



The biogeochemistry and oceanography of the East African Coastal Current

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ABSTRACT

The East African Coastal Current (EACC) is the dominant oceanographic influence along the coastlines of Tanzania and Kenya yet formal descriptions of the biogeochemical characteristics of these waters remain fragmented or poorly defined. Whilst the region remains undersampled, and information for many parameters is limited or even absent, the region is not understudied and complex patterns, due in part to the changing monsoon seasons, can be identified from extant observations. A critical distinction between the neritic waters of the narrow East African continental shelf, which may be more influenced by local tidal currents and terrestrial inputs, and the oligotrophic surface waters of the deeper offshore region under the influence of the EACC can be drawn, which cautions against the extrapolation of trends or seasonal patterns from limited datasets more widely throughout the region. Permanently N-limited, low $\text{NO}_3^-:\text{PO}_4^{3-}$ surface waters coupled with high ($> 25^\circ\text{C}$) sea surface temperatures are a key feature of the EACC Ecoregion and likely responsible for the presence of a regionally important population of the nitrogen fixing cyanobacterium *Trichodesmium*, though information on another key requirement, iron, is lacking. Phytoplankton diversity, abundance and the spatiotemporal variability of phytoplankton populations are considered poorly known due to limited sampling efforts. Recent and growing recognition of high coral biodiversity, high reef fish species endemism, of widespread reductions in mangrove forest coverage, and growing anthropogenic pressures on coastal waters suggest that the region deserves greater multidisciplinary study. Efforts to anticipate climate induced changes to these waters, which are expected to impact local fisheries with substantial socioeconomic impacts, would benefit from greater efforts to synthesise existing biogeochemical data, much of which resides within grey literature sources, theses, project reports, remains inaccessible or has been lost. Future biogeochemical and oceanographic observational efforts should simultaneously explore shelf and deeper offshore waters to determine shelf-to-ocean linkages and the spatio-temporal variability of parameter fields whilst also bridging the gap to research efforts on coral biodiversity, fisheries and marine management activities due to recognised gaps in underlying scientific data to support decision making in these areas.

1. Introduction

The tropical coastal waters of Tanzania and Kenya are bathed year-round by the northward flowing East African Coastal Current (EACC), a western boundary current of the Indian Ocean. The EACC influences a region containing important and highly productive mangrove forests, seagrass beds, coral reef ecosystems and estuaries which collectively sustain high levels of biodiversity including 10 species of mangrove tree, 12 species of seagrass, more than 300 species of coral and over 2000 species of fish (Spalding et al., 2001; Green and Short, 2003; Everett et al., 2010; Obura et al., 2012; Diop et al., 2016; Scheren et al., 2016; Bunting et al., 2018). The various ecosystems host high levels of endemism particularly amongst reef fish species, act as nursery grounds for important fish stocks that provide livelihoods for coastal communities, protein for human consumption as well as being a focus for

tourism and other cultural amenities (UNEP, 2015). Such ecosystems are increasingly threatened by rising sea levels, pollution, increased ocean temperatures and decreasing ocean pH, with the increased frequency and severity of coral bleaching events in the Western Indian Ocean (WIO) in recent years a particularly potent reminder of the sensitivity of tropical coastal ecosystems to their local environment (e.g. Salm, 1983; Wilkinson et al., 1999; Muhando, 2001; Obura et al., 2002; Grimsditch et al., 2009; Chauka, 2016; Spalding and Brown, 2015; Obura et al., 2017). Land use changes have resulted in reductions in mangrove forests regionally (Obura et al., 2012; Government of Kenya, 2017), increased soil erosion due to deforestation and poor farming practices (Bliss-Guest, 1983; Finn, 1983), whilst poorly regulated fishing practices and modernization of fishing gear are impacting biodiversity, destroying coral reef habitats and overexploiting fisheries resources (Kimani, 1995; Kimani et al., 2009; Katikiro et al., 2013;

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Braulik et al., 2015; Katikiro and Mahenge, 2016; Braulik et al., 2017). Eutrophication of coastal waters, due to growing human populations, untreated industrial and sewage discharge to the coastal ocean, and urbanisation are also increasing problems with a range of negative impacts (UNEP, 2009, 2015). Increased sediment discharge due to soil erosion has long been recognised as a major regional problem which leads to increased sedimentation and turbidity in coastal waters and the smothering of coral ecosystems (Finn, 1983). There is also growing recognition of the problems associated with marine litter and plastic pollution in these waters (UNEP, 2005; Lane et al., 2007; Government of Kenya, 2017; O'Brien, 2018; UNEP, 2018).

Despite this litany of negative impacts East African coastal waters remain comparatively undersampled compared to the wider Indian Ocean, which is itself generally considered to be less well studied than the Pacific or Atlantic Oceans (Mmochi et al., 2001; Richmond and Francis, 2001; UNEP, 2001, 2015). General oceanographic and planktonic descriptions from the 1950s and 1960s remain influential in the literature (e.g. Newell, 1957, 1959; Okera, 1974; Wickstead, 1961, 1962, 1963) and whilst results from the 1959–1965 International Indian Ocean Expedition (IIOE; Zeitzschel, 1973; Behrman, 1981) provided a broad and improved understanding of the Western Indian Ocean, observations were very limited in the coastal waters of East Africa. Against this background considerable progress has been made on the study of marine biodiversity within the Western Indian Ocean in the last 50 years (Richmond, 2001). Local infrastructure constraints on research prospects and a broad regional focus on fisheries research due to its socioeconomic importance, and on coral ecosystems due to their habitat importance for fisheries or due to their susceptibility to changing environmental conditions, have tended to constrain efforts to expand the knowledge of regional marine biogeochemistry. More recently the risk of piracy has greatly reduced accessibility and opportunities to work in the region (Vespe et al., 2015; Belhabib et al., 2019).

Here, a synthesis of existing observations from the tropical coastal and near coastal waters of East Africa (Tanzania and Kenya) is made to better understand the spatiotemporal variability of these waters and their response to monsoonal forcings. An examination of published scientific reports and of the extensive grey literature reveals a coherent picture of the biogeochemistry of the coastal Western Indian Ocean but one that is often based on scant information. The picture is therefore incomplete and whilst general descriptions of the seasonality and of the major physical forcing mechanisms of these waters have been around for 30 years or more (Wyrski, 1973; Bryceson, 1982; McClanahan, 1988), and with recognition of spatial variability in the productivity of coastal waters, including fisheries, extending back even further (Williams, 1956, 1958, 1963; Wickstead, 1961, 1962, 1963), biogeochemical observations remain uncommon and basic reports of many parameter distributions are limited, hard to find or even absent. Routine environmental sampling programmes are rare, even for water quality purposes, though there are areas of more regular sampling associated with local university or research centre activities (Mmochi et al., 2001). The region has though hosted many large international research programmes (e.g. Netherlands Indian Ocean Programme; NIOP) which collectively provide important insight and baseline observations of many processes and parameters. Whilst contemporary sampling efforts typically target coastal waters around the major urban areas and river networks routine sampling of the wider continental shelf including the North Kenya Banks, the largest regional extension to the continental shelf (Morgans, 1959), remains difficult.

2. The East African Coastal Current Ecoregion

The focus of this study is on that section of the East African coast permanently influenced by the East African Coastal Current, henceforth the EACC Ecoregion (Fig. 1). This region is reminiscent of the EACC hydrological region first described by Newell (1957, 1959) and the boundaries of this region (3–11°S) are comparable to the geographical

extent of the EACC along the African coast observed by Swallow et al., (1991). This region is more usually considered as part of the Somali Coastal Current Large Marine Ecosystem (Bakun et al., 1998; Sherman, 2005; Heileman and Scott, 2008), which stretches from the Comoros Islands (~10°S) to the easternmost tip of Africa (~12°N), or as part of the East African Marine Ecoregion, which extends from central Somalia (~2°N) to north-eastern South Africa (~27°S) (EAME, 2004). More recently the subdivision of the East African continental shelf into smaller discrete Marine Ecoregions has led to the area focussed upon here also being referred to as the East African Coral Coast or as part of the neighbouring North Monsoon Current Coast (Spalding et al., 2007). Recent research into coral diversity and biogeography patterns however argues for a redrawing of the boundaries between the Marine Ecoregions along the East African coast (Obura, 2012). There are also oceanographic grounds for the recognition of discrete sub-regions along the East African coast. The EACC ultimately forms from the bifurcation of the westward flowing Indian Ocean South Equatorial Current (SEC) at a point northeast of Madagascar (Swallow et al., 1991). This bifurcation produces the northeasterly and southeasterly flowing Madagascar Currents (NEMC and SEMC respectively). The SEMC flows south along eastern Madagascar whilst the NMEC continues westward reaching the African coast at ~11°S and turning northwards to become the EACC (Swallow et al., 1991; Manyilizu et al., 2016; Semba et al., 2019). Although exhibiting strong seasonality in response to monsoon forcing the EACC flows northwards year-round thus the EACC Ecoregion is directly and continually influenced by waters largely originating from the equatorial Indian Ocean (Semba et al., 2019). The coastline of Somalia and parts of northern Kenya are only seasonally influenced by the EACC and during the rest of the year they are strongly influenced by the southward flowing Somali Current bringing waters derived from the Arabian Sea (Schott and McCreary, 2001; Schott et al., 2009; Hood et al., 2017). This distinction between permanent or seasonal influence by the EACC forms the basis for the subdivision of the widely used Somali Coastal Current LME and the creation of the EACC Ecoregion. This region is distinct from the East African Coral Coast Marine Ecoregion described by Spalding et al (2007), though shares broad similarities.

Along the East African coast the EACC is recognisable as a distinct current up to 160–200 km (approximately 2° longitude) offshore and this broad current generally exhibits uniform surface velocities along the coast. Maximum velocities in excess of 1 m s⁻¹ associated with the main core of the current are usually found between 20 and 90 km offshore (Bell, 1969). Current velocities reduce to zero ~200 km offshore indicating the eastern boundary of the EACC and most of the transport associated with the EACC is typically restricted to the upper 400 m and occurs within 120 km of the coastline (Swallow et al., 1991). Closer to shore the influence of the EACC is weakened by coastal topography (Bell, 1969).

The EACC Ecoregion includes both continental shelf and deeper offshore waters. The continental shelf is narrow and ranges in width from <2 km to ~80 km. Extensions to the narrow shelf are evident at the North Kenya Banks (~3°S; Morgans, 1959; Obura, 2001), and in the vicinity of the islands of Unguja (also known as Zanzibar; ~6°S) and Mafia (~8°S), which are separated from the mainland by shallow channels <40 m deep and 20–40 km wide (Nyandwi, 2001; Masalu, 2008). Such extensions are important foci for artisanal and subsistence fishing which are restricted to the shallows. Pemba Island (~5°S) separated from mainland Tanzania during the early Miocene (~16 Ma (Stockley, 1942; Eames and Kent, 1955; Kent et al., 1971; Pickford, 2008) and remains separated by the deepwater Pemba Channel which is approximately 40 km wide and 800 m deep. The Pemba Channel is thus an important conduit bringing deeper ocean waters close to the coast.

3. Impact of the monsoon

The discovery of the monsoon winds is widely credited to Hippalus,

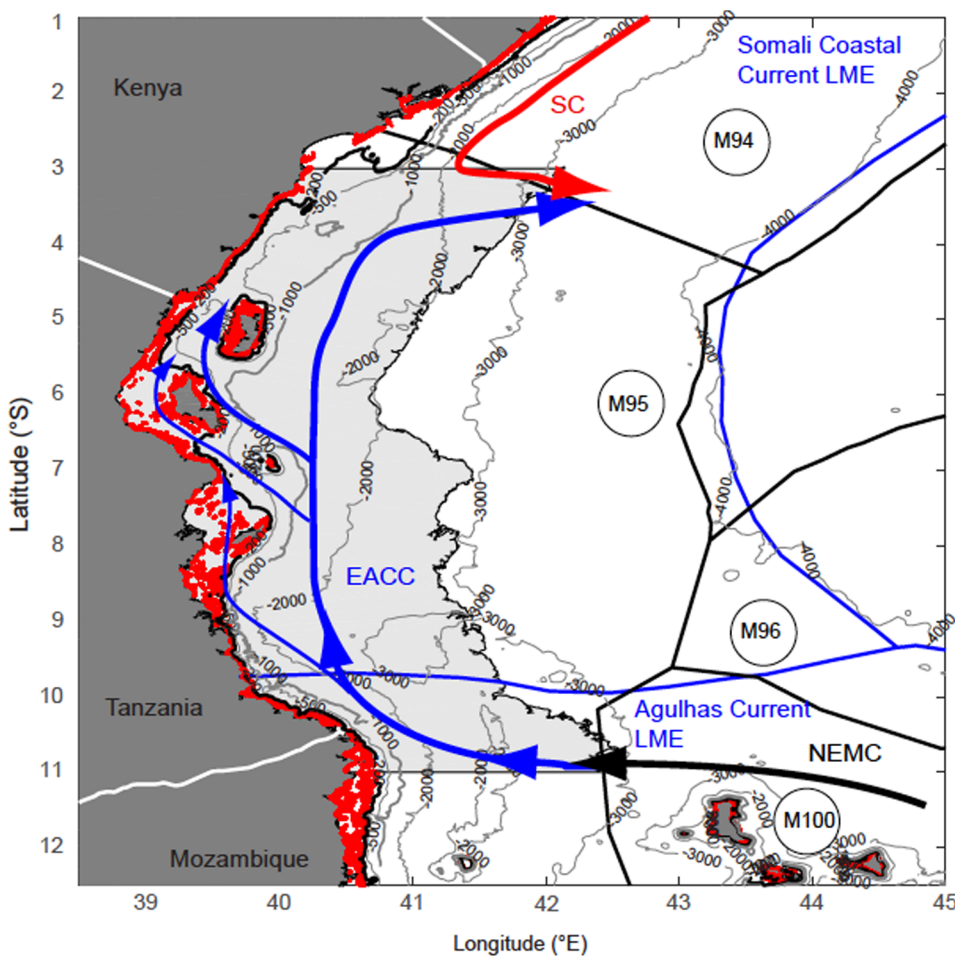


Fig. 1. Regional map showing the East African Coastal Current Ecoregion (3–11°S; light grey shading) during the NE monsoon period and boundaries between Large Marine Ecosystems (LME; blue boundary lines) and Marine Ecoregions of the World (black boundary lines) classification schemes. Major ocean currents shown include the North East Madagascar current (NEMC; thick black arrow), the East African Coastal Current (EACC; thick blue arrow) with suspected major (thick blue arrow) and minor pathways (thin blue arrows), and the Somali Coastal Current (SC; thick red arrow). Marine Ecoregions identified include Northern Monsoon Current Coast (M94), East African Coral Coast (M95), Seychelles (M96) and Western and Northern Madagascar (M100). Regional coral coverage (red dots) extracted from UNEP-WMC (2010), a global synthesis of warm-water coral distributions which includes contributions from (IMaRS-USF (Institute for Marine Remote Sensing-University of South Florida), 2005a; IMaRS-USF IRD (Institut de Recherche pour le Développement) 2005b) and Spalding et al., (2001). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

a Greek navigator from the first century BCE (Tripathi, 2011; Hatcher, 2013; Tripathi, 2017). This unique feature of the Indian Ocean is induced by the continental configuration of the Indian Ocean and the creation of a sea level atmospheric pressure gradient in response to differential heating of land and ocean and remains a major focus of current research efforts (Schott and McCreary, 2001; Schott et al., 2009; Hood et al., 2017). Cooling of the Asian continental landmass during boreal winter and simultaneous warming of south Indian Ocean establishes the NE monsoon with moderate northeasterly winds flowing along the pressure gradient from high pressure to low pressure regions. In contrast, warming of the Asian landmass and overlying atmosphere during boreal summer reverses the sea level pressure gradient and establishes the SE monsoon when strong southeasterly winds blow crossing the equator (Ramage, 1971; Hamilton, 1987).

An oceanographic consequence of the changing monsoon winds is the expansion and contraction of the EACC latitudinal range and the acceleration and deceleration of the EACC. During the SE monsoon (Jun-Oct) the EACC is accelerated and extends its range northwards across the equator to influence all of the Kenyan and much of the Somali coastline. During the NE monsoon months (Dec-Mar) downwelling is established over much of the Somali coastal region, the Somali Current flows southwards restricting the northern latitudinal extent of the EACC at the surface to 2–3°S. Where the EACC meets the Somali Current the currents turn eastwards into the Indian Ocean forming the South Equatorial Counter Current (Duing and Schott, 1978; Johnson et al., 1982). To the south the EACC weakens but does not reverse direction.

The seasonal alteration of high and low pressure atmospheric systems over Asia also has significant impacts on wind speeds and rainfall across the East African region (Okoola, 1999) and upon the upper ocean

more generally (McClanahan, 1988). Wind speeds and rainfall intensity are influenced by the seasonal movement of the Inter-tropical convergence zone (ITCZ) which moves northwards during the boreal summer and southwards during boreal winter (Galvin, 2008). The NE monsoon conventionally runs from Dec-Mar whilst the SE monsoon occurs between Jun-Oct, though the timing can and does vary depending upon location. The monsoon seasons are typically separated by periods of heavy rain, referred to as the long rains or “masika” (Apr-May) and short rains or “vuli” (Oct-Nov) (Johnson, 1962; Camberlin and Philippon, 2002; Conway et al., 2005; Nicholson et al., 2018). Passage of the ITCZ over the East African region coincides with these two significant rainfall seasons (Okoola, 1999). Atypical warming (cooling) of the sea surface, particularly in the equatorial region, can lead to significant flooding (drought) (Ntale et al., 2003), which can subsequently have an important impact on riverine discharges to near coastal waters (McClanahan, 1988; Nyandwi and Dubi, 2001). More recent research suggests that variability in East African rainfall is linked to the influence of both the Indian Ocean Dipole and the El Niño Southern Oscillation (Black et al., 2003; Black, 2005; Spencer et al., 2005); which are large scale cyclical temperature anomalies occurring in the Indian and Pacific Oceans respectively.

An indicative timing of the annual climatological conditions for Tanzania, which is broadly applicable to the EACC Ecoregion more generally is indicated in Fig. 2. Note that in Kenya (or in Somalia) the dominant wind direction between Jun and Oct is mainly from the SW whilst it is predominately from the SE along Tanzania (Heip et al., 1995), a distinction which can lead to some confusion in the literature (i.e. the SE and SW monsoon are one and the same).

During the NE monsoon mean monthly wind speeds are generally weaker (3–5.1 m s⁻¹) and air temperature is higher (> 30 °C) compared

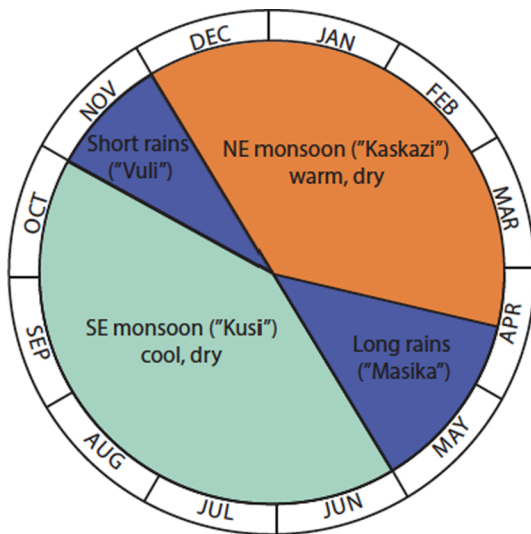


Fig. 2. The seasons of the EACC Ecoregion (redrawn from Bryceson, 1982).

to the SE monsoon when wind speeds are stronger ($3.7\text{--}6\text{ m s}^{-1}$) and air temperature is lower ($>25\text{ }^{\circ}\text{C}$) (Mahongo et al., 2011; ASCLME, 2012a). This generalization however masks significant spatial variability in the intensity and timing of seasonal wind speeds and along much of the Tanzanian coast mean monthly wind speed are $18\text{--}25\%$ stronger during the SE monsoon months (Dubé, 2001; Mahongo et al., 2011). The exception appears to be around Dar es Salaam where studies have found conflicting seasonality. Mahongo et al. (2011) found mean monthly wind speeds during the SE monsoon to be some 30% lower compared to wind speeds during the NE monsoon whilst Nyandwi (2013) reported a variation of 60% between seasons with mean wind speeds varying from 8 m s^{-1} during the SE monsoon to 5 m s^{-1} during the NE monsoon. In the vicinity of the Pemba Channel Semba et al. (2019) noted mean wind speeds of $4.86 \pm 1.56\text{ m s}^{-1}$ during the NE monsoon and $5.95 \pm 1.13\text{ m s}^{-1}$ during the SE monsoon, a seasonal difference of $\sim 20\%$. Along the Kenyan coast mean wind speeds in excess of 8 m s^{-1} occur during the SE monsoon months decreasing to an average of $\sim 4.3\text{ m s}^{-1}$ (range $3.5\text{--}5.5\text{ m s}^{-1}$) during the NE monsoon (Dec–Mar), a seasonal decrease of 47% (Government of Kenya, 2017). Mean monthly wind speeds reach annual minima of $1\text{--}1.5\text{ m s}^{-1}$ during the inter-monsoon months of May and November. These meteorological changes impact the upper ocean in several ways. SST typically varies from a maximum of $\sim 30\text{ }^{\circ}\text{C}$ during the NE monsoon to a minimum of $\sim 25\text{ }^{\circ}\text{C}$ during the SE monsoon. The strong southerly winds during the SE monsoon accelerate the EACC to typical velocities of $1\text{--}2\text{ m s}^{-1}$ (e.g. Swallow et al., 1991; Semba et al., 2019) and this, it is argued, aids flushing of the shallow sea channels across the region (Bryceson, 1982). Strong wind mixing deepens the mixed layer with the potential for entrainment of nutrients from depth whilst the vertical distribution of properties may also be modified by vertical mixing. The seasonal change in wind speed may also be important for larval dispersion patterns and inter-regional connectivity due to its influence on aspects of the regional circulation (e.g. Gamoyo et al., 2019). There is also an appreciable impact on beach erosion and sediment transport with a 30% increase in the average wave height from 0.9 m during the NE monsoon to 1.2 m during the SE monsoon months (Nyandwi, 2001).

Despite widespread generalisations of the prevailing climatic conditions within the EACC region important localised variations along the coastline of Tanzania and Kenya are now recognised (UNEP, 2001). In particular, the generalised occurrence of two rainy seasons becomes less accurate along the coast of southern Tanzania where a single longer rainy season between December and April is considered to be more accurate (UNEP, 2001). Whilst it is recognised that the state of

knowledge regarding environmental variability, including general patterns and frequency of rainfall events is lacking (ASCLME, 2012a), there is sufficient evidence to indicate a northwards increase in rainfall (UNEP, 2001) which suggests that the significance of riverine inputs to coastal biogeochemistry likely also changes northwards.

4. Regional hydrography and circulation

The initial hydrographic descriptions of these waters were presented by Newell (1957, 1959). Strong seasonal cycles in temperature in response to monsoonal forcing and the presence of a strong permanent thermocline were noted by Newell (1957, 1959) and are now widely recognised as characteristic features of the region but were only poorly understood at the time. A strong northerly current was noted year-round as was a slight shoreward deflection of the prevailing current which though suggestive of a downwelling regime was not specifically described as such by Newell (1957, 1959). One important conclusion of Newell's studies was that shallow shelf areas and coral reef systems – which line much of the East African coastline and which are important foci for fishing, separate the near coastal waters from the open ocean and play an important role as both habitats and barriers mitigating oceanic influences – are all bathed with the surface waters of the EACC and that cooler nutrient rich water from beneath the thermocline seldom reaches them.

Harvey (1977) updated the hydrographic description of Tanzanian waters and made the observation that monsoon driven variability is restricted to near surface waters predominately above the thermocline. A strong annual cycle in surface ($0\text{--}10\text{ m}$) temperatures was described ranging from $>29\text{ }^{\circ}\text{C}$ in Feb/Mar to $\sim 25\text{ }^{\circ}\text{C}$ in Jul/Aug due to the influence of the NE and SE monsoons. However, a longer-term decadal trend in temperature extending across the upper ocean was also identified which was attributed to interannual variations in heat penetration and which is now linked to coupled ocean-atmosphere processes (Spencer et al., 2005). Mean SST was found to increase by $1.4\text{ }^{\circ}\text{C}$ between 1957 and 1966 and decrease by $0.5\text{ }^{\circ}\text{C}$ from 1967 to 1972, whilst a weaker but similar interannual pattern was also identified at 125 m depth. In deeper offshore waters Harvey's (1977) analysis revealed the presence of a salinity maximum between 100 and 250 m depth and a salinity minimum at 500 m depth. Temperature decreased sharply between 100 and 250 m (main thermocline) but then more slowly thereafter. Surface waters ($<100\text{ m}$) were considered representative of the open Indian Ocean having been advected westwards by the South Equatorial Current.

