Fungal Diversity

Marine fungi: some factors influencing biodiversity

E.B. Gareth Jones[1]

Department of Biology and Chemistry, City University of Hong Kong, 83 Tat Chee Avenue, Kowloon, Hong Kong, and BIOTEC, National Center for Genetic Engineering and Biotechnology, 73/1 Rama 6 Road, Bangkok 10400, Thailand; e-mail: bhgareth@yahoo.com

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This paper reviews some of the factors that affect fungal diversity in the marine milieu. Although total biodiversity is not affected by the available habitats, species composition is. For example, members of the Halosphaeriales commonly occur on submerged timber, while intertidal mangrove wood supports a wide range of Loculoascomycetes. The availability of substrata for colonization greatly affects species diversity. Mature mangroves yield a rich species diversity while exposed shores or depauperate habitats support few fungi. The availability of fungal propagules in the sea on substratum colonization is poorly researched. However, *Halophytophthora* species and thraustochytrids in mangroves rapidly colonize leaf material. Fungal diversity is greatly affected by the nature of the substratum. Lignocellulosic materials yield the greatest diversity, in contrast to a few species colonizing calcareous materials or sand grains. The nature of the substratum can have a major effect on the fungi colonizing it, even from one timber species to the next. Competition between fungi can markedly affect fungal diversity, and species composition. Temperature plays a major role in the geographical distribution of marine fungi with species that are typically tropical (e.g. *Antennospora quadricornuta* and *Halosarpheia ratnagiriensis*), temperate (e.g. *Ceriosporopsis trullifera* and *Ondiniella torquata*), arctic (e.g. *Spathulospora antartica* and *Thraustochytrium antarticum*), while others are cosmopolitan (e.g. *Ceriosporopsis halima* and *Lignincola laevis*). Salinity is also important in affecting species composition. Many fungi occur primarily in fully saline waters (e.g. *Lindra inflata* and *Ondiniella torquata*), others are more frequent in brackish water (e.g. *Amylocarpus encephaloides* and *Aniptodera chesapeakenis*), while terrestrial and freshwater species may be able to grow at lower salinities (e.g. *Chytridium citriforme*, *Saprolegnia ferax* and *Stachybotrys atra*). In mangroves many species (e.g. *Halophytophthora* species), can tolerate great variation in salinity of the water. Some marine fungi are common in occurrence (e.g. *Ceriosporopsis halima*, *Lulworthia* spp., and *Zalerion maritimum* in temperate waters, and *Antennospora salina*, *A. quadricornuata* and *Lulworthia grandispora* in the tropics), while others are rarely collected (e.g. *Orbimyces spectabilis* and *Torpedospora ambispinosa*). For the latter group this may be due to seasonality (e.g. *Mycaureola dilsea* on

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[1] I dedicate this essay to three scientists who have greatly influenced my thinking and have been a wonderful source of inspiration: John Savory (for opening new horizons for a young undergraduate), Dr. David Houghton (who taught me a great deal about human nature) and Emeritus Professor John Levy (who by example, showed the way to look for the good in people).

Dilsea edulis) or have a specific temperature requirements (e.g. *Digitatispora marina* occurring during the winter months when water temperatures are below 10 C). For other species there is no apparent reason to explain their infrequent occurrence. A plethora of factors may govern the occurrence of marine fungi in a particular habitat or on a substratum. Many are subject to a consortium of factors operating together in controlling the biodiversity of fungi in the sea.

Key words: biodiversity, geographical distribution, habitats, inhibition competition, salinity, substrata, temperature.

Introduction

The ecology of marine fungi and their habitat preference, and the factors affecting and influencing their growth in the sea are examined. Particular reference is made to the effects of habitats, availability of substrata for colonization, geographical distribution and temperature, salinity, inhibition competition and microhabitats on marine fungal diversity. However, these are only a few of the factors that have an effect on the occurrence and distribution of marine fungi. Others include dissolved organic nutrients, hydrogen ion concentration, osmotic effects, oxygen availability, pollutants, abundance of propagules in the water, ability to impact on to and attach to suitable substrata, hydrostatic pressure, substrate specificity, temperature and tidal amplitude and perhaps even light (Booth and Kenkel, 1986). Species diversity of marine fungi is therefore controlled by an amalgam of interacting factors.

Examples selected for review are not meant to be exhaustive but rather indicative of observed trends.

