Micro-organisms in Action: Concepts and Applications in Microbial Ecology

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Preface

In the earlier volume [6] to which this is a sequel, the preface indicated the growth in interest of microbial ecology since 1975. Now there have been four International Symposia on Microbial Ecology at Dunedin [5], Warwick [3], East Lansing [4] and Ljubljana in 1986, with the next scheduled for 1989 in Kyoto, Japan. There have also been several texts published, notably those by Campbell [2] and Atlas and Bartha [1] as well as the series *Advances in Microbial Ecology* and the journals *Microbial Ecology* and *FEMS Microbiology Ecology*.

Constructive critical book reviews are always welcome but these can lead to unsuspected outcomes. When John Hobbie reviewed the earlier volume in *Ecology* in 1981 he indicated the need for a greater ecosystem approach. He became the obvious choice to replace Nigel Poole as co-editor when Nigel found his commitments to his company did not allow him time for the task. We thank the many students, teachers and researchers on microbial ecology everywhere who offered constructive comments. We also thank the authors and publishers listed below for allowing us to reproduce either original or copyright material.

Authors: Anderson & Sørensen (1986) (Fig. 3.2.18); Bazin & Saunders (1973) (Figs. 2.1.6, 2.1.7); Bedford (1981) (Fig. 4.2.6b); Bird & Akhurst (1983) (Fig. 4.2.2); Board (1969) (Fig. 4.3.4); Bunnell *et al.* (1977) (Fig. 3.1.14); Cliff *et al.* (1981) (Fig. 2.2.5); Cooper & MacCallum (1984) (Figs. 2.2.3, 2.2.4); Evans *et al.* (1987) (Fig. 4.1.1). Gibbs & Harrison (1976) (Fig. 2.2.2); Gieskes & Kraay (1984) (Fig. 3.2.6); Gregory (1973) (Figs. 3.5.2, 3.5.3); Griffin (1977) (Fig. 3.1.18); Haddock & Jones (1977) (Figs. 2.5.2, 2.5.6); Hamilton (1985) (Fig. 2.5.9); Harman *et al.* (1980) (Fig. 4.2.12); Jenkinson (1977) (Fig. 3.1.13); Jerlov (1976) (Fig. 3.2.1); Johnson *et al.* (1980) (Fig. 4.2.1); Jørgensen (1980) (Fig. 3.2.13), (1983a) (Fig. 3.2.12), (1983b) (Fig. 3.2.15); Kröger (1977) (Fig. 2.5.5); Lisansky (1984) (Table 4.2.1); Mack *et al.* (1975) (Fig. 4.4.4); Mandelstam *et al.* (1982) (Fig. 2.5.3); Odom & Peck (1981) (Fig. 2.5.8); Oglesby (1977) (Fig. 3.2.7); Parsons *et al.* (1977) (Fig. 3.2.4); Paul & Voroney (1984) (Table 3.1.6); Payne (1986) (Fig. 4.2.6); Payne *et al.* (1981) (Fig. 4.2.7); Ridout *et al.* (1986) (Fig. 4.2.11); Sieburth (1975) (Figs. 2.1.2, 2.1.3, 2.1.4), (1984) (Fig. 3.2.8); Simon (1985) (Fig. 3.4.3); Southward (1982) (Figs. 3.3.9, 3.3.10); Stanier *et al.* (1976) (Figs. 2.5.11, 2.5.12, 2.5.13); Stewart (1984) (Fig. 3.1.17); Thauer & Badziong (1980) (Fig. 2.5.7) Thauer *et al.* (1977) (Fig. 2.5.4); van Veen *et al.* (1984) (Fig. 3.1.16); White (1979) (Figs. 3.1.5, 3.1.15).

