

Chapter 2

The Marine Environment and the Role of Fungi

*How inappropriate to call this planet Earth, When it is quite
clearly Ocean...*

Arthur C. Clarke

Oceans cover more than 70% of the Earth's surface. The marine ecosystem is driven by an interaction between the physicochemical environment of the oceans and the organisms that live there (Lalli and Parsons 1997). Biological processes of the marine ecosystem have an impact on climate and human society.

Physical and chemical properties of seawater are crucial in determining marine ecological processes. The average depth of the oceans is about 4000 m, and the volume covered by seawater is nearly 1.35×10^9 cubic kilometers. Seawater has an average salt content of about 3.5%, expressed as salinity of 35 ppt (parts per thousand). The pH of seawater ranges from 7.5 to 8.5. Sodium followed by magnesium are the major cations in seawater, while chloride and sulfate are the major anions. Many other macro- and microelements contribute to the salinity of seawater (Table 2.1).

Temperature of seawater varies from about 30 °C in warm tropical surface waters to around −2 °C at the poles. Temperature also varies according to depth, the deep-sea environment being about 2–4 °C. Carbon dioxide and oxygen are the major dissolved gases in seawater. Oxygen levels vary from a maximum of 20 parts per million (ppm) to nearly 0 ppm at some sites. Most life processes in the ocean are supported by the photosynthetic, primary producers, the phytoplankton in the open ocean or macroalgae in coastal waters. The main nutrients for plant growth are nitrogen (as nitrate, nitrite and ammonia), phosphorus (as phosphate), potassium, sulfur, magnesium, and calcium. Iron is an essential trace element. Diatoms, the important primary producers, also require silicon.

Table 2.1 Composition of seawater

Chemical ion	Concentration in parts per thousand (ppt)	Proportion of total salinity
Chloride	19.245	55.03
Sodium	10.752	30.59
Sulfate	2.701	7.68
Magnesium	1.295	3.68
Calcium	0.416	1.18
Potassium	0.390	1.11
Bicarbonate	0.145	0.41
Bromide	0.066	0.19
Borate	0.027	0.08
Strontium	0.013	0.04
Fluoride	0.001	0.003
Other	Less than 0.001	Less than 0.001

2.1 Divisions of the Marine Environment

The marine environment is divided into various zones (Fig. 2.1). Each of these is defined by distinct physical and chemical characteristics that determine the organisms that live in it, their interactions, and ecosystem functioning.

Horizontally, the oceans are divided into neritic or coastal and oceanic or offshore habitats.

- **The neritic or coastal habitat** is strongly influenced by land. This region is generally understood to extend from the high tide level to the farther edge of the continental shelf that lies approximately at 200 m depth. The continental shelf lies beyond the edge of the continental margin that marks the edge of the continental shelf. The region between the high tide and low tide levels is the littoral.
- **The offshore or oceanic habitat** is much less influenced by land than the neritic. It encompasses the region extending beyond the continental margin at about 200 m depth.

On a vertical basis, the oceans are divided into the open water or pelagic and the sea bottom or benthic.

- **The pelagic habitat:** When we say that the oceans cover 70% of the earth, we are referring to the vast amount of water column or the open sea that fills most parts of the earth. The pelagic comprises the open waters of the oceans, which are divided into several vertical zones. The epipelagic region covers approximately the upper 200 m of the oceans, at level with the upper margin of the continental shelf. The well-lit upper zone of the epipelagic from the surface to roughly 80 m depth is called the euphotic. Below the epipelagic lies the

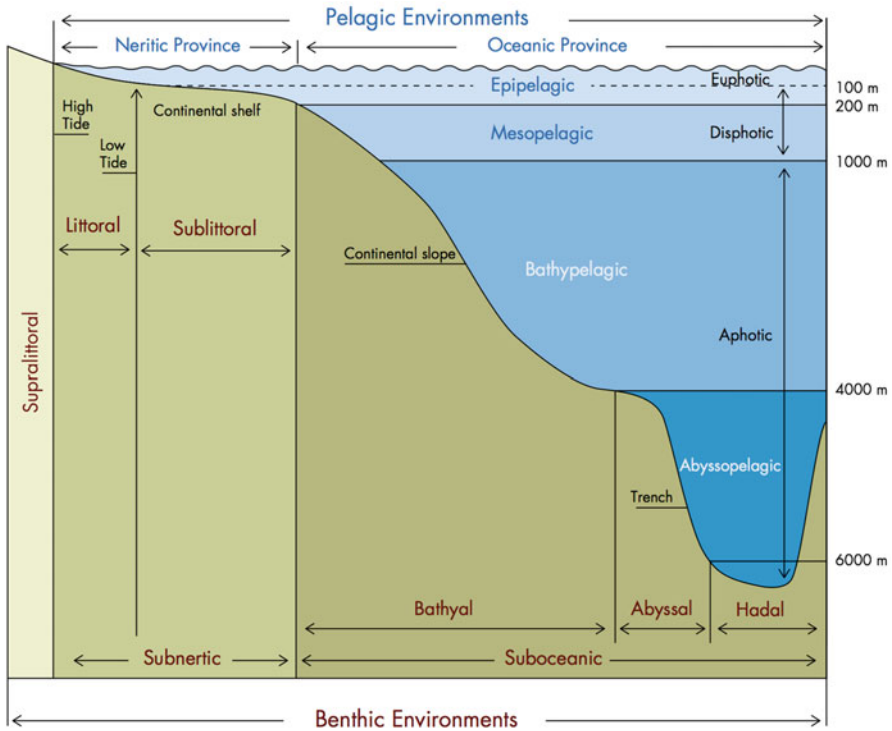


Fig. 2.1 The various divisions of the marine environment (Illustration by Craig Gladding)

mesopelagic till about 1000 m. This zone is dimly lit, while the deep-water or bathypelagic below 1000 m is almost totally dark or aphotic. The abyssopelagic zone lies below 4000 m, which is the average depth of the oceans.

- **The sea bottom constitutes the benthic zone.** The benthic zone extending from the high tide level to the low tide level is the **littoral benthic** and that below the low tide level to a depth of 200 m depth corresponding to the edge of the continental shelf is the **sublittoral benthic**. The bottom of the sloping continental shelf till about 4000 m is the **bathyal**, beyond which lie the **abyssal** and **hadal** zones. The average depth of the oceans is approximately 4000 m, the deepest part of the oceans being about 10,500 m. The deep sea is an extreme environment with temperatures of about 2–4 °C and high hydrostatic pressures that affect life processes. Hydrothermal vents occur in many parts of the deep-sea. These are characterized by a flow of super-heated seawater carrying a variety of dissolved minerals (see Sect. 12.2).

