

10. The Role of Fungi in Marine Detrital Processes

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Introduction

A variety of animals in the marine ecosystem feed upon detritus, the 'dead organic matter in various stages of decay with its associated microorganisms, which is formed from complex physical and chemical interactions mediated by the environmental conditions of the sediment and water column as well as the metabolism of micro- and macroorganisms closely associated with it' (Kenworthy et al., 1989). Detrital processes are crucial to the marine ecosystem and to detritivores (Mann, 1988). The pathway through which organic matter resulting from dead parts of organisms, including leachates and exudates, molts of animals and dead plant and animal tissues enter the foodweb through the intervention of decomposer microorganisms is vital both to remineralization processes, as well as the survival of detritivorous animals. Numerous studies have focused on detritus from coastal marine macrophytes, since these contribute an enormous amount of organic matter to the adjacent waters. Thus, for example, litter fall in the Chorao mangroves of Goa, India has been estimated as nearly 500 g C m⁻² yr⁻¹. The detritus input into Mandovi and Zuari estuaries through the 2000 hectares of mangroves in Goa may amount to 10.1 x 10³ tons of C yr⁻¹ (Wafar et al., 1997). The major role of microorganisms in detrital processes is the conversion of the less palatable dead organic matter to a more attractive food for the detritivores. The mechanisms by which this is achieved are the central themes of studies on detrital food webs. It is needless to say that this has a direct human interest, since many commercially important marine animals are detritivores. Along the west coast of Goa, production of the highly prized shrimps is believed to depend ultimately on the detrital food web. The role of bacteria in the detrital food web has been much studied. However, despite their widely acknowledged crucial role as decomposers in the terrestrial ecosystem, marine fungi find only a cursory mention in marine biology text books. No discussion on decomposition of coastal macrophytes, particularly mangrove plant parts, is complete without a consideration of the importance of fungi as major decay organisms. Contrary to popular belief, fungi

do form an important component of detritus in the neretic, as well as the oceanic realms. The greater awareness of bacteria in marine detritus as compared to fungi may be attributed to the absence of a comprehensive review on the role of fungi in detrital processes, bringing together information from widely scattered publications. While evaluating the role of fungi in these processes, it is essential to know their diversity, biomass, biodegradative role and importance as food to detritivorous animals. Much information is now available on these aspects. Much more, however, remains unknown. This article is an attempt to bring together information on fungi in marine detritus.

The Major Fungal Groups In Marine Detritus

It is important to recognize that bacteria and fungi occupy different ecological niches in detritus (Newell, 1984; Newell, 1994; Raghukumar, 1990). Unicellular bacteria live on surfaces of particulate detritus, are capable of rapid growth and multiplication and, have a high substrate affinity, thus being able to use even low concentrations of nutrients. Small particles of high surface to volume ratios tend to support bacteria more than fungi. Four major taxonomic and morphological groups, each with its own ecological significance may be discerned among fungi. These forms are found among fungi belonging to Kingdom Eumycota, as well as Kingdom Stramenopila or Chromista. The latter Kingdom comprises the Labyrinthulomycetes and Oomycetes (Porter, 1990; Dick, 2002; Raghukumar, 2002).

Mycelial fungi belonging to the Eumycotes grow more slowly when compared to bacteria, but are capable of penetrating relatively persistent particulate detritus much more efficiently than the latter by virtue of their filamentous habit and apical growth (Figs 1 and 2). They are particularly adept at utilizing large, lignocellulose-predominated substrates of high C:N ratios. Filamentous Oomycetes, such as species of *Halophytophthora* are likely to occupy the same niche as filamentous Eumycotes, residing within particulate detritus. Among the eumycotan fungi, the unicellular yeasts may occupy a similar niche as the bacteria.

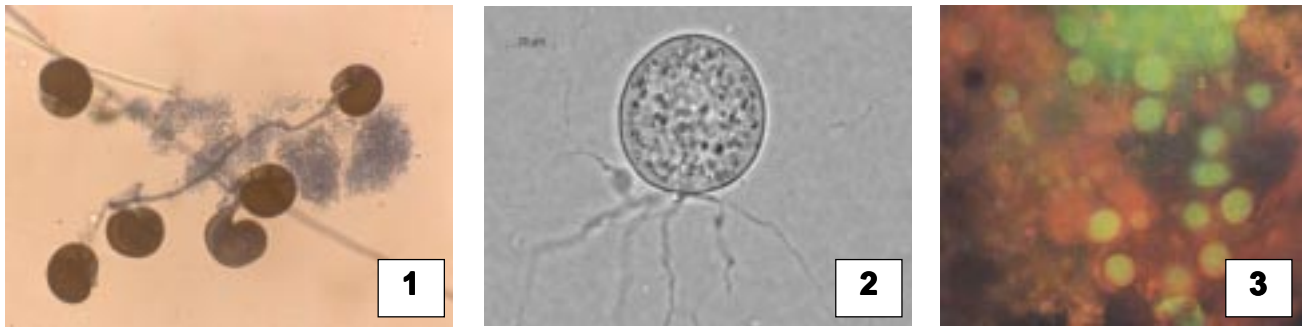


Fig. 1. The eumycotan mycelial fungus *Cirrenalia basiminuta* from decaying mangrove leaves.
 Fig. 2. Cell of a thraustochytrid, a stramenopilan fungus.
 Fig. 3. Thraustochytrids in marine aggregates (stained using the acriflavine direct detection technique)

