Exploring the Diversity of Marine Microbiome in Response to Changes in the Environment

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Abstract

For any environment, the total microorganisms along with their collective genetic material constitute a "Microbiome." The microorganisms being ubiquitous in nature inhabit the marine environment, i.e., the ocean, the seas, estuaries, bays, and their coasts as free entities or live in association with the marine animals (fish, sponges, corals, sea grass and algae, etc.). In the marine environment, coral reefs represent one of the most diverse ecosystems, having immense biodiversity and thus contributing to the primary productivity in the greater extent. Over last few decades, the researchers have explored much of the marine microbiology using new technologies and tools, but vast majority of the marine microbiome still remained to be uncovered, whose potential would definitely play an important role in future marine science. Up to the recent time, the number of marine microbes has reached to billions microbes per liter of seawater. Owing to their extreme diversity and versatility in terms of their metabolic activities, the marine microbes play an important role for supporting the marine food web. Generally, these microbes derive energy either through photosynthesis or through chemosynthesis. The marine microbiomes are responsible for more than half of the all primary production occurring on Earth. Moreover, these microorganisms contribute significantly to the biogeochemical cycling of the nutrients, oxygen production, and degradation of organic matters. In this chapter, the diversity and ecology of the marine microorganisms (Bacteria, Archaea, and Eukarya) and viruses are discussed along with their response to change in environmental factors like temperature, pressure, nutrient, oxygen and sunlight availability, and alterations in ocean stratification.

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6.1 Introduction

Seas and oceans are the largest biospheres on earth, covering more than 70% of its surface and hosting majority of its biomass (Whitman et al. 1998). Since all life forms originated from microbes in the ocean, these microbes dominate the living biomass after billions of years of evolution. Microorganisms are the most important entities in marine environments, representing about 90% of the biomass, and are responsible for about 98% of primary marine productivity (Alvarez-Yela et al. 2019). Marine microbes play a fundamental role in maintaining structure and function of marine ecosystem, as these microorganisms are the main source of mass and energy for all other life in the ocean and also sustain all life on earth by generating much of the oxygen in the planet. Marine microorganisms have the potential to mitigate the effects of climate change since they are the major processors of the world's greenhouse gases. Marine microbes play a central role in biogeochemical cycling of carbon, nitrogen, and sulfur and are potential source of biotechnologically important compounds (Tinta et al. 2019). Owing to the remarkable diversity and clear importance of the marine microbes, uncovering oceanic microbial taxa remains a fundamental challenge in microbial ecology (Gajigan et al. 2018). Major limitation in studying the diversity of marine microbial communities includes that vast majority (about 90–99%) of the microorganisms cannot be grown under standard laboratory conditions (Delmont et al. 2011). To overcome this limitation, molecular biology and sequencing technologies (metabarcoding and metagenomics) have been developed (Streit and Schmitz 2004; Pavan-Kumar et al. 2015), that are continuously enriching our knowledge about phylogenetic and functional diversity of the marine microbes (Debnath et al. 2007; Dionisi et al. 2012; Glöckner et al. 2012). With the advent of several new tools and technologies (such as deep sea sampling, metagenomics, next generation sequencing, etc.), there is possible opportunities for unlocking the potential of the marine microbiome in future (de la Calle 2017).

A coral reef is an important ecosystem found beneath the surface of the water and characterized by corals which form reefs. Often called sea rainforests, shallow coral reefs form one of the most diverse and productive ecosystems on Earth. Although they occupy less than 0.1% of the world's ocean's surface, coral reefs provide food, shelter, and habitat to about 25% of known marine species (Spalding and Grenfell 1997; Spalding et al. 2001; Mulhall 2009), including crustaceans, echinoderms, fish, molluscs, sponges, tunicates, worms, and other cnidarians (Hoover 2007). They offer various important economic services like coastal protection, fisheries, and tourism (Bourne et al. 2016; Silveira et al. 2017; Torda et al. 2017) (Fig. 6.1a).

Coral reefs are microbially driven ecosystems where microbes play a fundamental role in maintaining holobiont health and resilience of reef ecosystem under environmental perturbation (Vanwonterghem and Webster 2020).

6.2 Marine Microbiome

The "marine microbiome" is the diverse community of all microorganisms found in oceans and other aquatic environments. Marine microbiome controls the health of life on earth (de la Calle 2017). A drop of seawater may contain up to a million microbes with estimated number of 3.5×10^{30} microbes on the oceanic subsurface. In marine environments, microbes either live as free communities in the water column and benthonic substrates or in symbiotic association with other oceanic macroorganisms like macro-algae, corals, and sponges (Glöckner et al. 2012; Grossart et al. 2013). The symbiotic interactions between the oceanic microbes and host organisms could be harmful or beneficial depending on its microbial taxonomic structure and functionality (Konopka 2009; Kellogg et al. 2014). Any environmental factors or host characteristics (such as age, diseases, and physiological state) change the composition of associated microbial communities that ultimately influences the nutrient uptake, light absorption, and pathogen interactions of the hosts (Webster et al. 2008; Lachnit et al. 2011; Wahl et al. 2012; Zhang et al. 2015; Lawler et al. 2016).

