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Nutrient, Phytoplankton and Zooplankton Variability in the Indian Ocean

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Abstract

This chapter provides an overview of the physical and biogeochemical factors that control spatial and temporal variability in macro- and micro-nutrient concentrations, phytoplankton biomass and production, and zooplankton biomass and grazing in the Indian Ocean. As in other ocean basins, in the Indian Ocean there is a strong connection between the physics that drives (or suppresses) nutrient delivery to the photic zone and responses of phytoplankton and zooplankton. Wind forcing during the Southwest/Southeast Monsoon (boreal summer, austral winter) is a major biogeochemical and ecological driver with broad stimulatory effects throughout many regions, including the Arabian Sea, Bay of Bengal, Seychelles Chagos Thermocline Ridge, Java, and the central/eastern subtropical gyre. In contrast, substantial stimulatory response to the Northeast/Northwest Monsoon (boreal winter, austral summer) is manifested primarily in the Arabian Sea and Bay of Bengal. In addition, there are regionally specific processes that significantly modulate the biogeochemical and ecological responses. For example, strong advective impacts and Fe/Si limitation in the Arabian Sea; freshwater and stratification in the Bay of Bengal; the influence of Indonesian Throughflow nutrient inputs, poleward transport, downwelling and seaward-propagating eddies in the southeastern Indian Ocean; and alongshore-propagating eddies, meanders, upwelling and poleward transport in the southwestern Indian

Ocean. The southern subtropical gyre is extremely oligotrophic except when/where the Southeast Madagascar bloom occurs. Recommendations for future work include the need to reassess the potential effects of climate change on the biogeochemistry and ecology of the Indian Ocean basin, and motivate more planktonic food web studies.

Keywords: Indian Ocean, Arabian Sea, Bay of Bengal, Indonesian Throughflow, Leeuwin Current, Agulhas Current, Southern Subtropical Gyre, Mozambique Channel, Seychelles Chagos Thermocline Ridge, Sri Lanka Dome, Java Upwelling, South Equatorial Current, nutrients, nitrate, phosphate, silicate, iron, oxygen, salinity, stratification, zooplankton, microzooplankton, grazing, oxygen minimum zone.

1. Introduction

The northern Indian Ocean experiences strong monsoonal wind forcing that reverses seasonally due to seasonal heating and cooling over the Eurasian land mass (Schott and McCreary, 2001; Shankar et al., 2002; Schott et al., 2009). As a result, all of the boundary currents in the northern Indian Ocean also reverse seasonally which is unique among ocean basins. The combination of winds, boundary currents, and remote forcing from Kelvin waves drives localized regions of upwelling during the Southwest Monsoon (SWM) and downwelling (as well as buoyancy-driven convection) during the Northeast Monsoon (NEM). In addition, the partitioning of the northern basin of the Indian Ocean by the Indian subcontinent, combined with substantial differences in evaporation, precipitation, river runoff and connectivity to marginal seas, gives rise to large differences in salinity and stratification between the Arabian Sea and Bay of Bengal, which might otherwise be expected to have similar water masses. The surface waters of the Bay of Bengal are much fresher and more stratified than in the Arabian Sea. The northern Indian Ocean is also unique in having one of three major open-ocean oxygen minimum zones (OMZs) as well as large dust and aerosol inputs that occur all year round from both natural (Pease et al., 1998; Leon and Legrand, 2003; Guieu et al., 2019) and anthropogenic sources (Lelieveld et al., 2001; McGowan and Clark, 2008).

Unlike in the easterly trade-wind forced Pacific and Atlantic Oceans, upwelling in the equatorial Indian Ocean is not persistent because the mean winds along the equator are toward the east driving convergent rather than divergent Ekman transport (Schott et al., 2009; Wang and McPhaden, 2017). However, off-equatorial upwelling in the Seychelles-Chagos Thermocline Ridge (SCTR) and the Sri Lankan Dome is geographically extensive and persistent. The equatorial Indian Ocean is strongly influenced by oscillations and perturbations unique to it, such as the Wyrтки Jets and the Indian Ocean Dipole (IOD), as well as by the Madden-Julian Oscillation (MJO) which originates in the Indian Ocean (Madden and Julian, 1972). The equatorial region further influences the Indian Ocean more broadly through coastal Kelvin waves generated along the equator by the Wyrтки Jets that affect the eastern equatorial Indian Ocean and the northern boundary currents (Schott and McCreary, 2001; Shankar et al., 2002; Schott et al., 2009; Hood et al., 2017).

In the southeastern tropical Indian Ocean, the Indonesian Throughflow (ITF) connects the Pacific and Indian Ocean basins, altering water mass properties through exchanges of heat and freshwater (Schott and McCreary, 2001) and biogeochemical water mass properties through exchanges of nutrients (Talley and Sprintall, 2005; Ayers et al., 2014). Presumably, the ITF also influences Indian Ocean ecosystems directly through passive and active transport of plankton and other higher trophic levels from the Pacific and the Maritime Continent, but this has not been investigated.

The southern Indian Ocean subtropical gyre is an oligotrophic ocean habitat. To the north, the South Equatorial Current (SEC) transports warm, nutrient-enriched freshwater from the ITF across the basin (Schott and McCreary, 2001). To the east, the Leeuwin Current is a small downwelling-favorable current that is anomalous in being the global ocean's only poleward-flowing eastern boundary current and in having the largest eddy kinetic energy among all mid-latitude eastern boundary current systems (Hood et al., 2017). Combined with the topographic influence of the Ninety East Ridge, the SEC and Leeuwin Current generate numerous westward-propagating eddies (Gaube et al., 2013; Waite et al., 2007a) and unusual circulation patterns. To the west, the Agulhas Current is an unusually large, poleward-flowing, "upwelling-favorable" western boundary current (Bryden et al., 2005; Hood et al., 2017). To the south, the gyre is bounded by the Antarctic Circumpolar Current.

2. Nutrient, phytoplankton and zooplankton variability

Variability in nutrients and plankton communities in the Indian Ocean is strongly influenced by the physical characteristics, and by land-ocean coupling in different regions, which are presented separately as: 1) the Arabian Sea and the northwestern Indian Ocean; 2) the Bay of Bengal; 3) the equatorial Indian Ocean including the Java Upwelling and SCTR; 4) the eastern Indian Ocean and Leeuwin Current; 5) the southwestern Indian Ocean and Agulhas Current; and 6) the southern subtropical gyre.

2.1 Arabian Sea and the northwestern Indian Ocean

2.1.1 Macro Nutrients

During the SWM, strong upwelling occurs in the western Arabian Sea off Somalia, Yemen and Oman (Figure 1), where near-surface nitrate and silicate concentrations can increase to $>15 \mu\text{M}$ and phosphate to $>1 \mu\text{M}$ (Morrison et al., 1998). However, environmental conditions vary dramatically over the coastal to open-ocean gradient, with mixed-layer nitrate, silicate and phosphate all declining to very low concentrations offshore (Gupta and Naqvi, 1984; Mantoura et al., 1993; Morrison et al., 1998; Moffett et al., 2015; Moffett and Landry, 2020; Rixen et al., 2009). Inorganic nitrogen-to-phosphate ratios tend to be lower than the Redfield ratio of 16:1, suggesting that nitrogen is a more limiting nutrient than phosphorus (Morrison et al., 1998; Figure 1). Nitrogen to silicate ratios tend to be higher ($\sim 2:1$) than the uptake ratio (1:1) for diatom growth, suggesting the potential for silicate limitation of diatoms during the SWM (Morrison et al., 1998; Rixen et al., 2009; Figure 1). Modeling studies further indicate that

phytoplankton growth in SWM upwelled waters in the western Arabian Sea is prone to limitation by silicate (Koné et al., 2009; Resplandy et al., 2011) and/or iron (see section 2.2.2 below).

SWM winds and the southward-flowing West India Coastal Current in the eastern Arabian Sea also promote upwelling that outcrops at the surface along the west coast of India. This upwelling is most pronounced between $\sim 8^\circ$ N and 14° N (Shetye et al., 1990; Smitha et al., 2014) and gives rise to elevated nitrate, phosphate and silicate concentrations in the near surface layers (Hood et al., 2017), though this is not very evident in Figure 1. The Laccadive Low that develops off the southwest coast of India during the SWM is an anticyclonic upwelling circulation that is evident in sea surface height (SSH) (Bruce et al., 1998; Shankar and Shetye, 1997; Subrahmanyam and Robinson, 2000) but does not appear to have a strong influence on surface nutrient concentrations (Lierheimer and Banse, 2002; Figure 1).

Winds and circulation shift to downwelling favorable during the NEM. However, cooling and deep buoyancy-driven convection entrain nutrients that promote modest euphotic zone increases in nitrate, phosphate and silicate over much of the northern Arabian Sea (Wiggert et al., 2000; Koné et al., 2009; McCreary et al., 2009; Resplandy et al., 2012; Figure 2).

Between 200 and 400 m depth, denitrification in the central and western Arabian Sea OMZ reduces nitrate concentration to $\sim 20 \mu\text{M}$ (Figures 3 and 4) and nitrite concentration increases to $\sim 5 \mu\text{M}$ (Figure 2 in Moffett et al., 2015; Rixen et al., 2020), with nitrification also contributing to the latter (Li et al., 2006). The signature of denitrification is relatively low (<10) N:P ratios in these waters (Figures 3 and 4). Estimates of denitrification rates in the OMZ are still fraught with large uncertainties and amount to $\sim 7\text{-}16 \text{ Tg N yr}^{-1}$ according recent estimates (Rixen et al., 2020; Gaye et al., 2013). Moreover, the relative contributions and the regulating mechanisms regarding N_2 gas production and release by either anammox or [denitrification](#) are highly variable and still debatable in different oceans/regions ([Ward et al., 2009](#); [Dähnke and Thamdrup, 2016](#); [Choi et al., 2016](#)), and the anammox reaction has been shown to be an important sink for fixed nitrogen in other OMZs ([Dalsgaard and Thamdrup, 2002](#); [Dalsgaard et al., 2005](#); [Arrigo, 2005](#)). However, denitrification is the dominant loss process in the Arabian Sea (Ward et al., 2009). Therefore, the low nitrate and high nitrite concentrations emphasize the role of the OMZ as a significant sink for fixed nitrogen in the Arabian Sea due to denitrification.

Nitrogen fixation has been intensively studied in the eastern Arabian Sea, and according to the few estimates for the entire Arabian Sea, it contributes a modest 3.3 Tg N yr^{-1} (Ahmed et al., 2017; Bange et al., 2000; Parab and Matondkar, 2012). The modelling study of Guieu et al. (2019) suggests that nitrogen fixation displays strong seasonality in the Arabian Sea, mirroring the distribution of atmospheric iron deposition which is highest during the NEM (see next section), with maximum rates observed in the central and eastern Arabian Sea. However, the new nitrogen input from nitrogen fixation constitutes a small fraction (less than 1%) of primary production.

2.1.2 Iron

Iron concentrations in the Arabian Sea are influenced by dust from the Arabian Peninsula and India, redox processes associated with the oxygen minimum zone (OMZ), biological scavenging

and possibly hydrothermal inputs from the Gulf of Aden (Guieu et al., 2019; Moffett and German, 2020). Seasonal variability arises because biological scavenging and dust inputs are strongly influenced by the NEM and SWM. During the NEM, dust inputs (Pease et al., 1998; Tindale and Pease, 1999) elevate surface Fe and Al throughout the Arabian Sea (Measures and Vink, 1999). During the spring and fall inter-monsoon (SIM, FIM), dust deposition is lower than in winter (Pease et al., 1998; Tindale and Pease, 1999), but there is little biological scavenging of Fe due to prevailing oligotrophic conditions. Surprisingly, the SWM is the period of lowest Fe deposition (Tindale and Pease, 1999).

In the suboxic core of the OMZ, high levels of iron accumulate (Figures 5 and 6) as reduced Fe(II). Local Fe maxima coincide with the secondary nitrite maxima (Moffett et al., 2007, 2015; Kondo and Moffett, 2013; Figures 5 and 6), suggesting a relationship between Fe redox cycling and denitrification that has yet to be identified. Fe(II) and total dissolved Fe decrease outside the OMZ. Reductive mobilization of iron within the OMZ is probably an important mechanism for Fe supply from the Indian continental margin to the Arabian Sea interior (Moffett et al., 2015).

Naqvi et al. (2010) observed that chlorophyll-*a* (Chl*a*) and Fe:N conditions in the Omani upwelling region in 2004 were consistent with Fe limitation of primary production. Most importantly, the Arabian Sea becomes strongly depleted in Si relative to N during the SWM (Figure 1). Preferential depletion of Si relative to N is a powerful diagnostic of Fe limitation in upwelling systems like Central California and southern Peru, which overlie narrow shelves and resemble the Oman upwelling regime (Hutchins et al., 1998, 2002; Johnson et al., 1999). Moffett et al. (2015) showed that Chl*a* responded strongly to added Fe compared to controls in the central Arabian Sea during the 2007 SWM. The strongest response was at stations with high nutrients and low SST associated with filaments of upwelled coastal water from Oman. Nitrate was high ($\geq 6 \text{ mmole m}^{-3}$) but Si was depleted in most samples. Most of the growth was due to non-siliceous species, particularly the haptophyte *Phaeocystis*. Results were consistent with the modeling study of Wiggert et al. (2006), which predicted an intensifying region of Fe limitation in the western Arabian Sea through the SWM and into October (Figure 7). Modeling results of Guieu et al. (2019) suggest that without atmospheric Fe inputs through dust deposition during the SWM, annual net primary production would be reduced by half.

2.1.3 Phytoplankton

Ocean color images over the Arabian Sea show a seasonal cycle of phytoplankton characterized by two distinct growth periods, one in summer during the SWM, the other in winter during the NEM. The bloom areas during the SWM and the NEM show different regional patterns, with lags in bloom timing (Lévy et al., 2006). Due to upwelling, the western margin of the Arabian Sea transitions to a eutrophic coastal upwelling system during the SWM (Wiggert et al., 2005; Lévy et al., 2007; Hood et al., 2017; Figures 8 and 9). Satellite ocean color reveals dramatic Chl*a* increases along the coasts of Somalia, Yemen and Oman (Brock and McClain, 1992; Banse and English, 2000; Kumar et al., 2000; Lierheimer and Banse, 2002; Wiggert et al., 2005; George et al., 2013; Hood et al., 2017; Figure 8). They also show that the coastal SWM bloom onset occurs as early as March-April, peaks during the SWM and coincides spatially with wind-driven upwelling. Further offshore away from the direct influence of the upwelling, the bloom initiates one month later and is co-located with a pattern of deep-mixed layers (Lévy et al., 2007). The

modelling study of Resplandy et al. (2011) shows that the central Arabian Sea bloom is largely explained by lateral and vertical eddy supplies of nitrate associated with filaments originating from the coastal upwelling region, which is consistent with observations (Rixen et al., 2006a),

Vertically-integrated Chla in the western Arabian Sea can exceed 40 mg m⁻² during the SWM, with production rates of 2.5 gC m⁻² d⁻¹ (Marra et al. 1998; Wiggert et al., 2005; Hood et al., 2017; Figure 9). However, in the oligotrophic offshore waters, Chla and primary production decline dramatically (Brown et al., 1999; Wiggert et al., 2005; Hood et al., 2017; Figures 8 and 9). In the western Arabian Sea, larger cells (diatoms) dominate phytoplankton community structure during the SWM (Brown et al., 1999; Tarran et al., 1999; Shalapyonok et al., 2001), while picophytoplankton (e.g., *Prochlorococcus sp.*) predominate during the oligotrophic SIM and FIM periods (Garrison et al., 2000; Roy et al., 2015). During all seasons, subsurface Chla maxima occur between 40 and 140 m in the central southeastern Arabian Sea (Gundersen et al., 1998; Ravichandran et al., 2012; Figure 10), in some places below the oxyclines of the OMZ (Goericke et al., 2000).

During the SWM, topographically-locked eddies off Oman, Yemen and Somalia advect high Chla concentrations and coastal phytoplankton communities hundreds of kilometers offshore into more oligotrophic waters (Keen et al., 1997; Latasa and Bidigare, 1998; Manghnani et al., 1998; Gundersen et al., 1998; Roy et al., 2015; Hitchcock et al., 2000; Lee et al., 2000; Kim et al., 2001; Figure 8), which is also revealed by ocean-color images and models (Resplandy et al., 2011).

During the NEM, offshore waters are subject to shear and buoyancy-driven convection associated with cold dry northeasterly winds, driving mixing that entrains nutrients and increases Chla and primary production over the northern Arabian Sea (Wiggert et al., 2000, 2005; Lévy et al., 2007; Resplandy et al., 2011; Hood et al., 2017; Figures 8 and 9). The amplitude of this winter bloom varies between years and is significantly tied to the interannual winter mixed-layer depth anomaly (Keerthi et al., 2017). Convective mixing during the NEM in the northern Arabian Sea inhibits picoplankton (specifically *Prochlorococcus*) growth (Roy and Anil, 2015). Resplandy et al. (2011) suggests that, in addition to convective mixing, nearly 50% of NEM productivity could be sustained by eddy-driven vertical nutrient supplies. The NEM increases in Chla and primary production were associated with diatoms in early studies (Banse and McClain, 1986; Sawant and Madhupratap, 1996). However, *Phaeocystis* was first reported in Si-deficient upwelled waters in the central Arabian Sea during the JGOFS Arabian Sea Study (Garrison et al., 1998). Recent observations suggest a broader climate change-induced regime shift in the composition of winter phytoplankton blooms from diatoms to *Noctiluca scintillans*, a large mixotrophic dinoflagellate (Gomes et al., 2014; Goes et al., 2020). Indeed, *Noctiluca* and *Phaeocystis* blooms have become more common and widespread (Gomes et al., 2009). A succession from diatoms to *Phaeocystis* associated with Si removal may be common during the late SWM (Madhupratap et al., 2000).

SWM upwelling along the west coast of India gives rise to modest increases in Chla and primary production compared to the central Arabian Sea (Kumar et al., 2000; Naqvi et al., 2000; Luis and Kawamura, 2004; Lévy et al., 2007; Hood et al., 2017; Figures 8 and 9). In this region, upwelling is primarily forced by remotely-generated planetary waves, and secondarily by local winds (Shankar and Shetye, 1997; Shankar et al., 2002). This upwelling is associated with increased diatom abundance (Sawant and Madhupratap, 1996).

