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REVIEW

Fifty years of marine mycology

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Abstract Marine fungi have been widely studied over the past millennium and considerable progress has been made in documenting their phylogeny, biodiversity, ultrastructure, ecology, physiology and their ability to cause decay of lignocellulosic compounds. These studies have generated a wealth of publications and this review will focus primarily on research undertaken since 1995. During this period new topics have attracted marine mycologists especially: algicolous and manglicolous fungi, deep sea fungi, planktonic fungi, endophytes of marine plants, and the screening of taxa for new chemical structures and bioactive compounds. This review will also highlight areas that warrant further investigation, including surveys for marine fungi in Africa, artic waters and south America, more detailed studies of their physiology and biochemistry, and to determine the marine origin of so called "marine derived" fungi.

Keywords Biodiversity · Bioactive metabolites · Taxonomy and phylogeny · Substrata · Ultrastructure

Introduction

It is just over 50 years ago that I started working on marine fungi under the supervision of Dr. Irene Wilson, one of the pioner researchers of this group of fascinating organisms. Although various mycologists had reported on the occurrence of marine fungi (Desmaziéres 1849; Durieu de Maisonneuve and Montagne 1869; Crouan and Crouan 1867; Cesati 1880; Hennings 1908) there were no comprehensive studies of the group until those of Cotton (1909), Sutherland (1915, 1916a, b) and Sparrow (1934, 1936) concerning fungi found growing on seaweeds. However, it was a paper by Barghoorn and Linder (1944) on marine fungi on woody substrata that attracted further pioneer work on the group. These pioneers included Wilson (1951, 1954, 1956), Höhnk (1952, 1954a, b, 1955a, b), Meyers (1953, 1954), Johnson (1956a, b, c) and Kohlmeyer (1956). I was privelleged to have known all of these, all who helped me as a struggling postgraduate student. Between them they described some 100 marine fungi, predominantly from lignocellulosic substrata and currently some 530 species are documented (Jones et al. 2009a).

In 1995, the late Sam Meyers, in a keynote talk to the 6th International Marine Mycology Symposium held in Portsmouth, reviewed the first five decades of marine mycology (Meyers 1996), starting with the work of Barghoorn and Linder (1944). Therefore, this article will concentrate on developments in marine mycology since 1995, although reference will be made to earlier studies where appropriate. Research has focused on five major topics: 1. biodiversity, 2. taxonomical studies supported by molecular data, 3. ultrastructure of marine fungi with particular reference to spore appendage structure and fungal adhesion, 4. screening for bioactive compounds, and 5. their ability to cause decay of lignocellulose. These studies were initially centered on Europe and the USA, but over the past decade this has shifted to Asia, while other geographical locations are still little studied. These include Africa, South America and Artic regions. Approximately every 4 years, research progress has been the topic of at meetings of the International Marine Mycology Symposium (later the International Marine and Freshwater Mycology Symposium), often resulting in published volumes: Germany

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(Höhnk 1963; Gerlach and Höhnk 1966; Gaertner 1968), USA (Botanica Marina 1980), Portsmouth (Moss 1986) and Taiwan (Jones and Pang 2010). Because of the extensive published literature on marine fungi, it will be impossible to cover all the topics in detail, so I have been selective in those cited. Nevertheless, the references cited will give the reader a broad view of the research undertaken over the past 50 years.

Numbers of marine fungi

Various estimates of the number of marine fungi have been proposed: Jones and Mitchell (1996) estimated there were 1,500 species, but this was considered an under estimate by Liberra and Lindequist (1995) and Clement et al. (1999). Jones et al. (2009a) reported on 530 marine fungi in 321 genera which included 424 Ascomycota (251 genera), 94 mitosporic fungi (61 genera) and 12 Basidiomycota (9 genera). Most species were described between 1980 and 1999 and only 54 species between 2000 and 2011. Currently this figure is 549 with 16 new genera and 19 new species described since 2009 (Table 8), while others are in the process of being described. These figures are based on a very narrow interpretation of what can be considered to be marine, while yeasts and chytrids are rarely included. For example, it is estimated there may be some 1,500 yeasts and many new species are currently being described (Fell et al. 2010).

Jones (2011) has highlighted a wide range of fungi that should be considered as marine, and estimates the figure may be over 10,000 taxa. This is figure is based on ecological groups that have previously been labelled faculatative or marine derived. For example: fungi isolated from soils, sand, and water; planktonic fungi; deep sea fungi; unculturable fungi (environmental sequences); and cryptic species or taxa with similar morphology. Many fungi are incorrectly identified and therefore these are not considered in the estimates made. In many biodiversity studies species are only referred to genus or nonsporulating taxa, and again are not counted. In recent years studies of marine endophytes have been undertaken and more parasitic species discovered (Ananda and Sridhar 2002; Duc et al. 2009). Currently some 100 species are known from marine algae (Zuccaro and Mitchell 2005), but this figure is an underestimate as relatively few seaweeds have been examined. Considering the diversity of marine algae (estimated number of species 9,500 to 12,500), many more can be expected, especially as marine endophytes. Cryptic species are another source of marine fungi, those hidden within already described taxa, or species that are distinct but cannot be distinguished based on their morphology. This indicates that they were too broadly described, either morphologically, physiologically or ecologically. Application of molecular and incompatibility methods can also highlight the occurrence of cryptic species. Surveys of marine fungi are based on those sporulating on a substraum or isolated from them, while unculturable species go unaccounted. Molecular techniques are enabling many of these taxa to be documented, characterized and included in diversity estimates. Many sequences of unculturable fungi are already deposited in GenBank and it is important that this continues, because it will be the key to the identification of fungi yet to be discovered. It will also be necessary as barcoding of fungi is implemented (Seifert 2009; Begerow et al. 2010). Hibbett et al. (2009), in an analysis of data from three published studies, indicated there were 1120 potentially novel taxa from environmental samples, not assinable to any described species, thus highlighting the importance of molecular sequencing in ecological investigations. It is vital that we take the identification and characterization of "marine-derived fungi" seriously and not refer them merely to genera. They need to be fully documented and descriptions supported by molecular data so that their relationship to known terrestrial species can be determined. Further studies are warranted to determine if so "called terrestrial" fungi found in the marine milieu, are truly marine and adapted to life in the sea.

Biodiversity

Lignicolous marine fungi

Fungal biodiversity is the topic that has attracted the greatest research interest over the past 50 years. Initialy this was focused on temperate water fungi, especially wood-inhabiting taxa (Jones 1968; Schaumann 1968, 1969, 1975; Grasso et al. 1985, 1990; Cuomo et al. 1985, 1988; Shearer and Burgos 1987) with fewer studies in more recent years (Petersen and Koch 1997; Panebianco et al. 2002; Abdel-Wahab 2011a, b). The most intensive collections were made by Koch and Petersen (1996), Lintott and Lintott (2002), Jones et al. (1998), Jones (2010) and Abdel-Wahab et al. 2008 who reported 75 (Denmark), 38 (New Zealand), 92 (Friday Harbour, USA) and 41 (Italy) fungi, respectively. The most common temperate water species are listed in Table 1. Few of these studies offer any quantitative data, with the fungi collected from variable timber species and sample dimensions. However, Petersen and Koch (1997) attempted to quantify the species collected by removing 1440 standarised samples from *Quercus* and *Larix* mooring posts in Svanemollen Harbour, Denmark. They used a hollow punch to remove circular wood discs (3.5 diam., 1.5 thick, cm and 9.6 cm^2) from the mooring posts. Substrate specificity was noted for the two tree species: on oak: *Marinospora longissima*, *Halosphaeria*

Table 1 Ten most common temperate marine fungi from various studies

	Jones 1968	Byrne and Jones 1974	Cuomo et al. 1988	Grasso et al. 1985	Koch & Petersen 1996
Total fungi collected (total samples)	14 (16)	18 (14)	34 (766)	16 (120)	(number of poles sampled)
Cirrenalia macrocephala	4	5		20	
Dendryphiella salina	4				
Dictyosporium pelagica		2			
Trichocladium alopallonella	5				
Monodictys pelagica					97 (24)
Zalerion maritima	15	7		6	73 (22)
Digitatispora marina		2			
Aniptodera sp.					52 (25)
Arenariomyces trifurcatus			50	13	
Ceriosporopsis halima	10	6	44	19	
Corollospora maritima			240	67	
Halosphaeria appendiculata	2	8		10	163 (40)
Halosphaeriospis mediosetigera			153	11	49 (19)
Lignincola leavis		2	43		
Lulworthia fucicola					136 (36)
Lulworthia sp.					
L. purpurea	13	14	66	58	70 (32)
L. floridana	10				
Marinospora calyptrata					117 (34)
Marinospora longissima					201(38)
Phaeosphaeria oraemaris					95 (30)
Remispora hamata[a]	2	5	43		
Remispora maritima		4	36	29	
Remispora quadriremis			44	5	
Torpedospora radiata			53		

[a] Doubtfull species

appendiculata, *Lulworthia fucicola*, *M. calyptrata* and *Monodictys pelagica*; and on larch: *Remispora maritima* and *Dictyosporium pelagicum*. Observations on vertical fungal zonation were also made with samples taken from three zones: 1. Submerged zone, rarely exposed and 40–60 cm below daily sea level; 2. Interidal zone with wood exposed to rough sea, wind and greater variation in temperature and salinity and 3. Emersed zone 40 cm above daily sea level and exposed to periodic drying out, higher temperatures and salinity. Table 2 lists the species commonly found in the different zones on oak samples, with the greater diversity in the intertidal zone.

The common fungi recorded on lignocellulosic substrata vary with collecting/exposure methods employed e.g. drift material and entrapped wood (Cuomo et al. 1988; Koch and Petersen 1996; Jones et al. 1998; Lintott and Lintott 2002), sampling of fixed structures (Koch and Petersen 1996) or wood panels submerged in the sea (Miller et al. 1985; Panebianco et al. 2002). *Ceriosporopsis halima*, *Cirrenalia macrocephala*, *Corollospora maritima*, *Halosphaeria appendiculata*, *Halosphaeriopsis mediosetigera*, *Lulworthia* spp., *Marinospora calyptrata*, *Monodictys pelagica*, *Remispora maritima*, *R. stellata*, *Torpedospora radiata*, and *Zalerion maritima* can all be regarded as common lignicolous species in temperate waters (Hughes 1969; Byrne and Jones 1974; Grasso et al. 1985; Jones 1985; Cuomo et al. 1988; Petersen and Koch 1997). Most are members of the Halosphaeriales while very few bitunicate ascomycetes are to be found on submerged wood (Jones 1985).

Numerous studies of tropical marine fungi have been undertaken over the past 25 years largely those occurring on mangrove substrata. Kohlmeyer and Kohlmeyer (1979) listed 42 mangrove fungi, while Schmit and Shearer (2003) listed 625 taxa, but this figure inlcuded those growing on terrestrial parts of mangrove trees. Currently some 287 species can be regarded as growing on submerged mangrove substrata (Alias et al. 2010). Illustrated monographs of mangrove fungi have been published for India

Table 2 Vertical zonation of marine fungi on 480 oak wood samples from 40 mooring posts in Svanemollen Harbour, Denmark. (after Petersen and Koch 1997)

Fungi	Zone 1		Zone 2			Zone 3	Number posts with fungi
	−60	−40	−20	0	+20	+40	
Marinospora longissima	40	46	18	1			37
M. calyptrata	26	21	13	2			28
Lulworthia sp. (150–350 µm)	25	15	8	2			11
Halosphaeria appendiculata	24	23	23	2	3		34
Aniostagma rotundatum			1	16	2		15
Lulworthia fucicola		6	22	15	4		23
Phaeosphaeria oraemaris			3	10	19	2	18
Aniptodera sp.	1		8	9	2	1	15
Sphaerulina oraemaris			1	15		9	11

(80 species: Raveendran and Manimohan 2007), Malaysia (140: Alias and Jones 2009) and Taiwan (69: Pang et al. 2010a). Hyde and Jones (1988) recognized that mangrove fungi constituted the second largest ecological group of marine fungi which are widely distributed in Old and New world mangroves (Atlantic, Pacific and Indian Oceans). **Atlantic Ocean**: Bahamas (Jones and Abdel-Wahab 2005), Belize (Kohlmeyer and Volkmann-Kohlmeyer 1987a), Florida (Jones and Pugsili 2006); **Indian Ocean**: India (Maria and Sridhar 2002, 2004; Raveendran and Manimohan 2007; Vittal and Sarma 2006, Sarma and Hyde 2000), Mauritius (Poonyth et al. 1999), Seychelles (Hyde and Jones 1986, 1989a); **Pacific Ocean**: Brunei (Hyde 1988a, c; Hyde and Jones 1989b; Hyde and Sarma 2006), Hong Kong SAR (Jones and Vrijmoed 2003), Malaysia (Alias and Jones 2009), Thailand (Sakayaroj et al. 2004). Schmit and Shearer (2004) analysed the geographical distribution data published on mangrove fungi and found that different oceans supported varying numbers: Atlantic Ocean: 12–46 per site (14 sites: mean 25.6); Indian Ocean: 12–64 (14: 42.9) and the Pacific Ocean: 17–87 (16: 44). This would appear to indicate that more are to be found in the Pacific Ocean but this is more likely to reflect the intensity and frequency of sampling (Jones and Pugsili 2006; Alias and Jones 2009).

The Ascomycota are the most numerous and common taxonomic group in mangroves with the Basidiomycota the least frequenly collected (Alias and Jones 2009; Pang et al. 2010a). Biodiversity studies have shown a wide variation in the frequency and abundance of mangrove fungi; 154 Thailand (Sakayaroj et al. 2004), 139 Malaysia (Alias et al. 2010), 131 India (Vittal and Sarma 2006), 128 Hong Kong (Jones and Vrijmoed 2003) and 91 India (Maria and Sridhar 2003). However a core group of fungi can be identified and these are listed in Table 3. However the core mangrove fungi identified by Ananda and Sridhar (2004) and Sridhar and Maria (2006) differ from those listed in Table 3. Included in their core group are *Aniptodera* sp., *Arenariomyces parvulus* (generally more common on wood associated with sand), *Savoryella lignicola*, *Kallichroma tethys* and *Passeriniella mangrove*i and the mitosporic fungi *Arthrinium* sp., *Aspergillus* sp.1, *Penicillium* sp., which reflects the lower salinity of the water during the monsoon season. They also noted differences between dominant species on wood collected in the monsoon and the summer period. Various aspects of the ecology and biodiversity of mangrove fungi have been undertaken and these are briefly discussed below.

Colonization of other substrata

Other substrata that support the growth of marine fungi are seaweeds (Zuccaro and Mitchell 2005), sea grasses (Cuomo et al. 1982, 1985), salt marsh and other herbaceous mangrove plants. The most intensively surveyed salt marsh plant is *Spartina* (Gessner and Kohlmeyer 1976; Barata 2002). In a review of fungi growing on *Spartina* spp., Barata (2002) lists 123 species, from temperate and tropical salt marshes. The most diverse taxonomic group is the bitunicate ascomycetes with the genera *Leptosphaeria* (13 species), *Phaeosphaeria* (4 species) and *Pleospora* (6 species), well represented. In her study of marine fungi on *Spartina maritima* at three salt marshes in Portugal, the most frequently collected species were: *Natantispora* (as *Halosarpheia*) *retorquens*, *Phialophorophoma litoralis*, *Sphaerulina oraemaris*, *Phoma* sp., *Dictyosporium pelagicum* and *Byssothecium* (as *Passeriniella*) *obiones*.

Invariably when new substrata are surveyed for fungi, a wide range of new genera and species are encountered. This well illustrated by studies of the brackish water palm *Nypa fruticans* (Hyde et al. 1999) and the black needle rush *Juncus roemerianus*, a plant commonly found in coastal salt and brackish tidal marshes in the eastern USA (Kohlmeyer and Volkmann-Kohlmeyer 2001). In both cases the number of new species per host plant greatly exceeds the ration of fungi to host used by Hawksworth (1991) to estimate the global number of fungi.

