PARTICLE AGGREGATION DYNAMICS

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Significance of Particle Dynamics

Until the late 1970s it was thought that particulate organic matter sedimented to the deep sea via the slow downward sinking of tiny, suspended plants, animals, and debris. These particles supposedly produced a steady rain of fine detritus onto the deep seafloor. However, more recent studies using sediment traps (suspended cones or cylinders that intercept sedimenting material) demonstrate that large, rare, rapidly sinking particles are actually responsible for the majority of the downward vertical transport of matter from the surface waters of the ocean. The flux of these large sedimenting particles far exceeds that of the fine suspended particles, even though the large forms are far less numerous. Where do these large, rapidly sinking particles come from?

This article examines the processes that produce and destroy sedimenting particles in the ocean. The processes by which particles are transformed in size and composition are collectively known as 'particle dynamics.' An understanding of particle dynamics is essential for predicting marine sedimentation rates and ultimately, for estimating the quantity of carbon that can be sequestered in the deep sea. Most of the organic carbon in the ocean originates through the fixation of carbon dioxide by photosynthetic organisms near the surface. Sequestration of large quantities of this organic carbon in the sediments of the deep ocean can effectively remove carbon from the global carbon cycle and ultimately reduce concentrations of atmospheric CO_2, a major greenhouse gas, especially on long timescales of thousands of years. Thus oceanic sedimentation rates and particle dynamics are relevant to global climate change and the greenhouse effect. Particle dynamics also alters the sizes and types of particles available to animal grazers and microbial decomposers in the water column, making it important to the biology of many marine organisms. Moreover, processes that shift the particle size distributions in the ocean affect the optical properties of the water altering water clarity and signal transduction. Finally, particle dynamics involves transformation between the particulate and dissolved pools of matter in the ocean making it also relevant for marine chemistry.

Processes Forming Large Particles

The average depth of the ocean is about 4000 m. Sedimenting particles must sink at speeds of about 50 to several hundred meters per day in order to reach such great depths before they completely dissolve or decompose. Even then, a particle generated in surface waters and sinking at 100 m per day would require 40 days to strike the ocean bottom. Only particles bigger than about 0.5 mm in diameter or very dense particles, such as mollusk shells or sand grains, can sink at rates fast enough to reach the seafloor before destructive processes, including decomposition, dissolution, disaggregation, or consumption by grazers, completely destroy or transform them. Thus sedimentation rates in the ocean are governed by the mechanisms responsible for repackaging smaller particles into larger units capable of rapid settlement.

The most abundant types of large particles sedimenting to the seafloor fall into two general categories: fecal pellets and marine snow. Fecal pellets large enough to sink rapidly are produced by larger zooplankton such as euphausiids (krill), chaetognaths (arrow worms), amphipods, large copepods, pelagic crabs, salps (pelagic tunicates), pteropods (pelagic mollusks) and many other minor taxa. The generic term 'marine snow' describes aggregates of highly diverse origins, structure, and characteristics that are larger than 0.5 mm in diameter (*see* **Marine Snow**). Marine snow includes fragile, porous, loose associations of smaller particles, highly cohesive, robust gelatinous webs produced by zooplankton, and some flocculent, porous fecal pellets. The two classes of rapidly sinking particles are produced from smaller particles via two major pathways in the ocean. First, biologically mediated aggregation results when small particles are consumed and transformed into fecal pellets or feeding webs by the feeding activities of marine animals. Second, the coagulation of small discrete particles into larger heterogeneous aggregates occurs largely through physically mediated processes of collision and sticking.

Origins of Primary Particles

Both the coagulation and consumption pathways depend on the types and abundances of smaller particles available for physically or biologically mediated aggregation. These smaller particles are referred to as 'primary particles' because they are the basic units involved in aggregation. **Figure 1**

