

## The ubiquity and many roles of exopolymers (EPS) in aquatic systems\*

ROGER S. WOTTON

Department of Biology, University College London, Darwin Building, Gower Street, London WC1E 6BT.  
E-mail: r.wotton@ucl.ac.uk

**SUMMARY:** Exopolymers (EPS) are produced by unicellular and multicellular organisms. They consist largely of polysaccharides that hydrate rapidly on contact with water and link to form gels. EPS have many uses: in attachment; in locomotion on substrata; as a protection against predators, pathogens and changes in physico-chemical conditions; as a means of overcoming the threat of desiccation; in preventing abrasion; and in feeding. When free of organisms, some EPS form loosely associated polymer gels that are important in the development of organic matter aggregates. These aggregates, together with mucus-bound faecal pellets, play an essential role in nutrient cycling, and in the metabolism of ecosystems.

*Key words:* EPS, exopolymers, mucus, unicellular organisms, multicellular organisms, fibrils, flocs, aggregates.

**RESUMEN:** UBICUIDAD Y FUNCIONES DIVERSAS DE LOS EXOPOLÍMEROS (EPS) EN LOS SISTEMAS ACUÁTICOS. – Los exopolímeros (EPS) son producidos por organismos unicelulares y pluricelulares. Están constituidos fundamentalmente por polisacáridos que se hidratan rápidamente en contacto con el agua y se unen para formar geles. Los EPS tienen muchos usos; en la fijación; en la locomoción sobre sustratos; como protección contra los depredadores, los patógenos y los cambios en las condiciones fisicoquímicas; como una manera de contrarrestar el peligro de la desecación; para evitar la abrasión, y en la alimentación. Cuando se hallan libres de organismos, algunos EPS forman geles de polímeros asociados de manera laxa que son importantes para el desarrollo de agregados de materia orgánica. Estos agregados, junto con los paquetes fecales cohesionados con mucus, desempeñan un papel esencial en el ciclado de los nutrientes y en el metabolismo de los ecosistemas.

*Palabras clave:* exopolímeros, mucus, organismos unicelulares, organismos pluricelulares, fibrilas, copos, agregados.

### INTRODUCTION

Margalef (1985) describes the Mediterranean as “a living machine”. This is an excellent way of summarising the interactions of the living components of aquatic ecosystems and their transformation of chemicals. Living organisms also produce large numbers of waste products and exudates, many of which end up remote from the organisms that produce them. In this paper I will discuss exudates clas-

sified as exopolymers (EPS) and these include the products of single cells and of multicellular organisms. There are a number of common terms used to describe these exudates (e.g. glycocalyx, mucus, mucilage, slime) and EPS have a wide variety of chemical components depending on the particular organism from which they are produced (Decho, 1990; Leppard, 1995; Davies and Hawkins, 1998). The common component of all EPS is the presence of polysaccharide chains that hydrate on contact with water, the feature that gives them their physical properties.

\*Received September 18, 2001. Accepted November 19, 2002.

It seems likely that the earliest living organisms produced EPS and their secretion is a feature of the biology of many contemporary bacteria, cyanobacteria and unicellular algae. As evolution proceeded to the development of multicellular organisms, some cells of plants and animals became adapted solely to producing EPS, often in copious quantities. EPS have several features essential to their role in aquatic systems: the extent to which molecules of EPS form an hydrated gel; the changes in fluidity that occur in sol-gel and gel-sol transition; and their inherent “stickiness” and capacity for adsorption of other chemicals and of particles. These properties allow a wide range of applications both for the living organisms that exude them and, on becoming detached or after death, to the wider aquatic system. EPS are found everywhere there are living organisms: in water columns and over substrata; in the films of water surrounding terrestrial mineral grains; through to streams, rivers, pools, lakes, coastal margins and oceans. They are truly ubiquitous.

#### PRODUCTION AND FUNCTION OF EPS IN UNICELLULAR ORGANISMS

Many unicellular organisms produce EPS on occasions, or during some phases of their life cycle and they serve several roles (Table 1). The components of EPS are exported from the cell and then hydrate to form a fibrillar matrix (Decho, 1990; Lepard, 1995). Once produced, the resulting fibrils (or parts thereof) become interlinked and trap further water within the meshwork. Decho (1990), in his comprehensive review of microbial EPS in oceans, identifies slime and structural exopolymers. The latter have close interlinkages to form a capsule around bacteria that produce EPS, while slimes are looser associations with fewer links between fibrils. Capsule EPS are produced mainly during the log phase

TABLE 1. – Summary Table of the roles of EPS exuded by unicellular organisms. \*\*\* = important in majority of taxa; \*\* = important for some taxa; \* = found in some taxa; M = roles also found commonly in multicellular organisms.

Role	Status
Attachment (M)	***
Defence against attack (M)	**
Protection against change in physico-chemical conditions (M)	**
Formation of biofilms	**
Adsorption of nutrients and conservation of exoenzymes	**
Aid to locomotion (M)	*
Prevention of dessication (M)	*
Shunt for excess carbon generated within cells	*

of bacterial growth and slime EPS during the stationary phase (Plante and Shriver, 1998).

EPS are important in the attachment of bacteria to substrata and thus the development of biofilms (Costerton *et al.*, 1978), which are such features of all benthic habitats and of many water-air interfaces. Their ability to adsorb and retain nutrients is especially significant in biofilms (Lock, 1994) and the gel matrix also allows the conservation of exoenzymes that might otherwise be lost to the surrounding water. Many diatoms also attach to substrata using EPS.

