

PATHWAYS FOR THE UPTAKE OF DISSOLVED ORGANIC MATTER (DOM) BY AQUATIC ANIMALS

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Introduction

Life on Earth began after biochemical changes in, and the aggregation of, some of the dissolved organic materials (DOM) in the earliest seas. With time, the aggregations of molecules developed an integrity, the ability to copy themselves, and thus life appeared. The earliest organisms had a simple structure and, before the evolution of photosynthesis, energy for growth will have been obtained across cell walls from the pool of DOM in the water. After death, their contents will have been released back

into the water to maintain cycling through trophic pathways. Some organisms are probably little changed in structure and metabolism from these ancient times, and exist successfully today; others, however, continued to evolve, bringing the advantages of increasing multicellularity, viz. larger size and greater complexity.

The invasion of fresh waters by organisms brought similar mechanisms for processing DOM to those found in the ancient seas but, because the chemical environment of fresh waters is very different, some methods of acquiring DOM that are common in marine habitats are less common in lakes and rivers. For this article in *Freshwater Forum*, I will describe pathways occurring in freshwater habitats, but it is not possible to discuss these without making reference to the pathways found in the marine environment. It is not my intention to write a comprehensive review article so only a few (of many) pertinent references will be cited.

A cross-disciplinary approach is not often made by aquatic biologists as marine plants and animals (often the biota most studied) appear to be very different from their freshwater equivalents, though their functional roles may be quite similar. With the increasing use of information databases, more communication between the two major branches of aquatic biology will be possible, and advantageous.

What is dissolved organic matter (DOM)?

For many aquatic biologists, DOM is defined operationally as all the organic compounds which pass through a filter of pore size 0.45 μm , those retained on the surface of the filter being particulate organic matter (POM, often further identified into fractions of differing particle size). Using this operational, but arbitrary, separation, DOM therefore includes colloids and other particles (some living) and a wide range of hydrophobic chemicals in addition to those which are in aqueous solution. To add a further complication, some DOM can become trapped on the pores of filters used to make the separation of the two pools of material (Johnson & Wangersky 1985). In addition, if water samples for analysis are shaken, the proportion of POM can change as a result of particle formation, or disruption.

Some fractions of DOM are resistant to breakdown and remain apparently unaltered in water-bodies for long periods, perhaps years - humic compounds are examples. They are derived from plants, especially those parts which are used in strengthening, a function which may contribute to their resistance to decay. Anyone who has visited moorland streams, or bog pools in peat, will have been impressed by their dark colour, the result of staining by humic acids. This colouration creates "blackwater" rivers such as those of the sandy coastal plain of the southeastern U.S.A., where drainage is from adjacent marshes. Some

lakes in areas with large-scale peat deposits are similarly very darkly coloured, e.g. those in parts of Finland.

In contrast to these apparently refractory compounds, other fractions of DOM are rapidly utilized and transformed by the biota, especially by heterotrophic bacteria. Simple sugars and amino acids, for example, are readily taken up and used for metabolism or growth, and are examples of a labile fraction. This fraction is characterized by compounds of low molecular weight while refractory DOM typically contains those of high molecular weight.

Many studies investigate specific fractions of the DOM pool; examples of some of the components measured are given in Table 1. The extent to which one or more of these components are measured will depend on the needs of each study, and this can make comparison between studies difficult. The commonest measures are of total DOM by dry mass and dissolved organic carbon (DOC) determined using carbon analysers.

TABLE 1. Commonly-measured fractions of total dissolved organic matter (DOM): the choice taken by investigators will depend on the purpose of the study, and the techniques to be employed.

Total dissolved organic matter (DOM)
Dissolved organic carbon (DOC)
Dissolved organic nitrogen (DON)
Dissolved organic phosphorus (DOP)
Dissolved free amino acids (DFAA)
Total amino acids
Protein
Carbohydrate
Lipid
Volatile fatty acids
Non-volatile fatty acids
Aldehydes
ATP
Identification of individual organic compounds.

