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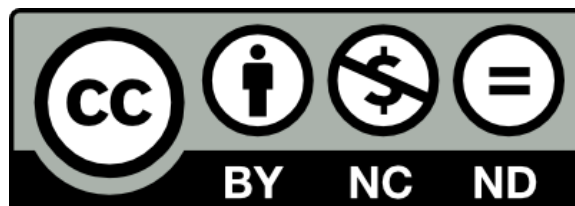
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Review

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Biogeochemical and Ecological Impacts of Boundary Currents in the Indian Ocean

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Abstract

Monsoon forcing and the unique geomorphology of the Indian Ocean basin result in complex boundary currents, which are unique in many respects. In the northern Indian Ocean, several boundary current systems reverse seasonally. For example, upwelling coincident with northward-flowing currents along the coast of Oman during the Southwest Monsoon gives rise to high productivity which also alters nutrient stoichiometry and therefore, the species composition of the resulting phytoplankton blooms. During the Northeast Monsoon most of the northern Indian Ocean boundary currents reverse and favor downwelling. Higher trophic level species have evolved behavioral responses to these seasonally changing conditions. Examples from the western Arabian Sea include vertical feeding migrations of a copepod (*Calanoides carinatus*) and the reproductive cycle of a large pelagic fish (*Scomberomorus commerson*). The impacts of these seasonal current reversals and changes in upwelling and downwelling circulations are also manifested in West Indian coastal waters, where they influence dissolved oxygen concentrations and have been implicated in massive fish kills. The winds and boundary currents reverse seasonally in the Bay of Bengal, though the associated changes in upwelling and productivity are less pronounced. Nonetheless, their effects are observed on the East Indian shelf as, for example, seasonal changes in copepod abundance and zooplankton community structure. In contrast, south of Sri Lanka seasonal reversals in the boundary currents are associated with dramatic changes in the intensity of coastal upwelling, chlorophyll concentration, and catch per unit effort of fishes. Off the coast of Java, monsoon-driven changes in the currents and upwelling strongly impact chlorophyll concentrations, seasonal vertical migrations of zooplankton, and sardine catch in Bali Strait.

In the southern hemisphere the Leeuwin is a downwelling-favorable current that flows southward along western Australia, though local wind forcing can lead to transient near shore current reversals and localized coastal upwelling. The poleward direction of this

eastern boundary current is unique. Due to its high kinetic energy the Leeuwin Current sheds anomalous, relatively high chlorophyll, warm-core, downwelling eddies that transport coastal diatom communities westward into open ocean waters. Variations in the Leeuwin transport and eddy generation impact many higher trophic level species including the recruitment and fate of rock lobster (*Panulirus cygnus)* larvae. In contrast, the transport of the Agulhas Current is very large, with sources derived from the Mozambique Channel, the East Madagascar Current and the southwest Indian Ocean sub-gyre. Dynamically, the Agulhas Current is upwelling favorable; however, the spatial distribution of prominent surface manifestations of upwelling is controlled by local wind and topographic forcing. Meanders and eddies in the Agulhas Current propagate alongshore and interact with seasonal changes in the winds and topographic features. These give rise to seasonally variable localized upwelling and downwelling circulations with commensurate changes in primary production and higher trophic level responses. Due to the strong influence of the Agulhas Current, many neritic fish species in southeast Africa coastal waters have evolved highly selective behaviors and reproductive patterns for successful retention of planktonic eggs and larvae. For example, part of the Southern African sardine (*Sardinops sagax)* stock undergoes a remarkable northward migration enhanced by transient cyclonic eddies in the shoreward boundary of the Agulhas Current.

There is evidence from the paleoceanographic record that these currents and their biogeochemical and ecological impacts have changed significantly over glacial to interglacial timescales. These changes are explored as a means of providing insight into the potential impacts of climate change in the Indian Ocean.

Keywords: Indian Ocean, boundary currents, monsoon, Southwest Monsoon, Northeast Monsoon, Southeast Monsoon, upwelling, downwelling, transport, nutrients, chlorophyll, primary production, zooplankton, fish, Somali Current, East African Coastal Current, Oman Coastal Current, West India Coastal Current, East India Coastal Current, Southwest Monsoon Current, Northeast Monsoon Current, South Java Current, Leeuwin Current, Mozambique Channel, East Madagascar Current, Agulhas Current, Agulhas Bank

Contents

1.   Introduction

1.1 The unique geomorphological and physical aspects of the Indian Ocean

Boundary currents are part of the major wind-driven circulations of the oceans, and they play an important role in the global thermohaline circulation. In addition, boundary currents mediate the fluxes of biogeochemical properties, and planktonic ecosystems, between major oceanic biomes. In so doing, they also impact higher trophic level (e.g., fishes) recruitment, production and behavior. The boundary currents in the Indian Ocean (Figure 1) are unique in many respects, compared to the boundary currents in the Atlantic and Pacific (Schott and McCreary, 2001; Hood et al., 2015). In the northern Indian Ocean the boundary currents reverse seasonally due to the influence of the monsoon winds (Figure 1). In the southeastern Indian Ocean, the Leeuwin Current flows poleward rather than equatorward (Figure 1). Although the Agulhas Current is a "normal" poleward-flowing western boundary current (Figure 1), it also has unusual attributes, which include large alongshore-propagating meanders and eddies that can substantially modify surface currents and upwelling and downwelling circulations (Lutjeharms, 2006a).

These unusual boundary current characteristics are directly related to the geography of the Indian Ocean (Figure 2). It is bounded to the north at low latitude by the Eurasian landmass so has no subtropical or temperate zones in the northern hemisphere. As a result, the northern Indian Ocean boundary currents do not flow into cooler water masses. Seasonal heating/cooling of the Eurasian land mass drives the intense semi-annual reversal of monsoonal winds (Figure 3; Slingo et al., 2005), which is a stark contrast to the gyre-scale atmospheric circulations operating in the northern Atlantic and Pacific basins. These monsoon winds, in turn, give rise to the seasonally reversing boundary currents in the northern Indian Ocean.

The partitioning of the northern basin of the Indian Ocean by the Indian subcontinent effectively creates two sub-basins and sub-gyres with distinct temperature and salinity characteristics and quasi-independent boundary current systems (though see section 2).

In particular, differences in evaporation, precipitation, river runoff, and connectivity to marginal seas, give rise to pronounced differences in salinity and stratification influences between the Arabian Sea and Bay of Bengal (Figure 4). As a result, the boundary currents in the former (where evaporation exceeds precipitation, river inputs are minor, and highly saline Persian Gulf and Red Sea waters contribute) are much saltier than they are in the latter (where precipitation exceeds evaporation and river inputs are large). Consequently, the signature of the salty source waters from the Arabian Sea that flow into the Bay of Bengal can be observed in the boundary currents in the Bay of Bengal. Similarly, freshwater signatures that propagate from the Bay of Bengal are apparent along the southwest coast of India (Shankar et al., 2002).

The Indonesian Throughflow (ITF) is another unique attribute of the Indian Ocean, allowing low latitude exchange between the western Pacific and eastern Indian Ocean through the Indonesian Archipelago (Gordon and Fine, 1996; Gordon et al., 1997), as opposed to the continental barriers that exist along the eastern Pacific and eastern Atlantic Oceans. The principal ITF pathway between the basins consists of flows that traverse the Makassar Strait, mix in the Banda Sea and then enter the Indian Ocean through the Timor Passage and Ombai Strait, with lesser contributions via Lombok Strait (Susanto and Song, 2015). The ITF inflow sets up the large-scale pressure gradients that drive the anomalous poleward-flowing Leeuwin Current in the southeast Indian Ocean which carries warm, and relatively fresh, water southward off the west coast of Australia (Figure 1; Schott and McCreary, 2001; Domingues et al., 2007). The Indonesian Throughflow also feeds and strengthens the Agulhas Current in the west via the South Equatorial Current (Figure 1; Lutjeharms, 2006a).

1.2 Recent advances in understanding biogeochemical, ecological and higher trophic level responses

In contrast to these relatively well-studied physical processes, we know much less about the impacts of Indian Ocean boundary currents on marine biogeochemistry, ecology and higher level trophodynamics and behavior. Much of our current understanding in the northern Indian Ocean derives from the international JGOFS (Joint Global Ocean Flux

Study) Arabian Sea process studies that were carried out in the 1990s (see, for example, *Deep-Sea Research II*, volumes 44-49 on the JGOFS Arabian Sea Expedition, and Smith, 2005). These studies primarily focused on trophic levels at or below mesozooplankton. There was a strong focus on how planktonic distributions, export fluxes and biogeochemical cycling are affected by monsoon-forced currents and upwelling on the western side of the basin off of Somalia, Oman and in the central Arabian Sea. Compared to the Arabian Sea, we know relatively little about the biogeochemical and higher trophic level impacts of the boundary currents in the Bay of Bengal and in the eastern Indian Ocean, though recent research has provided important new insights on the western side of the Bay of Bengal (see, for example, Vinayachandran 2009 and references cited therein). With a few exceptions, we can only speculate about the impacts of these seasonally reversing currents on commercially important higher trophic level species like sardines, tuna and squid, and on the massive myctophid populations.

As a result of numerous recent multidisciplinary studies that have been conducted off of Western Australia (see, for example, Waite et al. 2015 and references cited therein) we have a much deeper understanding of how the Leeuwin Current impacts biogeochemistry, ecology and higher trophic level species in this region. The latter includes important commercial species like the western rock lobster (*Panulirus cygnus*) as well as numerous coastal fishes whose larvae are strongly impacted by the southward transport and westward-propagating eddies that are associated with the Leeuwin Current.

Our understanding of the Agulhas Current and its tributaries has also benefitted from recent interdisciplinary international research initiatives (see, for example, Ternon et al., 2014; Marsac et al., 2014 and references cited therein for the Mozambique Channel and Fennessy et al., 2016 and references cited therein for the Kwa-Zulu Natal Bight) that have built upon a long history of research conducted off South Africa (e.g., Hutchings et al., 2002). This work has provided many insights into the impact of southwestern Indian Ocean boundary currents on biogeochemistry, ecology and higher trophic levels.

1.3 Review of the paper

In this paper, we explore and contrast how the unique physical attributes of Indian Ocean boundary currents influence biogeochemical fluxes, planktonic ecosystems and higher trophic level pelagic productivity, behavior and recruitment. The physical characteristics that we examine include differences in temperature, salinity, seasonality, transport, upwelling and mesoscale variability. These give rise to distinct differences among Indian Ocean boundary currents in the intensity, duration and timing of nutrient inputs and productivity responses (Table 1). To illustrate the impacts these currents have on higher trophic level productivity, behavior and recruitment we provide selected examples from each current system, which cover a wide range of sizes and trophic levels and include copepods, decapods and fishes. We show that these currents have profound biogeochemical and ecological impacts that differ in many respects from one another and that these differences can be linked to their physical attributes.

2. The Seasonally Reversing Currents of the Northern Indian Ocean

2.1 Introduction

During boreal summer heating over the Eurasian land mass, and more directly the Tibetan Plateau (e.g., Kripalani et al., 2003), drives the strong Southwest Monsoon (SWM) winds that flow across the Arabian Sea (where it is termed the Findlater Jet; Findlater, 1969), the Indian subcontinent and the Bay of Bengal from late May through August (Figure 3). Then, in the winter months (December through February) cooling and subsidence of the continental air masses over Eurasia and the Tibetan Plateau forms the Northeast Monsoon (NEM) that flows in, approximately, the opposite direction (Figure 3). In general, the monsoon winds drive anticyclonic and therefore upwelling favorable boundary current circulations during the SWM, versus cyclonic and downwelling favorable circulations during the NEM (Figure 2; Schott and McCreary, 2001; Shankar et al., 2002; Beal et al., 2013). This seasonality is more pronounced along the western sides of the Arabian Sea and Bay of Bengal sub-basins, and particularly, in the western Arabian Sea where the monsoon winds are most intense (Figure 3; Schott and McCreary, 2001; Shankar et al., 2002; Beal et al., 2013). Although most boundary current systems

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exhibit some seasonal variability in transport, as well as wind-induced reversals in near shore flows, the northern Indian Ocean is the only place where major boundary currents undergo full seasonal reversal.

2.2 Local versus remote forcing and seasonality

Local (monsoon) wind forcing impacts are very strong in the northern Indian Ocean as evidenced by the dramatic response of the basin's boundary currents. However, the changes in wind speed and direction associated with the monsoons are coherent over the entire northern Indian Ocean (Schott and McCreary, 2001; Schott et al., 2009; Shankar et al., 2002). As a result, the semi-annual changes in the boundary circulations (Figure 1) represent a quasi-coherent, basin-scale response. In addition, these boundary currents are influenced remotely and are modified significantly by coastally trapped Kelvin waves that initiate along the Sumatra coast as a result of the arrival of the eastward propagating Wyrtki Jet.

The Wyrtki Jet is a semi-annual, equatorially trapped Kelvin wave that is triggered during the inter-monsoon periods by equatorial westerly wind bursts in the western Indian Ocean (Wyrtki, 1973; Sprintall et al., 2000). Following the Jet's impingement on Sumatra it bifurcates and propagates northward and southward as coastal Kelvin waves. As they continue around the coastline, the coastal Kelvin waves influence the Bay of Bengal's circulation and boundary currents, eventually passing south of India and Sri Lanka and continuing into the Arabian Sea (McCreary et al., 1996; Schott and McCreary, 2001; Shankar et al., 2002; and references cited therein). The coastal Kelvin waves that propagate southward following the Wyrtki Jets' impingement on the Sumatra coast have been shown to trigger reversal of the South Java Current and influence the Indonesian Throughflow (Iskander et al., 2005; Sprintall et al., 2000; Sprintall et al., 2010).

These coastal Kelvin waves have significant influences, not only in the eastern equatorial Indian Ocean, but on the boundary currents throughout the northern Indian Ocean. They can cause them to respond in ways that seem paradoxical compared to what would be expected from the local wind forcing, i.e., they can drive abrupt changes in surface

currents, thermocline depth and upwelling that are in opposition to local wind forcing (Schott and McCreary, 2001; Shankar et al., 2002; and references cited therein).

2.3 The Arabian Sea and the western Indian Ocean

2.3.1 General physical attributes

The seasonally reversing currents in the Arabian Sea and the western Indian Ocean that are considered here include the Somali Current off Somalia and the Oman Coastal Current off of Oman, the West India Coastal Current that hugs the west coast of India, and the Southwest Monsoon Current that traverses eastward offshore around the southern tip of India and Sri Lanka during the SWM and enables exchange between the Arabian Sea and Bay of Bengal (Figure 1).

The Somali Current exhibits seasonal reversals and seasonal variations in its pathway along the east coast of Africa due to its association with the East African Coastal Current. During the NEM, the southwestward-flowing Somali Current merges with the East African Coastal Current to form the South Equatorial Countercurrent (Figure 1; Beal et al., 2013). In contrast, during the SWM, the East African Coastal Current traverses the equator and continues into the Arabian Sea as the Somali Current, with a portion of the current splitting off and turning southward again to form the "Southern Gyre" (Schott and McCreary, 2001; Shankar et al. 2002; Schott et al., 2009; Figure 1). However, recent observations suggest that this may not be a gyre but, rather, the retroflection of the East African Coastal Current, which feeds into eastward-flowing equatorial currents (Beal et al., 2013; Figure 1).

The Somali Current exhibits significant complexity as it flows northeastward off Somalia during the SWM, extending to a depth of ~500 m (Schott and McCreary, 2001; Figure 1). With an estimated transport of ~37 Sv (Beal and Chereskin, 2013), the Somali Current is the largest boundary current in the Northern Indian Ocean. The northward flowing phase of the Somali Current initiates south of the equator just prior to onset of the SWM. As it propagates along the African coast two anticyclonic eddies form, the somewhat cryptic

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Southern Gyre at ~ 3° N in late May and the Great Whirl at ~ 8° N in June as the
Findlater Jet (Findlater, 1969; Figure 1) becomes fully established (Beal and Donohue,
2013). Interestingly, the anticyclonic circulation indicative of the Great Whirl appears on
average in April, almost two months before the onset of the SWM winds (Beal and
Donohue, 2013). This early initiation is coincident with, and perhaps forced by, the
arrival of annual Rossby waves at the western boundary (Beal and Donohue, 2013). With
the onset of the SWM in early June, the Great Whirl intensifies quickly. Although most
of the flow associated with the Great Whirl turns offshore (eastward) before reaching the
Horn of Africa, some fraction continues to propagate northward, crosses the mouth of the
Gulf of Aden and proceeds along the coast of Oman as the Oman Coastal Current with an
estimated transport of up to 10 Sv (Cutler and Swallow, 1984; Elliot and Savidge, 1990;
Figure 1).

The Oman Coastal Current turns abruptly eastward to form the Ras al Hadd Jet that flows
across the northern Arabian Sea along the southern extent of the Gulf of Oman (Figure 1;
Wiggert et al., 2005). However, during the SWM, intense eddies and offshore
propagating flows (described as filaments and jets) develop, which tend to obscure the
northward alongshore flow in the western Arabian Sea. These eddies and offshore flows
are apparent in satellite SST and color measurements (e.g., Fischer et al., 2002 and see
Figure 7 below) and also by in situ observations and they appear to be linked to coastal
topographic features (Flagg and Kim, 1998; Manghnani et al., 1998; Lee et al., 2000).
However, there is poor understanding of the dynamics and transport associated with the
southwestern portion of the Oman Coastal Current and there are open questions regarding
its continuity and offshore mesoscale eddy interaction (Figure 1; Wiggert et al., 2005).

During the NEM, the Somali Current flows southwestward along the coast of Somalia
with a transport of ~5 Sv and it extends down to ~150 m depth (Schott and McCreary,
2001; Figure 1). As it crosses the equator, the Somali Current feeds into the eastward
propagating South Equatorial Countercurrent (Figure 1; Beal et al., 2013). Further north,
off the coast of Oman, the flow is generally southward during the NEM except across the
mouth of the Gulf of Aden where coastal currents from the north and south converge to

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form weak westerly flows (Figure 1). In the northern Arabian Sea, during the SWM, the mean flow along the coast is eastward (Figure 1; Schott and McCreary, 2001) and during the NEM it is westward (Figure 1; Shi et al., 2000).

Along the eastern boundary of the Arabian Sea during the SWM, the West India Coastal Current carries ~4 Sv of high salinity water southward along the west coast of India, extending to about 100 m depth (Figure 1). This current strengthens as it progresses southward from its first manifestation at ~15° N (Shetye et al., 1990). During the NEM the West India Coastal Current reverses and transports ~7 Sv of less saline water northward (Figure 1). This flow is in opposition to the prevailing (albeit weak) surface winds (Shetye et al., 1991). The poleward phase of the West India Coastal Current is better developed than the equatorward phase, extending to a depth of ~ 200 m with a lateral swath of ~ 400 km at 10° N (Shetye, 1998). Along with the seasonal reversal of the West India Coastal Current, anticyclonic/cyclonic circulations develop in the waters offshore of the southwest coast of India during the SWM/NEM (Figure 1). These 600-800 km wide eddies are identified as the Laccadive (Lakshadweep) Low/High (Bruce et al. 1994; Shankar and Shetye, 1997).

During the SWM the Southwest Monsoon Current extends from the southward flowing West India Coastal Current, as it wraps around the western edge of the Laccadive Low and turns eastward south of India with connectivity to the poleward flowing East India Coastal Current (Figure 1; Shankar and Shetye, 1997). This circulation, however, is complex. For example, the island of Sri Lanka deflects the eastward-flowing Southwest Monsoon Current southward, whilst along the eastern coast of Sri Lanka, a southward flow results from the Sri Lanka Dome recirculation (Schott and McCreary, 2001; de Vos et al., 2014; Figure 1). During the NEM the Southwest Monsoon Current is replaced by the Northeast Monsoon Current, which flows in the opposite direction (see section 2.4.1 below).

2.3.2 Upwelling and downwelling variability and mesoscale activity

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The changes in upwelling and downwelling associated with the monsoonal forcing and boundary current reversals in the Arabian Sea and the western Indian Ocean are dramatic (Figure 1). Strong upwelling is associated with the winds and the anticyclonic boundary current circulations that develop during the SWM, though the intensity and surface manifestation vary regionally. The strongest upwelling response is observed in the western Arabian Sea off of Somalia, Yemen and Oman (Figure 1) where near-surface nitrate concentrations increase to > 15 μM (Morrison et al. 1998). These regions exhibit very high eddy kinetic energy, particularly off of Somalia in association with the Great Whirl (Resplandy et al., 2009; McCreary et al., 2013; Figure 3). Modeling studies demonstrate that the aforementioned eddies and filaments facilitate offshore transport of coastally upwelled nutrients (Kawamiya, 2001; Resplandy et al., 2011).

Although less pronounced, the southward-flowing West India Coastal Current promotes upwelling that outcrops at the surface along the west coast of India (Figure 1). This upwelling is most pronounced between ~8° N and 14° N (Shetye et al., 1990; Smitha et al., 2014) and progressively extends from south to north during the SWM (Murty, 1987; Shetye and Gouveia, 1998). This upwelling is associated with the SWM winds, which strengthen in April, reach maximum velocity in August and then weaken in October (Shetye and Shenoi, 1988). However, it should be noted that, on average, the SWM winds do not blow alongshore, but rather onshore along the west coast of India (Figure 3). Moreover, numerical models suggest that the upwelling is predominantly forced remotely from the Bay of Bengal via northward propagation of coastal Kelvin waves (McCreary et al., 1993). Satellite color imagery suggests that seaward extension of upwelling off the west coast of India is much less pronounced than it is off of Somalia and Oman (Wiggert et al. 2006; Figure 2; Figure 5). Further, in comparison to the western Arabian Sea, the eddy kinetic energy is considerably lower (Resplandy et al., 2011; McCreary et al., 2013; Figure 3).

The Laccadive Low and High that develop off the southwest coast of India during the SWM and NEM are anticyclonic and cyclonic, and therefore result in upwelling and downwelling circulations, respectively (Figure 1). Although the impact of these

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circulations is evident in sea surface height (SSH) data (Bruce et al., 1994; Shankar and Shetye, 1997; Subrahmanyam and Robinson, 2000), they do not appear to have a strong influence on eddy kinetic energy (Figure 3) or on nutrient and/or chlorophyll concentrations at the surface (Lierheimer and Banse, 2002; see below).

Although the cyclonic boundary currents and northeasterly winds that are associated with the NEM are, generally, downwelling favorable in the Arabian Sea and the western Indian Ocean (Figures 1 and 3), the vagaries of local wind forcing and remote forcing via coastal Kelvin waves and their associated laterally propagating buoyancy fluxes can have counteracting effects. Observations show that remote forcing of the West India Coastal Current is present at all times and that this influence is most striking when the local winds are weak during the intermonsoon periods (Amol et al., 2012). The fresher waters of the West India Coastal Current that flow up the west coast of India during the NEM give rise to shallow mixed layers on the continental shelf off the southeast coast of India, and also northward displacement of maximum mixed layer depth from the location of peak net heat loss associated with the winter monsoon forcing (Shankar et al., 2015).

2.3.3 Impacts on primary production

The entire western side of the Northern Indian Ocean, and particularly the western Arabian Sea, transitions to a eutrophic coastal upwelling system during the SWM as a result of the monsoon-driven transition to upwelling favorable winds and currents (Wiggert et al., 2005; and references cited therein; Figure 2; Figure 5; Figure 6). These changes are revealed in ocean color data as dramatic increases in chlorophyll concentrations particularly along the coasts of Somalia, Yemen and Oman and, to a lesser extent, along the west coast of India (e.g., Brock and McClain, 1992; Banse and English, 2000; Kumar et al., 2000; Lierheimer and Banse, 2002; George et al., 2013; Figure 2; Figure 5). During the SWM, vertically-integrated chlorophyll-*a* concentrations in the western Arabian Sea can exceed 40 mgChla m^{-2} with areal primary production rates > 2.5 gC m^{-2}d^{-1} (Marra et al. 1998; Figure 6). However, during the SWM the environmental conditions vary dramatically between the eutrophic coastal zones off of Somalia, Yemen and Oman and the oligotrophic open ocean waters that are subject to pronounced wind-

curl induced downwelling south of the Findlater Jet (Lee et al., 2000). Over this coastal to open ocean gradient in physical environments, mixed layer nitrate and chlorophyll concentrations decline dramatically from > 10 to < 0.02 μM and from > 1.0 to < 0.2 mgChla m^{-3}, respectively (Brown et al., 1999). Past studies have shown that, in general, the phytoplankton community structure shifts to larger cells (e.g., diatoms) during the SWM in the western Arabian Sea (Brown et al., 1999; Tarran et al., 1999; Shalapyonok et al., 2001), albeit with small primary producers remaining active and important, even in areas strongly influenced by coastal upwelling where picophytoplankton can still comprise more than 30% of the phytoplankton carbon (Brown et al., 1999). In general, during the oligotrophic intermonsoon periods, surface waters in the western Arabian Sea are dominated by picoplanktonic *Prochlorococcus* and *Synechococcus* species (Garrison et al., 2000).

Off Somalia and Oman, the presence of the topographically-locked eddies not only drive the coastal currents, but they also generate strong offshore flows (i.e., filaments) that transport high nutrient and chlorophyll concentrations and distinct coastal phytoplankton communities hundreds of kilometers offshore (Keen et al., 1997; Latasa and Bidigare, 1998; Manghnani et al., 1998; Gundersen et al., 1998; Hitchcock et al., 2000; Lee et al., 2000; Kim et al., 2001; Figure 7). These advective effects are seen most clearly in association with the Great Whirl off of the northern tip of Somalia (Hitchcock et al., 2000) and the persistent filaments that consistently develop off of the Arabian Peninsula during the SWM (Wiggert et al. 2005; Figure 7). Although the circulation and winds transition to downwelling favorable during the NEM, the combination of buoyancy driven convection and moderate wind forcing drive entrainment of nutrients that promotes modest increases in chlorophyll and production over much of the northern and central Arabian Sea (Wiggert et al., 2000; Figure 5; Figure 6).