Cyanobacteria that glide over surfaces produce EPS fibrils from pores in the cell wall and these extrusions may result directly in locomotory force, or provide a platform against which contractions are used in propulsion (Hoiczyk, 2000). Pennate diatoms with a raphe use EPS in locomotion, but not as propulsive agents (Häder and Hoiczyk, 1992), and desmids also use EPS to move, exuding hydrating polysaccharides which drive the cell “like a jet” (Häder and Hoiczyk, 1992). Motile algae and cyanobacteria leave EPS trails on the substratum over which they are moving.

Unicellular algae produce EPS as a shunt for carbon produced in excess during photosynthesis (Smetacek and Pollehne, 1986), especially when cells are senescing (Liu and Buskey, 2000a). Production of large amounts of EPS also occurs when nutrients such as nitrogen are in short supply (Thornton *et al.*, 1999). Protein synthesis is then reduced and smaller amounts of the organic carbon generated during photosynthesis are required for growth and reproduction.

Just as with bacteria, the matrix of fibrillar EPS produced by algae has a defensive function and some algae that produce large quantities of EPS reduce grazing by protists (Liu and Buskey, 2000b). It has been suggested that bacteria and flagellates colonising the EPS, and using them as food, also incapacitate viruses that might otherwise invade algae and cause harmful infections (Murray, 1995). Protection is also afforded against adverse environmental conditions. As the EPS matrix is highly hydrated it is likely to prevent dessication should the unicellular organisms become exposed temporarily to the air and it protects algae against salinity changes (Liu and Buskey, 2000a). The matrix may act as a shield against harmful solar radiation, and this is likely to be significant in the dense biofilms that may develop at the water-air interface.

## PRODUCTION OF EPS BY MULTICELLULAR ORGANISMS

Multicellular organisms have cells specialised for the secretion of EPS. In plants and animals these secretions of glycosaminoglycans and glycoproteins (Davies and Hawkins, 1998) are referred to as mucus, or slime, and are commonly produced in bulk. Rapid hydration occurs when the polysaccharide-based components, accumulated within the lumen of the cells where they are produced, are discharged into water. The most dramatic illustration of this process is seen in the defensive response of the hagfish (Fig. 1), this secretion also serving to protect the fish when it invades the bodies of other fish to feed. In hagfish, the mucus is supported by proteinaceous threads (Koch *et al.*, 1991) so the integrity of the hydrated exudate, and its volume, is most impressive (Downing *et al.*, 1991).

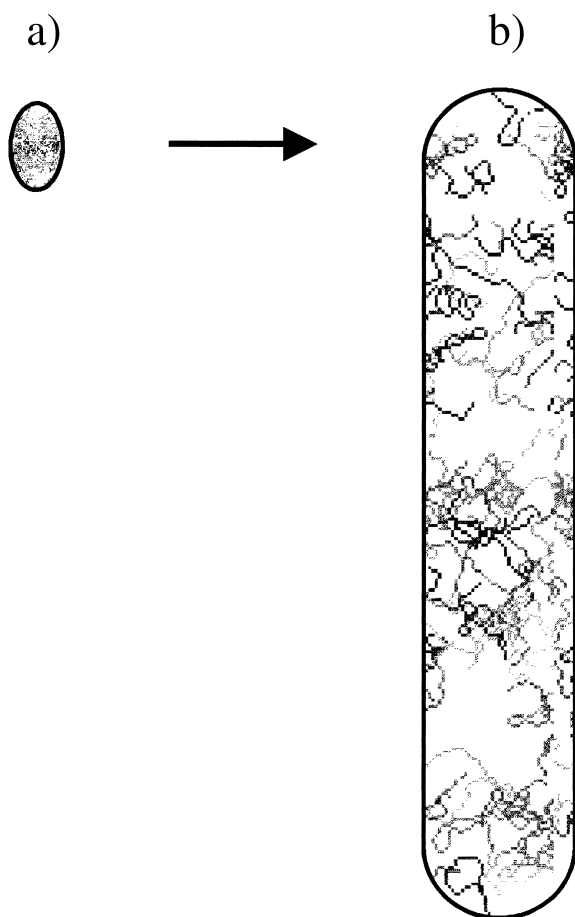


Fig. 1. – Diagrammatic representation of the rapid initial hydration of mucus produced from hagfish slime glands. A quantity of exudate from a slime gland (a) placed on to a spatula expands to form a column of mucus (b) within 10 seconds (with threads supporting the mucus mass). Drawn from photographs in the paper by Downing *et al.*, (1991).

TABLE 2. – Summary Table of the roles of EPS exuded by multicellular organisms. \*\* = important for some taxa; \* = found in some taxa; U = roles also found commonly in unicellular organisms.

