i>		
1.9-2.8	Monterey Bay, Calif.	Trent et al. 1978
0-8.0	Santa Barbara, Calif.	Alldredge, 1979
0-3.7	Gulf of California	"
0.7-14	Monterey Bay, Calif.	Shanks and Trent 1980
1.0-7.0	N.E. Atlantic	"
6.6-12	Monterey Bay, Calif.	Knauer et al. 1982
35	"	Hebel, 1983
9.4-12	Pt. Sur, Calif.	"
1-79	Santa Barbara, Calif.	Prezelin and Alldredge 1983
2.8-5.6	So. Calif. Bight	Beers et al. 1986
0.1-1.0	N.E. Atlantic	Alldredge et al. 1986
1.9-4.0	So. California	"
<i>Deeper Waters</i>		
.001-5.0	Sargasso Sea	Honjo and Asper 1982
0.2-7.5	California Current (off Monterey)	"
0.2-0.6	So. California (60 m depth)	Orzeck and Nielsen 1984
0.0005-.004	Subtropical NW Atlantic (130-650 m)	Alldredge and Youngbluth 1985
0.016-.038	Central Mexico Slope waters (80-900 m)	Alldredge and Silver unpub.
0.13-.005	Central Mexico, oceanic waters 0-400 m	"
0.014-.001	400-3000 m	"
0.5-2.5	Panama Basin (100-3000 m)	Asper, 1986
.0005-.01	NE Atlantic, warm core ring, 100-1000 m	Bishop et al. 1980

TABLE 2

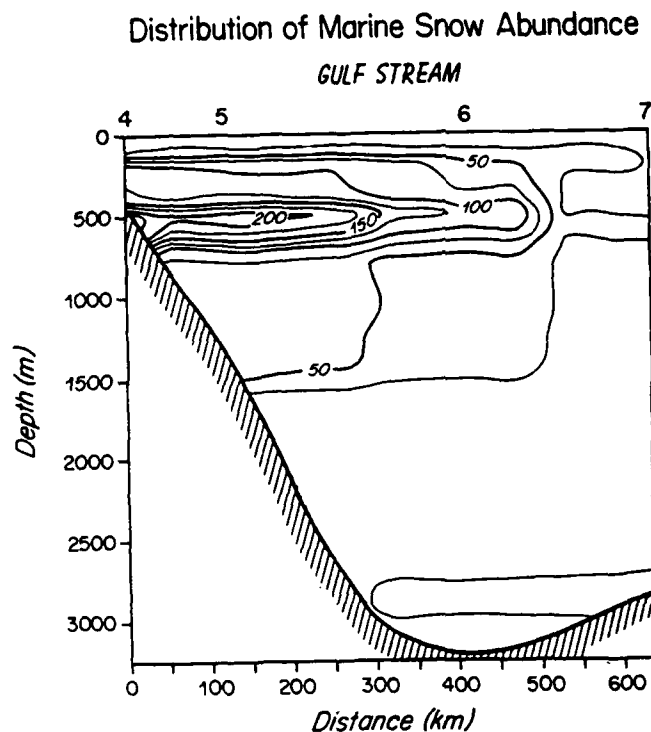
VOLUME OF FLOCCULENT MARINE SNOW FROM SURFACE WATERS

Month	Location	Volume ml/agg.	% of water column	Reference
June	Point Sur	0.025-0.08	<0.1	Hebel, 1983
June	Monterey Bay	0.15	<0.1	Hebel, 1983
July-Sept	Monterey Bay	0.003-2.24	0.01-0.67	Trent et al., 1978
April	Santa Barbara	0.034-1.0	0.1-0.27	Prezelin and Alldredge, 1983
June-Aug	Monterey Bay	0.01-0.29	0.006-0.33	Silver et al., 1978
Feb	So. Calif. Bight	0.08-0.2	0.02-0.04	Beers et al., 1986
March	"	0.01-0.05	0.002-0.009	Beers et al., 1986
Aug	"	0.002-0.2	0.001-0.1	Beers et al., 1986
Apr-June	Monterey Bay	0.0012-0.015	-	Davoll and Silver, 1986

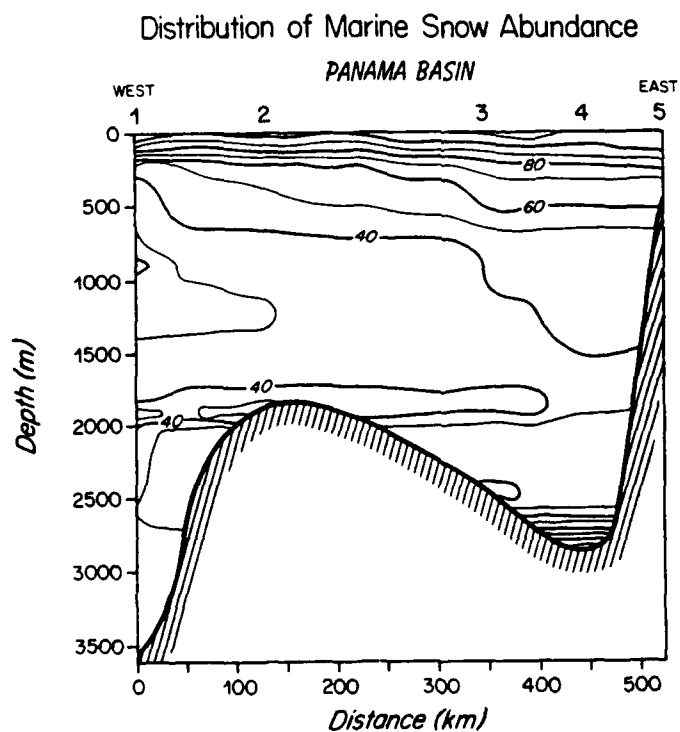
Marine snow is not only a prominent feature of near-surface waters, but has long been noted in deeper environments as well. Methods to quantitatively determine particle concentrations of the fragile aggregates in deep water have included a variety of approaches: techniques almost exactly analogous to the standard SCUBA approach, but with the observer inside a submersible (Silver and Alldredge, 1981); deep saturation divers in the lower euphotic and upper mesopelagic zone (Trent and Orzeck, 1984); in situ, large-volume pumps (Bishop et al., 1977); and remote cameras (Honjo et al., 1984). Observations on marine snow occurrence, using these various methods, are shown in Table 1. Marine snow abundances in the deep sea are considerably lower than in the surface waters, on the average. One important exception is the productive nearshore environment of Monterey Bay, in which the aggregate concentrations remained fairly high, like those of the overlying waters, to the sea floor (Honjo and Asper, 1982).

FIGURE 1. Vertical section showing marine snow volume concentrations (abundance in $\text{mm}^3 \text{L}^{-1}$), from Asper (1986)

a. North west Atlantic



b. Panama Basin



In the most extensive deep-water study to date, Asper (1986) presented vertical oceanographic sections of particles >1 mm in the Panama Basin and the North Atlantic, using the Honjo et al. (1984) camera system. These data, presented mostly as total aggregate volumes (sum of particle volumes for all size classes - in mm^3) show midwater maxima likely due to shelf resuspension in the Atlantic (Fig 1a) and resuspension from the basin sides in the Panama case (Fig 1b). Repeated sampling at the same site showed horizontal patchiness of aggregates on scales of 100s of m, otherwise profiles of abundance appeared relatively stable over the time scales of sampling.

Organic content of marine snow

Various authors have measured the organic contribution of larger aggregates to total suspended material in near-surface water. Such measures indicate marine snow contributions in neritic waters can range from 0 to 63% of the total particulate organic carbon, with these showing C:N ratios like those expected

TABLE 3

CARBON:NITROGEN RATIOS OF
MARINE SNOW FROM SURFACE WATERS

Month	Location	% of total POC on snow	C:N	References
June	Pt. Sur	5	7.1:1	Hebel, 1983
June	Monterey Bay	9	6.2:1	Hebel, 1983
July-Aug	Gulf of California	0-63	11.3:1	Allredge, 1979
Oct-March	Santa Barbara Channel	0-20	9.4:1	Allredge, 1979
April	Santa Barbara Channel	0.7	2.8:1	Prezelin & Allredge 1983
June-July	Monterey Bay	-	7.5:1	Shanks & Tren', 1980
Various	No. Atlantic	-	8.9:1	Caron et al., 1986

of microorganisms (i.e. about 3:1) to the more detrital-like ratios of 11:1 (see Table 3). On an individual particle basis, organic carbon and nitrogen can range from .1-4 ug C and .03-.5 ug N (Table 4).

TABLE 4

POC AND PON CONTENT OF
MARINE SNOW FROM SURFACE WATERS

Month	Location	mean ug C/agg	mean ug N/agg	References
June	Pt. Sur	3.21	0.48	Hebel, 1983
June	Monterey Bay	1.23	0.24	Hebel, 1983
July-Aug	Gulf of California	3.37	0.29	Allredge, 1979
Oct-March	Santa Barbara Channel	4.32	0.46	Allredge, 1979
April	Santa Barbara Channel	0.1	0.03	Prezelin/Allredge, 1983
June-July	Monterey Bay	1.36	0.33	Shanks/Trent, 1980
July	N.E. Atlantic	0.71	0.10	

Photosynthesis on marine snow

One of the most conspicuous features of near surface particles are their accompanying algal cells, noted by the earliest observers (Tsujiita, 1952; Riley, 1963). Such photoautotrophs can be assessed by measuring the chlorophyll a content of snow, found to range between .002 and 3 ug Chl a per aggregate from collections by divers in neritic waters (Table 5). Individual particles have been found to show 3-750 fold enrichments of this photosynthetic pigment over equal volumes of water at the same site and depth (Table 5). The cumulative contribution of chlorophyll on snow particles to the total suspended population has been shown to range between 0.1 and 34% (Table 5). Likewise, these algal cells are known to be actively

fixing carbon, as shown by carbon-14 incubations (Alldredge and Cox, 1982; Knauer et al., 1982; Prezelin and Alldredge, 1983) and oxygen electrode data (Alldredge, pers. commun.,). Contributions of marine snow to total production range from negligible to 58%, depending on the numbers and sizes of the snow particles, and the physiological conditions of the associated algal populations (see discussion in Prezelin and Alldredge, 1983). In general, the role of marine snow as a center for photosynthetic activity reflects its importance as a center for chlorophyll, but relative production rates (i.e. production per unit chlorophyll a) can be lower on snow than in the surrounding water on occasion (Alldredge and Cox, 1982; Prezelin and Alldredge, 1983).

TABLE 5

CHL. A CONTENT OF MARINE SNOW					
Month	Location	$\mu\text{g Chl. a/agg.}$	% of total on snow	Enrichment factor	Reference
July.-Aug.	Monterey Bay	0.0023-0.59	0.1-7.2	4-750	Trent et al., 1978
March-April	Southern California Bight	0.04-3.41	0.6-34	67-442	Alldredge and Cox, 1982
April	Santa Barbara Channel	0.02-0.2	0.3-20	3-74	Prezelin and Alldredge, 1983
March	Southern California Bight	.0002-.009	0.1-1.0	27-540	Beers et al., 1986
August	Southern California Bight	.0004-.003	1.3-1.6	15-72	Beers et al., 1986

Organisms associated with marine snow

The presence of high concentrations of microorganisms on near surface marine snow likely reflects its origins, coagulation efficiency, and status as a habitat. As discussed elsewhere in this workshop (see article by Alldredge), snow can originate from

algal agglomerates, mucus food collection devices, fecal pellets and other processes that give rise to organism-rich particles at their time of formation or release. Likewise the sticky, surface-rich snow can capture additional particles, including organisms, as it moves through the water (McCave, 1984; McCave, this volume). These benthic-like midwater surfaces likely attract organisms seeking refuges, possibly ones that orient to the chemical gradients provided by the chemically enriched microenvironments (Goldman 1984; Mitchell et al. 1985).

Hand collections by SCUBA divers have allowed measurements of the colonizers on marine snow. Data from various sites for different groups of microorganisms associated with the aggregates are shown Table 6. These data show highly variable concentration factors (i.e. organismal concentration on snow/organismal concentration in an equal volume of surrounding water) for microorganisms on marine snow, with concentrations of organisms commonly ranging from 1 to 3 orders of magnitude higher in marine snow than in equal volumes of surrounding water. These observations indicate that marine snow is a microbial center in the water column and that it concentrates some classes of microorganisms more than others.

Most studies on the populations associated with marine snow have been made on aggregates collected in surface water. A few collections have been made using submersibles, allowing studies on the microorganisms associated with single aggregates in deep water, and these are shown in Table 6. Recently, however, extensive saturation, deep-diver experiments have obtained many

TABLE 6

Marine Snow Content - Intact Cells

Organism	Environment	#/Aggregate	% total suspended population	Enrichment over surrounding water	Reference
1. Algae (photoautotrophs)					
Near Surface (0-35 m)					
Phytoplankton >2 μ m	So. Calif.	1.0×10^4	-	3.2×10^2	Trent 1985
"	So. Calif. Bight	6.1×10^3	0.2-2.5	6.7×10^2 - 3.0×10^3	Beers et al. 1986
phytoplankton <5 μ m	Monterey Bay, CA	8.0×10^2 - 2.2×10^4	-	1.0×10^2 - 1.8×10^3	Davoli & Silver, 1986
phytoplankton >5 μ m	Monterey Bay, CA	6.3×10^1 - 4.1×10^3	-	7.5×10^1 - 1.1×10^3	"
phytoplankton <2 μ m	NW All-shelf/slope	-	-	1.9×10^1 - 4.3×10^1	Caron et al., 1986
"	" warm core ring	-	-	1.9×10^1	"
"	Gulf Stream	-	-	4.2×10^1	"
"	Sargasso Sea	-	-	4.2×10^1	"
phytoplankton 2-20 μ m	NW All-shelf/slope	-	-	7.2×10^1	"
"	NW All-warm core ring	-	-	2.4×10^1	"
"	Gulf Stream	-	-	6.7×10^1	"
"	Sargasso Sea	-	-	5.8×10^1	"
phytoplankton >20 μ m	NW All-shelf/slope	-	-	2.4×10^2 - 2.7×10^2	Caron et al. 1986
"	NW All-warm core ring	-	-	2.0×10^1	"
"	Gulf Stream	-	-	1.3×10^3	"
"	Sargasso Sea	-	-	7.0×10^2	"
monads & flagellates					
"	So. Calif.	5.0×10^3	-	-	Trent 1985
"	So Calif Bight	5.5×10^2 - 4.7×10^3	-	5.5×10^2 - 4.7×10^3	Beers et al. 1986
diatoms					
"	Monterey Bay, CA	0.5×10^3	0-16	0.27×10^1	Silver et al. 1978
"	So. Calif.	2.4×10^3 - 3.1×10^4	11-14	5.9×10^1 - 1.1×10^2	Prezelin & Alldredge 1983
diatoms-pennate	So. Calif.	2.4×10^3	-	-	Trent 1985
diatoms-centric	So. Calif.	2.3×10^3	-	-	Trent 1985
diatoms-pennate	So. Calif.	2.7×10^1 - 4.1×10^3	-	2.8×10^1 - 6.0×10^3	Beers et al. 1986
diatoms-centric	So. Calif.	1.4×10^1 - 7.9×10^2	-	3.9×10^1 - 4.2×10^3	Beers et al. 1986
dinoflagellates					
"	Monterey Bay, CA	0.12×10^3	0-100	$0.10 > 2.1 \times 10^3$	Silver et al., 1978
"	So. Calif.	1.3×10^2	25	1.2×10^3	Prezelin & Alldredge 1983
"	So. Calif.	3.7×10^1	-	-	Trent 1985
"	"	2.6×10^2	-	-	Trent 1985
"	"	4.1×10^2	-	4.5 - 8.0×10^2	Beers et al. 1986
"	"	1.8×10^1 - 2.0×10^2	-	3.6 - 1.4×10^2	Beers et al., 1986
coccolithophores	So. Calif.	9.8×10^1	-	-	Trent 1985
"	So. Calif.	1.8×10^1 - 8.7×10^2	-	9.1×10^3	Beers et al. 1986
Deep Water					
cyanobacteria	"	-	-	-	"
algae 1-2 μ m	(100-1650 m)	2.3×10^3 - 3.8×10^5	-	-	"
diatoms	"	2×10^3 - 1×10^5	-	3.3×10^2 - 7.2×10^3	"
flagellates & monads	So. Calif. (75-260 m)	1.2×10^3 - 4.0×10^4	-	-	Trent 1985
"	"	7.9×10^2	-	-	"
diatoms-pennate	"	1.6×10^2 - 4.6×10^3	-	-	"
diatoms-centric	"	4.7×10^1 - 2.8×10^2	-	-	"
dinoflagellates-thecate	"	2.5×10^2 - 6.8×10^2	-	-	"
dinoflagellates-athecate	"	1.1×10^2 - 3.4×10^3	-	-	"
coccolithophores	"	-	-	-	"

TABLE 6 (cont.)

Marine Snow Content - Intact Cells					
II. Bacteria					
Near Surface (0-25 m)					
Organism	Environment	#S/aggregate	% total suspended population	Enrichment over surrounding water	Reference
	Sargasso Sea	$6.6 \times 10^5 - 3.3 \times 10^2$	-	2.1×10^2	Caron et al. 1982
	So. Calif.	$1.2 \times 10^7 - 2.5 \times 10^7$	7-78	(or more)	Prezlia & Alldredge 1983
	So. Calif.	$1.3 \times 10^6 - 1.7 \times 10^6$	0.9-3.0	$6.7 \times 10^1 - 1.2 \times 10^3$	Alldredge et al. 1986
	NW Atl (oceanic)	$1.8 \times 10^6 - 2.8 \times 10^6$	0.2-4.4	$3.0 \times 10^1 - 3.7 \times 10^1$	"
	Monterey Bay, CA	$4.2 \times 10^5 - 6.7 \times 10^6$	-	2.5×10^1	Davoll & Silver 1986
				$8.3 \times 10^1 - 3.0 \times 10^2$	
Deep Water					
	So. Calif. (1000-1650 m)	$1.0 \times 10^5 - 1.7 \times 10^5$	-	-	Silver & Alldredge, 1981
	NW Atlantic (oceanic) (30-650 m)	$3 \times 10^6 - 3 \times 10^7$	<.05	up to 10^2	Alldredge & Youngbluth 1985
III. Protozoa					
Near Surface (0-35 m)					
Organism	Environment	#S/aggregate	% total suspended population	Enrichment over surrounding water	Reference
ciliates	Monterey Bay, CA	0.13×10^2	0-100	5.86×10^3	Silver et al. 1978
2-20 μ m cells mostly flagellate	NW Atl-shelf & slope	-	-	$1.7 \times 10^1 - 2.7 \times 10^1$	Caron et al. 1986
	NW Atl-warm core ring	-	-	3.1×10^1	"
	Gulf Stream	-	-	1.1×10^2	"
	Sargasso Sea	-	-	5.2×10^2	"
bactiivorous flagellates	NW Atl-shelf & slope	-	-	$4.8 \times 10^1 - 5.1 \times 10^2$	"
	NW Atl-warm core ring	-	-	2.7×10^2	"
	Gulf Stream	-	-	7.6×10^4	"
bactiivorous amoeba ciliates	No. Atlantic	-	-	$4.1 \times 10^2 - 6.2 \times 10^3$	"
microflagellates	Monterey Bay, Ca	6.74×10^1	-	$1.1 \times 10^2 - 2.1 \times 10^3$	Davoll & Silver 1986
	"	$1.8 \times 10^2 - 5.5 \times 10^3$	-	$1.1 \times 10^2 - 9.9 \times 10^2$	"

specimens of marine snow to nearly 300 m (Trent and Orzeck, 1984). Additional collections of snow specimens are also possible in deep water using sediment traps supplied with fixatives, devices that obtain particles that settle through the water. Microscopic observations of trap samples show mixtures of marine snow-like aggregates, fecal pellets, and a wide range of biogenic and lithogenic debris and large quantities of living organisms being transported into deep water (Fellows et al., 1981). Populations on aggregates in traps, like those on surface marine snow, contains high concentrations of intact bacteria (Karl and Knauer, 1984; Taylor et al., 1986) algae (Silver et al., 1986), protozoa (Silver et al., 1984; Taylor et al., 1986) fecal pellets (Honjo, 1980; Urrer and Knauer, 1981) and a wide variety of other materials. Likewise, measurements of metabolic activity on trap collected particles suggest these are centers of microbial activity (Karl and Knauer, 1984; Karl et al., 1984). Comparisons of snow populations with those in surrounding waters are not yet possible, because sizes and contents of individual snow particles are not known from trap collections, which may either fragment large aggregates or coagulate finer materials during deployment. However, the sinking particles captured by traps appear to support highly enriched and active communities as compared with resident suspended communities through which they pass.

Successional Patterns on Marine Snow

Like other natural ecosystems, marine snow microenvironments experience predictable changes from their time of formation to

their final disruption or destruction. These changes occur in their associated populations and the chemical and physical characteristics of the habitat. Such changes are documented in a variety of detrital communities (see summary by Newell, 1984) and are now suggested for marine snow systems. For example, Pomeroy and Deibel (1980) and Pomeroy et al. (1984) describe the microbial succession on fecal aggregates, showing a rapid burst of bacterial growth upon release of the pellets, followed by increases in populations of protozoans that graze the growing bacteria, later decline of the bacterial populations after a few days, and final communities of sparse microorganisms on fragmenting remnants of the fecal material. Davoll and Silver (1986) describe the sequence of colonization on larvacean houses, a common near-surface form of marine snow. They note 3 phases: an inoculation phase when the larvacean pumps water and microorganisms through the house filter system; a second stage after house abandonment, when resident populations multiply and mobile immigrants enter, thereby changing the relative abundances of different trophic groups; and a final phase on the fragmenting house, during which trophic interactions in the house and exhaustion of the house matrix bring about a typical succession.

Successional changes in populations on marine snow and consequent alterations in the chemistry of the colonized aggregates can be expected both in particles that remain in surface waters and in those that settle to depth. Changes in the chemistry of settling materials are the subject of considerable interest and presently are being studied using sediment traps (Fowler and Knauer, 1986). Unfortunately the organisms and the

biological processes causing many of the alterations are still relatively poorly known. However, evidence clearly indicates that microbial destruction and substrate decomposition occurs as detritus settles through the water (Iturriaga, 1979; Gardner et al., 1983; Lorenzen et al., 1983; Ducklow et al., 1985; see also discussion below).

The nutrient status of marine snow

The abundance of microorganisms on marine snow would suggest that concentrations of metabolically active substances, both those produced and those consumed, would be altered in aggregates. A major difficulty in measuring these concentrations, however, is the practical one of sampling just the particle and its associated water volume: collections always simultaneously remove an unknown quantity of the surrounding water. A correction for this "contamination" from the surrounding water can be applied by measuring the bulk concentration of the desired property in a water sample nearby, and then subtracting the quantity of the test substance expected to occur in the sample volume in which the aggregate was collected. (Aggregates usually are μl in vol [see above] and commonly are collected in samples of ml size, thus occupying a small proportion of the total sample volume.) Especially for substances whose concentrations are elevated in marine snow, such measurements provide a reasonable measure of the marine snow contributions. However, estimates of concentration factors inside marine snow are more subject to error, since the true volume of water associated with the individually variable

aggregates usually is known only approximately. Thus measurements of nutrient levels associated with particles are better known than are the in situ concentrations, which are nevertheless the more important parameter for organisms inhabiting the aggregate.

Measurements of nutrient levels found in marine snow have been made by Shanks and Trent (1979). They found ammonia to be the most concentrated of the measured dissolved nutrients. Values as high as .5 mM were observed (Shanks and Trent, 1979), and these well may be underestimates because of dilution; such high values may even approach inhibitory levels for some phytoplankters, which can occur at 1 mM (Syrett, 1962). Prezelin and Alldredge (1983), who found snow particles to contain all the measurable ammonia in seawater at one of their study sites, suggest that chemoautotrophs, possibly nitrifiers, utilize these nutrients in the aggregate microenvironment. They provide evidence for substantive dark fixation of carbon that would be expected of nitrification in the ammonia-enriched aggregates. The same process is thought to occur in deep waters for the organically enriched, sinking particulates collected by traps (Karl et al., 1984). Very recently Alldredge (pers. commun.) found that persistent oxygen and pH gradients can occur out to 1 mm around marine snow particles 1-4 mm in diameter. These microzones apparently are maintained against diffusion and advection, suggesting marine snow represents a semi-isolated and chemically unique habitat in midwater.

The true nutrient concentrations associated with marine snow

and other aggregates are a subject of considerable importance. McCarthy and Goldman (1979) have stressed the possibility that nutrient enriched microenvironments occur in pelagic near surface habits, systems that otherwise usually support vanishing small concentrations of biolimiting nutrients. Predictions of nutrient concentrations rely on appropriate models of the diffusive regime of the aggregate. Jackson (1980) suggested that nutrient pulses introduced by single releases from zooplankters would quickly diffuse to background levels and Mitchell et al. (1985) calculated μm zones of enrichment around phytoplankton cells excreting dissolved materials. However, as Goldman (1984) and Paerl (1984) argue, the internal regime of an aggregate, especially the large marine snow particles, may be considerably different from the environment surrounding a small, solid particle and molecular diffusion may be constrained within the aggregate microenvironment.

Marine snow aggregates, as we presently understand them, are loosely organized, physically semi-enclosed structures consisting of clusters of individual particles. The physical processes that give rise to the clusters and the importance of biological aggregating processes have been described by McCave (1984). Such aggregates may physically correspond to fractals, including soot and snowflakes - structures that are presently of considerable interest to chemists and physicists (Witten and Cates, 1986). Such fractals or aggregates can develop as random aggregates of individual particles or clusters of particles, have loose and semi-open structures, are individually unpredictable in their shapes, but can be described surprisingly effectively in their

average properties. Such particles act as traps for dissolved molecules that adsorb on their surfaces: with their extensive though open structures, the Brownian motion paths of diffusing substances are so long that molecules rarely escape to the outside of the lattice before contacting an internal surface (Witten and Cates, 1986). Such trapping characteristics would apply to both substances (e.g. the ammonium ion) that could bond with the many charged organic molecules present in the matrix (see Goldman's 1984 discussion) or to the dissolved gases that could be utilized and removed by organisms in the aggregate. Such considerations would also suggest that molecules diffusing into the aggregate would likely be trapped well before then reached the aggregate's core, producing gradients and greatly slowing diffusive process between the inside and outside of the aggregate.

Sinking Rates of Marine Snow

Major interest in marine snow has focused on the role these particles may play in carrying adsorbed and associated materials into the deep sea. Considerable theoretical (McCave, 1975; McCave 1984) and empirical evidence shows that major flux of materials often occur via marine snow or "fecal matter", as it is sometimes called (Bishop et al., 1977, 1978 and 1980). However, ability to predict the behavior of marine snow is still limited because its sinking characteristics are poorly known (particles are not within the Stoke's regime) and their shapes and physical characteristics are still not well defined. Efforts have been made to measure the settling rates of naturally

occurring snow particles, and they are described below. However, such measurements are subject to many errors: the fragile particles may be altered (likely collapsed, to some extent) when collected; the container sizes may have been too limited or physical environment inside the experimental chamber altered so that accelerations in them not typical of those of unconfined particles; some "true" results discarded such as the occurrences of particles that rise rather than sink (Riley 1970, Shanks and Trent, 1980) and so on.

