

RESEARCH LETTER

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Key Points:

- Monsoon and ENSO teleconnections regulate Red Sea greenness
- Earth system processes unexpectedly result in a warmer but more fertile Red Sea
- The Red Sea chlorophyll is controlled by the intensity of winter monsoons

Supporting Information:

- Readme
- Figure S1
- Figure S2
- Figure S3
- Text S1

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Monsoon oscillations regulate fertility of the Red Sea

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Abstract Tropical ocean ecosystems are predicted to become warmer, more saline, and less fertile in a future Earth. The Red Sea, one of the warmest and most saline environments in the world, may afford insights into the function of the tropical ocean ecosystem in a changing planet. We show that the concentration of chlorophyll and the duration of the phytoplankton growing season in the Red Sea are controlled by the strength of the winter Arabian monsoon (through horizontal advection of fertile waters from the Indian Ocean). Furthermore, and contrary to expectation, in the last decade (1998–2010) the winter Red Sea phytoplankton biomass has increased by 75% during prolonged positive phases of the Multivariate El Niño–Southern Oscillation Index. A new mechanism is reported, revealing the synergy of monsoon and climate in regulating Red Sea greenness.

1. Introduction

In tropical oceanic ecosystems, phytoplankton growth in the euphotic layer is controlled primarily by the supply of nutrients. Monsoon winds reverse their direction biannually over the Indian Ocean, driving one of the Earth's most dynamic interactions between atmosphere, oceans, and continents [Clemens *et al.*, 1991]. This reversal has a profound influence on phytoplankton growth and biogeochemical processes as it facilitates nutrient input to the nutrient-depleted waters of the Arabian Sea [Smith *et al.*, 1998; Clemens *et al.*, 1991; Goes *et al.*, 2005]. The seasonal monsoon reversal is evident in the southern half of the Red Sea and the Gulf of Aden [Patzert, 1974] and is known to influence the local physical oceanographic processes [Murray and Johns, 1997; Sofianos and Johns, 2003; Aiki *et al.*, 2006; Johns and Sofianos, 2012]. Lack of riverine input and negligible precipitation mean that the nutrient-depleted ecosystem of the Red Sea relies principally on the horizontal intrusion of nutrient-rich waters from the Indian Ocean (through the Gulf of Aden) [Murray and Johns, 1997; Johns and Sofianos, 2012; Churchill *et al.*, 2014; Triantafyllou *et al.*, 2014], whereas in the northern end of the basin, nutrient enrichment is related to deep vertical mixing (winter convection and presence of a permanent cyclonic feature) [Sofianos and Johns, 2003; Triantafyllou *et al.*, 2014]. The reversal of the wind direction, during the onset of the winter monsoon, promotes the northward advection of nutrient-rich waters into the Red Sea [Murray and Johns, 1997; Johns and Sofianos, 2012]. The high mountains on the African and Arabian Peninsula constrain these surface winds orographically to blow parallel to the longitudinal axis of the Red Sea [Patzert, 1974; Jiang *et al.*, 2009]. Thus, the topography channels the northward propagation of the watermass from the Gulf of Aden (Figure S1 in the supporting information). The monsoon reversal in winter is reflected in the seasonal succession of the Red Sea phytoplankton [Raitsos *et al.*, 2013].

The Red Sea basin is a major economic asset to the region. At its southern end lies one of the most important straits in the world ocean, Bab-el-Mandeb, which provides the shortest commercial waterway between the Atlantic and Indian Oceans [Johns and Sofianos, 2012]. Therefore, the physics of the Red Sea—including circulation and water exchange with the Indian Ocean—have been well studied, in contrast with the paucity of knowledge on the biological processes [Acker *et al.*, 2008]. The only data source to investigate trends in the large-scale biological dynamics in the Red Sea is satellite-derived chlorophyll [Acker *et al.*, 2008; Brewin *et al.*, 2013]. Here we reveal profound and abrupt alterations in interannual variability of Red Sea phytoplankton and, furthermore, provide evidence that attributes these changes to a new mechanism involving the broader climate and monsoons.