They may occur on the surfaces of particles, or even in the presence of high concentrations of dissolved organic matter (DOM) (Fig. 2). The stramenopilan thraustochytrids, which belong to the Labyrinthulomycetes are unicellular and are the most ubiquitous marine forms. Their thalli grow on the surfaces of particles, while their ectoplasmic net elements penetrate them. They do not seem to have a high substrate affinity as the bacteria. The competitive advantage they ought to have over bacteria in occupying their specific ecological niche is not clearly known (Fig. 3). The labyrinthulids, which are yet another group of the Labyrinthulomycetes, are colonial forms, which may be found both epi- and endobiontically in particulate detritus.

Not much is known of the ecology of Oomycetes and thraustochytrids. Both of these groups are probably ruderal in their ecological strategy and colonize detritus much more rapidly than fungi, by production of motile zoospores. The numerous papers cited in this review should be consulted for isolating these fungi in culture from marine detritus.

Factors affecting detrital colonization, fungal diversity and biomass

Coastal macrophytic detritus: Vascular plants and macroalgae are the two major sources of detritus in coastal waters. Some of the most important among the former are the seagrasses, mangroves and salt marsh plants, such as the smooth cord or salt marsh grass, *Spartina alterniflora* Loisel. While the seagrasses are entirely submerged in water throughout their life, mangrove plant parts are allochthonous to the marine ecosystem and undergo decay only after they fall into the adjacent waters. The salt marsh grass forms extensive beds along southeastern Atlantic coast of the USA and is only partly submerged in the water.

Three phases of decomposition characterize macrophytes (Mann, 1988). The leaching phase lasts for a few days, during which a substantial amount of

weight loss takes place. The decomposition phase that follows may last a few weeks as in macroalgae, to several months as in vascular plants. The last phase is characterized by fine, particulate detritus. All macrophytes release substantial amounts of DOM into the water immediately upon their death (Koop et al., 1982). Conversion of DOM by bacteria into their biomass is an extremely important process that links the DOM to the foodweb through bacterivorous protozoans and microzooplankton (Biddanda, 1985; Mann, 1988). In some cases, the leachates may form flakes, which may be colonized by bacteria and are then consumed by larger invertebrates (Camilleri and Ribí, 1986). Thus, the annual dry weight of mucilage production during fragmentation from a small kelp bed of 700 ha was estimated to be 1458.38×10^4 kg and estimated to be capable of supporting a dry biomass of approximately 30×10^4 g bacteria and 3×10^4 kg dry biomass of flagellates and ciliates (Lucas et al., 1981). Little is known of the importance of fungi in this process. While mycelial fungi may not be expected to fill this niche, there is no reason why yeasts and thraustochytrids will not grow on high concentrations of DOM. Yet, this remains a poorly studied process for these fungi.

Colonization, diversity and biomass build-up in particulate detritus of coastal macrophytes are influenced by the chemistry of detritus. Living macrophytes contain substantial amounts of antimicrobial compounds, such as various phenolics and tannins (Valiela, 1979; Gonzalez-Farias and Mee, 1988). Leaves of different species of mangroves contain 5 to 42 % of tannins. The seagrass *Thalassia testudinum* contains a flavone glycoside that appears to confer protection to it from colonizing microbes (Jensen et al., 1998). Few thraustochytrids are found on living leaves of the sea grass, extracts of which have been shown to inhibit the growth of *Schizochytrium aggregatum* and attachment of its zoospores. Algae are well known to harbour antimicrobial compounds (Jones, 1988). Living algae, containing phenolics, inhibited the growth of thraustochytrids (Raghukumar et al., 1992). Despite

this, a few fungi are found in living macrophyte tissues. Phylloplane, or endophytic fungi, such as *Pestalotiopsis* sp., *Cladosporium cladosporioides* and other common primary saprophytes are found in living mangrove leaves (Newell, 1976; Fell and Newell, 198; Nakagiri, 1989; Raghukumar et al., 1995). Algal surfaces might be coated with epibiotic bacteria, which seem to play a symbiotic role by providing vitamins and other essential nutrients when the alga is alive (Austin, 1988). The aplanochytrid *Aplanochytrium minutum*, a stramenopilan fungus belonging to the Labyrinthulomycetes is present within the tissues of *Sargassum cinereum* (Sathe-Pathak et al. 1993). Many species of this fungus appear to be commonly associated with algae (Raghukumar, 2002).

