



Review

Metagenomic studies of the Red Sea

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ABSTRACT

Metagenomics has significantly advanced the field of marine microbial ecology, revealing the vast diversity of previously unknown microbial life forms in different marine niches. The tremendous amount of data generated has enabled identification of a large number of microbial genes (metagenomes), their community interactions, adaptation mechanisms, and their potential applications in pharmaceutical and biotechnology-based industries. Comparative metagenomics reveals that microbial diversity is a function of the local environment, meaning that unique or unusual environments typically harbor novel microbial species with unique genes and metabolic pathways. The Red Sea has an abundance of unique characteristics; however, its microbiota is one of the least studied among marine environments. The Red Sea harbors approximately 25 hot anoxic brine pools, plus a vibrant coral reef ecosystem. Physicochemical studies describe the Red Sea as an oligotrophic environment that contains one of the warmest and saltiest waters in the world with year-round high UV radiations. These characteristics are believed to have shaped the evolution of microbial communities in the Red Sea. Over-representation of genes involved in DNA repair, high-intensity light responses, and osmoregulation were found in the Red Sea metagenomic databases suggesting acquisition of specific environmental adaptation by the Red Sea microbiota. The Red Sea brine pools harbor a diverse range of halophilic and thermophilic bacterial and archaeal communities, which are potential sources of enzymes for pharmaceutical and biotechnology-based application. Understanding the mechanisms of these adaptations and their function within the larger ecosystem could also prove useful in light of predicted global warming scenarios where global ocean temperatures are expected to rise by 1–3 °C in the next few decades. In this review, we provide an overview of the published metagenomic studies that were conducted in the Red Sea, and the bio-prospecting potential of the Red Sea microbiota. Furthermore, we discuss the limitations of the previous studies and the need for generating a large and representative metagenomic database of the Red Sea to help establish a dynamic model of the Red Sea microbiota.

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Contents

1. Introduction	717
1.1. The Red Sea.	718
1.2. The Red Sea metagenomics	718
1.3. Exploration of the Red Sea microbiota for biotechnology-based applications	721
1.4. Discussion: future perspectives on Red Sea microbiota research.	721
References	722

1. Introduction

In recent years, significant advances were made in the field of environmental microbiology due to the advent of next-generation sequencing technology (NGS), which facilitated the establishment of metagenomics. Combined with NGS, metagenomics provides a powerful platform to examine and compare microbial fingerprints of different environments, their adaptation mechanisms, host microbe interactions,

Abbreviations: UV, ultraviolet; NGS, next-generation sequencing; psu, practical salinity units; DO, dissolved oxygen; BSI, brine–seawater interface; OUT, operational taxonomic unit; AOA, ammonia oxidizing Archaea; KAUST, King Abdullah University of Science and Technology.

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and microbial evolution. Metagenomic studies of water and soil provided significant insights into previously unknown terrestrial and marine microorganisms (Daniel, 2005; Simon and Daniel, 2011). Novel microbes, their genomes, and adaptation mechanisms were identified in extreme and inhospitable environments such as acid mine drainage sites (Tyson et al., 2004), deep-sea hyper-saline brine pools (Wang et al., 2013), Arctic soil (Lipson et al., 2013), and glaciers (Simon et al., 2009), providing evidence for extreme genomic plasticity and adaptation mechanisms of these microorganisms.

A substantial number of metagenomic-based studies have been conducted on marine environments, for several reasons. Water covers approximately three quarters of our planet, and is home to a vast range of microbial life forms that play essential roles in global ecosystems. The majority of marine niches are still unexplored, but those that were examined revealed a diversity of novel microbes with unique functions. Previous studies also strongly suggest that microbial diversity and functions are directly linked with their local environments, justifying examination of new and unusual niches for novel genes and species. In addition, marine microbes appear to have great prospect in biotechnology applications and many studies are underway to tap into these natural resources. Finally, monitoring changes in marine microbial diversity would provide an accurate index of environmental health and ecosystem sustainability.

Despite its unique physical and chemical attributes, the Red Sea is one of the least explored oligotrophic (low nutrients) marine environments. The Red Sea is characterized by its high year round temperature, high UV radiation, high salinity, low nutrients, extreme niches such as hot brine pools, and a vibrant coral reef ecosystem. The few metagenomic studies that were conducted on the Red Sea revealed that its microbiota is distinct from those found in other marine environments (Thompson et al., 2013). For example, the Red Sea hot brine pools harbor a diversity of halophiles, thriving in conditions thought to be inhospitable to organic life (Bougouffa et al., 2013). It is expected that such extremophiles have developed metabolic pathways and enzymes with potential biotechnology-based applications (Mohamed et al., 2013; Sayed et al., 2014). These pools, like many other unique niches in the Red Sea, remain understudied.

