Distribution of fungi on wood in the Tutong River, Brunei

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Five sites along the Tutong river and its tributary, the Sungai Kelakas, were sampled for fungi on decaying wood. Sixty-six taxa were found including two new genera and two new species. Nearly half of these (48%) are new records for Brunei. Although common taxa were generally not unique to any particular site, species distributions were correlated to the salinity gradient. These findings are consistent with previous studies showing that some marine fungi are tolerant to less saline conditions and that some freshwater species are tolerant to more saline conditions. Some species could be potentially classified as brackish water species. The ratio of ascomycetes to anamorphic fungi was higher in marine than freshwater sites. A checklist of fungi found in aquatic habitats in Brunei is included.

Key words: brackish, freshwater fungi, fungal diversity, marine fungi, salinity, wood.

Introduction

Biological diversity, especially in the tropics is under threat (Wilson, 1988). It is essential that the range of species present in different habitats be recorded rapidly for several reasons: (i) destruction of habitats is so rapid that species may be either locally or globally extinct before we discover them; (ii) many species contain medicinally important chemicals vital for humanity (Wilson, 1988); (iii) records of species within geographical areas is essential for environmental decision making (Hyde, 2003). Fungi are particularly poorly studied throughout the tropics and substantial funding, training and study are required to address this imbalance (Hawksworth, 2003; Hyde, 2003).

The diversity of fungi has been estimated to be 1.5 million (Hawksworth, 1991, 2001; Hyde, 2001). Although this estimate has been contested (May, 1994), there are approximately 72,000 fungal species currently described and

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about 1600 are currently being described each year as new (Hawksworth, 2001). This high species richness of fungi means that they are an important part of the biodiversity of an area.

The diversity of fungi in aquatic environments has been shown to be high (Goh and Hyde, 1996; Tsui *et al*., 2000; Cai *et al*., 2002, 2003; Kane *et al*., 2002; Luo *et al*., 2004), with more than 1000 species already discovered, most of which are either ascomycetes or anamorphic fungi (e.g. Goh, 1997; Hyde *et al*., 1997; Tsui and Hyde, 2003). The proportion of these species that actually grow and reproduce within the aquatic habitat is, however, unknown (Shearer, 1993).

Fungi utilise many different substrates within the aquatic environment including wood (Shearer and Von Bodman, 1983; Abdel-Raheem and Shearer, 2002; Bucher *et al*., 2004), leaves (Premdas, 1991), algae (Haythorn *et al*., 1980), coral (Morrison-Gardiner, 2002), soil (Mer *et al*., 1980), insects (Williams and Lichtwardt, 1990; Cafaro, 2002), and various other substrates (Czeczuga, 1996; Czeczuga and Muszyńska, 2004). Their spores even occur in tree holes and gutters (Gönczöl and Révay, 2003, 2004). There is often a different assemblage of fungi on each substrate, although some generalists utilise more than one substrate.

The distribution of wood-inhabiting fungi in aquatic habitats is affected by salinity and temperature (Shearer, 1972; Hyde and Lee, 1995; Jones, 2000; Tsui and Hyde, 2004). Jones and Oliver (1964) found that the assemblage of fungi in seawater was very different to that found in brackish and fresh water. However, several species were common to both fresh and brackish water. There have been many studies recording the distribution and abundance of fungi found in aquatic habitats (Hyde *et al*., 2000). Besides the study of Tsui and Hyde (2004) the distribution of fungi from fresh through to seawater in one system has not been studied.

In Brunei, nine studies on fungal diversity in aquatic habitats have revealed distinct assemblages of fungi in freshwater and marine habitats (Hyde, 1988a,b, 1989, 1990a,b, 1991, 1992; Wong, 1996; Ho *et al*., 2002). However, none of these studies examined fungi along a gradient from freshwater to marine habitats. It was our intention in this study to determine the pattern of fungal species abundance and distribution along a salinity gradient. The aim was to determine if there was a distinct assemblage of fungi in brackish sites or if there was simply a mix of freshwater and marine species.

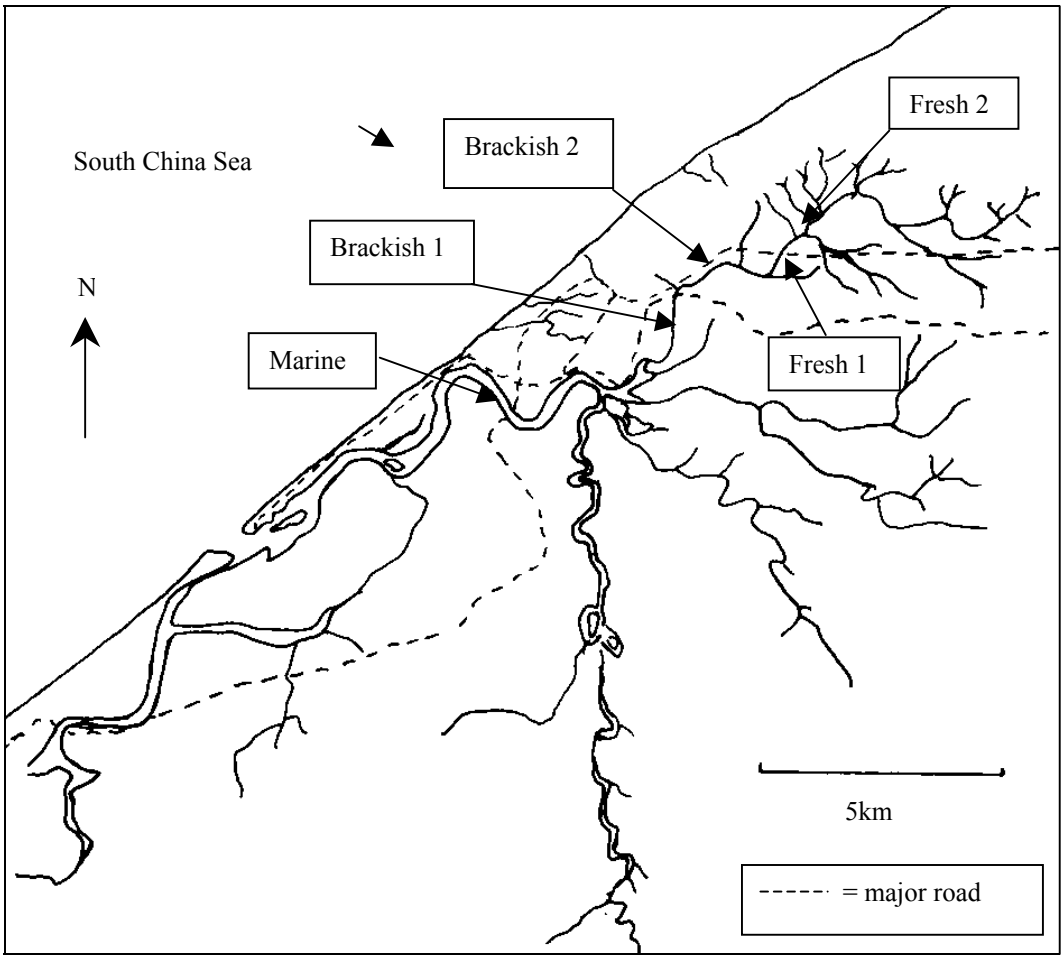

Fig. 1. Position of Brunei. **a.** Map of the study area; **b.** showing the Tutong river and its tributaries.