Publishers: Academic Press (Figs. 3.2.13, 4.2.6b, 4.2.7, 4.3.4); Am. Phytopathological Soc. (Fig. 4.2.12); Am. Soc. for Microbiol. (Figs. 2.5.2, 2.5.4, 2.5.6, 3.1.17, 3.4.3, Table 3.1.6); Annual Reviews (Fig. 2.5.9); *Appl. Environ. Microbiol.* (Fig. 3.4.3); Chapman & Hall (Figs. 2.2.3, 2.2.4, 3.1.18); CRC Press (Figs. 2.1.6, 2.1.7, 2.5.7); Cambridge University Press (Figs. 2.2.5, 2.5.5); Edward Arnold (Fig. 2.2.2); Elsevier (Figs. 2.5.8, 3.2.1); Forestry Commission (Fig. 3.3.1); *Fortschr. Zool.* (Fig. 4.2.6); Inter-Research (Fig. 3.2.18); *J. Fish. Res. Bd. Canada* (Fig. 3.2.7); *J. Gen. Microbiol.* (Fig. 4.2.11); *J. Invertebr. Path.* (Fig. 4.2.7); *J. Mar. Biol. Ass. U.K.* (Figs. 3.3.9, 3.3.10); S. Karger AG (Fig. 4.2.6a); Leonard Hill (Figs. 3.5.2, 3.5.3); Marine Biological Association (Figs. 3.3.9, 3.3.10); Martinus Nijhoff (Figs. 3.1.16, 4.1.1); *Microbiol. Ecol.* (Fig. 3.4.2); Nat. Research Council of Canada (Fig. 4.2.1); Online Publications (Table 4.2.1); Oxford University Press (Fig. 3.1.14); Pergamon Press (Figs. 2.1.6, 2.1.7, 3.1.14, 3.2.4, 4.2.2); Plenum Press (Figs. 3.2.6, 3.2.8); Prentice-Hall (Figs. 2.5.11, 2.5.12, 2.5.13); Society for General Microbiology (Fig. 4.2.11); Springer-Verlag (Figs. 3.1.19, 4.4.4); University Park Press (Figs. 2.1.2, 2.1.3, 2.1.4); Wiley (Fig. 3.2.12).

In times when there are so many pressures on scientists it can be difficult to secure delivery of manuscripts. Sue Bewsey not only typed the chapters where Lynch and/or Payne were authors, but she also typed many begging letters to authors pleading for their manuscripts; we as editors are extremely grateful to her. We also thank

Robert Campbell, Simon Rallison and Jane Andrew at Blackwell Scientific Publications for their help and support.

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REFERENCES

[1] Atlas R.M. & Bartha R. (1981) *Microbiol Ecology. Fundamentals and Applications*. Addison-Wesley, Reading, Mass.

[2] Campbell R. (1983) *Microbial Ecology*, 2nd edn. Blackwell Scientific Publications, Oxford.

[3] Ellwood D.C., Hedger J.N., Latham M.J., Lynch J.M. & Slater J.H. (eds.) (1980) *Contemporary Microbial Ecology*. Academic Press, London.

[4] Klug M.J. & Reddy C.A. (eds.) (1984) *Current Perspectives in Microbial Ecology*. American Society for Microbiology, Washington DC.

[5] Loutit M. & Miles J.A.R. (eds.) (1978) *Microbial Ecology*. Springer-Verlag, Berlin.

[6] Lynch, J.M. & Poole N.J. (eds.) (1979) *Microbial Ecology. A Conceptual Approach*. Blackwell Scientific Publications, Oxford.

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Part 1
Introduction

microbe, n. minute living being, micro-organism (esp. of bacteria causing diseases and fermentation); hence *microbial*, *microbic*, adjs. (F. f. Gk. *mikros* small + *bios* life).

ecology n. branch of biology dealing with organisms' relations to one another and to their surroundings [f. G *ökologie* f. Gk *oikos* house, see -LOGY].

From *The Concise Oxford Dictionary of Current English* (1982) 7th edn.

THE DICTIONARY definition of microbial ecology has not changed significantly since that used in an earlier form of this text [1], yet with so much publication and debate on the subject in 9 years it is useful to reflect on the boundaries of microbial ecology.