2. Materials and Methods

The remotely sensed chlorophyll data set (Sea-Viewing Wide Field-of-View Sensor (SeaWiFS), vR2010.0, level 3, monthly and 8 day binned products, 9 km resolution) were produced and acquired by the NASA Ocean Biology Processing Group (<http://oceancolor.gsfc.nasa.gov/>). Recent evaluations of different ocean color products indicated that the precision and accuracy of Red Sea chlorophyll is of adequate quality and falls within the global mission standards [Acker *et al.*, 2008; Brewin *et al.*, 2013; Labiosa *et al.*, 2003]. SeaWiFS offers the necessary requirements for ocean biogeochemistry and climate research, and it provides the longest and the highest-quality ocean color data record to date [McClain, 2009]. We also used SeaWiFS, as it is the longest single-sensor ocean color data set, providing very good coverage during the winter season (and less coverage in summer primarily due to atmospheric issues in the Southern Red Sea [Raitos *et al.*, 2013]). Remotely sensed chlorophyll data have known limitations especially in optically complex waters, where particulate and/or dissolved organic matter do not covary in a predictable manner with chlorophyll [Morel and Gentili, 2009]. Therefore, chlorophyll data may be influenced (generally resulting in an overestimation) by the factors mentioned above, especially in the coastal waters and/or very shallow waters of the Red Sea. However, not all the coastal high chlorophyll values are necessarily erroneous, as the large coral reef complexes may be sources of either nutrients or chlorophyll-rich detritus that enhance phytoplankton production near the reefs [Acker *et al.*, 2008; Raitos *et al.*, 2013].

The phytoplankton phenology (timings of initiation and termination of phytoplankton growth) was estimated using the long-term median threshold criterion [Racault *et al.*, 2012, 2015]. The median threshold criterion used herein to estimate the timings of initiation and termination of the phytoplankton growth was selected based on the following: (1) its robustness to large variability in the shapes of the main phytoplankton growing period [Siegel *et al.*, 2002; Racault *et al.*, 2012] and (2) its close comparativeness with another method that is not based on a threshold criterion (e.g., the rate of change method [Brody *et al.*, 2013]). The duration of the phytoplankton growth was calculated as the time elapsed between initiation and termination. The timing of peak in phytoplankton annual cycle is observed when chlorophyll concentration reaches maximum amplitude.

Quik Scatterometer version 4 (QuikSCAT-v4) monthly mean wind fields ($1/4^\circ$) were acquired from www.remss.com/data/qscat, the National Centers for Environmental Prediction (NCEP)/National Center for Atmospheric Research (NCAR) monthly reanalysis global zonal winds from <http://www.esrl.noaa.gov/psd/data/correlation/datasets.html>, the Multivariate ENSO Index (MEI) monthly data from <http://www.esrl.noaa.gov/psd/enso/mei/>, and the advanced very high resolution radiometer (AVHRR) nighttime (for methods see Raitos *et al.* [2011]) monthly sea surface temperature (SST) means (Pa V5) from <http://podaac.jpl.nasa.gov/AVHRR-Pathfinder>.

We constructed the net surface current (Ekman + geostrophic) and Ekman volume transport using satellite-derived wind and geostrophic current data (see Text S1 in the supporting information for detailed methods). We assessed the influence of several other climate indices on Red Sea chlorophyll, such as the Indian Ocean Dipole (IOD), which principally influences chlorophyll signals in Arabian Sea, but we did not find a relationship. In support with our findings, Currie *et al.* [2013] reported that El Niño–Southern Oscillation (ENSO) (and not IOD) variability is predominantly related to chlorophyll in the western Arabian Sea.

Anomalies in time series were computed as the difference between the values of a given year minus the overall mean.

