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Key Points:

- Reduction of up to 20% in marine phytoplankton in the Indian Ocean during the past six decades
- Reduction in marine productivity is attributed to the rapid warming in the Indian Ocean
- Future climate projections indicate further warming and subsequent reduction in marine productivity

Supporting Information:

- Texts S1-S3 and Table S1
- Figure S1
- Figure S2
- Figure S3
- Figure S4Figure S5
- Figure S6
- Figure S7
- Figure S8

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A reduction in marine primary productivity driven by rapid warming over the tropical Indian Ocean

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Abstract Among the tropical oceans, the western Indian Ocean hosts one of the largest concentrations of marine phytoplankton blooms in summer. Interestingly, this is also the region with the largest warming trend in sea surface temperatures in the tropics during the past century—although the contribution of such a large warming to productivity changes has remained ambiguous. Earlier studies had described the western Indian Ocean as a region with the largest increase in phytoplankton during the recent decades. On the contrary, the current study points out an alarming decrease of up to 20% in phytoplankton in this region over the past six decades. We find that these trends in chlorophyll are driven by enhanced ocean stratification due to rapid warming in the Indian Ocean, which suppresses nutrient mixing from subsurface layers. Future climate projections suggest that the Indian Ocean will continue to warm, driving this productive region into an ecological desert.

1. Introduction

Marine phytoplankton plays a central role in global biogeochemical cycles [Field et al., 1998], forms the base of the marine food web [Chassot et al., 2010], and regulates the global climate [Murtuqudde et al., 2002; Sabine et al., 2004]. Among the tropical oceans, the western Indian Ocean hosts one of the largest concentration of phytoplankton blooms in summer (Figure 1a) [Naqvi et al., 2003; Prasanna Kumar et al., 2001; Ryther and Menzel, 1965; Wiggert et al., 2005], supporting the second largest share of the most economically valuable tuna catch [Lee et al., 2005]. The monsoonal wind forcing is the strongest in the western Indian Ocean and leads to a strong coastal and open ocean upwelling resulting from coastal divergence of Ekman transport and from Ekman pumping, supplying nutrients to the surface and supporting elevated rates of primary productivity [Lévy et al., 2007; McCreary et al., 2009; Prasanna Kumar et al., 2001; Resplandy et al., 2011; Wiggert et al., 2005]. Interestingly, this is also the region with the largest long-term (~100 years) trend in sea surface temperatures (SSTs) in the tropics (Figure 1b) [Roxy et al., 2014, 2015a]—although the contribution of such a large trend in SST to productivity changes has remained ambiguous [Behrenfeld et al., 2006; Goes et al., 2005; Gregg and Rousseaux, 2014; Gregg et al., 2005; Prasanna Kumar et al., 2010]. This ambiguity has been due to the fact that the phytoplankton trend in the Indian Ocean has been estimated from a relatively short time series of observations over which the monsoon winds—a physical parameter which has a complex seasonality [Boyce et al., 2010]—also exhibit interannual changes and trends [Goes et al., 2005; Roxy et al., 2015b].

Rising sea surface temperatures (SSTs) can enhance near-surface stratification inhibiting vertical mixing, a critical process for introducing nutrients into the euphotic zone where sufficient light is available for photosynthesis [Behrenfeld et al., 2006]. This inhibits primary production and cascades through the entire food web in the region. Although Behrenfeld et al. [2006] indicate a reduction in net primary productivity (NPP) over most of the tropics as a result of surface thermal stratification, their results suggest an increase in NPP with respect to the rising SSTs over the western Indian Ocean from 1998 to 2004. Other studies [Goes et al., 2005; Gregg et al., 2005] arrive at similar results over the same period, indicating that the western Indian Ocean underwent the second largest increase in chlorophyll concentrations (indicator of phytoplankton biomass) among the open ocean regions. Goes et al. [2005] reported an increase of up to 350% in marine phytoplankton in this basin and attributed this to a strengthening of summer monsoon winds in the western Indian Ocean. The relatively short time series used in these previous studies put these results at a blind spot because long-term data are indispensable for the attribution of changes in phytoplankton to ocean warming [Beaulieu et al., 2013; Henson et al., 2010; Patara et al., 2012a].