Table 3 Core group of mangrove fungi as abstracted from published literature

Fungi	Hyde and Jones (1988)	Sarma and Hyde (2001)	Alias et al. 2010	Alias and Jones (2009)
Dactylospora haliotrepha	+	+	+	+
Halocyphina villosa	+	+	+	+
Halorosellinia oceanica	+	+	+	+
Kallichroma tethys	+	+	+	+
Leptosphaeria australiensis	+	+	+	+
Lulworthia grandispora	+	+	+	+
Verruculina enalia	+	+	+	+
Hydea pygmea	+	+	+	−
Lignincola laevis	+	−	+	+
Phoma sp.	+	−	+	+
Halosarpheia marina	+	−	−	+
Dictyosporium pelagicum	+	−	−	−
Matsusporium tropicalis	+	−	−	−
Trichocladium alopallonella	+	−	+	−

Several studies on the biodiversity of fungi on the intertidal brackish water palm *Nypa fruticans* have been undertaken (Pilantanapak et al. 2005; Hyde and Sarma 2006); however most describe new taxa (Hyde 1988d, 1992a, b; Jones et al. 1996a, b; Hyde and Alias 2000; Hyde et al. 1999). Pilantanapak et al. (2005) collected 81 species on the palm in Thailand while Hyde and Sarma (2006) documented 46 species from the Tutong River, Brunei. Of five surveys the most common species appear to be: *Linocarpon appendiculatum* (in all studies 20–53% frequency of occurrence), *L. nypae* (in 4, 17.5–32.5%), *Oxydothis nypae* (in in all 5, 12–26%) and *Astrosphaeriella striatispora* (in 4, 18–49.5%) (Hyde 1992a, b; Hyde and Alias 2000; Besitulo et al. 2002, 2010; Pilantanapak et al. 2005; Hyde and Sarma 2006). Many of the fungi, circa 45, are known only from *Nypa* and may be host specific, or host recurrent e.g. *Aniptodera nypae*, *Helicascus nypae*, *Linocarpon nypae*, *Tirisporella beccariana* and *Vibrissea nypicola*.

The Kohlmeyers have undertaken a detailed study of the fungi colonizing *Juncus roemerianus,* from the basal rhizomes subject to inundation by seawater to the terrestrial parts tolerant to sea spray. These have been grouped according to the parts of the plant they have been described from: obligate 6–52 cm above the rhizome), facultative (15–56 cm above the rhizome) and terrestrial or halotolerant (45–120 above the rhizome) (Kohlmeyer et al. 1997; Kohlmeyer and Volkmann-Kohlmeyer 2000). Their studies indicate that 107 species (44 obligate, 25 facultative and 38 halotolerant/terrestrial) are to be found growing on *J. roemerianus*, of which 48 species have been described, some supported by molecular data (Kohlmeyer and Volkmann-Kohlmeyer, pers. com.). These taxa belong to 7 orders, 20 families and 44 genera (Table 4) (Kohlmeyer and Volkmann-Kohlmeyer). In common with other studies of new host substrata for fungi, many of the species encountered cannot be assigned to a family or order e.g. *Aquamarina*, *Aropsiclus,* and *Heleiosa.* Taxonomic placement of other species has been resolved with sequence data, e.g. the halotolerant *Glomerobolus gelineus* to the Ostropales, Lecanomycetes (Schoch et al. 2006b).

Acanthus ilicifolius is a widely distributed shrubby herbaceous plant found in mangroves and a species surveyed for fungi by Sadaba et al. (1995). Forty four fungi were found on the decaying standing parts of *A. ilicifolius* in the intertidal zone at Mai Po Marshes, Hong Kong, with the aerial portions dominated by mitosporic fungi. The grass *Phragmites australis* and sedge *Schoenoplectus litoralis* supported 61 (17 ascomycetes, 44 mitosporic taxa) and 31 (6 ascomycetes, 25 anamorphic taxa) species, respectively in Mai Po Marshes, Hong Kong (Poon and Hyde 1998a, b; Wong et al. 1998). For both plants, the fungi present on the submerged regions differed from aerial regions, the latter supporting the greater diversity. Of the taxa documented, most were typically terrestrial-like, such as, *Cephalosporiopsis* sp., *Septoria*-like sp., *Phomopsis* sp. and *Colletotrichum* sp. Sridhar et al. (2010) followed fungal colonization, mass loss and biochemical changes during decomposition of the mangrove sedge *Cyperus malaccernsis* in the Nethravathi river delta, Katrnataka, India. Nineteen taxa were found (8 ascomycetes, 10 mitosporic taxa, one zygomycete). Initially terrestrial fungi were dominant, but followed by typical mangrove and marine fungi (*Acrocordiopsis patilii*, *Cumulospora* sp., *Okeanomyces cucullata*, *Leptosphaeria australiensis*, *Lignincola laevis*, *Lulworthia* sp., *Periconia prolifica*). Mass loss of the different parts of the sedge

Table 4 New fungi on *Juncus roemerianus* (Modified from Kohlmeyer and Volkmann-Kohlmeyer 2001)

ASCOMYCOTA
Dothideales
Dothideaceae
Scirrhia annulata Kohlm., Volkm.-Kohlm., & OE Erikss., Can J Bot 74:1835, 1996+

Pleosporales
Lentitheciacea
Keissleriella rara Kohlm., Volkm.-Kohlm. & OE Erikss., Mycol Res 100:303-404, 1995#

Massarinaceae
Massarina ricifera Kohlm., Volkm.-Kohlm. & OE Erikss., Mycologia 87:537, 1995*

Massarina carolinensis Kohlm., Volkm.-Kohlm. & OE Erikss., Mycol. Soc 100:393-404, 1995#

Montangulaceae
Tremateia halophila Kohlm., Volkm.-Kohlm. & OE Erikss., Bot Mar 38:166*, 1995*+

Phaeosphaeriacea
Paraphaeosphaeria apicicola Kohlm., Volkm.-Kohlm. & OE Erikss., Bot Mar 42: 505-511, 1999 #
Paraphaeosphaeria pilleata Kohlm., Volkm.-Kohlm. & OE Erikss., Mycol Res 100:393-404, 1995#
(anamorph *Coniothyrium* sp.)
Loratospora aestuarii Kohlm. & Volkm.-Kohlm., Syst Ascomycetum 12: 1-22, 1993+
Phaeosphaeria olivacea Kohlm., Volkm.-Kohlm. & OE Erikss., Bot Mar 40: *291-300, 1997*+
Phaeosphaeria roemeriani Kohlm., Volkm.-Kohlm. & OE Erikss., Can J Bot 76:470, *1998**
Phaeosphaeria anchiala Kohlm., Volkm.-Kohlm. & K.M.Tsui, Bot Mar 48: 306-317#

Pleopsorales incertae sedis
Massariosphaeria erucacea Kohlm., Volkm.-Kohlm. & OE Erikss*.,* Can J Bot 74: 1835, 1996+

Residual paraphyletic assemblage/clade
Floricola striata Kohlm. & Volkm.-Kohlm., Bot Mar 43:385-392, 2000+

Julella clade: Unresolved clade
Julella herbatilis Kohlm., Volkm.-Kohlm. & OE Erikss., Bot Mar 40:291-300, 1997+
Taxonomic position not confirmed by sequence data

Incertae sedis
**Heleiosa barbatula* Kohlm., Volkm.-Kohlm. & OE Erikss*.,* Can J Bot 74:1830-1832, 1996#

Capnodiales
Mycosphaerellaceae
Mycosphaerella eurypotami Kohlm., Volkm.-Kohlm. & OE Erkiss., Bot Mar 42: 505-511, 1999 #

Halosphaeriales
Halosphaeriaceae
Aniptodera juncicola Volk.-Kohlm. & Kohlm., Bot Mar 37: 109-114.1994*
Halosarpheia culmiperda Kohlm.,Volkm.-Kohlm. & OE Erikss*.,* Mycologia 87:532, 1995*

Ostropales
Stictidaceae
Glomerobolus gelineus Kohlm. & Volkm.-Kohlm., Mycologia 88:328-337, 1996+

Leotiales
Orbiliaceae
Orbilia junci Kohlm., Baral & Vokm.Kohlm., Mycologia 90:303-309, 1998#
(anamorph: *Dwayaangam junci* Baral & Vokm.Kohlm., Mycologia 90:303-309, 1998)

Xylariales

occurred over 4 weeks: bract 79%, basal stems 88% and top stems 51%. Enzyme production (cellulose, xylanase, pectinase) also peaked within the first 4 weeks of exposure.

The seagrasses *Enhalus acoroides*, *Halodule bermudensis*, *Halophila ovalis*, *Syringodium filiforme*, *Thalassia testudinum*, *Zostera japonica*, *Z. marina*, and *Z. muelleri* (mostly tropical) and the temperate water species *Cymodocea nodosa* and *Posidonia oceanica*, have been surveyed for saprobic and endophytic fungi (Newell and Fell 1980; Wilson 1998; Cuomo et al. 1982, 1985; Alva et al. 2002;

Table 4 (continued)

Amphisphaeriaceae/Cainiaceae
Atrotorquata lineata Kohlm. & Volkm,-Kohlm., Syst Ascomycetum 12:7-22,*1993**
Ommatomyces cotonatus Kohlm., Volkm.-Kohlm. & OE Erikss., Mycologia 87:538, 1995*
Anthostomella torosa Kohlm. & Volkm.-Kohlm., Mycol. Res 106: 365-374, 2002*
Anthostomella atroalba Kohlm., Volkm.-Kohlm. & OE Erikss., Can J Bot 76: 467-477, 1998#
Anthostomella semitecta Kohlm., Volkm.-Kohlm. & OE Eriks., Bot Mar 38:177, 1995+

***Xylariacea* Incertae sedis**
Hyponectriaceae
Physalospora citrogerminans Kohlm., Volkm.-Kohlm. & OE Erikss., Bot Mar 38: 183, 1995+

Incertae sedis
Phomatospora bellaminuta Kohlm., Volkm.-Kohlm. & OE Erikss., Bot Mar 38:181, 1995*

Lautosporaceae
Lautospora simillima Kohlm., Volkm.-Kohlm. & OE Erikss., Bot Mar 38: 165-174, 1995 *

Magnaporthaceae
Gaeumannomyces medullaris Kohlm., Volkm.-Kohlm. & OE Erikss., Mycologia 87:540, 1995*
(anamorph: *Trichocladium medullare* Kohlm. & Volkm.-Kohlm., Mycotaxon 53: 349-353, 1995)
Pseudohalonectria halophila Kohlm. & Volkm.-Kohlm., Bot Mar 48: 306-317, 2005 #

TBM clade
Juncigena adarca Kohlm.,Volkm.-Kohlm. & OE Erkiss., Bot Mar 40: 291-300, 1997*
(anamorph *Cirrenalia adarca* Kohlm.,Volkm.-Kohlm. & OE Erkiss., Bot Mar 40: 291-300, 1997*)

Papulosaceae
Papulosa amerospora Kohlm., & Volkm.-Kohlm.,Syst Ascom 11:96, 1993*

Saccardiaceae
Rivilata ius Kohlm.,Volkm.-Kohlm. & OE Erikss., Can J Bot 76: 467-477, 1998 #

Unitunicate Ascomycota *incertae sedis*
Aquamarina speciosa Kohlm., Volkm.-Kohlm. & OE Erikss., Mycol Res 100:303-404, 1995*
Aropsiclus junci Kohlm. &Volkm.-Kohlm., Syst Ascom 13:24, 1994*

BASIDIOMYCOTA
Unidentified (stilboid)

MITOSPORIC FUNGI
Hymenopsis chlorothrix Kohlm. & Volkm.-Kohlm., Mycol Res 105: 500-5005, 2001*
Hyphopolynema juncatile Kohlm. & Volkm.-Kohlm., Mycotaxon 70: 489-495+
Kolletes *undulatus* Kohlm. & Volkm.-Kohlm., Bot Mar 48: 306-317, 2005#
Koorchaloma galateae Kohlm. & Volkm.-Kohlm., Bot Mar 44:147-156, 2001*
Pestalotiopsis juncestris Kohlm. & Volkm.-Kohlm., Bot Mar 44:147-156, 2001+
Pycnodallia dupla Kohlm. & Volkm.-Kohlm., Mycol Res 105: 500-5005, 2001+
Septoriella unigalerita Kohlm. & Volkm.-Kohlm., Bot Mar 43:385-392, 2000#
Stagonospora abundata Kohlm. & Volkm.-Kohlm., Bot Mar 43:385-392, 2000+
Tetranacriella papillata Kohlm. & Volkm.-Kohlm., Bot Mar 44:147-156, 2001#
Tiarosporella halmyra Kohlm. & Volkm.-Kohlm., Mycotaxon 59:79-83, 1996+

* Obligate marine, + facultative marine, # halotolerant/terrestrial

Devarajan et al. 2002; Sakayaroj et al. 2010a). Early studies on seagrasses listed the basidiomycete *Falmingomyces* (=*Melanotaenium*) *ruppiae* on *Ruppia maritima* and *Halotthia posidoniae* and *Pontoporeia biturbinata* on *Posidonia oceanica* (Kohlmeyer and Kohlmeyer 1979). In Table 5 saprobic fungi currently known from seagrasses are listed. Banks of rotting seagrasses are common on the Mediterranean coast (Fig. 1) where they undergo decomposition by marine fungi, with *Corollospora maritima* being particularly common (Cuomo et al. 1985). These banks of rotting material are the feeding grounds of many invertebrates, e.g. *Paracentrotous lividus*. *Halotthia posidoniae* and *Ponto-*

Table 5 Marine saprobic fungi on seagrasses

Fungi	Host seagrass	Reference
Flamingomyces ruppiae (= *Melanotaenium ruppiae*)	*Ruppia maritima*	Bauer et al. 2007
Cladosporium algarum	*Thalassia testudinum*	Kohlmeyer and Kohlmeyer 1979
Corollospora maritima	*Th. testudinum Zostera marina*	Kohlmeyer and Kohlmeyer 1979; Cuomo et al. 1985
C. intermedia	*Posidonia oceanica*	Cuomo et al. 1985
C. lacera	*Th. testudinum*	Kohlmeyer and Kohlmeyer 1979
Lindra thalassiae	*Th. testudinum*	Kohlmeyer and Kohlmeyer 1979
Dendryphiella arenaria	*Th. testudinum*	Kohlmeyer and Kohlmeyer 1979
Varicosporina ramulosa	*Th. testudinum Z. marina*	Kohlmeyer and Kohlmeyer 1979
Halotthia posidoniae	*P. oceanica*	Cuomo et al. 1985
Pontopreia biturbinata	*P. oceanica*	Cuomo et al. 1985
Papulospora halima	*P. oceanica*	Cuomo et al. 1985

poreia biturbinata are frequently collected on the rhizomes of *Posidonia oceanica* along the Mediterranean coast. Cuomo et al. (1985) found both species on *P. oceancia* with a frequency of occurrence of 52% and 78%, respectively, but not on *Cymodcea nodosa*, another local seagrass. However collections made in Cyprus in December 2007 and February 2008 (Jones unpublished) showed *H. posidoniae* to be more abundant than *P. biturbinata.* Although *H. posidoniae* and *P. biturbinata* are commonly collected on drift *Posidonia*, little has been done to follow the process of colonization, indeed are they parasitic on the seagrasses?

Other unique marine fungi are those that occur on sand grains, corals and calcareous algae, shells of barnacles and molluscs, exoskeletons of hydrozoa and tubes of marine annelids (Kohlmeyer 1972a, b; Kohlmeyer and Kohlmeyer 1979). Some 40 arenicolous fungi have been documented, with members of the ascomycete genera *Arenariomyces*, *Carbosphaerella*, *Corollospora*, and the mitosporic species *Varicosporium ramulosa*, the most commonly found (Kohlmeyer 1966; Koch 1974; Rees et al. 1979; Tokura 1982; Koch et al. 1983; Farrant et al. 1985; Nakagiri and Tokura 1987) primarily from temperate water seashores. Accounts of arenicolous fungi from the tropics include those by Steinke and Jones (1993) from South Africa, and Sundari et al. (1996a, b) for Malysia and Singapore. *Corollospora* species are well adapted to growing on sand grains or other hard surfaces, with a well developed subiculum and ostioles and necks located basally adjacent to the subiculum. This is an advantage since long central necks to the ascomata would be abraded by the constant movement of the sand grains. The necks are plugged with thick walled cells that prevent entry of seawter into the centrum until ascospores are ready for discharge (Kohlmeyer and Volkmann-Kohlmeyer 1989). The appendaged ascospores also aide in floatation and their dispersal in seawater, and spores are often trapped in sea foam (Kohlmeyer 1966; Tokura 1982). Experimental studies on the sedimentation of spores (Rees 1980) and the effect of agitation on ascomata attachment to sand grains have been carried out by Sundari and Vikineswary (2002). Gonzáles and Hanlin (2010) suggest that arenicolous ascomycetes might be used as indicators of ecosystem disturbance of sandy beaches.

