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THE NINTH TANSLEY LECTURE*

What can ecologists learn from microbes: life beneath a square centimetre of sediment surface

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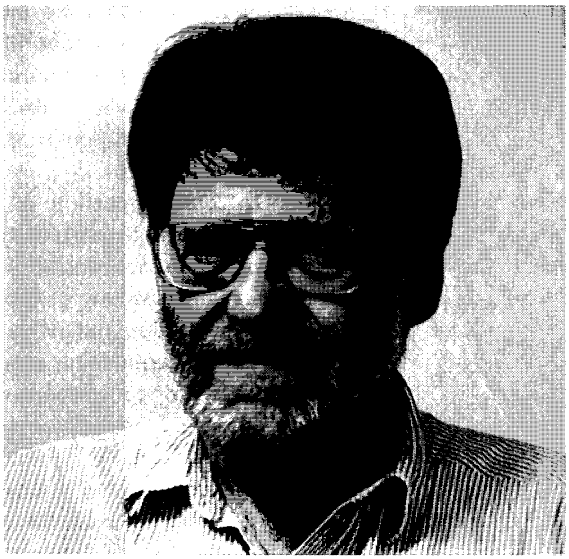
Introduction

The classical experiments of Gause (1934) are still cited in ecology textbooks as examples of species interactions. Beyond that, however, modern ecology and ecological theory is almost exclusively concerned with or draws inspiration from communities of terrestrial vertebrates, insects, vascular plants and other macroscopic organisms. This is remarkable, because some microbiologists have viewed assemblages of microbes in terms of modern ecological concepts since the turn of the century. For example, Winogradsky (1945) studied properties of whole microbial communities and coined the terms 'autochtonous' and 'zymogeneous' (soil bacteria) to describe a concept which is almost identical to that of 'K- *vs* r-strategists'. The term 'microbial ecology' has been established since Brock's (1966) book was published. The aim of microbial ecology is to find principles which explain the structure and function of microbial communities. Like 'general ecology' the approaches and objectives are diversified and include studies of the transfer of materials and energy in microbial ecosystems as well as interactions between species populations and community ecology. Microbial ecology has recently made substantial progress (see e.g. Fletcher, Gray & Jones 1987), but the field has developed in relative isolation from other ecological disciplines and has made little impact on ecological theory. It is my purpose here to show that microbes have much to offer to general ecology.

The particular properties of microbes and microbial communities are, of course, to a large extent related to scales of size and time. I use a broad definition of 'microbes' to include prokaryotes as well as unicellular eukaryotes. Most bacteria measure 0·5–1 μm in diameter and the largest Protozoa measure about 1 mm, a size range which is comparable to that of all vertebrates. Generation times of microbes range from less than 1 h for bacteria to a few days for the largest Protozoa. Whole microbial communities can therefore be studied in flasks or petri dishes, they are easily subjected to experimental manipulation, and populations can be followed over many generations within a short period of time. Many (and eventually perhaps all) microbes can be cultured axenically (that is, a pure culture containing only a single species or clone) or together with a few other defined species, allowing for studies on life cycles, interactions with other species and environmental requirements. Microscale ecology thus offers special opportunities for an experimental approach to ecology which are not available in studies of macroscopic organisms. Finally, and perhaps least appreciated, is the fact that many microbial communities display an astonishing diversity of species and a great variety of adaptations. The natural history of microbial communities is in many cases still in an exploratory phase and its appeal can be compared to that of tropical rain forests and coral reefs.



In order to be able to demonstrate all this within the limitations of a short paper, I have chosen to discuss the microbial life beneath 1 cm^2 of the surface of a sandy sediment in a shallow marine bay. I will especially emphasize the protozoan communities and refer to bacterial processes mainly to give a background understanding of the complex habitat constituted by sediments. Most examples or data presented derive from a particular site, Nivå Bay, situated along the coast between Copenhagen and Helsingør, Denmark. At intervals I have studied this locality during the last 25 years (e.g. Fenchel 1969). Studies carried out elsewhere, however, have elucidated certain aspects of the microbial ecology of shallow water sediments in much more detail and I will refer to these studies where appropriate.

* Based on the biennial lecture of the British Ecological Society, given at the University of Exeter on 18 December 1991.

The sediment ecosystem and an inventory of its microbial residents

THE SEDIMENTS OF NIVÅ BAY

Nivå Bay is a shallow bay with a negligible tidal amplitude. The salinity fluctuates between about 12 and 20 ppt due to the variable outflow of brackish surface water from the Baltic Sea. The sediment consists of fine sands with patchy growth of seagrasses (*Zostera marina* L.); water depths are everywhere less than a few metres. The sediments support dense populations of meiofauna (nematodes, harpacticoids, rotifers, etc.) as well as various molluscs, amphipods, crabs, prawns and other invertebrates and different species of fish (Muus 1967; Fenchel 1969).