In this review, we summarize the published metagenomic works conducted in the Red Sea, their significant findings, and the bio-prospecting potential of the Red Sea microbiota. We discuss the limitations of previous studies, and the need for spatio-temporal models of the Red Sea microbiota to gain insight into their community stability and dynamics. We also preview the scope of the Red Sea metagenomic explorations that are being conducted by the authors of this paper and colleagues at King Abdullah University of Science and Technology (KAUST).

1.1. The Red Sea.

In geological terms, the Red Sea rift began to develop approximately 30 million years ago (Dixon, 1990) through divergent movement and splitting apart of the African and Arabian lithosphere plates; this was followed by thinning out of the continental plates accompanied by a large number of volcanic activities, development of an active rift, and formation of typical oceanic crust in its axial zone (Gurvich, 2006). The maximum depth of the rift is approximately 2900 m in the South and 1500 m in North. The boundary between the thin continental plates and the oceanic crust extends along the central axis of the Red Sea basin, the area containing a large number of hot brine pools.

The Red Sea is the world's northernmost tropical sea located between arid and semi-arid deserts. It has a surface area of roughly 4.6×10^5 km², volume of 2.5×10^5 km³, length of ~2000 km, maximum width of 355 km, and a maximum depth of 3039 m (Rasul et al., 2015). Three distinct depth zones can be found within the Red Sea: 1) Shallow zone along its shoreline, with depth of less than 100 m covering approximately 40% of the sea; 2) Deep zone ranging

from 500 m to 1000 m; and 3) Deeper zone along its central axis with depth ranging from 1000 m to ~2900 m where the majority of brine pools are located (Rasul et al., 2015). The Red Sea is relatively isolated from the rest of the world's oceans (Thompson, 2014), connected to them only by a shallow strait (Bab-el-Mandeb, 310 m deep) in the south and an even shallower canal (Suez Canal, 25 m deep) in the north. The Strait of Bab-el-Mandeb connects the Red Sea to the Gulf of Aden in the south and the Suez Canal connects it to the Mediterranean Sea in the north (Fig. 1). The Red Sea is characterized as an oligotrophic environment with year-round UV irradiation and high surface temperature that can reach up to 34 °C during summer with only minor variations during winter. It contains one of the world's saltiest waters with the surface salinity ranging from 36 psu (south) to 41 psu (north), with an average salinity of 40 psu (Ngugi et al., 2012). The high salinity is attributed to the high rate of evaporation, the low annual precipitation, lack of river inflow, and relative isolation from the world body of oceans.

The Red Sea contains approximately 25 deep-sea brine pools, which contain mineralized hot brine with metalliferous deposits generated from dissolution of Miocene evaporites and hydrothermal activities deep in the sea floor. These brine pools are considered extreme environments with up to seven times higher salinity than the surrounding deep sea water, high temperatures (up to 60 °C and more), low pH, high concentrations of dissolved metals such as Fe, Mn, Zn, Cu, Pb, Co, Ba, Si, Li, and low concentration or complete absence of dissolved oxygen (Gurvich, 2006). The composition of sediments, percent salinity, pH, and temperature varies between different brine pools; even within the same pool, vertical stratification could occur resulting in distinctive layers of similar temperatures and salinity, beginning at the sea water-brine interface (Antunes et al., 2011). Due to their extreme nature, the Red Sea brine pools and their sediments can provide a perfect niche to examine extremophiles for their adaptation mechanisms and bio-prospecting potential.

Another unique feature of the Red Sea is its coral reef ecosystem. The Red Sea fringing coral reef complex extend some 2000 km along the shoreline, and provide the main source of food and shelter for a large number of species of fish and invertebrates. The Red Sea also contains numerous offshore reefs with a wide range of reef morphology that includes barrier reefs, atoll reefs, patch reefs, and platform reefs. These offshore reef formations are very unusual and do not follow the general reef classification schemes. The coastal and offshore reefs contain some of the most diverse corals with an unusual ability to survive in one of the world's saltiest and hottest waters. Increased overpopulation and industrialization along coastal regions, and the resulting anthropogenic activities have posed a significant threat to the Red Sea coral reef habitats specially those growing in the coastal regions.

1.2. The Red Sea metagenomics

Metagenomics is a powerful molecular and bioinformatics-based approach that enables characterization of the entire microbiome of a given environment by sequencing microbial DNA recovered directly from the environment without prior cultivation. Metagenomics can help establish microbial fingerprints of various environments and identify the microbial genes that carryout specific functions within the community metagenome. In addition, since microbial diversity is a function of the local environment, metagenomics-based approaches can identify the environmental factors responsible for shaping different microbial community structures. Accordingly, phenotypic changes in response to drastic environmental changes can be identified. Finally, metagenomics-based approaches can help identify novel microbial genes for biotechnology-based applications.

Surprisingly, few metagenomic explorations have been conducted in the Red Sea despite its unique characteristics: an oligotrophic environment containing one of the world's saltiest and hottest waters potentially harboring microbes with unique adaptation mechanisms.

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