

niches  
bacteria

## Speculations on niches occupied by fungi in the sea with relation to bacteria

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**Abstract.** The significance of fungi in the marine environment is poorly known when compared with the bacteria. Based on information available on bacteria and fungi in the sea and their structural characteristics, the various niches where the latter may play important roles is speculated upon in this article. Among the 3 niches discussed, the fungi, including thraustochytrids may be significant endobionts in substrates such as dead and living plants and calcareous shells. Substantial information is already available on fungi in decaying salt marsh grass and mangrove leaves, seedlings and wood and on parasites in macro- and microalgae. The need to investigate fungi as epibionts on surfaces of various organic and inorganic substrates and also sediments has been stressed. While bacteria are known to be significant as planktonic forms, thraustochytrids and yeasts in this and other niches have not been studied in detail.

**Keywords.** Fungi; bacteria; sea; niches.

### 1. Introduction

The role of fungi in terrestrial and freshwater ecosystems is well known when compared with information available on the marine environment. Although fungi occur commonly in the sea as parasites of living organisms and on dead organic matter (Jones 1976; Kohlmeyer and Kohlmeyer 1979; Moss 1986a), their importance in the processes in the sea has still not been sufficiently evaluated. Authors of standard works on marine microbiology and marine ecology (Sieburth 1979; Rheinheimer 1980; Parsons *et al* 1984; Knox 1986) have at most been able to make only vague remarks about their role in the sea. Several papers on the relative roles of bacteria and fungi in the sea have appeared (Fallon and Pfaender 1976; Morrison *et al* 1977; Cundell *et al* 1979; Morrison and White 1980). A few workers have even stated that fungi do not play a major role in the sea (Hanson and Wiebe 1977). These studies, however, have not paid attention to two points. (i) Most marine microbiological studies have not encompassed spatial niches which are likely to harbour great numbers of fungi. One of the objectives of this article is to elaborate that not all niches in the marine environment will be equally conducive to both bacteria and fungi. While the two groups of organisms might share the same niche in certain cases, either one of them might often also dominate certain other niches not preferred by the other. The key to these differences would lie in the structural and physiological characteristics of both these groups (Cooke and Rayner 1984). (ii) The role of yeasts and the unicellular marine microorganisms, the thraustochytrids, which for practical purposes are considered fungi by mycologists, have not been examined.

For the purpose of this discussion, the niches occupied by bacteria and fungi have been divided into 3 categories and each case examined independently.

## 2. Occupants of various niches

### 2.1 Planktonic forms: Utilising nutrients dissolved and uniformly distributed in an aqueous milieu

Oceanic water contains 0.4–2 mg l<sup>-1</sup> dissolved organic carbon (DOC) (Parsons *et al* 1984). Estuarine waters contain considerably more than this (Knox 1986). DOC in seawater arises due to phenomena such as leaching from macrophytes and microalgae, 'sloppy-feeding' of herbivores, autolysis, excretion of animals and terrestrial input (Valiela 1984; Knox 1986; Azam and Cho 1987).

Microorganisms can utilise DOC by living planktonically suspended. A small size is of advantage in this mode of life, by reducing the sinking rate (Hughes 1980) and increasing the surface to volume ratio. Many planktonic bacteria may be as small as 0.2 µm in size (Sieburth 1979). The mode of reproduction by bacteria, namely by division into two, followed by separation into two daughter cells results in a rapid dissemination in the aquatic environment. They have very high-affinity transport systems with saturation constants of up to 10<sup>-8</sup> M for readily assimilable compounds and can efficiently scavenge dilute dissolved organic compounds down to concentrations of a few µg per litre in the water (Pomeroy 1980; Azam and Cho 1987). Bacterial numbers vary from 0.1 × 10<sup>8</sup> l<sup>-1</sup> in the deep sea to 50 × 10<sup>8</sup> l<sup>-1</sup> in coastal waters, of which 80–90% may be planktonic (Azam *et al* 1983). Bacteria in the water column of kelp beds can convert up to 29.4% carbon of kelp mucilage into their own cell carbon (Lucas *et al* 1981). Leachates of *Spartina alterniflora* are utilised more efficiently by bacteria than fungi (Fallon and Pfaender 1976). Bacteria were also reported to be more important than fungi in the water column of seagrass beds and sediments (Moriarty *et al* 1985).