Numerous measurements of the sinking rates of marine snow have been made and are shown in Table 7. These range from 1-368 m/day and have been obtained for a variety of types of aggregates, using a number of different methods. Most recently,

TABLE 7

MARINE SNOW--SINKING RATES

Type Material	Method of Measurement	Sinking Rate	Site	Reference
Reaggregated, field collected marine snow from submersible	laboratory settling chamber	17-260 m/day	Japan neritic	Kajihara 1971
Field collected marine snow (3mm, spherical)	calculated	91 m/day	California, neritic	Allredge 1979
Field collected larvacean houses	laboratory settling chamber	57-64 m/day	California neritic	Silver and Allredge 1981
Field collected larvacean houses	laboratory settling chamber	103-368 m/day	neritic, Hawaii	Taguchi, 1982
aggregates of phytoplankton detritus from sea floor (2000 m)	calculated from time lapse <i>in situ</i> photography	100-150 m/day	north-east Atlantic	Billet et al., 1983
larvacean houses from lab cultured larvaceans	laboratory settling chamber	26-157 m/day	Monaco	Gorsky et al., 1983
aggregates of phytoplankton detritus from sea floor	calculated from time lapse <i>in situ</i> photography	100-150 m/day	north-east Atlantic	Lampitt, 1985
sediment trap samples from deep water (to 3560 m)	indirect calculation using <i>in situ</i> flux (trap) data and particle concentration data (<i>in situ</i> camera)	1 m/day and 36 m/day	Panama Basin	Asper, 1986
Sediment trap samples from deep water (to 5800 m)	calculated time lag from trap collections at different depths	175 m/day	North Pacific (Sta Papa)	Asper, 1986

Asper (1986) estimated snow sinking rates from in situ measurements of both flux and snow concentrations, (sinking rates are the quotient of flux and concentration), with time-series flux measurements made photographically of marine snow accumulating in a sediment trap. His results suggest that there are several kinds of snow, with some settling more rapidly than others. He suggests there are fresh, rapidly sinking particles that descend from the surface, accreting the slower particles at depth, and older, more refractory and lighter aggregates derived from resuspension at continental margins and advected at middepths to more oceanic environments. In his Panama Basin observations, the former would be smaller aggregates (1-2.5 mm) that sink more rapidly (36m/day) than the larger (4-5 mm) particles that sink slowly (1m/day). Asper's suggestion of slow settling for the marine snow in the Panama Basin is at variance with the prediction of Lal (1977) that only very small particles (ones <5um) are transported significant distances from nearshore environments to oceanic regions.

Considerable field evidence exists to show that marine snow, or large particulates, are sinking rapidly in the sea. Evidence comes from accounts describing the rapid sedimentation of phytoplankton blooms in some near-shore environments (e.g. van Bodungen et al., 1981; Smetacek, 1985; Skjoldal and Wasserman, 1986). Many of these blooms appear to settle when the populations become senescent, and researchers have suggested that mucus production by the cells aids in their aggregation and rapid descent (reviewed in Smetacek, 1985). Fresh aggregates of surface material have also been found in sediments in deep ocean basins,

as evidenced from in situ photographs showing the arrival of large, phytoplankton rich aggregates at the sediment-water interface (Billet et al., 1983; Lampitt 1985) and from collections with deep-water sediment traps (Honjo, 1982). Further evidence that near-surface material settles rapidly into deep water deep-water is provided by the strongly seasonal inputs found in bathypelagic environments, inputs that reflect the production and populations of overlying waters (Deuser et al., 1981; Honjo, 1982).

DISCUSSION AND CONCLUSIONS

This brief review on larger aggregates has emphasized their biological enrichment and the consequences of these enrichments. Primary producers are usually greatly concentrated here, as evidenced by chlorophyll analyses, cell counts, and primary production measurements. These primary producers can cause large diel oscillations in photosynthesis-related phenomena: oxygen concentrations (possibly even bubble formation), exudations of dissolved organics from algae during photosynthesis, pH changes related to dissolved carbon dioxide uptake, and so on. The presence of such photosynthetic centers could be detected in situ by local peaks in chlorophyll absorption and fluorescence, and by bioluminescence of some of the associated microorganisms (Orzeck and Nielsen, 1984).

Not only photosynthetic related processes and metabolites are enhanced on the macroaggregates, but also those related to the catabolic activities of the associated food webs. As shown in the review, bacteria are often concentrated here, as well as

protozoans of various trophic positions. These consumers likely cause the elevated concentrations of ammonia as by-products of ingestion and excretion and they also utilize oxygen and produce carbon dioxide, likely producing redox gradients in larger aggregates, especially at night or at aphotic depths. These conditions could affect the redox chemistry of many substances (Paerl, 1984) and may account for observations of diagenesis (Lee and Cronin, 1982) and dramatic changes in the composition of organic matter in particles sinking through deep water (Wakeham et al., 1980)

One of the themes reoccurring in the marine snow literature is the variability of naturally occurring marine snow particles. The literature on microbial succession indicates that enriched particles change very rapidly - on time scales of days - and such changes are beginning to be documented for marine snow. Associated events would include the leaching and rapid utilization by microbes of labile materials, the subsequent development of microbial populations which initially may help to stabilize the substrate, the consequent grazing and reduction of the bacterial populations by invasion and growth of mobile grazers, and the final substrate collapse or decline of populations following the loss of readily usable detritus within the habitat (Newell, 1984). Such "older" aggregates are indicated to occur in surface waters (Prezelin and Alldredge, 1983; Davoll and Silver, 1986) and now evidence (Asper 1986) suggests these may also exist in deep water. The older aggregates should be chemically more refractory, less populated,

and could make the properties of aggregates difficult to predict unless their sources or ages were known. Thus the marine snow systems should share the features expected from ecological studies of other communities, namely that variability and change are troublesome but entirely expected attributes of such complex natural detrital microcosms.

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PARTICLE SIZE SPECTRA AND AGGREGATION IN, AND REMOVAL FROM, THE OCEANS

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INTRODUCTION

The removal of particles from surface and mid-water depths in the ocean normally requires their aggregation into larger units having a settling speed greatly in excess of the original particles. The argument has been presented and corroborated by several authors including Rex and Goldberg (1958), Schrader (1971), McCave (1975), Honjo (1976), and in many papers based on sediment-trap data. The size distribution of suspended particles is a function of several variables including source and nature of the particles, physical or biological processes of aggregation and 'age' of the suspension.

There are few measurements of particle size spectra from the ocean. Particle number data can, in nearly all cases, be fitted by a power-law distribution over some part of the measured range. Expressed as cumulative number N as a function of particle diameter d this is $N = kd^{-\beta}$. A value of $\beta = 3$ signifies equal particle volumes in logarithmically increasing size grades. This was found by Brun Cottan (1971), Sheldon et al. (1972), McCave (1975), Lerman et al. (1977), and Pak et al. (1980) in regions well away from the bed or, if close to the bed (Lerman et al.), regions of very low concentration. In more concentrated nepheloid layers near the bed the sizes show a volume peak around 4 to 8 μm and the number distribution cannot be fitted by a straight line (McCave, 1983; Richardson and Gardner, 1985). Lambert et al. (1981) also maintained that the distributions of individual components (e.g.,

aggregates, goethite, aluminosilicate) they observed are not of power-law type but are log-normal by number. They found a distinct fall-off at the finest end of the distribution whereas Harris (1977) counted the finest particles down to $0.1\mu\text{m}$ and showed a power-law distribution with $\beta = 1.62$ in the region $d < 1\mu\text{m}$. Wellershaus et al. (1973) also found a decrease in numbers of fine particles but said that it was an artifact of the counting method. This is a well known artifact shown by comparisons of optical counting with other methods of size analysis (ASTM, 1983; McCave, 1979). The sum total of the components shown by Lambert et al. (1981) however, seems to be fitted by a straight line with $\beta \sim 3$ over a good part of the measured range. The only results from the Pacific (Baker et al., 1979) are fitted by a somewhat higher value of $\beta = 3.29$ for $3 < d < 8\mu\text{m}$ from mid-water samples.

The fine end ($< 1\mu\text{m}$) of the spectrum is a particular problem. In my 1984 paper I assumed that, in contrast with the atmosphere, there was no source of fine particles analogous to condensation nuclei other than from erosion of the sea bed, and thus that old suspensions in the ocean interior would not have a Brownian spectrum. However, there are at least two sources of submicron particles in the ocean. The abundant reservoir of dissolved organic carbon (DOC) yields some of the ocean's particulate organic carbon (POC) by condensation reactions (Parsons, 1975; Degens and Mopper, 1976). This is estimated to be about 1.5% of the phytoplankton production, or $\sim 1.5 \text{ g C m}^{-2} \text{ year}^{-1}$ (Mopper and Degens, 1979). This would provide about 10^7 particles mL^{-1} of $0.05\mu\text{m}$ diameter. Sharp (1973) estimates that up to 15% of the material reported as DOC (i.e. passing a $0.45\mu\text{m}$ filter) may in fact be colloidal, a potential $100\mu\text{g C mL}^{-1}$ (assuming with Mopper and Degens (1979), $700\mu\text{g C mL}^{-1}$ for the DOC reservoir). The second source lies in bacterial production. Azam et al. (1983) summarise the importance of microbes in the size range 0.3

to $1\mu\text{m}$ in consumption of DOM released from phytoplankton. The bacteria are fed on by flagellates and so on up the food chain. Deep water bacterial numbers are $\sim 10^4 \text{ m}^{-3}$.

In summary, most workers show data implying $B \sim 3$ in the size range 1 to $100\mu\text{m}$ in clear water. There is no consensus as to what is the size distribution of submicron particles. Their composition is also obscure. Relatively young (i.e., freshly eroded) suspensions in nepheloid layers have peaked volume size distributions, but old ones are flat (i.e., $B \sim 3$) according to McCave (1983). One view is that the overall distribution, whatever it may be, is made up of log-normal number distributions of several different components. The flat $B \sim 3$ distribution may extend to sizes well beyond $100\mu\text{m}$ shown by Sheldon et al. (1972).

PARTICLE DENSITY AND SETTLING VELOCITY

For model calculations some assumptions about density are necessary to obtain settling velocity. It is clear that density decreases with increasing aggregate size and there is a wide spread of values for any given size, partly because of the diversity of particle types. My best guess, justified in McCave (1984) is given below in Table 1.

PARTICLE INTERACTIONS

Although the interaction of particles must play an important role in controlling oceanic particle size spectra, there has been little work on the subject. There is every reason to believe that physically controlled particle aggregation occurs in the deep ocean, albeit slowly because of the low concentration. Within the water column and on the sea floor there are several types of organic-inorganic aggregates including those known as 'marine snow' and faecal pellets. Some such organic aggregates result from an organism actively

Table 1. Model particle parameters*

d (μm)	$\Delta\rho^\dagger$ (g cm^{-3})	w_s (cm s^{-1})	$Re^\ddagger$
0.1	1	3.63×10^{-7}	2.54×10^{-10}
0.2	1	1.45×10^{-6}	2.03×10^{-9}
0.5	1	9.08×10^{-6}	3.18×10^{-8}
1	1	3.63×10^{-5}	2.54×10^{-7}
2	0.746	1.08×10^{-4}	1.51×10^{-6}
5	0.506	4.60×10^{-4}	1.61×10^{-5}
10	0.378	1.37×10^{-3}	9.59×10^{-5}
20	0.282	4.09×10^{-3}	5.73×10^{-4}
50	0.191	0.0174	6.09×10^{-3}
100	0.0776	0.0282	0.0197
200	0.0315	0.0458	0.0641
500	9.58×10^{-3}	0.0870	0.305
1000	3.89×10^{-3}	0.1410	0.98
2000	3×10^{-3}	0.1447	2.03
5000	3×10^{-3}	0.1563	5.47
10^4	3×10^{-3}	0.1736	12.2

* Compared with Table 2 of McCave (1975) w_s is greater.

$^\dagger \Delta\rho = (\rho_s - \rho)$, where ρ_s is particle *in situ* bulk density and ρ is fluid density (here taken as 1.05 g cm^{-3}).

$^\ddagger Re = w_s d / \nu$ with $\nu = 0.0143$ Stokes.

gathering and consolidating sediment plus organic matter (e.g., faecal pellets), whereas others result from the passive collision of particles, whether organic or inorganic. In the latter case an organic component may simply provide a sticky substrate for particle accumulation. It may increase the coalescence efficiency (i.e., the fraction of collisions that result in particle sticking) but the organic matter does not play any active role in increasing the frequency of collisions. The principal control on aggregation is the frequency with which particles come into contact, which is controlled by physical and biological mechanisms.

The probability that a particle of volume v_j will encounter a particle of volume v_i is proportional to the number of v_i particles and is given by $K(v_j, v_i) n(v_i) dv_i$ (Twomey, 1977, p. 123), where $K(v_j, v_i)$ is the coagulation kernel with $n(v_i) = dn/dv$ at $v = v_i$. Coagulation mechanisms are ways of bringing particles together. The principal five mechanisms are:

1. Brownian motion. Spherical particles undergoing Brownian diffusion have a probability of colliding given by the kernel K_{Bij} times the number of particles.

$$K_{Bij} = 2\pi D_{ij} d_{ij} = \frac{2kT}{3\mu} \frac{d_{ij}^2}{d_i d_j} \quad (1)$$

where $D_{ij} = (D_i + D_j)$, the sum of the diffusion coefficients ($D_j = kT/3\pi\mu d_j$), and $d_{ij} = (d_i + d_j)$ the sum of the diameters of particles of size d_i and d_j . If all the particles are the same size at the beginning of coagulation (a monodisperse suspension) then the coagulation time t_c , the time to reduce the initial number N_0 of particles per unit volume by a half, is $t_c = 3\mu/4kTN_0E$. Using appropriate values for deep ocean nepheloid layers, $\mu = 0.017$ poise, $T = 275^\circ K$, $N_0 = 4.10^5$ particles cm^{-3} in the size range 0.5 to $1\mu m$, then $t_c \sim 8.6$ days assuming efficiency (E) of unity. With more realistic efficiency $E = 0.10$ from Edzwald et al. (1974), $t_c \sim$

3 months, which could be reduced to about 10 days for concentrated suspensions. The recent experimental results of Gibbs (1983) indicate coagulation efficiencies nearly double those of Edzwald et al. The effect of natural coatings has not yet been evaluated in this way but is clearly a necessity. Thus we expect appreciable Brownian pumping of particles from submicron size into aggregates a few μm in diameter on time scales of a few days to a few months to occur initially after introduction of suspended material into the water column. A similar situation should prevail in surface waters where concentrations are higher due to organic productivity. However, well away from the boundaries where the number of small particles is about 100 times less, the coagulation time is 20 years. Thus at mid-water depths, Brownian coagulation of small particles is very slow.

2. Laminar and turbulent shear. The laminar and turbulent shear kernels are similar:

$$K_{LSij} = \Gamma \frac{d_{ij}^3}{6} \quad (2)$$

for laminar shear with $\Gamma = dU/dz$ and

$$K_{TSij} = 0.163 d_{ij}^3 (\epsilon/\nu)^{1/2} \quad (3)$$

for turbulent shear with the shear rate Γ given in the terms of the turbulent dissipation rate ϵ and kinematic viscosity ν (Saffman and Turner, 1956). the coagulation time corresponding to equation 3 for a monodisperse suspension ($d_i = d_j$) is $t_c = 0.693 \pi/4V\Gamma$, where $V = \pi d^3 N_0/6$. The relative importance of Brownian and shear coagulation is approximately given by K_{Bij}/K_{LSij} or $2kT/\mu d^3 \Gamma$, and so for equal importance with shear rate $\Gamma = 0.0084 \text{ s}^{-1}$ in a mono-disperse suspension $d \sim 8\mu\text{m}$, but with $\Gamma = 1.0 \text{ s}^{-1}$ ($\epsilon = 1.4 \times 10^{-2} \text{ cm}^2 \text{ s}^{-3}$), $d = 1.7\mu\text{m}$. So Brownian coagulation dominates over shear in suspensions with low turbulence intensity for particles of diameter $< 8\mu\text{m}$, but in more turbulent suspensions shear dominates down to

about 2 μ m. With variable stresses the grain size region 2 to 8 μ m marks the transition from Brownian to shear-dominated behaviour of particles relative to their near neighbours in size. It appears that Brownian coagulation will create aggregates of a few μ m diameter faster than shear coagulation will remove them to larger sizes. Subsequently, as the number of submicron particles becomes relatively depleted, the 'bump' in the size distribution at values of a few μ m will be dissipated by transfer of particles to larger sizes.

3. Turbulent inertial coagulation. In turbulent flow local turbulent accelerations produce relative particle velocities for particles of unequal mass (Pruppacher and Klett, 1978, p. 375). This process is relatively unimportant. It is normally only significant when particles differ in diameter by more than about 1 cm.

4. Differential settling. The faster settling of larger particles through a suspension leads to collisions with slower settling particles and their capture to form aggregates. The kernel is given simply by the area swept out times the relative velocity, the collision efficiency E_{c1j} , and the efficiency of diffusive collection E_{d1j}

$$K_{G1j} = \frac{\pi d_{11}^2}{4} (w_{s1} - w_{sj}) (E_{c1j} + E_{d1j})$$

The collision efficiency is the ratio of the number of particles with which the settling particle makes contact to the number in the volume it sweeps out as it sinks. Small particles are also transferred by Brownian diffusion to the surface of the larger settling particle. For 5 μ m particles, most of the range of interest is dominated by collision save for particles <1 μ m, where diffusion is most important. Inertial capture of small particles by 'marine snow' is most inefficient and may not be important, but diffusive capture is relatively efficient (see Table 2). Settling through mid-water where there are

perhaps 3×10^4 particles cm^{-3} of size 0.35 to $0.7\mu\text{m}$, a piece of 'marine snow' of diameter 5mm and cross-sectional area 0.2 cm^2 sinking through 1000 m would collect 1700 particles in that size range assuming 10% coalescence efficiency. This may be important for the individual aggregate, but to sweep the water column clean of such particles would require about 35,000 more particles following the path of the first!

This view is based on the assumption of spherical particles. However, some components of 'marine snow' are discarded mucus webs whose shape is anything but spherical. It may well be that these irregular, deformable, porous, gelatinous particles have a much higher collision capture efficiency than a rigid sphere. At any event the behaviour of such particles should be examined theoretically.

Table 2. Settling capture efficiencies

Caught (μm)	Catcher			
	5 mm snow		50 μm aggregate	
	E_D	E_C	E_D	E_C
50	1.43×10^{-6}	<u>1.47×10^{-4}</u>	---	---
5	<u>6.16×10^{-6}</u>	1.5×10^{-6}	5.8×10^{-4}	<u>1.2×10^{-2}</u>
0.5	<u>2.85×10^{-5}</u>	1.5×10^{-8}	2.66×10^{-3}	1.47×10^{-4}

Underlined values are the most efficient for interactions of that pair of particles. E_D = diffusive capture, E_C = collision capture.

5. Biological aggregation processes. It is possible to write down a coagulation kernel for active particle catching and aggregate production by animals. Basically they sweep or filter a certain volume of water each second, $V = AU$, where A is the area of water column swept at speed U, and catch particles with an efficiency $E_{B,j,f}$, which depends on the type of organism j, the size d_i of the particle, and its perceived food value f. The kernel would have the

form $K_{b1j} = AUE_{b1j}f$. Animals are likely to have the major impact on particle spectra in the upper layers of the ocean where there is most food. It is not clear what the effects will be at great depths in mid-water and in the bottom nepheloid layer, where even the population densities are not well known (Wishner, 1980).

Coagulation Rates

The regions dominated by the different coagulation mechanisms are shown in Fig. 1 in a form based on the original suggestions by Friedlander (1965). The coagulation rate constants from the kernels are plotted for interactions with particles of size $d_1 = 5\mu\text{m}$. The conditions assumed are those of low shear, $\Gamma = 0.084$ to 0.0084s^{-1} , and deep-sea density and viscosity mentioned above with McCave's (1984) model particle properties. The 'giant' particles represented by marine snow appear to be dominated by shear in their interactions because of the d_1^3 term in the shear kernel. In particle collisions with near neighbours (in size) where small aggregates join to make bigger ones, and so on up to large sizes, the time scales calculated are very long (assuming 10% efficiency). Brownian coagulation times for $0.5\mu\text{m}$ particles are 3 months to 20 years for nepheloid layer and mid-water concentrations, respectively, and corresponding shear-coagulation times for $5\mu\text{m}$ particles are from 7 months to 7000 years! This makes it unlikely that small particles can aggregate progressively up the size spectrum to become big ones other than through biological intervention yielding faecal pellets. Apparently the mill grinds very slowly by physical means.

But does it? A feature of the turbulent shear kernel is that it attains high values for interactions involving large particles. One way of examining the effect of this is to calculate particle removal rate as suggested by Lerman (1979, pp. 288-299) [cf. Hidy's (1973) Tables 4 to 6 for aerosols]. This is

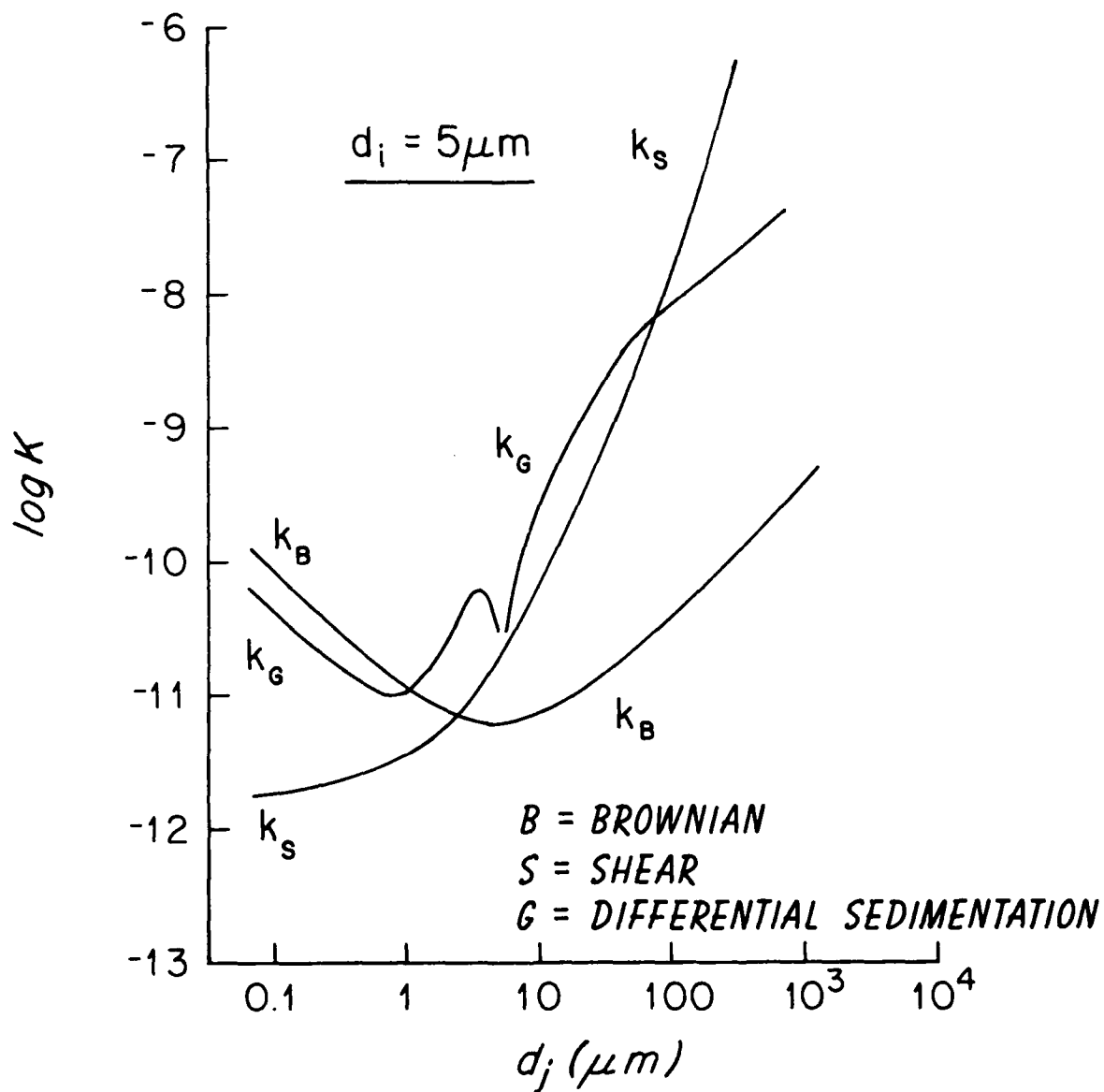


Fig. 1. Coagulation kernels K for collection of $5 \mu m$ particles plotted for $\epsilon = 10^{-4} \text{ cm}^2 \text{ s}^{-3}$ and oceanic conditions. Subscripts are B for Brownian, G for differential settling and S for shear.

given by the kernel times the numbers of interacting particles $K n(v_i)n(v_j)$ with units $\text{cm}^{-3}\text{s}^{-1}$. Table 3 shows the results of calculations for nepheloid layer and mid-water concentrations. The most important feature of Table 3 is that many of the collision frequencies are $<3.17 \times 10^{-8} \text{ cm}^{-3}\text{s}^{-1}$, or less than one collision per year per cm^3 .

The enhanced coagulation rates for small particles with large particles in nepheloid layers suggests that this will be a highly significant mechanism in surface waters too, where turbulence levels expressed as a shear rate may be an order of magnitude greater. In addition, the concentrations of marine snow may be two orders of magnitude greater than the figure given here [i.e. $5 \times 10^{-3}\text{cm}^{-3}$ from Shanks and Trent (1980) and 10^{-3}cm^{-3} from Honjo et al. (1984)]. Thus, in surface water the smallest particles are aggregated by Brownian motion. Such aggregates are lost by colliding with one another in motion controlled by differential settling, but they are scavenged even more rapidly by large particles with turbulent shear controlling the relative motion. They are probably collected by biological means even faster than both those physical mechanisms.

The above discussion has considered physical factors involved in aggregation. It must be tempered by the fact outlined above that some filter-feeding organisms can process the upper water column in a day. Brownian aggregation is likely to put small particles into sizes 1 to $8\mu\text{m}$, where they stand a good chance of being filtered by larger zooplankton if they have not already been collected by microzooplankton. More data on filtration rates and population densities of suspension feeders, particularly below the surface layers, will be essential in elucidating deep-sea particle dynamics. Animals may dominate at depth as it seems probable that they do in the surface.

Table 3. Particle removal rates*: $-dn/dt$ ($\text{cm}^{-3} \text{s}^{-1}$)

$d_i =$	Nepheloid layer ($\Gamma = 0.084 \text{ s}^{-1}$)				Mid water ($\Gamma = 0.0084 \text{ s}^{-1}$)		
	0.5 μm	5 μm	50 μm	0.5 μm	5 μm	50 μm	
L_B	6.74	6.07×10^{-5}	2.43×10^{-12}	6.74×10^{-4}	6.07×10^{-9}	1.22×10^{-14}	
L_S	1.37×10^{-2}	1.23×10^{-4}	4.93×10^{-9}	1.37×10^{-7}	1.23×10^{-9}	1.23×10^{-12}	
$L_S(2-4)$	1.86×10^{-2}	5.61×10^{-5}	1.18×10^{-8}	6.20×10^{-6}	1.87×10^{-8}	1.97×10^{-11}	
$L_G(50)$	5.68×10^{-4}	8.85×10^{-6}	—	2.84×10^{-7}	4.44×10^{-9}	—	
$L_G(2-4)$	2.42×10^{-3}	2.34×10^{-6}	1.35×10^{-8}	8.06×10^{-6}	7.80×10^{-9}	2.24×10^{-10}	
$N_i(\text{cm}^{-3})$	10^6	3×10^3	0.6	10^4	30	0.03	
$N_{2-4}(\text{cm}^{-3})$		6×10^{-5}			2×10^{-5}		

* Assuming 100% efficiency.