Fig. 1 Accummulation of rotting seagrass *Zostera marina* along the Danish coast

Many studies have examined the endophytes of various seagrasses and clearly show they are different from the saprobic fungi listed in Table 5 (Alva et al. 2002; Devarajan et al. 2002; Sakayaroj et al. 2010a). As for saprobic fungi on seagrasses, the number of endophytic species isolated is low: 8, 16 and 17 taxa from *Z. japonica*, *Z. marina* and *Th. testudinum*, respectively (Alva et al. 2002), 42 assemblages from *Enhalus acroides* (Sakayaroj et al. 2010a). Frequently isolated taxa from seagrasses include: *Alternaria alternata*, *Arthrinium arundinis*, *Aspergillus*, *Cladosporium*, *Fusa-*

rium, *Penicillium*, *Trichoderma* and *Phoma* spp. Sakayaroj et al. (2010a) used molecular techniques to identify their sterile isolates including a basidiomycete species, *Peniophora* sp. Most of the seagrass endophytes are similar to those isolated from mangrove trees (Suryanarayanan et al. 1998; Kumaresan and Suryananyanan 2001; Ananda and Sridhar 2002; Chaeprasert et al. 2010), and are predominatly terrestrial-like taxa. However, Ananda and Sridhar (2002) recovered the obligately marine fungi *Hydea pygmea*, *Lulworthia grandispora*, *Lulworthia* sp., *Trichocladium alopallonella* and *Zalerion maritima* from the roots of mangrove trees. Further studies are required to determine if these so called terrestrial isolates are adapted to life in the marine milieu.

Marine animals also harbor fungi, and have been shown to be a rich source of isolates yielding new chemical structures, often bioactive compounds (Kendrick et al. 1982; Höller et al. 2000; Morrison-Gardiner 2002; Proksch et al. 2008; Schulz et al. 2008; Li and Wang 2009; Aly et al. 2010; Rateb et al. 2010). Pivkin et al. (1999) isolated 27 fungi from tissues of three holothurians, while Proksch et al. (2008), Wang et al. (2008a, b), Baker et al. (2009), Liu et al. (2010) and Paz et al. (2010) isolated marine derived fungi from marine sponges, all with matches to known genera/species in the GenBank. Liu et al. (2010) opin that thousands of fungal strains have been isolated from different sponges with many yielding bioactive compounds (Bugni and Ireland 2004). Most isolated fungi are primarily genera and species considered terrestrial, such as, *Aspergillus*, *Cladosporium* and *Penicillium* spp. So are they marine, are they metabolically active in the marine environment, and how accurate is their identification? Paz et al. (2010) examined the ability of fungi isolated from the Mediterranean sponge *Psammocinia* sp., to inhibit the growth of fungi. From 400 isolates, 85 taxa were identified; with 28 possessing antifungal properties, predominantly *Trichoderma*, *Acremonium*, *Bionectria*, *Aspergillus*, and *Penicillium* spp. Paz et al. (2010) also consider the role of these marine derived fungi in the host sponge. As sponges are filter feeders, are the fungi simply trapped in the sponge tissues and therefore have no active role in the biology of their host?

Decomposition of mangrove substrata

Various studies have shown that mangrove fungi are able to degrade lignocellulose (Leightley 1980), Mouzouras (1986, 1989), Mouzouras et al. (1988) and Leong et al. (1991). Since most are ascomycetes and mitosporic fungi, they are able to cause soft rot attack of various timbers. However the basidiomycete *Halocyphina villosa* causes white rot attack of wood (Mouzouras et al. 1988). Maria et al. (2006) followed the decomposition of *Avicennia officinalis* and *Rhizophora mucronata* twigs in Udyavara mangrove, India over 18 months. Decay of twigs was slow over the first 10–12 months, but more rapid in the last 6 months. This topic is discussed further in a later section.

Factors affecting the distribution of mangrove fungi

The distribution of marine fungi is governed by a multitude of interacting factors, and no single one can be identified to explain their occurrence and frequency of occurrence. However some factors are more important than others, for example, availability of substrata, temperature, water salinity and geographical location are key elements in the occurrence and distribution of marine fungi (Booth and Kenkel 1986; Pang et al. 2009; Suetrong et al. 2009a, b; Vrijmoed et al. 1986). Jones (2000) highlighted a consortium of factors operating in determining the biodiversity of fungi in the sea: water temperature, salinity, seasonality, pH, nutrient availability, tidal amplitude, availability of substrata and their chemical composition, possession of specific enzymes to degrade the substratum, natural occurring substrata or baited samples, succession, period samples exposed to seawater, and depth at which samples are recovered (Fig. 2). A number of studies have discussed the importance of various factors in the ecology of marine fungi (Kohlmeyer and Kohlmeyer 1979; Hyde and Lee 1995; Sadaba et al. 1995; Schmit and Shearer 2003, 2004; Alias and Jones 2009), with Sarma and Hyde (2001) proposing a protocol for documenting the diversty of mangrove fungi.

Although a core group of mangrove fungi can be identified, there is great variation in the dominant fungi reported from different locations, especially when sampling drift or senescent attached wood. This can be accounted for by the different sampling methods adopted: size/volume of the sample, period exposed in the mangrove, presence or absence of bark on the wood, salinity of the water, sample size and frequency of collections. Fungi on mangrove wood can vary depending on collection of material, especially in the dry or wet season of mangroves subject to monsoons. Ananda and Sridhar (2004) documented 68 taxa on mangrove wood during the monsoon when the salinity was 0–1.05%, but only 55 species in the summer period when water salinity was higher. Species composition was also different with the terrestrial species *Arthrinium* sp., *Aspergillus* sp. 1, and *Penicillium* sp. dominant. Similar results were reported by Sadaba (1996) for fungi colonizing *Acanthus ilicifolius* during the dry season when salinity was high (20%0), marine fungi predominated; while in the wet season when salinities are low (1–5 ppm) typical terrestrial fungi occurred.

Sequence of colonization of mangrove substrata

Few studies have followed the process of colonization of substrata by marine fungi. This has usually involved the

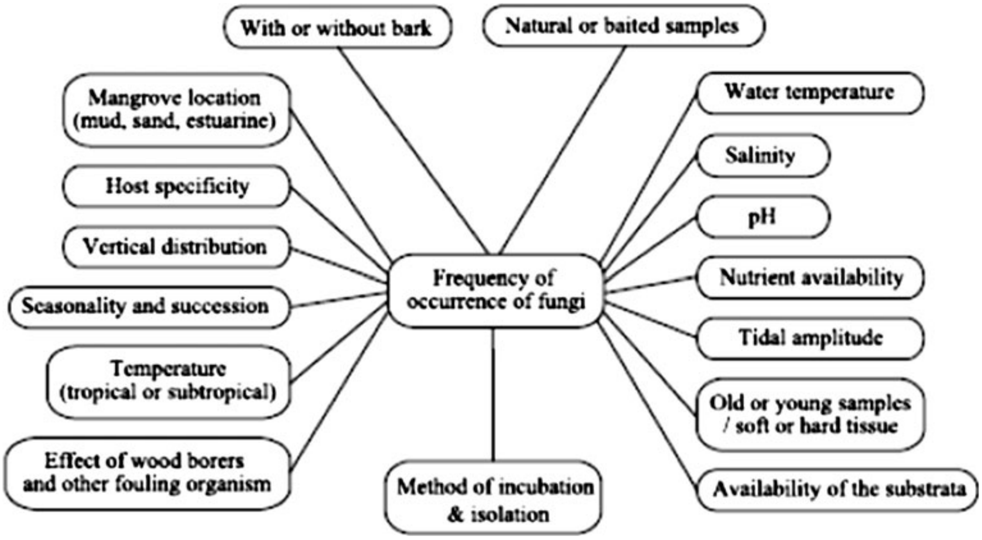

Fig. 2 Factors that influence the frequency of occurrenace of mangrove fungi (reproduced with permission of IOES, Kuala Lumpur)

submergence/exposure of test samples in the sea at various depths, with their retrival at specific time intervals, laboratory incubation to encourage sporulation and identification of the colonizing taxa. Early studies were by Meyers and Reynolds (1960) and Jones (1968) who reported the colonization of wood test blocks by *Ceriosporopsis* and *Lulworthia* speices after 12–18 weeks exposure. Subsequent studies in temperate localities were by Byrne and Jones (1974), Miller et al. (1985), Grasso et al. (1985) and Panebianco et al. (2002) while tropical studies focused on mangrove fungi (Tan et al. 1989a, b; Leong et al. 1991; Alias and Jones 2000a). Tan et al. (1989a, b) and Leong et al. (1991) followed fungal succession on four mangrove timbers (*Avicennia alba, A. lanata, Bruguiera cylindrica, Rhizophora apiculata*) at Mandai mangrove, Singapore, while Alias and Jones (2000a) exposed *Bruguiera parviflora* and *Avicennia marina* samples at Kuala Selangor mangrove, Malaysia. Although different timbers were used the most common species were similar: *Verruculina enalia*, *Lulworthia* sp., *Halosarpheia marina* and *Lignincola laevis*. Key findings from these studies include 1. There was 100% colonization of the test blocks, 2. Some core mangrove fungi did not appear on the test samples e.g. *Dactylospora haliotrepha*, *Halorosellinia oceanica*, and 3. There was a clear pattern of fungal colonization. Early colonizers (6–18 weeks) on both timbers at Kuala Selangor mangrove were *H. marina, N. retorquens, L. laevis, Neptunella longirostris* and *Lulworthia grandispora*. Intermediate colonizers (26–54 weeks) were *Dictyosporium pelagicum, Halocyphina villosa, Saagaromyces ratnagiriensis, Periconia prolifica, Savoryella lignicola, T. achrasoporum, T. alopallonellum* and *Verruculina enalia*. Late colonizers (60–96 weeks) were *Aigialus parvus, Leptosphaeria australiensis, Saagaromyces glitra, Quintaria lignatilis, Saccardoella marinospora* and *Tirispora unicaudata*.

The fungi colonizing timbers in mangroves are uniquely tropical and distinct from those occurring in temperate waters (Byrne and Jones 1974; Miller et al. 1985). Various laboratory studies have explored the factors that determine fungal colonization: fungal competition, interference verus exploitation and the chemical basis for such interactions (Strongman et al. 1987; Gloer 1995; Shearer 1995; Miller 1986, 2000). However few have explored these parameters under field conditions. Miller et al. (1985) followed the fungal colonization of beech panels in Langstone Harbour, England recording the number of perithecia of each fungus per 10 mm^2: 137 perithecia of *Lulworthia* sp. were present when it was the sole taxon sporulating on the wood, but only 53 when *Ceriosporopsis halima* also occurred on the panel. This figure dropped further to 3 per 10 mm^2 when *Amylocarpus encephaloides* also appeared on the wood. Panebianco et al. (2002) tested the effect of preconditioning balsa test blocks before submergence in the sea over 15 months, with the fungi *Corollospora maritima*, *C. halima*, *Halospaheriospsis mediosetigera* and *Marinospora calyptrata*. Control test blocks were colonised by *C. halima*, *Corollospora maritima*, *Halosphaeria appendiculata*, *Halosphaeriopsis mediosetigera*, *Lulworthia* sp. and *M. clalyptrata*, all typical fungi for the Langstone Harbour site (Jones 1968). On preconditioned blocks of *Corollospora maritima* it was the only fungus to sporulate on the wood for up to 6 months, similarly *H. mediosetigera*, suggesting that these taxa affected the colonization of the test blocks by “indigenous” species. However, *M. calyptrata* showed no such inhibition and became dominant at 9 months and the only species present at 15 months. Further studies are required to determine the nature of this inhibition, as many marine fungi have been shown to produce bioactive compounds.

Tan et al. (1995) have also shown that different fungi can affect the sporulation of other species when grown together on wood. *Aigialus parvus*, *Lignincola laevis* and *Verruculina enalia* were grown singly, or in mixed cultures, on mangrove test blocks in shake culture and periodically examined for the formation of ascomata. Sporulation of *L. laevis* was suppressed by *A. parvus*, while *L. laevis* enhanced ascomata production by *V. enalia*. All three fungi have been shown to produce bioactive compounds (Abraham et al. 1994; Isaka et al. 2002, 2009).

Vertical distribution of marine fungi

Early studies on the vertical distribution of marine fungi was undertaken by Schaumann (1968, 1969) in the Wesseer Estuary and Helgoland, Germany, and proposed that "the number of species increased from low-water mark towards the mean-tide mark. However, Kohlmeyer (1969a, b) reported there weas no vertical pattern of fungi on the roots, and prop roots of *Rhizophora* spp., and suggested further research was required. Vertical distribution of marine fungi may be influenced by tidal amplitude, e.g. at Morib mangrove, Malaysia with a wide intertidal zone (Alias and Jones 2009).

However, vertical distribution of marine fungi has been demonstrated for various fungi, while others are distributed throughout the tidal range (Hyde 1988a, b, c, 1990; Sadaba et al. 1995; Poon and Hyde 1998b; Alias and Jones 2000b; Besitulo et al. 2010). Sadaba et al. (1995) observed vertical distribution of fungi on standing plants of *Achanthus ilicifolius* in a study in Mai Po mangrove, Hong Kong. The apical portions were colonized by typical terrestrial fungi and the basal portions by marine fungi. The highest number of collections was from the basal portion, followed by middle and upper portions with mitosporic fungi the dominant group encountered at these levels. They attributed this to tissue type and varying degrees of exposure to tidal inundation which are important in governing species distribution along the vertical line. Kohlmeyer and Volkmann-Kohlmeyer (2001) also noted vertical distribution of fungi on *Juncus roemerianus*, those on the lower parts of the culm were regarded as obligately marine, with halotolerant species in the upper zone (aerial). For example, those occurring: 6–52 cm above the rhizome e.g. *Phaeosphaeria roemeriani* were obligate species, 15–56 cm above rhizome e.g. *Floricola striata* facultative, and 45–120 cm above rhizome e.g. *Septoriella unigalerita* terrestrial or halotolerant.

Alias and Jones (2000b) examined the vertical distribution of mangrove fungi, on the prop roots of *Rhizphora apiculata* at Morib mangrove in Selangor, Malaysia. Intertidal prop-roots were collected from three levels: upper 1.8–2.2 m above mean low water mark (samples were superficially dry for long periods), middle 0.8–1.8 m (submerged daily for varying periods) and lower: 0.2–0.8 m (waterlogged or submerged samples), with 100–200 samples per level placed in clean polythene bags and returned to the laboratory. Samples were washed to remove surface sediments and fouling organisms scraped off, then incubated in plastic boxes for up to 6 months at room temperature (Jones and Hyde 1988). Fifty-three fungi from 330 samples were collected, with *Pyrenographa xylographoides*, *Halosmassarina* (=*Massarina*) *thalassiae* and *Nectria* sp. common in the upper zone, while nine species occurred only in the lower zone, including the more oceanic species: *Antennospora quadricornuta*, *Haiyanga* (=*Antennospora*) *salina* and *Torpedospora radiata*. Most species occurred in the middle zone with nine species found only in this zone: *Ascocratera manglicola, Saagaromyces* (=*Halosarpheia*) *ratnagiriensis, Morosphaeria* (=*Massarina*) *ramunuculicola* and *Morosphaeria* (=*Massarina*) *velatospora* the most frequent. Only five species occurred at each level: *Quintaria lignatilis*, *Leptosphaeria australiensis*, *Lulworthia* sp., *Halocyphina villosa* and *Lulworthia grandispora*. However, Besitulo et al. (2010) found no evidence of vertical distribution of fungi on the palm *Nypa fruticans* in Siargao Island, Philippines, although at the same locality zonation occurred on *Rhizophora apiculata* and *Xylocarpus granatum*. *Cucullosporella mangrovei*, *Morosphaeria ramunculicola*, and *Marinosphaera mangrovei* were found in the upper level with *Acrocordiopsis patili* at the lower level only.

Factors that govern the vertical distribution of fungi include exposure during the intertidal and in particular desiccation, exposure to UV light, tolerance to freshwater in the form of rain, and reproduction with the need to release their spores. These aspects are further discussed by Kohlmeyer and Volkmann-Kohlmeyer (1987a, b), Jones and Tan (1987), Jones et al. (1988), Hyde (1991), Chinnaraj (1993) and Sarma and Vittal (2002).