What are the sources of DOM in fresh waters?

DOM is produced within a water-body (described as being an autochthonous input) or can enter a water-body from the terrestrial environment (described as being an allochthonous input).

Some allochthonous DOM enters rivers and lakes in the rain falling directly on to the water (a continuing echo of major primaeval input). Rainfall also causes DOM to be washed into water-bodies as a result of drainage through surface runoff and through discharge from the water table. The drainage water picks up DOM from terrestrial matter and from temporarily static films of water which become incorporated into the larger flows that follow precipitation. Water percolating to the water table will also pick up DOM as it descends through soil profiles.

Runoff after rainfall also carries allochthonous POM into rivers and lakes and this source, together with wind-blown material, has been of considerable interest to biologists investigating rivers which have deciduous woodlands in the upper part of their valleys. The seasonal input of leaves into these rivers, their conditioning by fungi and bacteria, and the subsequent reduction in size of the particles generated have been investigated by many biologists. Before, and during, conditioning the process of leaching occurs with water-soluble inorganic and organic materials present in dead matter passing out into solution. Research on the fate of allochthonous DOM and POM has led to the development of holistic models of river systems, the best known of which is that of the River Continuum Concept (Vannote et al. 1980).

Clearly, while DOM leached from leaves falling into the water is of importance in streams with wooded valleys, the open expanse of water found in most lakes makes DOM leached from terrestrial leaf fall of lesser significance in these water-bodies. It can have importance around the littoral margins (the site of greatest biological activity) and it may be a large input to small lakes and pools, as can be seen from the amount of leaf litter which builds up in shallow recreational ponds in parks. A more characteristic input of DOM to lakes and pools will be from decomposition of the macrophytes and planktonic organisms of the littoral margins, or elsewhere within the photic zone. While these plants must necessarily be resistant to leaching while alive, their decomposition after death will result in supplies of both DOM (and POM) to the surrounding water.

An important source of autochthonous DOM in all water-bodies comes from the production of exudates and secretions by living organisms. As a result of metabolic processes, the biota produce compounds which pass across their cell/body walls, or are excreted to the surrounding water. Many of these compounds are labile and they are often rapidly utilized by heterotrophs.

Diel, seasonal and local patterns of occurrence of DOM

As we have seen, there are several sources of DOM in fresh waters and their abundance will often be affected by diel or seasonal events. Almost all plants use light energy in photosynthesis, and biochemical processing of generated compounds occurs during darkness. As a result, the exudates produced by plants vary quantitatively through a 24-hour cycle depending on the diel light regime. DOM released during feeding by aquatic animals may also show diel variations, though this will be a minor factor in comparison with the diel cycle of production of plant exudates, the biomass and production of animals normally being much less than that of plants.

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Just as the light regime changes through a 24-hour cycle so there are seasonal changes in all but a narrow band of latitude around the Tropics; the further towards the Poles a water-body is situated the more marked is the seasonal change in light intensity. In many temperate and polar regions there are seasons when the growth of plants is inhibited by lack of light and this also has an indirect effect in that temperature is lower, having a major influence on the rate of metabolism and thus the amount of DOM generated. At the end of a growing season die-back occurs and this is often the time when there is the greatest input of POM and DOM from dead plants (and animals?).

Another seasonal effect comes with the meteorological changes: if there are rainy seasons, for example, these will be times of considerable input of DOM from terrestrial sources though, if the input is to rivers, much of this may be swept downstream by resulting spates. Even in normal river flows there is a considerable export of DOM to estuaries, though the influence of these exports on the oceans is probably minor for all but the largest rivers (e.g. Cai et al. 1988).