Coral reefs consist a complicated network of free living and host associated microbial communities with strong benthic-pelagic coupling (Lesser 2006; Bourne and Webster 2013). In order to flourish in oligotrophic waters, these communities help them in efficient capture, retention, and recycling of nutrients and trace elements (de Goeij et al. 2013; Cardini et al. 2014).

Corals obtain a small portion of their nutrients through heterotrophic feeding (predation of zooplankton), and mainly depend on their microbiome for the proficient acquisition and recycling of nutrients in the sea waters (Bourne et al. 2016). In addition, the coral-associated microbes also provide essential amino acids and co-factors (B vitamins) to the coral host and algal endosymbionts (Robbins et al. 2019; Matthews et al. 2020). Moreover, the native microbiome also protects the coral hosts from pathogens by colonizing the coral surface, by competing for nutrients, space, and the synthesis of antimicrobial compounds (Peixoto et al. 2017).

6.3 Marine Microorganisms (Bacteria, Archaea, and Eukarya) and Viruses

Microorganisms are the most abundant and diverse residents of marine environment. These microbes are the key players in maintaining marine ecosystems health owing to their integral contribution to biogeochemical cycles and other biological processes

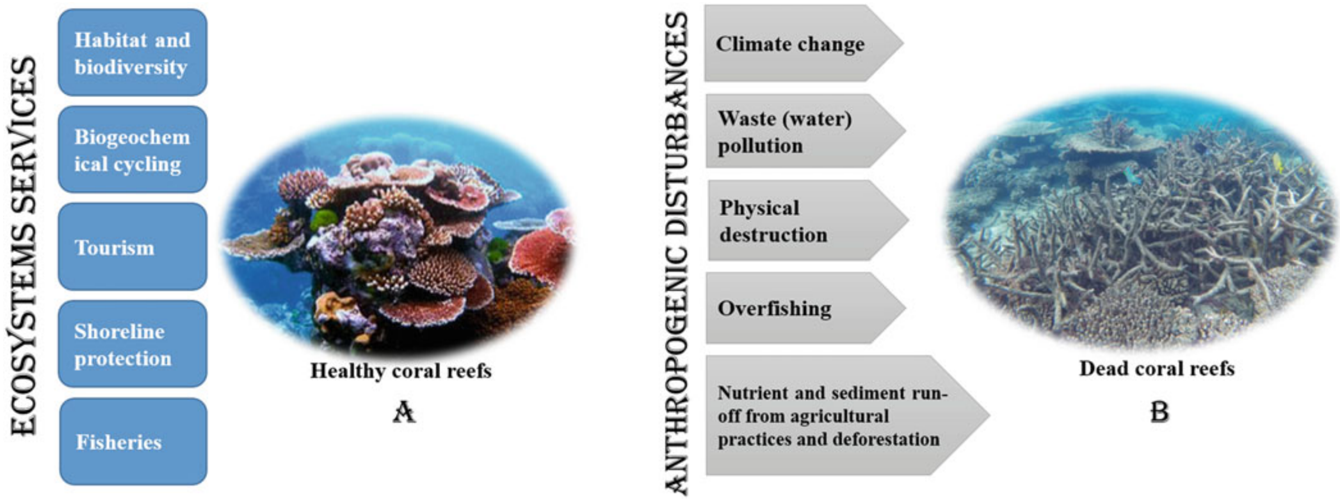

Fig. 6.1 (**a**) Overview of important ecosystem services provided by healthy coral reefs and (**b**) impact of anthropogenic perturbations that lead to decline of coral reefs

(carbon, nitrogen, sulfur cycling, etc.) (Caron 2005; Sogin et al. 2006). Marine microorganisms include archaea, bacteria, fungi, protists, and viruses which collectively comprise millions of cells in each milliliter of the oceanic water (Eakins and Sharman 2010).

Marine microorganisms acquire specific properties owing to extreme marine environmental conditions in which they live such as alkaline or acidic water, high or low temperature, high pressure and limited substrate in the deep sea water (Baharum et al. 2010).