Coupled physical-biological modeling studies have suggested that reversals in the coastal currents and changes in upwelling intensity lead to shifts in nutrient stoichiometry in the Arabian Sea, albeit with varied guidance on identifying the most-limiting nutrient (Wiggert et al., 2006; Koné et al., 2009; Resplandy et al., 2011). Specifically, these

studies indicate that, during the SWM, phytoplankton growth in coastally upwelled waters in the Arabian Sea are prone to silicate limitation (Koné et al., 2009; Resplandy et al., 2011) and/or iron limitation (Wiggert et al., 2006; Wiggert and Murtugudde, 2007) off the coasts of Somalia, Yemen and Oman (modeled iron limitation patterns are depicted in Figure 8). These model-based findings are supported by both direct and indirect observational evidence. High N:Si ratios (∼2/1 as compared to the ∼1/1 ratio often assumed as the ratio of uptake during diatom growth) measured in the water upwelled along the Omani coast suggest the potential for silicate limitation of diatom growth (Morrison et al., 1998). Similarly, N:Fe ratios in coastally upwelled waters measured during SWM cruises of the U.S. Arabian Sea JGOFS expedition range from 20,000– 30,000, where values above 15,000 are inherently iron limited (Measures and Vink, 1999). Moreover, both the N:Fe and N:Si ratios were observed to increase by the latter stages of the SWM, with the higher N:Si ratios (i.e. preferential Si depletion, Morrison et al., 1998) being indicative of iron limited diatoms (Moffett et al., 2015). Presumably, these elevated N:Fe and N:Si ratios are derived from upwelling of Fe and Si depleted water from depth, though the specific origin/depth of these source waters appears to be unknown.

In situ measurements reported by Naqvi et al. (2010) and Moffett et al. (2007) confirm low Fe concentrations and also low Si concentrations in upwelled water off the coast of Oman during the SWM. Naqvi et al. (2010) argue that these shifts in nutrient stoichiometry and limitation tend to inhibit diatom growth and promote, instead, blooms of smaller phytoplankton species. Such a shift in species composition potentially reduces vertical export to the deep ocean and would favor, instead, lateral advection of organic matter into the northern and central Arabian Sea (McCreary et al., 2013). In these deeper offshore waters, particle scavenging would tend to reduce the capacity for "local" retention of dissolved iron via remineralization, thus further contributing to Fe limitation. Naqvi et al. (2010) have suggested that the western Arabian Sea transitions to a High Nutrient Low Chlorophyll (HNLC) Fe-limited state during the SWM (as is observed, for example, in the eastern equatorial Pacific; Landry et al., 1997). In support of this HNLC hypothesis, Moffett et al. (2015) report up to 6-fold increases in chlorophyll

concentration in iron addition experiments on water samples from the western Arabian Sea. Interestingly, samples from within an upwelling filament that originated off Oman exhibited the strongest response to these enrichment experiments. Finally, with the depleted Si availability in upwelled waters, the dominant phytoplankton species apparent in these experiment responses was *Phaeocystis sp.*, rather than diatoms (Moffett et al., 2015), thus lending credence to the silicate limited response reported for the modeling efforts of Koné et al. (2009).

Finally, it should be noted that surface nutrient measurements reveal significant quantities of unused total inorganic nitrogen during the SWM in the western Arabian Sea (Morrison et al., 1998), which supports the HNLC hypothesis. However, whether or not the western Arabian Sea transitions to true HNLC conditions during the SWM remains a subject of debate.   Indeed, the high chlorophyll concentrations that develop off the coasts of Somalia, Yemen and Oman (> 40 mgChla m^{-2}) can hardly be described as "low chlorophyll". Further effort will be required to fully understand the role of iron as a limiting micro-nutrient in the northwestern Indian Ocean.

Off the west coast of India during the SWM the upwelling-favorable West India Coastal Current induces upwelling of nutrients adjacent to and over the West Indian shelf, which enhances phytoplankton concentrations by more than 70% compared to the central Arabian Sea (Kumar et al., 2000; Naqvi et al., 2000; Luis and Kawamura, 2004). However, the increases in chlorophyll and their offshore extent are modest compared to the western side of the basin (Figure 2 and Figure 5). The elevated phytoplankton concentrations near the coast are associated with increases in the abundance of diatoms (Sawant and Madhupratap, 1996). In contrast, during the NEM the downwelling-favorable West India Coastal Current tends to suppress primary production over the southwestern Indian Shelf.   The depletion of nutrients in this region during the NEM coincides with development of blooms of *Trichodesmium* and also several dinoflagellate species including *Noctiluca* (Parab et al., 2006; Matondkar et al., 2007). However, further north and offshore, nutrient entrainment enhances phytoplankton biomass and primary production during the NEM (Wiggert et al., 2000; McCreary et al., 2001; Luis

and Kawamura, 2004; Figure 5; Figure 6), and this has been associated with increased diatom abundance (Banse and McClain, 1986; Sawant and Madhupratap, 1996). (It should be noted, however, that, in the last decade, there appears to have been a shift in the composition of winter phytoplankton blooms in the northern Arabian Sea from diatom dominance to blooms of a large, green mixotrophic dinoflagellate, *Noctiluca scintillans;* Gomes et al., 2014). Off the west coast of India, The vertically-integrated primary production and near-surface chlorophyll-*a* estimated from satellite ocean color measurements (both averaged over the entire western India Shelf) increases from ~1 to 2.25 g C m^{-2} d^{-1} and from ~9 to 24 mgChla m^{-2}, respectively, from winter to the summer monsoon (Luis and Kawamura, 2004; Figure 5; Figure 6). The enhanced productivity during the SWM is modulated by the previously discussed remotely-forced coastal Kelvin waves from the Bay of Bengal that propagate along the West Indian Shelf and modify circulation patterns and upwelling (Luis and Kawamura, 2004).

Satellite ocean color observations suggest that phytoplankton pigment concentrations are relatively low all year-round in the Laccadive Sea in spite of the transition from anti-cyclonic upwelling circulations during the SWM to cyclonic downwelling circulations during the NEM (Lierheimer and Banse, 2002; Figure 5). Thus, it appears that the elevated chlorophyll concentrations and production rates caused by the upwelling off India during the SWM are largely restricted to the shelf. However, there are occasional large, zonal increases in chlorophyll that extend into the Laccadive Sea (Lierheimer and Banse, 2002). Whether or not there are cryptic subsurface phytoplankton blooms associated with the Laccadive Low upwelling is unknown.

2.3.4 Higher trophic level impacts and speculation

Microzooplankton and mesozooplankton grazing are both very important in the high-nutrient coastal aresa off of Oman during the SWM where the former can exceed 50% of total grazing. In contrast, microzooplankton grazing tends to dominate (> 80%) in the more oligotrophic offshore waters (Brown et al., 1999). Inverse and network analyses of multiple data sets collected during the JGOFS Arabian Sea Process study have suggested

that for most stations and seasons zooplankton grazing does not equal net phytoplankton production and that picophytoplankton production is an important and frequently dominant component of export (Richardson et al., 2006). It has been argued that this picophytoplankton domination of export is manifested through aggregation-related increases in sinking rate or consumption of picophytoplankton aggregates by mesozooplankton or salps (Richardson et al., 2006). These results contrast with the conventional ''microbial loop'' view that picophytoplankton production is predominantly recycled within the euphotic zone, and they suggest that primary production by the smallest algal cells is connected directly to export pathways via detritus and mesozooplankton. It should be noted, however, that subsequent studies indicate that the data from the JGOFS Arabian Sea Process Study are consistent with balanced production and grazing rates (Landry, 2009). Moreover, the idea that grazing is not coupled to primary production is incompatible with other results that are reported above, such as the similarity of the Arabian Sea to the HNLC equatorial Pacific, and below, such as the idea that *Calanoides carinatus* grazing can suppress phytoplankton growth during the SWM in the western Arabian Sea.

The dramatic reversals in the boundary currents and associated changes in upwelling and primary production in the northern Indian Ocean have led to the evolution of adaptive behaviors in higher trophic level species. For example, the crustacean zooplankter *Calanoides carinatus* migrates from hundreds of meters depth to the surface during the SWM in the western central Arabian Sea to feed when surface chlorophyll concentrations are high (Idrisi et al., 2004). Increases in *C. carinatus* nauplii have also been observed off the coast of Somalia during the SWM (Smith, 1992); this appears to represent a behavioral reproductive response to upwelling-enhanced chlorophyll concentrations. It has been suggested that grazing control by this species reduces accumulation of phytoplankton biomass in response to upwelling of nutrients during the SWM and that downward migration before the end of the SWM enhances phytoplankton concentrations and export due to the release of zooplankton grazing pressure (Smith, 2001).

We can expect that coastal fish species in the western Arabian Sea have evolved reproductive strategies that maximize the overlap between first-feeding larvae and the relatively predictable monsoon-driven periods of high productivity (Cushing, 1990). For example, analysis of the reproductive cycle of the kingfish (*Scomberomorus commerson*), which is one of the keystone species of the traditional fisheries along the Gulf of Oman, reveals a single spawning period, peaking in May/June just prior to the onset of the SWM (Claereboudt et al., 2004). Presumably, this behavior has evolved so that kingfish larvae can take advantage of the high productivity and high abundance of copepods associated with the SWM.

On the opposite side of the Arabian Sea, seasonal reversals in the winds and the West India Coastal Current and associated changes in upwelling intensity have profound impacts on oxygen concentrations and therefore higher trophic levels on the shelf off western India (Naqvi et al., 2000; Naqvi et al., 2006; Naqvi et al., 2009). From June to November, cold, saline, low oxygen (~22 μM) waters upwell onto the shelf. These waters are usually capped by a thick (5-10 m) warm, low-salinity layer of water derived from SWM-driven terrestrial runoff and local precipitation, which results in strong density stratification and poor ventilation of sub-pycnocline waters. This, in turn, results in depletion of oxygen concentrations to near-zero levels over the shelf where oxygen consumption is supported by both the upwelling and anthropogenically-enhanced terrestrial nutrient inputs (Naqvi et al., 2000). During the boreal fall (September-October) these low oxygen waters can be found over almost the entire western Indian shelf (Figure 9). These waters have deleterious impacts on both benthic and pelagic organisms and biodiversity on the shelf, including commercially important species, and they have been implicated in massive fish kills in the coastal zone (Naqvi et al., 2006; 2009).

Consistent with the satellite surface chlorophyll observations, acoustic and trawl surveys of zooplankton and micronekton (myctophid fishes, euphausiids and oceanic squids) abundance off of the southwest coast of India reveal much higher biomass in all of these groups along the continental shelf compared to the Laccadive Sea (Silas, 1972).

However, interestingly, the estimated mean standing stock of zooplankton in the Laccadive Sea increases sharply (by more than a factor of two) in July and August compared to other months of the year (Silas, 1972) revealing, perhaps, a higher trophic level response to the anti-cyclonic, upwelling favorable Laccadive Low that develops during the SWM. Whether or not these increases in zooplankton biomass significantly impact micronekton is unknown.

The northern Indian Ocean is also home to some of the largest fish stocks in the world. For example, the mesopelagic myctophid fish stock in the Arabian Sea has been estimated at 20-100 million tons with a potential yield of ~200,000 tons per year (Gjøsaeter 1981; Catul et al., 2011). Although there is considerable uncertainty in these estimates (Irigoien et al., 2013; T. Stromme, personal communication), it is likely that these myctophids have also evolved behaviors to deal with these dramatic monsoon-driven changes in Arabian Sea boundary currents, upwelling, productivity and food supply. There is also a potential linkage between myctophid behavior, the presence of oxygen minimum zones (OMZs), and boundary current processes via upwelling and downwelling influences on primary production, and export of particulate matter to the deep ocean. Through diurnal vertical migration, myctophids appear to use the OMZs as refuges from higher trophic level predators (Herring et al., 1998; Gjøsaeter, 1984; Kinzer et al., 1993). The enhanced primary production associated with upwelling favorable boundary currents during the SWM contributes to the biological oxygen demand that results in the formation of these OMZ refuges in the Arabian Sea (McCreary et al., 2013). These currents are also involved in both alongshore and offshore transport of organic matter and eddy-driven mixing that ventilates upper ocean waters, both of which are likely to impact the 3-dimensional distributions of the OMZs (McCreary et al., 2013). Thus, there is most likely a linkage between the boundary current reversals, upwelling variability and multiple higher trophic level behavioral responses and trophic interactions in the northern Indian Ocean.

2.4 The Bay of Bengal and the eastern Indian Ocean

2.4.1 General physical attributes

The seasonally reversing currents in the Bay of Bengal and the eastern Indian Ocean that are considered here include the Northeast Monsoon Current that traverses westward offshore around the southern tip of India and Sri Lanka during the NEM, the East India Coastal Current that hugs the east coast of India, and the South Java Current along Indonesia (Figure 1).

The East India Coastal Current is the Bay of Bengal counterpart to the West India Coastal Current. It transports ~10 Sv of relatively salty water northward during the Spring Intermonsoon (February through May) and SWM (Figure 1) when the hydrography is similar to many of the features that have been associated with the western boundary currents of the subtropical gyres (Shetye et al., 1993).   During the NEM, this current reverses, carrying 2-8 Sv of less saline water southward (Figure 1) (Shetye et al., 1996). To some degree, the East and West India Coastal Currents that bookend the Indian subcontinent provide linkages between the two sub-basins of the Northern Indian Ocean via the Southwest Monsoon Current and Northeast Monsoon Current, which traverse the coasts of India and Sri Lanka during their respective monsoon seasons. During the NEM the Northeast Monsoon Current flows from the southern part of the Bay of Bengal, merges with the equatorward flowing East India Coastal Current as it rounds Sri Lanka, and then turns to the north as it wraps around the western edge of the anticyclonic Laccadive High (Bruce et al., 1998; de Vos et al., 2014; Figure 1). During the SWM the Northeast Monsoon Current is replaced by the Southwest Monsoon Current, which flows in the opposite direction (see section 2.3.1 above). Off southern Sri Lanka the transport estimates for the Southwest Monsoon and Northeast Monsoon Currents are 8 Sv and 12 Sv, respectively (Schott and McCreary, 2001).

In the eastern Indian Ocean, the South Java Current (Figure 2) is particularly complex due to multiple influences. These include remote forcing associated with southeastward propagating coastal Kelvin waves generated by wind forcing over the equatorial Indian Ocean, and regional Southeast Monsoon (SEM) forcing and freshwater fluxes from the ITF (Quadfasel and Cresswell, 1992; Sprintall et al., 1999; Iskandar et al., 2005). During the SEM period (June through October), the flow of the South Java Current is generally

northwestward with an estimated transport of ~3 Sv over the upper 100 m (Quadfasel et al., 1996; Sprintall et al., 1999). Persistent, topographically-locked eddies and filaments develop in the South Java Current during the SEM in association with, for example, the southward ITF flow through Lombok strait (Figure 10). In November, the flow returns to a southeastward direction as Northwest Monsoon (NWM) forcing now acts in concert with the coastal Kelvin wave associated with the arrival of the (boreal) fall Wyrtki Jet. During these periods, the downwelling favorable flow extends to ~150 to 250 m depth with a transport of ~3-4 Sv (Meyers et al., 1995; Fieux et al., 1996; Schott and McCreary, 2001). However, transport time series of the South Java Current near the Sunda Strait have revealed considerable interannual variability with transports occasionally up to 10 Sv (Meyers, 1996).

South of the equator, Sumatra's coastal boundary current is primarily influenced by local wind forcing and remote forcing responses that propagate in from the equatorial Indian Ocean. The bulk of the remote response manifests as downwelling southeastward-propagating Kelvin waves that result as a consequence of semiannual Wyrtki Jet impingements that occur in May and November (Quadfasel and Cresswell, 1992). Coastal Kelvin waves along Sumatra can also be triggered by intraseasonal forcing in the form of near-equator westerly wind bursts, known as the Madden-Julian oscillation (Potemra et al., 2002). Signatures of these downwelling waves propagating along the coastal waveguide is evident in SSH measurements for the Lombok and Ombai straits (Iskander et al., 2014). The regional monsoonal cycle influences these semiannual and intraseasonal remote forcing impacts; during the SEM, local winds drive coastal upwelling that diminshes the downwelling aspect of the noted Kelvin waves. Further, upwelling Kelvin waves initiated by easterly wind bursts, which modulate the typical conditions just discussed, have been identified; however comprehensive observation and study remains to be done to clearly characterize their impacts (Drushka et al., 2010; Iskander et al., 2014). During Indian Ocean Dipole (IOD) events the northwest propagation of the South Java Current appears to be reinforced. This is a result of anomalous southeasterly winds over the southeastern Indian Ocean and the fact that the fall Wyrtki Jet does not manifest or is significantly diminshed (Wiggert et al., 2009; see

section 2.4.3 below for in depth discussion of the IOD phenomenon and its biogeochemical impacts).

2.4.2 Upwelling and downwelling variability and mesoscale activity

In the Bay of Bengal, the effects of the winds and the currents tend to be more cryptic, in part due to the influence of large freshwater inputs from rivers to the north (i.e., the Ganges-Brahmaputra and Irrawaddy), with upwelling sometimes occurring at depth but with no expression at the surface (Gomes et al., 2000; Vinayachandran et al., 2005). Some outcropping of upwelled water is observed at the surface along the eastern coast of India between 10° and 20° N in association with the upwelling-favorable, poleward-flowing East India Coastal Current during the spring intermonsoon (Gomes et al., 2000; Figure 11). This upwelling is enhanced during the SWM when upwelling favorable winds are coincident with the poleward-flowing current (Plant, 1992; Gomes et al., 2000; Figure 5). This region is also associated with modest increases in eddy kinetic energy during the SWM (Figure 3). However, satellite imagery shows that the influence of upwelling off the east coast of India is confined to a very narrow band near the coast and is much less pronounced in its spatial extent at the surface compared with the Arabian Sea (Wiggert et al., 2006; Figure 5 and Figure 11).

During both monsoon periods waters in the southwestern Bay of Bengal exhibit upwelling signatures and elevated chlorophyll concentrations (Figure 5) due to the interaction of the monsoonally reversing currents with Sri Lanka. Currents along the east and west coast of Sri Lanka propagate southward, converging along the island's southern coast with subsequent divergence associated with the offshore transport of water and contributing influence by the prevailing winds (de Vos et al., 2014). The upwelling and mesoscale variability in this region is particularly strong during the SWM when the eastward flow associated with the Southwest Monsoon Current develops a lee eddy commonly known as the Sri Lanka Dome, an upwelling recirculation that is reinforced by the overlying wind curl field (Vinayachandran et al., 2004; de Vos et al., 2014; Figure 12).

Off Indonesia, along the south coasts of the Sunda Islands, upwelling effects are strongly manifested as cold water at the surface in association with the northeastward-flowing upwelling favorable South Java Current and upwelling-favorable SEM (June through October) winds (Figure 10; Sprintall et al., 1999). This upwelling develops most significantly along the island chain stretching from southern Sumatra, Java, Bali, Lombok, Flores to Alor (Figure 10). The cool temperature signal of upwelling occurs first to the east of Lombok Island from late April to early May, then it proceeds westward along the south Java coast, reaching to the Sunda Strait in late June. From there it further progresses northwest to the west coast of the southern part of Sumatra in early August (Yu et al., 2016). At this time, peak upwelling is achieved with the strongest SST cooling located south of Java (Figure 10). In contrast, the retreat of upwelling is very rapid and simultaneous in October across the whole island chain, and is reinforced by the arrival of the fall Wyrtki Jet and subsequent downwelling coastal Kelvin Wave that propagates along the Sumatra and Java coasts (Iskander et al., 2005; Yu et al., 2016).

The Java-Sumatra upwelling area is also a region of enhanced mesoscale eddy activity, which is revealed in AVISO-derived eddy kinetic energy estimates (Figure 3). In addition, this region is associated with the major outflow straits of the ITF (Sunda, Lombok, Ombai and Timor) where topographically controlled mesoscale eddies play an important role in offshore transport of upwelled properties (e.g., Iskandar et al., 2010).

2.4.3 Impacts on primary production

Large inputs of freshwater in the Bay of Bengal from rivers and the resulting enhanced stratification act to inhibit upwelling-induced nutrient enrichment of surface waters (Madhupratap et al., 2003). In addition, although the supply of riverine borne nutrients (nitrate, phosphate and silicate) to the coastal zone of eastern India is large in the upper layers (up to 20 m) of the water column during the SWM, it is not observed to enhance the phytoplankton production rates to a large extent (Madhupratap et al., 2003; Madhu et al., 2006). Madu et al. (2006) report average primary production in the coastal waters of the eastern Bay of Bengal at ~350 mgC m^{-2} d^{-1} in summer, ~250 mgC m^{-2} d^{-1} in winter and ~300 mgC m^{-2} d^{-1} in spring intermonsoon periods, with diatoms dominating

phytoplankton abundance irrespective of seasons, and *Trichodesmium erythraeum* blooms developing in during the intermonsoon periods along with *Synechococcus* and heterotrophic dinoflagellate associations (Jyothibabu et al., 2008).

However, chlorophyll-*a* and primary production can be substantially increased over the shelf along the East Indian coastline by upwelling favorable boundary currents and/or winds. During the late spring intermonsoon period, the poleward-flowing East India Coastal Current brings nutrient-rich deep waters up toward the surface which gives rise to significant increases in phytoplankton biomass (~ 30 mgChla m^{-2}) and production (~ 1 gC m^{-2} d^{-1}) near the coast (Gomes et al., 2000; Figure 11). This upwelling has been shown to stimulate nearly monospecific diatom blooms in coastal waters (Sasamal et al., 2005). Wind-driven coastal upwelling (perhaps in combination with increased river-borne nutrient loads) during the following SWM season further increases phytoplankton biomass (> 100 mgChla m^{-2}). However, lower productivity occurs during this time (~0.55 gC m^{-2} d^{-1}), which suggests potential light limitation due either to cloud cover or increased turbidity (Gomes et al., 2000). In addition, modeling studies suggest that cryptic upwelling in Bay of Bengal coastal waters can also give rise to increased primary production during the SWM (Vinayachandran et al., 2005). Cryptic upwelling may be a common phenomenon in the Bay of Bengal where freshwater inputs tend to inhibit surface outcropping of upwelled water.

Satellite observations reveal that phytoplankton biomass and productivity near the coast is suppressed during the NEM when the East India Coastal Current flows equatorward (Figure 1; Figure 5; Figure 6). Presumably, this is due to a combination of the downwelling-favorable flow of the East India Coastal Current and downwelling-favorable winds. However, primary production over the shelf in the northern part of the Bay increases during the NEM (Gomes et al., 2000), possibly due to wind- and/or buoyancy-driven entrainment as is observed in the northern Arabian Sea during the NEM (Wiggert et al., 2000; 2005).

Although upwelling occurs along the southern coast of Sri Lanka during both monsoon periods the phytoplankton biomass and productivity response is much more pronounced during the SWM (de Vos et al., 2014, Figure 5; Figure 6; Figure12). Satellite SST and chlorophyll images reveal dramatic eastward advection of cool (< 28° C) chlorophyll rich upwelled water by the Southwest Monsoon Current (Vinayachandran, 2004; de Vos et al., 2014; Figure 12). Chlorophyll-rich waters from the southwestern coast of India are also advected by the Southwest Monsoon Current towards Sri Lanka during the SWM (Vinayachandran, 2004; Strutton et al., 2015). Satellite-derived surface chlorophyll concentrations along the southern coast of Sri Lanka can exceed 10 mgChla m^{-3} in July/August during the SWM, compared to much lower concentrations in January during the NEM when the Northeast Monsoon Current flows westward (de Vos et al., 2004; Figure 5). Similarly, satellite estimates of primary production suggest rates in excess of 1 g m^{-2} day^{-1} in August along the southern and western coasts of Sri Lanka, and along the southern tip of India, compared to much lower values in January (Figure 6). Vinayachandran (2004) attributes the productivity response during the SWM to nutrient enrichment from coastal upwelling driven by monsoon winds. Presumably, these high chlorophyll concentrations and production rates are associated with diatom blooms. Interestingly, however, the model results of Wiggert et al. (2006) suggest the potential for Fe limitation in these upwelling waters (Figure 8), which begs the question of whether or not there might be Si limitation as well, which would tend to inhibit diatom growth.

Upwelling enhanced chlorophyll and primary production are also observed along the southern coast of Indonesia in association with the northwestward-flowing, upwelling-favorable South Java Current and upwelling-favorable SEM (June through to October) winds (Figure 5; Figure 6; Figure 13). Monthly satellite climatologies show elevated chlorophyll-*a* concentrations (> 2 mgChla m^{-3}) off of Java first appearing in June and persisting into November (Figure 12) with primary production rates > 1 mgC m^{-2} day^{-1} in August (Figure 6). As discussed above, the relaxation of the SEM winds, combined with the passage of downwelling Kelvin waves associated with the arrival of the Wyrtki Jets (Sprintall et al. 1999) suppresses upwelling and, presumably, the productivity response in the late fall. Satellite climatologies also reveal that this upwelling-enhanced

phytoplankton biomass progresses northwestward during the SEM extending to the southwestern coast of Sumatra in September (Figure 12). Video plankton recorder imagery collected in the upwelled water off of Java during the SEM reveal that these elevated chlorophyll concentrations are associated with diatom blooms, e.g., "coil-shaped" chain-forming species (Yu et al., 2016; C. Davis, personal communication).

The upwelling regions off Sumatra, Java and Timor are almost certainly influenced by nutrient inputs associated with the ITF flows through the Lombok and Ombai Straits. Nutrient measurements collected during the World Ocean Circulation Experiment (WOCE line IR06, 1989) along a transect from the northwestern coast of Australia to Lombok Strait reveal the upwelling signature off of Java in both nitrate and phosphate distributions (Figure 14). The absolute N:P ratio of ~13.75 estimated from 200 m depth on the northern end of the transect, reveals what appears to be a denitrification and/or anammox signature. This signature may reflect the influence ITF source waters derived from shallow Indonesian Seas where sediment dentrification and/or anammox could result in nitrogen removal.

Interannual modulation of the impact of these currents and upwelling on phytoplankton biomass and production off Java (and Sumatra) can be clearly seen in ocean color data in association with the IOD (Wiggert et al., 2009; Currie et al., 2013). The IOD is an aperiodic coupled ocean and atmosphere phenomenon in the equatorial Indian Ocean that is associated with anomalous SST, wind and precipitation patterns (Saji et al., 1999). A positive (negative) IOD period is characterized by cooler (warmer) than normal water in the tropical eastern Indian Ocean and warmer (cooler) than normal water in the tropical western Indian Ocean. During positive IOD events unusually strong upwelling-favorable winds develop in the eastern Indian Ocean during the SEM. This, combined with a weakened or absent fall Wyrtki Jet, which allows for an anomalously shallow thermocline, results in unusually high chlorophyll-*a* concentrations off of Java and Sumatra. Indeed, during the 1997/1998 IOD, these conditions triggered a massive phytoplankton bloom in the eastern tropical Indian Ocean that extended from Sumatra

westward to 65 °E, with atypical bloom signatures that persisted into January/February (Murtugudde et al., 1999; Wiggert et al., 2009).

