Boom and bust dynamics of diatoms across marked seasonal transitions in the Gulf of Aqaba

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Introduction: Marine phytoplankton are a consortium of photosynthetic prokaryotes and unicellular eukaryotic algae, which drive nearly one half of the global primary production[1]. Among eukaryotes, diatoms (Fig. 1) are one of most prolific phytoplankton, generating around 40% of the marine primary productivity[2]. They also play a key role in the silica cycle, due to the biosynthesis of their silicified cell wall. Diatoms are a cosmopolitan group represented in many types of ecosystems across the ocean[3]. Principally, they prevail in well-mixed coastal and upwelling ecosystems where they rapidly form blooms which support the most important fisheries worldwide[4]. By contrast, the current understanding of diatom ecology in oligotrophic ecosystems is much less understood, although they can contribute around 30% to primary production in such areas[5]. The Gulf of Aqaba/ Eilat (GoA) is a model oligotrophic study-site. During the spring/summer seasons the water column is markedly stratified and oligotrophic, similar to oceanic gyres where nitrate and phosphate are considered to be both co-limiting, and phytoplankton biomass is low[6,7]. However, during winter progressive surface cooling drives a deep convective mixing over hundreds of meters that brings ample nutrients to the photic layer. When mixing stops due to warming around March a prominent bloom is formed[8]. This bloom reaches unique densities for subtropical ecosystems and appear to be dominated by diatoms[9]. However, the diversity and contribution to primary production of diatom communities in the GoA are poorly defined, limiting our understanding of a key player in such ecosystem.

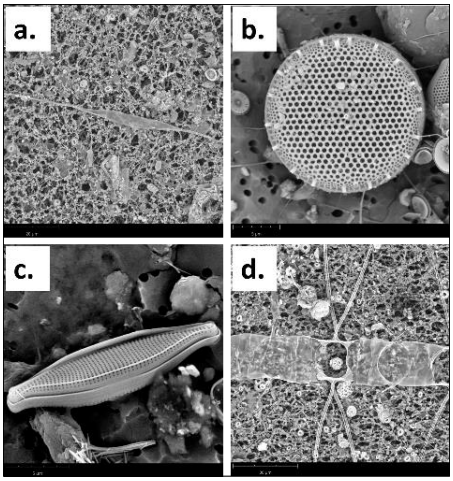

Figure 1. Main diatom species in the GoA: *C. closterium* (a), Thalassiosira (b), pennate (c), *C. hyalochaete* (d).

Aims: The overarching aim of my study was to define the importance of diatoms to primary production communities in the GoA. For that, I examined with high taxonomic and temporal detail the local diatom succession patterns over nearly 2 years. Specifically, I aimed to understand: i) how diverse are diatoms in the GoA as compared to other oceanic ecosystem; ii) Which ecological mechanisms underlie diatom ecological across seasons; iii) how diatom respond to winter-mixing conditions and under what pattern they bloom; iv) how important are they as primary producers during the bloom as compared to other phytoplankton groups; v) how they adapt and endure oligotrophic conditions.

Approach: A routine bi-weekly sampling for phytoplankton and environmental parameters was undertaken in the offshore Station A in the Gulf during nearly 2 years. Seawater samples were analyzed for macronutrients and other routine physical and chemical oceanographic parameters. Diatoms were analyzed by scanning electron microscopy and HPLC.

Results: The environmental framework of this study captured two cold winter seasons developing from approximately November to April, and one warm summer season from April to October (Fig. 2a). In 2022, mixing depth reached almost the bottom of the GoA to about 720m in March. During summer, the water was stratified. Broadly, concentrations of major macronutrients nitrogen (N), phosphate (P), and silicate (Si) varied in direct response to the mixing-stratified seasonal cycle (Fig. 2b). Diatom concentration remained low through the summer and early mixing season. A numerical rise was only detected in February. Then, during the bloom period along the mixing-stratification transition, diatom density reached maximal levels (Fig. 2c). The highest diatom densities were detected during the bloom of 2022, as this peak declined rapidly by May. Pigment analysis by HPLC unveiled that diatoms largely dominate photosynthetic biomass during the bloom, contributing >95% to total photosynthetic biomass (Fig. 2d). Electron microscopy enabled a high taxonomic resolution (Figs. 1, 3a). *Cylindrotheca closterium* was detected in all samples and numerically dominated during the stratified period. Small Thalassiosiraceae dominated during the winter mixing period, including the bloom. Much larger chain diatoms, particularly members of *Chaetoceros hyalochaete* species-complex specifically rose up in density during the large bloom in 2022, although it appeared at much lower densities throughout the year. Overall, diatom richness and diversity were markedly higher during the mixing and bloom periods with up to 20 morphospecies, which contrasts with other phytoplankton groups. Bray-Curtis similarity analysis was used to define the main diatom communities inhabiting the GoA, which were then associated with major seasonal events (Fig. 3b). Summer-Autumn communities were associated with high temperatures and low nutrients. A dynamic succession during winter was linked to high nutrient availability. Bloom communities were associated with high N : P ratios, and the bloom demise showed marked association with high Si : N ratio.