How is microbial colonization initiated upon the death of a macrophyte? There are two possibilities. (1) A few microorganisms are capable of living on or within living macrophytes despite the presence of antimicrobial substances. It is likely that such organisms are capable of tolerating phenolics present in the plants. These microorganisms may initiate decay, as soon as the plant parts die. (2) Select microbes in the water column that may withstand the antimicrobial substances in the freshly dead plants might colonize and initiate degradation. Thus, marine Oomycetes, particularly *Halophytophthora vesicula* colonized leaves of red mangrove (*Rhizophora mangle*) within 2 h of leaf submergence, probably finding them by chemotaxis. The frequency of occurrence of *H. vesicula* in submerged leaves reaches 100% within 30 h of submergence. By 43 h, most, if not all parts of leaves were occupied internally. Frequencies of the oomycete remained near 100 % through about 2 weeks of submergence and then declined to about 60 % in older (> 4 weeks) leaves. Leaves of white mangrove (*Laguncularia racemosa*) were also extensively occupied by the oomycete (Newell et al., 1987). Raghukumar et al. (1994) have shown that this species is capable of bringing down the levels of total phenolics when inoculated on to fresh detritus of leaves of the mangrove *Rhizophora apiculata* Blume. Species of *Halophytophthora* may be particularly well suited as first invaders of fallen mangrove leaves, due to their ability to readily utilize a rather wide variety of sugars and amino acids leaching from them. Their inability to attack more resilient compounds including polysaccharides and proteins prevent them from being successful competitors to fungi of later stages of succession (Bahnweg, 1978). Singh et al. (1991) have shown that after a week's submergence, microbial colonization intensified and the leaves appeared to be devoid of phenolic deposits.

Little is known of the role of bacteria in this connection. One of the earliest colonizers of detritus appears to be the thraustochytrids. Decaying leaves of the mangrove, *Rhizophora apiculata* as well as the brown alga *Sargassum cinereum* were colonized densely with thraustochytrids within one week of death (Sathe-Pathak et al., 1993; Raghukumar et al., 1995). However, more detailed studies, as have been carried out with Oomycetes as mentioned above, have not been made with thraustochytrids.

Parallel to initial colonization by microorganisms, the soluble tannins and phenolics may also leach out rapidly, facilitating further colonization and biomass build-up.

A typical succession of species, the mycosere, is found in decaying mangrove leaves (Newell, 1976; Fell and Newell, 1981). In fact, the seed for this is sown even when the plants are alive. The phylloplane and endophytic fungi mentioned earlier persist during the initial stages of decay characterized by the leaching phase. Species of *Halophytophthora*, particularly *H. vesicular* as well as thraustochytrids colonize the leaves as soon as they fall in the water, as mentioned above. Several terrestrial species of fungi and, the facultative marine fungi also colonize mangrove leaf detritus during this phase. Fungal colonization is promoted by the loss of phenolics from mangrove detritus. Raghukumar et al. (1994) grew several fungi isolated from mangrove detritus on similar detritus, but of various ages. While fungi grew well on aged detritus, growth on early stages of detritus, containing higher amounts of tannins was inhibited. Hence, initial colonization of the particulate detritus is slow, owing to the presence of phenolics and tannins, which are inhibitory to microbes (Valiela, 1979).

The second stage of decomposition, characterised by microbial decay is a protracted phase in the case of vascular plants, lasting several weeks to months. In the case of mangrove leaves, terrestrial species of fungi and, facultative marine fungi may colonize during the first one or two weeks. Obligate marine fungi such as species of *Cirrenalia* and *Lulworthia* appear subsequently. Terrestrial species of fungi colonize detritus once again towards the last stages of decomposition, when the detritus turns into fine particles. A summary of events relating to the mycosere is presented in Table 1.

The diversity of fungi in seagrasses has been a neglected field. One of the few significant studies is that of Cuomo et al. (1985), who reported the occurrence of several lignicolous fungi in the sea grass, *Posidonia oceanica* from Mediterranean coasts. The most common species were *Corollospora maritima*, *Papulospora halima* and *Lulworthia* spp. with the perthophytic fungus *Halothia posidoniae* the most

frequently recorded (Cuomo et al., 1985; 1988). Newell and Fell (1982) isolated fungi from the seagrass, *Thalassia testudinum* König, using surface-sterilization techniques. A single species, *Phaeosphaeria typharum*, an ascomycete dominates standing dead biomass of the salt marsh grass (Newell, 1996). Decaying woody material from mangroves, including dead wood, pneumatophores and viviparous seedlings have been highly researched substrates. More than 150 species of fungi typical of this substrate, the manglicolous fungi have been described so far.