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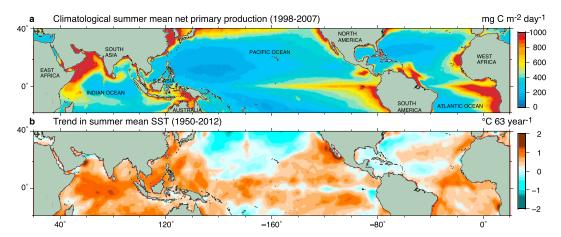


Figure 1. (a) Climatological boreal summer (June–September) net primary production (mg C m $^{-2}$ d $^{-1}$) during 1998–2007, derived based on SeaWiFS chlorophyll, photosynthetically active radiation, and advanced very high resolution radiometer SST using the vertically generalized production model [*Behrenfeld et al.*, 2006]. (b) Observed trend in summer SST ($^{\circ}$ C per 63 years) during 1950–2012, using HadlSST.

It is however imperative to have a firm understanding of the trends in productivity in this highly productive ocean basin, especially since it has been experiencing one of the largest warming trends over the tropical oceans. Any trend in primary production in this region can have greater implications for ecosystem processes and biogeochemical cycling. It is also likely that such changes feed back to the ocean-atmosphere dynamics, potentially modulating the ocean circulation on longer time scales [Murtugudde et al., 2002; Patara et al., 2012b]. Changes in plankton production can have immense impact on marine species as well as humans [Colwell, 1996; Harvell et al., 1999]. Downward trends in primary production over these upwelling areas can be detrimental to the marine food webs and the fishing industry. Data from the Food and Agriculture Organization (FAO) of the United Nations show that the Indian Ocean accounts for 20% of the total tuna catch, especially the most economically valuable bigeye tuna, making it the second largest supplier to world markets. Large-scale distribution of these dominant species of tunas is associated with the phytoplankton availability and abundance [Lee et al., 2005]. The need to understand the long-term trends in phytoplankton blooms in response to the rising temperatures can hardly be overemphasized.

2. Data and Methods

The chlorophyll data is obtained from version 2 of the European Space Agency's Ocean Color-Climate Change Initiative (OC-CCI) (S. Sathyendranath et al., Creating an ocean-colour time series for use in climate studies: The experience of the ocean-colour climate change initiative, submitted to *Remote Sensing of Environment*, 2016). The OC-CCI data is generated from merged normalized remote-sensing reflectances from multiple-satellite sensors (Sea-viewing Wide Field-of-view Sensor, Moderate Resolution Imaging Spectroradiometer, and Medium-Resolution Imaging Spectrometer). This brings the number of years of continuous data up to 16 years, bringing it close to the time required to extract trends in the tropical oceans including the western Indian Ocean [Beaulieu et al., 2013; Henson et al., 2010]. In order to validate the robustness of the satellite data, in situ data from Teledyne/Webb APEX—Argo floats deployed in the Arabian Sea—are used [Ravichandran et al., 2012]. See Text S1 and Figure S1 in the supporting information for details on observed data and validation.

Along with the extended array of satellite data, the historical simulations of chlorophyll derived by a suite of Earth system models participating in the Coupled Model Intercomparison Project phase 5 (CMIP5; Table S1 in the supporting information) [Taylor et al., 2012] facilitate long-term trend analysis (>50 years). However, many of the CMIP5 models fail to represent the spatial variability of mean chlorophyll concentrations in the Indian Ocean, particularly the western region which is a robust (coastal and open ocean) upwelling zone (Text S2 and Figures S2 and S3). Hence, a subset of models with pattern correlation coefficients (PCCs) above 0.4 (Table S1), which reasonably represent the spatial variability of chlorophyll in the Indian Ocean, are selected for examining the trends. This subset of models is used for preparing an ensemble mean of the chlorophyll trends. However, among the selected subset of models, many do not exhibit an interannual

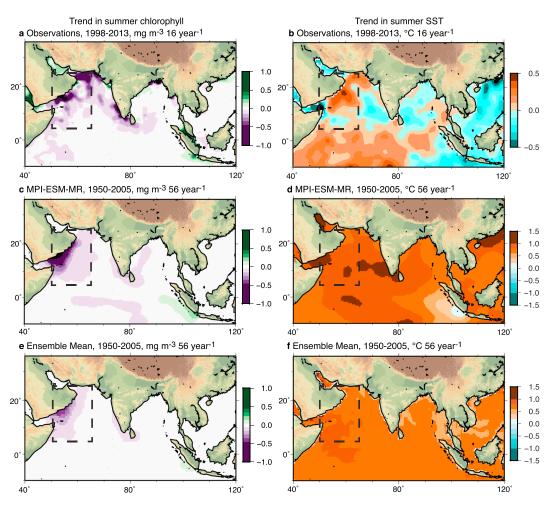


Figure 2. Chlorophyll and SST trend in (a and b) observations and historical simulations of (c and d) MPI-ESM-MR and (e and f) ensemble mean of selected five models, during summer. The inset box (50-65°E, 5-25°N) indicates the region under consideration, with the largest trends in chlorophyll concentrations.

variability comparable to observations (Figure S4). This will be a limitation as the response to climate variability will be weak in these models. Hence, based on interannual variability (standard deviations) and PCC, we have selected a single model to examine the biophysical response to increased warming, the Max-Planck-Institut-Earth system model-medium resolution (MPI-ESM-MR) [llyina et al., 2013].

