Role of fungi in marine ecosystems

KEVIN D. HYDE[1], E.B. GARETH JONES[2], EDUARDO LEAÑO[2],
STEPHEN B. POINTING[2], ASHA D. POONYTH[1] and LILIAN L.P. VRIJMOED[2]

[1]*Department of Ecology and Biodiversity, The University of Hong Kong, Pokfulam Road, Hong Kong*

[2]*Department of Biology and Chemistry, The City University of Hong Kong, Tat Chee Avenue, Kowloon Tong, Kowloon, Hong Kong*

Marine fungi are an ecological rather than a taxonomic group and comprise an estimated 1500 species, excluding those that form lichens. They occur in most marine habitats and generally have a pantropical or pantemperate distribution. Marine fungi are major decomposers of woody and herbaceous substrates in marine ecosystems. Their importance lies in their ability to aggressively degrade lignocellulose. They may be important in the degradation of dead animals and animal parts. Marine fungi are important pathogens of plants and animals and also form symbiotic relationships with other organisms. The effect of disturbances on marine fungi is poorly investigated. Keystone marine species may exist, especially in mutualistic symbioses. However, as many saprophytes appear to carry out the same function simultaneously, they may be functionally redundant. The need for a concerted effort to investigate the biodiversity and role of marine fungi globally and on as many substrata as possible is presented.

Keywords: biodiversity; biogeography; fungi; marine; nutrient cycling.

Introduction

Marine fungi are an ecological rather than a taxonomic group. However, the ascomycete order *Halosphaeriales* comprises largely marine species with 43 genera and some 133 species (Jones, 1995). This is approximately half of the total number of marine ascomycetes (Kohlmeyer and Volkmann-Kohlmeyer, 1991).

Definition of marine fungi

Various workers have attempted to define a marine fungus (Kohlmeyer and Kohlmeyer, 1979; Jones, 1988). Early workers determined the physiological requirements for the growth of marine fungi in sea water, or in particular concentrations of sodium chloride (Meyers, 1968; Jones and Jennings, 1964). The best working definition for a marine fungus is that proposed by Kohlmeyer and Kohlmeyer (1979): "obligate marine fungi are those that grow and sporulate exclusively in a marine or estuarine habitat; facultative marine fungi are those from freshwater and terrestrial milieus able to grow and possibly also sporulate in the marine environment."

Biodiversity of marine fungi

Kohlmeyer and Kohlmeyer (1979) stated "that considerable additions of new species in the future are unlikely", and indicated that there were then less than 500 marine fungi.

Several recent papers have addressed the issue of the diversity and numbers of marine fungi (Jones, 1995; Jones and Mitchell, 1996; Jones and Alias, 1997). Jones and Mitchell (1996) estimated that there are some 1500 species compared with 200,000 marine animals and 20,000 marine plants. The dramatic rise in the numbers of new marine fungi, which has occurred since the statement by Kohlmeyer and Kohlmeyer (1979), is due to the nature of the substrata examined for the occurrence of fungi. Kohlmeyer and Kohlmeyer (1979) listed 42 species of mangrove fungi, while the current number approaches 200 species (Jones and Alias, 1997). Similarly the number of fungi recorded by Kohlmeyer and co-workers from *Juncus roemerianus* has also increased dramatically (Kohlmeyer *et al.*, 1996). We believe that the documentation of marine fungi is still at the inventory stage and many new taxa await discovery.

Habitats for marine fungi

Marine fungi grow on a wide variety of substrata ranging from wood to sediments, muds, soils, sand, algae, corals, calcareous tubes of mollusks, decaying leaves of mangroves, intertidal grasses and living animals, to those growing in the guts of crustaceans (Kohlmeyer and Kohlmeyer, 1979; Hyde, 1996). Two substrata are predominant in terms of the marine fungi they support. Wood in the open ocean tends to favour the growth of members of the *Halosphaeriales* whose species have deliquescing asci, passive ascospores release and variously appendaged ascospores which are involved in flotation and attachment (Jones, 1994). In mangrove habitats, loculoascomycetes are especially common on decaying wood in the intertidal zone where they can eject their spores during low tides (Hyde, 1989b). Loculoascomycetes have the ability to forcibly eject their ascospores, and the ascospores generally have sheaths rather than appendages.