There is no proven instance of mycelial fungi growing planktonically in the sea. Although one might isolate a number of fungi from seawater, these either might come from dormant spores or from mycelium in solid debris from terrestrial habitats (Campbell 1983). The larger size of mycelial fungi as compared to bacteria and filamentous habit may not be suited for a planktonic mode of life. On the other hand, the unicellular fungi, yeasts are common in the water column (Fell 1976), although much lower in number than the bacteria. This might be due to the fact that the dissolved organic carbon levels of seawater are too low for the active growth of yeast cells, which are much larger in size than bacteria and have a lower surface to volume ratio and possess saturation constants of only up to 10<sup>-6</sup> M for easily assimilable compounds (Newell 1984). Where the seawater contains a high amount of dissolved organic carbon, as during algal blooms or in polluted waters, planktonic yeasts may be common (Sieburth 1979). Information on the number and role of yeasts in the sea is meagre and this area needs more detailed investigation.

Among fungi, the unicellular thraustochytrids (Moss 1986b) appear to be the commonest in the sea (Bremer 1976; Miller and Whitney 1981b), with numbers up to 640 cells l<sup>-1</sup> in the open sea, 6000 cells l<sup>-1</sup> in coastal waters (Raghukumar and Gaertner 1980) and 10,700 cells l<sup>-1</sup> in coral reef lagoons (Raghukumar 1987). Vegetative cells of thraustochytrids are 5–20 µm in size. Most known species produce a rhizoid-like ectoplasmic net system which is presumed to aid in penetration and/or attachment to particles and absorption of nutrients (Perkins 1973; Moss 1986b; Coleman and Vestal 1987). The presence of the ectoplasmic net

system would suggest that they live attached to particles. However, at least two species of thraustochytrids, *Althornia crouchii* Jones and Alderman (1971) and *Corallochytrium limacisporum* Raghukumar (1987) do not produce an ectoplasmic net system. Besides, many thraustochytrids display 'mini-cycles' of zoospore-cyst-zoospore which might help these organisms to persist or even thrive planktonically in nutrient poor waters (Kazama *et al* 1975). Still very little is known about their mode of life in the sea and the presently employed cultural techniques (Gaertner 1968; Raghukumar 1986) are not adequate to resolve if thraustochytrids occur as planktonic forms.

## 2.2 Endobionts: Organisms utilizing nutrients present within solid substrates

Dead plants and animals, particularly the former can be utilised by microorganisms either from the surface inwards or nutrients can be directly removed from within as well. Leaves and wood of mangroves, species of seagrasses such as *Thalassia* and *Zostera*, the salt marsh grass *Spartina* and the larger seaweeds such as *Sargassum* and *Laminaria*, as well as filamentous algae all provide such substrates. In coastal waters, macrophytic plants make an enormous contribution to primary production with productivities ranging from 2000–3400 g organic matter/m<sup>2</sup>/yr, comparable to that of many cultivated crop plants (Teal 1980; Knox 1986). In the pelagic ecosystem, diatoms and microalgae offer a substrate for microorganisms.

The ability to directly utilise nutrients present within a solid substratum by penetrating and growing within it is one of the most fundamentally important attributes of mycelial fungi (Cooke and Rayner 1984).

The interior of dead plant substrata in the sea may be heavily colonised by fungi. A great amount of work has been particularly carried out on fungi in wood submerged in the sea (Barghoorn and Linder 1944; Kohlmeyer and Kohlmeyer 1979; Mouzouras *et al* 1988). Mycelial fungi are common within dead tissues of the salt marsh grass (Gessner 1977; Newell *et al* 1986), mangrove leaves (May 1975; Fell and Master 1980), mangrove seedlings (Newell 1976) and mangrove wood (Kohlmeyer and Kohlmeyer 1979; Hyde and Jones 1988). Fell and Newell (1980) presented evidence on the role of fungi in carbon and nitrogen immobilization in coastal marine plant litter systems, based on regularly occurring mycoseres, electron microscopy, biochemical indicators and experiments with microecosystems.

