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LONG-TERM DECLINE IN PICOPHYTOPLANKTON ABUNDANCE AND CARBON BIOMASS IN THE ARABIAN SEA: EVIDENCE FROM 1995 AND 2019

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Abstract

Picophytoplankton play a critical role in marine primary production, particularly in oligotrophic regions such as the Arabian Sea. In this study, we assessed changes in the picophytoplankton abundance and carbon biomass of Prochlorococcus and Synechococcus between 1995 (US-Joint Global Ocean Flux Study-US-JGOFS) and 2019, revealing a significant decline in both groups. Picophytoplankton abundance declined by 23% for Prochlorococcus and 37% for Synechococcus in the basin. Estimated picophytoplankton carbon stocks in the Arabian Sea decreased from 8.8 Tg C (range: 4.0–20.16 Tg C) in 1995 to 2.8 Tg C (range: 0.81–13.75 Tg C) in 2019. These declines are consistent with broader reductions in chlorophyll a concentrations and net primary production, likely driven by increased ocean stratification and reduced nutrient supply under warming conditions. While uncertainties remain regarding long-term chlorophyll a trend, recent studies support the conclusion of declining productivity in oligotrophic oceans. Our findings highlight the vulnerability of picophytoplankton communities to climate-driven changes and suggest significant implications for carbon cycling and food web dynamics in the Indian Ocean.

Keywords: *Prochlorococcus, Synechococcus, ocean warming*

INTRODUCTION

Picophytoplankton—comprising the cyanobacteria *Prochlorococcus* and *Synechococcus*, along with picoeukaryotes— are the most abundant phytoplankton in oligotrophic tropical and subtropical oceans, contributing up to half of marine primary production and playing a central role in carbon cycling and export (Agawin et al., 2000; Agustí & Llabrés, 2007; Campbell et al., 1997). *Prochlorococcus* dominates nutrient-depleted, stratified open oceans, while *Synechococcus* is more prevalent in nutrient-rich coastal and upwelling zones, reflecting their niche partitioning across environmental gradients (Flombaum et al., 2013).

Climate-driven changes such as ocean warming, intensified stratification, and expanding oligotrophic gyres are reshaping marine ecosystems and nutrient dynamics, with conflicting predictions for picophytoplankton trends. Quantitative niche models, built from extensive global datasets, offer an alternative to Earth System Models (ESMs) for projecting picophytoplankton distributions by linking observed abundances to environmental gradients such as temperature, light, and nutrients (Agusti et al., 2019; Flombaum et al., 2013). These models suggest that warming may enhance the abundance of small, efficient cells like *Prochlorococcus* and *Synechococcus*, despite ESM and satellite-based studies indicating declines in chlorophyll *a*—a proxy for phytoplankton biomass—due to reduced nutrient flux and increased UV-B stress (Agustí & Llabrés, 2007; Behrenfeld et al., 2006; Boyce et al., 2010). This apparent contradiction underscores the complexity of interpreting chlorophyll-based trends and highlights the importance of regional variability, physiological plasticity, and community composition in shaping picophytoplankton responses to climate change (Duarte, 2015; Taucher & Oschlies, 2011).

The northern Indian Ocean, especially the Arabian Sea, is a hotspot of rapid oceanographic change. Long-term trends from satellite and modeling studies suggest a decline in productivity, but in situ community-level data remain scarce. While several studies have examined no shifts in total phytoplankton abundance and composition over time (Chowdhury et al., 2021). However, picophytoplankton have received comparatively little attention. To address this, we sampled to assess how picophytoplankton communities have changed over two decades. By comparing US-Joint Global Ocean Flux Study (US-JGOFS) (1995) and recent observations (2019), this study aims to: (i) assess shifts in vertical and horizontal distributions of *Prochlorococcus* and *Synechococcus*, (ii) evaluate climate-driven impacts on their relative abundances, and (iii) quantify changes in picophytoplankton carbon biomass in relation to physical and biogeochemical changes in the Arabian Sea. These insights are critical for understanding the vulnerability of microbial communities and the broader implications for carbon cycling in a warming tropical ocean.