Many marine fungi also sporulate on sand grains (35 species; Jones and Mitchell, 1996) or other hard calcareous material like coral (20 species; Jones and Mitchell, 1996). Arenicolous fungi are generally found on sand associated with wood from which they derive their nutrients.

A number of texts are available on marine fungi (Jones, 1976; Kohlmeyer and Kohlmeyer, 1979; Moss, 1986; Kohlmeyer and Volkmann-Kohlmeyer, 1991; Hyde, 1996) and these should be consulted for further information.

Biogeography of marine fungi

There appear to be two major groups of marine fungi: the pantemperate and the pantropical, but there is little evidence of species being restricted to countries or continents (Jones, 1993). In the regions between the tropics and subtropics, the composition of the mycobiota is dependent on water temperature, rather than air temperature. Tropical currents or colder currents often cross boundaries and influence the mycobiota therein. Where intermediate sea temperatures occur there is often a mixture of temperate and tropical fungi (Jones, 1993). This would be expected as these fungi are dispersed by separate propagules or on wood growing in the sea and therefore sea masses present no barriers to their dispersal.

Some marine fungi are cosmopolitan (Jones, 1993), including *Corollospora maritima* and *Halosphaeria appendiculata* which are common or less common in temperate and tropical seas respectively. The intertidal mangrove species *Halosarpheia fibrosa* and

Halosarpheia marina may have a subtropical distribution (Hyde and Lee, 1995). In most cases the occurrence of a fungus in a particular habitat is related to water temperatures and substrata. The effect of the latter is particularly striking as the fungi occurring on submerged wood in the open sea usually differ from those on intertidal mangrove wood. In turn these fungi differ from those occurring on leaves or algae (Hyde, 1988).

Role of marine fungi

Fungi are major decomposers of woody and herbaceous substrata entering marine ecosystems. Their importance lies in their ability to degrade lignocellulose. Fungi may also be important in the degradation of dead animals and animal parts. Some marine fungi cause disease of marine animals and plants, while others form mutualistic symbiotic relationships with other organisms.

Fungal degradation of wood

Lignocellulose degradation

Most marine fungi have been identified from substrata containing lignocellulose, and therefore it is not surprising that several genera have been implicated in wood decay activity within marine and estuarine environments. Although marine borers are recognised as particularly aggressive wood degraders in marine environments, they are unable to tolerate the reduced oxygen tensions found in sediments (Blanchette *et al.*, 1990). Many marine fungi appear to be able to tolerate low oxygen tensions and so may be the dominant agent of lignocellulose turnover in marine sediments, since although lignocellulolytic bacteria exist they are not aggressive degraders of this substratum (Holt and Jones, 1983; Singh *et al.*, 1990). This is of particular importance when considering the vast biomass represented by lignocellulose in the form of mangrove and other plant materials in coastal areas with high sediment loading. Fungi are also extremely important decomposers of wood in the upper intertidal region where marine borers are unable to survive.

Composition of lignocellulose

The structure, chemistry and association of lignocellulose in wood have been extensively studied and comprehensive review articles are available on this topic (Fengel and Wegener, 1989; Eaton and Hale, 1993). In terms of understanding lignocellulose as a substrate for fungi this heteropolymer can be considered as consisting of three main components: cellulose, hemicellulose, and lignin. The characteristics of these components are summarised in Table 1.

Lignocellulose degradation systems in fungi

The degradation of lignocellulose by terrestrial fungi is well studied, and mechanisms of attack are summarised in Table 1. Three decay types are recognised: *white rot*, where extensive enzymic and non-enzymic degradation of all wood components is observed; *soft rot*, in which extensive enzymic decay of cellulose and hemicellulose is accompanied by limited lignin degradation; *brown rot*, in which very rapid cellulose and hemicellulose decay is attributed to non-enzymic oxidation, with limited lignin degradation (Eaton and Hale, 1993). The brown rot fungi are not colonisers of very wet or waterlogged wood and

