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Morphology of the Zambezi River Plume on the Sofala Bank, Mozambique

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Keywords: Sofala Bank, Zambezi River, dispersion patterns, plume, density-driven current

Abstract — Hydrographic data collected in the vicinity of the Zambezi River plume between 2004 and 2007 is discussed alongside historical data to infer the plume morphology. Our strategy involved the establishment of 73 CTD stations. Satellite-derived wind speed data and river discharge measurements at an upriver gauging station were also analysed. The plume dispersion patterns indicated a tendency in its progressive propagation to move both equatorward and poleward. This tendency was not explored in previous studies and places the Zambezi River plume in a short list of plumes across the globe that propagate in a direction opposite to Kelvin or shelf waves. Visual inspection of the salinity profiles revealed that the Zambezi plume is super-critical, indicative of a faster freshwater inflow compared to the phase speed of long internal waves. The plume’s vertical structure was found to be surface-advected when the freshwater discharge measured at Tete was less than 2000 m³s⁻¹, and bottom-advected under larger discharges. A clear distinction was found between the plumes of the Zambezi and Licungo Rivers, characterised by a seaward bending of the salinity contours as the Zambezi freshwater flows downstream past the mouth of the Licungo River.

INTRODUCTION

Freshwater discharges from river basins into the ocean have an important influence on the dynamics of many coastal regions. In these regions, the input of freshwater generates a distinct physical regime, characterised by a surface layer of less saline water flowing over the denser ambient seawater. Following plume generation, a vast range of dissolved and suspended materials reach the ocean with various consequences. The most profound of these occur within the region of freshwater influence and vary from the physical alteration of the coastline, to changes in productivity and the availability of biological resources. For example, evidence of seaward extension of the Zambezi Delta in geological timescales caused primarily by high sediment flux is presented in Walford et al. (2005),
and the impact of the Zambezi freshwater on secondary production, in particular the shrimp fisheries in the adjacent coastal sea, is discussed by Mann and Lazier (2013). An accurate description of the dispersion of plume waters as well as of the plume structure is needed to elucidate these changes.

River plumes are often used as indicators of the spread of materials transported by rivers (e.g. nutrients, pollutants, sediments) to the ocean. For instance, Brakel (1984) analyzed satellite images and found distinctive patches of sediment dispersal in the Malindi Bay in Kenya, indicating a northward transport of the largest sediment plumes, promoted by the prevailing southern monsoon. A typical pattern in a positively buoyant plume is one in which a layer of freshwater spreads over the ambient waters. Within an estuary and near a river mouth, transport in the primary direction is dominated by advection of the river’s momentum and depends largely on the volume, timing and intensity of the river discharge (Fong & Stacey, 2003; Nezlin et al., 2005).

Despite numerous studies conducted along the Sofala Bank in recent years, as well as the proposed linkages between Zambezi River discharge and local secondary production, dispersal patterns of freshwater outflow from the Zambezi River have not been elucidated. However, a concise review of the coastal features along the coast of Mozambique has been provided by Lutjeharms (2006), and includes evidence that the seaward intrusion of freshwater from the Zambezi River can reach up to 50 km offshore, and is confined to a water depth of 15-30 m. The mean outflow of the Zambezi is 3000 m$^3$s$^{-1}$ (Gammelsrød, 1992) and its freshwater discharge is believed to influence not only the near-shore hydrodynamics and ecosystems, but also the offshore mesoscale circulation. This is particularly noticeable when freshwater runoff dominates the water masses within the continental shelf (Schumann, 1998; Sétre & da Silva, 1984).

The Zambezi River plume is documented in this paper, based on data published in a number of reports as well as in situ data collected, to describe its patterns of dispersion.

**METHODS**

**Study Site**

The Zambezi River meets the Indian Ocean on the Sofala Bank (Fig. 1). The connection is made through a relatively large delta, characterised by weak navigability due to obstruction by grass and reeds. The course of the Zambezi River is marked by a number of artificial lakes impounded by dams (Kariba and Cahora Bassa), which are mostly used for power generation rather than water retention during the wet season. Despite regulation of the river flow at the dams, the historical flood seasonality in the lower Zambezi remains undisturbed, with annual floods occurring during the rainy season. However, the current maximum extent of the flooded area is reported to be less than half what it was before the dams were constructed (Scodanibbio & Mañez, 2005). According to Beilfuss and dos Santos (2001), rainfall in the Zambezi river basin is strongly influenced by the movement of the Intertropical Convergence Zone, and in the delta region, this movement translates into a rainy season 4-6 months long between October and April. This region is also highly susceptible to torrential rain from tropical cyclones and depressions that can occur between November and April (Mavume et al., 2009). During the dry season, tidal influence is still noticed 80 km upriver, as noted during field work in September 2009 in this study.

**Data sampling**

The Mozambican National Institute of Fisheries Research (IIP) carried out an oceanographic cruise once every year between 2004 and 2007 on the Sofala Bank using vessels of the semi-industrial shrimp fishery fleet. Hydrographic measurements were collected at the stations illustrated in Figure 1 by deploying an enhanced Seabird CTD system with conductivity, temperature, depth, turbidity, dissolved oxygen and fluorescence sensors. The first measurement...
was taken as close to the surface as possible at each station and subsequent readings were taken in profiling mode at an average of every two decibars. Calibration of salinity or temperature was performed prior to sailing and the post-processing and archiving was undertaken at the IIP headquarters in Maputo.

In the late 1970s, three cruises were conducted on board the R/V Dr F. Nansen to survey the fish resources and fishing potential along the Mozambican coast. Data from these cruises included the physical properties of the water (IMR, 1977, 1978a, b) and these were also used to analyse plume patterns in the present study.

**Ancillary data**

Freshwater discharge from the Zambezi River is measured on a regular basis by the Mozambique National Water Directorate at an upriver station located about 440 km from the river mouth (Figure 2). Monthly-mean wind data for 2000-2008 were extracted from the QuikSCAT dataset in a 2° x 2° box centred at the river mouth. South-easterly winds predominate in this region throughout the year (Nehama, 2012), with a significant change to near easterlies from August to December. No information regarding sea or land breezes is available for this region due to a lack of observations by the national meteorological service.
RESULTS

Plume morphology from historical records

Surface salinity data collected in late September 1977 (IMR, 1977) clearly showed a tongue of less saline water leaving the delta and moving polewards (southwards). During these times, the ship drift indicated a weak equatorward surface current in the near-shore region, and a strong poleward current at the shelf break. Similar patterns were observed in January 1978, a few weeks prior to peak river discharges (IMR, 1978a). A striking seaward bending of isohalines was evident in front of the delta, as well as the occurrence of minimum surface salinity directly offshore of Beira where the shelf has its maximum extension. Vertical salinity profiles taken along the central line of

Figure 2. Seasonal variation in Zambezi River discharge based on 1976-2007 data from the Mozambique National Water Directorate.

Figure 3. Zambezi River discharge data (solid line) derived from the Tete gauge station and QuikSCAT wind data (arrow vectors) for 2004-2007. Shaded areas correspond to periods of plume observation.
the delta revealed a stratified water column, a feature that was less noticeable in the south where the water column consisted mainly of denser ambient water.

In early May 1978, shortly after peak river discharge, the horizontal salinity profile pointed to an equatorward movement of plume waters (IMR, 1978b). The salinity contours of 20.0-34.5 bent landwards in the region north of Quelimane, indicating a limit in the direct influence of freshwater from the Zambezi River; this was in agreement with the observations of Siddorn et al. (2001). The plume waters in May 1978 occupied the entire water column down to 50 metres in transects located near the delta, as noted by the authors of the cruise report. There were clear rise and recession periods, with respective maximum and minimum monthly mean discharges of 3039 and 1633 m$^3$/s$^{-1}$.

**River discharge and wind conditions**

Zambezi River discharge data during the hydrographic surveys in 2004-2007 (Fig. 3) revealed that river discharges were lower than the annual mean discharge (3000 m$^3$/s) in 2004 and 2006, and higher in 2005 and 2007. Daily readings varied a great deal during the

Figure 4. Near-surface salinity derived from CTD data collected in 2004-2007.
sampling period and, during peak discharges, the Zambezi distributaries overspilled their banks forming a broad channel to the ocean, particularly during spring tides (Beilfuss and dos Santos, 2001). Winds were very weak in 2004, moderate in 2005 and 2006, and moderate to strong in 2007. Their direction also varied considerably prior to, during and between plume observations. There was no predominant wind direction in 2004 but winds were mostly south-easterly in 2005, 2006 and 2007. During peak river discharges (January-March), easterly winds, followed by south-easterly winds, were most evident.

The plume observed in 2004

Hydrographic data recorded in 2004 is presented in Figures 4 and 5. The horizontal salinity and temperature profiles both reveal a feature representing plume waters (with a salinity and temperature of around 33.6 and 29.2°C respectively), apparently spreading southwards to 20°S. A re-circulating bulge was not evident in either the horizontal or the vertical salinity profiles. The plume occupied the surface layers at all stations located in the region immediately in front of the delta (Transect D), spreading from the coast to the position of the 100-1000 m isobaths. This

Figure 5. Near-surface temperatures derived from CTD data collected in 2004-2007.
pool of estuarine water of low salinity and high temperature followed the downstream coast, consistent with the theory of a density-driven coastal current (Garvine, 1999).

Vertical profiles at Transect I (Fig. 6), located about 200 km north of the river mouth, corroborated these findings.

The plume observed in 2005

The horizontal plume structure was similar to that observed in 2004 (Figs 4 and 5), except for the greater extent in southward movement by the plume waters. The salinity profile manifested a seaward bending in the isohalines and a second bulge near the mouth of the Licungo River. The extent of the offshore plume displayed in the vertical salinity profile (Fig. 6) was considerably smaller at the periphery of the Zambezi River mouth (Transect D) compared to the plume observed in 2004. The 2005 plume maintained contact with the seabed near the river mouth but elevated elsewhere. The coastal northward current attained its maximum depth at about 25 km from the coast (Transect I).

The plume observed in 2006

Low salinity (<35.0) waters were found almost throughout the study area in 2006 (Figs 4 and 5). The lowest salinities did not occur in the vicinity of the Zambezi mouth, but further south at the coast, directly offshore from Beira where other rivers might have contributed to the freshwater input. The equatorward movement of the Zambezi plume waters near the coast was not as marked in 2006, but rather offshore, suggesting their movement away from the coast. In spite of

Figure 6. Vertical profiles of salinity recorded in Transects D (at the Zambezi River delta) and I (located north of the delta).
this behaviour, the 2006 turbidity profile (Nehama, 2012) has indicated that sediments were transported primarily equatorward.

Vertical profiles of the plume in 2006 (Fig. 6) indicated that low-salinity water was limited to the surface layer to a depth of 20 m near the river mouth (Transect D); such water occupied the entire water column at Transect I further north.

**The plume observed in 2007**

Less dense water of low salinity (<31.0) and high temperature bounded the coast from the delta to the area north of the Zambezi River (Figs 4 and 5), indicating the presence of a strong, buoyancy-driven flow along the coast, extending beyond the limits of the sampled area. The salinity and temperature profiles bent seaward near the mouths of the Cuacua (at Quelimane) and Licungo Rivers, increasing the width of the buoyancy-driven flow considerably. This was more evident at the Licungo River than the Cuacua River. In addition, a considerable amount of suspended sediment was present some distance from the coast directly offshore of this river mouth.

Vertical profiles of this plume revealed that it occupied the entire water column from the coast to a considerable distance offshore (Fig. 6). Its surface layer at coastal stations in all transects consisted of water with <33.0 in salinity and the 33.0 isohaline was located farther offshore in Transect I.

**DISCUSSION**

The Zambezi River plume, as it is known today, is characterised as an estuarine plume that turns northward and proceeds along the coast (Mann & Lazier, 2013; Hoguane, 1997; Siddorn et al., 2001). Data presented here suggest that the above-mentioned northward and subsequent equator-ward flow of plume water might occur during high discharge periods, possibly only in years of extremely high discharge. During the present study, the average discharges were 1300, 2500, 1600, and 6000 m$^3$s$^{-1}$ in consecutive years from 2004, and the transport of plume waters north-eastwards (equatorward) was only found in 2007.

In contrast to earlier publications describing only a northward density-driven flow, plumes in the present study were also found to advect polewards (southwards) in a number of years, including in historical data provided in the IMR (1977, 1978a, b) reports. The exception to this pattern was the plume event recorded in 2007 (Figs 4 and 5) which featured strong north-eastward transport and greatly reduced poleward transport of less dense water.

It must be noted that this poleward transport differs from the upstream (i.e. opposite to the Kelvin wave direction) intrusion of plume waters expected from a number of previous simulation-based studies. For instance, according to Chapman and Lentz’s (1994) predictions, a coastally-trapped upstream flow attached to the coast, caused by "self-advection" of the plume, should be negligible in comparison with the downstream transport of plume waters. Garvine’s (1999) findings, however, yield predictions similar to the findings of this study: he hypothesized that little or no upstream intrusion would occur over a flat bottom, but plume waters would significantly penetrate upstream over even a gentle slope in the absence of a background downstream flow.

The dynamic basis for such upstream propagation was analysed in numerical simulations of the Suo-Nada River plume (Seto Inland Sea, Japan) by Magome and Isobe (2003). Their results supported findings which suggested that a stretched vortex line served as the main driver for the upstream intrusion. According to their review, upstream intrusion of freshwater has been observed in only a few natural systems, viz. the Changjiang River (East China Sea), major Siberian rivers (Arctic), the Mississippi River and the Suo- Nada outlet (Seto Inland Sea, Japan). The results presented here justify the inclusion of the Zambezi River in this short list, although the model results and explanations obtained for other plumes (for instance, Chapman and Lentz, 1994; Garvine, 1999; Magome & Isobe, 2003) cannot be applied in this case, as they link the upstream flow with re-circulation in front of the bulge, which has not been observed in the Zambezi River plume system.
The plumes discussed here are characterised as being super-critical (having a speed of freshwater inflow which exceeds that of the long internal waves), following the characterisation scheme of Chao (1988) and Kourafalou et al. (1966), since the width of plumes delineated by the 34 or 35 isohaline (Figs and 4 and 5) decreases from the bulge region towards the downstream coast. Note that the portion of plume water that spreads upstream was ignored in this classification, and in some cases extends over a larger area (cf. data collected in 2006).

The plumes observed in 2005 and 2007 are classified as being bottom-advected with respect to their vertical structure directly offshore from the riverine sources, while those observed in 2004 and 2006 fall into the category of intermediate. The latter are predominantly vertically stratified, yet with a small degree of homogeneity near the river mouth. The bottom-advected plumes exhibit a higher tendency towards homogeneity throughout their cross-shore extension (Yankovsky & Chapman, 1997). The base of the Zambezi River plume (where it reaches the seabed) extends offshore up to 15-30 km in the region immediately seaward from the centre of the delta (Transect D; Fig. 6).

Freshwater discharges from the Pungoe and Licungo Rivers, located near Beira and north of Quelimane respectively, make an important contribution to overall buoyancy forcing along the coast. The vast majority of the data presented here displayed seaward bending in salinity contours in the vicinity of the Licungo River, which is indicative of a clear distinction between the Zambezi and the Licungo River plumes; this corroborates the observations of Siddorn et al. (2001). We also suggest that the Licungo River plume will limit equatorward spreading of the Zambezi River plume during periods of exceptionally low Zambezi discharge, and it will generate a protuberance in the course of the plume waters during periods of high discharge. On the other hand, no clear distinction was found between the Zambezi and Pungoe plumes, as they merge seamlessly in the shallows of the Sofala Bank.

CONCLUSIONS

This study thus describes the morphological features of Zambezi River plumes observed during single-cruise campaigns conducted between 2004 and 2007. It has shown that the Zambezi River plume is one of a small group of plume systems that penetrate large distances upstream, opposing the Kelvin waves. The downstream portion of the plume is, in general, attached to the shoreline, spreading offshore to the 50 m isobath within a super-critical structure. Plume waters occupy the entire water column at the coast, and the upper 10 to 20 m away from the coast. The plume’s vertical structure is surface-advected under freshwater discharges weaker than 2000 m$^3$s$^{-1}$, and bottom-advected under larger discharges.

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Suitability of Selected Coral Species for Culture in the Ornamental Aquarium Trade

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Keywords: Ornamental coral culture, growth, survival, Pocillopora, Acropora, Porites, Kenya

Abstract — The culture of corals for the aquarium trade has been encouraged as a sustainable alternative to wild harvesting which has increasingly threatened coral reef ecosystems worldwide. A one-year experimental study was undertaken to assess the culture potential of seven scleractinian corals, Pocillopora damicornis, Pocillopora verrucosa, Pocillopora eydouxi, Porites rus, Acropora humilis, Acropora selago and Acropora verwei. Coral fragments obtained from the Mombasa Marine Reserve were transplanted onto artificial substrata placed in the Mombasa Marine Park, a no-take MPA. The fragments were monitored for survival and growth. The latter was measured in each fragment in terms of changes in linear extension of the main branch (axial growth) and branch width (radial growth). Survival after six months ranged from 91% (A. humilis), 88% (P. eydouxi), 80% (P. rus), 79% (A. selago), 62% (P. damicornis), 56% (A. verwei), and 29% (P. verrucosa). Survival increased with fragment size and a minimum size of 2cm in length proved optimum. Mean monthly growth (±SE) in axial length and branch width was highest in A. selago (29.6±4.1mm and 68.3±8.3mm respectively) and lowest for P. damicornis (13.5±4.7 mm and 33.8±7.7mm). This study demonstrated a low-tech method that can be used to establish parent stock for commercial ornamental coral culture.

INTRODUCTION

The value of the global trade in live aquarium organisms has been estimated to be US$ ~200-330 million p.a. (Grey et al., 2005; Wabnitz et al., 2003). The advent of home coral reef aquaria has led to a growing market for live coral (Delbeek, 2001; Wabnitz et al., 2003), involving more than 140 scleractinian coral species and a volume of 11-12 million fragments or colonies per year (Wabnitz et al., 2003). Popular coral genera traded include Trachyphyllia, Euphyllia, Goniopora, Acropora, Plerogyra, Catalaphyllia, Favia, Lobophyllia, Porites, Turbinaria, Montipora and Heliofungia (Wabnitz et al., 2003; Jones, 2008). According to the CITES (Convention on International Trade in Endangered Species of Wild Fauna and Flora) trade database, the top ornamental coral exporting countries are...
Indonesia (91%) and Fiji (8%), while the main importers are the USA (68%), European Union (24%), Japan (3%), Singapore (2%), Hong Kong (1%) and Canada (1%) (Jones, 2008). Kenya is a major supplier of marine ornamental species in the western Indian Ocean (Okemwa et al., 2009) and investors have shown keen interest in diversifying the trade to include cultured organisms to provide an alternative livelihood source for local fisher communities and reduce fishing pressure on the wild stocks.

Stony corals are listed in CITES Appendix II (vulnerable to overexploitation but not at risk of extinction). Their trade is permitted only if the specimens have been legally acquired and their export will not be detrimental to survival of the species or their role in the ecosystem. Culturing of stony corals has increasingly been cited as an alternative approach to reducing the impacts of harvesting on natural coral reefs in developing Indo-Pacific countries (Paletta, 1999). Cultured stony corals can be traded under CITES as long as the exporting country is satisfied that they have been grown from second generation cultured stock (Wells & Barzdo, 1991).

Interest in the culture of stony corals has grown tremendously (Arvedlund et al., 2003) with studies focusing on the development of both sexual and asexual culture techniques. Both farming techniques are encouraged as viable options to maintain a sustainable marine aquarium trade as well as to rehabilitate degraded reefs. Asexual culturing involves use of corals which have been fragmented either naturally or artificially. The coral fragments are cultured either in situ or in land-based aquaria (Delbeek, 2001; Arvedlund et al., 2003; Yap and Molina, 2003). Some costs and benefits may influence the choice of the culture environment. Although in situ culture systems may be more affordable, they may be compromised by predation and variable environmental conditions (Delbeek, 2001). On the other hand, the cost of propagating corals in ex situ systems is considerably higher due to the investment needed to recreate natural reef conditions in terms of water chemistry, nutrients, water flow and light intensity (Lindsay & Stanley, 2004). Comparisons between the two systems have revealed species-specific variations in survival and growth (Moothien Pillay et al., 2011).

Farming of corals in situ for the aquarium trade has been demonstrated to be economically viable in the Pacific region e.g. USA, Fiji, Solomon Islands, Philippines (Paletta, 1999; Delbeek, 2001; Herlan & Lirman, 2008; Lal & Kinch, 2005, Lindsay & Stanley, 2004). In the western Indian Ocean region, similar studies have been conducted at Mafia Island in Tanzania (Lindahl, 1998). Coral transplantation experiments have been conducted in Kenya, comparing growth and survival of coral fragments on natural and artificial substrata to assess their potential for reef rehabilitation in degraded areas (Tamelander et al., 2000). The aim of this study was to assess the suitability of potential ornamental coral species for the aquarium trade by comparing their survival and growth on artificial substrata in an in situ culture system.

**METHODS**

**Study Site**

The study was carried out in the Mombasa Marine National Park (MMNP) between April 2010 and April 2011 (Fig. 1). The MMNP was established in 1988 and, while all forms of resource extraction are prohibited in the park (McClanahan & Kaunda-Arara, 1996; Cros & McClanahan, 2003), it is surrounded by an adjacent reserve where traditional fishing activities are allowed. This reserve, which extends approximately 1 km to the north and 12 km to the south, served as the donor site for the collection of coral colonies for the experiment. The area is covered by seagrass patches, scattered coral bommies and bare sand. The MMNP and reserve have a similar reef structure, bottom topography and depth range, but differ slightly with respect to reef cover (Cros & McClanahan, 2003). The coast is enclosed by a fringing reef approximately 2 km offshore with a deep channel in the
south, and experiences a maximum tidal range of 4 m (Cros & McClanahan, 2003; Kirugara et al., 1998). The area is influenced by cyclic meteorological and oceanographic patterns caused by seasonal changes in the Inter-Tropical Convergence Zone (ITCZ) zone. These changes create two distinct seasons, the southeast monsoon (SEM) and northeast monsoon (NEM) that control many ecological processes. The SEM (April to October) is characterized by high cloud cover, rainfall, river discharge, wind energy, lower temperatures and reduced salinity, resulting in high water-column mixing, fast currents and wave energy. These parameters are reversed during the NEM (November to March). Sea surface temperatures range between 25°C and 31°C all year round.

Construction of culture tables and artificial substrate

Four 2.4 m x 1.2 m table frames were constructed using 20mm diameter round-bar metal rods (Fig. 2a). The table frames were deployed in situ and the legs were secured on concrete blocks to enhance stability. Artificial coral substrata were manufactured using a 50:50 sand-cement mixture. Palm-sized balls of the mixture were hand-pressed into circular disks with a small thumb depression on the centre and two small holes punctured on opposite sides, the design being adapted from similar studies elsewhere (e.g. Clark & Edwards, 1995; Edwards & Clark, 1998; Franklin et al., 1998; Yap et al., 1998; Lindahl & Stanley, 2004; Soong & Chen, 2003; Quinn & Kojis, 2006). A set of four 2ft x 4 ft wire mesh grids served as table tops for each table frame. A piece of nylon monofilament was threaded through the two holes of each dried cement disk and tied onto a wire mesh grid. Fifty cement disks were tied onto each wire mesh grid and labelled using Dymo tape® (Fig 2b).