3. Results and Discussion

Red Sea chlorophyll (as seen from space) has changed significantly in the last decade (Figure 1a). In particular, seasonality in chlorophyll (high to low from winter to summer) changed abruptly in 2002, as a result of a wintertime (October to April) enhancement in chlorophyll concentration, and to a lesser extent by a summertime decrease. The winter mean of Red Sea chlorophyll (Figure 1a) has increased significantly ($r=0.8$, $p=0.0001$), and after 2002 the average concentrations have shifted upward by 75% (compared to the pre-2002 era).

As the abrupt increase in the 2002 winter concentrations occurred during an El Niño event (positive MEI phase), we investigated the hypothesis that interannual variability in Red Sea chlorophyll and MEI are related (Figure 1b). The SeaWiFS-derived chlorophyll anomaly of the Red Sea clearly parallels the MEI variability to a significant degree ($r=0.71$, $p=0.003$). During negative MEI phases, the annual chlorophyll anomaly remains below the overall mean, whereas, when MEI shifts to a positive phase, it lies above the overall mean values

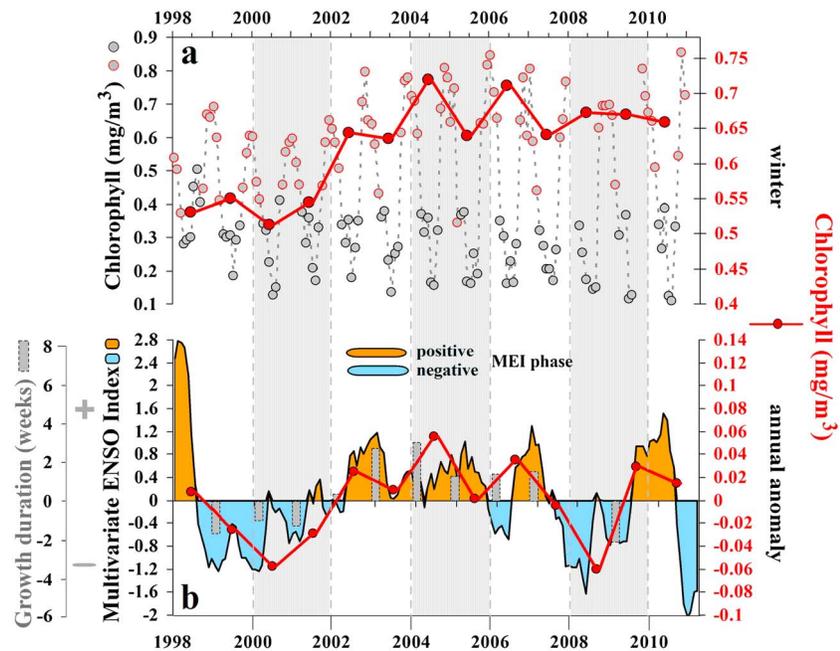


Figure 1. Interannual variability of Red Sea phytoplankton in relation to Multivariate ENSO Index (MEI). (a) Monthly (dashed line) and winter (red solid line) averages of chlorophyll concentration (mg/m^3) in the Red Sea. (b) The annual chlorophyll (red solid line) and growth duration (in weeks—grey vertical column) anomalies parallel the MEI oscillations (orange-blue shaded line).

(Figure 1b). In addition to the strong coherence between the interannual variability of Red Sea chlorophyll and MEI, the phenology (bloom timing) is also altered. Phenology is important because a delay in the initiation and shortening in duration of the main seasonal bloom may reduce survival of fish larvae, due to starvation during their most vulnerable stage [Platt *et al.*, 2003]. It appears that during positive (negative) MEI phases, the phytoplankton growth duration is prolonged (shortened) by 2 weeks on average (grey vertical columns in Figure 1b). These alterations in duration are due to an earlier initiation in growth of phytoplankton, rather than a delayed termination.