Table 1. The composition of wood and its degradation

	Cellulose	Hemicellulose	Lignin
% of wood mass	40–50	25–40	18–33
monomer	D-anhydrogluco pyranose	glucose, xylose, galactose, mannose, arabinose, rhamnose, fructose, uronic acids of glucose and galactose	p-coumaryl alcohol, coniferyl alcohol, sinapyl alcohol
polymeric structure	β1-O-4 linked linear chains	β1-O-4 linked linear chains, with substituted side chains	Dehydrogenative polymerisation to an amorphous polymer
Degradation	Hydrolysis by Endoglucanase (E.C. 3.2.1.4), Cellobiohydrolase (E.C. 3.2.1.91), β-glucosidases (E.C. 3.2.1.21); various cellobiose and glucose oxidases; non-enzymic oxidation	Various hydrolases (not well understood)	Enzymic modification by Lignin peroxidase (E.C. 1.11.1.7), Mn dependant peroxidase (E.C. 1.11.1.7), Laccase (E.C. 1.10.3.2); via production of highly reactive radicals

so are not found in marine environments (Mouzouras, 1989). However, there is evidence for enzyme mediated decay of lignocellulose by marine fungi.

Evidence for lignocellulose degrading systems in marine fungi

Despite the high incidence of fungi occurring on lignocellulose in marine environments, evidence for their ability to degrade this substratum is limited. Morphological decay features suggesting soft rot and white rot decay have been observed in wood samples colonised by marine fungi (Mouzouras, 1989). Evidence for the production of lignocellulose degrading enzymes by some isolates also exists, but this is mostly qualitative. Endoglucanase activity, as indicated by utilisation of a carboxymethylcellulose growth substrate, has been demonstrated in over 30 strains of marine fungi from diverse taxonomic groups (Rohrmann and Molitoris, 1992; Raghukumar *et al.*, 1994; Pointing *et al.*, 1998). Some of these isolates also displayed cellobiohydrolase activity as indicated by their utilisation of crystalline cellulose substrates.

Several strains warrant mention for their ability to rapidly utilise cellulose: *Corollospora maritima* and *Monodictys pelagica* (Rohrmann and Molitoris, 1992); and *Julella avicenniae*, *Lignincola laevis*, *Nia vibrissa*, and *Stagonospora* sp. (Pointing *et al.*, 1998). Cellulolytic marine fungi appear able to utilise cellulose growth substrates throughout the salinity range 0–34% (Pointing *et al.*, 1998). Hemicellulose degradation is usually assessed by the ability of a strain to degrade xylan, a major component of the polymer. Only one study has reported xylanolytic activity in marine fungi: Raghukumar *et al.* (1994) identified xylanase activity in 11 strains of marine fungi, recording comparatively high release of reducing sugars from hydrolysis of a xylan substrate by *Gongronella* sp., *Aigialus mangrovei*, *Lophiostoma mangrovei* and *Hypoxylon oceanicum*.

The mineralisation of lignin to CO_2 has been conclusively demonstrated in only two marine fungal strains, *Monodictys pelagica* and *Nia vibrissa* (Sutherland *et al.*, 1982). Decolourization of the polymeric dyes PolyR-478 and Azure B have been used in growth studies to suggest lignin degrading potential in marine fungi (Raghukumar *et al.*, 1994; Pointing *et al.*, 1998). Four fungi *Nia vibrissa* (basidiomycete), *Julella avicenniae* (ascomycete), *Lignincola laevis* (ascomycete) and *Stagonospora* sp. (a mitosporic fungus) are notable in their ability to completely decolourize such polymeric dyes whilst utilising either glucose or cellulose as a primary carbon source (Pointing *et al.*, 1998). Spectrophotometric enzyme assays have revealed manganese dependant peroxidase activity in three and laccase activity in 17 isolates, with lignin peroxidase undetected in 17 marine fungal strains tested (Raghukumar *et al.*, 1994). Dye decolourization assays further suggest enzyme activity may be affected by salinity. Whilst aggressive dye decolourizers such as *Nia vibrissa*, *Julella avicenniae*, *Lignincola laevis* and *Stagonospora* sp. are highly active at all salinities, several moderate or weak dye decolourizing isolates showed optimal activity at either low or high salinity (Pointing *et al.*, 1998).

It is clear that a comprehensive study of lignocellulolytic marine fungi is necessary to better understand their role in the environment. From existing studies it seems likely that several species may be cellulolytic, with some also capable of lignin degradation. These marine fungi are probably soft rot and white rot degraders of wood, and participate in the turnover of an abundant biopolymer. Furthermore, examining the physiology of lignocellulolytic marine fungi may reveal strains with novel commercial uses since ligninolytic and xylanolytic terrestrial fungi have a variety of potential biotechnological applications in biobleaching, biopulping and bioremediation technologies.