Collection of the corals and the propagation of coral fragments

Seven coral species were selected for the experiment on the basis of appeal and availability at the collection and experimental sites. These were *Acropora humilis*, *Acropora selago*, *Acropora verwei*, *Pocillopora damicornis*, *P. eydouxi*, *P. verrucosa* and *Porites rus*. Healthy (free of disease and bleaching) donor coral colonies were randomly selected and detached from the natural substratum using a hammer and chisel in the Mombasa Marine Reserve. The colonies ranged in size from 15 to 30 cm in diameter and were transported by boat to the experimental site in Mombasa Marine Park in 20 litre plastic buckets filled with sea water. The experimental site in the park was selected to minimise vandalism and interactions with...
fishing activities which occur in the reserve. The coral heads were left in situ overnight at the site, after which the tips of the branches were clipped off in fragments ranging from 1-4 cm in length. Excess water was removed from each fragment using a paper towel and the fragment was then glued using epoxy resin onto the cement discs already attached on the wire mesh (Fig. 2b and c). The glued fragments were left to set for approximately five minutes, after which each wire mesh grid was gently lowered onto the table frame and secured using plastic cable ties. Coral propagation was implemented in two trials during the SEM and NEM to compare seasonal variation in growth and survival. The SEM trial was initiated on 9 April 2010, while the NEM trial was initiated on 18 November 2010. In total, 800 coral fragments were propagated as shown in Table 1. The cement disks were gently cleaned every four weeks of all fouling organisms. A sample photo of the propagated fragments at the end of the experimental period is shown in Fig. 2d.

Environmental parameters
Sea surface temperature and salinity were measured monthly around midday using a mercury thermometer and a hand-held refractometer for three consecutive days at the experimental site. The data were later compared with remotely sensed satellite data for the same period obtained from www.worldseatemp.com/en/Kenya/Bamburi. In addition, three replicate samples of sea water were collected and

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Figure 2. a) Diagram of a culture table, b) coral fragment attached to a labelled cement disk and secured to the wire mesh grid with nylon monofilament, c) fragments prior to deployment and d) at the end of the experiment.
transported to the KMFRI laboratory where they were filtered through a 5µ GFF filter and dried at 60°C in a muffle oven to constant weight, after which they were reweighed to determine total suspended matter.

**Measurement of fragment growth and survival**

Fragment growth was monitored by measuring the change in linear extension of the main branch of each fragment (L: the total length to the apical tip) and its branch width (W: the widest diameter perpendicular to the axial length). The first measurements were taken using a metal vernier calliper one month after fragment deployment in May 2010 to allow for acclimatization. Measurements were thereafter recorded in July, September and December 2010 and April 2011. Survival rate was calculated as the percentage of the originally transplanted fragments still living at each measuring interval.

**Statistical analyses**

The linear measurements of the coral fragments were standardized to mm/month to compare growth rates between the coral species and seasons. Fragments that had lesions, or manifested negative growth, were excluded from the calculations. The data obtained between May and September 2010 for four species (A. humilis, A. selago, A. verwei and P. damicornis) were compared with data obtained for these species between September and April 2011 to determine variations in growth rate between the SEM and NEM. The number of healthy fragments used in the analyses ranged between 30 and 40 for each species. Linear regression analysis of the final L and W values was undertaken for five species (A. humilis, A. selago, A. verwei, P. damicornis and P. verrucosa) to determine the relationship between these dimensions. Mean growth rates for each species were then compared using one way ANOVA and Tukey’s Honest Significant Difference test within STATISTICA 6.0. The difference between the mean size of surviving and dead fragments during the first twelve-week period was tested using Student’s t-test. Variance in the sea surface temperatures and total suspended matter were compared between the NEM and SEM using Student’s t test. Correlation between in situ temperature and satellite temperature data was tested by linear regression.

**RESULTS**

**Environmental parameters**

Trends in the in situ mean temperature data correlated well with the satellite data ($R^2 = 0.74$), although the in situ temperature were slightly higher (Fig. 3). This difference was expected as the study area is isolated from the open ocean during low tide, causing temperatures to rise above that of the open sea during the NEM (McClanahan *et al.*, 2007). Temperature was lowest in June and July (~26°C) and highest in March (29°C). Salinity was lowest in August and September (29) and highest between November and February (35-36). Temperature during the NEM (November to March) was significantly higher than during the SEM (April to October), the salinity was significantly higher during the NEM, and total suspended matter was significantly higher during the SEM (Table 2).
Influence of initial fragment size on survival

The survival of fragments >2 cm (87.1%) was higher than that of fragments <2 cm (73.4%). When grouped by size class (Fig. 4), fragments <1 cm had the lowest survival rate, while those >3 cm had the highest. A significant difference between the mean size of surviving (2.5 cm ± 5.73) and dead fragments (1.65 ± 5.46) was observed during the first twelve-week period (p < 0.05, t-test).

Survival of the coral fragments

Survival of the coral fragments was high overall (mean 94%) after the first month but declined by the third month in July (Fig. 5). Six months after transplantation, 66% of the transplants had survived. Acropora species manifested higher survival (75%) than Pocillopora species (60%). At the species level, A. humilis exhibited the highest survival (91% after 6 months) followed by P. eydouxi (88.2% after 6 months), but the lowest survival occurred in P. verrucosa (29% after 6 months). After twelve months, A. humilis still exhibited the highest survival (86.6%) followed by A. selago (72.7%) and P. damicornis (43.3%). After twelve months, P. eydouxi and Porites rus had the poorest survival among all the species studied.

Growth of the coral fragments

No differences in mean monthly axial growth were observed among the species between the three tables deployed during the SEM, except for A. humilis on two of the tables (p = 0.0004); therefore, the growth rate data for the three tables were pooled for further analysis. The linear relationship between L and W was significant for all species except P. verrucosa, for which the sample size was

Table 2. Mean (±SE) temperature, salinity and total suspended matter at the coral culture site in the Mombasa Marine Park.

<table>
<thead>
<tr>
<th>Environmental Factors</th>
<th>SEM</th>
<th>NEM</th>
<th>Test Statistic</th>
<th>P</th>
<th>Annual mean</th>
</tr>
</thead>
<tbody>
<tr>
<td>Temperature</td>
<td>27.0±1.39</td>
<td>29.1±1.25</td>
<td>Z=6.30</td>
<td>&lt;0.05</td>
<td>28.2±1.65</td>
</tr>
<tr>
<td>Salinity</td>
<td>30.5±3.73</td>
<td>33.9±4.55</td>
<td>Z=2.65</td>
<td>&lt;0.007</td>
<td>32.4±4.53</td>
</tr>
<tr>
<td>Total suspended matter</td>
<td>0.07±0.017</td>
<td>0.04±0.047</td>
<td>Z=3.79</td>
<td>&lt;0.05</td>
<td>0.061±0.039</td>
</tr>
</tbody>
</table>

Figure 3. Mean monthly variation of temperature and salinity measured at the coral culture site and remotely sensed monthly sea surface temperature for Bamburi, Kenya (www.worldseatemp.com/en/Kenya/Bamburi).
low (Table 3). The mean initial and final sizes and the percentage growth in both L and W are presented for May 2010 and April 2011 in Table 4. Acropora species realised the highest growth rates after 329 days, their W increasing by 260-310% and their L by~100%; Pocillopora species grew the least with an increase in W of 65-113% and in L of 24-100%; Porites rus yielded medium growth rates of 133% (W) and 88% (L).

Mean axial growth in A. verwei, A. humilis and A. selago was lowest during May-July and highest during December-April (Fig. 6). Axial growth of P. damicornis, on the other hand, was lowest during September–December and highest during July-September. Acropora selago manifested higher mean growth in branch width than the other species. Growth in branch width was lowest in all the species during the May-July period except P. damicornis, in which this parameter was lowest in July-September and September-December. Growth in L and W was thus similar in pattern for all species except P. damicornis. Growth overall was higher in the NEM than the SEM except for P. damicornis and A. selago (Fig. 7). The former manifested little change in growth between the monsoon seasons, the latter lower growth in axial length but higher growth in branch width in the SEM.

Table 3. Results of linear regressions of axial and branch width growth of five coral species propagated in the Mombasa Marine Park.

<table>
<thead>
<tr>
<th>Species</th>
<th>Regression formula</th>
<th>R</th>
<th>DF</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acropora humilis</td>
<td>$W=28.9+0.915L$</td>
<td>0.618</td>
<td>90</td>
<td>&gt;0.001</td>
</tr>
<tr>
<td>Acropora selago</td>
<td>$W=23.6+1.220L$</td>
<td>0.730</td>
<td>20</td>
<td>&gt;0.001</td>
</tr>
<tr>
<td>Acropora verwei</td>
<td>$W=35.8+0.823L$</td>
<td>0.579</td>
<td>63</td>
<td>&gt;0.001</td>
</tr>
<tr>
<td>Pocillopora verrucosa</td>
<td>$W=12.1+0.822L$</td>
<td>0.607</td>
<td>5</td>
<td>0.147</td>
</tr>
<tr>
<td>Pocillopora damicornis</td>
<td>$W=10.7+0.402L$</td>
<td>0.723</td>
<td>55</td>
<td>&gt;0.001</td>
</tr>
</tbody>
</table>
Figure 5. Percentage survival of seven species of corals transplanted to the experimental culture tables for grow-out in the Mombasa Marine Park during April 2010-April 2011. N = the initial number of fragments that were transplanted.

Table 4. Mean (±SE) initial, final and percentage increase in axial length and branch width of Acropora humilis, A. selago, A. verwei, Pocillopora damicornis, P. verrucosa and P. eydouxi fragments (after 329 days), and Porites rus fragments (after 208 days).

<table>
<thead>
<tr>
<th>Species</th>
<th>Axial length</th>
<th>Branching width</th>
<th>% increase</th>
<th>Initial (mm)</th>
<th>Final</th>
<th>% increase</th>
<th>Initial</th>
<th>Final</th>
<th>% increase</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acropora verwei</td>
<td>19.0±5.4</td>
<td>37.9±9.3</td>
<td>99</td>
<td>15.5±6.7</td>
<td>60.2±16.3</td>
<td>287</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pocillopora damicornis</td>
<td>14.5±4.2</td>
<td>29.4±7.2</td>
<td>102</td>
<td>20.4±7.1</td>
<td>43.5±16.6</td>
<td>113</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Acropora humilis</td>
<td>19.6±6.0</td>
<td>36.7±12.4</td>
<td>82</td>
<td>13.3±3.9</td>
<td>48.8±18.8</td>
<td>266</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pocillopora verrucosa</td>
<td>19.5±3.3</td>
<td>26.7±8.7</td>
<td>36</td>
<td>25.2±7.6</td>
<td>47.1±8.0</td>
<td>86</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Acropora selago</td>
<td>18.2±4.6</td>
<td>39.5±13.6</td>
<td>116</td>
<td>12.2±4.2</td>
<td>58.3±21.9</td>
<td>374</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pocillopora eydouxi</td>
<td>24.0±6.9</td>
<td>29.8±8.3</td>
<td>24</td>
<td>18.4±6.9</td>
<td>30.5±8.9</td>
<td>65</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Porites rus</td>
<td>16.8±2.9</td>
<td>31.6±6.1</td>
<td>88</td>
<td>15.0±1.4</td>
<td>35.5±11.2</td>
<td>133</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
DISCUSSION

High survival rates (up to 100%) were recorded for three species of Acropora and Pocillopora damicornis in a coral culture system in a Mauritian lagoon until high temperatures dramatically reduced their survival (Moothien Pillay, et al., 2011). High survival rates, ranging from 75.3% to 87%, have also been recorded for A. grandis and A. muricata in a mid-water nursery in Thailand (Putchim et al., 2008). The high survival rates obtained in this study, particularly amongst the Acropora species, is thus not surprising.
Survival of the fragments was influenced by their initial size. While survival amongst fragments >4cm approached 100%, fragments <2cm experienced high mortality. Similar results have been obtained in other studies which have demonstrated that the survival of coral fragments is size-dependent, large fragments having a greater chance of survival (Lindahl, 1998, Tamelander et al., 2000, Herlan & Lirman, 2008). Forsman et al. (2006) found further evidence of size-specific mortality in an in situ Porites nursery where fragments <3cm had a low survival rate, but those in an closed nursery system did not undergo size-specific mortality where factors such as sedimentation, grazing, predation and competition were limited. Thus, larger coral fragments should be used in coral culture systems to obtain a high survival rate.

Apart from Pocillopora verrucosa, regression analysis revealed a close relationship between the axial growth and branch width expansion in the coral species investigated in this study, indicating that either parameter is suitable for monitoring early growth in coral fragments in culture systems. Overall, Acropora species grew faster than Pocillopora species, similar to findings from other studies (Yap & Gomez, 1981, 1985). The axial growth rates recorded for P. damicornis (~18 mm/year) in this study were nevertheless of the same order of magnitude to those measured in Australia (Harriott, 1999) Mauritius (Moothien Pillay, et. al., 2011) and India (Guzman & Cortes, 1989). The axial extension of Acropora species doubled and their branch width increased threefold over the 329 days that the experiment was conducted. Branch width increased faster than axial length in all species due to the formation of new branches. A. humilis and A. selago achieved the highest growth rates.

Generally, fragment growth was higher during the NEM than the SEM, although the differences were not statistically significant. Studies elsewhere in the Indian Ocean (e.g. Suresh & Mathew, 1993, 1995) have similarly yielded no significant differences in the seasonal skeletal extension rates of Acropora species (e.g. A. formosa and A. aspera), indicating that seasonal environmental factors such as temperature appear to have a minimal influence on coral growth in coral culture systems. On the other hand, skeletal extension was inversely correlated with currents, suspended matter and sedimentation in the aforementioned studies. In the present study, suspended matter was higher during the SEM, while salinity was lower, which may explain the lower growth rates perceived during this season.

Coral culture for ornamental purposes is clearly viable in Kenya using simple and relatively low-cost techniques. Three species were found to have a high potential for culture: A. humilis, A. selago and P. damicornis. The latter has been found to be an ideal culture candidate for the ornamental market due to its colouration, survival and growth potential (Borneman, 2009). This species also has relatively high recruitment rates in Kenya (Tamelander et al., 2000). The methods used in this study provide low-tech means of establishing mother colonies as a source for second generation seed for ornamental coral culture. However, before this technology can be adopted commercially, a protocol on standards and requirements should be developed. It will be important to ensure traceability of cultured corals from those harvested from the wild. More experimental studies should be conducted to assess the suitability of other ornamental species for culture to enhance the long-term sustainability of the marine ornamental trade in Kenya.

**Acknowledgements** – This study was conducted with financial support from the Kenya National Council of Science and Technology (NACOSTI). We thank the Kenya Marine and Fisheries Research Institute for logistical support. The Kenya Wildlife Service allowed us to conduct the study within the Mombasa Marine Park and provided logistical support during field work. We thank Mr Rene Jorgensen of Kenya Tropical Sea Life for his valuable support during the conceptualisation and initiation of the study. We acknowledge Masudi Juma, Brenda Obath and Tonny Nzioka for field assistance. Finally, we thank the anonymous reviewers whose criticism helped us to improve the manuscript.
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Quinn NJ, Kojis BL (2006) Evaluating the potential of natural reproduction and artificial techniques to increase Acropora cervicornis populations at Discovery Bay, Jamaica. Revista De Biologia Tropical 54:105-116


Keywords: Echinodermata, diversity, reef flats, reef slopes, lagoon, Juan de Nova

Abstract — Juan de Nova is one of the scattered islands known as Iles Eparses in the Mozambique Channel (Western Indian Ocean). Historically, they have been isolated from many anthropogenic influences which makes them ideal areas to study biodiversity for comparison with areas that are heavily impacted by urbanization and fishing. The programme BioReCie (Biodiversity, Resources and Conservation of Eparses Islands) undertook inventories of several marine groups, including echinoderms, which had hitherto not been assessed in Juan de Nova. A multidisciplinary team surveyed the reef slopes of the island using SCUBA to a depth of 25 m as well as the reef flats at low tide, collecting specimens and taking photos for identification. Sixty echinoderm species were found, with 51 occurring on the reef flats and in the lagoon and 22 on the reef slopes, comprising 21 species of Holothuroidea, 16 Ophiuroidea, 10 Echinoidea, 7 Asteroidea, and 6 Crinoidea. Commercial species of Holothuroidea, some of which are classified as endangered in the IUCN red list, i.e. *Thelenota ananas* and *Holothuria nobilis*, were present on the reef flats, reef slopes and in the lagoon of the island, indicating the value that protection has on biodiversity.

INTRODUCTION

Juan de Nova is one of the Iles Eparses (French Scattered Islands) which include Tromelin, Glorieuses, Bassas da India and Europa around Madagascar in the south-west Indian Ocean. Collectively, these islands, which have an EEZ (Exclusive Economic Zone) of approximately 650 000 km², have been governed as a strict Nature Reserve under statutes promulgated in 1975 (Gabrié, 1998) and 2007, and constitute the fifth district of Terres Australes et Antarctiques Françaises (Territory of the French Southern and Antarctic Lands). Juan de Nova is located in the Mozambique Channel (17°03’16”S; 42°43’30”E), 150 km from the west coast of Madagascar and 285 km from the East African coast (Fig. 1). The island is 5.48 km² in area and its coral reefs are 206.69 km² in extent, comprising 163.22 km² of reef flats and lagoon and 43.47 km² of barrier reef (Andréfouët et
The EEZ around Juan de Nova is 61,050 km² in area. A detailed presentation on the island covering its geomorphology and geopolitical and natural history is presented by Caceres (2003).

A survey of the island was undertaken during the BioReCie (Biodiversity, Resources and Conservation of Eparses islands) programme to map its reef areas and prepare inventories of several marine taxa for management purposes (Chabanet et al., 2012, 2013, 2014). Information on echinoderm diversity in the Iles Eparses has hitherto been very scarce (Vergonzanne, 1977; Mulochau & Conand, 2008) and inventories on the echinoderms were thus undertaken and presented for Europa (Conand et al., 2013a) and on the holothurians for the Glorieuses (Conand et al., 2013b) through the BioReCie programme.

Scientific studies within protected areas in the Indo-Pacific region that are not influenced by serious anthropogenic perturbation increase our knowledge on marine biodiversity, including echinoderms, and more particularly on commercially harvested holothurians (Conand et al., 2008; FAO, 2013; Purcell et al., 2013; Eriksson et al., 2015). The aim of this study was thus to compile the first inventory of echinoderms of Juan de Nova.

**METHODS**

Fieldwork was conducted during 7-17 December 2013 at Juan de Nova. An echinoderm species inventory was undertaken using an underwater visual census method (UVC) during SCUBA dives around the island at depths of 3-25 m, except on the reef flats.
where snorkeling was more efficient at depths of 0-3 m. The UVC method entailed a diver randomly swimming for a period of 50 minutes in the designated area. Most echinoderms were photographed but were collected when identification in situ was not possible, which was found to be the case particularly for the Ophiuroidea and Crinoidea. A total of 25 sites were sampled around the island, 19 on the reef flat and on reef patches in the lagoon, and six on the outer slopes (Fig. 2; Table 1). A total of 300 hours were spent searching for echinoderms on the reef surface, in cavities, under rubble blocks that could be overturned, and in the sand.

Indices of occurrence of each species were calculated as the number of sites where they were present in total and within the two main habitat types, viz. the reef flat and lagoons (rf), and outer reef slope (rs), divided by the total number of sites sampled in each habitat type. Taxonomic classification followed the World Register of Marine Species (Boxshall et al., 2014).

Table 1. Site codes, geomorphology, date sampled, coordinates and depth of sites sampled at Juan de Nova in 2013.

<table>
<thead>
<tr>
<th>Site code</th>
<th>Reef geomorphology</th>
<th>Date</th>
<th>Latitude</th>
<th>Longitude</th>
<th>Depth (m)</th>
</tr>
</thead>
<tbody>
<tr>
<td>2</td>
<td>Reef flat</td>
<td>08/12/2013</td>
<td>-17.06136</td>
<td>42.71416</td>
<td>0.2</td>
</tr>
<tr>
<td>3</td>
<td>Reef flat</td>
<td>09/12/2013</td>
<td>-17.07019</td>
<td>42.71046</td>
<td>0.5</td>
</tr>
<tr>
<td>8</td>
<td>Reef flat</td>
<td>12/12/2013</td>
<td>-17.05806</td>
<td>42.69461</td>
<td>0.5</td>
</tr>
<tr>
<td>15</td>
<td>Reef flat</td>
<td>15/12/2013</td>
<td>-17.04192</td>
<td>42.71683</td>
<td>1</td>
</tr>
<tr>
<td>17</td>
<td>Reef flat</td>
<td>16/12/2013</td>
<td>-17.04783</td>
<td>42.68040</td>
<td>1</td>
</tr>
<tr>
<td>20</td>
<td>Lagoonal reef patch</td>
<td>07/12/2013</td>
<td>-17.03259</td>
<td>42.73574</td>
<td>10</td>
</tr>
<tr>
<td>25</td>
<td>Lagoonal reef patch</td>
<td>10/12/2013</td>
<td>-16.95350</td>
<td>42.75982</td>
<td>15-18</td>
</tr>
<tr>
<td>27</td>
<td>Outer reef slope</td>
<td>11/12/2013</td>
<td>-17.08177</td>
<td>42.72536</td>
<td>13-16</td>
</tr>
<tr>
<td>28</td>
<td>Lagoonal reef patch</td>
<td>12/12/2013</td>
<td>-17.01960</td>
<td>42.68127</td>
<td>14</td>
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<tr>
<td>29</td>
<td>Outer reef slope</td>
<td>12/12/2013</td>
<td>-17.05418</td>
<td>42.67435</td>
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</tr>
<tr>
<td>30</td>
<td>Lagoonal reef patch</td>
<td>13/12/2013</td>
<td>-16.96562</td>
<td>42.69472</td>
<td>16</td>
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<tr>
<td>31</td>
<td>Lagoonal reef patch</td>
<td>13/12/2013</td>
<td>-16.94298</td>
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<td>18-19</td>
</tr>
<tr>
<td>33</td>
<td>Outer reef slope</td>
<td>14/12/2013</td>
<td>-17.01507</td>
<td>42.65688</td>
<td>20-22</td>
</tr>
<tr>
<td>34</td>
<td>Subtidal reef flat</td>
<td>15/12/2013</td>
<td>-17.01076</td>
<td>42.80413</td>
<td>17</td>
</tr>
<tr>
<td>35</td>
<td>Outer reef slope</td>
<td>15/12/2013</td>
<td>-17.07472</td>
<td>42.76651</td>
<td>14-20</td>
</tr>
<tr>
<td>36</td>
<td>Reef flat</td>
<td>16/12/2013</td>
<td>-17.03337</td>
<td>42.72390</td>
<td>1</td>
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<tr>
<td>37</td>
<td>Reef flat</td>
<td>16/12/2013</td>
<td>-17.03573</td>
<td>42.68453</td>
<td>2</td>
</tr>
<tr>
<td>38</td>
<td>Lagoonal reef patch</td>
<td>17/12/2013</td>
<td>-17.03507</td>
<td>42.77117</td>
<td>10</td>
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<td>52</td>
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<td>42.72429</td>
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</tr>
<tr>
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<td>Lagoonal reef patch</td>
<td>09/12/2013</td>
<td>-17.01781</td>
<td>42.71705</td>
<td>15</td>
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<tr>
<td>117</td>
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<td>42.72481</td>
<td>16</td>
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<td>140</td>
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<td>-17.01493</td>
<td>42.65645</td>
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<td>42.68913</td>
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<td>165</td>
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<td>-17.05728</td>
<td>42.77669</td>
<td>2</td>
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<tr>
<td>196</td>
<td>Lagoonal reef patch</td>
<td>17/12/2013</td>
<td>-17.03056</td>
<td>42.75651</td>
<td>10</td>
</tr>
</tbody>
</table>
RESULTS

Sixty echinoderm species were found, with 51 occurring on the reef flats and in the lagoon and 22 on the reef slopes (Table 2). Only a single echinoderm species was found at some stations (8, 15 and 36) which were all on the reef flats. Stations 86 and 30 located on lagoonal patch reef yielded the highest species richness with 17 and 16 echinoderm species. A mean of 8.5 echinoderm species was sampled per site on the reef slopes and 7.3 on the reef flats and lagoonal reef patches.