During the NEM, winds and currents along western India are downwelling-favorable, suppressing primary production most notably along the southwestern coast. Nutrient depletion in this region coincides with blooms of *Trichodesmium* and dinoflagellates during the NEM (Parab et al., 2006; Matondkar et al., 2007). Vertically-integrated Chla and primary production off western India decrease from ~ 24 to ~ 9 mg Chla m^{-2} and from ~ 2.25 to ~ 1 g C $m^{-2} d^{-1}$, respectively, from the SWM to NEM (Luis and Kawamura, 2004; Hood et al., 2017; Figures 8 and 9).

A comparison of the phytoplankton bloom cases reported before and after the 1950s (data from 1908 to 2009; D'Silva et al., 2012) reveals an increase in the number of algal bloom occurrences along the west coast of India, especially the southern part. The majority of these were caused by dinoflagellates. There have been 39 causative species responsible for the blooms, of which *Noctiluca scintillans* is one of the most common.

Satellite estimates of Chla and primary production are low year-round off southwestern India in the Laccadive Sea despite the transition from NEM downwelling (cyclonic) to SWM upwelling (anticyclonic) circulations (Lierheimer and Banse, 2002; Hood et al., 2017; Figures 8 and 9).

2.1.4 Zooplankton

Mesozooplankton sampling in the Arabian Sea has highlighted the relative seasonal constancy of biomass over much of the region, known as the “Arabian Sea Paradox” because it runs counter to expectations for a system with dramatic seasonal contrasts from intensive upwelling to subtropical oligotrophy (Madhupratap et al., 1992; Baars, 1999). During JGOFS, for example, biomass estimates in the northeastern Arabian Sea were 1.1 g C m^{-2} (upper 1000 m) in both coastal and oceanic waters during the SWM and NEM and slightly higher during the SIM (1.3-1.9 g C m^{-2} ; Smith and Madhupratap, 2005). Distributions of biomass and species at mid-water depths vary with the presence or absence of the OMZ (Wishner et al., 2008). In the western Arabian Sea, coastal stations averaged only 60% higher biomass in the upper 200 m compared to offshore (1.4 vs 0.9 g C m^{-2} , respectively) over four seasonal cruises, with ~ 2 -fold higher biomass during the SWM (1.5 vs 0.7 g C m^{-2}) and the peak shifting offshore during the NEM and SIM (Wishner et al., 1998). Along the same sampling transect, protistan microzooplankton (heterotrophic nanoflagellates, dinoflagellates and ciliates) averaged 0.52 ± 0.25 g C m^{-2} (upper 100 m), with similar ~ 2 -fold seasonal variability at individual stations but with biomass peaks shifting (opposite to mesozooplankton) to coastal stations during the late NEM and SIM (Garrison et al., 2000). In the eastern central sector, higher protistan biomass occurs both in coastal and open-ocean waters during the SIM compared to the SWM and NEM (Gauns et al., 1996). However, in the southeastern Arabian Sea ($15^{\circ}N$, east of $65^{\circ}E$), both microzooplankton abundances and mesozooplankton biomass are highest during the SWM (Jyothibabu et al., 2008a, 2010).

To first order, the observed Arabian Sea zooplankton biomass patterns are consequences of physical drivers and circulation features that connect primary production to zooplankton consumers. In the western Arabian Sea, fast currents, eddies and filaments disperse nutrients, production and zooplankton widely over the central and northern region (Baars, 1999; Kumar et al., 2001; Manghnani et al., 1998; Smith and Madhupratap, 2005; Resplandy et al., 2011). Nutrient entrainment by deep convective mixing during the NEM stimulates a second

productivity peak that sustains high zooplankton stocks over a broad region during winter (Banse and McClain, 1986; Madhupratap et al., 1992; 1996a,b). While productivity shows some seasonal variation between these peaks, it is notable that primary production during JGOFS exhibited only a 3-fold total range (0.8–2.4 g C m⁻² d⁻¹) among the 10 stations visited on 5 seasonal cruises, with only a 37% difference between the SIM and higher NEM and SWM averages (1.0 vs 1.6 g C m⁻² d⁻¹; Barber et al., 2001). South of 15°N, however, the southeastern Arabian Sea differs from the seasonally and spatially distributed productivity of the northern and western areas in being strongly stratified by the inflow of low salinity Bay of Bengal water during the NEM, which suppresses convective mixing and results in oligotrophic conditions in offshore waters for much of the year. Thus, zooplankton variability there aligns with the seasonal productivity peak driven by upwelling and river runoff during the SWM (Asha Devi et al., 2010; Jyothibabu et al., 2010).

Microzooplankton dominate Arabian Sea grazing processes, consuming an average of 71% of primary production for all coastal to offshore measurements during JGOFS (Reckermann and Veldhuis, 1997; Landry et al., 1998; Caron and Dennett, 1999; Edwards et al., 1999; Marra and Barber, 2005; as summarized in Landry, 2009). High microzooplankton grazing (58–97% of production) was also estimated for a eutrophic estuary during the SWM (Gauns et al., 2015). In a JGOFS synthesis of food web fluxes (Landry, 2009), carbon consumption by microzooplankton was 8 times higher than their grazing on heterotrophic bacteria (the “microbial loop”, Azam et al., 1983). Mesozooplankton, in turn, derived ~40% of their nutritional requirements (Roman et al., 2000) from predation on microzooplankton. Importantly, however, the relative grazing contributions of micro- and mesozooplankton are not fixed but vary seasonally and spatially in ways that modulate total impact in a manner consistent with hypothesized grazing control of phytoplankton biomass in the Arabian Sea (Smith, 2001; Marra and Barber, 2005). Where mesozooplankton biomass is highest in the coastal upwelling area during the SWM (coincident with large phytoplankton), their predatory pressure significantly diminishes the relative grazing impact of microzooplankton. When the mesozooplankton grazing peak shifts offshore during the NEM, microzooplankton grazing increases closer to the coast and the balance of production and grazing is maintained. Such dynamical flexibility is key to the idea of spatially separated co-regulation by iron and grazing in the Arabian Sea as suggested by Moffett and Landry (2020).

2.2 Bay of Bengal

2.2.1 Nutrients

The effects of the monsoon winds and associated currents are more cryptic in the Bay of Bengal due to weaker winds and large freshwater inputs from northern rivers (i.e., the Ganges-Brahmaputra and Irrawaddy). Most (95%) of the inorganic nitrogen and phosphorus loads are removed before the rivers reach the coast, with the remaining nutrients utilized within 10 km from the coast (De Sousa et al., 1981; Sarma et al., 2013a,b; Krishna et al., 2015). Freshwater in the Bay of Bengal surface layers leads to strong salinity stratification (Vinayachandran et al., 2009, Kumar et al., 2007; Wijesekera et al., 2016) that inhibits vertical mixing and upwelling processes (Gomes et al., 2000; Vinayachandran et al., 2002, 2005, 2009; Thushara et al., 2019). Coastal upwelling occurs along eastern India during summer (June to August) due to SWM

winds, but strong stratification prevents surface outcropping of nutrients in the northern Bay of Bengal (Shetye et al., 1991, 1993; Sarma et al., 2012, 2015).

In general, nutrient concentrations are much lower in the Bay of Bengal than the Arabian Sea, resulting in strong nutrient limitation of phytoplankton growth (Koné et al., 2009). In contrast to the Arabian Sea, there is little or no enhancement of climatological surface nitrate, phosphate or silicate concentrations in the Bay of Bengal coastal zones during the SWM (compare Figures 1 and 2). Nonetheless, nutrient ratios in east Indian coastal waters (11-15° N) over all seasons (molar ratios N:P<16; Si:P>7 and N:Si<1) indicate that nitrogen and silicate are the primary limiting nutrients (Thangaradjou et al., 2014). In the central Bay of Bengal, climatological nitrate, phosphate and silicate concentrations are all undetectable down to ~75 m (Figure 11, Baer et al., 2019). An interesting feature of the nutrient distributions is apparent in Figure 11, in which nitrate and phosphate are depleted below the primary nutricline between 100 and 200 m depth from 5 to 19°N leading to a local minimum imbedded within high nutrient conditions in the vertical. The cause of this feature is unknown. It does not co-occur with elevated fluorescence that might be associated with a secondary deep chlorophyll maximum (DCM) located within low oxygen waters that might serve as a refuge from predation (Figure 13).

Nutrient limitation experiments in the Bay of Bengal indicate that N is the primary limiting nutrient for autotrophic growth (Twining et al., 2019). However, experiments aimed at specific phytoplankton groups suggest a more complex, species-specific, nutrient-limitation mosaic, i.e., different phytoplankton groups can be limited by different nutrients (Twining et al., 2019). In addition, eddy-mediated processes have a strong influence on Bay of Bengal circulation (Sarma et al., 2020a) and euphotic zone nutrient concentrations and ratios (Kumar et al., 2007; Narvekar and Kumar, 2006; Nuncio and Kumar, 2013; Vidya and Kumar, 2013; Jyothibabu et al., 2015; Mahadevan, 2016). High N:P ratios (~25) observed in offshore upwelling eddies indicate the potential for phosphate limitation of phytoplankton growth, though these high ratios appear to have been observed in only one study (Sarma et al., 2020b).

In the southern Bay of Bengal, vertical stratification is weaker because of reduced riverine influence. As a result, monsoon-forced mixing and upwelling are strong enough to bring nutrients into the euphotic zone (Vinayachandran and Mathew, 2003; Vinayachandran, 2004; Vinayachandran et al., 2005; Lévy et al., 2006; 2007; Jyothibabu et al., 2015). The southern coasts of India and Sri Lanka are characterized by intense upwelling of nutrients during the SWM (Vinayachandran, 2004; Levy et al., 2007; de Vos et al., 2014). In addition, SWM winds drive open-ocean upwelling of nutrients in the Sri Lanka Dome east of Sri Lanka (Vinayachandran and Yamagata, 1998; Vinayachandran, 2004; Thushara et al., 2019). However, the impacts of these upwelling features are not readily apparent in climatological SWM surface nitrate, phosphate and silicate concentrations (Figure 1), suggesting rapid consumption by phytoplankton in the DCM (Figure 13). Indeed, direct measurements off southern Sri Lanka from August to October 2015 revealed only a small enhancement of surface nutrients (Thushara et al., 2019). Similarly, model simulations of the Sri Lanka Dome during the SWM reveal a distinct shoaling of the nitracline (2 mmol m⁻³ isoline) to 20 m, but with little surface nutrient enhancement (Thushara et al., 2019).

While oxygen is exceedingly low in the Bay of Bengal, surface oligotrophic conditions result in low export of carbon for bacterial consumption at depth which may limit the formation of a suboxic OMZ (for details on this topic see Hood et al., 2022b, this volume). There is no significant water-column denitrification (Naqvi et al., 2006; Bristow et al., 2017), but there is Fe enrichment in the OMZ (Figure 12) as in the Arabian Sea (Figure 6), which suggests that Fe can be mobilized and transported even in the absence of water-column denitrification. Recent surveys (Grand et al., 2015a,b,c; Chinni et al., 2019; Vu and Sohrin, 2013) show strong depletion of Fe in surface waters, consistent with Figure 6. However, prevailing oligotrophic conditions result in production limitation by macronutrients rather than Fe (Twining et al., 2019).

2.2.2 Phytoplankton

While strong salinity stratification generally depresses primary production in the Bay of Bengal, there are regions of elevated *Chla* and production associated with river plumes, upwelling eddies and where the monsoonal forcing can overcome the stratification (Lévy et al., 2006, 2007; Vinayachandran, 2009; Thushara et al., 2019). In general, *Chla* and primary production rates are elevated close to the coast, particularly off river mouths, with highest values occurring during the season of peak discharge (Vinayachandran, 2009; Figures 8 and 9). Along the Indian coast, the flow of *Chla* rich water is determined by the East Indian Coastal Current (EICC), which flows northward during the SIM and SWM and southward during the FIM and NEM. When the EICC meanders seaward from the Indian coast, it leads to offshore *Chla* increases (Vinayachandran, 2009). Eddies in the EICC and in the open ocean sometimes have relatively high *Chla*, but those nearer to the coast are typically more enriched by offshore entrainment of high *Chla* coastal water (Vinayachandran, 2009). As in the Arabian Sea, dinoflagellate blooms are common in east Indian coastal waters in the Bay of Bengal, with variations in species abundance attributed to seasonal variations in the stratification (Naik et al., 2011a). Pigment measurements also reveal the importance of diatom blooms in east Indian coastal waters, whereas prokaryotes and flagellates tend to dominate phytoplankton species composition offshore (Naik et al., 2011b).

A second region of elevated *Chla* and primary production occurs offshore in the southwestern Bay of Bengal during the NEM (Vinayachandran and Mathew, 2003; Lévy et al., 2006, 2007; Vinayachandran, 2009). Modeling studies suggest that elevated surface *Chla* is caused by wind-driven entrainment of both subsurface nutrients and phytoplankton from the subsurface *Chla* maximum that is present during the FIM (Vinayachandran et al., 2005; Vinayachandran, 2009). In contrast, coastal productivity is suppressed during the NEM when the winds and southward flowing EICC are downwelling favorable. Subsurface *Chla* maxima ($0.3\text{--}1.2\text{ mg m}^{-3}$) occur throughout the Bay of Bengal wherever wind forcing and currents are insufficient to entrain them into surface layer (Sarma and Aswanikumar, 1991; Murty et al., 2000; Sarojini and Sarma, 2001; Kumar et al., 2007; Thushara et al., 2019; Figure 13). The depth and intensity of these maxima are strongly influenced by eddies (Kumar et al., 2007; Figure 13) that tend to shoal near the coast (Sarma and Aswanikumar, 1991; Murty et al., 2000).

Elevated *Chla* and primary production are also observed along southern Sri Lanka during the SWM, along with *Chla*-rich waters advected from southwestern India by the Southwest Monsoon Current (Vinayachandran, 2004; 2009; Lévy et al., 2006, 2007; de Vos et al., 2014;

Strutton et al., 2015; Hood et al., 2017; Thushara et al., 2019; Figures 8 and 9). Surface Chl a and primary production can exceed 10 mg m $^{-3}$ and 1 g C m $^{-2}$ d $^{-1}$, respectively, compared to much lower values during the NEM, when the westward-flowing Northeast Monsoon Current and winds favor downwelling (de Vos et al., 2014; Hood et al., 2017; Figures 8 and 9). Diatom blooms are likely responsible.

2.2.3 Zooplankton

Density stratification and low oxygen content of waters beneath the pycnocline strongly affect the depth distributions of most mesozooplankton species such that 70-80% of the Bay of Bengal biomass to 1000 m generally resides above the thermocline and mainly in a thin mixed layer (Fernandez, 2008; Fernandez and Ramaiah, 2014). Within this upper layer, zooplankton abundances and trophic interactions are likely more vertically concentrated in the Bay of Bengal than in other regions, even if integrated biomasses are similar or less. Moreover, low oxygen concentrations and reduced salinity in the Bay of Bengal are associated with lower species richness (Sutton and Beckley, 2017). Depth-integrated biomass estimates have a large range (<0.2 to 6.7 g C m $^{-2}$), with 3-20X variability within seasons (Fernandez, 2008; Fernandez and Ramaiah, 2009, 2013, 2014). For most seasons, zooplankton biomass variability reflects the productivity. Along the western (coastal) bay, Ramaiah et al. (2010) indicated a >10-fold seasonal difference in mean mesozooplankton biomass from the SWM minimum to SIM maximum (0.22 and 2.43 g C m $^{-2}$), with the FIM and NWM being intermediate (0.91 and 0.99 g C m $^{-2}$). However, in the southwestern coastal region, Muraleedharan et al. (2007) found that wind-driven upwelling and a cyclonic eddy during the SWM enhanced local biomass estimates by 7-fold and 4-fold, respectively, compared to stratified waters. Seasonal averages were more similar for a transect along 88°E, with a SWM minimum and FIM maximum (0.59 and 1.04 g C m $^{-2}$) and 0.81-0.82 g C m $^{-2}$ during the NWM and SIM. Both western coastal and central stations show strong south to north biomass increases during the SIM (Fernandez and Ramaiah, 2019). On the eastern side of the basin (Andaman Sea), seasonal variability in zooplankton standing stocks and production indices are small, despite pronounced differences in environmental conditions (Nielsen et al., 2004; Satapoomin et al., 2004; Pillai et al. 2014).

Gauns et al. (2005) documented substantially lower microzooplankton biomass in the western and central Bay of Bengal than in the eastern and central Arabian Sea during all monsoon seasons. Mean biomasses are highest during the SIM in both the central and western bay (0.33 and 0.23 g C m $^{-2}$, respectively), decline by ~one-third during the SWM (0.22 and 0.14 g C m $^{-2}$) and drop precipitously during the FIM (0.02 and 0.03 g C m $^{-2}$) before increasing again during the NWM (0.09 g C m $^{-2}$) (Jyothibabu et al., 2008b; Ramaiah et al., 2010).

Zooplankton grazing studies are extremely rare in the Bay of Bengal. Fernandez and Ramaiah (2014) estimated that herbivorous feeding by copepods accounted for ~25% of primary production during the NWM. In the sole study of microzooplankton grazing, consumption of phytoplankton production in shallow coastal waters off SW India (Kochi) varied from 80% during the SIM to 26% during an SWM upwelling bloom (Anjusha et al., 2018). Among key issues unexplored in regional food-web investigations are the nutritional sources and grazing pathways that sustain zooplankton stocks during different seasons. Isotope measurements have

suggested, for example, that zooplankton in river-influenced areas during the SWM might derive more food value from suspended detritus than phytoplankton (Mukherjee et al., 2018). High zooplankton biomass during the SIM has also been attributed to enhanced fluxes via the microbial loop (Madhupratap et al., 1996a; Jyothibabu et al., 2008b; Anjusha et al., 2013), but the magnitudes of grazing flows from heterotrophic bacteria and dominant picophytoplankton (e.g., Brown et al., 1999, 2002) have not been measured for any season.