Decomposition of herbaceous substrata

The importance of the mangrove ecosystem in terms of their export of plant detritus and faunal biomass supporting offshore biological production is well documented (Lee, 1995). Microbes are responsible for the transformation of the polymeric compounds into dissolved or particulate organic matter utilizable by other consumers in the food web. These microbes comprise the bacteria, the eumycotic fungi including the ascomycetes, the mitosporic fungi, the chytrids, and the chromistan group which were formerly known as the oomycetes, the labyrinthulids and the hyphochytrids (Hawksworth *et al.*, 1995). There are numerous publications describing the association of these various groups with decaying plant litter in mangrove s (e.g. Fell and Master, 1973; Newell, 1976; Nakagiri *et al.*, 1996) and their presence in sediments (e.g. Lee and Baker, 1973; Ulken, 1984; Ito and Nakagiri, 1997). However, comparatively little information is available on their activity so their role in the recycling of nutrients is unclear. This was essentially hampered by the slow development of methods for the ecological study of the aquatic mycelial eukaryotic decomposers compared with the well established (published and field-tested) methods used for the measurement of prokaryotic productivity (Newell, 1994). The recently published or refined methods for measuring mycelial mass and productivity have enabled a better understanding of the role of the mycelial decomposers in different marine ecosytems. For example, it is now clear that different dominant fungal groups are responsible for the decomposition of herbaceous material in the mangroves and saltmarsh ecosytsems (Newell, 1996).

Numerous workers have studied the fungi associated with the decay of mangrove leaves (e.g. Fell and Master, 1973; Nagakiri *et al.*, 1996; Vrijmoed and Tam, 1990; Singh and

Steinke, 1992; Bremer, 1995). They incubated decaying leaves with or without a nutritive medium such as corn meal agar. Without exception, the dominant fungi which developed were non-marine species (e.g. *Cladosporium* spp., *Fusarium* spp., *Pestalotia* spp., *Penicillium* spp.) which are common inhabitants of the soil. *Halophytophthora* spp., thrauastochytrids and labyrinthulids were prevalent at the early stages of leaf submergence (Bremer, 1995; Nagakiri *et al.*, 1996; Newell and Fell, 1997). A small number of obligate marine fungi were also recorded but at lower frequencies (e.g. *Lulworthia grandispora*, Newell and Fell, 1992; *Lanceispora amphibia*, Nakagiri *et al.*, 1997; *Corollospora maritima*, Vrijmoed *et al.*, pers. obs.). *In vitro* cellulolytic activity has been demonstrated in some of the non-marine fungi (Singh and Steinke, 1992). However, it is unclear whether it is the marine eumycotic fungi, the 'soil fungi', or the oomycete chromistan group which are responsible for *in situ* decomposition in the mangroves. How can the occurrence data be interpreted in relation to activity when the fungi are only recognised after incubation in the laboratory? Can presence of fungi in mangrove leaves be quantified *in situ*?

Several attempts have been made to measure fungal biomass within decaying mangrove leaves. Blum *et al.* (1988), West, (1988), Newell (1992), and Raghukumar *et al.* (1995) were only able to detect very low fungal biomass (<1 mg g^{-1} organic decaying-system mass) using direct-microscope observations. Newell and Fell (1992) used the ergosterol technique (Newell, 1992) to estimate the living-fungal mass within submerged decaying leaves of red mangrove. They found averages of between 1 to 5 mg organic fungal mass g^{-1} for leaves with about 30% and 40–60% mass loss respectively. These values are low when compared with standing decaying cordgrass (*Spartina alterniflora*) in Florida saltmarshes (Newell, 1996), where a net increase from 66 to 85 mg organic fungal mass g^{-1} occurred from 2-12 weeks. The principal decomposer of the standing decaying cordgrass was *Phaeosphaeria spartinicola* and some other ascomycetes (Newell *et al.*, 1995). These fungi were dominant on the blades which senesced and died from the bottom upwards (Newell, 1993). Neither measures of mycelial production, nor enumeration of fungal fruiting structures, have been carried out in mangrove leaves and thus the importance of fungi *in situ* decomposition of leaves is unclear.