Macroscopic inspection of the surface of the sediment reveals heterogeneity at different scales. Seawards the surface consists of oxidized sands which are often tinted yellow or brown from diatoms or dinoflagellates, but further landwards, patches of black sulphide-containing sands appear which are often covered by conspicuous white mats of sulphur bacteria (mainly *Beggiatoa* spp.) or, during the summer, also purple patches of photosynthetic sulphur bacteria. Other patches are blue–green due to the formation of cyanobacterial mats. Along the shores large areas with accumulated dead *Zostera* leaves develop massive populations of photosynthetic sulphur bacteria to give the appearance of pink or red paint.

THE MICROBIAL POPULATIONS

Microscopical examination of sediment cores with a cross-sectional area of 1 cm^2 and a depth of about 10 cm reveals about 4×10^{10} bacterial cells, at least 10^4 heterotrophic flagellates and amoebae, some 10^8 chlorophyll *a*-containing cells (diatoms, various flagellates, cyanobacteria) and typically 1000–2000 (up to 4000) ciliates (Fenchel 1969; Fenchel & Straarup 1971; T. Fenchel, unpublished observations).

The diversity has been best studied in the case of the ciliates. An individual sediment core (1 cm^2) typically harbours about 30 species, but more than 100 species have been recorded from the sediments of the bay (Fenchel 1969). Other groups of protists are only incompletely known, but the work of Patterson, Larsen & Corliss (1989) and Larsen & Patterson (1990) suggests a great diversity of heterotrophic and photosynthetic flagellates in such sediments.

Certain spectacular prokaryotes (cyanobacteria, the large sulphide-oxidizing chemolithotrophic or photosynthetic bacteria) can be identified microscopically. Many other functional types of bacteria can be isolated into pure culture and identified although it is not known whether these particular strains are, in fact, important in the sediment. By and large, bacterial diversity of natural environments is still characterized only by the diversity of metabolic and biogeochemical activity (e.g. sulphate reduction, various types of fermentation, methane oxidation or the ability to hydrolyse various organic macromolecules). It is now possible to characterize bacteria of natural communities using immunofluorescent techniques or fluorescent probes based on ribosomal RNA sequences (Pace *et al.* 1986). It is likely that in years to come these techniques will give new insight into bacterial diversity and the relevance of the species concept to prokaryote organisms.

THE MAJOR MICROBIAL PROCESSES

At some depth, sediments are always anoxic and chemically reducing. The depth of the oxic zone varies according to water turbulence, load of organic decomposable material in the sediment and light intensity, but (excepting periods following strong wave action and sediment transport) oxygen is always absent below about 5 mm depth and often below 1 mm. The reason for this is that photosynthesis is limited to the upper few millimetres (Fenchel & Straarup 1971) and below this oxygen can only be supplied by molecular diffusion.

Beneath the oxic zone, microbial degradation of allochtonous organic material is fermentative, resulting in relatively few low molecular end-products and among them primarily volatile fatty acids (acetate, propionate, butyrate) and hydrogen (Sørensen, Christensen & Jørgensen 1981). Further mineralization takes place through anaerobic respiration in which electron acceptors other than oxygen are used. Nitrate respiration (denitrification) is energetically the most favourable process, but it usually plays a limited quantitative role due to the scarcity of nitrate in the sediment (Fenchel & Blackburn 1979; Sørensen, Jørgensen & Revsbech 1979). Sulphate respiration, on the other hand, is a dominating process because of the vast supply of sulphate in sea-water (about 100 times more oxidation equivalents than oxygen in air saturated water). Sulphate reduction may therefore account for more than 50% of the mineralization process of the sediment (Fenchel & Blackburn 1979). Its principle end-product is sulphide which in part combines with iron to produce the characteristic black colour of reduced marine sediments. Only when sulphate is almost depleted will methanogenesis play a significant role. This is due to competitive exclusion of methanogenic bacteria by sulphate reducers which obtain a larger cell yield per mole of consumed substrate (hydrogen or acetate) than do methanogenic bacteria (Ward & Winfrey 1985). The removal of hydrogen by sulphate reducers or methanogens is essential for the thermodynamic efficiency of fermenting bacteria. Fermentors (which are capable of hydrolysing polymers) and anaerobic respiring bacteria (which can use only a