In the tropics generally, stronger thermal stratification during a positive MEI phase (warmer period) reduces vertical mixing (nutrient supply) and thus limits phytoplankton growth [Doney, 2006]. However, the opposite is seen in the Red Sea ecosystem. To examine the mechanism driving this relationship, we explore next the differences in the intensity of winter net surface currents, monsoon (wind-induced horizontal advection of nutrients), and chlorophyll during consecutive periods of inverse MEI phases.

During the summer season (May to September) the prevailing northwesterlies in the Red Sea exhibit no significant variations, whereas the sea surface temperature (SST) attains a high level with maximum $\sim 33^\circ\text{C}$ (Figure 2a). In winter (October to April) the wind direction and the net surface currents are abruptly reversed over the southern half of the Red Sea (Figures 2b–2d). Further examination on the seasonal reversal of net surface currents shows clearly that during winter the surface flow remains northward, whereas the direction reverses (southward) abruptly in May (Figure S2). The winter surface currents in the Southern Red Sea facilitate the northward advection of colder nutrient-rich waters from the Gulf of Aden.

To investigate whether oscillations in MEI phase reflect alterations in the southeasterlies and surface flow (during winter monsoon), we examined differences in winter wind speed, and Ekman volume transport between two consecutive periods of negative (1999–2001) and positive MEI phases (2002–2004). The volume transport in the southern Red Sea and the Gulf of Aden indicates higher flux during the winter 2002–2004 period, with a general westward/northward flow in the Gulf of Aden/Southern Red Sea, as inferred from the average net surface current (Figure 3a). Further investigation of the surface flow in the southern Red Sea clearly shows stronger northward surface current during the positive MEI phase (Figure S3). Differences in wind speed between the two periods are similar to volume transport (Figure 3b). At about 19°N there is a strong convergence zone that marks the boundary between the monsoon-dominated atmosphere in the