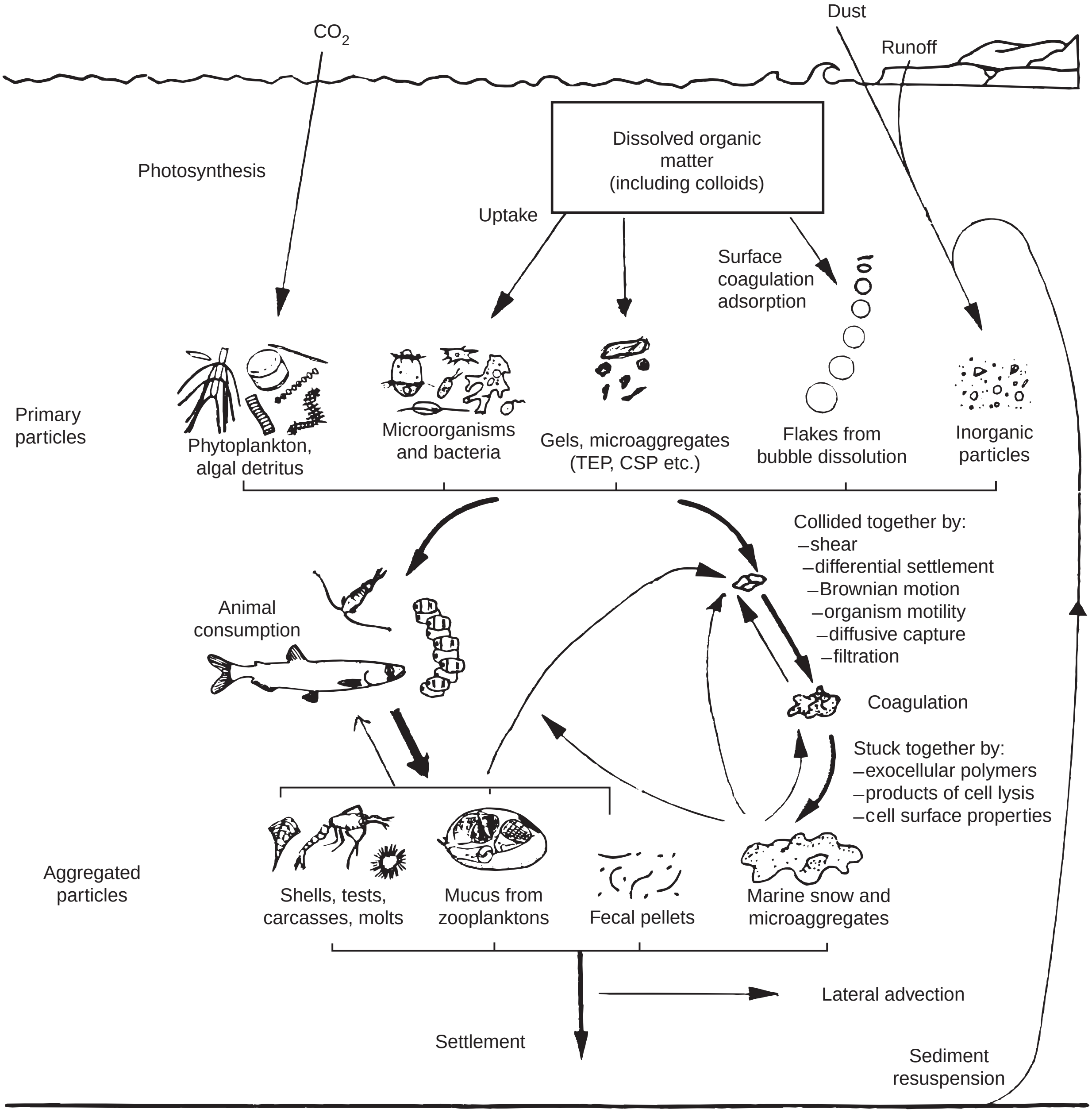


Figure 1 Major sources of particles in sea water. Primary particles are formed from inorganic or dissolved organic sources via processes such as photosynthesis, microbial uptake, and bubble dissolution. The large particles responsible for the sedimentation of particulate organic matter in the ocean are formed from primary particles via animal consumption (feeding webs, fecal pellets) and coagulation. TEP, transparent exopolymer particles; CSP, Coomassie stained particles. (Modified with permission from Hurd DC, Spencer DW (eds) (1991) *Marine Particles: Analysis and Characterization*. Washington DC: American Geophysical Union.

illustrates the most important types of primary particles.