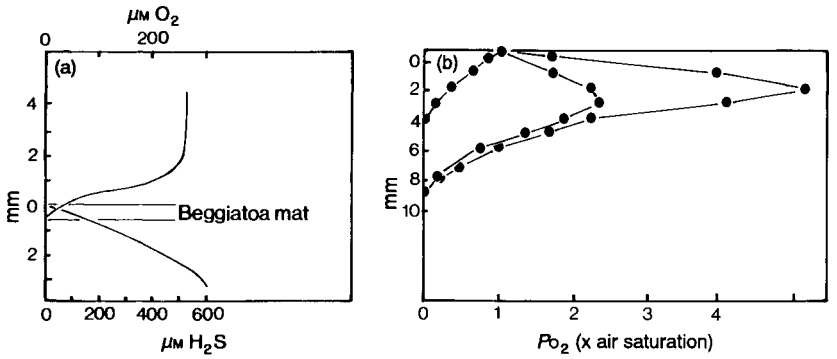


Fig. 1. (a) Gradients of O_2 and of H_2S in a sediment covered with a mat of the chemoautotrophic sulphur bacterium *Beggiatoa*. (Redrawn from Nelson *et al.* 1986.) (b) The O_2 gradient in the upper millimetres of an illuminated shallow water sediment 0, 30 and 260 min after the surface has been shaded. (Data from Revsbech *et al.* 1980.)

few types of low molecular substrates) thus interact in a sort of mutualistic association (syntrophy) and this hydrogen transfer plays a paramount role in anaerobic communities (Fenchel & Blackburn 1979).

The result of all this is a characteristic vertical zonation of the sediment with respect to the different processes and the chemical environment (Fenchel & Blackburn 1979). On the top of the sediments there is a thin oxic zone characterized by aerobic metabolism; below the oxic zone there is a narrow zone of nitrate reduction, beneath that again a zone of sulphate reduction and finally (and usually at a considerable depth) methanogenesis is the dominating terminal process of anaerobic degradation.

In marine sediments the methane produced is largely oxidized anaerobically in the sulphate zone and only small amounts reach the sediment surface (Iversen & Blackburn 1981). Reduced sulphur compounds (principally sulphide) are oxidized by oxygen at the aerobic–anaerobic boundary by chemolithotrophic bacteria or — if light reaches the anaerobic zone — by photosynthetic bacteria. The sulphide oxidizing chemolithotrophic bacteria, which depend on a chemically unstable mixture of oxygen and sulphide, form a dense (and often macroscopically visible) bacterial plate which separates the oxic and the anoxic zone over a distance of 1 mm or so (Fenchel 1969; Nelson, Jørgensen & Revsbech 1986; see also Fig. 1). These motile bacteria show a chemosensory behaviour towards oxygen and are therefore capable of moving to the preferred level of the sediment. Where sulphide reaches the photic zone a characteristic colour banding is seen in the upper 4 mm of the sediment: uppermost, a green layer of cyanobacteria and eukaryotic algae, beneath that a purple layer of photosynthetic sulphur bacteria and beneath that again black sediment.

SPATIAL AND TEMPORAL HETEROGENEITY

The foregoing description of the major microbial processes is to some extent idealized; in real sediments the vertical pattern is superimposed by heterogeneity on different scales. During periods with strong wave action the sediments are stirred or moved around. Oxygen and sulphate are mixed into the sediment, as is new detrital material which fuels the microbial processes. Therefore at any vertical level in the sediment successional events can be followed which resemble the spatial patterns described above: first oxygen disappears, then sulphate is slowly depleted and eventually methanogenesis takes place. The ideal vertical pattern is also modified by the burrowing activity of bivalves, amphipods and polychaetes which locally extend the oxic zone into the sediment and effectively increase the surface area of the sediment. Spatial heterogeneity is also a result of the uneven distribution of particulate organic material such as large lumps of dead *Zostera* leaves or macroalgal thallus.

Detrital particles may be responsible for the co-occurrence of opposing processes (e.g. sulphate reduction and sulphide oxidation) at the same vertical level in the sediment. This is because even in an oxic environment the internal surfaces of particle aggregates as small as 1 mm may become anoxic due to a high bacterial oxygen demand and because the oxygen transport is diffusion limited. Thus small anaerobic 'islands' occur in the oxic zone. In a similar way detrital particles may support methanogenesis in a sulphate-containing environment (Jørgensen 1977; T. Fenchel, unpublished observations).

The diurnal change in light intensity has a profound effect on the upper 0·5 cm of the sediment. This is because light is necessary for the activity of oxygenic as well as anoxygenic photosynthesis. In the upper part of the sediment, oxygen tension may change between supersaturation and zero over a short period (Revsbech *et al.* 1980; see Fig. 1) and the entire microbiological and chemical zonation shows diurnal vertical migrations (Fenchel 1969; Blackburn, Kleiber & Fenchel 1969).