2.2 The Marine Food Web

All heterotrophic organisms on earth, including bacteria, fungi, and animals, are sustained by organic carbon generated almost entirely by photosynthetic organisms, the primary producers. An exception is the life around hydrothermal vents in oceans, which is supported by chemosynthetic bacterial primary producers.

Photosynthetic primary producers form the base of the trophic pyramid (Fig. 2.2). These are grazed by herbivorous consumers, which are also termed secondary producers. These, in turn, are eaten by higher level carnivorous consumers towards the top of the trophic pyramid. Productivity of an ecosystem is considered by taking into account all trophic levels. Bacteria are well known to play an important role at each trophic level, as decomposers and parasites. The role of fungi in these processes is gradually coming to light.

The diversity of fungi, as also of all other organisms, at different trophic levels and their interactions depend upon the environment of the various coastal and oceanic ecosystems in which they grow.

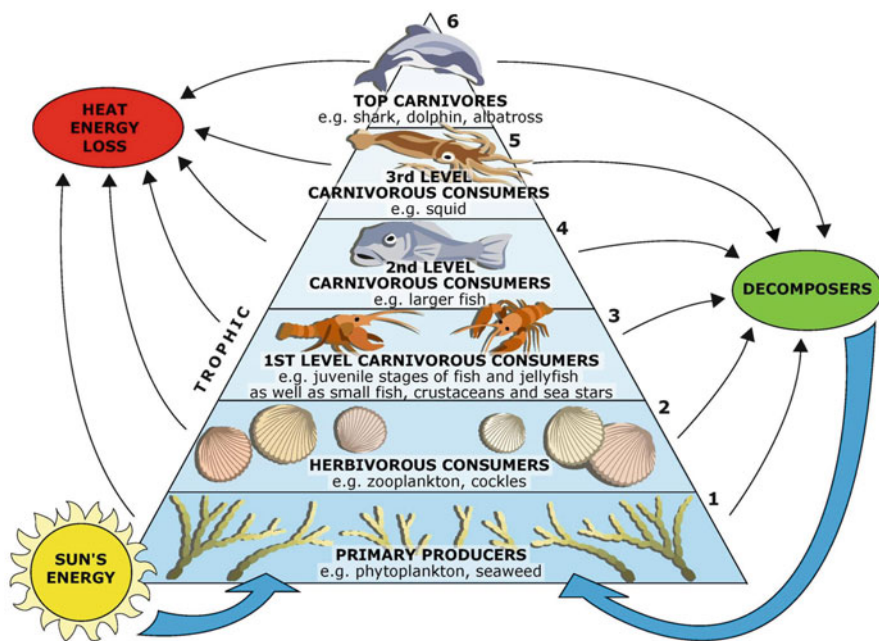


Fig. 2.2 The marine trophic pyramid (Copyright: University of Waikato. All Rights Reserved. <http://sciencelearn.org.nz>)

2.2.1 *Primary Production in Marine Ecosystems*

Primary production (PP) is the amount of organic matter fixed by photosynthetic organisms. Primary productivity is the rate of primary production. PP is usually expressed in terms of the amount of carbon fixed. The total amount of carbon fixed is the Gross Primary Production or GPP. Not all of GPP is converted into biomass. Part of the energy is used for respiration. **The amount of photosynthetically fixed energy that is converted into biomass is net primary production or NPP.** The level of primary productivity varies depending on the composition of photosynthetic organisms and varies among ecosystems and indicates how biologically productive an ecosystem is.

Part of the NPP is grazed by herbivores and enters the trophic chain, while the rest undergoes death and enters the microbial decomposition pathway. **The proportion of NPP that is consumed by grazers, or enters the detrital food chain upon their death, or is stored in sediments depends on the nature of the primary producers, which in turn is determined by the ecosystem.**

Coastal and oceanic waters together contribute a total NPP of nearly 52.14×10^9 metric tons of carbon per year (Fig. 2.3; Duarte and Cebrian 1996; Duarte et al. 2005; Bouillon et al. 2008). This roughly amounts to 50% of the Earth's photosynthetically fixed carbon, the rest coming from land plants.

Single-celled phytoplankton are the major primary producers in coastal as well as pelagic ecosystems. Of the 52.14 trillion metric tons of NPP produced every year in the oceans, phytoplankton are responsible for 89% or a total of 47.5×10^9 metric tons of carbon. The rest comes from vascular plants and macroalgae. About 40–50% of phytoplankton are consumed by herbivores. Coral reef algae, macroalgae, seagrasses, marsh plants, and mangroves are eaten by herbivores to a much lesser extent. These largely enter the decompositional, heterotrophic pathway rather than the grazer pathway.

