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Does size matter? Pico-phytoplankton cell size affects biomass distribution and nutrient limitation in the oligotrophic Eastern Mediterranean Sea

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Abstract. The Eastern Mediterranean Sea (EMS) is one of the most oligotrophic marine environments in the world, characterized by extreme nutrient scarcity and strong water-column stratification. In such systems, pico-phytoplankton typically dominate primary production, yet how cell size structures biomass distribution and nutrient limitation remains poorly constrained. Here, we examined the spatial and vertical variability of pico-phytoplankton cell size, abundance, and nutrient status in the easternmost Mediterranean Sea during oligotrophic summer stratification. Using flow cytometry and microscopy, we quantified the cell volumes of *Prochlorococcus*, *Synechococcus*, and pico-eukaryotes and combined these with ambient nutrient concentrations to estimate cellular nutrient quotas and Resource Supply Indices (RSI). All three groups exhibited increasing cell size with depth and from offshore to coastal waters, coinciding with higher nutrient availability and chlorophyll concentrations. *Synechococcus* and pico-eukaryotes were consistently larger in coastal and deeper waters, whereas *Prochlorococcus* maintained small and relatively constant cell size across environments. RSI analysis revealed widespread nitrogen limitation for *Synechococcus* and pico-eukaryotes (RSI_n<1), while phosphorus was generally sufficient (RSI_p>1). In contrast, *Prochlorococcus* remained largely unconstrained by either nitrogen or phosphorus, reflecting its low cellular nutrient demand and streamlined physiology. These results demonstrate that cell size is a powerful integrator of environmental forcing and ecological strategy in oligotrophic seas. The dominance of small *Prochlorococcus* cells under extreme nutrient scarcity imply how stable ocean stratification and nutrient decline may reshape microbial communities and biogeochemical cycling in the future oligotrophic oceans.

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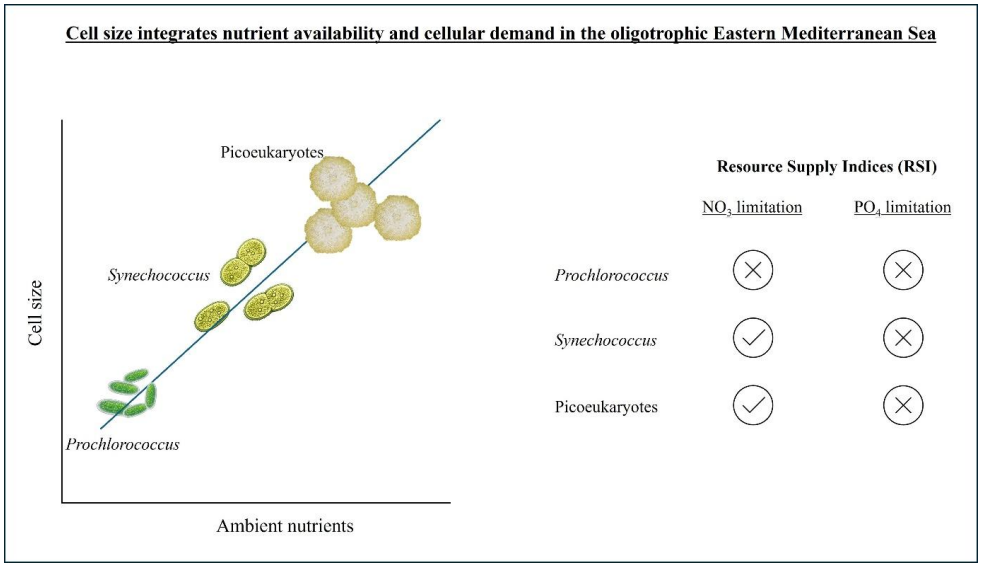
Graphical abstract



Keywords: Pico-phytoplankton; Eastern Mediterranean Sea, Resource Supply Indices, Oligotrophy; Cell-size

1 Introduction

Cell size is a foundational functional trait that shapes phytoplankton physiology, population dynamics, and community structure (Chisholm, 1992; Finkel et al., 2010; Litchman and Klausmeier, 2008). Across taxa, phytoplankton cell volume spans several orders of magnitude. Generally, in low-productivity oligotrophic water, pico-phytoplankton cells (<2-3 µm in diameter) dominate the autotrophic community (Reich et al., 2022; Yacobi et al., 1995). Pico-phytoplankton are small-sized phytoplankton that are composed of both prokaryotes and eukaryotes. They hold a pivotal role in the global primary production (some estimates suggest they contribute ~50% of the global rates, e.g., Field et al., 1998; Huang et al., 2021), making them a highly ecological-important group that affect the 'biological pump' and carbon sequestration in the deep oceans (Falkowski, 1997), and thus play an important role in regulating the global carbon cycle (Beardall et al., 2017; Chisholm, 2000).

Pico-eukaryotes are a taxonomically diverse group and include several algal phyla (Vaulot et al., 2008), while the prokaryotes belong to the phylum cyanobacteria are subdivided into the genera *Prochlorococcus* and *Synechococcus*, with each group having many ecotypes that

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dominate in different ocean regions (e.g., high-light vs. low-light adapted, Flombaum et al., 2013). Pico-phytoplankton often dominate the phytoplankton biomass under oligotrophic conditions such as in the subtropical gyres (Alvain et al., 2005), the northern Red Sea (Lindell and Post, 1995; Reich et al., 2024), and the Eastern Mediterranean Sea (Rahav and Berman-Frank, 2023). In contrast, productive waters are typically dominated by larger micro-phytoplankton such as diatoms and dinoflagellates (>20 μm) and exhibit simpler trophic pathways and higher particle sinking rates (Chkili et al., 2023). Under these conditions, the efficiency of the "biological pump" is greater than in oligotrophic systems, either directly via the sinking of ungrazed large cells or indirectly through aggregated particles and zooplankton fecal pellets (also referred to as "marine snow") (Boyd and Trull, 2007; Guidi et al., 2009).

Phytoplankton cellular composition, metabolic activity, nutrient uptake kinetics, and growth rate often exhibit pronounced cell-size dependence (Chisholm, 1992; Kiørboe, 1993; Marañón, 2015). Generally, as cells become larger, nutrient supply per unit volume theoretically declines (Kiørboe, 1993; Raven, 1998), raising the nutrient concentration threshold required to sustain a given growth rate (Chisholm, 1992). These biophysical constraints confer a clear advantage to small pico-phytoplankton cells due to their high-surface-to-volume ratio, which potentially makes them excellent competitors for nutrient acquisition from their surrounding in oligotrophic environments (Raven, 1998). Experimental studies consistently support an allometric pattern in which cell size is inversely related to growth rate and biomass-specific metabolic rate (Banse, 1982; Geider et al., 1986; Sommer, 1989). A key limitation of much of this literature, however, is taxonomic and size bias: most analyses have focused on large-size species, thereby excluding pico-phytoplankton (Marañón, 2015).