Table 2. Echinoderm classes sampled at Juan de Nova in 2013.

<table>
<thead>
<tr>
<th>Class</th>
<th>Reef flat and lagoon</th>
<th>Outer reef slope</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Holothuroidea</td>
<td>20</td>
<td>10</td>
<td>21</td>
</tr>
<tr>
<td>Ophiuroidea</td>
<td>14</td>
<td>4</td>
<td>16</td>
</tr>
<tr>
<td>Echinoidea</td>
<td>8</td>
<td>5</td>
<td>10</td>
</tr>
<tr>
<td>Asteroidea</td>
<td>7</td>
<td>2</td>
<td>7</td>
</tr>
<tr>
<td>Crinoidea</td>
<td>2</td>
<td>4</td>
<td>6</td>
</tr>
<tr>
<td>Total</td>
<td>51</td>
<td>22</td>
<td>60</td>
</tr>
</tbody>
</table>

CLASS HOLOTHUROIDEA

A total of 21 species of Holothuroidea were found at Juan de Nova (Table 3). The species with the highest occurrence was Holothuria atra (0.48), which was found at ten sites on reef flats and lagoonal reef patch and two sites on the outer slopes. Bohadschia subrubra (0.42) were also frequently sampled on reef flats and lagoonal reef patch, as were Bohadschia atra, Holothuria nobilis and Stichopus chloronotus each at an occurrence of 0.37. Thelenota ananas was the most abundant (0.83) species on the outer slopes but Actinopyga cf. obesa was also frequently sampled in this habitat (0.50).

We found at least one species of Holothuroidea at each station. Site 52, in the lagoon, had seven species, registering the greatest diversity for this class. Six species of Holothuroidea were recorded sites 17 and 86 in the lagoon, and site 140 on the outer slope.
Table 3. Occurrence of the Holothuroidea observed at Juan de Nova with the total number of sites at which species occurred, total occurrences (25 sites), occurrence on the reef flats and lagoonal reef patches (rf; 19 sites) and occurrence on the outer reef slopes (os; 6 sites).

<table>
<thead>
<tr>
<th>Species</th>
<th>N of sites</th>
<th>Total occurrence</th>
<th>rf</th>
<th>os</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Holothuria nobilis</em></td>
<td>7</td>
<td>0.28</td>
<td>0.37</td>
<td>0</td>
</tr>
<tr>
<td><em>Thelenota ananas</em></td>
<td>10</td>
<td>0.4</td>
<td>0.26</td>
<td>0.83</td>
</tr>
<tr>
<td><em>Stichopus chloronotus</em></td>
<td>10</td>
<td>0.4</td>
<td>0.37</td>
<td>0.33</td>
</tr>
<tr>
<td><em>Holothuria atra</em></td>
<td>12</td>
<td>0.48</td>
<td>0.53</td>
<td>0.33</td>
</tr>
<tr>
<td><em>Bohadschia subrubra</em></td>
<td>10</td>
<td>0.4</td>
<td>0.42</td>
<td>0.33</td>
</tr>
<tr>
<td><em>Bohadschia atra</em></td>
<td>9</td>
<td>0.36</td>
<td>0.37</td>
<td>0.33</td>
</tr>
<tr>
<td><em>Pearsonothuria graeffei</em></td>
<td>5</td>
<td>0.2</td>
<td>0.16</td>
<td>0.33</td>
</tr>
<tr>
<td><em>Stichopus herrmanni</em></td>
<td>1</td>
<td>0.04</td>
<td>0.05</td>
<td>0</td>
</tr>
<tr>
<td><em>Holothuria impatiens</em></td>
<td>2</td>
<td>0.08</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td><em>Actinopyga cf.miliaris</em></td>
<td>3</td>
<td>0.12</td>
<td>0.1</td>
<td>0.17</td>
</tr>
<tr>
<td><em>Actinopyga cf.obesa</em></td>
<td>5</td>
<td>0.2</td>
<td>0.05</td>
<td>0</td>
</tr>
<tr>
<td><em>Actinopyga mauritiana</em></td>
<td>4</td>
<td>0.16</td>
<td>0.21</td>
<td>0</td>
</tr>
<tr>
<td><em>Holothuria hilla</em></td>
<td>2</td>
<td>0.08</td>
<td>0.1</td>
<td>0</td>
</tr>
<tr>
<td><em>Holothuria pardalis</em></td>
<td>1</td>
<td>0.04</td>
<td>0.05</td>
<td>0</td>
</tr>
<tr>
<td><em>Actinopyga echnites</em></td>
<td>1</td>
<td>0.04</td>
<td>0.05</td>
<td>0</td>
</tr>
<tr>
<td><em>Thelenota anax</em></td>
<td>1</td>
<td>0.04</td>
<td>0.05</td>
<td>0</td>
</tr>
<tr>
<td><em>Holothuria fuscogilva</em></td>
<td>2</td>
<td>0.08</td>
<td>0.05</td>
<td>0.17</td>
</tr>
<tr>
<td><em>Holothuria difficilis</em></td>
<td>1</td>
<td>0.04</td>
<td>0.05</td>
<td>0</td>
</tr>
<tr>
<td><em>Holothuria sp. 1</em></td>
<td>1</td>
<td>0.04</td>
<td>0.05</td>
<td>0</td>
</tr>
<tr>
<td><em>Holothuria sp. 2</em></td>
<td>1</td>
<td>0.04</td>
<td>0</td>
<td>0.17</td>
</tr>
<tr>
<td><em>Holothuria cf.fuscocinerea</em></td>
<td>1</td>
<td>0.04</td>
<td>0.05</td>
<td>0</td>
</tr>
</tbody>
</table>

CLASS OPHIURIDEA

A total of 16 species of Ophiuroidea were sampled (Table 4) but not all were identified due to difficulties in their collection. Two species were recorded with the highest occurrence on the reef flats and lagoonal reef patches: *Ophiocoma (Breviturma) brevipes* (0.24) and *Macrophiothrix longipeda* (0.20). *Ophiocoma erinaceus* and *O. cynthiae* were also regularly observed. Only three species were sampled on the reef slopes, the most common being *Ophionereis porrecta* which was also found on the reef flats and in the lagoon. Site 30 in the north of the lagoon near the outer slope had the highest species richness of Ophiuroidea with six species.

Table 4. Occurrence of the Ophiuroidea observed at Juan de Nova with the total number of sites at which species occurred, total occurrences (25 sites), occurrence on the reef flats and lagoonal reef patches (rf; 19 sites) and occurrence on the outer reef slopes (os; 6 sites).

<table>
<thead>
<tr>
<th>Species</th>
<th>N of sites</th>
<th>Total occurrence</th>
<th>rf</th>
<th>os</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Macrophiothrix longipeda</em></td>
<td>5</td>
<td>0.2</td>
<td>0.26</td>
<td>0</td>
</tr>
<tr>
<td><em>Ophiocoma erinaceus</em></td>
<td>3</td>
<td>0.12</td>
<td>0.16</td>
<td>0</td>
</tr>
<tr>
<td><em>Ophiocoma (breviturma) brevipes</em></td>
<td>6</td>
<td>0.24</td>
<td>0.26</td>
<td>0.17</td>
</tr>
<tr>
<td><em>Ophiomastix venosa</em></td>
<td>1</td>
<td>0.04</td>
<td>0.05</td>
<td>0</td>
</tr>
<tr>
<td><em>Ophiocoma cynthiae</em></td>
<td>3</td>
<td>0.12</td>
<td>0.16</td>
<td>0</td>
</tr>
<tr>
<td><em>Ophionereis dubia</em></td>
<td>1</td>
<td>0.04</td>
<td>0</td>
<td>0.17</td>
</tr>
<tr>
<td><em>Ophiarcharnella gorgonia</em></td>
<td>1</td>
<td>0.04</td>
<td>0.05</td>
<td>0</td>
</tr>
<tr>
<td><em>Ophionereis sp.</em></td>
<td>1</td>
<td>0.04</td>
<td>0.05</td>
<td>0</td>
</tr>
<tr>
<td><em>Ophionereis porrecta</em></td>
<td>3</td>
<td>0.12</td>
<td>0.1</td>
<td>0.17</td>
</tr>
<tr>
<td><em>Ophiopeza fallax</em></td>
<td>1</td>
<td>0.04</td>
<td>0</td>
<td>0.17</td>
</tr>
<tr>
<td><em>Ophiactis savignyi</em></td>
<td>1</td>
<td>0.04</td>
<td>0.05</td>
<td>0</td>
</tr>
<tr>
<td><em>cf. Ophiactis</em></td>
<td>1</td>
<td>0.04</td>
<td>0.05</td>
<td>0</td>
</tr>
<tr>
<td><em>cf. Ophiolepis (juv)</em></td>
<td>1</td>
<td>0.04</td>
<td>0.05</td>
<td>0</td>
</tr>
<tr>
<td><em>Ophiura cf. kinbergi</em></td>
<td>1</td>
<td>0.04</td>
<td>0.05</td>
<td>0</td>
</tr>
<tr>
<td><em>Ophiocoma pusilla</em></td>
<td>1</td>
<td>0.04</td>
<td>0.05</td>
<td>0</td>
</tr>
<tr>
<td><em>cf. Ophiothele</em></td>
<td>1</td>
<td>0.04</td>
<td>0.05</td>
<td>0</td>
</tr>
</tbody>
</table>

CLASS ASTEROIDEA

Seven species of Asteroidea were sampled (Table 5), two of which were recorded with the highest occurrence on the reef flats and in the lagoon: *Culcita schmideliana* (0.20) and *Linckia laevigata* (0.20). Two species (*Neoferdina offreti* and *Acanthaster planci*) found in the lagoon were also sampled on the outer slopes. Site 86 has the highest species richness of Asteroidea with three species being recorded.

Table 5. Occurrence of the Asteroidea observed at Juan de Nova with the total number of sites at which species occurred, total occurrences (25 sites), occurrence on the reef flats and lagoonal reef patches (rf; 19 sites) and occurrence on the outer reef slopes (os; 6 sites).

<table>
<thead>
<tr>
<th>Species</th>
<th>N of sites</th>
<th>Total occurrence</th>
<th>rf</th>
<th>os</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Acanthaster planci</em></td>
<td>4</td>
<td>0.16</td>
<td>0.16</td>
<td>0.17</td>
</tr>
<tr>
<td><em>Culcita schmideliana</em></td>
<td>5</td>
<td>0.2</td>
<td>0.26</td>
<td>0</td>
</tr>
<tr>
<td><em>Linckia laevigata</em></td>
<td>5</td>
<td>0.2</td>
<td>0.26</td>
<td>0</td>
</tr>
<tr>
<td><em>Asteropsis carinifera</em></td>
<td>1</td>
<td>0.04</td>
<td>0.05</td>
<td>0</td>
</tr>
<tr>
<td><em>Neoferdina offreti</em></td>
<td>3</td>
<td>0.12</td>
<td>0.05</td>
<td>0.33</td>
</tr>
<tr>
<td><em>Dactylosaster cf.cylindricus</em></td>
<td>1</td>
<td>0.04</td>
<td>0.05</td>
<td>0</td>
</tr>
<tr>
<td><em>Linckia multifora</em></td>
<td>1</td>
<td>0.04</td>
<td>0.05</td>
<td>0</td>
</tr>
</tbody>
</table>
CLASS ECHINOIDEA

Ten species of Echinoidea were sampled (Table 6), two of which (Echinostrephus molaris and Echinothrix diadema) had the highest abundance on the reef flats and lagoonal reef patches. Echinostrephus molaris was frequently sampled at 14 of the 25 sites and, on the outer slopes, was always found associated with four other species: Echinothrix calamaris, Euclidaria metularia, Prionocidaris cf. pistillaris and Heterocentrotus mammilatus. Site 86 had the highest species richness of Echinoidea with three species being recorded.

Table 6. Occurrence of the Echinoidea observed at Juan de Nova with the total number of sites at which species occurred, total occurrences (25 sites), occurrence on the reef flats and lagoonal reef patches (rf; 19 sites) and occurrence on the outer reef slopes (os; 6 sites).

<table>
<thead>
<tr>
<th>Species</th>
<th>No. of sites/sp</th>
<th>total occ.</th>
<th>occ. rf</th>
<th>occ. os</th>
</tr>
</thead>
<tbody>
<tr>
<td>Echinothrix calamaris</td>
<td>9</td>
<td>0.36</td>
<td>0.42</td>
<td>0.17</td>
</tr>
<tr>
<td>Echinothrix diadema</td>
<td>2</td>
<td>0.08</td>
<td>0.1</td>
<td>0</td>
</tr>
<tr>
<td>Echinostrephus molaris</td>
<td>14</td>
<td>0.56</td>
<td>0.37</td>
<td>0</td>
</tr>
<tr>
<td>Echinometra mathaei</td>
<td>1</td>
<td>0.04</td>
<td>0.05</td>
<td>0</td>
</tr>
<tr>
<td>Stomopneustes variolaris</td>
<td>2</td>
<td>0.08</td>
<td>0.1</td>
<td>0</td>
</tr>
<tr>
<td>Plococidaris verticillata</td>
<td>1</td>
<td>0.04</td>
<td>0.05</td>
<td>0</td>
</tr>
<tr>
<td>Euclidaris metularia</td>
<td>3</td>
<td>0.12</td>
<td>0.1</td>
<td>0.17</td>
</tr>
<tr>
<td>Prionocidaris cf. pistillaris</td>
<td>1</td>
<td>0.04</td>
<td>0</td>
<td>0.17</td>
</tr>
<tr>
<td>Heterocentrotus mammilatus</td>
<td>1</td>
<td>0.04</td>
<td>0</td>
<td>0.17</td>
</tr>
<tr>
<td>Metalia spatagus</td>
<td>1</td>
<td>0.04</td>
<td>0.05</td>
<td>0</td>
</tr>
</tbody>
</table>

CLASS CRINOIDEA

Six species of Crinoidea were sampled (Table 7) with site 34 having six species, the highest number of crinoid species.

Table 7. Occurrence of the Crinoidea observed at Juan de Nova with the total number of sites at which species occurred, total occurrences (25 sites), occurrence on the reef flats and lagoonal reef patches (rf; 19 sites) and occurrence on the outer reef slopes (os; 6 sites).

<table>
<thead>
<tr>
<th>Species</th>
<th>No. of sites/sp</th>
<th>total occ.</th>
<th>occ. rf</th>
<th>occ. os</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stephanometra indica</td>
<td>1</td>
<td>0.04</td>
<td>0</td>
<td>0.17</td>
</tr>
<tr>
<td>Antedonidae</td>
<td>1</td>
<td>0.04</td>
<td>0</td>
<td>0.17</td>
</tr>
<tr>
<td>Tropiometra carinata</td>
<td>1</td>
<td>0.04</td>
<td>0.05</td>
<td>0</td>
</tr>
<tr>
<td>Cenometra bella</td>
<td>1</td>
<td>0.04</td>
<td>0</td>
<td>0.17</td>
</tr>
<tr>
<td>Crinoidea sp. 1</td>
<td>1</td>
<td>0.04</td>
<td>0.05</td>
<td>0</td>
</tr>
<tr>
<td>Crinoidea sp. 2</td>
<td>1</td>
<td>0.04</td>
<td>0</td>
<td>0.17</td>
</tr>
</tbody>
</table>

DISCUSSION

A total of 60 species of echinoderms were recorded at Juan de Nova, a lower number than that recorded at Glorieuses (67 species; Mulochau & Conand, 2008, 2013; Vergonzanne, 1977) but higher than Europa where only 39 species were found (Conand et al., 2013a). Indices of their abundance are provided but the data were qualitative and not amenable to further analysis; the objective of the study was a first inventory of echinoderms related to reef geomorphology within the broader context of the reef slopes and the reef flats with associated lagoonal patch reefs.

The occurrence of the Holothuroidea revealed that commercially valuable species such as Thelenota ananas, Bohadschia atra, B. subrubra, and Holothuria nobilis were present right around the island. Several species of Holothuroidea are listed on the IUCN list as endangered or vulnerable (Conand et al., 2014) and the strict Nature Reserve within which Juan de Nova lies represents an important area for the protection of this marine resource. A further survey will be necessary to quantify the Holothuroidea in the protected areas of the Les Eparses to compare their abundance with other areas that are highly fished (Conand, 2008; Purcell et al., 2012, 2013; FAO, 2013; Muthiga et al., 2014; Eriksson et al., 2015). The taxonomy of several species still needs more investigation and samples of tegument will be needed for their identification based on the spicules. DNA barcoding employing the COI gene may help to separate morphologically related species as Actinopyga miliaris, A. obesa and, perhaps a third morphotype.

Ophiuroidea are common on the reef flats and in the lagoon, whereas only two species were found on the reef slopes. Nevertheless, some Ophiuroidea are known to be negatively phototactic (Fell, 1966) and hide in the crevices of coral reefs during the day, making them difficult to find.
Amongst the Asteroidea, outbreaks of the crown-of-thorns sea star *Acanthaster planci* remain one of the most significant biological disturbances on tropical coral reefs (Baird, 2013). We did not encounter a high abundance of *A. planci*, although this species was present at Juan de Nova. *Linckia laevigata* and *C. schmideliana* are two large-sized species of Asteroidea that have frequently been found at Juan de Nova, Europa and the Glorieuses Islands (Conand et al., 2013a & 2013b).

Among the Echinoidea, *Echinostrephus molaris* was abundant at all the sites on the outer reef slopes and was the echinoderm with the highest occurrence. This concurs with our previous findings at the other Iles Eparses (Mulochau & Conand, 2008; Conand et al., 2013a).

Crinoidea, like the Ophiuroidea, have the ability to hide in crevices of a coral reef during the day to protect themselves from predators. DNA barcoding of two species encountered, *Stephanometra indica* and *Tropiometra carinata*, has revealed that their genetic diversity is higher than expected (Hemery, pers com). The specimens from Reunion Island and those collected elsewhere in the Mozambique Channel, e.g. the Glorieuses Islands and Madagascar have revealed significant genetic differences (Torrence et al., 2012; Hemery et al., 2013). *Stephanometra indica* and *T. carinata* could, therefore, constitute complexes of several species.

More field-work is needed to improve this first inventory for further comparison with other surveys in the south-western Indian Ocean. Sampling at night might produce a more complete inventory, especially for the Ophiuroidea, small species of Asteroidea and the Crinoidea. Further studies will also improve our understanding of their ecological role on the reefs of Juan de Nova in terms of their distribution, community structure and habitat utilization.

**Acknowledgements** – We would like to thank the administration of the TAAF (Terres Australes et Antarctiques Françaises) for research permits and financial support, the ‘Forces Armées de la Zone Sud ocean Indien’ (FAZSOI) for logistical support. Financial support for the expeditions to Juan de Nova island was also provided by the Institut Ecologie et Environnement du Centre National pour la Recherche (INEE-CNRS), the Institut National des Sciences de l’Univers (INSU), the Institut de Recherche pour le Développement (IRD), the Fondation pour la Recherche sur la Biodiversité (FRB), the Agence des Aires Marines Protégées (AAMP) and the Véolia Environment Foundation. We are thankful to all the participants in BioReCie Juan de Nova (P. Chabanet – the expedition leader, S. Andrefoüet, L. Bigot, C. Bourmaud, J-F Dupied, P. Durville, N. Gravier-Bonnet, S. Lauriol, H. Megalon, L. Mattio, J.B. Nicet, C. Russo, A. and N. Tisné, S. Turay and M. Zub) for their assistance, observations and photos. The assistance of E. Boissin in the identification of the ophiuroids, C. Mah in the identification of the asteroids and J.B. Nicet for the production of Figure 2 was appreciated. The comments of the anonymous referees have helped to improve the manuscript.

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Influence of Seasonality and Bathymetry on Decapod Crustacean Community Structure in Malindi - Ungwana Bay, Kenya

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Keywords: Decapoda, Penaeidae, abundance, monsoons, fisheries management, Kenya

Abstract — Decapod crustaceans support both artisanal and semi-industrial fisheries in the Western Indian Ocean (WIO) region. Despite their commercial value, data on their community structure is lacking in most of the region but are important for stock management. This study provides information on seasonal and bathymetric variation in decapod crustacean community structure in Malindi-Ungwana Bay, a biodiversity rich ecosystem in coastal Kenya. Samples were collected in the northeast (NEM) and southeast (SEM) monsoon seasons during an experimental bottom trawling survey in 2011. A total of 43 transects covering an estimated area of 1 873 km² were trawled in four depth zones (0-10, 10-20, 20-40 and 40-100 m) in both seasons. Twenty species of decapod crustaceans belonging to the Penaeidae, Portunidae, Calappidae, Majidae, Matutidae, Palinuridae and Scyllaridae were harvested. Overall crustacean biomass was higher in the SEM than the NEM. Penaeid prawns were numerically the most abundant in both the NEM (89.3%) and SEM (85.3%) seasons, Fenneropenaeus indicus being the most abundant in the NEM (58%) and SEM (42%). nMDS plots revealed separation of crustacean assemblages between depth zones but not the seasons. Two-way crossed ANOSIM indicated significant difference in species composition between the depth zones but not the seasons, with higher species diversity in the shallower depth strata. Canonical Correspondence Analysis revealed that temperature, salinity, Secchi depth and dissolved oxygen influence the bathymetric distribution of species in the bay. Recommendations are made that these factors be taken into consideration in the management of the crustacean fishery in the bay.

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INTRODUCTION

Marine decapod crustaceans account for nearly 6.9% of worldwide fin and shellfish landings by weight (FAO, 2011) and these landings have been on the upward trend in recent decades (FAO, 2008, 2012). The rise in decapod crustacean catches is mostly attributable to increased effort as a result of dwindling fish stocks worldwide (Jackson et al., 2001; Worm et al., 2006; FAO, 2010). Crustacean stocks are, however, increasingly being threatened with overfishing (FAO, 2012), mostly because of the global shift in targeting these resources.