Most primary particles consist of organic matter whose origins can be traced back to the fixation of inorganic carbon dioxide by photosynthetic phytoplankton. These microscopic algae are also at the base of the food web, supporting the growth of other living primary particles such as bacteria and protozoans. Certain phytoplankton, including diatoms, coccolithophorids (single celled, calcareous algae), and prymnesiophytes (golden-brown algae) contribute directly to marine snow formation. Chain-forming diatoms become entangled and aggregate to form large sinking composite particles and prymnesiophytes of the genus *Phaeocystis* exist within a mucus matrix and are often responsible for the large quantities of mucus reported to cause damage to fishing nets and beaches in the North

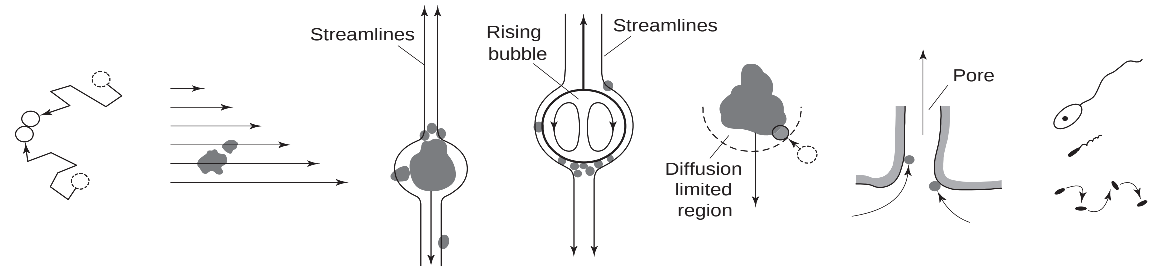
Atlantic. Phytoplankton also excrete copious polysaccharides and other organic molecules which increase the pool of dissolved organic matter in the ocean and support the growth of bacteria and the formation of primary particles from dissolved precursors. Finally, as they age, die, and decompose the broken spines and tests, cell walls, and cellular components of phytoplankton contribute to the pool of nonliving detritus.

Dissolved organic matter (DOM) in the ocean is also a major source of primary particles. There is about 10 times more DOM in the ocean than particulate organic matter (POM) and about 50% of this DOM consists of colloids. These tiny particles, between 1 nm and 1 μm in size, reach abundances as high as 10^7–10^9 per ml in the ocean and can readily coagulate into larger particles.

Three major types of primary particles important in the formation of sedimenting particles are generated from DOM: bacteria, flakes, and gels (**Figure 1**). First, new bacteria cells are produced when bacteria transport readily usable dissolved molecules such as amino acids, carbohydrates, and lipids across their cell membranes and use them to fuel cellular metabolism, growth, and cell division. Thus uptake of DOM by bacteria generates particulate matter in the form of new bacteria cells which are then available for further aggregation or consumption up the food web.

Second, flakes are produced by the dissolution of rising bubbles of air generated by white caps and waves breaking at the sea surface. Turbulent mixing forces these bubbles underwater, sometimes to depths of many meters or even tens of meters. As the bubbles rise surface active dissolved matter, including fatty acids, sterols, fatty alcohols, and proteins, adsorb to the bubble surface and many colloidal particles collide with and stick to the bubble surface through surface coagulation (**Figure 2**). The air within the bubble gradually dissolves causing the material adhering to the bubble surface to collapse into a small flake of particulate organic matter. The size of these flakes is dependent on the initial diameter of the bubble. Most bubbles generated by breaking waves in the ocean are < 100 μm in diameter and generate flakes of POM on the order of 2–20 μm in size. Anyone who has ever seen breaking ocean waves during high winds or violent storms can readily appreciate the potential magnitude of this process for producing particulate matter in the ocean.

Finally, transparent gel particles form from DOM, especially polysaccharides and proteins. Phytoplankton can excrete as much as 50% of their photosynthetically fixed carbon as long-chain polysaccharides. These molecules align in sea water, often via attractions between positively and negatively charged portions of the molecules, into colloidal-sized mucilaginous units called fibrils. These aggregate and swell to form gel-like material in water. These gel particles, known as transparent exopolymer particles (TEP), are discrete particles up to hundreds of micrometers long that appear as amorphous spheres, films, sheets, or strings on filters when stained with Alcian Blue, a dye specific for acidic polysaccharides (**Figure 3A**). In marine



(A) Brownian motion (B) Shear (C) Differential settlement (D) Surface coagulation (E) Diffusive capture (F) Filtration (G) Motility