The variability of nutrients, pico-phytoplankton abundance/biomass, and primary production in the EMS have been investigated previously (e.g., Belkin et al., 2022; Raveh et al., 2015; Yacobi et al., 1995). These studies (and others) generally showed that pico-phytoplankton cells predominate phytoplankton biomass in the EMS (Rahav and Berman-Frank, 2023; Yacobi et al., 1995), and that the variability in pico-phytoplankton standing stocks and primary production are often related to depth within the photic water column (Yogev et al., 2011), circulation patterns (e.g., cyclonic/anti-cyclonic eddies, Belkin et al., 2022; Rahav et al., 2013), and to a lesser extent seasonality (Reich et al., 2022). Although the EMS is considered as one of the most oligotrophic seas in the world (Krom et al., 2013), and a natural laboratory to investigate ocean warming and climate changes (Ben-Ezra et al., 2021), it has received little attention compared to other oligotrophic regimes, particularly in terms of phytoplankton cell sizes and how it affects community metabolism. Thus, investigating pico-phytoplankton size

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distribution and biomass in respect to key environmental factors (e.g., nutrients) is critical to understand their contributions to carbon cycles and sequestration in the oligotrophic oceans. Here, we investigated the spatial and vertical distribution of pico-phytoplankton and their size across the photic layer of Israel's Exclusive Economic Zone (EEZ), in the EMS. We show that pico-phytoplankton biomass and size generally increase with depth, and from the coast to the offshore water, coinciding inorganic nutrients availability. Additional calculations based on ambient nutrient concentrations and cell size of different pico-phytoplankton groups reveal that *Synechococcus* and pico-eukaryotes are primely N limited, while *Prochlorococcus* are not N nor P limited based on this matrix, suggesting other controls of this cyanobacterial genus in the EMS.

2 Material and methods

2.1 Seawater collection

Seawater samples were collected on-board the *R/V Bat-Galim* in 15 locations across the Israeli EEZ during August 2024 (Figure 1). Stations included coastal (close to shore, partly affected by perturbations and human activity, e.g., Rahav and Bar-Zeev, 2017; Raveh et al., 2019; Sisma-Ventura et al., 2022) and remote offshore (more pristine) locations. In each station, seawater was sampled at discrete depths between the surface (~0.5 m) and the bottom of the photic layer (~180 m) using Niskin bottles mounted on a rosette sampling system equipped with a Conductivity Temperature Depth (CTD) logger (Seabird 19 Plus), a fluorometer (Turner designs, Cyclops-7) and an oxygen optode (Seabird SBE 63). Water column samples were analyzed for dissolved inorganic nutrients (*i.e.,* NO_2+NO_3, PO_4), pico-phytoplankton abundance, size, biomass and primary production.

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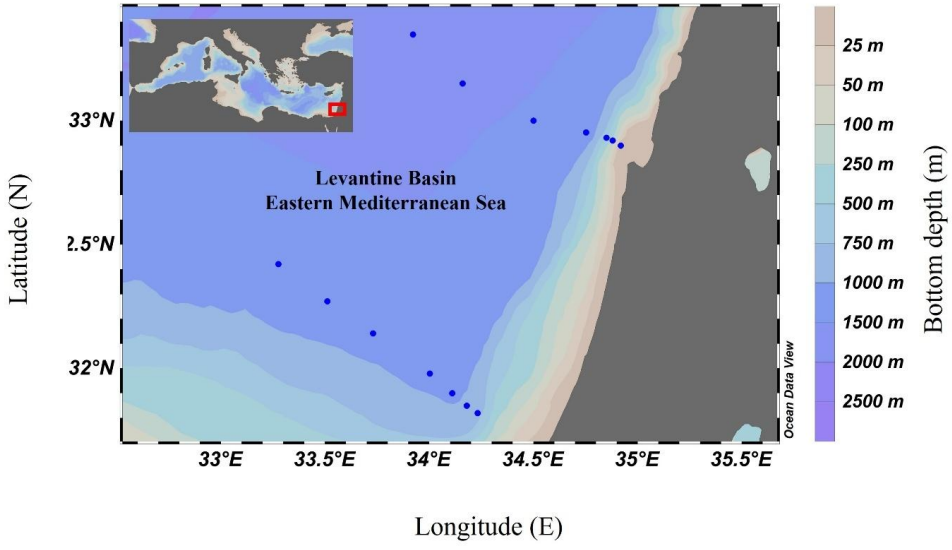

Figure 1: Map of the 15 sampling stations in the Levantine Basin, Eastern Mediterranean Sea. Stations extended along a coastal-to-offshore transect and were sampled in August 2024 aboard the R/V *Bat Galim*.

2.2 Inorganic nutrients

Pre-filtered (0.45 µm) samples were collected in acid-washed plastic tubes and were kept frozen at -20 °C until analysis within a few months. Nutrients were measured with a Seal Analytical AA-3 system (Kress et al., 2014). Nitrate+nitrite (NO_2+NO_3) was measured calorimetrically by Cd reduction and diazo dye (Kress et al., 2019). Orthophosphate (PO_4) was determined using the molybdate blue method (Murphy and Riley, 1962). The precision for NO_2+NO_3 and PO_4 was ±20 nM and 3 nM, respectively. The limits of detection (two times the standard deviation of the blank) for NO_2+NO_3 and PO_4 were 80 nM and 8 nM respectively. The quality of the nutrient measurements was confirmed by the results of the inter-comparison exercises (JAPAN, QUASIMEME).

2.3 Chlorophyll.a (chl-*a*)

Seawater samples (300 ml) were concentrated using a Whatman Glass Fiber Filter, GF/F (~0.7 µm pore size) at low pressure (<150 mbar) for chlorophyll-*a* (chl-*a*) analysis. The filters were placed in glass vials and frozen in the dark at -20 °C until analysis. Chl-*a* pigment was extracted overnight in cold acetone (90%) in the dark and determined by the non-acidification method (Welschmeyer, 1994) using a Turner Designs (Trilogy) fluorometer.

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2.4 Pico-phytoplankton abundance and size

Bacterial abundance samples (1.8 ml) were fixed immediately after sampling with 6 µl of microscopy-grade 50% glutaraldehyde after 10 min in the dark (0.2% final concentration, Sigma G-7651), frozen in liquid nitrogen and put at -80°C until analysis. Analysis was performed using an Attune NxT Acoustic Focusing Flow Cytometer (Applied Biosystems), equipped with a syringe-based fluidic system and 488 and 405-nm lasers. Taxonomic discrimination was based on the orange fluorescence of phycoerythrin (585 nm) and the red fluorescence of Chl-a (630 nm), on side-scatter (SSC, a proxy of cell volume), and on forward-scatter (FSC, a proxy of cell size) (Marie et al., 1997). Prior to the analysis, fixed samples were fast thawed at 37 °C water bath (Symphony) and the abundance of pico-phytoplankton (i.e. *Synechococcus*, *Prochlorococcus* and small eukaryotes) was determined.