It is necessary to understand the behaviour of micro-organisms under defined and controlled conditions in the laboratory in order to understand behaviour in natural environments. This book starts with a consideration of the microbial cell followed by some descriptions of interactions between cells of different microbial species. Viruses have frequently been omitted from discussions on microbial ecology and whereas they are non-cellular they are usually bound to cells of other micro-organisms, plants or animals. Recognition of the potential significance of plasmids in nature has increased greatly in the past few years and again it is critical to understand *in vitro* behaviour in order to predict behaviour in nature. Population and community dynamics can certainly be affected by plasmids. Ultimately, it is the metabolism of individual species and communities which determines the primary influence of micro-organisms on the environment and it is often useful to consider this from the energetic standpoint.

The term 'ecosystem' was first used by Tansley [2] to describe 'not only the organism complex but also the whole complex of physical factors, what we call the environment'. The second part of the book considers soil and water as well as animals and plants as environments for micro-organisms. Additionally aerial dispersal between environments and the effect of extreme environmental influences are discussed.

It is sometimes difficult to carry out cost–benefit analyses of scientific endeavour, especially when no obvious commercial benefit accrues but social amenities are improved. For example, the microbial deodorization of animal wastes on farms close to urban conurbations may make the environment more amenable to the residents but it is difficult to place a monetary value on this. Probably more scientific resources have been invested in studies on the fixation of dinitrogen than any other subject area in microbial ecology. Symbiotic processes are of major economic significance in agriculture and natural environments and this is the reason for their prominence in the chapter on dinitrogen fixation; this provides a complementary account to the earlier one [1] which had greater emphasis on free-living systems and physiology/biochemistry. The only other process where inoculation has proved an economic success is the biological control of pests and diseases. These beneficial activities of micro-organisms in the environment should be balanced by harmful microbial activities such as microbial spoilage of feeds and pollution of water. Also the effects of xenobiotic compounds in natural and man-made environments are discussed.

Our conclusion to the book will identify some areas of microbial ecology where the new developments in biotechnology might be exploited and studied.

The book is not intended as a comprehensive guide to microbial ecology but hopefully it will equip the reader to investigate chosen fields of study in the discipline and to think about them constructively.

REFERENCES

[1] Lynch J.M. & Poole N.J. (eds.) (1979) *Microbial Ecology. A Conceptual Approach*. Blackwell Scientific Publications, Oxford.

[2] Tansley A.G. (1935) The use and abuse of vegetational concepts and terms. *Ecology* **16**, 284–307.

Part 2
Principles of Microbial Behaviour in Ecosystems

'Yes, I have a pair of eyes,' replied Sam, 'and that's just it. If they wos a pair o' patent double million magnifyin' gas microscopes of hextra power, p'raps I might be able to see through a flight o' stairs and a deal door; but bein' only eyes, you see my wision's limited.'

Charles Dickens 1812–1870
Pickwick Papers

2.1 The potential of the microbial cell and its interactions with other cells

The basic consideration of this chapter will be the individual microbial cell. Much of microbiology considers populations of cells, and often the implicit assumption is that a pure culture, be it batch, chemostat or synchronous, is a collection of uniform cells or at least that any differences are averaged out. This is usually an acceptable generalization as, although there will be considerable phenotypic variations between adjacent cells, the characteristics of such cultures can only be reflections of the capabilities of each individual cell. In natural environments, microbial cells will almost always be in mixed cultures where they have to interact with cells of other species, but again these interactions are limited by the potential of each cell.

2.1.1 THE RANGE OF ORGANISMS

The taxonomic scope of microbial ecology

The microbial ecologist is concerned with a very wide range of organisms. There will likely be many different types of organism in any particular environment, and it is essential to any true understanding of their roles and interactions to be able to identify them as closely as possible. The micro-organisms encompass the three forms of life of the present day: eukaryotes, prokaryotes and viruses. These three groupings have no clear phylogenetic interrelationships, and apart from their chemical make-up the only thing that they have in common is that they are studied by microbiologists. Of the five-Kingdom classification of cellular forms [5, 34], microbiologists rightly claim three Kingdoms: (a) the Monera (Procaryotae, bacteria) [50]; (b) the Protista (protozoa, algae, slime moulds, and flagellated fungi or water moulds); and (c) the Fungi. These are dealt with in this chapter and the viruses and plasmids in the following two chapters.