Role	Status
Defence against attack (U)	**
Protection against change in physico-chemical conditions (U)	**
Aid to locomotion (U)	**
Protection against abrasion	**
Enhancing feeding on prey and on particulate and dissolved matter	**
Protection of the gut wall	**
Attachment (U)	*
Prevention of desiccation (U)	*
Preventing sessile organisms becoming covered by sediment	*
Building structures and for camouflage	*

Mucus produced by plants and animals has many roles (Table 2), depending on the organism (Denny, 1989). It often serves more than one function for organisms that exude it and the timing and volume of its secretion varies with need. Many fish produce mucus over their surface and this acts as a barrier to attack by both pathogens (Ebran *et al.*, 2000; Kosuga *et al.*, 2000), pollutants (Coello and Khan, 1996; Berntsson *et al.*, 1997) and predators (as in the hagfish). Anemonefish gain protection from living among sea anemones and it is their mucous covering that prevents them from being ensnared by the stinging cells of the coelenterates, possibly enhanced by sequestering of anemone EPS (Elliott *et al.*, 1994). In addition to providing many animals with a slippery physical barrier against predation by aquatic and terrestrial animals (Denny, 1989; Davenport, 1997) it is also likely that exuded mucus has chemical and microbiological defensive properties (Koh, 1997; Bryan *et al.*, 1998; Kelman *et al.* 1999).

Plants and animals of marine tidal coasts, and of temporary fresh waters, face the threat of exposure to the air and consequently of drying. On seashores, the mucus produced by coelenterates offers some protection against drying, as does the coating of mucus on macroalgae. In tropical fresh waters, aestivating snails (e.g. *Pila*) and bivalves (e.g. *Aspatharia*) secrete mucus at the opening of their shells and the EPS dehydrates to form a watertight seal that prevents further water loss (Beadle, 1974). Among vertebrates in drying habitats, lungfish (e.g. *Protopterus*) build a cocoon of mucus around their coiled bodies while buried within mud and this acts as a barrier to water loss. Some amphibians use a similar method (Beadle, 1974).

Like all coelenterates, corals produce EPS and this protects against coverage by sediment. The zooxanthellae that live symbiotically within many

corals are dependent on light for photosynthesis so these algae can no longer produce carbohydrates when sediment provides a barrier to light penetration. By exuding EPS, corals bind the covering mineral particles which are then swept away by the ebb and flow of currents across the reef. If corals receive too much light the damaging effect of UV rays can cause expulsion of their symbionts and damage to their own tissues so the secretion of mucus may then act as an UV barrier (Drollet *et al.*, 1997; Lyons *et al.*, 1998).

As mucus forms a slippery layer it prevents damage by abrasion. The EPS covering of macroalgal fronds allows them to slip over each other and also the rocks to which the alga is attached. Mucus exudates of burrowing annelids, echinoderms and molluscs serve a similar function, as movement though fine-grained mineral substrata would otherwise cause abrasion of the animals' surface. The sliminess of fish also offers protection against damage to the skin. For example, eels are able to live within gravels and all fish benefit by having a mucus coating over the gills, the delicate respiratory membranes being susceptible to abrasion by mineral particles, particularly where fish are living in turbid environments. The production of mucus by fish also aids in preventing osmotic stress caused by salinity change, just as with unicellular organisms. Thus, eels and salmon are protected by mucus, especially over the gills, as they migrate between salt and fresh water.

Some polychaete worms living within sandy deposits secrete tubes of mucus, or cement sand grains with EPS to make tubes (Dudgeon, 1994). This enables them to have a stable "home" within an unstable substratum, a means of avoiding the abrasive effect of moving mineral particles and, in some taxa, a framework to support their feeding tentacles. Some bivalves also use mucus in construction as they coat the outer surface of their shells which then adsorb detritus and mineral particles to provide camouflage (Morton, 2000). Other bivalves use mucus to hold mineral grains on to the shells to allow "cementing" by calcium carbonate deposited within the biofilm matrix (Taylor *et al.* 1999).

Mucus aids attachment in some multicellular animals and mucus trails are produced in locomotion. For example, flatworms are dorso-ventrally flattened and secrete EPS from cells in the ventral body wall that allow them to attach to surfaces, even to undersides. Many small, free-living flatworms move by means of cilia and these beat into a secreted trail

of mucus over which the animals glide. Some primitive snails also use this technique but most gastropods move by muscular contractions along the foot, the animal then sliding over secreted mucus. Snail trails are often visible to the human eye, although only 10-50  $\mu\text{m}$  thick (Connor and Quinn, 1984). It is likely that movement of the animal causes the gel structure to be broken, the sol-like state providing more effective lubrication (Denny, 1989). Trails then again become gels when linkages between EPS fibrils are re-established. These trails may remain for weeks (Davies and Hawkins, 1998) and are used by some limpets to navigate their return to "home scars" (Denny, 1989), to allow movement into aggregations, or to locate mates (Davies and Hawkins, 1998).

Mucus provides a slippery surface to reduce drag in fish (Denny, 1989), yet it provides very small planktonic organisms such as polychaete larvae (Nozais *et al.*, 1997) and larval mussels (Buchanan and Babcock, 1997) with a device to reduce sinking rate. The large surface area of their mucous threads increases frictional resistance as the animals sink through the water column. Perhaps the most unusual use of mucus in transport comes in the oceanic snail *Janthina* that produces a raft of bubbles coated with mucus to form a surface float that suspends the snail at the water-air interface (Ruppert and Barnes, 1994).

As mucus is sticky it is used as a trap for prey, as in some ctenophores. An unusual use of EPS in prey capture is found in *Euchirella*, a copepod that feeds by "firing" jets of mucus at potential prey (Klein and Koomen, 1994). Other invertebrates (e.g. *Chaetopterus*) use mucous threads "woven" into nets to catch particulate food (Ruppert and Barnes, 1994; Kappner *et al.*, 2000), and dissolved organic matter must also become adsorbed on to the matrix. Ingestion of nets therefore results in a wide array of foods becoming available, including some of the net material itself.