Figure 2 Physical collision mechanisms of particles in the ocean. (A) Brownian motion – particles smaller than a few micrometers collide while moving randomly. This is the major mechanism of collision for colloidal-sized particles. (B) Shear – particles carried by parallel streamlines of different velocities collide when one particle overtakes the other. This mechanism is most important for particles larger than a few micrometers in diameter. (C) Differential settlement – rapidly sinking particles overtake and collide with smaller, more slowly sinking ones. Collision depends on the smaller particle following streamlines close enough to the larger particle to produce contact. This process often results in collisions in the wake of the larger particle, generating comet-shaped aggregates. (D) Surface coagulation – the aggregation of colloids on rising bubbles is orders of magnitude more efficient than it would be if the bubbles were solid spheres because streamlines carrying the colloids are drawn to the bubble by internal gas circulation that moves the bubble surface. Colloids are also caught in the wake of the rising bubble. (E) Diffusive capture – rapidly sinking particles have boundary layers around them. Small particles may be carried across this boundary layer by diffusion and collide. (F) Filtration – large aggregates are porous with many channels through their interior. Smaller particles may be captured as they flow into these channels. (G) Organism motility – microorganisms swim and tumble leading to collision with other particles in the water.

environments TEP occur at concentrations up to thousands per millimeter. Similar transparent gel-like particles rich in proteins, rather than carbohydrates, known as Coomassie stained particles (CSP) after Coomassie, a stain specific for proteins, exist at even higher abundances than TEP. Cell lysis which releases protein-rich cell components, adsorption of proteins onto mucilage surfaces, and microbial exoenzymes may be sources of CSP.

The existence of both TEP and CSP was only discovered in the mid 1990s because unstained particles are totally transparent to the eye and the microscope. Since they exist as gels, they are mostly water. But their large size, high abundance, and sticky surfaces make them particularly important primary particles for the formation of large sinking aggregates. Gel particles appear to be the 'glue' that helps bind many of the other types of primary particles together to form larger aggregates (**Figure 3B**).

The last major class of primary particles is inorganic and includes primarily clay-minerals derived from sediment resuspension, terrestrial runoff, and wind-blown dust. Inorganic particles are relatively rare in the open ocean but can be a significant component of sedimenting aggregates near shore or near the water–sediment interface. The surfaces of inorganic particles entering the ocean become coated with absorbed organic molecules and develop a slight negative charge that affects their ability to aggregate.

Formation of Aggregated Particles

Despite the highly variable appearance and composition of large sedimenting particles (**Figure 4**) they are formed from combinations of primary particles by only two major pathways which are discussed here using **Figure 1** as a framework.

Biologically mediated aggregation: particles produced as by-products of animal consumption

Herbivorous zooplankton consume phytoplankton and microorganisms in the ocean and they, in turn, are consumed by carnivorous animals up the food chain. Flakes, gels, and detrital particles are also consumed. Feeding at all trophic levels brings together primary particles and transforms them into new animal growth, respired carbon dioxide, various dissolved excretory products, and fecal pellets. Several types of large particles result from feeding (**Figure 1**) including fecal pellets, feeding webs, and molts.

Assimilation efficiencies of zooplankton vary from about 60% to about 90%; thus 10–40% of the food consumed by zooplankton is repackaged into fecal pellets. Fecal pellets contain not only partially digested particles but also bacteria and some phytoplankton that escape digestion. They may be encased in a membrane (crustaceans, chaetognaths, larvaceans, etc.) or be loose, fluffy conglomerations of digestive waste (fish, doliolids). Larger pellets produced by big crustaceans (krill, amphipods, pelagic crabs), salps, chaetognaths, pteropods and many others can sink at rates of several hundred to over 2000 m per day. At these rates many large pellets reach the seafloor before decomposing completely. Smaller pellets produced by copepods, protozoans, and other small zooplankton may sink only a few meters per day. Small pellets rapidly decompose in the water column and rarely contribute significantly to the downward flux of particulate matter.