Molecular systematics

The advent of molecular systematics has greatly enhanced our understanding of the origin and evolution of marine fungi. The first molecular paper on marine fungi was by Spatafora and Blackwell (1994) when they included a sequence of *Halosphaeriopsis medisetigera* in their study of ophiostomid ascomcyetes. Subsequently Spatafora et al. (1998) established the independent terrestrial origins of the Halospaheriales, while the genera *Lindra* and *Lulworthia* formed a separate clade of marine perithecial ascomycetes. There followed extensive research into the phylogeny and taxonomy of marine fungi, which proceeded along three separate lines: 1. Resolution in the delineation of species and genera, 2. Higher order taxonomic placement of marine fungi, and 3. Application to ecological studies, especially the identification of sterile endophyte cultures and unculturable isolates.

Revision of genera

It had long been speculated that certain marine genera were a complex of unrelated species, e.g. *Corollospora*, *Halosarpheia* (Schmidt 1969, 1974) however, ultrastructural studies of ascospore appendage ontogeny gave partial resolution (Jones et al. 1983, 1984; Johnson et al. 1984, 1987). The delineation of other genera remained problematic, especially the genera *Halosarpheia* and *Massarina/Lophiostoma* (Hyde et al. 2002; Pang et al. 2003b). A wide range of genera have now been sequenced, especially members of the Halosphaeriales (Pang 2002; Sakayaroj et al. 2005a, b). This has resulted in taxonomic changes and the establishment of many new genera (Tables 6 and 8). Many genera were shown to be polyphyletic, e.g. *Cirrenalia*, *Cumulospora*, *Halosphaeria*, *Halosarpheia*, *Kirschsteiniothelia*, *Lulworthia*, *Massarina*, and *Remispora*, all resulting in transfer of species to new genera (Sakayaroj et al. 2010b) (Table 8). Sequence data also enabled the identification or confirmation of teleomorphs of many mitosporic genera: *Cirrenalia* (new genera for *Hydea pygmea* and *Matsusporium tropicale*), *Cumulospora* (new genus for *Moromyces varius*), *Zalerion* (Lulworthiales), *Halosigmoidea*, *Periconia* (Halosphaeriales), *Amorosia*, *Dendryphiella* (Pleosporales), *Halenospora* (Leotiales), *Glomerobolus* (Ostropales) and *Xylomyces* (Jahnulales) (Campbell et al. 2003, 2005; Schoch et al. 2006a, b; Jones et al. 2008a, 2009a, b; Abdel-Wahab et al. 2010).

Molecular data has been used to support the erection of new genera: *Haloaleurodiscus* (Russulales, Maekawa et al. 2005), *Pseudolignincola*, *Thalespora* (Halosphaertiales, Jones et al. 2006), *Halenospora* (Leotiales, Jones et al. 2009a), *Rostrupiella* (Lulworthiales, Koch et al. 2007), *Sedecimiella* (Hypocreales, Pang et al. 2010b) and new species: *Halosigmoidea parvula* (Halosphaeriales, Jones et al. 2009b), *Halosarpheia japonica* (Halosphaeriales, Abdel-Wahab and Nagahama 2011a, b). Other examples are listed in Table 8.

Other species referred to a family based on molecular sequences include: Ascomycetes: *Buergenerula spartinae*, *Gaumannomyces medullaris*, *Pseudhalonectria halophila* (Magnoporthaceae, Thongkantha et al. 2008), *Verruculina enalia* (Testudinaceae, Schoch et al. 2006a), *Neomassariosphaeria typhicola* (Amniculicolacae, Zhang et al. 2009b), *Keissieriella rarum*, *Lentithecium phragmiticola* (Lentitheiaceae, Zhang et al. 2009a), *Paraliomyces lentiferus* (Lophiostomataceae) *Kirschsteiniothelia maritima* (Mytilinidiales) Suetrong et al. 2009a) and the basidiomycetes: *Flammingomyces ruppiae* (Urocystaceae, Urocystales), and *Parvulago marina* (Ustilaginaceae, Ustilaginales) (Bauer et al. 2007). A number of new species could also be assigned with confidence to known families/orders: the yeasts *Candida*, *Cryptococcus*, *Kwoniella*, *Pseudozyma*, *Rhodotorula* (Statzell-Tallman et al. 2008, 2010; Fell et al. 2010), *Glomerulispora*, *Moheitospora* (TBM clade), and *Halzoon*, *Moleospora* (Lulworthiales) (Abdel-Wahab et al. 2010), and *Lanspora* (Ophiostomatales, Schoch pers. com.),

Other taxa that require further study when fresh material becomes available, include marine species of *Leptosphaeria*, *Lophiostoma*, *Massarina* in the Dothediomycetes

Table 6 Taxonomic revision of genera of marine fungi since 2000–2009, based on sequence data

Genus	Previous name	Taxonomic group	Reference
Flamingomyces	*Melanotaenium*	Urocystales	Bauer et al. 2007
Parvulago	*Ustilago*	Ustilaginales	Bauer et al. 2007
Decorospora	*Pleospora*	Pleosporales	Inderbitzin et al. 2002
Colemopsidium	*Verrucaria*	Pyrenulales	Grube and Ryan 2002
Haiyanga	*Antennospora*	Halosphaeriales	Pang et al. 2008a, b
Magnisphaera	*Halosarpheia*	Halospaheriales	Campbell et al. 2003
Morakotiella	*Haligena*	Halospaheriales	Sakayaroj et al. 2005a
Natantispora	*Halosarpheia*	Halospaheriales	Campbell et al. 2003
Neptunella	*Lignincola*	Halospaheriales	Pang et al. 2003a
Okeanomyces	*Halosphaeria*	Halospaheriales	Pang et al. 2004a, b
Panorbis	*Halosarpheia*	Halospaheriales	Campbell et al. 2003
Saagaromyces	*Halosarpheia*	Halospaheriales	Pang et al. 2003b
Kohlmeyeriella	*Lulworthia*	Lulworthiales	Campbell et al. 2005
Lulwoana	*Lulworthia*	Lulworthiales	Campbell et al. 2005
Lulwoidea	*Lulworthia*	Lulworthiales	Campbell et al. 2005
Halenospora	*Zalerion*	Leotiales	Jones et al. 2009a
Halosigmoidea	*Sigmoidea*	Halosphaeriales	Jones et al. 2009b
Nohea	*Nautofragella*	Halosphaeriales	Abdel-Wahab 2011a, b

(Suetrong et al. 2009a); *Lulworthia* species (*L. grandispora, L. purpurea, L. opaca*) and the polyphyly of the genus *Lindra* in the Lulworthiales (Koch et al. 2007); and the polyphyly of *Verrucaria*, Verrucariales (Gueidan et al. 2007). The genus *Lindra* has already been shown to be polyphyletic, but no fresh material of the type species (*Lindra inflata*) has been available to resolve the phylogeny of the genus (Koch et al. 2007). *Lindra obtusa* and its anamorph *Anguillospora marina* are distantly placed from *Lindra crassa* and *L. thalassiae*, and these two enties also differ morphologically (Jones et al. 2009a). Many marine genera are not assigned to any higher order position: the cleistothecial ascomycetes *Biflua*, *Drysophaera*, *Marisolaris* always found on wood and associated with sand (Koch and Jones 1989); *Biatriospora*, *Halotthia*, *Heleiosa*, *Pontoporeia*, *Tirisporella* (Pleosporales *incertae sedis*) (Suetrong et al. 2009a); and *Adomia*, *Lanceispora*, *Phomataospora* (Xylariales *incertae sedis*) (Jones et al. 2009a).

Families and orders: new lineages

Spatafora et al. (1998) were the first to identify marine fungal lineages, the Halosphaeriales and Lulworthiales, although the latter was not formally designated until later (Kohlmeyer et al. 2000). The Halosphaeriales (now regarded by some authorities as a family Halosphaeriaceae in the Microascales) comprises 126 species in 53 genera (Sakayaroj et al. 2010b). The diagnostic features of the order are perithecial ascomata, asci that are clavate to fusiform, lacking an apical apparatus and deliquescing early, presence of catenophyses, and primarily 1-septate, hyaline ascospores with various polar and equatorial appendages, and saprobes in aquatic habitats (Jones 1995; Pang 2002). The Lulworthiales comprise 8 genera: *Haloguignardia*, *Kohlmeyeriella*, *Lulworthia*, *Lulwoana*, *Lulwoidea*, *Lindra*, *Rostrupiella*, *Sapthluospora* and their anamorphs: *Cumulospora*, *Hydea*, *Matsusporium*, *Orbimyces* and *Zalerion* (Jones et al. 2008a; Abdel-Wahab et al. 2010). The teleomorphs all share a common feature in ascospores with an apical chamber from which a drop of mucilage may be released (Jones 1994). The genera *Koralionastes* and *Pontogenia* form a monophyletic clade basal to the Lulworthiales and are a third ascomycete marine lineage, the Koralionasteales (Campbell et al. 2009). This group differs from members of the Lulworthiales in that the ascospores lack an apical mucous-filled polar end chamber (appendages). *Koralionastes* is a unique genus of five species that occur on coralline-coated rocks and sponges, and known from the Atlanic Ocean, Belize, Central America, and Australia (Kohlmeyer and Volkmann-Kohlmeyer 1987c; 1990). *Pontogenia* species were initially referred to *Zigonella*, but were transferred to the new genus because of differences in the morphology of the ascomata, and in particular the hyaline, sepate ascospores parasitic on marine algae. Eight species have been described from green and brown algae (Kohlmeyer 1975).

Sakayaroj et al. (2005b) showed that the genera *Torpedospora* and *Swampomyces* formed a monophyletic group that was a sister group to the Hypocreales. Schoch et al. (2006a) confirmed that these genera, along with *Etheirophora* and *Juncigena*, formed a novel marine lineage in the Hypocreomycetidae grouping with the orders Coronophorales and Melanosporales and referred to as the TBM clade (*Torpedospora*, *Bertia*, *Melanospora*). However, the family and order relationships were not resolved and Schooch et al. (2006a) suggested further sampling was required with protein coding loci (RPB1, EF-1γ). A related lineage of aquatic fungi is the Savoryellales with the genera *Ascotaiwania*, *Ascothaliandia*, *Savoryella* and their anamorphs (*Canalisporium*, *Monotosporella*, *Helicoon*) and also form a relationship with the TBM clade (Boonyuen et al. 2011). Schoch et al. (2009) also highlight three nonlichenised lineages in the Dothideomycetes: plant pathogenic Coryneliales, lichen parasitic Mycocaliciomycetidae and the marine saprobic *Dactylospora*-clade (*Dactylospora haliotrepha*). For sure other new lineages of marine fungi remain to be discovered as further taxon sampling is undertaken.

Three marine lineages have been identified within the homobasidiomycetes, representing three to four independent transitions from terrestrial to aquatic habitats (Hibbett and Binder 2001; Maekawa et al. 2005). The *Nia* clade (*Halocyphina villosa*, *Nia vibrissa*, *Calathella mangrovei*) in the euagarics is primarily evolved from cyphelloid forms, with both mangrove and marine forms (Hibbitts et al. 1981; Binder et al. 2006). The second lineage in the euagarics, and not related to cyphelloid forms, is the physalacriaceae clade and comprises *Physalacria maipoensis* and *Mycaureola dilsea*, a parasite of the red alga *Dilsea edulis* (Porter and Farnham 1986; Binder et al. 2006). A third lineage includes *Haloaleurodiscus mangrovei* which occurs on dead trunks and branches of *Sonneratia alba* in Japanese mangrove forests (Maekawa et al. 2005). Sequence data phylogentically placed this species in the root of the Peniophorales clade, euagaric Homobasidiomycetes. Both *Ph. maipoensi* and *H. mangrovei* were reported from the more freshwater mangrove zone and regarded as halotoleratent, but the former has been collected at Futian mangrove growing on the intertidal senescent stems of *Acanthus ilicifolius* (Jones, unpublished data) (Inderbitzin and Desjardin 1999; Maekawa et al. 2005).

As the result of molecular studies a number of new families have been identified that have marine taxa. Within the Dothideomycetes eight new families have been proposed: Aigialaceae, Morosphaeriaceae (Suetrong et al. 2009a), Amniculicolaceae, Lentitheciaceae (Zhang et al.

2009a, b), and Trematosphaeriaceae (Suetrong et al. in press) (Pleosporales); Aliquandostipitaceae (Inderbitzin et al. 2001) (Jahnulales), Hypostromataceae (Mugambi and Huhndorf 2009) Lautosporaceae (Kohlmeyer et al. 1995) (Ascomycetes *incertae sedis*). *Lautospora gigantea* is a wood-inhabiting ascomycete with cylindrical asci with an ocular chamber and large, thick-walled hyaline, 4–7 septate ascospores lacking appendages or a sheath (Hyde and Jones 1989b). A second species *L. simillima* was described from *Juncus roemerianus* and because of the unusually large thick-walled ascospores a new family Lautosporaceae was erected to accommodate these two species and refered to the Dothideomycetidae *incertae sedis* (Kohlmeyer et al. 1995). No sequence data is available to resolve its higher taxonomic position (Suetrong et al. 2009a).

The Hypostromataceae was erected to accommodate two genera *Hypsostroma* and *Manglicola*, a family with no known relationship to any group in the Dothideomycetes, but with "probable affinities to the Melanommatales or Pleosporales" (Huhndorf 1994; Mugambi and Huhndorf 2009). Fresh collections enabled the referral of *Manglicola guatemalensis* to the Jahnulales based on sequence data, while the position of *Manglicola samuelsii*, collected on dead culms of bamboo in Guyana, remains unresolved. Inderbitzin et al. (2001) established the Aliquandostipitaceae for a new genus, *Aliquandostitpite*, with two freshwater ascomycetes collected in China and Thailand, but not referred to any order. The family can now be placed in the Jahnulales, an order described by Pang et al. (2002) with the genera *Aliquandostitpite, Jahnula*, and *Patescospora*, and the recently added *Manglicola* (Suetrong et al. 2009b), *Megalophylla* (Campbell et al. 2007), and the anamorphic genera *Brachiosphaeria*, *Xylomyces* (Campbell et al. 2007) and *Speiropsis* (Prihatini et al. 2008). The order is characterized by large-celled ascomata, often born on a stalk, broad vegetative hyphae (10–40 µm) and ascospores with a variety of gelatinous appendages, pads or sheaths. Shearer et al. (2009) opinioned that the order contains 4–5 separate lineages that require further molecular data to resolve their inter relationships.

The genera *Aigialus*, *Ascocratera* and *Rimora* (*Massarina mangrovei*), known only from mangrove habitats, form a monophyletic group with high statistical support, with the erection of a new family, Aigialaceae, in the Pleosporales (Suetrong et al. 2009a). Another new family in the Pleosporales is the Morosphaeriaceae which includes the marine genera *Heliscus*, and *Morosphaeria* and the freshwater ascomycete *Kirschsteiniothelia elaterascus* (Suetrong et al. 2009a). Suetrong et al. (2009a) referred the marine species *Halomassarina thalassiae* and *Falciformispora lignatilis* to the Trematosphaeriaceae; however this was not formally introduced in their paper. This has now been formally described (Suetrong et al. 2011) with *Trematosphaeria* as the type genus. Zhang et al. (2009a) erected the family Lentithiaceae to accommodate *Massarina* species that could not be assigned to the Massarinaceae, and included the marine fungi *Lentithecium* (*Massarina*) *phragmiticola* and *Keisieriella rarum*. *Verruclina enalia*, a common mangrove ascomycete, grouped in the Testudinaceae (Schoch et al. 2006a; Suetrong et al. 2009a) although in the anlaysis of Mugambi and Huhndorf (2009) it is placed in the Platystomaceae, with weak support.

Although there has been great progress in our understanding of the molecular phylogeny of marine fungi, many taxa await assignment to a family or order, in particular members of the Dothideomycetes (Suetrong et al. 2009a).

Application to ecological studies

A key question when undertaking ecological studies of marine fungi is, have you isolated/recovered all the species? Most of the biodiversity studies documented above have been of fungi sporluating on selected substrata or isolated from them on to agar media (Hyde et al. 1999; Raveendran and Manimohan 2007; Alias and Jones 2009; Jones et al. 2009a; Pang et al. 2010a, b). Also many of the fungi isolated as endophytes are sterile and do not sporluate in culture, in particular basidiomycetes and ascomycetes (Ananda and Sridhar 2002; Rungjindamai et al. 2008; Sakayaroj et al. 2010a). Such sterile strains can now be determined by the use of molecular techniques, as shown by the studies of Zuccaro et al. (2003, 2004) and Sakayaroj et al. (2010a). Forty four fungal asemblages were isolated from the seagrass *Enhalus acoroides* of which 25 were sterile cultures (Sakayaroj et al. 2010a), and sequence data enabled generic identification of these strains, and some to species. This will become an increasingly important technique for the identification of fungi in ecological studies (Pivikin et al. 1999; Pivkin 2000).