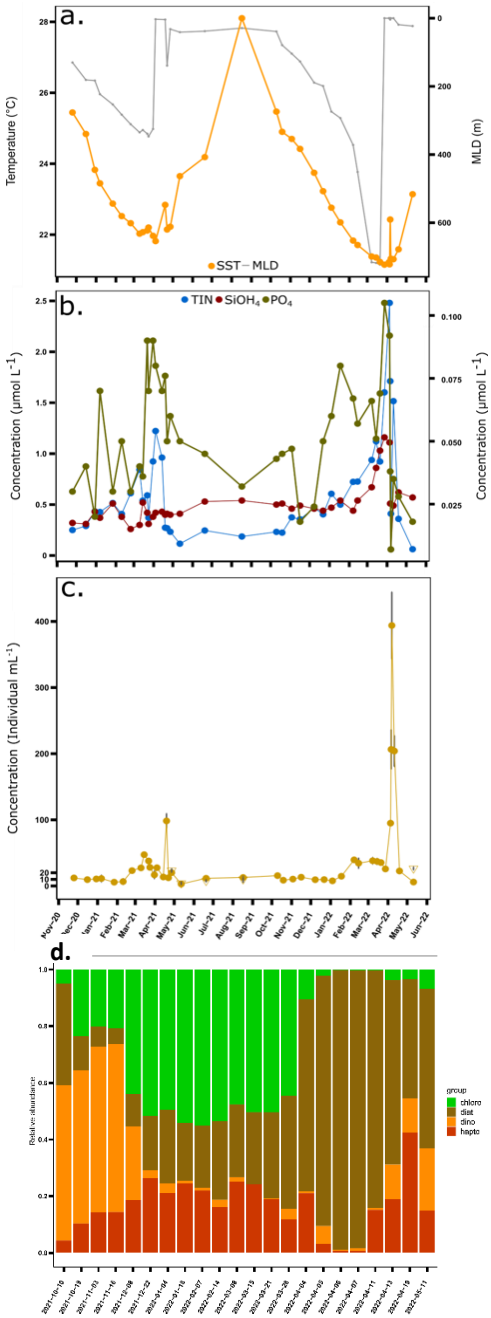

Figure 2. Seasonal variations in the GoA. Environmental settings of temperature and mixing depth (a), and macronutrients (b). Diatom abundance (c) and the relative contribution of diatoms (brown) to total chlorophyll a (d).

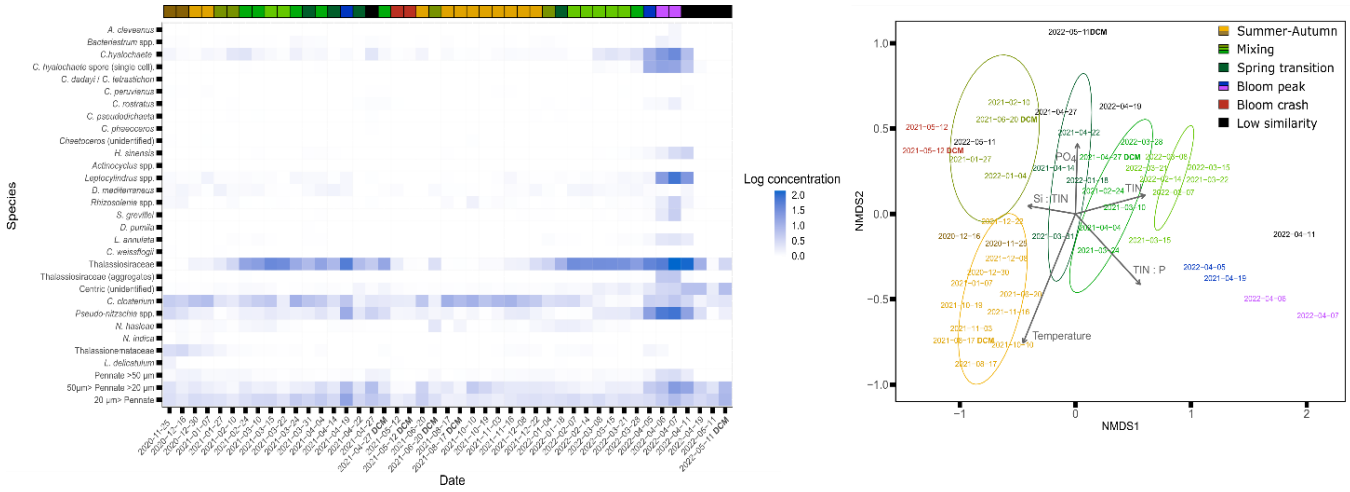

Figure 3. Community analysis of diatoms in the GoA. Heatmap of log-concentration of diatom species over 2 seasons (a). NMDS of main diatom communities based on Bray-Curtis dissimilarity, color coded by the state of the water-column. Arrows represent main environmental drivers that correlate with the different communities (b).

Significance: The GoA is often considered as an ecologically low-productive ecosystem principally dominated by cyanobacteria. The role of eukaryotes has been traditionally exempted due to low background concentration throughout most of the year. However, this work presents an opposite view, in which the local diatom assemblage is highly diverse and at times can account for over 95% of the Gulf's phytoplankton biomass. Moreover, they show a highly dynamic pattern of succession and bloom formation much more akin to boom-bust descriptions involving rapid growth and decay detected in mesotrophic ecosystem in the oceans. This emphasizes the contrasting oceanographic regimes mediated through seasonal and inherent geophysical properties of the northern Red Sea. Moreover, our study provide novel insights on the ecology of diatom in subtropical ecosystems that are less studied than high latitude and costal regimes. Further investigations will reveal the main abiotic and biotic governing diatom sucession in the GoA, the connectivity of the diatom community in the GoA to the main Red-Sea, and will determine the contribution of horizontal transport in the maintenance of the local GoA's communities.

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