2. MATERIALS AND METHODS

2.1 Sample collections

We collected seawater samples at 14 stations (SK1–SK14) in the Arabian Sea during the winter monsoon from 16 December 2019 to 6 January 2020, onboard ORV *Sagar Kanya* (SK-364) (Figure 1b). Seawater was collected from 6 to 8 depth up to 300 m using Niskin bottles fitted on rosette sampler. For comparative analysis, we utilized historical data from the US-Joint Global Ocean Flux Study (US-JGOFS) Arabian Sea Process Study Program, 1992 to 1997 (JGOFS Arabian Sea Process Study Program, 2002). Specifically, we compiled the picophytoplankton abundance data collected during cruise TN054, conducted from 29 November to 27 December 1995 (TN054) (Campbell et al., 1998). The sampling stations were categorized into two transects: (1) Northern transects (N1–N11), and (2) Southern transect (S1–S15) (Figure 1a). The samples were collected from 10 to 12 depths up to 200 m in the US-JGOFS.

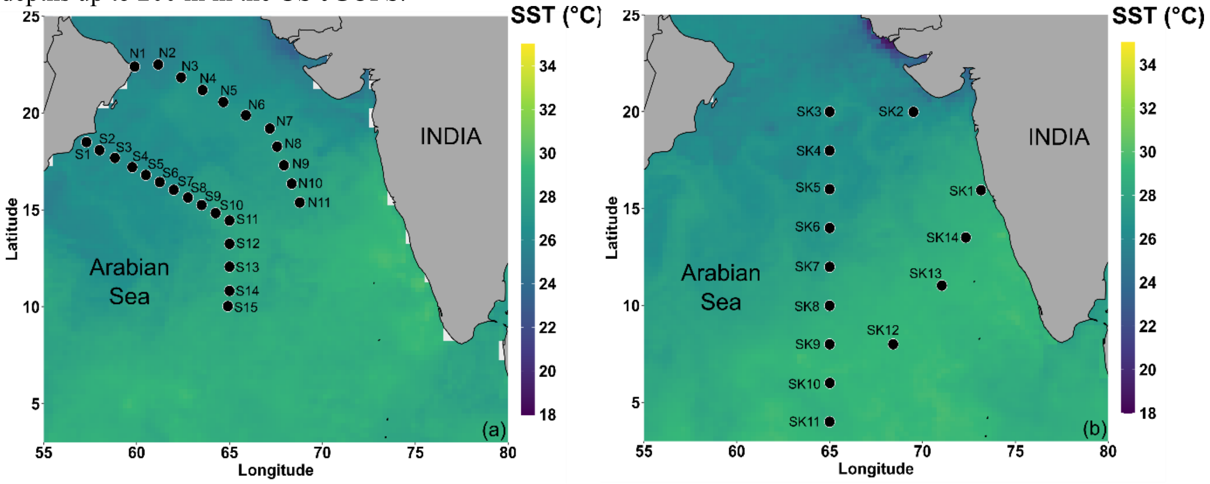

Figure 1: (a) Sampling locations along the northern (N1–N11) and southern (S1–S15) transects **in the Arabian Sea during the US-JGOFS cruise (**29 November to 27 December 1995)**, and (b) sampling locations (SK1**–SK14) in the Arabian Sea during the SK-364 cruise (16 December 2019 to 6 January 2020). The map is overlaid with sea surface temperature (SST, °C) corresponding to the respective sampling periods (E.U. Copernicus Marine Service Information (CMEMS), 2025; Guinehut et al., 2012; Mulet et al., 2012).

2.2 Picophytoplankton abundance analysis

Seawater was collected directly from Niskin bottles into 5 mL cryovials, immediately fixed with glutaraldehyde solution (final concentration 1%) for 10 minutes, and stored at −20 °C onboard. Samples were later transferred to −80 °C until analysis in an onshore laboratory. Prior to analysis, samples were thawed at room temperature in the dark. The picophytoplankton cells were enumerated using a sorter flow cytometer (BD FACS Aria Fusion), equipped with 405 nm and 488 nm laser. *Prochlorococcus* and *Synechococcus* populations were distinguished based on differences in cell size and pigment composition, specifically chlorophyll and phycoerythrin pigment. Standard beads (Fluoresbrite YG Microspheres, 2.0 µm, Polysciences, Inc.) were added to selected samples as internal standard for size calibration. Data acquisition and analysis were performed using FACS Diva software (version 8.5), following identification protocols based on side scatter and autofluorescence properties, as described by Marie et al., (2000). The previous picophytoplankton data were also obtained using flow cytometry; details of the methodology can be found in Campbell et al., (1998).