2.4.4 Higher trophic level impacts and speculation

Although there have been numerous studies documenting the impacts of the East India Coastal Current and upwelling on phytoplankton biomass and production (Gomes et al., 2000; Plant, 1992; Madhupratap et al., 2003; Chaturvedi, 2005; Sasamal et al., 2005; Madhu et al., 2006; and references cited therein), there is very little published information on higher trophic level impacts beyond linkages to zooplankton biomass and species composition. We know that the microzooplankton community in the coastal zone of the western Bay of Bengal is numerically dominated by heterotrophic dinoflagellates and ciliates with the highest abundance and diversity occurring during the spring inter-monsoon (Jyothibabu et al., 2008). In addition, historical surveys show that copepod abundance during the SWM increases dramatically over the East Indian shelf between 10° and 20° N (Stephen, 1992; Nair et al., 1977). Presumably, these increases are linked to the increases in coastal primary production that are associated with upwelling and the northward-flowing East India Coastal Current (Gomes et al., 2000). More recently, changes in zooplankton community structure in the coastal zone have been linked to the influence of upwelling eddies generated by the East India Coastal Current during the spring intermonsoon (Rakhesh et al., 2008). Specifically, this study documented the impact of a recurring, cyclonic, cold-core eddy generated by the East India Coastal Current that enriches coastal waters in the western Bay of Bengal north of 16°N during the spring intermonsoon. These observations reveal distinctly altered zooplankton species composition in the upwelled water associated with coastal current eddies, and apparent top-down control of diatoms that resulted in increased abundance of dinoflagellates.

There are even fewer published studies of higher trophic level responses to monsoonal forcing in the coastal zone of Sri Lanka. The coastal zone of Sri Lanka supports a rich

pelagic fishery that varies seasonally in response to monsoon-driven changes in upwelling and primary and secondary production (Joseph, 1975). Catch per unit effort (CPUE) for small pelagic fishes (e.g., sardine, herring, anchovy and mackerel) increases dramatically during the monsoons with highest CPUE observed during the SWM (Joseph, 1975). Although zooplankton are a major food source for these pelagic fishes and their larvae, there are few (if any) published data on zooplankton distributions, abundance and seasonal fluctuations in relation to environmental parameters that are needed to understand what drives seasonal variations in pelagic fishery resources in Sri Lankan coastal zones. All we can do is speculate (with some confidence) that there are commensurate seasonal fluctuations in zooplankton biomass and productivity associated with the satellite-observed seasonal changes in temperature, chlorophyll and primary production, and that zooplankton biomass and productivity are particularly high during the SWM when coastal upwelling is most intense off of Sri Lanka (Vinayachandran, 2004; de Vos et al., 2014, Figure 12).

Interestingly, although chlorophyll concentrations during the NEM are low compared to the SWM along the southern coast of Sri Lanka, feeding aggregations of blue whales (*Balaenoptera musculus*) occur in this region during the NEM, likely in response to the NEM-driven increases in primary and secondary production discussed above (Joseph, 1975; Alling et al., 1991; de Vos et al., 2014). Numerous whales are sighted along the southern coast of Sri Lanka during the NEM and there is a well-developed whale watching tourism industry in the region (Alling et al., 1991; de Vos et al., 2014). However, very little is known about the environmental factors that influence the distribution of blue whales in these waters.

Mooring-derived ADCP estimates of backscatter intensity in the South Java Current indicate that there are distinct seasonal increases in biomass and upward vertical migrations of crustacean zooplankton during the upwelling-favorable SEM period (Wang et al., unpublished) that are, perhaps, similar to the monsoon-driven seasonal migrations of *C. carinatus* that have been observed in the western Arabian Sea (Iridisi et al., 2004; Smith, 1992; 2001). It is possible that this seasonal migration impacts primary

production and export in the Java Current as well. SEM-driven increases in production associated with upwelling in the Java Current are also linked to increases in sardine (*Sardinella leumuru*) catch and (presumably) production in Bali Strait (Ghofar, 2005). The IOD-driven interannual variations in the strength of this current and the intensity of upwelling give rise to dramatic interannual variations in sardine catch, which impact supply relative to demand and therefore market prices (Sartimbul et al., 2010).

Relatively little is known about the impacts of boundary currents and upwelling on pelagic food webs supporting fisheries in the open ocean region between Indonesia and northwestern Australia, which is the only known spawning ground for southern blue fin tuna (*Thunnus maccoyii*) (Davis et al., 1989; Farley and Davis, 1998; Matsuura et al., 1997). This region is also a major spawning and fishing area for other tuna species. It is an area of complex currents and strong seasonal changes in upwelling and production associated with variation in monsoonal forcing and the influence of planetary waves. The region is also strongly influenced by freshwater and nutrient inputs from the ITF (Talley and Sprintall, 2005; Ayers et al., 2014). Satellite observations have shown strong eddy activity in the Lombok Strait area off southern Java during the SEM upwelling season (June through October) resulting in physical transport of chlorophyll-rich eddies directly south into the tuna-spawning region (Yu et al., 2016). Tuna may thus derive significant resource subsidy from offshore transport of seasonal upwelling production by these coastally-shed eddies that are associated with the South Java Current. The challenge is to understand the role of this offshore transport, along with all of the other potential influences, in providing resources and habitat for fish recruitment (Yu et al., 2016).

3. The Southward-Flowing Leeuwin Current

3.1 General physical attributes

The waters for the Leeuwin Current come from three main sources: 1) from the northeast through the Indonesian Throughflow (ITF) via the seasonal Holloway Current off of northwest Australia; 2) from the north via the South Equatorial Current; and 3) from the west via the Eastern Gyral Current (Domingues et al., 2007; Figure 15). As a result of

these tropical sources, which are subject to both low latitude warming and high precipitation, the Leeuwin Current emerges further south as a warm (Figure 16) and less saline current compared to adjacent surface water masses (Weller et al. 2011). The Leeuwin Current is relatively small compared to other eastern boundary currents, extending to a depth of only ~300 m with a transport < 5 Sv (Schott and McCreary, 2001). However, the Leeuwin Current has the largest eddy kinetic energy among all mid-latitude eastern boundary current systems (Figure 3; Feng et al., 2005). This induces strong cross-shelf transport (Figure 16, 17 and 18), particularly during the austral autumn and winter in the shelf region between ~27° S and 33° S (Feng et al., 2005; Feng et al., 2007; Feng et al., 2010). The Leeuwin Current becomes increasingly coherent, coalescing into a shelf-edge current as it flows southward, around Cape Leeuwin and then eastward along the Great Australian Bight towards Tasmania (Figures 15 and 16; Ridgway and Condie, 2004).

3.2 Local versus remote forcing and seasonality

The southward flow of the Leeuwin Current is driven by the large-scale pressure gradient that is set up by the ITF, which is, in turn, generated by the large-scale pressure gradient between the Pacific and Indian Oceans (Godfrey and Ridgway, 1985; Smith et al., 1991). The Leeuwin Current does not reverse seasonally like the northern Indian Ocean boundary currents. However, there is significant seasonal variability in Leeuwin Current transport with the largest flows occurring in austral winter and the smallest flows occurring in austral summer (Smith et al., 1991; Feng et al., 2003; Feng et al., 2010). Ridgway and Godfrey (2015) argue that this seasonality is driven by an annual sea level signal that propagates around the shelf edge waveguide extending from tropical waters off northwestern Australia to southern Tasmania. Apparently, this wave originates from a sea level pulse that emerges from the Gulf of Carpenteria (north-eastern Australia) during December–February that is forced by the seasonally reversing monsoon winds. The autumn-winter enhancement of the Leeuwin Current results from the geostrophic adjustment to the seasonal increase in the cross-shelf gradient of SSH as the wave progresses around the coastal waveguide. The timing of the appearance of this sea level

pulse results in a March-April peak in southwestward transport off northwest Australia and a June peak in southward transport at Fremantle.

Inter-annual and decadal variability of the Leeuwin Current is largely driven by tropical Pacific climate variability (Feng et al., 2013). As a result, ENSO-driven fluctuations in the strength of southeast trade winds in the Pacific Ocean have an impact on the strength of the Leeuwin Current. Remotely forced ENSO-driven upper ocean disturbances propagate poleward as internal coastal Kelvin waves along the coast of Western Australia (Meyers, 1996). These generate higher coastal sea levels and induce strong Leeuwin Current flow in La Niña years and weaker flow in El Niño years (Pearce and Phillips, 1988; Feng et al., 2003; Feng et al. 2005). Interannual variability in the Leeuwin Current is also driven by "Ningaloo Niño" events. These are associated with positive sea surface temperature anomalies off the west coast of Australia during El Niño and negative anomalies during La Niña (Doi et al., 2013; Feng et al., 2013; Kataoka et al., 2013). Ningaloo Niño events develop during October through December, they reach a peak in January-February, and then they decay (Doi et al., 2013). Long-term coral records reveal the existence and impact of ENSO and Ningaloo Niño/Niña events going back more than 200 years (Zinke et al., 2014).

3.3 Upwelling and downwelling variability

The Leeuwin Current is downwelling-favorable because the Coriolis effect on the southward flow in the southern hemisphere forces the current eastward toward the coast (Smith et al., 1991; Hanson et al., 2005a; Hanson et al., 2005b). This tends to suppress upwelling, and manifests as downward sloping isopycnals along the coast (Feng et al., 2003). However, local wind forcing can override this general tendency and drive upwelling and current reversals (Gersbach et al., 1999; Pearce and Pattiaratchi, 1999; Hanson et al., 2005a; Hanson et al., 2005b, Rossi et al., 2013a; 2013b). This happens, in particular, during the austral summer when the Leeuwin Current transport is low and upwelling-favorable southerly winds occur. This materializes, for example, off the southwest coast of Western Australia at Cape Mentelle (Figure 15) where localized upwelling forms the source of the relatively cool water of the northward-flowing Capes

Current (Gersbach et al., 1999), and off Ningaloo Reef near the North West Cape of Western Australia (Figure 15) where localized upwelling supplies cool water to episodic northward coastal flows (Woo et al., 2006; Xu et al., 2013, Rossi et al., 2013b).

3.4 Impacts on primary production

The tropical origins of the Leeuwin Current combine with its downwelling tendency to create a warm, oligotrophic current with low productivity. Seasonal nutrient climatologies from the southwestern Australian shelf, the Leeuwin Current and offshore show that the surface waters are all low in nitrate (< 0.5 μM) throughout the year (Lourey et al., 2006). This indicates that primary production is nitrogen limited. Relatively low levels of phosphate (< 0.25 μM) and silicate (< 2 μM) are observed in the shelf waters. Lourey et al. (2006) suggest that the low levels of silicate may limit diatom production. In contrast, phosphate concentrations are undetectable in the Leeuwin Current whereas silicate concentrations are relatively high (up to 4 μM; Lourey et al., 2006).   Thus, the Leeuwin Current appears to be a silicate source to the surrounding waters. The observed cross-shelf gradient in chlorophyll-*a* concentrations (Figure 16; Figure 17; Figure 18) indicates that terrestrial nutrient sources and/or near shore coastal upwelling make an important contribution to primary productivity (Lourey et al., 2006).

In the Leeuwin Current, chlorophyll-*a* concentrations are generally < 30 mgChla m^{-2} and primary production rates usually do not exceed 0.5 gC m^{-2} d^{-1} (Koslow et al., 2008; Lourey et al., 2006; Lourey et al., 2013). Productivity in this current is particularly low in summer, when the water column is stratified and subsurface chlorophyll maxima are ubiquitous between 50 and 120 m depth (Hanson et al., 2007; Figure 18) as observed typically in open ocean subtropical oligotrophic conditions (e.g., Venrick, 1991). However, primary production rates in isolated, near shore upwelling regions (e.g., off of the North West Cape during summer) can episodically reach very high levels (3–8 gC m^{-2} day^{-1}) characteristic of eastern boundary upwelling zones elsewhere in the world (Furnas, 2007). In general, primary production in the Leeuwin Current is highest in the austral fall and winter, coinciding with the period of strongest Leeuwin Current

flow and colder surface winds which contribute to increased eddy kinetic energy, vertical mixing and entrainment of nutrients from the nutricline into the mixed layer (Lourey, et al., 2006; Koslow et al., 2008; Thompson et al., 2011). During this time period, regions of relatively high chlorophyll (>30 mgChla m^{-2}) and primary production (> 0.5 gC m^{-2} d^{-1}) are found in association with mesoscale features (Lourey et al., 2013). Significant interannual variability in chlorophyll and primary production is observed in association with ENSO and Ningaloo Niño driven changes in the strength of the Leeuwin Current (Furnas, 2007; Narayanasetti et al., 2016).

Throughout the year, meanders in the Leeuwin Current generate warm core, anti-cyclonic eddies that transport relatively high chlorophyll coastal water offshore (Figure 18). The higher chlorophyll in these eddies is due to the presence of relatively productive coastal diatom communities. These diatoms are advected westward into cooler oligotrophic offshore waters that are dominated by small open ocean phytoplankton species (Waite et al., 2007a; Paterson et al., 2008; Waite et al., 2015). These eddies, which can extend to > 250 m depth (Figure 18), are enigmatic because they are anti-cyclonic, downwelling circulations that, in theory, should inhibit the introduction of new nutrients from depth. Yet, these eddies, and the higher chlorophyll concentrations associated with them, have been shown to persist for months (Feng et al., 2007; Moore et al., 2007; du Fois et al., 2014). It has been suggested that the diatom communities in these eddies are supported by lateral supply and/or internal nutrient recycling (Waite et al., 2007a; Paterson et al., 2013; Thompson et al., 2007). The latter is supported by the vertical scale of these features (Figure 18), which is potentially large enough to allow for almost complete remineralization of particulate matter generated near the surface before it can sink out and be exported through the base of the eddy (Waite et al., 2015).

There is prolific generation of these warm (and cold) core eddies in the Leeuwin Current between 20° and 35° S (Gaube et al., 2013). Most of them propagate directly westward and some appear to be quite long-lived (Feng et al., 2005; Feng et al., 2007; Moore et al., 2007; Gaube et al., 2013; du Fois et al., 2014). The persistence and potential impacts of these eddies in the open ocean have not been fully investigated.

3.5 Higher trophic level impacts and speculation

Studies of zooplankton in the Leeuwin Current are limited with only a few covering specific taxonomic groups embracing the latitudinal extent of the system (Holliday et al., 2012; Buchanan and Beckley, 2015; Sutton and Beckley, 2016). However, detailed inter-annual investigations of both the meso- and macrozooplankton have been conducted over the northwest shelf of Western Australia near the headwaters of the current. Cross-shelf transects have confirmed an onshore–offshore gradient in copepod community composition, with the inshore stations characterized by an abundance of small Paracalanidae and Oithonidae (McKinnon et al., 2008). Although copepods are more abundant inshore during El Niño conditions when the Leeuwin Current is weaker and there is more upwelling and higher primary production, copepod production rates do not differ substantially and remain low (Hanson and McKinnon, 2009). Suggested reasons for this anomaly include the highly pulsed nature of the upwelling, the strongly advective conditions and microbial processes dominating the food web. For the macro-zooplankton, during El Niño, distinct inshore and offshore assemblages are also observed that reflect the transition from upwelling-enriched shelf waters to the more oligotrophic Leeuwin Current waters offshore (Wilson et al., 2003). In contrast, during La Niña conditions, the stronger Leeuwin Current and downwelling regime weaken horizontal gradients in macro-zooplankton assemblages.

The Leeuwin Current has long been linked with the distribution and transport of biota along the west coast of Australia and it plays a crucial role in controlling larval retention and dispersal of many coastal species (e.g., Hutchins and Pearce, 1994; Gaughan and Fletcher 1997; Caputi, 2008; Muhling et al., 2008a; Muhling et al., 2008b; Beckley et al., 2009; Feng et al., 2010; Holliday et al., 2012). Lagrangian particle-tracking studies have shown that there is considerable spatial heterogeneity in retention rates along the coast and areas of low retention are associated with a narrower shelf, protruding coastal geography and strong alongshore currents. In contrast, areas of high retention are sheltered from the direct influence of the Leeuwin Current by coastal geography, e.g., by islands and embayments (Feng et al., 2010). The Leeuwin Current can enhance poleward

transport of marine populations and, for example, tropical species are observed in the demersal and pelagic fauna of the Great Australian Bight (southern Australia) (Condie et al., 2005). This has been attributed to the transport of tropical larvae and tropical conditions by the Leeuwin Current, which after passing Cape Leeuwin flows eastward along the southern coast of Australia (Maxwell and Cresswell, 1981; Figure 15). However, the high kinetic energy associated with the eddy field of the Leeuwin Current between ~27° S and 33° S (Figures 3, 16, 17 and 18) may disrupt long-shore connectivity and induce considerable cross-shelf transport (Holliday et al., 2012). For example, pre-flexion larvae of coastal anchovies can be advected offshore by such eddies and subsequently recorded in deep oceanic waters, far away from their normal shelf environment (Holliday et al., 2012).

Detailed studies of an evolving eddy as it formed from a meander in the Leeuwin Current (Paterson et al., 2008) showed that neritic fish larvae and krill species could be entrained and then, when the eddy detached from the main flow, they were trapped in the mesoscale feature with no return pathway to the coast (Holliday et al., 2011; Sutton et al., 2015). As these neritic fish larvae generally have pelagic larval durations of less than a month, not being able to find a suitable habitat in which to settle would result in larval mortality. This has been confirmed by detailed investigations in an older warm-core eddy, that detached five months previously and moved westward into the Indian Ocean. It contained no neritic fish larvae (Muhling et al., 2007). The fish larvae of the aged eddy were predominantly those of mesopelagic oceanic species such as myctophids, which may gain particular benefit by spawning in association with these more productive areas in the oligotrophic southeastern Indian Ocean (Muhling et al., 2007; Holliday et al., 2012). Stable isotope analysis suggests that larval fishes were preferentially targeting food sources derived from large phytoplankton carbon such as the large diatoms found in the warm-core eddy (Waite et al. 2007b). Interestingly, carnivorous zooplankton, particularly chaetognaths, dominated the zooplankton, and this anomalous trophic structure may reflect grazing down of the herbivorous/omnivorous component of the plankton (Strzelecki et al., 2007; Buchanan and Beckley, 2016).

Coastal animals that have long pelagic larval durations (9-11 months), such as the Western rock lobster (*Panulirus cygnus*), can be affected by these productive eddies in the oligotrophic southeast Indian Ocean in ways that contrast sharply from the planktonic impacts described above. The eddies could transport entrained phyllosoma larvae away into the central Indian Ocean or, if the eddy trajectory stalled and remained relatively close to the coast, it could reduce the distance necessary for the puerulus larvae to swim back to the coast after metamorphosis. The eddies may also provide a more generous food supply for the phyllosoma than the surrounding oligotrophic ocean (Säwström et al. 2014). Recent field studies have shown that, although ingesting a variety of planktonic prey (O'Rorke et al., 2012; Wang et al., 2014), they preferentially select chaetognaths from the pelagic smorgasbord (Saunders et al., 2012).

As the Western rock lobster is the target of Australia's largest and most valuable wild caught fishery, a crucial element in projecting catch is the long-term monitoring program that records the abundance of puerulus settling on inshore reefs along the west coast (mainly between August and January each year) (Phillips 1986; Caputi et al. 2014; Figure 19). Historically, high rock lobster puerulus settlement has been associated with strong Leeuwin Current transport in La Niña years (Caputi et al., 2001). Settlement has always shown a strong correlation with Leeuwin Current transport and commercial catches of lobsters three and four years later. However, correlations between transport and settlement have broken down in recent years (Feng et al., 2011). It has been suggested that successful settlement may be related to more subtle aspects of the Leeuwin transport and flow such as the presence or absence of strong landward flows associated with meanders in the Current and adjacent waters between 28° and 32° S that could bring the larvae back to shore (Säwström et al., 2014). Recent analysis of environmental variables potentially influencing puerulus settlement has suggested that an observed earlier onset of spawning (linked with higher bottom water temperatures) and reduced storm activity may have resulted in a mismatch with peak food availability and /or a favorable larval transport mechanism during the recent period of low settlement (de Lestang et al., 2015).

4. The Agulhas Current and its tributaries

4.1 General physical attributes

The Agulhas is a warm current with salinity between 35.0 and 35.5 that flows southwestward along the continental shelf/slope off the east coast of Africa from about Maputo (25°S) to the tip of the Agulhas Bank (40°S) where most of it retroflects sharply eastward back into the Indian Ocean (becoming the eastward-flowing Agulhas Return Current), while shedding eddies ("Agulhas Rings") that propagate into the Atlantic (Lutjeharms, 2006a; Figure 20).

The Agulhas Current plays an important role in surface return flow of the global thermohaline circulation with Agulhas Rings providing a vector for heat and volume transport between the Indian and Atlantic Oceans (Lutjeharms 2006a; Beal et al. 2011). The Agulhas is a very large current extending to > 1000 m depth with a transport of ~60-85 Sv (Lutjeharms 2006a; Beal et al. 2015), which is at least comparable to the Gulf Stream and the Kuroshio Current. The Agulhas is also similar to these currents in that it does not generate filaments or shed seaward propagating eddies as it flows along the continental shelf/slope.

A significant fraction of the Agulhas Current is derived from warm, tropical surface waters in the southwestern Indian Ocean. Its source waters from the north are from Mozambique Channel eddies and the East Madagascar Current, which coalesce off southern Mozambique (Figure 20; Lutjeharms, 2006a). Although there are conflicting estimates, the most reliable results to date suggest that the mean volume transport of the Mozambique Channel throughflow is ~8-15 Sv, but this transport is highly variable over a large range of time scales (Ridderinkhof and de Ruiter, 2003). The East Madagascar Current flows southward along the east coast of Madagascar (Figure 20) with a mean volume transport of ~20 Sv and it is also highly variable (Swallow et al., 1988; Roman and Lutjeharms, 2009). In addition, the Agulhas Current is supplied from the east via recirculation in the southwest Indian Ocean sub-gyre which contributes another ~ 35 Sv (Stramma and Lutjeharms, 1997).

4.2 Local versus remote forcing and seasonality

There is substantial interannual variability in the Mozambique Channel transport (~9 Sv) that appears to be remotely forced by the transport of the South Equatorial Current (SEC) that feeds the Mozambique Channel throughflow (Ridderinkhof et al., 2010). In addition, model simulations suggest that the Mozambique Channel transport has strong seasonality with a maximum in August (Biastoch et al., 1999), which can be explained by variability in the wind field over the western part of the Indian Ocean (Ridderinkhof et al., 2010). At intraseasonal timescales most of the transport variability is driven by local forcing from eddies that migrate through the Mozambique Channel (Figure 20; Harlander et al., 2009; van der Werf et al., 2010). About four to seven eddies per year are known to transit through the Channel, from north to south (Ridderinkhof and de Ruiter, 2003). Variability in the East Madagascar Current transport is also forced by fluctuations in the transport of the SEC and southward propagating eddies (Nauw et al., 2008) with significant contributions also from local winds (Hermes et al., 2007). In contrast, local winds seem to be the dominant forcing mechanism of variability in recirculation of the southwest Indian Ocean sub-gyre that supplies the Agulhas from the east (Hermes et al., 2007).

Given the variability in its sources, one would expect the Agulhas Current to have substantial transport variability over a similarly wide range of temporal scales. Multidecadal time series of geostrophic transport derived using a combination of SSH anomaly fields from satellite altimetry and climatological data suggest strong interannual variability in Agulhas transport that can be as large as a factor of two (see: http://www.aoml.noaa.gov/phod/altimetry/cvar/agu/transport.php). Satellite remote sensing, modeling and observational studies indicate significant seasonal variability as well with the highest transport during the austral summer and lowest during the austral winter (Matano et al., 1998; Pearce and Grundlingh, 1982; Beal et al., 2015). Most of the intraseasonal variability is derived from along-shore propagating eddies like break-away Durban eddies and Natal pulses (Bryden et al., 2005). Durban eddies are derived from persistent, cold-core, cyclonic, topographic lee eddies that form near Durban, South Africa and shed approximately every 14 days (Roberts et al., 2010). Natal pulses are

large, solitary, along-shore propagating, cold-core meanders on the inshore side of the

Agulhas Current (Lutjeharms and Roberts, 1988) that occur about six times per year

(Lutjeharms et al., 2003).

4.3 Upwelling and downwelling variability and mesoscale activity

The generation and southward propagation of mesoscale eddies in the Mozambique

Channel give rise to relatively high eddy kinetic energy (Figure 3). These eddies have a

profound and complex impact on upwelling and downwelling circulations in the channel

(e.g., Roberts et al., 2014). Coastal upwelling is also observed on the inshore side of the

upwelling-favorable East Madagascar Current (Figure 20). For example, a distinct,

coastal upwelling cell is observed inshore of the southern limb of the East Madagascar

Current where the current moves from a narrow continental shelf with a steep slope to a

wider shelf with a less steep slope (Figure 20; DiMarco et al., 2000; Lutjeharms and

Machu 2000; Machu et al., 2002). The lack of correlation between the local winds

suggests that the upwelling is topographically controlled. Eddy kinetic energy is

distinctly elevated to the south and west of Madagascar (Figure 3) where the East

Madagascar Current sheds eddies into the open ocean. These eddies coalesce with

Mozambique Channel eddies off the coast of Africa where they feed into the Agulhas

Current.