Habitats within the marine ecosystem

Five decades of marine mycology have clearly demonstrated that marine fungi are distinct from their terrestrial and freshwater counterparts, both in their taxonomy, morphology and adaptation to an aquatic habitat (Barghoorn and Linder, 1944; Johnston and Sparrrow, 1961; Jones, 1976; Kohlmeyer and Kohlmeyer, 1979; Meyers, 1996). Some of these fungi however, may occur in both seawater and freshwater or terrestial habitats. This is seen at both species (e.g. *Savoryella lignicola*, *Lignincola leavis* found in marine and freshwater habitats) as well as at the generic level [e.g. *Leptosphaeria*, *Pleospora*, *Trematosphaeria* (Ascomycota), *Calathella* (Basidiomycota) and *Alternaria* (mitosporic) found in marine and terrestrial habitats (Kohlmeyer and Volkmann-Kohlmeyer, 1991)].

Although the term "marine" is used to encompass all fungi that occur in the sea, they are often labeled marine, oceanic, manglicolous, arenicolous or estuarine. Mangrove fungi, for example, can be quite distinct from those occurring in the deep sea or oceanic and coastal waters. *Antennospora quadricornuata*, *Arenariomyces* species and *Corollospora* species and

Torpedospora radiata are typically fungi of coastal and oceanic waters, while *Hypoxylon oceanicum*, *Kallichroma tethys* and *Leptosphaeria australiensis* are generally found on mangrove substrata (Jones and Hyde, 1990). Some, such as *Ligníncola laevis* and *Periconia prolifica* are found in both habitats. Marine fungi occurring in specific habitats may be morphologically adapted to these. Oceanic fungi (e.g. Halosphaeriales) grow under submerged conditions, generally have asci that deliquesce early and release their ascospores passively (Fazzani and Jones, 1977). They also possess ascospores with elaborate appendages, which aid in floatation, impaction and increase the surface area for entrapment and attachment to suitable substrata (Rees, 1980; Rees and Jones, 1984; Hyde *et al*., 1986; Jones, 1994). Mangrove fungi on the other hand, tend to be intertidal, their ascospores have mucilaginous sheaths, lack elaborate appendages and are actively discharged (Hyde, 1990a,b; Read *et al*., 1992; Read *et al*., 1994; Au *et al*., 1999).

Deep-water fungi are also unique and different from those of mangroves and coastal waters. They include *Abyssomyces hydrozoicus* (recovered on wood from 631-641 m depth), *Bathyascus vermisporus* (1615-1720 m depth) and *Oceantis scuticello* (3975 m depth) (Kohlmeyer and Kohlmeyer, 1979). At these depths conditions differ significantly from those in coastal waters. Salinity is near 35 ‰, pH is 7.8-8, oxygen is 3-5 ml L, temperature is 2-2.4 C, pressure is high and substrata are sparse (Kohlmeyer and Kohlmeyer, 1979). The last three factors clearly have a profound effect on the diversity of species at these depths (Jones and Le Campion-Alsumard, 1970; Kohlmeyer and Kohlmeyer, 1979). Lorenze and Molitoris (1997) demonstrated that three marine yeasts could tolerate the pressures encountered in the deep sea: two tolerate pressures of 20 Mpa while the third tolerated 40 Mpa, which is equivalent to that at a depth of 4000 m. Raghukumar and Raghukumar (1998) have shown that two filamentous fungi (*Aspergillus ustus* and *Graphium* sp.), isolated from calcareous shells recovered from depths of 860 m and 965 m, were able to germinate, grow vegetatively and sporulate at a pressure of 100 bar. With further exploration of the ocean depths new marine fungi may be encountered. However, fungal diversity at these depths is likely to be low and new techniques for their enumeration would have to be developed.

Availability of fungal propagules and substrata in the marine ecosystem

A wide range of substrata are available in the sea and have been shown to be colonized by a number of fungi (Kohlmeyer and Kohlmeyer, 1979; Jones and Mitchell, 1996). The abundance of material for colonization varies from site to site and location. Mangroves are generally rich in substrata with an abundance of mangrove leaf litter and dead wood from trees cut for fire wood, and trees thinned out in managed forests, e.g. Matang mangrove, Malaysia

(Awang and Gan, 1989). Other habitats/localities may have little wood available for colonization by fungi [e.g. Spain in the Mediterranean Sea (Jones, unpublished data), Antarctic waters (Pugh and Jones, 1986) and the coast of Kuwait (Zainal and Jones, 1984)], with the result that fungal diversity is low with 20, 9 and 12 species respectively.

Fungal diversity may also vary from one mangrove to the next. This may range from 30 to 41 species for Singapore mangroves (Tan and Leong, 1990), 82, 51-64 species in Malaysian mangroves (Jones and Kuthubutheen, 1989; Alias *et al*., 1995), to 76 species from 650 samples in Ranong, Thailand (Hyde *et al*., 1990), to and 43-62 species in Belize (Kohlmeyer and Volkmann-Kohlmeyer, 1987). However, only seven species were recorded for Moorea mangroves, in Hawaii (Kohlmeyer and Volkmann-Kohlmeyer, 1993). The low species diversity at Moorea was attributed to the scarcity of dead wood arising from a small and young mangrove stand (established 30 years ago), and had only one mangrove tree species present (*Rhizophora stylosa*).