MPI-ESM-MR simulates the mean climatology of chlorophyll concentrations with a relatively lower bias and realistic spatial distribution in the Indian Ocean, particularly in the Arabian Sea where the primary production as well as the surface warming is most prominent. This model is also found to be skillful in simulating the mean state of the physical variables including SST and winds in the Indian Ocean [Prasanna, 2015], which are crucial in driving the chlorophyll variability on both interannual and long-term climate time scales in this monsoon-driven basin (Figure S5). See Text S2 and Figures S2-S5 for more details on model validation and selection. It is however to be cautioned that CMIP5 historical simulations are forced with the historical changes in greenhouse gas mixing ratios and aerosol concentrations, and represent the response to increasing temperatures alone, but will not have coincident interannual variability. CMIP5 simulations can hence be compared for climatologies and trends but not for year-to-year variations.

In order to further delineate the causal role of SST warming on the chlorophyll concentrations, a sensitivity experiment using an Earth system model with interactive biogeochemistry (Indian Institute of Tropical Meteorology Earth system model (IITM-ESM)) [Swapna et al., 2014] is performed. In the sensitivity experiment, positive SST anomalies similar to those in the observed SST trends were added to the Indian Ocean and the biophysical response is evaluated (see Text S3 for details).

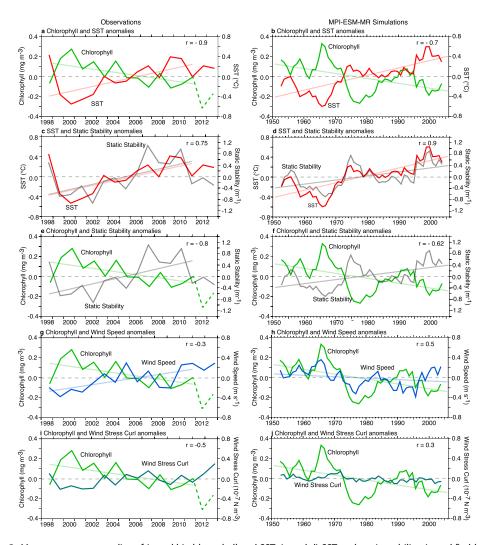


Figure 3. Mean summer anomalies of (a and b) chlorophyll and SST, (c and d) SST and static stability, (e and f) chlorophyll and static stability, (g and h) chlorophyll and wind speed, and (i and j) chlorophyll and wind stress curl in the western Indian Ocean ($50-65^{\circ}$ E, $5-25^{\circ}$ N; inset box in Figure 2), in (left) observations and (right) MPI-ESM-MR historical simulations. Positive wind stress curl anomalies indicate upwelling. All trend lines shown are statistically significant (P < 0.05). Dashed line in observed chlorophyll time series indicates the period with data uncertainty (see Methods). Note that the historical simulations are forced with changes in greenhouse gases alone, and can be used for comparing climatologies and trends, but not for year-to-year variations.

3. Results

A spatial distribution of the chlorophyll trends computed from the observations and the historical simulations indicate negative trends in the western Indian Ocean (Figure 2). Interestingly, the extremes in the observed chlorophyll trends also follow the large-scale spatial distribution of the observed trends in SST, with a significant reduction in chlorophyll in the western Indian Ocean where the warming is large, and a slight increase in values in the southeastern Indian Ocean where the surface warming is suppressed. This indicates that the dynamical processes driving the SST trends must also be affecting the primary production. It may appear that the largest negative trends in chlorophyll are not at the exact locations where the largest trends in SST occur. This is not unexpected, as the largest changes in chlorophyll (Figure 2) are over regions where the mean values are also large (Figure 1a). Figure 2a shows a mean decrease of up to 30% in the observations (P < 0.05). The MPI-ESM-MR and ensemble mean historical simulations indicate negative trends, similar to observations, and suggest a reduction of 20% (P < 0.05) during the past six decades (Figures 2c and 2e).