Like other western boundary currents, the Agulhas is upwelling favorable because the

oceanic density field reacts to the presence of the current by adjusting to geostrophic

equilibrium, which causes the thermocline and nutricline to tilt up toward the surface

along the inshore side of the flow. However, significant surface expressions of upwelling

are largely controlled by local wind and topographic forcing (Lutjeharms, 2006a). Shelf-

edge upwelling is observed primarily in association with specific headlands and

topographic features along the coast (e.g., the St Lucia upwelling cell; Pearce et al., 1978;

Lutjeharms et al., 2000; Meyer et al., 2002). For example, north of Durban in the

KwaZulu-Natal (KZN) Bight (Figure 20) the interaction of the Agulhas Current with the

topography results in three areas and types of upwelling: topographically induced

upwelling off St Lucia/Richards Bay in the north; shelf-edge upwelling; and cyclonic,

lee-trapped, eddy-induced upwelling to the south of Durban (Lutjeharms et al., 1989; Lutjeharms et al., 2000; Meyer et al., 2002; Lutjeharms, 2006a, 2006b). Upwelling is enhanced southward of the KZN Bight (downstream; Figures 20, 21 and 22) where increased meandering of the current and interactions with topography combine with wind forcing to lift deep water up toward the surface and onto the widening shelf (Lutjeharms 2006a). Upwelling is also observed off Algoa Bay and along the southeast coast to Port Alfred (Figure 21) (Beckley,1983; 1988; Beckley and van Ballegooyen, 1992; Goschen and Schumann, 1995; Goschen et al., 2012). Upwelling in this region is most intense in the austral summer in response to upwelling-favorable prevailing winds from the northeast and it is revealed by marked temperature variability at the coastline (Figure 21a; Beckley, 1983; 1988; Schumann 1999; Goschen et al. 2012; Jackson et al., 2012). Upwelling also occurs over the eastern Agulhas Bank (Figure 21a) where it is confined almost exclusively to prominent capes and headlands (Schumann et al., 1982; Goschen and Schumann, 1995). Typically, cold water is upwelled along the shoreline within a few days after the wind changes to northeasterly and upwelling progresses north-eastwards along the coast with the movement of the wind and weather systems (Goschen et al., 2012).

4.4 Impacts on primary production

In the Mozambique Channel phytoplankton abundance peaks in areas of nutrient enrichment that are often found in the core of cyclonic eddies, as well as on the continental shelf (Marsac et al., 2014). However, counter to conventional wisdom, modeling studies in the Mozambique Channel indicate that cyclonic upwelling eddies sometimes have low concentrations of chlorophyll at their cores, and that anticyclonic downwelling eddies sometimes have high concentrations of chlorophyll at their cores (José et al., 2014). These eddies also mediate lateral transport of nutrients and chlorophyll from the coasts of Africa and Madagascar (José et al., 2014; Lamont et al., 2014; Roberts et al., 2014). These results suggest that phytoplankton growth within both cyclonic and anticyclonic eddies in the Mozambique Channel often occurs in response to lateral nutrient injection into the euphotic zone by advection from the coastal zone rather

than upwelling and downwelling induced by the eddies themselves. In contrast, topographically-forced coastal upwelling in the East Madagascar Current brings cold, nutrient-rich water to the surface, which stimulates primary production (Lutjeharms and Machu, 2000; Ho et al., 2004; Quartly and Srokosz, 2004). This upwelling and its impacts are enhanced in both the austral winter and in the austral summer (Ho et al., 2004).

The concentrations, distribution and movement of nutrients 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 KZN Bight; Meyer et al., 2002). In general, inorganic nutrient concentrations (nitrate, silicate and phosphate) off southeastern Africa decline in the surface waters from the inner shelf to the outer shelf and into the Agulhas current (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 zone (Meyer et al., 2002; Barlow et al. 2015). Nutrient concentrations measured in the near-surface waters (10 m depth) over the shelf in the vicinity of the KZN Bight reveal enrichment of both phosphorus and silicate relative to nitrate compared to Redfield (Carter and d'Aubrey, 1988; Meyer et al., 2002; Barlow et al., 2015) suggesting the potential for nitrate limitation.

The Agulhas Current, itself, is warm and oligotrophic having been derived from nutrient poor surface waters from the southwestern tropical Indian Ocean (Lutjeharms, 2006a). In addition to driving upwelling through meandering and topographic interactions, it can dramatically suppress primary production when it impinges onto the shelf (Schumann et al., 2005). Downwelling oligotrophic Agulhas Current rings can also suppress primary production when they are shed into the Atlantic giving rise to well-documented negative impacts on higher trophic level (fisheries) production (e.g., Duncombe Rae et al., 1992).

In general, chlorophyll and primary production are enhanced along the inshore side of the Agulhas Current in the coastal zone of southeast Africa (Figure 20). This enhancement is

associated with the aforementioned wind and topographically-induced upwelling during summer. For example, recent measurements from the KZN Bight revealed chlorophyll concentrations that ranged from ~0.1 to 1.5 mgChla m^{-3} and integrated primary production that ranged from ~0.3 and 2.6 gC m^{-2} d^{-1} (Lamont and Barlow, 2015). Upwelling enhanced chlorophyll and primary production are also pronounced over the Agulhas Bank where surface chlorophyll-*a* concentrations can exceed 3 mgChla m^{-3} and carbon fixation rates are often greater than 0.5 gC m^{-2} d^{-1} (Figures 20, 21b and 22; Burchall, 1968; Carter and Schleyer, 1988; Boyd and Shillington, 1994; Lutjeharms et al., 1996a; Roberts, 2005; Jackson et al., 2012). Some of the highest surface chlorophyll concentrations are observed over the Agulhas Bank near the coast between Cape Agulhas and Algoa Bay (Figures 20, 21b, and 22; Probyn, 1994; Demarcq et al., 2003), between Algoa Bay and Port Alfred (Barlow et al., 2010; O'Donoghue et al., 2010) and in the KZN Bight north of Durban (Lamont and Barlow, 2015). Coastal diatom species are the primary contributor to the elevated phytoplankton biomass and primary production observed in these upwelling centers (Carter and Schleyer, 1988; Lamont and Barlow, 2015), with *Prochlorococcus* and *Synechococcus* dominant in the offshore regions (Barlow et al., 2015). A subsurface chlorophyll maximum is also observed to form over the shelf in the KZN Bight (Barlow et al., 2015) and in the central Agulhas Bank (Figure 22) when nutrient concentrations near the surface become limiting (Shannon et al., 1984; Probyn et al., 1995).

4.5 Higher trophic levels impacts and speculation

The Mozambique Channel mesoscale eddies (Figure 20) play a key role in marine ecosystem dynamics and higher trophic level behavior (Marsac et al. 2014). These eddies strongly influence zooplankton and micronekton abundance and also upper trophic levels. For example, Huggett (2014) showed that zooplankton biomass is highest in upwelling cyclonic eddies, intermediate in fronts and divergence zones, and lowest in anticyclones, and Béhagle et al. (2014) showed that acoustic-derived micronekton densities mirror these zooplankton patterns. Similarly, the average density of foraging seabirds tends to be lowest in downwelling anticyclones, highest in upwelling cyclones and at intermediate levels in divergence, shelf and frontal zones (see Marsac et al., 2014

and references cited therein). Complex higher trophic level behavioral responses are also observed in the Channel's highly variable environment. For example, swordfish tend to be associated with divergence zones and fronts (Potier et al., 2014). Similarly, the foraging patterns of Great Frigatebirds (*Fregata minor*) are closely tied to the boundaries of mesoscale eddies in the Mozambique Channel where good foraging conditions are promoted by lateral nutrient injections that enhance primary production and/or through accumulation or aggregation of biomass at fronts (Emilie and Marsac, 2010).

In contrast, relatively little is known about higher trophic level responses to variability in the East Madagascar Current (Lutjeharms, 2006b). The abundances of both pelagic and demersal fishes have been reported to increase toward the south in the East Madagascar Current (Lutjeharms, 2006b); whether or not this is related to the aforementioned upwelling that is observed inshore of the southern limb of the Current is unknown.

Interannual changes in the number, intensity and/or transport of eddies in the Mozambique Channel in response to large-scale remote forcing by the South Equatorial Current could potentially have profound effects on top predators like the Great Frigatebirds (Emilie and Marsac, 2010). Since the transport of the East Madagascar Current is also influenced by variability in South Equatorial Current forcing, we speculate that there are similar higher trophic level impacts, especially if this variability alters the timing of upwelling events or its intensity in the coastal waters of Madagascar. This could have significant impacts on the recruitment success of both pelagic and demersal fishes (Cushing, 1990).

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 Agulhas Current transports Indo-Pacific zooplankton species into waters over the Agulhas Bank (De Decker, 1973). Studies on zooplankton variability associated with the Agulhas Current have shown that biomass is greater inshore of the Current compared to within the Current itself, but with the Current harboring a higher diversity of species (Carter and

Schleyer, 1988; Pretorius et al., 2016). All of these observations are consistent with the fact that the Agulhas Current is oligotrophic and derived from the tropical southwestern Indian Ocean (Lutjeharms, 2006a).

The impact of the Agulhas Current on fish larvae is essentially similar to that observed for zooplankton. Spatial and temporal studies on fish larvae along the eastern seaboard of South Africa have revealed the importance of inshore upwelling on clupeiform larvae (Beckley and Hewitson, 1994), the influence of Agulhas Current intrusions in shoreward transport of mesopelagic myctophid larvae (Olivar and Beckley, 1994; Olivar et al., 1998; Harris et al., 2001) and the influence of the Agulhas Current on southward dispersal of larvae of tuna and other species from lower latitudes (Beckley and Connell 1996; Beckley 1998; Beckley and Leis 2000).

Off southeastern Africa, the KZN sardine run occurs in the austral winter when sardines (*Sardinops sagax*) of a distinct subpopulation move northward along the east coast of South Africa (Roberts et al., 2010; O'Donoghue et al., 2010a). Their dense shoals create a feeding frenzy along the coastline with dramatic higher trophic level responses (sharks, birds, dolphins, whales and people; O'Donoghue et al. 2010b). The existence and strength of the annual sardine run has long been a conundrum; the sardines' migration along the narrow shelf against the powerful, warm Agulhas Current is a particular enigma given that they are typically considered a cool, temperate species (Figures 20 and 23).

The persistence of cool, subsurface water on the eastern Agulhas Bank extending north along the Transkei coast has been demonstrated in the austral autumn (Beckley and van Ballegooyen, 1992; Roberts et al., 2010). Under the influence of southwesterly winds, northward-flowing coastal counter-currents exist at times between the Agulhas Bank and the KZN Bight. These currents provide a corridor for migration that can also be enhanced by transient cyclonic eddies that move downstream in the shoreward boundary of the Agulhas Current (Figures 23 and 24), i.e., break-away Durban eddies and the Natal pulses (Roberts et al., 2010). These eddies arrive at a frequency of 1-2 per month and their influence can last up to six days; thus, they potentially provide enhanced windows

for northward migration. Roberts et al. (2010) speculate that this is particularly important at prominent coastal headlands and where the shelf is narrowest. At these locations the pervasive influence of the Agulhas Current likely thwarts northward migration until assistance arrives with the passage of a transient cyclonic eddy allowing northward passage of the sardines and their associated megafauna predators.

The Agulhas Bank (Figure 25) is a productive region that supports several commercial fisheries that are economically important for South Africa. It is a major spawning ground for anchovy (*Engraulis encrasicolus*), sardine (*Sardinops sagax*), squid (*Loligo reynaudii*), hake (*Merluccius capensis*), kingklip (*Genypterus capensis*), sole (*Austroglossus pectoralis*), and yellow tail (*Seriola lalandi*) (Hutchings, 1994; Hutchings et al., 2002). The central-eastern Agulhas Bank also provides a nursery for several of these species in areas where topographically-forced recirculations promote retention and recruitment (Hutchings et al., 2002; Figure 25). The high fish productivity is supported by the wind and topographically-induced upwelling and enhanced plankton productivity over the Agulhas Bank.

Due to the strong influence of the Agulhas Current, most neritic fish species in southeast Africa coastal waters have evolved highly selective reproductive patterns for successful retention of planktonic eggs and larvae (Hutchings et al., 2002). Several appear to undergo northward spawning migrations, but entrainment of early life history stages into the powerful Agulhas Current is surely a non-advantageous mechanism for dispersal away from the known estuarine and coastal nursery areas (Figure 20; Figure 25). As discussed above, topographic influences of headlands and embayments along the relatively linear coastline of southeast Africa are important, not only for enhancing primary production and food supply, but also for providing retention areas for the larvae of coastal fish species. However, there are not many of these embayments. The KZN Bight, north of Durban, represents a significant area with a cyclonic circulation pattern that should favor retention of larvae in these warm sub-tropical waters. Another riskier reproductive strategy would be to avoid the core of the Agulhas Current by spawning in summer on the narrow shelf off the east coast and rely on southward transport induced by

the upwelling-favorable north-easterly winds which are more prevalent at that time. This would allow slower transport but retain the developing larvae in coastal waters from where they can easily access nursery areas but always with the possible threat of being entrained into the fast-flowing Agulhas Current.

5. The recent paleoceanographic history of the Indian Ocean and current trends

It is important to remember that the present day boundary currents of the Indian Ocean discussed herein have changed over recent geological time as a result of changes in climate and sea level. Paleo-climate records show that global sea level was 4 to 6 m higher during the last interglacial period, about 125 kyr before present, and it subsequently dropped by 80 to 150 m over the next 90 kyr to its lowest point between 30 and 15 kyr during the last glacial maximum (Waelbroeck et al., 2002). Proxy records for ocean temperature indicate a concomitant cooling of tropical sea surface temperatures over this 90 kyr BP period of 2°C and 3°C. Over the past 15 kyr these trends have completely reversed bringing us into the present day interglacial state. These global fluctuations in climate, sea level and sea surface temperature are clearly manifested in paleoceanographic records from the Indian Ocean and there is evidence, in at least some cases, that they had significant impacts on boundary current circulations and also biogeochemical and ecological responses.

In the northern Indian Ocean paleoceanographic records suggest that during glacial periods the SWM was weaker and the NEM was stronger compared to the present (Saher et al., 2007). Specifically, fossil records from the western Arabian Sea have identified a glacial monsoon mode between 20 and 13 kyr BP characterized by a weak SWM and stronger cooling by glacial NEM winds compared to the modern situation, as well as a modern monsoon mode, which started at ~8 kyr BP with a shift toward a strong SWM associated with strong upwelling, and weak influence of the NEM on SST.

Based upon our current understanding, we can speculate with some confidence that weaker SWM winds during glacial periods would give rise to less energetic boundary currents, weaker upwelling and suppressed biogeochemical and ecological responses in

both the Arabian Sea and the Bay of Bengal. It is somewhat more difficult to project how stronger cooling by NEM winds during glacial periods would impact biological processes in the northern Indian Ocean. Intensified wintertime convection over the Arabian Sea during the NEM would likely give rise to deeper mixing and greater nutrient enrichment of surface waters. However, with this deeper mixing, the signature winter phytoplankton bloom that is observed to occur in the northern Arabian Sea (e.g., Banse and McClain, 1986) could be reduced or eliminated completely due to increased light limitation (Wiggert et al., 2002; Wiggert et al., 2000). These kinds of effects would undoubtedly be less pronounced in the Bay of Bengal where there is much stronger stratification. Retrospective analysis of satellite chlorophyll and temperature data has suggested that the SWM is still intensifying, perhaps in response to climate change that has reduced Himalayan snow cover, and that this has led to further increases in upwelling and productivity in the western Arabian Sea during the SWM (Goes et al., 2005). However, more recent analysis of the satellite-based surface temperature and chlorophyll records (Prakash and Ramesh, 2007; Prakash et al., 2012; Rixen et al., 2013; Roxy et al., 2016) indicates that decadal variability may have influenced the earlier interpretation of a climate change-associated increase in SWM production (Rixen et al., 2013). Indeed, Prakash et al. (2012) argue that the earlier observed biological changes in the western Arabian Sea (Goes et al., 2005) are an artifact of the change in local winds and ocean dynamics that are part of the natural long-term variability.

In the eastern Indian Ocean, paleoceanographic data suggest that the transport of the ITF was reduced and the Leeuwin Current was "less active" during glacial periods (see Wyrwoll et al., 2009 and references cited therein). Specifically, fossil records from the western margin of Australia indicate that during the last glacial maximum (~21 kyr BP when sea level was ~130 m lower than today and there were much wider shelves along the coast of Western Australia and in the Indonesian Seas) the ITF transport was reduced, there were lower, low-latitude SSTs, and there were changes in the Western Pacific Warm Pool. These changes likely reduced the transport of the Leeuwin Current compared to the present day. Modern studies of the impact of changes in the intensity of the Leeuwin Current on primary productivity suggest that a less active Leeuwin Current

during glacial periods would have allowed increased upwelling during the austral summer months along the western margin of Australia with associated increases in nutrient supply, primary production and higher trophic level responses (Hanson et al., 2005a; Hanson et al., 2005b; Twomey et al., 2007). It is difficult to speculate on how these changes in transport may have impacted productivity during the austral winter months when both the Leeuwin Current transport and cooling winds and entrainment control nutrient supply (Koslow et al., 2008).

Reductions in Leeuwin Current transport can also have direct impacts on larval transport of higher trophic level species, which can lead to either reduced or enhanced recruitment depending upon the life history strategy of the species. For example, based on present day observations we might expect that a general decline in Leeuwin Current transport in the past would be associated with a decline in Western rock lobster (*Panulirus cygnus*) recruitment (Figure 19; Caputi et al., 2001). However, changes in eddy generation and the coastal circulation associated with lower sea level and/or reduced Leeuwin Current transport could easily override this relationship. We speculate in section 3.6 that the breakdown in the correlation between transport and settlement that has been observed in recent years could be related to subtle changes in the circulation or the timing of the spawning period of the lobsters.

In contrast to the northern Indian Ocean boundary currents and the Leeuwin Current, paleoceanographic data do not provide any conclusive evidence of major shifts in the Agulhas Current position, or of substantial cooling in the current's water during previous glacial maxima (Lutjeharms, 2006a). Indeed, it is believed that the position of the Agulhas Current has been fairly stable for >150 kyr and, that over this time period, it has also retroflected in approximately the same location as today (Winter and Martin, 1990). This does not, however, necessarily imply that the transport has remained unchanged. The fossil record on the eastern side of the Agulhas Bank shows that there was substantial glacial-interglacial variability in this region with the influence of Agulhas Current water reduced during glacial periods when the presence of sub-Antarctic water was increased (Rau et al., 2002). This change is consistent with inferred changes in ITF

transport, which was also reduced during glacial periods (Wyrwoll et al., 2009). This glacial-interglacial variability in Agulhas Current influence on the Agulhas Bank is also associated with unexplained changes in biological productivity that have been deduced from the fossil record (Winter and Martin, 1990). It has been suggested that past increases in production may have been related to increased meandering of the current (Lutjeharms and de Ruiter, 1996), which gave rise to increased upwelling of nutrient-rich water and greater primary productivity (Lutjeharms, 2006a). We can anticipate, based on our present understanding, that any changes in the transport of the Agulhas Current or productivity and/or meandering of the Current on the Agulhas Bank would have potentially profound impacts on higher trophic level production and recruitment. We can also expect that such changes would drive evolution of the reproductive patterns of most neritic fish species in southeast Africa coastal waters (Hutchings et al., 2002).

6. Summary and Conclusions

Due to the distinctive geography of the Indian Ocean basin, its boundary currents are complex and unique in many respects. These currents provide interesting contrasts in terms of upwelling, downwelling and mesoscale variability, relative influences of local versus remote forcing and biogeochemical and ecological responses. Specific examples from each current system have been presented to illustrate the impacts these currents have on higher trophic levels, which cover a wide range of size and trophic level and include copepods, decapods and fishes.

The northern basin is dominated by seasonally reversing currents that are driven by the monsoon winds. However, remote influences from planetary waves that originate in the equatorial waveguide can have significant impacts on the strength and direction of these currents and also on upwelling intensity. The seasonal reversals in these currents have very significant biogeochemical and ecological impacts that include seasonal switching from upwelling to downwelling circulations, and modification of primary productivity, nutrient stoichiometry, oxygen concentrations and phytoplankton species composition. There is also clear evidence that these seasonally reversing currents have profound effects

on higher trophic level species behavior and productivity. These effects are observed in in the behavior of crustacean zooplankton and large pelagic fish species in the western Arabian Sea, and in zooplankton community composition or behavior on the East Indian Shelf and off the coast of Java. The impacts of these seasonal current reversals and changes in upwelling and downwelling circulations are also manifested in West Indian coastal waters, where they influence oxygen concentrations and have been implicated in massive fish kills; in the Laccadive Sea where the standing stock of zooplankton changes by more than a factor of two; in the coastal waters of Sri Lanka where they impact chlorophyll concentration and catch per unit effort of fishes; and in the Bali Strait, where they strongly influence both seasonal and interannual variability in sardine catch.

In the southern basin, the Leeuwin Current is unusual in almost every respect due, in large part, to remote forcing that derives from the Indonesian Throughflow which sets up the large-scale pressure gradient that drives this southward flow. The Leeuwin Current does not reverse seasonally, but it does exhibit significant seasonal and interannual variability. The Leeuwin is an oligotrophic downwelling-favorable current but local wind forcing is also important as it can drive intermittent near shore current reversals and transient upwelling. This transient upwelling can give rise episodically high levels of primary production in isolated coastal regions. Although its transport is relatively small, the Leeuwin Current has the largest eddy kinetic energy among all mid-latitude eastern boundary current systems and this induces strong cross-shelf transport. As a result, the Leeuwin Current sheds anomalous, relatively productive, westward-propagating, warm-core eddies, the influence and fate of which are still being explored. The Leeuwin Current has long been linked with the distribution and transport of biota along the west coast of Australia and it plays a crucial role in controlling larval retention and dispersal of many coastal species. We speculate that successful settlement of rock lobster larvae may be related to relatively subtle aspects of the Leeuwin Current transport and flow.

In contrast, the southward-flowing Agulhas Current is among the largest boundary currents in the world. Its northern source waters derive from Mozambique Channel eddies and the East Madagascar Current. In addition, the Agulhas is supplied from the

west via recirculation in the southwest Indian Ocean sub-gyre. Mesoscale eddies have a profound and complex impact on upwelling and downwelling circulations in the Mozambique Channel and therefore also on nutrients, plankton productivity and higher trophic level behavior. Coastal upwelling and productivity response is observed on the landward side of the upwelling-favorable East Madagascar Current, but relatively little is known about higher trophic level responses to variability in this Current. We speculate that interannual changes in large-scale remote forcing by the South Equatorial Current could potentially have profound effects on top predators in the Mozambique Channel and the East Madagascar Current.

There is significant seasonal and interannual variability in Agulhas transport that is remotely forced by variability in its sources. In contrast, most of the intraseasonal variability in the current is due to local forcing, derived from along-shore propagating eddies like break-away Durban eddies and Natal pulses. The Agulhas Current is upwelling favorable but significant surface expressions of upwelling are largely controlled by local seasonal winds and topographic forcing. As a result, primary production is enhanced along the inshore side of the Agulhas Current at specific locations in the coastal waters of southeast Africa during the austral summer. The Agulhas Current, itself, is warm and oligotrophic having been derived from nutrient poor surface waters from the southwestern tropical Indian Ocean. In contrast, the Agulhas Bank and the KZN Bight are productive regions that support several commercial fisheries that are economically important for South Africa, including the sardine (*Sardinops sagax*). This species is responsible for the KZN sardine run off southeastern Africa, which is facilitated by coastal counter-currents and transient cyclonic eddies that provide a corridor for the northward sardine migration against the powerful Agulhas Current. Due to the strong influence of the Agulhas Current, many neritic fish species in southeast Africa coastal waters have evolved highly selective reproductive patterns for successful retention of planktonic eggs and larvae. Topographic influences of headlands and embayments in the relatively linear coastline of southeast Africa are important, not only for enhancing primary production and food supply, but also for providing retention areas for the larvae of coastal fish species.

It should be kept in mind, however, that the characteristics of all of these current systems have not been static over geological time. There is evidence in the paleoceanographic record that the boundary currents in the Indian Ocean have been influenced by global fluctuations in climate, sea level and sea surface temperature, and that glacial-interglacial changes in these currents had significant impacts on biological productivity and most likely also higher trophic levels.