There can be large differences in the abundance of DOM within very small regions of a water-body and this is also something which needs to be taken into account when the role of DOM in trophic dynamics is being considered. Smith (1986) has shown that there can be marked changes in DOM concentration over distances of a few metres and this would be expected when DOM is derived from many, heterogeneously distributed sources. Phytoplankton, heterotrophs, dead POM and DOM can become aggregated to provide a concentration of activity in an otherwise nutrient-poor medium. This, and many other features of detritus biology, is discussed in a stimulating paper by Mann (1988).

Direct uptake of DOM by animals

DOM can be taken up directly by animals by transfer across the body wall. This method of uptake is largely confined to marine habitats (or to internal parasites) as freshwater animals must minimize the incursion of water across the body wall by reducing its permeability. Direct uptake of DOM has been a topic of study since the beginning of this century and has been widened as the whole range of methods by which DOM is acquired by animals has been explored (see the comprehensive review by Jørgensen 1976).

Some marine animals appear to depend on the direct uptake of DOM, an example being the fan worms (Pogonophora) which do not have a functional gut. The direct uptake of DOM has been recorded in many Phyla but probably contributes only a small amount of the total organic uptake necessary for maintenance and growth. Although freshwater animals must prevent the excessive incursion of water across their body

wall, there is some evidence of direct uptake of DOM, for example in caddis larvae (Nilsson & Otto 1981) and molluscs (Efford & Tsumura 1973; Thomas et al. 1990).

DOM from ingested food

Animals which pass large quantities of water containing DOM through their feeding apparatus will pick up some DOM by adsorption on to its surface and this can be ingested after cleaning. Mucus, associated with the feeding organs of some aquatic insects, has good adsorption properties for DOM and this will increase the uptake, though the mass of DOM ingested will be small compared to that of POM.

Living or dead POM is the predominant diet of freshwater animals. Particles are either captured and ingested whole, or broken up by mouthparts where these are present (contributing small POM and DOM to the water column as a result of the delightfully-termed "messy eating" shown, for example, by some zooplankters). Once ingested, food particles are subjected to a variety of treatments within the gut to break them down. These are often a combination of the effect of strong acids or alkalis in hydrolysis and the action of digestive enzymes breaking up linkages between large molecules, thus releasing smaller molecules of DOM for transfer across the gut wall. When viewed in this way it is clear that all animals are feeding on DOM but this can only result after digestion has caused the break-up of POM and the "particulate fraction" of DOM (Fig. 1).

Those ingested particles which are not broken down by chemicals secreted by the animal, and/or by physical break-up using the mouthparts and other gut structures, can be attacked by microorganisms which may be ingested with the food, or are symbionts living within the gut. Investigations of the hind-gut wall of a detritivorous aquatic insect reveal that there is a well-developed resident gut flora (Klug & Kotarski 1980) and these symbionts probably play an important role in nutrition. Symbiotic microorganisms can take up DOM and transform it, thereby perhaps making altered DOM available to the host animal. Similarly, enzymes secreted by the ingested microflora assist in the breakdown of POM to DOM in the gut; this is then absorbed across the gut wall, or taken up by the symbiotic microbiota. This is an area of nutrition which needs to be investigated more widely.

In studies of crustacean zooplankton, Porter (1985) has shown that ingested gelatinous algae can pass through the gut relatively little affected by the processes of digestion: a sizeable proportion of ingested epilithic diatoms is also known to survive passage through the gut of grazing caddisfly larvae (Peterson 1987). Although they can be resistant to break-up, algae passing along the gut are exposed to an alien chemical

