



Picophytoplankton variability: Influence of winter convective mixing and advection in the northeastern Arabian Sea

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ABSTRACT

The deepening of mixed layer and ensuing changes in optical and physicochemical properties of euphotic zone can influence phytoplankton community dynamics in the northeastern Arabian Sea during winter monsoon. The response of picophytoplankton community to such changes during winter convective mixing is not well understood. Herein, we have compared variations in the picophytoplankton community structure during early (November–December 2012), peak (end-January 2014) and late (mid-February 2015) winter monsoon from three separate cruises in the southern northeastern Arabian Sea. The higher *Synechococcus* abundance owing to entrainment of nutrients in mixed layer was observed during peak winter monsoon, while the concomitant changes in nitrate concentration, light and oxygen environment restricted *Prochlorococcus* growth resulting in lower abundance during the same period. This highlights the diverse responses of picophytoplankton groups to physicochemical changes of water column during winter convective mixing. The divinyl chlorophyll *b/a* ratio (marker for *Prochlorococcus* ecotypes) indicated prevalence of one low-light adapted ecotype (sensitive to light shock) in sub-surface water, one high-light adapted ecotype in surface water during early winter monsoon and both disappeared during intense mixing period in peak winter monsoon. Subsequently, a distinct low-light adapted ecotype, capable to tolerate light shock, was noticed during late winter monsoon and we argue that this ecotype is introduced to southern northeastern Arabian Sea through advection from north by sub-surface circulation. The total picophytoplankton biomass available to microbial loop is restored during late winter monsoon, when stratification begins, with a higher abundance of *Synechococcus* and the re-occurrence of *Prochlorococcus* population in the region. These inferences indicate that variability in picophytoplankton community structure and their contribution to the microbial loop are driven by convective mixing and advection, which in turn influence ecosystem functioning and trophodynamics of the southern northeastern Arabian Sea.

1. Introduction

Seasonal reversal of wind pattern in the northeastern Arabian Sea (NEAS) is associated with the semi-annual monsoon systems, southwest and northeast, resulting in two distinct periods of elevated primary production (Banse, 1987). The high concentration of phytoplankton during southwest summer monsoon (June–September) has been attributed to strong upwelling while phytoplankton bloom during northeast winter monsoon (November–February) is linked to the convective mixing (Banse, 1987; Lévy et al., 2007; Koné et al., 2009).

The strong north-easterly dry wind causes evaporation to be higher than precipitation during the winter monsoon. As a consequence, the Arabian Sea High Salinity Water mass (> 36.5 psu) is formed in surface layers of NEAS in early November. This denser water mass sinks and

spreads southward with the progression of winter monsoon resulting in mixing of the water column in NEAS (Rochford, 1964; Kumar and Prasad, 1999). Shankar et al. (2016) show that the formation of deep mixed layer and spreading of Arabian Sea High Salinity Water mass in the southern NEAS is restricted by poleward advection of low saline water of West India Coastal Current thereby influencing the water column properties in month of February. The phytoplankton bloom which begins in November covarying with the deep mixed layer, ends by March as a shallow mixed layer inhibits nutrient supply from the sub-surface water (Madhupratap et al., 1996; Lévy et al., 2007). The convective mixing and subsequent mixed layer deepening together lead to change in optical and physicochemical properties of water column (Smayda, 1980; Lindell and Post, 1995) triggering community transition from microphytoplankton to picophytoplankton in the NEAS (Roy and Anil, 2015; Vijith et al., 2016).

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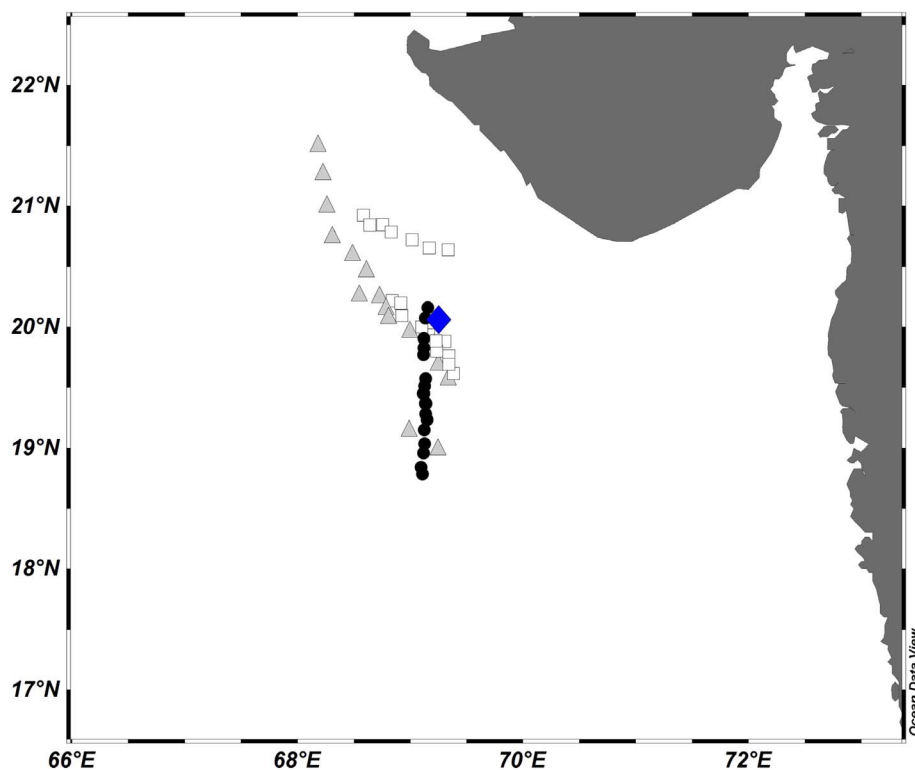


