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J. N. Am. Benthol. Soc., 1996, 15(1):127–135

Colloids, bubbles, and aggregates—a perspective on their role in suspension feeding

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Abstract. Suspension feeders capture a wide range of materials from water currents, and the type of food subsequently ingested varies with the catching device and with the animal's ability to be selective. Black fly larvae are examples of non-selective suspension feeders that ingest particulate and dissolved organic matter (POM and DOM). The DOM includes colloids originally produced as mucopolysaccharide (exopolymer) exudates from cells. Colloidal exopolymer particles (CEPs, those <1 μm in size) may be free in the water column, attached to each other or to surfaces of bubbles, or bound with other particles to form aggregates. CEPs, and their adsorbed coatings, may be important in the nutrition of animals that capture and ingest them. In this "Perspective" I consider some of the roles of CEPs in the biology of suspension feeders and in the biology of aquatic systems as a whole.

Key words: colloids, bubbles, aggregates, exudates, dissolved organic matter (DOM), surface microlayers, organic coatings, suspension feeders, digestion.

Suspension feeders collect particles and other matter from the water column, but what is the food, and thus trophic role, of these animals? In streams and rivers, most suspension feeders intercept existing currents with well-adapted feeding structures, e.g., nets of caddisfly larvae, silk strands of midge larvae, head fans of black fly larvae, and ctenidia of bivalves. In the earliest studies, the diet of suspension feeders was examined after dissection of their gut contents. Some particles were easily identified as being of mineral, plant, or animal origin, and the rest of the gut contents were described as detritus or amorphous matter. These terms were used because the origins of the materials were not known and their structure could not easily be resolved with light microscopy, especially if digestion was extensive. With the development of more sophisticated histological, microscopical, and experimental techniques, we now know more about suspension feeders and their diet (Merritt et al. 1996).

The earliest approach to trophic structure in ecosystems showed solar energy being converted to biomass by primary producers, which were eaten by primary consumers (herbivores). These, in turn, formed the diet of secondary consumers (carnivores) and tertiary consumers (top carnivores) (Odum 1957, Phillipson 1966). For suspension feeders that selectively ingest plants or animals, this trophic pathway *is* the dominant one; but what of those animals that ingest mainly detritus, and what part of this material is digested? As we learned more about aquatic detritivores, a new paradigm developed: detritus was viewed principally as the vehicle by which bacteria and fungi were ingested, these attached microorganisms forming the main food of detritivorous animals (Cummins 1974). Recent studies have shown that many suspension-feeding detritivores ingest a wide array of organic matter and gain their nutrition from many sources, including the detritus itself (Wotton 1994, Allan 1995).

Black fly larvae (Diptera:Simuliidae) are non-selective suspension feeders that ingest all the materials captured on their head fans. They capture colloids (categorised as having the longest axis ranging from 1 nm to 1 μm, Stumm 1992), and most particles in their guts are very small (Wotton 1976, 1977). Black fly larvae have a low assimilation efficiency and their gut contents appear little altered by digestion, although bacteria are known to be lysed in large numbers (Wotton 1994). When dispersed and mounted on slides, the gut contents contain much material that is difficult to resolve by light microscopy or scanning electron microscopy.

Black fly larvae often dominate the fauna of surface-release lake outlets, and very high population densities develop at these sites (Wotton 1994). Downstream from outlets, the quantity and/or quality of suspended particles decreases (Richardson and Mackay 1991) and the numbers of inorganic particles increase downstream in the erosive environment provided by most streams and rivers. In a study of the black fly larvae of a lake outlet in Swedish Lapland we suggested that particles <2 μm in diameter (i.e., mostly colloids) were important as food (Carlsson et al. 1977). Of course, larger particles were valuable in nutrition too, but the small particles *controlled* the extent of the downstream abundance of these suspension feeders. We did not know what these small particles were, how they were generated in the lake or the outlet stream, or their trophic significance. This "Perspective" explores some possible roles for such colloids.

Colloids and aggregation processes within the water column

Although information on the numbers of submicron particles in natural waters is limited because of sampling difficulties (Filella and Buffle 1993), estimates from several aquatic habitats have shown they are abundant in the water column. Among these very small particles (most being classified as dissolved organic matter, DOM, i.e., having a diameter of <0.45 μm) are many that are chemically active.