A major unknown when dealing with fungal ecology, is have all the species present in host/substrtum been determnined? This is particularly so for studies of marine soils and sediments. This is well illustrated by ecological studies of terrestrial soils when most of the fungi documented are mitosporic fungi or readily sporulating ascomycetes. Basidiomycetes are only occasionally listed, yet woodland soils are rich in such fungi. New techniques are therefore required to obtain a complete knowledge of the total mycological compliment of such substrata. Pang and Mitchell (2005) have outlined the range of molecular techniques available to assess fungal diversity in the marine environment, so that interactions between microbial diversity and ecosystem function can be better understood. PCR-DGGE (denaturing gradient gel electrophoresis) analysis of DNA exracted from various substrata has now been wildly used to document fungal communities using fungal specific primers e.g. May et al. (2001) Nikolcheva et al. (2005), Duong et al. (2006), and Seena et al. (2008). However its application to the study of marine fungi is relatively new (Pang and Mitchell 2005; Zuccaro et al. 2004, 2003, 2008). Zuccaro et al. (2004) extracted DNA from the brown alga *Fucus serratus* using primers nuSSU and nuLSU rDNA when a number of ascomycete phylotypes were identified. The majority of the environmental phylotypes isolated matched those of the culturable diversity, with representatives of the Dothideales, Halosphaeriales, Hypocreales and Lulworthiales. Four of the phylotypes could be matched with *Corollospora angusta*, *Halosigmoidea* (= as *Sigmoidea*) *marina*, *Lindra* cf *obtusa* and *Emeicellopsis/Acremonium* group. However, a number of phylotypes did not match those that were isolated by traditional methods. Such techniques are not without problems, short sequences and data interpretation, potential over estimates, number of sequences in the GenBank for comparison, estimation of taxon richness, and are these taxa ecologically active in the habitat. Zuccaro et al. (2004) further discuss the issues highlighted here and emphasise the importance of databases of fungal sequences for future ecological studies and "the development of probes for the detection of nonculturable and parasitic fungi".

Ultrastructure studies of marine fungi

Ulrastructural studies of marine fungi have focused on three topics: 1. The development of ascospores and their appendages, 2). To seek diagnositic features for the characterisation of species and 3. To observe the attachment of spores to various substrata.

Marine fungal spores and their appendages

As most unitunicate marine fungi possess ascospores with morphologically diverse appendages, it is natural that these features have been widely used in the delineation of species and genera (Jones et al. 1986). Jones (1995) outlined a scheme that characterised the different developmental forms in ascospore appendage development. A number of studies followed to examine the different ways ascospore appendages were formed at the scanning and transmission electron microscope level (SEM, TEM) (Read et al. 1993a, b; 1995), which often resulted in a reevaluation of the taxonomy of selected genera (Jones et al. 1983; Johnson et al. 1987; Jones 1995). Schmidt (1969) was the first to draw attention to the possibility that the genus *Corollospora* was polyphyletic which promoted Jones et al. (1983a) to examine ascospores structure and development of various species. This confirmed its polyphyly and species were assigned to the genera: *Kohlmeyeriella* (ascospores with polar endchambers formed by the epi- and mesosporium, and filled with mucilage), *Nereiospora* (appendages polar and equatorial, hair-like extensions of the spore wall), *Arenariomyces* (appendages sub-apical terminating in hook-like structures) and *Corollospora* (primary appendages apical formed by the epi- and mesoporium, secondary appendages formed by fragmentation of the exosporium). Similar studies showed other genera were polyphyletic: *Halosphaeria* and led to the reestablishment of the genera *Halosphaeriopsis*, *Remispora*, and the erection of the genera *Ondiniella*, *Ocostaspora* (Johnson et al. 1984; Jones et al. 1984); *Ceriosporopsis* and reestablishment of *Marinospora* while it was suggested that *C. tubulifera* should be referred to another genus (Johnson et al. 1984) and transfer of *Haligena amicta* to a new genus *Appendichordella* (Johnson et al. 1987).

Ascospores with hamate, bipolar unfurling appendages are common in the Halosphaeriales, but ultrastructural studies have shown that there is great variation in the orgin of these structures: appendages arising from a distinct pore (*Magnisphaera spartinae*); appendages emerging from a hood-like structure (*Cucullosporella mangrovei*); arising from discontinuities in the episporium (*Saagaromyces ratnagiriensis*) (Jones 1962; Alias et al. 2001; Baker et al. 2001). However, Yanna and Hyde (2003) showed that the genera *Linocarpon* and *Neolinocarpon*, with filiform ascospores, could not be delineated based on the ultrastructure of the polar appendages. Yusoff et al. (1995) undertook a similar study of the filiform ascospores of the genera *Lindra* and *Lulworthia*, with the latter genus possessing mucilage-filled polar end chambers formed by episporial and mesosporial wall layers. In *Lindra* species, the spore wall comprises an episporium and mesosporium with a mucilaginous layer around the spore poles but lack an end chamber. Thus descriptions of new genera and species have been considerably enhanced by electron micrographs of the ascomata, asci and ascospores.

One feature common to all the marine species investigated was the demonstration of a delimiting membrane (or membrane complex) which surrounds the developing spore and appendages and only breaks down once they have been released into water. This delimiting membrane prevents the premature expansion of the appendages until they are released from the ascomata. For example, ascospores of *Halosarpheia*, *Cucullosporella*, *Saagaromyces* spp., once released from the ascomata and in water, the delimiting membrane deliquesces and the hamate polar appendages unfurl to form long thread-like appendages (Alias et al. 2001; Baker et al. 2001; Jones 2006). Similarly, ascospore appendages of *Corollospora* species only expand when the delimiting membrane ruptures once in water and the exosporic layer peels away from the spore wall and undergoes a fragmentation process (Jones et al. 1983; Hsieh et al. 2007; Jones 2006).

While unitunicate ascomycetes possess ascospores with elaborate appendages, spores in bitunicate taxa generally have gelatinous sheaths, e.g. *Rimoria velatospora*, or are elaborated into wing like appendages e.g. *Decorospora gaudefroyi* (Yusoff et al. 1994). As most marine bitunicate fungi are intertidal and generally forcibly eject their asocospores, the presence of elaborate appendages would be a disadvantage if they expanded before release from the ascus. Thus the delimiting membrane prevents the premature expansion of ascospore appendages and sheaths until they are ejected into the surroung water (Read et al. 1994, 1997a, b; Jones 2006). The ultrastructure of a wide range of bitunicate ascomycetes have been investigated to determine the ontogeny of ascospore appendages and sheaths (Au and Vrijmoed 2002), in particular *Capronia ciliomaris* (Au et al. 1999b), *Leptosphaeria pelagica* and *Trematospheria malaysiana* (McKeown et al. 2001), *Paraliomyces* (Read et al. 1992), *Massarina* species (Read et al. 1994, 1997a, b), *Julella avicenniae* (Au et al. 1999a) and *Tirisporella beccariana* (Jones et al. 1996a, b), to list but a few. In unitunicate ascomycetes the ascospore wall generally comprises three layers: meso-, epi- and exosporium, but in bitunicte species the wall may be more elaborate with a bilamellate mesosporium (*Dactylospora haliotrepha*, *Julella avicenniae*, *Leptosphaeria pelagica*; Au et al. 1996, 1999a; McKeown et al. 2001).

Few detailed studies of ascomata and ascus development of marine fungi have been published, and mostly of sections observed at the light microscope level (Lloyd and Wilson 1962; Wilson 1956; Kohlmeyer and Kohlmeyer 1966; Schatz 1983; Pang et al. 2010a, b). Au et al. (1999b) showed at the TEM level, that the ascoma wall of *Capronia ciliomaris* comprised 2–3 layers with setae arising from the outer layer. Initially the upper third of the centrum was filled with rounded cells embedded in an extracellular matrix, but break down at maturity with the extension of the asci. Periphysoidal elements arose from the inner upper third of the ascomal wall and ostiolar canal, extended through the ostiole and merged with a crown of apical setae. Hsieh et al. (2007) followed ascoma development in *Corollospora gracilis* from ascogonium initiation, antheridium-ascogonium conjugation, production of ascogenous hyphae to peridium and ostiole development. Pit-connections of the centrum pseudoparenchyma have been reported for a number of marine ascomycetes, e.g. *Antennospora salina*, *Arenariomyces trifurcatus*, *Kohlmeyeriella tubulata* (Kohlmeyer and Kohlmeyer 1979; Kohlmeyer and Volkmann-Kohlmeyer 1987b) but their origin has not been determined. At the TEM level, pit-connections in *C. gracilis* were found to be modified ascomycetous septal pores, fluorescing with Calcoflour white, which stains material rich in 1, 4-β-glucans. Another observation made in this study was the occurrence of a plug of thick-walled non-melanized cells at the base of the ostiole that separated the rest of the centrum tissue by a thin melanised separation layer. Similar structures have been reported by Kohlmeyer and Volkmann-Kohlmeyer (1987a; b; c; 1989) in *Corollospora cinnamomea* and *C. armoricana,* and may occur in other species in the genus (Nakagiri and Tokura 1987). This plug may play a role in preventing the entry of seatwater into the centrum until ascospore release is imminent.

Attachment studies

Jones (1973) and his co workers, initiated various studies to investigate spore dispersal, attachment and colonization of substrata in the sea. Various stages can be identified leading to spore attachment: spore release, transport (dispersal, flotation), settlement, and deposition (attachment). These stages involve passive attachment (entrapment) to active attachment leading to the production and release of extracellular adhesive, spore differentiation, germination with germ tube development and formation of a hyphal sheath, development of appressoria and the penetration of the substrataum (Rees 1980; Rees and Jones 1984; Hyde et al. 1986a, b, 1989; Jones 1994, 2006). Fazzani and Jones (1977) carried out preliminary studies to document spore realese in various marine fungi, but this has not been followed with any further experimental work.

Spore entrapment to substrata has been documented for species such as, *Nantantispora retorquens* with its bipolar unfurling appendages wrapping around wood fragments, or conidia of *Orbimyces spectabilis* trapped to jagged wood cell walls (Rees and Jones 1984). Many marine ascomycetes have spores with mucilaginous appendages that aid passive attachment to the substratum: *Ondiniella torquata* (annulus-like equatorial appendage that forms an adhesive pad on contact with the substratum) and *Lautosporopsis circumvestita*; release of a drop of mucilage from apical end chambers, that form an adhesive pad that spreads out on the substratum to anchor the spore (*Kohlmeyeriella tubulata, Lulworthia* spp.) and sticky fibrous threads that aid attachment (*Carbosphaerella leptosphaerioides*, *Appendichordella amicta*, *Nereiospora cristata, Nautosphaeria cristaminuta*). Other species, especially bitunicate ascomycetes, possess mucilaginous sheaths that aid in spore attachment: *Halomassarina thalassiae*, *Julella avicenniae*, *Morosphaeria velatospora* (Rees and Jones 1984).

Active attachment results when ascospores have made contact with a substratum and begin to germinate, with the formation of germ tubes surrounded by mucilage (Hyde et al. 1986a, b). The trigger mechanism for this has not been elucidated. Subsequently hyphae are formed ensheathed by mucilage which further adhere the spore to the substratum (Hyde et al. 1986b). Mucilaginous hyphal sheaths have been known for some time (Szaniszlo et al. 1968; Palmer et al. 1983) but their function was speculative. Hyde et al. (1986a) followed the germination of 15 marine fungi on wood veneers and polycarbonate membranes and reported the development of hyphal sheaths in each species. It was postulated that these sheaths serve in the adhesion of the developing hyphae prior to penetration of the substratum. This is supported by the observations of other authors (Akai et al. 1967; Hau and Rush 1982).

Experimental studies of spore attachment of marine fungi have included factors affecting sedimentation rates of spores (Rees 1980), the use of waterjets to determine their strength of attachment to surfaces (Rees and Jones 1984), and a Fowler Radial Flow Chamber (Hyde et al. 1989). Hyde et al. (1989) found that ascospores of marine fungi became attached to the discs, albeit relatively weakly over 24 h. The spores of some species became more strongly attached (e.g. *Eiona tunicata*) than others (e.g. *Amylocarpus encephaloides*) and the strength of attachment increased with time with greater shear stress required to remove spores at time intervals up to 96 h. Hyde et al. (1993) studied the flotation, deposition and attachment of spores to solka flock, while Sundari and Vikineswary (2002) examined the effect of agitation on ascomata formation in the marine ascomycete *Corollospora gracilis*. Marine fungi must secure rapid attachment, often under turbulent wave action, and further studies are warranted to explore their ability to colonize substrata in the sea, especially pathogenic and endophytic taxa. Few mycologists have considered the world wide distribution/dispersal of marine fungi and their center of origin. While some taxa can be regarded as temperate (e.g. *Lindra inflata*), cold water species (e.g. *Toriella tubulifera*), tropical (e.g. *Halorosellinia oceanica*) others are cosmopolitan (e.g. *Corollospora maritima*, *Lignincola laevis*) (Abdel-Aziz 2010; Pang et al. 2009, 2010a, b; Abdel-Wahab 2011a, b).

Bioactive compounds

It is impossible to estimate how many marine/marine derived fungi have been screened for bioactive compounds or new chemical structures, but it runs into thousands, for example, Cuomo (1986) screened some 1500 marine strains. The Italian survey showed that the anamorphic fungus *Dendryphiella salina* was a prolific producer of new chemical structures yielding trinor-eremophilane or eremophilane sesquiterpenoids (Guerriero et al. 1988, 1989): dendryphiellin A, B, C, D, A1; dendryphiellic acid A, B, glyceryl dendryphiellate A, and five eremophilane derivatives. Since the discovery that the marine basidiomycete *Halocyphina villosa* produced the bioactive compound siccayne in 1981 (Kupka et al. 1981), our knowledge of their potential for production of secondary metabolities has increased dramatically. The result has been a number of extensive reviews of the subject: Biabani and Laatsch (1998), Miller (2000), Verbist et al. (2000), Faulkner (2002), Jensen and Fenical (2002), Lin and Zhou (2003), Bugni and Ireland (2004), Jones (2008) and Ebel (2010). The late Dr John Faulkner for a number of years reviewed the new secondry metabolites produced by marine microorganisms, which included marine fungi (Faulkner 2002, and references included therein) and this is being continued by Peter Proksch in Fungal Diversity (Aly et al. 2010; Debbab et al. 2011). The number of new bioactive compounds reported from marine fungi has increased steadily over the years: 1 (1981), 100 (2002), 272 (2004) and may be well over 400 now. These reviews document this information according to chemical structures (Verbist et al. 2000), activity of compounds (Aly et al. 2010) while Bugni and Ireland (2004) focus on the source of the fungi and their biological activity. Table 7 lists some recently published new compounds from marine fungi.

Bugni and Ireland (2004) have calculated that most compounds from marine fungi are from sponges (33%) followed by algae (24%) and wood (13%), with the number of new compounds following the same trend: 29, 27, and 10% from sponges, algae and wood, respectively. Although so called obligate marine fungi have been shown to produce a wide spectrum of secondary metabolites (e.g. *D. salina*: Guerriero et al. 1988, 1989, *Kallichroma tethys*: Alam et al. 1996, *Halorosellinia oceanica*: Schilingham et al. 1998; Chinworrungsee et al. 2001, 2002; Li et al. 2001), the most prolific are the marine derived fungi isolated from a wide range of substrata (Höller et al. 2000; Morrison-Gardiner 2002; Pivikin et al. 1999). Pivikin et al. (1999) isolated a large number of strains from bottom sediments, algae, animals and sea foam yielding 179 species from the Sea of Japan. From 418 strains tested 78 showed activity against Gram-positive and gram-negative bacteria. Of the marine derived fungi from a large number of studies, typical terrestrial taxa such as: *Aspergillus*, *Fusarium*, *Penicillium*, *Phoma* and *Trichoderma* were the most common but whether they are active in the marine environment is subject to debate. It is vital that molecular sequences of these strains are available so as that they can be compared with their terrestrial counterparts, and aid future studies. However, they generally produce quite different secondary metabolites to similar terrestrial strains (Bhakuni and Rawat 2005).