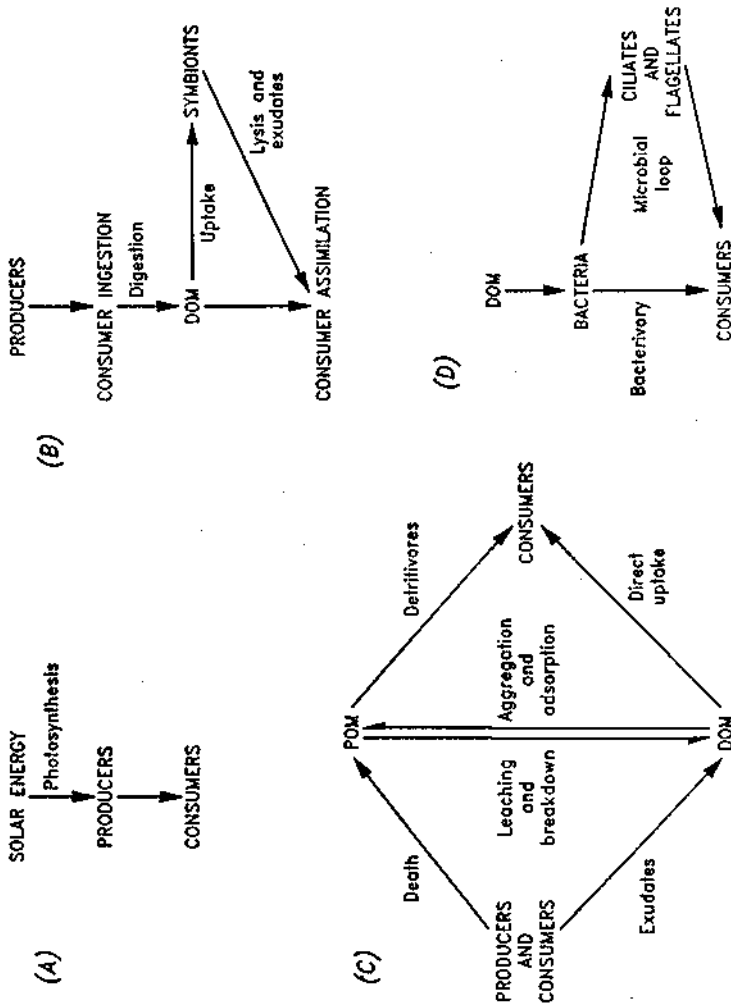


FIG. 1. Some trophic pathways: (a) a very simplified "conventional" trophic pathway; (b) a simple trophic pathway incorporating digestive processes within the gut of a consumer; (c) some pathways linking DOM, POM, producers and consumers; and (d) pathways of DOM through bacteria and the microbial loop.

environment and the "stress" which this creates may result in the release of exudates which can then be utilized by the consumer. Algae can thus provide a direct source of food when they are broken up, or an indirect source, the passage of survivors through the gut subjecting them to conditions that magnify the natural process of producing exudates.

There are advantages to animals in not killing all their live ingested food. If some food organisms can survive passage through the gut, they can be re-ingested at a later stage when more exudates will be produced, the cell contents having been replenished after egestion. It will be interesting to see if this is a common event, and what conditions must pertain to allow survival of algae other than those with gelatinous coats (and whether the latter produce exudates to any degree). Unfortunately, this trophic pathway is difficult to study since a radiotracer label would be incorporated into the animal's body tissues when an alga is broken up and assimilated, but also when it survives but produces exudates (containing radiotracer) which are then absorbed.

Just as some algae are seen to pass through the gut of freshwater invertebrates so do some bacteria, perhaps as many as 40-50% (Baker & Bradnam 1976). The bacteria that pass through the gut might also produce exudates in the altered chemical environment of the animal's gut and the arguments put forward above for the contribution of algal exudates to nutrition may also be made for bacteria. In addition, heterotrophs, which utilize extracellular enzymes, will be packed in close proximity to food items and thus increase the likelihood of breakdown of these materials. Clearly, an animal that can harbour symbionts, ingests heterotrophs, has the ability to utilize acidic or alkaline hydrolysis, and uses digestive enzymes, possesses a suite of methods to enhance the liberation of DOM within the gut, and allow for its uptake, and thence its utilization in growth and metabolism.