If water from lakes and streams is viewed under transmission electron microscopy it is possible to identify many very small particles and a less distinct matrix of much finer fibrils (see Mavrocordatos et al. 1994, Wilkinson et al. 1995 for recent techniques). These fibrils consist of mucopolysaccharides (a term used in this article to describe mucus-like exopolymers) which have been exuded from cells, and some fibrils appear to link particles together to form aggregates (Massalski and Leppard 1979, Leppard and Burnison 1983, Leppard 1984, Hicks and Hobbie 1985, Baxter et al. 1992, Filella et al. 1993, Jensen and Corpe 1994). Mucopolysaccharide exopolymers are produced by bacteria, some algae, and some animals and are found free in the water column after breaking off cell surfaces, or after surviving death of the organism that produced them (Massalski and Leppard 1979, Leppard and Burnison 1983, Leppard 1984, Hicks and Hobbie 1985, Baxter et al. 1992).

Decho (1990) and Decho and Lopez (1993) divided microbial mucopolysaccharide exudates into capsule exopolymers, which adhere closely to cells, and slime exopolymers that have a much looser association with cells and which are often produced as a metabolic shunt for excess carbon. I define fibrils of mucopolysaccharide exudate in the water column as colloidal exopolymer particles (CEPs). In addition to their release after excretion by biota within the water column, CEPs are also formed by sloughing and breakdown from other sources of exopolymer (e.g., biofilms, mucus trails, protective secretions, and secretions used to aid feeding), sometimes after breakdown from larger particles (Wotton 1994). CEPs have an affinity for organic molecules (Decho 1990, Decho and Lopez 1993, Filella and Buffle 1993, Passow et al. 1994, Passow and Wassmann 1994) and, in laboratory preparations, have been shown to bind heavy metal stains used in electron microscopy (Massalski and Leppard 1979, Leppard and Burnison 1983). DOM binds to adsorptive carboxyl ligands on the mucopolysaccharides (Decho 1990, Decho and Lopez 1993), a process that begins during the rapid hydration of these molecules after they are exuded.

Little is known about the biology of CEPs and larger exopolymer particles within the water column, and what we know is largely confined to marine environments (see the comprehensive review of Decho 1990). In contrast, there is considerable interest in the exopolymer associated with benthic biofilms, and we have a developing knowledge of the complex structure and function of these biofilms (Costerton et al. 1994, Lock 1994). Leppard and Burnison (1983) found that many lake-water samples showed particulate exopolymer to be abundant relative to other organic particles (Burnison and Leppard 1983).

Several mechanisms promote the aggregation of colloids to form larger particles within the water column, e.g., bubbling, changes in pH, in cation concentration, or shear stress (Wotton 1984, 1988); the physico-chemical mechanisms involved in aggregation are described by Stumm (1992) and by Johnson et al. (1994). There has been some discussion in the literature as to whether living bacteria are important in aggregation processes, but it is now known that whole bacterial cells are not essential (Kepkay et al. 1990a). Exopolymers attached to cells play an important role in ensuring the attachment of microbiota to each other, or to substrates, and the same "sticky" properties are probably true of free exopolymers (Passow and Alldredge 1995). Where live bacteria are not involved, CEPs exuded originally from bacterial or algal cells are probably the binding material within aggregates of organic and inorganic matter (Batoosingh et al. 1969, Carlough 1994, Logan et al. 1995, Mopper et al. 1995).

Aggregation of organic matter has been studied most thoroughly in the sea, and "marine snow" (describing its loose, floc-like appearance) is the most well-known form of aggregate. Marine snow is abundant during algal blooms and during the decline of these blooms (Riebesell 1991a, 1991b, Logan et al. 1995, Passow and Alldredge 1995). The aggregates are bound by CEPs and also by exopolymer exuded by living cells (Decho 1990, Decho and Lopez 1993, Passow et al. 1994, Passow and Wassmann 1994, Logan et al. 1995, Mopper et al. 1995). Exopolymer can also be fused into transparent particles 3–>100 μm long (TEP) which, in turn, bind the other ingredients of marine snow (Alldredge et al. 1993). Disruption of large aggregates of marine snow, caused by wind action and turbulence, is often temporary because aggregates re-form when the wind dies down (Herndl and Peduzzi 1988). Aggregation and disruption of aggregates are thus rapid and continuous processes.

Marine snow is found not only in water of high productivity but also in oligotrophic seawater where the limited nitrogen availability enhances the production of exudates by algae (Smetacek and Pollehne 1986). Marine snow then serves as a focus for grazing animals because other foods are in short supply within the water column. The aggregates also include populations of heterotrophs which mineralise detritus and make nutrients available for growth of incorporated algae. Marine snow aggregates thus form patches of biological activity in waters of low productivity (Herndl 1988, Decho 1990).