 N_i is the number concentration of particles of diameter d_i . $N_{2 \text{ to } 4}$ is the number concentration of 'snow' particles in the size range 2 to 4 mm.Subscripts for loss rates L are $B = \text{Brownian}$, $S = \text{shear}$, $G = \text{differential sedimentation}$, (2 to 4) mm and 50 μm . Frequencies $< 3.17 \times 10^{-8} \text{ cm}^{-3} \text{ s}^{-1}$ represent less than one collision per year.

Removal of Particles from Mid Water Depths

The distribution of turbidity at mid-water depths shows that there is more material present under mid-ocean high productivity areas (Eittrheim et al., 1976; Biscaye and Eittrheim, 1977), than under gyres. Thus the flux of large particles from the surface may reasonably be inferred to supply more material to mid-water depths than it removes, presumably by break-up of large aggregates. If the larger than average flux of large marine snow particles from high productivity results in net supply rather than removal of particles then there is reason to believe that under normal conditions in the open ocean the flux of large particles also performs no net scavenging function. However, this conflicts with the data of Honjo (1982) and Honjo et al. (1982) who show that vertical flux of aluminosilicate increases with depth and that the maximum flux of aluminosilicate coincides with a temporal maximum in surface organic carbon productivity and flux (and resulting carbonate flux). A similar, seasonally tied, result is given by Deuser et al. (1983) in the Atlantic. Do the sinking particles perform the scavenging of clays or does the presence of the organic-rich particles stimulate a scavenger (biological) to remove material indiscriminately? We must also consider the extent to which the downwards increase in flux reflects an increase in the particle concentration surrounding the trap.

Thus there seems to be no quick way of removing fine particles from mid-water depths via physical means and they must have a removal rate principally controlled by Brownian coagulation up to a size (about 5 μ m) where settling removal speeds up (~140m/year). This will take many years. It would explain why long residence times and slow sinking rates are inferred from analysis of radionuclides inasmuch as these are scavenged by the fine particles which are preferentially sampled by water bottles.

If there is some quicker way of removing particles from mid-waters then it must be biologically controlled.

THE RATE DETERMINING PROCESS FOR DEPOSITION

In a turbulent suspension, particles are brought into contact by several mechanisms and frequently stick, forming aggregates with a settling velocity greater than that of the individual particles. This raises the question of whether the rate of deposition to the bed is controlled by the rate at which larger aggregates are formed. If aggregates were not formed, would the rate of deposition be much slower?

One way of comparing rates due to these processes is to consider their respective half-lives, that is to say, the half-residence time of the number of particles in suspension. (Aggregation reduces the effective number of particles in suspension.) For deposition, this is $t_D = 0.693/(w_s/H)(1-\tau_0/\tau_1)_1$. For aggregation by Brownian motion, and turbulent shear, the coagulation times were given earlier. Let us assume deposition from a uniformly mixed nepheloid layer 50 m thick (H), with 100µg/litre of each size class (1, 5, and 20µm), and constant shear velocity $u_* = 0.1\text{cms}^{-1}$. For the 1µm material, $t_D = 6.1$ years, but $t_{cB} = 1.24$ years. Thus, it appears that clay (<2µm) will be moved up the size spectrum faster than it is deposited. For 5µm material, $t_D = 117$ days, but t_{cB} is 30 times as long at about 10 years.

One other case to consider is whether small particles will be scavenged out by large fast-settling ones and carried to the bottom faster than they would otherwise settle. McCave (1984) showed that the most effective means of scavenging is in the turbulent agitation of large particles among smaller ones. The collection rate is $K_{s1j}n_1n_j$, where $k_{s1j} = 0.163 d_{1j}^3$ in which d_{1j} is the sum of the diameters of the colliding particles and n_1 and n_j

are the number of i and j particles, respectively. For large "marine snow" particles of 2 to 4 mm diameter, we assume $n_j = 6 \times 10^{-5} \text{cm}^{-3}$ and for $1 \mu\text{m}$ particles, $n_i = 10^5 \text{cm}^{-3}$. With other parameters as before and 10% efficiency, the scavenging rate is $1.82 \times 10^{-4} \text{cm}^{-3} \text{sec}^{-1}$ or, in a layer 50-m thick, 0.91 particles/ cm^2/sec . The rate of deposition particle-by-particle is 1.8 particles/ cm^2/sec . Thus, scavenging of clay is not negligible, but neither is it dominant. In any event, it is less important than aggregation of small particles. For larger particles, scavenging becomes less important relative to their rate of deposition.

What is not at all clear is how important is the role of the benthopelagic plankton in aggregating sediment. Is it as important as the zooplankton of the upper 200 m? Good biological data are needed from great depths.

CONCLUDING QUESTIONS

I have raised a few questions, some implicit in assumptions one is forced to make, in this account. Important ones are: 1. What is the size distribution of submicron particles in the oceans? 2. What is the origin and composition of these submicron particles? (Chemists will doubtless wish to enquire into their scavenging capabilities for dissolved substances.) 3. What is the coagulation efficiency for different classes (size, composition) of oceanic particles? 4. What is the dynamical behaviour of sinking blobs, sheets and webs of mucus? 5. What are the biological scavengers of particles in the mid-water and bottom nepheloid layer regions? 6. What particle removal rates are associated with their activities?

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Aggregate Dynamics: Biological processes which form, alter and destroy
aggregates in the ocean

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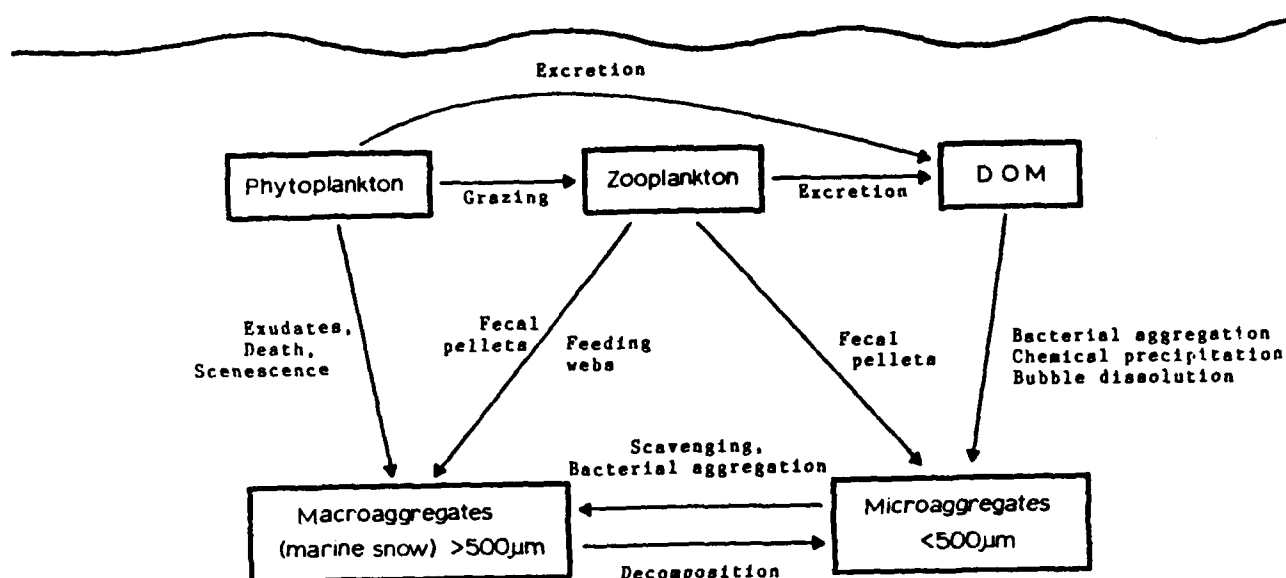
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INTRODUCTION

The processes which change the abundance, size distribution and characteristics of marine aggregates in nature are complex and diverse. Many biological and physical mechanisms are involved in the dynamics of particle formation and breakdown. Biological processes may be particularly important in the formation of aggregates in the sea. McCave (1984) examined physical processes of collision and coagulation and concluded that they were inadequate to explain the high degree of aggregation seen in particulate matter in the deep sea. He concluded that the size distribution of particles above submicron sizes was largely biologically determined.

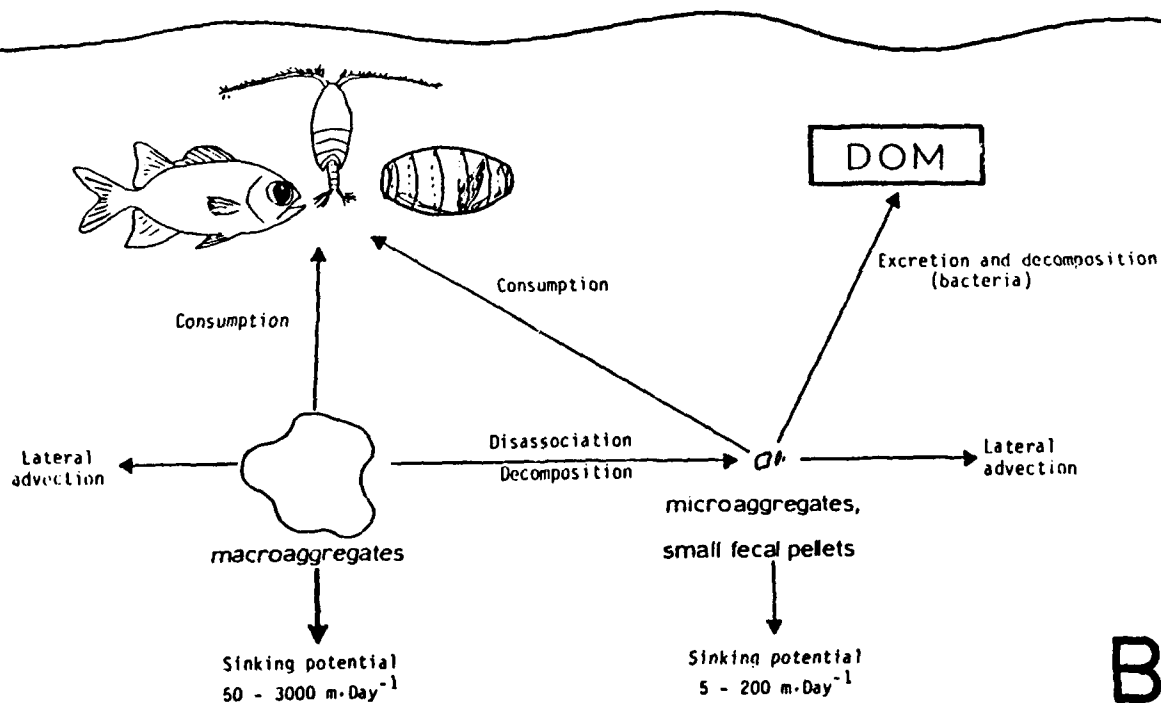
The major biological pathways by which marine aggregates are formed are illustrated in Fig. 1a. Macroaggregates, or marine snow, arise from the aggregation of senescent diatoms, from discarded zooplankton feeding webs, as flocculant fecal pellets, or from the microbial aggregation of microaggregates. Microaggregates form from bacterial aggregation and from dissolved organic

Biological Processes Producing Marine Aggregates



A.

Processes removing Marine Aggregates



B.

FIGURE 1: Biological processes which form, alter and breakdown marine aggregates.

matter through a variety of pathways, several of which are closely linked to physical processes as well.

The major pathways by which aggregates are destroyed or removed from the pelagic zone are illustrated in Fig. 1b. Significant biological processes of aggregate loss include consumption by zooplankton and nekton and decomposition by microorganisms. Physical processes of settlement, lateral advection, and fragmentation due to turbulence are equally important. In this review I will examine the major biological mechanisms by which aggregates are formed, altered and broken down in the ocean. Throughout I stress that many of these mechanisms can operate simultaneously to significantly change the abundance, size distribution and nature of marine aggregates.

FORMATION OF AGGREGATES

Direct production of aggregates by phytoplankton

Primary production is the ultimate source of most of the organic matter in the pelagic zone. Hence, phytoplankton contribute indirectly to most mechanisms of aggregate formation. However, phytoplankton also directly form macroaggregates through entanglement, aggregation and mass sinking following bloom conditions. Rapid mass sedimentation of phytoplankton through the water column has been documented in neritic environments (Smetacek, 1980; Wassmann, 1983), in the Baltic and North Seas (Smetacek et al., 1978; Davies and Payne, 1984), in the Panama Basin (Honjo, 1982) and in the north east Atlantic (Billet et al., 1983). Mass sinking has usually been equated with mass mortality of phytoplankton cells following bloom conditions (Walsh, 1983).

Smetacek (1985) challenges the concept of mass mortality and presents evidence that mass aggregation and sinking of certain phytoplankton groups may

be an adaptation for the transport of resting stages to the deep sea. Aggregation may insure the ultimate survival of the species via the maintenance of seed populations at depth. Diatoms, such as Thalassiosira, Skeletonema, Chaetoceros and Rhizosolenia are major genera contributing to aggregate formation. Diatom populations experiencing nutrient stress under bloom conditions produce large flocculant aggregates, identical to marine snow, which sediment at rates of 50 to 200 m day⁻¹, considerably higher than the <10 m d⁻¹ expected of individual diatom chains. These sinking diatom aggregates produce, for a few days, very high abundances of marine snow which Smetacek (1985) refers to as a "marine blizzard".

Three mechanisms apparently lead to the aggregation of diatom blooms. First, as nutrients become depleted, cell buoyancy is reduced and the cells begin to sink. Protuberances and spines on the cells entangle the sinking cells together, beginning the aggregation process. Second, the production of extracellular mucus, which increases under nutrient stress (Degens and Ittekkot, 1984) serves to adhere cells together as they collide. Third, although not addressed by Smetacek, some nutrient stressed cells actually die. Deterioration of the girdle upon death may split the diatom frustules apart, releasing protoplasm. This sticky gelatinous material could serve as a nucleus for the continued aggregation of particles. Although direct evidence for the aggregation of diatoms via these mechanisms has not yet been obtained directly in the sea, flocculation of diatoms in senescent cultures is commonly observed in the laboratory (Eppley et al., 1983), and considerable laboratory evidence exists to support mucus production and entanglement of nutrient stressed and negatively buoyant diatoms.

Diatom blooms usually progress from the coast toward the open sea. Strong lateral advection, such as the squirts and jets of the California coast, probably transport diatom blooms and aggregates off shore. Seasonal and regional patterns in cross-shelf transport will thus have a major impact on the distribution and abundance of diatom-generated marine aggregates. Moreover, evidence from marine sediments suggest that diatom-generated marine snow may be a widespread phenomenon throughout the world's oceans. The distribution of siliceous ooze in the sediments of the Pacific is closely correlated with phosphate concentration and primary production (Berger, 1984, Fig. 2). Areas of high productivity are the most likely areas for the production of macroaggregates by diatom blooms and the rapid sedimentation of silica to the sea floor.

Phytoplankton also directly produce marine snow via the formation of gelatinous colonies. The coccolithophorid, Emiliana huxleyi, and some diatoms such as Thalassiosira sp. can form gelatinous colonies (Fryxell et al., 1974), which serve as nuclei for macroaggregates. Although such colonies are occasionally abundant, the quantitative significance of gelatinous colonies as sources of marine snow remains unknown.

Production of aggregates by zooplankton

Zooplankton produce aggregates through two major mechanisms. 1) Large, flocculent aggregates are produced by appendicularians and pteropods as part of their feeding biology and, 2) animals repackage small particles into larger ones via consumption of food particles and defecation of the unassimilated portion as fecal pellets.

Zooplankton feeding webs can be a major source of marine snow at certain times and locations and may be particularly important in oligotrophic waters where conditions are less favorable for aggregate formation by other mechanisms.

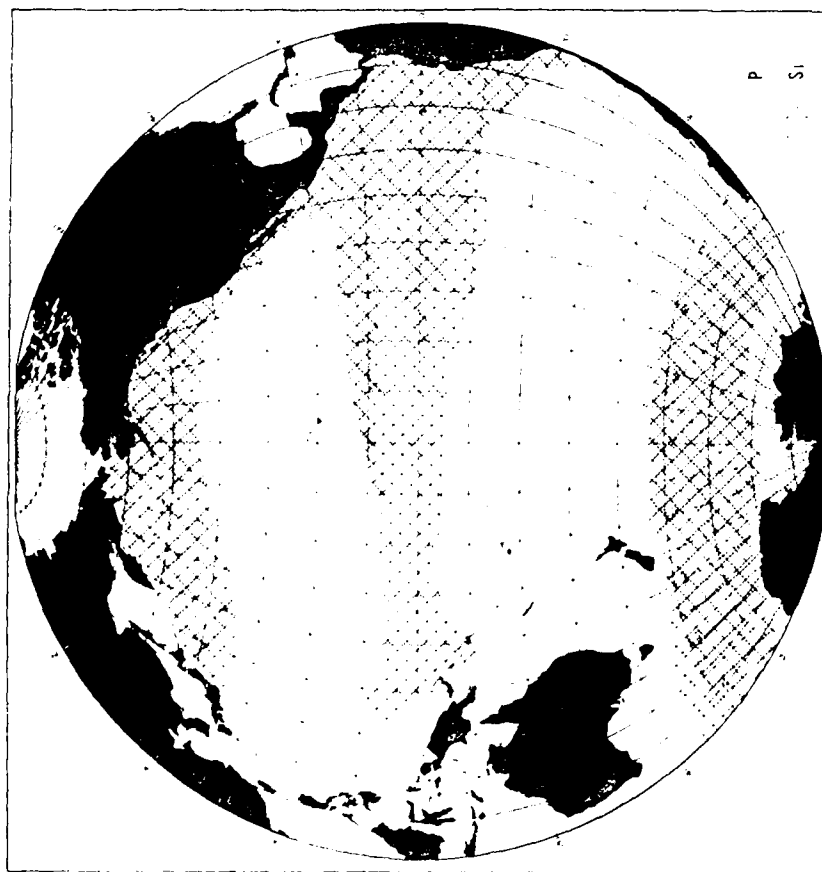


FIG. 29-25. Distribution of sediments rich in siliceous fossils ("Si") with respect to fertile areas, as indicated by the regions where PO_4^{3-} - P > 1 $\mu\text{g-at. l}^{-1}$ at 100 m depth ("P"). From Berger (1970b).

Figure 2: from Berger, 1984

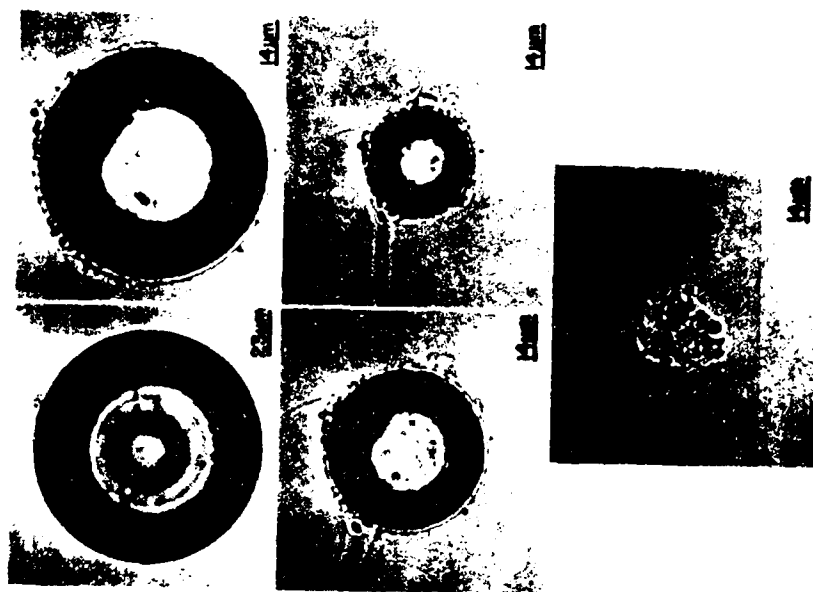


FIG. 5. Photomicrographs series showing dissolution of a bubble initially 62 μm in radius in filtered sea water. Bubble was aged in unfiltered seawater. Note inclusion of fibrous particles.

Figure 3: from Johnson and Cooke, 1980

Appendicularians, abundant planktonic tunicates, feed using a gelatinous feeding structure, the house, which contains a complex array of filters and passages. The house is composed a mucopolysaccharides and is secreted by specialized cells on the animal's trunk. The animal forces water through the filters of the house with its tail. Phytoplankton, bacteria, fecal pellets and microaggregates become concentrated, either on the external filters of the house or within the internal filter. The house is abandoned periodically and a new structure is secreted. Individual appendicularian houses may contain up to 50,000 phytoplankton cells and vary in diameter from a few hundred microns to 30 or more cms. Most are on the order of 3 to 20 mm in diameter (Alldredge and Madin, 1982).

Individual appendicularians produce and discard from 4 to 16 houses per day (Fenaux, 1985). These discarded houses become macroaggregates containing diverse detrital populations of phytoplankton, bacteria and protozoans (Alldredge, 1972). The rate of house production increases with increasing temperature and with increasing food concentration (Fenaux, 1985). Where appendicularians are abundant, houses may be the major macroaggregates in the water column. Discarded houses reach densities up to 80/l (Prezelin and Alldredge, 1983). A mean of 6% and 24% of macroscopic aggregates in the Santa Barbara Channel and the Gulf of California respectively are identifiable appendicularian houses (Alldredge, 1979).

Pteropods, gelatinous planktonic molluscs which feed with mucus sheets (Gilmer, 1972), are also sources of macroaggregates. Pteropods are ubiquitous and webs are occasionally abundant in surface waters (Caron et al., 1982), but no quantitative information exists regarding the rates of web production and the significance of pteropod webs as sources of macroaggregates in the pelagic zone.

The major impact of zooplankton on the size distribution and abundance of aggregates in the ocean is through the consumption and repackaging of food particles, primarily phytoplankton, into fecal pellets. Although a vast literature exists on the feeding rates of various zooplankton, previous research on zooplankton feeding has emphasized the impact of zooplankton on phytoplankton and other food populations or the growth rates and biological characteristics of the grazing animals themselves. Very little research has examined zooplankton feeding from the repackaging perspective.

Assimilation rates of most marine zooplankton are on the order of about 70% (Angel, 1984). If we assume that most of the primary production in surface waters is consumed by herbivores, then up to 30% of primary production eventually exists as fecal pellets. Fecal pellets form a special class of aggregates. The production of fecal pellets in the water column is controlled primarily by the abundance and feeding rate of the animals, and by their ingestion and assimilation efficiencies. Most available rates of pellet production are for crustaceans (Table 1). In copepods, the volume of fecal pellets produced per day is a linear function of animal dry weight (Paffenhofer and Knowles, 1979). Smaller individuals tend to produce more pellets per unit weight than larger individuals and small species have higher production rates than large species (Heyroud, 1979). Moreover, as assimilation efficiencies increase, pellet production decreases. Thus deep sea animals, which tend to have higher assimilation efficiencies may have lower fecal pellet production rates and we might predict that pellet production/individual would vary with depth (Angel, 1984).

Most zooplankton migrate in the top 1000 m of the water column and most micronekton in the top 1000-1500 m (Angel, 1984). Since most production of new particulate organic matter occurs in the euphotic zone, consumption and repackaging of new production is most significant in the upper 1000 m of the water

Table 1. Some observed fecal pellet production rates

From Angel, 1984

Species	Feeding Conditions	Fecal Pellets per day	Authors
<u>Acartia tonsa</u>	3 order of magnitude of food concentration	1-6	Reeve and Walter, 1977
<u>Acartia clausi</u>	5 x 10 ⁵ ml ⁻¹ natural particles	24.5	
	1.6 x 10 ⁵ ml ⁻¹ cocco- lithophores	91	Honjo and Roman, 1978
	2.0 x 10 ⁴ ml ⁻¹ cocco- lithophores	8	
<u>Temora turbinatus</u>	Natural conditions	10-169	
<u>Eucalanus pileatus</u>	Natural conditions	55-160	Paffenhof and Knowles, 1979
<u>Oikopleura longicauda</u>	Natural conditions	243±105	Taguchi, 1982
<u>Cyclosalpa affinis</u>	Excretion of animals	9.9*	
<u>Salpa maxima</u>	collected by SCUBA	13.0*	Madin, 1982
<u>Pegea confoederata</u>	divers and held in aquaria	17.8*	
<u>Meganyctiphanes norvegica</u>	25 mg animals fed on <u>Acartia</u> in laboratory	5.1 [†]	Small et al., 1973
<u>M. norvegica</u>	" "	5.3 [†]	Heyraud, 1979

*µg fecal C mg C⁻¹h⁻¹ †mg feces (mg animal dry wt)⁻¹ day⁻¹
(N.B. a Meganyctiphanes fecal pellet weights = 1.7 µg, Fowler, personal communication).

column. Repackaging of aggregates, both fecal pellets and other aggregates originating in surface waters, may occur throughout the water column (Turner and Ferrante, 1979). Fecal matter appears to be efficiently cycled in the upper layers of the ocean with relatively little fecal matter fluxing to the deep sea in some areas (Hoffman et al., 1981; Bishop et al., 1977) while high numbers of fecal pellets reach the sediments in others (Dunbar and Berger, 1981).

Fecal pellets, as a class of marine aggregates may be a considerably more abundant component of the pelagic zone than previously thought. Krause (1981) noted the prolonged residence of large numbers of copepod fecal pellets (up to 100 l^{-1}) in surface water in the North Sea, suggesting that not all pellets sank or were consumed. Macrocrustacean pellets, probably of Euphausia pacific, are abundant in the Santa Barbara and Santa Cruz Basins off Southern California, ranging from 550 to 98,000 pellets m^{-3} . Studies of the aging of the peritrophic membranes of these pellets in the laboratory indicate that up to 40% of pellets at 10 meter depths may be 3 or more days old, despite sinking rates of 18 to 170 m d^{-1} (Alldredge, unpublished). Turbulent mixing and entrainment events may maintain fecal pellets in surface waters, where they remain available for further repackaging via consumption by zooplankton.

Production of aggregates from dissolved organic matter (DOM)

The quantity of dissolved organic matter in the ocean generally exceeds that of particulate phase by an order of magnitude. Of this material about half is believed to be truly dissolved while the remaining half consists of colloidal sized particles (Cauwet, 1978). This DOM is composed of many types of complex organic molecules including proteins, lipids, and carbohydrates and is biological in origin. DOM is produced by the exudation of organic molecules by phytoplankton and marine microbes. It is excreted by zooplankton and is produced by

cell death and lysis and by decomposition processes. Some arises from nearshore and terrestrial environments. The conversion of matter from the dissolved to the particulate phase may be one of the major pathways forming marine aggregates. Such conversion may take place via one of three major mechanisms. Although 2 of these mechanisms involved physiochemical aggregation, they are included here since the primary source, DOM, is biological in origin.