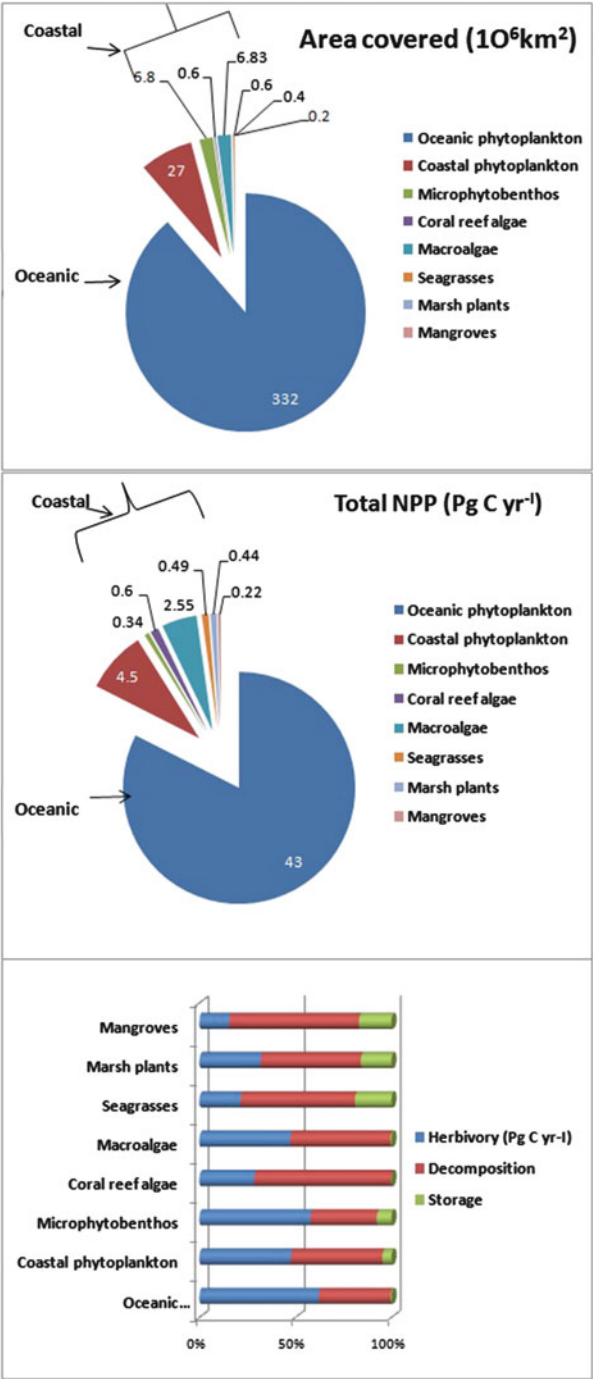
2.3 The Major Marine Ecosystems

The marine environment may be broadly divided into two distinct categories, the coastal and oceanic environments. Each contains distinct ecosystems that are driven by certain key groups of organisms.

2.3.1 *Coastal Environments*

Coastal fisheries and maritime activities have an enormous impact on human society. Coastal productivity, therefore, is of tremendous importance. **A variety**

Fig. 2.3 Major marine environments, their net primary productivity (NPP) and the fate of NPP (Based on information from Duarte and Cebrian 1996)



of coastal habitats, each with its unique characteristics, is found along the edges of continents.

Coastal oceans are biologically much more productive than the open oceans (Fig. 2.3).

- Coastal environment forms only about 12% of the ocean's area available for primary production. However, they are responsible for 18% of the NPP of the entire oceans. Net primary production in coastal environments equals nearly 9.14×10^9 metric tons of carbon.
- Of the above NPP, nearly 48% comes from mangroves, salt marsh plants, seagrass beds, coral reef algae, and macroalgae. Phytoplankton contribute around 52% of coastal NPP.
- NPP arising from vascular plants in mangroves, salt marsh plants, and seagrass beds is difficult to digest by herbivores, and only part of the NPP from this source enters the trophic web. Biomass produced by macroalgae and coastal phytoplankton are consumed to a larger extent by herbivores.
- A large portion of biomass produced by all primary producers enters the decompositional pathway.
- A greater portion of the NPP of vascular plants is recalcitrant and becomes stored in the sediments, compared to biomass from macroalgae and phytoplankton.
- Phytoplankton are easily grazed upon. Nearly 40% of the phytoplankton produced is grazed upon by herbivores. This, in turn, is passed on to higher trophic levels.

The following are the major coastal ecosystems.

- **The estuarine environment**, where a river meets the sea is characterized by a gradient in salinity, from about 35 ppt at the mouth of the estuary meeting the sea to nearly 0 ppt towards the upper reaches of the estuary. Riverine discharge from the estuary into the sea brings enormous amounts of nutrients into coastal waters. Wood from dead trees in coastal areas is often washed into the sea (see Chap. 4). Lagoons and networks of inland backwaters are other important coastal marine habitats.
- **Mangroves, salt marshes, and seagrasses** are important coastal vegetations (Chaps 5–7). Dense stands of mangrove trees are often found lining the estuarine margins and backwaters. Mangrove trees contribute to enormous organic material in the form of leaves and woody material that transport nutrients to coastal waters. Salt marshes are characteristic of lower salinity, brackish water regions. Seagrass beds are found in many shallow, sublittoral waters.
- **Coral reefs** are found in coastal waters of middle latitudes from 30° N to 30° S of the equator (Chap. 9). Fringing coral reefs along many coasts rival tropical rain forests in productivity and biodiversity. Hermatypic or reef-building corals that secrete calcium carbonate are the keystone species of this ecosystem, which is extremely rich in biodiversity. Coral reefs are found typically in coasts with clear waters and low nutrients.

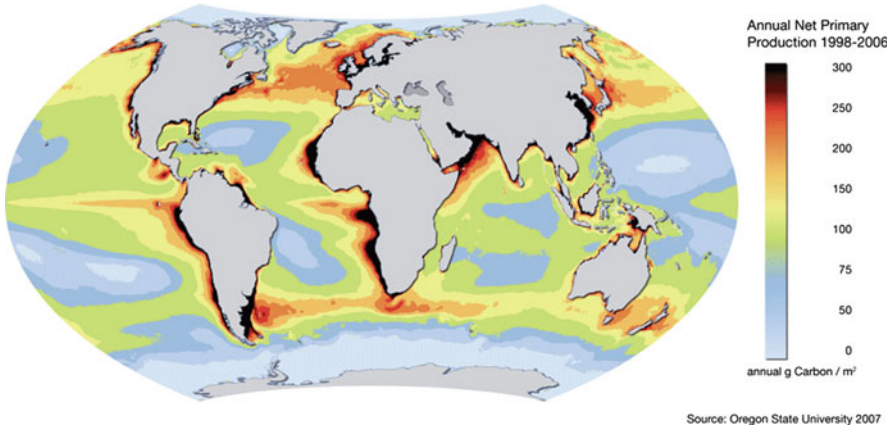


Fig. 2.4 Primary productivity in the global oceans. Note that the productivity is extremely high in certain coasts. Many parts of the world's oceans have extremely low primary productivity (Courtesy: GRID-Arendal. http://www.grida.no/graphicslib/detail/natural-resources-marine-resources_132a)

- **Algal beds**, comprising both micro- and macroalgae are often found in intertidal, rocky beaches (Chap. 8). Dense algal vegetations are often found in the sublittoral zones.
- **Coastal pelagic:** Primary productivity differs in various regions of the oceans, depending on the availability of nutrients and light and the presence of a suitable temperature (Fig. 2.4). Coastal waters are typically richer in nutrients than the oceanic. Therefore, primary production in the euphotic zone of the coastal pelagic is higher than in offshore pelagic. Phytoplankton, dominated by diatoms, drive the coastal pelagic ecosystem. Coastal waters of many continents experience seasonal or perennial upwelling that bring nutrients to the euphotic zone and are sites of intense primary production. Many coasts close to estuaries are enriched by nutrients brought from land by rivers resulting in enhanced productivity (Brink 2004). The coastal marine environment is extremely diverse in terms of its physicochemical characteristics and ecosystems. Primary production varies vastly in the euphotic pelagic of different oceanic regions depending on available light at different latitudes.