Fishing pressure can cause shifts in species community structure and ecosystem function (Jennings and Kaiser, 1998) with trophodynamic consequences (Leibold, 1996). Several abiotic and biotic factors may further influence the distribution patterns and community structure of marine benthic communities like crustaceans. Such abiotic factors include depth profile (Fanneli et al., 2007; Munoz, et al., 2008), salinity gradient (Gillett, 2008), substratum type (Lavrado et al., 2000) and rainfall patterns (Teikwa and Mgaya, 2003). Important biotic factors comprise environmental productivity (Follesa et al., 2009) and biological interactions (Jackson, et al., 2001).

A limited number of studies have been conducted on decapod crustaceans in the Western Indian Ocean (WIO) compared to the temperate latitudes. Most of the WIO studies have concentrated on species distribution (Mutagyera, 1984; Munga et al., 2012), the functional biology of single species (Wakwabi and Jaccarini, 1993; Wakwabi, 1996; Teikwa and Mgaya, 2003), and stock assessments and fisheries (Groeneveld and Melville-Smith, 1995; Groeneveld, 2000; Mwatha, 2005). Decapod crustaceans form an important link between lower and higher trophic levels and studies on factors that affect their community structure may offer useful information on ecosystem function at the local scale (Papiol et al., 2012). In ecosystems that are heavily fished and influenced by environmental variability, such as the expansive Malindi-Ungwana Bay in Kenya, information on variability in a resource’s community structure is useful in assessing spatio-temporal drivers of assemblages. This study therefore aimed to provide information on the environmental correlates of crustacean community structure in the Malindi-Ungwana Bay.

The bay is the most productive nearshore ecosystem in coastal Kenya (Nzioka, 1981; Mutagyea, 1984) and has thus been the focus of various trawling expeditions. Recent resource-use conflict and a fishing ban in the bay (Munga et al., 2012) requires that scientific information be available to support management.

METHODS

Study site and survey design

The study was carried out within Malindi-Ungwana Bay on the northern coast of Kenya (Fig. 1). The bay lies between 2° 30’ S - 3° 30’ S and 40° 00’ E - 41° 00’ E. It is the only known trawlable ground on the Kenyan coast, extends along ~200 km of coastline and has a continental shelf ranging from 15-60 km in width, with an estimated fishing ground of 35 300 km² (Iversen, 1984; Mueni, 2006). The Athi and Tana Rivers (Fig. 1) discharge an estimated 6 000 million m³ of freshwater and 3 million tonnes of sediment annually into the bay (Tychsen, 2006), which is affected by the monsoons that prevail on the Kenyan coast (McClanahan, 1988). Briefly, the northeast monsoon season (NEM, November–March) is a period of calm seas, elevated sea surface temperatures and higher salinities, while the southeast monsoon (SEM, April–October) is characterised by rough seas, cool weather, lower salinities and higher plankton productivity. The influence of this seasonality on community structure of crustaceans in coastal East Africa is not well documented.

The data were collected during two trawl surveys in the bay using the FV Vega, a medium-sized Kenyan prawn trawler. The first survey was conducted during 22 January - 4 February 2011 (NEM), the second between
22 May - 4 June 2011 (SEM). The trawler was fitted with two outrigger trawl nets made of nylon, comprising wings, a net body and cod-end with a total length of 44.3 m. The wings were 19.1 m long with a mesh size of 45 mm; the net body was also 19.1 m long but with a mesh size of 70.4 mm, and the cod-end was 6.1 m long with a mesh size of 45 mm. The nets each had a 22.5 m head rope length, a 25.4 m foot rope and a 28 m restraining chain.
between the two trawl doors. They were lowered simultaneously by hydraulic winch and the trawl start time recorded when the nets reached the sea floor, while the trawl end time was recorded when the vessel started retracting the nets.

A total of 43 trawl transects were surveyed within the bay during a 13-day period in each season. The surveys were stratified by depth into four zones: 0-10 m (zone 1); 10-20 m (zone 2); 20-40 m (zone 3) and 40-100 m (zone 4). The depth zone intervals were not uniform because the shelf steepens rapidly a few miles from the shore.

The percentage area of each depth zone within the trawlable area was used to determine the proportion of sampling time apportioned to each zone in each season, given that a maximum of four trawls could be conducted per day. The four depth zones were 471, 803, 468 and 133 km² in area and were allocated 8 (zone 1), 17 (zone 2), 13 (zone 3) and 5 (zone 4) trawls, respectively, totalling 43 trawls in each seasonal survey. The trawl transects ran parallel to the shoreline to remain within the respective depth zone as much as possible; shallow areas, coral and rocky areas were avoided. The geographical coordinates of the start and end point of each trawl transect were determined using a GPS. Trawling was done at a speed of 2.5-3.0 knots during the day between 06:00-18:00 h and each trawl lasted an hour. The same transects were trawled during the NEM and SEM.

### Sampling methods

Data on environmental variables were recorded at the start of each trawl during the NEM. A bottom water sample was collected using a Niskin bottle and dissolved oxygen, temperature and salinity measured using a digital meter. Water transparency was measured from the side of the boat using a Secchi disc. The depths of each transect position were measured using an echo sounder. The net was hauled onto the deck at the end of each trawl and the decapod crustaceans sampled using a protocol that depended on the catch size. When the catch was small and manageable (e.g. the total catch could be worked within an hour), the total haul was processed and sorted into the various crustacean groups. These were identified to species following identification keys by the FAO (1984) and De Grave and Fransen (2011) for prawns, and Stephenson (1948), Branch et al. (2007), Ng et al. (2008) and Richmond (2011) for crabs. Species were weighed to the nearest 0.1 g, and carapace lengths and widths measured to the nearest 1 mm using a Vernier caliper. Catches that were too large (requiring over an hour to work) were sub-sampled. All large specimens in the haul were first removed, identified and weighed individually to the nearest gram. The remaining catch was turned to achieve uniform mixing and then sub-divided into portions (sub-samples) of approximately equal size, one of which (b, kg) was randomly selected for analysis. The total weight (a, kg) of the other portions was also recorded. These weights were later added to that of the large specimens to determine the weight of the total haul. The weight of each species in the haul was estimated by multiplying their weight in the sub-sample (b, kg) by a raising factor (RF): RF = (a + b) / b.

### Data analysis

Biomass estimates of penaeid prawns were calculated using the Swept Area Method (Sparre & Venema, 1998). The distance trawled (D) per transect was estimated in units of nautical miles (nm) as:

\[
D = 60 \times \text{Sqrt}((\text{Lat}_1 - \text{Lat}_2)^2 + (\text{Lon}_1 - \text{Lon}_2)^2 \times \cos^2(0.5 \times (\text{Lat}_1 + \text{Lat}_2))) \tag{1}
\]

Where:
- Lat1 = Latitude at start of haul (degrees)
- Lat2 = Latitude at end of haul (degrees)
- Lon1 = Longitude at start of haul (degrees)
- Lon2 = Longitude at end of haul (degrees)

The estimated trawl distance was then multiplied by the length of the head rope (22.5 m) to get the trawled area (A, nm²), with a correction factor of 0.5 for the net configuration (Pauly, 1980):

\[
\text{Swept Area (A)} = D \times 22.5 \times 0.5 \tag{2}
\]
The catch densities (converted to kg.km\(^{-2}\)) of species were then derived for each haul, while species biomass (B, Kg) in each haul was derived as:

\[ B = \text{density} \times \frac{A}{X1} \]  

Where X1 is sampling proportion of crustaceans present in the swept area (X1 = 1, assuming all the crustaceans were fully accessible to the trawl).

Multivariate non-metric multi-dimensional scaling (MDS) was used to describe the community structure by depth zones and season (NEM and SEM) based on the Bray-Curtis similarity index (Clarke and Warwick, 2001). Two-way ANOSIM was used to test for differences in community structure with depth zones and seasons as factors, while two-way SIMPER analysis identified which crustacean species contributed most to the dissimilarity. The resulting R-values provided a measure of variation between samples, ranging from -1 to 1. Values tending to zero indicated little difference in species composition between depths/seasons, while values tending to +1 inferred differing composition (Clarke & Warwick, 2001). Canonical Correspondence Analysis (CCA) was used to analyse the influence of environmental factors (depth, temperature, dissolved oxygen, Secchi depth and salinity) on species distribution only during the NEM. The statistical analyses were performed using PRIMER version 6.

Two-way ANOVA (on log (x+1) transformed data) was used to test for the effect of seasons and depth on overall crustacean biomass, species richness and diversity in the bay. Taxonomic richness (S) and the Shannon-Wiener diversity index (H') were used to describe the community structure. As S reflected the total number of species of crustaceans in a stratum, the mean richness was calculated according to the depth zones and season. H' was calculated following Magurran (1988):

\[ H' = - \Sigma i \pi_i \log (\pi_i) \]

Where \( \pi_i \) is the proportion of the total count arising from the \( i \)th species in the stratum or season.

**RESULTS**

**Species composition, abundance and catch rates**

Totals of 767 and 1 808 crustaceans were sampled during the NEM and SEM, respectively, including 20 decapod crustacean species belonging to seven families. During the NEM, 11 species were harvested, mostly penaeid prawns (5 species), but relatively more portunids (9 species) made up the 19 species were caught during SEM (Table 1). Among the penaeid species, *Fenneropenaeus indicus* had the highest mean abundance (individuals, km\(^{-2}\) ± SE) of 8 318 ± 4 132, followed by *Metapeneus monoceros* (1 489 ± 689), *Penaeus semisulcatus* (1 069 ± 415) and *Penaeus monodon* (1 008 ± 439) (Table 1). The other crustaceans were recorded in low numbers of <400 individuals.km\(^{-2}\) (Table 1). Penaeid prawns were numerically the most abundant both in the NEM and SEM (89.7% and 85.3 %, respectively), with *F. indicus* making up the greatest proportion of the catch (NEM, 57.6%; SEM, 41.5%). The other penaeids occurred in variable proportions (Table 1). The Portunidae made up 9.4% and 12.3% of the numbers caught in the NEM and SEM, respectively, while the Palinuridae were very low in abundance in both seasons (Table 1).

Higher mean catch rates (kg.km\(^{-2}\) ± SE) were recorded in depth zone 1 (64.2 ± 18.7 kg.km\(^{-2}\)) during the NEM, with catch rates of 15.7 ± 5.5 and 17.9 ± 9.5 kg.km\(^{-2}\) being obtained in zones 2 and 3, respectively, during this season. During the SEM, catch rates of 67.14 ± 18.6 and 56.6 ± 18.1 kg.km\(^{-2}\) were obtained from depth zones 1 and 2, respectively, while zones 3 and 4 yielded lower rates of 14.25 ± 5.8 and 1.31 ±1.1 kg.km\(^{-2}\), respectively. Two-way ANOVA revealed that depth had a significant effect on the crustacean harvest (\( F = 3.89; \) df = 2, 130; \( P = 0.022 \)). This was not the case with season (\( F=0.014; \) df= 1, 130; \( P=0.95 \)), or the interaction of season and depth (\( F = 0.57; \) df= 2,130; \( P = 0.54 \)).
A greater harvest of prawns (the most abundant crustaceans in the bay) was obtained from depth zone 1 (78.7 ± 22.6 kg.km$^{-2}$) during the NEM. Depth zones 2 and 3 yielded near equal catches of 20.4±7.0 and 20.9±11 kg.km$^{-2}$, respectively. During the SEM, depth zones 1 and 2 yielded near equal catches of prawns of 112.4 ± 30.3 and 103 ± 31.01 kg.km$^{-2}$, respectively, higher than those recorded during the NEM. One-way ANOVA showed no significant difference in prawn catch rates during the NEM (F = 2.14; df = 2, 36; P = 0.13) or SEM (F=0.93; df= 2, 43; P = 0.40) in the three shallower depth zones. No prawns were harvested in depth zone 4 (40-100 m) in either season.

**Bathymetric and seasonal distribution of species**

Among the penaeid prawns, *F. indicus* and *M. japonicus* were restricted to depth zones 1 and 2 during both the NEM and SEM (Table 2). *M. monoceros* occurred in depth zones 1-3 during both seasons, but higher numbers were harvested in depth zones 1 and 2 during SEM. *P. monodon* and *P. semisulcatus* occurred in depth zones 1-3 during the SEM, with *P. semisulcatus* harvested in higher numbers in zones 1 and 2 during SEM (Table 2). Amongst the portunid crabs, only *Portunus sanguinolentus* was harvested in considerable numbers in both seasons.

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Table 1. Mean abundance (individuals.Km$^{-2}$ ± SE) and percentage composition of decapod crustaceans caught in trawls during the northeast (NEM) and southeast monsoons (SEM) in Malindi-Ungwana Bay. Values without standard errors indicate that species appeared in only one transect; (-) indicates absence of catch.

<table>
<thead>
<tr>
<th>Species</th>
<th>% NEM</th>
<th>% SEM</th>
<th>NEM</th>
<th>SEM</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Penaeidae</strong></td>
<td></td>
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<td></td>
</tr>
<tr>
<td><em>Fenneropenaeus indicus</em></td>
<td>57.6</td>
<td></td>
<td>347 ± 156.1</td>
<td>9.7</td>
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<tr>
<td><em>Marsupenaeus japonicus</em></td>
<td>0.9</td>
<td></td>
<td>0.05</td>
<td>0.05</td>
</tr>
<tr>
<td><em>Metapenaeus monoceros</em></td>
<td>12.5</td>
<td></td>
<td>9.3</td>
<td>9.7</td>
</tr>
<tr>
<td><em>Penaeus monodon</em></td>
<td>8.9</td>
<td></td>
<td>0.7</td>
<td>0.7</td>
</tr>
<tr>
<td><em>Penaeus semisulcatus</em></td>
<td>9.8</td>
<td></td>
<td>0.05</td>
<td>0.05</td>
</tr>
<tr>
<td><strong>Portunidae</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Portunus sanguinolentus</em></td>
<td>0.3</td>
<td></td>
<td>97</td>
<td>0.05</td>
</tr>
<tr>
<td><em>Thalamita crenata</em></td>
<td>0.1</td>
<td></td>
<td>0.05</td>
<td>0.05</td>
</tr>
<tr>
<td><em>Charybdis feriata</em></td>
<td>-</td>
<td>-</td>
<td>0.6</td>
<td>0.6</td>
</tr>
<tr>
<td><em>Charybdis hellerii</em></td>
<td>-</td>
<td>-</td>
<td>0.8</td>
<td>0.8</td>
</tr>
<tr>
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<td>0.2</td>
</tr>
<tr>
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<td>-</td>
<td>0.5</td>
<td>0.5</td>
</tr>
<tr>
<td><em>Podophthalmus vigil</em></td>
<td>-</td>
<td>-</td>
<td>0.05</td>
<td>0.05</td>
</tr>
<tr>
<td><em>Portunus pelegicus</em></td>
<td>-</td>
<td>-</td>
<td>0.3</td>
<td>0.3</td>
</tr>
<tr>
<td><em>Scylla serrata</em></td>
<td>-</td>
<td>-</td>
<td>33 ± 13</td>
<td>33 ± 13</td>
</tr>
<tr>
<td><strong>Calappidae</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Calappa calappa</em></td>
<td>0.3</td>
<td></td>
<td>40</td>
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</tr>
<tr>
<td><em>Calappa sp.</em></td>
<td>0.1</td>
<td></td>
<td>21</td>
<td>0.4</td>
</tr>
<tr>
<td><strong>Matutidae</strong></td>
<td></td>
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<td></td>
<td></td>
</tr>
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<td><em>Ashtoret lunaris</em></td>
<td>0.7</td>
<td></td>
<td>97</td>
<td>1.0</td>
</tr>
<tr>
<td><strong>Majidae</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Majid sp.</em></td>
<td>-</td>
<td>-</td>
<td>0.2</td>
<td>0.2</td>
</tr>
<tr>
<td><strong>Scyllidae</strong></td>
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<td></td>
</tr>
<tr>
<td><em>Thenus orientalis</em></td>
<td>0.4</td>
<td></td>
<td>20 ± 0.4</td>
<td>0.7</td>
</tr>
<tr>
<td><strong>Palinuridae</strong></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td><em>Panulirus ornatus</em></td>
<td>0.3</td>
<td></td>
<td>0.1</td>
<td>21± 0.3</td>
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</tbody>
</table>

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seasons, and mainly at shallower depths (Table 2). Amongst the Palinuridae (lobsters), *Thenus orientalis* was harvested in depth zones 1-3 in both seasons, while *Panulirus ornatus* was caught in depth zones 1 and 2 during the SEM. MDS plots revealed that different crustacean assemblages were found in the depth zones but not the seasons (Fig. 2). Two-way crossed ANOSIM indicated that the difference in these assemblages between

<table>
<thead>
<tr>
<th>Species</th>
<th>Zone 1 (0-10 m)</th>
<th>Zone 2 (10-20 m)</th>
<th>Zone 3 (20-40 m)</th>
<th>Zone 4 (40-100 m)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Fenneropenaeus indicus</em></td>
<td>11265 ± 5383</td>
<td>458 ± 386</td>
<td>-</td>
<td>-</td>
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<tr>
<td><em>Marsupenaeus japonicus</em></td>
<td>248</td>
<td>116 ± 16</td>
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<tr>
<td><em>Metapenaeus monoceros</em></td>
<td>1918 ± 953</td>
<td>735</td>
<td>367 ± 320</td>
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<tr>
<td><em>Penaeus monodon</em></td>
<td>1239 ± 539</td>
<td>199 ± 74</td>
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<tr>
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<td>-</td>
<td>564 ± 544</td>
<td>1405 ± 577</td>
<td>-</td>
</tr>
<tr>
<td><em>Portunus sanguinolentus</em></td>
<td>576 ± 201</td>
<td>117 ± 12</td>
<td>-</td>
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<td><em>Thalamita crenata</em></td>
<td>19</td>
<td>-</td>
<td>-</td>
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<td><em>Charybdis feriata</em></td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td><em>Charybdis hellerii</em></td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
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<td><em>Portunus pelagicus</em></td>
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<td><em>Calappa sp.</em></td>
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<td><em>Ashtoret lunaris</em></td>
<td>97</td>
<td>-</td>
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</tr>
<tr>
<td><em>Majidae sp.</em></td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td><em>Thenus orientalis</em></td>
<td>20</td>
<td>21</td>
<td>20</td>
<td>-</td>
</tr>
<tr>
<td><em>Panulirus ornatus</em></td>
<td>-</td>
<td>-</td>
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<table>
<thead>
<tr>
<th>Species</th>
<th>Zone 1 (0-10 m)</th>
<th>Zone 2 (10-20 m)</th>
<th>Zone 3 (20-40 m)</th>
<th>Zone 4 (40-100 m)</th>
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<tr>
<td><em>Fenneropenaeus indicus</em></td>
<td>15437 ± 4217</td>
<td>8208 ± 5210</td>
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<td><em>Marsupenaeus japonicus</em></td>
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<td>41 ± 12</td>
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<td><em>Portunus pelagicus</em></td>
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<td>-</td>
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<tr>
<td><em>Scylla serrata</em></td>
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<td>39 ± 19</td>
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<tr>
<td><em>Calappa calappa</em></td>
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<tr>
<td><em>Calappa sp.</em></td>
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<td>-</td>
<td>167</td>
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<td><em>Ashtoret lunaris</em></td>
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<td>42</td>
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<tr>
<td><em>Thenus orientalis</em></td>
<td>20 ± 0.2</td>
<td>54 ± 34</td>
<td>145</td>
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<td><em>Panulirus ornatus</em></td>
<td>20</td>
<td>21</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>
the depth zones were significant but again not the seasons (R = 0.410; p = 0.002 and R = -0.029; p = 0.598 respectively). A pairwise ANOSIM comparison test further confirmed the significance of the differences in the assemblages between depth zones 1 and 2, and between 1 and 3 (P < 0.05 in all cases; Table 3). A greater abundance of *F. indicus* in depth zone 1, and *P. semisulcatus* and *Charybdis natator* in depth zone 2, was responsible for the difference between these depth zones (two-way SIMPER: Table 4). Similarly, a greater abundance of *F. indicus* in zone 1 and *P. semisulcatus* and *Calappa pelii* in depth zone 3 (two-way SIMPER: Table 5) was responsible for the difference between these depth zones.

**Species richness and diversity**

Depth zones 1 and 2 were more diverse than zones 3 and 4, evidenced by the results on species richness (S) and the Shannon-Wiener diversity index (H') (Fig. 3a). Also, species diversity was higher in the SEM than NEM (Fig. 3b). Results of two-way ANOVA yielded significant differences in crustacean species richness (nos.transect^-1^) between depth zones (df = 2; F = 3.651; P = 0.039). However, the test revealed no significant difference between seasons or the interaction of depth zone and season (df = 1; F = 1.872; P = 0.182 and df = 2; F = 0.196; P = 0.823, respectively). A post hoc Fisher LSD
Table 3. Pair-wise ANOSIM comparison of differences in crustacean composition between depth zones in Malindi-Ungwana Bay based on abundance (%). Significance at $P \leq 0.05$ in bold.

<table>
<thead>
<tr>
<th>Depth zones</th>
<th>R statistic</th>
<th>p-value</th>
<th>Possible permutations</th>
<th>Actual permutations</th>
<th>Number $\geq$ observed</th>
</tr>
</thead>
<tbody>
<tr>
<td>1, 2</td>
<td>0.232</td>
<td>0.013</td>
<td>3185325</td>
<td>999</td>
<td>12</td>
</tr>
<tr>
<td>1, 3</td>
<td>0.806</td>
<td>0.001</td>
<td>54450</td>
<td>999</td>
<td>0</td>
</tr>
<tr>
<td>1, 4</td>
<td>0.952</td>
<td>0.125</td>
<td>8</td>
<td>8</td>
<td>1</td>
</tr>
<tr>
<td>2, 3</td>
<td>0.083</td>
<td>0.271</td>
<td>17325</td>
<td>999</td>
<td>270</td>
</tr>
<tr>
<td>2, 4</td>
<td>0.638</td>
<td>0.111</td>
<td>9</td>
<td>9</td>
<td>1</td>
</tr>
<tr>
<td>3, 4</td>
<td>0.5</td>
<td>0.400</td>
<td>5</td>
<td>5</td>
<td>2</td>
</tr>
</tbody>
</table>

Fig. 3. Bathymetric variation of diversity measures ($S \pm SE$ and $H' \pm SE$) of decapod crustacean species according to a) depth and b) season in Malindi-Ungwana Bay, Kenya.

Test confirmed that depth zone 2 differed significantly from depth zone 3 in both the NEM and SEM, and depth zone 3 differed significantly from depth zone 1 in the SEM ($P < 0.05$ in all cases).

Environmental measurements and species associations

No significant differences were encountered in temperature, salinity, dissolved inorganic nutrients (phosphates and nitrates), chlorophyll-$a$ or biological oxygen demand.
Turbidity (Secchi depth) decreased with depth (0-10 m to 40-100 m); i.e. with increasing distance from the shore. Canonical Correspondence Analysis (CCA) of the influence of these environmental variables on crustacean abundance during the NEM are presented in Figure 4. Depth zones 2 and 3 are dissimilar from zone 1 on the x-axis, the differences being attributable to water temperature in zone 1, and water clarity, dissolved oxygen and salinity in zones 2 and 3. Respective indicators of this are *Ashtoret lunaris* and *Calappa calappa* in zone 1, and *M. japonicus*, *P. monodon*, *M. monoceros*, *P. sanguinolentus* and *T. orientalis* in zone 2. The *Calappa sp.* was associated with depth zone 2 but apparently was not influenced in abundance by the selected environmental variables.