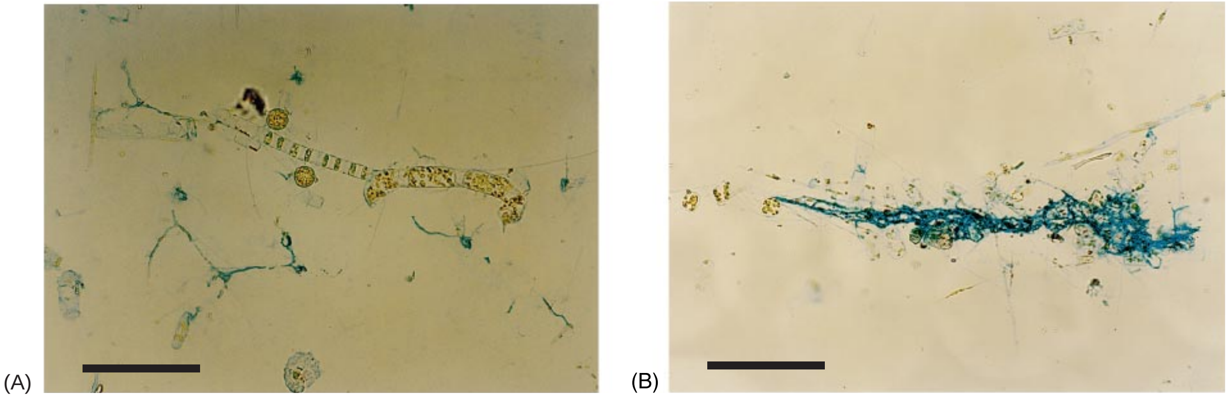


Figure 3 (A) Gel-like transparent exopolymer particles (TEP), here dispersed around a diatom chain, occur as stings, spheres, and sheets when stained with Alcian Blue, a stain specific for acidic polysaccharides. (B) These gels form the matrix of many marine aggregates of phytoplankton and detrital material. Scale bar, 100 μm. (B reprinted from Alldredge AL, Passow U and Logan BE (1993) The abundance and significance of a class of large, transparent organic particles in the ocean. *Deep-Sea Research*, 40, 1131–1140, with permission of Elsevier Publishing Co, London.)

Feeding webs are a second type of aggregated particle generated by zooplankton feeding. Planktonic tunicates known as larvaceans and planktonic snails, or pteropods, produce large mucous particles as part of their feeding biology. Larvaceans secrete a gelatinous 'house' around themselves with which they filter bacteria, small algae, and other particles from the surrounding seawater (**Figure 4C**). These houses are aggregates of gelatinous mucus and a variety of phytoplankton, bacteria, and smaller particles filtered from the water during feeding. The house filters clog quickly and an average larvacean may produce four to six houses per day, discarding each house sequentially. Most larvacean houses range from about 1 to 10 mm in diameter although species in the deep sea produce houses almost 100 cm across. Abundances up to 80 houses l^{-1} and particle fluxes as high as 9×10^4 houses $m^2 d^{-1}$ have been reported from tropical bays. Larvaceans are also common in the open ocean and can be an important source of sinking aggregates when abundant.

Mucus feeding webs produced by planktonic snails and foraminifera (spined calcareous amoeboid protozoa) are also a source of marine snow, especially in oceanic areas where these animals are abundant. However, no quantitative data presently exist as to the abundance of these webs or their contribution to particle flux in the ocean.

Finally, animals generate shells, tests, carcasses, and molts as they grow and die. These are included with aggregated particles because they are generated by animals through the consumption and transformation of primary particles. Shells, in particular, sink rapidly and can reach the bottom in many parts of the ocean before they dissolve, accumulating to form hydrocarbon oozes, such as pteropod and foraminiferal oozes, and calcareous and siliceous deposits.

Physically mediated aggregation: coagulation Although fecal pellets are important in particle flux, most POM sediments to the seafloor as marine snow. Marine snow is formed by the coagulation of the many types of smaller particles available in the water column including phytoplankton, bacteria, flakes, gels particles, detritus, fecal pellets, and inorganic particles. Coagulation is a two step process. First, primary particles must collide together. Second, they must stick together on collision to form an aggregate. This is an iterative process. Two primary particles collide and stick. This aggregate than collides with a third particle, then a fourth, and so on forming a larger and larger aggregate over time. All sizes of particles from colloids to marine snow can coagulate up the size spectrum to generate the large sedimenting particles important for particle flux.

Coagulating particles are brought together in the ocean largely by physical processes. The mechanisms that contribute to the collision of suspended particles in the water column are illustrated in **Figure 2**. The mechanisms most important for the aggregation of colloidal particles include Brownian motion, surface coagulation, diffusive capture, and possibly filtration. These mechanisms efficiently aggregate colloids up the size spectrum until they become large enough to contribute to the formation of even larger aggregates of marine snow. Aggregates in the marine snow size range (>0.5 mm in diameter) are produced primarily by collisions of larger primary particles and aggregates via shear and differential settlement (**Figure 2**). Swimming also brings motile bacteria, phytoplankton, and protists into contact with aggregates and facilitates colonization and the growth of complex detrital communities on particles.