Materials and methods

Study area

The Tutong River in Brunei feeds into the South China Sea on the northwest side of Borneo (Fig. 1). Samples were collected from five sites along the Tutong River and one of its tributaries, the Sungai Kelakas. Data on the physico-chemical conditions of the sites were collected during field sampling (Table 1). There was generally a gradient of salinity from 0 to 32‰, but at times of high river flow, all sites had salinity that was effectively 0‰.

Table 1. Physical properties of the water at each of the sites.

	Marine	Brackish A	Brackish B	Fresh water	Peat swamp
Salinity (‰)	0-31	0-11.9	0-10	0-3	0
pH	4.8-5.6	3.1-6.0	6.3	5.4	3.1-4.3
Temperature	26.1-30	26.4-30	29	26.6-29	29
DO_2 (%)	16-77	18-92	38	78	8-85

Marine site

The Tutong River at this site was approximately 50 m wide and 8.5 m deep at the mid-point. The riparian vegetation at this point was dominated by *Sonneratia caseolaris*, *Avicennia alba* and *Nypa fruticans*. The tidal range was approximately 2 m.

Brackish site A

Sungai Kelakas at this point was approximately 20 m wide and 2 m deep in the deepest part. The water was also tidal. A riparian strip approximately 50 m in width, bordered the river. The strip was inundated in times of high river flow (when the water was effectively fresh) and during high tides. The vegetation was a mixture of *Barringtonia* cf. *racemosa*, *Bruguiera gymnorrhiza*, *Cerbera odallam*, *Ficus* cf. *microcarpa*, *Gluta velutina*, *Heritiera globosa*, *Hibiscus tiliaceus*, *Nypa fruticans* and *Sonneratia caseolaris*.

Brackish site B

This site was 100 m upstream of Brackish site A, and had very similar vegetation. However, the topography of the site was more that of a floodplain. The channel at this point was less distinct and not as deep as at Brackish site A (approximately 1 m maximum). Plant growth was not restricted to the riverbanks, and some plants grew in the middle of the stream. Water at this site was also tidal.

Freshwater site

This area was a floodplain with no defined channel. Maximum depth was approximately 1 m. The riverine vegetation was dominated by species associated with disturbance such as *Dillenia suffruticosa*, *Ischaemum barbatum*, *Scleria* sp. and *Vitex pubescens* together with some regenerating peat swamp species.

Peat swamp forest (PSF)

Slightly further upstream from the freshwater site was a floodplain with a peat swamp forest. The forest was on shallow peat dominated by *Campnosperma coriaceum*, *Lophopetalum multinervium* and *Syzygium* sp. In times of high rainfall, the area was inundated with water up to approximately 1.5 m. During drier periods, the ground was exposed, but there was a series of pools throughout the forest. This site was referred to as a freshwater site.

Collection of samples

Thirty wood samples (approximately 40 × 5 × 3 cm) were randomly collected from the edge of the river (up to 50 cm deep) at each site. Samples were not collected if they were buried in the mud (and were therefore anaerobic), or had recently fallen into the water. Abiotic measurements, pH, salinity, temperature and dissolved oxygen (DO_2), of the water at each site were taken over two years. Samples were briefly washed in the river to remove excess mud and algae and placed individually into zip-lock bags and incubated at 27ºC in 24 hour light/dark cycles. After two weeks, the samples were observed at 200× magnification with a dissecting microscope for fungal fruiting bodies on the surface of the wood. Samples were observed again after 3 months of incubation. Fruiting bodies were identified at 400× magnification using a compound microscope, and the fungus isolated onto artificial agar media. Abundance was measured as presence/absence on a sample. That is, if a fruiting body of one species was seen more than once on a sample, it was counted only once.

Statistical analysis

Species abundance patterns

Shannon-Weiner diversity and evenness was calculated for each site along with Margalef species richness. Calculations were carried out according to Magurran (1988).

Multivariate analysis

Detrended Correspondence Analysis (DCA) was used to detect differences in species abundance patterns between sites. MultiVariate Statistical Package (MVSP) (www.kovcomp.com/mvsp) was used for this analysis.

Results

Sixty-six taxa were found during the survey (Table 2), 43 were ascomycetes and 23 anamorphic fungi. The most common species were *Cancellidium applanatum* (N = 93), *Sungaiicola brachydesmiella* (N = 38), *Aniptodera chesapeakensis* (N = 19), *Papulospora* sp. 2 (N = 18) and *Papulospora* sp. 1 (N = 17). *Cancellidium applanatum* was common at all sites, but was slightly more common in fresh and brackish water sites. *Sungaiicola brachydesmiella* occurred in all habitats, but was more common in brackish and marine sites. *Aniptodera chesapeakensis* occurred in brackish and marine sites, but not in fresh water. Both *Papulospora* sp. 1 and sp. 2 occurred only in brackish and marine sites. In fresh water no particular species were very common (apart from *Cancellidium applanatum* which was common in all sites).

Alysidium sp., *Annulatascus triseptatus*, *Aquaticola ellipsoidea*, Ascomycete sp. 1, *Ascotaiwania* sp., *Beverwykella pulmonaria*, *Brachysporiella gayana*, *Cataractispora applanatum*, *Cataractispora viscosa*, *Chaetosphaeria* sp., *Exserticlava vasiformis*, *Glomerella* sp., *Massarina* sp., and *Sporidesmium crassisporum* were all unique to freshwater. However, apart from *Beverwykella pulmonaria* and *Brachysporiella gayana* many of these species were rare (N = 1, 2 or 3) and so may also be rare in the other sites, but not observed during this study.

