the flow field. In particular, the amount of local shear or deformation contains information about the slant and tilt of surface patches. Deformation could be extracted or computed by detecting the changes in orientation of local line segments, without the need to detect motion *per se*. The oriented receptive fields found in the primary visual cortex of cat and monkey could well be involved in computing surface slant and structure from image flow in this way[10].

Higher-order shape characteristics, such as the curvature of surfaces, could also be detected using the local deformations in the flow fields generated when an observer moves with respect to a three-dimensional surface. The second spatial derivative of the flow field (the change of motion gradient across space), created by a curved three-dimensional surface, has the interesting characteristic that it does not change with the viewing distance to the surface (my own work). To extract the motion curvature in the flow field, the visual system would not necessarily have to differentiate the velocity field twice with respect to space (which sounds a rather unlikely biological operation). Instead, motion curvature could be computed by detecting the changes in the curvature of local line segments in the image, which has the advantage of being both more plausible from a biological point of view and more accurate than computations based on velocity vectors. At present, these ideas are speculative, but the potential for investigating these and other problems using psychophysical, physiological and computational techniques is a reason for optimism. □

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Oceanography

Effects of microbe activity

Erwin Suess

ORGANIC matter exists in many forms in the oceans — as detritus and microbes, which can be suspended or sinking, and also as dissolved organic matter. The way these pools interact is influenced by, and influences, the distribution of nutrients and oxygen dissolved in the water column. One point of current interest is the fate of large sinking phytodetritus particles and their interaction with microorganisms in the ocean's interior and at the sea floor. In two papers recently published in *Nature*, Karl *et al.*[1] and Cho and Azam[2] show that microbial activity on sinking phytodetritus decreases with depth and is minimal below 2,000 m in the ocean. On the other hand, on page 67 of this issue[3], Lochte and Turley show that phytodetritus, once it has reached the sea bed, hosts vigorous microbial activity.

The resolution of these contrasting results bears on several important issues in marine science. One long-standing problem is that the downward flux of sinking organic particles decreases with increasing depth. What is the fate of the lost particles? To what extent are they broken up into smaller suspended particles or else remineralized by microbes, releasing carbon dioxide and soluble nutrients, consuming oxygen in the process? Another problem concerns the microbial activity at and near the sea floor. This process can affect the local oxygen distribution and that mixed into the water column above, having consequences for palaeo-oceanography and ocean chemistry.

Lochte and Turley[3] demonstrate in this issue that large, fresh particles of phytodetritus recovered from the sea floor at 4,500 m depth in the north-east Atlantic are populated by heterotrophic bacteria, cyanobacteria and microflagellates (Fig. 1). The nutritious host particles must have arrived at the deep-sea floor only shortly before they were sampled because the cells of cyanobacteria, photosynthetically supported picoplankton that inhabit surface waters in summer, remain intact. The microbial population on the recovered detritus flourished when incubated under simulated deep-sea and shallow-water

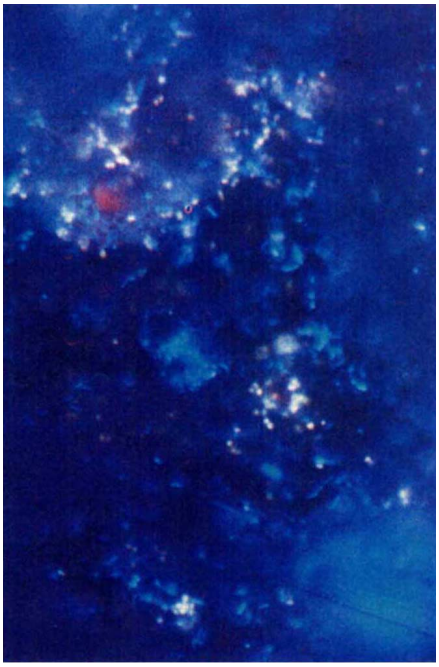

Fig. 1 Cyanobacteria (red) and non-pigmented bacteria recovered from the sea bed. (Photo courtesy of K. Lochte and C.M. Turley.)