Subsequent studies have largely confirmed and/or refined details of Newell's initial analysis yet despite the regional importance of the EACC the first detailed study of the transport associated with this current was only reported in the early 1990s (Swallow et al., 1991) and even by the mid-to-late 1990s information about the interlinkages of East African coastal ecosystems was considered very poorly known (Heip et al., 1995). Earlier ocean current observations reported by Leetmaa and Truesdale (1972) and Harvey (1977) revealed rapid current speeds within the EACC but no estimate of the transport was provided in either study. Leetmaa and Truesdale (1972) measured a maximum speed of $\sim 1.15\text{ m s}^{-1}$ during the NE monsoon east of Unguja Island whilst Swallow et al. (1991) observed a flow velocity closer to $\sim 2\text{ m s}^{-1}$ during the SE monsoon, comparable to the $1\text{--}2\text{ m s}^{-1}$ velocities reported by Newell (1957, 1959). Swallow et al. (1991) estimated a volume transport in the upper 500 m at $4\text{--}5^{\circ}\text{S}$ during the SE monsoon of 19.9 Sv , an observational based estimate that does not appear to have been refined since. Previously, Leetmaa et al. (1982) had estimated the EACC transport to be $\sim 13\text{ Sv}$ in the upper 100 m and $\sim 18.5\text{ Sv}$ in the upper 300 m using observational data collected between 1 and 3°S where the presence of the EACC is strongly seasonal. In the preliminary reports of the NIOP Heip et al. (1995) stated that the EACC transport may reach 65 Sv in the upper 200 m during the SE monsoon but it is unclear where or how this transport estimate was

derived. More recently Manyilizu et al (2016) modelled seasonality in ocean transport in the upper 1500 m which indicated typical mean monthly transports within the EACC of $\sim 30\text{--}40$ Sv but with a peak transport of ~ 40 Sv occurring in June during the SE monsoon and a minimum of $30\text{--}33$ Sv during the NE monsoon. Despite the utility of and wide reliance upon these general hydrographic descriptions observational evidence of the regional circulation remains limited, particularly for shelf regions and to some extent models are currently leading over observational efforts to understand the regional impact of the EACC.

Harvey (1977) noted that interpretations of the regional circulation were often based upon the presumption of a residual northwards flow induced by the broader northward movement of the EACC. Whilst a permanent northwards flow is well established for the EACC itself, Ngoile and Horrill (1993) noted that nearshore coastal waters are more likely to be influenced by tidal currents. Similarly, Obura (2001) noted that the fore reef and shallow inshore waters along the Kenyan coast were more likely to be influenced by terrestrial discharges and tidal flushing patterns with the EACC dominating the offshore waters. Nyandwi (2013) meanwhile highlighted the inaccuracy of presuming a residual northward flow influences the circulation of the shallow Zanzibar Channel. Using current measurements from a 2-year current meter deployment in the Zanzibar Channel Nyandwi (2013) found a northwards surface current flowing with a maximum mean speed of 0.26 m s^{-1} through the Zanzibar Channel during the SE monsoon but a reversed southwards surface current flowing with a maximum mean speed of 0.16 m s^{-1} during part of the NE monsoon. The current reversal was linked to the prevailing wind direction which was southwards during the NE monsoon. Nyandwi (2013) also noted that the maximum observed current speed within the Zanzibar Channel of 0.49 m s^{-1} was somewhat smaller than the maximum velocities of $1\text{--}2\text{ m s}^{-1}$ reported more generally for the EACC leading to the conclusion that no significant limb of the EACC funnels through the Zanzibar Channel. This conclusion was recently verified following analysis of 24-years of surface drifter trajectories which indicated that the shallow water Mafia and Zanzibar Channels were not conduits for drifters and thus were not directly flushed by the EACC whereas the deep water Pemba Channel most certainly was (Semba et al., 2019).

The analysis of surface drifter trajectories reported by Semba et al. (2019) also provided insight into the local circulation through the deep-water Pemba Channel. High northward current velocities in excess of 1.3 m s^{-1} were found in the central channel throughout the year but only during the SE monsoon, when the EACC is accelerated by southerly winds, is this evident as a continuous fast flowing current. Shallow waters on the margins of the Pemba Channel exhibited lower current velocities ($<0.8\text{ m s}^{-1}$), whilst overall the maximum current speed decreased by 22% from 1.73 m s^{-1} during the SE monsoon to 1.34 m s^{-1} during the NE monsoon.

Whilst in-situ observations are limited, numerical models have been successfully used to reveal further details of the regional circulation. Mahongo and Shaghude (2014) used the Regional Ocean Modeling System (ROMS) to better understand the dynamics of the EACC along the Tanzanian coast. They found that whilst the core of the EACC remains east (seaward) of the islands of Pemba, Unguja and Mafia branches of the EACC divert into and through the Zanzibar and Pemba Channels. The model results for the Zanzibar Channel seemingly disagree with (limited) observational efforts (e.g. Nyandwi, 2013; Semba et al., 2019), suggesting further work is required to clarify the path of the EACC through this channel. Mayorga-Adame et al. (2016) meanwhile identified two distinct coastal circulation regimes associated with the changing monsoon seasons along Tanzania and Kenya. During the NE monsoon, when the northward flow of the EACC is impeded by northeasterly winds, northward shelf flows are also reduced and in the shallow channels inshore of Mafia and Unguja Islands northwards transport can be obstructed by the shallow sill depths ($<40\text{ m}$). During the SE monsoon when the EACC is accelerated by southeasterly winds

there is strong northwards transport everywhere including through the shallow sea channels. A related modelling study by Zavala-Garay et al. (2015), which looked specifically at the circulation through the shallow Zanzibar Channel indicated that seasonal changes in the meridional (N-S) velocity through the channel were related to reversals of surface flows during the Dec-Feb period; a model result in keeping with observational data (Nyandwi, 2013). Supporting hydrographic observations from the SE monsoon period revealed the Zanzibar Channel to be well mixed with little variation in temperature ($\sim 26.2^\circ\text{C}$) or salinity (~ 35.3) with depth within the channel. The modelled transport through the shallow Zanzibar Channel during the NE monsoon of 0.029 Sv represented $\sim 1\%$ of the (model) estimated transport of the EACC east of the Zanzibar archipelago ($27.3 \pm 2.6\text{ Sv}$); a model result also in keeping with observational data (Semba et al., 2019). The model also indicated that the mean residence time for the Zanzibar Channel varied by a factor of 2 ranging from 40 days during the NE monsoon to 19 days during the SE monsoon. The ecological consequences of both the changing flow regime and the seasonal change in residence time are poorly known but sluggish flows through the shallow Mafia and Zanzibar Channels during the NE monsoon may potentially exacerbate the impact of thermal stress on neighbouring coral ecosystems whilst weaker seasonal flows have been implicated in the establishment of more neritic conditions and periods of higher marine productivity compared to the SE monsoon period (Bryceson, 1977, 1982).

Despite the EACC dominating the regional circulation there are clear emerging differences between the shallow shelf and deeper off-shelf areas which have yet to be fully resolved via observational efforts or described in more than general terms. Where models and observational studies agree however is that sea surface salinity generally decreases towards the coast due to riverine freshwater inputs and groundwater seepage which reduces the impact of the EACC on near coastal waters (Ngoile and Horrill, 1993; Obura, 2001; Mahongo and Shaghude, 2014). However, Zavala-Garay et al (2015) found seasonal decreases in surface salinity to be larger than expected from river inputs alone leading to speculation that low salinity water was also advected into the Zanzibar Channel by the EACC (with such water having a reduced salinity due to riverine inputs further south).

Observational reports of monsoon driven change to the mixed layer depth are limited. Harvey (1977) reported 2 distinct maxima and 2 minima throughout the year along the Tanzanian coast with the deepest MLD ($\sim 80\text{ m}$) occurring in July/August, whilst a shallower mixed layer depth of 30 m was found during March. Nguli (1995), working in Kenyan waters, also noted a seasonal oscillation in the mixed layer depth but found only 1 minima and 1 maxima. During the SE monsoon (June) the thermocline was located between 70 and 120 m and a homogenous nutrient poor layer was located above it. During the NE monsoon (Nov) Nguli (1995) found the thermocline to be 30 m shallower ($\sim 40\text{--}90\text{ m}$) with a $\sim 50\text{ m}$ shallow homogenous surface layer but nutrient concentrations were higher. The surprising contradiction of shallower mixed layer depths associated with higher nutrient concentrations during the NE monsoon was linked to increased riverine discharges which were observed to also reduce salinities at inshore stations (Nguli, 1995). Hartnoll (1974) reported a 2-fold variation in the mixed layer depth from $\sim 60\text{ m}$ during the NE monsoon to $\sim 130\text{ m}$ during the SE monsoon in the shelf waters near Kunduchi (north of Dar es Salaam at $\sim 6.7^\circ\text{S}$). The Argo based climatology of Holte et al (2017) suggests a comparable 2.8-fold variation in the mixed layer depth is also applicable in deeper offshore waters such as the Pemba Channel where the mixed layer varies from $\sim 24\text{ m}$ during the NE monsoon to $\sim 67\text{ m}$ during the SE monsoon (Fig. 3). Associated with this change in mixed layer depth is a pronounced change in the mean temperature and salinity of the mixed layer which decreases from 29.3°C to 25.5°C and from 34.95 to 35.62 g kg^{-1} respectively (Fig. 3). Consequently, fresher, warmer and lighter water is present in the Pemba Channel during the NE monsoon, whilst, cooler, more saline and denser water is present during the SE monsoon. ASCLME (2012a) reported a comparable

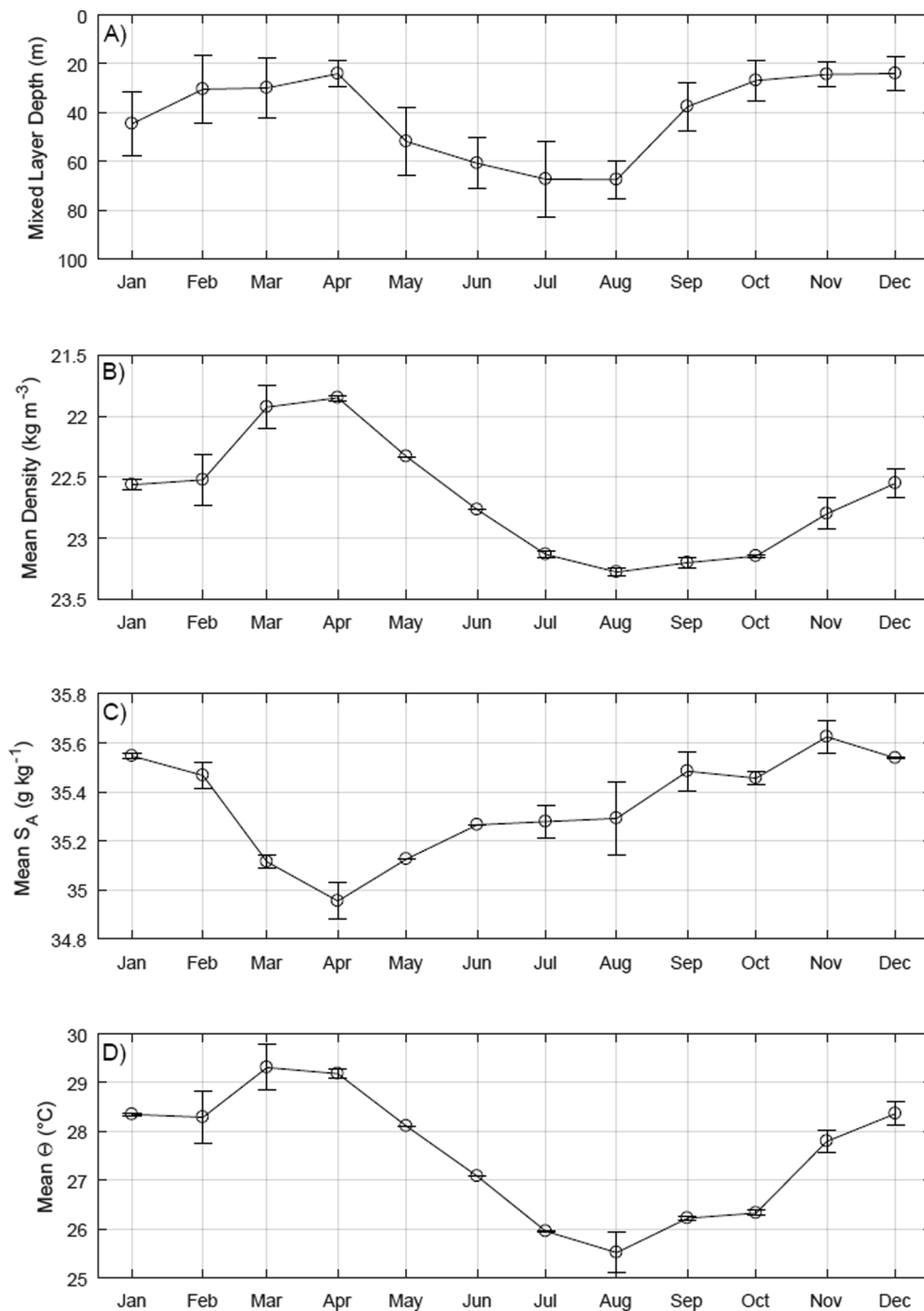


Fig. 3. Climatological annual cycle of (a) mean ($\pm$ s.d.) monthly mixed layer depth, (b) mean monthly mixed layer density, (c) mean monthly mixed layer absolute salinity and (d) mean monthly mixed layer conservative temperature for the Pemba Channel area (4.5–6.5°S, 38.5–40.4°E) based on the Argo mixed layer climatology of [Holte et al \(2017\)](#) and covering the period Jan 2000 – Apr 2018.

seasonal variation in surface salinity values along the Tanzanian coast with salinities generally lowest in May due to significant freshwater inputs and highest in November during the dry season. In addition to seasonal cooling, in situ entrainment, and riverine inputs explaining the observed changes in temperature and salinity [Manyilizu et al. \(2014, 2016\)](#) have argued that the hydrographic character of water along the Tanzanian coast is strongly linked to, and influenced by, the North East Madagascar Current with temperature and salinity changes along Tanzania mirroring those occurring north of Madagascar. [Swallow et al \(1991\)](#) previously anticipated this result when they argued that very little of the NEMC transport occurring in the upper 300 m of the ocean

north of Madagascar failed to enter the EACC.

5. Upwelling or downwelling regimes

Outside of the EACC Ecoregion strong wind-driven upwelling occurs along the Somalian coast during the SE monsoon and nutrient and chlorophyll concentrations, and zooplankton biomass are all elevated in the upwelling region ([Currie et al., 1973; Kampf and Chapman, 2016](#)). Within the EACC Ecoregion persistently low surface nutrient concentrations, a strong easterly component to the wind directions (i.e. onshore) and a consistent northerly flow of the EACC during both

monsoon periods have been cited as evidence for a permanent downwelling regime (Bell, 1966, 1969; McClanahan, 1988). Newell (1957) found strong persistent stratification along the East African coast and no evidence for mixing or upwelling of sub-thermocline waters to the surface. Similarly, Hartnoll (1974) stated that there was little or no evidence of upwelling or mixing between layers in the coastal waters of Kunduchi. From an ecological perspective the extensive fringing and patch reef complexes found along the coastlines of Tanzania and southern and central Kenya (Fig. 1), and which extend down to maximum depths of 45 m, though frequently shallower (Alusa and Ogallo, 1992; Wagner, 2000; Government of Kenya, 2017), are broadly indicative of a lack of persistent upwelling as the upwelling of cooler nutrient rich waters would negatively impact coral health, either directly through cooler water temperatures or indirectly through enhanced water column productivity and increased turbidity. As corals typically grow in water $>18^{\circ}\text{C}$ (Cohen, 1973; Lewis, 1981; Alusa and Ogallo, 1992), persistent upwelling of significantly cooler waters would likely impede coral growth in a detectable manner.

Nevertheless, evidence for short-lived or event-scale upwelling within the EACC Ecoregion is growing. Roberts (2015) suggested localised upwelling may occur north of Pemba Island induced by an island wake effect whilst Semba et al. (2019) noted that surface drifters were sometimes trapped in a permanent or semi-permanent eddy-like structure in the same area. Ochumba (1983) suggested that upwelling could be induced by eddies generated by islands or headlands interacting with the mean current flow. Upwelling indices meanwhile indicate favourable conditions for wind driven upwelling during the NE monsoon when northerly winds dominate and wind-driven Ekman transport would be (south)easterly offshore (Bakun et al., 1998). However, Bakun et al. (1998) also argued that such upwelling would be masked by the stronger downwelling effect induced during the SE monsoon. In essence strong downwelling during the SE monsoon depresses the nutricline/thermocline to depths deeper than wind induced upwelling can reach during the NE monsoon. Upwelling during the NE monsoon thus fails to entrain cooler nutrient rich waters but instead mixes shallower homogenous surface waters resulting in no appreciable surface signal. In contrast Jebri et al (submitted) recently reported that wind-driven upwelling could be identified in both biogeochemical

model and remote sensing datasets along much of Tanzania and Kenya during the NE monsoon. Upwelling may also be induced by the confluence and offshore movement of the EACC and Somali Current in the vicinity of the North Kenya Banks during the NE monsoon (Johnson et al., 1982; Jacobs et al., 2020). Confirmation of an upwelling effect is generally lacking from observational datasets but Jacobs et al. (2020) recently described short-lived wind-driven upwelling occurring during the NE monsoon in most years at the North Kenya Banks. Upwelling has also been reported in the equatorial region of the Western Indian Ocean in response to cross-equatorial winds as leading to high chlorophyll concentrations along the North Kenyan coast (Liao et al., 2017). Here, a combination of upwelled nutrients, deepening of the mixed layer north of the equator and subsequent southward advection of water during the NE monsoon was suggested to explain the presence of blooms at the North Kenya Banks (Liao et al., 2017).

The possibility exists therefore that interannual variability in the strength of the monsoon winds could be an important factor controlling upwelling intensity and thereafter phytoplankton productivity in this region. Under the Bakun et al. (1998) framework a weak SE monsoon with reduced vertical mixing followed by a strong NE monsoon with enhanced vertical mixing could lead to regionally significant periods of upwelling though far less intense than classically observed off Somalia and Oman. Interannual variability in the strength of the NE monsoon winds is also argued to drive variability in the position of the EACC/Somalia Current confluence zone thus shifting upwelling impacts latitudinally along the coast (Williams, 1963; Jacobs et al., 2020).

6. Rivers

Several large rivers drain from East Africa into the Indian Ocean. In Tanzania these include the Rufiji river ($\sim 7.8^{\circ}\text{S}$) with a mean annual discharge of $700\text{--}1200\text{ m}^3\text{ s}^{-1}$ and which alone is thought to account for 50% of all fresh water discharges from Tanzania, the Ruvuma river ($\sim 10.5^{\circ}\text{S}$; $475\text{ m}^3\text{ s}^{-1}$), the Wami river ($\sim 6.1^{\circ}\text{S}$; $\sim 60\text{ m}^3\text{ s}^{-1}$), the Ruvu river (6.38°S , $\sim 60\text{ m}^3\text{ s}^{-1}$) and the Pangani river (5.4°S , $27\text{ m}^3\text{ s}^{-1}$) (UNEP, 2001; ASCLME, 2012a) (Table 1). The Pangani river discharges directly into Pemba Channel, the Rufiji river discharges close to Mafia Island, whilst the Wami and Ruvu rivers discharge into Zanzibar

Table 1

Selected major rivers and mean annual discharges for the EACC Ecoregion. Timing of high and low flow taken from ^a Scheren et al (2016), ^b Anon (2008), ^c GLOWS-FIU (2014), ^d Global river discharge database (<https://nelson.wisc.edu/sage/data-and-models/riverdata/index.php>; last accessed 02/04/2019)

Country	River	Mouth ($^{\circ}\text{S}$)	Mean Annual Discharge ($\text{m}^3\text{ s}^{-1}$)	High flow month ^a	Low flow month ^a	Discharges to	Source
Tanzania	Ruvuma	10.5	475	Feb	Aug	Indian Ocean	ASCLME, 2012a
	Rufiji	7.8	~ 700 900–1133 ~ 1200 1100 950 820	Apr	Nov	Mafia Channel	UNEP, 2001 ASCLME, 2012a UNEP, 2015 UNEP / WIOMSA, 2009 UNEP / WIOMSA, 2009 Global River Discharge Database ^d
	Wami	6.1	~ 100 63	Apr ^b	Oct ^b	Zanzibar Channel	UNEP, 2001 ASCLME, 2012a
	Ruvu		43 63 65	May ^c	Oct ^c	Zanzibar Channel	UNEP, 2001 ASCLME, 2012a Global River Discharge Database
	Pangani	5.4	20 27	May	Sep	Pemba Channel	UNEP, 2001 ASCLME, 2012a; UNEP / WIOMSA, 2009
Kenya	Tana	2.6	150 230 285 156	May	Aug	North Kenya Banks / Indian Ocean	Kitheka and Ongwenyi, 2002 Kitheka et al., 2005; UNEP / WIOMSA, 2009 ASCLME, 2012b Tamooch et al., 2012; Government of Kenya, 2017
	Athi-Galana-Sabaki	3.2	73 50 63	Apr	Sep	Indian Ocean	UNEP / WIOMSA, 2009 UNEP / WIOMSA, 2009 Government of Kenya, 2017

Table 2

Water masses and suggested characteristics for the East African region of the Western Indian Ocean. Data from ¹ ASCLME (2012); ² UNEP (2001); ³ <http://dpo.cusat.ac.in/msc/ocee201/slides/unit2/Indian.pdf> (last accessed 15/12/2018); ⁴ Emery (2001); ⁵ Newell (1959); ⁶ Hartnoll (1974); ⁷ Iversen et al. (1984); ⁸ Rao and Griffiths (1998); ⁹ Emery and Meincke (1986); ¹⁰ Bell (1966).

Water Mass	Depth Range / Season	Temperature (°C)	Salinity (PSS-78)	Oxygen	Source
Surface Water	<100	22–30	<34.5	–	[2, 7]
East African Coastal water	<100	25–30	–	–	[10]
Tropical Surface Water	–	–	High	High	[1, 6]
	0 - thermocline	high	low	high	[5]
High Salinity Water	150–250	18–19	>35.4	–	[7]
Arabian Sea Water	–	–	High	Low	[1, 6]
	Thermocline – 240	–	high	low	[5]
	150–250	–	–	–	[2]
	0–500	24–30	35.5–36.8	–	[4, 8, 9]
Persian Gulf Water (PGW)	–500	–	–	–	[3]
	Summer	30–35	36.4–42	–	[8]
	Winter	14–15	36.4–42	–	[8]
	Winter	23	40	–	[8]
Red Sea – Persian Gulf Intermediate Water	500–1500	5–14	34.8–35.4	–	[4, 8, 9]
Red Sea Water (upon entering Indian Ocean)	–	22	38.0–40.0	–	[8]
Antarctic Intermediate Water (AAIW)	–	–	Low	High	[1, 6]
	>240	low	low	–	[5]
	500–1500	2–10	33.8–34.8	–	[4]
		2–10	33.8–34.6	–	[8, 9]
Indian Ocean Central Water	250–500	<18	–	–	[2]
	<1000	8–15	34.6 – 35.5	–	[3]
	250–500	<18	<35.4	–	[7]
	0–500	8–25	34.6–35.8	–	[4, 9]
Indian Equatorial Water	200–2000	4–17	34.9–35.2	–	[3]
	0–500	8–23	34.6–35	–	[4, 8, 9]
North Indian Deep Water	–	–	High	Low	[1, 6]
Indian Ocean Deep Water	500–3000	>2–12	High	–	[10]
Circumpolar Deep Water	–	0.1–2	34.62–34.73	–	[8, 9]

Channel. All rivers are strongly affected by the monsoon seasons with peak flows in April/May during the long rains intermonsoon period. Riverine impacts on coastal waters can be varied and freshwater influences are often spatially limited being dependent upon river discharge volumes and the circulation of near coastal waters. However, Nyandwi and Dubi (2001) observed short-lived but extreme changes in temperature and salinity along the coast of Tanzania following the onset of heavy rains in May 1998. The above average rainfall during this time, which was linked to the 1998 El Nino event, resulted in significant sediment discharge from many rivers to neighbouring tidal flats which trapped river waters close to the shore. As a result, near coastal temperatures and salinities decreased substantially compared to normal conditions.