De nova formation of particles in seawater by physiochemical processes may be a significant source of microaggregates. Particles spontaneously form in standing seawater even after ultrafiltration to remove all particles and molecules with a molecular weight greater than 2000 (Johnson and Cooke, 1980). ^{14}C labeled extracellular products of phytoplankton immediately form particles when added to seawater. Jensen and Sondergaard (1982) attribute this phenomenon to the absorption of organic molecules to the colloidal size fraction of DOM. Flocculation of humic materials in river water commonly occurs when freshwater mixes with seawater and 3 to 11% of the DOM in rivers may become particulate in this way (Sholkovitz, 1976). Wangersky (1978) has hypothesized that DOM may coprecipitate with CaCO_3 in seawater as well.

Adsorption of organic molecules to existing particles in seawater is well documented. Neihof and Loeb (1974) found that all particles in seawater are coated with high molecular weight organic molecules which produce a negative surface charge. Adsorption occurs via hydrogen bonding, Van der Waal forces and electrostatic attraction depending upon the nature of the particles and the organic molecules involved. Such adsorption enlarges colloidal particles. Reduction of the electrostatic charges which normally keep particles dispersed can result in aggregation. Sewage effluents are aggregated by chemical or bacterial treatments which accomplish this purpose (Riley, 1970). However, the physical and chemical processes behind de nova particle formation in seawater

have not been thoroughly explained and quantitative data on the conditions required and the rate of de nova particle formation do not exist.

Moreover, a twenty year old controversy is still raging regarding the necessity of bacteria in the de nova formation of aggregates from seawater. Biddanda (1985) found that particle formation occurred in filtered seawater kept idle, circulated or bubbled (with or without the addition of additional DOM and POM) only in the presence of bacteria. Bacteria growing at the expense of the DOM present formed large particles >100 μm by aggregation. Killed treatments did not show any particle formation of the type described by Baylor and Sutcliffe (1963), Sheldon et al. (1967) or Krank and Milligan (1980).

A second mechanism of aggregate production from DOM involves the adsorption of surface active dissolved molecules onto the surfaces of bubbles in the sea. The subsequent dissolution of the bubble results in a collapse of the surface coating forming a flake or microaggregate of particulate matter. Dissolved substances which are known to produce stable monolayers include fatty acids, proteins, sterols and fatty alcohols. The size of the aggregate produced is a function of the bubble size (Johnson and Cooke, 1980, Fig. 3), and small particles may also become incorporated into the flakes. Large bubbles appear to scavenge surface active materials less efficiently/unit surface area than smaller bubbles.

Although the qualitative process of aggregate formation from bubble dissolution is well documented, little quantitative information exists regarding its importance as a source of aggregates in nature. Dissolution rates indicate that most bubbles injected to a depth of 20 m in the ocean produce particles (Johnson and Cooke, 1980) although the surface organic coating can serve to stabilize the bubbles and prolong their life (Johnson and Cooke, 1981). While aggregate production from dissolving bubbles is clearly linked to wave action and weather

patterns at the sea surface, much additional quantitative information is needed on the rate of aggregate production in surface waters by this mechanism to assess its impact on the abundance and size distribution of aggregates in the sea.

A third mechanism by which DOM is converted to aggregated particulate matter is through the activity of marine microorganisms, primarily bacteria. Bacteria assimilate DOM and form capsular and fibrillar materials outside their cell walls. This material apparently helps to glue together particles, thus enlarging aggregates (Paerl, 1974). Although Paerl (1973) observed some aggregation of dissolved and particulate matter within sterile dialysis bags, aggregates were 10 times larger in non-sterile bags containing bacteria at natural concentrations. Particles formed by bacterial aggregation are held together by web-like structures of microfibrils produced by the bacteria on the particles. Considerable quantitative information exists on the assimilation and growth rates of marine bacteria, although this information has not been directly applied to problems of bacterial aggregation in situ.

In conclusion, while the mechanisms of the biological formation of aggregated organic matter are fairly well described, little quantitative information exists on the rates at which each of these mechanisms alters the abundance and size distribution of particles in nature. With the exception of the feeding biologies of zooplankton, the environmental factors altering those rates are largely unknown. Quantitative information on the environmental constraints of aggregate formation, the rate of aggregate production under various conditions and the relative significance of each mechanism in different oceanographic regimes or seasons is required in order to make accurate quantitative predictions of the abundances and size distributions of aggregates at any particular time and place in the ocean.

PROCESSES WHICH REMOVE OR BREAKDOWN AGGREGATES

The mechanisms by which aggregates are removed from the pelagic zone has been more extensively studied than processes of formation. Two major biological processes contribute to the removal or size reduction of aggregates; consumption by zooplankton or nekton and decomposition by microorganisms. Physical processes include settling, lateral advection, and particle fragmentation via turbulence and mixing.

1. Consumption: The primary result of consumption is to reduce the size and alter the physical and chemical characteristics of aggregates. While most zooplankton repackage small particles into larger ones, thus shifting the particle size spectrum toward the large size fractions, some zooplankton and nekton, including salps, doliolids and fish, consume large macroaggregates, repackaging them into smaller, but more compact and dense fecal pellets (Alldredge and Madin, 1982). Small copepods and euphausiid larvae also feed on the surfaces of macroaggregates and produce small fecal pellets (Alldredge, 1976). Many fecal pellets are consumed in the mixed layer. Hoffman et al. (1981) found only 0.2% of daily production reached the benthos as fecal pellets on the southeastern continental shelf. Likewise Bishop et al. (1977) found >94% of produced organic matter, much of it "fecal matter" and fecal pellets, was recycled in the upper 400 m of the North Atlantic.

Other investigations indicate that fecal pellets can be a significant component of vertical flux (Dunbar and Berger, 1981). Many are incorporated into marine snow (Turner and Ferrante, 1979), thus becoming unavailable to smaller particle feeders. Consumption of aggregates ultimately reduces their food value. Thus coprophagy may be most significant in nutritionally dilute environments where more nutritional foods are less available (Angel, 1984).

These and other studies suggest that consumption of aggregates, particularly fecal pellets, may be a significant sink for aggregated particulate matter.

2. *Decomposition*: The role of microorganisms as decomposers in the pelagic zone and the rates at which decomposition occurs have been the subject of considerable study. Bacterial decomposition primarily alters the chemical composition and nutritional value of aggregates. The C:N ratios and % of refractory matter in aggregates increases with depth (Riley, 1970) suggesting that aggregates become nutritionally depleted with age.

However, decomposition may not be a major pathway by which aggregates become fragmented or reduced in size in nature. Less than 10% of heterotrophic activity in seawater is associated with attached bacteria (Azam and Hodson, 1977; Ducklow and Kirchman, 1983). While the bacteria associated with aggregates are as metabolically active per cell as free-living forms, they are only rarely more active (Alldredge et al., 1986). Moreover, utilization of labile material on marine aggregates occurs very rapidly following formation. Rapid microbial growth occurs within the first 48 h and by 96 h most microbial activity had ceased (Pomeroy and Deibel, 1980). The majority of marine aggregates in nature appear to be nutritionally spent. Although some fragmentation of very flocculent particles may occur as labile matter is decomposed, microbial activity appears to aggregate rather than fragment particles (Paerl, 1973, 1974).

Fragmentation of fecal pellets may also be relatively insignificant. The peritrophic membranes of copepod fecal pellets decompose within 3 h at 20°C but 3 days at 15°C and 20 days at 5°C (Honjo and Roman, 1978). Pellets probably decompose slowly in surface waters of temperate and polar seas and experience reduced fragmentation once they sink to the thermocline in tropical seas. Much further research is needed to quantify decomposition as a process fragmenting aggregates in nature.

3. Sinking: Sinking is a major mechanism by which aggregates are removed from the pelagic zone. Dr. Silver (this publication) has described published rates of sinking for marine snow and fecal pellets. Although sedimentation is not a biological process, I wish to present some unpublished data here on sinking of marine snow which may prove relevant to later discussion.

We have determined the rate at which completely undisturbed aggregates of marine snow sink in nature by measuring the time required for particles to sink in situ relative to a stationary, neutral spot of dye placed 3 cm below them in the water column. We then photographed and collected these aggregates. Sinking rates of marine snow was a log function of particle mass and a linear function of mean particle length (Fig. 4). Sinking rates varied from 18 to 200 m d⁻¹ with maximum rates observed by particles 4-8 cm maximum length. Reynolds numbers ranged from hundreds to thousands. Densities of marine snow are near that of seawater. Greater than 80% of the particles have densities of 1.025-1.030 g cm⁻³ (Fig. 4).

Rapid settling rates such as these strongly suggest that settlement is a major mechanism by which aggregates, including fecal pellets and marine snow, are removed from the pelagic zone. These particles are the most abundant components of many sediment trap collections. However, the affects of turbulent mixing, entrainment and other physical processes on the sinking behavior and loss of aggregates has received relatively little attention. Rapid sinking rates do not necessarily mean that all particles settle out immediately. Many may be retained in the mixed layer or accumulate at the thermocline. Considerably more information on the affects of physical mixing processes on aggregate abundance, depth distributions and sinking is needed before the role of sedimentation as a mechanism of aggregate loss to the water column can be adequately accessed.

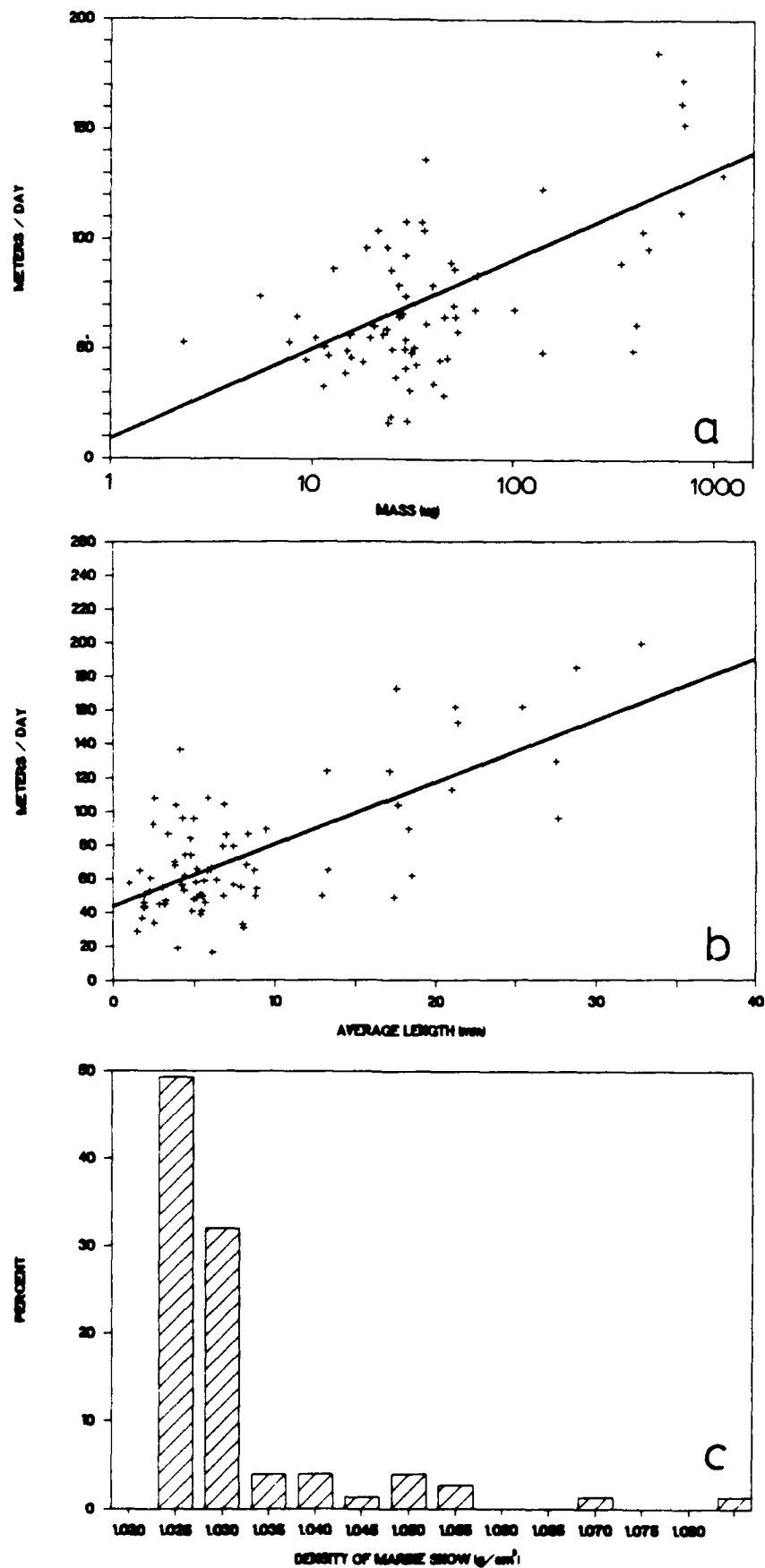


FIGURE 4: Sinking rate of marine snow measured in situ as a function of particle dry weight (A) and average length (B). C. Density of marine snow, $n = 85$. (Alldredge, unpublished).

CONCLUSIONS

While the major mechanisms of aggregate formation and loss have been identified, only in a few instances does our understanding of these mechanisms extend beyond mere qualitative description. If we are to clearly understand aggregate dynamics and make meaningful predictions regarding the abundance and size distributions of aggregated particulate matter occurring in the ocean on meaningful space and time scales, considerably more quantitative information is required. Information of the following types would greatly enhance our understanding of aggregate dynamics in the sea.

1. Mechanisms of aggregate formation must be more clearly understood. While some mechanisms, including fecal pellet formation, marine snow production by mucus-producing zooplankton, and microaggregate formation by bubble dissolution have been well studied, even good qualitative information is still needed for others. The mechanisms of de nova particle formation need to be clarified and the controversy regarding the role of bacteria in this process laid to rest. Mechanisms of bacterial aggregation need clarification, as do those for aggregation of senescent diatoms.
2. Chemical, biological or physical "markers" need to be identified for each mechanism of aggregate formation in order to identify the source of various aggregates in nature.
3. Quantitative information is needed for all processes including:
 - a. What conditions are necessary for each process to occur?
 - b. What are the physical, chemical and biological characteristics of aggregates produced by each process?
 - c. At what rate does each process occur in nature?
 - d. What factors influence these rates and how?

- e. What is the relative importance of each mechanism of formation and loss under various types of environmental conditions, seasons, or oceanographic regimes?

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State of the Art Instrumentation for Measuring Ocean Aggregates

by

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Introduction

Ocean aggregates, by their very nature, are more difficult to measure accurately than nonaggregated particles in a laboratory. They can be extremely friable and are easily disintegrated. Shear forces as small as 0.2 dyn cm^{-2} can break apart loosely associated, high order estuarine aggregates (Krone, 1976). Their size and shape may also change by colliding with other particles in the water column or on surfaces of vessels used in the sampling or measurement processes. Fresh biologically aggregated fecal pellets can often be handled repeatedly without disintegration. Older, biochemically altered pellicles, on the other hand may be quite friable.

Because of the susceptibility of aggregates to modifications in size, shape, and other properties prior to or during measurement, certain in situ techniques provide inherently less intrusive measurements of aggregates than do laboratory methods. Also, because of the heterogeneity of particle size and composition in the ocean, methods that extract individual particle characteristics or properties from the measurements are inherently superior to bulk measurements. As

a result, the major portion of this review will concentrate on in situ methods for measuring individual particles, or laboratory measurements that might be adapted to in situ applications.

Physical Structure

Perhaps the most fundamental measurement of particle size is volume, which does not require a shape discriminator. Because of this, the sphere-equivalent diameter or radius of a particle is often used as a de facto particle size standard. Thus, instruments that measure volume directly (e.g. by use of particle electrical resistivity methods) provide particle volume data unbiased by shape. Unfortunately, these methods draw particles through a small orifice in a dielectric tube, often disrupting aggregates.

On the other hand, particle shape is very important for purposes of identifying or categorizing particles, calculating their drag, surface area, settling speed, optical properties and diffusion. Mathematical relationships among size categories (e.g. major and minor axes, perimeter, cross-sectional area, surface area, volume) can be provided given a general shape category for a particle. Because of the dependence of scattering and absorption coefficients on the areal cross section of particles projected normal to the incident light, for example, the shape and orientation of a particle also have significant effects upon optical measurements of a particle. Shape and orientation are also quite important to particle settling dynamics, especially for noncompact particles (Lerman, 1979).

Internal Structure

The internal structure of a particle is also important to its settling dynamics and its microscopic identification. For solid particles such as mineral grains and most fecal pellets, the internal mass distribution or mass density directly affects settling speed. Knowledge of particle density permits the general classification of ocean particles into heavy mineral, nonheavy mineral, fecal pellet, and other categories. It also permits the calculation of mass from a measured volume. This is important since the mass of individual ocean particles is generally too small for direct measurement.

Aggregates and lysed phytoplankton cells have a somewhat open internal structure. If seawater can effectively flow through the interstices of a particle, this occluded water can be considered in somewhat the same way as are pore waters in sediment. While it reduces the apparent mean density of the particle, if water can flow through as well as around the particle, it provides complications when making particle settling velocity calculations (see Appendix 1).

The flow or diffusion rate of sediment pore waters is often described in terms of porosity and tortuosity (see Berner, 1980). The porosity is considered the ratio of the volume of the interstices to the volume of the sediment and interstices. Tortuosity is a measure of the mean path length a water parcel must travel to move a unit distance in the vertical through the sediment. These concepts may be helpful when conceptualizing the occluded water or pore water of aggregates. The simplest pore is a tube. When falling parallel to its length, it would have a tortuosity of 1. The same tube falling at a 45° angle would have a tortuosity of 1.41. However, we can show by a simple

example that the pore water flushing rate of a settling aggregate is somewhat different than that for sediment, due in part to the pressure differential across the particle induced by the balance between inertial and drag forces.

Because the water inside a cylindrical tube falling vertically is not restricted, it might appear at first to provide little of the added buoyancy to the tube that would occur if the ends were capped off. However, there is significant drag on the inside of the tube, so much of the fluid inside is not flushed when it settles a distance equal to the tube length. As the diameter is reduced to capillary dimensions under laminar flow conditions, and as the tube is lengthened, a much larger fraction of the original fluid remains after it has settled a distance equal to its length (see Fig. 1 and Appendix 1). The drag of this retained water has provided an added "buoyancy" to the pipe, even though its tortuosity is still 1.0. Adding tortuosity will increase the drag of pore waters, reduce their flushing, and increase the "buoyancy" provided by the occluded pore waters.

Since we don't know the internal structure of aggregates, we can only make some estimates of porosity based upon other measureables and some assumptions. If we consider an aggregate of diameter d consisting of a collection of solid particles of density ρ_s and occluded water of density ρ_w , the porosity of the particle or water fraction is f_w , and the solid fraction is f_s . The mean density of the particle can then be expressed as

$$\bar{\rho} = \frac{M_s + M_w}{V_s + V_w} = \rho_s f_s + \rho_w f_w = f_s(\rho_s - \rho_w) + \rho_w,$$

where M_s and V_s are mass and volume of the solid part of the aggregate,

respectively. M_w and V_w are the mass and density of the water, respectively, and $f_s + f_w = 1$. Since the water density is known, methods for determining $\bar{\rho}$ and ρ_s are required in order to determine f_s and f_w .

The density ρ_s of the solid or nonaqueous part of an aggregate can be determined by allowing it to settle to its own density level in an isotonic density gradient. Given time the original pore waters of the aggregate will be replaced by the density gradient media due to flushing and diffusion (Carder and Steward, 1984), and the density at any depth of the gradient can be determined from its index of refraction.

If one assumes that by a combination of tortuosity and high capillarity (long, narrow pores), flow through the aggregate is small compared to flow around it, the mean density of the aggregate $\bar{\rho}$ can be determined by inverting Stokes settling equation. For a sphere of diameter, d , this becomes

$$\bar{\rho} = \frac{\rho_w + 18w_a \eta}{980 d^2}$$

where w_a is the aggregate settling speed and η is the water viscosity. A method for measuring the flushing rate or flow through the aggregate in lieu of the above assumption is discussed in Appendix 2.

This exercise has allowed us to focus on the types of measurements required to better understand the settling dynamics of particles and aggregates, but the mechanics of aggregation and disintegration should also be mentioned. Aggregates form as a result of collisions between particles. These collisions can be caused by at least four mechanisms

(see Lerman, 1979): i) Brownian motion-induced particle diffusion; ii) water shear; iii) differential settling speeds; iv) and biological filtering or scavenging. In addition, retardation of settling and particle buildup on density interfaces enhances the probability of collisions or biological filtering and scavenging.

The first mechanism is most important in causing aggregation of colloidal or small particles under low shear conditions (e.g. $du/dz < 0.1 \text{ sec}^{-1}$), while differential settling is most effective for larger particles. Water shear is the dominant mechanism for $du/dz > 0.5 \text{ sec}^{-1}$ (Lerman, 1979). Water shear is typically most effective above the pycnocline and in the near bottom nepheloid layer. Both regions are usually regions of significant vertical shear. The sheet and layer, stepped density structure in the pycnocline provides a region where low density particles slow or accumulate at density interfaces, greatly increasing the probability of particle collisions. Here, also, there is a likelihood that detrital filter feeders would concentrate.

The primary disintegration mechanism for aggregates is high shear stress. Krone (1976) points out the shear strength of various orders of estuarine aggregates, above which disaggregation to a lower order aggregate occurs. Storms, breaking internal waves, and high bottom stress are candidate mechanisms for causing stresses exceeding ocean aggregate shear strength.

Optical Properties of Particles

The effects of particle shape and index of refraction are secondary to the effect of particle size on light scattering in the ocean (Jerlov, 1976). This property is exploited by particle sizing

instruments that measure the particle attenuation coefficient c_p or estimate the particle scattering coefficient b_p .

In general, all of the light energy impinging directly on a large particle of geometrical cross section G is scattered or absorbed, while an equal amount of light energy passing near the particle is scattered by diffraction (e.g. recall Babinet's principle, Van de Hulst, 1957). Thus the ratio of the total energy removed by a particle from a proceeding wave to the energy physically intercepted by a particle of cross sectional area G corresponds to an attenuation cross section or efficiency factor $Q_c \doteq 2 = Q_a + Q_b$. Q_a and Q_b are the absorption and scattering cross sections, respectively.

For sizing purposes, then, the attenuation coefficient for a spherical particle i is

$$c_i = G Q_c$$

or

$$c_i = \frac{\pi d_i^2}{4} Q_c \doteq \frac{\pi d_i^2}{4} (2) = \frac{\pi d_i^2}{2},$$

the absorption coefficient is

$$0 \leq a_i = \frac{\pi d_i^2}{4} Q_a \leq \frac{\pi d_i^2}{4} (1),$$

and the scattering coefficient is

$$1 \leq b_i = \frac{\pi d_i^2}{4} Q_b \leq \frac{\pi d_i^2}{2}.$$

An important question, then is "what constitutes a large particle?" For spherical particles with real refractive indices near 1.0 relative to the medium, Van de Hulst (1957) has derived

relationships among Q_a , Q_b , and Q_c , particle diameter d , and the refractive index m relative to the medium. These relationships are shown in Figure 2, where $\rho = 2\pi\eta_w d(m-1)/\lambda$, λ is the wavelength in vacuo, and η_w is the refractive index of water. It is clear that when ρ is smaller than about 3, the particle becomes an inefficient scatterer, and when ρ exceeds 8 to 10, $Q_c \approx 2$, regardless of the absorption coefficients (related to the imaginary part η' of the refractive index according to $\eta' = a_p \lambda / 4\pi$). Increases in η' force Q_c closer to 2 for smaller ρ values, and decrease Q_b values to 1.0. Again for large ρ values, Q_c is much less variable than Q_b .

For phytoplankton, the absorption coefficient a_p is less than 15% of the attenuation coefficient for much of the visible light spectrum (550-640 nm) (Bricaud et al. 1983).

Since $c_p = a_p + b_p$, then $b_p \geq 0.85 c_p$. For quartz grains, $b_p \approx c_p$. However, for large opaque particles such as certain fecal pellets, the absorption coefficient can equal the total scattering coefficient, or $b_p = 0.5 c_p$. Because of the variation in a_p in the oceans, attenuation or c meters are inherently more accurate than scattering or b meters as particle sizing devices.

In order that an optical particle sizing meter measure the signal due to a single particle rather than from an ensemble of particles, the measurement or sampling volume must be very small, or the particle concentration must be very dilute. Two methods are presently in use by automatic laboratory particle sizing and counting devices to increase the odds of measuring single particles. One method used by HIAC/ROYCO draws the media fluid through a narrow flow constriction (e.g. 100 μm x 1000 μm cross section), inducing turbulence to make the particles

tumble. The largest particle cross section presented to the $100\text{ }\mu\text{m} \times 100\text{ }\mu\text{m}$ cross section of collimated light passing across this constriction is recorded as a pulse height and counted.

A second method, used by Spectrex, focuses a scanning laser beam down to a narrow waist where an illuminated particle will intercept the greatest fraction of the incident radiant flux and provide the largest scattered or attenuated signal. Pulse length discrimination is used to reject signals that are too short (particle at the beam edge) or too long (particle not at the beam waist) to have been centered in the intensity maximum at the waist of the scanning beam. This method requires no fluid flow and thus is less destructive, but the pulse discrimination process provides about a 15% uncertainty in the projected cross sectional area of the particle. The methods also differ in that the first measures the "largest" areal dimension of a particle, while the second measures a random areal dimension. The scanning beam method in present use measures near-forward scattered light rather than light attenuation, adding an additional uncertainty if the particle absorption coefficient of particles is heterogeneous. However, the attenuation principle could be incorporated together with the scanning beam methodology to avoid the absorption uncertainty.

These automatic techniques are probably both adaptable to in situ observations, but discrimination of one particle type from another except by size would not be possible. That is the reason particle imaging and sizing systems are most commonly in use for studying marine particles and aggregates in situ.

Particle Imaging Methods

The in situ methods presently in use for imaging particles and aggregates fall into two categories: photographic and holographic. Because vidicon tubes and area array sensors for television have an order of magnitude lower resolution than photography, they can be considered for only low resolution photographic applications. For this reason, they are not considered independently in this review even though they provide real time data.

The choice of methodology used to image particles is often dependent upon the size of the particles of interest. As a rule of thumb, the number of particles of diameter d in the ocean decreases as the function d^{-k} , where k is typically between 3 and 5. For living particles Sheldon et al. (1972) found a value of about 3, while for all particles, a value near 4 may be more representative (see Lerman et al. 1977).

With a paucity of particles at larger sizes, one must either measure a given volume continuously for a long time to observe a statistically representative population of large particles, increase the volume of water imaged, or use a concentration mechanism. Because the depth of field of a photographic system is inversely proportional to its magnification, high magnification systems have very little depth of field. The odds of a free-falling or floating particle of the appropriate size occurring at the focal distance may be quite small, unless they come to rest on a fixed horizontal, optical surface such as the bottom of a sediment trap. However, photographic systems can be quite useful for the in situ imaging of large particles where magnification can be much less than 1.0, providing for adequate depths of field for large sample volumes.