2.3.2 Offshore Pelagic, Benthic, and Deep-sea Habitats

Although seawater covers most part of the earth, **the coastal (neritic) pelagic and offshore (oceanic) pelagic are very different from each other in their biological characteristics.** The sheer size of the oceanic waters is responsible for much of the global carbon budget.

- Nearly 81% of ocean's primary production and about 40% of global primary production take place in the offshore pelagic realm (Fig. 2.3).
- About 88% of herbivores depend upon oceanically produced NPP. This amounts to approximately 25.0×10^6 Pg C consumed by herbivores in the entire marine environment.
- Oceanic waters contribute nearly 26.0% of all oceanically produced NPP to the storage pool, most of these being deposited in the deep sea.
- Because of the size, NPP, and associated processes, oceanic waters are extremely important determinants of global climate.

Many parts of the oceanic pelagic waters, such as the North and South Pacific gyres, the North and South Atlantic gyres, and the South Indian gyre are perennially oligotrophic. As a result, primary production is extremely low in these regions. Microorganisms play a unique role in the food web even in such a harsh environment. No primary production can take place below the photic zone. Yet a high diversity of life and biological processes take place in the deep sea. Life in the aphotic deep sea is sustained because of a process termed the "biological pump" that transports dead organic matter from the euphotic zone to the deep sea.

The marine, benthic environment offers the largest surface area on earth for living organisms. Benthic diatoms and other algae form the food for consumers in shallow, well-lit littoral sediments. However, most of the benthic animals as well as microorganisms living in this zone **depend upon the supply of organic material falling from the water column.** The labile components of the deposited organic material are easily degraded or consumed by detritivores. Compounds which are more slowly degraded, or recalcitrant to degradation, such as humic material accumulates in the benthic environment. Microbial enzymatic hydrolysis of high-molecular weight and recalcitrant organic polymers is usually the rate-limiting step in mineralization in natural environments (Sigeo 2005).

Deep-sea sediments and hydrothermal vents harbor unique ecosystems, the latter being supported by chemosynthetic bacteria. Shallow water hydrothermal vents are not uncommon.

The study of marine fungi has to be addressed from the perspective of the diverse coastal and oceanic marine environments and the peculiarities of the trophic web in each of these.

- Physical and chemical properties of the seawater are crucial in determining marine ecological processes.
- The marine environment is divided into neritic or coastal and oceanic or offshore habitats.
- The water column represents the pelagic habitat, while the sea bottom constitutes the benthic zone. The benthic is divided into the intertidal or littoral, the sublittoral, bathyal, abyssal, and hadal zones.

(continued)

- Primary producers, herbivorous consumers, and carnivorous consumers at different levels make up the trophic pyramid. Microorganisms play an important level at each trophic level as decomposers and parasites. Productivity of an ecosystem is considered by taking into account all trophic levels.
- Oceans contribute about 50% of global primary production. Net Primary Production (NPP) by primary producers in the oceans roughly amounts to 53 trillion metric tons of carbon per. Part of the NPP is grazed by herbivores and enters the trophic chain, while the rest undergoes death and enters the microbial decomposition pathway. Recalcitrant organic matter is stored in marine sediments.
- Coastal oceans are biologically much more productive than the open oceans. The estuarine environment, coastal pelagic, mangroves, salt marshes, seagrasses, coral reefs, and algal beds are some of the important habitats of the coastal environment.
- Single-celled phytoplankton are the major primary producers in coastal as well as pelagic ecosystems. Vascular plants and macroalgae are also important primary producers in coastal ecosystems.
- Most of ocean's primary production comes from the vast oceanic pelagic waters.
- Most of the benthic animals as well as microorganisms depend upon the supply of organic material falling from the water column.
- The "biological pump" supplies food to animals in the deep-sea benthic in the form of dead organic particles from the euphotic, pelagic waters.
- Deep-sea sediments and hydrothermal vents harbor unique ecosystems, the latter being supported by chemosynthetic bacteria.

2.4 Fungi in Marine Ecosystem Processes

Fungi are associated with organisms of all trophic levels of the ecosystem in the form of (1) Symbiosis and (2) Saprotrophy (Cooke and Rayner 1984; Dix and Webster 1995; Kendrick 2000).

2.4.1 Symbiosis

Fungi may live as ectobionts on the surfaces of other organisms, or as endobionts, living within them. This association, **symbiosis, may be in the form of a commensal, a mutualist, or a parasite.**

- Commensals are casual residents within or upon other organisms. They neither cause any harm to the host nor do they obtain any particular benefits from them.
- Mutualists are those that confer benefits to their hosts and also derive advantages from them.
- Parasites obtain benefits from their hosts but are not useful to them. Parasites that cause harm to the health of their hosts are pathogens. Microbial parasites and pathogens are associated with organisms of all trophic levels. They play an important role in ecosystem functioning, similar to animal predators (Gachon et al. 2010).
 - Parasites prevent domination by any single species and maintain a balance in diversity and ecosystem functioning. Thus, they may confer resilience to the ecosystem against perturbation.
 - Pathogenic fungi may devastate the population of their hosts under exceptional circumstances and disturb ecosystem functioning or cause economic losses to human society.
 - Biotrophic fungi are obligate parasites. Biotrophs cannot live in the absence of their living host. Therefore, they rarely cause devastations of their host populations by becoming pathogenic. Facultative parasites are those that may live as commensals.
 - Pathogenic fungi may cause an accelerated leaching out of Dissolved Organic Matter (DOM) from the host, which is then available to other microorganisms for their growth. Parasites can cause the death of their hosts. These are then available to saprotrophs even earlier than the natural death of the hosts. Thus, parasites may be responsible for an accelerated recycling of organic matter.

Fungi are extremely common in marine organisms as parasites and pathogens. However, their dynamics in regulating natural populations is not sufficiently understood.

- **Endophytes are fungi that live as endobiontic symbionts within an algal or plant tissue without causing any external symptoms.** Endophytic fungi may be commensalistic, mutualistic, or weakly parasitic.