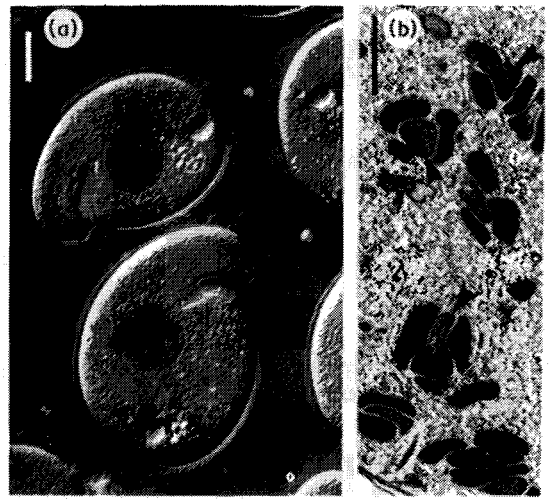


Fig. 2. The anaerobic ciliated protozoan *Plagiopyla frontata*. (a) Living cells (scale bar: 20 μm). (b) Endosymbiotic methanogenic bacteria (arrows) surrounded by hydrogenosomes, organelles which oxidize pyruvate into acetate and H_2 (scale bar: 1 μm). (Photographs by B.J. Finlay.)

The protozoan communities

The diversity of the protozoan biota of sediments can be divided into three distinct and spatially separated communities. These are the communities of the strictly anoxic and reducing zone, the microaerobic transition zone, and the oxic zone (Fenchel 1969). Different types of adaptations to particular characteristics of these three habitats (e.g. to special food resources) can be found, but the primary factor which controls the distribution of the organisms is in all studied cases the partial pressure of oxygen. All studied species show chemosensory behaviour in response to P_{O_2} (rather than to a variety of other chemical correlates (e.g. presence of sulphide, redox potential) and so the oxygen gradient in the sediment directly controls the (vertical) distribution of the species populations (Finlay, Fenchel & Gardner 1986; Fenchel, Finlay & Giannì 1989; Fenchel & Finlay 1990b). Diversity is also due to the existence of many different food resource niches (Fenchel 1968) and finally differential exploitation of spatial and temporal heterogeneity is important.

In the following I will first discuss the microbial communities belonging to the different vertical strata of the sediment. I will then proceed to discuss examples of special adaptations.

LIFE WITHOUT OXYGEN

It is often, but incorrectly held that eukaryotes, and hence phagotrophic food chains, are absent in completely anoxic environments. However, representatives of most major protozoan groups have adapted to life without oxygen. These organisms (among which ciliates and heterotrophic flagellates dominate) show a relatively low diversity and low population densities; for example there are less than 10 species of anaerobic ciliates commonly found in the sediments of Nivå Bay although by far the largest part of the sediment is anaerobic. The reason for this is the low energy yield of the anaerobic (fermentative) energy metabolism which is only about 10% of that of their aerobic counterparts and so gross growth efficiencies and maximum growth rates are only about 25% of those of aerobic species (Fenchel & Finlay 1990a). In terms of community structure this means that the ratio between predator and prey biomass is correspondingly lower and that food chains are short since little energy is preserved when going from one trophic level to the next. Thus by far the most species feed on bacteria and predators on protozoa are represented only by one or two rare species. A fourth trophic level does not occur.

The species which are found in the anoxic layer are obligatory anaerobes which to a varying degree survive microaerobic conditions ($P_{O_2} < 2\%$), the cells show strong adverse chemosensory reactions towards even traces of oxygen and they do not have cytochromes or catalase (Fenchel & Finlay 1990b). Representatives of several groups are capable of a fermentative oxidation of their substrate which involves hydrogen production; this increases energy yield above that of the glycolytic pathway. Most of these forms harbour endo- or ectosymbiotic bacteria. The endosymbionts have been shown to be methanogenic bacteria which use the hydrogen produced by the host to produce methane (Fenchel & Finlay 1991; see also Fig. 2). The metabolism is closely coupled to that of the host which maintains a constant number of symbionts and practically all the produced hydrogen is consumed by the bacteria. This relationship may be an example of hydrogen transfer: by sequestering hydrogen the methanogens maintain a low pH_2 inside the ciliate and this increases the thermodynamic efficiency of its energy metabolism (Fenchel & Finlay 1992).

LIFE IN AN OXYGEN GRADIENT

The oxic–anoxic boundary layer constitutes a zone of elevated biological activity. The reason is that in this zone chemolithotrophic bacteria utilize the reduced low molecular compounds (especially sulphide) which diffuse upwards from the anoxic zone. This bacterial production constitutes the basis for microbial food chains and the maximum density of protozoa is often found at this layer. The community is analogous to the deep sea hydrothermal vent biota which also depends on the bacterial production based on the oxidation of sulphide and methane.