2.3 Equatorial Indian Ocean including the Java upwelling and the SCTR

2.3.1 Nutrients

Unlike the Atlantic and Pacific, mean winds along the equator in the monsoon-dominated Indian Ocean are westerly and, therefore, predominantly downwelling favorable (Schott et al., 2009; Wang and McPhaden, 2017). As a result, near-surface waters along the equator tend to be oligotrophic, i.e., typically undetectable nitrate, phosphate and silicate down to ~100 m (Figures 4 and 11), and upwelling centers in the Indian Ocean are generally found in off-equatorial regions. One example is the Seychelles-Chagos Thermocline Ridge (SCTR), an upwelling region in the southern tropical Indian Ocean between ~ 5-15°S and ~50-80°E characterized by a thin (~30 m) mixed layer and relatively shallow thermocline (Vialard et al., 2009; Figures 4, 14). The thermocline ridge, and associated upwelling is driven by local wind stress curl (Xie et al, 2002; Hermes and Reason, 2008; Yokoi et al., 2008; McPhaden and Nagura, 2014; Nyadjro et al, 2017). The SCTR is coincident with the southernmost latitudes of monsoon-driven circulation in the Indian Ocean, south of which a steadier Trade Wind regime prevails. The SCTR influence on near-surface nutrients can be seen in Figure 4, where the nitricline, phosphocline and silicline shoal sharply at 20°S by 700 m over about 5° and remain near 100 m to the equator and beyond. This shoaling can also be seen in Figure 14 from Resplandy et al. (2009). Average nitrate concentration between the surface and 80 m depth exceeds 5 mmole m⁻³ in a bullseye centered at about 62°E, 8°S. The SCTR is the largest and most persistent upwelling region in the Indian Ocean.

The Java upwelling region off Indonesia is the only example of eastern boundary upwelling in the Indian Ocean. In contrast to the large eastern boundary upwelling in the Pacific and Atlantic Oceans, it occurs only seasonally during the SEM in association with the reversing South Java Current (Sprintall et al., 1999; Susanto et al., 2001) and, like the Bay of Bengal, is strongly influenced by freshwater inputs from the maritime Indonesian continent (Rixen et al., 2006b). Upwelling effects are strong along the coasts of the islands of Sumatra, Java, and Bali between ~5° and 10°S, and also influence the southern coasts of Lombok, Flores and Alor (Figure 10 in Hood et al., 2017). Nutrient measurements along a transect from the northwestern coast of Australia to Lombok Strait clearly show the upwelling signature off Java where elevated nitrate and phosphate concentrations (8 mmole m⁻³ and 0.8 mmole m⁻³, respectively) can extend to the surface near the coast (Figure 14 in Hood et al., 2017).

2.3.2 Phytoplankton

Satellite observations and model results reveal an annual cycle in surface Chl_a and primary production in the SCTR region, with highest values in austral winter (June-August; >0.20 mg m⁻³

and $>0.6 \text{ g C m}^{-2} \text{ d}^{-1}$, respectively, Figures 8 and 9) due to the strong southeasterly winds that increase wind stirring and induce upwelling (Resplandy et al., 2009; Dilmahamod, 2014). Vertical sections through the SCTR region also reveal a DCM that shoals and intensifies from $>100 \text{ m}$ at $18^{\circ}\text{S}, 55^{\circ}\text{E}$ to $\sim 50 \text{ m}$ at $10^{\circ}\text{S}, 55^{\circ}\text{E}$ due to upwelling (George et al., 2013; Figure 10).

There is significant seasonal variability in near-surface *Chla* and primary production in equatorial waters (10°N - 10°S) associated with monsoon forcing, with lowest concentrations ($<0.1 \text{ mg m}^{-3}$) and rates ($<0.8 \text{ g C m}^{-2} \text{ d}^{-1}$) occurring during the SIM (Figures 8 and 9, Wiggert et al., 2006; Strutton et al., 2015). During the SWM, *Chla* and production increase with wind mixing and upwelling in far western equatorial waters, but stay relatively low ($<0.5 \text{ mg m}^{-3}$, $<0.8 \text{ g C m}^{-2} \text{ d}^{-1}$, respectively) in the central and eastern equatorial waters. Island wake effects give rise to high *Chla* water ($>0.5 \text{ mg m}^{-3}$) advected eastward along the equator from the Chagos-Laccadive ridge at 73°E during the FIM and westward during the SIM by Wyrтки Jets (Figure 1 in Strutton et al., 2015).

Well-developed DCM are observed in the western, central and eastern equatorial Indian Ocean centered between 50 and 100 m (Sorokin et al., 1985; George et al., 2013; Figures 10 and 13). It is unknown whether this subsurface maximum exists along the equator throughout the year, but it is probably present whenever the water column is stratified. Models predict the presence of a deep (60 m) maximum along 87°E in eastern Indian Ocean equatorial waters throughout the year except when high *Chla* surface water is advected into the region from the west during the SWM (Wiggert et al., 2006). Pigment measurements indicate that prokaryotic cyanobacteria and flagellates dominate the flora in the central equatorial Indian Ocean (Naik et al., 2020).

Enhanced *Chla* and primary production are also observed along southern Indonesia during the SEM (Figures 8 and 9). Satellites reveal that elevated *Chla* ($>2 \text{ mg m}^{-3}$) first appears off Java in June and persists into November (Lévy et al., 2006, 2007; Hood et al., 2017), with primary production estimates in August exceeding $1 \text{ g C m}^{-2} \text{ d}^{-1}$ (Figure 9). Relaxation of SEM winds and downwelling Kelvin waves (Sprintall et al., 1999) suppress productivity in the fall. Satellite observations also reveal that upwelling-enhanced *Chla* progresses northwestward during the SEM and extends to southwestern Sumatra in September (Hood et al., 2017). These *Chla* and production responses are associated with diatom blooms (Yu et al., 2015; Hood et al., 2017; Romero et al., 2009).

The biogeochemistry of the equatorial Indian Ocean is strongly influenced by physical processes at intraseasonal to interannual time scales (i.e., Wyrтки Jets, MJO and IOD). For example, IOD events can significantly increase *Chla* and production in eastern equatorial waters, and it has been shown that relaxation of an IOD event can decrease biological productivity (Wiggert et al., 2009; Kumar et al., 2012; Currie et al., 2013; Marsac et al., 2022, this volume). In the SCTR region, wind-induced mixing during MJO episodes (typically between January and March) can also lead to enhanced *Chla* at intra-seasonal time scales; their efficacy is strongly related to basin-scale interannual variability of the thermocline depth (Resplandy et al., 2009; Dilmahamod et al., 2016).

2.3.3 Zooplankton

Although the central equatorial Indian Ocean and the off-equatorial SCTR and Java upwelling regions lack modern systematic plankton studies comparable to the Arabian Sea and Bay of Bengal, historical net sampling in these areas provides some basis for comparing their seasonality and relative magnitudes of mesozooplankton biomass (Figure 15). The narrow sampling band close to the equator (1°S - 2°N) shows lowest biomass during and following the NEM into March, ascending to \sim three times higher level for the remainder of the year, with no additional increase during the SWM. Given the general downwelling characteristics of this region, such a seasonal pattern may be more consistent with advective transport of zooplankton into the central equatorial area than local secondary production. Zooplankton communities dominated by calanoid copepods of the family Pontellidae (bright blue-pigmented calanoid copepods) have been observed at the ocean surface in the open equatorial Indian Ocean during the SWM (Venkataramana et al., 2017), which could also be related to advective transport.

In the SCTR upwelling area directly to the south (2 - 10°S), biomass is relatively low for most of the year with a pronounced four- to five-fold increase during the SEM upwelling in August (austral winter) (Figure 15). West of 60°E , in the SCTR area renowned for its tuna fishery, Gallienne et al. (2004) reported a 10-fold increase in optically-sensed zooplankton biovolume in April-May 2001 relative to subtropical waters to the south, which they attributed to upwelling production driven by the collision of the South Equatorial Current (SEC) with the shallow (20-200 m) ridge crest of the Mascarene Plateau. In addition to zooplankton biomass being elevated downstream (west) compared to upstream (east) of the Mascarene Plateau in June-July 2002 (3-6 fold over 12 - 19°S), it was also elevated 6-fold or more over the northern plateau compared to the southern part, increasing northwards from the gap between Saya de Malha and Nazareth Banks (13 - 14°S ; Gallienne and Smythe-Wright, 2005). A similar N-S contrast in zooplankton biomass (as well as phytoplankton biomass and particulate organic matter) was observed in October-November 2008, with mean values of 0.2 g C m^{-2} (max 1.3) over Seychelles Bank (4 - 6°S), 0.1 g C m^{-2} (max 0.4) over Nazareth Bank (14 - 17°S), and 0.05 g C m^{-2} (max 0.3) north of Mauritius (19 - 20°S ; Huggett and Kyewalyanga, 2017). Sampling with a very coarse net (1-mm mesh that would have missed smaller size fractions), Roger (1994) found little seasonal difference in zooplankton biomass on the Mascarene Plateau from March (SIM) to September (SWM). However, total large zooplankton biomass was 4-fold higher in this area than in southern subtropical waters, and the biomass of specific zooplankton that contribute most to the tuna food chain was enriched seven-fold, with a maximum at 4 - 6°S (west of the Seychelles).

The Java upwelling region is at the northern end (9.5°S) of the 110°E transect line sampled \sim bi-monthly from August 1962 to August 1963 during the International Indian Ocean Expedition (IIOE, Tranter and Kerr, 1969, 1977), providing most of the seasonal biomass data and consistent methods for that area (Figure 16). Following standard conversions from mostly wet weight measurements to carbon and from $333\text{-}\mu\text{m}$ to $200\text{-}\mu\text{m}$ nets (Moriarty and O'Brien, 2013), zooplankton carbon estimates increase by about an order of magnitude seasonally in the Java upwelling (Figure 15). The maximum of $\sim 5 \text{ g C m}^{-2}$ occurs during the SEM when upwelling prevails along southern Indonesia. The biomass minimum of $\sim 0.6 \text{ g C m}^{-2}$ occurs during the NWM (December-January, Austral summer) when downwelling prevails. At least for the 1962-63 year from which most of the data derive, the seasonal changes were smooth, with a broad

peak of $>2 \text{ g C m}^{-2}$ persisting from June to October (Figure 15). The 110°E transect was revisited in May/June of 2019, but did not go far enough north to sample the Java upwelling region (the northernmost station was located at 11.5°S). The 2019 data do reveal increases in mesozooplankton biomass (up to $\sim 0.5 \text{ g C m}^{-2}$) at the northern most stations in early June, consistent with observations from the 1960s (Landry et al., 2022).

2.4 Eastern Indian Ocean and the Leeuwin Current

2.4.1 Nutrients

The South Equatorial Current carries ITF waters into the Indian Ocean, flowing westward between $10\text{-}20^\circ\text{S}$ (Talley and Sprintall, 2005; George et al., 2013; Van Sebille et al., 2014). The ITF influences Indian Ocean biogeochemistry by supplying a net flux of nutrients primarily to thermocline waters (Ayers et al., 2014). A comparison of N:P ratios in the ITF and Indian Ocean by Ayers et al. (2014) shows that the ITF water is enriched in nitrate, which increases the N:P ratio of the Indian Ocean thermocline, though it remains below the classical Redfield ratio of 16:1. The ITF also represents a significant silicate source to the Indian Ocean, which is evident as a broad tongue of elevated silicate concentration between 10° and 20°S extending from the ITF region on the $31.96 \sigma_1$ density surface ($\sim 1000 \text{ m}$) across the basin to 60°E and beyond (Figure 9b in Talley and Sprintall, 2005). This silicate feature, associated with westward advection of Indonesian Intermediate Water, can also be seen along 90°E between 5° and 20°S in association with less pronounced increases in nitrate and phosphate extending from 1000m to 100m depth (Figure 11). Elevated silicate concentrations derived from ITF sources have also been observed in the Leeuwin Current (Thompson et al., 2011).

The tropical origins of the Leeuwin Current combine with its southward-flowing downwelling tendency to create a warm oligotrophic current. However, local wind forcing during the austral summer can override this general tendency and drive localized upwelling (Gersbach et al., 1999; Pearce and Pattiaratchi, 1999; Hanson et al., 2005a,b; Rossi et al., 2013a,b). Seasonal nutrient climatologies from the southwestern Australian shelf, the Leeuwin Current and offshore show low surface nitrate ($< 0.5 \mu\text{M}$) throughout the year, suggesting N-limitation of primary production (Lourey et al., 2006). Phosphate concentrations in the Leeuwin Current are also low, but its relatively high levels of silicate (up to 4 mmole m^{-3}) may be a source of silicate for surrounding waters (Lourey et al., 2006). Shelf waters inshore of the current also generally have low levels of nitrate ($< 0.5 \text{ mmole m}^{-3}$), phosphate ($< 0.25 \text{ mmole m}^{-3}$) and silicate ($< 2 \text{ mmole m}^{-3}$) year-round, but deepening of the mixed layer can lead to nutrient entrainment in offshore waters during austral winter (Lourey et al., 2006). In addition, the Leeuwin Current generates numerous warm (downwelling) and cold core (upwelling) eddies between 20° and 35°S (Gaube et al., 2013; Waite et al., 2007a, 2015). These eddies propagate directly westward, and some appear to be very long-lived (Feng et al., 2005; 2007; Moore et al., 2007; Waite et al., 2007a; Gaube et al., 2013; Dufois et al., 2014), although their persistence and potential impacts on open-ocean biogeochemistry have not been fully investigated.

Low oxygen, high-nitrate layers have been observed in the eastern Indian Ocean off northwest Australia (Thompson et al., 2011; Waite et al., 2013). These layers are formed from multiple

subduction events of the Eastern Gyral Current beneath the Leeuwin Current and have been shown to directly impact the ecological function of western Australian coastal waters. Isotopic measurements suggest that 40–100% of the nitrate in these layers is derived from nitrogen fixation (Waite et al., 2013). Slightly elevated N:P ratios at 400m in Figure 3 are consistent with these data. Based on measurements from several cruises in the region bounded by 28°S–34°S and 110°E and 114°E, Raes et al. (2015) similarly concluded that nitrogen fixation is an important source of fixed nitrogen in the eastern Indian Ocean, with most of the nitrate in the photic zone derived from oxidized ammonium with a nitrogen-fixation origin.

2.4.2 Phytoplankton

Satellite estimates of Chl a and primary production are generally elevated in the SEC in the eastern Indian Ocean, with Chl a varying from ~0.10 to 1.0 mg m $^{-3}$ and production from ~0.4 to 1 g C m $^{-2}$ d $^{-1}$ (Figures 8 and 9). The highest values for the eastern SEC occur in July-August during the SEM (austral winter) associated with ITF nutrient sources and Java upwelling. The lowest values are observed in January (austral summer, Figures 8 and 9).

The downwelling Leeuwin Current is a warm, oligotrophic current with low Chl a (<30 mg m $^{-2}$) and production (<0.5 g C m $^{-2}$ d $^{-1}$; Koslow et al., 2008; Lourey et al., 2006, 2013). Productivity is lowest during austral summer, when the water column is stratified and the Chl a maximum is between 50 and 120 m (Hanson et al., 2007). However, primary production in nearshore regions can attain very high levels of 3–8 g C m $^{-2}$ d $^{-1}$ in localized upwelling centers (Furnas, 2007). For some examples of local upwelling mechanisms along the Western Australia coastline see review by Vinayachandran et al. (2021).

Meanders in the Leeuwin Current give rise to the aforementioned warm-core anticyclonic eddies that carry high-chlorophyll water and coastal diatom communities offshore into cooler oligotrophic waters dominated by open-ocean picophytoplankton (Waite et al., 2007a; 2015; Paterson et al., 2008a). These eddies, which can extend to more than 250 m depth, are unusual because they are downwelling (anticyclonic) circulations with high chl a .

2.4.3 Zooplankton

Zooplankton distributions in the eastern Indian Ocean off western and northwestern Australia reflect the influences of distinct tropical and subtropical/temperate habitats (Tranter, 1977; Buchanan and Beckley, 2016), transport by the Leeuwin Current, and the ecotones and mesoscale features where they mix and interact. In the oceanic realm along 110°E, tropical waters north of ~17°S have the highest total biomass of mesozooplankton as well as the highest abundances of copepods, chaetognaths, appendicularians, euphausiids and foraminiferans (Tranter and Kerr, 1969, 1977; Landry et al., 2022). Seasonality in this tropical area is driven by upwelling off of Java and northwest Australia during the SEM, leading to a broad mesozooplankton maximum across the ITF region in August-September and minimum biomass during the NWM downwelling season in December-January (Tranter and Kerr, 1977), with the former also observed in June of 2019 (Landry et al., 2022). Larger predators follow the seasonal development of smaller prey, with larger size classes of zooplankton peaking in September and the micronekton maximum occurring later in October-November (Legend, 1969).

Compared to the tropical region, biomass seasonality in subtropical/temperate waters south of 27-28°S display a more bimodal pattern, with peaks during the winter SEM and summer seasons (Tranter and Kerr, 1969, 1977). Total mesozooplankton biomass is generally 2-5 fold lower in subtropical than tropical waters (Tranter and Kerr, 1969; Säwström et al., 2014; Landry et al., 2020; Landry et al., 2022), but mean biomasses of chaetognaths and pteropods are reported to be higher in the subtropics (Legand, 1969; Tranter and Kerr, 1969). Gelatinous predators appear to have a biomass maximum at intermediate latitudes where tropical and subtropical waters mix (Legand, 1969).

From its low-latitude origin, the Leeuwin Current transports the enhanced zooplankton biomass and species assemblages of tropical waters southward along the continental margin of Western Australia (Buchanan and Beckley, 2016; Sutton and Beckley, 2017). The current's contribution to mesoscale zooplankton variability in the oceanic region is well established. The center areas of the anticyclonic warm-core eddies that form off of western Australia contain Leeuwin Current water, with a tropical signature of lower salinity and higher zooplankton biomass as well as the aforementioned coastal phytoplankton (diatom) influences (Feng et al., 2007; Paterson et al., 2007). The center areas of cyclonic cold-core eddies are waters of subtropical origin with higher salinity, lower chlorophyll and ~2-fold lower zooplankton stocks than the warm-core eddies (Feng et al., 2007; Strzelecki et al., 2007). Microzooplankton standing stocks are correspondingly higher in warm-core eddies (Strzelecki et al., 2007; Paterson et al. 2007), and Waite et al. (2007b) have argued, based on $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ isotopic indices, that zooplankton are also healthier in warm-core eddies. Paradoxically, however, the oceanic phyllosoma larvae of western rock lobster, the most valuable fishery of western Australia, accumulate more lipid and fatty acids as energy stores in the cold-core eddies (Wang et al., 2014), which Waite et al. (2019) attributed to more efficient energy transfer in the flagellate-dominated food webs and shallower mixed layers of cold-core features relative to the deeper diatom-dominated food webs of warm-core eddies. The flow fields between warm and cold eddy pairs that direct loops of the Leeuwin Current shoreward are also believed to be an important mechanism returning phyllosoma larvae from oceanic subtropical waters to their recruitment into the benthic habitat and fishery on the continental margin (Säwström et al., 2014).