2.3 Carbon biomass calculation

Carbon biomass was estimated by multiplying picophytoplankton abundance with the appropriate carbon conversion factor. A value of 53 fg C Cell^{-1} was used for *Prochlorococcus*, and 175 fg C Cell^{-1} for *Synechococcus*, based on published estimates (Campbell et al., 1994; Strathmann, 1967; Veldhuis et al., 1997). Additionally, we calculated the picophytoplankton carbon stock in the euphotic zone of the Arabian Sea by integrating the carbon biomass over depth and scaling it to the total surface area of the basin.

2.4 Statistical analyses

A *t*-test was performed to evaluate whether the mean values of picophytoplankton abundance and carbon biomass differed significantly between the two time periods in the Arabian Sea, with the significance level set at $p < 0.05$. The analysis was performed using the "ggpubr" package (Kassambara, 2023) in R software (v 4.2.3).

Table 1: ***Depth-integrated carbon biomass (mg C*** m^{-2}***) of Prochlorococcus (Pro) and Synechococcus (Syn) in the Arabian Sea during the US-JGOFS and the present study (SK-364). The northern and southern transects correspond to the US-JGOFS and SK-364 cruise to the present study.***

Station	Northern transect		Station	Southern transect		Station	SK-364	
	Pro	***Syn***		***Pro***	***Syn***		***Pro***	***Syn***
N1	16.71	599.20	**S1**	228.24	**2805.85**	**SK1**	**24.97**	**314.22**
N2	39.88	1510.09	**S2**	362.86	**1638.52**	**SK2**	**32.91**	**348.24**
N3	109.73	799.52	**S3**	263.47	**1063.74**	**SK3**	**18.14**	**301.04**
N4	257.63	1373.14	**S4**	278.51	**791.35**	**SK4**	**47.07**	**402.22**
N5	255.74	1087.69	**S5**	118.98	**591.10**	**SK5**	**45.60**	**2024.09**
N6	429.37	616.37	**S6**	194.97	**1224.81**	**SK6**	**20.25**	**660.43**
N7	145.92	683.33	**S7**	260.12	**1200.78**	**SK7**	**12.27**	**478.39**
N8	157.74	1223.11	**S8**	280.76	**797.61**	**SK8**	**173.91**	**68.48**
N9	402.15	565.24	**S9**	219.46	**1492.97**	**SK9**	**74.67**	**60.09**
N10	488.08	409.39	**S10**	225.13	**1439.22**	**SK10**	**102.28**	**19.98**
N11	564.21	421.64	**S11**	494.04	**1636.23**	**SK11**	**102.07**	**30.47**
			S12	612.47	**650.65**	**SK12**	**187.66**	**17.43**
			S13	931.49	**304.05**	**SK13**	**127.80**	**35.44**
			S14	523.65	**117.86**	**SK14**	**46.23**	**117.49**
			S15	1239.56	**312.99**			

3. RESULTS AND DISCUSSION

3.1 Climate effects on picophytoplankton

Synechococcus exhibits a widespread distribution across marine environments, thriving in nutrient-rich waters and predominant within the sunlit upper layer. In contrast, *Prochlorococcus* is typically dominant in oligotrophic oceans and extends to deeper, low-light zones (Partensky et al., 1999). Likewise, a**cross the studied locations of the Northern Transect (US-JGOFS), Southern Transect (US-JGOFS), and SK-364, both *Prochlorococcus* and *Synechococcus* displayed a distinct vertical distribution (Figure 2).** *Prochlorococcus* was more abundant (median: 36.2 × 10^3 cells mL^{-1}) at offshore stations, while *Synechococcus* was abundant across all stations (Coastal stations: 17.6 × 10^3 cells mL^{-1} and open ocean stations: 17.0 × 10^3 cells mL^{-1}) in the northern transect (Figure 2a and 2b). Similarly, *Synechococcus* was abundant at coastal (6.37 × 10^3 cells mL^{-1}) and open ocean (26.4 × 10^3 cells mL^{-1}) stations in the southern transect, whereas *Prochlorococcus* was higher at open ocean (50.9 × 10^3 cells mL^{-1}) than coastal stations (15.5 × 10^3 cells mL^{-1}) (Figure 2c and 2d). Interestingly, higher *Synechococcus* abundance was restricted to coastal waters (4.93 × 10^3 cells mL^{-1}) than open ocean stations (6.03 × 10^1 cells mL^{-1}) (Figure 2e). *Prochlorococcus* showing a subsurface maximum that appeared to have shifted and decreased in abundance compared to the southern transect (Figure 2c and 2e). Furthermore, the distribution of *Synechococcus* differed in the present study, showing higher abundance at the coastal station with some presence in open ocean stations, whereas it was largely restricted to the coastal station with very low abundance offshore as compared to earlier data (Figure 2b, 2d, and 2f).