The photographic methods are typically used to image large particles and aggregates with fractional magnification values to increase the depth of field. A large sample volume increases the probability that a particle of interest (e.g. marine snow) will be in the sampling volume. The cost of increasing the sample volume in this way is an image that appears to be perhaps 25% longer and wider at the near edge of the volume than it does at the far edge, even with a "perfect" pinhole camera (see Fig. 3). For an actual camera with a finite aperture, the particle images will appear to be out of focus at the near and far edges of the sample volume. Reduction in the depth of the sample volume ameliorates both the magnification and the focusing problem, but reduces the number of particles imaged. Increasing the radiant flux of the source and/or the sensitivity of the film can provide a larger f-stop for the system, improving the depth of focus by reducing the camera aperture.

At least two in situ photographic particle imaging and sizing systems are presently in use for measuring aggregates and particles. One of moderate resolution (diameter $> 50 \mu\text{m}$) measures backscattering along with photographic images with $1/4$ magnification (Johnson and Wangersky, 1985). The backscattering meter is used to activate a strobe only when imaging larger particles or organisms. While the sample volume of the imaging system is not discussed, it appears to be of order 10-20 ml.

A system of lower resolution (diameter $> 500 \mu\text{m}$; $1/40$ magnification) but much larger sample volume ($.66 \text{ m}^3$) has been described by Honjo et al. (1984) for studying large amorphous

aggregates or marine snow. A particle at the near edge of the sample volume relative to the camera would appear to be about 29% larger than would the same particle at the far edge (e.g. see Fig. 3). This $\pm$ 14.5% uncertainty in size could be easily reduced by narrowing the depth of the lighted or sample volume viewed. This modification and others will be discussed in detail by Vernon Asper in a later talk.

Methods using holographic microscopy are more useful for measurement systems requiring image magnification, since the diffraction patterns from all particles in a volume are recorded rather than the images from the particles at a given focal plane. In the image reconstruction process the diffraction patterns on the film diffract light such that images of the original particles can be formed by moving an image screen along the optical axis of the system (see Fig. 4). Transmission or Gabor holography has been the method of choice in ocean applications because of the inherent stability and low power requirements of the method.

Magnification of the diffraction patterns (already much larger than the original particle) onto the holographic film can be achieved with lenses (see Thompson et al., 1967; Carder et al., 1982), but most of the magnification is performed during the holographic reconstruction process. Total system magnification factors of more than 500 can be achieved (Costello et al., in press) with a sample depth of more than 3.5 cm. Typical sample volumes range from about 1 to 4 cm³ (Carder et al., 1982). Adequate resolution of the reconstructed image is achieved if three or more diffraction rings are captured on the hologram and if the particle moves a distance less than 1/10 its diameter during the exposure (Thompson et al., 1967).

Holography is of additional interest in studies of aggregate behavior at density interfaces because the phase contrast due to differences in refractive index across the interface and mixing induced by settling particles can be visualized. Transmission or Gabor holography is adequate to visualize mixing between fluids of relatively high contrast in refractive index (see Appendix II), but for more sensitivity, multiple beam, multiple wavelength, multiple pass or double exposure holographic interferometry methods can be employed (Vest, 1979). Such studies are important because i) density interfaces increase the probability of aggregate formation, ii) aggregates cause mixing by flushing occluded water below the interface as low density, low viscosity cylindrical streamers, iii) these streamers provide a faster, preferred pathway for subsequent aggregates, and iv) because vertically elongated aggregates are formed when subsequent aggregates overtake slower aggregates in the streamer (see Appendix II). These density interface processes involving aggregates have ramifications on aggregate collision probabilities, size, shape, settling speed, fluid mixing, and most likely feeding behavior, and should be considered for study as the technology becomes available.

Photographic and holographic methods can both be used to measure particle settling speeds by taking sequential photographs or holograms. However, the fluid must not be moving relative to the imaging system, and gravity should be the only acceleration on the particles. Carder et al. (1982) and Costello et al. (in press) have achieved platform stability and stationary fluid conditions by holographically imaging particles inside a large sediment trap suspended from the surface by a system of damped buoys in tandem (see

Fig. 5). A constant downward particle settling velocity through multiple images confirms platform stability.

For studies of eolian mineral transport from Asia to and through the central north Pacific we have developed a multiple sample sediment trap equipped with vertical and horizontal axis holographic cameras. Figure 5 shows a 0.66 m^2 collection cone, horizontal camera and laser housings, a vertical camera housing, the sampling chamber assembly and battery pack/timer. The vertical laser is inside the collection cone. The sampling chamber has six collection cups with windows which are sealed except during sampling. The cone is deployed and retrieved open. One-way valves permit filling and flushing of the cone. A programmable delay of typically six hours is used to avoid sampling of most particles entrained in the cone during deployment. Then the first cup is pulled by a lead weight and locked into place. Burn wires are used to control the cup progression by releasing an elastic locking mechanism upon a signal from the timer.

A dense (1.11 gm/ml), viscous (0.053 poise), isotonic mixture of sugar, dextran and saltwater in the cup dramatically slows the speed of fecal pellets and minerals to permit multiple holograms of the same particles before they leave the 1 cm diameter laser beam. Typical frame rates are 1/minute to 1/15 sec. for the horizontal camera, and 1/6 minutes for the vertical camera. Each camera contains 250 exposures of 35 mm high speed holographic film (Kodak 50-253).

Reconstructed holograms of typical quartz-like particles, heavy minerals, fecal pellets, and aggregates are shown in Figure 6. The Stokes settling equation for prolate spheroids was used to calculate density values of about 2.6, 5.0, 1.136, and 1.12 gm/ml for

these classes of particles (Carder et al., in press). Fecal pellets captured at greater depth had densities as high as 1.21 gm/ml.

Other Methods

For robust particles such as some fecal pellets, laboratory measurements can be made to enhance our understanding of their nature. Light microscopy of carefully collected aggregates by SCUBA divers has been used (Alldredge, 1972). Scanning electron microscopy with individual particles electron dispersive x-ray analysis might be used on similarly collected aggregates to better determine the composition of the heavier elements of the aggregate components.

It is known that large aggregates break apart when passing through the Coulter Counter (Sheldon, 1967; Hunt, 1982), and the same fate may await aggregates passing through a flow cell cytometer, an instrument used to estimate individual particle size and fluorescent properties by light absorption, scattering and fluorescence (e.g. see Olson et al., 1985; Yentsch et al., 1983). For robust fecal pellets, it may be possible to qualitatively estimate their pigment content by fluorescence, and their degree of opacity may be a useful fecal pellet classifier. Sizing can be performed by either light attenuation or near-forward scattering techniques similar to those discussed earlier, and scattering at large angles is thought to provide a measure of internal structure and/or index of refraction (R. Spinrad, personal communication). More details about flow cell cytometry are provided later in the talk by K. Stolzenbach.

A final laboratory method useful for sizing nonodisperse distributions of very small (30 Angstroms to 3 μm) particle populations

is Photon Correlation Spectroscopy (PCS). It may be useful for studying Brownian motion induced aggregation since it provides a measure of the particle diffusion coefficient A_p . Since large particles diffuse more slowly than small ones due to the frictional drag of the water viscosity, the particle diameter can be expressed by the Stokes-Einstein equation as

$$d = \frac{kT}{3\pi A_p},$$

where k is the Boltzman constant and T is the absolute temperature (Ford, 1983). The Brownian motion of each particle imparts a small Doppler shift in the wavelength of the scattered light. This Doppler shift is too small to be effectively analyzed spectroscopically. However, interference between this doppler-shifted scattered light and that of incident light as a function of time produces a beat frequency at the receiver which increases as the Doppler-induced wavelength difference increases. Recalling that these beats are a measure of group wave or envelope frequency, the beat period γ is proportional to $\lambda/\Delta\lambda$. The spectra of beat frequencies due to interference of scattered light from all particles in the sample volume are analyzed using the auto-correlation function of the scattered signal (Ford et al., 1973). The spectral distribution of the scattered intensity as a function of frequency ω is Lorentzian in shape

$$I(\omega) = \frac{(\text{constant})}{2 + (\omega - \omega_0)^2},$$

where ω_0 is the incident frequency. It is centered around the

incident frequency w_0 , with half-width at half-height of

$$\Gamma = A_p \frac{4\pi\eta}{V_0} \sin^2(\theta/2),$$

where A_p is the particle translational diffusion coefficient, η is the index of refraction of the medium, λ_0 is incident wavelength, and θ is the scattering angle. Combination with the Stokes-Einstein expression permits determination of the effective diameter of a spherical particle.

It may be possible to use this photon correlation spectroscopy technique to observe the increase in the effective or mean diameter of a population of colloidal particles as Brownian motion induces aggregation. Instruments such as Langley Ford or the Coulter Model N4 are designed for laboratory use, and the method is vibration sensitive. Even the motility of micro-organisms affects the results, so use in a shore-based facility is probably a firm requirement for PCS applications at present. However, many colloidal particles form at the river-ocean interface, so this restriction may not be as severe as it first appears.

Summary

A number of optical methods are in use presently in laboratory instruments which may be adaptable for in situ applications. These include automatic particle sizing by light attenuation or light scattering methodologies. These methods do not provide particle shape and orientation discrimination, however.

For large particles (diameter $> 50 \mu\text{m}$) photographic techniques have been developed to measure particle size and shape, and these methods could be modified by particle measurement inside a stable sediment trap to measure particle settling speeds by taking sequential photographs of particle position. These methods sample volumes from about 10 ml to 0.6 m^3 , with sizing accuracies of better than $\pm 15\%$, depending upon the magnification and sample depth.

For intermediate to small particles (nominally $5 \mu\text{m}$ to $5000 \mu\text{m}$ diameter), transmission holographic microscopy is being used to sequentially image particles in sample volumes of $.5$ to 4 cm^3 , depending upon the application. Particle size, shape, orientation, position in three-space, and velocity in three-space are determined holographically for all particles in the sample volume. Magnification is uniform with particle distance from the camera, so size ambiguities do not result from the position of the particle in the sample. Particle size, shape and settling speed used with Stokes settling equations then provide a measure of the particle density. The flushing rate of occluded water for aggregates can be determined at density interfaces either holographically or using holographic interferometry.

A number of laboratory methods are not expected to be successfully adapted to in situ application. Flow cell cytometry equipped with

particle sizing by attenuation or scattering methodologies and fluorescence provides single particle or cell characteristics for classification and sorting. Shipboard sea trials have been successful. Photon correlation spectroscopy is not expected to be useful at sea because of effects of ship vibration on the motion of colloidal and small particle populations. For shore based facilities, experiments on the growth in size of colloidal and small aggregates due to Brownian motion induced collisions may be directly observable use photon correlation spectroscopy.

Acknowledgements

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Figure Legends

Figure 1. Family of approximate settling velocity curves as a function of radius R for open (solid) and capped (open) circular tubes of varying length L , falling parallel to the long axis. The wall thickness dr is 0.1 times the radius, and the wall density is 2.65 gm/ml. Sea water density is 1.02 gm/ml and viscosity is 0.01 poise. Note that for long open tubes the settling speed approximates those of capped tubes (see Appendix 1 for details)

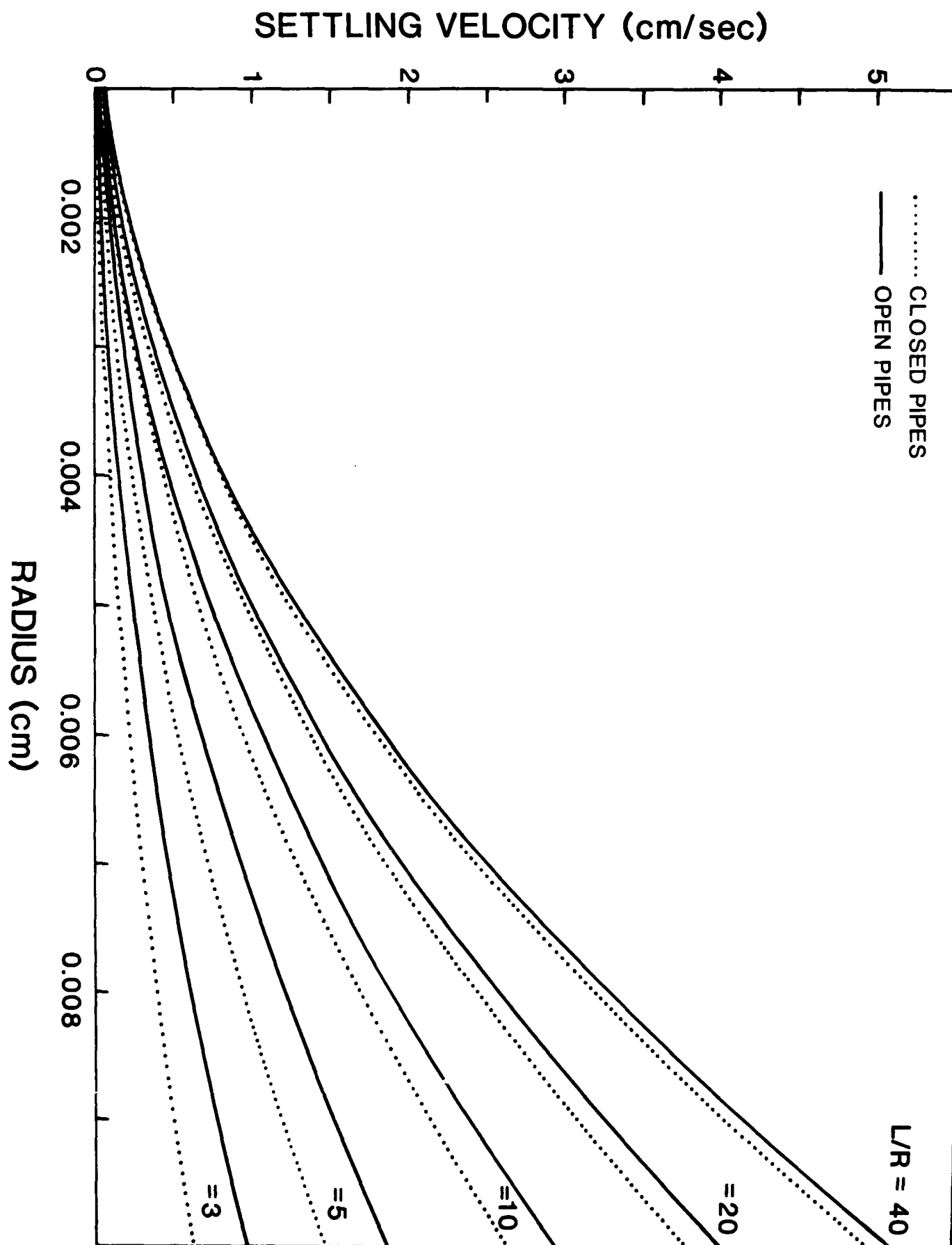
Figure 2. Families of curves for the cross sections for attenuation, total scattering and absorption as a function of ρ for different values of the imaginary or absorbing part η' of the index of refraction. The parameter ρ is the optical size of a particle and is defined in the text.

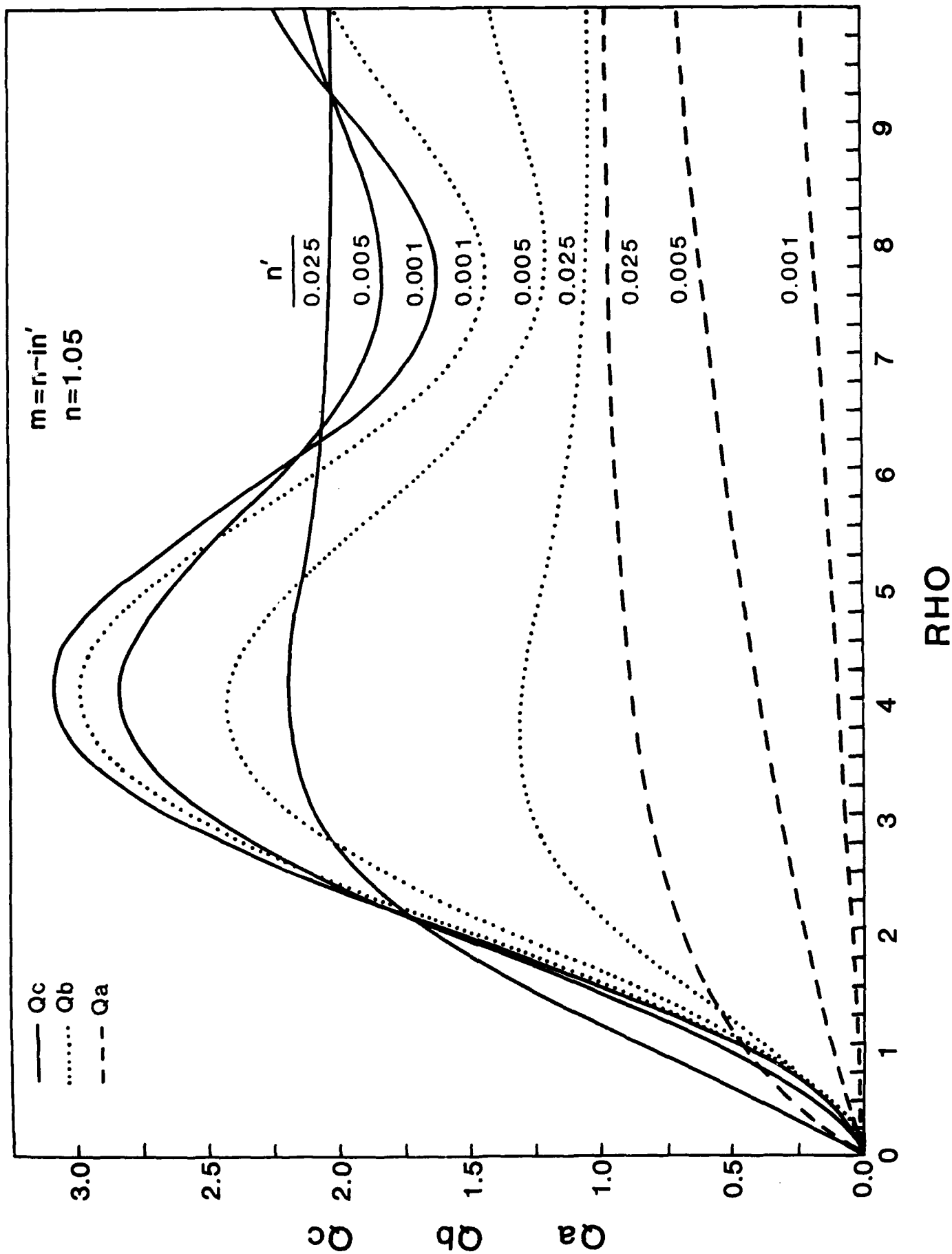
Figure 3. A schematic representation showing the ambiguity in particle size for a pinhole camera with a large depth of field. L_1 is the image on the film of either object L_1 or L_2 , at the front and rear edges of the sample volume. L_2 is about 30% longer than is L_1 .

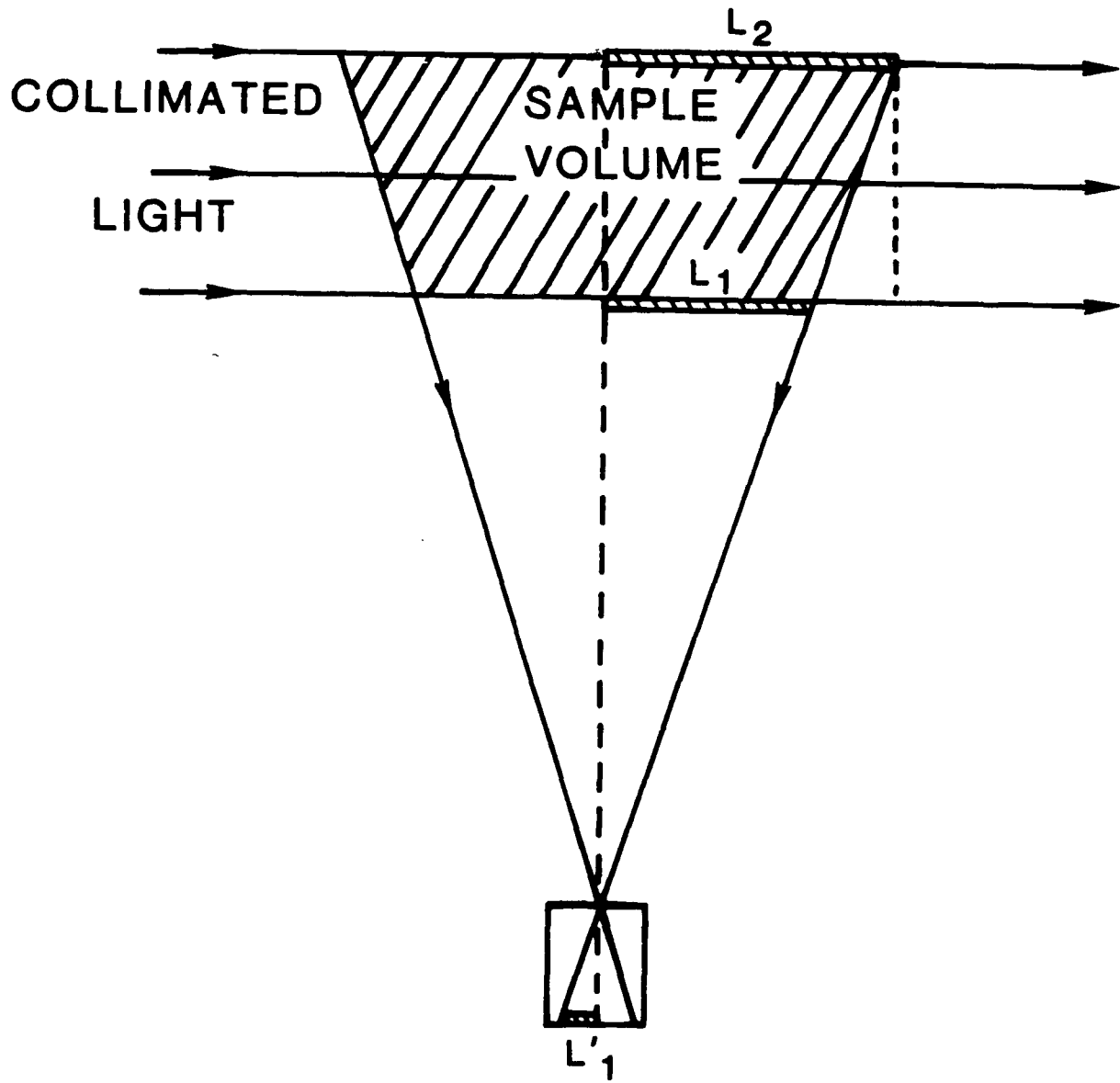
Figure 4. A schematic of Gabor or transmission holography. Planar wavefronts of a collimated laser beam are diffracted by a particle P. Diffracted light (spherical wavefronts) constructively interfere with planar wavefronts at the film plane producing high density or dark circular diffraction rings. Destructive interference occurs between the dark rings, providing low density or light rings. Placing the developed hologram back in the film plane and passing a collimated laser beam through it in the opposite direction causes light scattering off the diffraction rings themselves such that constructive interference occurs at P, creating the image of the original particle at the position P.

Figure 5. Drawing of a sediment trap equipped with horizontal and vertical axis holographic camera systems for viewing particles orthogonally. At the apex of the inverted conical concentrator (A) is the six-cup viewing and sampling assembly (B). The timer/battery pack (horizontal cylinder at bottom) controls the timing sequence of cups (C), laser on/off cycles, and camera firing. Motive force for advancing cup assembly through sequentially fired registration pins (D) is provided by a lead weight in the long plexiglass sleeve (E) vertically attached to the trap frame. The horizontal laser housing (F), horizontal camera housing (G), and vertical camera housing (H) are shown.

Figure 6. Photographs of reconstructed of in situ particles captured in the north central Pacific gyre during March/April, 1986.







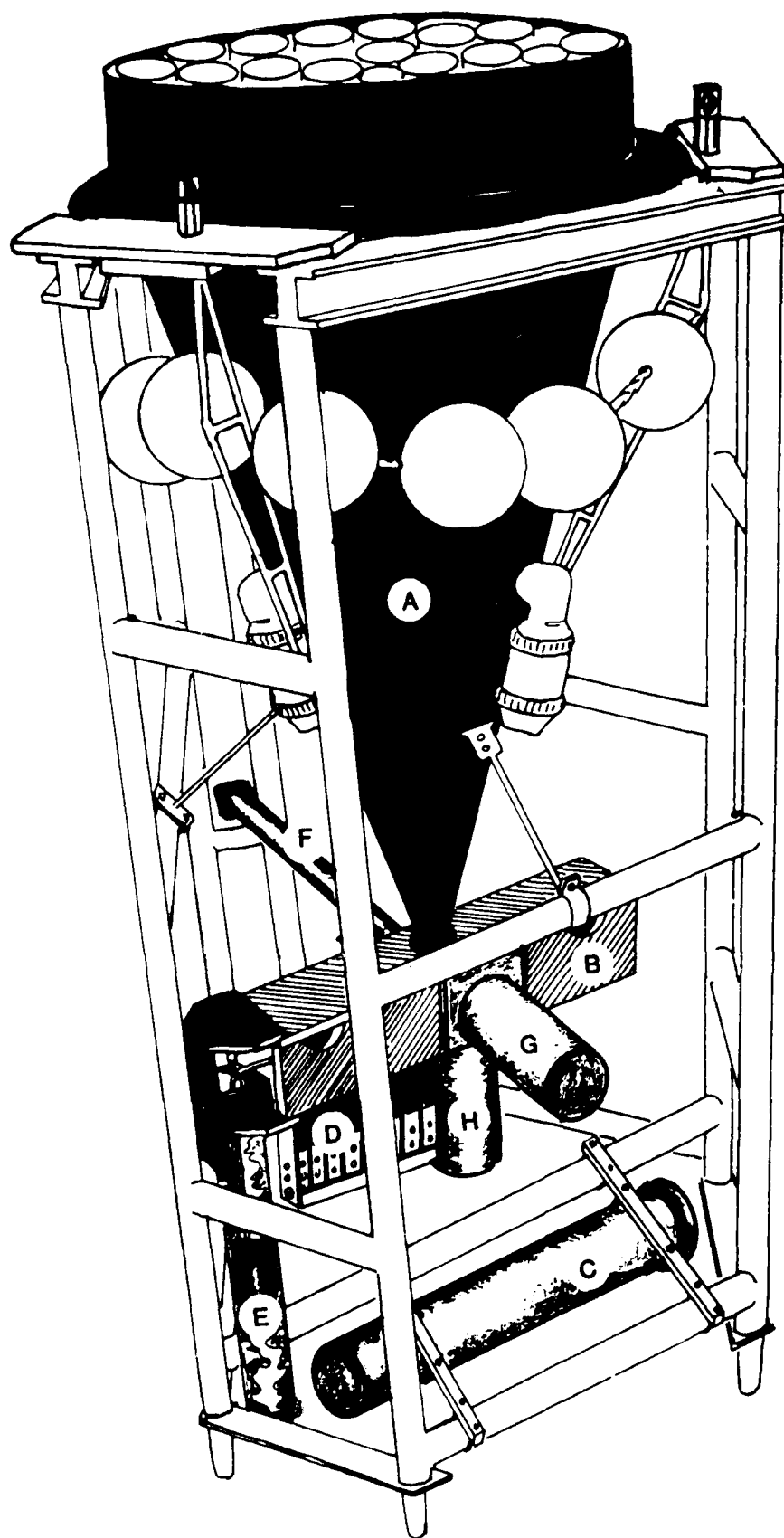


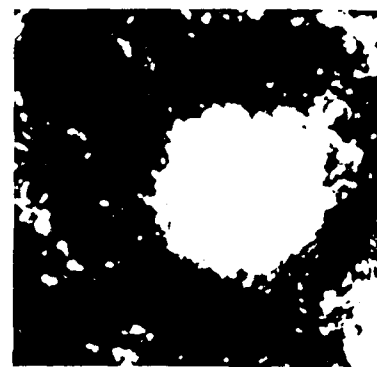
Figure 6. Holographic reconstructions of particles imaged in situ



a) Copepod: (37X)
850 μm X 550 μm



b) Fecal pellet: (513X)
48.7 μm X 22.2 μm
1.136 g/cc



c) Fecal pellet: (258X)
90 μm dia., 1.137 g/cc
1.137 g/cc



d) Aggregate: (513X)
62.8 μm X 41.9 μm
1.12 g/cc



e) Aggregate: (513X)
54.2 μm X 52.4 μm
1.12 g/cc



f) Aggregate: (513X)
35.7 μm X 36.1 μm
1.12 g/cc



g) Quartz: (513X)
31.6 μm X 21.1 μm
2.61 g/cc



h) Heavy Minerals: (513X)
21.4 μm X 15.3 μm
5.1 g/cc

APPENDIX I

The flushing rate of aggregates is important to consider in terms of its effect on the buoyancy of particles. For many flocculated mineral materials, the flushing rates are of the order of minutes to tens of minutes and appear to be controlled by the rate of diffusion (Lerman, 1979; p. 312). In cases of aggregates stopping on density interfaces, the flushing time is of the order $t = L^2/D$, where L is the particle length and D is the molecular diffusion coefficient for salt or temperature. Except at density interfaces, the time it takes such aggregates to settle a distance L is typically short compared to the diffusional flushing rate, and flushing has little effect on the Stokes settling rate calculations.