Zooplankton respiration, grazing and production have been systematically investigated based on biogeochemical indices and size-rate relationships in shallow tropical coastal habitats of northwestern Australia (Moritz et al., 2006; McKinnon et al., 2015a,b), but rate measurements are rare for deeper waters. During a time (May) when zooplankton biomass along 110°E is seasonally minimal, Landry et al. (2020) determined that mesozooplankton consumed 3% of phytoplankton (*Chla*) standing stock d^{-1} in subtropical waters and 21% in the tropical region. In addition, Landry et al. (2020) showed that there is a strong and positive correlation between the mesozooplankton grazing rates and temperature ($r^2 = 0.85$), which exceeded the temperature effects on gut turnover and metabolic rates. Paterson et al. (2007) found that microzooplankton consumed all or most phytoplankton production in both warm- and cold-core eddies, with large dinoflagellates as major grazers in the diatom-rich warm-core eddies while ciliates dominated in the flagellate-rich cold-core eddies. In seasonal studies from the continental slope to a coastal lagoon, microzooplankton grazing also generally balanced cell growth of picoplankton

populations, while the total phytoplankton community exhibited positive net growth (Paterson et al., 2008b).

2.5 Southwestern Indian Ocean and the Agulhas Current

2.5.1 Nutrients

Surface waters in the Mozambique Channel are generally warm and nutrient depleted having been derived from oligotrophic surface waters from the southwestern tropical Indian Ocean. However, areas of nutrient enrichment (nitrate $> 0.2 \text{ mmole m}^{-3}$) are sometimes found in the core of cyclonic eddies, as well as on the continental shelf (Marsac et al., 2014; José et al., 2014; 2016). Counter to conventional wisdom, modeling studies of the Mozambique Channel indicate that anticyclonic downwelling eddies sometimes have high nutrient concentrations at their cores while cyclonic upwelling eddies sometimes have low nutrients (José et al., 2014; 2016). These eddies mediate lateral transport of nutrients from the coasts of Africa and Madagascar (José et al., 2014; 2016; Lamont et al., 2014; Roberts et al., 2014). In contrast, along eastern Madagascar, topographically-forced coastal upwelling in the East Madagascar Current brings cold nutrient-rich water to the surface (Lutjeharms and Machu, 2000; Ho et al., 2004; Quartly and Srokosz, 2004; Ramanantsoa et al., 2018). This upwelling and its impacts, which are most pronounced along the southern and southeastern coasts of Madagascar, are enhanced in both austral winter and summer (Ho et al., 2004).

The Agulhas Current is also derived from oligotrophic surface waters from the southwestern tropical Indian Ocean (Lutjeharms, 2006). Its northern source waters are from the Mozambique Channel eddies and the East Madagascar Current, which coalesce off southern Mozambique (Lutjeharms, 2006). The Agulhas Current is additionally supplied from the east via recirculation in the southwest Indian Ocean sub-gyre (Stramma and Lutjeharms, 1997). Even at 400 m depth, climatological concentrations of nitrate, phosphate and silicate are all relatively low (<10 , <1 and $<10 \text{ mmole m}^{-3}$, respectively) off southeastern Africa (Figure 3). N:P ratios in these waters appear low, however, data from only a single cruise drives this signature so it should be further investigated (Figure 3). Nutrient concentrations over the southeast African shelf can be strongly influenced by the Agulhas Current via topographically forced upwelling at specific locations (e.g., the St. Lucia upwelling cell in the KwaZulu-Natal Bight; Meyer et al., 2002). In general, inorganic nutrient concentrations (nitrate, silicate and phosphate) off southeastern Africa decline in surface waters from the inner to outer shelf and into the Agulhas Current, where they drop to very low (oligotrophic) levels (Carter and d'Aubrey, 1988; Barlow et al., 2015). However, the interaction of upwelling with horizontal advection and mixing can give rise to complex nutrient distribution patterns in the coastal waters of southeastern Africa (Meyer et al., 2002; Barlow et al. 2015).

2.5.2 Phytoplankton

Chla and production in Mozambique Channel surface waters are generally low ($<0.4 \text{ mg m}^{-3}$ and $<0.7 \text{ g C m}^{-2} \text{ d}^{-1}$) and not significantly different in cyclonic and anticyclonic eddies (Lamont et al., 2014; Barlow et al., 2014; Hood et al., 2017; Figures 8 and 9). DCMs occur between 25 and 125 m depending on eddy influences and shelf proximity (Barlow et al., 2014; Lamont et al.,

2014). Enhanced production in both cyclonic and anticyclonic eddies in the Mozambique Channel often occurs in response to nutrient inputs by lateral advection from the coasts of Madagascar and Africa rather than eddy-induced upwelling (Kyewalyanga et al., 2007; José et al., 2014; Lamont et al., 2014; Roberts et al., 2014). In contrast, the topographically-induced coastal upwelling in the East Madagascar Current gives rise to high Chl*a* and production (Lutjeharms and Machu, 2000; Ho et al., 2004; Quartly and Srokosz, 2004).

The Agulhas Current itself is oligotrophic (Lutjeharms, 2006). Chl*a* and production in surface waters are particularly low during austral summer ($<0.2 \text{ mg m}^{-3}$ and $<0.5 \text{ g C m}^{-2} \text{ d}^{-1}$) and higher in austral winter (Machu and Garcon, 2001; Hood et al., 2017; Figures 8 and 9). However, the Agulhas Current can elevate primary production in the coastal zone through meandering and topographic interactions that drive upwelling and it can suppress primary production when it impinges onto the shelf (Schumann et al., 2005; Hood et al., 2017).

In general, Chl*a* and production are elevated in southeast coastal Africa along the inshore side of the Agulhas Current (Machu and Garcon, 2001; Goschen et al., 2012; Hood et al., 2017). This effect is most pronounced in austral summer and further southward, associated with upwelling favorable (southeasterly) winds and topographically-induced upwelling. For example, Chl*a* concentrations from the Kwa-Zulu Natal Bight range from ~ 0.1 to 1.5 mg m^{-3} and primary production ranges from ~ 0.3 to $2.6 \text{ g C m}^{-2} \text{ d}^{-1}$ (Lamont and Barlow, 2015). Elevated values are also observed over the Agulhas Bank where near-surface Chl*a* can exceed 3 mg m^{-3} and production rates often exceed $0.5 \text{ g C m}^{-2} \text{ d}^{-1}$ (Burchall, 1968; Carter and Schleyer, 1988; Boyd and Shillington, 1994; Lutjeharms et al., 1996; Roberts, 2005; Jackson et al., 2012).

2.5.3 Zooplankton

Surveys off Mozambique between 1977 and 2014 (Nehring et al., 1987; reviewed by Huggett and Kyewalyanga, 2017) have generally shown lower mesozooplankton biomass in the monsoon-influenced region north of 18°S compared to the southern sector. For example, lower biomass was measured in the north during winter 2009 (mean 0.3 , maximum 1.4 g C m^{-2} ; Huggett, unpublished), while values up to 5.7 g C m^{-2} (mean 1.2 - 1.7 g C m^{-2}) were recorded in the south in early summer 2014 (Huggett and Kyewalyanga, 2017). Macrozooplankton biomass ($>500 \mu\text{m}$, upper 100 m) averaged 0.5 g C m^{-2} on the Mozambique shelf during seasonal sampling in 1977-78, with maximum values of 2.1 g C m^{-2} during summer (Oct-Dec), but unlike mesozooplankton showed no clear longitudinal patterns (Huggett and Kyewalyanga, 2017). Monthly zooplankton density has been shown to track the Chl*a* seasonal cycle on the Mozambique shelf, with a primary peak in March/April following the summer rains and high nutrient inputs from rivers, and a lesser peak in September (Paula et al., 1998).

Mesozooplankton biomass measured over four surveys from 2007 to 2010 in the Mozambique Channel averaged 0.4 g C m^{-2} in the upper 200 m (range 0.1 - 1.8 g C m^{-2}), concentrated in the upper 100 m (Huggett, 2014). Biomass was significantly higher in cyclonic eddies (and divergence areas) compared to anticyclonic eddies (and convergence areas), but highest overall in the shelf region. Off the southern Madagascar shelf, a young cyclonic eddy entrained material from the productive shelf region in its periphery during July 2013 (Noyon et al., 2019),

demonstrating the potential to transport meroplankton across the Mozambique Channel (Ockhuis et al., 2017). Zooplankton data are scarce for the rest of the Madagascan perimeter (Huggett and Kyewalyanga, 2017).

The biogeographical distributions of zooplankton species off South Africa clearly reflect the influence of the Agulhas Current, with specific assemblages associated with Agulhas water (De Decker, 1984; Schleyer, 1985). It has also been shown that the current transports Indo-Pacific zooplankton species southward (Sutton and Beckley, 2017) and into waters over the Agulhas Bank (De Decker, 1973). In general, zooplankton biomass is greater inshore of the current compared to within, but species diversity is higher in the current (Carter and Schleyer, 1988; Pretorius et al., 2016), consistent with its tropical origins. Measurements for the northeastern continental shelf of South Africa indicate relatively low mean biomass of 0.4 g C m⁻² (max 1.1; Huggett, unpublished). Further downstream in the KwaZulu-Natal Bight, sampling during 2010 indicated high spatial variability with greater zooplankton biomass during the dry winter compared to the wet summer (~0.6 vs 0.2 g C m⁻²; from data in Pretorius et al., 2016), as observed for phytoplankton biomass. In contrast, biomass on the southeastern shelf (between Port Edward and Cape St Francis) during 2017 was greater in summer (mean 0.3, max 1.0 g C m⁻²) compared to winter (mean 0.2, max 0.5 g C m⁻²; Huggett, unpublished).

Off the south coast of South Africa, the shelf broadens into the extensive Agulhas Bank, where the zooplankton community is dominated by the large calanoid copepod *Calanus agulhensis* (De Decker and Marska, 1991; Huggett and Richardson, 2000). Hutchings et al. (1991) estimated mesozooplankton biomass there to average 0.9 g C m⁻² (range 0.2-2.0 g C m⁻²) and macroplankton biomass 0.1 g C m⁻². During annual surveys in late spring to early summer 1988-1990, mean copepod biomass over the Agulhas Bank ranged from 1.1 to 1.6 g C m⁻² (Verheye et al., 1994), with highest biomass east of Cape Agulhas (mean 1.7-1.8 g C m⁻²), dominated (85%) by *C. agulhensis*. These years likely represent a short-term peak in biomass, with a long-term (24-years, 1988-2011) mean of 1 g C m⁻² for the whole bank, and 1.1 g C m⁻² for the area east of Cape Agulhas (Huggett, unpublished). Seasonal studies are limited, but De Decker and Marska (1991) noted peak abundance of *C. agulhensis* from August to November 1964 (austral spring), and extremely high settled volumes in late spring or summer due to vast swarms of Thaliaceans over the southern and central Bank (De Decker, 1973). High biomass of *C. agulhensis* on the central and eastern Agulhas Bank is associated with a quasi-permanent shallow but mainly subsurface 'ridge' of cool upwelled water over the midshelf (Boyd and Shillington 1994). This feature, which is most prominent in summer (Roberts, 2005), is thought to stimulate primary and secondary production, and enhance local retention of copepods through cyclonic circulation around the ridge, although there is a net westward advection of copepods across the Bank (Huggett and Richardson, 2000).

Copepod feeding studies on the Agulhas Bank are few but suggest that younger stages of *C. agulhensis* graze preferentially on small cells prevalent in the upper mixed layer, while older stages prefer larger cells more commonly found at the subsurface maximum (Verheye et al., 1994), and are thus more likely to be food-limited when chlorophyll concentrations are low (Huggett and Richardson, 2000). Grazing estimates vary, but copepod grazing impact during

spring and summer, based on a daily consumption of 0.6-0.9 g C m⁻², was estimated as 30-50% of daily primary production for a wholly phytoplankton diet, and 15-25% for a diet with equal proportions of phytoplankton and microzooplankton (Verheye et al., 1994). Gibbons (1997) estimated that grazing impact by high densities of *Thalia democratica* on the Agulhas Bank could exceed 100% of phytoplankton production.

2.6 The southern subtropical gyre

2.6.1 Nutrients

The core of the southern Indian Ocean subtropical gyre between 20° and 40°S is oligotrophic, with undetectable nitrate, phosphate and silicate concentrations in near-surface waters (Figures 1, 2, 3 and 4; Harms et al., 2019). N:P ratios are generally below 7.5, suggesting nitrogen limitation (Figure 4 and 11) consistent with nutrient addition experiments conducted in the southern subtropical gyre along 95° E (Garcia et al., 2018; Twining et al., 2019). Climatological nutrient concentrations reveal greater depression of the nitracline and phosphocline (between ~25° and 35° S) in the western gyre (Figures 3, 4 and 11). The vertical section along 95° E (Figure 11) reveals a sharp increase in N:Si (>10) in the surface waters of the subtropical front between 35° and 50° S and subduction of this high N:Si water northward beneath the subtropical gyre. These features are visible, though less pronounced, in the vertical section along 50° E (Figure 4). High N:Si water in the Subtropical Front is a circum-global feature where silicate can limit diatom growth (e.g., Bishop et al., 2004; Coale et al., 2004; Martin et al., 2013). Analysis of satellite-derived ocean currents, sea level anomalies, and thermohaline distribution in the Subtropical Front of the Indian Ocean suggests that, despite the high mesoscale variability and turbulence in this region, the primary supply of nutrients is a result of advection (vertical or zonal) rather than vertical mixing (George et al., 2018).

2.6.2 Phytoplankton

In the southern Indian Ocean subtropical gyre, near-surface Chl_a and primary production are low (<0.1 mg m⁻³ and <0.5 g C m⁻² d⁻¹, respectively; Figures 8 and 9). A well-defined DCM generally occurs between 50 and 150 m (Figures 10 and 13). Figure 13 reveals a particularly pronounced DCM along 95° E, with concentrations exceeding 0.125 mg m⁻³ between 100 and 150 m. This feature may be associated with the aforementioned subduction of high N:Si water between 35° and 50° S. Pigment measurements indicate that prokaryotic cyanobacteria and flagellates dominate the phytoplankton community composition in the gyre, transitioning to flagellate dominance in the Subtropical Front (Naik et al., 2020).

The SE Madagascar bloom (SMB) is a prominent exception to the general oligotrophy of the southern Indian Ocean subtropical gyre. The SMB occurs in the late austral summer/fall (Jan-April) and extends eastward into the subtropical gyre. It can cover a 2,500 km² area with near-surface Chl_a of 2-3 mg m⁻³ (Longhurst, 2001). While the mechanism that generates the bloom is not entirely clear, it occurs within a warm (>26.5°C), shallow mixed layer (~30 m) overlying a strong pycnocline (Uz, 2007; Srokosz and Quartly, 2013; Dilmahamod et al., 2019). It has been suggested that new nitrogen from N₂ fixation fuels the bloom, with eddies and/or the South Indian Counter Current (SICC) advecting and dispersing it eastward while potentially also

contributing additional nutrients and/or phytoplankton biomass (Uz, 2007; Poulton et al., 2009; Dilmahamod et al. 2019; Huhn et al., 2012; Raj et al., 2010; Srokosz and Quartly, 2013; Srokosz et al., 2004, 2015). This hypothesis is supported by observations of nitrogen fixing species southeast of Madagascar in the SMB region (Poulton et al., 2009) and elevated nitrogen fixation rate measurements in the western part of the southern subtropical gyre (Horstmann et al., 2021) during austral summer/fall. An alternative explanation is that the SMB initiates off Madagascar from coastal processes that bring limiting nutrients into the photic zone (Srokosz et al., 2004).

2.6.3 Zooplankton

Measurements in the subtropical region south of Madagascar during the IIOE showed two peaks in zooplankton diversity, one in the surface layers along a northern transect at $\sim 26^\circ$ S, and a second between 750 and 1500 m along the southern transect (~ 34 - 37° S) (Rand, 1964; De Decker and Mombeck, 1964). The vertical distributions of 274 copepod species clustered into four groups linked to different water masses, described as Mozambique and Agulhas Currents (0-500 m), surface and subsurface water (0-200 m), central water (200-600 m), and Antarctic Intermediate water (600-1300 m). A recent update of calanoid copepod biogeography in the region by Cedras et al. (2020) revealed three main species clusters corresponding to water masses associated with the Agulhas Return Current, the Subtropical Front and the Sub-Antarctic Front, all with distinct *Chla* concentrations.

Mean mesozooplankton biomass in the western subtropical zone, including both open-ocean and seamount stations, increases latitudinally from 0.1-0.2 g C m⁻² in the north (~ 27 - 33° S) to 0.3-0.4 g C m⁻² at seamounts farther south and in the Subtropical Front (~ 36 - 42° S) (Sonnekus et al., 2016). Zooplankton communities differ among seamounts, which has been attributed to latitudinal or mesoscale (e.g., eddy-related) oceanographic variability and connectivity with the Madagascar shelf rather than topographic effects on mesozooplankton biomass or size composition (Noyon et al., 2020). These findings are consistent with the observations of Asha Devi et al. (2020) from the Subtropical Front (40 - 43° S, 52 - 60° E), which reveal a strong impact of eddies on productivity, food web structure and zooplankton community composition. Venkataramana et al. (2019) observed a high-standing stock of small copepods in the Subtropical Front ($\sim 42^\circ$ S, 57° E), transitioning to larger copepods further south in the Polar Front.