Analysis of depth-integrated cell abundance revealed consistent patterns between the two sampling periods (Figure 3), with *Prochlorococcus* being the dominant group and a trend of decreasing *Synechococcus* abundance. Specifically, depth-integrated *Synechococcus* abundance was 1.2–10, 1.5–3, and 2.5–5 fold higher for the northern, southern, and SK-364 coastal stations, respectively. In contrast, depth-integrated *Prochlorococcus* abundance generally increased with distance from the coast and was 2.3–4.5, 0.5–15, and 1–35 fold higher in the northern, southern, and SK-364 coastal stations, respectively. Notably, in the southern transect during the earlier study, *Synechococcus* abundance was similar to or slightly higher than *Prochlorococcus* (Figure 3b), a distinction that appears to have shifted in the present study, where the distribution of the two groups is more clearly differentiated (Figure 3c).

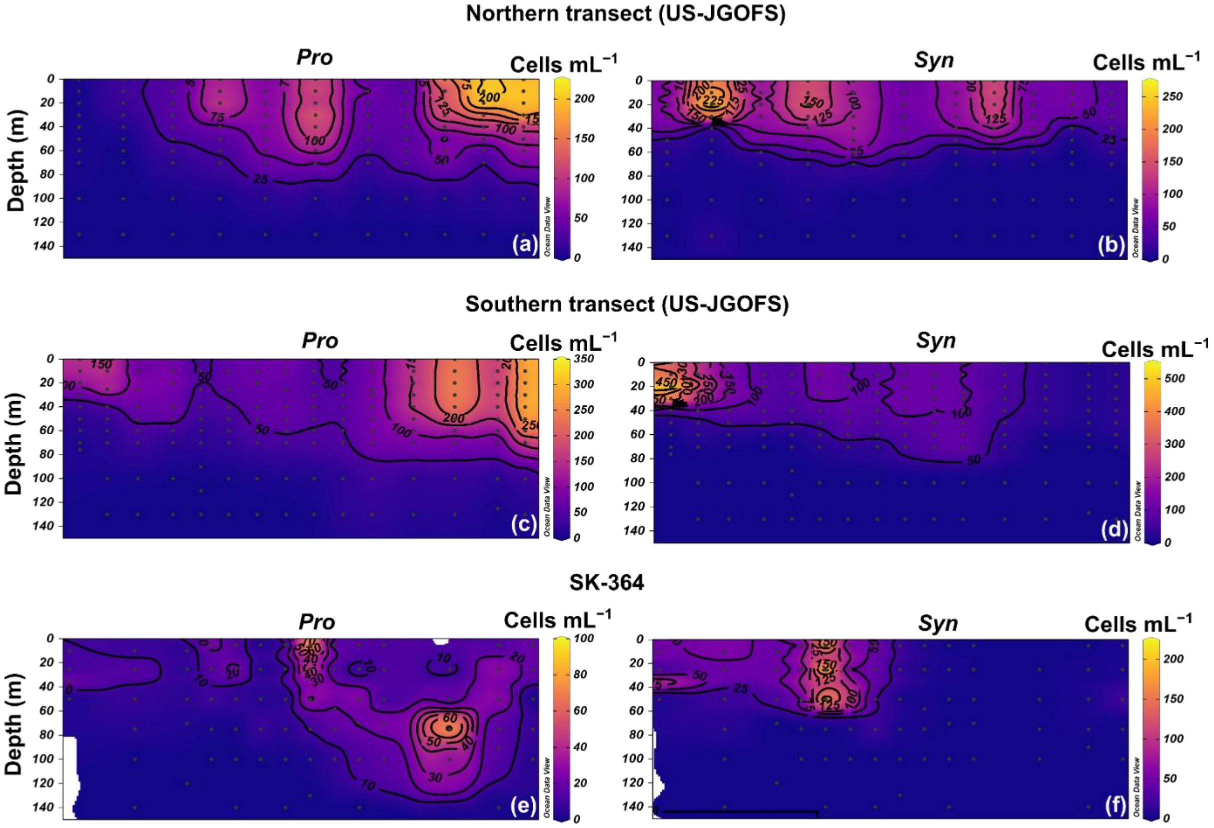

Figure 2: Vertical distribution of *Prochlorococcus* (*Pro*) (cells mL^{-1}) and *Synechococcus* (*Syn*) abundance (cells mL^{-1}) in the Arabian Sea: (a, b) northern transect, (c, d) southern transect during the US-JGOFS cruise, and (e, f) SK-364 cruise. Please note that the abundance values are represented on a scale of × 10^3 cells mL^{-1}.