The cell size distribution of the pico-phytoplankton communities was determined using flow cytometry based on FSC and side scatter SSC signals. The instrument was calibrated prior to each run using a mixture of fluorescent polystyrene microspheres of known diameters (0.2, 0.5, 1.0, 3.0, and 10.0 µm; Applied Biosystems). These size-standard beads were run under the same flow cytometer settings as the samples, and their FSC and SSC signals were used to construct a calibration curve relating light scatter to particle size (Figure S1A). Additionally, 21 random samples of ~300 ml were concentrated onto polycarbonate GTTP filters (Millipore, 0.2 µm pore size) using support nitrocellulose filters below (Millipore, 0.47 µm pore size) at low vacuum pressure (<150 mmHg) to minimize cell deformation or rupture, fixed as above in a petri plate (0.2% glutaraldehyde final concentration) and analysed with a Nikon Eclipse 80i microscope equipped under x400 magnification within a few days. A minimum of 20 random fields of view per filter were examined, ensuring coverage of >100 cells per sample. Size estimates were measured using ImageJ and were compared to the flow cytometry reads, which gave a good fit and a ~1:1 slope (r^2=0.92, n=21, Figure S1B).

2.5 Cellular nutrient quotas (Q_{min} and Q_{max}) and resource supply index (RSI)

The theoretical cellular demand for nitrogen (N) and phosphorus (P) for the different pico-phytoplankton groups (i.e., *Synechococcus*, *Prochlorococcus* and pico-eukaryotes) was calculated based on the cells' diameter. These matrixes quantify the amount of a given nutrient required by a single cell to sustain metabolic processes and growth. Where, Q_{min} represents the minimum cellular content of a nutrient that is necessary to maintain basic cellular functions and support balanced growth under ambient nutrient conditions (e.g., a "baseline" stoichiometric requirement that cannot be reduced without impairing growth). The Q_{max} matrix

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reflects the upper limit of nutrient storage capacity within a cell under replete (nutrient-rich) conditions. It represents the total nutrient content a cell can accumulate, including surplus stored beyond immediate metabolic needs (e.g., a 'luxury update').

Cell diameters (d, µm) were measured using the FSC signal in the flow cytometric analyses. Assuming spherical cell morphology, cell volume (V, µm³) was calculated as shown in Eq. 1:

$$(1)\ V = \frac{\pi}{6} x\ d^3$$

We then converted the cell's volume to cellular carbon content (fg C cell^{-1}) using the empirical allometric relationship derived by Menden-Deuer and Lessard, (2000) and shown in Eq. 2:

$$(2)\ \text{C content} = 0.216\ x\ V^{0.939}$$

The cellular N and P content were estimated from the cellular C content by using the canonical Redfield molar ratios (C:N = ~6.6:1 and C:P = ~106:1, Redfield, 1934).

The calculated per-cell quotas were the Q_{min} (i.e., Q_{min},N = N content and Q_{min},P = P content). Q_{max} was defined as twice Q_{min} (Marañón et al., 2013).

The Resource Supply Index (RSI) integrates cellular nutrient demand with ambient nutrient availability to provide a dimensionless measure of nutrient sufficiency at the population level. RSI was calculated as shown in Eq. 3, defined as the ratio between the total nutrient concentration in the surrounding environment and the total cellular demand for that nutrient if all cells reached Q_{max}.

$$(3)\ \text{RSI} = \frac{[\text{Ambient nutrient}]}{Q_{max}\ x\ \text{cell abundance}}$$

Where, RSI>1 indicate that ambient nutrient concentrations are theoretically sufficient to satisfy cellular nutrient requirements for the observed population size, whereas RSI<1 suggests that environmental supply is inadequate to meet cellular demand.

2.6 Statistical analyses

Principal Coordinates Analysis (PCoA) were generated based on Euclidean distance matrices to visualize patterns of multivariate environmental variation and to identify the principal gradients structuring the sampled water column. The analysis was performed on the standardized environmental matrix. Environmental variables were subsequently fitted as vectors (envfit approach) onto the ordination space, with vector direction indicating the gradient of increasing values and vector length representing the strength of correlation

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(Pearson's *r*) between each variable and the ordination axes. To examine how cell size variability is related to these environmental gradients, we projected the average cell diameter of *Synechococcus*, *Prochlorococcus*, and pico-eukaryotes onto the PCoA as passive vectors. This approach allowed us to assess the strength and direction of the correlation between cell size and the major environmental gradients without influencing the underlying ordination structure. Additionally, we quantified the proportion of size variability explained by the combined environmental matrix using multiple linear regression for each group, reporting the coefficient of determination (R^2) as a measure of explanatory power. All multivariate analyses were conducted in Python (v3.10) using the numpy, pandas, and scikit-learn libraries, with visualization performed in matplotlib.

3 Results

3.1 Biogeochemical characteristics of the Low-Nutrient Low-Chlorophyll (LNLC) EMS

The water column was stratified with well defined water masses within the photic layer (Figure 2A). The upper mixed layer depth (MLD) ranged from ~25-30 m, with Sigma-theta (density) of ~25-26 kg m^{-3} and surface temperatures of ~28-30 °C. The water density increased with depth, reaching 28-29 kg m^{-3} at the bottom of the photic layer (~180 m). Such a stable stratification minimizes nutrients replenishment from deeper depths lead to low, often below the detection levels, of inorganic nutrients (Figure 2B,C) and thus to low phytoplankton biomass represented by chlorophyll-*a* (Figure 2D). Surface water NOx (NO_2+NO_3) ranged from ~0.04 µmol L^{-1} in the offshore water and increased near the coast fivefold; ~0.20 µmol L^{-1} (Figure 2B). NOx increased with depth and was >0.1-0.3 µmol L^{-1} below ~100 m till the bottom of the photic zone (Figure 2B). These values, although higher than the very top surface water, are still considered low and representative of oligotrophic seas (Siokou-Frangou et al., 2010). Orthophosphate (PO_4) was overall homogeneous throughout the water column, ranging from below detection (<0.008 µmol L^{-1}) to ~0.02 µmol L^{-1} (Figure 2C). Nevertheless, the resulting N:P ratio was often higher than the 16:1 'Redfield ratio', suggesting N limiting conditions for phytoplankton. In agreement, the spatial distribution of chlorophyll mirrored that of NOx (Figure 2B vs. 2D), suggesting high dependence of phytoplankton to nitrogen species. Where, the surface chlorophyll concentrations were typically low (<0.1 µg L^{-1}) and increased with depth reaching maximal values around the Deep Chlorophyll Maxima (DCM) of ~0.3 µg L^{-1} (Figure 2D). The location of the DCM in the water column changed westward and deepened from ~75 m in more coastal locations to ~140 m in the offshore (Figure 2D).