The role of the oomycetes in the decay process of submerged mangrove leaves is well documented. In all mangrove ecosystems, *Halophytophthora* spp. (notably *H. vesicula*) can be found at high frequencies where there is a high input of leaf litter (Newell and Fell, 1995). *H. vesicula* has been shown to be an aggressive competitor in field experiments (Newell and Fell, 1997). Not only was it able to occupy substrata that were already colonised by mycelial marine fungi (e.g. *Lulworthia* sp. and *Zalerion varium*), but it was also capable of inhibiting colonisation by *H. spinosa*. This character may explain its rapid colonisation of submerged mangrove leaves. Ragukumar *et al.* (1994) were also able to show that *H. vesicula* could degrade cellulose, and phenolics, and capture labile-carbohydrate rapidly.

Labyrinthulids and thraustochytrids (*Thraustochytrium* sp., *Schizochytrium* spp.) have also been isolated from *Sonneratia* and *Rhizophora* leaf disks submerged in mangroves (Bremer, 1995). These species were isolated after 24 hours, through to 14 days of immersion. Cellulase activity was also detected in culture filtrate of *Schizochytrium aggregatum* (Bremer 1995). There are presently no biochemical methods to measure the mass of oomycete fungi within mangrove leaves, since ergosterol is not present in their membranes. Their dominance and enzymatic activities, however, indicate that these fungi are the main decomposers of submerged leaves (Newell, 1996).

Decomposition of animal remains

Little is known of the role of fungi in the decomposition of animal remains in the sea. Tunicin is an animal cellulose which occurs in the test of tunicates and it has been shown that marine fungi may play a role of degrading tunicate cellulose in nature (Kohlmeyer & Kohlmeyer, 1979). Marine fungi are also known to invade calcareous substances, such as the shells of molluscs, test of barnacles, or linings of burrows. It is also thought that thraustocytrids and other oomycete fungi play an important role in the recycling of elements tied up in animals remains, although evidence is lacking.

Importance as symbionts in the marine environment

Literature on fungal marine symbionts is scant. Mutualistic symbiotic associations of marine fungi occur with other organisms in three forms: lichens, mycophycobioses, and mycorrhizas.

Lichens

Most marine lichens grow on rock surfaces in the intertidal zone and are immersed or sprayed with seawater at high tide; a few may be permanently submerged Santesson (1939) gave a detailed account of intertidal, pyrenocarpous lichen taxonomy. Fletcher (1975) enumerates 428 marine or maritime fungi in the British Isles, of which only 18 might be obligate marine species. In some primitive lichens the association between the fungal and algal components is loose. The algal component, which is usually microscopic, can be free-living. *Chadefaudia corallinarum* can associate with the algae *Dermatoliton* and *Epilithon*, which grow as epiphytes on macroalgae. A few other genera of fungi which form similar associations are *Pyrenocollema*, *Stgmithum*, and *Turgidosculum* (Kohlmeyer and Kohlmeyer, 1979). The lichen genera *Verrucaria*, *Lichina* and *Pyrenocollema* have been found to have terrestrial and marine counterparts (Fletcher, 1975; McCarthy, 1991).

Mycophycobioses

Mutualistic symbiotic associations between a systemic marine fungi and macroalgae are called mycophycobioses. Such associations are obligate and the habit of the alga predominates. *Blodgettia* and *Mycosphaerella* are two genera of fungi which form mycophycobioses (Kohlmeyer and Kohlmeyer, 1979). The fungus *Turgidosculum complicatum*, which lives in association with the green algae *Praseola borealis* and *P. lessellata*, are thought to confer resistance to desiccation at low tides (Kohlmeyer and Kohlmeyer, 1979).

Mycorrhizas

Vesicular arbuscular mycorrhizas in a salt-marsh plant were first reported by Mason (1928). Subsequently, halophytic plants were found to be associated with arbuscular mycorrhizas (Boullard, 1958; Nicolson, 1960; Khan, 1974; Rozema *et al*., 1986). The presence of mycorrhizas may enhance oxygen uptake and enhance stress resistance to salt in salt marshes (Khan and Belik, 1995). So far, no mangrove plants have been shown to have mycorrhizas (Mohankumar and Mahadevan, 1986).