Many suspension feeders have coatings of mucus on their feeding apparatus. Bivalve molluscs use cilia on the gills to draw water through the mantle cavity and specialised ciliary bundles of adjacent gill filaments overlap to produce a filtering mesh. Captured particles are transferred to the frontal surface of the gill and become mixed with mucous secretions (Ruppert and Barnes, 1994). These help retain particulate and dissolved food and make these materials easy to transport along the gill to the labial palps where, after sorting, some is transferred to

the mouth. All muco-ciliary feeders use cilia to transport food bound in mucus, but EPS gathered from the water column is also found on structures that intercept currents and may act to retain particulate and dissolved matter (Wotton, 1994). For example, it is likely that some pelagic fish that feed using gill rakers use mucus to enhance retention of captured food particles (Eiras-Stofella *et al.*, 2001).

The gut of multicellular animals provides a barrier between the animals' tissues and the environment within the gut lumen. Foods concentrated within the gut are subjected to dramatic physico-chemical changes resulting in digestion, and assimilation of products across the gut wall. These physico-chemical conditions are potentially damaging to the walls of the gut, as are abrasive foods, and the gut of many animals contains cells that secrete EPS. Mucus thus serves the same functions in lubrication and protection as it does when secreted over the external surface of the organisms. Secretion of EPS by ingested algae and bacteria also serves as a defence against digestion and is likely to increase their chances of survival (Hansson and Tranvik, 1997). Capsule EPS provides the resistance to digestion, but susceptibility to attack by enzymes varies from one taxon to another and probably results from the quality of the EPS, and of the cell wall (Plante and Shriver, 1998). This mechanism thus replicates the defensive systems evolved by animals to prevent auto-digestion.

#### EPS REMOTE FROM THE ORGANISMS THAT EXUDE THEM

Whether secreted in fibrillar form or as mucous masses, some EPS become remote from the organisms that secrete them: as free colloidal exopolymer; fibril meshworks; components of a biofilm matrix; mucous trails and attachments; or as sloughed mucus from surfaces. This EPS plays significant roles in the functioning of aquatic ecosystems (Table 3).

Free fibrils become intertwined as they impact with each other to form a loose hydrated matrix analogous to that found around many unicellular organisms (Decho, 1990; Leppard, 1995). This matrix forms a polymer gel (Chin *et al.*, 1998) and all water bodies contain these loose aggregates of EPS fibrils, together with other organic chemicals. The polymer gels assemble, and disassemble, easily and the distribution of these loose gels is very patchy, varying both with environmental conditions

TABLE 3. – Summary Table of the roles of EPS free within the water column. \*\*\* = highly significant generally; \*\* = significant generally; \* = occurs in some habitats. Roles in brackets are uses made by humans of processes dependent on EPS.

Role	Status
Formation of polymer gels	***
“Glue” in the development of marine, lake and river “snow”	***
Formation of a substratum at the water-air interface	***
Formation of transparent exopolymer particles (TEPs)	**
Food for many organisms, especially suspension feeders	**
Binding for faeces	**
Stimulant for “gardening” of bacteria and algae	*
Providing cues that warn of predators	*
(Treating drinking water)	*
(Treating effluent)	*

and with location. However, they form foci for the development of larger, more permanent aggregates such as transparent exopolymer particles (TEPs) that form when the negatively charged EPS fibrils bond with divalent cations. EPS, in both TEP and fibrillar form, provide adhesive bridges that allow larger aggregates to form. Colonising microorganisms add to the EPS and further bind the components of flocs. These flocs are a feature of all water bodies and they play essential roles in the industrial treatment of water for drinking and safe discharge to the environment.

Loose flocs of organic matter resemble snowflakes and they have been termed “marine snow” by oceanographers. As would be expected, these flocs are also found in lakes and rivers and are referred to as “lake snow” and “river snow” respectively (Grossart *et al.*, 1997; Neu, 2000). Flocs are moved by currents and thus collect other materials and organisms by impaction. They usually contain many bacteria and bacterial EPS and it is likely that some bacteria colonise after moving actively towards these substrates using chemical gradients (Blackburn *et al.*, 1998). The bacteria begin the breakdown of organic matter that results in recycling and nutrient release.

EPS also gather at the surface of water bodies and help to support the active community of organisms that live there, many of which also secrete EPS. In some small water bodies the surface biofilm is so highly developed that immersion of objects picks up a coating that feels slimy and consists of large amounts of EPS (as revealed by staining with alcian blue). Any time that bubbles form at the surface of water bodies, as in waves or river rapids, they pick up a coating of surface film materials, including EPS and micro-organisms. When the bubbles break the

coatings form small aggregated particles that are known to have an enhanced biological activity (Kepkay *et al.*, 1990), just as do snow particles. The role of surface films in cycling of organic matter, protection of organisms against damage by UV light and many other roles is poorly known, or unknown, yet the surface of the planet largely consists of water-air interface with its potentially abundant EPS.

