



Nutrients as a Driving Factor in Genetic Diversity and Genome Plasticity of Marine Cyanobacteria

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Annual marine primary production contributes roughly 50% of the annual global productivity. This primary production takes largely place in the vast, nutrient-deplete or oligotrophic waters of (sub)tropical ocean provinces including the Red Sea. Picophytoplankton ($<2\ \mu\text{m}$) are the main primary producers in such waters with the globally abundant cyanobacteria *Prochlorococcus* and *Synechococcus* as the most abundant genera. These cyanobacteria dominate the phytoplankton biomass in the surface waters of the Gulf of Aqaba, northern Red Sea, year-round. The nutritional status of the waters in the Gulf varies between nutrient-deplete, oligotrophic conditions in summer to nutrient-replete, mesotrophic conditions in winter. Conceptually, nutrition may form a persistent stress factor which is met by the expression of an adaptive potential in the, marine *Synechococcus* and *Prochlorococcus*. The adaptive response may then be dependent on the expression of nutrient stress responses by genotypically homogeneous populations. Alternatively, that nutrient stress may be a transient phenomenon which exerts selective pressure on the cyanobacterial populations thereby yielding a competitive advantage to those genotypes carrying a gene pool best fit to meet current nutritional conditions. While nitrogen (N) and phosphorus are considered as potentially productivity limiting nutrients, iron availability is considered to be sufficient due to the high dust input into the Gulf. Whether N is the rate-limiting factor for primary production in these waters (as well as in the open ocean) is still an open question. Ambient nutrient concentrations and primary production measurements suggest N limitation to occur in the surface layers during summer. Moreover, populations of nitrogen-fixers, including occasional blooms of *Trichodesmium* spp., appear during the summer stratification. N stress responses in marine cyanobacteria are conveyed by the N-specific transcriptional regulator NtcA. We determine the genetic make-up

of natural communities (based on *ntcA* sequence information), the occurrence of N-stress (based on *ntcA* expression) and the genotype-specific gene pool for N-utilization (NtcA regulon) in an environmental genomics approach. Recent studies indicate that genotypic diversity of *Synechococcus* in the Gulf of Aqaba, using *ntcA* as a marker gene, is extensive. The genotypic make-up of the cyanobacterial community varies in a seasonal fashion. Clades of "eutrophic genotypes" are abundantly represented in winter and "oligotrophic genotypes" are found in summer. Molecular probing indicates that *Synechococcus* (and possibly the smaller *Prochlorococcus* as well) are not limited by N-availability in any season. Intermediate levels of *ntcA* expression indicate that *Synechococcus* may utilize nitrate during the spring bloom, but otherwise this cyanobacterium is ammonium sufficient. Other lines of research suggest that these populations may actually be P limited. Lastly, whole genome analyses show that closely related marine cyanobacteria have widely different gene complements for N-acquisition and may thus occupy different ecological niches. Moreover, available genome sequences indicate that these cyanobacteria may utilize N compounds which at present have not been recognized as N sources common to the marine environment.