Where there is a copious production of sulphide, the oxic–anoxic boundary zone of sediments is only a few millimetres thick due to the formation of bacterial films (Fig. 3); in sediments with a less intensive anaerobic microbial activity, the zone may extend for several centimetres or consist of anaerobic

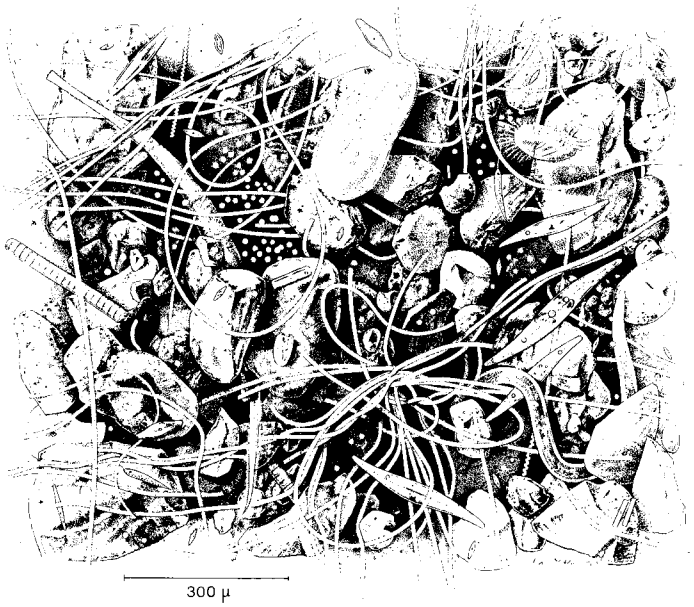


Fig. 3. Surface of a sediment dominated by the chemoautotrophic sulphur bacteria *Beggiatoa* (the filaments) and *Thiovulum* (the white spherical cells). Also seen are species of diatoms, euglenoid flagellates, cyanobacteria, ciliates and a nematode. (After Fenchel 1969.)

islands (detrital particles) immersed in an otherwise microaerobic sediment.

The oxic–anoxic boundary layer hosts a great variety of Protozoa which fill many different food niches. Among them the ciliate genus *Kentrophoros* is remarkable in that the dorsal side of the ciliate is densely covered by rod-shaped sulphide oxidizing bacteria (Fig. 4). The ciliate has no mouth, but it phagocytizes the bacterial symbionts through its dorsal surface (Fenchel & Finlay 1989). It is thus a phenomenon similar to the benthic invertebrates from hydrothermal vents and from marine sediments, which depend on symbiotic sulphur bacteria for food (see Southward 1987).

The ability of the Protozoa to orient themselves in the chemical gradient is, in all investigated cases, due to chemosensory responses towards oxygen partial pressure (Fenchel & Finlay 1986, 1989; Fenchel *et al.* 1989). Most studied species have a preference for a P_{O_2} of around 5% atm. sat. They all show a clear avoidance reaction towards higher O_2 tensions (Fig. 5) and they are affected by oxygen toxicity (in terms of reduced survival or growth rate constants) above a certain value of P_{O_2}, but they are very tolerant towards anoxia and the presence of sulphide (Finlay *et al.* 1986; Fenchel *et al.* 1989).

PROTOZOAN BIOTA OF THE SURFACE LAYER

The surface layers are characterized by a diversity of photosynthetic protists including diatoms, euglenoid, cryptomonad and chrysomonad flagellates and dinoflagellates in addition to the prokaryote cyanobacteria. Heterotrophic protists also include a great variety of species belonging to various groups of flagellates, rhizopods and ciliates (Fenchel 1969; Patterson *et al.* 1989).

Altogether the surface layers of the sediments harbour the highest number of species. This is mainly due to the availability of a great variety of food items. There is also a considerable variation in cell size, shape and behaviour which in part reflects habitat diversification: the extremely long or flattened species of ciliates are obviously adapted to slide along sand grains in the interstitia of the sediments (Fenchel 1969) while others such as the oligotrich *Strombidium sulcatum* live immediately above the sediment surface (Fenchel & Jonsson 1988).

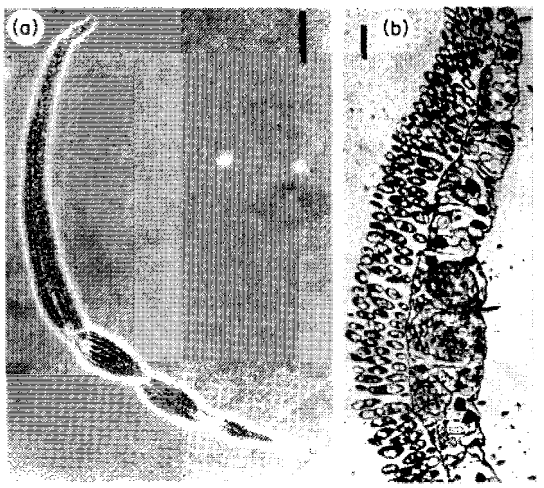


Fig. 4. The ciliate *Kentrophoros facsiolatum* which depends on its ectosymbiotic sulphur bacteria for food. (a) A living cell (scale bar: 50 µm). (b) A transversal section showing the bacteria aligned perpendicularly on the dorsal side of the ciliate and food vacuoles filled with the bacteria (scale bar: 2 µm).