Eleven species were unique to brackish water sites: *Aniptodera* sp. 1, *Aniptodera* cf. *haispora*, *Annulatascus lacicola*, *Annulatascus palmietensis*, *Aquaticola* sp., *Dactylospora mangrovei*, *Mangrovispora pemphii*, *Monodictys* sp. 1, *Monodicyts* sp. 2, *Savoryella verrucosa* and *Trichocladium achrasporum*.

Eleven species were unique to the marine site: *Aniptodera megalospora*, *Ceratosphaeria* sp. 1, *Chaetosphaeriaceae* sp., *Lasiosphaeria* sp. 3, *Lophiostoma bipolare*, *L. frondisubmersum*, *Phomatospora* sp., *Savoryella lignicola*, *S. paucispora*, *Swampomyces* sp. and *Chalara* sp.

Only seven species occurred in all habitats: *Annulatascus velatisporus*, *Aquaticola longicolla*, *Fluviatispora reticulata*, *Lasiosphaeria* sp. 1, *Sungaiicola brachydesmiella*, *Cancellidium applanatum* and *Sporidesmium* cf. *anglicum*.

With the exception of *Beverwykella pulmonaria* and *Brachysporiella gayana*, no species that occurred more than three times were unique to any one habitat. Species that were common in any one habitat were either common in the other habitats, or at least occurred in them.

Table 2. Fungal species found at each of five sites. Numbers refer to the number of wood pieces (maximum 30) on which each fungus occurred.

Site	Fresh	PSF	Brackish A		Brackish B	Marine	
Collection period	**1**	**2**	**1**	**2**	**1**	**1**	**2**
Ascomycetes							
Unidentified Ascomycete sp. 1	1	-	-	-	-	-	-
Aniptodera sp. 1	-	-	-	-	1	-	-
Aniptodera sp. 2	-	-	2	-	-	1	-
Aniptodera chesapeakensis Shearer & M.A. Mill.	-	-	1	-	1	14	3
Aniptodera cf. *haispora* Vrijmoed, K.D.Hyde & E.B.G. Jones	-	-	1	-	-	-	-
Aniptodera megalospora K.D. Hyde, W.H. Ho & K.M. Tsui	-	-	-	-	-	-	4
Annulatascus sp.	-	-	1	-	-	-	-
Annulatascus palmietensis K.D. Hyde, Goh & T.D. Steinke	-	-	-	1	-	-	-
Annulatascus triseptatus S.W. Wong, K.D. Hyde & E.B.G. Jones	-	3	-	-	-	-	-
Annulatascus velatisporus K.D. Hyde	2	-	1	-	4	-	3
Aquaticola sp.	-	-	1	-	-	-	-
Aquaticola ellipsoidea W.H. Ho, K.M. Tsui, Hodgkiss & K.D. Hyde	1	1	-	-	-	-	-
Aquaticola longicolla W.H. Ho, K.M. Tsui, Hodgkiss & K.D. Hyde	-	3	-	1	-	-	1
Ayria appendiculata Fryar & K.D. Hyde	-	-	1	-	3	1	-
Ascotaiwania sp.	1	-	-	-	-	-	-
Cataractispora appendiculata K.D. Hyde, S.W. Wong & E.B.G. Jones	-	1	-	-	-	-	-
Cataractispora viscosa K.D. Hyde, S.W. Wong & E.B.G. Jones	-	1	-	-	-	-	-
Ceratosphaeria sp. 1	-	-	-	-	-	-	1
Ceratosphaeria sp. 2							
Chaetosphaericeae sp.	-	-	-	-	-	2	-
Chaetosphaeria sp.	1	-	-	-	-	-	-
Dactylospora mangrovei E.B.G. Jones, Alias, Abdel-Wahab & S.Y. Hsieh	-	-	-	1	-	-	-
Fluviatispora reticulata K.D. Hyde	3	2	-	1	1	-	1
Glomerella sp.	-	1	-	-	-	-	-
Lasiosphaeria sp. 1	1	-	-	2	-	1	-
Lasiosphaeria sp. 2	-	-	-	1	1	-	1
Lasiosphaeria sp. 3	-	-	-	-	-	-	1
Lophiostoma bipolare (K.D. Hyde) Liew, Aptroot & K.D. Hyde	-	-	-	-	-	-	1
Lophiostoma frondisubmersum (K.D. Hyde) Liew, Aptroot & K.D. Hyde	-	-	-	-	-	-	1

N = total number of individuals, S = total number of species.

Table 2 continued. Fungal species found at each of five sites. Numbers refer to the number of wood pieces (maximum 30) on which each fungus occurred.

Site	**Fresh**	**PSF**	**Brackish A**		**Brackish B**	**Marine**	
Collection period	**1**	**2**	**1**	**2**	**1**	**1**	**2**
Lulworthia spp.	-	-	1	1	-	3	-
Mangrovispora pemphii K.D. Hyde & Nakagiri	-	-	1	-	-	-	-
Massarina sp.	1	-	-	-	-	-	-
Orbilia sp.	-	3		-	1	-	-
Phaeosphaeria capensis T.D. Steinke & K.D. Hyde	1	-	-	-	1	-	-
Phomatospora sp.	-	-	-	-	-	-	1
Savoryella lignicola E.B.G Jones & R.A. Eaton	-	-	-	-	-	3	-
Savoryella paucispora (Cribb & Cribb) Jørgen Koch	-	-	-	-	-	1	-
Savoryella verrucosa Minoura & Muroi	-	-	-	-	1	-	-
Sungaiicola brachydesmiella Fryar & K.D. Hyde	1	1	15	-	2	18	1
Swampomyces sp.	-	-	-	-	-	1	-
Torrentispora crassiparietis Fryar & K.D. Hyde	-	2	-	-	1	-	-
Torrentispora fibrosa K.D. Hyde, W.H. Ho, E.B.G. Jones, K.M. Tsui & S.W. Wong	-	3	-	1	-	-	-
Torrentispora fusiformis Fryar & K.D. Hyde	3	-	-	1	-	-	-
Number of individuals of ascomycetes	**16**	**21**	**25**	**10**	**15**	**47**	**19**
Number of species of ascomycetes	**11**	**11**	**10**	**9**	**11**	**10**	**12**
Anamorphic fungi							
Alysidium sp.	1	-	-	-	-	-	-
Berkleasmium sp.	-	2	-	3	-	-	-
Beverwykella pulmonaria (Beverw.) Tubaki	7	-	-	-	-	-	-
Brachysporiella gayana Bat.	7	-	-	-	-	-	-
Cancellidium applanatum Tubaki	22	18	20	6	15	6	6
Candelabrum sp.	1	-	-	-	1	-	-
Chalara sp.	-	-	-	-	-	1	-
Dactylella sp.	6	-	-	-	1	-	-
Exserticlava vasiformis (Matsush.) S. Hughes	1	-	-	-	-	-	-
Monodictys pelagica (T.W. Johnson) E.B.G. Jones	1	2	1	3	-	-	-
Monodictys sp. 1	-	-	1	-	-	-	-
Monodictys sp. 2	-	-	-	1	-	-	-
Papulospora sp. 1	-	-	-	6	1	7	3
Papulospora sp. 2	-	-	7	3	-	7	1
Phaeoisaria clematidis (Fuckel) Hughes	1	5	1	1	1	-	-
Pleurophragmium-like	6	-	-	-	1	-	-
Sporidesmium cf. *anglicum* (Grove) M.B. Ellis	1	-	1	1	-	-	3
Sporidesmium crassisporum M.B. Ellis	2	-	-	-	-	-	-
Trichocladium achrasporum (Meyers & Moore) Dixon	-	-	-	1	-	-	-
Tritirachium sp.	2	-	-	-	1	-	-