Mycelial fungi have been isolated from decaying seaweeds (Miller and Whitney, 1981). Terrestrial species, such as species of *Acremonium*, *Alternaria*, *Aspergillus*, *Curvularia*, *Paecilomyces* and *Phoma*, as well as marine species such as *Lindra thalassiae* have been reported from *Sargassum cinereum* (Sathe-Pathak et al., 1993). However, they do not appear to play an important role in macroalgal decomposition. Stramenopilan fungi appear to be more important in this process. As in the case of vascular plants, algal decomposition is also probably initiated by microbes already present in living thalli. As mentioned earlier, species of *Aplanochytrium* are commonly found in living algae and may be responsible for the initial stages of decomposition. The Labyrinthulomycetes appear to be more important than mycelial fungi in decaying macroalgae. The build up of thraustochytrid biomass appears to be due to the decline of phenolics in decaying macroalgae. Thus, thraustochytrids grew well on autoclaved detrital material, resulting in a total loss of phenolics (Raghukumar et al., 1992).

Sathe-Pathak et al. (1993) reported *Aplanochytrium minutum* and *Ulkenia visurgensis* to be the important fungi in the decaying brown alga, *Sargassum cinereum* from the coastal waters of Goa. The former is found as an endobiont even in living thalli of the brown alga and persist during decay. *Ulkenia visurgensis* makes its appearance only after the death of the brown alga. Milller and Jones (1983) have discussed colonization of detritus of the kelp *Fucus serratus*.

Why are mycelial fungi fewer and thraustochytrids more common in macroalgae than in vascular plants? The reason could be that macroalgae decompose much faster than vascular plants, allowing little time for a high diversity of mycelial fungi to colonize the substrates. This depends on the chemistry of macroalgal detritus, which is characterized by more soluble organics and little or no lignocellulosic fibres, as is the case with vascular plants. Thraustochytrids, which colonize rapidly through zoospores and grow faster, therefore, have a better chance to thrive upon algal detritus. The lower C:N ratio of macroalgae might also favour thraustochytrids more than mycelial fungi. Once again, a study of yeasts in macroalgal detritus could prove to be interesting. Vascular plant detritus persists for a long time through decay and allows an opportunity for the k-strategy fungi to colonize and establish.

The total biomass of microorganisms in detritus is generally low (Table 2). The various methods of fungal biomass and productivity estimations in detritus have been reviewed by Newell (1994). Fungal mycelium in detritus may be directly stained and fungal biovolume measured manually using a microscope (Sathe and Raghukumar, 1991; Raghukumar et al., 1995), or using an image analysis software). The signature molecule, ergosterol, may be estimated. Ergosterol contents provide an estimate of living fungal biomass, but its conversion to fungal biomass depends on the conversion factor used, which may vary according to the fungus (Newell, 1994). Despite these drawbacks, a rough idea of fungal biomass in marine detritus is emerging (Table 3). Microbial biomass, including that of fungi, generally peaks during intermediate stages of decomposition (Table 4). Raghukumar et al. (1995) found the highest mycelial fungal biomass in mangrove leaves by 21 days of decomposition. Findlay et al. (2002) found that while bacterial biomass was higher on fine particles relative to leaves or wood surfaces and that of ergosterol concentrations, representing fungi were significantly greater on leaves and wood, confirming the predominance of fungal biomass in these larger size classes.

Table 1. Fungal dynamics during decomposition of a macrophyte

Living - Senescent	Death phase	Decompositional phase	Recalcitrant phase
1. High levels of soluble organics and phenolics; high C/N ratios	Rapid leaching of soluble organics and phenolics; High C/N ratios.	Low levels of soluble organics and phenolics	Scant levels of soluble organics and phenolics; Low C/N ratios.
2. Endophytic fungi present	Colonisation by Labyrinthulomycetes (eg., thraustochytrids and Oomycetes) and yeasts	Colonisation by mycelial, marine fungi	Colonisation by terrestrial species
3. Low fungal biomass	Increasing fungal biomass.	Peak fungal biomass.	Low fungal biomass.

Findlay et al. (1986) and Findlay and Fell (1988) used the following fatty acid signatures for microbial biomass and colonization in green, senescent, yellow floating, yellow sunken, brown sunken and black sunken leaves of the mangrove, *Rhizophora mangle*.

Based on these signatures, they determined that fungi contribute a biomass in senescent leaves and were most prevalent during intermediate stages of decomposition, namely yellow sunken leaves (0.0538 % of detrital dry weight). Bacteria were present in low levels in senescent leaves and remained throughout the decay process, becoming most abundant in black leaves and fine particulate detritus. Thraustochytrids were not present in senescent leaves but were found in all leaves recovered, suggesting that they colonized the leaves soon after they entered the water; thraustochytrids increased in abundance as the leaves decayed and became significant in black leaves. Use of fatty acid markers by Mflinge et al. (2003) has once again confirmed the rapid increase of fungal biomass from 0 to 2 weeks.