Table 4. Two-Way SIMPER Analysis of decapod crustacean species contribution to dissimilarity in terms of abundance (%) between depth zones 1 and 2 in Malindi-Ungwana Bay. The average dissimilarity was 65.3%, notable contributors to this being highlighted in bold.

<table>
<thead>
<tr>
<th>Species</th>
<th>Depth zone 1 Average abundance (%)</th>
<th>Depth zone 2 Average abundance (%)</th>
<th>Average dissimilarity (%)</th>
<th>Contribution (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Fenneropeneus indicus</em></td>
<td>58.11</td>
<td>22.89</td>
<td>19.35</td>
<td>29.63</td>
</tr>
<tr>
<td><em>Penaeus semisulcatus</em></td>
<td>1.32</td>
<td>29.05</td>
<td>14.47</td>
<td>22.15</td>
</tr>
<tr>
<td><em>Metapenaeus monoceros</em></td>
<td>22.26</td>
<td>18.65</td>
<td>10.89</td>
<td>16.67</td>
</tr>
<tr>
<td><em>Portunus sanguinolentus</em></td>
<td>7.13</td>
<td>6.95</td>
<td>7.07</td>
<td>10.81</td>
</tr>
<tr>
<td><em>Penaeus monodon</em></td>
<td>9.43</td>
<td>5.45</td>
<td>4.43</td>
<td>6.78</td>
</tr>
<tr>
<td><em>Charybdis natator</em></td>
<td>0.00</td>
<td>6.67</td>
<td>3.18</td>
<td>4.87</td>
</tr>
</tbody>
</table>

Fig. 4. Canonical Correspondence Analysis (CCA) showing the influence of physico-chemical factors on crustacean species abundance in the three shallower depth zones within Malindi-Ungwana Bay during the NEM. Species names are as shown on Table 1.
DISCUSSION

Higher abundances of crustaceans were harvested during this study in the oceanographically rougher SEM than the calmer NEM season using the same vessel. Although previous studies have yielded similar results (e.g. Mwatha, 2005; Munga et al., 2012), the causes of this difference are unclear. Contributory factors may be higher recruitment to the fishery by the Penaeidae (the most abundant group), higher vulnerability to gear or higher environmental productivity during the SEM. Nonetheless, more studies are needed to determine the causal factors for seasonal variability in crustacean abundance in the Malindi-Ungwana Bay.

Significant differences in the relative abundance of penaeid prawns have been found between dry and wet seasons elsewhere (Teikwa & Mgaya, 2003; de Freitas, 2011), suggesting the influence of rainfall and hence salinity on prawn catches. Rainfall is thought to initiate the migration of prawns offshore from estuaries, either by lowering salinities or simply the mechanical disturbance of runoff and of the bottom sediments (Meager et al., 2003; de Freitas 2011). Juvenile prawns are known to move to offshore fisheries as a result of a reduction in inshore salinities during the rainy season (Staples and Vance, 1986). The SEM in coastal Kenya is typically a wet season and there is an increase in river discharge into the Malindi-Ungwana Bay during this season which introduces organic matter to the bay (Tychsen, 2006). This probably increases primary productivity in the bay, as it does in the Mediterranean.
(de Juan & Cartes, 2011). Such increased nutrient input into Malindi-Ungwana Bay would suggest that productivity-induced seasonal differences cause changes in crustacean abundance in the bay. This would suggest the need for seasonally structured management regulations for exploitation of its penaeid prawns.

The penaeid prawns were mostly restricted to the shallow zones 1 and 2 (0-10 and 10-20 m) during both seasons. However, *Penaeus semisulcatus*, *Metapenaeus monoceros* and *P. monodon* had a wider bathymetric distribution that was more distinct during the SEM. This may be attributable to a higher tolerance of environmental variability by these species than the other penaeids. A similarly wide bathymetric distribution associated with temperature tolerance has been reported for *P. semisulcatus* in Kuwait (Ye et al., 1999), for *M. monoceros* in the Iskenderum Bay (Can et al., 2004) and in the Gulf of Antalya in Turkey (Yilmaz et al., 2009), and for both species in Mozambique (de Freitas, 2011).

Changes in salinity and temperature probably contributed to high species richness in Malindi-Ungwana Bay during the SEM, with a peak in diversity in depth zones 1 and 2. Increased runoff during the SEM results in temperature and salinity stratification (Papiol et al., 2012) and this may contribute to higher larval survival (due to differential thermal warming of strata) and, hence, high species diversity in the bay during this season. Other studies have found that crustacean diversity is affected by temperature, salinity and prey availability within estuaries and bays (Vance et al., 1985; Meager et al., 2003; Papiol et al., 2012).

The distribution of species is affected by a number of environmental variables such as temperature and productivity, which can affect both their maximum densities and the extreme limits in their distribution (Fanelli et al., 2007). Wienner and Read (1982) observed that decapod crustacean communities show definite changes in structure (species abundance and composition) with season and depth. However, Munoz et al. (2008) found no seasonality in decapod communities in the West Mediterranean Sea due to spatial interactions between assemblages. The presence of most of the species in depth zones 1 and 2 in this study may have been due to high primary productivity and other favourable environmental factors such as salinity, dissolved oxygen and substratum type. However, the study did not cover some of these parameters.

Although some studies (e.g. Fanelli et al., 2007; Wienner & Read, 1982) have reported the influence of both seasonality and depth on crustacean distributions, this study, like others (e.g. Munoz et al., 2008) found that seasonality had less influence on the crustacean assemblages than depth. Environmental variables directly related to depth, such as temperature and dissolved oxygen, may play an important role in structuring the assemblages. Canonical Correspondence Analysis indicated that temperature influenced the composition of species in depth zone 1 during the NEM, while dissolved oxygen, water clarity and salinity had a greater effect on species composition in depth zones 2 and 3. A lack of environmental parameters during the SEM precluded determination of the effects of these environmental variables during this season.

In conclusion, the study found that penaeid prawns were the most abundant group in all the depth zones and seasons in Malindi-Ungwana Bay. All crustacean groups occurred in higher abundance in the SEM than in the NEM. This variation was attributed to seasonal changes in oceanographic conditions and crustacean behaviour. Decapod crustacean assemblage structure in the bay appeared to be more influenced by depth than seasonality, and most of the biomass was found at shallower depths. The study also revealed higher crustacean species diversity in the bay during the SEM than the NEM in all depth zones. Taking these results into consideration, it is recommended that the spatial and temporal variation in crustacean community structure should be considered when developing a fisheries management plan for the bay, and that future studies should determine the parameters that influence the seasonal abundance in populations.
Acknowledgements – We are grateful to the South West Indian Ocean Fisheries Project (SWIOFP) crustacean scientific trawl team led by Dr Edward Kimani and team members (Julius Manyala, Rashid Kaka, Thomas Mkare, Captain Joseph Mwanthi, Dickson Odongo, Boaz Orembo and Joseph Kilonzi) and the FV Vega crew for their good team work. We thank the SWIOFP for funding this study through a fellowship to CKN. The Kenya Marine and Fisheries Research Institute (KMFRI) provided laboratory space and logistical support. The Kenyan Permanent Secretary, Ministry of Fisheries Development, and Director of Fisheries provided work leave to CKN.

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Reproductive Biology of the Common Octopus 
(*Octopus vulgaris* Cuvier, 1797) in South Kenya


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**Keywords:** *Octopus vulgaris*, reproduction, Shimoni, Vanga, Kenya

**Abstract** — Although common octopus catches are increasing globally, lack of information on the reproductive biology of the species has been a major concern in its management, particularly in Kenya. The present study aimed to investigate the reproductive biology of common octopus at Shimoni and Vanga on the Kenyan south coast. Sampling was undertaken monthly from November 2010 to November 2012 using a traditional fishing spear. The body weight (BW), total length (TL), dorsal mantle length (DML), ventral mantle length (VML) and gonad weight was recorded for each specimen. Maturity stages and gonadosomatic indices (GSI) were determined using standard methods. A total of 1 599 specimens (746 males and 853 females) were collected. The sex ratio was 1:1.1 (males: females) at both Shimoni and Vanga during the study period. Sexual staging of gonads indicated that the common octopus was breeding year round with a spawning peak from June to August. Fecundity estimates ranged from 5 200 to 389 000 oocytes (mean 154 057.6 ± 29 132). The lowest gonadosomatic index values were recorded during the month of September, indicating the end of the spawning period. The female length at first maturity (DML50) was 10.8 cm, that for the male was 10.5 cm.

**INTRODUCTION**

The common octopus has been shown to spawn year-round with two main peaks in spring and autumn, although this varies depending on the study site (Hernández-García *et al.*, 2002; Silva *et al.*, 2002; Caverivière *et al.*, 2002; Oosthuizen & Smale, 2003). Zguidi (2002) reported that female common octopus normally attain sexual maturity at an average weight of 1 200-1 450 g in the Gulf of Gabès, Tunisia. He further found that females spawn from February to September with a peak between March and July. Mature males were recorded all year round. The breeding season was preceded by an inshore migration in autumn, with males migrating before the females (Zguidi, 2002). In early spring, a large number of adult females isolated themselves in shelters for spawning (Caverivière, 1990).
Because of their solitary lifestyle, mating in common octopus does not involve long-term pairing, monogamy or intricate courtship (Hanlon & Messenger, 1996). Common octopuses are oviparous and have separate sexes with no sex reversal or hermaphroditism. After a successful mating and when conditions are right for fertilization, a female lays 100 000-500 000 eggs (Hanlon & Messenger, 1996). These are attached to the substratum inside the den, either individually or in a clump, and she protects and cares for them until they hatch. The hatchlings are then carried away by currents and they feed on plankton for 45-60 days. Only a few of the hatchlings survive to adulthood (Scheel, 2002). Sexual maturity drastically changes the female’s life processes and activities. Her body stops growing and she remains in the den without food, discontinuing eating for the rest of her life. According to Anderson et al. (2003), female common octopus die soon after their eggs hatch as they are too weak to eat due to a massive decrease in their digestive gland weight. After mating, male octopuses are often seen engaged in undirected activities, even during the day, in the wild and in captivity. In captivity, this behaviour may continue for some time but, in the wild, it probably results in the octopus quickly becoming an easy prey. The entire life cycle of common octopus only lasts between twelve and fifteen months (Katsanevakis & Verriopoulos, 2005).

Gonzalez et al. (2011) found that the gonadosomatic index of female common octopus increased with sexual maturation in the Gulf of Alicante in the north western Mediterranean. Maximum values of the index occurred when reproductive activity was at its highest. In males, the testis and the Needham sac increase in weight before the beginning of the spawning season (Mangold, 1983)and males usually reach sexual maturity ahead of the females, but this does not prevent reproduction (Silva et al., 2002). This is possible because females store sperm in their oviducal gland until they are sexually mature and the ova are ready for fertilisation (Hanlon & Messenger, 1996). The female can retain sperm inside their oviducal gland for up to two thirds of their life span. This also allows the females to collect sperm sacs from various partners before fertilisation of eggs.

Information on the common octopus reproductive biology is important as it provides an insight to the fishery needed for its management. For example, while fecundity studies provide an understanding of the reproductive potential of the species, information on the spawning season, mode of reproduction and spawning migrations yield information on the recruitment potential of the stock. The small-scale fishery on the common octopus is of great socio-economic importance on the Kenyan coast and it is an valuable resource, yielding almost 394 metric tonnes a year (McClanahan & Mangi, 2001). Nevertheless, no reproductive biology studies have been undertaken on the species in Kenyan coastal waters (State Department of Fisheries, unpubl. data). This study on the reproductive biology of the species is intended to inform policy in the management of the fishery in Kenya.

METHODS

Sampling for common octopus was carried out at Shimoni and Vanga along the Kenyan South coast between November 2010 and November 2012 (Fig. 1). The two study sites are among the main fishery landing sites on the Kenyan coast. Shimoni is at 4°38’ S; 39°23’ E, lying some 70 km south of the main octopus markets in Mombasa. Vanga is at: 4°39’ S; 39°14’ E and it is the southernmost fishing village on the Kenyan border with Tanzania.

Common octopuses were collected on a monthly basis at both Shimoni and Vanga, predominantly during low spring tides, using a traditional spear. The following was recorded for each individual: sex, total body wet weight (BW), total length (TL) - measured from the end of the longest arm to the posterior end of the mantle, total gonad wet weight, dorsal mantle length (DML) - measured from the midpoint between the eyes to the posterior tip of the body, and the ventral mantle length (VML) - measured from the anterior border of the mantle ventral midline to the apex of the mantle.
Assessment of the sex ratio

Sex was determined by the presence of a spermatophoric groove and hectocotylus on the third right arm of males and the absence of these features in females. Only common octopus whose sexes could successfully be determined were used to calculate sex ratios and these were analysed on a monthly, seasonal and annual basis.

Significant deviations in the ratios from 1:1 were tested using the chi-squared ($\chi^2$) test.

$$\chi^2 = \sum \frac{(f-F)^2}{F}$$

Where;
- $f$ = observed number of individuals of each sex.
- $F$ = expected number of individuals of each sex.
Assessment of the size at first maturity

Maturation and reproduction were assessed using a four point maturity scale (Inejih, 2000) for males (Table 1) and five point maturity scale for females (Table 2).

Common octopus belonging to maturity stage II onwards were considered mature and were used in the size at first maturity calculations; all the sampling data were pooled for this. The DML at which 50% of common octopuses were mature was considered the length at first maturity.

The size at first maturity (DML<sub>50%</sub>) was estimated by fitting the length-frequency distribution of the proportion (P<sub>i</sub>) of mature females to a logistic model, P<sub>i</sub> = 1/(1+exp[-a + bDML<sub>i</sub>]), where DML<sub>50%</sub> = -a/b, using nonlinear methods, and deriving the regression line by the least squares method using the Gauss-Newton algorithm (Quinn & Keough, 2002).

Here:

P<sub>i</sub> = represents the relative frequencies of fully mature individuals in length class DML<sub>i</sub>.
‘a’ and ‘b’ = are the regression constants, and DML<sub>50%</sub> = is the dorsal mantle length at 50 % sexual maturity.

The body weight (BW) at first maturity was estimated following the same procedure.

Table 1. The four reproductive stages of male common octopus.

<table>
<thead>
<tr>
<th>Stage</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stage I: Immature</td>
<td>Indistinct accessory gland systems and testis.</td>
</tr>
<tr>
<td>Stage II: Maturing</td>
<td>Testis was larger than the accessory gland and visible through the wall of the genital bag.</td>
</tr>
<tr>
<td>Stage III: Mature</td>
<td>Testis and accessory gland of similar size and spermatophores present in the Needham’s sac and/or penis.</td>
</tr>
<tr>
<td>Stage IV: Post-spawning</td>
<td>Testis small and striated and spermatophores present in the penis and/or Needham’s sac.</td>
</tr>
</tbody>
</table>

Table 2. The five reproductive stages of female common octopus.

<table>
<thead>
<tr>
<th>Stage</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stage I: Immature</td>
<td>Ovary small, generally weighing &lt;3 g with no follicles and a thick outer wall; small white oviducal glands located mid-way down very narrow proximal and distal oviducts.</td>
</tr>
<tr>
<td>Stage II: Maturing</td>
<td>Ovary slightly larger with a thinner wall than stage I and follicles and/or very small eggs; oviducts longer and white oviducal glands larger and positioned further up the proximal oviduct.</td>
</tr>
<tr>
<td>Stage III: Mature</td>
<td>Ovary very large (&gt;20 g), packed tightly with elongated, striated but unstalked eggs; oviducal glands large and dark in colour and positioned high up the proximal oviduct.</td>
</tr>
<tr>
<td>Stage IV: Pre-spawning</td>
<td>Majority of remaining eggs stalked, fully formed and less compressed than in stage III; eggs present in the oviducts and dark oviducal glands, located further down the proximal oviduct.</td>
</tr>
<tr>
<td>Stage V: Post-spawning</td>
<td>Ovary shrunken with only follicles and a few fully-formed eggs; oviducts slightly reduced in size unless containing eggs; oviducal glands smaller but still dark in colour.</td>
</tr>
</tbody>
</table>
Assessment of gonad maturity

In the laboratory, portions of the middle region of the ovary were cut and preserved in Bouin’s solution for histological study. These were dehydrated in an alcohol gradient (30%, 50%, 70%, 80%, 90%, 95%, 100%), cleared in xylene, embedded in paraplast wax, sectioned in 5 µm slices and stained in iron haemotoxylin and eosin (Carson, 1992). The final preparations were examined under a dissecting microscope (40× magnification) for identification of the maturity stages.

Assessment of Gonadosomatic Index

The gonadosomatic indices (GSI) were calculated by comparing the monthly frequency of males and females in each maturity stage with their monthly average body mass (Kume & Joseph, 1969).

\[
\text{GSI}_m = \frac{\text{Testis weight}}{\text{Total Tissue Weight}} \times 100
\]

\[
\text{GSI}_f = \frac{\text{Ovary weight}}{\text{Total Tissue Weight}} \times 100
\]

Where:

- \( m \) = males
- \( f \) = females

Assessment of relative fecundity

The fecundity of approximately ten female octopus with mature ovaries was analysed each month. Gonad sections from these specimens were stored in Gilson’s fluid for three months in plastic bottles, vigorously shaken from time to time to aid in the release of oocytes from the ovarian walls. Before counting the eggs, the contents of each bottle were poured into a petri dish and oocytes not liberated from the ovarian tissue were removed by teasing. The oocytes were repeatedly washed in tap water and transferred to a one litre beaker containing tap water. A plastic ruler was used to stir the egg suspension vigorously to ensure an even distribution of the oocytes and, after ten strokes of the ruler, a subsample was removed using a Labsystem pipette. One aliquot usually yielded sufficient numbers of large and small oocytes to counts and measure. The oocytes were pipetted into a zooplankton chamber, and their diameter was measured using a calibrated eye-piece graticule under a dissecting microscope at 40× magnification.

The fecundity (F) of each octopus was calculated following the formula published by Simpson (1951):

\[
F = \left( \frac{V}{V_i} \right) n \times \left( \frac{W}{W_i} \right)
\]

Where:

- \( n \) = number of oocytes in the subsample;
- \( V \) = volume of the egg suspension;
- \( V_i \) = volume of subsample;
- \( W \) = weight of the ovary;
- \( W_i \) = weight of fixed portion of the ovary.

RESULTS

Sex ratios

While the sex ratio (M:F) of common octopus at Shimoni was 1:1.2, at Vanga it was 1:1. The monthly ratios were variable (Figure 2) but a chi-squared test (Shimoni: \( \chi^2 = 6.2, \ df = 1, p >0.75; \ Vanga: \chi^2 = 1.7, \ df = 1, p >0.05 \)) revealed no significant differences in the monthly or annual sex ratios. Seasonally, a significant difference emerged in the sex ratios \( (p <0.05) \) in favour of females during the northeast monsoon (NEM) months of February-September. No significant difference was detectable during the southeast monsoon (SEM) months of May-August.

Sex ratio at different sizes

There were no significant differences \( (p >0.05) \) in the sex ratio (M:F) in most size classes at either Shimoni or Vanga up to 18 cm (Shimoni) or 19 cm (Vanga) DML, at which size only females were found (Figure 3); females clearly grew larger than males. At Vanga, only females were found in the length class of 5 cm; this was probably a sampling artefact.

Size at sexual maturity

Analysis of the length at first maturity revealed that the female size at first maturity (DML_{50}) was 10.8 cm and that of males was 10.5 cm (Fig. 4).
Figure 2. Variation in monthly sex ratios of common octopus at a) Shimoni and b) Vanga.

Figure 3. Sex ratios in the different size classes of common octopus at a) Shimoni and b) Vanga.

Figure 4. Cumulative frequency curves of length of maturity stages II, III and IV in common octopus in southern Kenya: a) females at Shimoni, b) females at Vanga, c) males at Shimoni and d) males at Vanga.
Gonad maturity

The monthly gonad development of common octopus at Shimoni and Vanga is shown for the entire sampling period in Figure 5.

**Gonadosomatic Index (GSI)**

Gonadosomatic indices of male and female common octopus at Shimoni revealed that low GSI values occur during the months of August and September. High GSI values were recorded during the months of April, May, November, and December. Both sexes yielded high GSI values during the northeast monsoon, compared to the southeast monsoon. The monthly GSI values for females and males at Vanga were low during the months of August and September. High GSI values were recorded during the months of April, October, and November.

**Fecundity**

The lowest number of oocytes counted in a single female octopus was 5 200 while the highest was 389 000. The mean fecundity was 154 057.61 ± 29 131.97 (SD). Fecundity was highest in the months of January, September and April and lowest in the months of March, August and, particularly, May. No significant difference in annual fecundity was noted (p>0.05, t = -0.7279, d = 22 and p = -0.474). Variations in the seasonal (NEM and SEM) mean fecundity were significantly different (p<0.05, t = 0.5185, df = 22 and p = 0.031). The mean diameter of the long axis of eggs in common octopus was 0.14 ± 0.02 cm.
DISCUSSION

The sex ratio recorded in the current investigation concurs with studies by Otero et al., (2007), who reported a sex ratio of 1:1 for common octopus in the Balearic Islands and along the Galician coastline in the northwestern Mediterranean. The dominance of females in the larger class sizes in this study (Fig. 3) was also evident in several parts of the Atlantic Ocean (Silva et al., 2002). This was attributed to a number of factors, among them differences in growth rates of the two sexes (Silva et al., 2002; Mangold, 1983). A slightly greater prevalence of males detectable in some months in the current study (Fig. 2) may be an indication that females were moving from fishing grounds for breeding purposes; similar shifts in the sex ratio have been found in the Mediterranean Sea (Mangold-Wirz, 1963) and Morocco-Mauritania (Hatanaka, 1979; Dia, 1988). It has been stated that such variations in the sex ratio are difficult to explain but some authors attribute it to a combination of factors such as migration associated with sexual maturation and spawning processes (Mangold-Wirz, 1963); feeding behaviour related to reproduction; post-spawning mortality; and differences in the growth rates of the sexes (Mangold, 1983). Differences in the sex ratios found in other areas could be attributed to the sampling strategy (Caverivière et al., 2002). In South Africa, Oosthuizen (2003) established that females were dominant in intertidal areas but no differences were found sub-tidally. Most females found in the sub-tidal zone, where they gather for mating, were mature (Mangold, 1983).

The size at first maturity recorded in the present study of 10.8 cm DML for females and 10.5 cm DML for males was lower than that reported by Mangold (1983). Sánchez and Obarti (1993) recorded a size at first maturity of 11-13 cm DML for both males and females in Spanish Mediterranean waters. Similar studies by Guerra (1975) in the Mediterranean revealed that males reached sexual maturity much earlier than females. Dia (1988) found that males in the Gabes Gulf were smaller than females at sexual maturity. Other studies have also indicated that males reach sexual maturity earlier than females (Gonçalves, 1993; Silva et al., 2002; Oosthuizen & Smale, 2003; Mangold-Wirz, 1963; Dia, 1988) but the size at which this occurs varies.