Once collided together, particles must stick together. Most particles in the ocean are relatively unsticky. When marine sediments, healthy phytoplankton, and other small marine particles collide generally less than 1 in 10 collisions actually results in the two colliding particles sticking together. Often rates are even lower with only 1 in 100 inorganic particles or phytoplankton joining on collision. Such low sticking efficiencies imply that coagulation rates should be very low in the ocean. However, gel particles are quite sticky and facilitate aggregation. Sedimenting marine snow is formed primarily from the collisions of particles on the order of tens to hundreds of micrometers in size. The polymers associated with marine snow increase stickiness to the point where 70–80% of collisions between larger aggregates result in sticking. This is about 10 times higher than the sticking probabilities of smaller particles of marine sediment which lack the extensive biological communities and polysaccharide glues associated with marine snow.

Our theoretical understanding of coagulation in marine systems has been guided largely by the work of colloidal chemists, atmospheric scientists and waste water engineers. The coagulation theory that marine scientists inherited from these disciplines was developed to describe simple systems containing identical, spherical, nonliving particles. In theory, any aggregates formed were larger but otherwise identical in shape and density to the original particles. These assumed particle properties are contradicted in almost every way in natural marine systems that contain heterogeneous mixtures of particles from many sources. The physical and chemical properties of natural particles vary; their shapes are seldom spherical; and they often contain spines. Furthermore, living particles grow and divide, even within aggregates. When particles do coagulate, they form porous aggregates with properties described by fractal rather than Euclidean geometry. Fractal aggregates have smaller mass and slower sinking rates than predicted for Euclidean particles of similar size. Finally, quantifying and modeling the impact of each individual collision mechanism given the diversity of both particle characteristics and physical conditions in various regions of the ocean is a daunting task.

These complexities have made it very difficult to accurately predict coagulation rates in the ocean and quantitative estimates of coagulation rates in nature and the development of theory to accommodate complex oceanic systems are both in their infancy. However, basic theoretical considerations can still identify significant factors governing aggregation. Coagulation rates for the formation of larger, sinking particles are primarily a function of three major factors: the abundance and size distribution of primary particles; sticking efficiency between particles; and the intensity of the particular physical process colliding particles, especially shear and differential settlement. Early application of coagulation theory to particle dynamics in the water column indicated that the abundance of primary particles and the intensity of physical processes, especially shear, were simply too low to explain the high abundance of marine snow and other aggregates observed in nature. However, recent applications of coagulation theory that take into account increased particle abundances and sizes resulting from the presence of TEP and CSP, increased sticking efficiencies of larger particles, and nonspherical particle sizes and shapes indicate that coagulation is an important process controlling maximum phytoplankton concentrations and the vertical flux of organic matter, even in the nonbloom conditions of the oligotrophic ocean. Although biological aggregation through animal consumption is certainly the most significant processes regulating the aggregation of particles smaller than about 5–10 μm in the ocean, coagulation appears to be as or more important than grazing for aggregating particles larger than about 10 μm. However, extensive quantitative comparisons of these two pathways have not been made.

One system where coagulation is particularly important and greatly increases the flux of large particles is phytoplankton blooms. Aided by increasing abundances of TEP from phytoplankton exudation, blooms of chain-forming diatoms, particularly the chain-forming genera *Nitzschia* and *Chaetoceros*, aggregate into centimeter-sized particles of marine snow, often coinciding with nutrient depletion (**Figure 4A, B**). These flocs settle at velocities of 100–200 m day^{-1} and quickly transport photosynthetically derived carbon directly to the seafloor, often before it can be consumed by zooplankton. The rapid sinking of large flocs formed by diatoms helps to explain why diatoms and the shells of other small organisms are often distributed in deep-sea sediments directly below the surface populations originally forming them. Previously these distributions had been surprising given the relatively slow settling rates of individual shells and the possibility for horizontal displacement by underlying ocean currents. We now know that these organisms reach the seafloor in large, rapidly settling flocs of marine snow.

Processes that Destroy and Transform Large Particles

Particle dynamics also includes processes that either directly consume and destroy aggregates or that transform them into nonsinking or more slowly sinking forms. These destructive processes are very effective. Generally less than 10% of photosynthetically fixed carbon sinks to the seafloor in shallow coastal seas and less than 1% reaches the seafloor over most of the deeper ocean. Five major processes are responsible for the transformation of large sinking particles in the ocean. Quantitative estimates of the significance of these various destructive and transformative processes are very rare and considerable future research is needed to fully understand their role in particle dynamics.