Using the immunofluorescence technique, Sathe-Pathak et al. (1993) estimated the biomass of the thraustochytrid *Ulkenia visurgensis* in brown algal detritus. The fungus produced 0.07 % of the detrital carbon, while the total bacterial biomass corresponded to 1.1 %. It is likely that if the biomass of *Aplanochytrium minutum*, which was also present in culturable numbers in the detritus had been accounted for, total thraustochytrid biomass might have been considerably higher. More studies are required to evaluate biomass production of thraustochytrids in macroalgal detritus.

Some of the highest fungal biomass is found in standing, naturally positioned dead leaves of the salt marsh grass, *Spartina alterniflora* (Newell, 1989, 1993, 1996). Most of the biomass appears to be formed by the Ascomycete, *Phaeosphaeria typharum*,

which produces about 1000 ascomata per square centimetre of the decaying-leaf abaxial surface. Using the enzyme-linked immunosorbent assay (ELISA), Newell (1989) estimated that fungal biomass formed >98 % of the microbial standing crops. Standing bacterial bio-volume or mass is lower than that of fungi on/in the decaying substrates, at least during much of the decay period. The ratio of bacterial: microalgal: fungal standing crop by 8 weeks of post senescence in standing stock of the cordgrass is approximately 1:4:600. Fungal biomass can rise to >10 % of the detritus, with specific rates of fungal organic mass increase of 0.001 to 0.02 per h during periods of water saturation of leaves (Newell, 1989, 1996). In absolute values, fungi can produce 106 mg of organic biomass per gam of detrital weight. Fungal dominance of microbial standing crops declined when autumn leaves bent downward and acquired a large sediment content, at which time the bacterial biomass rose to 7 % of the total. Fungal productivity was negative late in the decay period for autumn leaves, and was approximately equal to bacterial productivity for late winter-spring leaves.

Pelagic detritus

Fungi have generally been considered unimportant in open water detrital processes. However, there is increasing evidence for a major role for thraustochytrids fungi in detrital dynamics of the water column Raghukumar (2002). Thraustochytrids are the most abundant and ubiquitous of fungi in the marine ecosystem. Direct detection and biomass estimations of these fungi have now become easier through the use of the acriflavine direct detection method (AfDD, Raghukumar and Schaumann, 1993). Thraustochytrids have been found in/on a variety of substrates, such as faecal pellets of salps and marine snow (Raghukumar and Raghukumar, 1999; Raghukumar et al., 2001). Thraustochytrids

Table 2. % Microbial biomass in detritus of various macrophytes

Macrophyte	Biomass	Reference
Leaves of the seagrass <i>Halophila decipiens</i>	0.70	Kenworthy et al., 1989
Leaves of the seagrass <i>Thalassia testudinum</i>	0.14	Blum et al., 1988
Leaves of the mangrove <i>Rhizophora mangle</i>	0.08	Blum et al., 1988
Leaves of the seagrass <i>Syringodium filiformis</i>	0.47	Blum et al., 1988
Fronds of the brown alga <i>Laminaria pallida</i>	1.70	Stuart et al., 1981
Leaves of the seagrass <i>Halodule wrightii</i>	0.15	Blum et al., 1988
Leaves of the mangrove <i>Rhizophora apiculata</i>	0.10	Raghukumar et al., 1995
Fronds of the brown alga <i>Sargassum cinereum</i> (Thraustochytrids only)	1.17	Sathe et al., 1991

Table 3. Some examples of maximum % fungal biomass in detritus

Substrate	Biomass	Reference
Decaying mangrove leaves (mycelial fungi)	0.052 % of detrital dry wt.	Raghukumar et al., 1995
Decaying mangrove leaves (mycelial fungi)	0.1 % of detrital dry wt.	Blum et al., 1988
Decaying seagrass leaves (mycelial fungi)	3.2 % of detrital dry wt.	Sathe and Raghukumar, 1991
Decaying mangrove leaves (thraustochytrids)	0.043 % of detrital dry wt.	Findlay et al., 1986
Water column of the Arabian Sea (thraustochytrids)	0.027 mg C L ⁻¹	Raghukumar et al., 2001
Standing dead salt marsh grass	Up to 20 % of detrital dry wt.	Newell, 1996

Table 4. Peak microbial biomass during macrophyte decomposition

Decomposition duration (d)	Substrate	Peak biomass (d)	Reference
360	Leaves of the mangrove <i>Rhizophora satylosa</i>	40	Roberson, 1988
180	Leaves of the seagrass <i>Thalassia testudinum</i>	40	Rublee and Roman, 1982
40	Leaves of the seagrass <i>Thalassia testudinum</i>	40	Blum et al., 1988
40	Leaves of the mangrove <i>Rhizophora mangle</i>	40	Blum et al., 1988
34	Fronds of the brown alga <i>Laminaria pallida</i>	10	Stuart et al., 1984
36	Fronds of the brown alga <i>Laminaria</i> sp.	36	Robinson et al., 1982
160	Fronds of the seagrass <i>Halophila decipiens</i>	160	Kenworthy et al.,
56	Leaves of the mangrove <i>Rhizophora apiculata</i>	21	Raghukumar et al., 1995
28	Fronds of the brown alga <i>Sargassum cinereum</i>	14	Raghukumar et al., 1995
Bacteria:	15:0; cy 17:0; cy 19:0.		
Thraustochytrids:	22:5w6; 22:6w3.		
Fungi:	18:2w6; 18:3w3.s		