Mature females and males were collected throughout the sampling period which may indicate that common octopus spawn throughout the year on the Kenyan south coast. This concurs with the findings of Silva et al. (2002) and Oosthuizen and Smale (2003) in the Gulf of Cádiz and South Africa. In a similar study conducted in the Mediterranean, the reproductive period of common octopus seemed to extend almost throughout the year from January to October, but with one or more spawning peaks (Mangold-Wirz, 1963). In the present study, mature females at stage III were recorded in all months except June - August which may indicate that the majority of mature females were in their nests spawning. A high number of spent females were recorded in the months of November and December, providing evidence of a post-spawning season.

The low GSI values we encountered during the months of August and September may be an indication of reduced spawning during that period. Guerra (1975) reported that, in female common octopus, the GSI increases with sexual maturation and maximum values are attained when reproductive activity is at its highest. In males, the testis and the Needham sac (which acts as a reservoir for spermatophores before mating) increase in weight before spawning commences in females.

The range in fecundity of 5 200 and 389 000 eggs we measured in gravid females fell within the range recorded by Oosthuizen and Smale (2003) in South Africa and Silva et al. (2002) in the Gulf of Cádiz; their estimates fell between 12 000 and 500 000 eggs per female. The high fecundity we recorded in the month of April may be indicative of a pre-spawning peak in their development, and the drop in fecundity which commenced in June may be an indication that this was the start of spawning. The spawning season of common
octopus in the Kenyan South coast may thus occur during the months of June, July and August. The mean egg diameter of 0.14 ± 0.02 cm recorded in the present study was lower than that measured by Isshiki et al. (2012) in Tokyo Bay, Japan, where the mean diameter of the long axis of common octopus eggs was 0.23 ± 0.03 cm. Other similar studies by Hatanaka (1979) estimated a mean length of oocytes at 0.32 ± 0.08 cm, ranging from 0.17 to 0.49 cm. The smaller mean egg size we recorded may be attributable to the smaller mean body sizes of octopus in our study.

The northeast and southeast monsoon seasons seemed to have no influence on the spawning patterns of common octopus on the Kenyan south coast. This is in contrast with results from the Gulf of Cádiz (SW Spain) and the north western coast of Africa which revealed that a number of factors such as climatic conditions affected the spawning pattern of common octopus (Hatanaka, 1979; Hernández-García et al., 2002; Silva et al., 2002). In Spain, spawning peaked during spring and extended up to the onset of winter Silva et al. (2002).

Based on the results of this study which have revealed that female common octopus attain maturity at 10.8 cm DML and males at 10.5 cm DML on the Kenyan coast, it is recommended that a minimum size limit of 10.8 cm DML be imposed as a precautionary measure for their harvest to ensure maturation of both males and females before they enter the fishery.

Acknowledgements – GMK is extremely grateful to the Ministry of Education, Science and Technology, Kenya, for financial support which enabled him to undertake this study. Our sincere thanks also go to the artisanal fishermen, the staff of the State Department of Fisheries, Kenya Marine and Fisheries Research Institute, the University of Nairobi and all those who helped us in one way or another in this study.

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Diel and Lunar Variations in Larval Fish Supply in Malindi Marine Park, Kenya

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Keywords: Fish larvae, diel patterns, lunar patterns, larval supply, Malindi Marine Park,

Abstract — Larval fish supply to reefs influences the structure of adult populations and their response to exploitation. Despite this, few studies have examined patterns of larval fish supply to reefs in the Western Indian Ocean. The temporal variability in fish larval occurrence was thus studied in Malindi Marine Park, Kenya, to assess diel and lunar patterns of larval replenishment. Monthly and 24-hour sampling for fish larvae were undertaken between March 2005 and March 2007. Replicate samples were obtained by towing a 2 m long plankton net (500 µm mesh size, 0.2 m² mouth area) for six minutes within the park. Larval abundance (larvae.100 m⁻³ ± SE) in the park was significantly higher during spring tides (951 ± 408) than neap tides (394 ± 260). Nocturnal larval abundance was 13-fold greater than daytime concentrations, regardless of tidal regime. The dominant fish families in the larval pool were Engraulidae, Labridae, Blenniidae and Gobiidae. Spectral time-series analysis revealed that larval fish supply occurred in a 30-day cyclical pattern associated with the new moon and was synchronised in the long-term with the northeast monsoon season.

INTRODUCTION

Elucidation of the patterns and processes associated with the supply of fish larvae to habitats is critical to understanding the replenishment and structure of their fish populations (D’Alessandro et al., 2007). Larval supply to habitats is affected by stochastic factors such as chemical, physical and biological oceanographic conditions during planktonic phases (Richards & Lindman, 1987; Kaunda–Arara et al., 2009), and by more deterministic factors such as spawning regimes and seasonal cues (Johannes, 1978; Valles et al., 2001). It is unlikely that biological or physical factors...
will exclusively control variability in the larval supply to reefs. However, larvae have been reported to frequently settle on a cyclical basis, correlated with short-term factors such as lunar cycles or tidal amplitude (Johannes, 1978; Taylor, 1984; Leis, 1993; D’Alessandro et al., 2007; Kaunda-Arara et al., 2009), and with large-scale factors such as inter-annual variability in ocean conditions (Doherty, 1987). In terms of the lunar cycle, greater larval settlement onto reef sites has been associated with new moon phases (Dufour & Galzin, 1993), perhaps as a strategy to avoid predation (Johannes, 1978). Environmental factors such as wind direction and speed can influence larval settlement at different temporal scales (Dufour & Galzin, 1993) and have been reported to affect larval distribution in nearshore habitats (Jenkins et al., 1998). Despite the effects of currents and wind on larval transport, some late-stage larvae of fish are known to actively control their position and dispersal (Leis, 1993).

The composition, structure and timing of fish larval settlement from distant sites on reefs probably influence the population dynamics of the settled adult populations and their response to exploitation. Reefs with a high and diverse supply of fish larvae are likely to be less susceptible to and recover faster from the effects of overfishing (D’Alessandro et al., 2007). Therefore, it is important to understand both the temporal and the spatial scales of larval supply to these habitats. Moreover, larval transport between reef sites influences levels of connectivity and hence the genetic differentiation of reef populations (Sinclair, 1988; Botsford et al., 2009). Despite this, few studies have examined temporal and spatial variability in larval fish supply in the Western Indian Ocean (WIO) (but see Kaunda-Arara et al., 2009). Patterns in larval supply to reefs in the WIO at fine temporal scales are virtually unknown. The temporal variability in fish larval occurrence was thus studied in Malindi Marine Park, Kenya, to assess diel and lunar patterns of larval abundance.

### METHODS

#### Study site

The study was carried out in Malindi Marine Park (Fig. 1), a marine park created in 1968 which is 6.3 km² in extent and includes part of Kenya’s continuous nearshore fringing reef and a patch reef system. The park encloses a shallow lagoon with interspersed sand, algae, coral rubble and live coral bommies. Beds of the seagrass *Thalassodendron ciliatum* and isolated coral heads dominated by species of *Porites* and *Galaxea* occur on the upper edges of the east and south-west slopes of the North Reef (Fig.1). Malindi Marine Park is surrounded by a marine reserve (a traditionally-fished area) which has been fished for many years. However, no resource extraction is allowed in the park.

#### Field sampling

Fish larvae were sampled monthly (March 2005 to December 2006) at stations 1-3 (Fig. 1) using a 2 m long plankton net with a mesh size of 500µm and mouth area of 0.2 m² towed behind a boat at a constant speed of ~1 m.s⁻¹ for six minutes. Three replicate tows were collected during the day at high tide at each station, working from close (1-3 m) to the bottom to just below the water surface at depths ranging from 10-18 meters. A calibrated General Oceanics flowmeter was installed at the center of the mouth of the net to measure volume of seawater filtered. After each tow, samples were preserved in 5% buffered formaldehyde in seawater.

Six 24-hour sampling sessions were undertaken at Station 1 (Fig. 1) to determine diel variation in larval abundance. Sampling was undertaken during neap and spring tides on 15-16 March 2005 (spring tide), 18-19 March 2005 (neap tide), 27-28 May 2005 (spring tide), 29–30 June (neap tide), 24 –25 January 2007 (spring tide) and 29-30 March 2007 (neap tide). The tidal state and amplitude on sampling dates were derived from the Kenya Port Authority tide tables. Tows were
conducted using the net described above along randomly selected transects parallel to the shore (Fig. 1) at six-hour intervals beginning at 1200 hrs noon to 1200 hrs the next day. A total of five samples were collected from five tows during each sampling session.

All fish larvae were separated from the samples under a Wild Heerbrugg M3C stereo microscope in the laboratory and identified to the lowest taxonomical level using keys provided by Leis and Rennis (1983), Leis and Trnski (1989) and Leis and Carson-Ewart (2000).

Figure 1. Map of Malindi Marine National Park, Kenya, showing the stations (1-3) sampled monthly for fish larvae and the location of transects for the 24-hr sampling sessions (●).
Table 1. Differences in mean (±SE) fish larval abundance (larvae.100 m$^{-3}$), total larvae and development stage (preflexion, pr; flexion, fl; and postflexion, po) between spring and neap tides during six 24-hr sampling sessions in Malindi Marine Park, Kenya. n.d. indicates undetermined species; the t-test compared spring vs neap tides.

<table>
<thead>
<tr>
<th>Taxa</th>
<th>Stage</th>
<th>Spring tide Mean abundance</th>
<th>Total larvae</th>
<th>Neap tide Mean abundance</th>
<th>Total larvae</th>
<th>t</th>
<th>p</th>
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<tbody>
<tr>
<td>Acanthuridae</td>
<td>pr</td>
<td>10 ± 10</td>
<td>50</td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Acanthurus sp.</td>
<td>pr</td>
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<td>100</td>
<td></td>
<td></td>
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<td>Apogonidae</td>
<td>pr</td>
<td>8 ± 8</td>
<td>40</td>
<td>28 ± 9</td>
<td>142</td>
<td>-0.66</td>
<td>0.52</td>
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<td>Balistidae</td>
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<td>7</td>
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<td></td>
</tr>
<tr>
<td>Blenniidae</td>
<td>pr, fl, po</td>
<td>131 ± 41</td>
<td>465</td>
<td>46 ± 25</td>
<td>230</td>
<td>0.53</td>
<td>0.60</td>
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<td>96 ± 48</td>
<td>482</td>
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<td>4 ± 4</td>
<td>20</td>
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<td>Carangidae</td>
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<td>4</td>
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<td>Caranx sp.</td>
<td>fl</td>
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<td>33</td>
<td>-1.43</td>
<td>0.17</td>
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<td>Dactylopterus sp.</td>
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<td>2</td>
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<td>Gerreidae</td>
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<td>20</td>
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<td>Gobiidae</td>
<td>pr</td>
<td>1 ± 1</td>
<td>4</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Gobies ria</td>
<td>pr</td>
<td>1 ± 1</td>
<td>7</td>
<td>7 ± 7</td>
<td>33</td>
<td>-1.43</td>
<td>0.17</td>
</tr>
<tr>
<td>Haemulidae</td>
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<td>5 ± 5</td>
<td>25</td>
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<tr>
<td>Pomadysis maculatum</td>
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<td>5 ± 5</td>
<td>25</td>
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<td>Labridae</td>
<td>pr, fl, po</td>
<td>250 ± 250</td>
<td>1075</td>
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<tr>
<td>Lethrinidae</td>
<td>pr, fl, po</td>
<td>215 ± 215</td>
<td>175</td>
<td>7 ± 7</td>
<td>33</td>
<td>-1.36</td>
<td>0.19</td>
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<td>Lutjanidae</td>
<td>pr</td>
<td>2 ± 2</td>
<td>8</td>
<td>1 ± 1</td>
<td>5</td>
<td>-0.66</td>
<td>0.51</td>
</tr>
<tr>
<td>Monacanthidae</td>
<td>pr</td>
<td>2 ± 2</td>
<td>8</td>
<td>1 ± 1</td>
<td>5</td>
<td>-0.66</td>
<td>0.51</td>
</tr>
<tr>
<td>Monacanthus ciliatus</td>
<td>pr</td>
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<td>7</td>
<td>4 ± 4</td>
<td>20</td>
<td>1.13</td>
<td>0.27</td>
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<td>pr</td>
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<td>8</td>
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<tr>
<td>Nemipteridae</td>
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<td>-</td>
<td>3 ± 3</td>
<td>13</td>
<td>-</td>
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<tr>
<td>Platyccephalidae</td>
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<td>2</td>
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<tr>
<td>Platycephalidae n.d.</td>
<td>fl</td>
<td>-</td>
<td>1 ± 1</td>
<td>7</td>
<td>-</td>
<td></td>
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<tr>
<td>Pomacentriderida</td>
<td>pr</td>
<td>5 ± 5</td>
<td>25</td>
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<tr>
<td>Chromis sp.</td>
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<td>2 ± 2</td>
<td>8</td>
<td></td>
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<tr>
<td>Abudeddyf sp.</td>
<td>pr</td>
<td>1 ± 1</td>
<td>13</td>
<td></td>
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<tr>
<td>Pomacanthidae</td>
<td>pr</td>
<td>2 ± 2</td>
<td>8</td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Siganus sutor</td>
<td>pr, po</td>
<td>20 ± 20</td>
<td>100</td>
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<tr>
<td>Siganus canaliculatus</td>
<td>pr, po</td>
<td>7 ± 7</td>
<td>33</td>
<td>4 ± 4</td>
<td>20</td>
<td>0.64</td>
<td>0.53</td>
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<td>Sparidae</td>
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<tr>
<td>Leptocaras vaigiensis</td>
<td>pr</td>
<td>100 ± 100</td>
<td>500</td>
<td></td>
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<td></td>
</tr>
<tr>
<td>Calotomus sp.</td>
<td>pr</td>
<td>3 ± 3</td>
<td>13</td>
<td></td>
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<td>pr</td>
<td>6 ± 5</td>
<td>30</td>
<td></td>
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</tr>
<tr>
<td>Sigynidae</td>
<td>pr</td>
<td>11 ± 10</td>
<td>57</td>
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<tr>
<td>Sphyraena barracuda</td>
<td>fl, po</td>
<td>10 ± 10</td>
<td>50</td>
<td>2 ± 2</td>
<td>4</td>
<td>1.93</td>
<td>0.07</td>
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<tr>
<td>Sygnathidae</td>
<td>pr</td>
<td>1 ± 1</td>
<td>3</td>
<td>1 ± 1</td>
<td>4</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Symphostoma sp.</td>
<td>fl</td>
<td>9 ± 3</td>
<td>47</td>
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<td>Tetraodontidae</td>
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<td>2 ± 2</td>
<td>8</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Totals</td>
<td></td>
<td>951 ± 408</td>
<td>4562</td>
<td>394 ± 260</td>
<td>1890</td>
<td>2.10</td>
<td>0.03</td>
</tr>
</tbody>
</table>
Data analysis

Data from all three stations were pooled to represent monthly supply of larvae into the park environment as no significant difference was detected in the monthly larval abundance between stations (2 way-ANOVA, $F = 1.62$, $p = 0.198$). The data were standardised according to the volume of water sampled to obtain larval abundance per day. The total daily abundances were then averaged to obtain mean daily abundances (larvae.100 m$^{-3}$) which were then subjected to time-series spectral analysis to examine fine-scale temporal variations of larval abundance in the park (Taylor, 1984). In addition, Autocorrelation Function (ACF) plots were used to validate significant periodicities identified by the power spectra (Platt & Denman, 1975; Taylor, 1984).

RESULTS

Diel cycles

A total of 394 larvae were collected from the six 24-hour samples, comprising 39 species in 27 families (Table 1), mainly Blennidae, Gobiidae, Engraulidae, Labridae and Scaridae in a complete range of stages (principally preflexion, but also flexion and postflexion; Table 1). During neap tides, Stolephorus commersonii (Engraulidae), an Apogon sp. (Apogonidae), Parablennius sp. (Blenniidae) and a Gobiidae sp. (not determined, n.d.) dominated the park samples, while Stolephorus commersonii, Leptoscarus vaigiensis (Scaridae), Labridae n.d. and Parablennius sp. were the dominant larvae during spring tides. The total mean abundance (100 m$^{-3}$ ± SE) of larvae in the park was significantly higher during spring tides (951 ± 408) than neap tides (395 ± 261; $t = 2.02$, $p < 0.05$; Table 1).

During spring tides, the mean larval abundance (100 m$^{-3}$ ± SE) increased from 205.3 ± 197 at 1800 hrs to a peak of 1 184 ± 1060 at 2400 hrs (Fig. 2a). Larval abundance increased from 205.3 ± 197 at 1800 hrs to a peak of 1 184 ± 1060 at 2400 hrs (Fig. 2a). Larval abundance

<table>
<thead>
<tr>
<th>Species</th>
<th>Season</th>
<th>F</th>
<th>p</th>
<th>Time of day</th>
<th>F</th>
<th>p</th>
<th>Season and time of day</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total catch</td>
<td>0.575</td>
<td>0.455</td>
<td>1.771</td>
<td>0.195</td>
<td>2.003</td>
<td>0.169</td>
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<tr>
<td>Stolephorus commersonii</td>
<td>2.014</td>
<td>0.168</td>
<td>2.504</td>
<td>0.126</td>
<td>2.341</td>
<td>0.138</td>
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<tr>
<td>Blennidae n.d.</td>
<td>3.520</td>
<td>0.124</td>
<td>0.801</td>
<td>0.378</td>
<td>1.198</td>
<td>0.283</td>
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<tr>
<td>Gobiidae n.d.</td>
<td>0.06</td>
<td>0.806</td>
<td>2.41</td>
<td>0.132</td>
<td>0.03</td>
<td>0.851</td>
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</tbody>
</table>
was lowest in the park at 1200 hrs (26.0 ± 13.3) during spring tides (Fig. 2a). During neap tides, the mean larval abundance (100 m⁻³ ± SE) increased from 57.1 ± 47.4 at 1200 hrs to a peak of 246.3 ± 210.4 at 1800 hrs (Fig. 2b). Thereafter, the larval occurrence in the park declined to levels of 90 ± 50.8 and 103 ± 68.1 at 2400 and 0600 hrs, respectively. No significant effects of season (p = 0.455), time of day (p = 0.195) or their interactions (season x time of day; p = 0.169) were found on larval abundance in the park (Table 2). Similarly, no significant effect season or time of day were found on the occurrence of the most abundant taxa, Stolephorus commersonii (p = 0.168 and p = 0.126), Gobiidae n.d. (p = 0.806 and p = 0.132) and Blennidae n.d. (p = 0.124 and 0.378)

The larval supply of the dominant species (e.g. Stolephorus commersonii, Labridae n.d. Parablennius sp. and Gobiidae n.d.) to the park was highest during nocturnal spring tides (2400 hrs; Fig. 3), suggesting that these larvae entered the park mostly under these conditions. However, during daytime spring tides, the abundance of most species was low except for the Parablennius spp. at 0600 hrs (Fig. 3). During neap tides, larvae of these species were almost absent during the day and appeared at night in comparatively low numbers (Fig. 3). The cardinalfish, Apogon sp., was not caught during spring tides most of the time except at 0600 hrs. However, during neap tides, this species, unlike the others, was more abundant during the day at 1200 hrs and

![Figure 3. Diel variation in abundance (vertical bars represent the SE) of the dominant fish larval species collected during six 24-hr sampling sessions in Malindi Marine Park, Kenya.](image-url)
at 1800 hrs (Fig. 3). Larval abundance was positively correlated with tidal height (r = 0.58), suggesting that larvae used high tides to enter the park.

**Lunar patterns**

The number of larvae sampled during new moon periods (2,886 larvae) was higher than during the full moon periods (2,824 larvae). However, no significant differences in mean larval abundance were detected between the two lunar periods for the comparable sample sizes of 204 and 200 tows during the new and full moon periods respectively (t = 1.84, p = 0.066). Spectral analysis of total larval (all families) and dominant species data revealed that peak larval supply occurred in a 25-30 days cycle, as shown in the spectral analysis periodogram (Fig. 4). This observation was corroborated by the Autocorrelation Function plot (ACF) that revealed a significant peak in larval arrival at 30-day intervals (p <0.05; Fig. 4).

The Blenniidae n.d. manifested a major peak in larval abundance at 30 days and a minor peak at 15 days with significant activity in the ACF plot at 30-day intervals (Fig 5). This pattern is suggestive of a lunar and semi-lunar frequency in its larval supply to the park. The *Stolephorus commersonii* larvae also manifested a strong peak in larval abundance in the park at 30-day intervals, and a minor peak at 27 days; the 30-day cycle again being confirmed by the ACF plot (Fig. 6). Finally, the Gobiidae n.d. larvae manifested some evidence of a similar pattern to the preceding in its abundance in the park (Fig. 7).

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![Figure 4](image_url)

**Figure 4.** Time-series of mean total fish larval abundance from March 2005 to December 2006 in Malindi Marine Park, Kenya (upper graph; = full moon and = new moon). The lower left spectral density plot shows the cyclical peaks within the time series (period in days) of larvae confirmed by the Autocorrelation Function plot (lower right) of the raw data, where the horizontal bars represent 2x the SE.
Figure 5. Time-series of larval abundance of a *blenniid* sp. from March 2005 to December 2006 in Malindi Marine Park, Kenya (upper graph; = full moon and = new moon). The lower left spectral density plot shows the cyclical peaks within the time series (period in days) of larvae confirmed by the Autocorrelation Function plot (lower right) of the raw data, where the horizontal bars represent 2x the SE.

Figure 6. Time-series of larval abundance of *Stolephorus commersonii* from March 2005 to December 2006 in Malindi Marine Park, Kenya (upper graph; = full moon and = new moon). The lower left spectral density plot shows the cyclical peaks within the time series (period in days) of larvae confirmed by the Autocorrelation Function plot (lower right) of the raw data, where the horizontal bars represent 2x the SE.
DISCUSSION

The supply of fish larvae to Malindi Marine Park seems to be both diel and lunar in pattern. Overall, greater numbers of larvae entered the park at night compared to the day, with evidence of lunar periodicity. Larval abundance was highest at 2400 hrs during spring tides, with abundances being twice that of neap tides and about 13 times more in the night compared to the day for a given tidal regime. It has been hypothesised that larvae are predominantly spawned or dispersed during the night or new moon to reduce the risk of mortality from visual predators (Johannes, 1978; Taylor, 1984; Dufour & Galzin, 1993). Additionally, it is likely that olfactory and sound cues for dispersal and settlement onto reefs may be more enhanced at night (Kingsford et al., 2002; Wright et al., 2005).