Another function of pronounced changes in pH within the gut may be in releasing DOM which has become adsorbed on to surfaces in the environment. For example, does the DOM adsorbed on to mucus and particles remain there once these are ingested, or can it be released? Does the re-ingestion of faecal material result in a higher efficiency of utilization of foods by allowing longer exposures of some heterotrophs to their substrates in conditions that suit breakdown?

Transformed DOM

There are a number of ways in which DOM is transformed before ingestion, in addition to its direct utilization by animals. To what extent the rapidly-utilized fractions of the DOM pool are involved in these processes remains to be seen, but refractory DOM may be more easily broken down when formed, for example, into aggregations that include

heterotrophs. Bacteria are involved in all three of the processes described in this section and, if not directly promoting aggregation or adsorption, they certainly colonize aggregates and may aid in adsorption by altering the physico-chemical nature of the surface of existing particles.

(i) *Ingestion of DOM by bacteria and the "microbial loop"*

As already discussed, DOM is taken up by heterotrophs and transformed into microbial tissue; any animal which then feeds on bacteria will be indirectly feeding on the DOM. Similarly, dissolved nutrients taken up by plants and transformed into plant tissue will be taken up by herbivores. Animals, such as protozoans, that ingest bacteria may themselves be eaten by other animals and this has led to the concept of the "microbial loop" (Azam et al. 1983) (Fig. 1). On the face of it this represents a key mechanism whereby DOM can be returned to trophic pathways, but the efficiency of the microbial loop in aquatic systems may be low. Certainly, as the number of connections within a food web increases, the amount of energy that is transferred across these connections decreases as energy is lost in partial assimilation and in respiration.

There is some debate on the importance of the microbial loop. Ducklow et al. (1986), in an experiment in a sea loch, found that little DOM found its way through the microbial loop to higher consumers, though their study has been criticized by Sherr et al. (1987) for being a single experiment in a habitat atypical of much of the sea. In lakes with heavy loadings of humic compounds, microflagellates may form the dominant food of zooplankton and Salonen & Hammar (1986) suggest three trophic pathways involving this link. Zooplankters can ingest microflagellates which (i) grow autotrophically, (ii) grow heterotrophically by ingestion of bacteria, or (iii) grow heterotrophically after feeding directly on transformed DOM. The DOM - bacteria - protozoan - metazoan loop may also be an important trophic pathway in blackwater rivers (Carlough & Meyer 1990), the lotic equivalent of humic-rich lakes.

Debate on the significance of the microbial loop has centred on whether the pathway by which DOM passes to bacteria is a "link" to higher trophic levels or whether it is a "sink" leading either to sedimentation, or to respiration of carbon dioxide from the water-body. It is, of course, both a link and a sink and the extent to which it is either will depend on the type of water-body, its trophic status, the concentrations of the biota, and seasonal events. It will be interesting to see just how important microbial loops are in a wide range of aquatic systems, though one of the problems facing investigators may be how to identify ingested Protozoa, these being so easily broken up.

(ii) *Aggregation processes*

Leached DOM can be transformed into particles (e.g. Camilleri & Ribi 1986) and aggregation will also occur between the fractions of "DOM" which are more obviously particulate in nature. There will also be aggregation between DOM and small-sized POM to produce larger aggregates. Whatever their origins, aggregates will be ingested by detritivores. Laboratory, and field, experiments have identified many mechanisms by which particles can be formed and these include changes in pH, changes in salinity (important for the formation of aggregates in estuaries), changes in calcium ion concentration, the effect of turbulence, and the effect of collapsing bubbles which have coatings of hydrophobic compounds. These mechanisms have been outlined by Wotton (1984) and by Johnson et al. (1990). In essence, the process of aggregate formation, and subsequent ingestion by detritivores, forms a parallel to the "microbial loop" as a means of readmitting DOM to trophic pathways (Fig. 1).