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Together, these physiochemical and biological characteristics highlight the LNLC oligotrophic nature of the study area, in accordance with previous studies from the area (abovementioned references).

3.2 Pico-phytoplankton cell size is an indicator for oligotrophy in the EMS

Pico-phytoplankton communities consisted of the two cyanobacterial genera *Prochlorococcus* and *Synechococcus*, along with photoautotrophic pico-eukaryotic cells (Figure 3). *Synechococcus* was typically more abundant in surface waters (~20,000-25,000 cells ml^{-1}) and in coastal stations (~25,000-60,000 cells ml^{-1}) compared to the deeper water layers >100 m (~5,000-15,000 cells ml^{-1}) (Figure 3A). Differently than its abundance, *Synechococcus* biovolume was generally smaller in the upper 100 m than in the 100-180 m layer, averaging 0.98±0.13 μm^3 (range: 0.8-1.2 μm^3) in the surface layer vs. 1.12±0.20 μm^3 (range: 0.8-1.5 μm^3) at depth (Figure 3B). Larger *Synechococcus* cells were found in coastal nutrient-richer water than in offshore oligotrophic regimes (Figure 4). *Prochlorococcus* was generally more abundant at the DCM, where its concentrations ranged from ~10,000 to ~80,000 cells ml^{-1} compared to surface waters where they ranged from as low as ~1,000 cells ml^{-1} to ~58,000 cells ml^{-1} (Figure 3C). *Prochlorococcus* biovolume was smaller than that of *Synechococcus* and showed a clear increase with depth (Figure 3D). The average surface biovolume of *Prochlorococcus* was 0.62±0.07 μm^3 (range: 0.51-0.73 μm^3), increasing to 0.68±0.04 μm^3 (range: 0.62-0.74 μm^3) at the DCM. No significant differences in *Prochlorococcus* cell biovolume were observed between coastal and offshore stations (Figure 4), thus suggest a lower cell plasticity compared to *Synechococcus* or pico-eukaryotes (discussion below). Pico-eukaryote abundance was generally higher in the upper 100 m (~100 to 3,700 cells ml^{-1}) compared to deeper waters (below detection to ~1,100 cells ml^{-1}), with consistently greater concentrations in coastal stations than offshore (Figure 3E). Generally, pico-eukaryotic cells were larger than of *Synechococcus* and *Prochlorococcus*, averaging ~1.9, 1.0 and 0.6 μm^3 across all depths and stations, respectively. Nevertheless, pico-eukaryotes biovolume increased with depth (Figures 3F), as well as showed an increasing trend from coastal toward offshore waters (Figure 4). At the upper 100 m, pico-eukaryotes biovolume was ~1.75±0.37 μm^3 (range: 1.16-2.60 μm^3), while at 100-180 m it was 2.07±0.48 μm^3 (range: 1.15-2.95 μm^3).

Taken together, pico-phytoplankton dominated across different depths and water masses; however, all three groups exhibited overall similar vertical and spatial patterns in cell size with an increasing trend with depth, as well as from coastal toward offshore waters (Figures 3,4). These overarching trends mirrored the spatial distribution of nutrients, particularly NOx, and,

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consequently, the distribution of chlorophyll (Figure 2). These observations suggest that cell size serves as a good environmental cue/indicator of oligotrophic conditions in the EMS and likely in other oceanic regimes (discussion below).

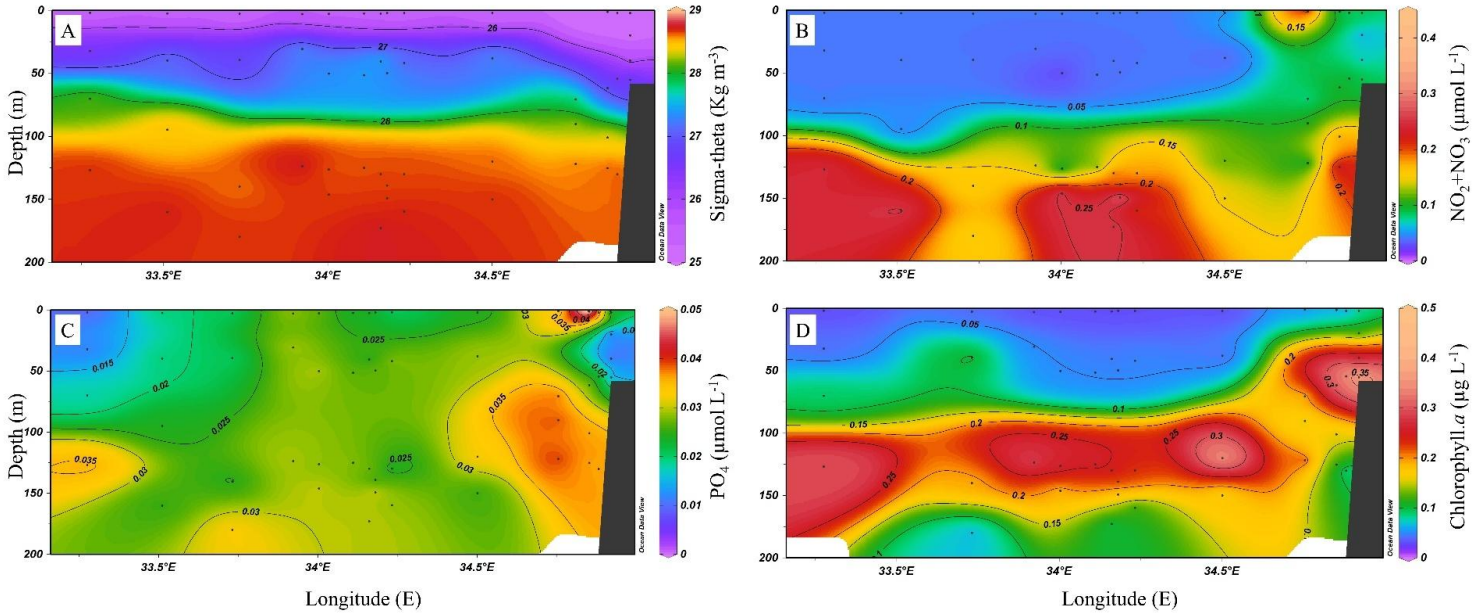

Figure 2: Spatial and depth patterns of Sigma-theta (A), dissolved NO_2+NO_3 (B), PO_4 (C) and chlorophyll.*a* (D) within the photic layer of the Eastern Mediterranean Sea during summer 2024.