The vertical distribution pattern observed along the northern and southern transects were closely linked with surface mixed layer (Campbell et al., 1998). Our findings showed that depth-integrated *Synechococcus* abundance was higher in areas experiencing pronounced convective mixing. This mixing likely enhanced the upward transport of nutrients, supporting *Synechococcus* growth in the surface waters. In contrast, *Prochlorococcus* abundance appeared

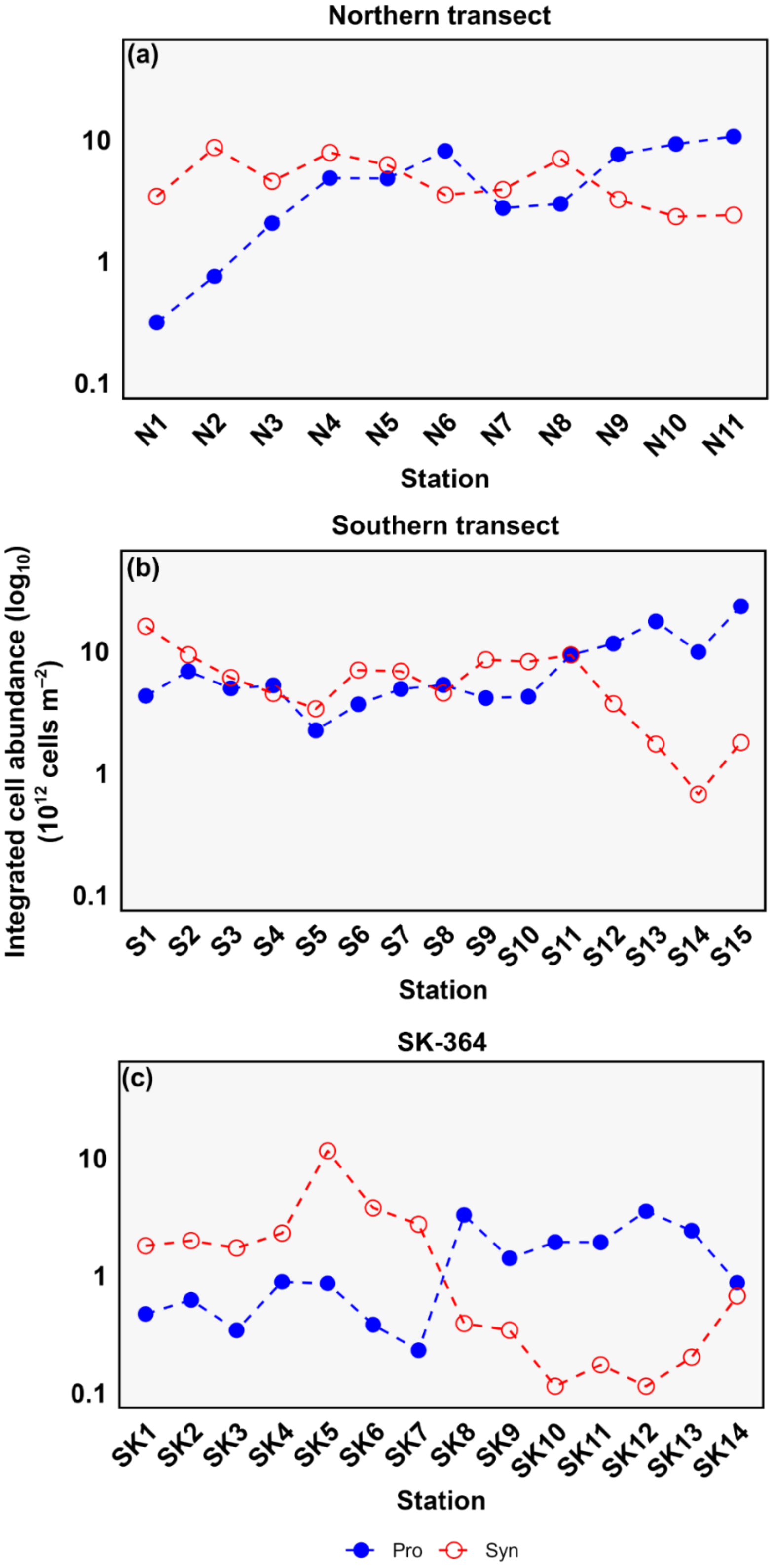

Figure 3: Depth-integrated cell abundance (×10^{12} cells m^{-2}) of *Prochlorococcus* and *Synechococcus* in the Arabian Sea during the US-JGOFS and the present study (SK-364). The northern and southern transects correspond to the US-JGOFS and SK-364 cruise to the present study. Please note that the *y*-axis scale is logarithmic ($\log_{10}$).

unaffected by convective mixing or nutrient availability and was consistently higher in the surface layers across both transects. *Synechococcus*, however, was scarce in the open ocean, possibly due to intense oligotrophic conditions that do not favor its proliferation. Interestingly, our results contrast with previous studies that found no significant linkage between nutrient supply and *Synechococcus* abundance. However, our observations align with prior finding showing a negative relationship between *Prochlorococcus* abundance and nutrient concentrations (Agusti et al., 2019; Flombaum et al., 2013).

In addition to these vertical distribution patterns, we observed a significant decline in picophytoplankton abundance in the Arabian Sea over the past two decades (Figure 4). We also analysed picophytoplankton abundance data from an earlier study in the Arabian Sea during 2012, which showed a similar trend of decline in picophytoplankton abundance during winter monsoon (Bemal et al., 2018). Specifically, depth-integrated *Prochlorococcus* abundance declined by 27.8% and 17.5% (average 22.6%) as compared to the northern and southern transects, respectively, while *Synechococcus* abundance