Among species with pelagic eggs and oceanic larvae (e.g. Stolephorus commersonii and the Labridae n.d. found in this study), a possible strategy in reproduction is to time spawning to coincide with the ebb of spring tides to maximise the offshore tidal transport of larvae to reduce predation (Johannes, 1978). Among demersal spawners (e.g. the Parablennius sp., Gobiidae n.d., Apogon sp. found in this study), hatching is similarly believed to occur predominantly at dusk or at night to prevent predation (Johannes, 1978; Dufour & Galzin, 1993). The presence of all stages of larvae in the families Gobiidae, Blennidae, Engraulidae, Labridae and Scaridae in this study suggested that they completed their pelagic larval phase within the lagoon (Mwaluma, 2010; Patrrick & Strydom, 2008).
In this study, fish larval abundance was cued to lunar phases in cyclical patterns of 30 days (with a semi-lunar peak in the Blenniidae). If larval supply was cued entirely to lunar or tidal cycles, then two peaks (pulses) in larval supply would occur in the park every month. However, sampling effort in this study had to be concentrated in the second half of the month for logistical reasons, thus missing potential semi-lunar peaks. The dominant species of larvae (Blenniidae n.d., Stolephorous commersonii and Gobiidae n.d) nevertheless manifested a synchronous abundance at 28-30 days, indicating similarities in factors that regulated their larval supply in the park. These results are similar to those reported by D’Alessandro et al. (2007) in the Florida Keys where the fish larval abundance peaked between 21 and 30 days. Factors related to the arrival of pre-settlement larvae at reef sites in different lunar phases have been associated with adult spawning behaviour (Taylor, 1984; Robertson, 1991; D’Alessandro et al., 2007), larval behaviour (Thorrold et al., 1994), spawning prior to recruitment (McIlwain, 2003) and passive delivery by currents (D’Alessandro et al., 2007). However, in this study, data were lacking to determine whether there environmental regulators determine lunar-based supply of fish larvae to the park.

Spectral analysis nevertheless revealed that larval fish supply to the park at a temporal scale is significant within a narrow diel and lunar period or window; this may be linked to environmental productivity (Johannes, 1978; Cushing, 1987), favourable oceanic conditions (McClanahan, 1988) and increased spawning activity (Mwaluma et al., 2011).

Larval fish supply to Malindi Marine Park thus appears to be influenced by lunar cycles with larvae arriving in the park in cycles of 30 days within a narrow window. The larvae displayed a tidally-induced diel, peak abundance during spring tides at midnight, suggesting a behavioural component in their replenishment. These results are useful for modelling of their dispersal and recruitment, needed to elucidate the population dynamics of coral reef fish communities.

Acknowledgements – We are grateful to the Director: Kenya Wildlife Service for permission to work in the Malindi Marine Park, and the Warden of the park for logistical support. We thank Bakari Faiz (KWS), Masudi Zamu (Kenya Marine and Fisheries Research Institute, KMFRI) and Anthony Nzioka (KMFRI) for assistance in the field. Funding was provided by the Western Indian Ocean Marine Science Association Marine and Coastal Science for Management grant number WIOMSA/MASMA/AG/2004/03.

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Phenotypic Divergence in the Reproductive Traits of Marbled Parrotfish *Leptoscarus vaigiensis* (Quoy and Gaimard, 1824) on Variably Protected Reefs in Kenya

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*Keywords:* *Leptoscarus vaigiensis*, fishing pressure, fecundity, evolutionary response, MPAs, Kenya

**Abstract** — Phenotypic divergence in the reproductive traits of marbled parrotfish (*Leptoscarus vaigiensis*) was studied during May 2011-April 2012 at six reef sites exposed to varying levels of fishing pressure in coastal Kenya. Baited fish traps were used to capture fish within two no-take marine parks (Malindi and Watamu) and adjacent reserves in which regulated fishing is allowed. Fish samples were also obtained from fishers operating at two unprotected sites (Kanamai and Vipingo). Reproductive attributes (fecundity, oocyte size and length at first maturity) were determined and revealed significant differences in fecundity between sites (F=3.742, P=0.004), fish in the parks and reserves having a higher mean fecundity (110 128±75 492 and 145 570±88 873 respectively) than those on unprotected reefs (76 250±55 337). Fish at unprotected sites had higher fecundities at smaller sizes relative to larger fish at protected sites. In terms of length at first maturity (L50), females at unprotected sites matured at lower lengths (11.2 cm, 11.1-11.4 cm, 95% CI) than those in marine parks (16.7 cm, 15.7-17.3 cm, 95% CI) and reserves (16.8 cm, 16.6-17.1 cm, 95% CI). Overall, the results indicated some level of phenotypic divergence of the fish between sites, which is possibly an adaptive strategy to enhance their resilience to fishing pressure, thereby serving to sustain local populations. The real causes of this divergence cannot be partitioned between fishing mortality, genetic variability or habitat-induced variation. The data provide the basis for future research on causes for differences in the life history traits of marbled parrotfish on variably protected reefs.

**INTRODUCTION**

Parrotfishes (Scaridae) play an important role in enhancing coral reef resilience to perturbation through their grazing activities and sediment removal (Mumby, 2006). Widespread harvesting of these and other fishes may affect local community structure and cascade to declines in ecosystem function and changes in coral reef dynamics. It is likely
that mechanisms such as phenotypic plasticity (production of different phenotypes by the same genotype under different conditions, sensu Morita & Morita, 2002) causes divergence in the life history attributes of reef fishes, thereby making them resilient to the effects of fishing (Gomes & Monteiro, 2007; Candolin, 2009), hence their ability to sustain populations and coral reef function.

Fishing mortality alters inter- and intra-specific competition, which may lead to enhanced availability of food per capita and production of earlier-maturing individuals through phenotypic plasticity (Rijnsdorp, 1993; Taylor & Stefa´nsson, 1999; Law, 2000). Alternatively, fisheries can cause differential selection through gear/size selectivity, favouring genotypes coding for high fecundity and early maturation (Rijndorp, 1993; Law & Grey, 1989). Thus, fisheries can trigger changes in the maturation process via two pathways, either by influencing phenotypic plasticity or divergence, or through evolutionary selection (Dieckmann & Heino, 2007). Phenotypic and evolutionary changes can co-occur in harvested fish populations, although they may operate on different time scales, at different rates and even in different directions (Sharpe & Hendry, 2009). Phenotypic divergence in life history traits can occur following an exploitation-mediated reduction in the population density (Hutchings & Baum, 2005) with a resultant decrease in maximum sizes (Jennings & Kaiser, 1998) and the earlier maturation of individuals (Heino & Godo, 2002; Kuparinen & Merila, 2007). Evolutionary change can also occur due to fishing if some of the phenotypic variation within a species is due to genetic differences within the stock (Law & Grey, 1989; Law, 2000).

In this study, we describe changes in the reproductive traits of the commercially important marbled parrotfish (Leptoscarus vaigiensis) on Kenyan reefs. Here they are exposed to varying degrees of fishing intensity and protection, and, therefore, provide an opportunity to test the hypothesis of fisheries-induced phenotypic plasticity in the life history traits of fish. L. vaigiensis is an ideal candidate for the study as it is a reef fish that is resident in nature (Kaunda-Arara & Rose, 2004).

**METHODS**

**Study area**

Reefs in Kenya can be divided into three conservation categories depending on their level of exposure to fishing pressure, these categories being protected (or marine parks), partially protected (or marine reserves) and unprotected, thereby providing a gradient in protection level. Extractive exploitation of resources is prohibited on protected reefs in Kenya, also designated as marine parks. “Reserves” or partially protected reefs (in the Kenyan context) are buffer areas in which regulated fishing is allowed adjacent to the parks with “traditional” methods that include baited fish traps, fish trapping fences and cast nets; and “unprotected” reefs are open access sites with no formal regulatory framework (McClanahan & Obura, 1995). Samples of Leptoscarus vaigiensis were obtained from protected reefs in the Malindi and Watamu Marine Parks, reserves adjacent to these Marine Parks and from unprotected (Vipingo and Kanamai) reefs (Fig. 1). Kenyan reefs are described by Kaunda-Arara and Rose (2004) as predominantly shallow (~10-12 m at high tide), lagoonal fringing reefs that run parallel to the coastline with a mosaic of substrata (seagrass beds, sand, rubble, live coral, etc.) common to all coral reefs. The Kenyan coast experiences seasonal weather caused by both north-easterly and south-easterly monsoon winds described by McClanahan (1988). Briefly, the northeast monsoon season (NEM, November–March) is a period of calm seas, elevated sea surface temperatures (SSTs) and higher salinities, while the southeast monsoon season (SEM, April–October) is characterized by rough seas, cool weather, lower salinities and higher productivity.
Figure 1. Map of Kenya showing the sites sampled for marbled parrotfish, *Leptoscarus vaigiensis*. 
Field and laboratory procedures

Samples of *L. vaigiensis* were caught within protected sites (Malindi and Watamu Parks and their reserves; Fig. 1) on a monthly basis from May 2011 to April 2012 using local traps called *demas*. The baited traps were deployed during low tide and retrieved during the subsequent low tide the following day, having soaked for about 12 hours. Monthly samples were obtained at the unprotected sites (Vipingo and Kanamai; Fig. 1) during the same period, from fishers harvesting *L. vaigiensis* at these sites using cast nets and spear guns. An effort was made to obtain a wide size range of *L. vaigiensis*. All specimens were transported to the laboratory on ice for further processing.

The total (TL) and standard lengths (SL) of the specimens were recorded to the nearest millimetre and total weights to the nearest 0.1 g. The fish were then dissected and the sex and maturity stages determined visually. The gonads were staged following Bagenal’s (1978) maturity stages as I - immature, II - immature, III - maturing, IV - mature, V - active, and VI - spent. The gonads were weighed to the nearest 0.001 g and sections were excised monthly from all mature and active ovaries (stages IV-V) to determine their fecundity. These were weighed to the nearest 0.001 g and stored in Gilson’s fluid for at least two months, with frequent shaking to aid the release of oocytes from the ovarian wall (Kaunda-Arara & Ntiba, 1997). Portions of ovaries were taken from either lobe following a preliminary analysis of variance that revealed no significant differences (P>0.05) in oocyte size distribution along the antero-posterior axis of either the right or left lobes of the ovary. Fecundity was then determined following the volumetric method described by Bagenal (1978). Briefly, the contents of each bottle containing ovarian portions were poured into a petri dish and the oocytes washed repeatedly in tap water. The clean and separated oocytes were transferred to a one litre beaker containing a known volume of water. A plastic stirrer was used to stir the egg suspension to ensure an even distribution of the oocytes. After 15 strokes of the stirrer, a 5 ml subsample was extracted with a Labsystem finelet pipette. The oocytes in this aliquot were examined, counted and their diameters measured along their horizontal axis using a calibrated eyepiece graticule under a standard dissecting microscope at 40× magnification.

Data analysis

The fecundity (F) of each active/mature female fish was estimated from the egg counts in the subsamples according to the formula:

$$F = \frac{V}{V_1} \times \frac{N}{W/W_1}$$

Where N is the number of eggs in a subsample, V is the volume of the egg suspension; $V_1$ is volume of the subsample; W is the weight of the whole ovary; and $W_1$ the weight of the portion of ovary fixed in Gilson’s fluid. Fecundities at sites were log ($x + 1$) transformed to satisfy ANOVA assumptions of normality and homoscedasticity (Zar, 1999) and then compared using one-way ANOVA. A Student–Newman–Keuls (SNK) multiple comparison test was performed post hoc to establish whether the means were significantly different (Zar, 1999).

Relationships between fecundity (F) and standard length (SL) in specimens from park, reserve and unprotected sites were established using the formula:

$$F = aSL^b$$

Where a and b are derived from least-squares regression of the log-transformed variables. The length exponent (b) was compared between sites using Analysis of Covariance (ANCOVA) with log standard length as the covariate. Multidimensional scaling (MDS) ordination was used to test for similarity between sites based on the fecundity estimates.

Mean oocyte diameters at the active stage V were compared between sites using one-way ANOVA after log ($x + 1$) transformation of the data, and the size-frequency distribution of the oocytes was examined using graphical plots.

The length at first maturity (L50) of the specimens was determined per site by calculating the proportion of mature (stages
IV-V) individuals for each length class (King, 1995). The results of these analyses were fitted to a logistic function using least-squares regression with the SOLVER routine in Microsoft Excel:

\[ P(L) = \frac{1}{1 + e^{-(a+bL)}} \] ........................... Equation 3

Where \( P(L) \) is the proportion of mature individuals at length \( L \), and \( a \) and \( b \) are parameters of the logistic equation. The length at which 50% of fish were mature (stages IV-V) was regarded as the size at first maturity. A non-parametric bootstrapping technique (Efron & Tibshirani, 1993) was used to resample the data to form three site-specific subsets of the length data. The \( L_{50} \) was estimated separately for females for each of these subsets using the above procedure. It was not computed for males, largely due to the small sample size of mature male gonads at unprotected sites and inherent difficulties in estimating their maturity stages.

**RESULTS and DISCUSSION**

**Sample structure**

A total of 1 281 *Leptoscarus vaigiensis* were caught during the study period, of which 860 (67.14%) were caught during the SEM and 421 (32.86%) during the NEM (Table 1). There were more males than females at all sites but the overall sex ratio (M:F) of 1.29:1 was not significantly different from unity (\( \chi^2 = 12.723, P = 0.364; \) Table 1).

**Fecundity**

Fecundity estimates from 117 active/mature female *L. vaigiensis* differed significantly between sites (\( F = 3.742, \) df = 2, \( P = 0.004; \) Table 2), being significantly higher in Malindi Reserve (156 456 ± 99 233) and Watamu Marine Park (137 669 ± 88 048) than at the unprotected sites of Vipingo (92 299 ± 53 647) and Kanamai (77 459 ± 62 275; Table 2). SNK post hoc tests confirmed these differences but revealed no significant differences between the fecundity at sites with the same level of protection viz. the Malindi and Watamu Marine Parks, associated reserves, and the unprotected sites of Kanamai and Vipingo (Table 2). Values of ‘a’ and ‘b’ (equation 2) varied between sites, with higher values for ‘a’ in reserves and unprotected sites relative to those in the marine parks, suggesting that fish at the fished sites had higher fecundities than those at protected sites at equivalent sizes (Fig. 2). Also, the ‘b’ exponents for fish in the marine parks were higher (\( b \approx 3 \)) than those in reserves and at unprotected sites (\( b < 3 \)), indicating that they grew isometrically relative to those at the other sites (Fig. 2). However, ANCOVA of the b values indicated

<table>
<thead>
<tr>
<th>Sites</th>
<th>M</th>
<th>NEM</th>
<th>Immature</th>
<th>SEM</th>
<th>Immature</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Malindi Marine Park</td>
<td>39</td>
<td>27</td>
<td>0</td>
<td>87</td>
<td>28</td>
<td>181</td>
</tr>
<tr>
<td>Watamu Marine Park</td>
<td>34</td>
<td>12</td>
<td>1</td>
<td>48</td>
<td>29</td>
<td>126</td>
</tr>
<tr>
<td>Watamu Reserve</td>
<td>3</td>
<td>5</td>
<td>0</td>
<td>7</td>
<td>6</td>
<td>21</td>
</tr>
<tr>
<td>Malindi Reserve</td>
<td>58</td>
<td>56</td>
<td>0</td>
<td>134</td>
<td>90</td>
<td>338</td>
</tr>
<tr>
<td>Kanamai</td>
<td>28</td>
<td>28</td>
<td>2</td>
<td>99</td>
<td>112</td>
<td>285</td>
</tr>
<tr>
<td>Vipingo</td>
<td>67</td>
<td>53</td>
<td>8</td>
<td>80</td>
<td>106</td>
<td>330</td>
</tr>
<tr>
<td>Overall sex ratio (M:F)</td>
<td>1.28:1</td>
<td>( \chi^2 = 12.723, P = 0.364 )</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 2. Mean fecundity (±SD) estimates of sexually active/mature Leptoscarus vaigiensis caught at protected (marine parks), partially protected (reserves) and unprotected sites in coastal Kenya.

<table>
<thead>
<tr>
<th>Sites</th>
<th>Mean fecundity (oocytes)</th>
<th>N</th>
</tr>
</thead>
<tbody>
<tr>
<td>Watamu MarinePark</td>
<td>137 669 ± 88 048</td>
<td>9</td>
</tr>
<tr>
<td>Malindi Marine Park</td>
<td>108 655 ± 64 314</td>
<td>14</td>
</tr>
<tr>
<td>Watamu Reserve</td>
<td>106 610 ± 67 289</td>
<td>3</td>
</tr>
<tr>
<td>Malindi Reserve</td>
<td>156 456 ± 99 233*</td>
<td>46</td>
</tr>
<tr>
<td>Vipingo (unprotected)</td>
<td>92 299 ± 53 647</td>
<td>27</td>
</tr>
<tr>
<td>Kanamai (unprotected)</td>
<td>77 459 ± 62 275</td>
<td>18</td>
</tr>
</tbody>
</table>

ANOVA: F = 3.742, p = 0.004, df = 5

*Difference in fecundity between Malindi Reserve and other sites (except Watamu Park) significant (p<0.05).

Figure 2. Relationships between fecundity (F) and standard length (SL) in Leptoscarus vaigiensis at reef sites with different levels of protection in coastal Kenya. N denotes number of ovaries examined at sites.
a non-significant interaction between length (covariate) and sampling site (independent variables), suggesting that the effect of length on fecundity was independent of sites; this may be an artefact of small sample sizes from the marine parks (Table 3). The sites were uniformly distributed in the MDS analysis (data not shown).

Differences in the fecundity of *L. vaigiensis* at the various sites may be attributable to variability in fishing intensity between them, which, in turn, would be attributable to differences in their level of protection. *L. vaigiensis* is largely a resident reef fish (Kaunda-Arara & Rose, 2004), thereby precluding the likelihood of movement between sites. Fishing selectively removes large and highly fecund individuals from sites (Jennings & Kaiser, 1998), leaving small individuals with the reduced fecundity reported here and in other studies (e.g. Jennings & Phillips, 1992; Wilson *et al.*, 2010). However, even if harvesting is not size-selective, intensive exploitation will always lead to truncation of age and size structures of fished stocks, since members of a cohort do not survive to attain a relatively old age or large body size (Marteinsdóttir & Pardoe, 2008); this may further explain the lower fecundity of fish at the intensely fished, unprotected sites in this study relative to the reserves and marine parks. However, there could be other causes for spatial changes in fecundity, including genotypic variation (Dieckmann & Heino, 2007) and differences in inter- and intra-species interactions at the sampling sites (Law, 2000). We found that levels of fecundity of small-sized fish at heavily-fished sites were higher than those of equivalent-sized fish at less fished and unfished sites. It is likely that this is caused by the early maturation observed at fished sites,

### Table 3. ANCOVA output for the comparison of slopes of log fecundity and log standard length relationships in *Leptoscarus vaigiensis* caught on different reefs in coastal Kenya.

<table>
<thead>
<tr>
<th>Source</th>
<th>SS</th>
<th>df</th>
<th>MS</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Corrected model</td>
<td>2.519E11</td>
<td>11</td>
<td>2.290E10</td>
<td>4.173</td>
<td>0.000</td>
</tr>
<tr>
<td>Sites</td>
<td>1.388E10</td>
<td>5</td>
<td>2.776E9</td>
<td>0.506</td>
<td>0.771</td>
</tr>
<tr>
<td>SL</td>
<td>4.048E10</td>
<td>1</td>
<td>4.048E10</td>
<td>7.376</td>
<td>0.008</td>
</tr>
<tr>
<td>Sites×SL</td>
<td>1.174E10</td>
<td>5</td>
<td>2.347E9</td>
<td>0.428</td>
<td>0.828</td>
</tr>
<tr>
<td>Error</td>
<td>5.763E11</td>
<td>105</td>
<td>5.488E9</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

### Table 4. Oocyte diameters (±SD) in active gonads (stage V) in *Leptoscarus vaigiensis* caught on different reefs in coastal Kenya.

<table>
<thead>
<tr>
<th>Sites</th>
<th>Mean size (mm)</th>
<th>Modal size (mm)</th>
<th>Size range (mm)</th>
<th>N</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kanamai</td>
<td>0.17 ± 0.07</td>
<td>0.20</td>
<td>0.06-0.28</td>
<td>1 209</td>
</tr>
<tr>
<td>Vipingo</td>
<td>0.19 ± 0.06</td>
<td>0.20</td>
<td>0.10-0.28</td>
<td>632</td>
</tr>
<tr>
<td>Malindi Marine Park</td>
<td>0.23 ± 0.08</td>
<td>0.20</td>
<td>0.10-0.36</td>
<td>3 363</td>
</tr>
<tr>
<td>Malindi Reserve</td>
<td>0.19 ± 0.07</td>
<td>0.20</td>
<td>0.08-0.30</td>
<td>14 714</td>
</tr>
<tr>
<td>Watamu Marine Park</td>
<td>0.18 ± 0.07</td>
<td>0.20</td>
<td>0.08-0.28</td>
<td>2 295</td>
</tr>
<tr>
<td>Watamu Reserve</td>
<td>0.18 ± 0.07</td>
<td>0.20</td>
<td>0.08-0.28</td>
<td>537</td>
</tr>
</tbody>
</table>

ANOVA

<table>
<thead>
<tr>
<th>F</th>
<th>p</th>
<th>df</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.147</td>
<td>0.345</td>
<td>5</td>
</tr>
</tbody>
</table>
Figure 3. Length at first maturity ogives (solid lines) of female *Leptoscarus vaigiensis* caught at sites with different levels of protection in coastal Kenya; confidence intervals of the estimates are given in parentheses. The dashed lines represent the 95% confidence intervals for lengths at first sexual maturity ($L_{50}$).

- **Unprotected sites**
  - $L_{50} = 11.2$ cm (11.1 - 11.4 cm)
  - (n = 209)

- **Reserve sites**
  - $L_{50} = 16.8$ cm (16.6 - 17.1 cm)
  - (n = 133)

- **Marine Park sites**
  - $L_{50} = 16.7$ cm (15.7 - 17.3 cm)
  - (n = 67)
possibly mediated by reduced competition between individuals as a result of population declines due to fishing pressure (Heino & Godo, 2002; Kuparinen & Merila, 2007), among other factors. The distance between the heavily fished sites on the south coast and the unfished and reserve sites in the north (Fig. 1), together with the resident nature of this fish, would isolate these populations from each other and possibly thereby facilitate selection for higher fecundity and earlier maturation at smaller sizes at the fished sites.

**Oocyte diameters**

Oocyte diameters were estimated from 22,740 oocytes at maturity stage V (Table 4). The diameters ranged from 0.18 mm in Vipingo to 0.26 mm in Malindi (Table 4), with a modal value of 0.2 mm at all sites. Mean oocyte diameters were not significantly different between sites ($F = 1.147; P = 0.345$; Table 4).

Higher survival is expected amongst juveniles emanating from large larvae (Tomkiewicz *et al*., 2003; Raventos & Macpherson, 2005) developing from large eggs (Pitcher & Hart, 1993). It is therefore intuitively expected that fish under heavy predation (e.g. fishing pressure) may develop larger eggs relative to those in protected sites (Einum & Flemings, 2000; Heath *et al*., 2003) as a phenotypic response to stress. However, in this study we found a higher proportion of small eggs in *L. vaigiensis* at fished sites, although the mean egg diameter was not significantly different between sites. It is possible that *L. vaigiensis* at unprotected sites invest more energy into somatic growth to attain maturity faster as a trade-off against larger gonadal development which is energetically more demanding (Jennings & Phillip, 1992). Clearly, studies on predator-prey manipulations would be required to test this hypothesis.