reproduce by means of heterokont, biflagellate zoospores that may rapidly swim towards a substrate and colonize it. Their importance in coastal macrophytic detritus has already been discussed earlier. Towards the decaying stages of a bloom, many species of phytoplankton, particularly the diatoms secrete large amounts of mucus that form conspicuous aggregates in the water column. These marine aggregates, or marine snow contribute enormously towards pelagic detritus and are believed to be responsible for a large-scale flux of organic material to the deep sea. Such aggregates appear to be an

important niche for thraustochytrids. Recent papers by Naganuma et al., (1998), Kimura et al., (1999) and Raghukumar et al. (2001) suggest that thraustochytrids can attain substantial biomass in the water column, often rivalling that of the bacteria (Table 3). It is likely that thraustochytrids residing in these aggregates are transported to the deep-sea along with their substrates. Raghukumar and Raghukumar (1999) have shown that thraustochytrids in salp faecal pellets withstand high hydrostatic pressure and low temperature characteristic of the deep-sea, indicating their role in detritus in the deep-sea.

The role of thraustochytrids in marine aggregates is not clear. Polysaccharides of marine snow formed by phytoplankton may be recalcitrant to bacterial degradation. It is likely that thraustochytrids perform the important task of remineralization of marine aggregates, in the place of bacteria. The enzymes involved in this process and degradation rates could form a potential topic for the future. Although mycelial fungi have been considered unimportant in detritus in oceanic water column, we have often observed fungal hyphae in Transparent Exopolysaccharides (TEP) in the water column. It will be worthwhile to examine the role of fungi in this substrate.

Decomposition and biochemical alteration of detritus by fungi

Fungi play a key role in the decomposition and biochemical transformation of macrophytic detritus in two major ways. Much of the material is highly resistant to microbial attack and perhaps, as with the phenolics, even inhibitory to marine bacterial and fungal activity (Hodson et al., 1983). Production of degradative enzymes is the key to biochemical transformation. For example, mangrove leaves consist of approximately 50 % lignocellulosic structural polymers and 50 % soluble organics, rich in tannins and phenolics (Hodson and Moran, 1983). Microorganisms that break down these recalcitrant compounds will have a major role in detrital dynamics. Secondly, fungi may play a major role in nitrogen immobilization by converting inorganic nitrogen into fungal biomass, thus resulting in a decrease of the C:N ratio of the detritus (Fell and Newell, 1981). This is crucial to the food web, as will be discussed later.

Raghukumar et al (1994) have investigated degradative enzyme production by fungi isolated from detritus of the leaves of the mangrove *Rhizophora apiculata*. Cellulases were produced by all species tested, while some produced xylanase, pectin lyases, amylase and proteases. Twenty one higher filamentous fungi isolated from *Spartina alterniflora* and other salt marsh substrata were shown to be capable of degrading cellulose, cellobiose, lipids, pectin, starch, tannic acid and xylan (Gessner, 1980). *Phaeosphaeria spartinicola* from salt marsh grass was shown to mineralise radiolabeled lignin moiety to CO₂ and solubilize part of it to DOC, after 45 days incubation at 20°C. Mineralization of polysaccharides was seven times faster than that of lignin. The fungus caused a 50 % loss of organic plant material of the plant during incubation (Bergbauer and Newell, 1992). Electron microscopy further confirmed their lignocellulolytic capabilities (Newell, 1996). Manglicolous marine fungi in decaying wood cause soft-rot (Mouzouras, 1989). One of these, the

basidiomycete, *Halocyphina villosa*, causes white-rot (Mouzouras, 1989). Many of these fungi cause a weight loss of wood. The relative roles of fungi and bacteria in degradation of detrital lignocellulose have been contentious issues. While fungi play a dominant role in this process on standing dead tissues of *Spartina alterniflora*, bacteria appear to be more important in degrading lignocellulose of detritus submerged in the water (Benner et al., 1984). Bacteria may also be more important in lignocellulose degradation of fine particulate mangrove and seagrass detritus (Hodson et al., 1983). However, the substantial biomass of mycelial fungi in larger particles lends circumstantial evidence for their greater importance in such material. As a matter of fact, marine detrital fungi producing lignocellulolytic enzymes appear to have much biotechnological potential in bioremediation and paper and pulp industries (Raghukumar, 2002). In addition, the role of thraustochytrids in possible lignocellulose degradation has not been addressed. Thraustochytrids do elaborate cellulases (Raghukumar et al., 1994; Bremer, 1995) and it is worth examining their lignin-degrading enzymes. Fungal degradation of lignocellulose may result in dissolved organic carbon (LC-DOC), which might be utilized by bacteria, or contribute to the humic material of the surrounding environment.