Acknowledgements

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Table and Figures

	Boundary Current	Relative Temperature	Relative Salinity	Seasonality	Transport	Depth (m)	Nutrients	Primary Production	Mesoscale Variability
Seasonally Reversing Currents in the Northern Indian Ocean	Somalia/EACC	Cold (SWM) /Cold (NEM)	Fresh (SWM) /Salty (NEM)	Seasonally Reversing	~20-40 Sv (SWM) / 5 Sv (NEM)	~500 (SWM) /150 (NEM)	>15 μM NO_3 at the surface, Potential Fe and Si limitation (SWM/OMAN)	>40 mgChla/m^2 >2.5 gCm^{-2}d^{-1} (SWM/OMAN) P/B ~ 62	Very High during SWM off of Somalia
	WICC	Weak temperature signatures Warm (SWM) /Warm (NEM)	Salty (SWM) /Fresh (NEM)	Seasonally Reversing	~4 Sv (SWM) / 7 Sv (NEM)	~100 (SWM) / 200 (NEM)	<5 μM NO_3 at the surface, Elevated DIP/DIN ratios in low O_2 waters (SWM over shelf), Potential Fe limitation (SW coast)	9 mgChla/m^2 1 gCm^{-2}d^{-1} (NEM) P/B~111\n\n24 mgChla/m^2 2.25 gCm^{-2}d^{-1} (SWM) P/B~94	Relatively low and confined to the coast during SWM
	EICC	Warm (SWM) /Cold (NEM)	Salty (SWM) /Fresh (NEM)	Seasonally Reversing	~10 Sv (SWM) / 2-8 Sv (NEM)	200 (SWM/NEM)	<5 μM NO_3 surface (12-13°N SWM) >20 μM NO_3 surface from river influence	~30 mgChla/m^2 ~0.3-1 gCm^{-2}d^{-1} (SWM-SIM) P/B~10-33 ~0.25 gCm^{-2}d^{-1} (NEM)	Moderate extending into offshore waters during SWM and N
	SMC/NMC	Warm (SWM) /Cold (NEM)	Salty (SWM) /Fresh (NEM)	Seasonally Reversing	11.5 Sv (SWM) / 9.6 Sv (NEM)	unknown	NO_3 unknown, potential Fe limitation	>10 mgChla/m^2 ~0.55 gCm^{-2}d^{-1} Upwelling South of Sri Lanka (SWM) P/B~55	High during SWM and NEM
	Java Current	Warm	Fresh	Seasonally transient (June-October)	4-10Sv (SEM)	~150-250	<5 μM NO_3 at the surface (off Lombock Strait, SEM), low DIN/DIP ratios at 200 m	>5 mgChla/m^3 >0.5-1 gCm^{-2}d^{-1}	High during SEM
Leeuwin Current	Leeuwin Current	Warm	Fresh	Moderate seasonal transport variability	<5 Sv	<300	NO_3 BTL* and elevated Si (>4 μM) at surface in LC, <0.5 μM NO_3 and low PO_4 and Si over shelf (SW Australia)	<30 mgChla/m^2 <0.5 gCm^{-2}d^{-1} P/B ~ 17	High especially during SEM
Agulhas Current	Agulhas Current	Warm	Weak salinity signature (salty)	Small seasonal transport variability	~60-85 Sv	>1000	NO_3 BTL* in AC, >0.5 μM NO_3 and high PO_4 and Si over shelf in Natal Bight at the surface	>3 mgChla/m^3 >0.5 gCm^{-2}d^{-1} (Agulhas Bank during austral summer) 0.1-1.5 mgChla/m^3 0.3-2.6 gCm^{-2}d^{-1} (KZNB**)	High in Mozambique Channel and south of Madagascar. High nearshore in Agulhas Current

Table 1: Summary of the major Indian Ocean boundary currents in terms of: relative temperature, salinity, seasonality, transport, depth, nutrient concentrations, chlorophyll concentrations, production rates and P/B ratios, and amount of mesoscale variability, based upon the discussion and references cited in this paper. *BTL = Below Detection Limit. BTL is assumed for Agulhas Current. **KZNB = KwaZulu-Natal Bight.
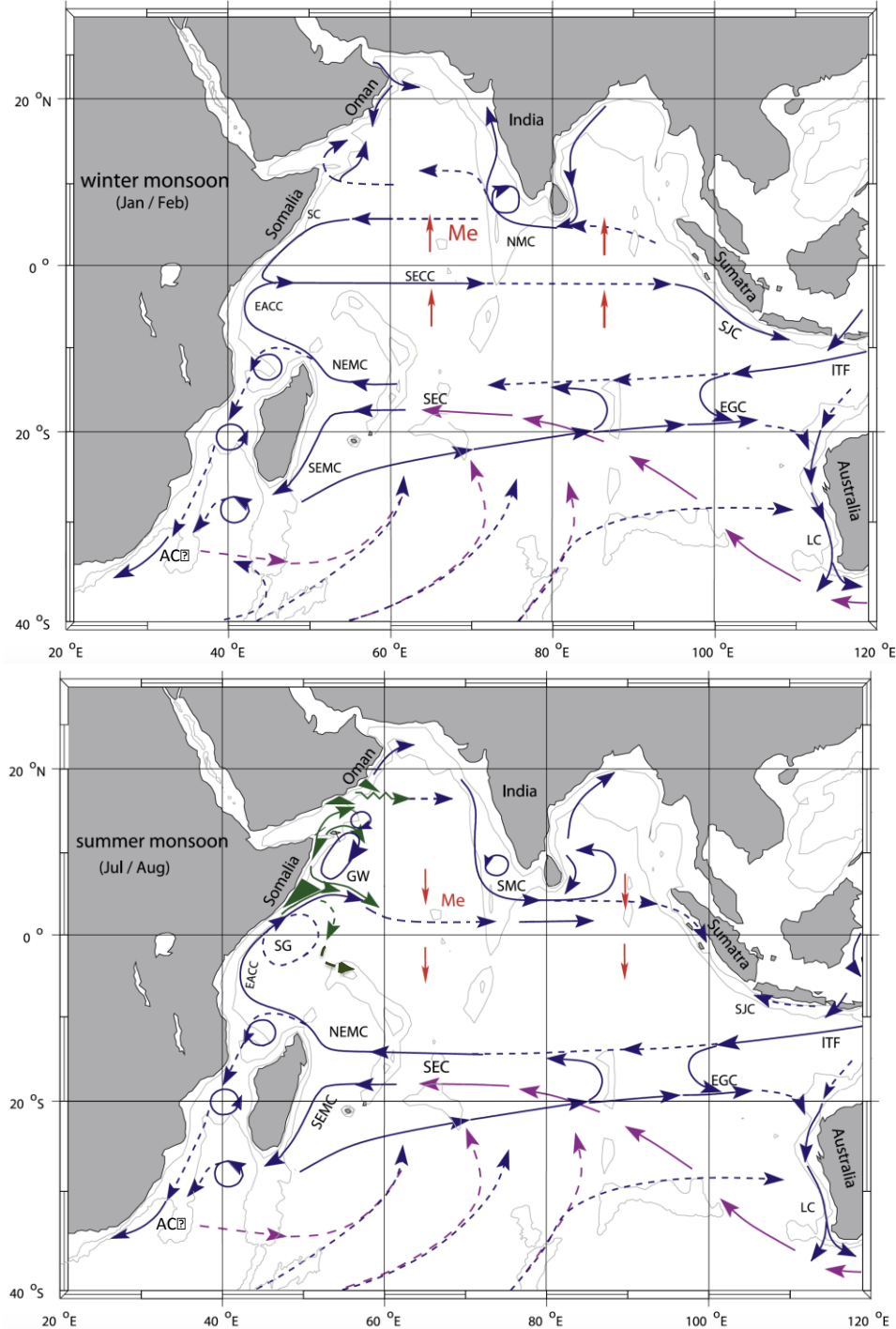
Figure 1: Schematic representation of currents during the NEM (top) and SWM (bottom). The currents indicated are the South Equatorial Current (SEC), South Equatorial Countercurrent (SECC), Northeast and Southeast Madagascar Current (NEMC and SEMC), East African Coastal Current (EACC), Somali Current (SC), Southern Gyre (SG) and Great Whirl (GW) and associated upwelling wedges (green shades), Southwest and Northeast Monsoon Currents (SMC and NMC), South Java Current (SJC), East Gyral Current (EGC), Leeuwin Current (LC) and Agulhas Current. The subsurface return flow of the supergyre is shown in magenta. Depth contours shown are for 1000 m and 3000 m (grey). The red vectors (Me) show directions of meridional Ekman transports. ITF indicates Indonesian Throughflow. Dashed arrows indicate uncertain flows. Figure and caption modified from Schott et al. (2009) following Beal et al. (2013).