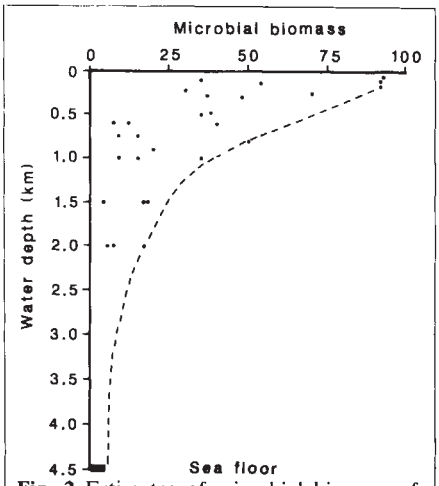

Fig. 2 Estimates of microbial biomass of fast-sinking, organic particles in the ocean[1,2] and at the sea floor[3] as weight per cent of total detritus.

conditions. Its respiratory activity and the rates at which it converted carbon into biomass affected the chemistry and mass of the entire suspended-particle pool. The rate of carbon respiration during the experiment simulating deep-sea conditions indicates that phytodetritus from the sea surface would be consumed within two months of settling on the sea floor.

Microbial populations attached to sinking particles in the water column and estimates of their biomass have been reported before. Biomass estimates from the north-east Pacific, reported by Karl *et al.*[1] and Cho and Azam[2], extrapolated down the oceanic water column, give a distribution of microbial biomass decreasing with depth to reach the sea-floor value found by Lochte and Turley[3] (Fig. 2). This distribution is at odds with the rapid rates of decomposition observed by Lochte and Turley. Karl *et al.* trapped sinking organic particles in the top 2,000 m of the ocean. The microbial population in these consistently died during *in situ* incubation experiments, despite the nutritious environment provided by the host particles.

How then is it possible that the microbial population attached to particles recovered from the sea floor is so unusually active? The incubation experiments provide an interesting possible explanation. The activity of the cyanobacteria initially attached to the particles at the sea surface lasted only a few days, whereas the high activity of heterotrophic bacteria was sustained for the duration of the experiment. Could it be only after the phytodetritus reaches the sea floor that the specialized barophilic heterotrophs populate the particles? These heterotrophs would be better able to use the nutritious detritus than the attached cyanobacteria. Particles recovered from the water column by trapping[1], of course, could not have been populated by sea-floor microbes. Clearly, the mechanism of decomposition at the sea floor is not merely an extension of that

in the water column.

The rapid response of the deep-sea microbes has consequences for palaeo-oceanography. At the same north-east Atlantic site where the microbe-containing particles were collected, certain species of rare benthic foraminifera populated the freshly arrived phytodetritus in great abundance[4]. These species are specially adapted consumers feeding opportunistically as others remain unaffected by the organic influx. Hence, the abundance pattern of benthic foraminifera would be a direct reflection of the organic influx. Also, their habitat would become enriched in metabolic carbon dioxide from respiratory consumption. These conditions could be recorded in the species' assemblages[5] and the stable carbon isotopes of their calcareous shells[6].

The deep-sea floor along productive continental margins has been identified by respiration data[7] as the main site of oxygen consumption in response to organic influx. Previous models of the oxygen distribution, based largely on fast-sinking particle fluxes, favoured the shallow water column as the site of high consumption. The new concept implies that bottom water, after having its oxygen extracted by the adjacent sea floor and being advected laterally, could control the oxygen and nutrient chemistry of the ocean's interior. These studies[4-7] show that the rapid turnover of phytodetritus at the sea floor is the key process.

The low microbial activity observed by Karl *et al.*[1] also throws light on the reduction of the flux of sinking organic particles. These particles are poor hosts to attached microbes, which therefore cannot be responsible for the lost flux, as was previously thought. Instead the sinking particles probably disaggregate before free-living microbes turn the suspended fragments into soluble nutrients.