Table 2 continued. Fungal species found at each of five sites. Numbers refer to the number of wood pieces (maximum 30) on which each fungus occurred.

Site	**Fresh**	**PSF**	**Brackish A**		**Brackish B**	**Marine**	
Collection time	**1**	**2**	**1**	**2**	**1**	**1**	**2**
Xylomyces sp.	-	-	2	-	-	1	-
Xylomyces chlamydosporis Goos, R.D. Brooks & Lamore	1	-	1	-	-	-	-
Xylomyces giganteus Goh, W.H. Ho, K.D. Hyde & K.M. Tsui	-	-	4	-	-	1	-
Number of individuals of anamorphic fungi	59	27	38	21	21	23	13
Number of species of anamorphic fungi	14	4	9	9	7	6	4
Total no. of individuals	75	48	63	31	36	70	32
Total no. of species	25	15	19	18	18	16	16

Several species demonstrated a gradient in abundance between habitats. During the first sampling *Aniptodera chesapeakensis* was common in the marine site, rare in the brackish sites and did not occur in the freshwater site. Similarly, during the first sampling *Sungaiicola brachydesmiella* was common at the marine site and the brackish site closest to the sea and rare in the other brackish site and freshwater site. This pattern was however not observed in the second sampling.

No basidiomycete fruiting bodies were seen on the samples. However some samples had thick white hyphal cords that may have been basidiomycetous.

The ratio of ascomycetes to anamorphic fungi increased with increasing salinity in the first set of samples (both number of species and number of individuals) (Table 3). However, in the second sample, the ratio was lowest for brackish water, and highest for sea water.

New species and genera

During this study two new genera (*Ayria* and *Sungaiicola*) and two new species (*Torrentispora crassiparietis* and *T. fusiformis*) were discovered and are presently being described. Several other species were also new (e.g. *Aniptodera* sp. 1, and *Aquaticola* sp.) However, there was insufficient material to describe these as new. The material has been lodged in the HKU(M).

Table 3. Descriptive statistics for each of the samples.

Measure	Fresh	PSF	Brackish A		Brac B	Marine	
Sampling time	**1**	**2**	**1**	**2**	**1**	**1**	**2**
No. of species (S)	25	15	19	18	18	16	16
No. of individuals (N)	60	46	63	32	36	70	32
Shannon-Weiner index (H')	1.29 ± 0.05	0.99 ± 0.07	0.90 ± 0.06	1.14 ± 0.06	1.01 ± 0.09	0.96 ± 0.05	1.11 ± 0.05
H' evenness	0.925	0.818	0.717	0.906	0.789	0.799	0.918
Species richness (Margalef)	12.8	8.92	9.76	11	10.8	7.93	9.97
No. species per branch	2.5 ± 1.5	1.6 ± 1.2	2.1 ± 1.5	1.2 ± 0.9	1.2 ± 1.1	2.3 ± 1.6	1.1 ± 1.3
No. branches with no fungi	2	6	5	8	7	6	14
No. ascomycetes/No. anamorphic	0.3	0.8	0.7	0.5	0.7	2	1.5
No. of species of ascomycetes/ anamorphic	0.8	1.8	1.1	1	1.6	1.7	3

New records for Brunei

Thirty-two species found during this survey are new records for Brunei. A checklist of fungi found in aquatic habitats in Brunei in presented in Table 4. The 246 fungal taxa consists of 158 ascomycetes, 3 basidiomycetes and 85 anamorphic taxa.

Species diversity

Generally more species and individuals were observed in the first set of samples (Table 3) and overall, species diversity (H') was highest at the freshwater site during the first sampling (individual t-tests $p<0.05$). Although the species richness and evenness of the samples canot be compared statistically, the higher species diversity in the freshwater site appeared to be due to both higher species richness and evenness at the site (Table 3).

The high species richness of the freshwater site was not as distinctive, however, when the number of species per samples was observed. The freshwater sample along with the Brackish A (1) and Marine (1) samples all had more species than the other samples (ANOVA, $F_{6,203}=5.96$, $p<0.001$; LSD, $p<0.05$).

An average of 1.7 species were found on each branch in this survey. However this number was highly variable (s.d. = 1.4). Many samples (23%) had no fruiting bodies and some were found with up to 6 taxa.

Table 4. Checklist of fungi from aquatic habitats in Brunei.