Suspension feeders that capture small particles are capable of acquiring both polymer gel components and snow. Some animals also capture colloidal particles (< 0.1  $\mu\text{m}$  in diameter) from water and thus accumulate fibrillar EPS. Feeding on colloidal particles has been demonstrated in larval mosquitoes that live in lakes (Dadd, 1971), larval blackflies that inhabit rivers (Wotton, 1976) and in the tunicate *Oikopleura*, a suspension feeder in oceans (Flood *et al.*, 1992). Whatever their origins, some EPS are digested (Decho, 1990; Couch *et al.*, 1996) and materials that adsorb on to them are likely to be desorbed in the vigorous physico-chemical conditions provided by the gut (Decho, 1990; Wotton, 1996). Some EPS, either ingested or exuded by bacteria and algae within the gut, are not broken down and these are egested. They are commonly the binding agents of faeces (Wotton and Malmqvist, 2001) which, in the absence of the surrounding membrane found in many crustaceans, serve to maintain the integrity of pellets. Mucus also binds the pseudofaeces (bundles of rejected particles) produced by bivalves. Binding of faecal pellets is a vitally important indirect role of EPS, as pellets are dense and move through water columns (Wotton and Malmqvist, 2001). Unless they are broken apart, or become diffuse, pellets sediment or are transported by currents and the movement of faecal pellets within oceans, lakes and rivers represents a significant vertical and/or horizontal movement of carbon (Malmqvist *et al.*, 2001; Wotton and Malmqvist, 2001).

Mucus produced by multicellular organisms also provides food for animals. As we have seen, coral mucus becomes free in the water over the reef and undergoes conditioning. Organic matter and micro-organisms attach to the mucus and it becomes broken into smaller particles. Some of these are ingested and assimilated by corals (Coffroth, 1984) but these particles are also available as food for other animals. Derivatives of coral mucus are powerful surfactants and accumulate at the water-air interface where they have dampening effects on the sea state, providing conditions suitable for the growth of delicate corals (Denny, 1989). Particles generated at the

surface contain these surfactants and their adsorbed chemicals and this is a further likely source of food for reef suspension feeders.

Motile foraminiferans leave trails of EPS that become colonised by “lawns” of bacteria and fungi that use the exudate as a substrate (Langer and Gehring, 1993). The foraminiferans graze over the lawns and show evidence of using chemical cues emanating from the micro-organisms to move towards dense patches of cells. The mucus trails of some gastropods also stimulate the growth of bacteria and algae (Peduzzi and Herndl, 1991; Davies and Beckwith, 1999) that are subsequently grazed (Connor and Quinn, 1984). Gastropod mucus is highly adsorptive of organic chemicals (Brereton *et al.*, 1999) and these, too, are likely to encourage the conditioning process. Brereton (1998) noted that snail faecal pellets were associated with their mucus trails, providing a source of fertiliser for the developing microbial and algal community. A similar use of nitrogenous waste as fertiliser is found in some species of limpets that develop a “garden” of algae over which they graze (Plagányi and Branch, 2000). Bivalves return some energy lost in mucus production, as conditioned EPS released within the faeces and pseudofaeces stimulates the growth of algae that form bivalve food (Cognie and Barille, 1999).

EPS provide cues (kairomones) that warn of the presence of predators. For example, some prey organisms have been shown to sense mucus by-products originating from predatory fish (Forward and Rittschof, 2000). As Forward and Rittschof (2000) point out, mucus is constantly sloughing off swimming fish, so prey animals able to sense mucus degradation products can detect, and avoid, predators. It is to be expected that EPS, in addition to providing direct cues, also act as carriers of many chemical signals, a result of the adsorptive properties of these exudates.

In addition to their role in natural systems, EPS have been utilised by humans for cleaning water for drinking, and for the treatment of effluent for safe discharge back to the environment. Biofilms that grow over sand grains adsorb dissolved organic matter, while the sand grains and their coatings also act as physical filters (Weber-Shirk and Dick, 1997). It has long been known that fresh waters draining through sands are often fit for drinking and this is the basis of many of the bottled mineral waters that are available commercially. The water industry also uses sand filters to clean drinking water and these filters remain an effective means of removing harm-

ful micro-organisms, the biofilm community of the sand grains being maintained in active growth by the grazing of protists and invertebrates (Wotton, 2002). Another method for purification of drinking water is to generate flocs of EPS that adsorb DOM and small particles, the floc then being filtered or settled to leave drinking water.

Flocculation is also a key process for cleaning effluent in the activated sludge process (Mason, 2002). After settlement of particles the effluent is seeded with flocculated aggregate from earlier treatments and subjected to vigorous mixing and/or aeration. The result is a massive growth of microbial floc that is allowed to sediment and this reduces organic matter and pathogenic organisms to levels that allow discharge back to rivers or the sea. Another method of cleaning effluent uses porous substrata that develop an effective covering of biofilm that is grazed by a community of organisms analogous to that found in the sand filters used to clean drinking water.

Occasionally, untreated effluent is released into natural aquatic systems and this stimulates algal growth. Blooms also result from discharges of plant nutrients that are applied to land to stimulate crops or animal feeds. The algal blooms "swamp" the feeding activities of herbivores and when algae deplete nutrients and enter the senescent phase they produce large quantities of EPS that are present as stable aggregates (Thornton *et al.*, 1999). On occasions, the sea then develops a mucous coating, gas bubbles maintaining huge aggregates at the water surface where they are carried by currents and winds, often ending up on shores (Stachowitsch *et al.*, 1990).