First, many types of zooplankton including copepods, euphausiids, salps, pteropods, and some fish, such as midwater myctophids, eat marine snow and others are known to consume fecal pellets. Animal feeding transforms marine snow into smaller (and usually more slowly sinking) fecal pellets, new animal growth and reproduction, and respired carbon dioxide. Although the consumption of rapidly sinking particles by zooplankton and fish has not been quantified, it is most likely a major loss process given the abundance of zooplankton. In the deep sea, in particular, where food is relatively scarce, rapidly sinking particles may be particularly attractive for grazers.

A second major process is microbial decomposition, mostly by bacteria inhabiting sinking particles. These organisms utilize the particulate matter on the sinking particles to generate new bacteria cells but much of the organic carbon is lost to respiration.

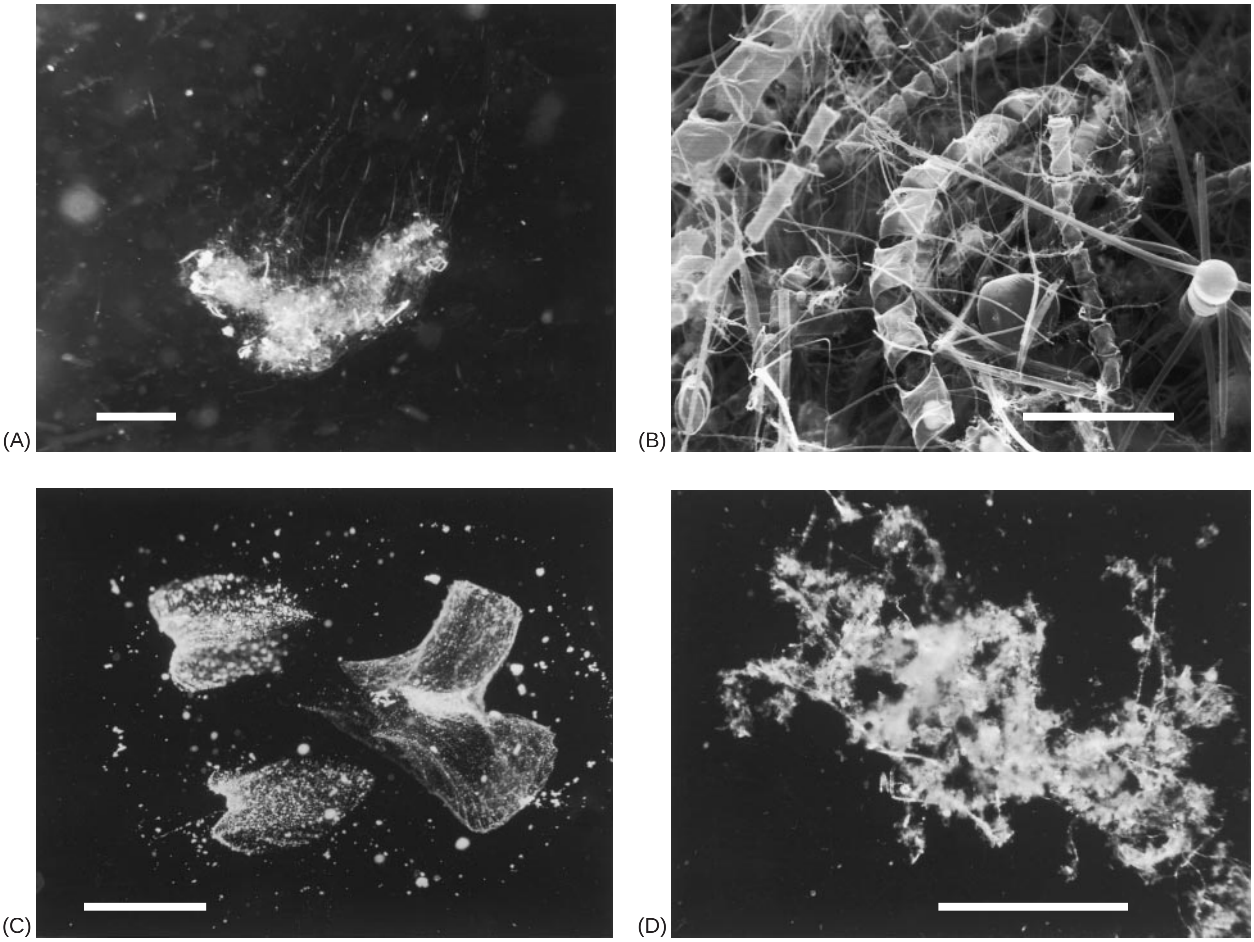


Figure 4 Examples of large aggregated particles. (A) Aggregate formed by the coagulation of living, chain-forming diatoms; scale bar, 1 cm. (B) Scanning electron micrograph of the interstices of a diatom floc composed predominantly of individuals of the genus *Chaetoceros*; scale bar, 40 μm. (C) Abandoned house of a larvacean with filtering structures evident. This particle is formed via the animal consumption pathway; scale bar, 5 mm. (D) Light micrograph of a typical aggregate of detritus and debris formed by the coagulation pathway; scale bar, 1 mm.