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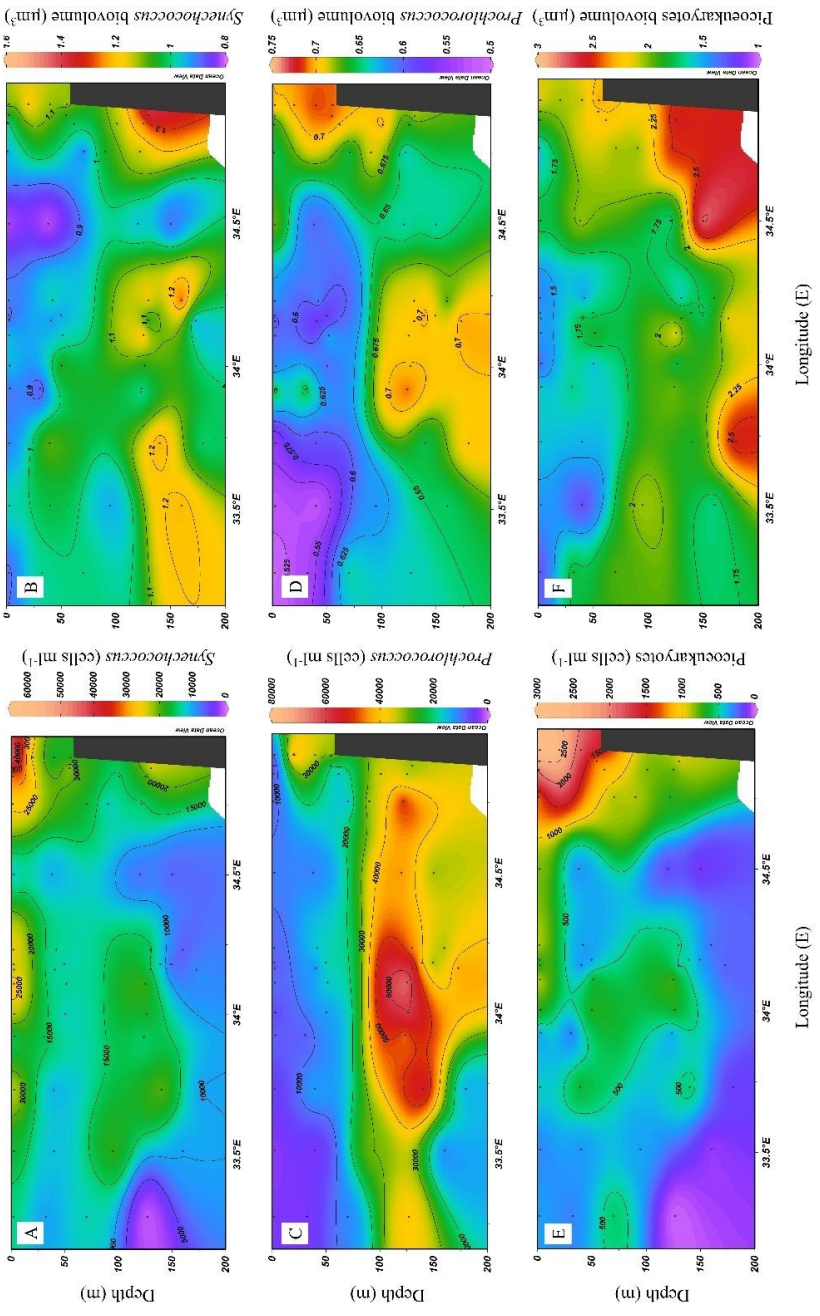

Figure 3: Spatial and depth patterns of *Synechococcus* (A,B), *Prochlorococcus* (C,D) and pico-eukaryotes (E,F) abundance (A,C,E) and biovolume (B,D,F) in the Eastern Mediterranean Sea during summer 2024.

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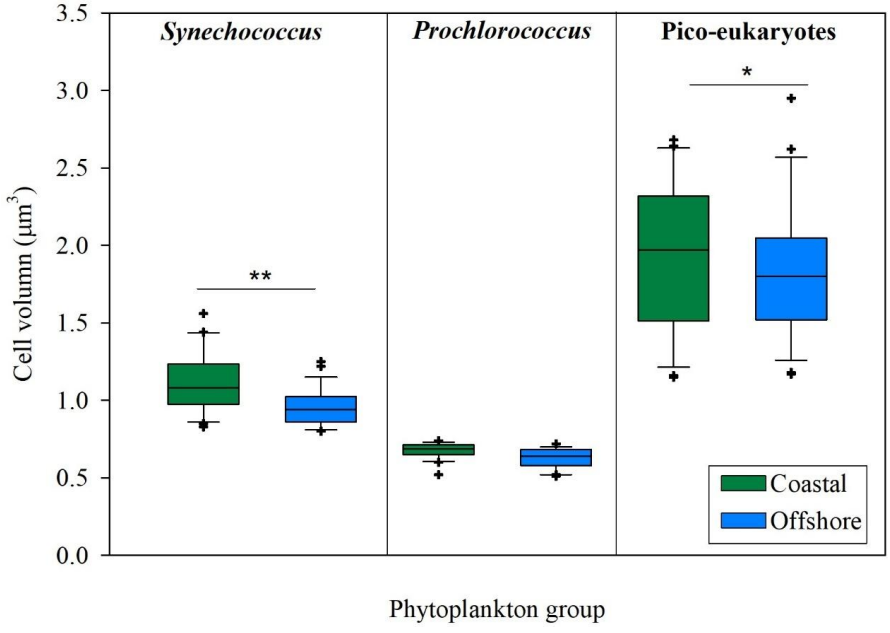

Figure 4: Comparison of single-cell volumes (µm³) of *Synechococcus*, *Prochlorococcus*, and pico-eukaryotes between coastal (green) and offshore (blue) waters in the Eastern Mediterranean Sea. Box plots show the median, interquartile range, and overall distribution of cell volumes. Statistically significant differences between coastal and offshore populations were determined using Welch's *t*-tests or Mann–Whitney *U* tests. * $p<0.05$, ** $p<0.01$.

3.3 Can the ambient nutrients pool meet pico-phytoplankton's growth requirements?

Based on the cell's biovolume, abundance and the inorganic nutrient standing stocks we calculated the per-cell quotas and RSI values of the three pico-phytoplankton populations in the EMS (Marañón et al., 2014). These 'back of the envelope' calculations provided valuable insights into the minimal and maximal nutrient requirements of the different pico-phytoplankton cells and their theoretical nutrients limitations derived from cell size. Generally, our results demonstrate that being a small cell have significant benefits in oligotrophic seas like the EMS. Where, the relatively low Q_{min} values of *Prochlorococcus* reflected its small cell size and streamlined metabolic machinery, while *Synechococcus* and pico-eukaryotes exhibited higher quotas due to their larger biomass and more complex cellular organization. These

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differences translated into distinct nutrient demands per cell and thus influence each group's ecological strategy and competitive capacity under the oligotrophic conditions of the EMS.