dropped by 41.3% and 32.5% (average 36.9%) in the same regions. Previous studies have attributed such declined in tropical and subtropical waters to thermally driven reductions in vertical nutrient supply (Behrenfeld et al., 2006; Boyce et al., 2010). The Indian Ocean regions has recorded the fastest warming among the global oceans (Roxy et al., 2014, 2016, 2020), with significant sea surface temperature increases in the Arabian Sea contributing to enhanced stratification and reduced nutrient supply (Roxy et al., 2016). In the last decade, this rapid warming has been overlaid with extremes in the form of frequent and intense marine heatwaves (Phillips et al., 2021), further exacerbating stress on marine ecosystems, thereby declining in phytoplankton (Roxy et al., 2016).

As a result, *Synechococcus* populations were largely restricted to coastal stations where convective mixing was more active, while remaining low in the open ocean regions. Evidently, there has been a notable decrease in marine phytoplankton abundance—by approximately 30% based on observational data (1998–2013) and around 20% according to CMIP5 model (1950–2015) (Roxy et al., 2016), which is consistent with our observations in declining of picophytoplankton in the Arabian Sea. However, models projections are not unanimous, some predict an increase in picophytoplankton abundance under warming scenarios (Agusti et al., 2019; Flombaum & Martiny, 2021).

Yet, other studies suggest that rising temperatures, coupled with decreasing chlorophyll a concentrations, actually lead to a reduction in picophytoplankton abundance (Agusti et al., 2019). Additional stressors such as increased photosynthetically active radiation (PAR) and intensified oligotrophication further contribute to decline in picophytoplankton abundance (Agusti et al., 2019). Notably, *Prochlorococcus* and *Synechococcus* are projected to decrease by 18% and 32%, respectively, under a 2 °C warming scenario with associated oligotrophication is considered, which aligns with our findings (Figure 4).

