



Salinity and macrophyte drive the biogeography of the sedimentary bacterial communities in a brackish water tropical coastal lagoon



Pratiksha Behera^a, Sofia Mahapatra^a, Madhusmita Mohapatra^a, Ji Yoon Kim^b, Tapan K. Adhya^c, Vishakha Raina^c, Mrutyunjay Suar^c, Ajit K. Pattnaik^{a,1}, Gurdeep Rastogi^{a,*}

^a Wetland Research and Training Centre, Chilika Development Authority, Barkul, Balugaon, 752030, Odisha, India

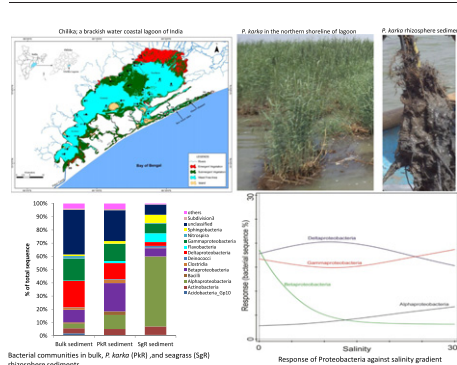
^b Department of Integrated Biological Science, Pusan National University, Geumjeong-gu, 46241 Busan, South Korea

^c School of Biotechnology, KIIT University, Patia, Bhubaneswar, 751024, Odisha, India

HIGHLIGHTS

- Bulk and rhizosphere sediment communities were investigated in a brackish water coastal lagoon.
- Spatiotemporal patterns in bacterial communities were linked to salinity and 'the rhizosphere effect'.
- Proteobacterial lineages revealed differential response against the salinity gradient.
- Metabolic mapping provided detailed insights on the biogeochemical potential of bulk and rhizosphere communities.

GRAPHICAL ABSTRACT



ARTICLE INFO

Article history:

Received 3 February 2017

Received in revised form 28 March 2017

Accepted 29 March 2017

Editor: D. Barcelo

Keywords:

Coastal lagoon

Illumina sequencing

Bulk sediment

Phragmites karka

Halodule uninervis

ABSTRACT

Brackish water coastal lagoons are least understood with respect to the seasonal and temporal variability in their sedimentary bacterial communities. These coastal lagoons are characterized by the steep environmental gradient and provide an excellent model system to decipher the biotic and abiotic factors that determine the bacterial community structure over time and space. Using Illumina sequencing of the 16S rRNA genes from a total of 100 bulk surface sediments, we investigated the sedimentary bacterial communities, their spatiotemporal distribution, and compared them with the rhizosphere sediment communities of a common reed; *Phragmites karka* and a native seagrass species; *Halodule uninervis* in Chilika Lagoon. Spatiotemporal patterns in bacterial communities were linked to specific biotic factors (e.g., presence and type of macrophyte) and abiotic factors (e.g., salinity) that drove the community composition. Comparative assessment of communities highlighted bacterial lineages that were responsible for segregating the sediment communities over distinct salinity regimes, seasons, locations, and presence and type of macrophytes. Several bacterial taxa were specific to one of these ecological factors suggesting that species-sorting processes drive specific biogeographical patterns in the bacterial populations. Modeling of proteobacterial lineages against salinity gradient revealed that α - and γ -Proteobacteria increased with salinity, whereas β -Proteobacteria displayed the opposite trend. The wide variety of biogeochemical functions performed by the rhizosphere microbiota of *P. karka* must be taken into consideration while formulating the management and conservation plan for this reed. Overall, this study provides a comprehensive understanding of the spatiotemporal dynamics and functionality of sedimentary bacterial communities and

* Corresponding author.

E-mail address: rastogigurdeep@gmail.com (G. Rastogi).

¹ State Project Management Unit, Integrated Coastal Zone Management Project, Bhubaneswar, Odisha 752003, India.

highlighted the role of biotic and abiotic factors in generating the biogeographical patterns in the bacterial communities of a tropical brackish water coastal lagoon.

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1. Introduction

Coastal wetlands such as those exemplified by the lagoons are located at the interface of freshwater and marine ecosystems (Tagliapietra et al., 2009). Due to their intermediate position between the rivers and sea, coastal lagoons are highly productive, support habitat for a wide diversity of flora and fauna, and provide numerous ecosystem services. At the same time, these lagoons are also at the high risk of eutrophication as riverine discharge and terrestrial run-off from the catchment area drains a significant amount of nutrients and organic inputs into them (Viaroli et al., 2008; Obi et al., 2016). The sedimentary microbial communities not only prevent the occurrence of eutrophication in these lagoonal ecosystems, but also reduce or prevent the transport of nutrients and contaminants into ocean by sequestering or transformation of carbon and nitrogen (Hunter et al., 2006; Oni et al., 2015; Obi et al., 2016). The sediments of the coastal lagoons acts as a terminal repository for a wide range of organic and inorganic compounds including heavy metals and pesticides before they enter into the ocean. The water column, however, is more susceptible to the regular changes in physicochemical variables than the sediments. Thus, sediment provides a much stable environment where active microbial biogeochemical processes occur (Hunter et al., 2006; Oni et al., 2015). Sediment particle provides a very complex and heterogeneous niche with respect to nutrients and oxygen availability, thus supporting a diverse assemblage of aerobic and anaerobic microbial communities (Oni et al., 2015). The co-existence of different microbial communities in the sedimentary micro-habitat carry out efficient cycling of carbon, nitrogen, and sulfur, and detoxification of xenobiotics such as polychlorinated biphenyls and polycyclic aromatic hydrocarbons (Hunter et al., 2006; Oni et al., 2015).