In Kenya the Tana River (~2.5°S) discharges, via its extensive delta, almost directly onto the North Kenya Banks making this river a major focus of research efforts due to perceived impacts of riverine sediments on coastal productivity (Kitheka, 2002; Kithika et al., 2005; Fulanda et al., 2011). Mengesha et al (1999) however observed no significant influence by the Tana river discharge on coastal nutrient distributions. This may either be due to the timing of this particular study (June–July and Nov–Dec) or more likely due to the Tana's influence being greatly restricted to the delta and near coastal waters and having limited impact across the wider continental shelf. The Tana river watershed occupies ~23% (132,000 km²) of the total land area of Kenya and contributes ~32% of Kenya's total river runoff (Kitheka and Ongwenyi, 2002). The mean annual discharge is ~150 m³ s⁻¹ but varies from <10 m³ s⁻¹ during the dry seasons to >2000 m³ s⁻¹ during the wet season (Kitheka and Ongwenyi, 2002). Significant sediment load is carried by the Tana with high sedimentation rates along the coast generally assumed to explain the lack of coral reef complexes within Ungwana Bay (McClanahan and Obura, 1997; Kithika, 2002, 2013), the coastal embayment receiving water from the Tana river (Fig. 1). The reduction of coral coverage has also been linked to mangrove forest destruction which reduces sediment trapping efficiencies resulting in increased terrestrial sediment flux to, and increased turbidity in, coastal

waters (Kitheka and Ongwenyi, 2002). Heip et al. (1995) noted that despite considerable silt discharge occurring during the rainy seasons from the Tana and the nearby Galana-Sabaki rivers the quantity and fate, and therefore impact, of this material was largely unknown. More recent research has addressed some of these unknowns. The annual sediment flux from the Tana river to the coastal ocean is estimated to range from 3×10^9 kg yr⁻¹ (Syvitski et al., 2005) to 6.8×10^9 kg yr⁻¹ (Kitheka et al., 2005). Bouillon et al. (2007) independently estimated an annual flux of 3.2×10^9 kg yr⁻¹ and argued that the higher estimate reported by Kithika et al (2005) may have been biased by analysis of a short 1.5-year time-series. At an upstream location Geeraert et al (2015) reported annual sediment fluxes for 2009–2013 that ranged from 3.5 to 8.8×10^9 kg yr⁻¹ yet whilst this range encompasses the sediment flux of Kithika et al (2005), these upstream flux estimates cannot be used to infer sediment fluxes to the coastal zone due to significant retention, recycling and remineralization of terrestrially derived material in the lower riverine and estuarine system (Bouillon et al., 2007, 2009). As to the fate of any sediment reaching the coastal zone Brakel (1984) found that sediment plumes from the Tana and Athi-Sabaki rivers were typically advected northwards along the coast and away from the river mouths during the SE monsoon and southwards during the NE monsoon months. There was limited indication that sediments derived from the Tana river influence the outer shelf of the North Kenya Banks, a region where higher chlorophyll concentrations are observed and, pending in-situ confirmation, where higher productivity is assumed. It is most likely therefore that enhanced productivity over the outer shelf originates from oceanic influences and wind-driven or shelf-break upwelling.

7. Water masses

Hydrographic investigations of the EACC Ecoregion are limited but the general characteristics have been known for some time (Newell, 1957; Bell, 1966). Nguli (1995) identified five water masses along the Kenyan coast consisting of (i) Arabian Sea Water, (ii) Subtropical

Surface Water (shallow), (iii) Red Sea Water, (iv) Subtropical Surface Water (deep), and (v) Intermediate Antarctic Water, stating that they compared favourably to similar water masses discussed by Tomczak and Godfrey (1994). Hartnoll (1974) and ASCLME (2012a) drawing upon earlier work by Newell (1957, 1959), both identified four water masses along the Tanzanian coast. These were (i) Tropical Surface Water, (ii) Arabian Sea Water, (iii) Antarctic Intermediate Water and (iv) North Indian Deep Water (Table 2). In contrast, Iversen et al. (1984) and UNEP (2001) list only 3 water masses which they refer to as (i) Surface Water, (ii) High Salinity Water or Arabian Sea Water and (iii) Indian Ocean Central Water. The discrepancy between these studies off Tanzania is due to differences in sampling depth with Iversen et al. (1984) being restricted to 500 m and the UNEP (2001) summary being based on the results of Iversen et al. (1984). In contrast, Emery (2001) indicates that Indian Equatorial Water is likely the dominant surface (0–500 m) water mass found along Tanzania and Kenya. Between 500 and 1500 m Red Sea-Persian Gulf Intermediate Water, with a prominent salinity maximum, is more likely to be found than Antarctic Intermediate Water which has a salinity minimum (Table 2). At depths greater than 1500 m Emery (2001) indicates the Indian Ocean is filled with Circumpolar Deep Water. There are then some inconsistencies in the knowledge of regional hydrography close to the East African coast. Repeat hydrographic sections within the WIO are currently limited to line I07 (nominally along 55°E) under the GO-Ship programme with this line last occupied in 2018. Observations closer to or within the EACC Ecoregion are not planned under GO-Ship but during the earlier WOCE programme hydrographic line I02 undertook observations between 4 and 5°S from the coast out to ~45°E.

As the current information about water masses seems incomplete or at the very least inconsistent and as modern repeat hydrographic sections are not optimally placed for the purposes of clarifying water mass identity in the region of interest an analysis of hydrographic profiles from the World Ocean Database was undertaken (WOD; (Boyer et al., 2013)). In total 239 profiles were extracted and examined with these profiles covering the shelf and deeper offshore waters of the EACC Ecoregion (Fig. 4). Maximum sampling depths varied from 14 to 3000 m and the observations cover the period 1913–1996. Water properties ranged from an average temperature of 27.4 °C and salinity of 35.0 at the surface (0–10 m) to 1.4 °C and 34.7 at 3000 m. There is considerable near surface (0–10 m) scatter with salinities ranging from 34.37 to 35.67 and temperatures ranging from 24.6 to 30.03 °C. Despite being collected in different years, in different monsoon seasons and over different depth ranges the T-S profiles are broadly consistent (Fig. 5). Superimposed onto Fig. 5 is the mean T-S profile (0–3000 m) based on depth bin-averaging of the WOD13 observations. This is supplemented with the mean T-S profile for the EACC reported by Schott and McCreary (2001). The two mean profiles are very similar. Also included in Fig. 5 are the conventional limits of core water masses for the Western Indian Ocean (Table 2). Whilst a typical inventory of four core water masses is approximately correct for the EACC region, the conventional definitions have overlapping T-S characteristics which may lead to confusion (Fig. 5). The occasional appearance of a further two water masses is also evident suggesting that four water masses is perhaps not correct. The core water masses include (i) Circumpolar Deep Water, (ii) Red Sea – Persian Gulf Intermediate Water, (iii) South Indian Central Water and (iv) Tropical Surface Water. The additional water masses include Antarctic Intermediate Water which was observed in the southern areas of the EACC Ecoregion and Arabian Sea Water which was observed in the north, though neither appears common.

Whilst indicative temperature and salinity ranges for each water mass exist (Table 2; Fig. 5) (Emery and Meincke, 1986; Emery, 2001) these can vary regionally due to mixing. There do not appear to be corresponding summaries of the typical oxygen or nutrient concentrations for these same water masses specifically for the EACC Ecoregion. Based on Fig. 5 and on a simple separation of water masses along isopycnal lines this indicative information is provided in Table 3.

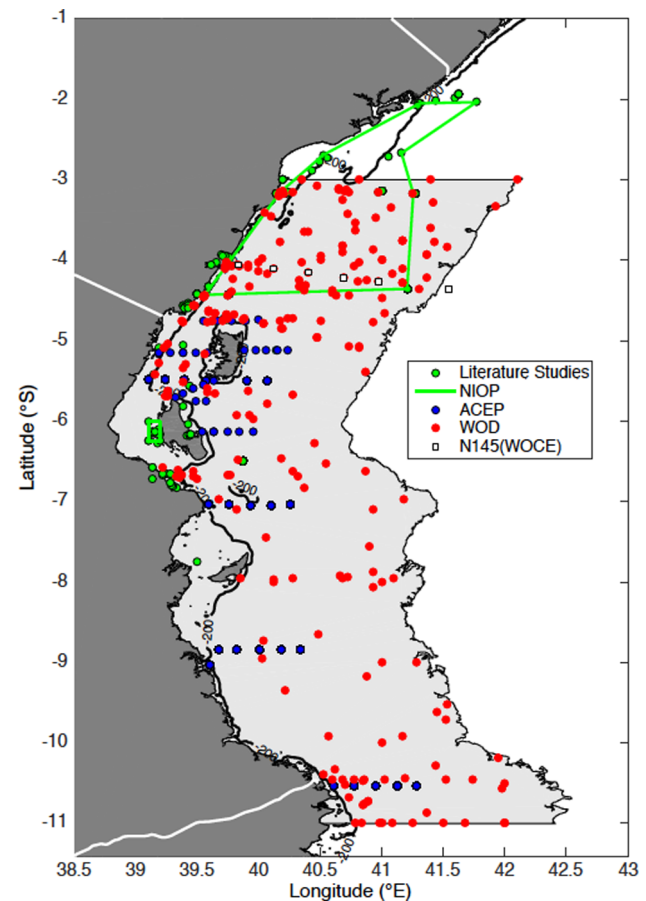


Fig. 4. Summary map showing the distribution of hydrographic and biogeochemical data identified for the EACC Ecoregion. Major programmes indicated include the Netherlands Indian Ocean Programme (NIOP; green polygon), the African Coelacanth Ecosystem Programme (ACEP; blue dots), the World Ocean Database (WOD; red dots) and the World Ocean Circulation Experiment (cruise N145; white squares). Literature data contributing to Tables 5, 6 and 10 are indicated by the green circles. The small green rectangle indicates the study site of Zavala-Garay et al. (2015) Biogeochemical sampling positions during ACEP and NIOP are not explicitly indicated here. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

This isopycnal based separation reveals a warm surface water mass (~0 m-thermocline; Tropical Surface Water; $<24.4 \text{ kg m}^{-3}$) with a mean temperature of 26.3 °C and a salinity of 35. This surface water mass is oxygen rich but nutrient poor and occupies the water column above the thermocline (which varies from ~60 m during the NE monsoon to ~130 m during the SE monsoon; Hartnoll, 1974). Note however that nitrate measurements within this density interval vary widely leading to a comparatively high mean concentration. Beneath this is a prominent salinity maximum, which typically peaks between 150 and 200 m depth. Morales et al. (1996) working near the raised coral atoll of Aldabra (9.42°S, 46.3°E), and thus upstream of the EACC proper, associated this salinity maximum with Subtropical Surface Water (SSW; $24.4\text{--}26.2 \text{ kg m}^{-3}$) a water mass formed within the subtropical gyre of the Southern Indian Ocean. SSW has a mean temperature of 18.1 °C, a mean salinity of 35.3 and a mean oxygen concentration 25% lower than observed in TSW. Nutrient concentrations have however increased substantially as this water mass is beneath the permanent thermocline. Beneath SSW lies South Indian Central Water (SICW; $26.2\text{--}27.2 \text{ kg m}^{-3}$) with a characteristically linear T-S distribution. Temperatures range from 5.8 to 15.7 °C and salinity from 34.47 to 35.6, values which are comparable to conventional definitions (Table 2). The mean oxygen concentration of $155 \mu\text{mol kg}^{-1}$ in SICW is

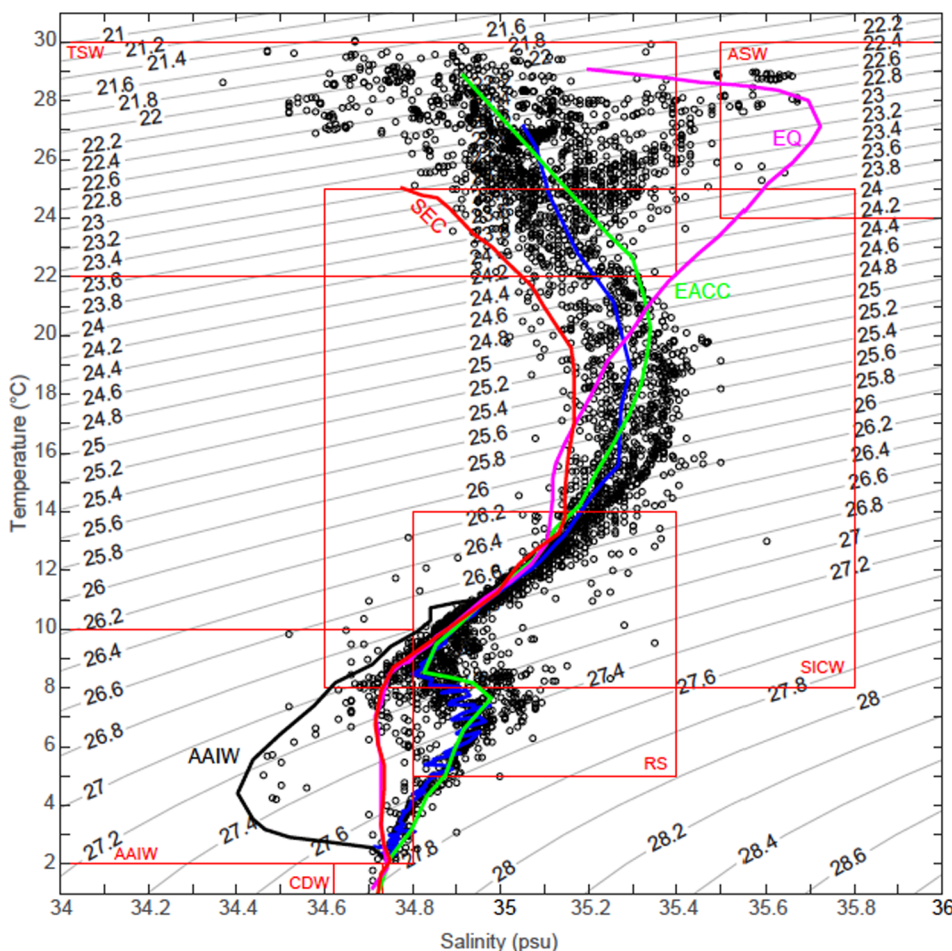


Fig. 5. Temperature-Salinity diagram of World Ocean Database (WOD13) observations for the EACC Ecoregion (open circles) with a mean profile (blue line) based on 20 m depth bin averaging of all observations. Conventional limits of core water masses are indicated by the red boxes and represent Circumpolar Deep Water (CDW), Antarctic Intermediate Water (AAIW), Red Sea Water (RS), Southern Indian Central Water (SICW), Arabian Sea Water (ASW) and Tropical Surface Water (TSW). Water mass limits are based on summaries by Iversen et al. (1984), Rao and Griffiths (1998), and Emery (2001). Mean TS lines for AAIW (black line), the Southern Equatorial Current (SEC; red line), the equatorial region of the western Indian Ocean basin (EQ; magenta line), and the East African Coastal Current (EACC; green line) are digitized and approximated from Fig. 7 of Schott and McCreary (2001). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

similar to that of SSW ($152 \mu\text{mol kg}^{-1}$) but with nitrate and silicate concentrations of $\sim 20 \mu\text{mol kg}^{-1}$ nutrient concentrations are roughly twice as high as found in SSW. A discontinuity in the T-S profile indicates the presence of Red Sea-Persian Gulf Water (RSPGW; $27.2\text{--}27.7 \text{ kg m}^{-3}$), a cool and saline water mass found at a mean depth of $\sim 1000 \text{ m}$. RSPGW is also oxygen poor ($82.7 \mu\text{mol kg}^{-1}$) but rich in nutrients. Finally, at depths between 1500 and 3000 m Circumpolar Deep Water (CDW; $> 27.7 \text{ kg m}^{-3}$) is observed. CDW is comparatively rich in oxygen ($144.2 \mu\text{mol kg}^{-1}$) and silicate ($116 \mu\text{mol kg}^{-1}$) compared to overlying water masses but is also cold and fresh.

In summary, five water masses would seem to be more indicative of the EACC region than the four usually assumed (e.g. Hartnoll, 1974), though the distinction between TSW and SSW is subtle and arguably subjective. These five water masses extend from the sea surface to 3000 m. This increase by one in the total number of water masses is due to previous identification efforts using set T-S ranges which are predominately based on observations from the open WIO or central Indian Ocean regions without consideration of the effects of mixing which can alter the T-S characteristics locally or of local circulation which can draw water northwards from the southern subtropical gyre.

The general distribution of water masses along the Tanzanian and Kenyan coasts has been broadly understood for several decades but the region remains undersampled within the context of modern repeat hydrographic programmes. A broad consensus for the number and depth distribution of different water masses exists for extant hydrographic studies for the upper ocean. However, differences in maximum sampling depth hinder direct comparison between studies and observations below 2000 m are limited. There is insufficient data to evaluate temporal variability in water mass distributions or properties and consequently the hydrographic nature of the water column appears

stable in time. Near surface waters experience well understood monsoon driven fluctuations in temperature and salinity but relationships between hydrographic changes in near coastal surface waters and far-field influences advected into the region remain poorly described.

8. Regional biogeochemistry

8.1. Nutrient observations

The World Ocean Database 2013 (WOD13) contains 239 stations lying within the geographical limits of the EACC Ecoregion (Fig. 4). These stations cover the period 1909–1996 yet the temporal distribution of observations is skewed with 148 stations sampled between 1960 and 1980 and 73 stations sampled between 1980 and 1996. Data from more recent decades is absent. The dataset provides reasonable spatial coverage of the EACC Ecoregion but not all nutrients were measured at each station or at all sampled depths. Despite such shortcomings there is a usable quantity of data with which to broadly characterise these waters. Fig. 6 summarises the upper 200 m of the EACC Ecoregion. Reported nutrient concentrations show large variabilities with increased variability at depth. All results consistently show reduced nutrient concentrations in surface waters and an increase in concentration with depth. There is a nutricline at $\sim 70 \text{ m}$ depth. Characteristic mean annual conditions for the EACC Ecoregion are reported in Table 4 which is based on a simple 20 m vertical bin-averaging of the available data. This indicates typical surface nutrient concentrations of 0.21 ± 0.25 , 0.18 ± 0.08 and $3.67 \pm 1.69 \mu\text{mol L}^{-1}$ for NO_3^- , PO_4^{3-} and Si respectively, an average SST of $27.2 \pm 1.3^\circ\text{C}$ and a typical salinity of 35.04 ± 0.22 . Whilst these results are broadly indicative of mean annual conditions the presence of significant monsoon driven

Table 3
Mean water mass properties (range in brackets) based on isopycnal separation of water masses found in the EACC Ecoregion. Analysis based on World Ocean Database 2013 (WOD13).

Water Mass	Isopycnal range - σ (kg m^{-3})	Temp ($^{\circ}\text{C}$)	Salinity (pss-78)	Oxygen ($\mu\text{mol kg}^{-1}$)	Nitrate ($\mu\text{mol kg}^{-1}$)	Phosphate ($\mu\text{mol kg}^{-1}$)	Silicate ($\mu\text{mol kg}^{-1}$)
Tropical Surface Water (TSW)	< 24.4	26.34 (21.49–30.03)	35.07 (34.37–35.67)	201.21 (133.44 – 250.98)	1.2 (0.03–8.01)	0.22 (0.02–0.75)	4.08 (0.98–13.68)
Subtropical Surface Water (SSW)	24.4–26.2	18.08 (13.16–22.21)	35.29 (34.79–35.5)	151.96 (109.7–223.64)	11.48 (0.78–18.91)	0.8 (0.19–1.27)	11.41 (3.22–26.43)
South Indian Central Water (SICW)	26.2–27.2	10.87 (5.76–15.7)	34.98 (34.47–35.6)	154.95 (57.83–213.15)	19.31 (6.92–34.66)	1.35 (0.29–2.64)	21.03 (4.29–54.52)
Red Sea Water (RSW)	27.2–27.7	6.11 (2.59–9.58)	34.89 (34.46–35.35)	82.65 (45.21–167.45)	33.23 (18.4–42.54)	2.5 (1.65–3.02)	77.73 (50.62–142.07)
Circumpolar Deep Water (CDW)	> 27.7	2.69 (1.65–3.2)	34.76 (34.71–34.9)	144.22 (131.23–196.41)	27.71 (21.31–38.24)	2.37 (2.1–2.58)	115.98 (105.09–125.52)

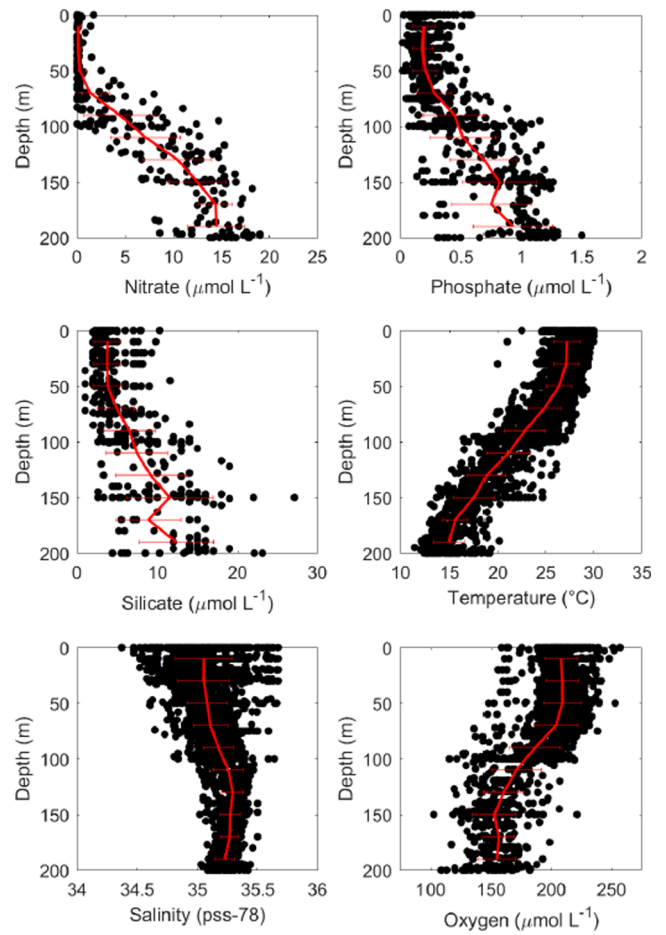


Fig. 6. WOD13 observations of (a) nitrate, (b) phosphate, (c) silicate, (d) temperature, (e) salinity and (f) dissolved oxygen for the EACC Ecoregion over the 0–200 m depth range. Red curves are 20 m depth bin averaged mean profiles with standard deviations presented for each depth bin. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

seasonality in these waters must be recognised (McClanahan, 1988). This seasonality is not clearly evident in the WOD nutrient dataset. The hydrographic data however does exhibit the seasonality discussed by Newell (1959), Bryceson (1982) and McClanahan (1988). Fig. 7 presents mean annual cycles of physicochemical parameters based on monthly averaging of WOD13 data over the upper 50 m of the water column; a depth chosen to represent the upper ocean away from the nutricline. Monthly mean nitrate concentrations are typically in the range 0.1–0.2 $\mu\text{mol L}^{-1}$. The substantial increase to $\sim 1.6 \mu\text{mol L}^{-1}$ in December appears atypical and originates from a single station conducted in 1929 during the Dana Expedition (Schmidt, 1931). Phosphate concentrations are more stable across the year ranging between 0.14 and 0.24 $\mu\text{mol L}^{-1}$. Silicate concentrations range from 2.2 to 5.4 $\mu\text{mol L}^{-1}$ across the year and appear to be lowest during April–May ($< 3 \mu\text{mol L}^{-1}$), a time of significant rainfall regionally (ASCLME, 2012a), and highest in October ($> 5 \mu\text{mol L}^{-1}$). This pattern is comparable to that reported by Wallberg et al (1999) who observed higher silicate concentrations in August ($2.61 \pm 0.66 \mu\text{mol L}^{-1}$) compared to April ($1.35 \pm 0.58 \mu\text{mol L}^{-1}$) around Unguja Island. A strong seasonal cycle is evident in the temperature data with highest temperatures ($> 28^{\circ}\text{C}$) between February and May (NE monsoon), and lowest between August and October ($\sim 25^{\circ}\text{C}$; SE monsoon). Salinity shows a pronounced seasonal cycle with lowest monthly salinities during Feb–June (34.78–34.98) and highest salinities in December/January (> 35.3). Dissolved oxygen concentrations also show a seasonal cycle with

Table 4

Mean annual conditions in the upper 200 m of the EACC Ecoregion as derived from data held within the World Ocean Database.