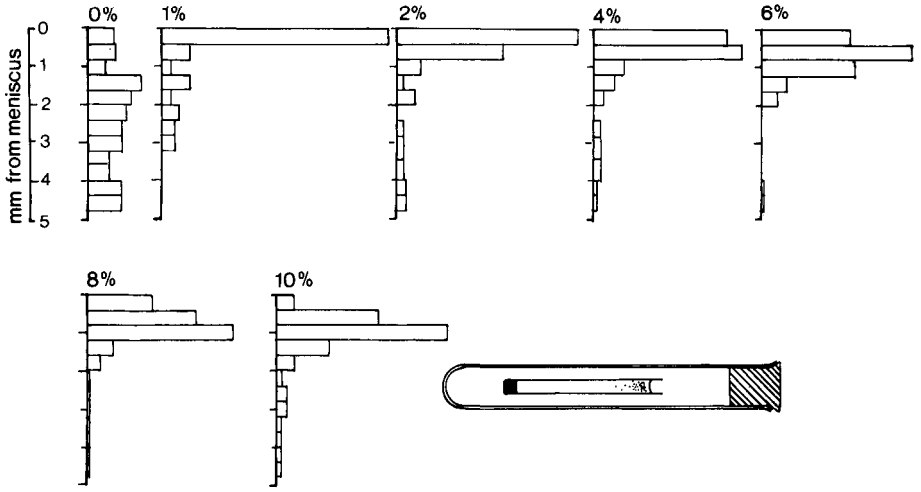


Fig. 5. The distribution of a population (about 100 cells) of the microaerophilic ciliate (*Euplotes* sp.) in a capillary tube. The sea-water in the capillary was initially anoxic and the capillary was placed in a stoppered test tube with a N_2-atmosphere. When small, known amounts of air are injected into the tube, the O_2 tension of the meniscus is that of the surrounding atmosphere and an O_2 gradient is formed in the capillary due to the balance between diffusion and respiration of the ciliates. Numbers are % atm. O_2. When PO_2 exceeds about 4% atm. sat. in the headspace, the ciliates retreat from the meniscus. (Data from Fenchel *et al.* 1989.)

FOOD NICHES

The high diversity of the sediment Protozoa is first of all due to specializations to different food items. Suspended bacteria are consumed by raptorial heterotrophic flagellates and by the larger filter-feeding ciliates. The filter-feeding forms seem only to discriminate food particles according to size. Raptorial flagellates and ciliates are often specialized to feed on certain classes of prey organisms, and they discriminate between food particles on the basis of other properties in addition to size. Thus some forms are specialized for feeding on different size classes of diatoms, filamentous bacteria, various types of flagellates and on other ciliates. Guilds of species share certain classes of food items according to size (Fenchel 1968, 1987). Some large suspension feeding ciliates have a more generalist utilization of food resources and feed on a variety of sufficiently large prey cells. Some forms have become specialized in feeding on attached bacteria and algae, and finally, some ciliates ('histophages') specialize in feeding on metazoan tissue of wounded or molested invertebrates (Fenchel 1968). Altogether the microbes of sediments form a complex food web.

Endosymbiotic photosynthetic algae or 'chloroplast-symbiosis' (that is, maintaining intact and functional chloroplasts from photosynthetic prey species) are far less common phenomena in sediments than in protozoan biota of the water column. However, a few sediment ciliates (e.g. *Condylostoma tenuis*) harbour endosymbiotic algae and some shallow-water foraminifera are known to retain functional chloroplasts (Fenchel 1968; Lopez 1979).

ADAPTATIONS TO A FEAST AND FAMINE EXISTENCE

The life cycle of unicellular organisms is generally held to be a simple alternation between a growth phase and a division phase which reflects a cell cycle with successive phases of DNA duplication and synthesis of RNA and proteins. Such an orderly state of affairs is referred to as balanced growth in which the cell population increases exponentially and in which cells of any given stage of the cell cycle constitute a constant fraction of the entire population. Such populations in balanced growth can be maintained in the laboratory (e.g. in a chemostat). Sexual phenomena (in eukaryote forms), polymorphic life cyles and evolutionary changes are all, of course, known to complicate the picture. However, it is more rarely appreciated that micro-organisms show a variety of adaptations for the differential exploitation of environmental heterogeneity in time and space. These adaptations are reflected in different types of life cycles and behaviour and these phenotypic traits are again reflections of plasticity with respect to the cell cycle within a given genotype as well as between different species or genotypes. I will elaborate on this by discussing three ciliate life cycles which reflect different ways of exploiting environmental patchiness.