For aggregates with larger structural components and pores, the effect of flushing rate on Stokes settling calculations and particle buoyancy may need to be considered. As a simple illustration, suppose a pore is modelled as a long, hollow tube of radius R and length L . If it settles parallel to L , a first order estimate of its drag is that for a long cylinder (Happel and Brenner, 1975):

$$F_D = \frac{2 \pi \eta U_s L}{\ln (L/R) - .72} \quad (A1)$$

where η is the fluid viscosity and U_s is the settling speed. The pressure differential dp required at low Reynolds numbers to force water through the tube at mean internal velocity U_i is (Schlichting, 1955)

$$dp = - \frac{4 \eta L U_i}{R^2} \quad (A2)$$

In order to estimate the pressure differential between the bottom and top of the tube created by a settling velocity U_s , consider the drag force F_{DD} on a disk settling face down (Lamb, 1945; Happel and Brenner, 1973) in the limit of no thickness:

$$F_{DD} = 5.1 \pi \eta U_s R. \quad (A3)$$

This equation approximates the part of the drag on a cylinder that results from the flat end surfaces.

Combining equations A2 and A3

$$dp (\pi R^2) = F_{DD}$$

$$\frac{4 \eta L U_i}{R^2} (\pi R^2) = 5.1 \pi \eta U_s R$$

or

$$\frac{U_i}{U_s} = \frac{5.1 R}{4 L} = 1.275 R/L. \quad (A4)$$

Thus, for $L/R = 10$, the pore velocity U_i is about 13% of the settling speed. This result is for a vertically oriented tubular pore of uniform cross section and no tortuosity.

To consider the settling speed of a circular, thin-walled tube, the buoyancy force on the tube must be calculated, including that of the internal pore water carried with it. The volume of pore water carried with the tube in settling a distance equal to its length L is

$$V_{\text{pore}} = \pi R^2 L f_{\text{pore}}, \quad (A5)$$

$$\text{where } f_{\text{pore}} = \frac{U_s - U_i}{U_s} \quad (\text{A6})$$

is the fraction of the pore retaining unflushed water.

The volume of the tube is

$$V_c = \pi L [(R + dr)^2 - R^2] \doteq 2 \pi L R dr \quad (\text{A7})$$

for $dr \ll R$. The average density of the tube and entrained pore water is

$$\bar{\rho} = \frac{V_{\text{pore}} \rho_w + V_c \rho_c}{V_{\text{pore}} + V_c} \quad (\text{A8})$$

Combining eqs. A4, A5, A6, and A7,

$$\bar{\rho} = \frac{(1 - 1.275 R/L) \rho_w + 2dr/R \rho_c}{(1 - 1.275 R/L) + 2 dr/R}.$$

Setting the buoyant force equal to the drag force for the open tube,

$$\pi(R + dr)^2 L g(\bar{\rho} - \rho_w) = \frac{2\pi\eta U_s L}{\ln(L/R) - .72},$$

and solving for the settling velocity provides

$$U_s = \frac{g(R + dr)^2 (\ln(L/R) - .72)(\bar{\rho} - \rho_w)}{2\eta}. \quad (\text{A9})$$

This equation provides the family of curves shown in Fig. 1 for an open tube with $dr/R = 0.1$, $\rho_c = 2.65$, and variable values of R/L . The settling curves for capped tubes are also shown, and the fraction of pore water retained can be calculated from the curve differences.

Appendix II: Evaluation of Stokes Settling Equation
for Variable Density Aggregates

by

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I. Introduction

Reduction of viscous drag has been cited as a reason for the relatively faster settling speeds than expected for aggregates using Stokes settling equation with a particle packing model density (Chase, 1979; Hawley, 1982). However, the inability to measure the actual density of individual particles in these studies has made it necessary to make gross estimates of one or more of the Stokesian parameters, usually the aggregate density. If settling aggregates were assigned too small a density based upon a given density packing model, it would appear that viscous reduction had occurred in order to provide faster-than-Stokes settling speeds. Also, if aggregates settled and then broke up at depth, the smaller aggregate components observed would appear to have settled faster than Stokes equation allows. Again, viscous reduction could erroneously be used to explain this settling behavior. Our program objectives were to conduct settling-chamber/density-gradient experiments to measure aggregate particle density and viscous drag independently.

A key element of the project was the independent measurement of particle density by the use of high density fluids (isotonic with the seawater) in density gradient columns. Although the holographically-measured settling velocity and Stokes equation predicted montmorillonite aggregate densities of the order 1.05 g/ml (similar to the high-order aggregates found by Krone (1976)), none of the aggregates remained buoyant in the columns of high-density sugar solutions, which reached densities of 1.40 g/ml. This suggested that the occluded water or pore water of the aggregate was constantly being

flushed and replaced by the density of the surrounding media. This would remove the buoyancy due to lower density occluded waters of the original aggregate, and the settling aggregate would have a net negative buoyancy due to the clay (montmorillonite) component. Holographic investigation of the behavior of the aggregates as they traversed a sharp density interface has demonstrated some aspects of aggregate settling behavior which are of more importance than the objectives of the initial program. Pore water flushing has been demonstrated holographically to occur and to have significant effects on the settling behavior of aggregate particles.

As a summary of the work performed under this contract, this report will describe the behavior of inorganic aggregates encountering fluids of differing composition than those in which they were created. Holographic techniques have been used to show that the interstitial water of these aggregates is not tightly bound. In fact, it is exchanged rapidly, and suggests an initiation mechanism for the formation of vertical sediment fingers in stratified water columns.

II. Experimental Design

The settling chamber was constructed for this project with the following features: an upper cylinder to dampen injection forces and allow the settling particles to achieve terminal settling velocity, and a lower chamber equipped with dual ports for holographic velocimeters crossed at 90° to each other and the settling direction. Below the horizontal laser paths, the particles came to rest on another optical plate providing an opportunity to holographically image the particles in the vertical direction.

Three types of aggregates were prepared in filtered, abiotic artificial seawater. Three standard clays, kaolinite, montmorillonite, and illite from the U. S. Geological Survey were each allowed to aggregate in 35ppt artificial seawater for about one month. Flocculated aggregates on the order of 20-300 μm were gently withdrawn and introduced both to the settling chamber and the density gradient chamber.

Two different density media were used in the gradients. In the initial setup runs and test, serum dextran was used to save the extremely expensive metrizamide for later runs. Metrizamide-heavy water solutions isotonic with 35ppt seawater were created with densities as high as 1.40 g/ml. Even at these high densities, the aggregates consistently failed to become buoyant, even those with densities determined using Stokes settling equation (with measured water viscosity) to be less than 1.05 g/ml.

III. Results

To examine the behavior of the aggregates as they settled into the higher density fluids, the holographic microvelocimeter was employed. A two-layer, isothermal, isotonic density gradient was prepared from artificial seawater (35ppt, 1.0241 g/ml, 23.5°C, 0.92 centipoise) and dextran-artificial seawater (35ppt, 23.5°C, 1.054 gm/ml, 7.45 centipoise). The 1 cm diameter laser beam crossed the settling chamber at the sharp interface. Time-sequential transmission holograms revealed why the particles were not reaching density equilibrium with the heavier medium. As the particles

encountered the interface, they slowed down. After a pause of less than a second, the larger particles punched through the interface, leaving a streamer of lower-density, extruded pore water in their wake. This streamer shows up holographically since the difference in index of refraction between the pore water streamer and medium results in interference patterns.

An example of this behavior is shown in Figure 1a-c. This was the second experiment performed with this density gradient, so the original step-like structure had broken down somewhat near the interface due to the mixing induced by the settling particles of the first experiment (some ten minutes earlier). These unreconstructed holographic images show only the diffraction fringes. An in-focus reconstruction of Figure 1b is shown in the Appendix.

The first visible particle to resume settling after hitting the interface is labelled A. This particle is 256 microns diameter and extrudes a low viscosity conduit in its wake that influences the settling of particles B and C. In addition to channelizing the subsequent particle settling paths, this conduit also tends to affect particle morphology and settling orientation. The reduced viscosity and density in the conduit and the alignment of the particle long axes with it, permits increased settling speed by the subsequent particles. This increases the likelihood that particles will collide with slower moving particles downstream, and can result in elongate aggregates with their long axis oriented vertically (shown in Figure 2). A detailed explanation of the settling behavior and flushing rate of the particles in Figure 1 is provided in the discussion.

IV. Holography of Pore Water Streamers

The tube-like conduits of flushed aggregate pore waters contain a lower density, lower viscosity, and lower refractive index media than that surrounding the conduits. The maximum refractive index contrast is $\Delta n = .0046$: that difference between that of the upper and lower layers. The streamer left by particle A stretches to about .2 cm below the original interface (about 8 diameters of particle A). If we calculate the diameter D of a cylinder .2 cm long that contained only seawater, its diameter would be on the order of .0075 cm in order that its volume match that of the volume of particle A (.0256 cm diameter).

A light ray ($\lambda = 632.8$ nm in vacuo) passing through the center of a seawater cylinder ($n = 1.3396$) of .0075 cm diameter would exit 0.54 wavelengths ahead in phase of the part of that wave front that passed just outside the cylinder. Since the index of refraction contrast is so small, very little refraction will occur ($n_{sw}/n_d - 1 \ll 1$). Rays passing just outside the cylinder diffract toward the central axis, where interference occurs with those having traversed through it. For a cylinder such that

$$\rho_c = \left| \frac{2\pi d}{\lambda} \left(\frac{n_{sw}}{n_d} - 1 \right) \right| \approx 3.9 ,$$

the largest anomalous diffraction constructive interference peak occurs (Van de Hulst, 1957). Here d is the diameter of the cylinder, λ is the wavelength in the medium, and n_{sw} and n_d are the refractive indices of seawater (1.3396) and dextran (1.3442), respectively. For our model cylinder, the value of $\rho_c \approx 3.41$, producing a constructive

interference peak (bright fringes) which is very close to the maximum value possible. For larger cylinders with similar refractive indices, the axial interference peaks decrease, but never by more than 50%. For cylinders with $d < .0025$ cm, the amplitude of the interference peak decreases rapidly toward background values. Small destructive interference fringes (dark fringes) will occur at an angle of about 0.5° off axis and downstream from the cylinders and will be most apparent for cylinders about twice (or increments thereof) the diameter of our model cylinder ($\rho \pm 7, 14, 20, \dots$).

In summary, maximum fringe formation will occur on our film if $\rho_c \pm 3.9$. For lower refractive index contrast (smaller $|n_{sw}/n_d - 1|$), a larger cylinder (presumably created by a larger aggregate) is required to produce similar constructive fringes. For fresh water over salt water (e.g., $m = n_{fw}/n_{sw} \pm \frac{1.3330}{1.3390}$), the maximum refractive contrast approaches that of our model cylinder. Only iceberg melt or river plumes over deep water scenarios (e.g., Amazon, Magdalena) might provide that much refractive contrast. However, less contrast from larger diameter cylinders (larger particles) would produce similar fringes to the ones we have viewed.

V. Particle Dynamics Model for Aggregates with Occluded Water Flushing

To understand the dynamics of porous aggregates which exchange their occluded waters at some unknown rate with that of the surrounding medium, we developed a model to estimate the density of the occluded waters as a function of a flushing factor. To begin, we require some definitions.

A wet primary particle is defined as a particle containing no voids but has water bound in the molecular matrix. The density of such a particle, ρ_p , is defined as

$$1) \quad \rho_p = \frac{M_s + M_w}{V_s + V_w}$$

where M_s and M_w are the masses of the solid material and water respectively, and V_s and V_w are volumes of the same respective materials. We have determined in previous work that the density of our samples of wet, primary montmorillonite particles is 1.77 gm/ml (Gartner and Carder, 1977).

As the material aggregates, internal voids are created, partially enclosing occluded water (ow). If this ow is tightly bound, a static density results as defined by

$$2) \quad \rho_{\text{static}} = \frac{M_s + M_w + M_{ow}}{V_s + V_w + V_{ow}}.$$

If the ow is exchanged with the surrounding medium, then a dynamic density (ρ_{dynamic}) results as

$$3) \quad \rho_{\text{dynamic}} = \frac{M_s + M_w + M'_{ow}}{V_s + V_w + V_{ow}}.$$

M'_{ow} is an apparent mass of ow as defined by the Stokes equation for a sphere of diameter D settling with velocity v_s in a medium of density ρ_m and viscosity η . If aggregates or phytoplankton contain the occluded water (or cytoplasm) tightly enough that there is no significant flushing or exchange of pore waters with the surrounding isotonic medium, then it follows that

$$4) \quad \rho_{static} = \rho_{dynamic}.$$

Otherwise

$$\rho_{static} < \rho_{dynamic}.$$

We can describe, to the first order, the effect of the flushing of aggregate pore waters on the Stokes settling speed by developing a relationship to describe ρ_{ow} , in terms of a flushing rate for the particle. Suppose that some fraction f of the ow is flushed each time the particle settles a distance of one diameter D . Then $f/D = F$ is the flushing rate per unit distance settled. If $\rho_{ow}(Z)$ and $\rho_{ow}(Z + \Delta Z)$ are the occluded water density values at depths Z and $Z + \Delta Z$, and the density of medium ρ_m increases linearly with depth then

$$5) \quad \rho_m(Z) = \rho_m(0) + KZ,$$

where K is a constant that describes the change in ρ with depth.

A first order approximation of the change in ρ_{ow} in settling over a short depth $\Delta Z = D$ can be expressed as

$$\begin{aligned} \frac{\Delta \rho_{ow}(Z)}{\Delta Z} &\approx \frac{\rho_{ow}(Z + \Delta Z) - \rho_{ow}(Z)}{\Delta Z} \\ &\approx \frac{f \rho_m(Z + D) + (1 - f) \rho_{ow}(Z) - \rho_{ow}(Z)}{D} \\ 6) \quad &= \frac{f[\rho_m(0) + K(Z + D)] - f \rho_{ow}(Z)}{D}, \end{aligned}$$

where the fraction f of $\rho_{ow}(Z)$ that is flushed is replaced by the denser water of the medium $\rho_m(Z + D)$ found at depth $Z + D$. Rearranging terms, we can write the equation as a differential equation

$$\rho_{ow}'(Z) + \frac{f}{D} \rho_{ow}(Z) = \frac{f}{D} KZ + \frac{f}{D} (\rho_m(0) + KD)$$

or

$$\rho_{ow}'(Z) + F \rho_{ow}(Z) = FKZ + F(\rho_m(0) + KD),$$

where $F = f/D$.

The solution to this equation is

$$7) \quad \rho_{ow}(Z) = \rho_{ow}(0)e^{-FZ} + e^{F/Z}[\rho_m(0) + K(Z + D - 1/F)] \\ - \rho_m(0) - K(D - 1/F).$$

To simulate our two-layer, density-gradient, particle dynamics problem, we let $\rho_{ow}(0) = \rho_m(0) = 1.024 \text{ g/ml}$ and the density contrast gradient, $K \doteq .12 \text{ g/cm}^4$.

We chose to exercise F over a range of values in order to evaluate the effect that the density contrast of the occluded waters with the media has on the particle settling speed for various aggregate densities. As mentioned previously, the variation in viscosity across the interface had a more significant effect on settling speed than did the change in density, and in order to arrive at a solution, we originally assumed the density contrast of the aggregate ($\rho_{dynamic} - \rho_m$) to be constant with depth. We can now estimate how much in error that assumption may have been for the various particles in this study.

Now that ρ_{ow} can be estimated as a function of flushing rate F and depth, one can solve Stokes equation for viscosity as a function of depth, given the measured settling speeds of the particles.

Since the streamer from particle A (Figure 1) affected the viscosity of the cylinder in which particles B and C traveled, it is important to analyze the viscosity encountered by particle A first. It is clear even at .2 cm below the original interface (position of particle A in Figure 1e) that a gradient in refractive index between the streamer and surrounding waters remains. Thus, we chose .25 cm

below the interface as the depth at which the density, viscosity, and refractive index gradients of the medium with depth disappeared (medium of purely layer 2 type properties). Thus,

$$K = (1.054 - 1.024)/0.25 \text{ cm} = .12 \text{ g/cm}^4.$$

$$8) \quad \eta(Z,F) = \frac{980[1.77 \text{ g/ml } VF_s + (1 - VF_s)\rho_{ow}(Z,F) - \rho_m(Z)]D^2}{18 v_s(Z)}$$

where

$$9) \quad VF_s = \frac{\rho_{dynamic}(Z,F) - \rho_{ow}(Z,F)}{1.77 \text{ g/ml} - \rho_{ow}(Z,F)},$$

and $\rho_{ow}(Z,F)$ and $\rho_m(Z)$ are known from equations 7 and 5, respectively, and VF_s is the volume fraction of the aggregate occupied by solid matter. To solve exactly this set of equations, $\eta(Z,F)$ should be known at some point where a velocity measurement $v_s(Z)$ is known. We do know that $\eta(Z > .25 \text{ cm})$ is about .0745 poise; however, no velocity measurements were available at that depth since it was out of our field of view. We thus assumed a relatively smooth transition between the viscosity at .25 cm below the interface or viscosity at .175 cm, our deepest particle velocity observation.

VI. Application of Model

The resulting viscosities associated with the velocities of each particle for four depth intervals and two F factors are shown in Figure 2, with the upper and lower points representative of F factors

of 0.5/cm and 0.2/cm, respectively. The flushing factor had little or no effect on particles A and C since montmorillonite made up larger fractions of their mass values than for particle A (62% and 15% versus 8.6%, respectively).

The dotted lines represent regions where two different settling transitions occurred: i) in Figure 1b and 1c particle A can be seen to be settling along or just adjacent to a streamer from an earlier particle, and ii) in Figure 1d and 1e, particle C seems to have moved out of the streamer tube of particles A and B. Particle A apparently encountered a relatively constant viscosity when in the proximity of the old streamer, with the viscosity sharply increasing as it moved away from the streamer remnant. Particle C also encountered fluid of relatively constant viscosity within the streamer of particle A, with an abrupt increase occurring on passage out of it. Figure 2 reflects these facts.

Particle B settled within the streamer of particle A until Figure 1d, where it seems to have edged out of the tube. In Figure 1e it appears to be slightly behind the tube. Figure 3 also corroborates this fact, since the viscosity encountered by particle B is clearly much less (within the streamer tube) than that encountered by particle A at the same position before the streamer was extruded.

An estimate of the effective viscosity increase outside versus inside a streamer is indicated by the arrow bar of .8 centipoise on Figure 3. That represents a viscosity increase of about 25%, a significant effect.

Summary

Holography of aggregates settling through density interfaces provides a direct observation of pore-water flushing due to the contrast in refractive index between the extruded pore waters and the medium. These extruded pore-water tubes provide a pathway where subsequent particles encounter reduced viscous drag and less buoyancy than would be available outside the tube. Viscosity reductions of at least 25% were observed. This means that if two particles of similar settling speeds are following each other in a streamer tube, the second will settle faster since it encounters lower viscosity. The probability of collisions, in such a system, then, changes from one with a random or Gaussian likelihood to one that favors low density, highly porous aggregates, capable of providing a reduced viscosity, funnel-type of pathway at density interfaces for subsequent particles to traverse and within which to collide. As these aggregates build in size, they increase even more the probability of subsequent collision. Figure 2 shows several elongated aggregates apparently created by particle collisions in a streamer tube.

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Figures 1a (top), 1b (middle), 1c (bottom)

A sequence of holograms taken with 10 second intervals. The top hologram has an arrow on the left showing the original level of the density gradient interface which represent in the reference point ($Z = \phi$). Three aggregates labelled A (246 μm diameter), B (76.5 μm diameter), and C (113 μm diameter) are settling along the same conduit which is marked by a bright pore water streamer flushed out of particle A. Note in formation of elongate particles in the streamer above particle C.

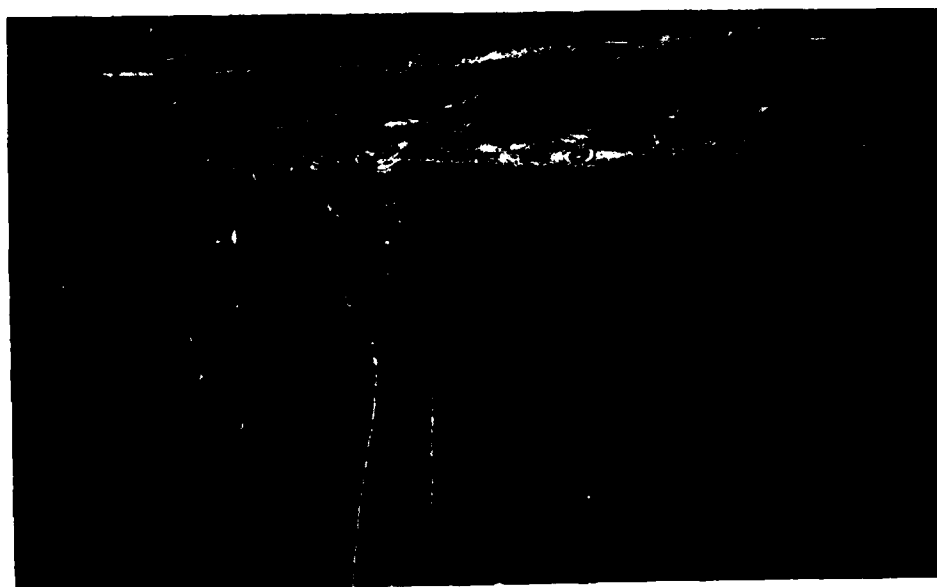


Figure 2. Hologram of several elongated aggregates found about 1 cm below the interface (note especially the lower left corner). These streamlined morphologies suggest their formation to have occurred in a streamer. Note the continued presence of low index streamers even this far below the interface, suggesting relatively slow flushing rates.

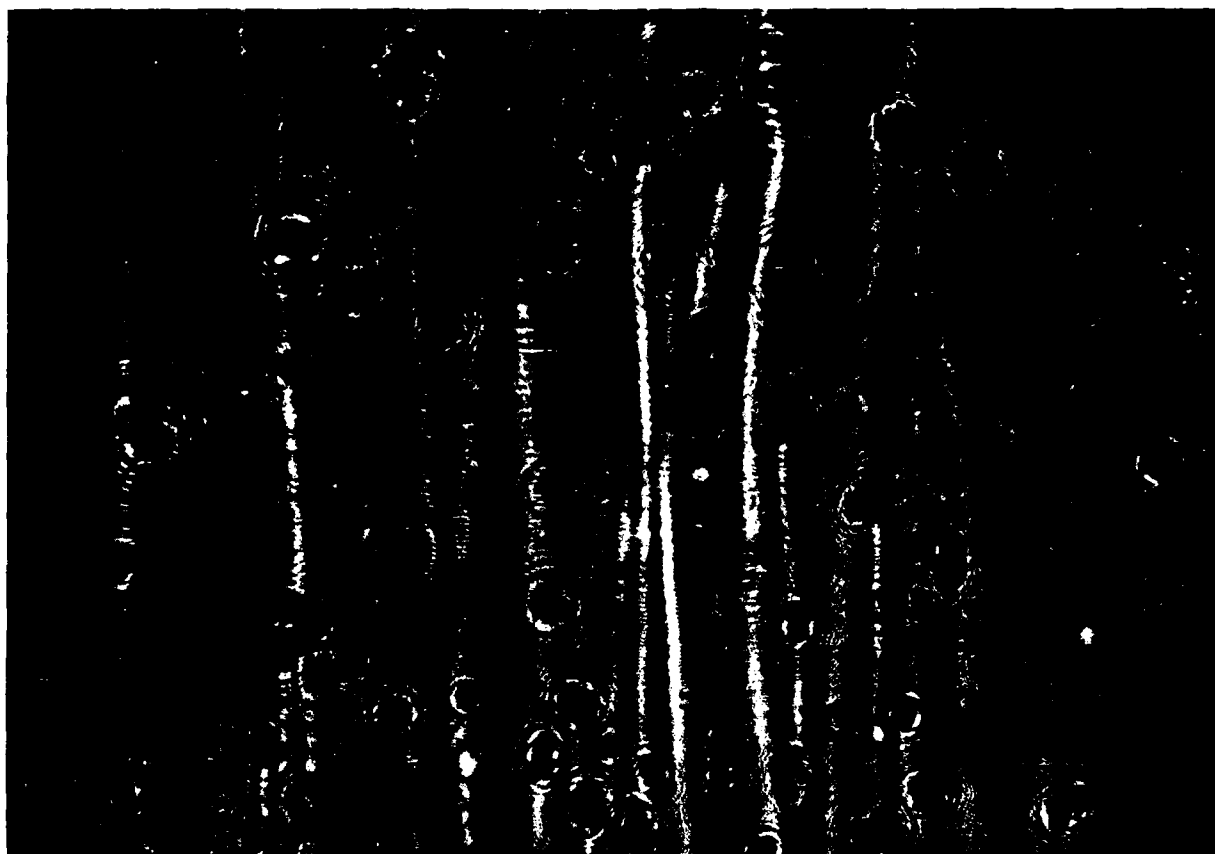
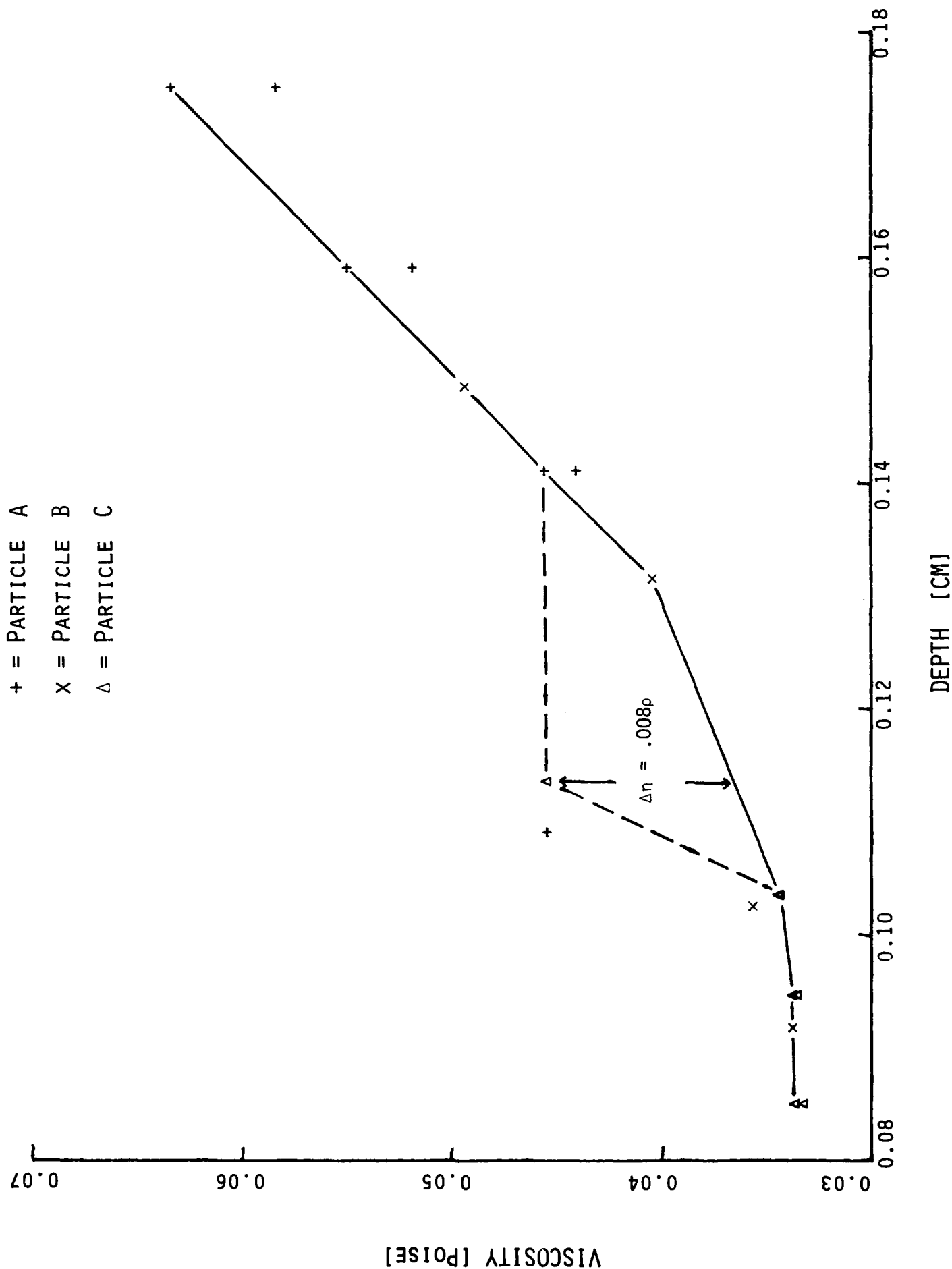


Figure 3. Viscosity profile in the density gradient traversed by and inferred from particles A, B, and C. The sudden increase in viscosity observed for particle C some .11 cm below the interface occurred when the particle left the low viscosity streamer and suddenly encountered more resistance to settling.