## CONCLUSIONS

EPS have properties that make them invaluable to the organisms that secrete them. They are sticky, adsorptive, and form gels that have many uses. As they are hydrated, and form loose aggregates, their functional volume is very large compared to their mass and estimates of abundance based on mass are likely to severely underestimate the significance of EPS, and their turnover (although some will be resistant to breakdown and remain little changed for long periods of time). The fibrillar nature of much EPS also presents a huge surface area for impaction and adsorption and the total surface of EPS, in the form of fibrils, gels and biofilms, makes them easily the dominant surface in aquatic systems.

In concluding his review, Decho (1990) poses a series of questions that need to be addressed in research on EPS secretions. These concern the amounts of EPS; their turnover; their role as foods (directly and as carriers of adsorbed coatings); their role in aggregation processes; and their effect in the development of biofilms. Many of these questions are currently being addressed and the role of EPS and mucus is now also receiving attention in the popular scientific press (Copley, 2000; Crystall, 2000; McFee, 2000; Pain, 2000; Zalasiewicz and Freedman, 2000). We are only just beginning to realise the extent to which these exudates play important roles not just for the organisms that secrete them, but for other organisms and for the functioning of aquatic systems. Clearly, many more exciting discoveries on the role of EPS await those investigating the biology of rivers, lakes and the oceans.

## ACKNOWLEDGEMENTS

I would like to thank Terry Preston, Conrad King and two anonymous referees for their comments on the manuscript. Thanks also to students on the UCL Aquatic Biology course for discussion.

## REFERENCES

- Azam, F. – 1998. Microbial control of oceanic carbon flux: the plot thickens. *Science*, 280: 694-696.
- Beadle, L.C. – 1974. *The Inland Waters of Tropical Africa: an Introduction to Tropical Limnology*. Longman, London.
- Berntsson, M.H.G., F. Kroglund, B.O. Rosseland and S.E.W. Bonga. – 1997. Responses of skin mucous cells to aluminum exposure at low pH in Atlantic salmon (*Salmo salar*) smolts. *Can. J. Fish. Aquat. Sci.*, 54: 1039-1045.
- Blackburn, N., T. Fenchel and J. Mitchell. – 1998. Microscale nutrient patches in planktonic habitats shown by chemotactic bacteria. *Science*, 282: 2254-2257.
- Brereton, C. – 1998. *The role of mucus and silk as attachment and sorption sites in streams*. Ph.D. thesis, Univ. London.
- Brereton, C., W.A. House, P.D. Armitage and R.S. Wotton. – 1999. Sorption of pesticides to novel materials: snail pedal mucus and blackfly silk. *Environ. Pollut.*, 105: 55-65.
- Bryan, P.J., J.B. McClintock and B.J. Baker. – 1998. Population biology and antipredator defenses of the shallow-water Antarctic nudibrach *Tritoniella belli*. *Mar. Biol.*, 132: 259-265.
- Buchanan, S. and R. Babcock. – 1997. Primary and secondary settlement by the Greenshell mussel *Perna canaliculus*. *J. Shellfish Res.*, 16: 71-76.
- Chin, W.-C., M.V. Orellana and P. Verdugo. – 1998. Spontaneous assembly of marine dissolved organic matter into polymer gels. *Nature*, 391: 568-572.
- Coello, W.F. and M.A.Q. Khan. – 1996. Protection against heavy metal toxicity by mucus and scales in fish. *Arch. Environ. Contam. Toxicol.*, 30: 319-326.
- Coffroth, M.A. – 1984. Ingestion and incorporation of coral mucus aggregates by a gorgonian soft coral. *Mar. Ecol. Prog. Ser.*, 17: 193-199.
- Cognie, B. and L. Barille. – 1999. Does bivalve mucus favour the