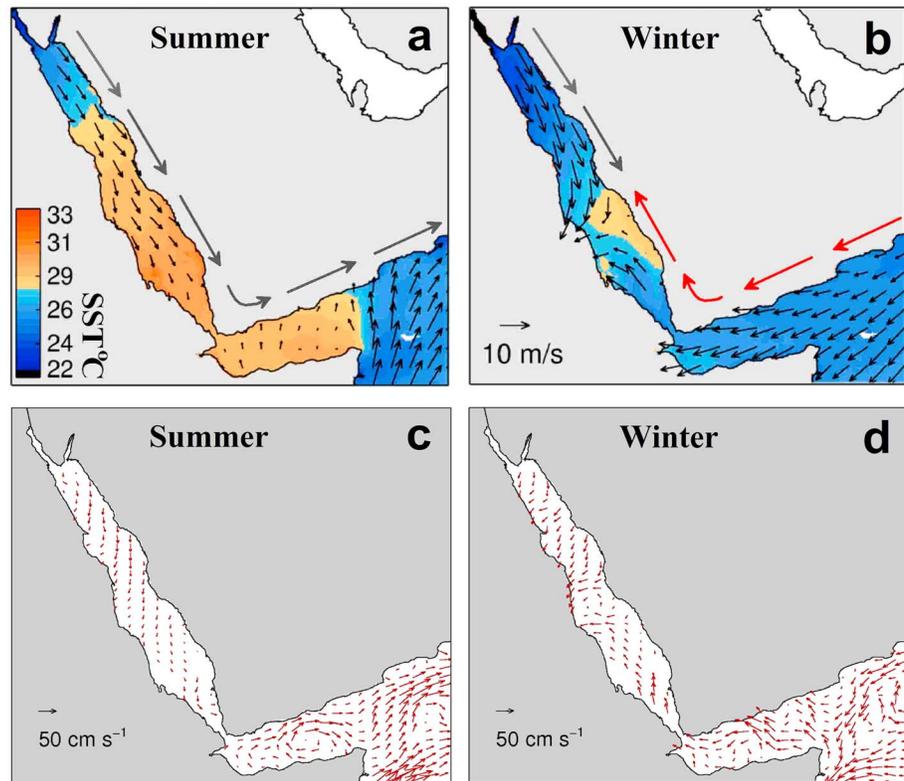


Figure 2. Climatology of wind magnitude, SST, and net surface currents averaged during summer and winter seasons (monsoonal reversal). (a, b) Climatology of wind speed (m/s), wind direction, SST, and (c, d) net surface current (cm/s) during summer and winter. A noticeable change in wind speed, direction, and net surface currents is observed during the winter season (October to April) in the southern half of the Red Sea (northward flow) and the Gulf of Aden (westward). This sudden wind reversal is responsible for the surface nutrient-rich waters influx into the Red Sea.

south and the midlatitude continental atmospheric circulation in the north [Papadopoulos *et al.*, 2013]. The prevailing winds in the northern half of the Red Sea remain predominantly southward with no significant seasonal variations in direction, and their intensity appears to decrease during positive MEI phases (Figures 3a and 3b). In contrast, in the southern half of the Red Sea, the winter Ekman volume transport and southeasterly winds are intensified during positive MEI phases (Figures 3a and 3b), facilitating the northward horizontal advection, and consequently enhancing the phytoplankton biomass and growth duration almost everywhere in the Red Sea (Figures 3c and 3d). The growth duration is on average 2 weeks longer (earlier initiation), and the duration may locally increase up to 10 weeks (Figure 3d). Interestingly, the only area that does not conform to this pattern is the convection area (western part of the northern Red Sea),

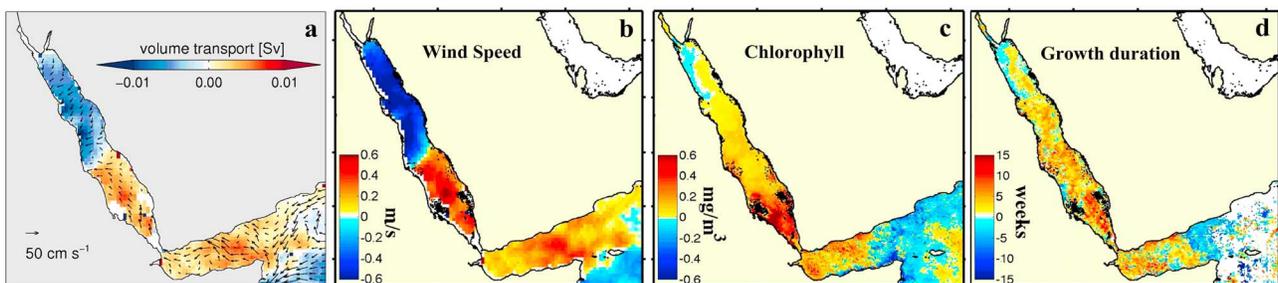


Figure 3. Comparison of water volume transport, surface wind, and chlorophyll concentrations in the Red Sea and the Gulf of Aden between two consecutive periods of negative (1999–2001) and positive MEI phases (2002–2004). Differences in winter (a) Ekman volume transport, (b) wind speed, (c) chlorophyll concentrations, and (d) growth duration between two opposed MEI phases (2002–2004 minus 1999–2001). Note that the net surface current vectors in Figure 3a represent the overall mean of the wintertime net surface flow.