Species	Habitat	Reference
Ascomycetes		
Acrocordia-like sp.	M	1,2,3
Acrocordiopsis patilii Borse & K.D. Hyde	M	4,5
Aigialus grandis Kohlm & Schatz	M	1,2,3,4,5
Aigialus mangrovei Borse	M	6,5
Aigialus parvus Schatz & Kohlm.	M	1,2,3,4,5,7
Aniptodera sp.	M	1,2,3,4
**Aniptodera* new species	B	10
Aniptodera sp. (spores <15 µm)	M	1
Aniptodera chesapeakensis Shearer & M.A. Mill.	F,B,M	1,2,3,5,6,9,10
**A*. cf. *haispora* Vrijmoed, K.D. Hyde & E.B.G. Jones	B	10
A. inflatiascigera K.M. Tsui, K.D. Hyde & Hodgkiss	F	9
A. lignicola K.D. Hyde, W.H. Ho & K.M. Tsui	F	9
A. longispora K.D. Hyde	M	5
A. mangrovii K.D. Hyde	M	1,2,3,4,5,6,7
**A. megalospora* K.D. Hyde, W.H. Ho & K.M. Tsui	F,M	10
**Annulatascus* sp.	B	10
Annulatascus bipolaris K.D. Hyde	F	9
A. triseptatus S.W. Wong, K.D. Hyde & E.B.G. Jones	F	8,10
A. velatisporus K.D. Hyde	F,B,M	8,9,10,11
Antennospora quadricornuta (Cribb & J. Cribb) T.W. Johnson	M	1,2,3,4
**Anthostomella* sp.	B	11
Aquaticola sp. 1	F	9
Aquaticola sp. 2	F	9
**Aquaticola ellipsoidea* W.H. Ho, K.M. Tsui, Hodgkiss & K.D. Hyde	F	10
**A. longicolla* W.H. Ho, K.M. Tsui, Hodgkiss & K.D. Hyde	F,B,M,R	10,11
Arenariomyces trifurcatus Höhnk	M	2,3
**Ayria appendiculata* Fryar & K.D. Hyde	M	10
Ascocratera manglicola Kohlm.	M	5
**Ascotaiwania* sp.	F	10
+*Ascotaiwania pallida* K.D. Hyde & Goh.	R	11
Bathyascus grandisporus K.D. Hyde & Jones	M	1,2,4,5
Belizeana tuberculata Kohlm. & Volkmann-Kohlm.	M	2,3,4,5
Biatriospora marina K.D. Hyde & Borse	M	2,5
Biconiosporella corniculata Schaumann	M	2,3
Bionectria sp.	F	9
+*Bruneiapiospora* sp.	R	11
Capillataspora corticola K.D. Hyde	M	6
Carbosphaerella leptosphaerioides I. Schmidt	M	2,3
Caryospora mangrovei K.D. Hyde	M	5
Caryosporella rhizophorae Kohlm.	M	1,2,4,5
Cataractispora appendiculata K.D. Hyde, S.W. Wong & E.B.G. Jones	F	8,10
**C. viscosa* K.D. Hyde, S.W. Wong & E.B.G. Jones	F	10

Table 4 continued. Checklist of fungi from aquatic habitats in Brunei.

Species	Habitat	Reference
**Ceratosphaeria* sp.	B,R	11
+*Chaetosphaeria* sp.	R	11
Chaetosphaeria anglica P.J. Fisher & Petrini	F	9
Clohiesia corticola K.D. Hyde	F	9
Corollospora colossa Nakagiri & Tokura	M	2,3
C. maritima Werdermann	M	3
C. pulchella Kohlm., I. Schmidt & Nair	M	2,3
Crinigera mangrovei K.D. Hyde & E.B.G. Jones	M	2
C. maritima I.Schmidt	M	1
Cucullospora mangrovei K.D. Hyde & E.B.G. Jones	M	2,3,4,5
Cytospora rhizophorae Kohlm. & E. Kohlm.	M	1
Dactylospora haliotrepha (Kohlm. & Kohlm.) Hafellner	M	1,2,3,4,5
**D. mangrovei* E.B.G. Jones, Alias, Abdel-Wahab & S.Y. Hsieh	B	10
Didymosphaeria sp.	M	2
Didymosphaeria enalia Kohlm.	M	1,2,3,4,5
Didymella avicenniae Patil & Borse	M	2,5
Diluviocola capensis K.D. Hyde, S.W. Wong & E.B.G. Jones	F	8
Etheirophora blepharospora (Kohlm. & E. Kohlm.) Kohlm. & Volkm.-Kohlm.	M	4
Eutypa sp.	M	5
**Fluviatispora boothii* Fryar & K.D. Hyde	B	11
**F. reticulata* K.D. Hyde	B	11
**Glomerella* sp.	F	10
Gnomoniella rubicola Pass.	F	9
Haligena salina Farrant & E.B.G. Jones	M	2,3
Halocyphina villosa Kohlm. & E. Kohlm.	M	1,4
Halosarpheia abonnis Kohlm.	M	2,3,5,7
H. cincinnatula Shearer & Crane	M	2,3
H. fibrosa Kohlm. & E. Kohlm.	M	2,4,5
H. heteroguttulata K.D. Hyde, S.W. Wong & E.B.G. Jones	F	9
H. marina (Cribb & J. Cribb) Kohlm.	M	1,2,3,4,5,6
H. minuta Leong	M	5,6
H. ratnagiriensis Patil & Borse	M	2,3,4,5,6
H. retorquens Shearer & Crane	M	2,5
H. viscosa I. Schmidt	M	2,3,4,5
Halosphaeria appendiculata-like	M	2,3
H. cucullata (Kohlm.) Kohlm.	M	2,3,5
H. salina (Meyers) Kohlm.	M	2,3
Helicascus kanaloanus Kohlm.	M	2,3,5,7
Hydronectria tethys Kohlm. & E. Kohlm.	M	1,2,3,4,5
Hypophloeda rhizospora K.D. Hyde & E.B.G. Jones	M	4,5,6
Hypoxylon oceanicum Schatz	M	4,5,6,7
Hypoxylon kretzschmarioides Y.M. Ju & J.D. Rogers	F	9
Jahnula australiensis K.D. Hyde	F	9
Kirschsteiniothelia elaterascus Shearer	F	9

Table 4 continued. Checklist of fungi from aquatic habitats in Brunei.