The formation of snow-like flocs, bound by exopolymer and CEPs, has been reported in lakes (Klut and Stockner 1991, Logan et al. 1995) and rivers (Carlough 1994), although the effects of shear, created by currents, limit floc size in flowing waters. Nevertheless, average aggregate diameter was 16 μm in a blackwater river (Carlough 1994), and aggregates are colonised by many bacteria and protozoans. Small mineral particles bound in aggregates in most streams and rivers are also likely to promote the sedimentation of aggregates. Clearly, aggregation processes are universal in aquatic systems (Wotton 1994, Logan et al. 1995), and aggregates and their constituent parts are food for suspension feeders. Were CEPs and disrupted aggregates the important materials that limited the downstream abundance of the black fly larvae we studied (Carlsson et al. 1977) in Sweden? How important are colloids and aggregates in the trophic biology of lake outlets and of lotic waters generally?

Bubbles and aggregation at air-water interfaces

Bubbles within the water column are a feature of many turbulent waters. Thirty years ago, Baylor and Sutcliffe (1963) produced particles by bubbling air through samples of seawater that had been filtered through a 0.45-μm-pore filter. DOM adhering to bubbles in their experiment would have included CEPs, which bound the aggregate particles resulting from the bubbles' collapse (cf. Alber and Valiela 1994, Mopper et al. 1995). CEPs with hydrophobic properties accumulate at air-water interfaces. Kepkay and coworkers (Kepkay and Johnson 1989, Kepkay et al. 1990a, 1990b, Kepkay 1991) have shown that colloids adhering to the surface of bubbles produce aggregates that enhance microbial respiration, especially where the numbers of suspended particles are low (Kepkay et al. 1990a). Thus, while living bacteria are not essential for the development of aggregates, these microorganisms benefit from aggregate formation.

Extensive bubbling occurs in the surf zone of the marine littoral. Foams generated here contain hydrophobic materials and aggregates formed in the surf, bound with CEPs, and have a longer duration than those formed solely by impaction forces. As surf diatoms are "sticky" (Talbot and Bate 1988), these aggregates are probably bound by exopolymer sloughed from their surfaces, as well as from bacteria (cf. Mopper et al. 1995). Many CEPs are visible in electron micrographs of foam generated by wave action on the surface of lakes (Massalski and Leppard 1979).

Bubbles greatly increase the area of air-water interface, and microlayers that accumulate just under the surface film will quickly coat the bubbles. The surface microlayers of most water bodies are thin (Maki and Hermansson 1994) but extensive (think of the total area of water on Earth). Eutrophic lakes and ponds often have much thicker microlayers, and slicks commonly develop during still periods in summer. In streams and rivers the microlayers are frequently disrupted, but layers of surfactants rapidly re-form at the surface film, coating the surface of "dead zones" and pools. Particles falling into lakes, rivers, and streams (e.g., leaves, pollen grains, etc.) pick up a coating of surface-active material as they pass across the surface microlayers, probably enhancing the adsorption of other organic matter. Exopolymer-producing organisms are found in high concentrations near the water surface (Maki and Hermansson 1994), and conditions here (e.g., high ultraviolet radiation, high temperature) stimulate the production of exudates. Death of cells also contributes CEPs to the surface microlayers although some CEPs will be broken down by heterotrophs. Labile organic matter is also formed by photolytic breakdown of refractory materials at the water surface (Herndl et al. 1993, Maki and Hermansson 1994, Karentz et al. 1994). This labile DOM stimulates bacterial growth (Lindell et al. 1995) and becomes adsorbed to the surface of CEPs and CEP-bound aggregates.

Petersen (1986) showed a 66% increase in the number of particles of diameter 4–6 μm below a waterfall. These particles were probably generated from DOM and many must have included surface film components. Aggregates of this kind, bound by CEPs, are a common feature in rivers and streams where bubble formation is a frequent event, e.g., below riffles or waterfalls. Although many factors are important in the distribution of suspension feeders (e.g., high current velocities for rapid delivery of food and high oxygen tension for efficient metabolism), could the high numbers of suspension feeders often present in riffles be explained partly by an increase in food availability created by floc/aggregate formation after bubbling?