Seasonal variability of zooplankton biomass in the central southern subtropical Indian Ocean shows a primary peak during the late SEM (August-September, winter), a broad secondary peak during and following the NEM (January-April, summer), and minima during May and December (Figure 16). Biomass magnitudes differ by a factor of two, however, between the western-central region (55 - 100° E) and the eastern area along 110° E, which retains water mass characteristics of South Indian Central Water (Rochford, 1969; 1977). The primary maximum in the central southern subtropical Indian Ocean is probably related to increased wind mixing and nutrient entrainment during winter. In contrast, the summertime secondary maximum might be related to increased primary production during the most stratified summer period due to nitrogen fixation, as observed at station ALOHA in the subtropical North Pacific (Landry et al., 2001; Valencia et al., 2016). The higher biomass values in all seasons along 110° E compared to the central-eastern

subtropics may reflect the intensification of winds and increased eddy activity due to proximity to the Australian land mass and Leeuwin Current.

Based on gut pigment analyses of mesozooplankton in eastern subtropical waters along 110°E, Landry et al. (2020) determined grazing rates of 3.0 ± 0.4 % of euphotic zone Chl*a* d⁻¹, equivalent to 14 ± 2 % of zooplankton C standing stock d⁻¹. For two stations in the central subtropical region, Jaspers et al. (2009) used measured rates of fecal pellet production, biomass scaling and literature relationships to estimate total consumption by copepods and larvaceans of 7-18% of zooplankton C d⁻¹. These estimates are indicative of highly oligotrophic waters where the dominant pico-sized phytoplankton largely escape direct feeding by mesozooplankton and microzooplankton are the major grazers and trophic intermediaries.

2.7 Long-term trends

There have been several studies of long-term changes in Chl*a* and primary production in the Indian Ocean. Rising sea surface temperatures (SSTs) due to global warming can enhance near-surface stratification and inhibit vertical mixing of nutrients, which, in turn, inhibits primary production (Behrenfeld et al., 2006; Roxy et al., 2016). This is consistent with remote sensing studies that indicate a reduction in net primary productivity (NPP) over most of the tropics associated with El Niño-induced increases in stratification (Behrenfeld et al., 2006). In contrast, remote sensing studies suggest an increase in NPP in the northwestern Indian Ocean linked to a climate-induced change in the intensity of the SWM that has increased upwelling and productivity (Goes et al., 2005; Gregg et al., 2005). However, recent analyses of satellite surface temperature and chlorophyll records (Prakash and Ramesh, 2007; Prakash et al., 2012; Roxy et al., 2016) suggest that decadal variability may have influenced the earlier interpretation of a climate change-associated increase in SWM production (Rixen et al., 2014). In contrast, remote sensing and model simulations indicate that there has been a significant multi-decadal decrease (of up to 20%) in phytoplankton biomass in the western Indian Ocean driven, indeed, by enhanced ocean stratification due to rapid warming (Roxy et al., 2016; Gregg et al., 2017). Though much less pronounced, stratification increase and phytoplankton decline appear to extend over most of the Indian Ocean basin (Jena et al., 2013; Roxy et al., 2016). Roxy et al. (2016) further argue that continued warming in future decades will turn large areas of the Indian Ocean into an ecological desert. However, surface satellite measurements do not include the robust and ubiquitous DCMs that are so evident in Figures 10 and 13. Moreover, similar trends were observed in the central Pacific decades ago before it was recognized that vibrant, productive communities of microbes could exist and support relatively healthy levels of zooplankton stocks in oligotrophic waters (as this review of different Indian Ocean regions also shows). The Roxy et al. (2016) findings are also inconsistent with apparent trophic amplification due to warming on phytoplankton and zooplankton communities that was observed meridionally along 110°E, which might be explained by enhanced trophic coupling efficiency via mixotrophy (Landry et al., 2020).

As discussed above, there also appears to have been a shift in the composition of winter phytoplankton blooms in the northern and central Arabian Sea over the last decade from diatoms to *Noctiluca scintillans*. This change in species composition has been linked to climate-change induced decreases in the intensity of the NEM that increase stratification and expansion of the OMZ, which has altered nutrient stoichiometries to favor *Noctiluca*'s mixotrophic feeding strategy (Gomes et al., 2014; Goes et al., 2020).

3. Summary and Conclusions

The Indian Ocean has many special attributes that impact its biogeochemical and ecological dynamics. The Arabian Sea and the northwestern Indian Ocean are strongly influenced by monsoon winds, dust deposition, upwelling/downwelling circulations and the OMZ. Strongest upwelling occurs during the SWM, driving nutrient enrichment and elevated phytoplankton productivity in coastal waters off Somalia, Yemen and Oman and to a lesser extent along western India. However, multiple lines of evidence suggest that maximum production is capped by Si and Fe limitation. Questions regarding a potential link between iron redox cycling and nitrite maxima remain unanswered. In contrast, the NEM drives downwelling except in the northern central Arabian Sea where wind-driven nutrient entrainment increases primary production. There is surprisingly weak seasonal and spatial variability in mesozooplankton biomass in the Arabian Sea. Nonetheless, the relative grazing contributions of micro- and mesozooplankton vary seasonally and spatially in a manner consistent with spatially separated co-regulation by iron and grazing. Potential changes in zooplankton biomass, community composition and trophic transfer associated with the observed community shift towards *Noctiluca* and *Phaeocystis* during the NEM in the Arabian Sea need to be investigated.

The Bay of Bengal is influenced by the same factors that impact the Arabian Sea, but seasonal wind effects are more muted due to weaker winds and strong freshwater stratification. Although the Bay of Bengal generally exhibits surface oligotrophy, there are regions of high Chl a and production associated with river plumes, upwelling eddies and wind-induced nutrient entrainment, which drive significant variability in mesozooplankton biomass. Low oxygen content of waters beneath the pycnocline force Bay of Bengal mesozooplankton to reside in a thin mixed layer where trophic interactions are likely more concentrated than in other Indian Ocean regions. The lack of zooplankton biomass and grazing rate measurements in the Bay of Bengal leads to uncertainty in zooplankton grazing impacts and trophic transfer in the region.

The equatorial Indian Ocean encompasses important open-ocean and coastal upwelling systems driven by monsoon winds. South of the equator, observations and models of the SCTR show strong nutrient, Chl a , production and zooplankton responses to SEM wind forcing in austral winter. Along the southern coasts of the Indonesian island chains, SEM winds and the upwelling-favorable South Java Current also drive nutrient inputs that give rise to enhanced productivity and seasonal zooplankton biomass an order of magnitude higher than in open-ocean waters further south.

The eastern Indian Ocean and the Leeuwin Current are strongly influenced by the ITF, downwelling circulations and seaward-propagating eddies. In the Leeuwin Current, a unique poleward-flowing eastern boundary current, tropical zooplankton are transported southward and warm-core anticyclonic eddies carry moderately high *Chla* coastal water offshore. In the oceanic realm, tropical waters to the north have the highest total biomass of mesozooplankton, with seasonality driven by upwelling off of Java and northwest Australia during the SEM.

The southwestern Indian Ocean is dominated by alongshore-propagating eddies in the Mozambique Channel and Agulhas Current that elevate (suppress) nutrients and productivity by meanders and topographic interactions that drive upwelling (downwelling) and lateral transport. In general, zooplankton biomass is also low in these waters, except in coastal/shelf regions. The Agulhas Current transports Indo-Pacific zooplankton southward and over the Agulhas Bank, where primary production is somewhat elevated and the zooplankton community is dominated by the large calanoid copepod *Calanus agulhensis* in austral spring.

The southern Indian Ocean subtropical gyre is extremely oligotrophic except when the SE Madagascar bloom occurs in the late austral summer/fall. It has been hypothesized that this bloom is driven by nitrogen fixation, but the causes remain unclear. Low N:P ratios in the gyre suggest perennial nitrogen limitation. Phytoplankton production and mesozooplankton abundance are particularly low in the western subtropical gyre, with variability linked to different water masses and chlorophyll concentrations. Zooplankton biomass is highest in the eastern subtropical gyre which likely reflects the intensification of winds and increased eddy activity associated with proximity to the Australian land mass and Leeuwin Current. Grazing rate estimates from the southern subtropical gyre of the Indian Ocean are indicative of highly oligotrophic waters where microzooplankton are the major grazers.

In general, it is clear that in all subregions of the Indian Ocean there is a strong connection between the physics that drives (or suppresses) nutrient delivery to the photic zone and responses of phytoplankton (*Chla*), primary production and zooplankton. Wind forcing during the SWM/SEM (boreal summer, austral winter) is a major biogeochemical and ecological driver with broad stimulatory effects throughout many regions (Arabian Sea, Bay of Bengal, SCTR, Java, central/eastern subtropical gyre). In contrast, substantial stimulatory response to the NWM/NEM is less pronounced (Arabian Sea and Bay of Bengal). In addition, there are regionally specific processes that significantly modulate the biogeochemical and ecological responses. For example, strong advective impacts and Fe/Si limitation in the Arabian Sea; freshwater and stratification in the Bay of Bengal; the influence of ITF nutrient inputs, poleward transport, downwelling and seaward-propagating eddies in the southeastern Indian Ocean; and alongshore-propagating eddies, meanders, upwelling and poleward transport in the southwestern Indian Ocean. The southern subtropical gyre is just extremely oligotrophic except when/where the Southeast Madagascar bloom occurs.

It should be emphasized that, other than basic patterns, the details of mechanisms and biogeochemical and ecological responses are poorly explored in many of these Indian Ocean sub-regions, despite evidence that a main driver, the monsoon winds, is being impacted by climate change. There is clearly a need for more studies aimed at improved understanding of

planktonic food web dynamics in the Indian Ocean, especially in regions other than the Arabian Sea. Moreover, important questions remain unanswered. For example, why is there so little seasonal and spatial variability in zooplankton biomass in the Arabian Sea? What is the spatial and temporal extent of iron limitation and nitrogen fixation in the Indian Ocean? How does the ITF influence ecological connectivity between the Pacific and Indian Oceans? How do Leeuwin Current eddies impact connectivity and primary productivity as they transit the Indian Ocean? What causes the Madagascar bloom? To name just a few. Finally, given the variability in projections of how climate change is influencing basin scale biogeochemistry and ecology, more work needs to be done to reassess the potential effects of climate variability and change on the biogeochemistry and ecology of the entire Indian Ocean basin.

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5. Educational Resources

-Ocean Data View, free software for plotting oceanographic data. Available at: <https://odv.awi.de>

-World Ocean Atlas, a collection of objectively analyzed, quality controlled temperature, salinity, oxygen, phosphate, silicate, and nitrate means based on profile data from the World Ocean Database. Available at: <https://www.ncei.noaa.gov/products/world-ocean-atlas>

-Satellite ocean color data. Available at: <https://oceancolor.gsfc.nasa.gov>

-GFDL Sea Surface Temperature Simulation for the Indian Ocean. Available at: <https://www.youtube.com/watch?v=ZVssbK0K4wc>

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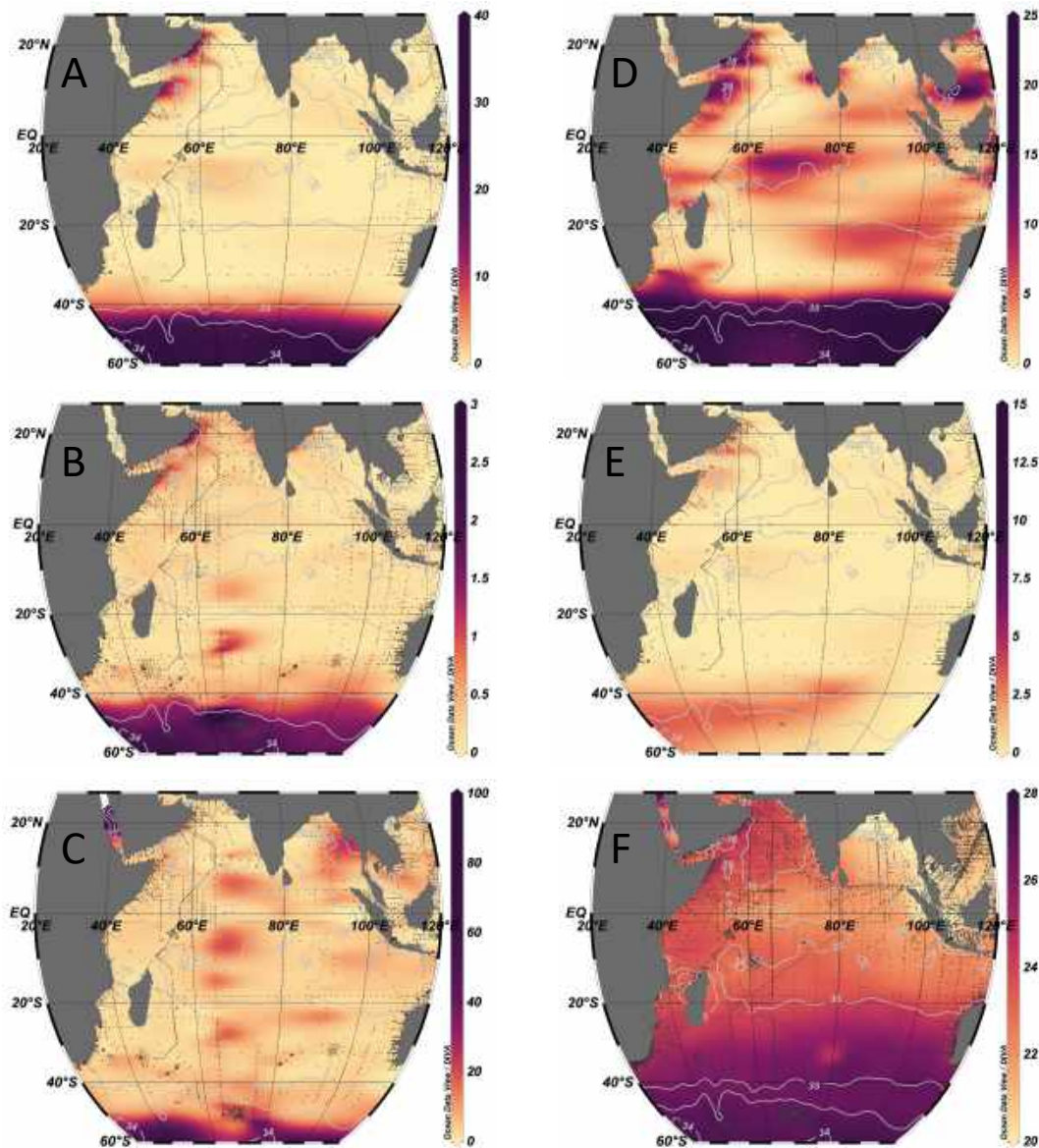


Figure 1: Maps of the SWM period (July – August) for A) 10m nitrate (mmol m^{-3}) B) 10m phosphate (mmol m^{-3}), C) 10m silicate (mmol m^{-3}) D) 10m nitrate to phosphate ratio, E) 10m nitrate to silicate ratio, F) 10m potential density anomaly. The grey contours are surface salinity. The station locations are shown as dots. Near surface nutrient ratios may have large errors due to the small surface nutrient concentrations. Data from the World Ocean Database (2018).

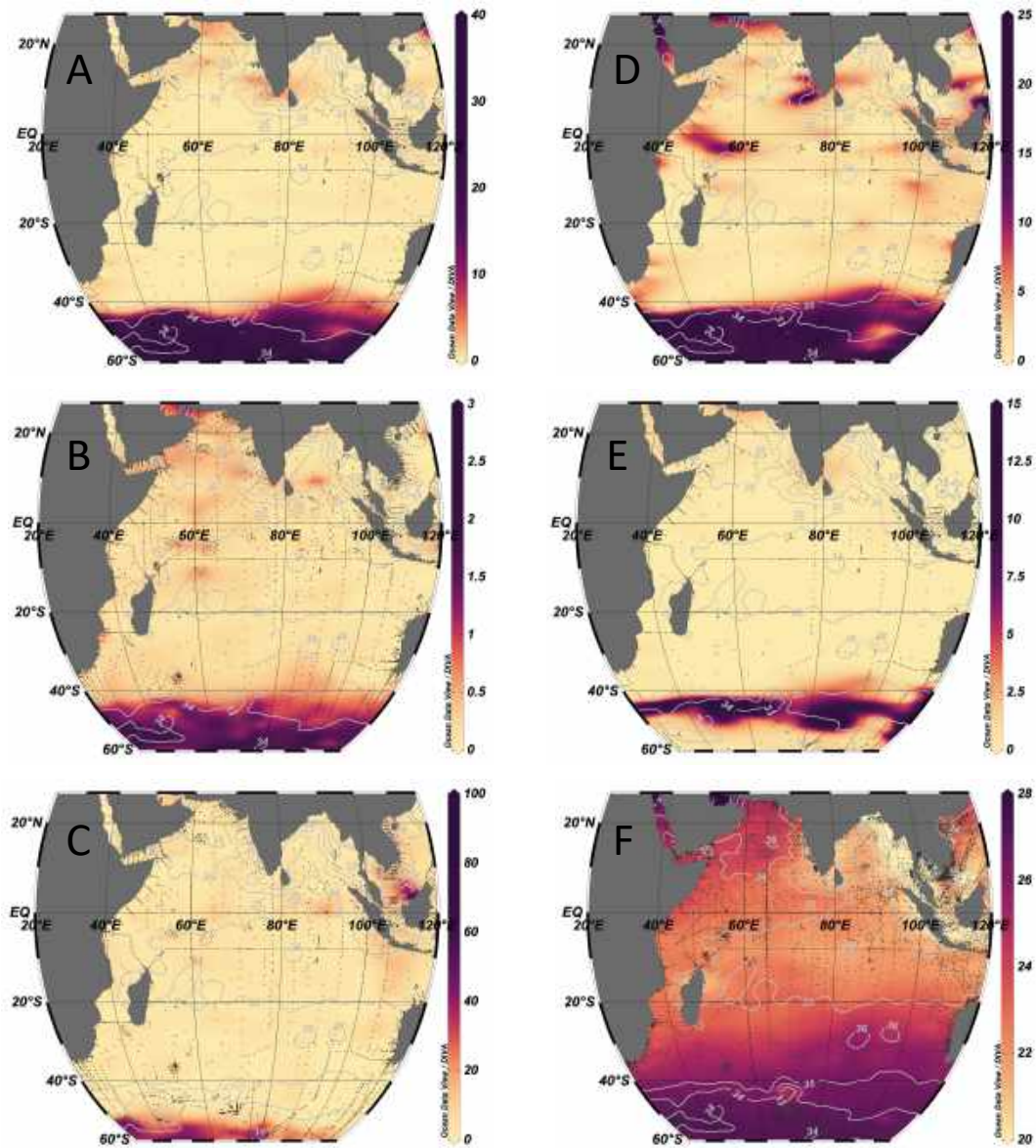


Figure 2: Maps of the NEM period (December - January) for A) 10m nitrate (mmol m⁻³) B) 10m phosphate (mmol m⁻³) , C) 10m silicate (mmol m⁻³) D) 10m nitrate to phosphate ratio, E) 10m nitrate to silicate ratio, F) 10m potential density anomaly. The grey contours are surface salinity. The station locations are shown as dots. Near surface nutrient ratios may have large errors due to the small surface nutrient concentrations. Data from the World Ocean Database (2018).