Species	Habitat	Reference
**Lasiosphaeria* sp. 1	B	11
**Lasiosphaeria* sp. 2	B,R	11
Lasiosphaeria breviseta P. Karst.	F	9
**L. immersa* P. Karst.	B	11
Lautospora gigantea K.D. Hyde & E.B.G. Jones	M	5
Leiosphaerella sp.	M	2
Leptosphaeria sp.	M	1,2,3,4,5
Leptosphaeria australiensis (Cribb & J. Cribb) G.C. Hughes	M,R	1,2,3,4,5,6,11
L. cf. *avicenniae* Kohlm. & E. Kohlm.	M	1,2,3,4,5,7
Lignincola laevis Höhnk	M	1,2,3,4,5,7
L. tropica Kohlm.	M	1,2,3,4,5
Lindra marinera Meyers	M	2
L. thalassiae Orpurt, Meyers, Boral & Simms	M	2
Linocarpon pandani (Syd. & P. Syd.) Syd. & P. Syd.	M	2,3
Linocarpon sp.	M	2,3
Lophiostoma aquaticum (Webster) Aptroot & K.D. Hyde	F	9
L. bipolare (K.D. Hyde) Liew, Aptroot & K.D. Hyde	F,M	9,10
**L. frondisubmersum* (K.D. Hyde) Liew, Aptroot & K.D. Hyde	F,M	8,10
**L. tetraploa* (Scheuer) Aptroot & K.D. Hyde	B	11
Lulworthia sp. (spores 136-195 µm)	M	2,3,4
Lulworthia sp. (spores 220-335 µm)	M	1,2,3,4,5,6
Lulworthia sp. (spores 340-490 µm)	B,M	1,2,3,4,5,7,10,
Lulworthia grandispora Meyers	M	11
Mamillisphaeria dimorphospora K.D. Hyde, S.W. Wong & E.B.G. Jones	F	1,2,3,4,5,6,7, 8,9
Manglicola guatemalensis Kohlm. & E. Kohlm.	M	1,2,4,6
**Mangrovispora pemphii* K.D. Hyde & Nakagiri	B	10
Marinosphaera mangrovei K.D. Hyde	M	1,4,5
Massarina sp. 1	F	8
Massarina sp. 2	M	2
Massarina sp. 3	M	2
+*M. rubi* (Fuckel) Sacc.	R	11
M. thalassiae Kohlm. & E. Kohlm.	M	1,2,5
M. velataspora K.D. Hyde & Borse	M	1,2,3,4,5
Mycosphaerella pneumatophora Kohlm.	M	5
Nais glitra Crane & Shearer	M	5
Nectria cf. *byssicola*	F	9
+*N. haematococca* Berk. & Broome	R	11
Nimbospora bipolaris K.D. Hyde & E.B.G. Jones	M	2,3
N. octonae Kohlm.	M	2
Ophioceras dolichostomum (Berk. & Curtis) Sacc.	F	9
Ophiodeira monosemeia Kohlm. & Volkm.-Kohlm.	M	4,5
**Orbilia* sp.	F,B,R	10,11
Orcadia cf. *ascophylli*	M	1,2,3
Oxydothis sp.	M	3

Table 4 continued. Checklist of fungi from aquatic habitats in Brunei.

Species	Habitat	Reference
Passeriniella savoryellopsis K.D. Hyde & Mouzouras	M	2,4,5
+*Phaeosphaeria* sp.	R	11
**Phaeosphaeria capensis* T.D. Steinke & K.D. Hyde	F,B	10
**Phomatospora* sp.	M	10
Phomatospora kandeliae K.D. Hyde	M	7
Pleospora sp.	M	1,2,3
Pleospora state of *Stemphylium majusculum*	F	9
Quintaria sp.	F	9
Remispora crispa Kohlm.	M	2,3
R. galerita Tubaki	M	2,3
Rhizophila marina K.D. Hyde & E.B.G. Jones	M	3,4,5
Rosellinia sp.	M	2,3
Salsuginea ramicola K.D. Hyde	M	7
Savoryella sp.	M	2,3
Savoryella aquatica K.D. Hyde	F	9
S. fusiformis W.H. Ho, K.D. Hyde & Hodgkiss	F	9
S. lignicola E.B.G. Jones & R.A. Eaton	M,F	1,2,3,4,5,7,9,10
S. paucispora (Cribb & J. Cribb) Koch	M	1,2,5,10
S. verrucosa Minoura & Muroi	F,B	9,10
Sphaerulina cf. *oraemaris*	M	2,5
**Sungaiicola brachydesmiella* Fryar & K.D. Hyde	F,B,M	10,11
Swampomyces cf. *armeniacus* Kohlm. & Volkm.	M	4,5
+*S. triseptatus* K.D. Hyde & Nakagiri	R	11
Thalassogena sphaerica Kohlm. & Volkm.-Kohlm.	M	4,5
Torpedospora radiata Meyers	M	2,3,4,5
**Torrentispora crassiparietis* Fryar & K.D. Hyde	F,B	10
**T. fibrosa* K.D. Hyde, W.H. Ho, E.B.G. Jones, K.M. Tsui & S.W. Wong	F,B	10
**T. fusiformis* Fryar & K.D. Hyde	F,B	10
Trematosphaeria lignatilis Kohlm.	M	1,2,4,5
T. striataspora K.D. Hyde	M	4,10
Trematosphaeria sp.	M	2,3
Tubeufia palmarum (Torrend) Samuels, Rossman & E. Müll.	F	9
Verruculina enalia (Kohlm.) Kohlm. & Volkm.-Kohlm.	M	7
Basidiomycetes		
Calathella mangrovei Jones & Kohlm.	M	7
Halocyphina villosa Kohlm. & E. Kohlm.	M	2,3,5,7
Nia vibrissa Moore & Meyers	M	2,3
Anamorphic fungi		
Acrogenospora sphaerocephala (Berk. & Broome) Ellis	F	9
**Alysidium* sp.	F	10
Aquaphila albicans Goh, K.D. Hyde & W.H. Ho	F	9
**Arthrobotrys oligospora* Fresen.	B,R	11

Table 4 continued. Checklist of fungi from aquatic habitats in Brunei.