Thraustochytrids present in detritus of the macroalga *Sargassum cinereum* were seen to produce proteases, but not alginases, which degrade the structural polysaccharides of the brown algal cell wall. Degradation of the internal tissues of mangrove plant parts was shown to be associated with fungal activities (Singh et al., 1991). Miller and Whitney (1981) grew seven fungi isolated from living and cast seaweeds on different carbon compounds and found that the fungi were generally unable to grow on the algal polysaccharides, but showed good growth on the other algal compounds. Wainwright (1980); Schaumann and Weide (1990) have shown that several marine fungi are capable of producing alginate-degrading enzymes.

Fell and Findlay (1988) have argued that fungi are the key to increase in detrital nitrogen owing to the fact that they are found within the detritus, unlike bacteria that inhabit the surface. In the case of the salt marsh grass, all dead-leaf nitrogen is initially scavenged by fungi and it is only during the later stages of decay that they immobilize N from the surrounding waters (Newell et al., 1989). Up to 75 % capture of system nitrogen in detritus of this plant is constituted by living fungal biomass (Newell et al., 1996). Mfilinge et al. (2003) noticed a rapid loss of C by 2 weeks, and a rapid increase in N in leaves of the mangrove *B. gymnorrhiza* and loss of N in *Kandelia candel*,

corresponding to fungal biomass build up. They concluded that the rapid loss of N from *K. candel* was due to mineralization and its accumulation in *B. gymnorhiza* was probably due to immobilization, suggesting that fungi play a central role early in decay, in particular in C loss, in loss of leaf biomass and cellulosic materials and in enriching the detritus with N. Most of the increase in detrital nitrogen may not be through microbial biomass build up, but to complexing of nitrogenous material, including extracellular enzymes of the microbes with plant phenolics and lignin (Hicks et al., 1991).

Importance of fungi in improving nutritional quality of detritus

Many detritivores can assimilate more than 50 % of the non-microbial part of detritus as food (Table 5). In some animals, like the oyster *Crassostrea virginica* feeding on salt marsh grass detritus, this value can be low as 3 %, while in others, such as the shrimp *Palaeomonetes pugio* feeding on seagrass, it may be as high as 72 %. However, it has been unequivocally shown that microorganisms generally play a major role in transforming detritus into a more palatable food. The extent and nature of their involvement in this process varies, depending upon the source and chemistry of the detritus itself. Besides, different microorganisms may vary in their importance. Mann (1988) discusses the various detrital pathways and the role of microbes in them. The best studied examples of fungal enhancement of detritus are from studies on freshwater allochthonous detritus (Chandrashekar et al., 1989). Freshwater detritivores are strongly attracted to detritus colonized by fungi (see Graca, 1993). Thus, fungi serve as cues for the animals to select appropriate food. Several studies on freshwater detritus have examined the reasons why fungi could be useful to detritivores (Kostal and Seymour, 1976; Graca, 1993; Suberkroopp and Arsuffi, 1984; Suren and Lake, 1989). These studies can be used as guidelines for future studies on marine detritus, which have not been studied in such detail.

One of the most important roles of fungi in marine detrital transformation could be the removal of antigustatory compounds present in just-dead plant parts. The tannins, phenolics and various other compounds deter feeding of living plants and early stages of detritus by detritivores (Rietsma et al., 1988). Although much of these compounds are leached out, a substantial amount could also be degraded by fungi, as appears likely with early-colonizing fungi such as species of *Halophytophthora* (see earlier). In the case of vascular plants, the fibrous lignocellulose tissues may be softened by the activity of lignocellulose-degrading fungi. Change in physical texture is an indirect way of enhancing palatability. Bärlocher and Kendrick (1975) have shown that freshwater detritus softened by chemical means was as palatable as that softened by fungi. Fungi may enhance the nitrogen levels of detritus and diminish C/N ratios (Fell and Findlay, 1986; Newell, 1996). This would make the detritus more nutritious. However, this enhanced nitrogen may not be the result of high fungal biomass, since microbial standing stocks in general are quite low in detritus. On the other hand, increased N may be the result of the complexing by microbial extracellular enzymes with plant polysaccharides, resulting in 'humic nitrogen'. Although such nitrogen was originally considered a dead end as for as nutrition goes. Bärlocher et al., (1989) shown that such nitrogen can contribute substantially to the N nutrition of freshwater detritivores.