Interval (m)	Mid bin depth (m)	Nitrate ($\mu\text{mol L}^{-1}$)	Phosphate ($\mu\text{mol L}^{-1}$)	Silicate ($\mu\text{mol L}^{-1}$)	Temp ($^{\circ}\text{C}$)	Salinity (pss-78)	Oxygen ($\mu\text{mol L}^{-1}$)
0–20	10	0.21 ± 0.25	0.18 ± 0.08	3.67 ± 1.69	27.2 ± 1.4	35.05 ± 0.24	207.42 ± 12.65
20–40	30	0.22 ± 0.3	0.18 ± 0.08	3.74 ± 1.67	27.1 ± 1.3	35.05 ± 0.21	208.86 ± 13.12
40–60	50	0.56 ± 0.98	0.2 ± 0.1	3.82 ± 1.86	26.4 ± 1.3	35.08 ± 0.17	208.97 ± 15.46
60–80	70	1.65 ± 2.12	0.27 ± 0.14	4.92 ± 2.22	24.8 ± 1.7	35.11 ± 0.14	203.42 ± 18.22
80–100	90	4.64 ± 3.67	0.44 ± 0.25	6.5 ± 3.26	22.8 ± 2.1	35.17 ± 0.13	186.05 ± 21.23
100–120	110	7.11 ± 3.62	0.51 ± 0.27	7.44 ± 3.86	21.1 ± 2.3	35.26 ± 0.12	170.62 ± 20.65
120–140	130	10.43 ± 3.57	0.69 ± 0.28	9.17 ± 4.42	18.9 ± 2	35.29 ± 0.09	160.09 ± 16.45
140–160	150	12.5 ± 2.94	0.82 ± 0.31	11.55 ± 5.43	17.5 ± 2.1	35.27 ± 0.08	152.23 ± 18.23
160–180	170	14.38 ± 1.74	0.75 ± 0.33	8.89 ± 4.02	15.6 ± 1.3	35.27 ± 0.08	155.86 ± 13.1
180–200	190	14.46 ± 2.99	0.93 ± 0.33	12.36 ± 4.66	14.9 ± 1.6	35.23 ± 0.08	154.31 ± 15.93

monthly mean concentrations tending to be lower ($\sim 205 \mu\text{mol L}^{-1}$) between February and June and higher ($> 220 \mu\text{mol L}^{-1}$) between July and October, a pattern that is strongly linked to coincident changes in temperature (Fig. 7).

Based on a regression between all coincident observations of NO_3^- and PO_4^{3-} the WOD dataset indicates a mean $\text{NO}_3^-:\text{PO}_4^{3-}$ of 13.89 for the region, which is indicative of a predominately N-limited system (e.g. Tyrrell, 1999). In near surface waters however the extent of N limitation may be greater with mean annual nutrient concentrations (Table 4) suggesting a $\text{NO}_3^-:\text{PO}_4^{3-}$ for these waters as low as ~ 1.1 and a typical $\text{NO}_3^-:\text{Si}$ of ~ 0.06 . There is weak seasonality and low $\text{NO}_3^-:\text{PO}_4^{3-}$ conditions ($< 2:1$) persist from January to November with a possible increase to ~ 6.5 in December; a result again driven by a single station. Persistently low $\text{NO}_3^-:\text{PO}_4^{3-}$ conditions are compatible with the widespread presence of diazotrophy in these waters (e.g. Lugomela et al., 2002) and the largely unchanged stoichiometry throughout the year implies limited vertical mixing.

Additional cruise data sources include nutrient data from R.V. Knorr cruise 316N145_15 (WOCE cruise, January 1996), R.V. Algoa cruises ALG130 (August 2004) and ALG160 (October 2007) conducted as part of the African Coelacanth Ecosystem Programme (ACEP) (Fig. 4). Data from these cruises were extracted for the EACC Ecoregion and averaged over the upper 50 m, as for the WOD13 data. For the R.V. Knorr cruise, which transected the northern part of the EACC Ecoregion at approximately 4.2°S (Fig. 4), we obtained very comparable estimates of nitrate and silicate concentrations for January compared to the WOD13 based January mean (0.12 ± 0.04 vs $0.19 \pm 0.14 \mu\text{mol L}^{-1}$ for NO_3^- ; 3.0 ± 0.54 vs $2.58 \pm 0.67 \mu\text{mol L}^{-1}$ for Si). PO_4^{3-} concentrations were slightly lower (0.15 ± 0.01 vs $0.20 \pm 0.11 \mu\text{mol L}^{-1}$) but within the range of WOD13 observations.

The ALG130 cruise conducted 4 CTD transects perpendicular to the coast covering the majority of the EACC Ecoregion and is thus of particular value for revealing spatial (latitudinal) variability. 50 m averaged NO_3^- and PO_4^{3-} concentrations were very comparable at

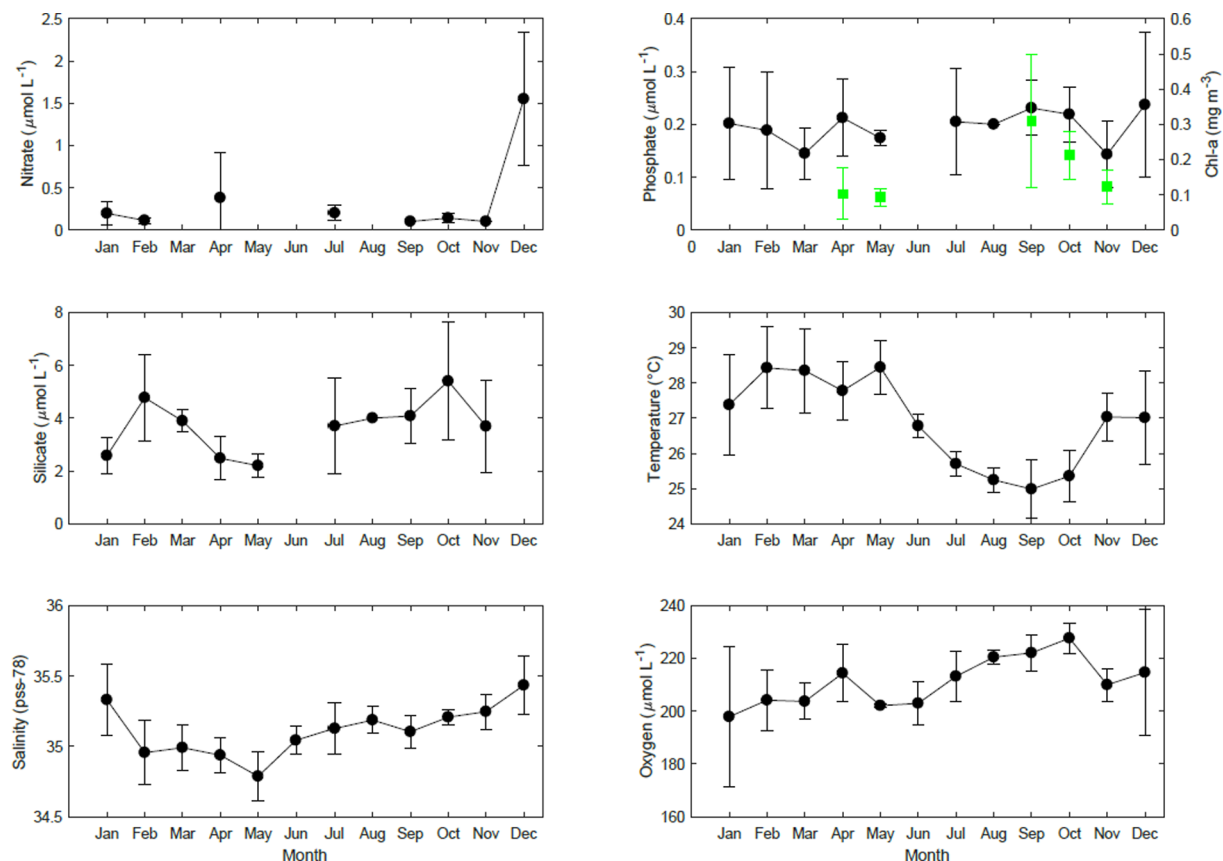


Fig. 7. Mean annual cycles of (a) nitrate, (b) phosphate (black) and chlorophyll (green), (c) silicate, (d) temperature, (e) salinity and (f) dissolved oxygen within the EACC Ecoregion based on monthly averaging of World Ocean Database (2013) data between 0 and 50 m. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 5
Surface nutrient observations for the EACC Ecoregion collated from the literature.

Location	Season / Date	Nitrate ($\mu\text{mol L}^{-1}$)	Phosphate ($\mu\text{mol L}^{-1}$)	Silicate ($\mu\text{mol L}^{-1}$)	Ammonium ($\mu\text{mol L}^{-1}$)	Source
Tanzania (10.5°S)	Aug 2004	0.42 ± 0.42	0.26 ± 0.07	2.46 ± 0.38		ALG130
Tanzania (8.8°S)	Aug 2004	0.41 ± 0.27	0.19 ± 0.04	1.22 ± 0.71		ALG130
Tanzania (7°S)	Aug 2004	0.14 ± 0.16	0.22 ± 0.09	1.97 ± 1.41		ALG130
Tanzania (5.5°S)	Aug 2004	0.46 ± 0.47	0.22 ± 0.05	1.57 ± 0.78		ALG130
Around Pemba Island (4.7 – 6.1°S)	Sep-Oct 2007	0.28 ± 0.39	0.14 ± 0.19	0.85 ± 0.99		ALG160; Barlow et al., 2011
Around Pemba Island (4.7 – 6.1°S)	Sep-Oct 2007	<0.25	0.03–0.8	0.2–0.5		Barlow et al., 2011
Dar es Salaam (6.67°S)	1975–1976			2.6–7.1		Bryceson, 1977
Dar es Salaam (6.67°S)	1975–1976	<LOD – 7.5	0.1–0.5			Bryceson, 1982
Kenyan coastal waters (2.05–4.42°S)	SE monsoon	0–1.1	0.09–0.48	1–3.3	0.21–1.89	Goosen et al., 1997
Kenyan coastal waters (2.05–4.42°S)	Intermonsoon	0–1.84	0.14–0.66	0.2–3.1	0.03–0.65	Goosen et al., 1997
Dar es Salaam coastal waters (6.8°S)	Aug 2008 to Jul 2009	0.01 ± 0.5–4.5 ± 0.04	0.1 ± 0.078 ± 0.05			Hamisi and Mamboya, 2014
Kenyan coast (2–4.5°S)	SE monsoon	<LOD	<0.2		<0.5	Heip and de Bie, 1995
Kenyan coast (2–4.5°S)	Intermonsoon	<LOD	<0.2		<0.2	Heip and de Bie, 1995
Kenyan Shelf (2–4.42°S)	Nov-Dec 1992	<0.1 ± 0	0.249 ± 0.113	1.267 ± 0.553	0.145 ± 0.104	Heip et al., 2013
Malindi coast (3°S)	Dec-86 - Apr-87	70.9				Juma, 1987
Sabaki river (3.17°S)	Dec-86 - Apr-87	99.7				Juma, 1987
Gazi (4.42°S)	Dec-86 - Apr-87	75.5				Juma, 1987
Kenya - Tudor estuary (4.02°S)	Apr-86	0.45	0.03	2.05	0.44	Kazungu, 1986
Kenya - Kilindini estuary (4.06°S)	May-86	0.05	0.02	0.37		Kazungu, 1986
Kenyan coastal waters (2.05 – 4.42°S)	June/Jul 1992	<0.1	0.1–0.2	0.5–3	<0.5	Kromkamp et al., 1997
Kenyan coastal waters (2.05 – 4.42°S)	Nov-Dec 1992	<0.1	0.2–0.35	<2		Kromkamp et al., 1997
Around Unguja Island (5.8–6.3°S)	March 2008 - Feb 2009	0.015–0.127	0.008–0.046			Limbu and Kyewalyanga, 2015
Dar es Salaam (6.65–6.8°S)	Aug96 - Jul 97	0.18–2.41	<1.47		2–8.9	Lugendo et al., 2001
Zanzibar Channel (6.15–6.66°S)	Jul2004 - Jun 2005	0.02 – 0.08	0.0002 – 0.03			Lugomela, 2007
Dar es Salaam - Kunduchi (~6.6°S)	Aug 2008 - Jul 2009	0.85–2.59	0.41–1.23			Lugomela, 2013
Dar es Salaam - Kunduchi (~6.6°S)	Aug 2008 - Jul 2009	0.62–2.84	0.22–0.9			Lugomela, 2013
Sn 1: Chwaka Bay (East coast Unguja) - Mangrove	Apr 94 - Mar 95		0.1–1.4			Lugomela and Semesi, 1996
Sn2: Chwaka Bay (East coast Unguja) - seagrass	Apr 94 - Mar 95		0.05–0.45			Lugomela and Semesi, 1996
Sn3: Bawe Island - Coral reef	Apr 94 - Mar 95		0.05–0.45			Lugomela and Semesi, 1996
Sn 4: Open Channel waters	Apr 94 - Mar 95		0.1–0.8			Lugomela and Semesi, 1996
Zanzibar Channel (6.1°S)	93/94, 94/95 and 98/99	0.08	0.0052			Lugomela et al., 2002
Dar es Salaam (Ocean Road-1) (6.81°S)	Aug 2005 - Aug 2006	0.2–9.9	0.3–10.9			Lyimo, 2009
Dar es Salaam (Ocean Road-2) (6.8°S)	Aug 2005 - Aug 2006	0.6–54.3	0.4–45.2			Lyimo, 2009
Dar es Salaam (Oyster Bay) (6.78°S)	Aug 2005 - Aug 2006	0.4–8.6	0.4–1.8			Lyimo, 2009
Dar es Salaam (Kunduchi) (6.67°S)	Aug 2005 - Aug 2006	0.4–9.1	0.4–5.1			Lyimo, 2009
Dar es Salaam (Mtwoni) (6.57°S)	Aug 2005 - Aug 2006	0.3–6.2	0.3–2.8			Lyimo, 2009
Zanzibar (6.15°S)	Mar 93 - Feb 94	0.002–1.06	0.08–0.25			Lyimo, 2011
Dar es Salaam (6.66°S)	Sep08 - Aug09	0.37–1.17	0.01–0.5			Lyimo, 2011
WTO - Region around Zanzibar (~5.56°S)	1973	<1	<0.2			McGill, 1973
Kenyan coast (2–4.5°S)	SE monsoon 1992	<0.03–0.41			0.03–0.51	Mengesha et al., 1999
Kenyan coast (2–4.5°S)	Intermonsoon 1992	<0.03–0.13			<0.03–0.21	Mengesha et al., 1999
Zanzibar Channel (6.12°S)	June 96 - July 97	2.14–3.23			0.44–0.76	Mohammed and Mgaya, 2001
Chwaka Bay, Unguja Island (6.18°S)	Jul-Aug 1997	17.5 ± 1.6–23.2 ± 4.8	0.21–0.23			Mohammed et al., 2001
Zanzibar coastal waters (6.16°S)	May 2012-May 2013	0.001–0.035	1.2 ± 0.1–9.5 ± 0.01			Moto and Kyewalyanga, 2017
Kenya - Mtwapa Creek (3.9°S)	Aug 99 - Oct 99	0.414–1.429	0.001–0.005		0–0.19	Mutua, 2000
Kenya - Ramisi Creek (4.55°S)	Aug 99 - Oct 99	0.536–1	0.181–0.471		0.729–1.071	Mutua, 2000
Kenya - Shirazi Creek (4.5°S)	Aug 99 - Oct 99	0.414–0.479	0.29–0.303		0.45–0.857	Mutua, 2000
25 miles East of Unguja Island (6.49°S)	Jan-Oct 1956		0.145–0.613		0.5–0.536	Newell, 1959
Kenyan coast (2–4.5°S)	1992	<2	0.3–0.6	<3		Nguli, 1995

(continued on next page)

Table 5 (continued)

Location	Season / Date	Nitrate ($\mu\text{mol L}^{-1}$)	Phosphate ($\mu\text{mol L}^{-1}$)	Silicate ($\mu\text{mol L}^{-1}$)	Ammonium ($\mu\text{mol L}^{-1}$)	Source
EACC – Mean (2–4.5°S)		<5	0.1–0.6		<1–4	Obura, 2001
Kenyan Reef (2–4.5°S)		<3	0.1–0.75		0.01–3	Obura, 2001
Kenyan shelf (2–4.5°S)	SE monsoon	<0.03–0.41			0.24	Semenh et al., 1995
Kenyan shelf (2–4.5°S)	Intermonsoon	0.03–0.12			0.12	Semenh et al., 1995
North Kenya Bank (2.25°S)	Jul-92	0.5				Van Kouwelaar, 1997
Zanzibar Channel (6.1°S)	April average	0.03 $\pm$ 0.02	0.04 $\pm$ 0.03	1.35 $\pm$ 0.58	5.9 $\pm$ 7.7	Wallberg et al., 1999
Zanzibar Channel (6.1°S)	Aug Average	0.03 $\pm$ 0.03	0.04 $\pm$ 0	2.61 $\pm$ 0.66	2.5 $\pm$ 0.6	Wallberg et al., 1999
EACC Ecoregion (3–11°S)	Mean Annual	<0.01	0.2–0.3	3 to 8		WOA13 / This study
Kenyan coastal waters (~4°S)	Jan-96	0.132 $\pm$ 0.03		0.144 $\pm$ 0.01		WOCE, 2002 (Section 102W)

different latitudes but quite variable for Si. For transects conducted at 10.5°S, 8.8°S, 7°S and 5.5°S the 50 m averaged NO_3^- concentrations ranged from 0.51 ± 0.29 to $0.59 \pm 0.35 \mu\text{mol L}^{-1}$ whilst mean PO_4^{3-} concentrations ranged from 0.23 ± 0.04 to $0.27 \pm 0.05 \mu\text{mol L}^{-1}$. Mean Si concentrations were more variable between transects ranging from 1.20 ± 0.73 (8.8°S) to $2.51 \pm 0.32 \mu\text{mol L}^{-1}$ (at 10.5°S). Si concentrations were generally higher along the southern transect at 10.5°S (range 2.2–2.9 $\mu\text{mol L}^{-1}$) than elsewhere (0.5–2.5 $\mu\text{mol L}^{-1}$) suggesting the presence of a latitudinal gradient, the cause of which remains unclear. The (August) monthly mean NO_3^- and PO_4^{3-} concentration derived from ALG130 data was slightly higher than the WOD13 mean whereas the mean Si concentration was lower (2.5 vs 4 $\mu\text{mol L}^{-1}$).

The ALG160 dataset was collected around Pemba Island in Oct 2007 (Barlow et al., 2011). Mean concentrations were 0.45 ± 0.39 , 1.24 ± 0.98 and $0.18 \pm 0.2 \mu\text{mol L}^{-1}$ for NO_3^- , Si and PO_4^{3-} respectively. NO_3^- and PO_4^{3-} concentrations were again comparable to the WOD13 October average whilst Si was considerably lower. Variability within the ALG160 dataset was not consistent for all nutrients, with the highest (single profile) 50 m average NO_3^- concentration ($1.36 \mu\text{mol L}^{-1}$) found close inshore to the east of Pemba Island, highest average Si ($3.5 \mu\text{mol L}^{-1}$) found southwest of Pemba Island at the entrance to the Pemba Channel and highest average PO_4^{3-} ($0.84 \mu\text{mol L}^{-1}$) found adjacent to the Tanzanian coast near the major port city of Tanga; thus it is conceivable that this is indicative of municipal activities.

Nutrient observations extracted from more recent regional scientific studies and grey literature reports suggest that typical nutrient conditions in the near shore waters of Zanzibar and Pemba Channels and along the Kenyan coast, and frequently in the vicinity of mangrove forests, seagrass meadows and fringing coral reefs may be somewhat or significantly modified from the typical conditions discussed above (Table 5). Though generally recognised as nutrient poor near coastal waters along Tanzania and Kenya can display significantly elevated nutrient concentrations due to the discharge of sewage and industrial effluents from major urban areas, run-off from agricultural lands or riverine influences (Mohammed, 2000). For example, Lyimo (2009) reported NO_3^- and PO_4^{3-} concentrations of up to $54 \mu\text{mol L}^{-1}$ and $45 \mu\text{mol L}^{-1}$ respectively in surface waters close to Dar es Salaam. Such concentrations are 360-fold and ~240-fold higher than the mean WOD-derived concentrations found in EACC surface waters (Table 4). Whilst eutrophication and the presence of organic pollutants and high concentrations of faecal coliform bacteria are increasingly recognised as serious and growing regional problems (e.g. Lyimo, 2009; UNEP, 2009; ASCLME, 2012a), the spatial impacts remain unclear due to limited monitoring surveys (Mmochi et al., 2001). Nevertheless, it is generally accepted that low nutrient concentrations close to the coast are essential for the healthy development of coral reef and seagrass ecosystems (Hemminga et al., 1995) and, for the most part, extant nutrient observations demonstrate this to be the case (Table 5). Reported surface PO_4^{3-} concentrations range from <0.01 to $45.9 \mu\text{mol L}^{-1}$ but for most studies surface concentrations are typically $<0.5 \mu\text{mol L}^{-1}$ and thus broadly comparable to the mean annual WOD derived concentration of $0.18 \pm 0.08 \mu\text{mol L}^{-1}$ (Table 4). NO_3^- measurements range from 0.01 to $70.9 \mu\text{mol L}^{-1}$ and can be quite variable between studies (Table 5). Away from rivers and municipal discharge points NO_3^- concentrations have a typically magnitude of $\sim 0.4 \mu\text{mol L}^{-1}$, slightly higher than the mean annual WOD derived concentration of $0.21 \pm 0.25 \mu\text{mol L}^{-1}$ (Table 4). Silicate is the least reported nutrient with concentrations ranging from 0.2 to $7.1 \mu\text{mol L}^{-1}$, though most studies typically report concentrations of 1–3 $\mu\text{mol L}^{-1}$, again comparable to the WOD-derived mean annual surface concentration of $3.67 \pm 1.69 \mu\text{mol L}^{-1}$.

Not all of the variability in measured nutrient concentrations in near coastal waters can be wholly attributable to anthropogenic discharges and seasonal and/or spatial variability must also be recognised for its impact on nutrient concentrations. For instance, Newell (1959)

observed that surface phosphate concentrations at a fixed station east of Unguja Island ("Station Z", $\sim 6.49^\circ\text{S}$, 39.87°E) varied from 0.3 to $0.6 \mu\text{mol L}^{-1}$ between January and October signifying seasonality. Babenerd and Boje (1973) meanwhile reported a northward increase in phosphate concentrations during the NE monsoon months with concentrations ranging from $<0.15 \mu\text{mol L}^{-1}$ at $\sim 5^\circ\text{S}$, to 0.15 – $0.3 \mu\text{mol L}^{-1}$ along the Kenyan coast and peaking at $>0.3 \mu\text{mol L}^{-1}$ along parts of the Kenyan/Somali border at ~ 1 – 2°S . In contrast McClanahan (1988) reported PO_4^{3-} concentrations of 0.4 – $0.6 \mu\text{mol L}^{-1}$ off Tanzania during the SE monsoon period and linked the elevated concentrations to increased river discharges and vertical entrainment due to higher mean seasonal wind speeds and a deeper thermocline. Increased nutrient concentrations in the vicinity of river outflows were similarly reported by Kromkamp et al (1997). More recently, Barlow et al (2011) measured a 26-fold variation in mixed layer phosphate concentrations which ranged from 0.03 to $0.8 \mu\text{mol L}^{-1}$ in the surface waters of the central Pemba Channel (~ 5 – 6°S) in a region away from major riverine influences and which may therefore indicate a role for mesoscale driven variability.