MEASURING THE ABUNDANCE AND FLUX OF MARINE SNOW AGGREGATES

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INTRODUCTION

Marine Snow aggregates are thought to be important in the vertical and lateral transport of particulate matter in the oceanic water column (Alldredge, 1984; Asper, 1986; Asper, in press; Shanks and Trent, 1980; Silver, 1981). Their delicate nature and relative low abundance (0.1 to 1.0 aggregates liter⁻¹ in deep water) have prohibited assessment of their in situ flux, abundance and sinking speeds using standard oceanographic sampling techniques. These parameters have only been measured in the uppermost water column which is accessible by SCUBA. To learn more about marine snow aggregates in the deeper water column we have developed two complimentary photographic systems; the first measures the abundance (number liter⁻¹) and the second measures the flux (number m⁻² day⁻¹) of aggregates at any depth in the water column.

MEASURING THE ABUNDANCE OF AGGREGATES

Figure 1 shows a diagram of the Marine Snow Survey Camera (MSSC) developed by Susumu Honjo at Woods Hole (Honjo et al., 1984). This system consists of one or two deep-sea strobe lights mounted at the focal point of a compound Fresnel lens, producing a collimated 'slab' of illumination. Mounted at approximately 90° to this slab, a deep-sea camera photographs an intersecting volume of water (600 liters). The light scattered image of marine snow particles within this well-defined slab of light are photographed against a background of dark (unilluminated) water. The system is lowered slowly (10-20 m min⁻¹) through the water column on a trawl wire, exposing frames at a time interval of 7 to 20 seconds calculated to yield 800 frames between the surface and the sea floor at a distance of 1.2 to 5.6 m frame⁻¹ throughout the water column. Depth is monitored and recorded using a pinger and the ship's precision depth recorder. Lowering is halted when the frame is within 2 to 10 meters of the sea floor. Film from the camera is developed as a continuous roll in order to insure consistent development. The negatives are then analyzed directly using a computer aided image digitizer and the abundance of marine snow is plotted vs. the depth at which the image was obtained.

MEASURING THE FLUX OF AGGREGATES

From a sedimentological point of view, the existence of marine snow in the water column becomes important only when it can be shown that these aggregates are settling at significant rates and contributing to the flux of material. The second photographic system (Marine Snow Flux Camera, MSFC) was constructed in order to assess the flux of these aggregates through the water column. This system (figure 2) consists of a polypropylene cylinder (0.069 m² opening) which

is open at the top (with a closing mechanism) and closed at the bottom by a clear plexiglass plate. Four flash tubes from Vivitar^T strobe heads are attached to Impulse^T connectors which are threaded into clear plexiglass rod. These pressure-tight strobe units are mounted just above the trap bottom and flush with the walls of the cylinder so as to illuminate any material lying on the clear plate. A deep-sea camera is mounted one meter beneath this apparatus, so that the bottom of the trap is in focus and only material lying on the plate is photographed. Using a 30 m roll of film, 800 frames can be exposed, each showing successive additions of material to the trap. Experimental results show that a resolution of approximately 50 μm is attainable using fine grain film (Kodak^T Panatomic-X).

This system is deployed on a mooring (either floating or bottom-tethered) and allowed to collect material for a specified time interval. After recovery of the system, negatives are developed and analyzed in the same manner as for the MSSC except that the numbers are plotted vs. time rather than depth. Sealing off the top of the trap prior to recovery allows retention of the material which settled into the trap and which was photographed by the camera system. Examination of the composition and quantity of this material provides some insight into the types and amounts of particles delivered to the sea floor by marine snow aggregates.

MEASURING THE SINKING SPEED OF MARINE SNOW AGGREGATES

Probably the most difficult to obtain measurement relating to marine snow aggregates is their sinking speed. The work by Shanks and Trent (1980) in surface water indicates the value of this number but also demonstrates the difficulties associated with obtaining it, even near the surface. However, estimates of in situ sinking speeds are obtainable either using a combination of the MSFC and MSSC numbers or else using a proposed, but not yet developed in situ settling tube system.

Use of MSSC/MSFC in combination. The amount of new material added to the flux camera per area per time interval between frames in the photograph is flux of that material. When this flux value is divided by a concentration value obtained by lowering the MSSC to the depth of the MSFC, an effective average sinking speed of all aggregates imaged by the MSSC can be obtained:

$$\frac{\text{number}}{\text{volume}} * \frac{\text{distance}}{\text{time}} = \frac{\text{number}}{\text{area} * \text{time}}$$

This procedure can be employed over any practical time scale; temporal resolution is determined by the time interval between frames. Also, flux and abundance numbers can be obtained for several size classes of aggregates, allowing the determination of a sinking speed estimate for each size aggregate.

In addition to questions relating to the hydrodynamics of trapping particles (e.g., over/under trapping, swimmer interactions, effects of entrapment on aggregate morphology etc., which will not be addressed here), several assumptions inherent in this experimental design limit the usefulness of these sinking speed estimates. First, material falling into the MSFC must represent the same

material as that photographed by the MSSC for each size class. Any temporal or spatial variability in the input of material either vertically or horizontally will influence the results unless both instruments are deployed in close proximity along the same mooring. Second, all material of a given size is assumed to be sinking at the same speed. This assumption is problematic because particles of a given size will not necessarily be of uniform density. Even within a population of aggregates, differences in content and porosity could foreseeably result in a wide range of densities and therefore sinking speeds. The sinking speed obtained by this method represents the average sinking speed for all particles photographed by the MSSC and not the average sinking speed of particles actually entering the MSFC; some particles (aggregates) observed by the MSSC may not be sinking at all while others settle at rapid speeds, resulting in an intermediate overall value.

Direct sinking speed measurement. An average sinking speed for all aggregates obtained this way is useful for modelling "typical" water column residence times for large particles; however, measuring the actual in situ sinking speeds of individual aggregates would be of considerably more value in modelling particle transport. To this end, a new camera system capable of measuring the fall of aggregates in a quiescent volume of water is proposed (figure 3). This system would consist of dual settling tubes with a camera mounted normal to their vertical axis. Particles settling through the tubes would be photographed several times over a programmed time interval; settling speed could be determined by the distance traversed during that time interval. Ball valves mounted at the openings of the tubes could be used to open and close the trap, sealing the contents for retrieval and subsequent analysis. Duplicate tubes are used either for the collection of replicate samples or for investigating the effects of poisons, preservatives, density gradients, baffles, screens, and tube geometry (aspect ratio, etc.) on the quantity and quality of material retained. A second camera mounted beneath the trap would record material arriving on the bottom of the trap (flux estimate) and would observe any material which might settle through the tubes quickly enough to be missed by the side-looking camera. This approach is thought to be capable of yielding some extremely useful information relating to the flux and in situ sinking speeds of aggregates.

SUMMARY

In order to be important in the vertical transfer of particulate matter in the world's oceans, marine snow aggregates must be present in significant concentrations and must settle at sufficient rates to produce an appreciable mass flux. The two photographic systems which have previously been built and tested have been shown to be capable of assessing the abundance and flux of relatively undisturbed aggregates in the water column. A third system has been proposed which would also measure the in situ sinking speed of individual aggregates and thus provide even more useful information relating to the contribution of these aggregates to oceanic sediment flux.

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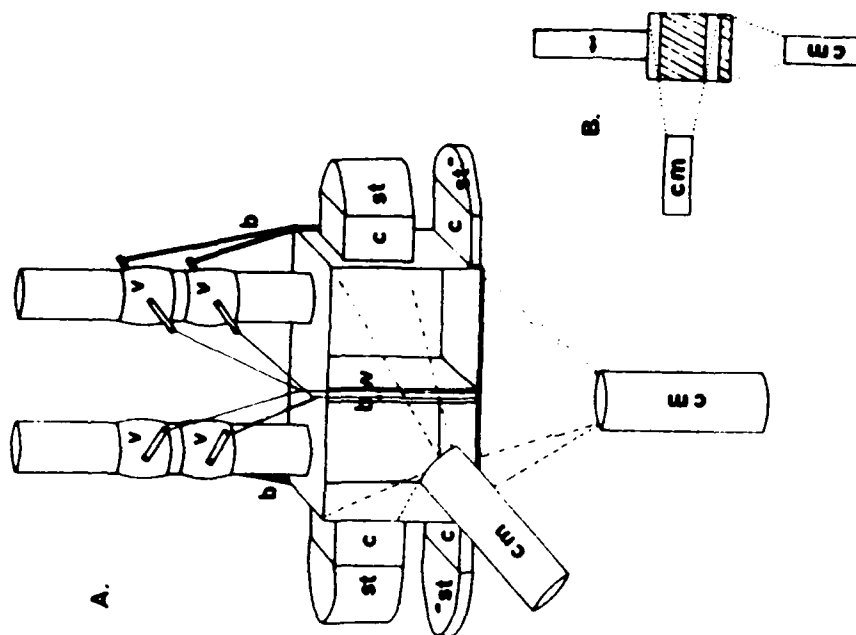


Figure 3. a) Sketch of proposed ASTAC (Aggregate Settling Tube And Collector) showing closing valves (V), burn wire (BW), light sources (ST) with collimators (C), and cameras (CM). Particles settling into the device will be photographed as they settle through a quiescent chamber (sinking speed) by the side-mounted camera and again upon their arrival on the clear bottom plate by the bottom-mounted camera (flux). The chambers can be sealed prior to deployment and again upon their arrival. Ball valves counted above the settling chamber. Suspend cords (B) pull the valves closed upon release of the burn wires. Activation of the valves is confirmed photographically by observing the burn wire. Duplicate systems are used to provide replicate samples or to evaluate the effects of poisons, baffles or tube geometry, in which case one tube/chamber is used as a control. b) Diagram of the ASTAC showing illuminated areas (hatched) and geometry of the system.

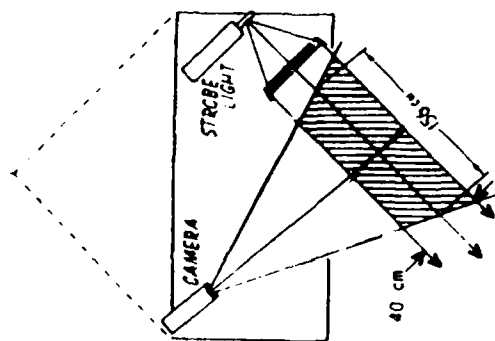


Figure 1. Diagram of Marine Snow Survey Camera (MSSC) showing dimensions of light slab. 600 liters of water are included in the photograph.

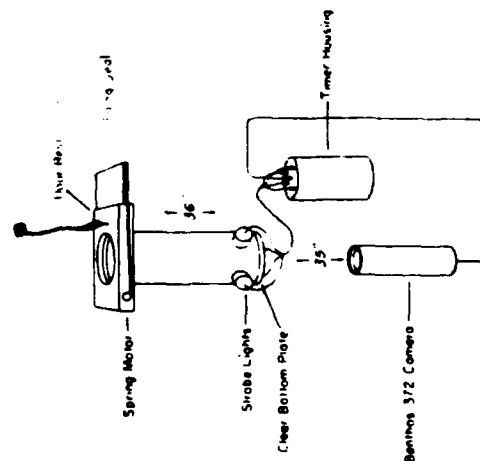


Figure 2. Schematic showing principal components of the Marine Snow Flux Camera (MSFC). Only particles lying on the clear bottom plate are photographed.

Youngbluth, M.J., T.G. Bailey, C.A. Jacoby, P.J. Davoll and P.I. Blades-Eckelbarger. Submersible-based measurements of the sources, densities, distributions and sinking rates of marine snow aggregates and euphausiid fecal pellets.

Manned submersibles and the technical equipment they carry represent one kind of sampling system that has been used to define various properties and characteristics of macroscopic (> 0.5 mm) particulate matter in marine environments. Water column investigations with mobile undersea vehicles have been conducted primarily in the uppermost 1000 m. Visual observations coupled with photography (still and video), pumps and traps, and environmental data logging systems have provided new information about the diversity, distribution, abundance and behavior of marine particles on relatively small spatial scales.

Qualitative and quantitative data from over 300 dives in the uppermost 800 m of temperate and tropical seas with the JOHNSON-SEA-LINK vehicles have revealed:

(1) Most macroscopic particles are irregularly-shaped flakes and flocs (0.5-5 mm) but larger masses (5 mm-1.5 m) in globular, string and sheet forms are common.

(2) Particles are frequently concentrated at physical interfaces. For example, massive numbers ($> 3000 \text{ m}^{-3}$) of flocs (3-5 mm) have been observed repeatedly near the pycnocline (90-150 m) in the Bahamas. The origin of these particles has not been determined. A portion of this material may represent degradation products of periodically abundant organisms or the remains of mucilaginous secretions of soft-bodied zooplankton. Strings (3-100 cm long x 0.5-2 mm OD) of mucoid material formed by the foraminiferan Hastigerina pelagica, were frequently abundant ($10-50 \text{ m}^{-3}$) throughout the uppermost 400 m and the largest aggregations of these particles often appeared in the 90-150 m interval. Sheet-like feeding webs ($25 \text{ cm}^2-2.3 \text{ m}^2$) of mucous, produced by the pteropods Gleba cordata and Cavolina tridentata, were numerous only in the pycnocline region of Exuma Sound. Neither reliable estimates of the number of webs nor the density of pteropods could be made owing to the fragile nature of the webs and the photonegative behavior of these zooplankton.

In addition to aggregate material derived from animals, tufts (clusters of strands 0.5 cm long x 0.2 mm OD) of the blue-green alga Trichodesmium sp., have appeared within the mixed layer (uppermost 40 m) in substantial numbers ($400-20,000 \text{ m}^{-3}$).

Relatively dense aggregations ($3-9$ individuals m^{-3}) of the giant larvacean Bathocordaeus charon, have developed in the Gulf Stream during springtime periods and were concentrated in a narrow depth interval (45-65 m) which overlapped with the subsurface chlorophyll maximum (50-70 m). The ovoid filter-houses (30 cm OD) they produced and abandoned, constituted a major source of marine snow debris, especially along the continental shelf off eastern Florida where thick masses of this mucoid matter extended from the surface downward to the sea floor at 200 m. At midwater depths (400-750 m) in Bermuda and the Bahamas spherical filter-houses (2-5 cm OD) were common ($0.1-2 \text{ m}^{-3}$). They were made by several

undescribed and vertically segregated (100-m intervals) species of kowalevskiid larvaceans.

High densities ($100-1000\text{ m}^{-3}$) of fecal pellets (2-6 mm long x 0.2 mm OD) occurred in discrete layers (7-12 m thick) coincident with the thermocline (15-30 m) throughout the Gulf of Maine and over the submarine canyons south of Georges Bank (Youngbluth et al. 1985). High standing stocks ($1-100\text{ m}^{-3}$) of the euphausiid Meganyctiphanes norvegica, were the source of these pellets.

(3) Large particles originate both in the epipelagic and the mesopelagic zones. As they sink from these zones of origin into deeper water and to the benthos, they transport nutritive material. Extrapolations based on the abundance of two of the particle types noted above (i.e., euphausiid fecal pellets and midwater larvacean filter-houses) and measurements of their carbon contents, daily production rates and sinking velocities suggested the potential for significant amounts of carbon export to deeper waters. For example, pellets from the single euphausiid species could supply, on the average, $50\text{ mg C m}^{-2}\text{d}^{-1}$ to the benthos. This amount represented 29% of the daily primary production in the mixed layer and 11% of the total benthic community respiration.

Flux rates of $3-65\text{ mg C m}^{-2}\text{d}^{-1}$ could originate from the filter-houses. If these estimates of flux are correct, the mesopelagic larvaceans may be modifying, repackaging and transporting the elevated microbial production noted in sediment trap collections from midwater regions.

(4) Individual larvacean filter-houses collected from 400-750 m in Bahamian and Bermuda seas had bacterial densities ($7 \times 10^5 - 3 \times 10^6$ per house) equal to marine snow aggregates from surface waters in the Atlantic and Pacific Oceans. Houses that were incubated for 4 d showed higher bacterial densities ($6 \times 10^6 - 1 \times 10^7$ per house). Bacterial production on houses varied widely ($0.01-4\text{ ng C ml house}^{-1}\text{h}^{-1}$) and represented substantial enrichments over equal volumes of the surrounding water (10-5000X). However, the bacterial activity on these particles was a small portion of the total bacterial production (0.01-0.4%). The midwater filter-houses and the larvacean fecal pellets they contained also were laden with olive-green bodies (2-20 μm OD), numbering $4 \times 10^3 - 2 \times 10^5$ per house. Only low densities (50-130 per house) of eukaryotic photoautotrophs (2-4 μm) and cyanobacteria (1 μm) were attached to the houses.

(5) Most macroscopic particles appear to bioluminesce. Presumably microbial organisms attached to these particles were the sources of the bioluminescent light. The size and number of bioluminescent flashes, stimulated by turbulence from movements of the submersible or its thrusters, was usually greatest above and within the thermocline. However, on several occasions an unusual bioluminescence was induced within narrow layers at midwater depths (frequently at 250-300 m) while the submersible was stationary. Hundreds of luminescent spheres (3-6 cm OD) would glow for 5-15 s immediately after a flashlight or strobe lamp was activated. The particles responsible were almost indistinguishable under incandescent light.

Distributions of macroscopic aggregates in the Northwest Atlantic Ocean

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Macroscopic aggregates play an important role in the vertical transport of chemical elements in the ocean. Vertical profiles of > 1 mm sized aggregates in the "fecal matter" and "fecal pellet" categories (Bishop et al. 1977) were obtained from the upper 1000 m by large volume in-situ filtration as part of the Warm Core Rings Program in 1982. Stations were occupied in the Slope Water, Warm Core Rings (WCR) 82B and 82H, The Gulf Stream and Sargasso Sea.

Greater than 1 mm sized aggregate abundances in the upper 100 m of the NW Atlantic ranged from 2 m^{-3} to 1000 m^{-3} . Abundances ranged from $< 0.1 \text{ m}^{-3}$ to 30 m^{-3} in deeper waters. The lowest levels of this material were found at stations in the Gulf Stream and Sargasso Sea. Highest abundances were found in waters of greatest primary productivity. These results indicate a correlation between aggregate abundance and water column productivity. The correlation is not linear since the dynamic range of aggregate abundance (500:1) greatly exceeds that of primary productivity (approx 10:1; Hitchcock et al. 1985).

Data also show that zooplankton are important in determining the vertical concentration gradients of large aggregate particles (Bishop, Conte, Wiebe, Roman and Langdon, 1986). For example, profiles of aggregate abundance and zooplankton biomass were obtained from the core waters of WCR 82B in April and June 1982. In April, $> 333 \text{ } \mu\text{m}$ zooplankton biomass ranged between 400 and $100 \text{ nmol C kg}^{-1}$ over the depth interval 50 - 400 m. At the same time, aggregate abundances varied less than a factor of 3 over the same depth interval and averaged 10 m^{-3} . In June 1982, zooplankton biomass ranged between 2000 and $100 \text{ nmol C kg}^{-1}$ from 25 m to 400 m. At this time, however, aggregate abundances decreased from 1000 m^{-3} at 25 m to 2 m^{-3} by 150 m. Thus, aggregate abundances in the water column appear to be governed by the activities of zooplankton. Once again, the relationship is not linear.

In spite of the large dynamic range of aggregate abundance and the importance of large aggregates to sedimentation, the above demonstrates that we have incomplete knowledge about the mechanisms of formation and destruction of these particles in the oceanic water column. More emphasis needs to be placed on understanding of the hydrographic, physical and biological factors controlling these important particles.

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Bioluminescence of Marine Snow

J. K. Orzech and K. H. Nealson

In this research, we employed both scuba and saturation divers to hand-collect samples of marine snow and surrounding water in separate syringes for discrete analyses. The samples were taken at depths as great as 260 m during 16 saturation dives from 1982 through 1984. Within hours of collection, the samples were brought to the surface and measured for emitted light flux (ϕ) in an integrating photometer calibrated for its response to light in the blue-green (480 nm) spectral region characteristic of bioluminescence. Of the 250 macroaggregate samples collected, 44% were luminous emitting measurable light from two to six orders-of-magnitude greater than that found in comparable volumes (0.01 ml) of the surrounding water. Only about 4% of the samples, however, were bright enough to be seen at 10 cm.

Our analyses further have shown that this light was produced by bacteria, dinoflagellates, radiolarians and/or other luminous micro-organisms associated with the marine snow.

The use of saturation divers and deep-diving systems to collect samples at depths unattainable to conventional divers has been a major innovation and an integral part of this research. Operating from the Deep-Diving System Mk 2 (DDS) on board the Diver Training Vessel ELK RIVER and the U.S.S. Pigeon, U.S. Navy saturation divers have performed a variety of scientific tasks to depths between 26 and 260 m including the collection of marine snow. These extremely fragile macroaggregates are most successfully sampled by hand because of the diver's excellent manual dexterity and hand-to-eye coordination. Prior to this program, DDSs had been used only twice for marine research although they are used extensively for military and commercial diving. By working in cooperation with the U.S. Navy's Submarine Development Group ONE, and by employing the DDSs during their already scheduled certification and training dives, the substantial costs of operating a DDS were circumvented.

Using underwater video and stereo photography, we estimated the size distributions and concentrations of the macroaggregates during several dives in which light flux also was measured. A light budget was obtained for two dives one week apart in September 1982. During the first of these dives, nearly all of the ambient light (97%) emanated from the marine snow. One week later at the same location, 98% of the light flux originated in the surrounding water.

These studies have indicated that marine snow frequently is an emitter of light in the sea. As the macroaggregates form and then disintegrate, they have a significant role in defining the distribution of light-emitting organisms as well as other optical properties of the sea. This work was funded by the Office of Naval Research.

ACOUSTICAL TECHNIQUES FOR REMOTELY DETECTING AND CLASSIFYING PARTICLES IN THE OCEAN

by

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Sonar systems can be used to remotely detect and classify particles (Fig. 1). These systems can provide high volume coverage in relatively short amounts of time. Furthermore, the results can be displayed in real time to allow directed sampling. For example, a system with 100 m range, 10° beamwidth and towed at 6 knots can scan about 10 million cubic meters of water per hour. While this produces large amounts of data, the scan can be qualitatively summarized in real time intensity plots or "echograms" (Fig. 2).

A common quantity used to describe each object's ability to reflect sound is the backscattering cross section σ_{bs} and the resultant target strength TS:^(1,2)

$$\sigma_{bs} \equiv R^2 I_{bs} / I_0$$

$$TS \equiv 10 \log \sigma_{bs}$$

where I_0 and I_{bs} are the incident and backscattered intensities of the sound, respectively, and R is a reference distance at which I_{bs} is evaluated. σ_{bs} is essentially the fraction of acoustical intensity reflected back toward the transmitter. Even for simple objects like a sphere, σ_{bs} is a very complicated function of size, shape, density and speed of sound contrast with respect to the surrounding water, and acoustic wavelength. In general, the larger the size, density, and/or speed of sound contrast, the greater the echo from the object. At low frequency, the size-to-wavelength ratio is especially important. Figure 3 shows that for low frequencies and/or small size (i.e. $ka \ll 1$) σ_{bs} is small but increases rapidly with ka to $ka \sim 1$ where a characteristic "wiggly" pattern develops. The $\sigma_{bs}/\pi a^2$ curve approaches a constant level for sufficiently high ka .

The effectiveness of the sonar system not only depends on each particle's target strength, but the spatial resolution of the sonar. Counting and classifying objects becomes much more straight forward when they are resolved. To obtain adequate angular resolution a sonar transducer that is large compared to a wavelength is required (i.e. higher frequencies are required). Also with higher frequencies, shorter transmission pulse durations can be achieved, providing better range resolution. However, because of absorption effects in seawater, the higher the frequency of sound, the less the penetration. Because of these factors investigators tend to use the highest frequency (shortest wavelength) possible that can penetrate to the desired range.