Probably the most important role of fungi is the supply of essential nutrients to detritivores (Phillips, 1984). Both fungi and bacteria are a source of vitamins and amino acids, which are extremely essential for the detritus-feeding animals. Some examples are essential amino acids that cannot be synthesized by the animals, such as lysine and methionine; various vitamins; sterols that contribute to the cholesterol of animal tissues and polyunsaturated fatty acids (PUFAs). The role of PUFAs for detritivores has attracted much attention in recent years, since some of these, such as the docosahexaenoic acid (DHA) are essential for growth and maturation of crustaceans (Harrison,

Table 5. Contribution of non-microbial component to food of detritivores

% Assimilation efficiency	Animal	Reference
30 - 50 % C	Mysid, <i>Mysis satemnopis</i> on hay	Foulds and Mann, 1978
34 %	Prosobranch, <i>Hydrobia ventrosa</i> on hay	Kotoed, 1975
3 %	Oyster <i>Crassostrea virginica</i> on suspended matter	Langdon and Newell, 1990
9 %	Mussel, <i>Geukensia demissa</i> on kelp detritus	Langdon and Newell, 1990
50 %	Mussel, <i>Aulacomya ater</i> on kelp detritus	Stuart et al., 1982
72 %	Shrimp, <i>Palaeomonetes pugio</i> on sea grass detritus	
46 %	Gastropod, <i>Bittium varicum</i> on seagrass detritus	

1990). Thraustochytrid fungi are typically high in DHA and have become a major commercial source of DHA in recent years (Lewis et al., 1999). Unfortunately, their ecological role in supplying this essential PUFA to the food web has remained largely ignored. Just the presence of thraustochytrids in detritus could make the substrate so much more nutritious to detritivores.

Do microbes serve directly as food for detritivores? The low microbial biomass that occurs on particulate macrophytic detritus would suggest that this may not be so. However, microbial biomass on highly labile substrates, such as leached out DOM and macroalgal mucus may be so substantial that these could serve directly as food even to macroinvertebrates (Table 6). Thus, the mussel *Geukenssia demissa* was estimated to derive a substantial portion of C and N from bacteria. High densities of bacteria on these substrates would naturally be a favoured source for bacterivorous flagellates and ciliates. Bacterivory by these microzooplankton is extremely important in the food web, representing the 'microbial loop', which sustains larger organisms through the intervention of mesozooplankton and fish (see Mann, 1988).

Table 6. Microbial contribution to food of detritivores

% Contribution	Animal	Reference
25% C	Polychaete, <i>Nereis succinea</i> on various sources	Cammen, 1980
5.5% C; 10% N	Oyster, <i>Crassostrea virginica</i> from suspended particles	Langdon and Newell, 1990
31% C; 71% N	Mussel, <i>Geukenssia demissa</i> from water column bacteria	Langdon and Newell, 1990
7% C; 73% N	Kelp bed community, through the faeces loop	Newell and Field, 1983
0.14% - 22.5% C	General	Blum et al., 1988

While mycelial fungi may not be important in this process, thraustochytrids and yeasts are quite likely to be. The high biomass of thraustochytrids on marine aggregates could be an excellent source of not only C and N, but also DHA. Are flagellates and ciliates that consume thraustochytrids enriched in this PUFA? If so, how important are thraustochytrids in the microbial loop? Large particulate aggregates with dense thraustochytrids biomass, as in the case of diatom aggregates or salp faecal pellets could be of direct use as food to mesozooplankton. Future studies might throw more light on this. Although similar possibilities exist for marine yeasts, no studies have been carried out on their ecological role in the sea. The interesting

possibility of fungal enzymes ingested along with detritus colonized by fungi being active in the guts of a detritivore is indicated in a paper by Bärlocher (1982). This may be yet another role of fungi in detritus.

Conclusion

A high diversity of eumycotan mycelial fungi and yeasts, as well as stramenopilan fungi (Oomycetes and Labyrinthulomycetes) prevails in coastal marine macrophytic detritus, as well as oceanic detritus. The diversity of these fungi depends on the detrital source. A typical succession of fungal species occurs in vascular plant detritus, such as mangrove leaves and wood. This mycosere may depend upon the chemistry of the detritus. Microbial biomass, including both fungi and bacteria is generally low in macrophytic detritus. However, they may play an important in the biochemical transformation of detritus by the production of extracellular enzymes and nitrogen enhancement. Thraustochytrids and yeasts may be important in utilizing DOM that is leached out of detritus, similar to bacteria. The former group may develop substantial biomass in marine aggregates of the ocean. Fungi may transform detritus into a more palatable food for detritivores. Various mechanisms of doing this may be present, the details of which have not been clearly worked out. One of the most important of these might be the supply of essential nutrients, such as vitamins, amino acids and polyunsaturated fatty acids to the detritivores. We are still quite ignorant about the biomass and productivity of fungi in marine detritus. Newell (1994) has presented detailed discussions relating to these aspects, by using ergosterol, the signature sterol of eumycotan fungi. Wider application of the techniques described in these papers and further refinement of the techniques may provide us more insight into the dynamics of fungi in marine detritus.

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