Over 100 species of bacteria can be found in just a single drop of sea water. Their size may vary from the smallest, i.e., one-hundredth of a millimeter to the largest, i.e., three-quarters of a millimeter (found in ocean sediments off the coast of Namibia). Marine bacteria are well adapted to their environmental condition in the ocean. Bacteria living close to the water's surface obtain energy through photosynthesis like cyanobacteria. In contrast, bacteria living at deeper depths where there is no sunlight, acquire unique adaptations to obtain energy through different chemical reactions and this leads to greater bacterial diversity at water depth. Some marine bacteria feed either on other bacteria (like *Bdellovibrio*) or on dying phytoplankton. Among marine bacteria, *Prochlorococcus*, (a cyanobacterium) and *Pelagibacter* are of particular interest. The ocean surface (rich in sunlight) is home to some of the world's biggest photosynthesizers. *Prochlorococcus*, being one of the most abundant photosynthesizer on the planet, is responsible for producing 20% of the O_2 in the atmosphere. *Pelagibacter* accounts for about 25% of all the microbes in the water column. This bacterium plays significant role in cleaning the ocean as it feeds on organic matter, dissolved in the ocean water.

Archaea constitute about 40% of the marine microbes. In addition to living in extremely hot, acidic, or low oxygen environments, archaea are found in both freshwater and saltwater environments.

Viruses are the most abundant entities in the oceanic water, with estimated number of more than 10^{30} viruses in the ocean. Since viruses living in the ocean generally infect specific hosts, the number of viruses fluctuates with change in the host bacterial communities. It is found that in the sunlit portion of the water column, viral infection rates are comparatively higher.

Although protists are one of the least studied microbes in the ocean, they can have significant impacts on ecosystems. Some protists are voracious predators that impose check on the number of bacteria in the ocean. A type of protist, a dinoflagellate, live in symbiotic association with corals.

In the marine environment, although fungi are comparatively hard to find, they play important roles in the marine ecosystem (recycling nutrients). Generally, marine fungi live in association with the decomposition of plant materials or as parasites within marine plants, algae, and animals.

6.4 Importance of Marine Microbes

6.4.1 Biogeochemical Cycling of the Nutrients

Marine microbes are of critical importance for maintaining environmental and human health. They are key players to biogeochemical cycles, fluxes, and processes which occur in marine environment; and thus these microorganisms are very crucial for the functioning of marine ecosystems. Marine phototrophic microbes produce most of the global oxygen that is indispensable for all life on Earth.

6.4.2 Degradation of Organic Matters

Marine microorganisms are responsible for the degradation of organic compounds in the ocean, thus maintain the balance between free and fixed carbon dioxide (CO_2). Due to their extreme abundance and diversity, these microbes produce and release carbon products (CO_2 and CH_4) that regulate the Earth's climate.

6.4.3 Source of Novel Bioactive Compounds

Marine microorganisms are potential source of biotechnologically important enzymes and compounds that are used in industrial and medical sectors. Polymer degrading enzymes and robust enzymes have been isolated from extremophilic marine microbes and are being successfully used in several industries like laundry and food processing industries (Antranikian 2007; Kennedy et al. 2008). Marine bacteria are also a source of biosurfactants and (extracellular) polymeric substances that are used as bio-adhesives, biodegradable plastics, dyes, drag reducing coatings on ship hulls, sunscreens, underwater surface coatings, etc. (Munn 2011). Moreover several bioactive compounds have been isolated from marine microbes and tested for their biomedical potential (anticancer and anti-inflammatory drugs, antibacterial, antifungal and antiviral agents, drug delivery agents, etc.) (Fenical 2006; Newman and Hill 2006; Williams 2009; Choudhary et al. 2017).

6.4.4 Tackling Pollution

Owing to their incredibly diverse genes, marine microorganisms are being studied and explored for their bioremediation activities. It has been found that these microbes have significant potential to break down the environmental pollutants, e.g., oil, Br-containing pesticides and flame retardants. Several marine bacteria have natural tendency to breakdown and remove oil in the ocean. Ocean plastic pollution is another issue of concern. Marine bacteria have been found to grow and feed on plastics (Yoshida et al. 2016). Moreover, marine microbes are being investigated as a source of new sustainable bioplastics (Narancic and O'Connor

2017). Various marine bacteria act as indicators of effluent discharges and find application in heavy metal bioremediation (Ramaiah et al. 2007; Selvin et al. 2009; Dash and Das 2016).

6.4.5 Maintenance of Marine Food Chain and Food Web

Marine microorganisms occupy the critical bottom trophic level in ocean foodwebs through continuously supplying the seafood products. The microscopic remnants of dead organisms and their waste products are fed by marine microbes, which in turn are consumed by tiny creatures called nanoflagellates. Then, the slightly larger creatures called ciliates feed on those nanoflagellates. These ciliates are the food source of copepods (bug-like crustaceans) and other zooplankton, which are further engulfed by small fish.