2.4.2 *Saprotrophy*

Saprotrophic microorganisms utilize dead organic matter for food. All living organisms eventually die and undergo microbial decomposition. **Saprotrophic fungi and bacteria play a key role in the trophic web by organic matter degradation and nutrient recycling.** Dead particulate organic matter (POM) with its associated saprobic microorganisms is termed **detritus**. Dissolved Organic Matter (DOM) generated from biotic and abiotic activities are also substrates for saprotrophic microorganisms. Since carbon is the major element in POM and DOM, these are often discussed in terms of Particulate Organic Carbon (POC) and Dissolved Organic Carbon (DOC). Saprobic fungi play three major roles.

Saprotrophic fungi have a greater advantage compared to bacteria in decomposition of particulate organic matter large enough to support endobiotic growth. Bacteria grow mostly on the surfaces of organic particles. Bacterial degradative activity is mostly confined to the surfaces of plant tissues. Fungi, on the other hand, are capable of penetrating solid substrates. This may be accomplished by hyphae, rhizoids, or ectoplasmic nets (Sect. 1.1). Hence, their degradative ability also prevails in the interior of particles. Many mycetaen fungi are excellent degraders of lignocellulose and therefore are commonly associated with decomposition of vascular plants. They can also efficiently withstand periodic wetting and drying. On the other hand, bacteria are more efficient in utilizing small particles with a large surface area and in using DOM (Torzilli and Andrykovitch 1986; Raghukumar 1990; Newell 1984, 1996a; Newell and Porter 2000).

Degradation of organic matter by saprotrophic marine microorganisms is characterized by a few key features (Fig. 2.5).

- **DOM leached out by dead organisms during initial stages is a major nutrient source for saprotrophs.** Microorganisms rapidly take these up through absorption and convert them into their biomass. Conversion of DOM by bacteria and unicellular fungi into their biomass is an extremely important process, since the biomass can be fed upon by phagotrophic protozoans and microzooplankton. The phagotrophs may serve as food for higher level consumers. Thus, the DOM is linked to the food web through a process termed the microbial loop (Raghukumar 2005). In some cases, DOM may first aggregate to form flakes. These may subsequently be colonized by microorganisms. These detrital flakes are consumed by larger invertebrates.

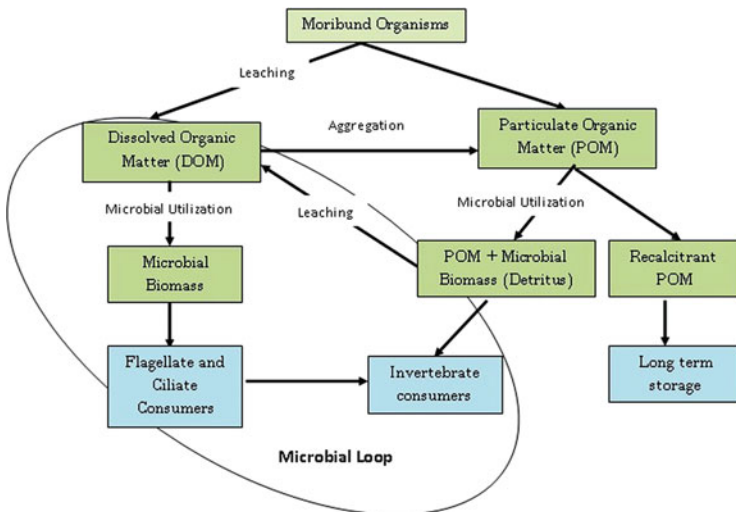


Fig. 2.5 Key features of organic matter degradation and microbial saprotrophy in marine ecosystems

- **Saprotrophic bacteria and fungi breakdown complex organic matter of the POM** by use of degradative enzymes and absorb the labile dissolved nutrients thus formed. As a result, organic matter which was originally formed of large and complex molecules is gradually converted into microbial biomass. Growth and enzymatic activity of fungi and bacteria on detritus transforms it biochemically. Detritus is nutritionally enriched because of the microbial activities and their biomass. Detritus forms the food of many detritus-feeding animals or detritivores.
- **Enzymatic degradation of POM by bacteria and fungi results in the release of DOM, as well as inorganic nutrients.** This DOM may again enter the microbial loop.
- **Organic matter that is highly resistant to microbial decay is stored away in marine sediments.** Decay and long-term storage processes are determined to a large degree by the biochemical nature of dead organic matter (Walker and McComb 1988; Harrison 1990; Duarte and Cebrian 1996; Enriquez et al. 1993; Short et al. 1993). For example, structural polysaccharides of vascular plants are composed of lignocellulose, comprising cellulose, hemicellulose, and lignin. Lignocellulose is extremely resistant to decomposition. Hence, decomposition of vascular plant detritus is complex and lasts over a period of several months. In the marine ecosystem, seagrasses, marsh plants, and mangrove detritus are rich in lignocellulose. In addition, an enormous amount of allochthonous, lignocellulosic material in the form of wood and other terrestrial plant material enters the sea. These too contribute to marine, lignocellulosic detritus. Additionally, the belowground parts of marine macrophytes are nutrient-poor relative to that of photosynthetic tissues and are found in deeper, anaerobic sediments with a low rate of decomposition. Hence, although marine vascular plants contribute only 4% of the total ocean NPP, they contribute to nearly 30% of the stored carbon in marine sediments because of their recalcitrance to microbial decomposition,.

Contrary to vascular plants, tissues of macroalgae are made of polysaccharides which are more easily degraded by bacteria and fungi. Phytoplankton detritus is rich in nutrients and very easily decomposed. Most of this enters the consumer pathway.

Saprotrophic fungi exhibit several ecological strategies.

- **Some fungi possess an r-strategy**, in which they use up readily available labile nutrients and rapidly colonize a substrate. They reproduce fast and prolifically, following which their population declines. **Several others display a k-strategy**, in which the fungi utilize more complex substrates for their nutrition and grow slowly. Many fungi overcome competition with others by means of antagonism, in which compounds inhibitory to competing organisms are produced. Such strategies define the fungi that colonize various substrates in the sea.
- **Fungal colonization on complex substrates is characterized by a succession of species, the mycosere.** The decomposition of large-sized, macroscopic particulate organic matter takes place over a period of time, depending on its

complexity. The decompositional phase of detritus plays an important role in determining the mycosere.