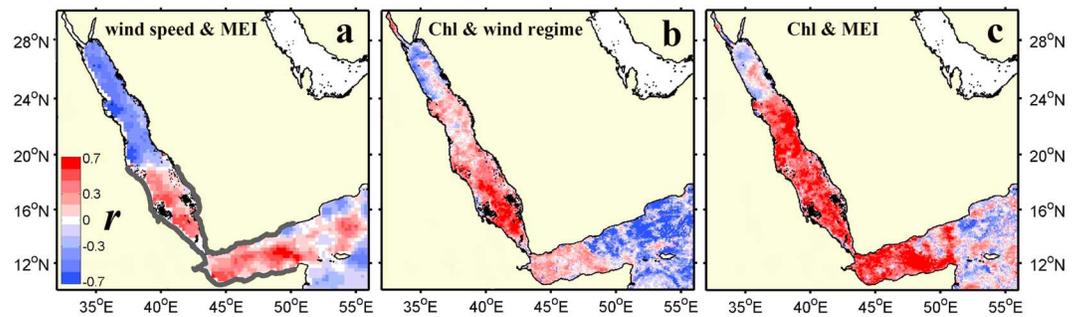


Figure 4. Correlation coefficient (r) between annual anomalies of wind speed, chlorophyll concentrations, and MEI during 10 years of concurrent satellite-derived data sets (2000–2009). (a) The annual wind speed anomalies and MEI are significantly related, indicating that during positive MEI phases the wind speed is intensified over the southern half of the Red Sea and the Gulf of Aden (grey contour line along the coast). This area is characterized by seasonal monsoon reversal and is responsible for nutrient facilitation. (b) Correlation between the wind index (average wind over the grey contour coastline area) and chlorophyll concentrations. (c) Correlation between Red Sea chlorophyll concentrations and MEI.

where phytoplankton growth depends on vertical transport of nutrients controlled by deep convection/upwelling [Sofianos and Johns, 2003; Triantafyllou *et al.*, 2014]. This area follows the typical regime seen in the tropics, where warmer conditions lead to higher thermal stratification, which in turn limits the vertical transfer of nutrients to the illuminated surface, thus reducing phytoplankton concentration [Behrenfeld *et al.*, 2006; Doney, 2006].

We have demonstrated alterations of the winter wind regime, surface flow, and the chlorophyll response (Figures 3 and S3) between two opposed MEI phases—these periods include La Niña and El Niño events (in 1999 and 2002, respectively) [Wolter and Timlin, 2011]. However, this is an indirect way to investigate the apparent mechanistic link between monsoons, MEI and chlorophyll. Taking advantage of 10 years of concurrent satellite-derived data sets, we have also examined the direct relationships between the annual anomalies of wind speed, chlorophyll, and MEI (Figure 4). A positive MEI intensifies the annual wind speed anomalies over the southern Red Sea and Gulf of Aden, whereas the opposite relation is found for the northern half of the Red Sea (Figure 4a). The southern wind regime (averaged wind speed over the area surrounded by the grey contour—Figure 4a) covaries positively with the Red Sea chlorophyll (Figure 4b). It is evident that alterations in the southern wind regime influence the chlorophyll nearly everywhere in the Red Sea, with the exception of the northernmost part. Similarly, the interannual variability of the Red Sea chlorophyll parallels significantly the MEI oscillations (Figure 4c).

There is a growing interest in identifying links between global climate indices and biological processes [Behrenfeld *et al.*, 2006; Martinez *et al.*, 2009]. For instance, ENSO influences the global climate on seasonal to interannual time scales [Wolter and Timlin, 2011] and it is known to have profound impacts on every trophic level of the marine ecosystem [Behrenfeld *et al.*, 2006; Chavez *et al.*, 2003]. The MEI provides a more complete and flexible description of ENSO events compared with other indices, because it encompasses information about variations of coupled ocean-atmosphere processes [Wolter and Timlin, 2011]. Positive phases of MEI have been shown to be associated with a warmer global climate [Wolter and Timlin, 2011; Reid and Beaugrand, 2012]. The observed tight coupling between Red Sea chlorophyll and MEI is different from the type of climate-plankton relationships that have been reported earlier for the tropics [Behrenfeld *et al.*, 2006; Doney, 2006]. Using disparate data sets, we describe the mechanistic link between climate, ocean physics, and biological response in the hitherto relatively unexplored Red Sea ecosystem (schematized in Figure 5). The regression between zonal winds and MEI for the winter season shows a clear negative relationship over the Arabian Sea and Gulf of Aden (Figure 5a), indicating that during elevated MEI periods the easterlies in the Gulf of Aden are strengthened. During positive (negative) MEI phases, the easterlies that control the horizontal nutrient inflow from the Arabian Sea are intensified (reduced) (Figure 5b). We conclude that strengthening (weakening) of this wind regime enhances (reduces) the surface chlorophyll concentrations by ~50% on average (Figure 5c).