Calcareous shells of animals harbour abundant mycelium of microboring fungi within, the fungi probably utilising the organic components in the shells (Kohlmeyer 1969; Rooney and Perkins 1972; Sieburth 1979). Perkins and Halsey (1971) found fungi to be the most widespread and abundant microboring organisms in all their 165 samples of animal calcareous material from continental margin sediments off North and South Carolina, from the intertidal to 758 m depth. The extremely frequent occurrence of fungi in skeletons of reef corals led Bak and Laane (1987) to believe that fungi might play a major role in the coral ecosystem. Foraminiferan tests harbour endobiontic fungi (Kohlmeyer 1984). The importance of mycelial fungi in the recycling of calcareous animal structures in the sea deserves detailed studies.

Fungi have also been reported to be able to penetrate and grow inside a man-made material, polyurethane in the sea (Jones and LeCampion-Alsumard 1970). In general, substrata large enough to support the growth of mycelium and not too

rapidly decomposed by bacteria before the mycelium can establish itself can be expected to harbour filamentous fungi.

Apart from filamentous fungi, the thraustochytrid and labyrinthulid fungi can also penetrate solid substrata. Perkins (1973) demonstrated the penetration of plant cell walls by the ectoplasmic net elements of thraustochytrids and their subsequent growth within the cell lumen. Miller and Jones (1983) have observed thraustochytrids within the kelp, *Fucus serratus* L. In spite of numerous reports, detailed studies on the role of thraustochytrids in the decomposition of macrophytic plants, and phyto- and zooplankton are not available.

Fungi are important agents of plant diseases on land since they can penetrate and grow within the plant substratum. They could be important plant parasites in the sea as well. Numerous mycelial fungi, mostly belonging to the Ascomycetes parasitise larger thallose algae (Andrews 1976; Kohlmeyer and Kohlmeyer 1979; Porter 1986). Single-celled phycomycetous fungi and thraustochytrids may live as epiparasites on filamentous algae and diatoms. The rhizoids of phycomycetous fungi and the ectoplasmic net elements of thraustochytrids penetrate the host cells and draw nutrients. They may also be endoparasites (Gaertner 1979; Chandralata Raghukumar 1986, 1987; Porter 1986). *Labyrinthula* sp. grow within living tissues of the seagrass *Zostera* and causes the wasting disease (Short *et al* 1987).

Unicellular bacteria are not capable of substantially penetrating solid substrata and growing inside. Even the burrowing bacteria in wood (Mouzouras *et al* 1988) and the actinomycetes have only a limited capability to do so.

This difference in niche between bacteria and fungi has not been sufficiently appreciated by many workers who have looked for mycelial fungi only on the outside of macrophytic material (Morrison *et al* 1977; Bobbie *et al* 1978; Morrison and White 1980). Cundell *et al* (1979) observed fungal infestation of *Rhizophora* leaf surfaces only after 14 days using SEM, whereas Fell and Master (1980) using cultural techniques found them to be present throughout the decomposition of mangrove leaves. Using direct observation as well as other techniques, Newell and Hicks (1982) showed that fungi contributed up to 27% of the volume of decomposing leaf of *Spartina* and bacteria, 0.7%.

In their studies on decomposing salt marsh grass, Benner *et al* (1986) concluded that bacteria were more important than fungi in lignocellulose degradation. However, it would appear that the authors have not observed decompositional stages most likely to harbour lignocellulolytic fungi. Biomass and species of fungi in detritus depend on the stage of decomposition, those actively utilising lignocellulose appearing late (Cooke and Rayner 1984). The biomass of thraustochytrids, likewise may depend on the decompositional stage, such as after leaching out of carbohydrates and phenols (Miller and Jones 1983).

Blum *et al* (1988) concluded that bacterial biomass was considerably higher than that of fungi in seagrass and mangrove detritus. However, the direct microscopy technique involving homogenisation used by these authors might seriously underestimate fungal biomass (Newell *et al* 1986).

In order to assess fungal biomass, the following points will have to be considered: (i) Mycelial fungi should be looked for within solid organic substrata using suitable techniques, (ii) different decompositional stages must be examined and (iii) the presence and abundance of thraustochytrids must be considered.