- **Succession of mycetaen fungi in large particulate organic matter is deduced by observing the appearance of sporulating structures, such as ascocarps, basidiocarps, and conidial structures on the surface of the substrate.** A study of these events requires regular observations over a long period of time. Most mycetaen fungi occur in their vegetative, mycelial stage within large particulate matter, such as wood during early stages of colonization and growth. They produce fruiting bodies or sporulating structures on them only during their late stages of colonization and growth. Succession studies based on the appearance of fruiting bodies does not truly represent the process. Culturing method cannot be successfully employed to understand succession because many fungi may not grow in culture. Even if they did, many of them do not sporulate in culture. Therefore, they cannot be identified using microscopic features and can be identified only using molecular methods.

There are three major phases of decomposition of large particulate detritus in marine environments (Valiela et al. 1984).

1. **The initial phase of leaching out of labile and soluble compounds:** Coastal plants and algae may be inhabited by endophytic fungi prior to their senescence and death. Rapid, abiotic leaching of soluble and labile organic matter takes place immediately upon their death. An important consequence of leaching is the removal of inhibitory compounds such as phenolics from decomposing tissues. Some microorganisms colonize detritus during this early decomposition. These too may play a role in breaking down phenolics and enabling further colonization by other microorganisms that would be deterred by high levels of phenolics. Endophytic fungi present earlier in the living tissues often persist for a while after death of the plant or alga. Besides, a few other fungi also colonize the detritus at this stage and initiate decomposition. This leads to further leaching of Dissolved Organic Matter (DOM). Such abiotic and biotically induced leaching causes a rapid loss of weight of detritus. Duration of this phase depends on the host plant and may last a few days to several months. **Fungi with an r-strategy colonize the substrate and rapidly utilize labile, soluble organics during the initial decomposition phase. Diversity during this period is low. A few stress-tolerant species are found during this period.**
2. **The intermediate phase of microbial degradation of refractory components:** A second phase of colonization by fungi takes place after the initial leaching phase and decomposition. Refractory compounds such as lignocelluloses in vascular plants or structural polysaccharides in algae are decomposed by bacteria and fungi. Fungal biomass rapidly builds up during this phase and fungal hyphae pervade the substrate. **Mycosere during this intermediate phase is characterized by colonization from a high diversity of species. These often exhibit a combative strategy and possess antagonistic properties against other fungi, thus preventing them from colonizing.**

3. **The final phase of physical and biological fragmentation of detritus:** The third phase is characterized by declining microbial activities. Biotic activities including microbial degradation, as well as animal activities, combined with abiotic activities such as abrasion result in fragmentation of detritus into fine, particulate detritus. Bacterial biomass is higher on fine particles relative to large POM. Mycosere during this final phase is represented by highly stress-tolerant species with a k-strategy. Diversity during this phase is low. Thus, fungal colonization of substrates takes place by a succession of species with different ecological strategies.

Degradative activities of bacteria and fungi play a key role in the detrital food web (Raghukumar 2005).

- **Microbial degradative activities alter the biochemical properties of detritus.** Fungi and bacteria growing in detritus take up inorganic N and P from the environment and incorporate these into microbial protein. This “immobilization” of the inorganic ions alters the chemistry of detritus by enriching it with nitrogen and phosphorus. This results in the lowering of C/N and C/P ratios. Nitrogen-fixing bacteria on detritus may also contribute to increase in nitrogen.

Easily decomposable organic detritus, such as those from phytoplankton and macroalgae, become highly enriched in total nitrogen owing to buildup of microbial protein.

On the other hand, increase in nitrogen of vascular plant detritus (mangroves, salt marshes and seagrass) takes place through microbial protein, as well as an increase in humic nitrogen (Rice 1982). Microbial degradative activities result in reactive carbohydrates, phenols, small peptides, and amino acids. These react with microbial enzymes and condense to form humifying detritus.

- **Detritus enriched with bacterial and fungal biomass is a major nutrient source to detritivorous animals.** Growth on detritus results in buildup of microbial biomass. The enormous quantity of microbially mediated detritus serves as a major food source to many marine animals, particularly those in coastal environments. These include crabs, gastropods, crustaceans such as prawns, fish, and smaller invertebrates like amphipods and gastropods. Vast amounts of plant and algal detritus from coastal marine vegetations are exported to coastal waters. This process, called “outwelling,” is characteristic of coastal wetlands and was first postulated by E. P. Odum and J. M. Teal in the 1960s (Lee 1995). Hence, the importance of detritus as food is not just locally confined to the environment of the coastal vegetation, but extends farther into the coastal waters.
- **Detritus is a nutritious food** for several reasons.
 - Palatability of detritus by detritivores is improved because recalcitrant compounds such as lignocelluloses are degraded or modified.

- Fungal and bacterial biomass may be substantial in detritus from certain sources, such as salt marsh grass. In such cases, fungi may serve as a large pool of proteins to detritivores.
- Fungal biomass may provide essential nutrients to detritivores (Mann 1988; Raghukumar 2005). Some of these are amino acids lysine and methionine, various vitamins, polyunsaturated fatty acids, and sterols, an important precursor for the manufacture of cholesterol in marine animals (Phillips 1984). These nutrients are vital for the survival of detritivorous animals, which are unable to synthesize such compounds by themselves. For example, Crustacea require the polyunsaturated fatty acid docosahexaenoic acid for growth, which may be provided by straminipilan fungi (Harrison 1990).
- Fungi may provide important cues for detritivores to feed on detritus.

The relationship between a fungus and its host is delicately balanced, based upon the health of the host and environmental conditions. Hence, the gamut of relationships from commensal, mutualist, and saprotroph or parasite is a continuum which can change from one to another.

Various aspects of marine fungal ecology have been discussed in many reviews (Hyde et al. 1998; Raghukumar 2002, 2008; Hyde 2002; Raghukumar and Damare 2011; Jones and Pang 2012; Nakai and Naganuma 2015).

- Fungi are associated with organisms of all trophic levels in the ecosystem in the form of (1) Symbiosis and (2) Saprotrophy.
- Symbiosis may be in the form of a commensal, a mutualist, or a parasite.
- Endophytic fungi live as endobiontic symbionts without causing any external symptoms.
- Saprotrophic fungi and bacteria play a key role in organic matter degradation and nutrient recycling. All organisms in the trophic web undergo microbial decomposition upon death.
- Dead particulate organic matter (POM) with its associated saprobic microorganisms is termed detritus.
- Saprotrophic fungi exhibit r- or k-strategy in colonizing substrates. Growth on detritus results in buildup of fungal biomass.
- Fungal degradative activities alter the biochemical properties of detritus.
- Decomposition of vascular plant detritus in the marine environment consists of (1) the leaching phase, (2) the microbial decomposition phase, and (3) the physical and biological fragmentation phase.
- The enormous quantity of microbially mediated detritus serves as a major food source to many marine animals, particularly those in coastal environments.
- The relationship between a fungus and its host is delicately balanced, based upon the health of the host and environmental conditions. Hence, the gamut of relationships from commensal, mutualist, and saprotroph or parasite is a continuum which can change from one to another.