- growth of their main food source, microalgae? *Oceanol. Acta*, 22: 441-450.
- Connor V.M. and J.F. Quinn. – 1984. Stimulation of food species growth by limpet mucus. *Science*, 225: 843-844.
- Copley, J. - 2000. Ooze cruise. *New Sci.*, 2229: 27-29.
- Costerton, J.W., G.G. Geesey and K.-J. Cheng. – 1978. How bacteria stick. *Sci. Am.*, 238: 86-95.
- Couch, C.A., J.L.Meyer and R.O. Hall. – 1996. Incorporation of bacterial extracellular polysaccharide by black fly larvae (Simuliidae). *J. N. Am. Benthol. Soc.* 15: 289-299.
- Crystall, B. – 2000. Monstrous mucus. *New Sci.*, 2229: 38-41.
- Dadd, R.H. – 1971. Effects of size and concentration of particles on rates of ingestion of latex particulates by mosquito larvae. *Ann. Entomol. Soc. Am.*, 64: 687-692.
- Davenport, J. – 1997. Comparisons of the biology of the intertidal subantarctic limpets *Nacella concinna* and *Kerguelenella lateralis*. *J. Molluscan Stud.*, 63: 39-48.
- Davies, M.S. and S.J. Hawkins. – 1998. Mucus from marine molluscs. *Adv. Mar. Biol.*, 34: 1-71.
- Davies, M.S. and P. Beckwith. – 1999. Role of mucus trails and trail-following in the behaviour and nutrition of the periwinkle *Littorina littorea*. *Mar. Ecol. Prog. Ser.*, 179: 247-257.
- Decho, A.W. – 1990. Microbial exopolymer secretions in ocean environments: their role(s) in food webs and marine processes. *Oceanogr. Mar. Biol. Annu. Rev.*, 28: 73-153.
- Denny, M.W. – 1989. Invertebrate mucous secretions: functional alternatives to vertebrate paradigms. In: E. Chandler and N.A. Ratcliffe (eds.), *Mucus and related topics*: 337-366. Society for Experimental Biology Symposium XLIII.
- Downing, S.W., W.L. Salo, R.H. Spitzer and E.A. Koch. – 1991. The hagfish slime gland: a model system for studying the biology of mucus. *Science*, 214: 1143-1145.
- Drollet, J.H., T. Teai, M. Faucon and P.M.V. Martin. – 1997. Field study of compensatory changes in UV-absorbing compounds in the mucus of the solitary coral *Fungia repanda* (Scleractinia: Fungiidae) in relation to solar UV radiation, sea-water temperature, and other coincident physico-chemical parameters. *Mar. Freshwat. Res.*, 48: 329-333.
- Dudgeon, D. – 1994. The functional significance of selection of particles by aquatic animals during building behavior. In: R.S. Wotton (ed.), *The biology of particles in aquatic systems*, pp. 289-312. Lewis, Boca Raton.
- Ebran, N., S. Julien, N. Orange, B. Auperin and G. Molle. – 2000. Isolation and characterization of novel glycoproteins from fish epidermal mucus: correlation between their pore-forming properties and their antibacterial activities. *Biochim. Biophys. Acta - Biomembranes*, 1467: 271-280.
- Eiras-Stofella, D.R., P. Charvet-Almeida, E. Fanta and A.C.C. Vianna. – 2001. Surface ultrastructure of the gills of the mullets *Mugil curema*, *M. liza* and *M. platanus* (Mugilidae, Pisces). *J. Morphol.*, 247: 122-133.
- Elliott, J.K., R.N. Mariscal and K.H. Roux. – 1994. Do Anemonefishes use molecular mimicry to avoid being stung by host anemones? *J. Exp. Mar. Biol. Ecol.*, 179: 99-113.
- Flood, P.R., D. Deibel and C.C. Morris. – 1992. Filtration of colloidal melanin from sea water by planktonic tunicates. *Nature*, 355: 630-632.
- Forward, R.B. and D. Rittschof. – 2000. Alteration of photoreponses involved in diel vertical migration of a crab larva by fish mucus and degradation products of mucopolysaccharides. *J. Exp. Mar. Biol. Ecol.*, 245: 277-292.
- Grossart, H.-P., M. Simon and B. E. Logan. – 1997. Formation of macroscopic organic aggregates (lake snow) in a large lake: The significance of transparent exopolymer particles, phytoplankton, and zooplankton. *Limnol. Oceanogr.*, 42: 1651-1659.
- Häder D.-P. and E. Hoiczky. – 1992. Gliding motility. In: M. Melkonian (ed.), *Algal cell motility*, pp. 1-38. Chapman & Hall, New York.
- Hansson, L.A. and L.J. Tranvik. – 1997. Algal species composition and phosphorus recycling at contrasting grazing pressure: An experimental study in sub-Antarctic lakes with two trophic levels. *Freshwat. Biol.*, 37: 45-53.
- Hoiczky, E. – 2000. Gliding motility in cyanobacteria: observations and possible explanations. *Arch. Microbiol.*, 174: 11-17.
- Kappner, I., S.M. Al-Moghrabi and C. Richter - 2000. Mucus-net feeding by the vermetid gastropod *Dendropoma maxima* in coral reefs. *Mar. Ecol. Prog. Ser.*, 204: 309-313.
- Kelman, D., Y. Benayahu and Y. Kashman. – 1999. Chemical defence of the soft coral *Parerythropodium fulvum fulvum* (Forskal) in the Red Sea against generalist reef fish. *J. Exp. Mar. Biol. Ecol.*, 238: 127-137.
- Kepekay, P.E., D.K. Muschenheim and B.D. Johnson. – 1990. Surface coagulation and microbial respiration at a tidal front on Georges Bank. *Cont. Shelf Res.*, 10: 573-588.
- Klein, J.C.V. and P. Kooimen. – 1994. The possible origin of mucus jets used for immobilizing prey in species of *Euchirella* (Copepoda, Calanoida, Aetideidae). 1. Theoretical considerations in relation to swimming and feeding behavior. *Crustaceana*, 66: 184-204.
- Koch, E.A., R.H. Spitzer, R.B. Pithawalla and S.W. Downing. – 1991. Keratin-like components of gland thread cells modulate the properties of mucus from hagfish (*Eptatretus stouti*). *Cell Tissue Res.*, 264: 79-86.
- Koh, E.G.L. – 1997. Do scleractinian corals engage in chemical warfare against microbes? *J. Chem. Ecol.*, 23: 379-398.
- Kosuga, Y., N. Mano and H. Hirose - 2000. Bacterial agglutinins in the skin mucus of Japanese eel. *Fish Pathol.*, 35: 73-77.
- LaFee, S. – 2000. Meet me at the goo. *New Sci.*, 168: 44-47.
- Langer, M.R. and C.A. Gehring. – 1993. Bacteria farming – a possible feeding strategy of some smaller, motile Foraminifera. *J. Foramin. Res.*, 23: 40-46.
- Leppard, G.G. – 1995. The characterization of algal and microbial mucilages and their aggregates in aquatic ecosystems. *Sci. Total Environ.*, 165: 103-131.
- Liu, H.B. and E.J. Buskey. – 2000a. Hypersalinity enhances the production of extracellular polymeric substance (EPS) in the Texas brown tide alga, *Aureoumbra lagunensis* (Pelagophyceae). *J. Phycol.*, 36: 71-77.
- Liu, H.B. and E.J. Buskey. – 2000b. The exopolymer secretions (EPS) layer surrounding *Aureoumbra lagunensis* cells affects growth, grazing, and behavior of protozoa. *Limnol. Oceanogr.*, 45: 1187-1191.
- Lock, M.A. – 1994. Dynamics of particulate and dissolved organic matter over the substratum of water bodies. In: R.S. Wotton (ed.), *The biology of particles in aquatic systems*, pp. 137-160. Lewis, Boca Raton.
- Lyons, M.M., P. Aas, J.D. Pakulski, L. Van Waasbergen, R.V. Miller, D.L. Mitchell and W.H. Jeffrey. – 1998. DNA damage induced by ultraviolet radiation in coral-reef microbial communities. *Mar. Biol.*, 130: 537-543.
- Malmqvist, B., R.S. Wotton and Y. Zhang. – 2001. Suspension feeders transform massive amounts of seston in large northern rivers. *Oikos*, 92: 35-43.
- Margalef, R. – 1985. Introduction to the Mediterranean. In: R. Margalef (ed.), *Western Mediterranean*, pp. 1-16. Pergamon, Oxford.
- Mason, C.F. – 2002. *Biology of Freshwater Pollution*. Prentice Hall, Harlow, England.
- Morton, B. – 2000. The anatomy of *Callocardia hungerfordi* (Bivalvia: Veneridae) and the origin of its shell camouflage. *J. Molluscan Stud.*, 66: 21-30.
- Murray, A.G. – 1995. Phytoplankton exudation: exploitation of the microbial loop as a defence against algal viruses. *J. Plankton Res.*, 17: 1079-1094.
- Neu, T.R. – 2000. *In situ* cell and glycoconjugate distribution in river snow studied by confocal laser scanning microscopy. *Aquat. Microb. Ecol.*, 21: 85-95.
- Nozais, C., J.C. Duchene and M. Bhaud. – 1997. Control of position in the water column by the larvae of *Poecilochaetus serpens* (Polychaeta): The importance of mucus secretion. *J. Exp. Mar. Biol. Ecol.*, 210: 91-106.
- Pain, S. – 2000. Slime scene. *New Sci.*, 2229: 35-37.
- Peduzzi, P. and G.J. Herndl. – 1991. Mucus trails in the rocky intertidal: a highly active microenvironment. *Mar. Ecol. Prog. Ser.*, 75: 267-274.
- Plagányi, É.E. and G.M. Branch. – 2000. Does the limpet *Patella cochlear* fertilize its own algal garden? *Mar. Ecol. Prog. Ser.*, 194: 113-122.
- Plante, C.J. and A.G. Shriver. – 1998. Differential lysis of sedimentary bacteria by *Arenicola marina* L.: examination of cell wall structure and exopolymeric capsules as correlates. *J. Exp. Mar. Biol. Ecol.*, 229: 35-52.
- Ruppert, E.E. and R.D. Barnes. – 1994. *Invertebrate zoology*. Saunders, Fort Worth.
- Smetacek, V. and F. Pollehne. – 1986. Nutrient cycling in pelagic systems: a reappraisal of the conceptual framework. *Ophelia* 26: 401-428.