If a dense bacterial suspension or anything that will stimulate the development of bacterial populations such as a dead animal tissue or easily decomposable material is added to a small sediment sample the dish will be swarming with one or more species of bacterivorous ciliates within 2–3 days. This mimics

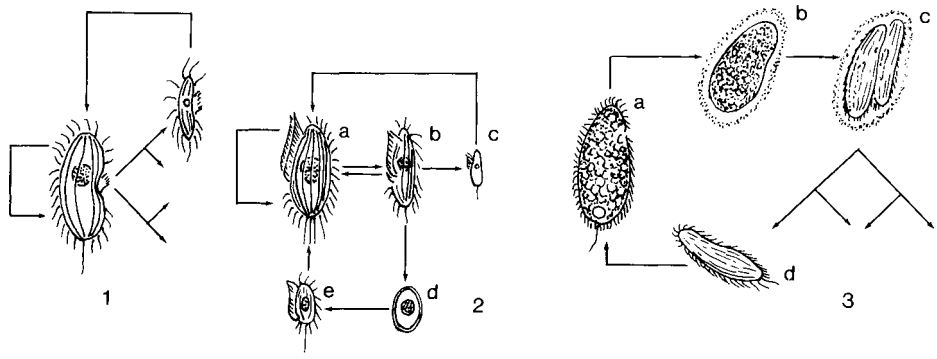


Fig. 6. Life cycles of three species of ciliates (1, *Uronema marinum*; 2, *Pseudocohnilembus pusillus*; 3, *Porpostoma notatum*) representing differential exploitation of spatial and temporal heterogeneity of food resources. For explanation see text. (1 and 2 based on data in Fenchel 1990; 3 based on unpublished data of S. Naeem & T. Fenchel.)

what happens regularly in nature. Among these ciliates, *Uronema marinum* (about 30 μm long) is common (Fenchel 1990). Cell populations grown in pure cultures with bacterial suspensions as food grow exponentially with a generation time of about 3·5 h (at 20°C). These growing cells move slowly, and they frequently change swimming direction by ciliary reversals ('tumbles'). If suddenly deprived of food, the ciliates immediately increase swimming velocity (by a factor of about 20) and tumbling frequency is reduced to about one-third of that of feeding cells. The cells will still divide for two to three generations producing small, rapidly swimming swarmer cells (Fig. 6.1). These will survive for more than 100 h without food. The reason this is possible is that the ciliates reduce their metabolic rate to about 10% within a few hours after being starved, and the rate of O_2 uptake falls further during the following day. Once the swarmers encounter food they slow down and feed.

The long survival time of starving cells is brought about by a drastic reduction in the synthesis of macromolecules, and also autophagy of cell components, especially mitochondria (Fenchel 1982, 1990). The consequence of this is that once food is found it takes a long time before the ciliates resume cell division because the machinery of protein synthesis and for catabolic metabolism must first be re-established. Thus cells which have starved for only a few hours will have a lag time of about 10 h (i.e. more than twice the generation time) and after 60 h of starvation the lag time will have increased to more than 15 h.

The behaviour of *Uronema* reflects an adaptation to spatially heterogenous resources such as carrion with copious bacterial growth. One or more cells will arrive at such patches and will increase in numbers until the resource has been exploited. Once starvation sets in, the additional cell divisions can be considered as a way in which each genome maximizes the probability of finding a new resource patch; the trait will be selected for so long as the survival of the smaller division products (4–5 per cell) is more than one-quarter to one-fifth of the starvation survival of a cell that had stopped dividing once food is depleted. The rapid swimming and long survival during starvation of the swarmer cells also maximizes the probability of finding new resource patches. Based on the motility of the swarmer cells, the mean displacement of the swarmer cells after 150 h (their expected time of survival) can be calculated to be about 40 cm from their origin (unless they are displaced by turbulence or advection in the water column). A radius of 40 cm can therefore be considered the 'spatial scale' of *Uronema* (Fenchel 1990).

Trophic stages of the related *Pseudocohnilembus pusillus* may also appear in sediment samples when enriched with bacteria. The life cycle of this ciliate, however, is different (Fig. 6.2). If starved, the *Pseudocohnilembus* cells will not divide further, and their metabolic rate is not depressed as strongly. They also swim more rapidly than the trophic cells, but for the duration (10–40 h) of this stage (Fig. 6.2b) their mean displacement will be only about 10 cm. If offered food, these cells can resume growth within 2–3 h and they are then at an advantage relative to *Uronema* cells which have been starved for the same period. After 10–40 h the starving *Pseudocohnilembus* cells may do one of two things. They may divide to form tiny swarmer cells (Fig. 6.2c) which survive for another 20–30 h if not offered food. The time lag for cell division increases with time. Alternatively the cells may form resting cysts (Fig. 6.2d). About 50% of the cells encyst. The metabolic rate of the cysts becomes undetectable between 50 and 300 h after encystment. The cysts remain viable for about 4 months. They will excyst (Fig. 6.2e) if bacterial suspensions (or filtrate from bacterial suspensions or sterile peptone solutions) are added, but the lag time before excystment and subsequent cell divisions increases with age (eventually to 50 h or more) so that the fitness of the cysts decreases with age (Fenchel 1990).