Food collection, digestion and nutrition in suspension feeders

In addition to the collection and concentration of CEPs, black fly larvae capture particles generated within the water column that are bound by CEPs (i.e., fragments of the freshwater analogue of marine snow) and particles formed from bubbles. (As they capture such a wide range of particles I shall continue to use black fly larvae as examples of suspension feeders in this section of the "Perspective".) All particles, whether classified as POM (particulate organic matter, i.e., particles >0.45 μm in diameter) or DOM, may be filtered from the water column by these suspension feeders. Black fly larvae may feed continuously in a water current >50 cm/s and therefore strain material from an impressive amount of water during their lifetime of 2 wk or more. The feeding mechanism therefore functions in the same way as membrane filters or glass-fibre filters in retaining and concentrating matter from large volumes of fluid.

Ross and Craig (1980) and Nübel (1984) noted mucopolysaccharide on the feeding organs of black fly larvae and thought that this material was secreted by glands in the head (Ross and Craig 1980). A similar mucosubstance was found around the mouthparts of suspension-feeding mosquito larvae (Merritt and Craig 1987), and head glands were again suspected as the secretion site. Later studies have shown that the mucopolysaccharide was not produced by the larvae but came from an external source (Fry 1994), probably the accumulation of CEPs. The cephalic fans of black fly larvae, with their abundant microtrichia, may not only concentrate colloids from the water column but also generate shear stress that aids the local aggregation of CEPs over the surface of the fans (J. J. H. Ciborowski, University of Windsor, and D. A. Craig and K. M. Fry, University of Alberta, personal communications). By collecting a mucopolysaccharide coating on their feeding organs, the insects acquire a filtering surface with properties shown by mucous coverings on gills and meshes of many marine suspension feeders and freshwater molluscs. Mucopolysaccharide coatings promote adhesion of particles (Ross and Craig 1980) and act as adsorption sites for DOM (cf. Decho 1990) from water passing through the feeding apparatus. Organisms that have bubbles and floc striking their feeding apparatus are able to retain bubble coatings if adsorbed to an impacted mucopolysaccharide, or another charged surface. It is not known how much of the mucopolysaccharide coating is removed when black fly larvae clean their fans, or why the fans of some larvae lack these coatings.

The nutritional role of the total diet is not known. Once inside the gut, food is often subjected to a dramatic change in pH. For example, black fly larvae have highly alkaline mid-guts and food is exposed to a pH of 10 within minutes of ingestion (Lacey and Federici 1979). Organic matter adsorbed on some ingested CEPs and on other particles is likely to become dissociated by changes in pH (Bärlocher et al. 1989, Decho 1990). If proteins are dissociated from their adsorption site they are subject to further enzymatic breakdown, with alkaline proteases a feature of the gut of black fly larvae (Martin et al. 1985). CEPs are thus vehicles for bringing bound organic matter into the gut where it becomes available for nutrition after dissociation and hydrolysis. The rapid throughput rate of black fly larvae (Wallace and Merritt 1980) also favours stripping of adsorbed coatings rather than enzymatic attack on substrates unless ingested materials are easily broken down.

Studies on marine animals have shown that components of seafoam are digested (Bärlocher et al. 1988). Decho and Lopez (1993) showed that slime exopolymers were readily labile when ingested by a deposit-feeding polychaete, and these mucopolysaccharides provided nutrition in addition to the DOM bound on the polymers. The extent to which exopolymers are digested depends on gut physiology and gut retention time. However, it is important to note that CEPs may function as direct sources of nutrition as well as vehicles from which DOM is stripped on passage through the gut.

Exopolymers may also be important when live organisms are captured and ingested. An aura of exopolymer (Massalski and Leppard 1979, Leppard and Burnison 1983) is maintained around phytoplankters, providing a mechanism whereby labile exudates are conserved, by adsorption, close to the cells that generate them (analogous to the role of exopolymer in benthic biofilm, Lock 1994). The trapped exudate supports the growth of bacteria which destroy viruses harmful to the algal cells (Murray 1995), and the exudate may convey the "taste" of cells used by some selectively feeding zooplankters (Kerfoot and Kirk 1991), although feeding in some copepods is inhibited by the presence of exudates (Malej and Harris 1993). Black fly larvae do not use these cues (although other lotic suspension feeders might), but exudates and coatings of cells can be digested. The stressful environment within the gut also provides conditions whereby more exudate is likely to be produced by the process called "milking" (causing living cells to exude high quantities of DOM) by Thomas (1990). Therefore, living cells provide sources of nutrition even if their walls remain intact on passage through the gut of suspension feeders. This nutritional source should be considered when conducting radiotracer studies of assimilation efficiency. In such studies the measured uptake of radiotracer may come from exudates as well as from lysis.