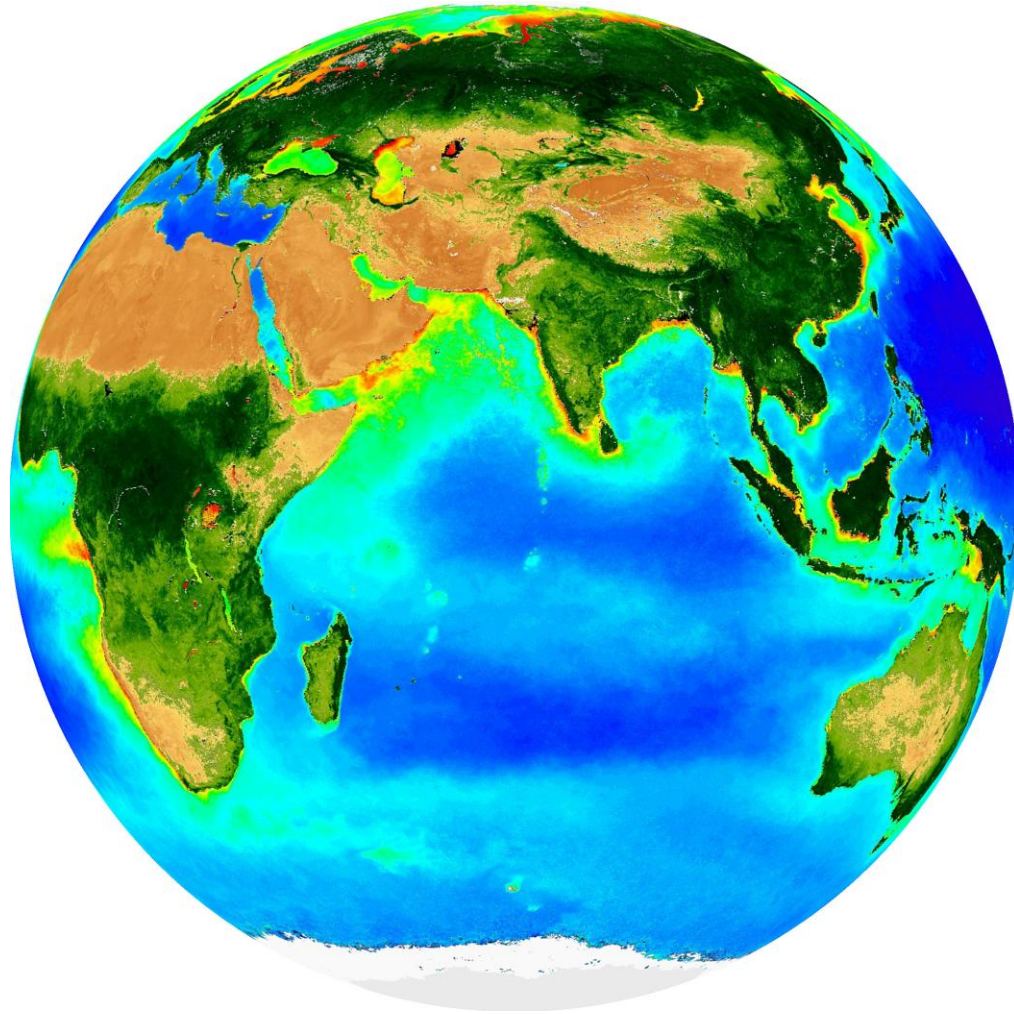
Figure 2: Climatology of SeaWiFS near-surface Chlorophyll focusing on the Indian Ocean and showing also land vegetation in surrounding continents. Note that the averaging over time in the ocean tends to obscure mesoscale variability. Image from http://oceancolor.gsfc.nasa.gov
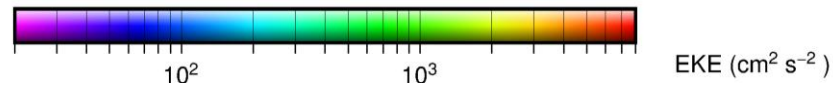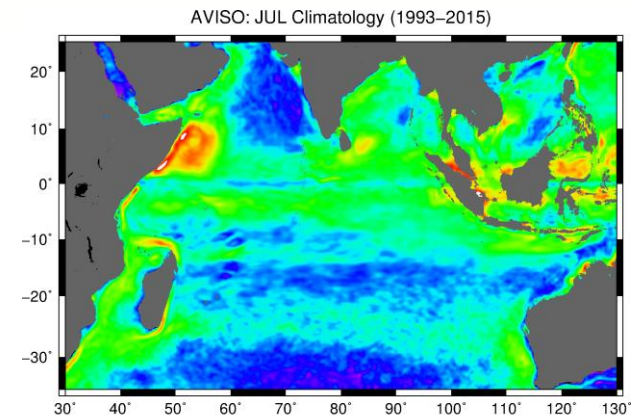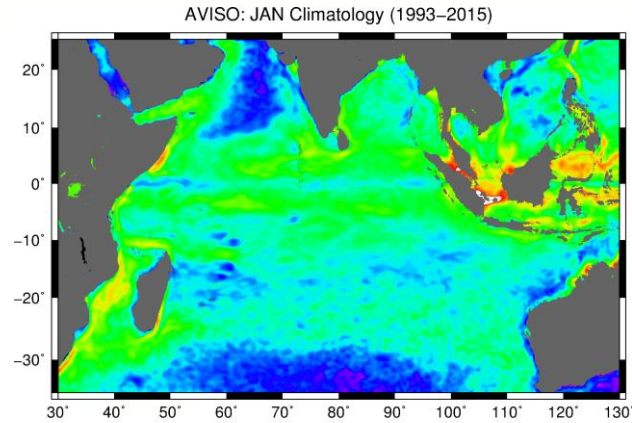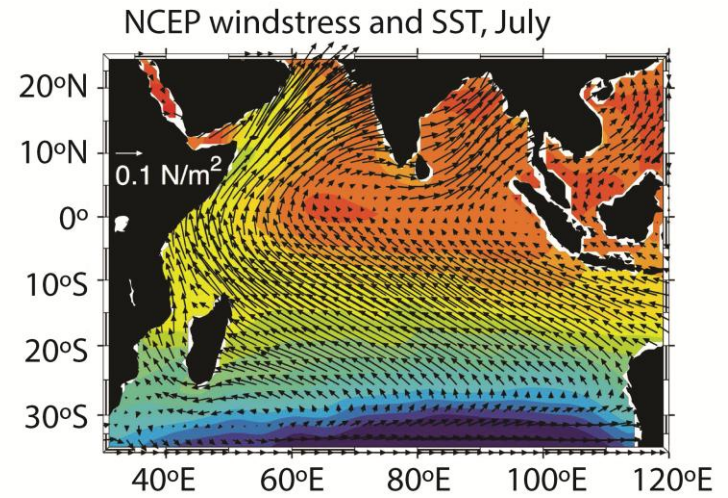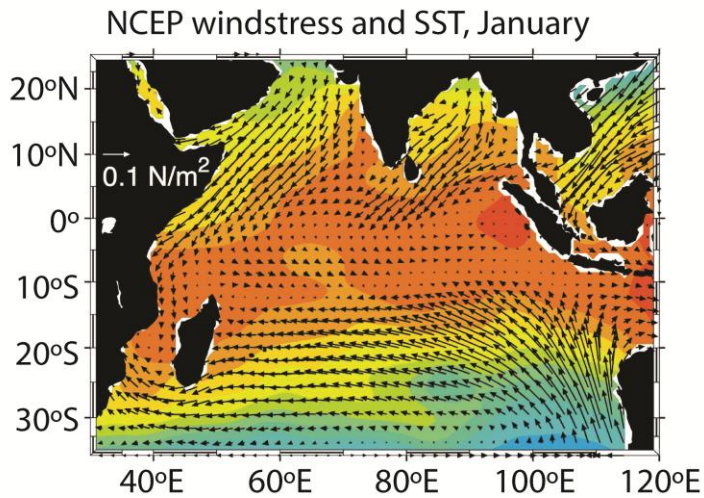
Figure 3: Top panels: Surface wind speed and direction over the Indian Ocean with sea surface temperature during the NEM (left) and the SWM (right) modified from Schott and McCreary (2001). Wind speed units are m/sec and the warmer colors represent warmer temperatures. Bottom panels: Surface ocean eddy kinetic energy during the Northeast Monsoon (left) and the Southwest Monsoon (right) derived from AVISO sea surface height data.
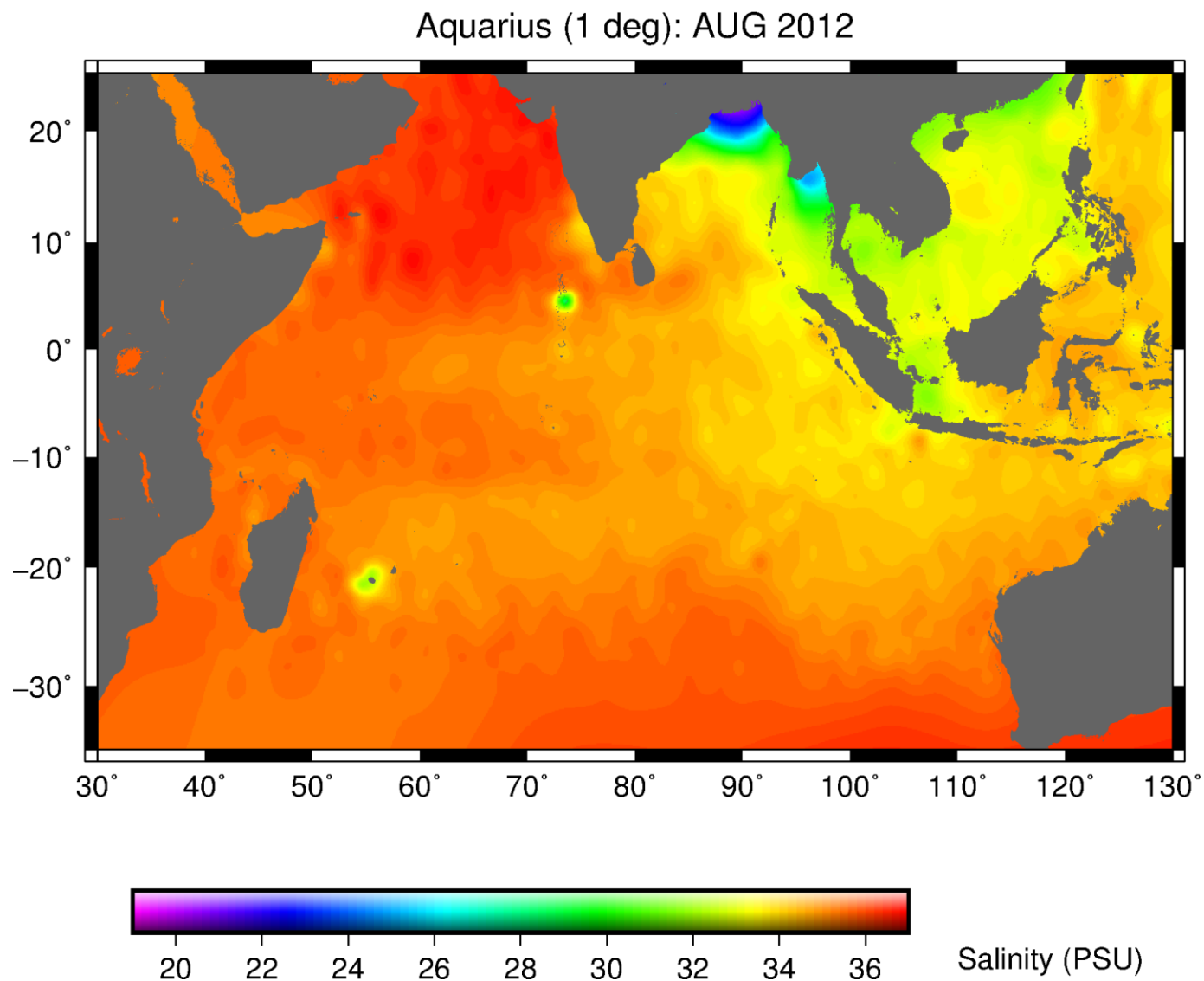
Figure 4: Sea surface salinity form Aquarius (1/4 degree resolution, August 2012). Data obtained from the JPL PO-DAAC (http://podaac.jpl.nasa.gov/). Note that the fresh areas around Mauritius and the Maldives are likely artifacts.
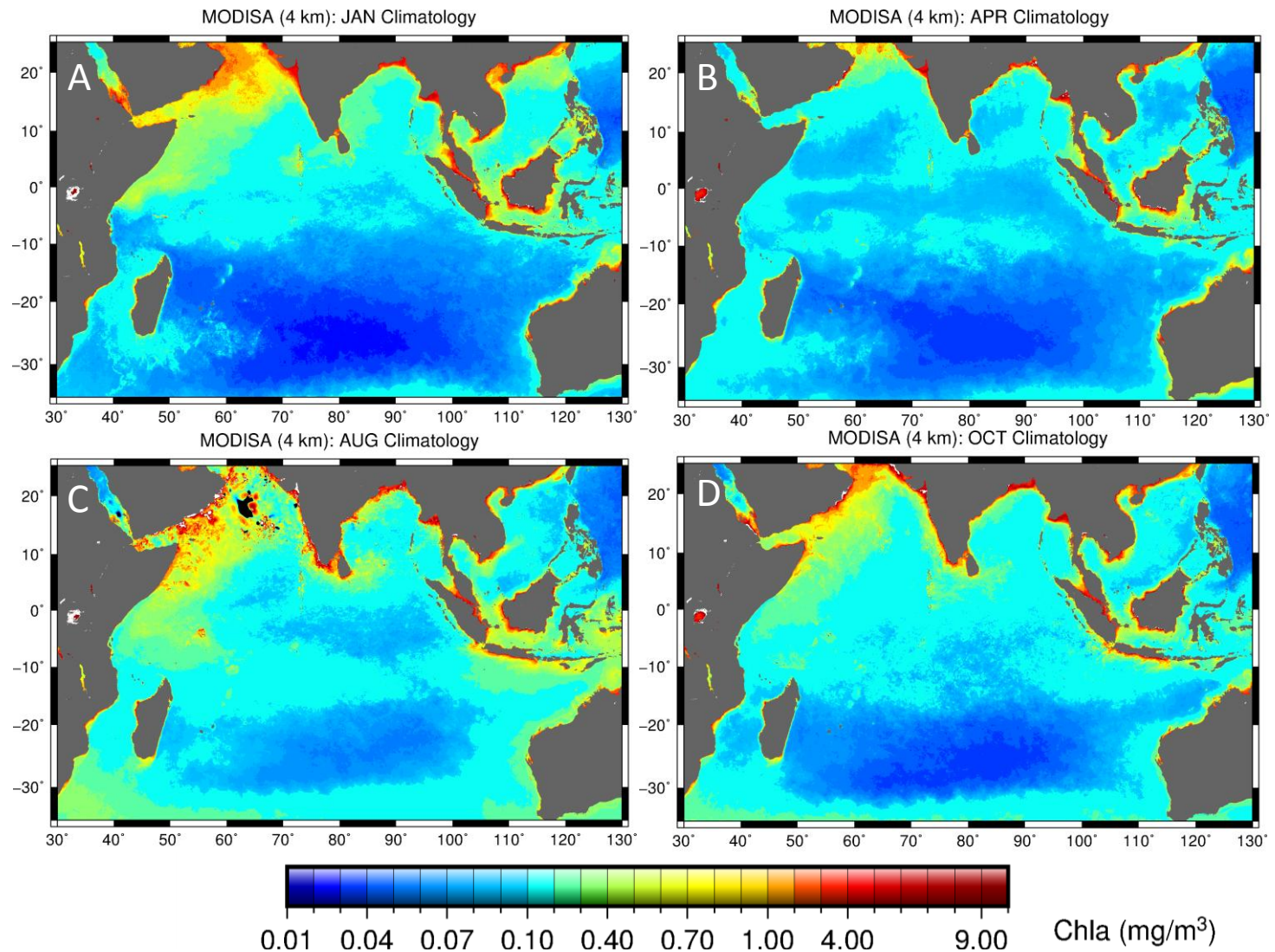
Figure 5: Monthly climatology of MODIS-Aqua (4 km resolution) chlorophyll: A) January, B) April, C) August, D) October. The climatology fields were obtained from the Goddard DAAC (http://daac.gsfc.nasa.gov).
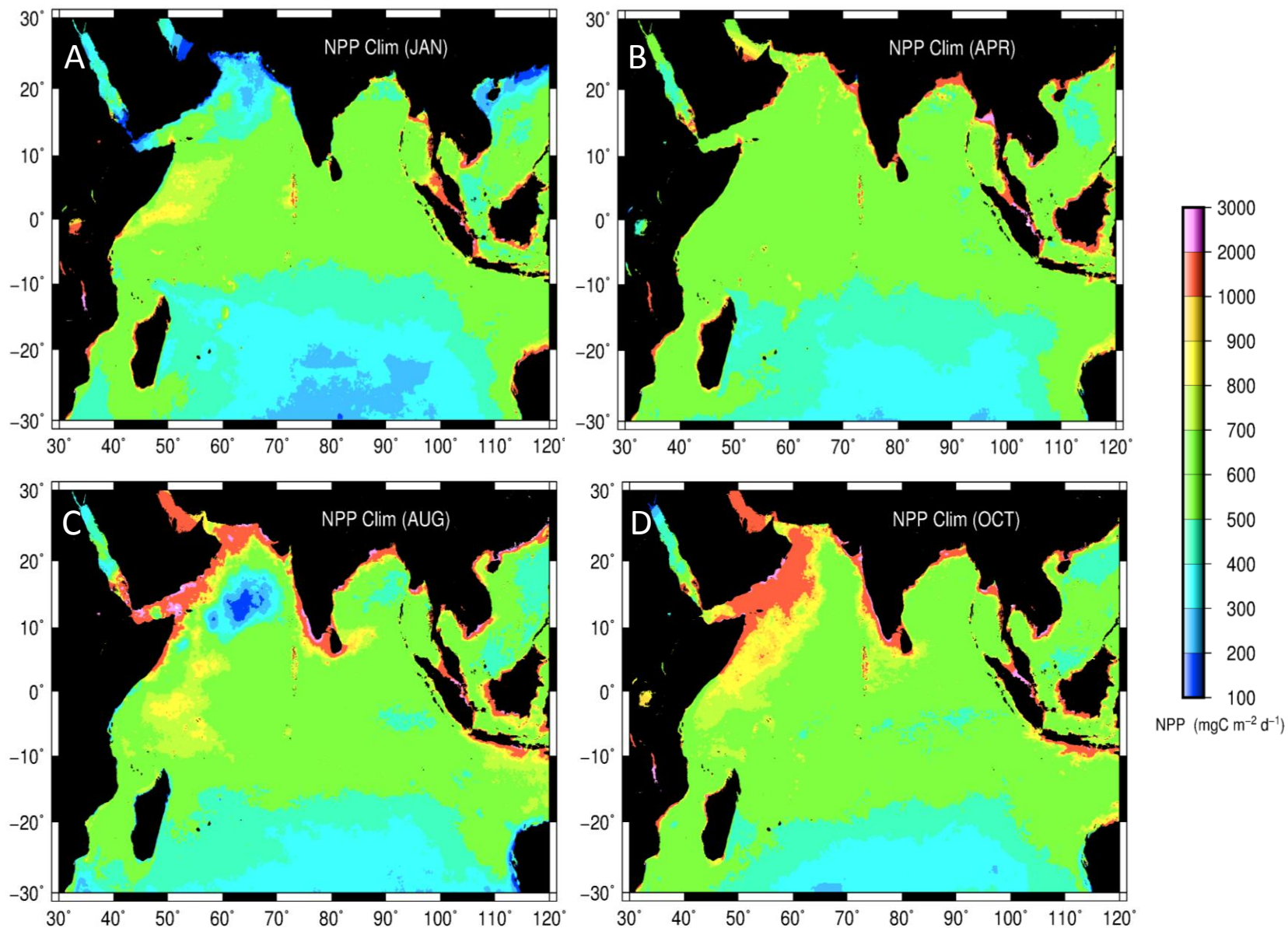
Figure 6: Monthly climatology of net primary production (mgC m^{-2} d^{-1}) estimated from SeaWiFs data: A) January, B) April, C) August, D) October. The climatology fields were obtained from the Goddard DAAC (http://daac.gsfc.nasa.gov).
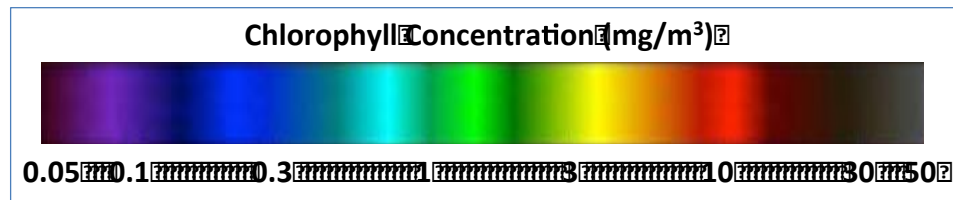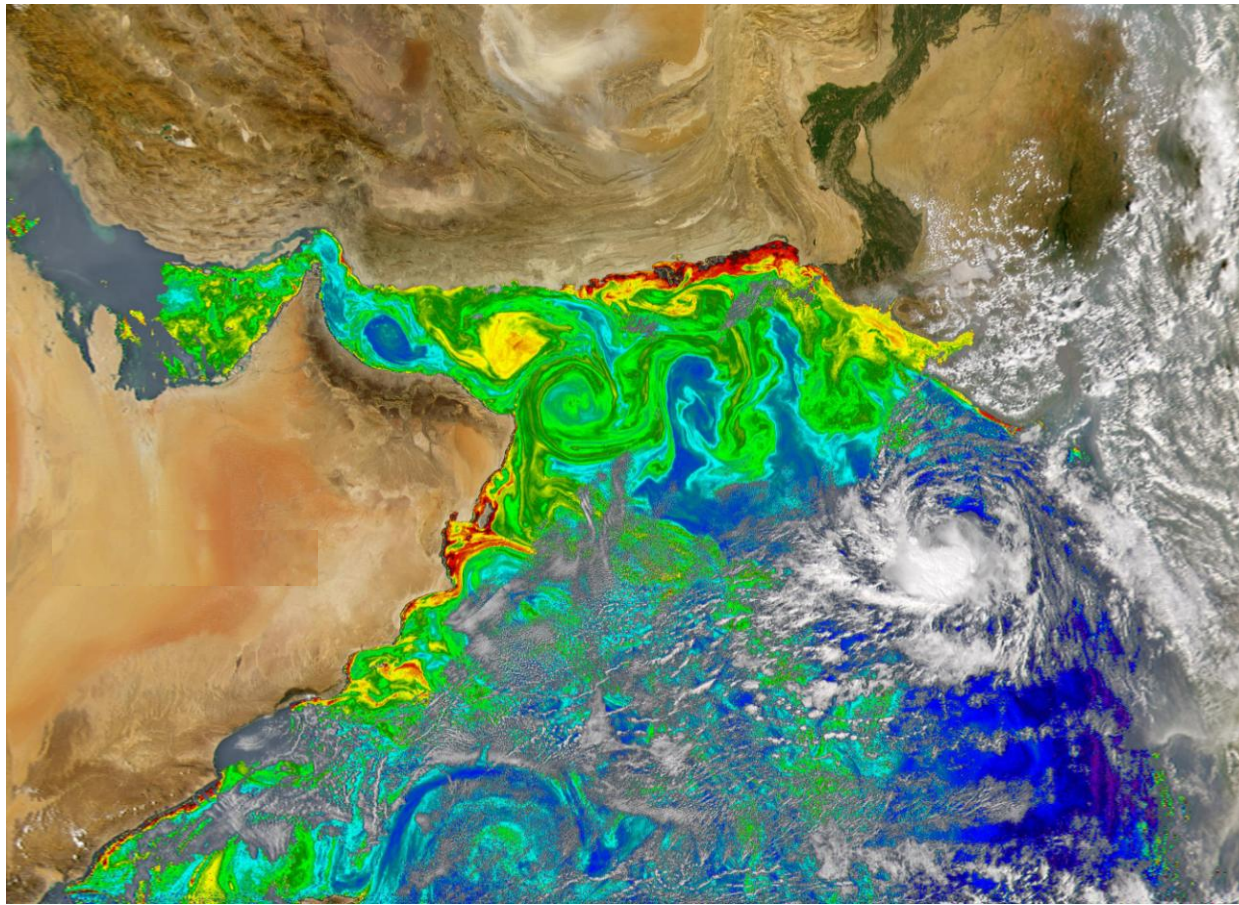
Figure 7: Near-surface chlorophyll-a concentration (mg/m³) in the Arabian Sea and the Gulf of Oman showing intense mesoscale variability at the end of the Southwest Monsoon (October 6, 2004). From http://oceancolor.gsfc.nasa.gov.
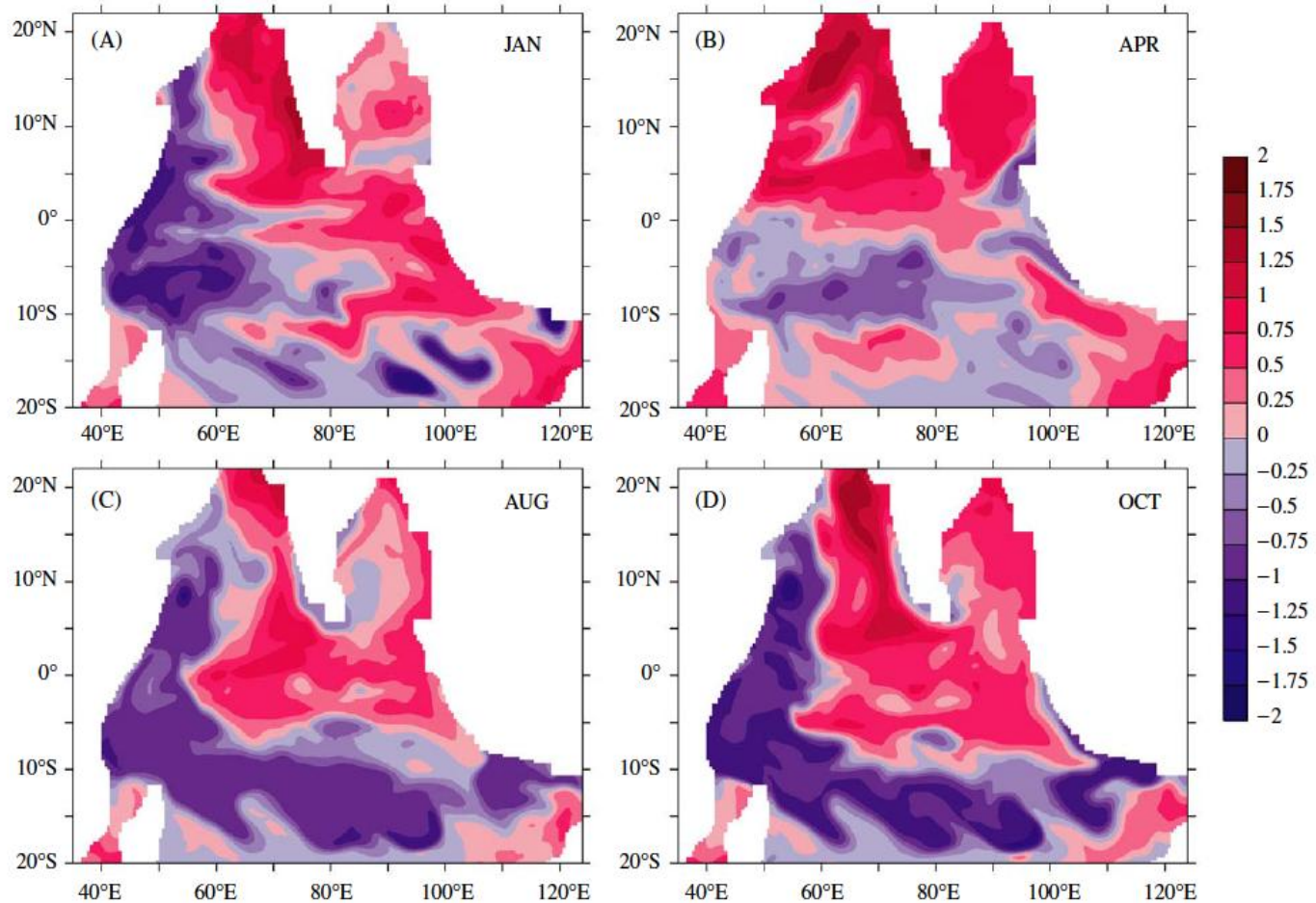
Figure 8: Model-simulated seasonal evolution of most limiting surface nutrient for net plankton with blue (red) indicating Fe (N) limited growth (i.e., red is iron replete). The four seasons consist of (A) January (NEM); (B) April (Spring Intermonsoon); (C) August (SWM); and (D) October (Fall Intermonsoon). Figure and caption modified from Wiggert et al. 2006.
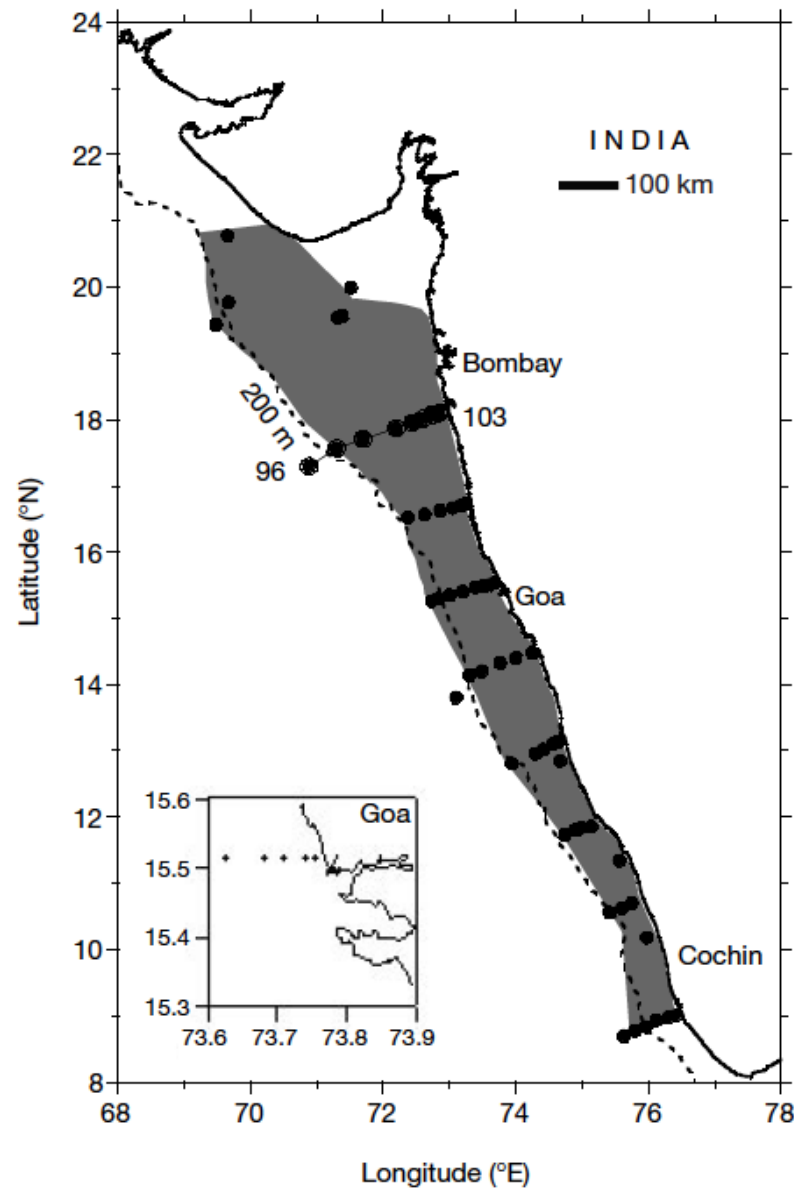
Figure 9: Zone of severe hypoxia on the western Indian shelf during September-October 1999 and locations of sampling sites. Zone of hypoxia is shown as shaded region ($O_2 < 0.5$ ml l^{-1}). Figure and caption modified from Naqvi et al. (2000).
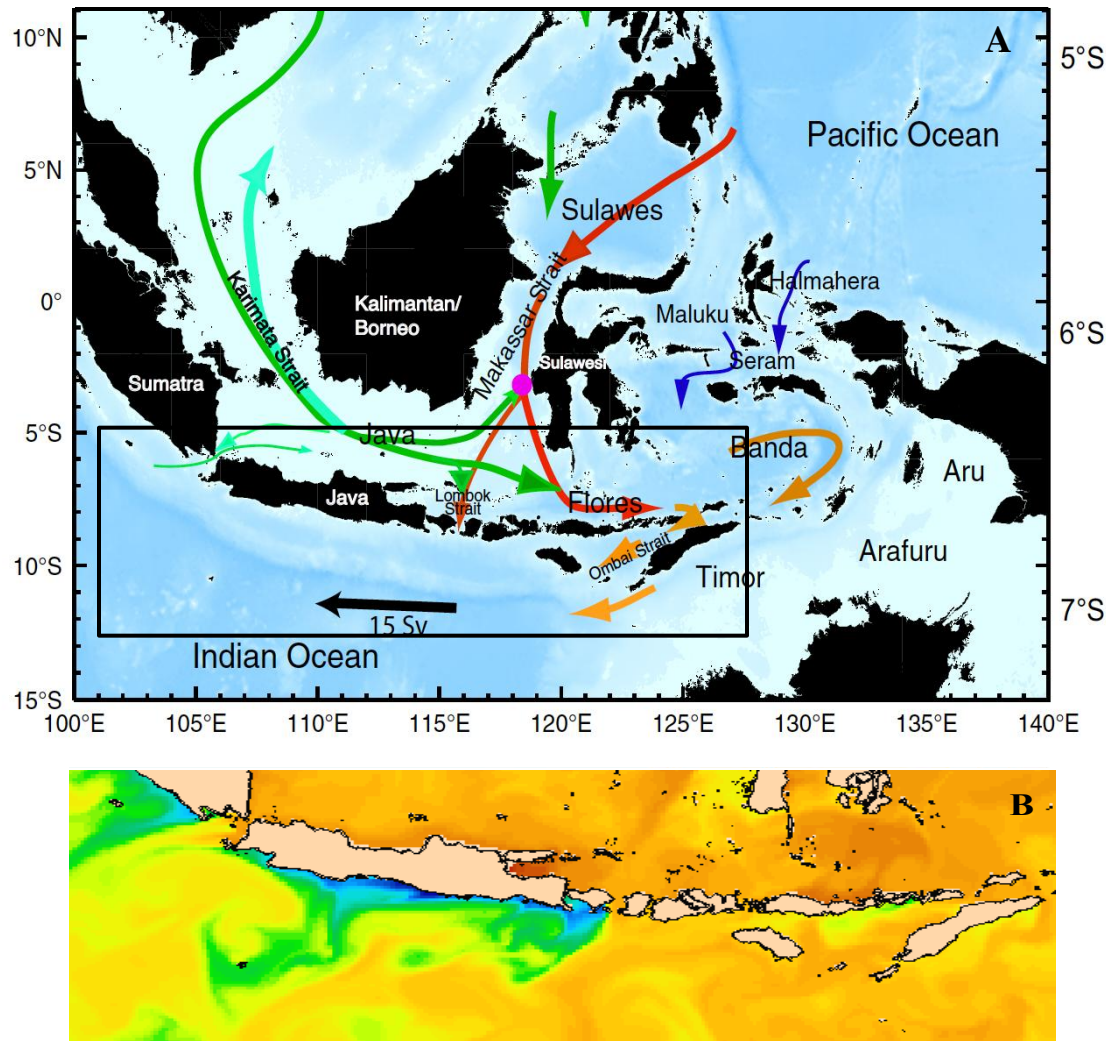
Figure 10: A) Map of the Indo-Pacific region and Indonesian Throughflow pathways. Most of the Throughflow (red line) passes through the Makassar Strait. The South China Sea Throughflow is shown in green. The Throughflow via the eastern part of Indonesia/Maluku Sea is shown in blue. All these ITF inputs are mixed in the Banda Sea before exiting into the Indian Ocean, mostly via Timor passage and Ombai Strait (orange). Figure and legend modified from Susanto and Song (2015). B) Subregion showing cold water upwelling along the coast of Java during the Southeast Monsoon simulated with the Ocean Forecasting Australia Model (OFAM). Cold water is indicated by the cool colors (green to blue) and warm water is indicated by the warm colors (yellow to orange). Figure courtesy of A. Schiller.