The MPI-ESM-MR simulations are further employed for an extended analysis on long-term trends in chlorophyll and related physical entities. Time series of chlorophyll, SST, static stability, and wind speed anomalies

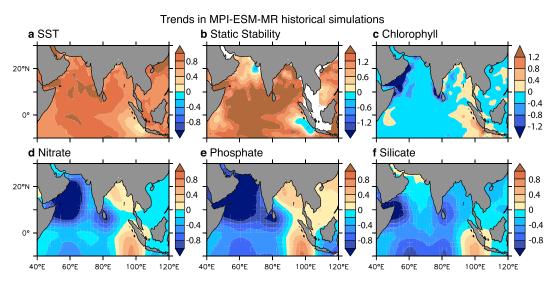


Figure 4. Trends in (a) SST ($^{\circ}$ C); (b) static stability; (c) chlorophyll (mg m $^{-3}$); and (d-f) nitrate (μ mol L $^{-1}$), phosphate $(10^{-1} \mu mol L^{-1})$, and silicate ($\mu mol L^{-1}$) anomalies in the MPI-ESM-MR historical simulations for June–September, during 1950-2005 (56 years).

are computed for the region (50-65°E, 5-25°N; inset box in Figure 2) where the trends in chlorophyll concentrations are the largest. SST and chlorophyll anomalies during the past several decades exhibit a significant trend, and a strong correlation between these two variables (r = -0.9 in observations and r = -0.7 in MPI-ESM-MR; P < 0.05), indicating the larger role of SST trends in the Indian Ocean being detrimental to marine primary production (Figures 3a and 3b). Rising surface temperatures can reduce chlorophyll because they are an indication of increased surface stratification and hence suppressed vertical mixing of nutrient-rich subsurface waters [Behrenfeld et al., 2006]. Density difference between the surface and subsurface layers provides a useful measure of stratification and can be represented by the static stability parameter [Behrenfeld et al., 2006; Dave and Lozier, 2013; Pond and Pickard, 1983] (Text S1). Summer mean anomalies of the static stability exhibit increasing trends indicating enhanced stratification of the western Indian Ocean under rising surface temperatures (r=0.75 in observations and r=0.9 in MPI-ESM-MR; Figures 3c and 3d). Further, the stratification is strongly correlated with the changes in chlorophyll (r = -0.8 in observations and r = -0.62 in MPI-ESM-MR; Figures 3e and 3f). These results clearly link the rising Indian Ocean SSTs to increased stratification and subsequent reduction in marine primary productivity over the region, during the past half century.

It is also possible that a changing monsoon circulation and winds [Roxy et al., 2015b] affect the chlorophyll variability by influencing the upwelling dynamics over the region [Goes et al., 2005]. An examination of the wind speed anomalies over the western Indian Ocean indicates a relatively weak correlation with the chlorophyll anomalies (Figures 3g and 3h). Also, the long-term change over the same region is only about 0.2 m s⁻¹ (Figure 3h), which is minor compared to an SST trend of 0.6°C during the same period (Figure 3b). The wind stress curl anomalies do not show any significant trends (Figures 3i and 3i), indicating that trends in the wind-induced upwelling and associated changes in chlorophyll are trivial during this period. In fact, the results indicate a strengthening of winds in the recent decade, which should have favored an increase in the nutrients and chlorophyll, but the correlation during this period is negative. It is obvious that increasing SSTs are playing a larger role than the changing winds, contrary to what earlier studies have proposed, albeit for relatively shorter-term records [Goes et al., 2005; Gregg et al., 2005].

The MPI-ESM-MR historical simulations also provide estimates of available nutrients, which can be used to investigate whether the nutrients are indeed decreasing as a result of reduced mixing due to warmer surface waters. Trend analyses of nitrate, phosphate, and silicate concentrations indicate that the nutrient availability has reduced in the western Indian Ocean and around the southern tip of Indian peninsula, regions where the chlorophyll concentrations have also gone down (Figure 4). At the same time, there is an increase in nutrient availability and chlorophyll concentrations in the southeastern Indian Ocean where the corresponding SSTs show suppressed surface warming. The anomalous increase of chlorophyll in this region may be due to the decreasing stratification (Figure 4b) driven by faster rates of warming in the subsurface relative to the surface [Dave and Lozier, 2013].