Marine fungi produce a wide spectrum of secondary metabolites and some examples are included here:

> **lipids**: ceramide was obtained from *Lignincola laevis* (Abraham et al. 1994), and asperamides A and B from an endophytic *Aspergillus niger* isolated from *Colpomenia sinuosa* (EN-13), a brown alga (Zhang et al. 2007);
>
> **heterocycles**: penicilazine from a *Penicillium* sp. (Lin et al. 2000) and is related to the compound triochode-

Table 7 Examples of some new compounds from marine fungi 2008–2011

Fungus	Substratum	2nd metabolite	Reference
Alternaria sp.	*Sonneratia alba* China	xanalteric acids I, II	Kjer et al. 2009
Unidentified ascomycete	Marine sponge, Figi	New dibenzofurans:	Rateb et al. 2010
Fasciatispora nypae	Mangrove wood, Malaysia	2,2,7-trimethyl-2H-chromen-5-ol	Zainuddin et al. 2010
Phomopsis sp.	Mangrove bark China	phomopsin A	Tao et al. 2008
Penicillium aurantiogriseum	Marine mud China	verrucosidinol verrucosidinol acetate	Yu et al. 2010
Unidentified	Red Sea Egypt	deuteromycol A, B	Nawwar et al. 2010
Fusarium sp.	Gorgonian sea fan, Thailand	anthraquinone cyclopentanon derivatives	Trisuwan et al. 2010
Talaromyces sp.	Bark *Kandelia candel*, China	7-epiaustdiol, 8-0-methylepiaustdiol	Liu et al. 2010
Paecilomyces sp.	Bark mangrove tree, Taiwan	paecilozocins A, B	Wen et al. 2010
Phoma sp.	Caribbean marine sponge, Dominica	epoxyphomalins C, D, E	Mohamed et al. 2010
Penicillium sp.	Sediment sample, China	meleagrin D, E roquefortine H, I	Du et al. 2010
Unidentified sp.	Leaves *Xylocarpus granatum*, Thailand	merulin A, B, C	Chokpaiboon et al. 2010
Unidentified sp.	Marine brown alga, Japan	phomactin	Ishino et al. 2010
Penicillium chrysogenum	Marine sponge, Italy	sorbifurans A-C	Bringmann et al. 2010
Aspergillus insulicola	Sediment, Hawaii	azonazine	Wu et al. 2010

mamide from the marine derived fungus *Trichoderma virens* isolated from a marine ascidian (Eliane et al. 2003);

allenolic series: xyloallenolide A, isolated from a mangrove *Xylaria* sp. strain #2508 (Lin et al. 2001a), allenic moieties are rather uncommon, with most from marine habitats;

ketal series: xyloketals 9–16 were isolated from a *Xylaria* strain #2508 (Lin et al. 2001b). Xyloketals have importrant phamacological activities with great efforts being made for their synthesis under laboratory conditions;

depsipeptides: a novel cyclic depsipeptide enniatin G was isolated from the mangrove fungus *Halosarpheia* sp. collected on mangrove wood in Thailand (Lin et al. 2002a);

alkaloids: two new diketopiperazines were obtained from a *Penicillium* sp. isolated from a deep ocean sediment sample, and roquefortine H, J and I (Du et al. 2010);

cyclic peptides: marine fungi produce a wide range of peptides as illustrated with *Beauveria felina* isolated from the marine alga *Caulerpa* yielding two new cyclic depsipeptides; pseudodestruxin C and β-Me-pro destruxin E chlorohydrin (Lira et al. 2006); *Spicellum roseum* isolated from a Caribbean sponge *Ectyplasia perox* produced two new cyclohexadepsiptides spicellamide A and B (Kralj et al. 2007); mangrove strain #2516 yielded three new cyclotetrapeptides and four cyclic dipeptides, while strain #2524 isolated from seeds of *Avicennia marina* produced two new cyclic pentapeptides (cyclo-(L-Phe-L-Leu^1-L-Leu^2-L-Leu^3-l-lle, and cyclo-(Phe-Val-Leu-Leu-Leu), the former exhibiting cytotoxic activity against human cancer cell line Bel-7401 (Li et al. 2004), and the hexacylic dipeptide azonazine was isolated from the marine derived fungus *Aspergillus insulicola* (Wu et al. 2010);

isocumarins: two new isocumarins avicennin A and B, and vermopyrone were isolated from the leaf endophyte of *Avicennia marina* (Lin et al. 2001c), while isoculmorin was obtained from the mangrove fungus *Kallichroma tethys* (Alam et al. 1996; Kong and Kim 2002);

terpenes: a number of marine fungi produce these compounds: *Dendryphiella salina* (dendryphielins A-D, Guerriero et al. 1988); endophyte #2492 and *Halorosellinia oceanica* (two unique dipterpenes isomers hypoxylin A and B, and a sesquiterpene lactone: Luo et al. 2004; Li et al. 2001); unidentified marine fungus (MPUC 046), isolated from a brown alga *Ishige okamurae* (phomactin I, 13-epi-phomactin I and phomatcin J: Ishino et al. 2010); *Penicillium* sp., isolated from sea mud (two new eremophilane sesquiterpenes: 3-acetyl-9,7(11)-dien-7a hydroxyl-8-oxoeremophilane and 3-acetyl-13-deoxyphemenon: Huang et al. 2008);

diketopiperazines: an *Aspergillus* sp. isolated from *Mytilus edulis* (mussel) yielded a series of prenylated diketopiperazines, notoamides A-D and F-K (Kato et al. 2007); while another species *A. fumigatus* isolated from *Stichopus japonics* (holothurian) produced seven such compounds including spiro-3-indolinone, spirotryprostatin C, D and E, and *Eurotium rubrum* and *P. bilaii* yielded dehydroariecolorin L and dehydroechinulin and bilains A, B and C respectively (Li et al. 2008);

lactones: *Helicascus kanaolanus*, a mangrove ascomycete yielded helicascolides A and B (Poch and Gloer 1989), while a *Eutypa* sp. isolated from *Avicennia marina* yielded eutpoid A a new α,β-unsaturated-γ-lactone (Lin et al. 2002b), while others have been reported by Yang et al. (2006) and Shao et al. (1999);
anthraquinones: many marine fungi have been shown to produce known and new anthraquinones: *Halorosellinia* sp. (Jiang et al. 2000), an endophytic fungus from *Avicennia* sp. (Zhu et al. 2004), *Paecilomyces* sp. (Wen et al. 2007) and an endophytic strain isolated from *Acanthus ilicifolius* (Shao et al. 2007).

Marine fungi have been shown to have activity against a broad range of microorganisms and pharmacological conditions; however few have made it commercially. In comparing the activity of 1,500 marine and 1,450 terrestrial strains, the major difference in antimicrobial activity was in that terrestrial isolates were more active against gram-negative bacteria, while those from marine fungi were active against fungi (e.g. *Candida albicans*, *Pythium dabaryanum*, *Botrytis cincerea*). Biological activities range from:

antibacterial: nigrospoxydon A showed activity against *Staphylococcus aureus* (NIC 64 μg/mL) (Trisuwan et al. 2008);
antifungal: isoculmorin (Alam et al. 1996), culmorin (Strongman et al. 1987), microsphaeropsin from a *Microsphaeriopsis* sp. (Höller et al. 2000), mactanamide (Lorenz et al. 1998), two macrodiolides from *Cladosporium herbarum* (Jadulco et al. 2001), three lipodepsipeptides affect fungal cell wall synthesis and thus have a potential in the control of dermatophytes (Schilingham et al. 1998), while Paz et al. (2010) showed that 36 marine derived fungi isolated from a Mediterranean sponge *Psammocinia* sp. possessed antifungal activity;
broad antimicrobial activity: halymecins A-C (from a *Fusarium* sp.) and D-E (from *Acremonium* sp.) (Chen et al. 1996);
antimalarial: hypothemycin and aigialomycin D activity at IC50 values of 2.2 and 6.6 μg/ml (Isaka et al. 2002), while bostrycin showed weak activity (Trisuwan et al. 2010);
cytotoxic (penochalasins A-C most potent against P388 leukemia cell line (Numata et al. 1996; Iwamoto et al. 1999), while trichdenones A-C are mildly cytotoxic (Amagata et al. 1998), communesins A and B are cytotoxic alkaloids from a *Penicillium* sp. (Numata et al. 1993, 1996), paeciloxocin A against HepG2 cell line (Wen et al. 2010), pentostatin A-D, nigrosporanene A against MCF-7 and Vero cells (IC50 values of 9.37, 5.42 μg/mL, respecvtively) (Rukachaisirikul et al. 2010); *Xylaria psidii* and strain KT31 (a sterile algicolous strain from *Kappaphycus alvarezii*) showed strong cytoxic activity at IC50 values of 4 μg/mL and 1.5 μg/mL, respectively (Tarman et al. 2011);
platelet activating factor PAF) antagonists: phomactins are a new class pf specific PAF antagonsis (Sugano et al. 1995). Other uses of metabolites from marine fungi are dicussed by Verbist et al. (2000).

Pan et al. (2008) screened more than 100 fungal strains isolated from various substrata collected in the South China Sea, with 25 yielding 40 new compounds of which 20 were new bioactive compounds. Intensive screening of marine and marine derived fungi has yielded a huge number of interesting compounds, with a wide range physiological activity. Some marine fungi have been shown to be a prolific source of compounds: *Dendryphiella salina* isolated from seaweeds and other marine substrata, yielded some 12 new chemical structures some with bioactivity. Jensen and Fenical (2002) indicate that Dendryphiellin A is "an unpresentented sesquiterpene esterified with a branched C9 carboxylic acid". *Halorosellinia ocenaica* is another species that yields a wide range of novel compounds: 15G256α, 15G256β, 15G256γ, 15G256δ, 15G256ε (Abbanat et al. 1998; Schilingham et al. 1998), halorosellinic acid (Chinworrungsee et al. 2001), a sesquiterpenoid lactone (Li et al. 2001, 2005), while a *Halorosellinia* sp. (#1403) yielded seven anthraquinones, one of which was a new compound (Jiang et al. 2000). Of equal interest are two *Fusarium* strains isolated from the gorgonian sea fan (*Annella* sp.) which yielded five new metabolites (a modified anthraquinone fusaranthaquinone, cyclopentanon fusarone, a naphthquinone fusarnaphthoquinone, fusarnaphthoquinone B, furanaphthoquinone C and 18 known compounds (Trisuwan et al. 2010). In the search for new sources for bioactive compounds, marine fungi have yielded a wide range of novel compounds both chemical structures and in their pharmacologically activity. Fungi isolated from mangrove wood, and marine derived strains from sponges, algae and tunicates top the list as sources for novel chemistry (Bugni and Ireland 2004). More recently endophytes of various plants and animals have also been shown to be an excellent source of new compounds (Schulz et al. 2002; Jones 2008; Pan et al. 2008; Chaeprasert et al. 2010; Rateb et al. 2010) with Schulz et al. (2008) demonstrating that endophytic fungi were a better source of novel secondary metabolies than fungi associated with marine algae. Schulz et al. (2008) further concluded that "neither plant organ from which endophytes originated nor host species affected antifungal activity of the culture extracts and the genera *Geniculosporium*, *Nodulisporium* and *Phomopsis* species produced the greatest numbers of metabolites per isolate". It is not surprising that the first two genera produced so many novelties, as they are xylariaceous mitosporic fungi, a known rich source of bioactive compounds (Stadler and Hellwig 2005). This is an area of marine mycology that will continue to expand and yield fascinating results.

Wood decay

Wood decay research in the 1960–1970's was the result of the great losses in timber structures in the marine environment by wood boring animals (molluscs and crustaceae) and the role of fungi in the preconditioning of wood prior to larval settlement. This led to the setting up of a special working group by OECD on the preservation of wood in the sea, and was later incooperated into Comité International pour la Recherch sur la Préservation des Matériaux en Millieu Marin COIPM (Jones 2009).

Some of the early studies of the physiology and biochemistry of marine fungi dealt with their ability to cause decay of wood (Jones 1971; Meyers 1971a, b) in particular their ability to cause soft rot attack of wood cell walls (Mouzouras 1986; Mouzouras et al. 1988). Later studies have focused on: 1. Mechanism of wood cell wall breakdown, 2. Enzymes produced by marine fungi, and, 3. Potential use of marine fungi in bioremediation.

Mechanism of wood cell wall breakdown

Early studies examined the ability of marine fungi to cause soft rot attack of wood, cordage and cellulose, although the number of species screened was low (Jones 1971). *Corollospora maritima*, *Monodictys putredinis* and *Lulworthia purpurea* caused weight losses of wood of 25.7, 16.8 and 9.8%, respectively over an 18 week exposure period. Soft rot cavities were observed in the middle layer of the secondary wall in transverse sections, and as diamond shaped cavities in longitudinal sections in polarized light. Mouzouras (1986) screened 24 species for soft rot attack and cell-wall penetration, with cavity formation observed in 16, and weight losses was dependent on the wood used. Significant weight loss was observed by the anamorphic fungus *Monodictys pelagica* (40%), and basidiomycetes *Nia vibrissa* (28%) and *Halocyphina villosa* (23%) on balsa wood (*Ochroma lagopus*), lower weight loss on *Fagus sylvatica* (21, 5.5 and 8%, respectively), with no losses on *Pinus sylvestris*. Mouzouras (1989) and Mouzouras et al. (1988) showed that temperature affected the degree of weight loss caused: the cold water basidiomycete *Digitatispora marina* cuased 14% weight loss of balsa wood at 10°C but only 5% at 22°C, while the opposite was noted for the mangrove basidiomycete *H. villosa* (0% at 10°C and 23% at 22°C). The results for *Nia vibrissa*, a cosmopolitan species, were 13 and 28% loss at 10 and 22°C, respectively. Butcher et al. (2004) also determined the wood mass loss under exposed and submerged conditions by 48 marine strains, with the greatest losses by *Ascocratera manglicola* (20%), *Cryptovalasa halosarciicola* (20%) and *Rhizophila marina* (12%). Weight losses were much lower under submerged conditions. Two terrestrial fungi included for comparison caused losses of 56% (*Phanerochaete chrysosporium*) and 73% (*Pycnoporus sanguineus*), indicating marine fungi were less active in the decay of wood.

The marine basidiomycetes caused white rot decay of wood and this has been demonstrated by Leightly and Eaton (1979) for *Nia vibrissa* and by Mouzouras (1989) for *Halocyphina villosa*.

The mechanism of soft rot attack had been widely speculated on until Hale and Eaton (1984, 1985a, b) observed cavity formation in two marine fungi (*Trichocladium alopallonella* and *Monodictys putredinis*) using a combination of continuous photomicrography and Scanning and Transmission Electron microscopy. They were able to observe the oscillatory growth of the fine proboscis hyphae in the wood cell wall and the stop start mycelial growth leading to the formation of cavities.

Enzymes produced by marine fungi

Early studies of the enzyme activity of obligate marine fungi was by Chesters and Bull (1963) who studied the enzymes associated with various algal polysaccharides, e.g. laminarin, and Sam Meyers and his group (Meyers 1968, 1971b) on wood decay fungi isolated from wood and cordage (Meyers 1971a, b). These studies also included observations on their ability to sporulate under laboratory conditions, to degrade seagrasses (Meyers et al. 1965) and the relationship between marine fungi and nematodes in the marine environment (Meyers et al. 1964). These and other more recent studies have been reviewed by Verbist et al. (2000) who list redox enzymatic activity laccase, tyrosinase, peroxydase, polyphenoloxydase), xylanasic and cellulosic activities (xylanase, β-D-xylosidase, cellulose, β-D-glucosidase) and amylasic, pectinasic, alginastic and laminarinasic activities. Most of the fungi screened were isolated from *Spartina*, wood, decaying mangrove wood and seagrasses and “showed a great variety of enzymatic activities for a given genus”.