2.5 Diversity of Marine Fungi

According to popular estimates, about 1,500,000 species of mycetaen fungi inhabit earth. Studies using sequencing of internal transcribed spacer (ITS) markers from soil DNA samples have even suggested a global total of 3.5–5.1 million species of fungi (O’Brien et al. 2005). Only about 80,000 species of fungi have been described so far.

The total number of marine fungi has been estimated at about 10,000 species (Jones et al. 2009, 2015; Jones and Pang 2012).

There are two major ecological categories of marine fungi.

- **“Obligate marine fungi”** grow and reproduce exclusively in the marine environment.
- **“Facultative marine fungi”** are terrestrial species, which actively grow and reproduce in marine environments.
- Fungi which are recovered from marine environments through culturing or metagenomic methods, but whose obligate, or facultative marine nature is not certain are called **“marine-derived fungi.”**

Fungi may be detected in marine substrates by two methods (Fig. 2.6).

1. **Direct detection of obligate and facultative marine fungi:** Marine substrates are examined microscopically to detect sporulating structures of fungi, followed by identification and isolation in culture. This method unequivocally establishes whether the fungus actively grows in a substrate and whether it is an exclusively marine species or a terrestrial species. However, many fungi may be present

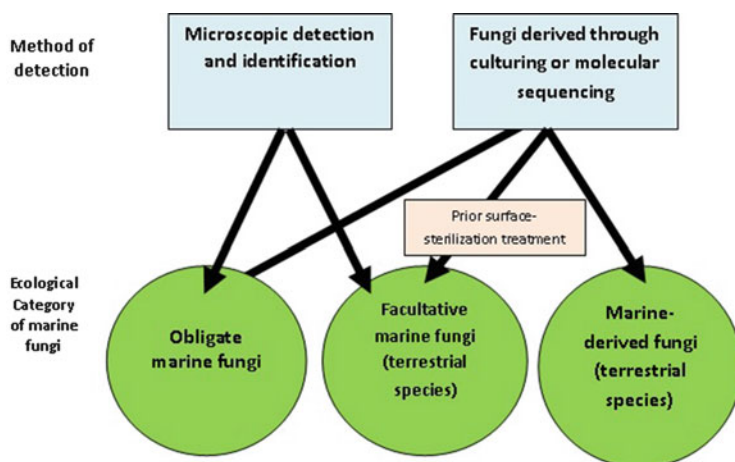


Fig. 2.6 Methods of detecting different groups of marine fungi

Table 2.2 Diversity of various groups of marine fungi (Adapted from data by Jones et al. 2015)

Kingdom	Group	Obligate marine species	Facultative/Marine-derived species
Mycetae	Microsporidia	6	–
	Cryptomycota	12	–
	Chytridiomycota	25	–
	Ascomycota	531	447
	Basidiomycota	12	62
	Asexual fungi of unknown affinities		42
Straminipila	Hyphochytriomycetes	7	–
	Oomycetes	73	–
	Labyrinthulomycetes	50	–
Total		716	551

within a substrate but may not produce sporulating structures. These may not be detected by this method.

2. **Culturing and metagenomics:** Fungi in marine substrates may be detected by culturing them or by retrieving their molecular sequences. These methods help in discovering the following groups of fungi.

- **Cultures or sequences may belong to known, or hitherto undescribed obligate marine fungi.**
- **Facultative marine fungi may be obtained if the substrates are surface sterilized prior to obtaining cultures or sequences.** Terrestrial species of fungi obtained after surface sterilization confirm that they are growing actively in the form of hyphae within the substrate.
- **“Marine-derived fungi”** are those that are detected by culturing or by detection of their sequences and whose obligate or facultative marine nature is not confirmed.

Using the above methods, more than 700 species of obligate marine fungi and nearly 550 species of facultative and marine-derived fungi have been described so far (Jones et al. 2015; Table 2.2). Thus, only a small fraction of nearly 1.5% of fungi from a total of nearly 80,000 species that have been described have been reported till now from marine habitats.

About 130 species of straminipilan fungi, all of which are obligately marine, are known from the marine environment.

2.5.1 Kingdom Mycetae

Members of the Ascomycota are the most frequent among marine mycetaen fungi. Approximately, 550 obligate marine species and 450 species of facultative or

marine-derived ascomycetes have been reported. Nearly 430 of the obligately marine species occur in association with decomposing lignocellulosic materials, such as decaying wood and litter. About a hundred species grow on algae as parasites, saprobes, commensals, and mutualists. Many are associated with animal shells and coral rocks.

Most of the obligate marine mycetaen fungi belong to Class Sordariomycetes and Class Dothideomycetes of the Ascomycota.

- Sordariomycetes are characterized by ascocarps which are perithecia or cleistothecia. Asci are single-walled or unitunicate. Asci are arranged basally or peripherally within the ascocarps. Asexual states or anamorphs are produced by many members.
- Dothideomycetes produce perithecia. Asci are double-walled or bitunicate. The inner wall expands and projects out during spore liberation.

Facultative marine fungi and marine-derived fungi are common in the oceans. Most of these belong to asexual states of Ascomycota. These occur on lignocellulosic materials as animal and algal parasites and also in the deep-sea sediments. Members of Eurotiomycetes, comprising mostly anamorphic species of the terrestrial genera *Aspergillus* and *Penicillium*, are the most widely represented among these in the sea.

Basidiomycota are poorly represented among obligate marine fungi. Thus, only 12 are known to be truly marine. Most of these occur on lignocellulosic materials. Many species of terrestrial Basidiomycota such as mushrooms and bracket fungi have large, macroscopic fruiting bodies or basidiocarps. On the contrary, those of marine species have small basidiocarps, presumably as an adaptation to their aquatic habitat.