This notion agrees with Cho and Azam's observation[2] that most of the suspended organic matter in the upper ocean is bacterial. (Specifically, they find that 90 per cent of the surface area of suspended particles is on microbes.) Additional evidence of free-living microbes in the water column comes from Wakeham[8] who shows that suspended particles are associated with fresh, unaltered steroids typically found in living organisms, whereas sinking particles are associated with steroids altered by extracellular degradation. □

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Transposition immunity

Action at a distance

Neville Symonds

THE biggest revolution in our thinking about genetics in recent years has been the belated acceptance of the idea first proposed by Barbara McClintock in the 1940s, that there are small genetic elements which can move from one location to another within the genomic DNA present in cells. These mobile elements, now called transposons, have been identified in bacteria, fungi, insects, plants and animals, and shown to be responsible for effects ranging from the spread of antibiotic resistance in bacteria to the onset of cancer in animals. An unexpected observation noted over 10 years ago with bacterial transposons was that insertion of a bacterial transposon into a plasmid (a small circular DNA molecule) within a cell was severely inhibited if the plasmid already contained a copy of the same transposon[1]. This phenomenon, called transposition immunity, was first reported for the transposon Tn3, and has since been found in other members of that family, in Tn7 and in phage Mu (refs 2–4). An intriguing feature of transposition immunity is that a single copy of the transposon located at a site within the plasmid can inhibit the insertion of another copy at sites up to 50 kilobases (kb) away[5]. A paper by Adzuma and Mizuuchi[6] in the 22 April issue of *Cell* gives the first clear account of the biochemical basis underlying an example of transposition immunity, and in so doing opens up ways of investigating this 'action at a distance' aspect of the phenomenon.

Transposons become inserted into new locations in genomes by a special type of recombination process in which specific enzymes (transposases) recognize and bind to unique sequences present at each end of the transposons. Plasmids occur naturally in bacteria and are transferred from one cell to another during bacterial conjugation. They provide the vehicles by which transposons, many of which carry determinants conferring resistance to antibiotics, spread through bacterial populations and are able to establish themselves in new bacterial strains.

There is now general agreement on some aspects of the phenomenon of transposition immunity[1-6]. It has become clear that it is not caused by the inability of the plasmid to carry more than one copy of a particular transposon as plasmids containing more than one copy can easily be made. The immunity must therefore result from a block in the successful completion of the transposition cycle. It is also clear that immunity is not dependent on a complete transposon being present within the target. The essential factor is that there is a binding site for transposase. Further, immunity of several orders of magnitude can be obtained with target molecules of up to 100 kb in length. Just a few molecules of transposase located at a single site in a molecule therefore determine the immunity.

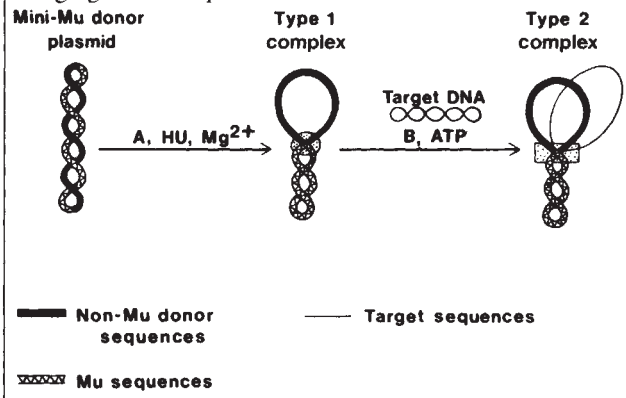

Fig. 1 Steps in the strand-transfer reaction.

Before I describe the new work of Adzuma and Mizuuchi, I shall review briefly what is now known about the molecular nature of transposition in the bacteriophage Mu, as deduced from *in vitro* experiments[7]. The key step in this transposition is one of strand-transfer, leading to the formation of a branched DNA molecule in which the 3′ termini of Mu DNA are joined to the 5′ termini of a 5-base-pair staggered cut in the target DNA (ref. 7). A defined *in vitro* system that efficiently supports this reaction is now available. It consists of Mu A protein (the transposase), Mu B protein (a non-specific DNA-binding protein which is also an ATPase), *Escherichia coli* HU protein (a histone-like protein), ATP and Mg^{2+}. Into this milieu are introduced small circular donor and target DNA molecules, the donor containing a mini-Mu derivative of phage Mu[7,8].

Two steps have now been identified in the strand-transfer reaction[9,10]. In one, the Mu A protein binds to the Mu end sequences and with the HU protein introduces specific nicks at the termini of the Mu DNA, so leading to the formation of a stable type 1 complex in which the Mu ends are held together by protein. In the second, this type 1 complex interacts with target DNA in the presence of Mu B protein and ATP to complete the strand-transfer reaction and form the branched type 2 complex.