Little is known of the number of fungal propagules in seawater. Fazzani and Jones (1977) recorded eight spores of marine fungi per L, while high densities have been documented for thraustochytrids in seawater (10-710 per L) and sediments (2,000-18,500 per L sediment) (Gaertner, 1968). Kirk (1983) outlined a technique for the enumeration of spores of higher marine fungi in foam and sediments. Storm generated sea foam yielded 2813 propagules per 50 mg sediment with the following groups of marine fungi: 10 arenicolous, 8 caulicolous, 5 lignicolous and 6 geofungi. The most common fungi were *Arenariomyces trifurcatus* and *Corollospora maritima* with 1171 and 872 ascospores respectively. Whatever the number of propagules in seawater, rapid colonization of substrata has been documented, especially in tropical areas: days for *Halophytophthora* species on mangrove leaves (Newell *et al*., 1987; Newell and Fell, 1994, 1997; Nakagiri *et al*., 1996), to weeks or months for the higher marine fungi on wood (Furtado *et al*., 1977).

Nature of substrata and their effect on fungal diversity

Table 1 lists the common fungi collected on different substrata: *Avicennia alba Bruguiera cylindrica* and *Rhizphora apiculata* test blocks and drift mangrove wood (Tan *et al*., 1989; Leong *et al*., 1991), *Acanthus ilicifolius* culms (a perennial, herbaceous, Angiosperm and a mangrove associate) (Sadaba, 1996) and *Nypa fruticans* fronds (a mangrove palm) at different mangroves (Hyde, 1993a). Lignocellulosic substrata support typically marine mangrove fungi (Vrijmoed *et al*., 1996; Jones and Vrijmoed, 1997), while the fungi colonizing *A. ilicifolius* and *N. fruticans* differ from each other and with those on timber (Sadaba *et al*., 1995). Many of the fungi colonizing *N. fruticans* are similar to the genera found on terrestrial palms (e.g. *Linocarpon*

Table 1. Fungi colonizing different substrata in mangroves.

Substrata	Driftwood (Vrijmoed *et al.*, 1996)	*Nypa fruticans* (Hyde, 1992)	*Acanthus ilicifolius* culms (Sadaba *et al.*, 1995)	*Bruguiera cylindrica* test blocks (Leong *et al.*, 1991)
Total species	13	43	120	60
Total samples	303	250	44	24
Common species	*Hypoxylon oceanicum*, *Lignincola laevis*, *Marinosphaera mangrovei*, *Trichocladium linderi*	*Astrosphaeriella striatispora*, *Lignincola laevis*, *Linocarpon appendiculatum*, *Oxydothis nypae*	*Acremonium* sp., *Colletotrichum gloeosporioides*, *Phoma* sp., *Tunercularia* sp.	*Aigialus parvus*, *Halosarpheia marina*, *Lulworthia* sp., *Lignincola laevis*, *Verruculina enalia*

appendiculatum, *Oxydothis nypae* and *Astrosphaeriella stratispora* (Hyde and Nakagiri, 1989; Hyde, 1993a, 1994; Hyde *et al.*, 1997). These and a number of other genera described are unique to *Nypa* (e.g. *Frondicola* and *Nypaella*) (Hyde, 1993a). The biodiversity of fungi on *Nypa* can be accounted for by the nature of the substratum and the lower salinity of the water in which this palm thrives. On *A. ilicifolius* typical terrestrial/geofungi or facultative marine fungi (*sensu* Kohlmeyer and Kohlmeyer, 1979) are encountered e.g. *Colletotrichum gloeosporioides*, *Tubercularia* sp. and *Phialophora* sp. (Sadaba *et al.*, 1995).

Mangrove leaf litter is also and important substratum supporting a very different fungal community to that found on lignocellulosic materials (*Halophytophthora* species and thraustochytrids) (Newell, 1992; Newell and Fell, 1994; Tan and Peck, 1997). Higher marine fungi are not common on such leaf material (Nakagiri *et al.*, 1996, 1997).

A number of workers have shown that driftwood supports a greater diversity of fungi than on exposed test panels [e.g. 26 species on driftwood, 9 species on test blocks (Miller and Whitney, 1981)], while Alias (1996) recorded 104 species on mangrove driftwood, but only 77 on exposed test blocks of mangrove wood. However, Poonyth *et al.* (1999) recorded 67 fungi on intertidal attached wood and 59 on exposed test blocks mangrove wood in Mauritius.