Mutua (2000) measured surface NO_3^- and PO_4^{3-} concentrations of up to 1.4 and $0.6 \mu\text{mol L}^{-1}$ respectively in Mtwapa, Ramisi and Shirazi estuaries in Kenya whilst nutrient observations around Unguja Island have been reported at nanomolar levels (Wallberg et al., 1999; Lugomela et al., 2002). Frequently however, observations from the same sites can be highly variable and occasionally without obvious explanation. For instance Wallberg et al. (1999) and Moto and Kyewalyanga (2017) reported NO_3^- concentrations of $\sim 30 \text{ nmol L}^{-1}$ near Bawe Island, a small coral atoll offshore of Stone Town, Unguja, whilst Mohammed and Mgaya (2001) reported concentrations of 2 – $3 \mu\text{mol L}^{-1}$. Moto and Kyewalyanga (2017) have drawn attention to the variability in nutrient concentrations in Zanzibar coastal waters which can vary by an order of magnitude or more between studies and which they suggested could be related to rainfall patterns.

NO_3^- appears particularly limited in these waters and some studies have reported NO_3^- concentrations below detection limits. For instance, Nguli (1995) reported surface nutrient concentrations of $<3 \mu\text{mol L}^{-1}$ for Si, $<0.6 \mu\text{mol L}^{-1}$ for PO_4^{3-} and $<2 \mu\text{mol L}^{-1}$ for NO_3^- but also documented surface NO_3^- concentrations close to zero in June. Meanwhile Heip and de Bie (1995) noted that NO_3^- was nearly or completely absent in surface waters during both monsoon periods. In June (SE monsoon) NO_3^- was undetectable throughout the upper ~ 70 m but increased rapidly to $15 \mu\text{mol L}^{-1}$ at 150 m depth and increased further to $\sim 39 \mu\text{mol L}^{-1}$ at 1200 – 1400 m depth. In November (NE monsoon) the nutricline had shoaled to 50 m following uplift of the thermocline but NO_3^- concentrations were still undetectable in the upper 50 m. NH_4^+ concentrations meanwhile were $\sim 0.5 \mu\text{mol L}^{-1}$ in June, decreasing to $\sim 0.2 \mu\text{mol L}^{-1}$ in November and broadly stable with depth. Surface PO_4^{3-} concentrations were $\sim 0.2 \mu\text{mol L}^{-1}$ above the thermocline in both monsoon periods increasing to $\sim 3 \mu\text{mol L}^{-1}$ at 800 m.

A significant proportion of studies have examined anthropogenic influences on nutrient concentrations but do not always agree on the severity of impacts. Mohammed and Mgaya (2001) measured nutrient concentrations around two coral islands within the Zanzibar Channel to quantify the impact of anthropogenic discharges. Chapwani Island which is located ~ 3.5 km north of Stone Town and directly downstream of a major sewage outflow was compared to Bawe Island a coral island situated in unaffected waters approximately 6 km west of Stone Town. The year-long study found little difference in PO_4^{3-} concentrations between the two sites with typical concentration of $0.2 \mu\text{mol L}^{-1}$ at both localities. This concentration is comparable to the WOD-derived mean PO_4^{3-} surface concentration for the region (Table 4) and to many other recent studies (Table 5). NO_3^- concentrations were steady at $\sim 2.6 \mu\text{mol L}^{-1}$ at Chapwani whilst at Bawe concentrations varied significantly particularly over the tidal cycle reaching $3.2 \mu\text{mol L}^{-1}$ during neap tides and $2.1 \mu\text{mol L}^{-1}$ during spring tides, a variation of

$\sim 35\%$. These concentrations are all elevated compared to typical NO_3^- concentrations reported elsewhere in the literature (Table 5). The authors concluded that whilst coral reefs close to Unguja Island may be threatened by anthropogenic nitrogen enrichment the intensity of tidal flushing over the spring-neaps cycle might provide a degree of control on the severity of short-term eutrophication impacts. A separate study by Hamisi and Mamboya (2014) however found significantly elevated NO_3^- and PO_4^{3-} concentrations associated with sewage discharge points close to Dar es Salaam suggesting that both N and P enrichment are likely problematic. Mean annual concentrations of 5.45 ± 0.04 and $0.78 \pm 0.05 \mu\text{mol L}^{-1}$ for NO_3^- and PO_4^{3-} respectively were significantly higher than observed at far-field stations where the mean annual concentrations were 0.01 ± 0 and $0.1 \pm 0 \mu\text{mol L}^{-1}$ respectively. In this particular study seasonal variability was also observed in NO_3^- concentrations which were higher during the NE monsoon at all stations but no seasonality was reported for PO_4^{3-} .

The impacts of nutrient over-enrichment on seagrass and macroalgae communities were studied by Lugendo et al (2001) who reported nutrient concentrations from several beaches near Dar es Salaam. At 'Ocean Road', which was considered a polluted site, mean monthly NO_3^- ranged from 0.18 to $2.41 \mu\text{mol L}^{-1}$, NH_4^+ peaked at $8.9 \mu\text{mol L}^{-1}$, and PO_4^{3-} peaked at $1.47 \mu\text{mol L}^{-1}$. At Kunduchi, considered an unpolluted site, mean monthly NO_3^- ranged from 0.22 to $2.41 \mu\text{mol L}^{-1}$, NH_4^+ peaked at $2.01 \mu\text{mol L}^{-1}$, and PO_4^{3-} peaked at $0.87 \mu\text{mol L}^{-1}$. At both sites NO_3^- , NH_4^+ and PO_4^{3-} concentrations were higher during the NE monsoon period than during the SE monsoon period with the suggestion that riverine discharges were important for coastal nutrient concentrations and potentially thereafter for coastal productivity. Mean monthly NO_3^- concentrations were generally higher at Kunduchi than at Ocean Road contrary to expectations, whilst NH_4^+ concentrations were generally higher at Ocean Road than at Kunduchi in agreement with expectations. No significant difference in PO_4^{3-} concentrations was observed between the two sites. The primary focus of this study was on assessing the impact of pollution on macrophytes and whilst Lugendo et al (2001) observed no significant difference in seagrass biomass between the polluted and unpolluted study sites macrophyte biomass and species composition did differ with the higher biomass of green macroalgae at the polluted site tentatively connected to higher ambient NH_4^+ concentrations.

Variability in nutrient concentrations has also been observed in conjunction with the presence of unusual phytoplankton species. Lugomela (2007) reported 'unusually low' nitrate and phosphate concentrations from both sides of the Zanzibar Channel between July 2004 and June 2005 when coincidentally the large bioluminescent dinoflagellate *Noctiluca Scintillans* was also observed. This species has only recently been identified within these waters (Lugomela, 2007) and is usually found further north (Rosario Gomes et al., 2014). On the western side of the channel close to mainland Tanzania NO_3^- and PO_4^{3-} ranged from 0.02 to 0.08 and <0.01 – $0.02 \mu\text{mol L}^{-1}$, whilst on the eastern side concentrations ranged from 0.02 to 0.08 and <0.01 – $0.03 \mu\text{mol L}^{-1}$ respectively. NO_3^- concentrations were considered to be significantly higher during the NE monsoon months but PO_4^{3-} concentrations were more constant. It was suggested that the seasonal accumulation of NO_3^- was due to increased residence times of water during the NE monsoon when the EACC slows allowing shelf waters to attain a more neritic characteristic.

Nutrient observations for the EACC Ecoregion remain limited. Existing observations, whilst broadly covering the region, reveal important spatial and temporal variability in nutrient concentrations that may be attributable to multiple causes and widespread routine sampling remains difficult. The majority of recent nutrient observations are generally made in shallow near coastal waters with limited sampling in deeper offshore waters which tends to bias the interpretation of the aggregated dataset. Individual datasets can vary in quality, quantity and duration of sampling. The influence of municipal discharges on nutrient concentrations can be significant, though rarely does the

impact appear to be geographically widespread and the impacts of nutrient over-enrichment need to be set against more in-depth observations from uncontaminated waters. The existing data indicate low N:P conditions and thus widespread N limitation but also reveal moderate concentrations of Si within surface waters. There is widely reported to be seasonal variability in NO_3^- concentrations which are often higher during the NE monsoon contrary to the mixed layer seasonal cycle which is deepest during the SE monsoon. There is no indication of a similar seasonal cycle in PO_4^{3-} which remains at measurable concentrations year-round. This anomaly has yet to be adequately explained but may relate to terrestrial and riverine inputs to near coastal waters, in which case, the true spatial extent of seasonality in NO_3^- concentrations and of any fundamental distinction between shelf and offshore areas remains to be fully described. There is currently insufficient data to adequately subdivide the EACC Ecoregion into smaller shelf and offshore regions though such a distinction is highly likely.

8.2. Chlorophyll observations

Chlorophyll measurements are widely reported for the region as they provide a quick estimate of phytoplankton biomass but extant observations are not centralised. The limited WOD chlorophyll dataset indicates monthly mean surface concentrations of 0.1 to 0.3 mg m^{-3} and although chlorophyll concentrations appear to peak in September when SST is lower, a pattern that would be in agreement with the annual cycle of productivity of the WIO (Kabanova, 1968; Cushing, 1973), the chlorophyll data are generally insufficient to describe the phenology of these waters (Fig. 7). A broad summary of literature

observations from within the EACC Ecoregion is presented in Table 6. The majority of studies typically report mean surface chlorophyll concentrations of $\sim 0.3 \text{ mg m}^{-3}$ from open water locations or from the central waters of the various sea channels, although Peter et al. (2018) note that knowledge of monsoon driven variability in chlorophyll concentrations in shallower waters is rather poorly known. Many studies reveal significant seasonal or spatial variability within the shallows. For instance, Krey (1973) indicated average chlorophyll concentrations for the region 0–10°S and for June to September to be in the range 0.2–0.3 mg m^{-3} whereas between Dec and March concentrations could exceed 0.3 mg m^{-3} over the North Kenya Banks and simultaneously be $< 0.1 \text{ mg m}^{-3}$ along the southern Kenyan and Tanzanian coastline. Bryceson (1977) described higher chlorophyll concentrations during the NE monsoon months in shelf waters close to Dar es Salaam, whilst Moto and Kyewalyanga (2017) found either weak seasonality or no seasonality at all in the coastal waters around Unguja Island. Such variability suggests that generic descriptions of monsoon driven seasonality in shelf waters (e.g. McClanahan, 1988) require careful ground-truthing for individual study sites. Reported chlorophyll concentrations can be significantly higher than the mean. In estuaries chlorophyll concentrations can exceed 5 mg m^{-3} (Mutua, 2000) and in one extreme case a chlorophyll concentration of 19 mg m^{-3} was reported from the mangrove dominated waters of Chwaka Bay (east coast of Unguja Island), though annual average concentrations from the same location were far lower at 3.7–5.5 mg m^{-3} (Kyewalyanga, 2002). Near-shore chlorophyll concentrations can display rapid temporal fluctuations in response to rainfall/riverine discharges (e.g. Lugomela et al., 2001a, 2001b) suggesting that results from individual studies need to be interpreted carefully when results are aggregated as the quantity of

Table 6

Surface chlorophyll-a concentrations for the EACC Ecoregion collated from the literature. For most studies the reported range in concentration is reported (mean concentration where presented is shown in brackets).

Location	Date/Season	Chl-a concentration (mg m^{-3})	Source
Around Pemba Island (4.7–6.1°S)	Sep-Oct 2007	0.12–0.68 (0.25 $\pm$ 0.15)	ALG160 dataset; Roberts et al., 2007
Around Pemba Island (4.7–6.1°S)	Sep-Oct 2007	0.16–0.5 (0.29 $\pm$ 0.12)	Barlow et al., 2011
Gazi Creek (Kenya 4.4°)	01/10/1992	0.06–0.3	Bollen et al., 2016
Dar es Salaam coastal waters ($\sim 6.7^\circ\text{S}$)	Jan 1975 - Jan 1976	0.2–1.4	Bryceson, 1977
Somali Coastal current LME (12°N–10°S)	Mean annual	0.19	GEF/TWAP, 2015
Coastal WIO (0–10°S)	Mean June to September (SE monsoon)	< 0.3	Krey, 1973
Coastal WIO (0–10°S)	Mean Dec to March (NE monsoon)	≤ 0.3	Krey, 1973
Kenyan coastal waters (2.05–4.42°S)	June/Jul 1992	0.06–0.31	Kromkamp et al., 1997
Kenyan coastal waters (2.05–4.42°S)	Nov/Dec 1992	0.04–0.26	Kromkamp et al., 1997
Zanzibar coastal waters (6.19°S) - range	22/07/99–21/07/00	0.11–19.17	Kyewalyanga, 2002
Zanzibar coastal waters (6.19°S)	22/07/99–21/07/00	3.7 – 5.5	Kyewalyanga, 2002
Around Unguja Island (5.8–6.7°S)	March 2008 - Feb 2009	0.3–0.7	Limbu and Kyewalyanga, 2015
Zanzibar coastal waters	Yearly	0.04–0.5	Lugomela, 1996
Dar es Salaam - Kunduchi ($\sim 6.6^\circ\text{S}$)	Aug 2008 - Jul 2009	0.11–0.20	Lugomela, 2013
Dar es Salaam - Kunduchi ($\sim 6.6^\circ\text{S}$)	Aug 2008 - Jul 2009	0.15–0.22	Lugomela, 2013
Stn 1: Chwaka Bay (East coast Unguja) - Mangrove	Apr 94 - Mar 95	0.12–0.51	Lugomela and Semesi, 1996
Stn2: Chwaka Bay (East coast Unguja) - seagrass	Apr 94 - Mar 95	0.04–0.1	Lugomela and Semesi, 1996
Stn3: Bawe Island - Coral reef	Apr 94 - Mar 95	0.04–0.1	Lugomela and Semesi, 1996
Stn 4: Open Channel waters	Apr 94 - Mar 95	0.04–0.21	Lugomela and Semesi, 1996
Zanzibar Channel (6.1°S)	93/94, 94/95 and 98/99	0.2–1	Lugomela et al., 2001a, 2001b
Zanzibar Channel (6.12°S)	June 96 - July 97	0.81–0.9	Mohammed and Mgaya, 2001
Kenyan coastal waters (2.8°S)	05/07/1977	0.44–0.5	Mordasova, 1980
North of Pemba Island (4.7°S)	17/07/1977	0.77–1.74	Mordasova, 1980
Pemba Channel (5.4°S)	11/07/1977	0.58	Mordasova, 1980
Zanzibar coastal waters (6.16°S)	May 2012–May 2013	0.69–1.86	Moto and Kyewalyanga, 2017
Mtwapa Creek Kenya (3.9°S)	01/08/1999	0.5–3.2	Mutua, 2000
Ramisi Creek Kenya (4.5°S)	01/08/1999	2.3–5.5	Mutua, 2000
Shirazi Creek Kenya (4.5°S)	01/08/1999	1.5–2	Mutua, 2000
Kenyan offshore waters (EACC influenced) (2–4.5°S)	Mean annual conditions	< 1	Obura, 2001
Kenyan coastal waters (2–4.5°S)	Mean annual conditions	< 0.5	Obura, 2001
Unguja Island (5.8–6.3°S)	NE monsoon	0.41	Peter et al., 2018
Unguja Island (5.8–6.3°S)	SE monsoon	0.36	Peter et al., 2018
Mafia Channel (8°S)	Jul-13	0.15–0.28	Semba et al., 2016
Zanzibar Channel (6.1°S)	April (Rainy season)	1.2 $\pm$ 0.7	Wallberg et al., 1999
Zanzibar Channel (6.1°S)	Aug (Dry season)	1 $\pm$ 1.2	Wallberg et al., 1999
Zanzibar Channel ($\sim 6^\circ\text{S}$)	Jul/Aug 2011	0.33–0.34	Zavala-Garay et al., 2015

data available for the EACC Ecoregion is still limited. Hamisi and Mamboya (2014) drew attention to the impact of sewage discharge on chlorophyll concentrations in coastal waters noting elevated chlorophyll concentrations at those stations closest to the discharge point. Chlorophyll concentrations were reportedly $>100 \text{ mg m}^{-3}$ at the most severely impacted station but the magnitude or the units reported by Hamisi and Mamboya (2014) seem unfeasible and these results are excluded from Table 6. All stations studied by Hamisi and Mamboya (2014) exhibited maximum chlorophyll concentrations during Nov-Dec coincident with the short rains of the intermonsoon period when river flows, and terrestrial runoff likely peaked. All stations revealed 40–60% higher chlorophyll concentrations in Feb-Mar during the NE monsoon months compared to the SE monsoon period (Jun-Sep) suggesting that even in regions influenced by sewage discharge a strong degree of seasonality remains.

The majority of studies report short-term observations of chlorophyll associated with particular research programmes whilst the few studies that report observations over annual timescale can produce different seasonal patterns or different seasonal concentrations (e.g. Peter et al., 2018). There are insufficient data to resolve latitudinal gradients, if any, a question that remains best answerable with Earth Observation datasets. Bulk chlorophyll measurements dominate the reported observations with limited size-fractionated measurements, particularly estimates of the picoplankton contribution to total chlorophyll. Picoplankton are known to be particularly important for productivity in these and surrounding waters (Ranaivoson and Magazu, 1996; Wallberg et al., 1999; Lugomela et al., 2001a, 2001b) suggesting that they certainly represent a major, if not the major, component of the total chlorophyll pool, as is expected for tropical waters (Partensky et al., 1999; Veldhuis and Kraay, 2004). In a rare study Kromkamp et al. (1997) estimated that 40–60% of total chlorophyll was found in the picoplankton size fraction ($<3 \mu\text{m}$) in Kenyan waters. This compares very well to the 34–66% contribution estimated by Ranaivoson and Magazu (1996) off Madagascar. However, Barlow et al. (2011) noted contrasting instances of micro- and nanoplankton dominance and nano- and picoplankton dominance of the chlorophyll pool around Unguja Island suggesting that there are important but as yet poorly understood

spatial patterns in the distribution of phytoplankton size classes across the region. Indeed, Kromkamp et al. (1997) found that picoplankton tended to dominate the community biomass only at deeper offshore stations which had a more oceanic influence whilst diatoms were more prevalent at the shallower inshore stations which had a more neritic character. At four stations around Unguja Island Lugomela and Semesi (1996) also observed a nanoplankton ($<20 \mu\text{m}$) dominance with this size class representing 65–88% of chlorophyll biomass.

More recently, Semba et al. (2016) reported chlorophyll concentrations from the Mafia Channel during the SE monsoon. They found a slight variation in surface chlorophyll concentrations as a function of water depth with concentrations ranging from $<0.2 \text{ mg m}^{-3}$ in deep stations ($>10 \text{ m}$) to 0.9 mg m^{-3} at shallow stations ($<5 \text{ m}$). Similarly, surface chlorophyll concentrations varied with distance from shore decreasing from a mean of $0.65 \pm 0.24 \text{ mg m}^{-3}$ at distances of $<5 \text{ km}$ from shore to $0.18 \pm 0.12 \text{ mg m}^{-3}$ at stations situated $>10 \text{ km}$ from shore. A supporting analysis of satellite chlorophyll data for the Mafia Channel indicated that peak chlorophyll concentrations occurred in Mar-Apr (NE monsoon/inter-monsoon period) possibly in response to increased riverine discharges from the Rufiji river which experiences peak discharge in April (UNEP / WIOMSA, 2009).

8.2.1. Remote sensing perspective

To better understand the variability reported in the literature observations a supporting analysis of MODIS Aqua (R2018.0) surface chlorophyll data was undertaken. The mean annual cycle and the annual mean and median concentrations for the shelf region of the EACC Ecoregion were calculated (Fig. 8). The mean concentration for this region, representing the entire shelf from 3 to 11°S and waters ranging in depth from 20 to 200 m, thus excluding shallow (case II) waters, was $0.36 \mu\text{g L}^{-1}$, whilst the median concentration was 0.33 mg m^{-3} (range $0.16\text{--}2.0 \text{ mg m}^{-3}$). Throughout the EACC Ecoregion mean chlorophyll concentrations for the shelf regions are typically above the annual mean concentration in early January, below average from mid-February to early April, above average from mid-April to October and below average from mid-October through to late December. This annual cycle, and particularly the timing of peaks and troughs, suggests monsoon

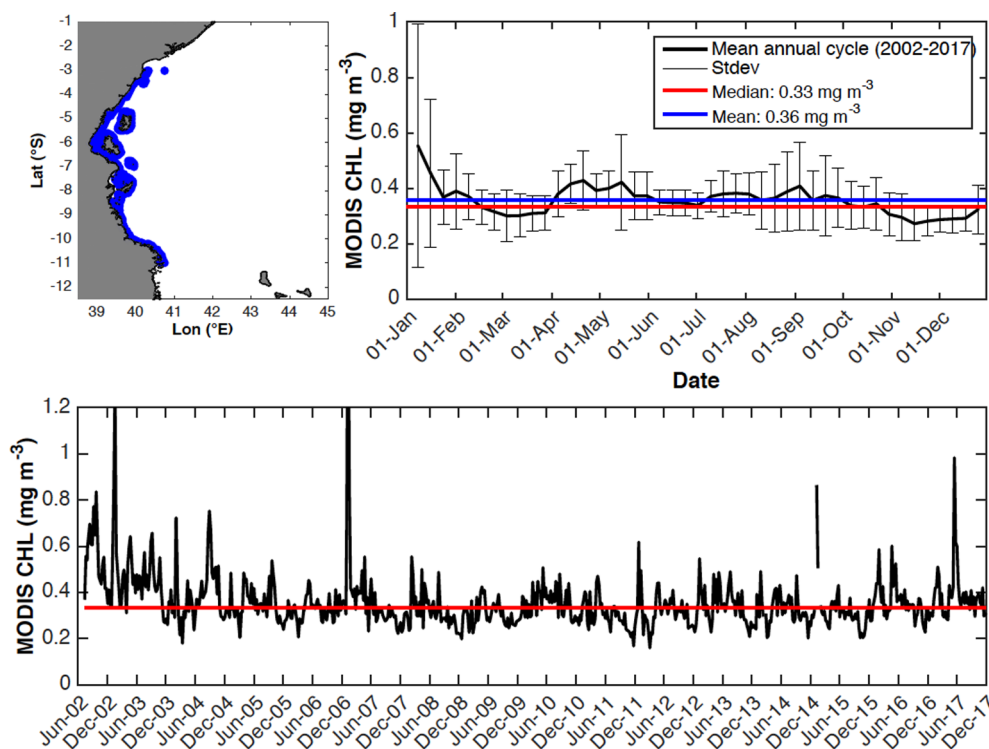


Fig. 8. Analysis of MODIS Aqua chlorophyll concentrations for the shelf regions of the EACC Ecoregion (blue shading in panel a) with data filtered to remove (case II) shallow waters $<20 \text{ m}$ deep; (b) the mean annual cycle of chlorophyll concentrations for this region including the long term mean (blue line) and median (red line) values and (c) the corresponding 2002–2017 time series averaged over the shelf regions (blue shading in panel (a)). MODIS Aqua (R2018.0) data obtained from the Nasa Ocean Color website (www.oceancolor.gsfc.nasa.gov). Chlorophyll concentrations derived using the OCI algorithm described by Hu et al. (2012). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

driven variability with above average chlorophyll concentrations during the SE monsoon months, in agreement with observations from the wider Indian Ocean (e.g. Signorini and McClain, 2012; Signorini et al., 2015), and yet the highest annual chlorophyll concentrations occur during the NE monsoon month of January as reported by Bryceson (1982) and McClanahan (1988). The large variability in January is however indicative of significant interannual or spatio-temporal variability within this region which is obscured by the large scale regional averaging approach used.

To better understand the seasonality and spatiotemporal variability of chlorophyll within these waters mean seasonal composites and time series for selected subregions were created. The mean seasonal composites clearly show seasonality and/or spatial variability in some areas (Fig. 9). For instance, high chlorophyll concentrations occur at Mtwara (~11°S), a region where the Ruvuma river discharges to the Indian Ocean and where the NEMC/EACC first makes contact with the coast, whilst the mean boreal winter composite (21Dec-20Mar) - which largely corresponds to the NE monsoon period - shows elevated chlorophyll in the region 1-4°S (North Kenya Banks and Malindi Banks) compared to all other seasons. This latter observation is likely due to the influence of the southward flowing Somali Current which results in the 0.2 $\mu\text{g L}^{-1}$ contour moving south by 2° of latitude relative to its mean position in autumn (21Sep-20Dec). During the SE monsoon (Summer, 21Jun-20Sep) the whole EACC region appears to be more productive, the 0.2 $\mu\text{g L}^{-1}$ contour is moved offshore compared to its position during other seasons, and shelf waters generally exhibit higher chlorophyll concentrations. Note however that the waters around Mafia Island (7-9°S) are generally more productive during the NE monsoon as noted previously (e.g. Semba et al., 2016).