Linkage to other groups of organisms

Diseases of marine animals

Fungal diseases can act as major limitors of natural and cultured populations of marine animals (Alderman and Polglase, 1986). Mycopathogens of aquatic animals have become the focus of considerable attention because of the high occurrences of fungal diseases in wild populations and aquaculture (Johnson, 1983; Polglase *et al.*, 1986; Noga, 1990). Marine fungal pathogens are predominantly straminipilous organisms (oomycetes), but also include some mitosporic fungi. The oomycetes are probably most important and include several genera (e.g. *Aphanomyces*, *Halocrusticida* (= *Atkinsiella*), *Haliphthoros*, *Lagenidium*, *Leptolegnia*, *Saprolegnia*, *Sirolpidium*) comprising species that are notoriously destructive pathogens (Rand, 1996). Most of these have been described from finfish, bivalve molluscs, or crustaceans (Stewart, 1984; Porter, 1986; Noga, 1990). Thraustochytrids and labyrinthulids have also been reported to cause infections in many marine animals, including abalones *Haliotis* spp., the large nudibranch *Tritonia diomedea*, and the lesser octopus *Eledone cirrhosa* (Polglase, 1980; Bower, 1986; McLean and Porter, 1987).

The most important mitosporic fungal pathogens are *Fusarium* species (e.g. *F. solani*) which have been reported to be associated with shell disease of marine crustaceans (Lightner, 1988), and mycotic infections in hermit crabs (Smolowitz *et al.*, 1992) and lobsters (Stewart 1984). Other mitosporic fungal pathogens include an unnamed *Scolecobasidium* which causes infection among massive coral species from the Andaman Islands (Raghukumar and Raghukumar, 1991), *Ochroconis humicola* which causes ulcerative lesions in devil stinger (*Inimicus japonicus*) cultured in Japan (Wada *et al.*, 1995), and *Lasiodiplodia theobromae* which was isolated from an infection in a juvenile boring clam (*Tridacna crocea*) cultured in Australia (Norton *et al.*, 1994). Most marine fungal infections, once established in an individual, are often fatal and difficult to treat. This indicates that these fungi will continue to be problematic pathogens of marine animals (Noga, 1990).

Significance as pathogens of plants

Relatively few fungi have been reported as pathogens of marine plants, as compared to the number of saprophytic fungi identified on decaying mangrove wood and leaves. The intertidal fungus *Cytospora rhizophorae* is thought to be parasitic on *Rhizophora* spp. prop roots (Kohlmeyer and Kohlmeyer, 1979). *Phomopsis mangrovei*, which is probably pathogenic, was described from dying prop roots of *Rhizophora apiculata* in Thailand (Hyde, 1996). Terminal dieback of *Avicennia marina* was shown to be caused by an intertidal *Phytophthora* species (Pegg *et al.*, 1980; Weste *et al.*, 1982). A *Phytophthora* species was also found to be pathogenic on *Avicennia marina* var. *resinifera* in New Zealand (Maxwell, 1968). *Halophytophthora* species were also thought to be responsible for diseased mangrove forests over vast areas in Sydney (Garrettson-Cornell and Simpson, 1984). Dieback in *A. marina* was also suspected to be due to the low resistance of this host to the *Halophytophthora* species (Hutchings and Saenger, 1987). The pathogenicity of these marine pathogens are generally unproven, but have been inferred from their association with disease symptoms, rather than experimental evidence.

Foliage diseases, root rots, butt and heart rots of mangroves

Amongst the few pathogens reported most cause leaf spots (Nag Raj and Ponnappa, 1968; Kohlmeyer and Kohlmeyer, 1969; Farr *et al.*; 1989; Chalermpongse, 1991; Hyde and

Cannon, 1992; Ho and Hyde, 1996, 1997). Chalermpongse (1991) also reported two fungi causing root rot of *Rhizophora apiculata* and six fungi causing butt and heart rots of some mangrove plants in Ranong mangrovein, Thailand. However, these diseases are caused by terrestrial fungi and cannot be considered as truly marine diseases.

Diseases of marine algae

All groups of algae are parasitised by true and straminipilous organisms, and fungal diseases appear to be a common feature of the marine algae (Raghukumar, 1986). Members of the *Labyrinthulomycetes* are considered to be the most important pathogens of marine algae (Muehlstein *et al.*, 1988). Several species of *Labyrinthula* cause infections of marine algae (e.g. *Cladophora* sp., *Rhizoclonium* sp., *Zostera marina*) and cyanobacteria (e.g. *Lyngbya* spp.) (Raghukumar, 1986; Raghukumar, 1987a, b; Muehlstein *et al.*, 1988; Rheinheimer, 1992).