Host specificity

Jones (1968) and Byrne and Jones (1974) observed that certain fungi preferred *Fagus sylvatica* test blocks (*Halosphaeria appendiculata*, *Nautosphaeria cristaminuta*, *Halosarpheia hamata*) to *Pinus sylvestris* (*Lautisporopsis circumvestita*, *Cirrenalia macrocephala*, *Trichocladium alopallonellum*) and similar data was reported by Grasso *et al.* (1985) for other timber species. Petersen and Koch (1997) found that *Halosphaeria appendiculata*, *Marinospora calyptrata* and *M. longissima* were most common on oak poles, while *Remispora maritima* and *Dictyosporium pelagicum* were common on larch, and were not found on oak. There has been little evidence of substrate specificity by mangrove fungi (Hyde and Lee, 1995; Alias, 1996), although Hyde (1990a,b, 1992, 1993b) has shown that some fungi were specific to single mangrove trees (e.g. *Caryospora mangrovei* on *Xylocarpus granatum*; *Aigialus mangrovis* and *Eutypa* sp. on *Avicennia alba*; *Trematosphaeria mangrovis* on *Rhizophora racemosa*; *Hypophloeda rhizophora* and *Rhizophila marina* on *Rhizophora* spp.). A number of fungi growing on the mangrove palm *Nypa fruticans* may also be host specific and this aspect warrants further investigation (Hyde, 1993a).

Newell and Fell (1994) found that the zoosporic halophytophthoras showed substrate specificity in that *Halosphytophthora masteri* was predominant on *Avicennia germinans*, while *H. vesicula* and *H. spinosa* var. *spinosa* were predominant on *Laguncularia racemosa*.

Incubation of substrata

Woody substrata are generally examined immediately after collection and subsequently after a period of incubation (Jones, 1971). Many fungi are not sporulating on freshly collected material, but require a period of incubation. Prasannarai and Sridhar (1997) have shown that 70% of the fungi produced fruit bodies on incubation for 6 months, while others appeared after 12-18 months incubation (*Corollospora* sp.1, *Dactylospora haliotrepha*). This is therefore a factor that must be taken into account when estimating the biodiversity of fungi on materials collected from the sea, especially when examining driftwood.

Ecological studies of marine fungi have largely focused on those sporulating on the incubated substratum. This may lead to an underestimated diversity, because the fungi are present only as mycelium and sporulation may be inhibited by the presence of other fungi (Tan *et al.*, 1995). This can only be resolved by the development of molecular techniques to enable the detection, identification and enumeration of both culturable and non-culturable fungi (Liew *et al.*, 1999; Jones, 1999). Such techniques have been developed and employed for the detection of marine yeasts (Fell and Kurtzman, 1990; Fell *et al.*, 1992; Fell and Blatt, 1999; Fell *et al.*, 2000).

Inhibition competition

Studies on the colonization of test blocks in temperate waters showed that *Lulworthia* species were common and often dominant (Jones, 1968, Byrne and Jones, 1974). Miller *et al.* (1985) reported the same trend with 137 perithecia of *Lulworthia* per 10 mm^2 when it was the sole species on the test blocks. However, when *Ceriosporopsis halima* or *Amylocarpus encephaloides* were present, the number of *Lulworthia* perithecia dropped significantly to 53 and 3 per 10 mm^2, respectively ($p < 0.001$). This observation led to a number of studies to examine interference competition between selected species of marine fungi (Miller *et al.*, 1985 on agar media; Strongman *et al.*, 1986, on small test blocks). An index of antagonism was developed and *in vitro* data confirmed *in vivo* observations for *Lulworthia* spp., *C. halima* and *A. encephaloides*. Strongman *et al.* (1986) were also able to extract a compound with antifungal activity from the fermentation of *Leptosphaeria oraemaris* (the sesquiterpene culmorin) which had activity against the marine fungi tested.

This observation on interference competition was tested under field conditions when *Corollospora maritima* was inoculated onto test blocks of balsa and allowed to completely colonize them. They were then exposed in the sea and the fungi sporulating on the wood determined at 2, 6, 9 and 15 months. The control test blocks were colonized by a number of marine fungi: *Corollospora maritima*, *Halosphaeriopsis mediosetigera* and *Ceriosporopsis halima* at 2 months; and *C. halima*, *Halosphaeria appendiculata*, *Lulworthia* sp., and *Marinospora calyptrata* at 6 months. However, *Corollospora maritima* was the only species to appear on the *C. maritima* inoculated blocks up to 6 months, suggesting that the fungus was producing metabolites affecting other fungi present in the surrounding water (Panebianco, 1991). This clearly shows how the rapid colonization of a substratum by a species can markedly affect fungal diversity. Panebianco (1991) also demonstrated the same phenomenon for *Halosphaeriopsis mediosetigera* for up to 6 months, and *Ceriosporopsis halima* for up to 2 months. *Marinospora calyptrata* showed no such inhibition, but became the dominant species on the test blocks after 9 months and the only species sporulating on the wood at 15 months. It would be interesting to extend the experiment to monitor colonization at the molecular level and assess if secondary metabolites are produced.