6.5 Environmental Factors Affecting the Marine Microbiome

Environmental pollution and climate change have significant hazards to the corals, sponges, and other marine organisms, which in turn, may introduce risks to human health and economic growth. Coral reefs are facing unprecedented losses on local and global scales leading to its degradation. Under future climate change conditions, they are expected to be among the most adversely affected ecosystems. Localized reef degradation is caused by declining water quality, disease, overfishing, physical destruction, pollution, and outbreaks of coral predating fish (De'ath et al. 2012; Pawlik et al. 2016; Hoegh-Guldberg et al. 2017) whereas climate change (i.e., elevated temperature, oceanic acidification) is responsible for reef degradation at a global scale (Hoegh-Guldberg et al. 2007).

In 1988, the first mass coral bleaching event was recorded (Cziesielski et al. 2019), and prominent coral reef ecosystems such as the Great Barrier Reef have lost about 50% of shallow-water corals in the past 4 years alone (Hoegh-Guldberg et al. 2019).

Climate change may cause a destabilization of the coral natural microbiome, resulting in a dysbiosis that will in turn cause the emergence of opportunistic and potentially pathogenic microorganisms, resulting in an increased incidence of disease, bleaching and eventually host mortality (Littman et al. 2011; van Oppen and Blackall 2019) (Fig. 6.1b).

6.5.1 Global Climate Change

Due to anthropogenic activities, there is an increase of greenhouse gases in the atmosphere that in turn results in increasing the average global temperature. This increase in global temperature will also cause a rise in oceanic temperature that pose significant effects on the marine microbiome and other oceanic life it supports.

Metabolic activity and growth rate of marine microorganisms are differentially affected by temperature. One of the important consequences of increased water temperature results in the occurrence of harmful "algal bloom," where microorganisms grow rapidly in large quantities, producing toxins and deplete vital nutrients in the water. Thus the algal bloom presents significant hazards to aquatic life, seabirds, and humans.

Due to the increased global temperature, the polar icecaps are melting and massive volumes of freshwater are released in the oceans that results in sea level rise. This sudden release of water will change the salinity of the receiving water bodies, i.e., oceans, seas, etc., which will affect marine microorganisms causing dramatic shifts in the microbial community composition (Gao et al. 2012; Thomas et al. 2012).

Moreover, high temperature of the ocean affects the availability of certain nutrients and lowers the amount of dissolved oxygen in the water. This may affect the growth of some microorganisms particularly, planktons, which are an important food source for other oceanic life (Hutchins and Fu 2017).

Marine environment is also affected by the anthropogenic emissions of CO_2 to the atmosphere that results in ocean acidification. About one-third of the CO_2 emitted into the atmosphere by combustion of fossil fuel enters the ocean surface (Orr et al. 2005). CO_2 dissolution in seawater disturbs the "equilibrium of the seawater carbonate buffer system" thus lowering its pH. However the effects of low pH on the growth and activity of marine microorganisms are not fully understood.

In case of coral reef ecosystems, it has been reported that due to higher ocean temperature and/or acidification, there is a microbial community shift, i.e., from beneficial bacterial taxa (Endozoicomonas) to opportunistic and pathogenic groups (Alteromonadaceae and Vibrionaceae) that will result in elevated incidence of disease (Bourne et al. 2016; O'Brien et al. 2016; McDevitt-Irwin et al. 2017).

Another impact of high CO_2 is alteration of ocean stratification (i.e., a physical barrier/density driven structure in a water column in which colder and/or more saline water underlies warmer and/or less saline water). The intensified "stratification" process leads to lowering of vertical fluxes of critical deep-water nutrients, thus affecting the growth of plankton in the surface ocean (Hutchins and Fu 2017).

6.5.2 Environmental Pollution

Inadequately planned and poorly managed agriculture and aquaculture practices are generating nutrient-abundant wastes being dumped into aquatic environments. It may cause eutrophication, algal bloom events, and oxygen-depleted "dead zones."

The effect of oil pollution on marine microbial community is not fully understood. Some marine bacteria have natural tendency to breakdown the oil in the ocean. Discharge of large amount of oil in the ocean results in growth of their numbers, which in turn, may cause reduction in overall marine microbial biodiversity (Yang et al. 2016).

6.6 Conclusion

Marine microbiome represents the totality of all microbes and viruses in the ocean/seas and in any related environment (the seafloor and marine animals/plants). The diversity of microbial life remains largely unidentified, and may represent a secret treasure for human society. Moreover, in today's ocean, the abundance, distribution, diversity, interactions, and functions of marine microorganisms are either directly or indirectly affected by the climate change and anthropogenic disturbances, resulting in altered nutrient cycling, loss of microbial diversity and biomass, local extinction, and community shifts. Although coral reefs support enormous biodiversity and provide critical ecosystem services, they suffer rapid degradation on a local and global scale. Therefore, a detailed understanding of the mechanisms involved in coral bleaching and resilience is required, coupled with concerted global action to reduce carbon emissions to prevent further decline in coral reefs.

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