More recent studies have focused on the cellulolytic and ligninolytic activity of marine fungi, especially ascomycetes. Pointing et al. (1998) screened 15 fungi for cellulolytic activity with all displaying endoglucanase and cellobiohydrolase activity. Lignolytic activity was determined by well established dye discolouration methods, with seven and 14 displaying peroxidase and laccase activity, respectively. Similar results were obtained by Raghukumar et al. (1994) when they isolated and screened mangrove and seagrass fungi for laccase activity. A few produced significant levels of laccase (*Saagaromyces ratnagiriensis*, *Hydea pygmea*, *Gliocladium* sp.), three showed manganese-dependent peroxidase activity but none had lignin peroxidase activity. Butcher et al. (2004) screened 48 strains of marine fungi for lignolytic acitivity, 89% were celluloytic, 84% xylanolytic, 60% decolourised Poly-R, 23% oxidized syringldazine and 12% decolourised Azure B. Luo et al. (2005) screened 29 fungal isolates collected from tropical and subtropical mangrove/marine habitats for the presence of lignocellulose-degrading enzyme activities in agar media. Endoglucanase and xylanase were the most common enzymes produced. However, none of the fungi exhibited an ability to decolourise Poly-R-478 dye, indicating the lack of ligninolytic peroxidases. Three groups of fungi were categorised according to their cellulolytic, xylanolytic, and ligninolytic enzymes. Group I contained 21 isolates (ca. 72% of the test fungi) able to produce the three enzymes: endoglucanase, xylanase and laccase. Group II comprised two isolates lacking the ability to utilise filter paper and/or xylan, whereas Group III consisted of six isolates (ca. 21%) with no laccase activity. Laccase activity would appear to be widespread in marine fungi but other lignin degrading enzymes were less common. This may be accounted for by the fact most species screened were ascomycetes.

Typical terrestrial-like basidiomycetes have been shown to occur in brackish water mangroves e.g. *Phellinus* sp. causing butt rot of *Xylocarpus granata*, while *Grammothele fuligo* has been repeatedly collected on the decaying frond bases of *Nypa fruticans* (Jones and Choeyklin 2008). Basidiomycetes have also been isolated as endophytes from marine plants: *Peniophora* from the seagrass *Enhalus acoroides* (Sakayaroj et al. 2010a), while Menezes et al. (2010) and Bonugli-Santos et al. (2010a, b) isolated a number of basidiomycetes from the marine sponges *Amphimedon virdis* and *Dragmacidon reticulata* from the coastal town of São Sebastião, São Paulo state Brazil. They showed that isolates of *Marasmiellus* sp. *Peniophora* sp. and *Tinctoporellus* sp. showed great laccase gene diversity and new putative laccases. These laccases were produced when the fungi were grown on seawater media, suggesting they may be active in the marine environment. However the number of basidiomycetes recovered from marine habitats remains low and further studies involving innovative isolation methods is warranted.

Potential use of marine fungi in bioremediation

The ability of marine fungi to produce lignin degrading enzymes has stimulated research into the decolourization of bleach plant effluent from pulp and paper mills, effluent from textile and dye making industries and molasses spent wash from alcohol distilleries (Raghukumar 2008). Various authors have screened marine fungi for their ability to decolourize a range of dyes or produce lignin degrading enzymes (Pointing et al. 1998; Raghukumar et al. 1999; Raghukumar 2002, 2008). Raghukumar (2002) screened 11 marine fungi for lignin degrading enzymes and their ability to decolourise industrial dyes, with 70% showing laccase activity, and 82% cellulose activity. Three and one showed manganese peroxidase and peroxidase activity, respectively. A white rot basidiomycete, *Flavodon flavus*, isolated from a decaying sea grass in a coral lagoon in India, produced all three major classes of lignin degrading enzymes: manganese-dependent peroxidase, lignin peroxidase and laccase, and was the most effective in the decolourization of dyes. For example: Congo red, remazol brilliant blue, and 80% of pigments in spent molasses were decolourised.

Although various fungi (especially white rot species) have been shown to decolourise a wide range of dyes and effluents, there has been no commerical application. One of the major problems is the rate at which reactions take place, e.g. to achieve 80% decolourization of spent molasses pigments takes 8 days, and this is unrealistic when thousands of gallons per hour have to be treated. Raghukumar (2002) has also discussed some of the problems related to bioremediation of water born pollutants and dyes by fungi. Pointing (2001) reviewed the wide range of pollutants in the environment, the ability of white rot fungi to bring about their transformation and minerlization, and set out some of the conditions that have to be met for their use in bioremediation. White rot fungi, such as *P. chrysosporium*, *Pycnoporus cinnabarinus* and *Tramtes versicolor*, have been used in bioreactors (Das et al. 1995; Schliephake and Lonergan 1996; Leidig et al. 1999). However, marine fungi may have a greater potential in the bioremediation of oil spills in coastal waters (Sadaba and Sarinas 2010).

Deep sea fungi

Initial records of deep sea fungi were by Jones and Le Campion-Alsumard (1970) and Kohlmeyer (1977) on wood or polyurethane covered panels and retrieved as part of other ongoing projects. More recently Dupont et al. (2009) recovered two fungi (*Alisea longicola*, *Oceanitis scuticella*) from depths of 1,000 m in the Pacific Ocean, off the Vanuatu Islands. All these studies were based on the fungi sporulating on the retrieved substrata. The study of deep sea fungi has been hampered by the cost of such research and available sampling methods and equipment (Raghukumar et al. 2010).

Current studies utilize a combination of culturing and molecular techniques to characterize the diversity of fungi in the deep-sea, especially those present in deep-sea sediments (Nagano et al. 2010; Raghukumar et al. 2010). Damare et al. (2006) and Singh et al. (2010) have recovered 163 cultivable fungi from the Central Indian Basin deep-sea sediments, most filamentous strains were ascomycetes, and most yeasts basidiomycetes. Common genera were *Aspergillus*, *Cladosporium* and *Penicillium*, thus complementing the data for marine derived fungi from various substrata, endophytes of marine plants and algae and sediments from mangrove and coastal waters. The fungal diversity reported has been surprisingly low with few novel taxa recovered (Bass et al. 2007), however Le Calvez et al. (2009) did recover new species from three fungal phyla, using DNA extracts from hypothermal vent samples. Further innovation using molecular techniques (Groβ et al. 1994; Takishita et al. 2006), wider sampling of the world's oceans (Raghukumar et al. 2010), and habitats in the deep-sea: hypothermal vents (Lopez-Garcia et al. 2001, 2003) and methane seeps (Lai et al. 2007), will undoubtedly yield an even wider range of undocumented fungi.

Algicolous fungi

The first marine fungi were those collected on algae (Sutherland 1915, 1916a, b), but the discovery lignicolous species (Barghoorn and Linder 1944) attracted marine mycologists with a consequent loss of interest in algicolous fungi. Bugni and Ireland (2004) commented that fungi isolated or growing on algae were the second largest source of marine fungi. They include parasites, saprobes and endophytes of seaweeds and planktonic taxa, and most are ascomycetes. Algal genera that have been shown to support fungi include: *Ascophylum* (Sutherland 1915; Webber 1967), *Ballia* (Kohlmeyer 1967), *Chondrus* (Schatz 1980a, b), *Dilsea* (Stanley 1992), *Fucus* (Zuccaro et al. 2008), *Laminaria* (Kohlmeyer 1968), and *Sargassum* (Kohlmeyer 1972a, b) to name but a few. Jones (2011) draws attention to the large number of algae that have yet to be explored for the occurrence of fungi. Not only are algae very numerous in marine habitats (9,200 to 12,500 described seaweeds) but also cover vast areas of the sea bottom, e.g. circa 30% of bottom surface in the Maritime Antarctica are algal beds, yielding an estimate of 74,000 tons of wet biomass (Nedzarek and Rakusa-Suszczewski 2004). Harvested seaweeds in Japan and Korea are 655,000 and 777,090 tons wet weight, respectively, which again indicate the potential source for marine fungi (Ohno and Largo 1998; Sohn 1998). An estimate of the standing crop of kelp bed biomass for British Colubmia was 651,697 WT of which 130,34WT was harvested for various products (Lindstrom 1998). These extensive standing seaweed crops are in urgent need of more intensive surveys for marine fungi (Fig. 3). Algae in storage, prior to extraction of phycocolloids, are often subject to deterioration by mitosporic fungi, such as *Penicillium*, *Trichoderma* (Critchley and Jones, unpublished data).

Marine algae are known to harbor endophytes (Jones et al. 2008b), but few taxa have been studied in any detail. Zuccaro and Mitchell (2005) list some 79 marine fungi growing on seaweeds as parasites or saprobes, with only a few new algicolous species described over the last two decades (Zuccaro et al. 2004; Janson et al. 2005; Mantel et al. 2006; Jones et al. 2009a, b). In a study of the "endophytes" and saprobes of *Fucus serratus* Zuccaro et al. (2003) reported 84 species, from six Ascomycota orders, with membeers of the Dothideales the most numerous. *Halosigmoidea marina* and *Acremonium fuci* were the most common species when algal tissue was surface sterilized. Only phylotypes from four orders were detected from living and dead *F. serratus*: Dothideales (33%), Halosphaeriales (17%), Hypocreales (33%) and Lulworthiales (17%). Further studies are warranted especially of the larger seaweeds: tropical *Sargassum* spp. and the extensive kelp beds of temperate waters (Fig. 3).

Recently there has been a resurgent of interest in fungi growing on marine algae. Loque et al. (2009) studied the filamentous fungi and yeasts associated with the marine algae *Adenocystis utricularis*, *Desmarestia anceps* and *Palmaria decipiens* from Antarctica. Seventy five species were isolated (27 filamentous fungi, 48 yeasts) belonging to the genera *Geomyces*, *Antarctomyces*, *Oidiodendron*, *Penicillium*, *Phaeosphaeria*, *Aureobasidium*, *Cryptococcus*, *Leucosporidium*, *Metschnikowia* and *Rhodotorula*. Chytrids and the Chromistan (Straminipiles) oomycetes parasitic on algae have also attracted interest (Sekimoto et al. 2008a, b; Strittmatter et al. 2009; Gachon et al. 2006, 2009, 2010).

Fig. 3 Brown algal bed of *Durvillea antarctica* in the Falklands, to illustrate substrata for colonization by marine fungi (Photo Dr R.L. Fletcher)

Many of these studies have been concerned with commercially important algae, e.g. *Pophyra* in the production of nori, and the resultant economic losses (Gachon et al. 2010). Filamentous marine algae, e.g. *Pylaiella*, have also been examined for marine oomycetes (Sekimoto et al. 2008b).

Planktonic fungi

Planktonic fungi include unicellular yeasts, chytrids and chromistan organisms and their study has varied greatly over the years. Some of the early studies of marine chytrids were by Cohn (1865), and Sparrow (1934, 1936) with greater research interests in the period 1950–1970: Höhnk (1955a, b, 1961), Höhnk and Aleem (1953), Harder and Uebelmesser (1955), Ulken (1967, 1968, 1969, 1974), Chakravarty (1974), Booth (1969, 1971) and Sparrow (1969). Some of these dealt with parasitic chytrids, while others were saprobic species (Patersen 1958). Catastrophic collapse of planktonic organisms, such as unicellular algae, zooplankton, by chytrids is well documented (Walsh 1983; Tillmann et al. 1999; Kagami et al. 2007). Marine yeasts were intensively studied by Fell (1967, 1974, 1976), Fell et al. (1960), Meyers et al. (1967), van Uden and Casttelo-Branco (1963), van Uden and Fell (1968), van Uden and Zobell (1962) and Ahearn and Crow (1986). Kohlmeyer and Kohlmeyer (1979) listed some 140 facultative marine yeasts, largely based on the studies of Fell (1967, 1976), Ahearn et al. (1968) and van Uden and Casttelo-Branco (1963). Recent studies of marine yeasts have been by Kutty and Philip (2008), Chen et al. (2009) and Fell and his co-workeers (Fell et al. 2004, 2010). Currently there may be as many as 1,500 marine yeasts and they are particularly common in mangroves (Fell pers. comm.). Statzell-Tallman et al. (2008) reported 55 and 58 species, respectively, of ascomycetes and basidiomycetes yeasts from three mangrove habitats, 50% of which are un-described. Subsequently, Fell et al. (2010) and Statzell-Tallman et al. (2010) described other marine yeasts from the Everglades and coral reefs in the Florida Keys, and mangrove regions in Belize and Bahamas (Table 8). In the Everglades study, 74 previously described species were documented with an equal number of new taxa (Fell et al. 2010). Not only are yeasts abundant in coastal waters, they also form extensive communities in open ocean waters and may be more numerous than filamentous fungi (Lachance and Starmer 1998).

Chromistan organisms have been widely isolated by sampling water at various depths, and most belong to the Thraustochytriales and Labyrinthulales (Höhnk 1955b; Goldstein 1963; Gaertner 1972, 1974). Thraustochytrids are rarely seen growing on recently recovered substrata, and pollen baiting techniques have been used for their isolation and growth in culture (Gaertner 1968; Clokie and Dickinson 1972; Bahnweg and Sparrow 1974; Clokie 1974). In recent years this group has attracted considerable interest for their ability to producte high yields of polyunsaturated omega-3-fatty acids (Bajpai et al. 1991; Singh et al. 1996; Yaguchi et al. 1997; Bowles et al. 1999; Fan et al. 2000).

Culture techniques have been used to document planktonic fungal communities, but these are very selective and do not include unculturable organisms. Total biodiversity estimates are only possible by the use of molecular techniques; such are denaturing gradient gel electrophoresis (DGGE), and other more advanced techniques. These have been applied to characterize saprobic fungal communities (Pang and Mitchell 2005) but have not been extensively used to study planktonic fungal communities (Gao et al. 2010). However, densities of 10^3 to 10^4 fungal cells per milliliter of seawater have been reported by Kubanek et al. (2003). In a study of Hawaiian coastal waters, Gao et al. (2010) identified 124 clones including 46 fungal species that belonged to the Ascomycota (n=4) and Basidiomycota (n=42), however 39 of the latter were likely new fungal phylotypes. Thus coastal waters harbor as yet many unidentified fungi, and our estimates of the marine fungal community may be well off target.

Marine derived fungi

In the previous sections, the isolation of terrestrial-like fungi has been frequently referred to, species that show no morphological affinities with the so called obligate or facultative fungi recovered from substrata such as driftwood and attached mangrove wood, intertidal seagrasses (*Spartina*, *Posidonia*) and some seaweeds. Marine derived species have been isolated from a broad spectrum of substrata: saprobic fungi on marine algae, woody substrata (but not sporulating on the wood), sediments and sand, in the water column; or parasitic on algae and marine animals; or as endophytes (Udea 1980; Udea and Udagawa 1983; Mantel et al. 2006; Phongpaichit et al. 2006; Jones et al. 2009b; Duc et al. 2009). Many of these species are known from studies of mangrove and marine sediments (Swart 1958, 1963; Chowdhery and Rai 1980) or in the isolation and screening for new bioactive compounds (Jensen and Fenical 2002; Janson et al. 2005).