A third related process is solubilization. All bacteria must first convert particulate matter into dissolved form in order to transport it across their cell membranes. Bacteria attached to particles produce copious exoenzymes which solubilize the particulate matter and convert it into dissolved organic molecules that diffuse into the surrounding sea water. Simultaneously, the attached bacteria divide and release many of their offspring into the surrounding sea water, as well. Thus, the attached forms seed the sea water with both offspring and the dissolved food to help sustain them by exploiting particulate matter on rapidly sinking particles. Solubilization of marine snow adds to the pool of dissolved organic matter in the ocean at the expense of the particulate pool. Decomposition and solubilization processes degrade aggregates over long time spans of weeks to months. These rates are slow enough to allow larger aggregates time to reach the seafloor.

Physical processes such as fluid shear from currents, upwelling and mixing can physically break sinking particles into smaller more slowly sinking forms. These smaller particles remain longer in the water column making them even more susceptible to animal grazing and decomposition by bacteria. Finally, turbulence generated by the swimming and vertical migration patterns of larger animals, especially krill, salps, medusa, and other large zooplankton also disrupt marine snow and break it into smaller, more slowly sinking particles. This latter process may be more important than shear generated by mixing since average shear rates in most of the ocean have been shown to be far too low to disrupt most types of marine snow.

These five destructive processes and the various aggregation processes all act on marine particles simultaneously. The ultimate fate of any particular particle depends greatly on which processes dominate its transformation and its interactions with other particles and organisms in the water column.

Conclusions

Particle dynamics affects not only the rate of sedimentation in the ocean but also the ecology of the organisms living in the water column, the sizes of the pools of important chemical constituents such as carbon and nitrogen, and the optical properties of the water itself. The complex array of processes that contribute to particle dynamics have been identified. However, the relative importance of each of these processes at different times and places in the ocean has yet to be fully investigated. A quantitative understanding of particle dynamics will be necessary in order to accurately predict sedimentation rates and the role of the ocean in global scale problems such as climate change.

Summary

Most of the material sedimenting to the seafloor sinks as large fecal pellets or as rapidly settling aggregates of phytoplankton and organic debris known as marine snow. Particle dynamics encompasses the processes by which these particles are produced, transformed, and consumed in the ocean. Large, rapidly settling particles are formed from the aggregation of small, slowly sinking particles including phytoplankton, microorganisms, gels, flakes, detritus, and clay-minerals by two pathways. First, primary particles can be transformed biologically into fecal pellets, molts, and mucus feeding webs through the feeding activities of zooplankton. Second, they can collide with each other and stick together to form progressively larger aggregates through the physical process of coagulation. Although it may take large particles many days or weeks to sediment to the seafloor, some reach the ocean bottom before they are destroyed by animal consumption, bacterial decomposition, or disaggregation. The balance between the processes of production and destruction determines the quantity and size distribution of particulate organic matter in the water column and the quantity of material deposited on the seafloor.

Glossary

Assimilation efficiency the percentage of consumed food that is absorbed through the gut wall and becomes available for cellular metabolism.

Colloids Particles from 1 nm to about 1 μm in size. Colloids do not sink and they are considered to be part of the pool of dissolved organic matter in the ocean.

Detritus Non-living particulate organic matter including algal debris.

Dissolved Organic matter Organic matter that passes through a filter with a pore size of 0.7–0.8 μm.

Fractal geometry A nonlinear, noninteger mathematics that has evolved to describe rugose, wrinkled objects such as clouds, coastlines, and aggregates.

Marine snow Aggregated marine particles larger than 0.5 mm in diameter.

Oligotrophic Regions of the ocean characterized by low nutrient concentrations, low phytoplankton biomass, and high water clarity.

Particle Flux The quantity of particulate matter sinking through a given area of the water column, usually a square meter, at a given depth per unit time.

Phytoplankton Plant plankton.

Zooplankton Animal plankton, including protozoans.

See also

Carbon Cycle. Floc Layers. Gelatinous Zooplankton. Marine Snow.

Further Reading

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