At the upper 100 m nitrogen supply was often below demand (RSI_n<1) for *Synechococcus* and pico-eukaryotes (Figure 5A,E) but not *Prochlorococcus* (Figure 5C) that lacks the genetic and enzymatic machinery required for NO_3 assimilation (e.g., they do not carry the genes *narB* and often *nirA*, López-Lozano et al., 2002; Moore et al., 2002). Differently, the RSI values for phosphorus (RSI_p) were larger than 1 in all pico-phytoplankton groups (Figure 5B,D,F). These results suggest that PO_4 was not the main limiting nutrient for neither of the pico-phytoplankton groups and that N was the primary limiting element. Importantly, these results suggest physiological and ecological trade-offs among the pico-phytoplankton groups. Where, *Prochlorococcus* typically shows higher RSI values, and therefore a greater likelihood of sustaining growth due to its minimal nutrient requirements per cell, even under low-nutrient conditions. In contrast, *Synechococcus* and pico-eukaryotes frequently experience more severe N limitation (but to a lesser extent P based on RSI calculations), driven by higher per-cell quotas and large population standing stocks. Such differences in nutrient standing stocks likely contributed (along with other variables such as light intensities etc.) their depth distributions, seasonal dynamics, and competitive interactions in oligotrophic marine ecosystems.

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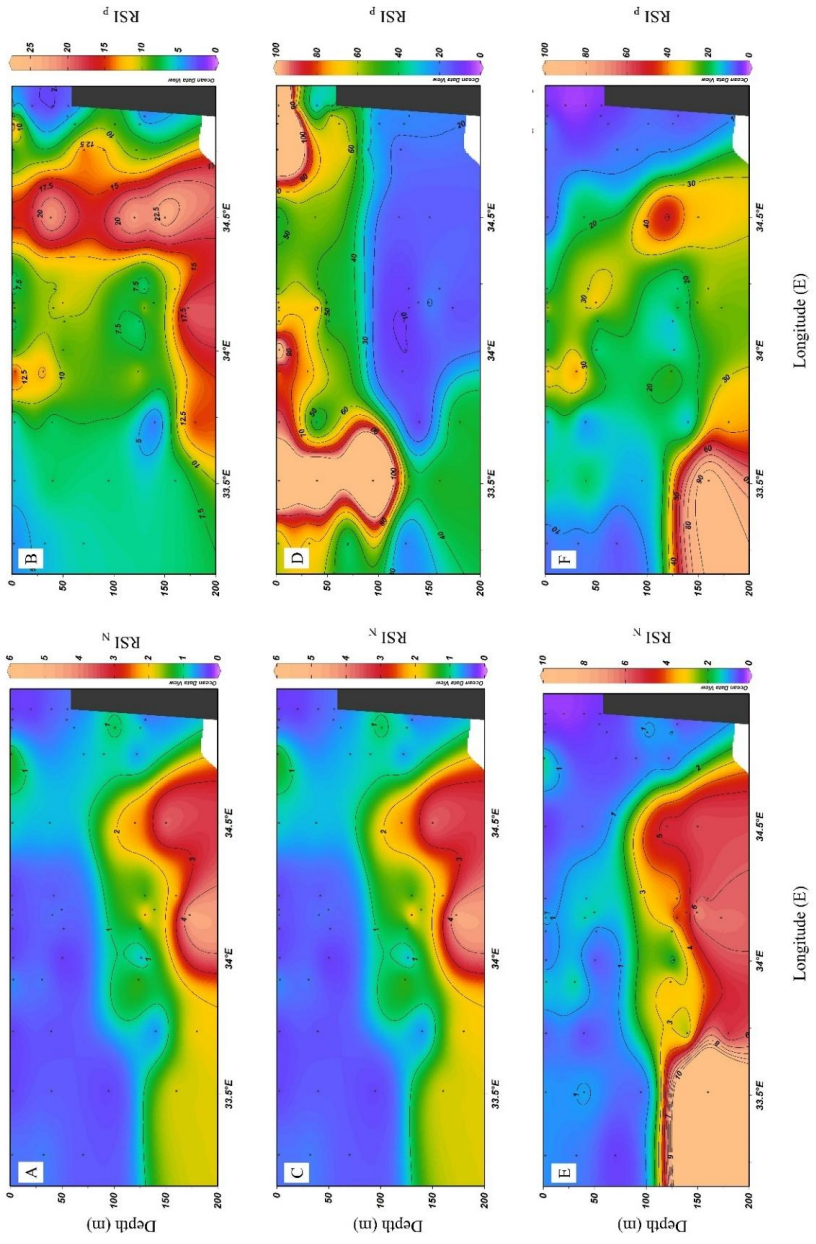

Figure 5: A theoretical Resource Supply Index (RSI) of *Synechococcus* (A,B), *Prochlorococcus* (C,D) and pico-eukaryotes (E,F) calculated for NOx (A,C,E) and PO4 (B,D,F) in the Eastern Mediterranean Sea during summer 2024. RSI values <1 suggest nutrient limitation.

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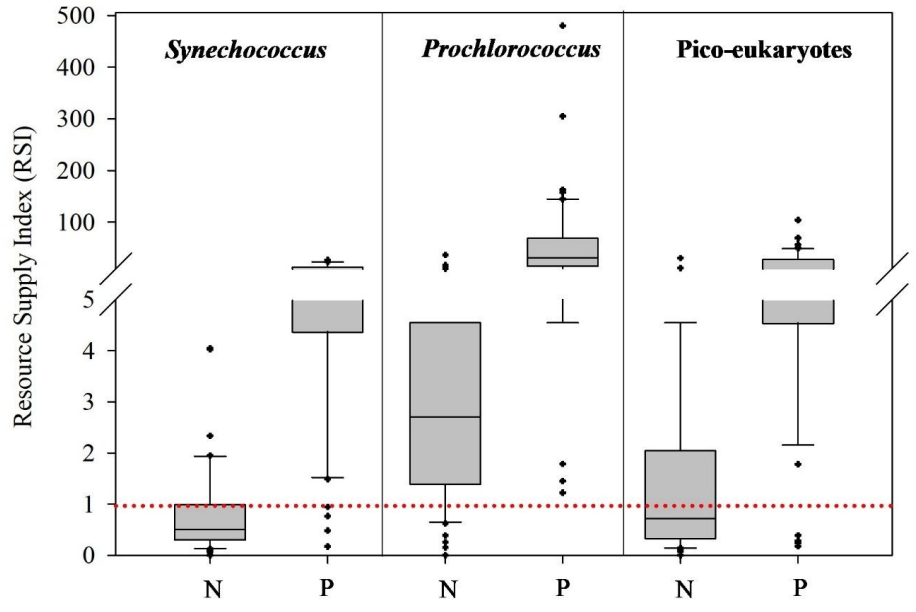

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307 **Figure 6:** Box Whisker plots showing the data distribution of the RSI values for NO_3 and PO_4
308 for the different pico-phytoplankton groups. The black line inside the box shows the median.
309 The dotted red line shows the RSI threshold, where RSI<1 imply on a nutrient limitation.