Prokaryotes

The starting point for any work with prokaryotes must be *Bergey's Manual* [11, 29], which firmly establishes the Kingdom Procaryotae for the bacteria.

With the advent of the use of nucleic acids in the study of the classification of bacteria, in particular the sequencing of 16S ribosomal RNA, new light has been cast onto their phylogenetic relationships. Thus, taxonomy current-

ly is in an exciting state of flux. We can expect many surprises in the next few years, hence the need for simplicity in the meantime. The *Shorter Bergey's Manual* [25] gives three rules of the game:

1 Use all the information available to you.
2 Apply common sense at each step.
3 Use the minimum number of tests to make the identification. It also gives seven practical steps to follow:

1 Make sure you have a pure culture.
2 On the basis of the isolation procedure, establish whether you have a chemolithotrophic autotroph, a photosynthetic organism or a chemoheterotrophic organism (see Chapter 2.5).
3 Examine living cells by phase contrast and Gram-stained cells by light microscopy.
4 Examine gross growth appearances.
5 Test for oxygen requirements.
6 Test the dissimilation of glucose.
7 Complete additional tests appropriate to genera suggested by results from tests listed above.

They add the cautionary note that the most frequent cause of mistaken identity of bacteria is errors in determination of shape, Gram-reaction and motility.

THE EUBACTERIA

These bacteria inhabit virtually every ecological niche in the biosphere. They may be divided conveniently into Gram-negative bacteria, Gram-positive bacteria, and the permanently wall-less mycoplasmas which are mostly pathogenic in animals and plants.

The Gram-negative bacteria consist of the following: green and purple sulphur and non-sulphur bacteria, a diverse group of organisms which are photosynthetic in anoxic environments; pseudomonads, aerobic rods respiring a wide range of organic compounds; aerobic nitrogen-fixing bacteria; facultatively anaerobic rods: dissimilatory sulphate-reducers; spiral and curved aerobic bacteria; anaerobic fermentors; coccobacilli; sheathed bacteria; budding and prosthecate bacteria; chemolithotrophic bacteria; rickettsias; spirochaetes; and gliding bacteria.

The Gram-positive bacteria consist of the following: endospore formers; asporogenous rods and cocci; and actinobacteria.

THE ARCHAEBACTERIA

In recent years an apparently disparate group of bacteria have been shown to have a series of biochemical characteristics that set them completely apart from all other bacteria; they have walls of unusual polysaccharides instead of peptidoglycan, membranes often with unusual glycerol ether isoprenoid lipids instead of phospholipid bilayers, and characteristic ribosomes and ribosomal RNA sequences [48]. Moreover, they characteristically inhabit extreme environments. They include the red halophiles of brine pools and salted fish, the methanogens of anaerobic muds, animal guts and anaerobic digesters, and the thermoacidophiles of hot acid springs and smouldering coal wastes (cf. Chapter 3.4).

THE CYANOBACTERIA

The Cyanobacteria [14] are of great importance as primary producers. They evolve oxygen during photosynthesis and many can fix nitrogen. They occur as major constituents of marine and freshwater blooms, and also thrive in the upper layer of damp nutrient-poor soil and on wet rocks. Thermophilic species grow in clear successions down the progressively cooling effluents of hot springs. Some species produce toxins, and their blooms can cause fish mortalities. Cyanobacteria occur as symbionts; e.g. *Nostoc* spp. in the lichen *Peltigera canina* and in the water fern *Azolla filiculoides*. Their capacity for nitrogen fixation (see Chapter 4.1) plays a major role in the nutrition of these symbioses, and in lichens their photosynthesis is the major source of carbon and energy. Some, called cyanellae, occur as symbionts in some protozoa such as *Cyanophora* spp. These cyanellae still retain a thin peptidoglycan coat, but their DNA complexity is much less than that of free-living cyanobacteria and quite close to that of the algal chloroplasts. In fact, the recently discovered Prochlorophytes are very close to chloroplasts, as they contain chlorophylls *a* and *b* instead of the chlorophyll *a* and phycobiliproteins of cyanobacteria; these were discovered as extracellular symbionts of tropical marine ascidians.