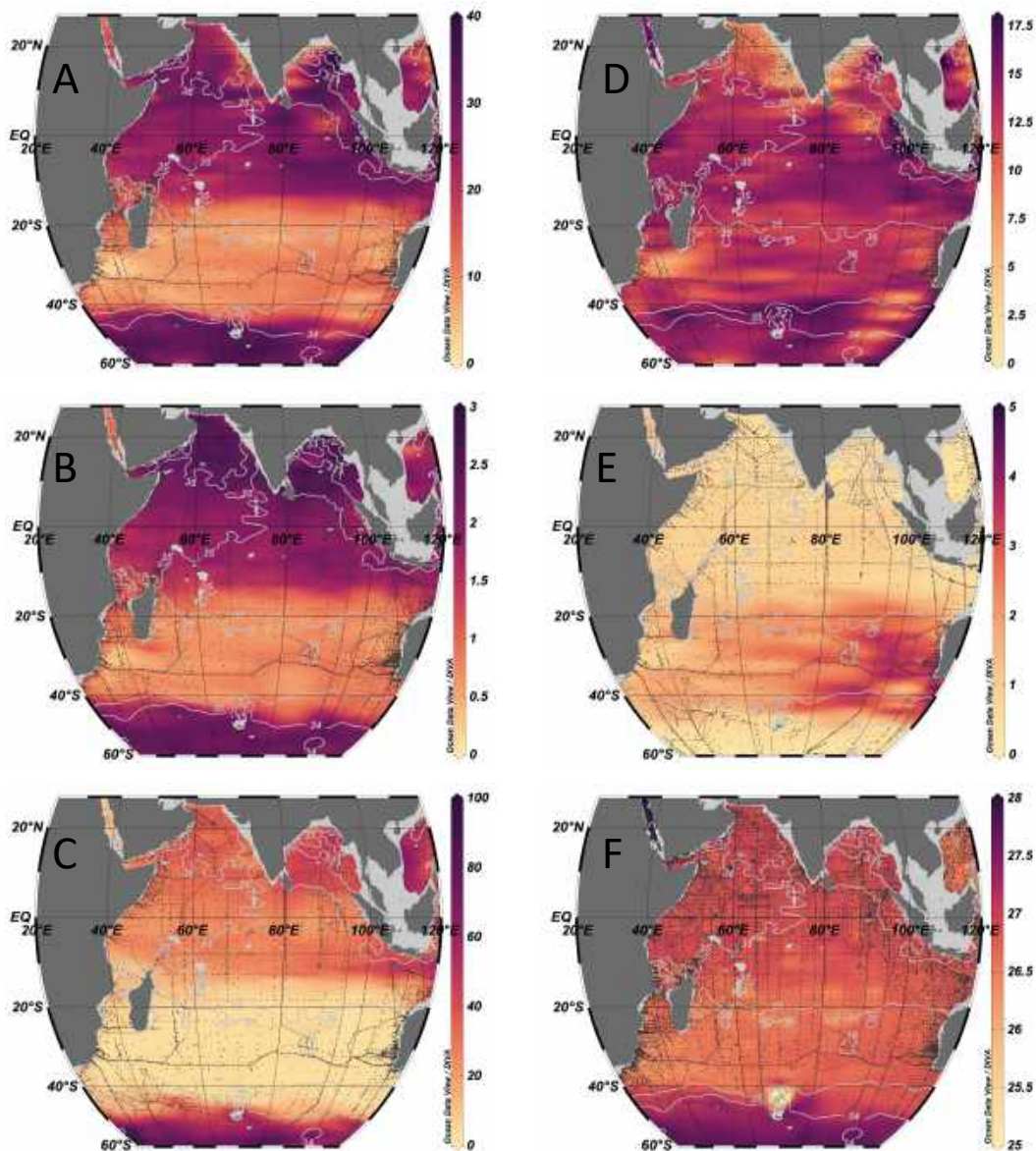


Figure 3: Maps of A) 400m nitrate (mmol m^{-3}) B) 400m phosphate (mmol m^{-3}), C) 400m silicate (mmol m^{-3}) D) 400m nitrate to phosphate ratio, E) 400m nitrate to silicate ratio, F) 400m potential density anomaly. The grey contours are surface salinity. The station locations are shown as dots. Data from Soviet cruises were removed for nutrient biases. Data from the World Ocean Database (2018).

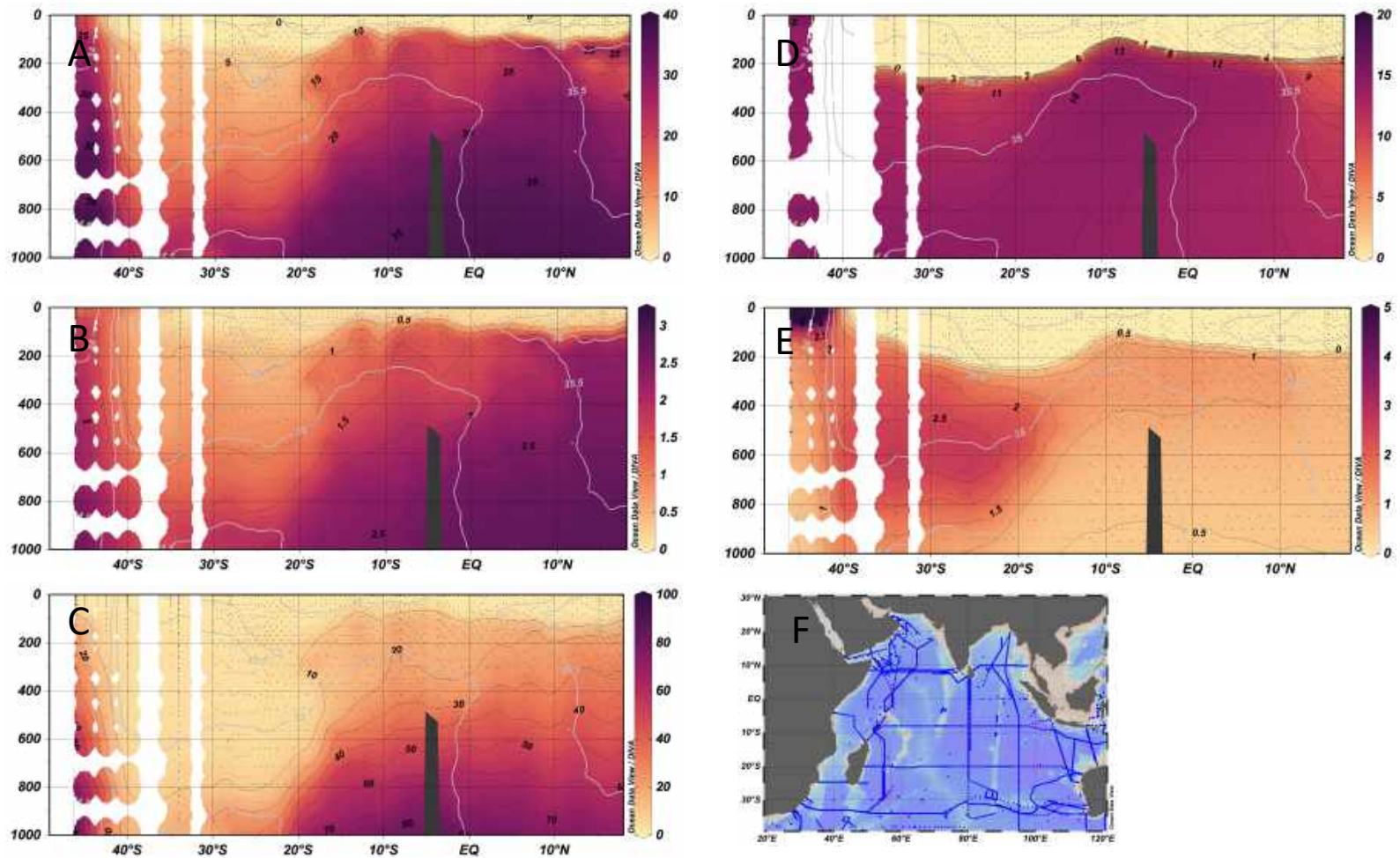


Figure 4: Vertical sections nominally along 55°E of A) nitrate (mmol m⁻³) B) phosphate (mmol m⁻³) , C) silicate (mmol m⁻³) D) nitrate to phosphate ratio, E) nitrate to silicate ratio, F) map of the section. The grey contours are salinity, and the black contours the colored property. The station locations for each property are shown as dots. Data from the World Ocean Database (2018), comprising mainly data after 2005 and the 2018 IO7 GoShip line. Only data from the 70°E N-S section are used in the section plots.

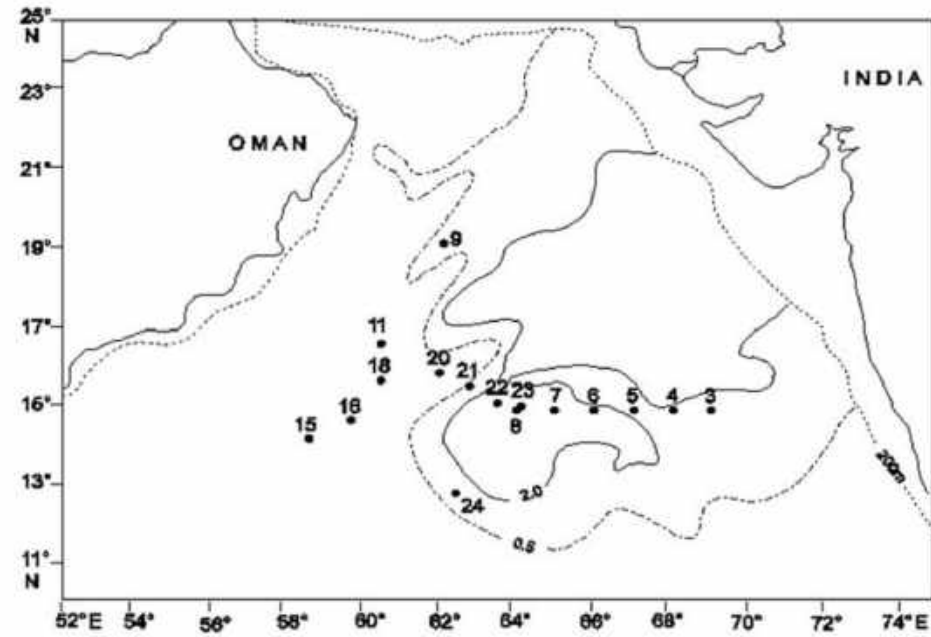
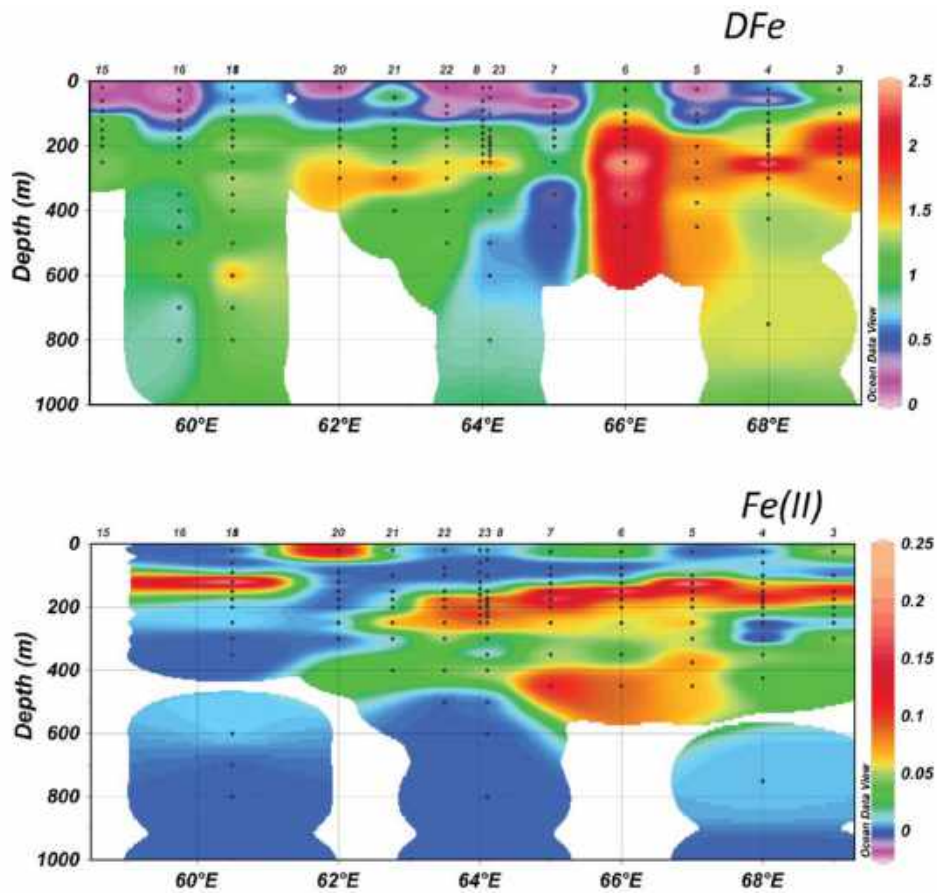


Figure 5: East to west section of dissolved iron (Dfe) and Fe⁺² (Fe(ii)) in the Arabian Sea down to 1000 meters depth. The units are umoles m⁻³ The station locations are shown in the map inset. Figures from Moffett et al. (2015).

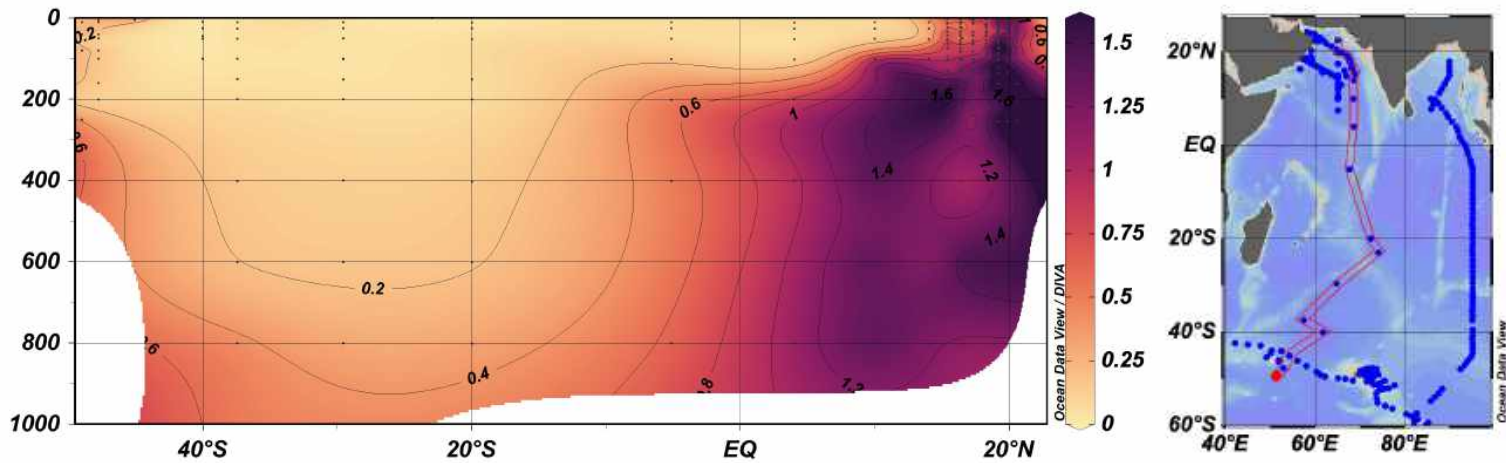


Figure 6: Dissolved Iron (umoles m⁻³) along approximately 70° East in the Indian Ocean. The station locations are shown in the map inset. Data from Tagliabue et al. (2012) database. Only data from the 70°E N-S section are used in the section plots.