310

311 **4 Discussion**

312 **4.1 Coastal-offshore variability in pico-phytoplankton cell size and abundance at the**
313 **EMS**

314 Significant differences in pico-phytoplankton cell volumes were detected between coastal and
315 offshore waters, reflecting clear shifts in trait composition across environmental gradients.
316 Both *Synechococcus* and pico-eukaryotes exhibited larger mean cell volumes in nutrient-richer
317 coastal waters than in offshore environments. These differences in cell size are likely attributed
318 by human-induced perturbations typical to coastal water (e.g., Herut et al., 2024; Kress et al.,
319 2019; Rahav et al., 2020; Raveh et al., 2019) and reflects greater allocation to metabolic and
320 structural components, potentially improving competitive ability and storage capacity when
321 resources are not limiting. In contrast, *Prochlorococcus* displayed small and statistically weak
322 differences in cell volume between coastal and offshore stations. This minimal divergence
323 likely underscores the strong evolutionary and physiological constraints on this genus (e.g.,

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Daakour et al., 2024), which remains highly specialized for life in chronically oligotrophic and stratified surface water. Its small and relatively invariant cell size reflects optimization for nutrient-poor conditions, where minimizing metabolic demands and maximizing surface-area-to-volume ratios provide a selective advantage.

The strong size structuring observed in the EMS is consistent with patterns reported from other marine oligotrophic systems such as the subtropical gyres, the Sargasso Sea, the North Pacific Subtropical Gyre (Station ALOHA), and the Red Sea (Buitenhuis et al., 2012; Coello-Camba and Agustí, 2021; Glover et al., 2007; Pearman et al., 2017). In all these regions, pico-phytoplankton dominate biomass and primary production, and small cell size is a defining adaptive trait under chronic nutrient scarcity. For example, in the North Pacific Subtropical Gyre, *Prochlorococcus* and small *Synechococcus* populations exhibit cell diameters and biomass comparable to those measured here and dominate where nitrate and phosphate are persistently near detection limits (Karl and Church, 2017; Winter et al., 2025). Similarly, the northern Red Sea shows depth-dependent increases in pico-phytoplankton cell size associated with nutricline proximity and the deep chlorophyll maximum (Rahav et al., 2015).

The EMS, however, represents one of the most phosphorus-depleted marine systems on Earth (Krom et al., 2010). While many subtropical gyres experience combined N and P limitation, the EMS is characterized by extremely low phosphate and high N:P ratios (Krom et al., 2005). Despite this, our RSI calculations show that phosphorus was not the primary limiting element for any of the pico-phytoplankton groups during summer, whereas nitrogen limitation was widespread for *Synechococcus* and pico-eukaryotes. This agrees with recent experimental and field studies in the EMS showing that nitrate availability often controls phytoplankton productivity during stratified periods even in coastal areas that have more NO_3 to begin with (Rahav et al., 2018).

Larger *Synechococcus* and pico-eukaryotes cell volumes requires higher cellular nitrogen and phosphorus quotas, which in the EMS frequently exceeded ambient nitrogen supply, as indicated by $RSI_n<1$. This could explain, at least partly, why *Synechococcus* and pico-eukaryotes are often found in greater abundances in coastal water where nutrient inputs are higher (Kress et al., 2019). In contrast, *Prochlorococcus* remained largely unconstrained by both N and P, highlighting its exceptional adaptation to nutrient scarcity and/or that this cyanobacterium is limited by other nutrients such as organic molecules (e.g., urea, Hetharua et al., 2025; Moore et al., 2002; Zubkov et al., 2004). This physiological adaptation 'allows' *Prochlorococcus* to dominate in the most nutrient-poor surface and warm water but also constrains its ecological niche: it is less competitive in nutrient-rich or turbulent environments

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where larger phytoplankton with higher storage capacity and growth potential prevail (Biller et al., 2015; Partensky and Garczarek, 2010). Thus, we surmise that the weak spatial variation in *Prochlorococcus* cell size in the EMS reflects its highly specialized adaptation to the persistent ultra-oligotrophic conditions characterising this sea (Berman-Frank and Rahav, 2012; Siokou-Frangou et al., 2010).

Taken together, the alterations in cellular size highlights important ecological implications. Where, larger cell volumes in *Synechococcus* and pico-eukaryotes not only enhance nutrient storage and metabolic potential but also increase their visibility to grazers and affect their position within microbial food webs (Charalampous et al., 2021; To et al., 2024; Ward et al., 2017). Such size shifts can therefore influence trophic transfer efficiency, carbon export potential, and the balance between autotrophic and heterotrophic processes. Conversely, the little/moderate change of *Prochlorococcus* cell size underscores its role as a persistent, small-celled specialist that dominates biomass and productivity in nutrient-depleted offshore regions. Collectively, these results demonstrate that cell size is a highly responsive functional trait that integrates environmental forcing with microbial community structure, revealing how resource availability and physical conditions shape ecosystem-level processes in oligotrophic marine systems such as the Eastern Mediterranean Sea.

4.2 Environmental drivers explain a large fraction of cell-size variability in the EMS

A multivariate ordination analysis reveals a relationship between *Synechococcus* cell size and the surrounding environmental gradients (Figure 7). The size vector for *Synechococcus* was closely aligned with NO_3 and PO_4 levels, as well as with chlorophyll.*a* concentrations that were greater in coastal water (Figure 2). This pattern indicates that *Synechococcus* cells tend to be larger under less oligotrophic conditions, often coinciding with regions of higher primary production (Raveh et al., 2015). These results are consistent with the ecological strategy of *Synechococcus*, which exhibits considerable physiological plasticity and is known to thrive in environments where higher nutrient supply 'allows' higher growth rates and increased cellular investment in metabolic machinery (Badger et al., 2006; Ungerer et al., 2018). Larger cell sizes under such conditions may reflect a shift toward improved nutrient storage capacity and enhanced uptake kinetics when compete (Garcia et al., 2016; Kerimoglu et al., 2012; Verdy et al., 2009). In contrast to *Synechococcus*, *Prochlorococcus* maintains smaller cell sizes under highly oligotrophic surface waters that prevail in the EMS during the summer (Ben-Ezra et al., 2021). The 'tendency' toward small cell size in such environments reflects *Prochlorococcus*'s

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evolutionary optimization for efficient nutrient uptake and minimal metabolic cost under severe resource limitation. Smaller cells possess a higher surface-area-to-volume ratio, which enhances nutrient acquisition at nanomolar concentrations, and they require fewer resources for cellular activities. Pico-eukaryotes cell size showed an intermediate response to environmental variability. The size vector was most strongly associated with depth, PO_4, and chlorophyll.*a*, and to a lesser extent with NO_3 and temperature, indicating that picoeukaryote size tends to increase under conditions of higher nutrient availability. This trend suggests that pico-eukaryotes respond dynamically to shifts in resource supply and water column structure, with larger cells occurring in environments that can support greater metabolic and structural complexity.