Yeasts, which are single-celled, belong to both Ascomycota and Basidiomycota. **More than 200 yeasts have been reported from marine environments** (Fell 2012; Jones et al. 2015). Of these, about 140 are ascomycetes and 70 are basidiomycetes. Most yeasts from marine habitats belong to terrestrial species. Sixteen species of yeasts belonging to Saccharomycetes of the Ascomycota may be truly marine. The ascomycete genus *Metschnikowia* is frequent in oceanic waters and also as parasites of marine animals. Species belonging to *Malassezia* (Exobasidiomycetes, Phylum Ustilaginomycotina of Basidiomycota) are also common in the marine environments, including the deep-sea water column and sediment samples. Marine yeasts may be associated with high nutrient concentrations as occurs in polluted waters, plankton blooms, etc.

Chytridiomycota are poorly represented in the oceans and only about 24 species, most of which are probably obligately marine, have been reported so far (Gleason et al. 2012a). However, analyses of environmental samples using molecular techniques have revealed unknown clades of zoosporic true fungi along with other groups of heterotrophic eukaryotic microorganisms in many diverse marine ecosystems.

Members of Cryptomycota may be important in oceanic systems. Metagenomic studies have identified several novel groups within Cryptomycota from a variety of marine habitats (Richards et al. 2012; Jebraj et al. 2012).

Six species of Microsporidia parasitic in marine animals and one species of aphelids parasitic in a marine diatom have been described so far (Stentiford et al. 2013; Karpov et al. 2014).

Obligate marine species are not yet known from many taxonomic groups of fungi belonging to Kingdom Mycetozoa. Only a few obligately marine mycetozoa fungi have been reported from pelagic and benthic habitats of the sea.

Most of what we know about the diversity of marine mycetozoa fungi is based on either direct observation of sporulating structures of fungi on various substrates or culturing of fungi from different habitats. Metagenomic studies based on environmental clone library sequencing has in recent years provided strong evidence that that members of Ascomycota and Basidiomycota are much more diverse and prevalent in oceanic habitats than believed so far.

2.5.2 Kingdom Straminipila

About 130 species of marine straminipilan fungi have been reported so far. Oomycetes and Labyrinthulomycetes are important straminipilan fungi in the oceans (Beakes et al. 2014; Nakai and Naganuma 2015; Laby Base: http://syst.bio.konan-u.ac.jp/labybase/index_en.html).

- Oomycetes are widespread in terrestrial and freshwater environments as saprobes and plant parasites. Nearly 72 species of marine Oomycetes are known, most of which are animal and algal parasites. Only about 7 species of marine Hyphochytriumycetes are known (Marano et al. 2012). Members of the Labyrinthulomycetes are the most widespread and ubiquitous among straminipilan fungi in oceans. A total of 13 genera are known, with approximately 30 described species. Among the three groups of Labyrinthulomycetes, the thraustochytrids appear to be most diverse, comprising 11 genera and 20 species. Aplanochytrids and labyrinthulids are the other two groups of Labyrinthulomycetes. Members of labyrinthulomycetes occur mostly as saprobes on dead organic matter and a few are animal parasites. They are found almost in every marine habitat and may play a major role in marine ecosystem dynamics (Raghukumar 2002; Bongiorno 2012). **Thraustochytrids, belonging to Labyrinthulomycota, are important sources of omega-3 polyunsaturated fatty acids (ω -3 PUFAs), particularly docosahexaenoic acid (DHA), which are required in the diet of many marine animals.**

Our knowledge of fungal diversity in the marine ecosystem is still very rudimentary. It is expected that many more marine fungi will be discovered in future.

- According to popular estimates, about 1,500,000 species of mycetaen fungi inhabit earth.
- The total number of marine fungi has been estimated at about 10,000 species.
- There are two major ecological categories of marine fungi, the “Obligate marine fungi” and the “Facultative marine fungi.” “Marine-derived fungi” are those whose obligate or facultative nature is not certain.
- Fungi may be detected in marine substrates by direct (microscopic detection) and indirect (culturing and metagenomic) methods.
- Using the above methods, more than 700 species of obligate marine fungi and nearly 550 species of facultative and marine-derived fungi have been described so far.
- About 130 species of stramenipilan fungi, all of which are obligately marine are known from the marine environment.
- Members of the Ascomycota are the most frequent among marine mycetaen fungi. Approximately 550 obligate marine species and 450 species of facultative or marine-derived ascomycetes have been reported. Most of the obligate marine mycetaen fungi belong to Class Sordariomycetes and Class Dothideomycetes of the Ascomycota. Facultative marine fungi and marine-derived fungi are common in the oceans. Basidiomycota are poorly represented among obligate marine fungi. More than 200 yeasts have been reported from marine environments Chytridiomycota are poorly represented in the oceans
- Members of Cryptomycota may be important in oceanic systems.
- Obligate marine species are not yet known from many taxonomic groups of fungi belonging to Kingdom Mycetae. Only a few obligately marine mycetaen fungi have been reported from pelagic and benthic habitats of the sea.
- About 130 species of marine straminipilan fungi have been reported so far. Oomycetes and Labyrinthulomycetes are important straminipilan fungi in the oceans
- Thraustochytrids, belonging to Labyrinthulomycota, are important sources of omega-3 polyunsaturated fatty acids (ω -3 PUFAs), particularly docosahexaenoic acid (DHA), which are required in the diet of many marine animals.
- Our knowledge of fungal diversity in the marine ecosystem is still very rudimentary.

Future Directions

- Existing culture methods may be inadequate to culture many novel fungi. Novel methods need to be developed to isolate marine fungi from various marine habitats and to understand their role in ecosystem processes.

- Presently used methods of taxonomic identification do not reveal “cryptic species” which may resemble known ones, but which may actually be novel. Further developments in molecular phylogeny and taxonomy may reveal many cryptic species of fungi belong to novel taxa of fungi.
- Many geographical areas have not yet been studied for marine fungi. Future studies in such areas will help provide a more complete picture of the diversity and role of marine fungi.
- Many fungi may have specific substrate and host associations. Studies on benthic fungi and those associated with different plants and animals will help to better elucidate the role of marine fungi.
- Metagenomic studies have revealed the presence of many fungi that have not been cultured and whose role has not been understood. Recent analyses of existing unique fungal SSU rDNA sequence data have suggested that filamentous fungi within Ascomycota and Basidiomycota are more diverse in marine habitats than previously believed. Marine environments may host a significant number of highly novel groups closer to Chytridiomycota. This aspect needs further elucidation and clarification.

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