MODISA (4 km): 5–12 MAR 2006

MODISA (4 km): 17–24 JAN 2006

Chla (mg/m³)

0.01   0.04   0.07   0.10   0.40   0.70   1.00   4.00   9.00
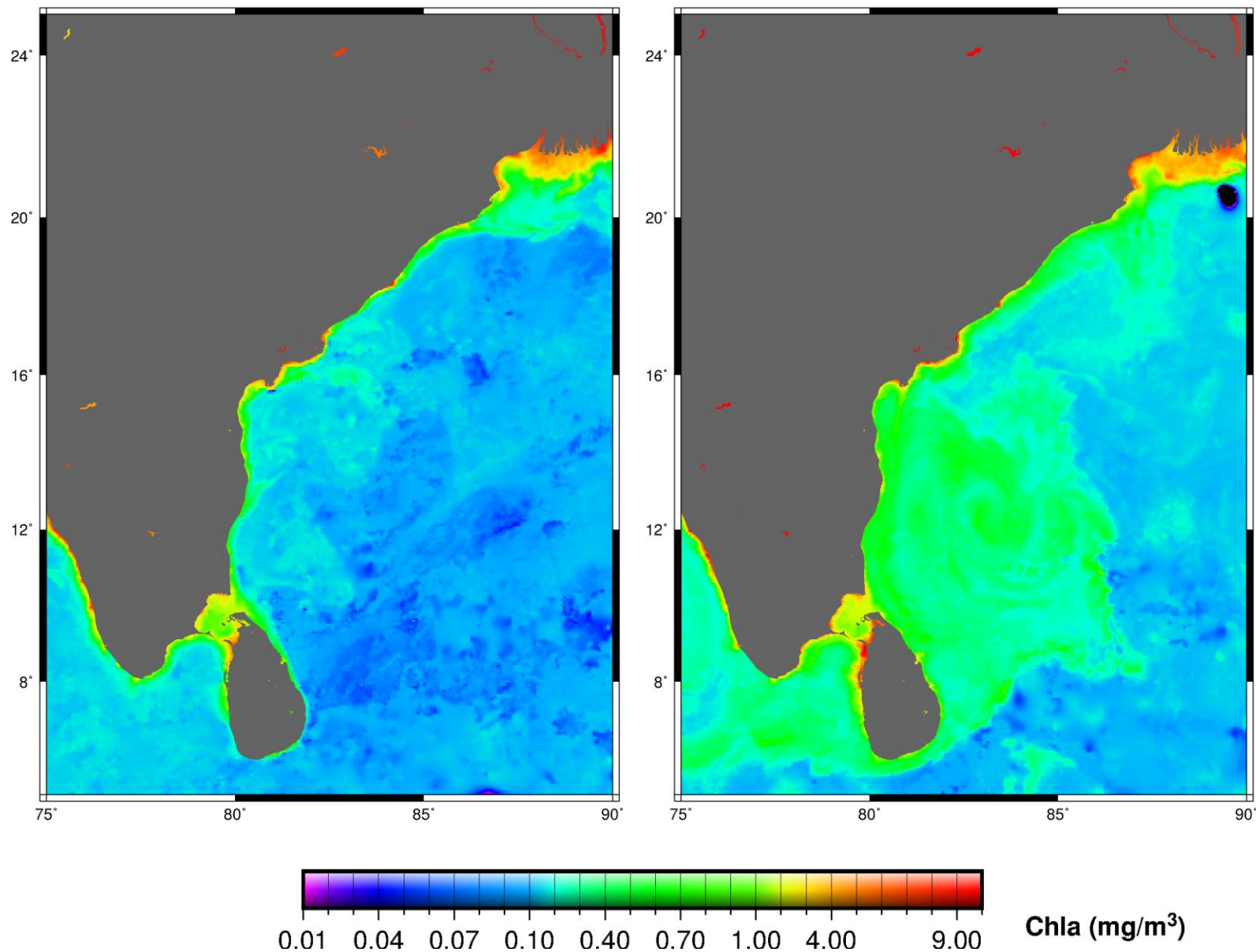
Figure 11: 8-day composite chlorophyll-a images for the western Bay of Bengal from MODIS Aqua. Left panel: 5-12 March 2006; Right panel: 17-24 January 2006. The fields were obtained from the Goddard DAAC (http://daac.gsfc.nasa.gov).
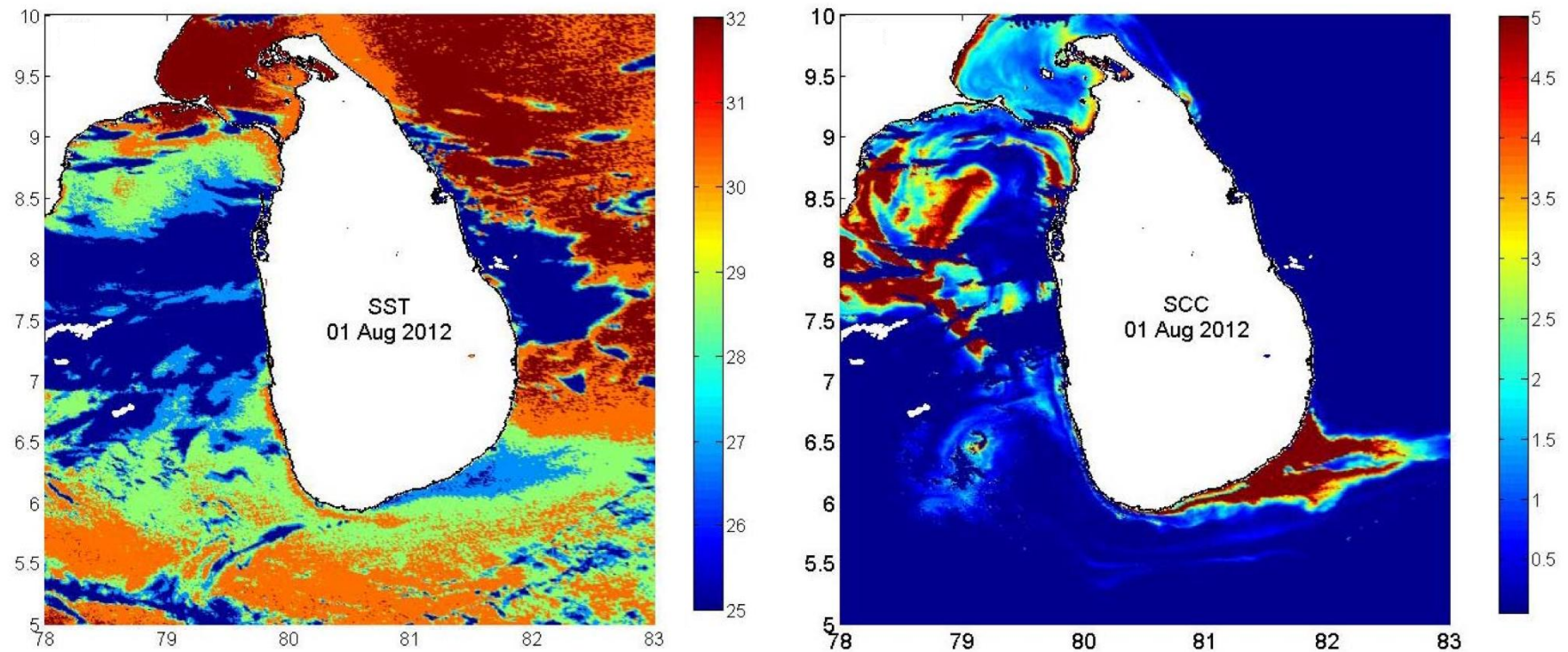
Figure 12: Surface temperature in degrees C (left panel) and chlorophyll concentration in mg m^{-3} (right panel) obtained on 1 August 2012. From de Vos et al. (2014).
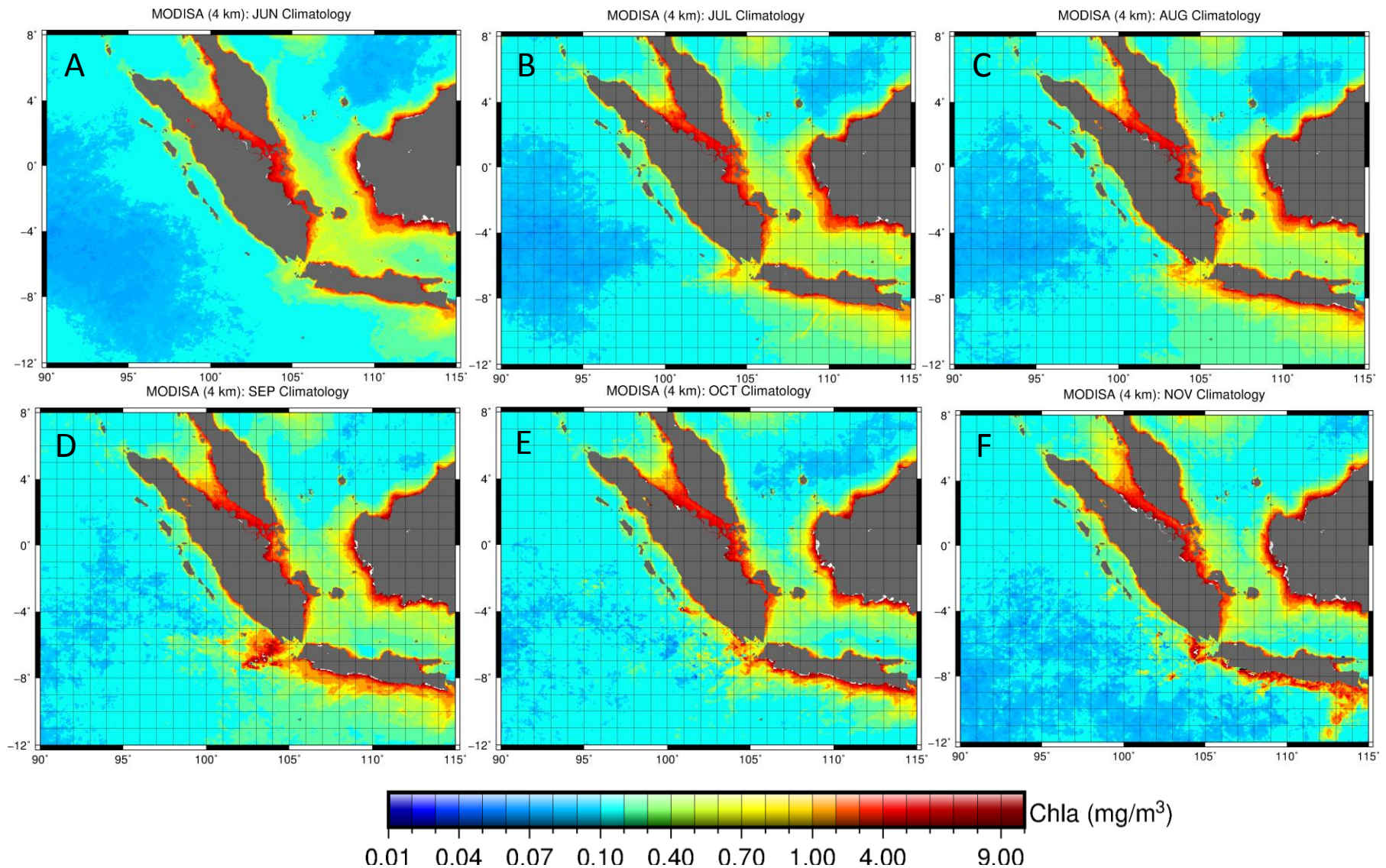
Figure 13: MODIS-derived monthly chlorophyll-a (mg m^{-2}) climatologies for the eastern equatorial Indian Ocean in the vicinity of Java and Sumatra: chlorophyll: A) June, B)July, C) August, D) September, E) October, F) November. The climatology fields were obtained from the Goddard DAAC (http://daac.gsfc.nasa.gov).
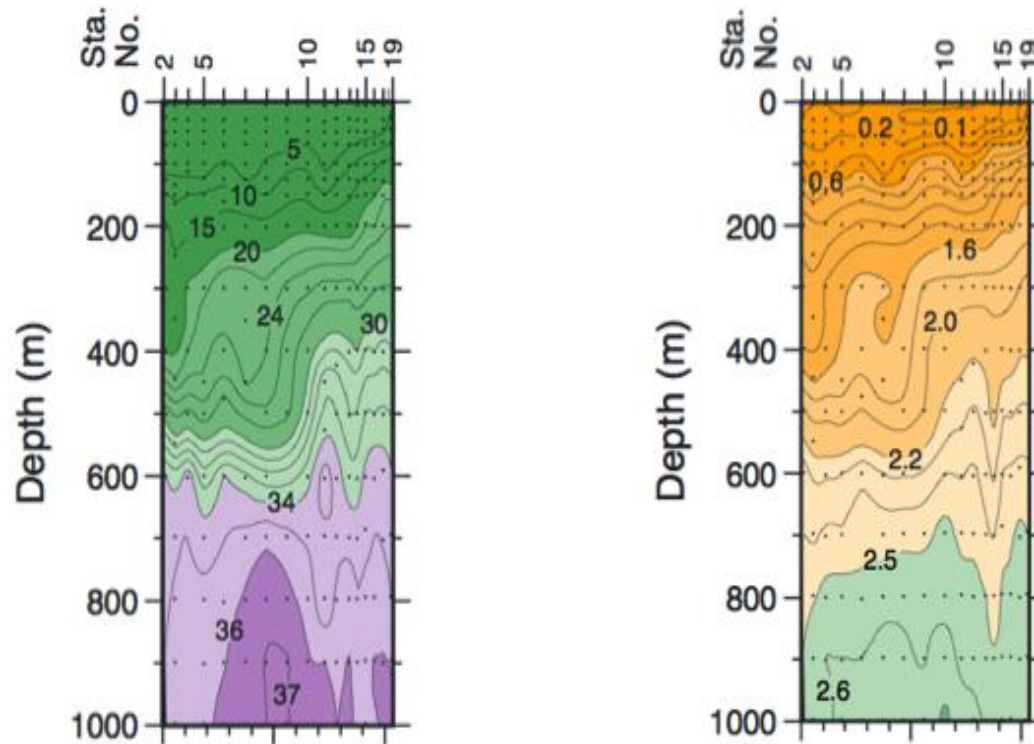
Figure 14: Nitrate (left panel) and phosphate (right panel) sections from WOCE line IR06, extending from northwest Australia (station 2) to Lombok Strait (station 19).
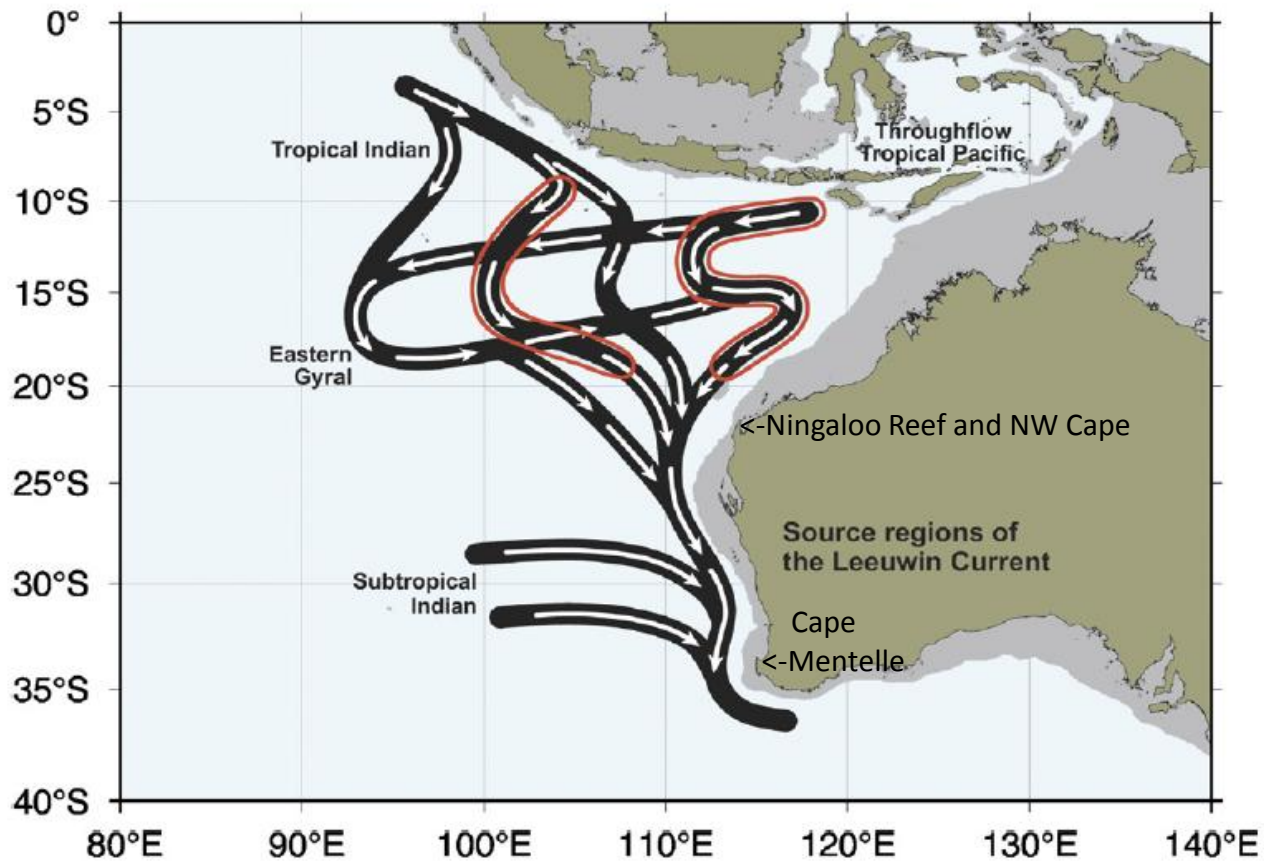
Figure 15: Schematic diagrams of the upper ocean circulation of the southeast Indian Ocean near Australia associated with the source regions of the Leeuwin Current. Figure and caption modified from Domingues et al. 2007.
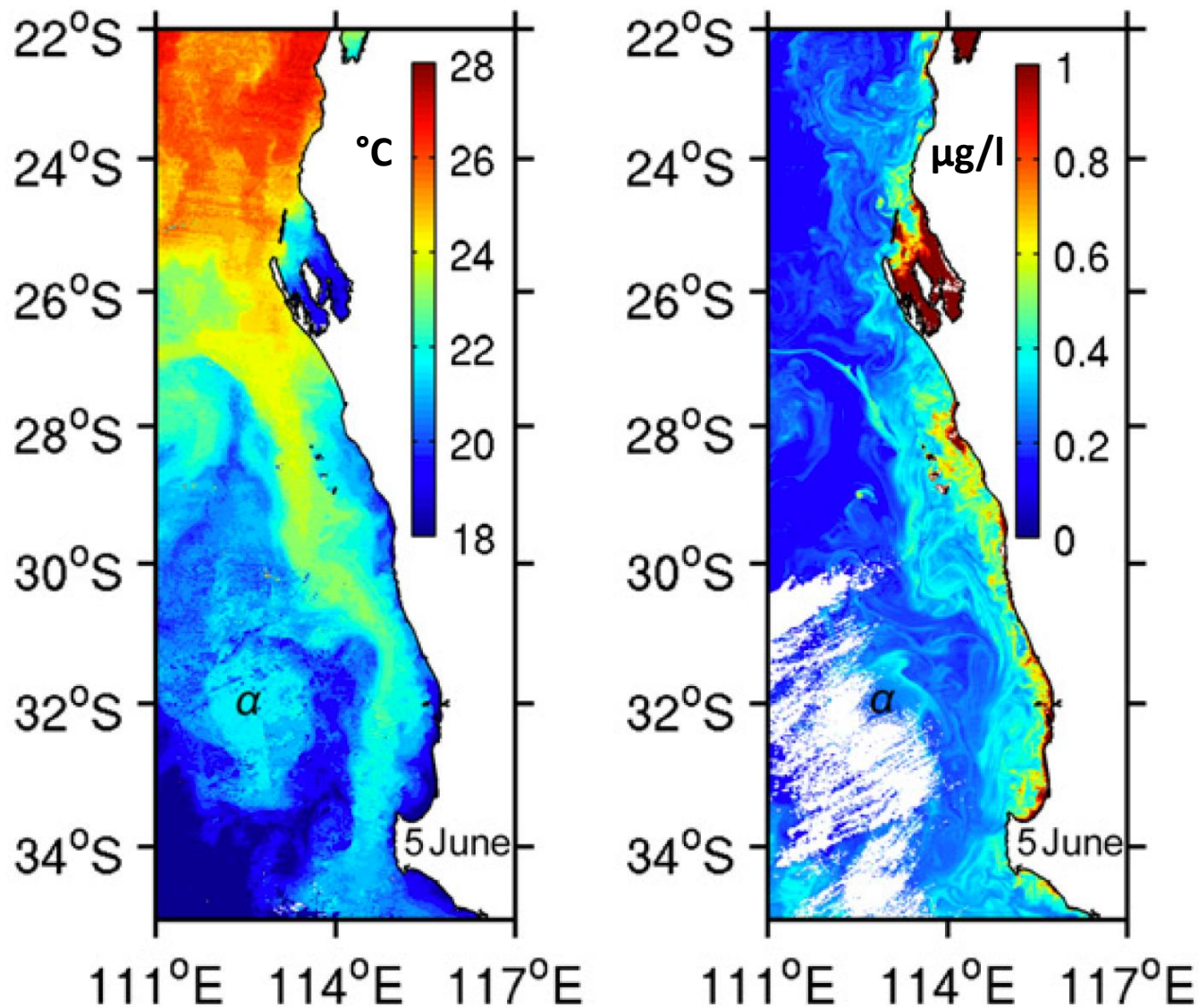
Figure 16: Single-day sea surface temperature (left pane) from GHRSST (1 km resolution) and surface chlorophyll a distribution (right panel) from the MODIS-Aqua satellite (1 km resolution) off Western Australia on 5 June 2007. Alpha (α) highlights a warm core, high chlorophyll feature. Figure and caption modified from Weller et al. (2011).
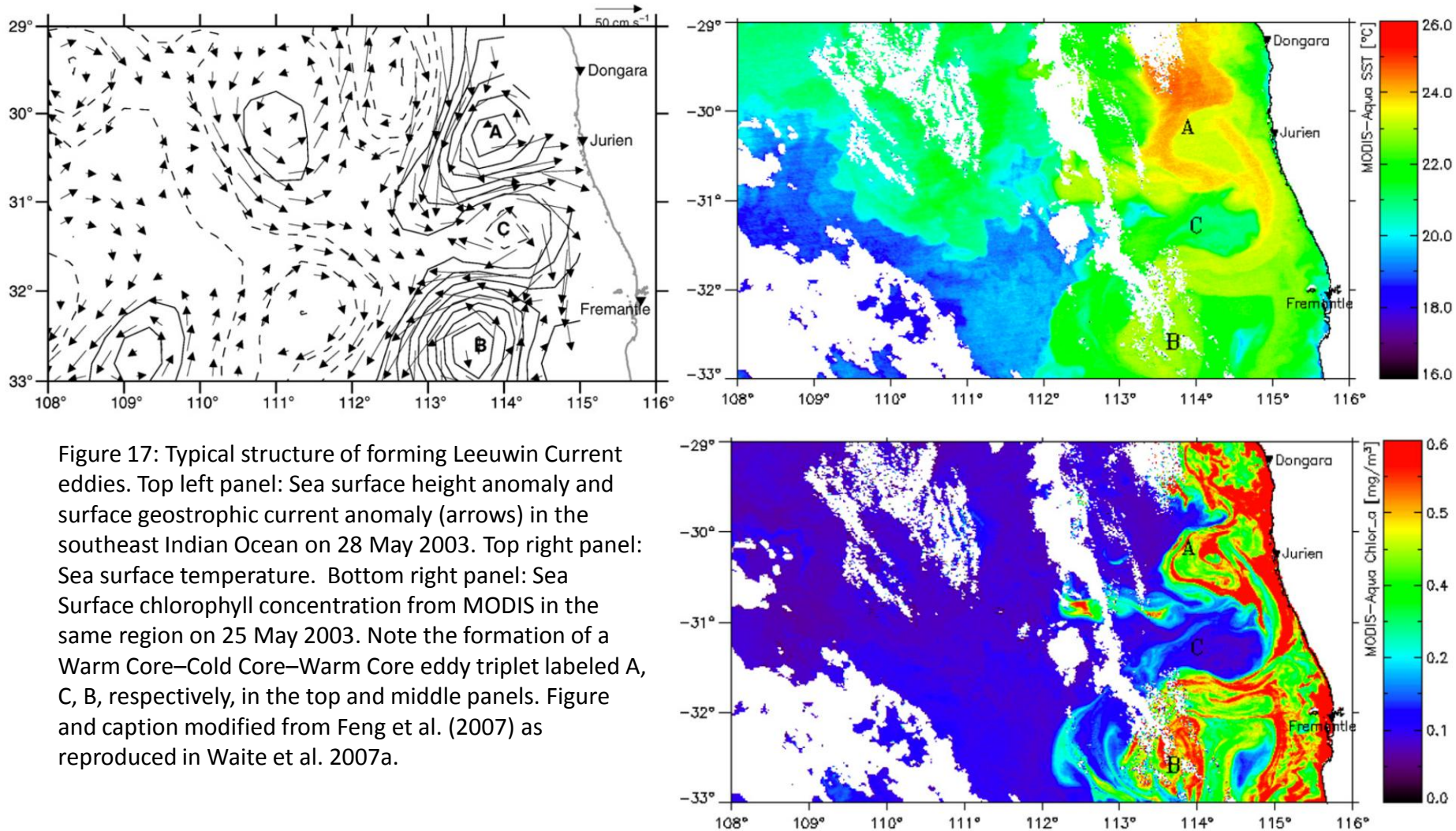
Figure 17: Typical structure of forming Leeuwin Current eddies. Top left panel: Sea surface height anomaly and surface geostrophic current anomaly (arrows) in the southeast Indian Ocean on 28 May 2003. Top right panel: Sea surface temperature. Bottom right panel: Sea Surface chlorophyll concentration from MODIS in the same region on 25 May 2003. Note the formation of a Warm Core–Cold Core–Warm Core eddy triplet labeled A, C, B, respectively, in the top and middle panels. Figure and caption modified from Feng et al. (2007) as reproduced in Waite et al. 2007a.

Figure 18: Top Panel: Chlorophyll a biomass integrated to 150 m as estimated from calibrated fluorescence as seen in Middle Panel. Middle Panel: A composite of four SeaSoar transects showing regional scale variation of subsurface fluorescence within the cold-core (CC) and warm-core (WC) eddies separated by the warm surface jet (WSJ) generated between the eddies (solid arrow). East of the WC eddy is Subtropical Front Water (SFW), a mild CC feature typified by an intense fluorescence maximum at depth. White lines are isopycnals. Note that the more diffuse layer of chlorophyll a in the WC eddy in general contains more vertically integrated chlorophyll a biomass than any other regional feature. Bottom Panel: SeaWIFS sea-surface temperature image showing the location of the CC, WC, WSJ and SFW and the actual ship track for the SeaSoar transects (solid black lines). Figure and caption modified from Waite et al. 2007c.
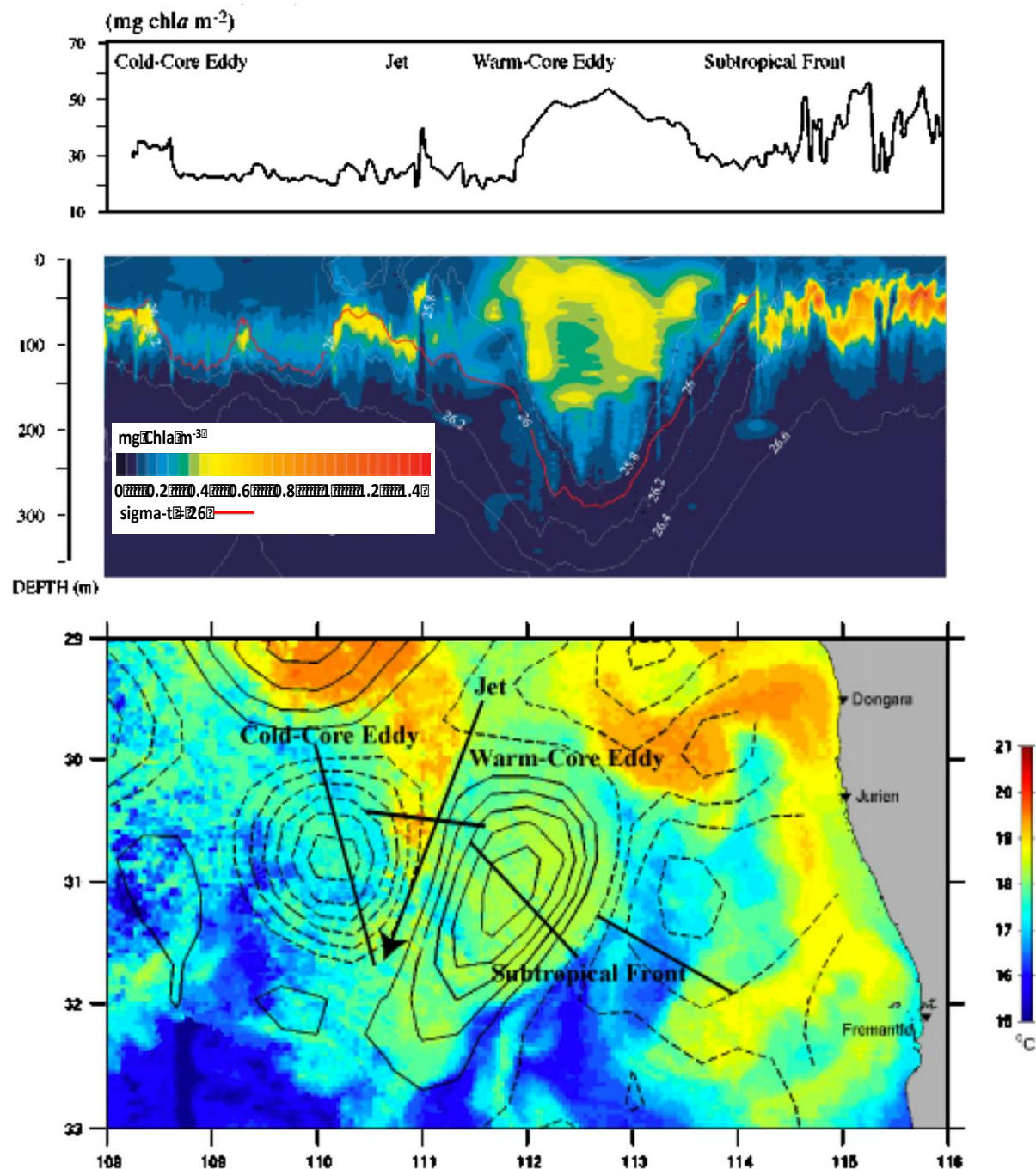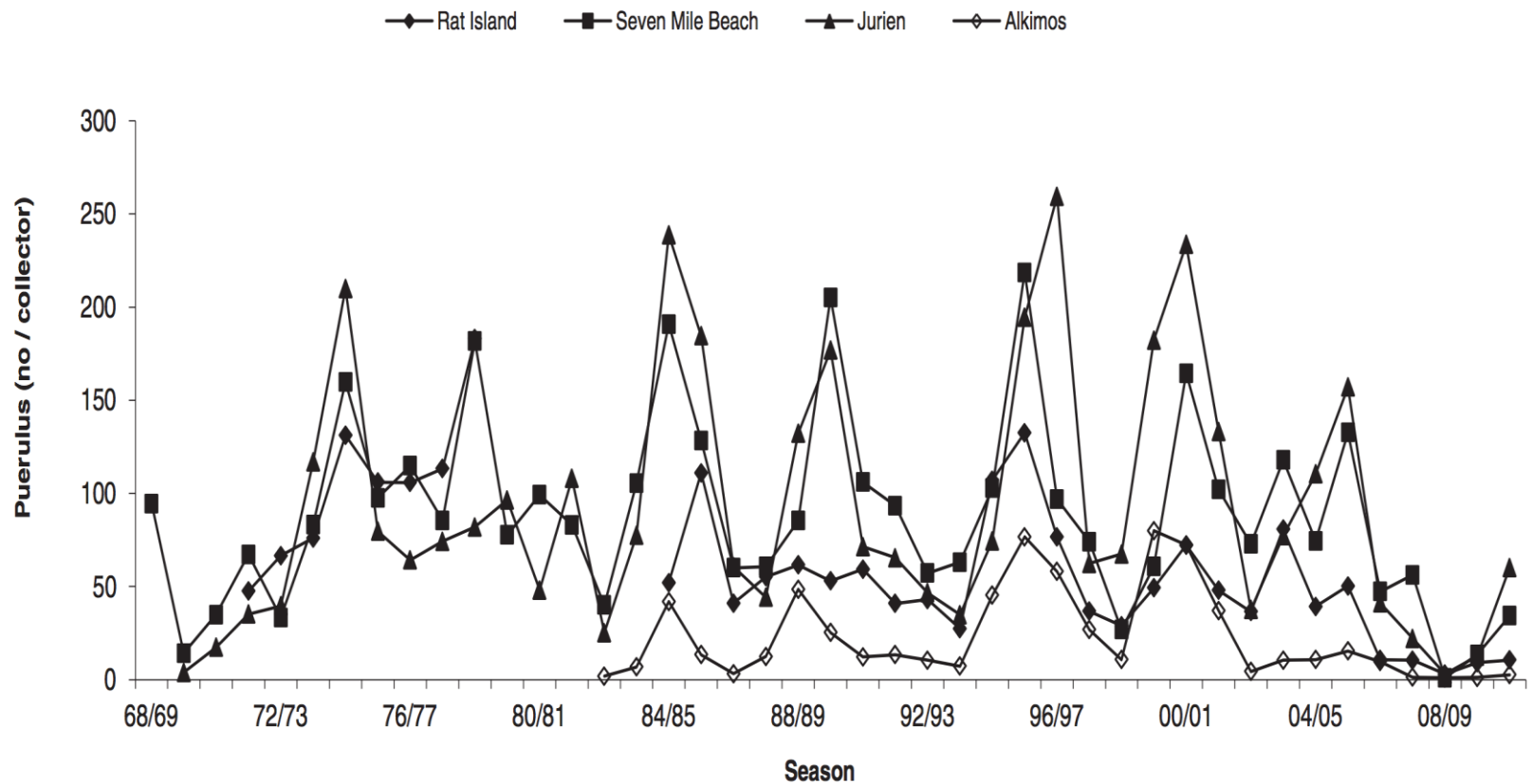
Figure 19: Puerulus settlement (numbers per collector) from 1968 through 2009 at four collector sites off of Western Australia in the western rock lobster fishery. High rock lobster puerulus settlement is associated with strong Leeuwin Current transport in La Niña years with a three to four year lag. Figure and caption modified from Caputi et al. (2014).
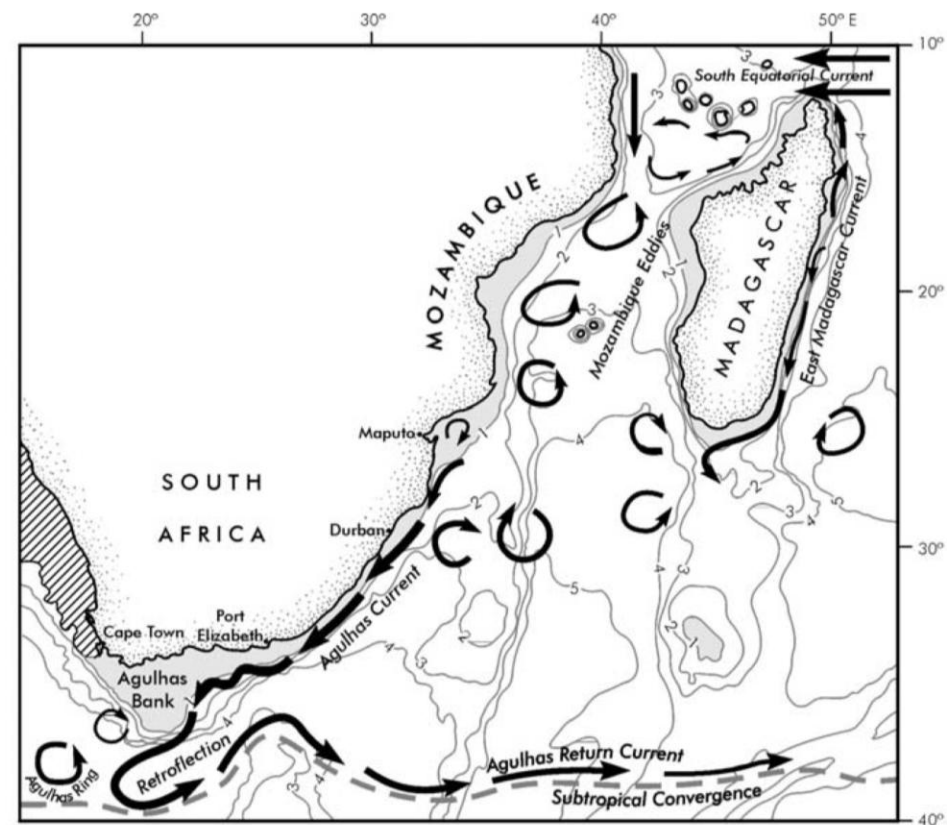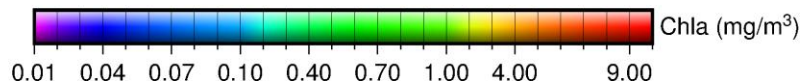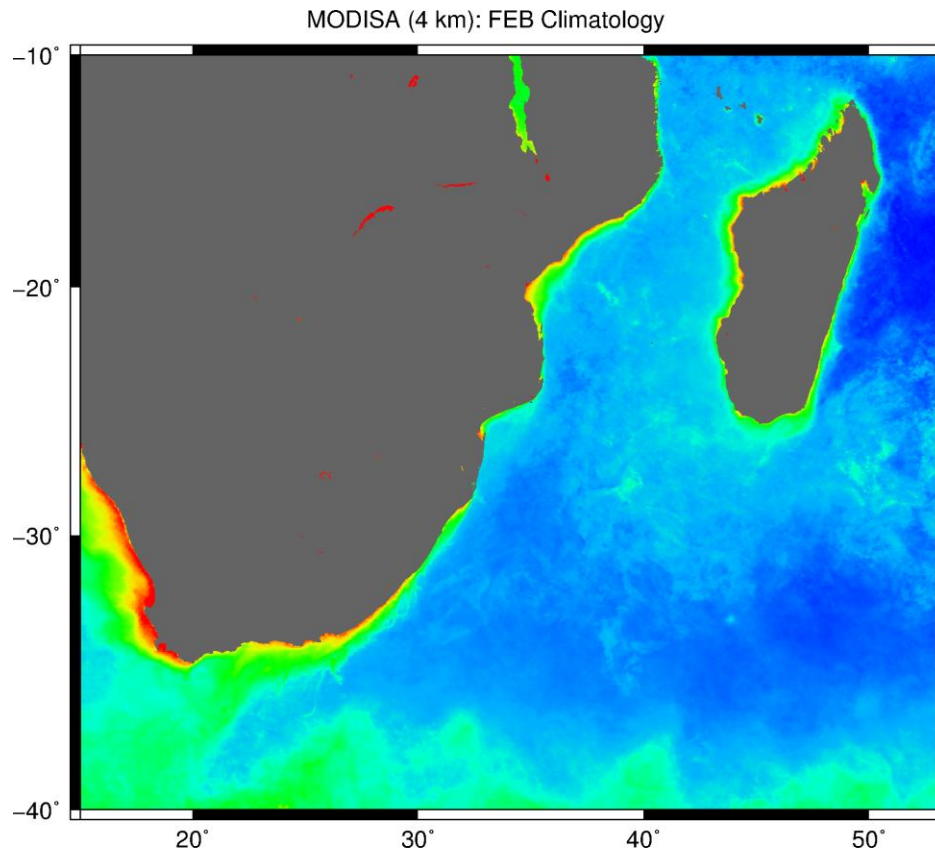
MODISA (4 km): FEB Climatology

Chla (mg/m³)

0.01 0.04 0.07 0.10 0.40 0.70 1.00 4.00 9.00

Figure 20: Right Panel: Source waters, eddies and retroflection in the Agulhas Current. From Lutjeharms (2006). Left Panel: MODIS February chlorophyll concentration climatology around South Africa and Madagascar and in the vicinity of the Agulhas Current and retroflection. The climatology fields were obtained from the Goddard DAAC (http://daac.gsfc.nasa.gov).