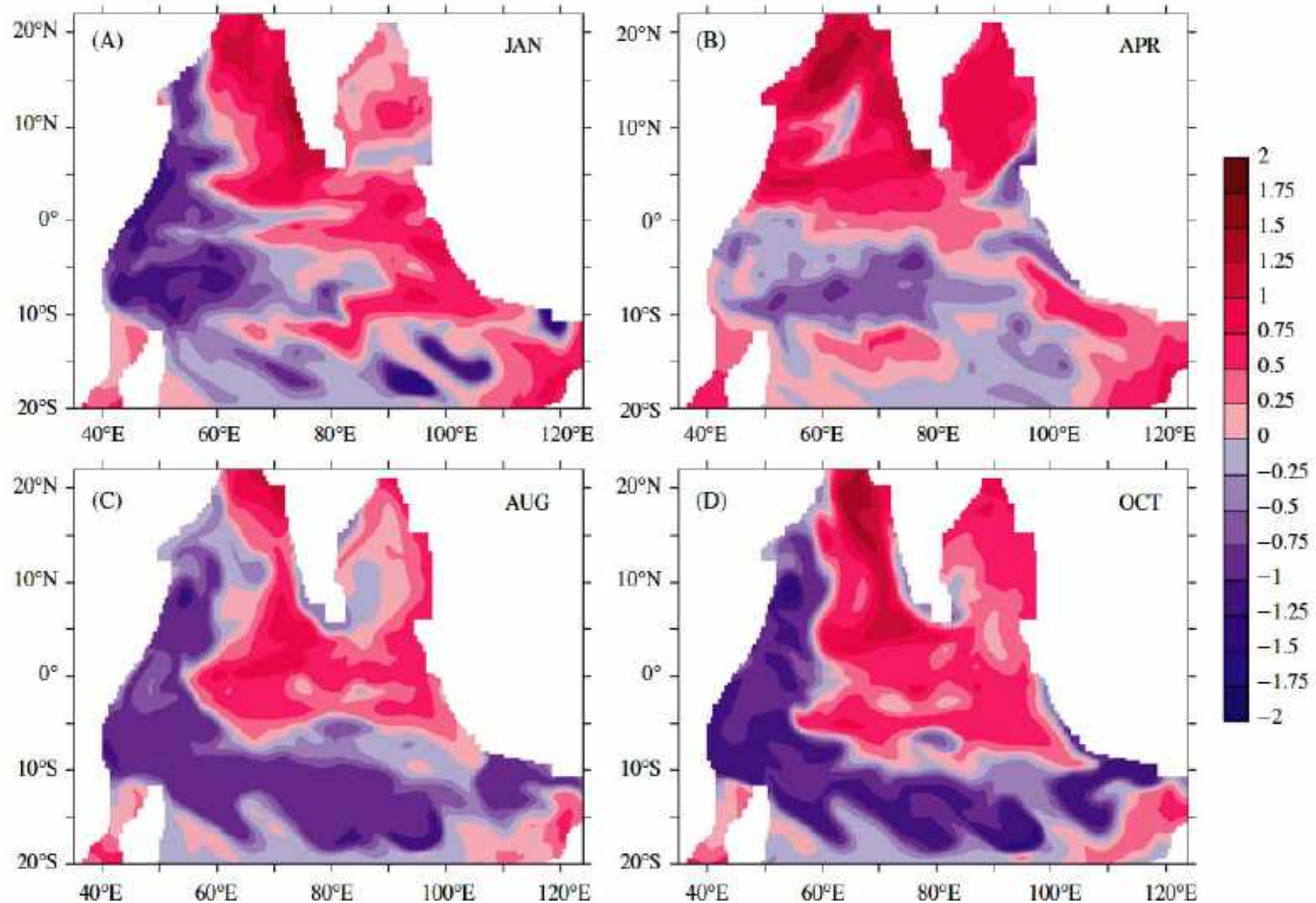


Figure 7: Model-simulated seasonal evolution of most limiting surface nutrient for net plankton with blue (red) indicating Fe (N) limited growth (i.e., red is iron replete). The four seasons consist of (A) January (NEM); (B) April (Spring Intermonsoon); (C) August (SWM); and (D) October (Fall Intermonsoon). Figure and caption modified from Wiggert et al. 2006.

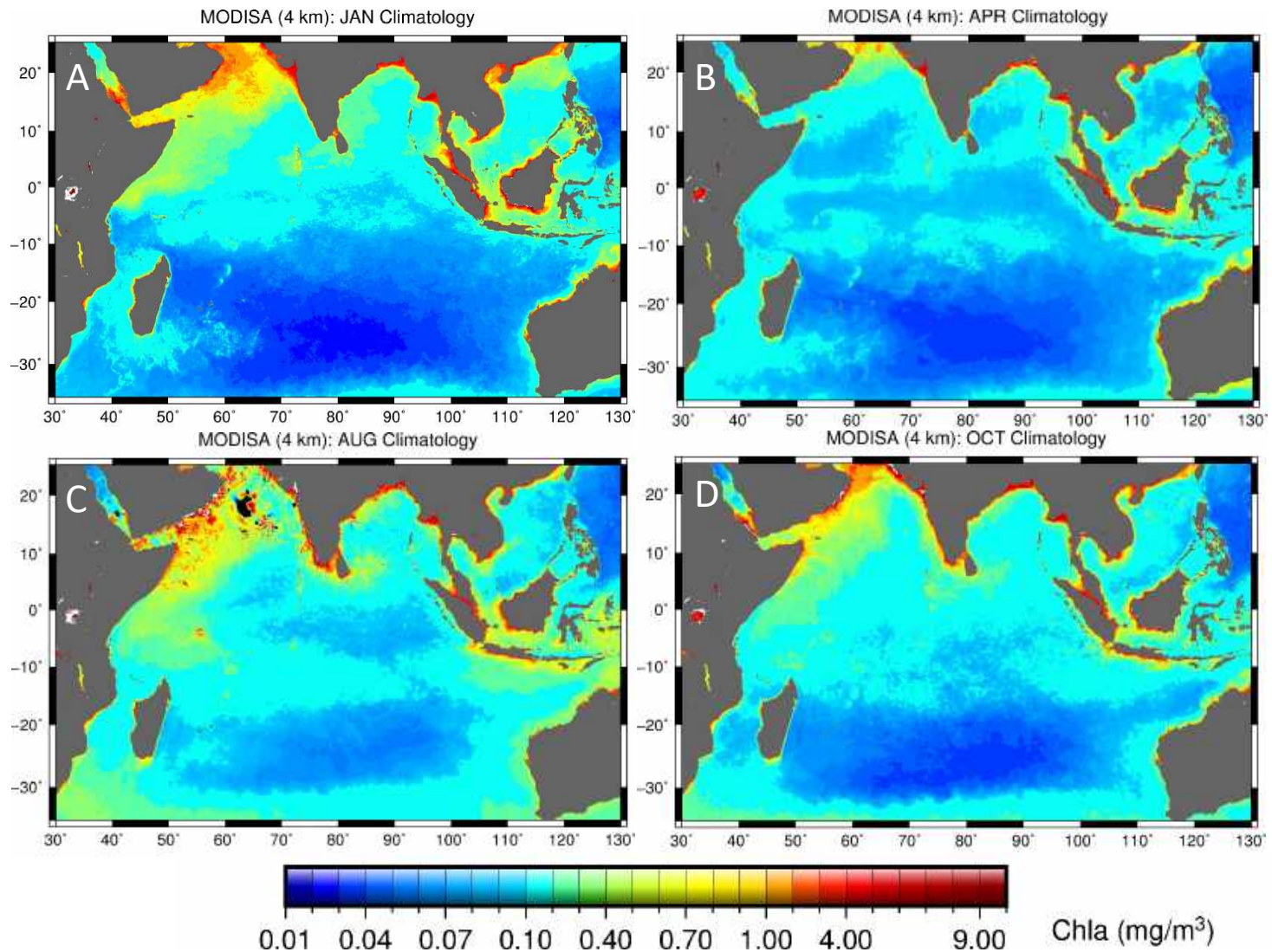


Figure 8: Monthly climatology of MODIS-Aqua (4 km resolution) chlorophyll: A) January, B) April, C) August, D) October. The climatology fields were obtained from the Goddard DAAC (<http://daac.gsfc.nasa.gov>). Figure and Caption from Hood et al. (2017)

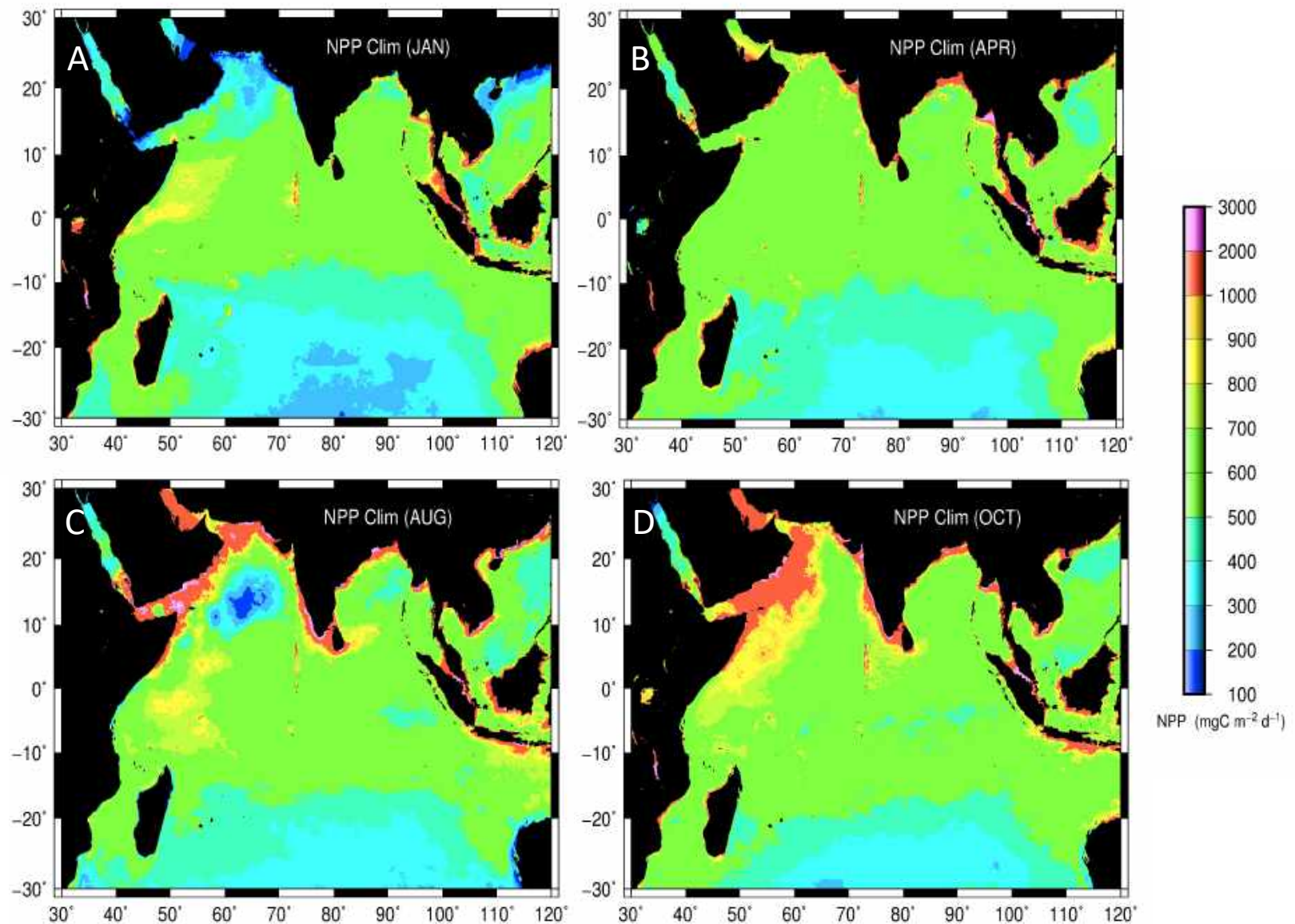


Figure 9: Monthly climatology of net primary production (NPP; $\text{mgC m}^{-2} \text{d}^{-1}$) estimated from SeaWiFs data: A) January, B) April, C) August, D) October. The climatology fields were obtained from the Goddard DAAC (<http://daac.gsfc.nasa.gov>). Figure and Caption from Hood et al. (2017).

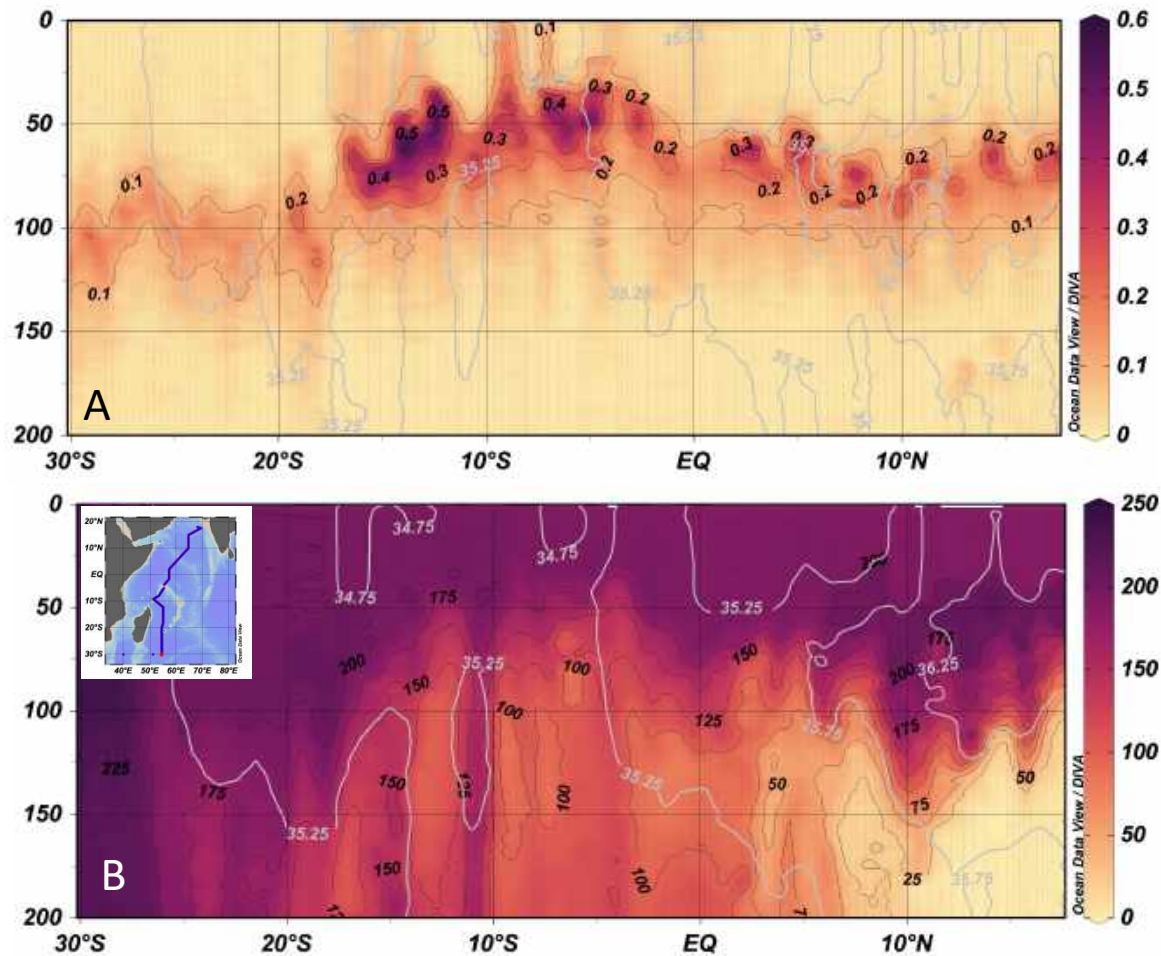


Figure 10: Vertical sections nominally along 55°E of A) Chlorophyll-a (mg m^{-3}) B) oxygen (mmol m^{-3}). The grey contours are salinity, and the black contours the colored property. The station locations for each property are shown as dots. Data from the 2018 IO7 GoShip line.

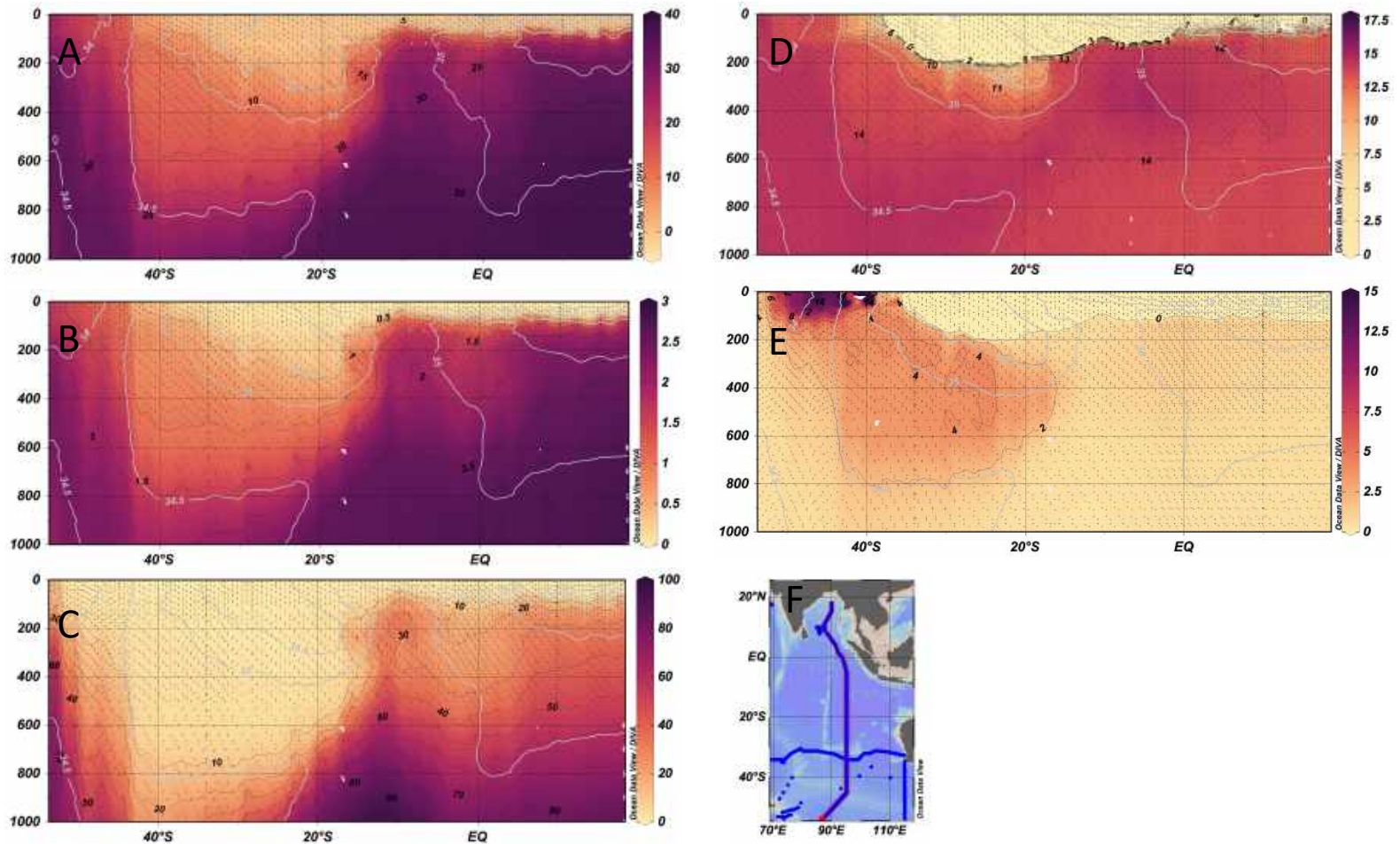


Figure 11: Vertical sections nominally along 90°E of A) nitrate (mmol m^{-3}) B) phosphate (mmol m^{-3}), C) silicate (mmol m^{-3}) D) nitrate to phosphate ratio, E) nitrate to silicate ratio, F) map of the section. The grey contours are salinity, and the black contours the colored property. The station locations for each property are shown as dots. Data from the World Ocean Database (2018), comprising mainly data from the IO9N and IO8S repeat hydrography lines. Only data from the 90°E N-S section are used in the section plots.