In most studies, the estimation of fungal diversity depends on the fungi present sporulating on the substratum. Tan *et al.* (1995) grew three marine fungi (*Aigialus parvus*, *Lignincola laevis* and *Verruculina enalia*), singly and in mixed cultures, on three mangrove test blocks in shake culture and determined the number of ascomata formed. All three species formed abundant ascomata, when grown singly on the test blocks, but at different time intervals on the three timbers. Sporulation however, was markedly affected when they were grown in combination; e.g. sporulation of *L. laevis* was suppressed by *A. parvus* and/or *V. enalia*. In contrast, the presence of *L. laevis* enhanced ascomata formation by *V. enalia*. *Aigialus parvus* has been shown to produce a number of bioactive compounds: hypothemycin (a known antibiotic), 4 new macrolides and a new ketene acetal (Youtathai *et al.*, pers. comm.). This indicates that interference competition among these fungi can affect enumeration of fungal diversity.

Another interesting observation that shows how fungal diversity can be affected by external factors (e.g. chemical compounds) was conducted by Jensen *et al.* (1998). Extracted compounds from the sea-grass *Thalassia testudinum*, impregnated into agar discs, inhibited the zoospores of the thraustochytrid *Schizochytrium aggregatum*. The compound was a new flavone glycoside characterized as luteolin 7-0-β-D glucopyranosyl-2" sulfate. Miller and Jones (1983) noted that there were few thraustochytrids on living brown algae compared to cast seaweeds, but their number increased once carbohydrates and phenolics had been leached from the alga (*Fucus serratus*). These and similar observations require further research in our quest for a better understanding of the whole issue of fungal diversity in the marine milieu and why some substrata support few fungi while others yield a rich species diversity.

Geographical distribution and temperature

Another major factor that governs fungal diversity is geographical distribution and the temperature of the sea. Booth and Kenkel (1986) suggest sea temperature is the single most important factor in the geographical distribution of marine fungi. A striking effect of temperature is the appearance of the marine basidiomycete *Digitatispora marina* on test blocks of *Fagus sylvatica* in Langstone harbour, Portsmouth, England. When the temperature dropped below 10 C, *Digitatispora marina* appeared on the wood, but when the temperature reaches 10 C, and above, the fungus stopped fruiting on the wood (Byrne and Jones, 1974). Similarly, when water spraying the Tudor ship Mary Rose was chilled to 4 C *Digitatispora marina* appeared on the bow of the ship (Dr M.A.Jones, pers. comm.).

Hughes (1974) was the first to publish distribution maps of marine fungi and divide the oceans into zones based on their average temperature range over the year. This has led to a number of maps showing the world distribution of marine fungi (Kohlmeyer, 1983, 1984; Jones, 1993; Kohlmeyer and Volkmann-Kohlmeyer, 1993; Hyde and Lee, 1995; Jones and Alias, 1997; Whalley *et al.*, 2000). While these maps help, at a glance, to indicate trends in the geographical distribution of marine fungi, they are limited to the extent that vast areas have not been sampled (e.g. South America, West Coast of Africa).

Few marine fungi have been recovered from Antarctic waters: *Thraustochytrium antarticum*, *Leucosporidium anatartica* and *Spathulospora antartica*. This may be attributed to the low temperature of the seawater and the availability of suitable substrata (Pugh and Jones, 1986). Many other fungi have been collected only in tropical waters [e.g. *Adomia avicenniae*, *Antenospora quadricornuata*, *Massarina acrostichi*) (Hyde, 1989a; Jones, 1993; Panebianco, 1994)], while there is a characteristic temperate group of marine fungi (e.g. *Ceriosporopsis trullifera*, *Lindra inflata* and *Ondiniella torquata*) (Kohlmeyer and Kohlmeyer, 1979; Jones, 1985; Jones *et al*., 1998). Many fungi also have a cosmopolitan distribution (e.g. *Arenariomyces trifurcatus*, *Corollospora maritima* and *Torpedospora radiata*) (Kohlmeyer, 1983). There is evidence to suggest that some cosmopolitan species may form distinct geographical races as in *Corollospora maritima* (Beboute *et al*., 1987), based on physiological responses to temperature. Roberts *et al*. (1995) sequenced the 18S gene of seven isolates of *Corollospora maritima*, and found that five isolates from temperate localities grouped together, those from subtropical collections formed a separate group, while the strain from Aldabra separated from both groups.