To further delineate the causal role of the Indian Ocean warming on chlorophyll variability, model sensitivity experiments were carried out using an Earth system model with an interactive ocean biogeochemistry [Swapna et al., 2014] (Text S3 and Figure S6). On a large spatial scale, the results are similar to the changes observed in the MPI-ESM-MR historical simulations. Clearly, the enhanced warming has resulted in weakened nutrient mixing and a reduction of chlorophyll concentrations over most of the Arabian Sea, affirming the conclusions drawn above from observations and a CMIP5 model.

4. Discussion

Earlier studies on changes in chlorophyll had described the western Indian Ocean as among the open ocean regions with the largest increase in marine phytoplankton but based on relatively short-term records. In the recent decades, the coastal winds over this region have strengthened, and ideally, this should enhance the nutrient mixing and phytoplankton blooms. On the contrary, the current study using quality-controlled blended chlorophyll data and Earth system model simulations points out an alarming decrease of up to 20% in marine phytoplankton during the past six decades. The observations indicate that the phytoplankton decline is large during the past 16 years, with a decrease of up to 30%. We find that these trends in chlorophyll are driven by enhanced ocean stratification due to the rapid warming in the Indian Ocean, which suppresses nutrient mixing from subsurface layers.

While the current study demonstrates a decreasing trend in chlorophyll (during 1998-2013), why did the earlier studies [e.g., Goes et al., 2005] indicate an increasing trend in the chlorophyll concentrations (during 1998–2005)? On a closer inspection, the time series in Figure 3 indeed shows a slight increase in chlorophyll during 1998-2005. This trend is dominated by the changes during the years 1998-1999 which saw large El Niño-Southern Oscillation variability—which has a strong association with the SST anomalies in the western Indian Ocean [Yu and Rienecker, 1999; Murtugudde et al., 2000]. Specifically, 1998 was a strong El Niño year which warmed up the western Indian Ocean, immediately followed by La Niña conditions in the year 1999 which cooled the region. This can be observed as a large dip in SST from 1998 to 1999, perfectly matched with an increase in the chlorophyll anomalies during this period [Murtugudde et al., 1999]. If 1998–1999 is treated as an outlier, the entire time series indicates a secular trend of decreasing chlorophyll concentrations. Apart from this, a major difference with Goes et al. [2005] is that their study considers only the coastal region of the western Arabian Sea (47–55°E, 5–10°N), where the biophysical processes are dominated by strong coastal dynamics, entrainment, advection, and river runoff [Vialard et al., 2011]. Meanwhile, the current study employs a much larger region (50-65°E, 5-25°N) including the open basin where coastal processes are less of a player but the large-scale monsoon forcing is dominant and the effect of wind and stratification changes on chlorophyll is easier to detect.

Establishing relationships between a warming Indian Ocean and primary productivity relies heavily on the accuracy to which changes in the phytoplankton distribution can be detected. Unfortunately, the chlorophyll concentration discerned by satellites or models is only a gross indicator of a multitude of phytoplankton species which have a fairly diverse response to environmental alterations [Huisman et al., 2006]. Other than warming temperatures, plankton fluctuations may also occur due to the limiting effects of light, zooplankton grazing, and viral infection [Behrenfeld, 2014]. Nevertheless, the extended satellite data and the state-of-the-art model simulations used in our study provide a quantitative and causal evaluation of the overall chlorophyll trends and allow for a general understanding of the changes in marine primary productivity in a monotonically warming Indian Ocean.

Available data show that the tuna catch rates in the Indian Ocean have declined by 50-90% during the past five decades [Myers and Worm, 2003; Polacheck, 2006] (Figure S7). Increased industrial fishery is a major cause for such a huge decline. However, the reduced phytoplankton may add up as a potential stress factor in the recent decades and exploiting a resource that may be in decline can tip it over to a point of no return. Despite a long-term decline in the tuna catch rates, there is a slight increasing trend in the catch rates in the recent decades during which the chlorophyll concentrations decreased, which suggests that ecosystem responses in the food web are complex, especially when highly migratory species are involved. Careful data gathering is needed to understand the totality of the ecosystem response to changing stratification, especially in terms of the fishery yields and disease pressures. It is however definitive that the Indian Ocean is warming, and CMIP5 future simulations project a further decline in marine primary productivity in the coming decades [Bopp et al., 2013] (Figure S8). This is a



cautionary tale considering that ecosystems can extract even weak climate links [Taylor et al., 2002] and human activities are providing increasingly strong climate forcing. The Indian Ocean may thus need to be monitored more closely to see if it is acting as an early indicator of physical-biological interactions in a warming world.

Acknowledgments

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