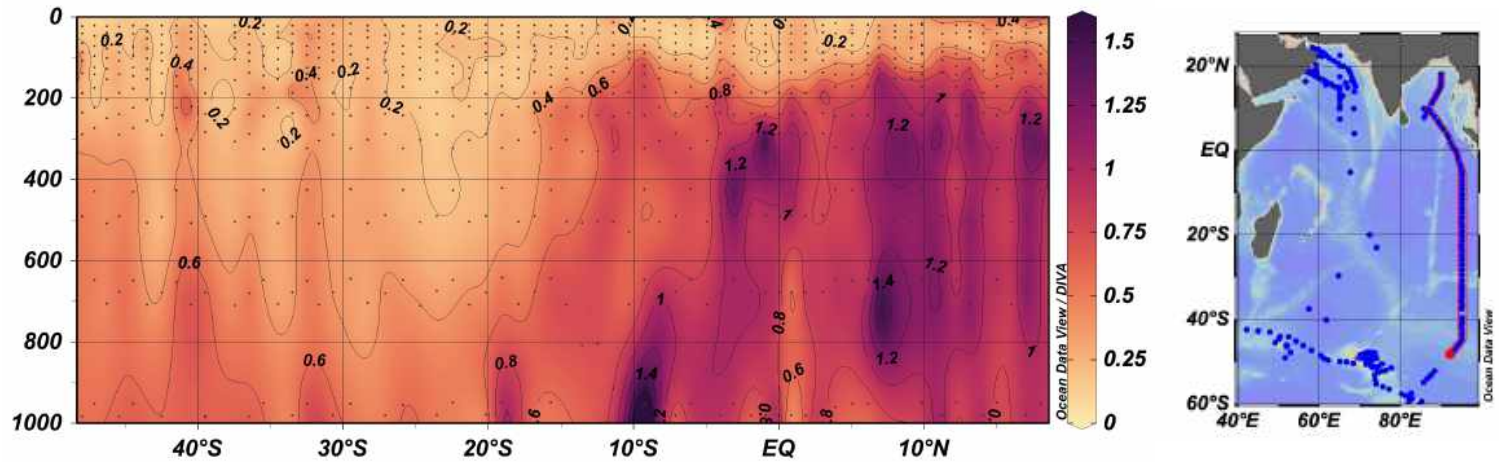


Figure 12: Dissolved Iron ($\mu\text{mole m}^{-3}$) along approximately 90° East in the Indian Ocean. The station locations are shown in the map inset. Data from Tagliabue et al. (2012) database. Only data from the 90°E N-S section are used in the section plots.

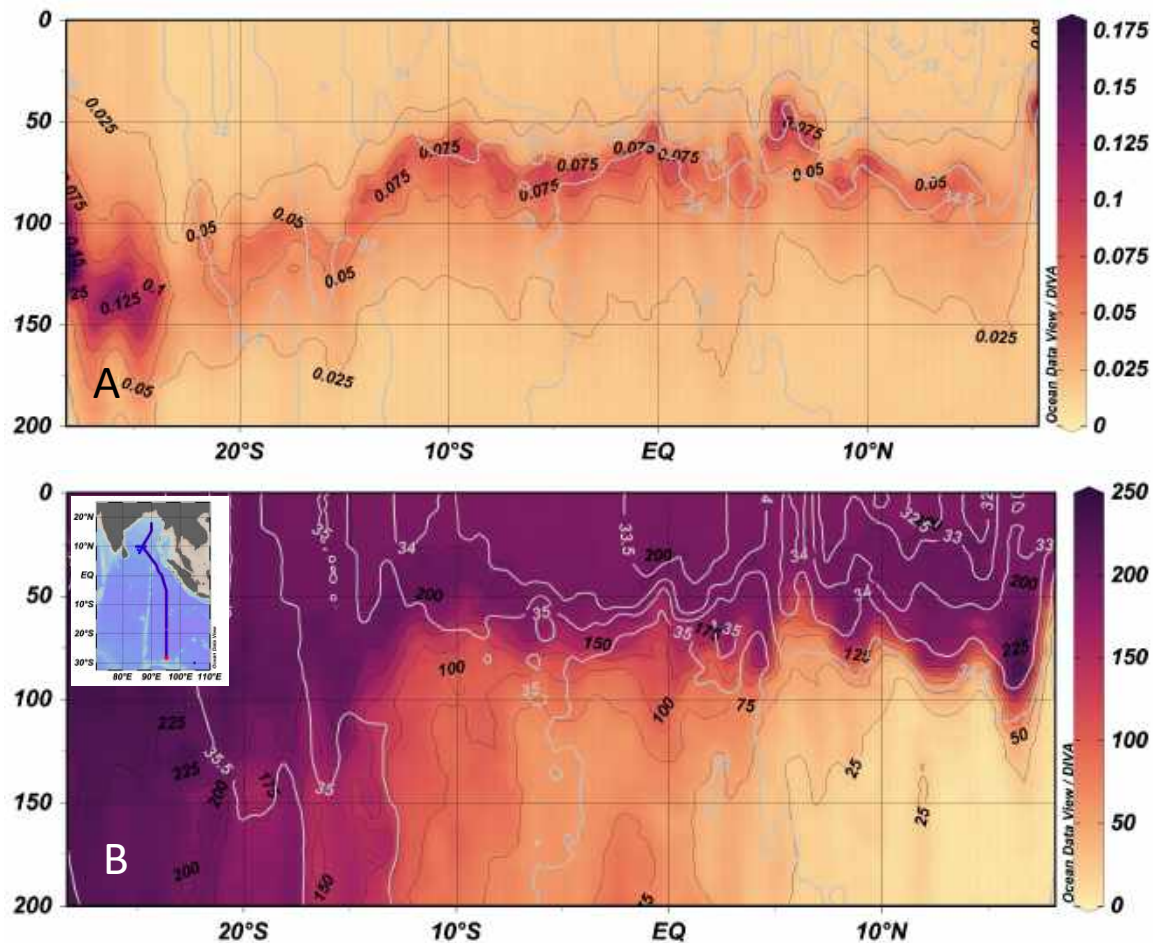


Figure 13: Vertical sections nominally along 95°E of A) CTD Fluorescence (volts) B) oxygen (mmol m⁻³). The grey contours are salinity, and the black contours the colored property. The station locations for each property are shown as dots. Data from the 2017 IO9 GoShip line.

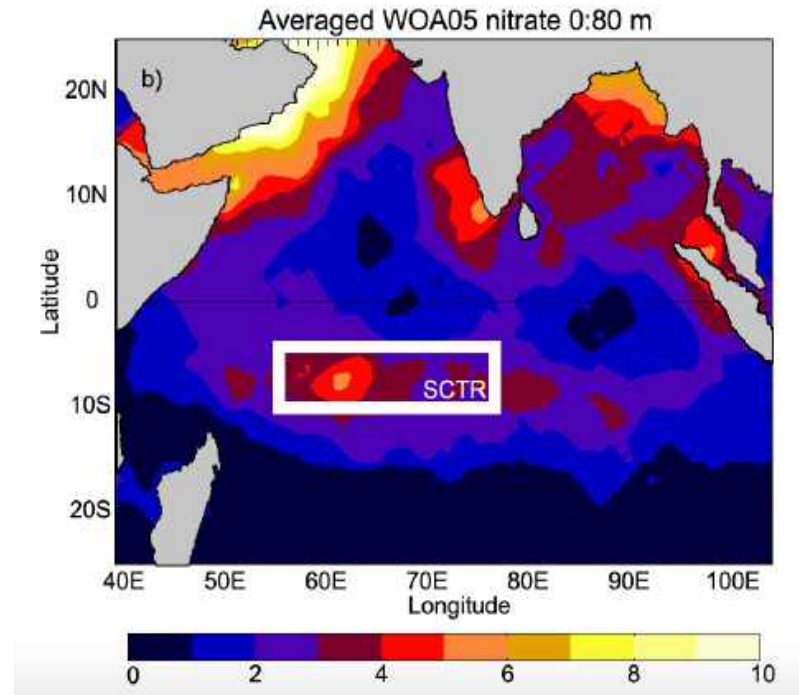
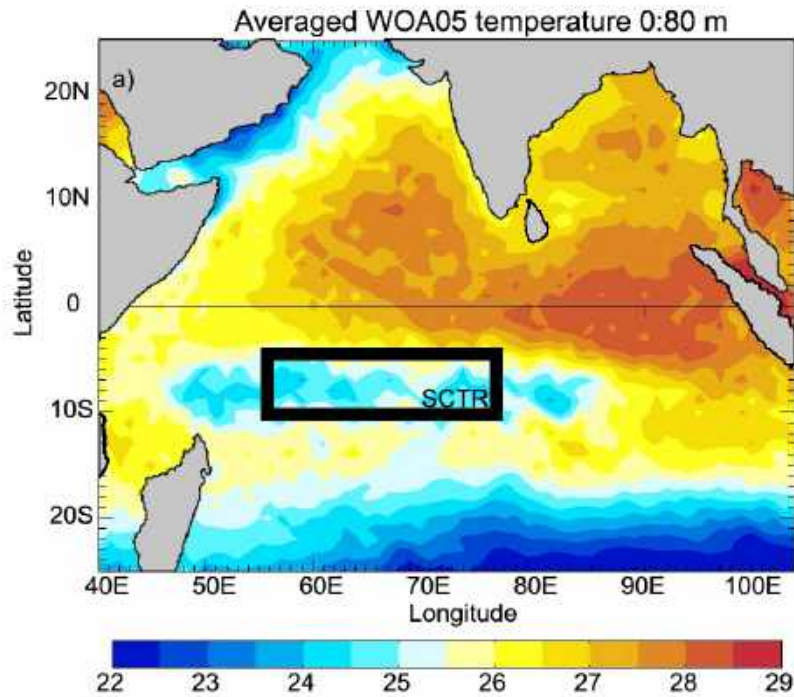


Figure 14: Annual World Ocean Atlas (2005) (a) temperature and (b) nitrate concentration (in mmol N m^{-3}) averaged between the surface and 80 m in the Indian Ocean. Figure and caption modified from Resplandy et al. (2009).

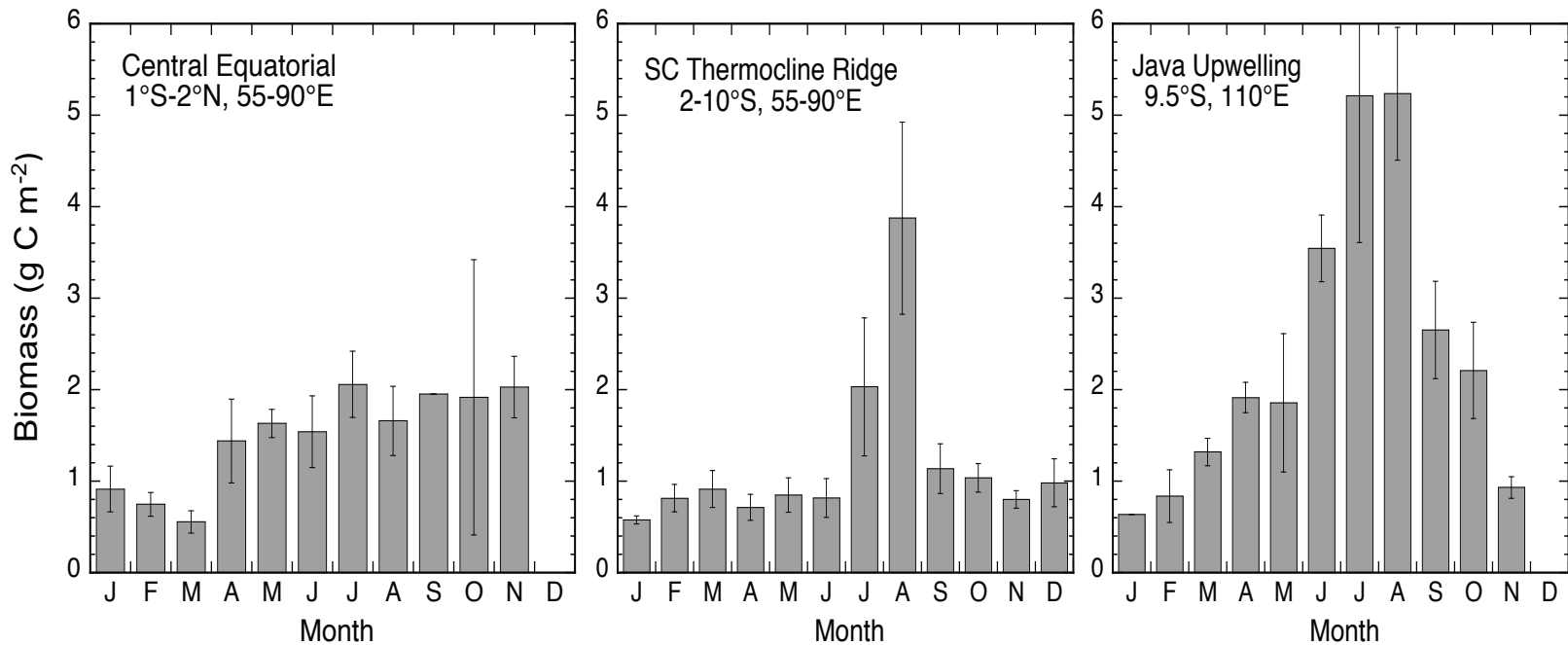


Figure 15: Monthly mean estimates of mesozooplankton biomass in the equatorial and off-equatorial upwelling systems of the Indian Ocean. Data are from historical collections in the Coastal and Oceanic Plankton Ecology, Production, and Observation Database (COPEPOD, <http://www.st.nmfs.noaa.gov/copepod>) were measured as wet weight and displacement volume (upper ~200 m) and corrected for different mesh sizes to carbon equivalents m⁻² for a 200- μ m mesh net according to Moriarty and O'Brien (2013). Uncertainties are standard errors of mean estimates. Plots are meant to compare and contrast seasonal patterns in different regions. Carbon may be overestimated where gelatinous animals are abundant.

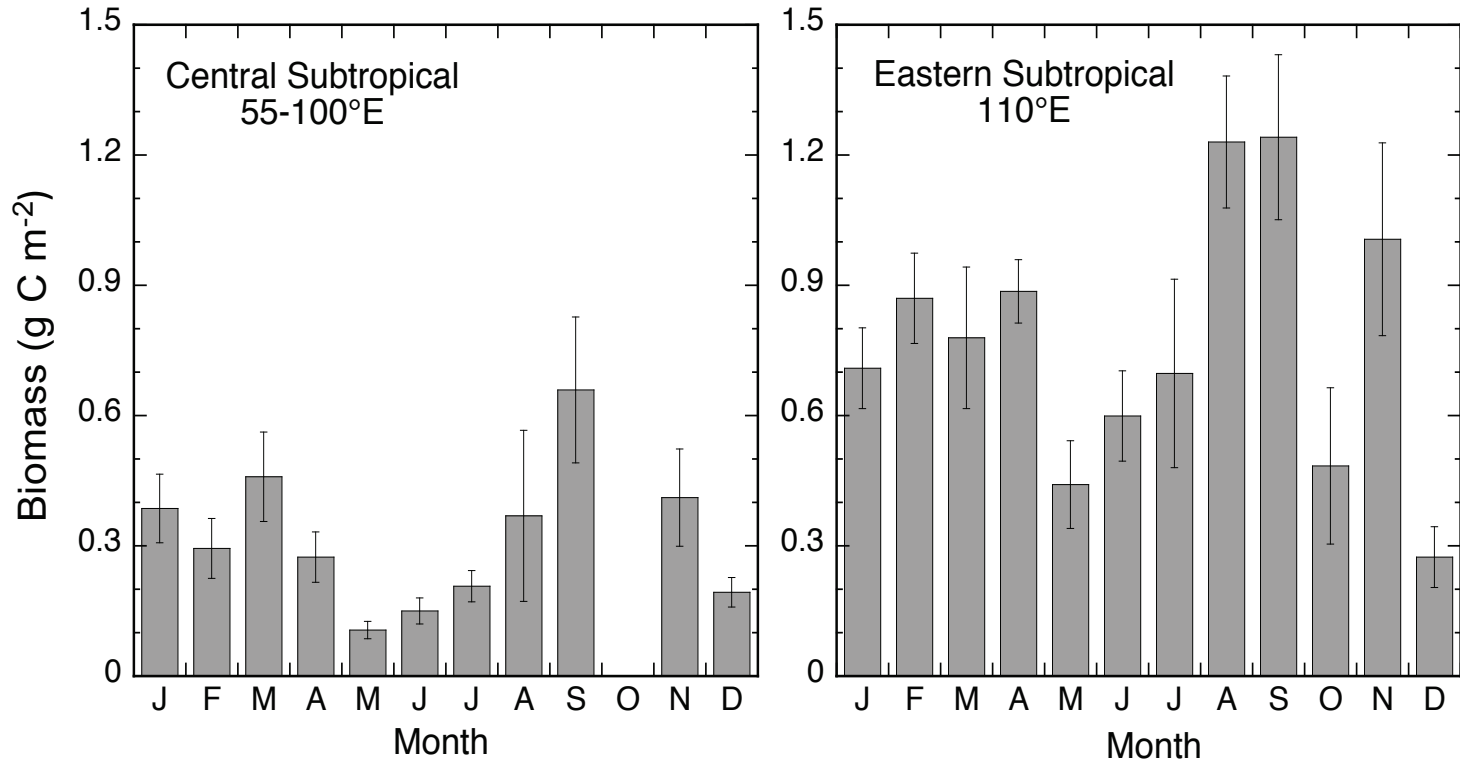


Figure 16: Monthly mean estimates of mesozooplankton biomass in the central and eastern subtropical regions of the Indian Ocean. Data source and caveats as in Figure 15.