Species	Habitat	Reference
Bactrodesmium sp.	M	2
B. linderi (Crane & Shearer) Palm & Stewart	M	4
**Berkleasmium* sp.	F,B	10,11
**Beverwykella pulmonaria* (Beverw.) Tubaki	F	10,11
**Brachysporiella gayana* Bat.	F,B	10,11
Canalisporium caribense (Hol.-Jech. & Mercado) Nawawi & Kuthub.	F	9
C. elegans Nawawi & Kuthub.	F	9
C. pulchrum (Hol.-Jech. & Mercado) Nawawi & Kuthub.	F	9
**Cancellidium applanatum* Tubaki	F,B,M	10,11
Candelabrum brocchiatum Tubaki	F	9
Ceuthospora gaeumannii Nag Raj	F	9
**Chalara* sp.	M	10
Chloridium lignicola (Mangenot) W. Gams & Hol.-Jech.	F	9
Chrysosporium sp.	M	1,2,3
Cirrenalia pseudomacrocephala Kohlm.	M	2,4,5,6
C. pygmea Kohlm.	M	1,2,3,4,5, 6,7
C. tropicalis Kohlm.	M	1,2,3,4,5,6
Cladorrhinum samala (Subram. & Lodha) W. Gams & Mouchacca	F	9
Clavariopsis bulbosa Anastasiou	M	2,3
+*Coleodictyospora cubensis* Charles	R	11
+*Conioscypha* sp.	R	11
Cordana abramovii var. *seychellensis* K.D. Hyde and Goh	F	9
Cytospora rhizophorae Kohlm. & Kohlm.	M	5
Dactylaria triseptata (Matsush.) R.F. Castañeda & W.B. Kendr.	F	9
**Dactylella sp.*	F,B	10
Denticularia limoniformis de Hoog	F	9
Dictyochaeta fertilis (Hughes & Kendrick) Holubova-Jechova	F	9
Dictyosporium alatum van Emden	F	9
D. pelagicum (Linder) G.C. Hughes	M	2,3,4,5
Diplodia sp.	M	5,6
**Exserticlava vasiformis* (Matsush.) S. Hughes	F,B	10,11
+*Graphium putredinis* (Corda) Hughes	R	11
Haplochalara angulospora Linder	F	9
**Helicomyces* sp.	B	11
Helicomyces roseus Link	F	9
H. torquatus L.C. Lane & Shearer	F	9
Humicola alopallonella Meyers & Moore	M	1,2,3,4,5
**Intercalarispora nigra* J.L. Crane & Schokn.	B	11
+*Lasiodiplodia* sp.	R	11
Megaloseptoria mirabilis N.A. Naumov	F	9
Microsphaeropsis olivacea (Bonord.) Höhn.	F	9
Monodictys capensis R.C. Sinclair, Boshoff & Eicker	F	9
M. pelagica (T.W. Johnson) Jones	F,B,M,R	1,2,3,10,11

Table 4 continued. Checklist of fungi from aquatic habitats in Brunei.

Species	Habitat	Reference
Monotosporella setosa var. *macrospora* G.C. Hughes	F	9
Nawawia filiformis (Nawawi) Marvanová	F	9
**Papulospora* sp. 1	B,M	10,11
**Papulospora* sp. 2	B,M	10,11
Periconia prolifica Anastasiou	M	1,2,3,4,5,6
Phaeoisaria clematidis (Fuckel) Hughes	F,B,R	9,10,11
P. sparsa Sutton	F	9
Phialocephala xalepensis Maggi & Persiani	F	9
Phialogeniculata africana Goh, K.D. Hyde & T.D. Steinke	F	9
Phialophorophoma litoralis Linder	M	2,4,5,6
Phoma sp.	M	2,3,4,5
Phomopsis sp.	M	4,7
Phragmospathula sp.	M	2,5
Pleurothecium recurvatum (Morgan) Höhn.	F	9
Polystigmina sp.	M	5
Pseudospiropes cubensis Hol.-Jech.	F	9
Robillarda rhizphorae Kohlm.	M	2
Scolecobasidium dendroides Pirozynski & Hodges	F	9
Sibrina orthospora W. Gams	F	9
**Spacidoides* sp.	B	11
**Sporidesmium* cf. *anglicum* (Grove) M.B. Ellis	F,B,M,R	10,11
**S. crassisporum* M.B. Ellis	F,R	10,11
S. ellipticum Moore	M	2
S. macrurum (Sacc.) M.B. Ellis	F	9
Sporidesmium sp.	M	2
Sporoschisma saccardoi E.W. Mason & S. Hughes	F	9
S. uniseptatum Bhat. & W.B. Kendr.	F	9
Stilbella holubovae Seifert, S.J. Stanley & K.D. Hyde	F	9
Tiarosporella paludosa (Sacc. & Fiori) Höhn.	F	9
Topospora sp.	M	1
Trichocladium sp.	M	3,4,5,7
Trichocladium achrasporum (Meyers & Meyers) Dixon	M	2,3,4,5
Trichocladium cf. *opacum* (Corda & Shearer)	M	1,2,4,5
Varicosporina ramulosa Meyers & Kohlm.	M	2
Verticillium sp. 1	F	9
Verticillium sp. 2	F	9
Virgariella atra S. Hughes	F	9
Xylomyces sp.	B,M	2,3,4,5,6,11
Xylomyces chlamydosporis Goos, R.D Brooks & Lamore	F,B	9,11
**X. giganteus* Goh, W.H. Ho, K.D. Hyde & K.M. Tsui	B	11
Zalerion varium Anastasiou	M	2,3

*indicates species which are new records for Brunei in either this study or Fryar *et al*., 2004b, + indicates species which have been found only in the riparian vegetation i.e. not from an aquatic habitat. F = freshwater, B = brackish, M = marine, R = in riparian vegetation. 1 = Hyde, 1988a, 2 = Hyde, 1988b, 3 = Hyde, 1989, 4 = Hyde, 1990a, 5 = Hyde, 1990b, 6 = Hyde, 1991, 7 = Hyde, 1992, 8 = Wong, 1996, 9 = Ho *et al*., 2001, 10 = This study, 11 = Fryar *et al*., 2004a.

Multivariate community analysis

Detrended Correspondence Analysis (DCA) showed a trend of marine sites on the left through to the freshwater sites on the right (Fig. 2). Axes 1 and 2 explained 35% of the variation. The species that explained the most variation in axis 1 were *Alysidium* sp., Ascomycete sp. 1, *Ascotaiwania* sp., *Beverwykella pulmonaria*, *Brachysporiella gayana*, *Chaetosphaeria* sp., *Dactylella* sp., *Exserticlava vasiformis*, *Massarina* sp., *Pleurophragmium*-like, *Sporidesmium crassisporum*, *Torrentispora fusiformis* and *Tritirachium* sp. Axis 2 was mostly explained by *Aniptodera megalospora*, *Ceratosphaeria* sp. 1, *Lasiosphaeria* sp. 3, *Lophiostoma bipolare*, *Lophiostoma frondisubmersum* and *Phomatospora* sp.

Discussion

Salinity is one of the most important factors influencing the distribution of fungi in aquatic habitats (Shearer, 1972). Studies consistently find different assemblages of fungi in fresh and marine habitats (e.g. Shearer and Von Bodman, 1983; Shearer, 1993; Czeczuga, 1996; Alias and Jones, 2000; Sarma and Vittal, 2000, 2001; Sivichai *et al*., 2002). However, the distribution of fungi in intermediate habitats (brackish water) is less well known. Shearer (1972) found that significant changes occurred to the species composition at points where salt and freshwater mixed. Although several species were able to tolerate a wide range of salinities, many only occurred at brackish water sites (7.8-17.9‰) (Shearer, 1972). Similarly, in this study several species were found at all sites, and were common, whereas others were unique to the brackish water sites.