Why are some marine fungi so rare?

A number of fungi have only been infrequently collected despite intensive studies in recent years. *Orbimyces spectabilis* has been collected infrequently, but Dr. J. Koch (pers. comm.) has found it in soil or peat associated with wood along the Danish coast, suggesting it might be a pH effect or the organic nutritive content that controls its distribution. *Torpedospora ambispinosa* was described from wood collected at Friday Harbour, San Juan Island, U.S.A. by Kohlmeyer (1960) and collected again by Jones (1985) but has not been collected elsewhere. Similarly, *Digitatispora lignicola* was also described from Friday Harbour and is known only from that locality (Jones, 1986). *Sporidesmium salinum* collected on beech test blocks exposed in the sea at Port Erin, England, has not been reported from other localities (Jones, 1963). *Mycaureola dilsea*, a marine basidiomycete, grows on the red alga *Dilsea edulis*. Its appearance is seasonal and therefore the fungus must be sought during the latter part of the year (e.g. September to November) in the U.K. (Stanley, 1992).

Are these infrequently observed fungi particularly rare or do they occupy specific niches? There are many such species, their precise niche and role in the marine environment awaits elucidation.

Two groups of marine fungi that are found on unique substrata are the arenicolous fungi and the Trichomycetes. The latter are found as commensals within the digestive tracts of living marine amphipods, decapods and isopods (Lichtwardt, 1976) with 20 species.

The ascomata of arenicolous fungi are attached to sand grains by a subiculum and tolerate extreme environmental conditions, including exposure to high temperatures, abrasion, desiccation and variation in salinity (Sundari *et al*., 1996a,b). Sundari (1997) has shown that ascomycetes grow on sand grains in the range 425 to 600 µm. *Corollospora* species have ascomata with a carbonaceous wall that can withstand abrasion and desiccation, while the necks are in a lateral and basal position, and often in cooperated into the subiculum tissue (Kohlmeyer and Volkmann-Kohlmeyer, 1997) thus subject to less abrasion from adjoining sand grains. Ascomata may be attached to more than one sand grain, producing a number of subicula while the outer layer of cells of the peridium may comprise thick walled collumnar cells as in *C. besarispora* (Sundari *et al*., 1996a). Arenicolous species occur widely, with some cosmopolitan in their distribution e.g. *Corollospora maritima*, *Arenariomyces trifurcatus* (Kohlmeyer and Volkmann-Kohlmeyer, 1993; Nakagiri and Tokura, 1994).

Another group of interesting marine fungi is encountered on mangrove prop roots at the high water mark. These fungi include the ascomycetes *Pyrenographa xylographoides*, *Kallichroma tethys*, *Anthostomella* spp., *Melespilea mangrovei* and *Massarina* spp. (pers. observ.). Species diversity can be low in this zone due to the prevailing environmental conditions of desiccation, varying salinity and temperature and exposure to UV light. Many of the ascomycetes survive these conditions because the developing asci are embedded in mucilage in the centrum or the ascomata are immersed deeply within the wood (Au *et al*., 1999).

Vertical zonation of intertidal fungi

Schaumann (1968, 1969) was the first to consider vertical distribution of marine fungi on stationary wooden structures. Kohlmeyer (1969) however, found no evidence for vertical zonation on the prop roots of *Rhizophora* spp. and the pneumatophores of *Avicennia* sp. Vertical zonation of fungi on salt marsh grasses and perennial herbaceous plants has been well documented: *Spartina* (Gessner and Kohlmeyer, 1976); *Acanthus ilicifolius* (Sadaba *et al*., 1995); *Juncus roemarianus* (series of papers by Kohlmeyer and Volkmann-Kohlmeyer, 1998, 1999) and *Phragmites australis* (Poon and Hyde, 1998) with marine fungi growing at the bases of the plants and terrestrial species on the apical part of the shoots. Petersen and Koch (1997) found evidence of vertical zonation of marine fungi over a narrow tidal range on oak and larch poles. *Marinospora calyptrata*, *M. longissima*, *Lulworthia* sp., *Halosphaeria appendiculata* and *Ondiniella torquata* were commonly recorded from the lower zone (subtidal) while *Sphaerulina oraemaris*, *Marinosphaera mangrovei*

Table 2. Variation in the salinity of selected mangroves.