Chytrids and oomycetes have been reported to cause infections in many species of marine algae. The chytrid *Chytridium polysiphonae* has been found to cause infection on *Sphacelaria* sp. Other examples include *Rhizophydium littoreum* on *Bryopsis plumosa*, *Coenomyces* sp. on *Cladophora* sp. and *Rhizoclonium* sp., and *Olpidium rostiferum* on *Cladophora* sp. (Raghukumar, 1986; Amon, 1984). The oomycete *Pontisma lagenidiodes* has been reported to cause the browning disease of the green alga *Chaetomorpha media* (Raghukumar, 1987a), and *Sirolpidium bryopsidis* has been reported to cause infection in *Cladophora* sp. (Raghukumar, 1986). *Lagenisma coscinodisci* has also been reported to cause infections in marine diatoms (Schnepf and Deichgraber, 1978). Further, *Petersenia* and *Pythium* species have been reported as parasites of several marine algal species (van der Meer and Pueschel, 1985; Molina, 1986; Raghukumar, 1987a, b; Kerwin *et al.*, 1992).

Effects of disturbance on marine fungi

The marine environment is subject to increasing human disturbances such as sewage and industrial effluent discharge, oil spills, and leachates containing pesticides. Coastal areas are most vulnerable to the above disturbances, and mangroves are another ecosystem that is particularly exposed to stress factors.

Contamination by petroleum hydrocarbons from oil spills and oil refineries is a major threat to all marine organisms. Hyde (1989a) reported that the presence of hydrocarbons might reduce the diversity of marine fungi. However, the diversity of fungi may be naturally low at some sites, and it is difficult to infer that pollution by hydrocarbons reduces fungal diversity because baseline data prior to contamination is not available. In a study of the intertidal fungi in Mauritius, highest diversity (36 sp.) occurred at Beau Champ mangrove, an area contaminated with oil from an effluent of a sugar factory (Poonyth, unpubl.). The presence of hydrocarbons on substratum surfaces is known to reduce aeration and slow down fungal activity (Scherrer and Miller, 1989). Data for the effects of most types of disturbance on marine fungi are poor.

Are there keystone species?

It is unknown if there are keystone fungi in marine ecosystems. A particular marine fungus may be a keystone species depending on its position in the food web. A fungus associated with an alga in a lichen or one involved in a mycorrhizal association may be a keystone

species whose extinction might cause a change in the ecosystem. However, as many sap-robic fungi appear to carry out the same function simultaneously, some could be functionally redundant (Hawksworth, 1991).

Major gaps in our knowledge

Although inventory data are available for the marine fungi occurring on various substrata in several countries (e.g. Australia, Hyde, 1996; Brunei, Hyde, 1988, 1989a; Malaysia, Jones and Alias, 1997), there are still many regions and types of substrata which have not been investigated. Many substrata found in the sea require further study for the occurrence of marine fungi: these include dead and living coral, rhizosphere fungi in mangroves, mycorhizal associations with mangrove trees, and sea grasses especially in the tropics. Our knowledge of strictly marine lichens and myxomycetes is also fragmentary with some 28 and 3 known species respectively. The last 20 years has also seen a significant decrease in the study of marine chytrid and straminopilous organisms. A concerted effort is needed to investigate the biodiversity of marine fungi across the world and on as many substrata as feasible. Particular attention should be paid to understudied continents such as Africa, and the numerous substrata mentioned above require targeting.

The role of marine fungi in the decay of leaves and woody tissue requires further investigation, including interactions between fungi and invertebrates. There is little knowledge of the role of marine fungi in sediments and in the decay of dead animal parts. When fungi are isolated from marine sediments, typical fast-growing weedy species (e.g. *Aspergillus*, *Penicillium*) are usually recovered. It is unclear if these fungi are active in sediments or if dormant spores are being isolated. Although fungi are also known to occur in the deep sea (Kohlmeyer and Kohlmeyer, 1979), we have little data of their role or importance.

Both bacteria and fungi are active in the decay of wood in marine environments. However, the biomass of fungi and bacteria in decaying wood has not been quantitatively evaluated. Fungi are probably more important, especially in all but the late stages of decomposition (Barghoorn and Linder, 1944). In submerged wood marine borers play a crucial role, whereas, intertidal wood, especially in the upper intertidal region, is probably decomposed solely by fungi. Various methods should also be employed to investigate the importance of marine fungi in nutrient cycling (e.g. of leaves, wood, sediments and animal parts).

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