### 2.3 Epibionts: Organisms utilising nutrients present on the surfaces of solid substrata

The surfaces of both organic and inorganic substrata suspended in an aqueous medium offer a niche for microorganisms. In the former, nutrients could be exuded by the substratum. Larger algae, seagrasses and diatoms constantly exude dissolved organic compounds (Valiela 1984; Knox 1986; Azam and Cho 1987). The external surfaces of living animals may be colonised by microorganisms (Sieburth 1979). The surfaces of animal guts are bathed in nutrients and could provide a niche for bacteria and fungi. In the case of inorganic substrata, various nutrients including biological macromolecules get adsorbed onto the surfaces, thereby offering better conditions for microbial growth than the surrounding water (Campbell 1983; Costlow and Tipper 1984; Characklis and Escher 1988).

Bacteria are the first settlers on surfaces of uncolonised substrata in water. Bacteria growing on the surfaces of dead macrophytes and phytoplankton play an important role in their decomposition (Stuart *et al* 1981; Fukami *et al* 1985; Biddanda and Pomeroy 1988; Blum *et al* 1988). An abundant bacterial flora is found in the guts and on surfaces of animals (Sieburth 1979). On fresh inorganic surfaces, bacteria grow rapidly to form a primary film and are responsible for biofouling and corrosion in the sea (Costlow and Tipper 1984; Characklis and Escher 1988).

Dead macrophytic substrata in the sea internally colonised by fungi may also harbour fungal mycelia on their surfaces (Cundell *et al* 1979; Morrison *et al* 1977; Bobbie *et al* 1978). Fungi grow on surfaces of mangrove prop roots and are avidly fed upon by snails (Kohlmeyer and Bebout 1986). Fungal hyphae may be present on live algal surfaces, although in low numbers (Miller and Whitney 1981a). Fungal hyphae which had penetrated polyurethane coatings were also found on their surface (Jones and LeCampion-Alsumard 1970). Filamentous fungi may not be rare in the guts of marine animals. Hibbits (1978) found large numbers of fungi belonging to Trichomycetes in the guts of 17 of 45 species of Crustacea she examined.

However, mycelial fungi appear to be rare in the primary film of inorganic substrates when compared to bacteria, as judged by the numerous observations using SEM (Sieburth 1975; Bobbie *et al* 1978). This is probably due to the fact that bacteria are at a greater competitive advantage on such surfaces and take up the dilute nutrients more rapidly. However, a particular situation in this connection seems to have been overlooked. The arenicolous or sand-inhabiting fungi (Kohlmeyer and Kohlmeyer 1979; Koch and Jones 1984) draw nutrients from a discrete organic base in the sediment and produce a profusion of hyphae which spread out and grow on the surfaces of sand grains producing ascocarps strongly adhering to them. This space-invading mode of life is one of the characteristics of mycelial fungi and is well known among fungi in terrestrial soils (Campbell 1983; Cooke and Rayner 1984). Many terrestrial species of fungi have also been isolated from marine sediments (Kohlmeyer and Kohlmeyer 1979) and probably live similar to the arenicolous fungi. However, the conventional techniques employed in such isolations do not provide evidence as to whether terrestrial species of fungi grow actively in the marine muds or occur only as dormant spores. Mycelial fungi are highly adaptable and therefore, theoretically it is not impossible for fungi to thrive in aerobic marine sediments.

Yeasts occur on the surfaces of animals, their guts and on seaweeds (Sieburth 1979). A very high number of them might occur during certain stages of decomposition of plant organic matter as has been reported for the salt marsh grass *Spartina* by Meyers (1974). However, little information on their role in surface films of organic and inorganic substrata is available.