Most marine derived fungi are mitosporic taxa belonging to the genera *Aspergillus, Cladosporium, Fusarium, Gliocladium, Microsphaeriopsis, Paecilomyces*, *Penicillium, Phoma, Phomopsis, Trichoderma* and *Ulocladium* (Bugni and Ireland 2004). They have been isolated in high numbers from various sources: 617 from coral reefs (Morrison-Gardiner 2002), 1000 strains from marine sediments (Pivikin et al. 1999), 800 as mangrove endophytes

Table 8 New genera, species and taxonomic changes since Jones et al. (2009a; b)

Species	Previous name	Taxonomic group	Reference
Candida rhizophorensis Fell, Gutiérrez, Statzell-Tallman & Scorzetti	Saccharomycetales		Fell et al. 2010
Candida sharkiensis Fell, Gutiérrez, Statzell-Tallman & Scorzetti	Saccharomycetales		Fell et al. 2010
Candida spencermartinsiae Statzell-Tallman, Scorzetti & Fell	Saccharomycetales		Statzell-Tallman et al. 2010
Candida taylorii Statzell-Tallmanm Scorzetti & Fell	Saccaromycetales		Statzell-Tallman et al. 2010
Ceriosporopsis intricata (Jorj. Koch & E.B.G. Jones) Sakayaroj, K.L. Pang & E.B.G. Jones	*Bovicornua intircata* Jorj. Koch & E.B.G. Jones	Halosphaeriaceae	Sakayaroj et al. 2010b
Corollospora mesopotamica Al-Saadoon	N/A	Halosphaeriaceae	Al-Saadoon 2006
Cryptococcus mangaliensis Fell, Statzell-Tallman & Scorzetti	Tremellales (Bulleromyces clade)		Fell et al. 2010
Gesasha pediatus Abdel-Wahab & Nagahama[a]		Halosphaeriales	Abdel-Wahab and Nagahama 2011
Gesasha unicellularis Abdel-Wahab & Nagahama		Halosphaeriales	Abdel-Wahab and Nagahama 2011
Gesasha mangrovei Abdel-Wahab & Nagahama[b]		Halosphaeriales	Abdel-Wahab and Nagahama 2011
Glomerulispora mangrovis Abdel-Wahab & Nagahama[a]	N/A	TBM clade	Abdel-Wahab et al. 2010
Halokirschsteinionthelia maritima (Linder) S. Boonmee & K. D. Hyde[a]	*Kirschsteinionthelia maritima* (Linder) D. Hawksw.	Mytilinidiaceae (Mytilinidiales)	Boonmee et al. in press
Halazoon fuscus (I. Shmidt) Abdel-Wahab, K.L. Pang, Nagahama, Abdel-Aziz & E.B.G. Jones[a]	*Cirrenalia fuscus* I. Shmidt	Lulworthiales	Abdel-Wahab et al. 2010
Halazoon melhae Abdel-Wahab & Nagahama[a]	N/A	Lulworthiales	Abdel-Wahab et al. 2010
Halosarpheia japonica Abdel-Wahab & Nagahama	N/A	Halosphaeriales	Abdel-Wahab and Nagahama 2011
Hydea pygmea (Kohlm.) K.L. Pang & E.B.G. Jones[a]	*Cirrenlaia pygmea* Kohlm.	Lulworthiales	Abdel-Wahab et al. 2010
Kwoniella mangroviensis Statzell-Tallmanm, Belloch & Fell[a]	Tremellales		Statzell-Tallman et al. 2008
Kochiella crispa (Kohlm.) Sakayaroj, K.L.Pang & E.B.G. Jones[a]	*Remispora crispa* Kohlm.	Halosphaeriales	Sakayaroj et al. 2010b
Matsusporium tropicale (Kohlm.) E.B.G. Jones & K.L. Pang	*Cirrenalia tropicalis* Kohlm.	Lulworthiales	Abdel-Wahab et al. 2010
Moheitospora adarca (Kohlm., Volkm.-Kohlm. & O.E. Erikss.) Abdel-Wahab, Abdel-Aziz & Nagahama[a]	*Cirrenalia adarca* Kohlm., Volkm.-Kohlm. & O.E. Erikss.	TBM clade	Abdel-Wahab et al. 2010
Moheitospora fruticosa Abdel-Wahab, Abdel-Aziz & Nagahama[a]	N/A	TBM clade	Abdel-Wahab et al. 2010
Moleospora maritima Abdel-Wahab, Abdel-Aziz & Nagahama[a]	N/A	Lulworthiales	Abdel-Wahab et al. 2010
Moromyces varius (Chatmala & Somrith.) Abdel-Wahab, K.L. Pang, Nagahama, Abdel-Aziz & E.B.G. Jones[a]	*Cumularia varia* Chatmala et Somrith.	Lulworthiales	Abdel-Wahab et al. 2010
Sediecimiella taiwanensis K.L. Pang, Alias & E.B.G. Jones[a]	N/A	Hypocreales	Pang et al. 2010b
Halomassasrina thalassiae (Kohlm. & Volkm-Kohlm.) Suetrong, Sakayaroj, E.B.G. Jones, Kohlm., Volkm.-Kohlm. & Schoch[a]	*Massarina thalassiae* Kohlm. et Volkm-Kohlm.	Trematosphaeriaceae	Suetrong et al. 2009a
Morosphaeria velatospora (K.D. Hyde & Borse) Suetrong, Sakayaroj, E.B.G. Jones & Schoch[a]	*Massarina velatospora* K.D. Hyde & Borse	Morosphaeriaceae	Suetrong et al. 2009a
*Morosphaeria ramunculicola (*K.D. Hyde) Suetrong, Sakayaroj, E.B.G. Jones & Schoch[a]	*Massarina ramunculicola* K.D. Hyde	Morosphaeriaceae	Suetrong et al. 2009a
Nohea delmarensis (Kohlm. & Volkm.-Kohlm.) Abdel-Wahab	*Naufragella delmarenis* Kohlm. & Volkm.-Kohlm.	Hlaopshaeriales	Abdel-Wahab 2011a
Nohea spinibarbata (Jørg. Koch) Abdel-Wahab	*Naufragella spinibarbata* (Jørg. Koch) Kohlm. & Volkm.-Kohlm.	Halosphaeriales	Abdel-Wahab 2011a

Table 8 (continued)

Species	Previous name	Taxonomic group	Reference
Neomassariosphaeria typhicola (P. Karst.) Yin. Zhang, J. Fourn. & K.D. Hyde[a]	*Massariosphaeria typhicola* (P. Karst.) Leuchtm.	Amniculicolaceae	Zhang et al. 2009a
Pseudozyma abaconensis Statzell-Tallmanm Scorzetti & Fell	Ustilaginales		Statzell-Tallman et al. 2010
Rhodotorula cladiensis Fell, Statzell-Tallman & Scorzetti	Cystobasidiomycetes (Sakaguchia clade)		Fell et al. 2010
Rhodotorula evergladiensis Fell, Statzell-Tallman & Scorzetti	Sporidiobolales		Fell et al. 2010
Rimora mangrovei (Kohlm. & Vittal) Kohlm., Volkm.-Kohlm., Suetrong, Sakayaroj, & E.B.G. Jones[a]	*Lophiostoma mangrovei* Kohlm. & Vittal	Aigialaceae	Suetrong et al. 2009b
Toriella tubulifera (Kohlm.) Sakayaroj, K.L. Pang & E.B.G. Jones[a]	*Ceriosporopsis tubulifera* Kohlm.	Halosphaeriaceae	Sakayaroj et al. 2010b
Tubakiella galerita (Tubaki) Sakayaroj, K.L. Pang et E.B.G. Jones[a]	*Remispora galerita* Tubaki	Halosphaeriaceae	Sakayaroj et al. 2010a, b

[a] New genera

[b] Doubtdfull species

(Pang et al. 2008a) and 1743 from diverse marine taxa (Schulz et al. 2008). Many of these strains were sterile and others could only be identified to genus. While sequence data has greatly aided in the identification of these strains, especially those isolated as endophytes (Sakayaroj et al. 2010a), their true origin remains unclear. What role do they play in the ecology of oceans? Are they truly adapted to life in the marine environment? Preliminary studies indicate that "so-called" terrestrial species may have evolved into marine forms and this aspect warrants continued study (Alker et al. 2001; Zuccaro et al. 2004).

Marine fungi on animal hosts

Few studies have examined shells, calcareous algae, coral and soft corals in any detail to determine what role marine fungi play in their biology (Kohlmeyer 1969a, b). More recently, Le Campion-Alsumard et al. (1995) showed endolithic septate fungal hyphae in coral skeletons and soft coral tissue, while Porter and Lingle (1992) found thraustochytrids boring into mollusk shells. Kendrick et al. (1982) have also found evidence for "microborings" (light and scanning electron microscopy) in aragonite of coral skeletons. Vast quantities of mollusk shells are cast up on our shores (Fig. 4) and undergo decomposition (Fig. 5) and fungi may utilize the conchyolin which makes up part of the shells (Alderman and Jones 1967).

Marine fungi also cause diseases of marine animals and plants but this is a realtively unexplored topic (Kohlmeyer 1973, 1979; Kohlmeyer and Demoulin 1981; Gachon et al. 2010; Jones 2011; Gleason et al. 2011). Crustacean species, fish and algae are the most frequently cited hosts of pathogenic marine fungi. Various *Fusarium* spp. have been

Fig. 4 Shells of marine molluscus washed on to the shore at Koh Chan, Thailand

Fig. 5 Cast conch shells undergoing minerlization along the Bahamas coast

reported to cause disease of prawns (Khao et al. 2005), tiger prawn (Khao et al. 2004), infections of the eggs of loggerhead sea turtle (Sarmiento-Ramirez et al. 2010), *Aphanomyces sinensis* infections of juvenile soft-shelled turtle (Takuma et al. 2011) and various fungi causing skin infections of southern right whale (Reeb et al. 2011). Algae susceptible to fungal infections include: the red algae *Bangia, Palmaria, Polysiphonia* and *Porphyra* (Pueschel and Vandermee 1985; Müller et al. 1999; Sekimoto et al. 2008a, b), and the brown algae *Cystoseira*, *Halidrys*, and *Pylaiella* (Alongi et al. 1999; Gachon et al. 2006; Harvey and Goff 2010). A fuller list of parasitic marine fungi is given by Zuccaro et al. (2004).

Many new fungi have been described as pathogens: *Trichomaris invadens* in tanner crab (Sparks 1982), *Labyrinthuloides haliotidis* of juvenile abalone (Bower 1987), *Haliphthoros milfordensis* juvenile stages of lobster (Fisher et al. 1975), *Atkinsiella panulirata* from spiny lobster (Kitancharoen et al. 1994), and *Plectosporium oratosquillae* in mantis shrimp (Duc et al. 2009). The role of marine zoosporic fungi in parasitizing plants and animals is imperfectly known and greater attention is required of this important group (Gleason et al. 2011).

Physiology of marine fungi

Early physiological studies of marine fungi focused on their salinity tolerance (Jones and Jennings 1964; Jennings 1986b), temperature requirements (Jones et al. 1971), nutrient requirements (Amon 1986), enzyme production (Molitoris and Schaumann 1986; Schaumann et al. 1986), aspects of wood decay (covered above) and ability to grow on different polysaccharides (Barghoorn and Linder 1944; Meyers 1971b). Marine fungi can be defined based on their morphology, physiology and ecology, and their ability to reproduce in the marine environment. Although these are important, for others no single criterion may apply, e.g. so called terrestrial species, as they may not be morphologically or physiologically adapted to the marine habitat. Studies of the effect of salinity on their growth and morphology were undertaken in order to try and definie them based on their physiology and need for seawater for growth and reproduction. It soon became apparent that marine fungi showed a broad response to growth in seawater, while vegetative growth occurred at all salinities, maximum growth was often at 20–60% seawater (Jones and Jennings 1964; Meyers 1971b). Similar variation was noted for sporulation: most required salinities of 40–100% seawater (*Luworthia floridana*, *Lindra thalassiae*), others formed peritheca in media made up with distilled water (*Halosphaeriospsis mediosetigera, Torpedospora* sp.).

However, zoozporic fungi were shown to be more sensitive to changes in salinity (Harrison and Jones 1974; Tsui et al. 2011). Studies progressed to examine what elements in seawater were necessary for the growth of marine fungi, was sodium a requirement? For some, such as, *Haliphthoros* and some *Thraustochytrium* spp., sodium was required as a macronutrient (Jennings 1986a, b). Further investigations focused on the mitosporic fungus *Dendryphiella salina* as it was aminable to laboratory experimental studies (Jennings 1986a, b). Topics that were studied included ion concentration within the mycelium (Jones and Jennings 1965; Wethered et al. 1985; Gibb et al. 1986), carbohydrate metabolism in relation to salinity (Holligan and Jennings 1972), sodium sequestered in spores and their germination (Galpin and Jennings 1975; Galpin et al. 1978), and the role of polyols in maintaining turgor in mycelium (Wethered and Jennings 1985; Wethered et al. 1985). More recently Tsui et al. (2011) have shown that thraustochytrids are well adapted to mangrove habitats producing the greatest number of zoopsores at 7.5 to 15‰ salinity, and suppressed at salinities above 15‰. Zoospore motility was also investigated (both curvilinear velocity and straight-line velocity), with the highest motility at 7.3‰ salinity, but this decreased with increasing salinity (Tsui et al. 2011). Physiological determinants for the growth of fungi in the sea include: polyol concentration in the mycelium, an alkaline environment, sodium extrusion from the mycelium and tolerance to high salinity. Marine yeasts have also been studied for their ability withstand high salinities (Norkrans 1966; Norkrans and Kylin 1969), while the mitosporic species *Asteromyces cruiciatus* has been shown to tolerate concentrations of sodium chloride of 2.5 M, providing a divalent ion, such as calcium, is present in the medium.

Marine fungi have been shown to produce a wide range of enzymes with Chesters and Bull (1963) screening some 160 organisms for laminarin-hyrolyzing enzymes. *Dendryphiella salina* was shown to produce siginificant laminarinase activity as well as to degrade alginate and cellulose.

Widespread screening has followed with the studies of Meyers (1971b), Molitoris and Schaumann (1986), Sadaba et al. (2000a) and these, and other studies, have been collated by Verbist et al. (2000). Complex organic matter in the sea includes lignocellulose (discussed above), algal polysaccharides (Meyers 1971b), and chitin, estimated at billions metric tonnes (Yu et al. 2010). Grant et al. (1996) showed that the ascomycetes *Corollospora maritima* and *Lindra obtusa* produced chintinolytic enzymes, while Velmurugan et al. (2011) reported a novel low temperature chitinase from the marine fungus *Plectosphaerella* sp.

With major oil spills all to common, it is not surprising that many studies have focused on the role of marine fungi in hydrocarbon utilization (Crow et al. 1976; Ahearn and Crow 1986), fungal communities on bunker oil (Okereke et al. 2007; Obire and Anyanwu 2009; Sadaba and Sarinas 2010) to the effect of oil spill dispersants on fungal spores (Curran et al. 1997). Other topics that have attracted attention of marine mycologists include: osmoregulation in *Hydea pygmea* (Ravishankar et al. 2006), marine fungi as fish food (Cuomo 1986; Jaritkhuan 2002), and fungal protein production (Jones and Irvine 1972).

Conclusions

Although marine fungi have been studied for some 100 years, and increasingly over the past 50 years, many aspects still remain poorly documented. Our knowledege of the marine Chytridomycota, Oomycota, Zygomycota, are fragmentary, but there is evidence of greater awareness of these groups, in particular their role in marine food webs (Gleason et al. 2011). Are these groups poorly adapted to marine habitats, or are suitable hosts/substrata lacking for their growth and reproduction? The more plausible explanation is lack of mycologists interested in these groups. Data on the occurrence of pathogens of the larger seaweeds, plankton, animals, are also lacking. This may well be due to the availability of material for study as such disease outbreaks often go undocumented and mycologists fail to sample on a wide enough scale. However, over the past 5 years there has been a reawaking of interest in this topic (Sekimoto et al. 2007, 2008a, b; Gachon et al. 2006, 2009; Strittmatter et al. 2009; Loque et al. 2009; Kubanek et al. 2003).

While our knowledge of deep sea fungi has increased in recent years, those present in the plankton remain poorly documented. Biodiversity studies have dominated the marine mycology literature overe the past decades, but these are often just lists of taxa sporulating on the substrata, offering little of ecological vaule. What is now required is a greater in depth study of the process of substratum colonization, and the documentation of non sporulating fungi by the use of molecular techniques to elucidate sequential colonization. The technology is now available and biodiversity studies need to capatilise on this. Most endophytes of marine algae, seagrasses and mangrove plants are not truly obligate marine fungi. Again these studies simply document the sporluating species and the use of molecular techiques needs to be undertaken to include taxa not isolated by the usual methods.

The greatest challenge for marine mycology is to investigate the physiology and biochemistry of these unique fungi, their ability to produce bioactive compounds, enzymes to tolerate both salinity and pH, and their use for commercial application. Also to document their role in the turn over of complex organic matter in the sea and their contribution to the food web of marine ecosystems. Marine fungi have been shown to have ability to breakdown of hydrocarbons, so can they be developed to play a role in marine bioremediation of oil spills?

Surveying for marine fungi needs to continue as many substrata, habitats remain unexplored (e.g. fungi colonizing mollusk shells, marine lichens, fungi within soft marine rocks) (Figs. 4, 5 and 6). Also many taxa documented colonizing mangrove substrata are misidentified or insufficient material was available for their identification, so continued studies are required. Although there is a substantial body of data on marine fungi, in many respects much needs to be tackled, and some of these areas have been highlighted above. Some may regard the study of marine fungi as somewhat esoteric but they do play a vital role in ecology of marine ecosystems and in the food web of the oceans.

New marine fungi described since 2009

The last update of new fungi described from marine substrata was by Jones et al. (2009a) when 530 species were listed. Table 8 lists those described over the past 18 months including nomenclature changes introduced as

Fig. 6 Soft rocks on shore at Kog Samui, Thaiand, potenial source of marine fungi

the result of phylogenetic studies (Suetrong et al. 2009a; Abdel-Wahab et al. 2010; Abdel-Wahab 2011a, b; Abdel-Wahab and Nagahama 2011a, b).

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