Eukaryotic microbes

Following the five-Kingdom classification introduced above, the eukaryotic micro-organisms are the Fungi and the Protista — the water moulds, slime moulds, algae and protozoa. Also to be included are the lichens which, although symbiotic associations, are classified as discrete species. In contrast to the prokaryotes, the traditional taxonomy of these groups was established using morphological characters by biologists in the 19th century and earlier. For the most part their classification has stood the test of time. However, the phylogenetic relationships

both between and within the different groups remain topics of healthy dispute and speculation, chiefly because there is little fossil record except for such organisms as diatoms or coccolithophorids which have silicified or calcified cell components of characteristic morphology.

THE FUNGI

The true fungi have two major cell types, the hypha and the yeast [13]. These two forms have different properties, and they are very important determinants for growth in different environments. Some fungi can only form hyphae, others can only form yeast cells, while others can grow as either depending on conditions. Another characteristic is that fungi have a rigid cell wall. This limits them to being saprophytic on organic substrates, or parasitic on living animals, plants, algae, protozoa or other fungi. The classification of the fungi is based on the pattern of their spore formation. The four phyla are:

1 Zygomycotina: typically ephemeral saprophytic opportunists, spreading quickly through habitats rich in simple carbohydrates or starch, and rapidly sporulating; sporangiospores formed in large numbers, readily dispersed by air current or water droplets; and mycelium coenocytic, i.e. without regular cross-walls. A few species are parasitic on other fungi, animals or plants.

2 Ascomycotina: septate hyphae; saprophytes and parasites. Many cause the soft rots of stored products. The hemiascomycetes (with their ascospores formed in a naked ascus, and not in a structured fruiting body) include the familar yeast, *Saccharomyces cerevisiae*.

3 Deuteromycotina: lacking a known sexual phase, most probably allied to Ascomycotina.

4 Basidiomycotina: mushrooms and toadstools, as ephemeral fruiting bodies, produce large numbers of basidiospores from a parent mycelium made of a continuum of interconnecting hyphae that can be very large and old (e.g. as old as the tree in the case of a mycorrhizal fungus, and sometimes many hundreds of years old in the case of fairy rings); many are important wood rotters, giving rise to brown rots and white rots. Heterobasidiomycetes, with septate basidia, include the smuts and rusts, important plant parasites.

THE PROTISTA

Although forming a coherent Kingdom, these eukaryotic microbes present an enormous variety of form, function and habitat. Their diversity is such that phylogenetic considerations have little relevance to the ecologist. Thus the Euglenophyta contain many phototrophic species, but also many saprotrophic species and phagotrophic species. In this and many other cases, it is best for the ecologist to take a functional view and to call the phototrophs algae and the heterotrophs protozoa.

The algae [44] are of immense importance as the primary producers in the seas and lakes, but are also found in the surface layers of soil and on such substrates as moist tree trunks. The limits of microbiology become blurred when dealing with the algae. For example, a giant kelp many metres long is not usually considered grist for the microbiologist's mill. However, nearly all groups of algae contain species that are solely unicellular, and so are unequivocally microbes. Some algae can live heterotrophically. For example, living diatoms without chlorophyll are found in the darkness of marine sediments, where they survive on dissolved organic matter and may produce cellulases. Some algae occur as phototrophic symbionts of invertebrates. The most important of these in terms of global productivity are the 'zooxanthellae', now known to be dinoflagellates, which are intracellular symbionts in corals. Here they photosynthetically fix carbon dioxide and at the same time control the calcification of the coral skeleton. Some algae which lack a rigid cell wall can also engulf particles of food, and so can practise photosynthetic, absorptive or phagocytic acquisition of nutrients.

The algae have been classified traditionally by pigmentation and life cycle. The principal phyla of interest to microbial ecologists, i.e. those with planktonic or single-celled existence, are summarized below:

1 Rhodophyta, the red algae: principally marine and multicellular, immotile, some unicellular forms occur in sand or encrusting rock pools.

2 Chlorophyta, the green algae: many planktonic species, freshwater and marine, motile by flagella, others multicellular, motile or sessile.