Location	Salinity(‰)
Mai PO, Hong Kong	4-25
Kuala Selangor, Malaysia	13-20
Port Dickson, Malaysia	25-30
Sinai, Egypt	44
Acklins Island, Bahamas	55-70

and *Leptosphaeria pelagica* were recorded from the upper tidal zone (supralittoral). Hyde (1989b, 1990a,b, 1993b) has examined the zonation of mangrove fungi on a number of mangrove trees. This involved collection of dead wood from trees and the prop roots of *Rhizophora* species. Distinct fungal communities were found on young prop roots with bark at the lowest level (e.g. *Phomopsis mangrovei* and *Lulworthia grandispora* predominated), while *Hypophloeda rhizospora*, *Halosarpheia abonnis*, *Ascocratera cf. manglicola* and *Aigialus grandis* were common on old roots with bark in the mid level. This demonstrates that fungal diversity is affected by the degree of exposure they are subjected to. Also of importance here is the tidal amplitude which can also affect species diversity.

Various studies have provided evidence of fungal succession on mangrove wood exposed in seawater (Tan *et al*., 1989; Leong *et al*., 1991). Hence, the timing of sample collection will influence the diversity recorded. Many species will not be sporulating when recovered from the sea and such samples must be incubated in moist chambers (Jones, 1963, 1968). This aspect has also been discussed above.

Effects of salinity

Salinity and temperature are the major factors affecting the diversity of marine fungi as is well illustrated by the data of Booth and Kenkel (1986). They produced a distribution model for lignicolous marine fungi comprising 9 groups from cool homeohalothermic to mixed euryhalothermic and to warm homeohalothermic. The model was limited by the lack of good data on the temperature and salinity regimes of the sites used for the analysis. The oceans of the world vary greatly in intertidal amplitude and salinity of the waters, all features that can dramatically affect fungal biodiversity (Table 2).

Early physiological studies of marine fungi concentrated on their salinity requirements in the belief that they had a requirement for sodium chloride at concentrations found in seawater (Jones and Jennings, 1964; Meyers, 1968; Jones *et al*., 1971; Byrne and Jones, 1975a,b; Jones and Harrison, 1976; Jennings, 1983, 1986). Indeed zoosporic fungi such as *Althornia*, *Haliphthoros* and *Thraustochytrium* species had a sodium requirement for growth at the macronurtient level (Alderman and Jones, 1971) (Table 3). However, *Schizochytrium* species have recently been isolated from mangrove habitats with low salinities (Fan *et al.*, unpublished data), while *Halophytophthora* species exhibit a wide tolerance to salinity in nature and under laboratory conditions (Nakagiri *et al.*, 1996; Leano *et al.*, 1998). This suggests that these organisms are well adapted to the varying salinity in a mangrove such as Mai Po, with greatly fluctuating water salinity.

The higher mycelial marine fungi also do not appear to have a sodium requirement at macronutrient levels (Jennings, 1983, 1986) (Table 3). Jennings (1986) concludes that a combination of factors enables these fungi to grow in the sea: they can tolerate concentrations of ions present in seawater and prefer the alkaline pH of seawater. Hyphal water potential is maintained at a more negative value than the surrounding sea water by the synthesis of compatible solutes including polyols and amino compounds (Wethered *et al.*, 1985), along with the accumulation of ions (Clipson *et al.*, 1990; Edwards *et al.*, 1998). These conditions may restrict invasion by terrestrial fungi. Stanley *et al.* (1995) suggested there is genetical basis for salinity tolerance in *Dendryphiella salina*.

Many studies on the effect of salinity on fungal growth consider only vegetative growth. Harrison and Jones (1975) clearly demonstrated that many freshwater saprolegniaceous fungi cannot reproduce at salinities above 30% seawater (10.5 ‰), and suggest this is the major reason that they do not grow in the sea. However, Padgett (1978) and Padgett *et al.* (1988) were able to show that although saprolegniaceous organisms survived salinities as high as 18 ‰, they were "not physiologically adapted to, nor morphologically active in highly saline environments".

That salinity affects the diversity of fungi colonizing *Acanthus ilicifolius* culms is illustrated by data presented in Table 4. During the dry season when salinities are high, marine fungi predominate, conversely in the wet season when salinities are low terrestrial/geofungi are dominant (Sadaba, 1996). However, the higher number of geofungi may be attributed by terrestrial run off from the Pearl Estuary and their ability to grow at these low salinities. Ragukumar (1986) has shown that colonization of the red alga *Centroceras clavulatum* by the parasite *Chytridium polysiphonae* is dependent on salinity of the water in the Goa area.