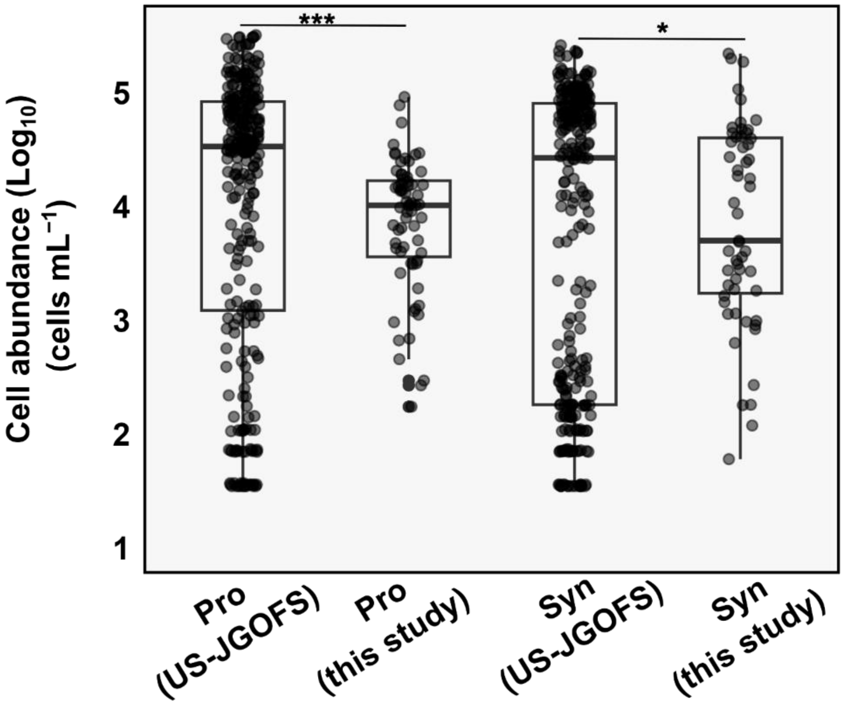

Figure 4: Comparisons of picophytoplankton abundance (cells mL^{-1}) (*Prochlorococcus* and *Synechococcus*) between the US-JGOFS cruise (1995) and this study (2019-2020, SK-364 cruise) in the Arabian Sea. The boxplots show the distribution of cell abundance overlaid with individual data points. The horizontal line within each box represents the median. Only statistically significant values are shown (*: $p < 0.05$, ***: $p < 0.001$). Please note that the *y*-axis scale is logarithmic (Log_{10}).

This suggests that temperature alone does not govern picophytoplankton dynamics, rather a combination of environmental factor may responsible for such dynamics. Furthermore, increasing atmosphere CO_2 concentration are driving ocean acidification, with significant implication for picophytoplankton. Low pH conditions have been shown to negatively impact *Prochlorococcus* growth, while enhancing that of *Synechococcus* (Fu et al., 2007). Projections suggest that ocean acidification could exert a stronger influence on these organisms than warming or nutrient limitation (Dutkiewicz et al., 2015). Sreeush et al., (2019) reported that the Indian Ocean is undergoing acidification due to the absorption of anthropogenic CO_2 from the atmosphere, leading to decrease ocean pH. The pH in the Indian Ocean had decreased by ~0.1 unit, with the most significant decline observed in the western Indian Ocean, indicating decline in *Prochlorococcus* abundance in the Arabian Sea. However, decrease of *Synechococcus* abundance could not be explained by increase in CO_2 concentration in the basin.

3.2 Distribution of Carbon biomass

Similar to the observed decline in overall picophytoplankton abundance, the carbon biomass of *Prochlorococcus* and *Synechococcus* also showed significant differences ($p < 0.001$) between the two time periods, with both groups exhibiting a notable reduction in 2019 compared to the US-JGOFS in 1995 (Figure 5) (Table 1). Niche-based models that incorporate chlorophyll *a* as a predictor for *Prochlorococcus*, *Synechococcus*, and picoeukaryotic phytoplankton showed a decrease in their abundance under future warming scenario (Agusti et al., 2019). Although increase in PAR in a deeper layer may lead to photoacclimation and subsequently lower chlorophyll *a* concentration—often used to estimate phytoplankton biomass—this effect does not fully offset the overall declining trend (Behrenfeld et al., 2016; Graff JR et al., 2016). Globally, chlorophyll *a* concentration has declined since the onset of oceanographic observations. However, regional patterns vary, with the north and south Indian Ocean showing positive trends since the 1950s, although the increase in the northern Indian Ocean has not been statistically significant (Boyce et al., 2010). The methodology of Boyce et al., (2010) has faced scrutiny due to concerns about temporal sampling biases (Rykaczewski & Dunne, 2011), yet their conclusions have been corroborated by subsequent independent studies that account for such limitations (Agusti et al., 2019; Signorini et al., 2015). The persistent decline in chlorophyll *a* supports the observed decrease in picophytoplankton carbon biomass in the region.