To explore seasonality within the main regions of high chlorophyll shown in Fig. 9, namely (i) Malindi and North Kenya Banks (2-3.5°S), (ii) Dar es Salaam/Zanzibar Channel coastal waters (5.5-7°S), (iii) Mafia Channel (7-9°S), and (iv) Mtwara (10-12°S), mean annual cycles were calculated for each subregion out to the 200 m bathymetric contour excluding waters <20 m deep. Mean annual chlorophyll concentrations for the shelf regions at Malindi/North Kenya Banks, Dar es Salaam/Zanzibar Channel, Mafia Channel and Mtwara were 0.49 ± 0.31 , 0.33 ± 0.13 , 0.49 ± 0.17 , 0.52 ± 0.25 mg m^{-3} respectively. At some locations therefore the mean annual chlorophyll

concentration can be more than 40% higher than the EACC average (Fig. 8).

At North Kenya Banks, the (seasonal) confluence zone for the EACC and Somali Currents, observed chlorophyll concentrations ranged from 0.11 to 3.5 mg m^{-3} but averaged 0.49 mg m^{-3} (Fig. 10). Mean chlorophyll concentrations are generally below average from February to mid-June and higher than average from mid-June to late September but over the year the mean conditions are broadly stable. Highest chlorophyll concentrations (>0.8 mg m^{-3}) occur in January and again in July for the mean annual cycle whilst the 2002-2017 time series makes clear that both months can exhibit significantly higher chlorophyll concentrations (up to 3.5 mg m^{-3} in July 2013).

Around Dar es Salaam and Zanzibar, a region with a 2-fold seasonal variation in residence times (Zavala-Garay et al., 2015), observed chlorophyll concentrations ranged from 0.14 to 1.6 mg m^{-3} but averaged 0.33 mg m^{-3} (Fig. 11). The mean annual chlorophyll concentration for this subregion (0.33 mg m^{-3}) is comparable to the mean concentration obtained for the entire shelf area of the EACC Ecoregion (0.36 mg m^{-3}) but is the lowest of the four subregions examined here being at least 30% lower. Concentrations peak in January (~0.5 mg m^{-3}) and again in May whilst being above average from April to mid-September. There is a notable decrease in chlorophyll concentrations to <0.25 mg m^{-3} during November and December.

To the south around Mafia Island, a shallow region with important seasonal riverine inputs, observed chlorophyll concentrations ranged from 0.13 to 1.5 mg m^{-3} but averaged 0.49 mg m^{-3} (Fig. 12). Chlorophyll is highest during April (~0.75 mg m^{-3}), presumably in response to riverine discharge given the coincident timings (Table 1), but generally above average from January through to mid-June (N.B. satellite algorithms are challenged by high sediment concentrations thus the peak in April should be treated with care). Chlorophyll concentrations are close to the annual average during the SE monsoon months (June to October) and noticeably below average from October through to December when concentrations are <0.4 mg m^{-3} .

At Mtwara, a distinctly different seasonal timing is evident. This is the receiving region for the NEMC/EACC (Fig. 1) and observed chlorophyll concentrations range from 0.09 to 2.8 mg m^{-3} and average 0.52 mg m^{-3} (Fig. 13). Chlorophyll concentrations peak between late March and mid-May (~0.75 mg m^{-3}), are below average from June to

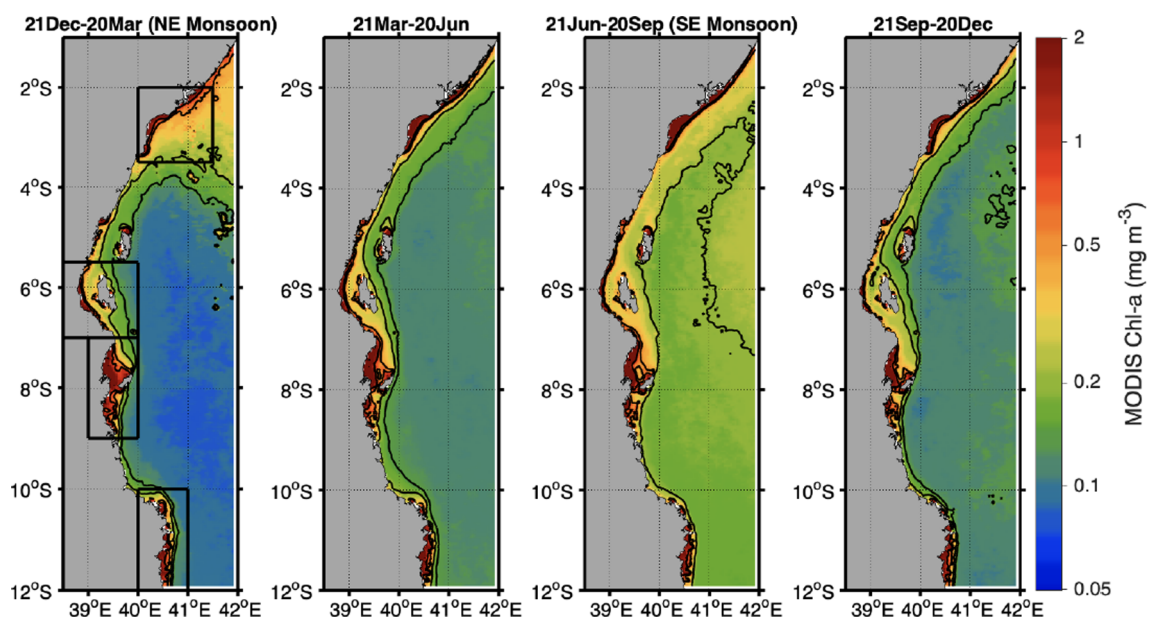


Fig. 9. Mean seasonal composites of surface chlorophyll concentrations for the EACC Ecoregion based on MODIS Aqua full mission climatologies (Reprocessing 2018.0). Black boxes in panel a indicate the approximate areas examined in Figs. 10 to 13 and represent from north to south (i) North Kenya Banks, (ii) Dar es Salaam/Zanzibar coastal waters, (iii) Mafia Island and (iv) Mtwara.

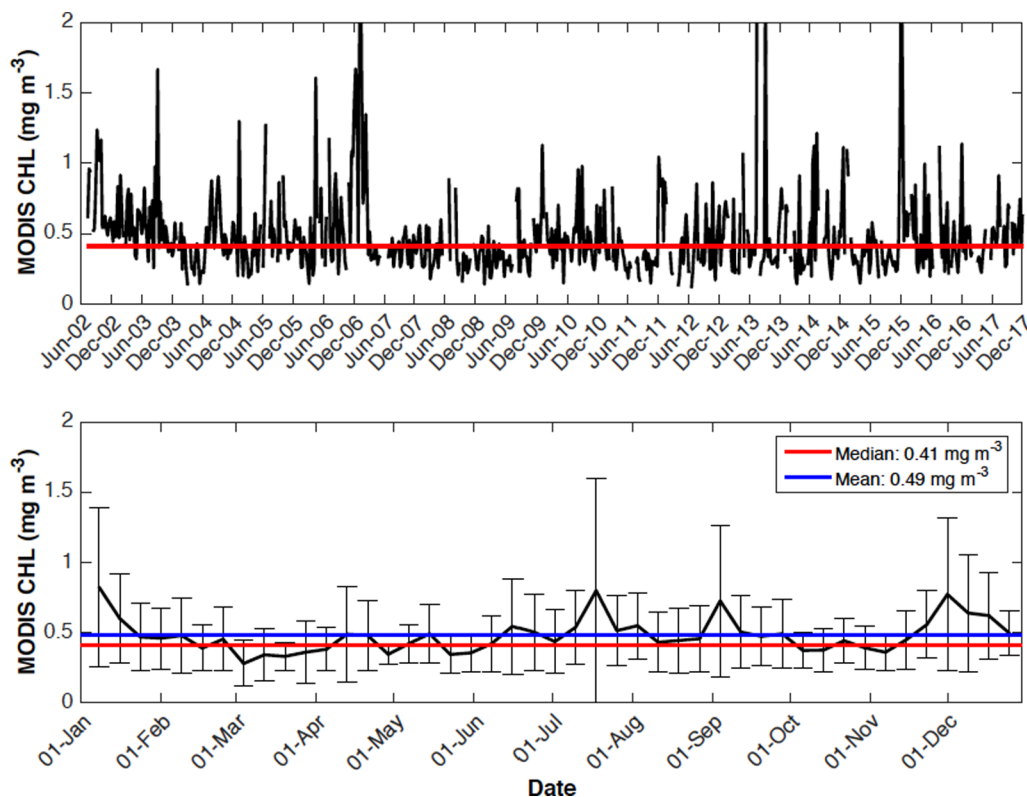


Fig. 10. Analysis of MODIS Aqua chlorophyll concentrations for the shelf regions of the Malindi Banks/North Kenya Banks subregion with data filtered to remove (case II) shallow waters < 20 m deep; (a) the 2002–2017 time series averaged over the shelf region approximated by the box indicated on Fig. 9(a), (b) the mean annual cycle of chlorophyll concentrations for this region including the long term mean (blue line) and median (red line) values. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

mid-August and below average again during November and December. The minima during the SE monsoon period may be related to annual minima river discharge from the Ruvuma river at this time (Table 1).

Offshore gradients in chlorophyll have an important impact on the derivation of mean annual concentrations. Averaging to the offshore position of the 500 m bathymetric contour reduces the mean annual

concentration by 15–31% at Mtwara, Mafia and Dar es Salaam and by 40% at North Kenya Banks (Table 7). For the EACC region as a whole the reduction is 20%.

Satellite chlorophyll climatologies (Fig. 9) also reveal two hotspots of intense chlorophyll around Pemba Island. One is located to the north (downstream) of the island and is characteristic of a classic island wake

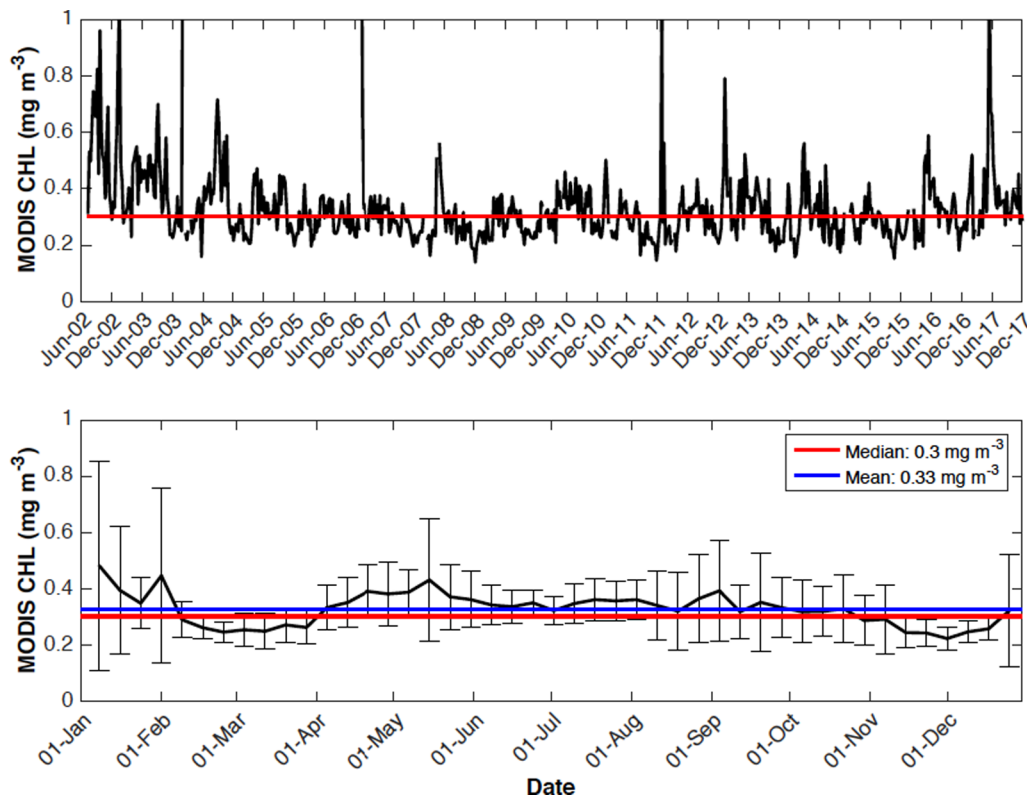


Fig. 11. Analysis of MODIS Aqua chlorophyll concentrations for the shelf waters of Dar es Salaam/Zanzibar subregion with data filtered to remove (case II) shallow waters < 20 m deep; (a) the 2002–2017 time series averaged over the shelf region approximated by the box indicated on Fig. 9(a), (b) the mean annual cycle of chlorophyll concentrations for this region including the long term mean (blue line) and median (red line) values. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

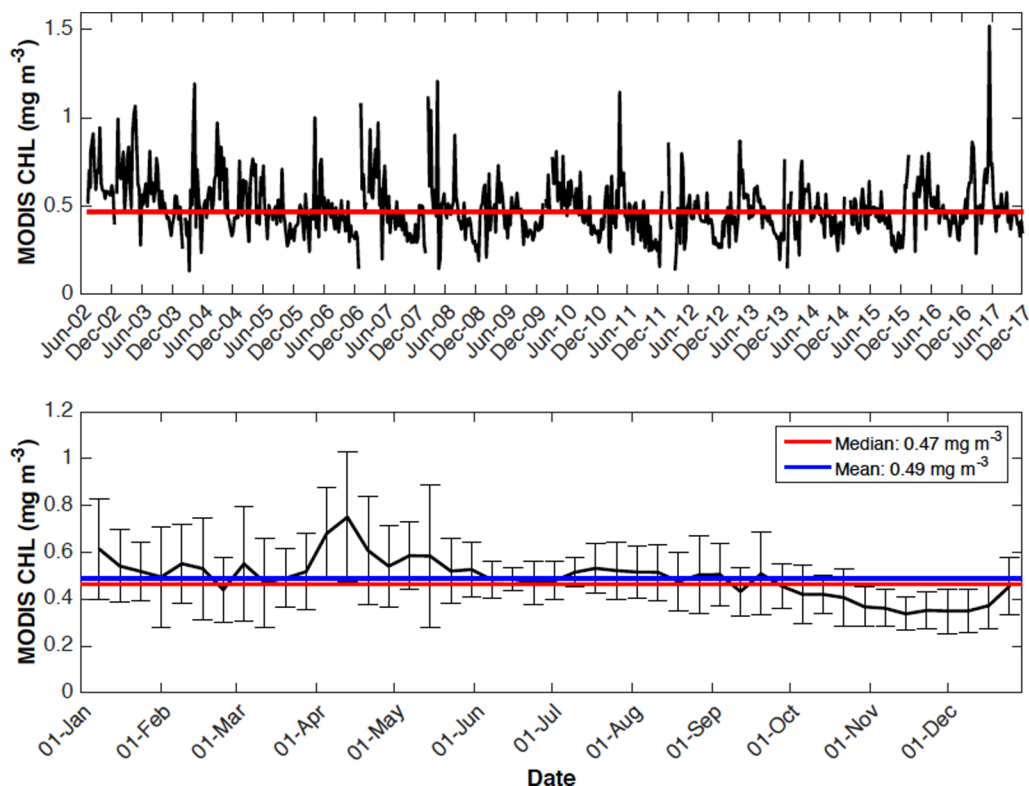


Fig. 12. Analysis of MODIS Aqua chlorophyll concentrations for the shelf waters of the Mafia Island subregion with data filtered to remove (case II) shallow waters <20 m deep; (a) the 2002–2017 time series averaged over the shelf region approximated by the box indicated on Fig. 9(a), (b) the mean annual cycle of chlorophyll concentrations for this region including the long term mean (blue line) and median (red line) values. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

effect whilst the other is located to the west of Pemba and may be indicative of a recirculating cell or eddy formed by the geography of Pemba Island (the southern coastline of Pemba Island protects the broad and shallow continental shelf of Chake Chake Bay from direct influence by the EACC). The island wake effect and localised upwelling of nutrient rich water to support the higher observed chlorophyll

concentrations has been observed (Roberts, 2015), and eddy shedding downstream of Pemba Island may also impact productivity rates further north. Whilst the southern coastline of Pemba Island protects the waters and sediments of Chake Chake Bay from the EACC the flushing time of water within the Bay is currently unknown.

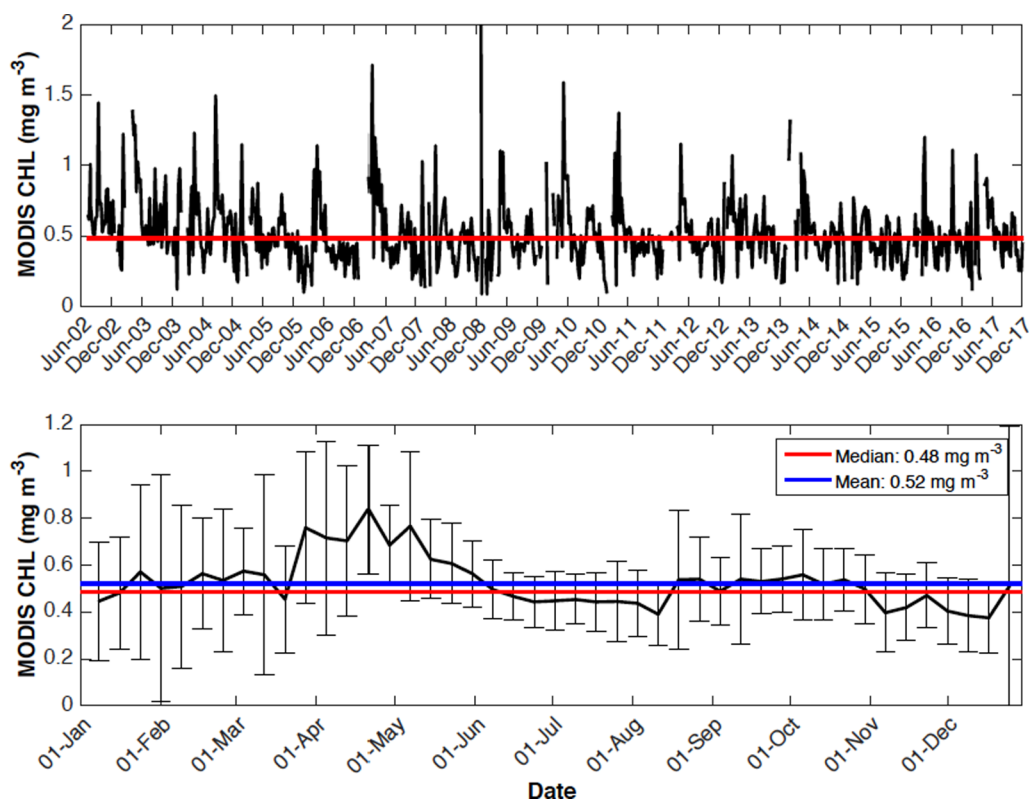


Fig. 13. Analysis of MODIS Aqua chlorophyll concentrations for the shelf waters of the Mtwara subregion with data filtered to remove (case II) shallow waters <20 m deep; (a) the 2002–2017 time series averaged over the shelf region approximated by the box indicated on Fig. 9(a), (b) the mean annual cycle of chlorophyll concentrations for this region including the long term mean (blue line) and median (red line) values. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 7

Mean annual chlorophyll concentrations at 4 subregions within the EACC Ecoregion averaged out to the 200 m and 500 m bathymetric contour.

Region	Mean Annual Chlorophyll to 200 m (mg m^{-3})	Mean Annual Chlorophyll to 500 m (mg m^{-3})	% change
EACC Ecoregion	0.36	0.29	−20
Malindi and North Kenya Banks (2–3.5°S)	0.49	0.29	−40
Dar es Salaam (5.5–7°S)	0.33	0.28	−15
Mafia Island (7–9°S)	0.49	0.37	−25
Mtwara (10–12°S)	0.52	0.36	−31

8.3. Phytoplankton

Studies conducted on phytoplankton diversity within the EACC Ecoregion, mainly sampling in Tanzanian coastal waters, have so far identified ~200–265 individual species (e.g. Bryceson, 1977; Lugomela, 1996; Lugomela and Semesi, 1996; Mgaya, 2000; Limbu and Kyewalyanga, 2015; Moto et al., 2018). This however is likely to be an underestimate given recent observations of previously undocumented dinoflagellate species like *Noctiluca Scintillans* in these waters (Lugomela, 2007), very limited study of the picoplankton (e.g. Kromkamp et al., 1997) and no systematic sampling of the region. Most phytoplankton studies focus on nano- or microplankton size classes due to the relative ease of microscopic identification (e.g. Lugomela and Semesi, 1996), or on rates of community primary production and chlorophyll seasonal dynamics thereby side-stepping the need for taxonomic identities (e.g. Kyewalyanga, 2002). The spatiotemporal variability in phytoplankton distribution and abundance is acknowledged as being poorly known (Kyewalyanga, 2012), in part due to studies on phytoplankton being a minor component of regional botanical research efforts (Nyika and Francis, 1999; Erftemeijer et al., 2001).

Within the limits of available published reports, and with many relevant theses and datasets remaining inaccessible, existing observations suggest a greater diversity of larger phytoplankton species, higher phytoplankton biomass and potentially greater productivities in shelf waters during the NE monsoon than during the SE monsoon months (e.g. Bryceson, 1982; McClanahan, 1988; Kyewalyanga and Lugomela, 2001; Lugomela et al., 2002). This pattern differs markedly from the productivity cycle of the Western Indian Ocean which experiences highest productivities during the SE monsoon (Cushing, 1973). This seasonality is not however universally reported. For example, whilst Kyewalyanga and Lugomela (2001) reported the greatest phytoplankton diversity between January and May for the shallow coastal waters around Unguja Island Lugomela and Semesi (1996) reported no significant difference between monsoon periods in the abundance of diatoms and dinoflagellates. In contrast, Moto et al (2018) reported different community compositions, species abundances and in some cases even different seasonal cycles on either side of Unguja Island indicating that results from limited sampling efforts cannot be extrapolated to cover wider general areas. The seasonal productivity cycle of inshore waters is also reportedly higher during the low turbulent conditions of the NE monsoon months perhaps promoting greater phytoplankton diversity (Bryceson, 1982; Ochumba, 1983), and higher (zoo) plankton abundances at this time (Wickstead, 1961, 1962, 1963; Okera, 1974).

Working in the open waters of the Western Indian Ocean (58–67°E, 16°N–19°S) Thorrrington-Smith (1970) observed a seasonal increase in phytoplankton abundance during the SE Monsoon which was considered coincident with an increase in primary production (citing productivity data from Kabanova (1968)). Both were linked to the seasonal increase in phosphate concentration in response to a shoaling of the thermocline caused by an increase in the transport of the South Equatorial Current at this time. Thorrrington-Smith (1970, 1971) also identified 11 different floral assemblages and 4 phytohydrographic regions. A large number of species (50) were found to be endemic in the waters of the South Equatorial Current and these species, which included

pennate and centric diatoms, dinoflagellates, and coccolithophores dominated all samples regardless of the phytohydrographic region. As the equatorial region is the source region for water ultimately entering the EACC via the NEMC, the phytoplankton assemblages reported by Thorrrington-Smith (1971) provide an important point of comparison for more coastal studies. Krey (1973) subsequently noted that a significant characteristic of the region was the widespread occurrence of *Trichodesmium* whilst also concluding that dinoflagellates and coccolithophores were likely to dominate over diatoms and cyanobacteria in the coastal waters of the Western Indian Ocean. In contrast, Currie et al. (1973) suggested that diatoms particularly *Helicotheca tamesis* (synonym *Streptotheca tamesis*), *Chaetoceros* sp. and *Fragillaria* sp. were likely the most abundant species in the coastal belt. More recent work indicates that the dominant diatom species are typically *Rhizosolenia* sp., *Nitzschia* sp., *Chaetoceros* sp., *Bacteriastrum* sp., and *Navicula* sp., whilst dominant dinoflagellate species are *Ceratium* sp., *Dinophysis* sp., *Prorocentrum* sp. and *Prorocentrum* sp. (Limbu and Kyewalyanga, 2015). Moto et al. (2018) found that in more exposed settings *Chaetoceros* sp., *Rhizosolenia* sp. and *Nitzschia* sp. dominated the phytoplankton community being up to 15 times more abundant than dinoflagellates whilst in more sheltered waters total diatom and dinoflagellate abundances were more balanced, an observation likely related to differences in turbulent mixing (e.g. Margalef, 1978).