ENSO oscillations influence the entire Indian Ocean (including Arabian Sea and Gulf of Aden), through a well-established atmospheric bridge [Alexander *et al.*, 2002]. Yu and Rienecker [1999] observed a sea surface

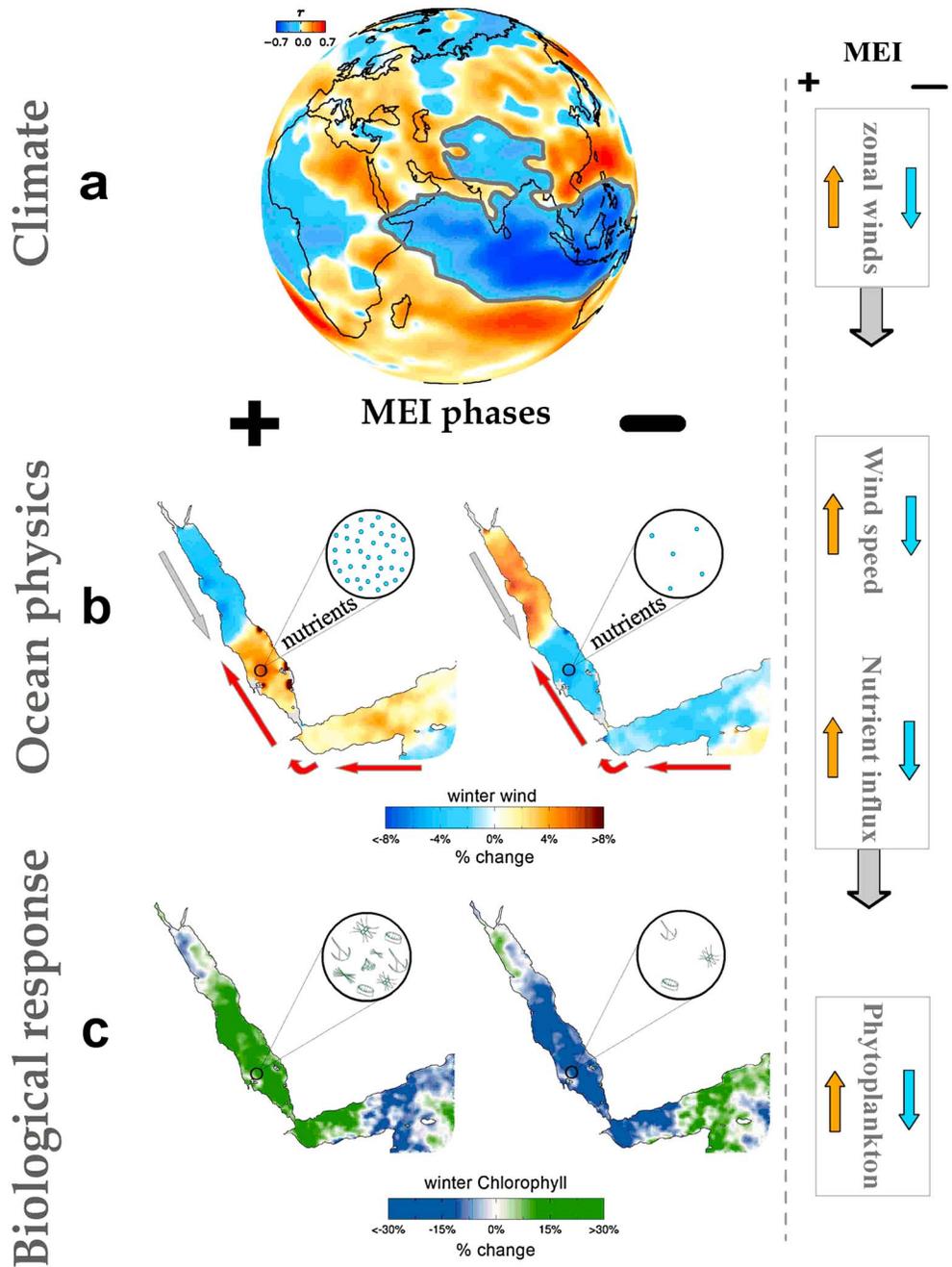


Figure 5. Mechanistic link between climate variability, ocean physics, and the biological response in the Red Sea ecosystem. (a) Correlation between winter zonal winds and MEI (1950–2010). The grey contour line, highlights the influence of MEI on the zonal winds (strong negative correlation). The negative correlation indicates that during positive MEI phases the easterlies in the Gulf of Aden are enhanced. (b) Differences in the percentage of change of winter wind speed between negative and positive MEI phases (2002–2004 minus 1999–2001). During positive (negative) MEI phases, the easterlies that control the horizontal nutrient inflow from the Indian Ocean are intensified (reduced). The regional circulation distributes the nutrient-rich waters up to the northern Red Sea. (c) Differences in the percentage of change of winter chlorophyll between negative and positive MEI phases (2002–2004 minus 1999–2001). The strengthening (weakening) of the winter wind enhances (reduces) the surface chlorophyll concentrations (mg/m^3) by 50% on average.

height (SSH) dipole during strong positive ENSO phases attributed to enhanced easterlies along the equatorial Indian Ocean. Stronger than usual easterlies, displaced north of the equator, drive sea water masses westward, increasing SSH over the western ocean boundary. This could explain the stronger inflow of the Indian Ocean water entering the Red Sea during MEI positive phase (Figure S3).

4. Conclusions

Our results raise the possibility that warmer climate conditions could make the Red Sea ecosystem more productive, contrary to what may have been expected [Behrenfeld *et al.