The ocean is composed of many objects of different sizes and composition. If the nature of the backscattering cross sections of these objects is known then one can combine data from a multiple frequency sonar with inverse analytical techniques to derive size distributions of the objects.^(3,4) If it is not known, then one can use a high resolution single frequency sonar, whose frequency is chosen to detect a specific size class, to count the objects.⁽⁵⁻⁸⁾

Depending on the method, there are several levels of expertise, technology, and effort involved. To detect and locate objects, a simple commercial sonar can be used along with some basic knowledge of acoustics to produce data such as in Fig. 2. Counting objects may involve more specialized (and expensive) yet available equipment and much more knowledge of acoustics. Finally, determining the size distribution with a multifrequency sonar requires mostly custom technology and expert knowledge (and a great deal of effort I might add).

In summary, sound can conveniently be used to probe the ocean rapidly and versatily. Depending on the level of technology and expertise involved, simple detection and location, counting, and even determining size distribution of the objects are possible.

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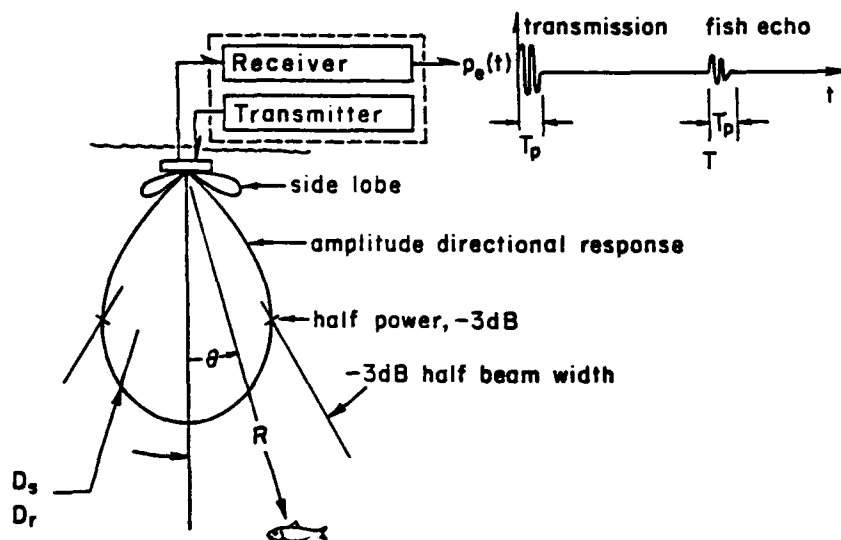


Figure 1. Sonar system that transmits pulse and receives echo from fish at a time T later.

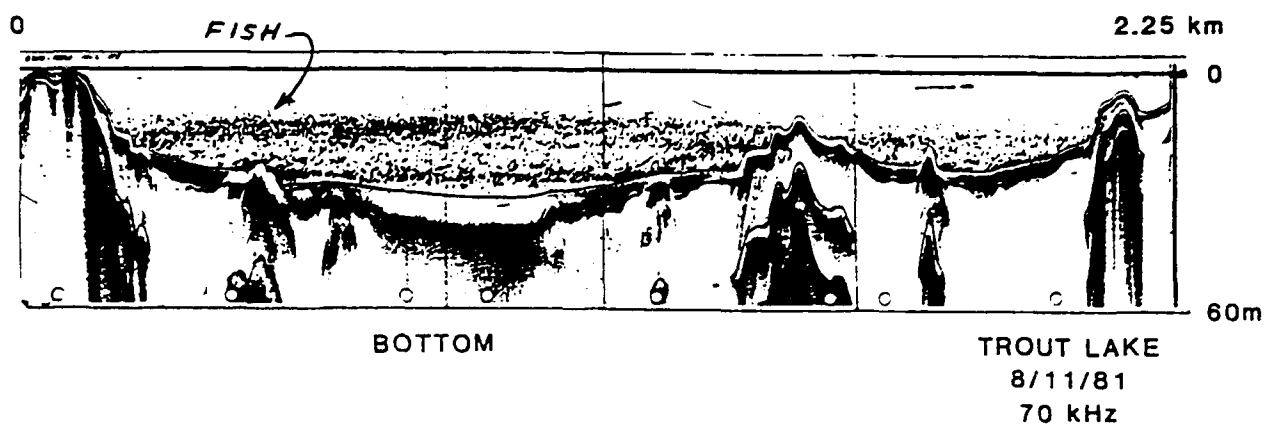


Figure 2. "Echogram" or intensity plot of sonar echoes from fish and lake bottom. Private communication, Lars Rudstam, Center for Limnology, University of Wisconsin, Madison, WI.

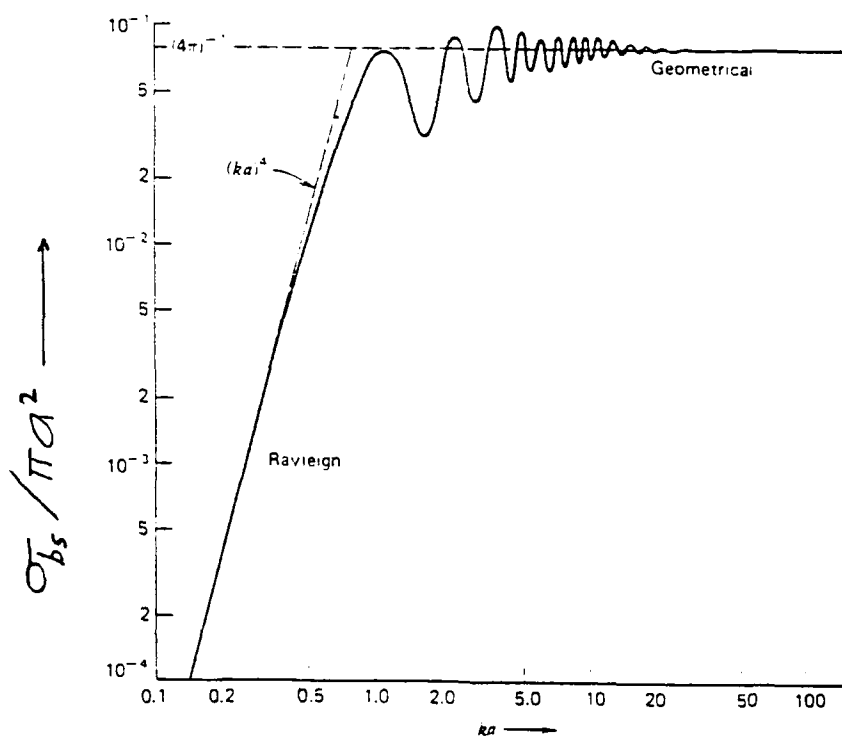


Figure 3. Backscattering cross section σ_{bs} normalized by projected area of sphere πa^2 versus ka where a is the radius of the rigid and fixed sphere and k is the acoustic wavenumber which is proportional to frequency.⁽¹⁾

Flow Cytometric Tracing of Fluorescent Particles

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We have developed a new methodology for studying the transport and deposition of particles in the field using fluorescent pigment particles as a tracer and flow cytometry for their detection. Our initial interest in these studies has been the fate of particles in sewage discharged into relatively shallow coastal waters, but we believe our findings have general relevance to particle dynamics in other environments.

The pigment particles used are available commercially (DayGlo Corp.), fluoresce intensely at 600 nm, have a specific gravity of 1.4, and range in diameter from 0.1 to 10 microns. The corresponding settling velocity range is 0.0002 to 2 m/day. Laboratory sedimentation experiments with these particles show that they do not coagulate with themselves or with sewage particles at concentrations typically observed in the water column (1 to 100 mg/l).

The pigment particles are detected in field samples using a flow cytometer. This instrument measures the intensity of fluorescence emission from individual particles as they flow in single file past the detection optics. Our instrument utilizes an epifluorescence microscope adapted by mounting a flow cell beneath the objective (Olson et al., 1983). The emitted light is split into two separate beams which are then filtered optically to yield sensitivity to different wavelength ranges. The tracer particles are identified among background particles by the characteristic ratio of the two signals. Particle size is calculated from the fluorescence intensity relative to that of a known standard. Tracer concentration is calculated from the number counted in a known volume. Sediment cores are prepared for analysis by suspension in water, agitation, and filtration through a 10- μ m Nitex screen. Sediment trap samples are agitated and filtered. Agitation by sonification yields quantitative recovery of tracer mass from the sediment; agitation by gentle shaking leads to loss of tracer on the screen but maintains the sample's tracer particle size distribution in the filtrate.

We have applied this technique to a site in Salem Sound, Massachusetts. Two hundred kilograms of tracer slurry (50:50, wt:wt) was discharged over several hours through the sewage outfall of the South Essex Sewerage District (10 mg/l at a flow rate of 23 mgd). Water and sediment samples were taken at 18 stations within 5 km of the outfall before and 1, 3, and 8 days following the tracer release. Sediment traps were set at three locations the day before and collected 9 days after the release.

Quantitative analysis of cores collected after 8 days shows that roughly 7% of the mass of released tracer particles was deposited in the study area. This value is consistent with estimated rates of particle deposition and removal by tidal flushing. Most interestingly, size distribution analysis of both core and sediment trap samples reveals that the size distribution of the sedimented particles is indistinguishable from that in the initial tracer

slurry. That is, deposition of particles is independent of their size and thus independent of their Stokes settling velocity. As the laboratory experiments rule out coagulation in the water column, we conclude that the particles are mixed down to sediment interface where they are indiscriminately removed by some mechanism. We postulate that this may be achieved by circulation through and coagulation with a high-concentration fluidized sediment layer.

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Particle aggregation kinetics and ocean energetics at Gulf Stream
boundaries

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Rates of particle aggregation in the ocean are determined by both environmentally dependent and particle dependent variables. Data for spatial and temporal variabilities of environmental parameters can be used in particle aggregation models to better assess hypotheses about the effects of particle dependent variables on aggregation. Energy fluxes to the density and current shear fields are known to be crucial environmental data needed for aggregation studies. A method for incorporating 1-3 dimensional oceanic mixing data (acoustic current profiles and density structure profiles) into encounter probability particle aggregation models is presented. Data are furnished for this model from the Gulf Stream western and eastern boundaries, where particle aggregation is actively ongoing. Model runs are used to predict the potential importance and effect of various particle dependent data in these environments.

Observation of marine particles with laser techniques

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The purpose of our work is to construct an instrument which will enable us to observe in situ particles suspended in the marine water column in real time. The system is designed for a resolution better than 15 μm in all three dimensions and will allow 30 observations/ second. With these specifications, the field of observation is about 15 mm wide, 15 mm long and 12 mm high. The optical pathway has been described previously (Fig. 1, Strickler 1977, 1982, 1985) and is a modification of a Schlieren optical pathway. A collimated light beam is focused by a condensing lens. At the focal point, a small black spot stops the light from reaching the image plane. Hence, there is only a dark exposure. Any light scattered by a particle within the collimated beam will miss the spot and reach the image plane, forming a light image on a dark background. Out of focus particles do not form a sharp image on the image plane, but particles up to a few centimeters out of focus can be detected. Three-dimensional information is obtained by photographing the same field of view with two cameras at 90 degrees to one another. An infrared laser, which does not disturb marine life in the dark, is used as a light source.

We have already tested and used this method in the laboratory, video taping live zooplankters interacting with each other and with algae. We have observed the behavior of sinking particles of marine snow and subjected them to shear in order to observe particle cohesiveness.

Deployment of this instrument directly in the ocean will allow investigation of many questions arising in the study of particles in marine environments. Analysis of video images taken in situ will give information of particle size distributions, abundances, and particle spacing, shape, and potential origin. Information on processes of particle fragmentation and flux may also be possible. For example, we have observed that phytoplankton become entrained around sinking copepods, particularly near their mouth parts, and thus are transported to depth more rapidly than single cells. Similarly, sinking patterns of particles, behavior of zooplankton and processes occurring at boundary layers may be

observed directly.

This system is different from most systems used for the observation of suspended particles in that 1) we videotape the temporal behavior of the particles allowing us real-time first evaluation of the observation as well as computerized image processes of the observations and 2) we observe suspended particles in a frontview-sideview fashion allowing us to use the computer assisted design (CAD) programs for the analyses.

This system can be modified to resolve particles of around 1 μm in size, or to scan large volumes of water. Further application may use the same basic optical path because it allows simultaneous observations of suspended particles in the size range of 10 μm to 3 cm.

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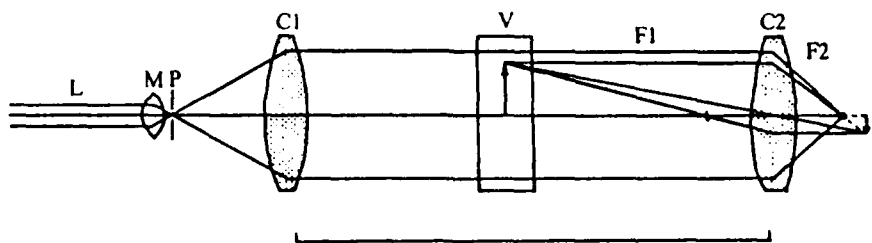


Fig. 3. Optical pathway used to obtain Fig. 1. The collimated light beam (4 cm diameter) is an enlarged laser beam (L) which passed a spatial filter (M = microscope lens, P = pinhole, C1 = collimator lens). All collimated light is focused by the condenser lens (C2) onto the black dot in the back focus (F2). The image (I) of the object in the vessel (arrow in V) is formed by diffracted light (F1 = front focal point). Bar equals ~ 100 cm.

In Situ Measurements of
Single Particle Optical Observables

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Measurement of the light scattering properties of single particles permits the development of certain sets of "optical observables" by which means such particles may be characterized, classified, and/or identified. Ideally, these particles should be measured in situ, but until this time, instrumentation to achieve this has not existed.

Under the on-going ONR Contract N00014-85-L-0067 we have developed an instrument that may be operated at any depth and which measures the scattered light intensity at many angles from single particles entering the approximate one microliter field of view. Although the contract is devoted primarily to phytoplankton characterization and identification, its broad range of application certainly includes bacteria, bubbles, and many types of aggregates. For example, a dual read head instrument was delivered to NORDA in July for the in situ measurement and discrimination bubbles in the $2\mu\text{m}$ to $100\mu\text{m}$ range at depths down to 250m.

The typical read head structure is comprised of a polarized laser light source, a set of 16 optical collimators (optical fibers plus field of view limiting lens), 16 polarizing analysers, and an open framework to support the optical collimators at up to 72 different angular positions. The framework consists of three intersecting great circles whose common diameter is the laser beam. Small radially-aligned apertures in these circles permit the insertion and holding of the optical collimator/analyser structures at any unoccupied angular position. The optical collimator/analysers have a very restricted angular acceptance angle ($\pm 1^\circ$) which, in turn, limits the field of view seen to about 2mm of the laser beam ($1/e^2$ diameter = 0.8mm). This corresponds to an effective "target" volume of about 1 microliter at the center of the sphere defined by the great circle framework.

As a particle enters the target volume, it scatters light outwardly in spherical waves. Each collimator/analyser collects the light reaching it and transmits it through optical cables corresponding, remote photomultiplier detectors. The 16 PMT signals are converted by means of a 16-channel A/D multiplexer and stored in a computer memory unit for subsequent processing.

By varying the multiplexer scanning frequency, the light scattering profile of the single particle as it traverses the beam may be followed. The collection of these light scattering data is triggered by selecting a required minimum threshold signal at any one of the 16 detectors. Once the threshold signal is detected, the collection and storage of all angular scattering data proceeds until terminated.

The collected data are analysed and reduced to a set of optical observables on which basis the source particle may be characterized. Some of these observables are described that permit velocity, size, density and structural inhomogeneity to be monitored. For example, measurements are presented that permit the differentiation of bubbles (spheres) from aggregates, as well as motile from immobile particles.

Finally, other applications of the optical observables are discussed. Foremost among these are the generation of bulk radiative transfer properties such as bulk scattering and absorption coefficients. Such coefficients may be synthesized by the suitable combination of optical observable catalogs corresponding to the unique particle population distributions hypothesized to exist at specific locations.

IN SITU PARTICULATE DIAGNOSTICS*

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Characteristics of the radiation scattered by a unit volume of sea water containing suspended particulates depend upon several parameters, such as the wavelength of the incident radiation and the particulate properties. In general, particulate properties can be divided into two categories: (1) properties that appear as parameters in the Mie theory of scattering which are the relative index of refraction, particle size, and size distribution. These parameters must be specified to predict laser beam propagation and light transmission through absorbing media such as atmospheric haze, clouds, and sea water; and (2) properties that involve an approximation, such as the shape of the particle, orientation relative to the scattering plane, and optical depth; i.e., single or multiple scattering. For this discussion we assumed locally homogeneous distribution with spherical particles and that the single scattering (optically thin) condition exists.

Determination of the aerosol cloud number density distribution function, which is essential to the application of the Mie computer codes, can be achieved by two methods, direct sampling and optical scattering measurement. The direct sample method involves collecting samples from the aerosol cloud and sizing the particulate individually. Various sampling techniques are available, but they are subject to calibration errors.

Optical scattering measurement provides an indirect way to determine the cloud particulate size distribution function. Optical techniques have been used for particulates with narrow size distribution functions. However, with the availability of lasers and better computational tools, these indirect diagnostic techniques can be extended to wide size distribution functions. In this technique, measurements are made of the attenuation and scattering of laser radiation from a small volume containing the particulates. By making these measurements at several wavelengths and angles, the data can be used to deduce the particle size distribution and refractive index. This is accomplished by using an accurate matrix inversion scheme and efficient Mie computational subroutines.

Based on our experience with Mie scattering and electro-optical instrumentation, we developed a diagnostic concept to obtain the aerosol size distribution function and the index of refraction. Our approach has two main features: (1) experiments that include a multiwavelength and multiangle bistatic measurements, simultaneously measured spectral extinction, and a time of flight (TOF) velocimetry correlation method, and (2) data analysis that includes the Mie scattering theory and the Backus-Gilbert data matrix inversion technique.

*This research was done under Lockheed funding.

To prove our diagnostic concept, we have performed a mathematical experiment utilizing atmospheric cloud models, since most of our applications are atmospheric related. However, the method may be directly applicable to underwater conditions as well. We assumed a modified gamma function for particle size distribution representing large $0.01 \leq R (\mu\text{m}) \leq 20$ droplets that exist as a cumulus cloud layer, or $0.01 \leq R (\mu\text{m}) \leq 1.0$ polydispersion that can be found under a hazy atmospheric condition. Cloud averaged angular intensity functions $\sigma(\theta) [\text{cm-sr}]^{-1}$ have been obtained from Mie theory. Arbitrary error ϵ (2 to 10 percent) have been added to represent realistic measurements data set. Application of the Backus-Gilbert inversion algorithm provided "experimentally" obtained size distribution function. Careful study of our results (shown in Fig. 1) indicates that a multiwavelength bistatic data set matrix inversion yields the best fit to the originally assumed function.

Application of this method to marine aggregate in situ diagnostics is straightforward with the appropriate wavelength selection. TOF laser velocimetry technique can be applied to measure the suspended aggregates' fall velocity. Two parallel ribbon-like laser beams are transmitted into the measurement volume. When a particle crosses the first beam, it scatters light into the receiver. This light is detected and a correlator clock started. When the same particle crosses the second beam, the light is detected by a second detector and the clock is stopped. The time (t) to cross the distance (d) between the two light sheets is obtained from the correlator. Velocity components perpendicular to the two beams can be determined by $v=d/t$.

At the Lockheed Palo Alto Research & Development Division, we have built and tested a 3-dimensional TOF laser velocimeter system to measure aircraft velocity to a very high degree of accuracy. In principle, we can see no difficulty in combining a 3-dimensional TOF laser illumination system to a bidirectional nephelometer to provide marine aggregates in situ diagnostic information.

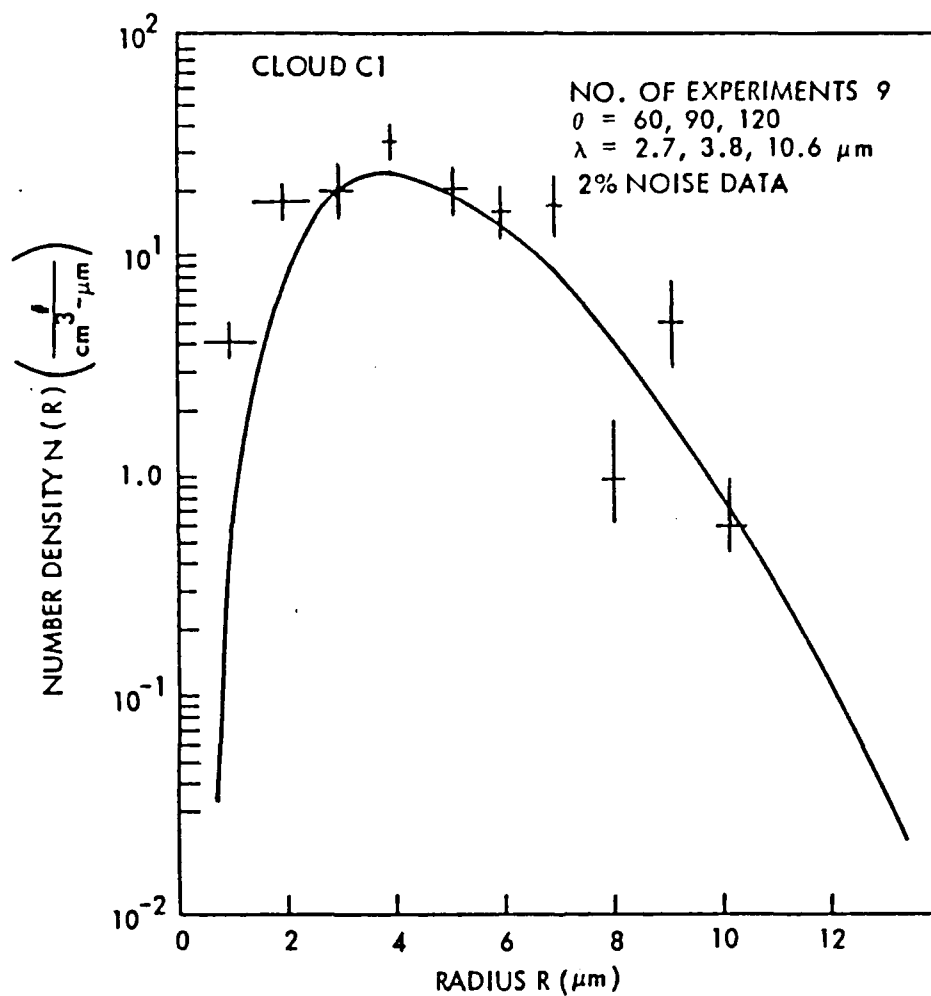


Fig. 1 Actual and Recovered Size Distribution (Mathematical Experiment)

GEOMETRY AND SCALING OF HYDROSOL ENCOUNTER MECHANISMS

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Suspension feeding is a major removal mechanism for particles from seawater. Rubenstein and Koehl (1977) provide a listing and parameterization of mechanisms whereby the particle-collecting surfaces of suspension feeders can encounter hydrosols. Their approach is drawn directly from aerosol filtration theory. Focus in aerosol engineering is on efficiency of removal of particles, while success in suspension feeding depends on rate of particle capture. A further major difference between aerosol filtration and many kinds of suspension feeding is that flow is constrained, usually by a duct or pipe, to go through an aerosol filter. One of the consequences, since the aerosol filter occupies some volume, is that flow velocity in the filter will exceed that upstream of it. While not especially important at the single-fiber level (other than with respect to fiber orientation to the flow and gravity vectors) this difference in aerosol filtering versus feeding on hydrosols becomes extremely important when fibers or filter-feeding appendages are close enough to each other to interact. The geometry of suspension feeding resembles the constrained arrangement of aerosol filtration in bivalves, tunicates, appendicularians, and some polychaetes and crustaceans with enclosed filtering systems, resembles it less well for suspension feeders sweeping collecting appendages through open water, and resembles it very poorly for passive suspension feeders. In aerosol filtration a denser filter packing will remove particles with greater efficiency (percent of total particle number); in a passive suspension feeder denser packing of filtering structures may deflect flow around the collector and lead to capture at a lower rate (particles per time) than would a sparser array.

We choose to focus directly on incident particle flux per individual, inherently a biologically more meaningful quantity than filter efficiency. We first provide simple, dimensional parameterizations for each of the hydrosol encounter mechanisms listed by Rubenstein and Koehl (including sieving) and show how they may be generalized to capture structures of any geometry. We do not suggest ours as a replacement for that provided by Rubenstein and Koehl (1977), but rather as an alternative perspective that may be more suitable for some purposes and less suitable for others. The re-analysis we present here makes the physical homology with particle aggregation mechanisms (McCave, this symposium) and with deposition (on the seabed) more obvious.

As one example of the benefit of retaining the dimensional form of the equations or of an alternative non-dimensionalization (i.e., dividing the actual encounter flux by the the particle flux required to just prevent weight loss but not allow growth), consider encounter by gravitation. Flux [particles per time] to the collector surface is simply maximal collector area [length squared] in the plane normal to the gravity vector times particle concentration [number per length cubed] times particle settling velocity [length per time]. Intensity of capture [dimensionless] in the aerosol filtration sense of fiber efficiency is the ratio of particle settling velocity to flow velocity. The dependence on flow velocity and the independence from both particle concentration and collector size arise in the aerosol filtration-intensity term in the process of nondimensionalization. While use of the aerosol intensity-of-capture indices often leads to the conclusion that gravitational capture is unimportant in suspension feeders, consideration of the geometry and

dimensions of the gravitational flux lead to the alternative conclusion that an organism using gravitational mechanisms in particle capture would probably not use a fiber. Since the mechanism does not require a relative (to the collector) flow velocity but does benefit from a large collector area in the horizontal plane, particularly likely users are the net-spinning pteropods. The other mechanisms of capture can be analyzed similarly, retaining important information on the geometry and flow orientation of the collector.

All these equations are written for rigid particles that can be characterized by a single length scale and a single excess density with respect to seawater. It is clear that the physical dynamic properties of aggregates cannot be characterized in the same way. Therefore we are examining several alternative characterizations of particle aggregates from the dynamic perspective, with foci on relaxation times, densities (mass per unit volume), sizes, and behavior in shear flows. These dynamic properties are needed to predict suspension-feeding encounters as well as the behavior of aggregates during settling and deposition.

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Mechanisms of bio-particle interactions as suggested by
chemotactic models

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A potentially important mechanism for aggregation in the marine environment involves the interactions among organisms. Examples include the concentration of phytoplankton by feeding zooplankton and the chemotactic accumulation of bacteria around leaking algae. Simulations of bacterial chemotactic behavior under a range of conditions helps to understand the potential role of chemotactic interactions in bioparticle interactions. Results show that the efficiency of chemotactic detection is a strong function of the size and chemical efflux rates. Particles smaller than 2-5 μm in diameter are undetectable by chemotactic means. Such a limitation on chemotactic behavior could explain the drop in efficiency of copepod feeding on particles less than about 5 μm . It implies that the mechanisms that organisms use to find particles, either to eat them or to colonize them, depend on the particle size and the leakage of material from the particle. This has implications for the dynamics of aggregate formation and removal.