Coccolithophore diversity within the EACC Ecoregion is poorly studied but the region is known to host a community assemblage that is distinct from that of the open Indian Ocean. Stolz et al. (2015) identified 56 species from a single study within the Pemba Channel during the NE monsoon period (February). Coccosphere abundance proved to be highly variable between samples ranging from 0 to ~23,000 coccospheres L^{-1} . However, only the species *Florisphaera profunda*, *Gephyrocapsa oceanica*, and *Emiliania huxleyi* were considered numerically important with *G. oceanica* unusually dominating the coccolithophore assemblage of the upper euphotic zone (<50 m). These findings contrast with the identification of 26 coccolithophore species in the Eastern equatorial Indian Ocean during approximately the same monsoon period (Liu et al., 2018) with temperature suggested as a factor altering the diversity in coastal waters (Stolz et al., 2015). Both studies however report fewer species than the 83 taxa reported from the Arabian Sea (Schiebel et al., 2004), or the 171 taxa reported from the open waters of the subtropical and tropical Atlantic Ocean (Poulton et al., 2017). It is not known from in-situ observations if coccolithophore diversity or abundance decreases during the SE monsoon period as seems to be the case for the cyanobacterium *Trichodesmium* and other larger phytoplankton (Kyewalyanga and Lugomela, 2001; Lugomela et al., 2002). Satellite retrievals of calcite concentrations suggest peak calcite concentrations during June/July in the very near coastal waters which, if true, would distinguish them from offshore waters where peak calcite occurs during the NE monsoon months (Hopkins et al., 2015). Anecdotal observations recorded by Taylor (1973) suggest that coccolithophores were notably abundant at station 417 of the “Anton Brun” cruise (Nov’64, 7.05°S, 42.56°E) but apparently less abundant closer to the coast thus more observational evidence is required to understand the spatiotemporal variability in coccolithophore populations.

The extensive analysis of dinoflagellates within the Indian Ocean reported by Taylor (1973, 1976) identified over 300 species from 40 genera. Coverage of the tropical coastal WIO was limited to a single

transect from Mombasa to Madagascar, and thus through the centre of the EACC Ecoregion. Species of the genus *Ceratium* (75 species) dominated oceanic waters whilst the second most dominant genus *Peridinium* was generally restricted to neritic waters. During the SE monsoon and intermonsoon period (July–Nov) dinoflagellates were poorly recorded in the Mozambique Channel, with coastal stations generally exhibiting higher abundances than offshore stations. Stations off Kenya (near Mombasa) were particularly rich and also contained numerous diatom and coccolithophore species. Insufficient data prevented a NE monsoon classification for the waters near Africa. More generally however, dinoflagellates were more uniformly abundant in the WIO during the SE monsoon and patchy during the NE monsoon, with the exception of shear zones such as between the equatorial and counter currents when dinoflagellate abundances were notably higher.

Early demonstrations of the importance of small phytoplankton for total primary productivity in the Indian Ocean were reported by Saijo (1964) and Saijo and Takesue (1965) who identified a significant contribution of between 15 and 37% to total productivity from organisms passing through a 0.8 μm filter. Mullin (1965a, 1965b) subsequently demonstrated that the 1–10 μm size fraction was the dominant contributor to total particulate organic carbon with this size fraction providing an average of 58% of total POC, though in an addendum to this work Mullin (1965a, 1965b) argued that detrital or heterotrophic carbon was the major component of this size fraction. The subsequent discoveries of *Synechococcus* (diameter 0.8–1.5 μm) (Waterbury et al., 1979) and particularly *Prochlorococcus* (diameter 0.5–0.7 μm) (Chisholm et al., 1988) readily explain these initial findings and it is now recognised that primary production in tropical oceanic waters is dominated by *Prochlorococcus* which can account for 50% of biomass and productivity, with *Synechococcus* making significant contributions in coastal and mesotrophic waters (Liu et al., 1997; Partensky et al., 1999; Agawin et al., 2000; Johnson et al., 2006). There have been no studies of *Prochlorococcus* or of *Synechococcus* distributions or abundances within the EACC Ecoregion and observations from the wider Indian ocean are still limited (Buitenhuis et al., 2012). Nevertheless, a genetically distinct high-light, low iron adapted clade of *Prochlorococcus* has been identified from the equatorial Indian Ocean (Rusch et al., 2010). Given the prevailing circulation, the linkages between equatorial waters and the EACC Ecoregion, and the nutrient depleted nature of the EACC it is likely that the waters host *Prochlorococcus*. Thus the apparent maximum seen in satellite chlorophyll measurements during the SE monsoon and the conflict with in-situ studies that show peak nano- and microplankton abundances during the NE monsoon may resolve itself once appropriate measurements of the picoplankton community are made. The increase in surface chlorophyll during the SE monsoon could therefore be due to the advection of open ocean *Prochlorococcus* populations into the EACC Ecoregion. The advection of water from the open Indian Ocean into the region may also explain the seasonal disappearance of *Trichodesmium* from these waters as it is conceivable that low Fe conditions are advected into the EACC region during the SE monsoon.

The recent identification of *Noctiluca scintillans* in the Zanzibar Channel may be related to the appearance of large scale blooms of this species in the Arabian Sea during the NE monsoon (Rosario Gomes et al., 2014), though *N. scintillans* is certainly present elsewhere in the Indian Ocean (Conway et al., 2003). Over recent decades near surface waters of the Arabian Sea have displayed increased hypoxia which coincides with the increased dominance of *N. scintillans*, and which has resulted in the displacement of previously dominant diatom populations. Grazing experiments conducted by Rosario Gomes et al. (2014) suggest that as the dominance of *N. scintillans* grows there will be a shift from a diatom-copepod based food web to one where salps and jellyfish dominate due to *N. scintillans* being too large to be grazed by copepods. As jellyfish and salps represent a minor component of fish diets compared to copepods there could also be a subsequent impact on regional fisheries. Whether the identification of *N. scintillans* in

Tanzanian waters marks the start of a floral shift in the phytoplankton community or a belated identification of a species long present in these waters is unclear. As *N. scintillans* is a prominent source of bioluminescence its historical presence may well be inferred from anecdotal accounts of bioluminescence – accepting that several other species may also be responsible – but such accounts do not appear to exist for this region. Further observational effort to determine the presence and distribution of this species would be advisable, particularly in relation to future changes to fisheries.

A key biogeochemical attribute of these waters is the presence of a regionally important population of *Trichodesmium*. Pelagic nitrogen fixation is recognised as an important process in the Western Indian Ocean (e.g. Westberry and Siegel, 2006) but there have been limited in-situ investigations to date, either within the WIO or across the wider Indian Ocean (Mulholland and Capone, 2009). Williams (1958) recorded the regular occurrence of *Trichodesmium* blooms during the NE monsoon months (December–January) along the Kenyan coast for the years 1951–1954 and anecdotal accounts of surface slicks attributed to *Trichodesmium* across the wider north Indian Ocean are common (e.g. The Royal Society, 1961, 1962, 1963, 1964, 1965). Direct enumeration of *Trichodesmium* abundances or measurement of nitrogen fixation rates in East African coastal waters does not appear to have occurred earlier than the mid 1970s (Bryceson, 1977, 1980; Bryceson and Fay, 1981; Bryceson, 1982) though *Trichodesmium* was certainly observed and quantified further east in earlier years (e.g. Thorrrington-Smith, 1971). *Trichodesmium* is common to the coastal waters of Tanzania and Kenya during the NE monsoon months but appears largely or totally absent during the SE monsoon months, with most explanations for this focussing upon increased windiness and turbulence and deeper mixed layers during the SE monsoon period (Bryceson and Fay, 1981; Lugomela and Semesi, 1996; Kromkamp et al., 1997; Kyewalyanga and Lugomela, 2001; Lugomela et al., 2002). Surface abundances of up to 60×10^6 trichomes m^{-3} have been recorded off Tanzania with lower abundances of $<8 \times 10^6$ trichomes m^{-3} further north off Kenya (Kromkamp et al., 1997; Lugomela et al., 2002; Luo et al., 2012). However, in what were considered exceptional circumstances Kromkamp et al (1997) observed abundances as high as 6.63×10^9 trichomes m^{-3} in Kenyan waters. Five species of *Trichodesmium* (Janson et al., 1995) have so far been identified within the region with *T. erythraeum* representing up to 70% of the community (Lugomela et al., 2002). *Trichodesmium* primary production can contribute up to 20% of total water column productivity during the NE monsoon period being lower at other times of year (Lugomela et al., 2002). N_2 fixation rates have been less frequently recorded than *Trichodesmium* abundances but the most comprehensive study to date suggests a mean annual N_2 fixation rate of $42.7 \text{ mmol N m}^{-3} \text{ yr}^{-1}$ for the surface coastal waters off Tanzania (Lugomela et al., 2002). This would equate to a mean daily surface fixation rate of $\sim 117 \mu\text{mol N m}^{-3} \text{ d}^{-1}$ which is towards the upper limits of global nitrogen fixation estimates (Luo et al., 2012), but comparable to Kromkamp et al. (1997) who reported surface nitrogen fixation rates off Kenya ranging from 0.4 to $434 \mu\text{mol N m}^{-3} \text{ d}^{-1}$ and increasing to almost $80,000 \mu\text{mol N m}^{-3} \text{ d}^{-1}$ within a dense *Trichodesmium* bloom. Integrated nitrogen fixation rates remain rare for this region. The results reported by Kromkamp et al (1997) indicate typical integrated rates of $<87 \mu\text{mol N m}^{-2} \text{ d}^{-1}$ increasing to $15.6 \text{ mmol m}^{-2} \text{ d}^{-1}$ under exceptional bloom conditions.

Also present in these waters is the nitrogen fixing cyanobacterium *Richelia intracellularis*, a heterocystous forming endosymbiont of several diatom genera such as *Hemiaulus* and *Rhizosolenia* e.g. (Venrick, 1974; Villareal, 1991). Diatom-Diazotroph Associations (DDA's) are widely noted across much of the Western Indian Ocean from the southern tip of Madagascar (Poulton et al., 2009) to the west Indian coast (Jabir et al., 2013). The regional significance of *R. intracellularis* is therefore considered to be high but not yet fully evaluated (Bergman, 2001; Lugomela et al., 2001a, 2001b) with study of *R. intracellularis* within the EACC Ecoregion limited to the work of Lyimo (2011). In that study *R.*

intracellularis was found to be present in the Zanzibar Channel throughout the year with peak monthly abundances of 428 ± 105 filaments L^{-1} occurring during the SE monsoon (August). The timing of peak abundance is notable as both *Trichodesmium* abundance and bulk rates of nitrogen fixation peak during the NE monsoon but Lyimo (2011) cautions that further observational support is required to confirm this seasonal cycle due to significant spatiotemporal variability within the observations and the small dataset of *R. intracellularis* currently available for these waters.

Nitrogen fixation requires a source of iron but measurements of dissolved iron (dFe) concentrations in the Western Indian Ocean are very rare and there are no measurements from East African coastal water (Tagliabue et al., 2012; Grand, 2014). Limited measurements along 70°E indicate typical surface dFe concentrations of $<0.1\text{--}0.3$ nmol L^{-1} (Niskio et al., 2013), measurements from 67°E suggest concentrations of ~ 0.3 nmol L^{-1} (Saager et al., 1989) whilst measurements around 56°E indicated dFe concentrations below detection limits (1.7 nmol L^{-1} ; (Morley et al., 1993)). Models suggest Fe limitation of the tropical coastal ocean including the EACC Ecoregion (Wiggert et al., 2006). Nevertheless, close proximity to the islands of the Zanzibar archipelago, the mainland continental shelf and the African continent may provide sufficient Fe to support the prevalence of diazotrophs and nitrogen fixation in these waters.

Enhanced phytoplankton biomass and productivities in shallow water areas during the NE monsoon and intermonsoon months may also be strongly linked to river discharges which peak around April–May (UNEP / WIOMSA, 2009). Remote sensing data for the deeper waters of the Pemba Channel however reveal a potential contradiction. Whilst it is true that warmer, more stable conditions occur during the NE monsoon months and coincide with a shallower mixed layer, surface chlorophyll concentrations are highest over deep water areas during the SE monsoon months (Jul–Oct), when wind speeds are higher, SST's are cooler and the mixed layer is deeper (e.g. Fig. 3). Ordinarily, stronger winds and a deepening mixed layer would indicate entrainment of water from depth. Extant nutrient observations generally show low nutrient conditions extend down to the thermocline year-round thus the significance of any downward movement in the position of the thermocline for nutrient enrichment of the overlying surface waters during the SE monsoon is unclear. The analysis of WOD and literature nutrient data is inconclusive on the timing of peak nutrient concentrations due both to the paucity of data available and the contrasting conclusions reached (e.g. Fig. 7, Table 5).

The changing monsoon seasons represent the dominant influence on the region. In recent years repeated observational effort around Unguja Island has highlighted both the impact of the changing monsoons on coastal waters but also the scale of natural variability between geographically closely located but ecologically distinct sites. Conditions during the NE (hot calm conditions) and SE (cooler, windier conditions) monsoons have an appreciable impact on the upper ocean and in particular on the East African Coastal Current (Newell, 1957, 1959; Leetmaa and Truesdale, 1972). Bryceson (1982) documented the impact the monsoons have on the phytoplankton community in coastal waters around Dar es Salaam noting, as have others, that a strong floristic shift between seasons is characteristic of the Western Indian Ocean. However, a growing number of studies are beginning to reveal inconsistencies and an explanation for this is currently lacking. All phytoplankton studies report *Trichodesmium* abundances to be highly seasonal with peak abundances during the NE monsoon and a total or near total absence during the SE monsoon. For diatoms and dinoflagellates however, some studies suggest higher abundances during the NE monsoon whilst others suggest peak abundances occur during the early SE monsoon months e.g. (Kyewalyanga and Lugomela, 2001; Limbu and Kyewalyanga, 2015). There are insufficient taxonomic observations to readily resolve these discrepancies but observations from sheltered or exposed locations, from east or west of the islands or from areas subject to riverine influences almost certainly differ in both their

communities and in their responses to monsoonal forcings.

Monsoon seasonality is not just restricted to the autotrophs. Wallberg et al (1999) examined the plankton community during the rainy (April) and dry (August) seasons in 1995–97 and found significant differences in bacterial and phytoplankton production, and in heterotrophic nanoflagellate growth rates between the seasons. Heterotrophic organisms increased their growth rate but not their biomass during the rainy season whilst the results of a simple carbon budget indicated a 3-times higher carbon flow from heterotrophic and autotrophic bacteria to heterotrophic nanoflagellates during the rainy season. Despite higher growth rates during the rainy season Wallberg et al (1999) suggest that heterotrophic microorganisms may actually be a more important carbon source for higher trophic levels during the dry season due to coincident lower productivity by larger phytoplankton.

8.4. Harmful algal blooms (HABs)

Knowledge of HAB species in East African coastal waters is considered lacking due to the absence of established research groups and the expense of establishing routine monitoring programmes (Hansen et al., 2001). As the region is highly dependent upon artisanal fisheries and as aquaculture is a rapidly developing industry in Kenya, Tanzania and Madagascar there is recognition of the need to consider toxic algal problems across the region given their prevalence (Tamele et al., 2019). In constructing a guide and taxonomic key to potentially toxic marine microalgae of the Western Indian Ocean Hansen et al. (2001) noted the presence of 60 potentially toxic species which may occasionally be present at high concentrations. However, different species were found in coastal waters off Kenya, Tanzania and Madagascar suggesting that each country will need to focus resources on the problem locally as well as considering the broader regional problem. A recent review of marine toxins in East African waters by Tamele et al. (2019) highlighted the presence and potential impact of toxic or potentially toxic cyanobacteria, diatom and dinoflagellate species along the Tanzanian and Kenya coasts. Comparatively more toxic diatom and dinoflagellate species were reported from Kenyan waters than from Tanzanian waters whilst cyanobacteria were more prevalent in Tanzanian waters.

To improve knowledge of HAB species in the region Kyewalyanga and Lugomela (2001) reported results of an exploratory study of microalgae at four sites close to Unguja Island conducted between September 1998 and June 1999. They documented 40 diatom species of which one, *Pseudo-nitzschia* spp., was potentially harmful, 26 dinoflagellate species of which 19 are known to be harmful and 10 cyanobacteria species, of which 4 are potentially harmful. Though cell abundances were not reported in this study the results do reveal important temporal patterns. For instance, diatoms displayed two diversity peaks being most diverse in Oct/Nov (up to 12 species) and again in Apr/May (up to 26 species). Dinoflagellates meanwhile had a low assemblage diversity during Oct/Nov (3 species) but this peaked in Feb (17 species) and again in May (14 species). A minor diversity peak was also noted in June (6 species). Finally, the diversity within cyanobacteria was at a minimum in Nov/Dec (1 species – *Trichodesmium* spp.) but peaked during Jan/Feb (6 species). *Trichodesmium* spp. were mainly present during Jan/Feb when cyanobacterial diversity was highest and thus coincident with the NE monsoon months. The study concludes with a warning that harmful species are indeed present around Unguja Island and may respond negatively to increased human pressures including pollution and sewage outflows, problems which are well recognised around the major urban areas (UNEP, 2009, 2015). More recently Moto et al. (2018) identified a further five potentially harmful and previously unobserved species around Unguja Island with the suggestion that shipping ballast waters may have introduced these species.

Kiteresi et al. (2013) documented 39 potentially harmful algae along the Kenyan coast including 18 diatom species/genera's, 20 dinoflagellate species/genera's, 9 cyanobacteria, 2 flagellate species, 2

Table 8
Indian Ocean productivity estimates.

Region	Productivity (g C m ⁻² d ⁻¹)	Source
Indian Ocean (mean annual)	0.22	Koblentz-Mishke et al., 1970
Indian Ocean (mean annual)	0.21	Prasad et al., 1970
Indian Ocean (mean annual)	0.31	Cushing, 1973
Indian Ocean (mean annual)	0.18	Berger et al., 1987; 1988
Indian Ocean (mean annual)	0.26	Antoine et al., 1996
Indian Ocean (mean annual)	0.24	Behrenfeld and Falkowski, 1997
Indian Ocean (mean annual)	0.38	Carr et al., 2006
Western Indian Ocean (mean annual)	0.35	Ryther et al., 1966
Western Indian Ocean (mean annual)	0.24	Prasad et al., 1970
Eastern Indian Ocean (mean annual)	0.19	Prasad et al., 1970
Indian Ocean NE monsoon (mean season)	<0.1	Kabanova, 1968
Indian Ocean NE monsoon (mean season)	0.15 ± 0.15	Cushing, 1973
Indian Ocean SE monsoon (mean season)	0.27	Kabanova, 1968
Indian Ocean SE monsoon (mean season)	0.5 ± 0.34	Cushing, 1973
Western Indian Ocean (NE monsoon)	0.4–0.5	Krey, 1973
Indian Ocean (mean annual) MONS province	0.29 ± 0.07	Longhurst et al., 1995
Indian Ocean (mean annual) ARAB province	1.26 ± 0.88	Longhurst et al., 1995
Indian Ocean (mean annual) EAFR province	0.52 ± 0.13	Longhurst et al., 1995
NE monsoon (MONS province)	0.26 ± 0.02	Longhurst, 1995, 1998
SE monsoon (MONS province)	0.33 ± 0.09	Longhurst, 1995, 1998
NE monsoon (ARAB province)	0.68 ± 0.09	Longhurst, 1995, 1998
SE monsoon (ARAB province)	1.93 ± 1.00	Longhurst, 1995, 1998
SE monsoon (ARAB province non-upwelling)	0.7 ± 0.4	Smith and Codispoti, 1980
NE monsoon (EAFR province)	0.62 ± 0.12	Longhurst, 1995, 1998
SE monsoon (EAFR province)	0.43 ± 0.05	Longhurst, 1995, 1998

haptophyte species and 2 raphidophytes species. This study suggests that there has been an increase in the number of harmful species identified in Kenyan waters since 2001 but whether this is a real increase or the result of improved observational effort is unclear.

A more detailed examination of the environmental controls on *Pseudo-nitzschia* distribution in the coastal waters of Dar es Salaam was reported by Lugomela (2013). The abundance of *Pseudo-nitzschia* spp. was low throughout the 1-year study period (<16 cells L⁻¹) and no seasonality was evident. No correlation between *Pseudo-nitzschia* spp, particularly *Pseudo-nitzschia pungens* which was the most common species, and the measured variables of salinity, temperature, pH, dissolved oxygen, chlorophyll, NO₃⁻ or PO₄³⁻ was identified. Consequently this study argues for awareness of the presence of a known toxic species but understanding the environmental controls on its abundance or distribution requires further work.

8.5. Primary production in the Western Indian Ocean

Several estimates of Indian Ocean productivity have been published (Table 8). In a seminal paper, Ryther et al. (1966) estimated a mean productivity rate for the WIO of 0.35 g C m⁻² d⁻¹ based on 231 stations sampled during 1963–1964. Despite significant spatiotemporal variability in productivity rates and a noted lack of seasonal coverage, Ryther et al. (1966) concluded that the WIO was ‘somewhat more productive than other oceanic regions’. However, the spatial resolution of data was poor and the extrapolation of productivity results into under-sampled regions produced a wide range of daily productivity rates, particularly for East African waters (a weakness noted by Ryther et al., 1966; Bryceson, 1984). Rates ranged from >1 g C m⁻² d⁻¹ near Mombassa (~4.04°S), to between 0.51 and 1 g C m⁻² d⁻¹ in a south-easterly direction from the Kenyan coast towards Madagascar or to 0.26–0.5 g C m⁻² d⁻¹ southwards along the Tanzanian coastline, a gradient that cannot be justified given the lack of sampling in these waters.

A more comprehensive and detailed map of Indian Ocean production was reported by Kabanova (1968) who synthesised productivity data from over 1600 stations collected in the Indian Ocean between 1951 and 1965. The WIO was found to be more productive than the Eastern Indian Ocean (EIO) and the Indian Ocean as a whole was less

productive during the NE monsoon (1.2 × 10⁹ tons C yr⁻¹) than during the SW monsoon (2.7 × 10⁹ tons C yr⁻¹). Integrated productivities for the NE monsoon period (Dec-May) were low over much of the open ocean (<0.1 g C m⁻² d⁻¹) but elevated along the East African coast (0.5–1 g C m⁻² d⁻¹), exceeding 1 g C m⁻² d⁻¹ in some locations. During the SW monsoon (June-Nov) production was generally higher across the whole Indian Ocean with a mean rate of 0.27 g C m⁻² d⁻¹. Along the East African coast productivity estimates were scarce or absent with the few observations reported by Ryther et al. (1966) strongly influencing the summary. Productivity in Kenyan coastal waters was again reported as 0.5–1 g C m⁻² d⁻¹ and higher than open ocean waters. These data were subsequently incorporated into the global productivity synthesis of Koblentz-Mishke et al. (1970) which revealed higher mean productivity rates in the Indian Ocean than in the Pacific or Atlantic Oceans (0.22, 0.13 and 0.19 g C m⁻² d⁻¹ respectively). Koblentz-Mishke et al. (1970) estimated a mean productivity for inshore waters globally of 0.25–0.5 g C m⁻² d⁻¹, a range that matched the limited data from the East African region.

Cushing (1973) subsequently reanalysed the global primary production database compiled by Koblentz-Mishke et al. (1970) regridding the data on to a 5° by 5° grid. Along East Africa highest productivity rates occurred during the SE monsoon (1.1–1.45 g C m⁻² d⁻¹) than during the NE monsoon (0.55–0.75 g C m⁻² d⁻¹) (Table 9). When scaled by 180 days to produce an estimate of production during the monsoon periods Cushing estimated monsoon productivities of 198–262 g C m⁻² per 180 days during the SE monsoon and slightly lower productivities of 144–196 g C m⁻² per 180 days for the NE monsoon. A subregional analysis for coastal East Africa (0–15°S)

Table 9

Summary of East African productivity estimates derived from the compilation of Cushing (1973).

Region	SE monsoon (g C m ⁻² d ⁻¹)	NE monsoon (g C m ⁻² d ⁻¹)
Coastal 0–5°S	1.45	
Coastal 5–10°S	1.1	
Offshore 0–5°S		0.55
Offshore 5–10°S	1.1	0.75
Seasonal (per 180 days)	198–262	144–196

obtained a mean productivity of $1.22 \pm 0.2 \text{ g C m}^{-2} \text{ d}^{-1}$ during the SE monsoon and a lower rate of $0.63 \pm 0.1 \text{ g C m}^{-2} \text{ d}^{-1}$ during the NE monsoon. East African coastal waters thus appear more productive during the SE monsoon period.