Bacteria help in maintaining the integrity of particles formed by aggregation and this also locks them to potential substrates (some aquatic scientists believe that bacteria are essential for particle formation). Exudates of polysaccharides from bacteria can form adhesive bridges between the fractions of an aggregate, and the polysaccharide fibrils found free in the water (resulting originally from bacteria) will also aid in binding. In addition, the exudates may carry a charge which favours adsorption of dissolved organics, so the aggregate can be enriched after it has been formed by whatever initial process was responsible. Aggregated particles are thus rather like living particles in that they will take up materials from within the water column and also pass them out. In oceans the flocs that form by aggregation can be very large (centimetres in diameter) and this "marine snow" may serve as a means of transport of organic material (and its associated biota) around the surface waters. The flocs are highly enriched with heterotrophs (Caron et al. 1982) and cause increased activity in the water surrounding the floc (Herndl 1988).

In fresh waters the particles formed by aggregation of fractions of DOM and small-sized POM are, at most, tens of micrometres in diameter, and usually very much smaller in size. If loosely consolidated, they are easily disrupted again, and estimating their abundance in natural waters presents difficult sampling problems as a result. Some particles formed from DOM, however, appear to be robust (see the photographs in Pomeroy 1980) and these flakes have been shown to be a source of food for animals (Camilleri & Ribi 1986).

That aggregation of DOM occurs within regions of turbulent flow was demonstrated by Petersen (1986) and it will be interesting to see just

how important these aggregates are in the nutrition of the particle feeders that abound where there is a high level of turbulence adjacent to regions of calmer water (e.g. at lake outlets or over the rocky/stony littoral of lakes and the sea). Certainly animals at these locations are able to ingest surface film (Wotton 1982) and this may be a good source of food at periods of the life cycle if, for example, fatty compounds are required for the development of reserves. It is not known whether these compounds enter as small particles but the hydrophobic nature of many surface film components (Hermansson 1990) cause them to coat bubbles. The impaction of bubbles on feeding organs, with retention on charged surfaces, is a likely mechanism whereby these organic compounds are retained, and then ingested.

(Hi) Adsorption processes

Particles (both inorganic and organic) within the water column may pick up coatings of DOM from the surrounding water and this will be dependent on attractant properties of the particles (charge and chemical nature). It is probable that some particles, or some sites on particles, have a greater attractant property than others which may, as a result, have little or no coating of DOM. This is an area which is now receiving considerable research interest, especially with the need to develop attractant surfaces for harmful dissolved organic compounds such as pesticides. Animals which ingest particles may strip away coatings of DOM and POM, though the extent to which this material is utilized in nutrition, and whether it is present in anything but small amounts, are not known. It should be borne in mind that animals ingesting large quantities of small particles will have a considerable surface area of potential substrate available for digestion.

Just as polysaccharides produced by free-living bacteria cause adsorption of DOM so do the polysaccharides generated by bacteria contributing to the biofilm characteristics of shallow benthic habitats (the structure and function of biofilms have been well described by Lock 1990 and Lock et al. 1984). DOM leached from leaves falling into the water, and that from other sources, is taken up by the community of microorganisms living over the substratum of streams (Lock & Hynes 1976; Lush & Hynes 1978) by direct adsorption, and after flocculation and sedimentation, thus preventing it being washed downstream. This is important as leaf leachates may form a major seasonal input of energy to support trophic pathways and, after microbial transformation of these compounds, the accumulating biofilm is available to consumers. These will be of the scraper functional feeding group (Cummins 1973), not the particle collectors feeding on suspended aggregates, so different parts of the complex food web are involved. It would be intriguing to calculate

what proportion of the DOM in streams is processed through the benthic biofilm to consumer pathway and how much is processed through the suspended aggregate to consumer pathway. We also need to find out how important these pathways are when compared with the direct consumption of detritus particles, free-living bacteria, benthic and planktonic plants and animals.