Thraustochytrids are common as epibionts on living macrophytes (Sparrow 1969; Miller and Jones 1983) and diatoms (Gaertner 1979; Chandralata Raghukumar 1986). A high number of thraustochytrids are present in the guts of various animals such as sea urchins (Wagner-Merner *et al* 1980), sponges (Höhnk and Ulken 1979; Richter 1985) and hydroids (Raghukumar 1988). These fungi have been isolated from plastic surfaces submerged in the sea (Sparrow 1969). Sediments harbour a high number of 73,000 thraustochytrids per litre (Raghukumar and Gaertner 1980; Jacobsen 1983; Riemann and Schrage 1983). One might expect thraustochytrids to be present on particles as small as 20  $\mu\text{m}$  diameter, since the individual cells of known species of thraustochytrids are 5–20  $\mu\text{m}$  in size. The role of these organisms on various surfaces in the sea deserves attention.

### 3. Conclusion

It has been rightly pointed out by Karl (1982) that 'future studies in microbiological oceanography and marine biogeochemistry would undoubtedly benefit from a careful analysis of the structure of individual microbial assemblages'. It has been the aim of this article to speculate upon the niches in the sea where fungi might contribute significantly to the microbial assemblage. The utilisation of low concentrations of nutrients in the water column of the oceans might be carried out more efficiently by the bacteria by virtue of their small size and high affinity transport systems. However, the role of fungi in the sea might be greater than hitherto recognized, since niches suitable for growth of different groups of fungi are plentiful as schematically indicated in figure 1. There is strong evidence for an important role for fungi in many niches. (i) Large macrophytic tissue such as that of *Spartina*, mangroves and wood may be colonised extensively by mycelial fungi.

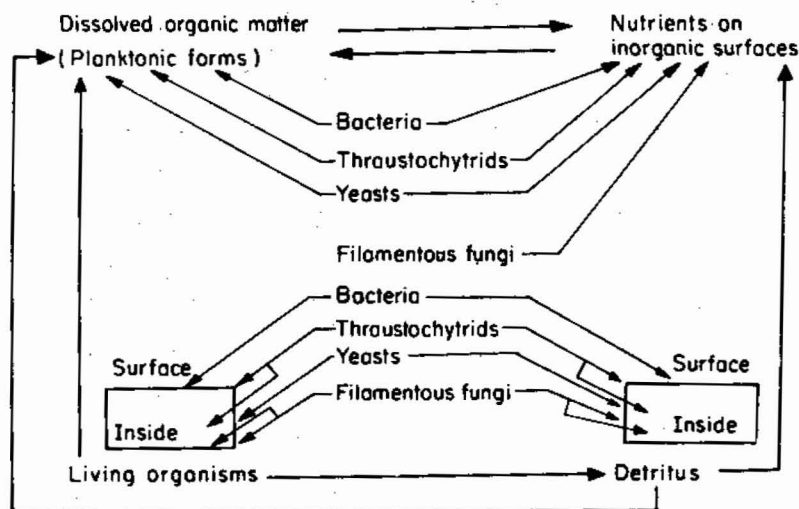


Figure 1. Various niches in the sea occupied by bacteria and different groups of fungi.

(ii) Thraustochytrids and yeasts are present in numbers of up to several hundreds each per litre water in the sea. (iii) Thraustochytrids are extremely abundant in the marine sediments. Thraustochytrids, yeasts and Trichomycetes are common in guts of animals. Numerous situations in the sea have not been adequately explored for fungi. Thus, the role of mycelial fungi in marine muds has still not been satisfactorily answered. The role of thraustochytrids in the decomposition of macrophytic plants as well as phyto- and zooplanktonic organisms has not been investigated. Studies on the role of fungi should consider mycelial fungi, yeasts and thraustochytrids together. A major handicap in resolving many problems on the role of fungi in the sea has been the lack of suitable techniques to estimate the biomass of fungi. Mycelial fungi cannot be estimated in terms of numbers as can be done for bacteria. Their sheltered habitat inside plant substrates adds to the problem. Yeasts and thraustochytrids cannot be easily recognised by microscopic observation of natural samples. Wider application of recent techniques including direct microscopy (Newell and Hicks 1982), use of chemical indicators such as ergosterol (Lee *et al* 1980), fatty acid profiles (Findlay *et al* 1986) and immunological techniques (Newell *et al* 1986; Raghukumar 1988), besides development of newer techniques to estimate fungal biomass might lead to a more complete understanding of the role of fungi and microbial processes in the sea.

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