3 Euglenophyta: unicells, motile by a single flagellum and also by 'euglenoid motion', a squirming of the body of the cell; common in nutrient-rich freshwater pools, also found in the sea and in the soil.

4 Bacillariophyta, diatoms: in microplankton of seas and lakes; motile by gliding; with silica frustules which are species-specific, and which readily survive in sediments and fossil deposits to enable a picture of the phytoplankton existing at former points in time to be built up.

5 Dinophyta, dinoflagellates: in microplankton of seas and lakes; motile with two flagella; some cause 'red tides', which can result in fish mortality by the production

of toxins, others are luminescent and cause the nocturnal phosphorescence of warmer seas.

6 Chrysophyta; biflagellate cells, chiefly found in fresh water, also the marine silicoflagellates.

7 Haptophyta: biflagellate planktonic algae; many are species of the nanoplankton. The coccolithophorids have a covering of calcified scales; blooms of these species can give the sea a milky appearance and coccoliths from dead cells can build up in the sediments.

There is much information on the occurrence and distribution of many of the algae in the microplankton [46] as diatoms are readily collected in plankton-sampling nets and microscopically identified. However, in many parts of the ocean and in most lakes the most abundant and the most productive algae are the nanoplankton; these forms may be as small as 2 μm in diameter and pass readily through the finest netting. Special techniques such as the use of inverted microscopes, epifluorescence, and electron microscopy, are needed to identify and count them.

The protozoa [37] exhibit a very wide range of form and way of life. In some species the adult cell is very large and has a remarkably complex structure. Many are predators on bacteria, fungi (see Section 2.1.8), algae, yeasts or other protozoa, and many are parasitic or symbiotic in animals (see Chapter 3.3). As mentioned above, many shown close phylogenetic affinities with unicellular algal forms. Some can lead a secondary phototrophic existence by having algal endosymbionts (see Section 2.1.8). The major phyla of interest to the microbial ecologist are summarized below:

1 Sarcodina, the amoeboid protozoa: in a wide variety of habitats; free-living amoebae as predators in the soil; the foraminiferans and radiolarians, with their intricate calcified and silicified skeletons in the marine plankton, accumulating in the bottom ooze to form beds of sediments; human and animal pathogens; and the slime moulds, whose feeding stage is as amoebae (see below).

2 Ciliophora: includes the familiar ciliates of hay infusions, *Tetrahymena* and *Paramecium*, and many other very intricately structured cells; some such as *Vorticella* are important in sewage treatment processes, where bacteria, other microbes and detritus form their food (Chapter 4.4).

Also phylogenetically clearly in the Kingdom Protista, not least by virtue of their having motile stages and '9 + 2' flagella, are the following groups that ecologically can be thought of as fungi:

3 Phycomycota: including the oomycetes, water moulds or pathogens of plants or fish; and the hyphochytridiomycetes, water moulds.

4 Chytridiomycota: water moulds living on detritus such as fallen leaves or parasitic on algae, protozoa or cyanobacteria.

5 Labyrinthomorpha: marine amoeboid cells moving in tubes of their own making; *Labyrinthula macrocystis* has caused considerable coastal ecological changes during this century in Britain by causing wasting disease of the marine eel grass, *Zostera marina*.

6 Slime moulds: phylogenetically they are best thought of as amoebae, but they have been considered as fungi as they produce macroscopic fruiting bodies, either by aggregation of amoebae to form a pseudoplasmodium (e.g. *Dictyostelium*) or by the amoeba forming a multinucleate feeding plasmodium which then forms the fruiting body (e.g. *Physarum*).

2.1.2 THE SIZE OF MICROBES

The small size of a bacterium means that a habitat can be correspondingly small. It also means that a small volume can contain a very large number of organisms or potential propagules. From a practical point of view it also means that only rarely can direct observations be made of the numbers and identities of microbes in natural environments.