DOM as an attractant and repellent

Some living particles (e.g. blue-green algae) may release dissolved organic compounds which are distasteful, providing a protection against their ingestion, or causing regurgitation if the algae are ingested.

The exudates of other plants provide cues by which they are detected by herbivores, producing an "aura" which can be detected by the sense organs of feeding animals (see the review by Vanderploeg 1990). For example, it is probable that some zooplankters are able to identify suitable food particles before they physically encounter them (if one assumes that the aura is not physically associated with the particle). The coating of particles has also been shown to be important once a particle is encountered; animals as diverse as zooplankters and marine benthic polychaetes, for example, can be made to feed on plastic beads which have an organic coating (Taghon 1982; DeMott 1986).

Some predators use olfactory stimuli (as opposed to tactile or visual ones) to detect the DOM emanating from their prey. Spacing between organisms can also be facilitated by sensing metabolic by-products of neighbours, though the extent to which this mode of spacing occurs relative to those of physical or visual contact remains to be thoroughly investigated.

Some conclusions and speculations

The earliest forms of life will have taken up DOM across the cell wall and this remains a process which continues in primitive organisms today. With the development of higher levels of organization, particles were taken into the body through an aperture in the cell wall (perhaps temporary in nature) and ingested particles were of living, or dead, cellular origin, or aggregates of DOM, a method retained by contemporary protozoans. With the evolution of photosynthesis came the ability to generate energy within living particles and their higher food value meant that some animals evolved selective herbivory. The evolution of selective carnivory then brought the benefit of a diet rich in proteins and other building chemicals, though this was compensated by a decrease in general availability of food items compared to the availability of plants or detritus. Animals that lacked the ability to be selective

continued with a diet consisting of particles of many sources, and may have had reduced competition with other metazoans for their food as a result. They also retained a digestive system, or feeding strategy, adapted to a diet of mixed quality.

The food, whether living or dead, will have a variety of DOM associated with it as a result of exudate production, microbial associations, etc. and we need to find out just how important all the DOM sources reviewed in this article are in nutrition: it may be minor, we do not know. Unfortunately, many experimental techniques do not allow the accurate delimitation of the trophic role of DOM as this presents problems with scaling effects, and accurate means of measurement of processes. The complexity of food webs in most aquatic systems also needs to be understood, as individual components of webs can change the type of food which they ingest over short time periods. This will influence the amount of DOM from the various sources that will be ingested and utilized, something which is dependent on gut retention time, and thus further dependent on temperature, quantity of food available and also on a range of other environmental variables (Wotton 1990). Any model must take this variability into account.

We also need to define what we mean by "refractory". Detritus particles and POM considered as being refractory are digested and utilized by animals with, and without, the aid of symbionts (Fong & Mann 1980; Kreeger et al. 1988; Mann 1988; Pomeroy & Wiebe 1988). "Refractory" DOM may be easier to attack than "refractory" POM, especially when it is aggregated and embedded within mucus. Does this provide an explanation of why mucus is found on the mouthparts of some insects and is then ingested when these mouthparts are cleaned? And why do such insects (blackfly larvae), and bivalve molluscs (with mucous coatings over the gills), show such high levels of production (Wotton 1990) at sites where particles are formed from DOM? It may, of course, be a coincidence as these sites - lake outlets and estuaries, respectively - are rich in particles of many types and have good delivery systems to transport them to the particle feeders. There are clearly many questions which are awaiting answers.

If large quantities of DOM pass to a sink which cannot be readily utilized by metazoan animals, we have lost a very abundant resource (at least DOM is generally abundant in some systems, and locally abundant in others). If we can find a means of more efficiently harnessing this energy source for the growth of metazoans there are potentially high commercial dividends to be obtained. Perhaps a first step in the link will be to use cultured heterotrophs selected for their ability to attack "refractory" compounds. But how are these heterotrophs to be selected: would genetically engineered organisms provide an answer?

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