Pseudocohnilembus is therefore bet hedging. The fact that the cells do not encyst immediately after being starved demonstrates the significance of

dispersal. The cells first try to find a new food patch in the vicinity of the old one. If this fails, a fraction of the cells continue this approach for some time, but the rest rely on temporal heterogeneity (e.g. that a dead worm will at some time appear next to the cyst).

It is very rare to find trophic cells of *Pseudocohnilembus* in fresh samples of surface sediment. However, they are easily recovered from cysts by adding bacteria to sediment samples. Using this fact and a 'most probable number' technique the cysts can be quantified in field samples. In a study it was found that the average density of *Pseudocohnilembus* cysts is about 7 per cm^2 sediment surface. Their distribution is contagious, however, and small areas with high densities probably reflect the previous occurrence there of a dead polychaete or whatever. In a sense, *Pseudocohnilembus* is reminiscent of annual weeds in which by far the largest part of the population at any time is made up of dormant seeds in the soil.

The so-called histophagous ciliates feed on wounded invertebrates or pieces of living tissue which may become available on the sea bottom as a result of a more or less successful attack by predators. The ciliates feed on the tissue which is first partly lysed through the excretion of extracellular enzymes.

Histophagous ciliates include different species belonging to several different taxa (Fenchel 1987). They are easily collected by adding a cut worm to a dish with sediment and water. If present, the ciliates will appear in the wound within a few minutes. In this way it has been shown that in the surface layers of Nivå Bay there are about 20 cells of the histophagous ciliate *Porpostoma notatum* per cm^2 in the summer (S. Naeem & T. Fenchel, in preparation).

The food resources of histophagous ciliates are very emphemeral because even if the pioneer ciliates are not able to exploit it all within a short period it is bound to be found by some carrion-feeding invertebrate or fish before long. The life cycle of these ciliates (Fig. 6.3) is therefore polymorphic, and the trophic stage cannot reproduce itself. *Porpostoma* feeds for at most 30 min during its life cycle, but during this period it increases its volume by a factor of five to 10 (Fig. 6.3a). After feeding it swims around for a few minutes and then attaches to a surface and forms a cyst covered by mucous (Fig. 6.3b). The encysted stage is the metabolically most active part of the life cycle. It lasts for 15–18 h. During this period digestion takes place followed by RNA and protein synthesis and eventually cell division. If the ciliate had an undisturbed meal for at least 15 min and if it had not starved for very long before it found food it may divide twice inside the cyst to produce four swarmer cells (Fig. 6.3c,d); otherwise it will only produce two to three cells. The swarmer cells leave the cyst and can now search for a new food patch for 2–3 days before they succumb to starvation (S. Naeem & T. Fenchel, in preparation).

In this ciliate the cell cycle has thus been compartmentalized into well-defined stages: feeding, digestion, synthesis of macromolecules and division and a searching stage. Only the searching stage varies in duration according to the probability of finding a food patch, while the other stages have a fixed duration.

The histophagous ciliates are promising objects for studying adaptations to environmental heterogeneity (S. Naeem & T. Fenchel, in preparation). This is particularly so because different species vary according to details in the life cycle. Thus species of *Ophryoglena* tend to produce a larger number of smaller swarmer cells or they are polymorphic in this respect so that they may either produce many small or few large swarmers (Canella & Rocchi-Canella 1976).

Conclusions

The diversity and complexities of microbial communities of sandy marine sediments do not allow for a complete description in a short paper. Here I have emphasized the natural history aspect, especially with respect to ciliated Protozoa. Nevertheless, the examples show that microbial communities and their individual components also pose many general ecological problems; they also show that microbial communities are extremly well suited for studying these problems through the combination of field observations and laboratory experiments.

There is one additional aspect of microbial ecology which I find to be of particular interest. There are many views on what ecology is supposed to be; the subject ranges from systems ecology to population ecology, and many different definitions of ecology can be found. Many ecologists have expressed the desirability of a unified ecology, but have not succeeded. As mentioned in the Introduction, microbial ecologists too may be divided with respect to what they think is worthy of study.

Even so, microbial ecology does engender a sense for the unity of biology if not for ecology. When looking at how unicellular organisms interact with their surroundings the approach often broadly overlaps with that of cell biologists or biochemists. The symbiotic relationships between different microbes (e.g. the endosymbiont methanogenic bacteria in anaerobic Protozoa) is an example of interaction between two species populations, but it is also a cell biological phenomenon and the cell biologist and the population ecologist will actually ask the same questions and study it in a quite similar way. Understanding the evolution and adaptive significance of different life cycles in microbes requires insight into the cell cycle at the molecular level. The strong connection between microbial ecology and the study of basic biological phenomena, I believe, should be an important inspiration to general ecology.

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