*, 2006; Doney, 2006]. This is because a large part of the Red Sea ecosystem depends on horizontal advection (wind induced) of nutrients. We show that during warmer global climate phases (positive MEI), although higher thermal stratification is expected in the Red Sea, the winds are also intensified significantly, amplifying the transfer of nutrient-rich waters from the Indian Ocean. The frequency of El Niño events is predicted to increase due to global warming [Cai *et al.*, 2014]. Although our findings are of immediate importance to regional African and Arabian Peninsula fisheries, our insights have broader implications for other ecosystems globally. We evidence that tropical ecosystems may not rely exclusively on convective vertical nutrient transfer, highlighting the importance of changes in the horizontal (wind-induced) advection of nutrients on productivity under a warmer climate scenario. Recent studies in the global oceans challenge the fundamental stratification/productivity paradigm [Dave and Lozier, 2013] and emphasize the importance of the horizontal advection on nutrient levels [Lozier *et al.*, 2011; Hartman *et al.*, 2010]. The Red Sea ecosystem encompasses both examples—the predominantly advection-dependent part of the basin and the northernmost convection-dependent area. Alterations in phytoplankton biomass and bloom timing (as we show here) may have important ramifications for trophic interactions that may influence food-web structures and lead to eventual ecosystem-level changes [Platt *et al.*, 2003; Richardson and Schoeman, 2004; Chavez *et al.*, 2011]. Higher phytoplankton blooms due to favorable climatic conditions enhance food supply to larval fish and therefore survival rates [Lo-Yat *et al.*, 2011], especially when the food availability appears earlier (as seen in Red Sea during positive MEI phases). Although these mechanisms were proposed more than 100 years ago for temperate latitudes, restriction of technology and data sets meant it was only recently that these relationships could be tested, thanks to the advent of remotely sensed information [Platt *et al.*, 2003]. It is vital that these high-quality satellite data sets are maintained long into the future.

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