Previous studies in Brunei had found distinct assemblages of fungi in fresh and sea water (Hyde, 1988a,b, 1989, 1990a,b, 1991, 1992; Wong, 1996; Ho *et al*., 2002). However, as salinity was generally not recorded it was unknown whether there is a mixture of 'freshwater' and 'marine' species or a completely different assemblage of fungi i.e. 'brackish water' species. The current data suggests that there are both. Some freshwater species also occurred in brackish habitats, but not in marine habitats (e.g. *Torrentispora crassiparietis*, *T. fibrosa, T. fusiformis* and *Dactylella* sp.). Similarly some marine species occurred in brackish habitats but not in freshwater (e.g. *Aniptodera chesapeakensis* and *Lulworthia* spp.). This suggests that brackish water supports a mixture of freshwater and marine species. There were, however, several rare, unique species in the brackish habitats (e.g. *Annulatascus hongkongensis*, *A. palmietensis* and *Savoryella verrucosa*) that

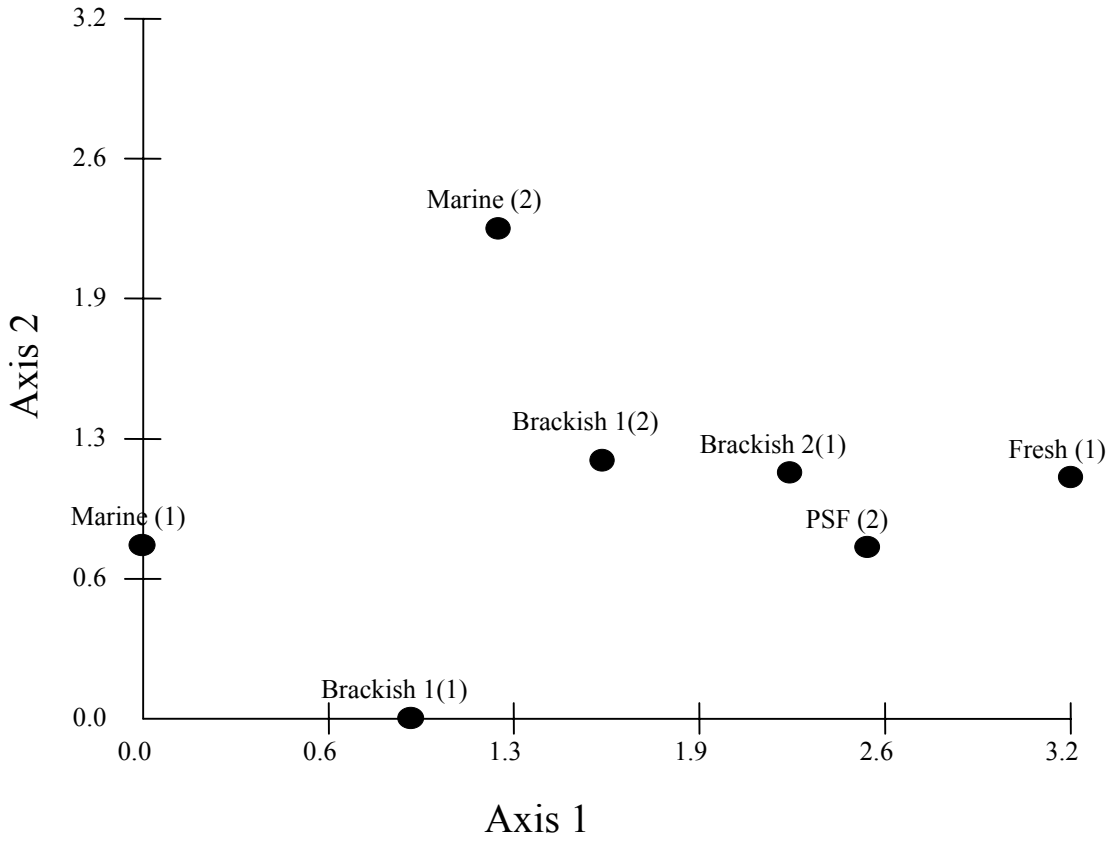

Fig. 2. Plot of axis1 vs. axis 2 scores from Detrended Correspondence Analysis.

indicate brackish habitats support an assemblage of fungi distinct from freshwater and marine assemblages.

The Detrended Correspondence Analysis indicated that the assemblages of fungi in the brackish sites were intermediate between marine and freshwater sites, i.e. that there is a continuum of species rather than distinct communities at each site. Research in other parts of the world has found that some 'marine' species have a tolerance for brackish water and can even grow in freshwater, but not as vigorously (Byrne and Jones, 1975; Curran, 1980). Likewise, 'freshwater' species (and even some terrestrial species) have been found to have some tolerance for salinity (Curran, 1980). This was also observed in this study with *Aniptodera chesapeakensis* and *Sungaiicola brachydesmiella* showing a gradient of abundance from marine to freshwater sites. However, some species (*Annulatascus velatisporus*, *Exserticlava vasiformis*, *Papulospora* sp. 1, *Papulospora* sp. 2, *Xylomyces* sp., and *Xylomyces*

giganteus) were more abundant in brackish water habitats than freshwater or marine suggesting these are 'brackish water' species that can also live in either freshwater or marine habitats. A good example is *Monodictys pelagica* that was found in brackish and freshwater habitats. *Monodictys pelagica* has previously been noted as being a brackish water species (Tubaki, 1969) based on physiological evidence. Optimum salinity for this fungus is 20-60% sea water (Jones and Jennings, 1964; Tubaki, 1969).

Shearer (1972) found that the ratio of ascomycetes to hyphomycetes increased with increasing salinity. This trend was also seen in the first set of samples of this study. The reason for this is unknown, but perhaps there are different stimuli for sporulation in marine and freshwater habitats, or the osmotic potential of salt water is too great for many conidia.

This is only the second time that *Fluviatispora reticulata* has been found. It was described from fruiting bodies found on rachides of *Livistona* sp. in the Bensbach River, Papua New Guinea (Hyde, 1994).

Cancellidium applanatum was common at all sites. This aero-aquatic hyphomycete was originally described from balsa-wood test blocks in a lake in Japan (Tubaki, 1975). However, it has since been recovered from submerged decaying leaves in Malaysia (Webster and Davey, 1980) and Queensland, Australia (Shaw, 1994). It has not been previously recorded in Brunei.

The significant finding of two new genera and two new species is indicative of the lack of knowledge of fungi in aquatic habitats, and the general lack of funded fungal taxonomists (Miller, 1995; Hyde, 2003).

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