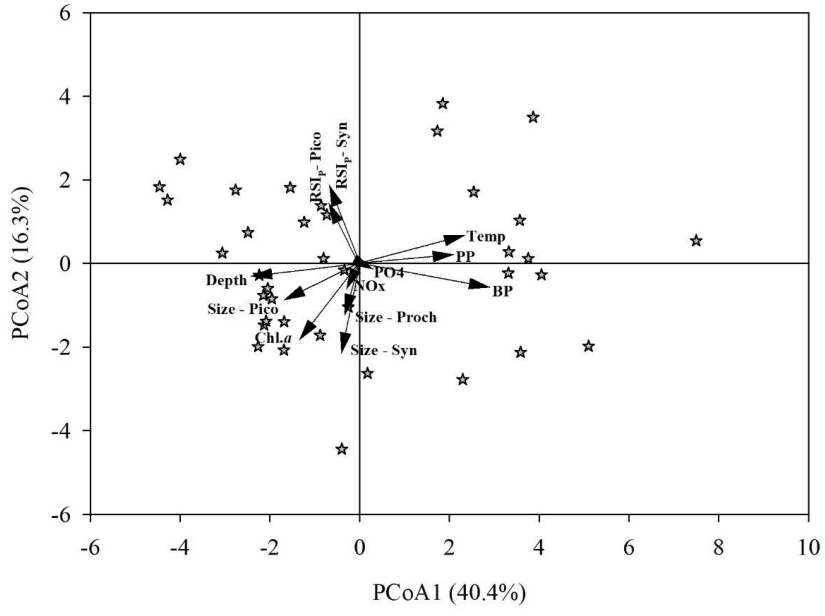

Figure 7: Principal Coordinates Analysis (PCoA) of environmental gradients and their relationship to pico-phytoplankton cell size in the oligotrophic Eastern Mediterranean Sea. The ordination was performed using Euclidean distances based on standardized environmental variables. Arrows represent the direction and strength (vector length) of correlations between individual environmental variables and the first two PCoA axes (Axis 1 and Axis 2, which together explain ~57% of total variance). Longer vectors indicate variables with stronger correlations to the ordination space.

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The patterns revealed by Q_{min}, Q_{max}, and RSI analyses have important implications for how pico-phytoplankton communities may respond to future climate-driven changes in the marine environment. Ocean warming, enhanced stratification, and reduced vertical nutrient fluxes are expected to further intensify oligotrophic conditions in many subtropical and semi-enclosed basins (Ducklow and Doney, 2013). Such shifts will likely exacerbate phosphorus scarcity (Mansour et al., 2025) and increase the frequency and severity of N&P co-limitation (Browning and Moore, 2023), further constraining primary production and altering microbial food-web dynamics (Ibáñez et al., 2023). Species with lower nutrient requirements and greater physiological flexibility such as *Prochlorococcus* may therefore gain a competitive advantage under these conditions, potentially reshaping community composition and biogeochemical cycling. At the same time, changes in nutrient stoichiometry and supply ratios could modulate carbon export efficiency and the coupling between primary production and nutrient regeneration. Together, these findings underscore the value of cellular quota and RSI-based approaches not only for diagnosing present-day nutrient limitation but also for predicting ecosystem responses to future climate and nutrient regime shifts in oligotrophic ocean regions. Additionally, the spatial heterogeneity in cell physiology and biochemical composition can introduce systematic biases when converting pico-phytoplankton cell volume to carbon and nutrient quotas using a single universal conversion factor. Both laboratory and field studies show that cellular carbon density, chlorophyll content, and macromolecular composition in pico-phytoplankton may vary with nutrient regime, light availability, and growth rate (Finkel et al., 2010; Stawiarski et al., 2016; Wang et al., 2022). In nutrient-richer coastal waters and or in deeper water, these taxa tend to exhibit higher protein, pigment, and storage compound content per unit volume, leading to higher carbon and nutrient content for a given cell size than in oligotrophic offshore waters (Bertilsson et al., 2003; Givati et al., 2023; Liefer et al., 2019). Conversely, under extreme oligotrophy, cells are less pigmented, have lower ribosomal content (as they grow more slowly), and allocate a greater fraction of their volume to low-density structural components, resulting in lower carbon and nutrient quotas per unit volume (Fuszard et al., 2012; Hartmann et al., 2014). Applying a single global biovolume-to-carbon conversion factor across these contrasting environments would therefore overestimate offshore biomass and underestimate coastal biomass for *Synechococcus* and pico-eukaryotes and to a lesser extent *Prochlorococcus* that displays remarkably constrained cellular composition across environmental gradients (Figures 3-5). This is likely due to *Prochlorococcus*'s streamlined genome, reduced pigment suite, and tightly regulated cellular architecture. Together, applying

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a single universal biovolume-to-carbon conversion across both coastal and offshore regimes and/or surface vs. deep water may introduce a biased biomass estimates of pico-phytoplankton in the oceans. Therefore, it is advised to measure pico-phytoplankton cell size along with its abundance.

5 Conclusions

This study highlights pico-phytoplankton cell size as a key functional trait linking nutrient scarcity to ecosystem-level carbon cycling in ultra-oligotrophic seas. Rather than abundance alone, size-dependent nutrient demand and physiological plasticity may determine which taxa will likely be dominating phytoplankton biomass under persistent nutrient limitation in the EMS. This size-structured trade-off has direct consequences for carbon fate, where dominance of very small cells promotes tight recycling within the microbial loop, reduces trophic transfer efficiency, and ultimately weakens the biological pump by limiting the formation of fast-sinking particles.

Additionally, our findings indicate that using a single, fixed carbon-per-cell conversion factor for each pico-phytoplankton group throughout the photic zone can introduce bias in depth-integrated biomass estimates in the EMS, and likely in other stratified oligotrophic oceans. We therefore recommend applying size-adjusted conversion factors of ~36-40 fg C cell^{-1} for surface and deep *Prochlorococcus*, ~255 and ~290 fg C cell^{-1} for surface and deep *Synechococcus*, and ~2590 and ~3050 fg C cell^{-1} for surface and deep pico-eukaryotes, respectively. Adoption of these depth-resolved factors will refine carbon standing stock assessments and enable more robust comparisons across coastal-offshore gradients and vertically structured oligotrophic systems.

Lastly, as ocean warming and enhanced stratification continue to expand low-nutrient, low-chlorophyll regions, selection for small cell size and low cellular quotas is likely to intensify. Such shifts are expected to promote recycling-dominated food webs, decoupling primary production from carbon export and reducing long-term carbon sequestration efficiency in oligotrophic oceans. Incorporating cell-size variability into biomass estimates and biogeochemical frameworks is therefore essential for predicting how future oceans will regulate carbon export under increasing stratification and nutrient decline.

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curation, formal analysis, investigation, methodology, project administration, writing original draft.

Data availability. The data are presented in full in the main text or the supplementary material. The hydrographic data is openly available from https://isramar.ocean.org.il/isramar2009/.

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