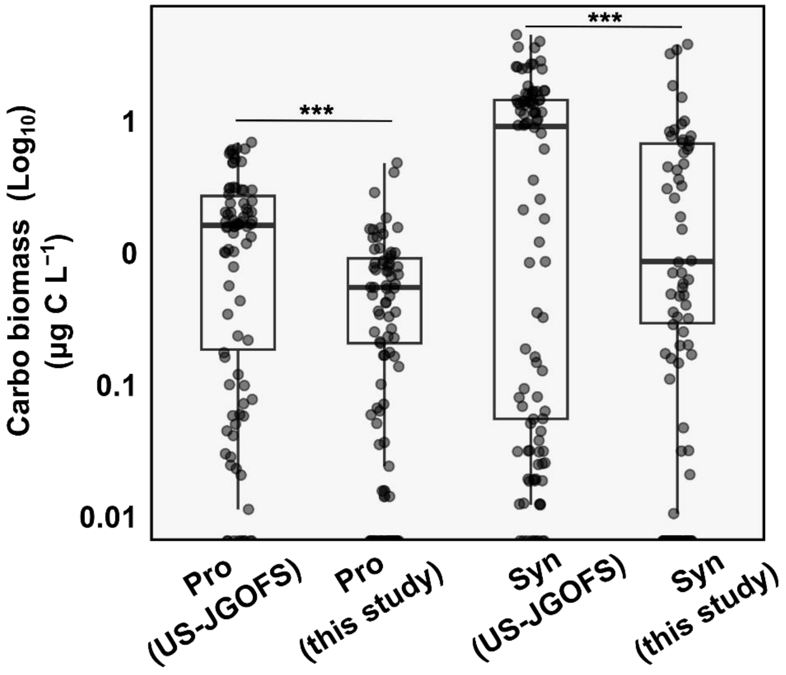

Figure 5: Comparisons of picophytoplankton carbon biomass (µg C L^{-1}) between the US-JGOFS cruise (1995) and this study (2019-2020, SK-364 cruise) in the Arabian Sea. The boxplots show the distribution of cell abundance overlaid with individual data points. The horizontal line within each box represents the median. Only statistically significant values are shown (***: $p < 0.001$). Please note that the *y*-axis scale is logarithmic (Log_{10}).

Furthermore, a substantial reduction in global marine net primary production was recorded during 1997–2006, attributed to increased ocean stratification and warming (Behrenfeld et al., 2006). In the Arabian Sea, intensified stratification and weakened convective mixing may have reduced wintertime productivity over the past two decades. Recent studies also report a decline in primary productivity in the Arabian Sea in this period (Roxy et al., 2016; Saxena et al., 2022), indicating a reduced contribution to the oceanic carbon pool. Furthermore, the western Indian Ocean showed the most productive region of the northern Indian Ocean (Singh & Ramesh, 2015), which showed a decline in carbon contribution in this study. Additionally, Singh et al., (2019) reported that a surplus amount of nitrogen was available for primary producers, which contribute to carbon biomass. However, other environmental factors may outweigh these parameters, ultimately contributing to the observed decline. We estimated the picophytoplankton carbon stock in the Arabian Sea to be 8.8 Tg C (4.0–20.16 Tg C) in 1995 and 2.8 Tg C (0.81–13.75 Tg C) in 2019, that showed ~31% decrease in carbon biomass in past two decades. Taken together, these findings underscore a long-term decline in picophytoplankton carbon biomass, likely driven by climate-induced changes in ocean stratification, nutrient availability, and light conditions, with important implications for regional biogeochemical cycles and carbon flux.

CONCLUSION

This study reveals a substantial decline in the carbon biomass of picophytoplankton, specifically *Prochlorococcus* and *Synechococcus*, in the Arabian Sea from 1995 to 2019. The observed reduction in biomass is closely linked to declining chlorophyll *a* concentration and reduced primary productivity, likely resulting from increased ocean stratification, warming, and limited nutrient availability. Our estimate shows a more than threefold decrease in picophytoplankton carbon stock over the past two decades, indicating a weakening of the region's microbial carbon reservoir. These findings align with global trends of declining marine productivity and underscore the sensitivity of microbial communities to climate variability. Continued monitoring and improved predictive modelling are essential for understanding the long-term implications of these shifts on biogeochemical cycling and ecosystem functioning in the Indian Ocean.

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