Mucopolysaccharides that are resistant to digestion by suspension feeders are egested and probably help to bind faecal pellets. Binding of organic matter may be especially strong in acidic waters (e.g., blackwater rivers and ponds). McLachlan et al. (1979) found that faecal pellets of midge larvae inhabiting the sediments of a bog lake were more difficult to disperse than pellets from other sites, perhaps reflecting more effective binding by exopolymer. In acidified streams, suspension feeders such as black fly larvae increase in number at the expense of other taxa (Chmielewski and Hall 1993). With their high gut pH they are capable of releasing adsorbed organic matter from CEP-bound materials, e.g., faecal pellets egested by animals upstream. Any animal inhabiting waters with low pH may be able to dissociate valuable food molecules from refractory organic substrates if they have guts with alkaline regions.

Black fly larvae living in thin films of water at lake outlets ingest hydrophobic material from the surface microlayers (Wotton 1982) either by direct interception or after the capture of bubbles. Bubbles formed at the stream surface are coated by this material, which is enriched with hydrophobic compounds such as lipids (Napolitano and Richmond 1995). Female black flies from the site I used for a study of feeding on surface microlayers (Wotton 1982) were facultatively autogenous in the first gonotrophic cycle (i.e., they were able to mature a first batch of eggs from reserves accumulated from larval life; a second batch required a blood meal). It is tempting to speculate that ingestion of surface microlayer material was an important factor allowing autogeny, especially in view of the possible enrichment of the microlayers by lipids and polypeptides (Maki and Hermansson 1994). Were hydrophobic CEPs, and the coatings of mucopolysaccharide on the head fans, important in ensuring the capture of these materials?

Clearly, much has yet to be discovered about the diet of black flies and of the many other aquatic invertebrates that feed on mucopolysaccharide exudates.

Conclusions and questions

The diet of suspension feeders differs according to their catching device and their ability to select for size or quality. As a group, suspension feeders capture and digest animals, protists, plants, microorganisms, and a diverse array of other organic matter. In this "Perspective" I have only alluded to some of these types of food and my central theme has been on the role of exopolymer, both as CEPs and as a binding material for aggregates. Exopolymer provides a possible answer for several questions about the one group of suspension feeders, black fly larvae, that I took as an example. What is the mucopolysaccharide on the rays of the head fans? What limits downstream abundance below lake outlets? What is the amorphous material found in the gut? I hope these questions will soon have answers.

CEPs may play a significant part in the nutrition not just of suspension feeding animals but of a wide range of other aquatic organisms. All detritivores feed on materials that have attached exopolymer, or which are formed into flocs, but what is the importance of the exopolymer in nutrition relative to the cell contents of microorganisms and algae that exude it? The answer depends on the degree to which lysis of microorganisms and algae occurs and on the gut environment. The gut of aquatic invertebrates contains organic matter concentrated from the surrounding water and exposed to "hostile" conditions. The conditions within the gut should promote the release of further exudate in addition to allowing hydrolysis. Just how important is the former process?

Investigations on CEPs are few because they require a high level of focus. Transmission electron microscopy of water samples is necessary before CEPs can be seen as anything other than the aggregates of "amorphous detritus" seen using most other preparation techniques. CEPs, however, are ubiquitous and may have an important role to play in the functioning of aquatic systems, although static measures of the abundance of CEPs do not reveal their true biological significance. CEPs have an enormous total surface area for adsorption of other organic matter; some CEPs are readily metabolised and therefore turn over rapidly; and they form coatings on surfaces throughout the water column.

Finally, just how important are bubbles in streams and rivers? We have seen that bubbles have coatings that are metabolically active and particles are generated from bubbles after implosion. Have we made sufficient investigations of bubbles and their coatings and have we considered the importance of both in the functioning of streams and rivers?

The more we look the more we will see.

Acknowledgements

I thank Rosemary Mackay and Fred Benfield for their comments on both the scientific content and the English of this article. Doug Craig, Anne Hershey, Randy Hicks, Mike Miller, Rich Merritt, Mike Kaufmann, Patrick Armitage, Alan House, Dominic Chaloner, Costas Joicey, and two anonymous referees provided many useful suggestions on earlier versions of this paper and these have led to its improvement. I am grateful to Jan Ciborowski, Doug Craig, and Ken Fry for providing unpublished information on uptake of DOM by black fly larvae.

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Received: 26 July 1995
Accepted: 8 November 1995