More recent efforts to compile and synthesise productivity measurements were made by Berger et al (1987, 1988, 1989). This effort collated ~8000 production profiles for the period 1944–1985 based largely on the ^{14}C method. Based on the reported Indian ocean productivity of 4.7 Gt C yr^{-1} and assuming a surface area of $70.56 \times 10^6 \text{ km}^2$, a mean Indian Ocean productivity of $0.18 \text{ g C m}^{-2} \text{ d}^{-1}$ can be obtained (Table 8). It is evident from this more recent synthesis however that productivity rates in the EACC Ecoregion are, like most coastal margins, considerably higher than the oceanic mean with rates reaching $1.4 \text{ g C m}^{-2} \text{ d}^{-1}$.

The introduction of remote sensing methods to estimate primary production immediately addressed some of the spatiotemporal difficulties older syntheses faced. Longhurst et al. (1995) estimated mean productivities of $0.29 \text{ g C m}^{-2} \text{ d}^{-1}$ for the open ocean MONS province and of $1.24 \text{ g C m}^{-2} \text{ d}^{-1}$ for the coastal ARAB province. The coastal province covers the coastal regions of Tanzania, Kenya and Somalia as well as parts of the Arabian Sea thus includes regions of pronounced monsoon driven seasonality and is not directly comparable to the EACC Ecoregion defined here. Nevertheless, from that dataset indicative productivities of 0.68 and $1.93 \text{ g C m}^{-2} \text{ d}^{-1}$ can be calculated for the NE and SE monsoon periods seeming to again confirm the SE monsoon as the more productive period. Antoine et al. (1996) used CZCS data to estimate an annual productivity for the Indian Ocean of 6.6 Gt C yr^{-1} equivalent to a mean daily productivity of $0.26 \text{ g C m}^{-2} \text{ d}^{-1}$, and similar to prior observational syntheses. Behrenfeld and Falkowski (1997) meanwhile estimated a mean annual productivity of 6.2 Gt C yr^{-1} for the Indian Ocean based on monthly mean CZCS data and the vertical generalised production model (VGPM) from which a mean daily rate of $0.24 \text{ g C m}^{-2} \text{ yr}^{-1}$ can be calculated. More recently Carr et al (2006) compared 24 different remote sensing models which estimated a mean Indian Ocean productivity of 9.9 Gt C yr^{-1} equivalent to a daily rate of $0.38 \text{ g C m}^{-2} \text{ d}^{-1}$ (Table 8).

8.6. East African coastal productivity

Whilst typical mean productivities for the Indian Ocean are generally in the range of $\sim 0.2\text{--}0.3 \text{ g C m}^{-2} \text{ d}^{-1}$; (Table 8), such estimates do not adequately reflect the spatiotemporal variability of primary production found more generally within the Indian Ocean or more specifically within the more productive coastal waters of East Africa. At the largest scale for instance, Prasad et al. (1970) showed the WIO to be more productive than the EIO with a mean annual productivity of $0.24 \text{ g C m}^{-2} \text{ d}^{-1}$ compared to $0.19 \text{ g C m}^{-2} \text{ d}^{-1}$. The east–west imbalance in mean productivities is largely driven by the enhanced primary production occurring in the Arabian Sea during the SE monsoon period when intense upwelling occurs. Studies that seasonally resolve productivity rates within the WIO suggest a 2–3 fold variation in mean productivities between seasons with mean productivity estimates ranging from $<0.1\text{--}0.15 \text{ g C m}^{-2} \text{ d}^{-1}$ during the NE monsoon to $0.25\text{--}0.5 \text{ g C m}^{-2} \text{ d}^{-1}$ during the SE monsoon (Kabanova, 1968; Cushing, 1973; Krey, 1973). Seasonally therefore, mean primary production in the central WIO is generally viewed as being highest during the SE monsoon period (Jun–Oct) (e.g. Nair and Pillai, 1983). These broad spatial averages however conflict with more detailed in-situ observations from coastal waters.

Productivity estimates for the EACC Ecoregion are presented in Table 10. At Station ‘Z’ (approximately 6.49°S , 39.87°E) located to the east of Unguja Island Newell (1959) estimated a mean productivity of $0.21 \text{ g C m}^{-2} \text{ d}^{-1}$ for the NE monsoon period based on dissolved oxygen profiles. This mean estimate was set against a background of significant variability with coincident measurements of phosphate and plankton distributions revealing a seasonal plankton cycle beginning

with the onset of the NE-monsoon ($\sim$ Nov) and peaking in March before declining through May and June. The intraseasonal variability in daily productivity rates was not recorded by Newell (1959) but may have varied significantly relative to the mean productivity value reported. Coastal waters were considered to be less productive between June and September during the SE monsoon implying a typical productivity rate of $<0.2 \text{ g C m}^{-2} \text{ d}^{-1}$ and thus an opposing seasonality compared to the open WIO. Newell’s (1959) mean productivity estimate for the NE monsoon period matches a productivity rate of $0.21 \text{ g C m}^{-2} \text{ d}^{-1}$ from a single station within the EACC reported by Steemann Nielsen and Jensen (1957) for the intermonsoon period (May) and is comparable to productivity estimates for the NE monsoon period from within the South Equatorial Current ($\sim 0.23 \text{ g C m}^{-2} \text{ d}^{-1}$; (Steemann Nielsen and Jensen, 1957)). In contrast Lugomela et al. (2001a, 2001b) reported productivity rates reaching $4.1 \text{ g C m}^{-2} \text{ d}^{-1}$ in the shallow coastal waters of the Zanzibar Channel during May and June. Such rates are significantly higher than the Indian Ocean mean (Table 8) and even higher than rates of $1.7\text{--}2.5 \text{ g C m}^{-2} \text{ d}^{-1}$ reported from the upwelling regions off Somalia (Smith and Codispoti, 1980; Owens et al., 1993).

The inconsistency in the timing of peak production between the shelf and the open ocean likely reflects broader scale variability as well as sparse sampling of the region. Newell (1959) found little evidence of photosynthetically driven changes in oxygen concentrations during the SE monsoon months but noted that phosphate concentrations were generally higher than during the NE monsoon months. Together these observations were interpreted as indicating minimal productivity during the SE Monsoon. Newell’s (1959) coastal observations therefore suggest higher productivity during the NE monsoon in contrast to the inferences obtained from larger scale WIO mean syntheses (Table 8) (Kabanova, 1968; Cushing, 1973). Subsequent studies in Tanzanian coastal waters by Bryceson (1982, 1984) and McClanahan (1988) indicate more favourable conditions for phytoplankton production – as evidenced by higher chlorophyll concentrations – during the NE monsoon. However, whilst working on the east coast of Unguja Island Kyewalyanga (2002), found no appreciable seasonality in primary production and concluded that chlorophyll alone was not a reliable proxy for productivity due to the occurrence low chlorophyll concentrations during periods of higher productivity. This latter observation conflicts with the analysis of the ARAB and MONS biogeographical provinces reported by Longhurst (1995) who found that changes in chlorophyll was usually a very good indicator of changes in productivity rates. Subsequent work by Peter et al (2018) tends to support the conclusion that there is little or limited seasonality in chlorophyll concentrations around Unguja Island as they found no significant difference in seasonal chlorophyll concentrations which raises the possibility that the seasonality reported by Bryceson (1982) and McClanahan (1988) is not indicative of the wider East African coastal region but perhaps representative of the coastal waters around Dar es Salaam only. The observations reported by Peter et al (2018) lend some credence to this possibility as whilst there was no overall seasonality identified in the data higher chlorophyll concentrations occurred to the east of Unguja Island during the SE monsoon whilst the inshore and more sheltered stations to the west of the island exhibited peak chlorophyll concentrations during the NE monsoon. Peter et al (2018) linked this discrepancy to the influence of sewage and municipal discharges to the west of Unguja Island rather than to oceanographic factors.

As with chlorophyll measurements, size-fractionated productivity measurements are seldom reported. Lugomela et al. (2001a, 2001b) however presented a carbon budget for the Pemba Channel based on plankton composition and carbon cycling observations which included productivity estimates for four size classes. A single sampling site in the Zanzibar Channel was visited 12 times over a 2-month period in May/June 1999 coinciding with the end of the long-rain intermonsoon period and onset of the SE monsoon. Bulk integrated primary production ranged over 20-fold from 204 to $4142 \text{ mg C m}^{-2} \text{ d}^{-1}$ possibly in response to rainfall and/or tidal state but the contribution to total

Table 10
Primary productivity estimates from the EACC Ecoregion.

Region	Season / time period	Productivity ($\text{g C m}^{-2} \text{d}^{-1}$)	Productivity ($\text{mg C m}^{-3} \text{h}^{-1}$)	Source
Around Pemba Island (4.7–6.1°S)	Late SE monsoon	0.79–1.89		Barlow et al., 2011
Coastal East Africa (0–10°S)	SE monsoon (mean)	1.2		Cushing, 1973
Coastal East Africa (0–10°S)	NE monsoon (mean)	0.6		Cushing, 1973
Gazi estuary (4.4°S)	SE monsoon (Jul)	0–0.11		Goosen et al., 1997; Kromkamp et al., 1997
Sabaki estuary (3.166°S)	SE monsoon (Jul)	<0.01–0.07		Goosen et al., 1997; Kromkamp et al., 1997
Kiwayuu estuary (2.05°S)	SE monsoon (Jul)	0.03–0.60		Goosen et al., 1997; Kromkamp et al., 1997
Gazi estuary (4.4°S)	Intermonsoon (Nov/Dec)	0.12–2.5		Goosen et al., 1997; Kromkamp et al., 1997
Sabaki range (3.166°S)	Intermonsoon (Nov/Dec)	0.16–1.08		Goosen et al., 1997; Kromkamp et al., 1997
Kiwayuu range (2.05°S)	Intermonsoon (Nov/Dec)	0.08–0.70		Goosen et al., 1997; Kromkamp et al., 1997
Coastal East Africa (0–10°S)	NE monsoon (mean)	~0.5		Krey, 1973
Chwaka Bay (6.17°S)	Annual range		1.66–132	Kywalyanga, 2002
	Annual means		14.8–53.1	
Zanzibar Channel (6.16°S)	Intermonsoon (May/June)	0.2–4.1		Lugomela et al., 2001a, 2001b
Zanzibar (Station Z; 6.49°S)	NE monsoon	0.21		Newell, 1959
Offshore EACC (4.26°S)	Intermonsoon (May)	0.21		Steemann Nielsen and Jensen, 1957
Tanzanian coastal waters (5–11°S)	Intermonsoon (Oct/Nov)	0.26–0.5		Ryther et al., 1966
Somali Coastal Current LME (10°N–12°S)	Annual Mean	0.76		GEF/TWAP, 2015
Gazi Creek (4.44°S)	Annual cycle	0.31–1.74		Wawiye, 2016

production by the four size classes were broadly similar. The $>100 \mu\text{m}$ and $10\text{--}100 \mu\text{m}$ size fractions contributed $\sim 30\%$ each to total primary production, while the $0.2\text{--}2.0 \mu\text{m}$ and $2.0\text{--}10 \mu\text{m}$ size fractions contributed $\sim 20\%$ each.

Kromkamp et al. (1995, 1997) observed higher productivity during the inter-monsoon months of Nov-Dec than during the SE monsoon months of Jun-Jul in Kenyan coastal waters (Table 10), a pattern that supports the satellite derived cycle of productivity reported by Carr et al., (2006) for the $10^\circ\text{S}\text{--}10^\circ\text{N}$ region of the Indian Ocean. Nutrient concentrations were low in surface waters (<0.1 , <3 and $<0.2 \mu\text{mol L}^{-1}$ for NO_3^- , Si and PO_4^{3-} respectively), and nitrogen was considered the limiting nutrient during the SE monsoon (Mengesha et al., 1999). Production measurements along transects at 4.5°S , 3°S and 2°S during the SE monsoon revealed latitudinal dissimilarities and strong cross shelf gradients in production. At 4.5°S primary production exceeded $0.5 \text{ g C m}^{-2} \text{d}^{-1}$ at the shallowest inshore stations and decreased offshore to $<0.1 \text{ g C m}^{-2} \text{d}^{-1}$ over deeper waters. At 3°S productivity increased from $\sim 0.18 \text{ g C m}^{-2} \text{d}^{-1}$ at the shallowest inshore stations ($\sim 20 \text{ m}$ depth), to $\sim 0.25 \text{ g C m}^{-2} \text{d}^{-1}$ at 50 m deep mid shelf stations before finally peaking at $\sim 0.29 \text{ g C m}^{-2} \text{d}^{-1}$ at 500 m deep stations, thus indicating an increasing offshore productivity gradient. This particular offshore gradient was related to a widening of the continental shelf at this latitude which may have had an impact on nutrient upwelling. However, further offshore production rates decreased suggesting a localised enhancement. At 2°S productivity was high due to the influence of the North Kenya Banks with rates $>0.50 \text{ g C m}^{-2} \text{d}^{-1}$. This enhanced productivity extended offshore to stations located over deep waters which may have been due to advection.

In a supporting study examining new and regenerated production during the SE and inter-monsoon periods Mengesha et al. (1999) found that NH_4^+ uptake dominated at both neritic and oceanic stations leading to low f -ratios (0.01–0.24) during both seasons. NO_3^- uptake rates (new production) varied seasonally being highest during the November inter-monsoon period though ambient NO_3^- concentrations were largely unchanged. NH_4^+ uptake rates (regenerated production) were similar throughout both seasons despite 2-fold higher ambient NH_4^+ concentrations during the SE monsoon period. NH_4^+ typically represented 72% of the DIN pool of the upper mixed layer. Importantly, Mengesha et al. (1999) observed functional differences between neritic and oceanic phytoplankton populations with regards to NH_4^+ concentrations, uptake rates and physiological adaptiveness arguing that a persistent state of high NH_4^+ affinity existed in the (pico-) phytoplankton found offshore but not in the coastal populations. The implications of this study are that whilst the waters of the EACC Ecoregion are typical of oligotrophic waters worldwide that (i) NH_4^+

concentrations should be more widely measured as they appear to be more important for overall productivity rates, (ii) that clear ecological adaptations to neritic and oceanic conditions exist within the phytoplankton community that require closer scrutiny and (iii) that productivity responses to nutrient inputs and environmental stressors is likely to vary between coastal and oceanic regions.

In the Pemba Channel Barlow et al (2011) reported a detailed investigation of phytoplankton productivity from October 2007 (late SE monsoon/inter-monsoon period). Regionally primary production varied from 0.79 to $1.89 \text{ g C m}^{-2} \text{d}^{-1}$ but was $1\text{--}1.3 \text{ g C m}^{-2} \text{d}^{-1}$ in the channel itself (Table 10). Nitrate concentrations in the surface mixed layer within the channel were generally $<0.25 \mu\text{mol L}^{-1}$ (Table 5). A subsurface chlorophyll maxima was present ranging in depth from 28 to 90 m . In the channel chlorophyll was generally dominated by micro- and nanoplankton but east of the islands pico- and nanoplankton dominated. Chlorophyll normalised production (P_{max}^B) ranged from 0.5 to $10.8 \text{ mg C [mg Chl-a]}^{-1} \text{hr}^{-1}$. Such results demonstrate the existence of significant spatial variability in productivity.

8.7. Implications for regional coral ecosystems and fisheries

Warm-water corals are found continuously along two thirds of the Tanzanian coastline, along most of the Kenyan coastline, apart from the far north, and are predominately fringing reefs or patch reefs (Fig. 1; Wagner, 2000; UNEP, 2001; Obura et al., 2002; Arthurton, 2003). Corals grow best in clear warm waters ($>20^\circ\text{C}$) receiving high incident sunlight and regions of high turbidity, regions prone to significant temperature fluctuations (both high and low), or regions exposed to nutrient eutrophication are not amenable locations for coral development (Cohen, 1973; Lewis, 1981; Lerman, 1986; Spalding et al., 2001; Spalding and Brown, 2015). The widespread presence of corals within the EACC Ecoregion (Spalding et al., 2001, 2007), the high regional biodiversity (Obura, 2012), and the likely presence of some species since the Palaeogene ($56\text{--}24 \text{ Ma}$, Obura, 2016), suggests favourable environmental conditions have existed for some time.

It has been estimated that coral reefs support 70–80% of artisanal fish production in East Africa (Ngoile and Horrill, 1993; Maina, 2012) with surrounding mangrove forests and seagrass beds providing important nursery grounds for coral fish populations (van der Velde et al., 1995). Artisanal and subsistence fishing plays a substantial socio-economic role and most fishing typically takes place close to the shoreline (Richmond, 2011). Sardines (*Clupeidae*), anchovies (*Engraulidae*) and mackerel (*Scombridae*) are common target species and are predominantly filter-feeders preying upon zooplankton and in some cases larger phytoplankton (van der Lingen et al., 2009). The dynamics

of phytoplankton and zooplankton populations and their relationship to local environmental conditions are therefore important to understand as they ultimately link to fisheries. It is acknowledged however that further work is required to understand both the variability in marine productivity and the associated trophodynamics underpinning fish stocks within the EACC Ecoregion (ASCLME, 2012b). Furthermore, some fisheries such as the small pelagic fishery of Tanzania are considered poorly understood and at risk of overexploitation (Breuil and Bodiguel, 2015; Anderson and Samoilys, 2016). Across the wider Western Indian Ocean basic information linking small and medium size pelagic fisheries to local environmental conditions or to the implications of climate change is also recognised as being inadequate (van der Elst et al., 2005), even though the projected implications of climate change for the region and for regional fisheries are significant (Cinner et al., 2012; Hoegh-Guldberg et al., 2014; Moustahfid et al., 2018).

Though the information collated here provides improved understanding of the range and variability in a number of basic biogeochemical parameters associated with the EACC Ecoregion there are still numerous difficulties in extrapolating from this information to regional fisheries. Whilst recent paleo-productivity studies based on coccolithophores suggest oligotrophic-like conditions have prevailed for at least the last 300 ka and probably longer (Tangunan et al., 2017) there is a degree of spatiotemporal variability in nutrient (Table 5) and chlorophyll (Table 6) concentrations and in productivity estimates (Table 10) particularly across the shelf region that is poorly understood and which may be related to different physical forcings (e.g. Figs. 10–13). Existing descriptions of biogeochemical seasonality in East African waters (e.g. McClanahan, 1988) are thus incomplete and whilst models can provide insight into the regional circulation they do not yet capture all scales of variability. Similarly, whilst remote sensing can capture aspects of the spatiotemporal variability of chlorophyll and productivity it remains difficult to understand the detailed dynamics and composition of the phytoplankton community via such methods.

The lack of sustained observational programmes focussing on the pelagic realm and infrastructure limitations preventing access to deeper offshore waters may not change quickly but there are alternative actions that can be undertaken to improve knowledge of these waters. Due to the strong current velocities associated with the EACC (up to 2 m s^{-1}) water first encountering the coast at 11°S could in theory travel the $\sim 1000 \text{ km}$ to the confluence with the Somali Current at $\sim 3^\circ\text{S}$ in as little as 7 days. The oceanographic linkages between Tanzania and Kenya are thus extremely strong and consequently the offshore region should be viewed as one oceanographic continuum rather than as a series of discrete sites as is often the case today. Differences in the behaviour and biogeochemical functioning of shallow waters areas are important but the lack of a coherent broader research and synthesis activity has to date prevented commonalities and generalities of the EACC Ecoregion from being articulated. It is evident therefore that only with further study will progress be made in developing the links needed between marine biogeochemistry and regional ecosystems.

9. Conclusions

- The EACC Ecoregion is undersampled but not understudied – A rich picture can be drawn from the varied sources of information available. However, whilst mean annual conditions have been presented here it has not been possible to examine interannual variability due to insufficient data. Furthermore, considerable recent observational information resides in grey literature or other non-traditional publications, and difficulties of access to source data and a lack of consolidation and synthesis prevent the full value of these data sources being realised. Despite widespread efforts to expand knowledge of these waters (e.g. UNEP, WIOMSA) there is still a need for a critical synthesis and examination of existing marine

biogeochemical data from the region as a whole rather than on the basis of territorial or EEZ waters and efforts to move beyond generalities, often the result of inadequate data, must be encouraged.

- General oceanographic descriptions of the region have been available for several decades and are frequently referred to. More recent observations that conflict with the established generalities of the regional circulation however have so far been generally overlooked. Marine biogeochemical observations remain limited and often are geographically restricted to a few key areas of interest (e.g. Dar es Salaam, Unguja (Zanzibar) Island, Kenyan waters), and other easily accessible shallow shelf regions.
- Lack of regular sampling, whether for water quality/pollution monitoring, HAB species monitoring or biogeography purposes inhibits a deeper understanding of processes and biological variability within the region. The few extended or long-term sampling studies reported to date on phytoplankton for instance have typically been located in shallow easily accessible waters and reveal contrasting patterns. The outer shelf and deeper waters of the central sea channels are poorly sampled and study of these areas depends upon international research efforts coming into the region.
- General observations of many basic parameters appear to be missing. Numerous recent global syntheses almost always show the coastal WIO to be devoid of study. Older observations or research programmes still have enormous influence even if the data are of questionable quality or even, in the case of HIOE, if they did not actually sample East African coastal waters.
- World Ocean Database data holdings for the EACC Ecoregion are limited and currently temporally biased to data collected prior to 1996. The submission of more recent data to WOD is encouraged but there are notable discrepancies in coverage and data quality that must first be overcome. WOD data form the basis for most general descriptions of the region given the ease of access.
- There is evidence of inconsistencies in how more recent observational data is generated and reported and efforts to improve data quality control / quality assurance should be considered a priority. Some data (e.g. nutrients) may be improved with increased training efforts. Use of international standards such as nutrient certified reference materials and adoption of best working practices may in some circumstances be feasible but there are financial implications which may be difficult to overcome.
- There is considerable variability in the shallow water areas of the EACC Ecoregion. Such regions are often distinguishable from the waters of the EACC itself. This variability is however poorly described, with a few key studies taken as indicative of the broader region. Long-term measurement programmes are required to fully understand the linkages between various physical forcing mechanisms, marine productivity and fisheries. Several year-long studies conducted around Unguja (Zanzibar) Island or close to Dar es Salaam give contrasting insight into the annual cycle of productivity and thus on the dominant forcing mechanisms. The general perception of year-round downwelling may mask periods of active upwelling either wind-driven or due to island wake effects, that may be important for priming the upper ocean for subsequent productive events.
- International efforts to monitor HABs species and assess the impacts of toxicity events in the WIO region have revealed a general shortcoming of national monitoring programmes which are only now being addressed.
- Primary production estimates from the WIO region, either by season or as an integrated mean, are highly comparable. Nevertheless, primary production measurements in the EACC Ecoregion are rare. Recent time-series around Unguja (Zanzibar) Island have begun to examine the seasonal dynamics of productivity in these waters but the region remains under sampled. Though productivity rates are

low and in keeping with other tropical waters, broad consensus estimates of typical productivity rates in the range $0.5\text{--}2\text{ g C m}^{-2}\text{ d}^{-1}$ appear appropriate but as with all such summaries there are exceptions. These exceptions can be geographically or ecosystem specific i.e. near municipal or sewage outflows or close to mangrove areas. Nevertheless, understanding the productivity of these waters is key for understanding the factors that influence fisheries and to a lesser extent the extensive coral reef network of the region.

- Less evident in the literature are detailed studies examining the interannual variability in productivity due to the scale of the task required. Large-scale observational campaigns of the size of IIOE are difficult to orchestrate and out of necessity could not address all research interests at the required spatiotemporal scales. Limited sampling in the coastal waters of East Africa has long been a major criticism of the IIOE programme and there remain major logistical considerations preventing this from being rectified. The move to remote sensing techniques can ameliorate the logistical difficulty and financial expense of mounting long-term and spatially extensive field campaigns but the continental margins are frequently excluded from basin scale assessments due to shallow water effects. For many of the ecosystems within the EACC Ecoregion productivity within the shallow continental seas is critical but satellite algorithm accuracy for these waters remains unverified.
- There is a rich literature on regional fisheries given its socio-economic importance and multiple large international efforts exist to better assess fish stocks, evaluate stock reliance to fishing pressures and understand the threat posed by climate change along coastal East African and within the Western Indian Ocean more generally. There is widely recognised to be limited information available linking regional marine productivity to fish stocks and that fisheries management efforts are poorly supported by scientific information. Whilst fisheries research now includes efforts to understand natural and anthropogenic drivers of variability in fish catch there remains a recognised gap between the socioeconomic focus of fisheries studies and the link to environmental variability. Uncertainties in the annual cycles of nutrients and primary production, of the environmental drivers of interannual variability in annual productivity rates and the underlying yet distinct behaviour of different fishing grounds are important topics that require attention.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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