- Stachowitsch, M., N. Fanuko and M. Richter. – 1990. Mucus aggregates in the Adriatic sea: An overview of stages and occurrences. *P.S.Z.N.I: Mar. Ecol.*, 11: 327-350.
- Taylor, J.D., E.A. Glover and C.J.R. Braithwaite. – 1999. Bivalves with 'concrete overcoats': *Granicorium* and *Samarangia*. *Acta Zool. (Stockholm)*, 80: 285-300.
- Thornton, D.C.O., D. Santillo and B. Thake. – 1999. Prediction of sporadic mucilaginous algal blooms in the Northern Adriatic Sea. *Mar. Pollut. Bull.*, 38: 891-898.
- Wotton, R.S. – 1976. Evidence that blackfly larvae can feed on particles of colloidal size. *Nature*, 261: 697.
- Wotton, R.S. – 1994. Methods for capturing particles in benthic animals. In: R.S. Wotton (ed.), *The biology of particles in aquatic systems*, pp. 183-204. Lewis, Boca Raton.
- Wotton, R.S. – 1996. Colloids, bubbles and aggregates - a perspective on their role in suspension feeding. *J. N. Am. Benthol. Soc.*, 15: 127-135.
- Wotton, R.S. – 2002. Water purification using sand. *Hydrobiologia*, 469: 193-201.
- Wotton, R.S. and B. Malmqvist. – 2001. Feces in aquatic ecosystems. *BioScience*, 51: 537-544.
- Zalasiewicz, J. and K. Freedman. – 2000. The dawn of slime. *New Sci.*, 2229: 30-33.

[Illustration material to support this article can be found as links in the Internet Book "Life in Water" published by R.S.Wotton at <http://www.ucl.ac.uk/~ucbt212>.]