Fig. 1. Location map in the northeastern Arabian Sea. Station symbols: black circles, cruise SSK-41 (20 stations); empty rectangle, SSK-60 (17 stations); grey triangles SSK-77 (15 stations). Blue diamond is the ADCP location. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Although the importance of picoplankton (defined here as plankton $< 2.0 \mu\text{m}$ in size) has been recently acknowledged, our understanding of this community still remains primitive for the Indian waters, especially in the Arabian Sea (Campbell and Carpenter, 1986; Campbell et al., 1998; Barber, 2007; Richardson and Jackson, 2007). Picoplankton includes both chemotrophic and heterotrophic bacteria, small phagotrophic eukaryotes (animals) and photosynthetic forms (picophytoplankton) such as picoeukaryotes and picokaryotes (*Synechococcus* and *Prochlorococcus*) (Olson et al., 1990; Veldhuis et al., 1993). The recent advances in cell physiology and molecular biology of *Synechococcus* and *Prochlorococcus* have indicated considerable genetic and physiological diversity among these populations. These two genera are phylogenetically clustered into several subpopulations characterised with diverse physiological adaptations reflecting variety of niches occupied in the oceans. The existence of two *Synechococcus* types, namely, the ‘dim’ and ‘bright’ have been reported during US JGOFS (Joint Global Ocean Flux Studies) cruises in the western and the central Arabian Sea. *Synechococcus* strains of both types contain two chromophores: phycoerythrobilin (PEB) and phycourobilin (PUB) in different ratios. The high-PUB (bright type) group is prevalent in oligotrophic waters, whereas the low-PUB (dim type) group is usually found in onshore eutrophic waters (Campbell et al., 1998; Liu et al., 1998; Wood et al., 1999; Bernal and Anil, 2016a). On the other hand, two physiologically distinct *Prochlorococcus* groups, referred to high light (HL) – and low light (LL) – adapted ecotypes have been found in surface stratified waters and deep below the oxygen minimum zone in the Arabian Sea (Goericke et al., 2000). Information about physiological adaptation and biogeography of different *Synechococcus* and *Prochlorococcus* lineages provides insight into underlying processes that control the picophytoplankton niche partitioning and community structure in diverse aquatic environments. The habitat reconstruction and phylogenetic analysis of picophytoplankton in the Indian Ocean indicate that the large *Synechococcus*-like ancestors expanded their ecological niche from coastal waters to open ocean oligotrophic waters and subsequently evolved to *Prochlorococcus* through lineages diversification and associated streamlining of genomes (Díez et al., 2016). Though *Prochlorococcus* abundance is thought to be restricted to oligotrophic waters, several recent

observations indicate its prevalence in nutrient rich mixed water column of the various water bodies and in particular, the Mediterranean Sea (Vaulot et al., 1990; Vaulot and Partensky, 1992; Li et al., 1993), Sargasso Sea (Goericke and Welschmeyer, 1993), Suruga Bay (Shimada et al., 1995) and Gulf of Aqaba (Lindell and Post, 1995). The physicochemical changes in water column due to vertical mixing significantly influence the relative abundance of *Prochlorococcus* in surface water of the Atlantic, Pacific and Indian Ocean (Bouman et al., 2006). Recent studies suggested HL – and LL – adapted *Prochlorococcus* ecotypes constitute a notable fraction of picophytoplankton community structure in surface and sub-surface water during early winter monsoon (November–December) in the NEAS (Roy et al., 2015). However, complete disappearance of both these ecotypes from the water column with the onset of deep convective mixing has recently been reported in this region (Roy and Anil, 2015). The mixing intensity and water column depth may regulate picophytoplankton community composition, vertical distribution and seasonal succession (Lindell and Post, 1995). Whether the *Prochlorococcus* population grows or is advected to the southern NEAS in the subsequent season remains an unresolved question. Detailed observations on community dynamics of picophytoplankton in NEAS will elucidate the complex nature of inter-relationship between physical and biological processes involved in convective mixing. In this context, we have conducted measurements on cell abundance and pigment concentration of picophytoplankton during different phases of convective mixing to answer the following questions: 1) How do the physicochemical changes in water column influence the picophytoplankton community structure? 2) How does *Prochlorococcus* population surge in NEAS after its apparent disappearance during intense mixing period?

2. Material and methods

2.1. Study area and water sampling

A total of 52 water column profiles were sampled in the southern NEAS during three consecutive winter seasons: fall 2012, early winter 2014 and mid-winter 2015 (Fig. 1). Observations were made onboard

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