Considering the importance of sedimentary bacterial communities in the biogeochemical processes, numerous studies have investigated their ecological roles and biogeographical patterns in a variety of aquatic ecosystems. Bacterial community structure, function, and their environmental drivers have been examined in a variety of marine [bay (Urakawa et al., 1999; Zheng et al., 2014), coastal lagoon (Mohit et al., 2015), brackish lakes (Zhang et al., 2016)], and freshwater ecosystems [lakes (Song et al., 2012; Sheng et al., 2016), rivers (Febria et al., 2012; Liu et al., 2015; Thoetkiattikul et al., 2017)]. Compared to the marine and freshwater ecosystems, estuarine coastal lagoons are highly dynamic due to a sharp physicochemical gradient in parameters such as salinity, nutrients, and dissolved oxygen which is generated mostly due to the mixing of freshwater with seawater (Srichandan et al., 2015a).

Estuarine coastal lagoons offer a unique model system to investigate the biogeographical patterns of the sedimentary bacterial communities and their environmental drivers. However, literature search reveals that compared to the marine and freshwater ecosystems, estuarine lagoons are poorly understood with respect to the biogeography of their sedimentary communities (Thompson et al., 2011; Ghai et al., 2012). This was mostly due to the use of low-resolution molecular techniques (e.g., clone-library sequencing, denaturing gradient gel electrophoresis, and terminal restriction fragment length polymorphism) in earlier studies which are technically not suited to address questions related to spatial and temporal variation in communities at large geographical distances (Freitag et al., 2006; Mosier and Francis, 2008; Ikenaga et al., 2010; Song et al., 2012; Tsuboi et al., 2013). Additionally, most of these studies were temporally limited in the sense that sediment communities were examined only in a single season which would not

provide any clue regarding their seasonal variability (Mosier and Francis, 2008; Ikenaga et al., 2010).

The advent of high-throughput sequencing of community DNA (i.e. metagenomics) and 16S rRNA genes has provided a detailed comprehensive insight on the sedimentary microbial communities (Bowen et al., 2011; Wang et al., 2012; Xiong et al., 2014; Zheng et al., 2014; Kou et al., 2016). However, comprehensive biogeographical investigations especially on the estuarine brackish sediment communities using high-throughput sequencing data are still limited. We conceived this study to improve the understanding of sedimentary bacterial communities in a brackish water estuarine lagoon, Chilika (India). A previous study on sedimentary bacterial communities has applied pyrosequencing analysis of 16S rRNA genes to a limited number of samples ($n = 3$) collected from Chilika Lagoon which did not provide any information on the spatiotemporal variability in bacterial communities (Pramanik et al., 2015). In this background, we applied Illumina sequencing of 16S rRNA genes to elucidate the spatiotemporal variation in the bacterial communities of the bulk sediments ($n = 100$) collected across 30 stations in 3 different seasons from the Chilika Lagoon.

The outer channel area of the Chilika Lagoon supports luxurious growth of seagrasses. In contrast, the northern shoreline of the lagoon is heavily infested with dense stands of a common reed, *Phragmites karka* (Fig. 1). The ground survey of reed covered area suggested that around 50 km² area in the northern shoreline is occupied with *P. karka* (personal communication, Chilika Development Authority). In addition, small and sporadic dense patches of this reed are also present in the central and southern shoreline of the lagoon. In an earlier study, we characterized the spatiotemporal variability in the rhizosphere sediment communities ($n = 60$) of *P. karka* from Chilika Lagoon. The Illumina 16S rRNA sequence data corresponding to the rhizosphere sediments of *P. karka* was available from the GenBank Sequence Read Archive accession number SUB2357802 under the BioProject accession number PRJNA369297. In the present study, as large number of bulk sediment communities were sequenced, we expanded our investigation to conduct a more detailed comparative assessment of bulk and *P. karka* rhizosphere communities to examine how sedimentary bacterial communities are structured by the presence of an emergent macrophyte such as *P. karka*.

Our hypothesis was that bacterial communities would exhibit biogeographical patterns which would be strongly associated with the biotic (e.g., the rhizosphere effect) and abiotic (e.g., salinity) factors. The aims of this study were (i) to characterize the spatial and temporal dynamics of sedimentary bacterial communities along estuarine salinity gradient, and (ii) to compare the bacterial communities of the bulk sediments with the rhizosphere communities of a common reed (*P. karka*) and a native seagrass (*Halodule uninervis*) species. The functional mapping of the bacterial 16S rRNA gene taxonomic data using METAGENassist program, allowed us to predict the 'metabolic' and 'energy source' relevant functions of the sedimentary bacterial communities in the context of 'the rhizosphere effect', biogeochemical cycles, and the detoxification of contaminants in a brackish water coastal lagoon.

2. Materials and methods

2.1. Study area and site characterisation

Chilika Lagoon (Ramsar site No. 229), is a tropical brackish water coastal estuarine lagoon (19° 28'–19° 54' N and 85° 06'–85° 35' E),

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