Figure 21: Panel (a) shows the sea surface temperature (degrees C) on September 2, 2010 from the blended microwave and infrared optimally interpolated product (http://www.remss.com/sst). The grey lines indicate the bathymetry in 1000 m intervals starting at 1000 m. The black lines indicate the absolute dynamical height (ssh anomaly from Aviso, plus the mean of Maximenko and Niiler) that ranges from 0.5 to 0.8 m. Transects are numbered east to west from 1 to15.The cruise track commenced on thee astern Agulhas Bank on August 30, 2010 and finished on the western Agulhas Bank on September 22, 2010. Note the Natal Pulse (NP) in the Agulhas Current near sections 1–3 and the Agulhas Current meander (ACM) at sections 4–6. Panel (b) shows a 3-day composite from MODIS aqua of chlorophyll (mg/m^3) measured from 1 to 3 September 2010. The spatial resolution of the chlorophyll a data is 4 km. To emphasize spatial variability, chlorophyll concentrations are presented in logarithmic values (base10). Figure and caption are modified from Jackson et al. (2012).
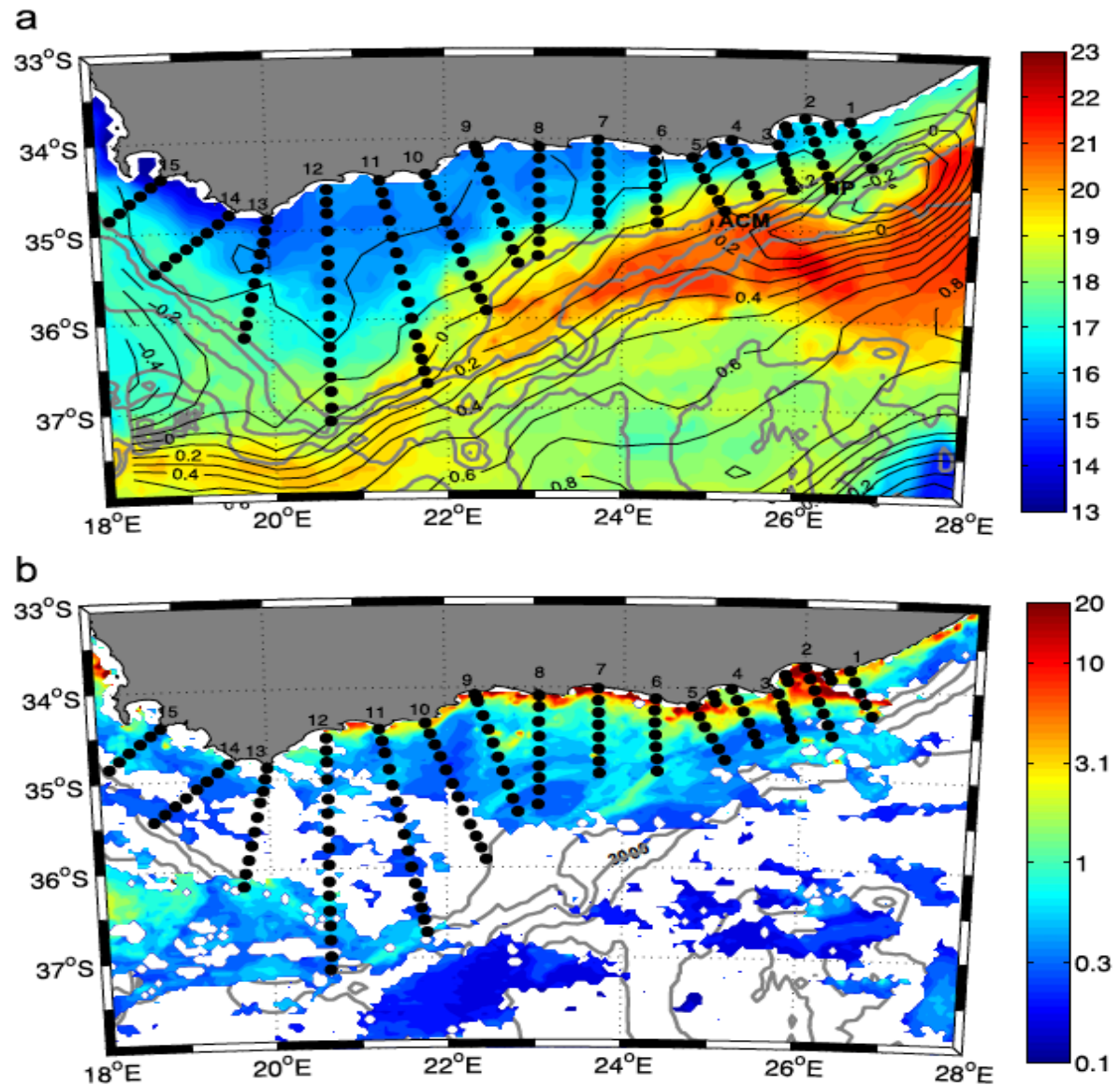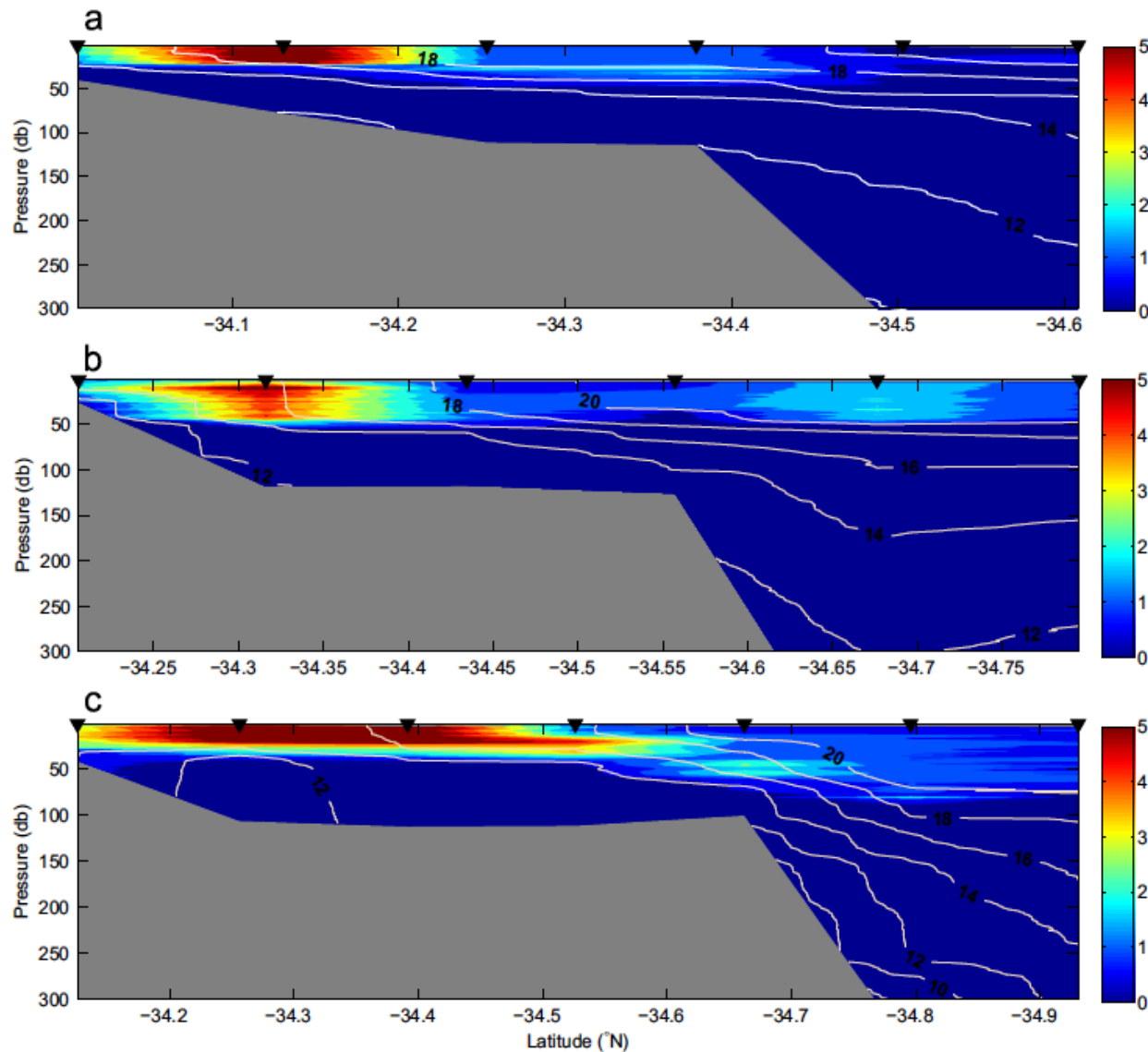
Figure 22: Vertical sections of chlorophyll (mg/m^3) across (a) section 4, (b) section 5, and (c)section 6 in Figure 21. Chlorophyll is colored and conservative temperature is shown as contour line. Black triangles indicate the station position. Figure and caption modified from Jackson et al. (2012).

Figure 23: S–ADCP data collected in May 2005 between Port Edward and East London: (a) near-surface current field measured along interconnected trans-shelf transects A–A', B–B', C–C', and D–D', and a complementary SST satellite image recorded on 7 May 2005. Note the close proximity of the Agulhas Current (red) on the KZN south coast and between Mbhashe and Kei rivers in both datasets, and the counterflow on the shelf near Port St Johns distinguished in the satellite image by cooler coastal water (green); (b) vertical section to a depth of 600 m of the S–ADCP data collected along transect A–A', highlighting the close proximity of the core of the Agulhas Current (yellow-orange) to the shelf edge; and (c) vertical section of the S–ADCP data collected along transect D–D', highlighting core velocities of the Agulhas Current (yellow-orange) over the shelf edge. Figure and caption modified from Roberts et al. (2010).
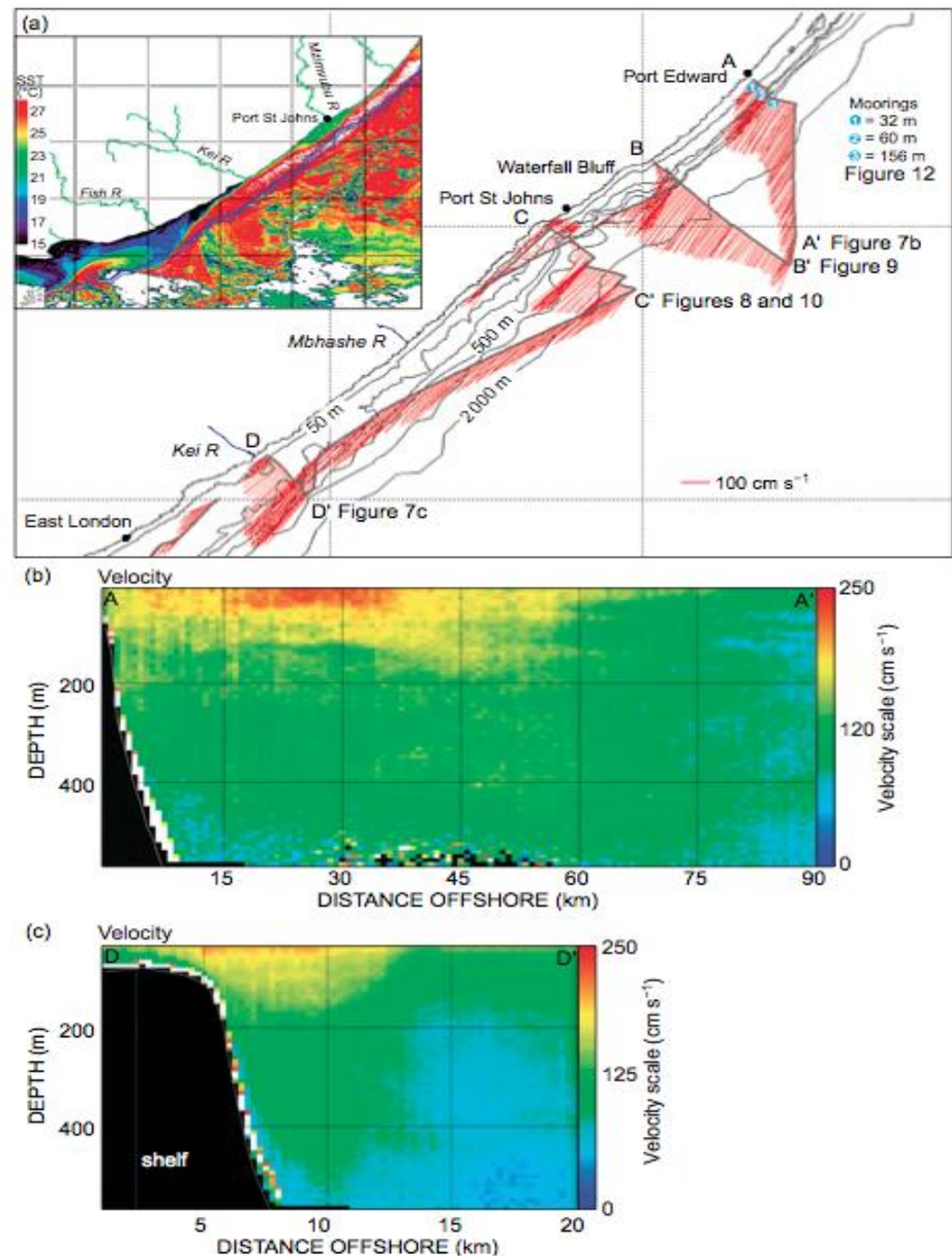
Figure 24: (a) Expanded view of the near-surface circulation measured by S–ADCP near Port St Johns, highlighting distinct onshore flow in the vicinity of Rame Head and to the east, north-eastward flow. Combined with the offshore flow on the inner shelf of the Waterfall Bluff transect, these data indicate a lee-trapped cyclonic eddy between Rame Head and Waterfall Bluff. Red dots 1–6 indicate CTD stations; (b) vertical sections (velocity and direction) of the S–ADCP data collected along transect C–C' to a depth of 600 m depicting the high-velocity core of the south-westward-flowing Agulhas Current (yellow-red) and a 10 km-wide distinct north-eastward counterflow (blue). Note the subsurface velocity maximum (>100 cm s−1) over the shelf slope. Figure and caption modified from Roberts et al. (2010).
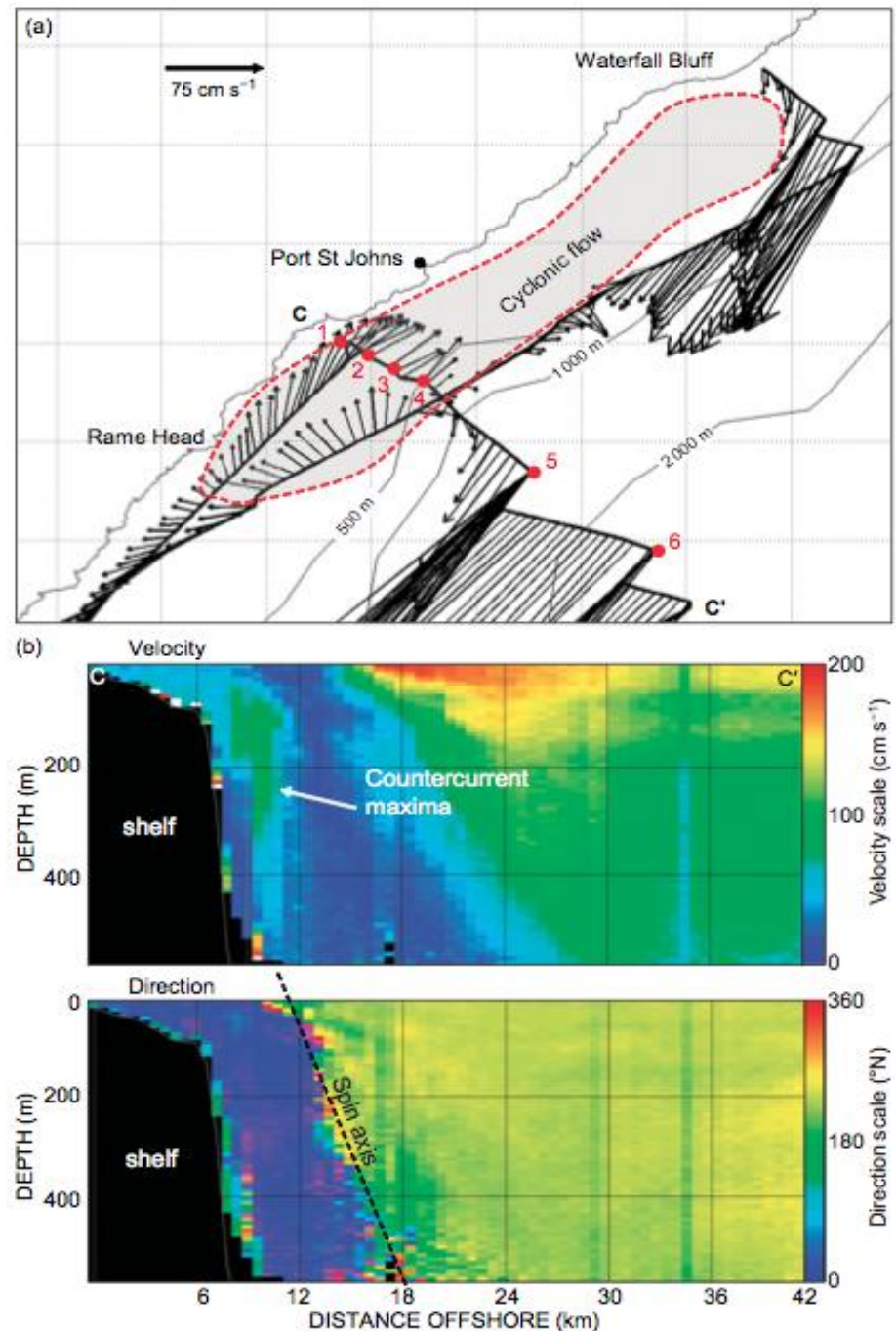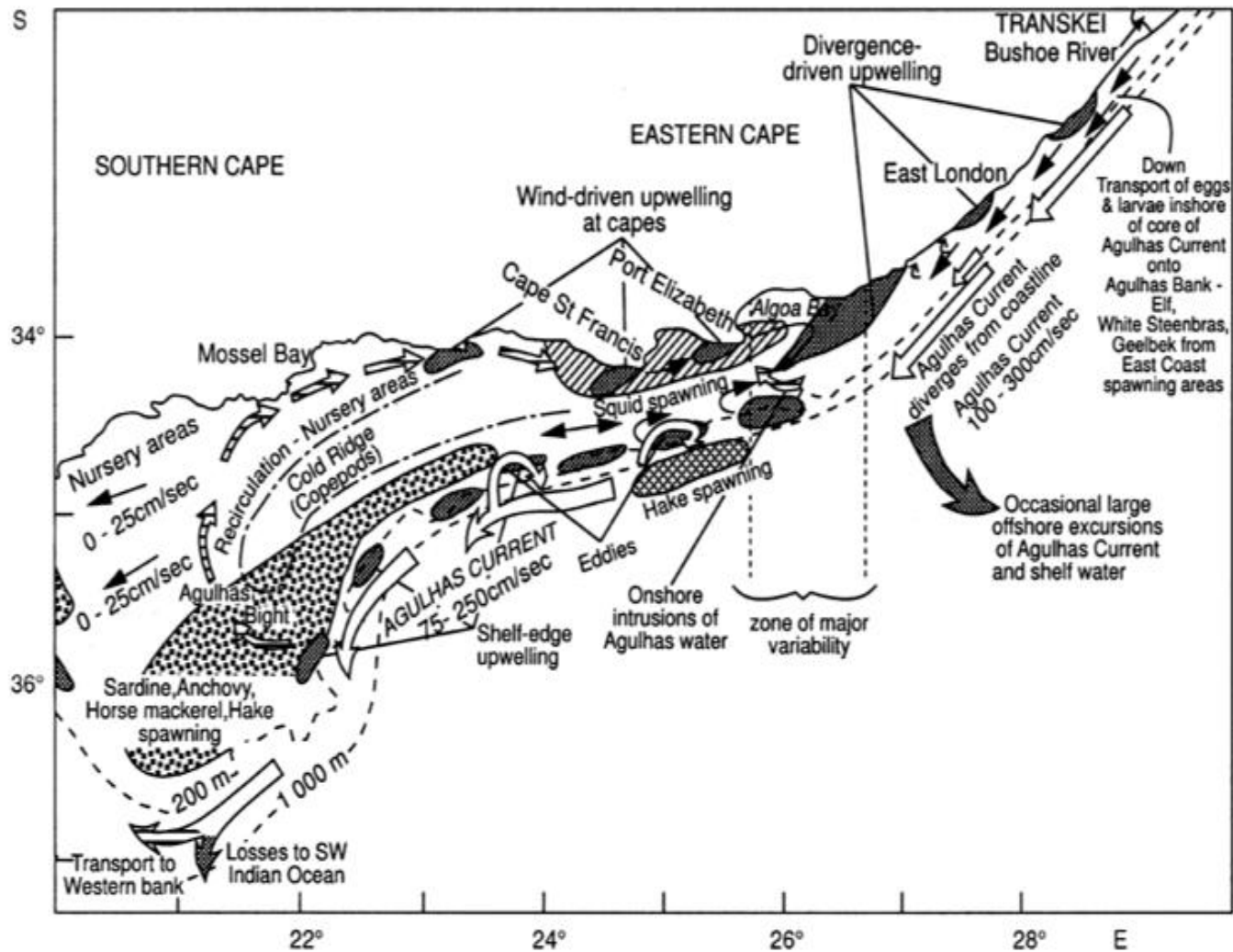
Figure 25: The central-eastern Agulhas Bank nursery/spawning ground showing the spawning areas of several different species along with key zones of Agulhas Current influence. The latter include, from east to west, a region where the Agulhas diverges from the coastline between 27° and 28° E with occasional large offshore excursions of Agulhas Current and shelf water; A zone of major variability between 25.5° and 26.5° E which includes a region where onshore intrusions of Agulhas water often occur; A region between 23.5° and 25° E where eddies impinge on the shelf; A zone of shelf-edge upwelling between 22° and 24° E; and finally the region between 20° and 22° E were losses of larvae to the SW Indian Ocean and transport to the Western Bank likely occur. Figure and caption modified from Hutchings et al. (2002).

Highlights

Indian Ocean boundary currents are complicated compared to the Atlantic and Pacific.

All of the boundary currents in the northern Indian Ocean reverse seasonally in response to monsoon forcing. These include the Somali Current (East Africa Coastal Current) the Oman Coastal Current, the West India Coastal Current, the Southwest Monsoon Current, the East India Coastal Current, the Northeast Monsoon Current and the Java Current.

All of these reversing currents have large biogeochemical and ecological impacts.

The Leeuwin Current flows poleward and has very high eddy kinetic energy.

It sheds seaward-propagating, warm-core eddies that impact higher trophic levels.

The Agulhas Current is very large and generates eddies that propagate alongshore.

As a result, neritic species have evolved highly selective reproductive behaviors.