Comparison of the fungi colonizing *A. ilicifolius* culms at Kat O (a seawater site), with samples exposed at Mai Po mangrove (low salinity), Hong Kong shows that marine fungi again predominate at high salinities (Table 5). This data also demonstrates that species diversity was much greater at the mangrove site when compared with the samples from the open ocean site, and this accounted for by the larger number of terrestrial fungi recorded. Nineteen

Table 3. The effect of salinity (percent seawater) on the growth of selected marine fungi. Figure in brackets indicates optimum growth (after Alderman and Jones, 1971; Jones, 1976).

Fungi with wide tolerance	Salinity (‰)	Fungi with a narrow tolerance level	Salinity (‰)
Asteromyces cruciatus	0-100 (90)	*Althornia crouchi*	40-100 (80-100)
Corollospora maritimum	0-100 (100)	*Labyrinthula* sp.	35-100 (60-100)
Dendryphiella salina	0-100 (60-70)	*Ostracoblabe implexa*	20-100 (80-100)
Dendryphiella arenaria	0-100 (20)	*Thraustochytrium multirudimentale*	20-100 (70-100)

Table 4. The effect of salinity on fungi colonizing the basal culms of *Acanthus ilicifolius* at Mai Po mangrove, Hong Kong (after Sadaba, 1996).

	Dry winter season	Wet summer season
Salinity (‰)	20-23.5	1.8-12.3
Total species	22	17
Total samples	27	29
Common fungi	*Acremonium* sp.	*Acremonium* sp.
	Aniptodera chesapeakensis	*Graphium* sp.
	Lignincola laevis	*Periconia prolifica*
	Lulworthia sp.	*Trichocladium achrasporum*
	Tirispora unicaudata	*Tirispora unicaudata*

Table 5. The effect of salinity on common fungi colonizing *Acanthus ilicifolius* culm samples during summer season (after Sadaba, 1996).

Test site	Mai Po mangrove, Hong Kong	Kat O, Hong Kong, open sea
Salinity (‰)	1.8-12.3	29-38
Total species	87	34
Total samples	196	55
Common fungi	*Acremonium* sp.	*Cirrenalia basiminuta*
	Cladosporium cladosporioides	*Lulworthia* sp.
	Nectria sp.	*Periconia prolifica*
	Phoma sp.	*Trichocladium achrasporum*

marine fungi were recorded on *Kandelia candel* collected at Kampong Tutong mangrove, Brunei, where salinity fluctuated between 3-24 ‰ (Hyde, 1992). This shows that these fungi may also tolerate wide fluctuations in salinity.

Another effect of salinity is on the production of lignocellulolytic enzymes. High salinities generally reduce production of cellulases (Pointing *et al*., 1999). Peroxidase production was favoured at higher salinities, while laccase activity was more pronounced at lower salinities (Pointing *et al*., 1998).

This is another factor that can play a role in determining species diversity in the marine environment.

Most studies on the effect of salinity on fungal growth have been conducted at a fixed temperature usually, 25 C. However, there is an interrelationship between temperature and salinity as has been demonstrated by the "*Phoma*" pattern described by Ritchie (1957). Some marine fungi (e.g. *Dendryphiella salina* and *Zalerion maritimum*) exhibit an increase in their salinity optimum for growth with elevation in temperature (Molina and Hughes, 1982; Lorenz and Molitoris, 1992; Torzili, 1997). What effect this has on the growth of the fungi in nature and whether it can affect fungal diversity is not known. This is another area for future investigation.

Future scope

Many substrata (mangrove fruits; herbaceous, mangrove associates; marine animals) have yet to be sampled intensively for marine fungi. Similarly, many habitats await exploration, as few exploratory studies having been undertaken: rhizospheres of mangrove trees (Ito and Nakagiri, 1997); soil and mud of coastal beaches and mangroves (Rees and Jones, 1985; Gonzalez, *et al.*, 1998); hypersaline waters (Buchalo *et al.*, 1998); commensal Trichomycetes of arthropods (Lichtwardt, 1976); mortalities of marine animals (Le Campion-Alsumard *et al.*, 1995; Smith, *et al.*, 1996) and marine salterns (Gunde-Cimerman *et al.*, 1996a,b). For many of these topics, new isolation media and procedures need to be developed if we are to determine the true fungal diversity of the oceans.

In this essay I have tried to consider a number of factors that can affect the diversity of fungi in the marine environment. No single factor can account for the diversity we observe, the marine environment being a complex ecosystem with great variation in many parameters from ocean to ocean, from mangrove to mangrove and from shore to shore, and sometimes over a narrow range. However, by considering the different factors that influence the occurrence of fungi we can obtain a better picture of their ecology and perhaps consider the important issue of long term conservation of our marine habitats.

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