The sizes of microbes (Table 2.1.1) show steps greater than an order of magnitude of increasing size between typical viruses, prokaryotes and eukaryotes. There is little variation in the size of the bacteria, most of the cultured forms being in the range 1–3 μm by 0.5–1.5 μm. However, most planktonic bacteria in lakes and oceans are small cocci or rods between 0.2 and 0.6 μm in diameter. Extremes of size include cells of *Mycoplasma* spp. at 0.1 μm in diameter and the purple sulphur bacterium *Thiospirillum jenense* at 40 by 4 μm. There is a much greater range of cell size among the eukaryotic microbes, with a range in the algae represented by the prasinophycean marine alga *Micromonas pusilla* at 1 by 0.7 μm and the giant marine diatom, *Ethmodiscus rex*, at 2000 μm in diameter.

Within any species there can be a marked range of sizes of vegetative cells (see Table 2.1.2) as they tend to increase in size with increasing growth rate. For example, for ten species of bacteria [24] the log phase cells in batch culture were an average of 2.4 times as large as stationary cells. The primary hyphae of *Neurospora crassa* quoted in Table 2.1.2 were growing nearly three times as fast as the secondary branches. Many diatoms also show a range of size, as on cell division each daughter cell forms a new

Table 2.1.1. The sizes of micro-organisms (from various sources)

Organism	Dimensions (μm)	Generation time (h)	Swimming speeds (μm sec^{-1})
Viruses			
Poliovirus	0.03 × 0.03	—	—
Tobacco mosaic	0.3 × 0.02	—	—
T_2-Bacteriophage	0.2 × 0.06	—	—
Prokaryotes			
Marine bacteria	0.2 diam.	?	?
Pseudomonas aeruginosa	1.5 × 0.5	0.5	60
Serratia marcescens	1.7 × 1.0	0.5	30
Bacillus megaterium	7.6 × 2.4	0.3	20
Eukaryotes			
Mucor hiemalis	8 diam.	3	—
Euglena gracilis	50 × 15	7	230
Paramecium caudatum	250 × 50	10	1000
Stentor coeruleus	1000 × 200	34	—

Table 2.1.2. Range of cell size in some species (from various sources)

Species	Size (μm)	Volume (μm^3)	Conditions	Remarks
Salmonella typhimurium	1.43		Doublings h^{-1} 2.73	Size is cell thickness
	0.87		Doublings h^{-1} 0.61	
		1.24	Doublings h^{-1} 2.0	
		0.33	Doublings h^{-1} 0.13	
Nostoc species	5 × 13	240	In oldest leaf	The symbiont of *Azolla*
	4 × 5	40	In youngest leaf	
Neurospora crassa	11.7	(1075)	Primary hyphae	Volume quoted for 10 μm of hypha
strain spco-9	5.7	(255)	Secondary branches	
Stephanodiscus astraea	70.6	62 603		Range of diameters of the diatom in Britain
var *minutula*	18.4	2657		
Saccharomyces cerevisiae		49.1	Doublings h^{-1} 0.33	
		29.0	Doublings h^{-1} 0.14	

silica valve to fit inside its respective parent valve. Thus, the average surface area of the valves of an actively growing population gets progressively smaller, until eventually, after perhaps several years, a new large cell is formed from an auxospore. This decrease in surface area may to some extent be compensated for by the cells becoming thicker, but nevertheless the size and shape of a diatom cell in plankton must be an important determinant for such properties as sinking rate, photosynthetic yield, and growth rate. These properties presumably are not critical for the cells' survival within the limits imposed by the changes in size. Another diatom, *Stephanodiscus astraea*, shows a seasonal change in size, being larger in the winter (34 μm diameter) than in summer (24 μm).

Increasing size has a number of consequences for a microbial cell. Larger cells have the potential for greater adaptability as they have more space for genetic material and the enzymic machinery. There is clearly a lower limit of size for a cell to contain the essential equipment for self-replication, and presumably the smallest free-living bacteria approach this size. Thus, any increase in size for such a modest bacterium would give it the chance of packaging more information, which would permit it to be more adaptable. Increasing size, however, reduces the vital ratio of surface area to the volume as the former is a function of the square of the cell radius and the latter of the cube. This decreasing ratio must limit the upper size of a prokaryotic cell, which is dependent on its cell