**Length at first maturity (L\textsubscript{50})**

A comparison of the estimates of length at first maturity (L\textsubscript{50}) indicated that the lowest L\textsubscript{50} for female *L. vaigiensis* occurred at unprotected sites (mean 11.2 cm, range 11.1-11.4 cm, 95% CI), whereas the highest L\textsubscript{50} occurred at reserve sites (mean 16.8 cm, range 16.6-17.1 cm, 95% CI; Fig. 3). The L\textsubscript{50} of female *L. vaigiensis* in the marine parks was 16.7 cm (range 15.7-17.3 cm, 95% CI; Fig. 3).

The earlier maturity of female fish at unprotected sites relative to those in marine parks and reserves is possibly a compensatory response to ensure that fish at the former sites reproduce before capture (Hutchings & Baum, 2005). Fishing has been identified as one of the main factors for declines in size and age at maturation in exploited fish stocks (Jennings & Kaiser, 1998; Olsen *et al*., 2004; Kuparinen & Merila, 2007). Apart from causing a decline in stock biomass, fishing can trigger changes in individual fish growth in response to an increase in per capita food availability (Trippel, 1995) and, hence, enhanced growth rates that result in earlier maturation at fished sites (Haug & Tjemsland, 1986). Conversely, high levels of competition and predation in protected marine parks mediated by the high biomass and diversity of fishes at these sites (McClanahan & Kaunda-Arara, 1996) probably reduces relative growth rates and hence increased size at maturity. Differences in growth rate and maturation may thus be a phenotypic response to changes in food availability. However, it may also develop over time in response to selective mortality (Law, 2000).

This study has thus shown divergence in the reproductive attributes of *L. vaigiensis* which is probably induced by fishing pressure. Fish at unprotected sites have equivalent or higher fecundities at smaller sizes relative to larger fish at protected sites. They mature earlier, possibly as an adaptive strategy which enhances their resilience to fishing pressure and helps to sustain local populations. Although the results suggest some level of phenotypic divergence or plasticity, the real causes of this plasticity cannot be apportioned between fishing mortality, genetic variability or habitat-induced variations. The results, however, provide a basis for future research aimed at partitioning the observed divergence in the reproductive traits of *L. vaigiensis* to its actual causes.
Acknowledgements – We thank the PADI Foundation and Kenya National Council of Science and Technology (NCST) for funding this study through a fellowship to GAL; the Director Kenya Wildlife Service (KWS) for permitting research in the Marine Protected Areas; and field staff for their support, especially Michael Kazungu, Ben Ogola and Boaz Orembo. We appreciate the criticisms and comments of two anonymous reviewers that greatly improved the quality of the manuscript.

References


Diet Composition of Hawksbill Turtles
(*Eretmochelys imbricata*) in the Republic of Seychelles

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Keywords: *Eretmochelys imbricata*, Seychelles, diet, in-water observation, stomach contents, oesophageal lavage

Abstract — Effective conservation of the critically endangered hawksbill turtle (*Eretmochelys imbricata*) in the western Indian Ocean is hindered by a lack of basic ecological information about its diet and habitat requirements. This study utilised stomach samples from dead turtles and oesophageal lavage, together with in-water observations of foraging turtles, to identify the relative importance of species contributing to the diet of hawksbill turtles at five localities in the Republic of Seychelles. Diets were remarkably similar to those of hawksbill turtles from the Atlantic and Pacific in that they fed predominantly on demosponges and anthozoans. In total, ten demosponges, four anthozoans, three seaweeds, one seagrass, one ascidian and the egg cases of a mollusc were identified. The most prevalent taxa encountered were *Stelletta* sp., *Spheciospongia* sp. (both demosponges) and *Zoanthus sansibaricus* (anthozoan). Five genera are new to the global list of taxa consumed by hawksbill turtles, viz. *Stelletta*, *Rhabdastrella*, *Haliclona*, *Pseudoceratina* and *Discosoma*. The relative merits of the various methods of dietary determination are discussed and it is concluded that in-water observations of turtle feeding yields results that are in many ways superior to oesophageal lavage or the collection of gut contents from dead animals. Recommendations are made for further research and conservation efforts, including the identification of adult hawksbill foraging grounds offshore, and the protection of habitats rich in hawksbill food.

INTRODUCTION

Populations of the hawksbill turtle (*Eretmochelys imbricata*) are more than 80% reduced globally, primarily as a result of over-exploitation in recent centuries (Mortimer & Donnelly, 2008). Effective conservation initiatives are hindered by insufficient basic ecological information about their diet and
habitat requirements. Despite several major hawksbill diet studies in the Pacific and Atlantic Oceans (reviewed by Bjorndal, 1997), ours is the first such study in the western Indian Ocean.

Hawksbill turtles forage in a variety of soft and hard bottomed habitats throughout the tropics. Demosponges dominate their diet in the Pacific and Atlantic (Meylan, 1988), although zoanthids and corallimorphs are favoured at some sites (Mayor et al., 1998; Leon & Bjorndal, 2002). As the largest spongivore on tropical reefs, hawksbill turtles play a key role in the coral reef ecosystem by relieving corals from space competition with sponges (Hill, 1998; Leon & Bjorndal, 2002; Bjorndal & Jackson, 2003) and promoting biodiversity and ecosystem function through bio-excavation of the coral reef (von Brandis, 2011).

Hawksbill turtles are widespread in the neritic environment of the Seychelles Bank, Amirantes Bank and especially in shallow waters adjacent to some 115 islands that comprise the Republic of Seychelles (Mortimer, 1984). Sea turtles received full legal protection in the Seychelles in 1994 and anecdotal accounts suggest that the foraging population is now increasing.

The Seychelles government is currently contemplating expansion of its Marine Protected Area (MPA) network. Considering that the numbers of foraging hawksbill turtles appear to be increasing, sufficient foraging habitat needs to be identified and protected. This study will help define suitable habitats by identifying and ranking the importance of species that comprise hawksbill diet.

**METHODS**

The dietary composition of hawksbill turtles was determined by oesophageal lavage, examination of the stomach contents of dead turtles and in-water observations at five locations throughout the Seychelles, viz. the Inner Islands group (Mahé and Praslin Islands), D’Arros Island in the Amirantes Group, and the Aldabra, Cosmoledo and Farquhar Atolls (Fig. 1). The inner islands comprise some 41 islands (mostly granitic) situated on the Seychelles Bank (depth range 10-60 m; area ~40 000 km²). D’Arros Island is a small sand cay located on the Amirantes Bank (depth range 10-60 m; area ~3 500 km²). Aldabra, Cosmoledo and Farquhar are mid-oceanic, upraised limestone atolls situated 1 100 km southwest of the inner islands. All islands in the Seychelles are encircled by fringing reefs comprising a shallow reef flat extending from the shore to the reef crest followed by a gradually deepening reef slope.

Oesophageal lavage was conducted on immature turtles foraging on the reef flats of D’Arros Island in 2006 (n = 20) and Aldabra Atoll in 1992 (n = 19) by the first and second authors respectively. Oesophageal lavage involves the non-lethal extraction of ingesta from the anterior region of the oesophagus by means of a water pump (Forbes & Limpus, 1993). Turtles were hand-captured using the ‘beach jump’ and ‘rodeo’ methods (Limpus & Reed, 1985) and restrained in an upside-down and posteriorly elevated position. Gentle pressure was applied to the tip of the mandible using a tongue depressor. As the mouth opened, another depressor was positioned between the mandible and maxilla to maintain the opening. Next, a lubricated, flexible plastic tube was inserted through the mouth into the bottom of the oesophagus. The tube length was determined prior to insertion by laying it along the midline of the plastron and measuring from the junction of the humeral and pectoral scutes to the tip of the mouth. An inner tube diameter of 5 mm was used for turtles larger than 40 cm in curved carapace length and 3.5 mm for smaller individuals. Saltwater was delivered via a hand pump at a steady rate of approximately 10 l min⁻¹. Expelled food items were collected in a mesh bag below the head and stored in 70% ethanol. The turtles were tagged with conventional flipper tags, measured and released unharmed.

Stomach contents of salvaged dead hawksbill turtles were collected opportunistically between 1982 and 2003 by the second author. Those from Cosmoledo (n = 26) and Farquhar (n = 2) were collected in 1982-83 from animals legally killed for their shell (Mortimer, 1984). Those from the Inner Islands (n = 20) were collected between
1995 and 2003 and were derived animals that died from accidental entanglement in nets, propeller strikes, dynamite blasting or unknown causes. A single gut sample from Aldabra was collected in 1987 from a turtle that had died from unknown causes. The date, location, carapace length and relative state of maturity were noted for each dead turtle and the contents of the oesophagus and stomach were surgically removed, fixed in 5% formalin for 24 h and stored in 70% ethanol.

Stomach and lavage samples were drained before analysis, blotted dry and inspected under a dissecting microscope (Olympus SZ61, 0.67-4.5x). Distinguishable ingesta were separated and their wet weight measured to the nearest tenth of a gram; indeterminate slurry was disregarded. Species in the diet were identified to the lowest possible taxonomic rank based on gross appearance and spicule morphology (sponges) using available literature (Gosliner et al., 1996; Allen & Steene, 1996; Debelius, 2001; Richmond, 2002; Hooper & van Soest, 2002). A small fragment of each sponge (± 0.3 cm$^3$) was dissolved in sodium hypochlorite (NaOCl) for 15 minutes for spicule analysis. Settled material was extracted and photographed under a compound microscope (Olympus BX45) at 50x, 100x and 400x.

The percentage occurrence, percentage weight and an Index of Relative Importance (IRI) was calculated for each diet species encountered per lavage and gut sample:

\[
\text{% occurrence of species } x = \frac{\text{number of samples in which species } x \text{ occurred}}{\text{total number of samples}} \times 100
\]

\[
\text{% weight of species } x = \frac{\text{combined weight of species } x \text{ in the samples}}{\text{total weight of all samples}} \times 100
\]

\[
\text{IRI of species } x = \frac{\text{% occurrence} \times \text{% weight}}{100}
\]

In-water observations of juvenile hawksbill foraging behaviour (n = 501) were conducted at D’Arros Island by the first author over a period of eight months between 2006 and 2009 on a small (approx.

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Figure 1. Map of Seychelles indicating locations where hawksbill diet samples were collected.
1 ha) insular platform reef (6-25 m depth) situated approximately 100 m from the shore (von Brandis et al., 2010). The reef was systematically searched using SCUBA gear, up to four times daily (n = 235 dives, mean duration = 86 min) and, upon locating a turtle, it was observed for as long as possible. Several turtles with distinct natural markings (damaged marginal scutes and/or presence of epibionts) were re-sighted almost daily and became increasingly habituated to the presence of observers, eventually enabling close observation of their natural behaviour for extended periods. Each time the turtle stopped to feed, the observer positioned himself no less than 1.5 m from the turtle’s head and recorded the species consumed and feeding duration on an underwater writing slate. If species of a selected dietary item was unknown, a sample was collected for later identification.

The frequency of consumption was used as an Index of Relative Importance (IRI) for each diet species selected during in-water observations:

\[
IRI = \frac{\text{number of feeding events in which species } x \text{ was ingested}}{\text{total number of feeding events}} \times 100
\]

RESULTS

Diet species included sixteen animal and four plant species. With the exception of one ascidian, all could be identified to at least genus level (Table 1). Animals comprised 10 sponges, four cnidarians, one chordate and the egg cases of a mollusc. Sponges belonged exclusively to the class Demospongiae (sponges containing siliceous spicules and/or spongin fibres). Cnidarians were all from the class Anthozoa and comprised a hard coral, soft coral, zoanthid and a corallimorph. The chordate was an unidentified ascidian (class Asciacea) and the molluscan egg cases belonged to the triton shell (Charonia sp.; class Gastropoda). Plants included three seaweeds (Rhodophyta and Phaeophyta) and a seagrass (Magnoliophyta).

The stomach contents of 17 turtles (age classes: 8 adults, 8 immature and 1 unknown) that perished in the vicinity of Mahé and Praslin Islands contained seven demosponges, three plant species and the unidentified ascidian (Table 1). These gut samples weighed between 2.1 and 114 g and comprised 1-7 dietary species. Demosponges (Stelletta sp., Chondrilla australiensis, Tethya sp. and Chondrosia sp.) were the most important taxa in the diet (IRI = 17, 12, 10 and 5 respectively). The remaining three demosponges, the three plant species and the unidentified ascidian featured poorly in the samples (IRI <1).

The combined stomach contents of the eight resident immature turtles from the inner islands contained all 11 of the above diet species but the adults lacked Rhabdastrella rowi, Aaptos suberitoides and Hypnea cornuta. Adults (7 males and 1 nesting female) were presumed to be transient breeding turtles since the nearshore foraging population comprises exclusively juveniles (first and second authors pers. obs.) and they all died during the annual nesting season (October – January; Mortimer & Bresson, 1999).

At D’Arros Island, the foraging population comprised only resident immature turtles. The dietary components included four demosponges, four anthozoans, one seaweed and one seagrass (Table 1). The 20 turtles from the shallow reef flats that were subjected to oesophageal lavage yielded the demosponge Spheciospongia sp. (IRI = 43) and the anthozoan Zoanthus sansibaricus (IRI = 24). The seagrass Thalassia hemprichii and the seaweed Eucheuma denticulatum were also ingested but scored IRIs of less than one. Lavage samples were generally small (0.5-9 g) and contained between one and three diet species.

In-water observations of 501 feeding events on the deeper platform reef at D’Arros Island yielded consumption records of three demosponges and three anthozoans. Feeding events lasted on average nine minutes (SD
Demosponges were considerably more important in the diet, consisting of *Stelletta* sp., *Pseudoceratina purpurea* and *C. australiensis* (IRI = 45, 13 and 6 respectively). The anthozoans *Discosoma* sp., *Dendronephthya* sp. and *Physogyra lichtensteini* (IRI = 3, <1 and <1 respectively) were rarely ingested.

At Aldabra Atoll, samples were derived only from resident immature turtles foraging on the shallow (<2 m) reef flats. Oesophageal lavage of 19 different turtles revealed four demosponges, three seaweeds, one anthozoan and one seagrass (Table 1). Sample weights varied between 0.1-9.3 g and comprised 1-3 diet species. The seaweed *H. cornuta* and the demosponges *Spheciospongia* sp. and *Ecionemia acervus* were most important in the diet (IRI = 17, 13 and 3 respectively) followed by *Stelletta* sp., *Haliclona cymaeformis*, *Z. sansibaricus*, *T. hemprichii*, *E. denticulatum* and *Turbinaria* sp., all of which scored IRIs of <1. The single gut sample from Aldabra belonged to an immature turtle that was found dead in the shallow lagoon and comprised *Stelletta* sp., *H. cornuta* and *Spheciospongia* sp (IRI = 48, 29 and 23 respectively).

At Cosmoledo Atoll, the gut contents of 26 different turtles (age classes: 9 adults, 17 immature) contained four demosponges, the unknown ascidian, three seaweeds and egg cases of the giant triton shell (*Charonia* sp.) (Table 1). Sample weights varied between 9.1-170 g and comprised 1-5 diet species. The important dietary components comprised exclusively demosponges, i.e. *Spheciospongia* sp., *E. acervus*, *H. cymaeformis* and *Stelletta* sp. (IRI = 23, 10, 6 and 2 respectively). *Tethya* sp., *T. hemprichii*, *E. denticulatum*, *H. cornuta*, the unknown ascidian, and the eggs of the giant triton shell (*Charonia* sp.) all scored IRIs of <1. It was not possible to establish whether the adults were resident or transient, but their guts contained all the above taxa except *Tethya* sp. and *E. denticulatum*. The guts of the immature turtles contained all the above dietary components, excluding the triton shell egg cases.

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The guts of two turtles from Farquhar Atoll, of unknown age, comprised mostly *Z. sansibaricus* (IRI = 29) followed by demosponge *A. suberitoides*, the unknown ascidian and *T. hemprichii* (IRI = 9, 9 and 3 respectively).

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Table 1. Index of Relative Importance (IRI) of diet species consumed by hawksbill turtles in the Seychelles at the Inner Islands (I), D’Arros Island, and the Aldabra, Cosmoledo and Farquhar Atolls.

<table>
<thead>
<tr>
<th>Kingdom</th>
<th>Phylum</th>
<th>Class</th>
<th>Order</th>
<th>Family</th>
<th>Genus</th>
<th>Species</th>
<th>Inner Islands n=17</th>
<th>D’Arros Island n=20</th>
<th>Aldabra Atoll n=19</th>
<th>Cosmo. Atoll n=1</th>
<th>Farqu. Atoll n=2</th>
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<tr>
<td>Animalia</td>
<td>Chordata</td>
<td>Asciidae</td>
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<td>-</td>
<td>-</td>
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<td>-</td>
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<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Cnidaria</td>
<td>Anthozoa</td>
<td>Corallimorpharia</td>
<td>Scleractinia</td>
<td>Zoantharia</td>
<td><em>Stelletta</em> sp.</td>
<td>&lt;1</td>
<td>-</td>
<td>-</td>
<td>-</td>
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<tr>
<td>Mollusca</td>
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<td>Demospongia</td>
<td>-</td>
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<td>-</td>
<td>&lt;1</td>
<td>-</td>
<td>-</td>
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<td>-</td>
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<tr>
<td>Hadromerida</td>
<td>Suberitida</td>
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<td>&lt;1</td>
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<td>-</td>
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</tr>
<tr>
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<td>Chalinidae</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
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<td>-</td>
<td>-</td>
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<td>-</td>
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<tr>
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<td>Pseudoceratinida</td>
<td>-</td>
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<tr>
<td>Plantae</td>
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<td>Hydrocharitaceae</td>
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<td>45</td>
<td>5</td>
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<td>1</td>
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<tr>
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<td>Solieraceae</td>
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</table>

Note: IRI = Index of Relative Importance, G = Gut contents, L = Oesophageal lavage, I = In-water observation.
DISCUSSION

Demosponges predominated in the diets of the Seychelles hawksbill turtles, as has been reported in earlier studies in the Indian Ocean (Ross, 1981; Frazier, 1985; Meylan, 1988), Pacific (Balazs, 1978; Alcala, 1980) and Atlantic Oceans (Carr & Stancyk, 1975; Den Hartog, 1980; Acvedo, 1984; Meylan, 1988; Vicente & Carballeira, 1992; Vicente 1993; Anderes & Uchida, 1994; van Dam & Diez, 1997; Leon & Bjorndal, 2002; Martinez et al., 2002; Valeris et al., 2002; Flores et al., 2003; Blumenthal et al., 2009). Principal sponges in the diet were *Spheciospongia* sp. and *Stelletta* sp., both scoring high IRIs at multiple locations (Table 1). Interestingly, six of the ten sponge genera (*Spheciospongia*, *Ecionemia*, *Chondrilla*, *Chondrosia*, *Aaptos*, and *Tethya*) are also common in the diets of Caribbean hawksbill turtles (Meylan, 1988), while the remaining four genera (*Stelleta*, *Rhabdastrella*, *Haliciona* and *Pseudoceratina*) have not previously been reported in the hawksbill diet.

Anthozoans in the diet consisted of the genera *Zoanthus*, *Dendronephthya*, *Physogyra* and *Discosoma*, of which only the latter is new to the global list of species consumed by hawksbill turtles. *Zoanthus sansibaricus* is an important dietary component of hawksbill turtles foraging on the reef flats of Seychelles. The only other location where zoanthids comprise a significant portion of the diet is at Buck Island Reef National Monument in the Caribbean (Mayor et al., 1998; Pemberton et al., 2000). There, a congener, namely *Zoanthus sociatus*, accounted for 85% of the lavage weight recorded by Mayor et al. (1998). In-water observations of turtles in Brazil (Stampar et al., 2007) and Honduras (Dunbar et al., 2008) revealed that hawksbill turtles also consume the zoanthid *Palythoa caribaeorum*, which is known to be extremely toxic (Mereish et al., 1991). *Ricordea florida*, a corallimorph similar to that eaten at D’Arros Island (*Discosoma* sp.), occurred in 63.6% of lavage samples in the Dominican Republic (Leon & Bjorndal, 2002) and less frequently at Buck Island (Mayor et al., 1998).

At D’Arros, turtles occasionally consumed *Physogyra lichensteinii* (bubble coral) and *Dendronephthya* sp. (thistle coral). Obura et al. (2010) observed hawksbill turtles eating *P. lichensteinii* at Aldabra Atoll and reported anecdotal accounts of similar behaviour in Thailand, Madagascar and the Sudanese Red Sea. Because these anthozoans secrete copious mucus when disturbed (first author’s pers. obs.), their infrequent ingestion may provide greater physiological than nutritional benefits, i.e. the mucus may protect the alimentary canal from abrasion by sponge spicules as suggested by Leon & Bjorndal (2002) in the case of mucus secreted by *Ricordea florida*.

Ascidians were consumed at the Inner Islands, Cosmoledo Atoll and Farquhar Atoll. Elsewhere, they have appeared in the hawksbill diet at Costa Rica (Carr & Stancyk 1975), Cuba (Lazara & Anderes 1998) and in Venezuela where ascidians accounted for 63% of a stomach sample (Valeris et al. 2002). Isolated instances also suggest that Seychelles hawksbill turtles occasionally ingest a variety of obscure items such as the eggs of giant triton shells (*Charonia* sp.), plastic, fishing bait, and even fish and bread (second author’s pers. obs.).

Seaweeds and seagrass occurred frequently in samples but, because they tend to grow in close association with certain demosponges and generally accounted for <5% of sample weight, it appears that they may be ingested incidentally. Yet, at Aldabra, turtles seemed to target *H. cornuta* (IRI = 17). Also, the seaweed *E. denticulatum* at D’Arros comprised 83% of one lavage sample and a turtle was observed feeding on floating fragments of *Turbinaria* sp. for over half an hour. Several authors have reported plant matter in hawksbill stomach samples (Carr, 1952; Carr & Stancyk, 1975; Alcala, 1980; Meylan, 1988; Green, 1996; van Dam & Diez, 1997; Lazara & Anderes, 1998; Mayor et al., 1998; Leon & Bjorndal, 2002; Martinez et al., 2002; Valeris et al., 2002; Flores et al., 2003), although only Green (1996) and Lazara and Anderes (1998) reported noteworthy quantities (80% and 25% of gut contents...
Respective of its potential nutritional benefits, perhaps occasional gorging of plant material facilitates digestion. Unlike other spongivores, hawksbill turtles do not possess morphological adaptations to facilitate the passage of copious sponge spicules (Meylan, 1988).

Gut content removal from salvaged dead animals and oesophageal lavage are valid diet determination methods that have been used extensively (e.g. Balazs, 1980; Forbes & Limpus, 1993; van Dam & Diez, 1997; Forbes, 1999; Leon & Bjorndal, 2002, Berube et al., 2012). Nevertheless, both methods pose limitations that may introduce bias in the assessment of dietary composition and selectivity. In the case of gut contents, some items may have been ingested incidentally, differential digestion may hamper diet identification and, where cause of death is unknown, samples may not reflect the diet of healthy individuals. Limitations of oesophageal lavage include the fact that samples are small (mean = 3.2 g in this study) as only small pieces of recently ingested items are removed, some items may have been ingested incidentally, and certain ingesta may flush more easily from the oesophagus on account of their size, shape and texture.

There are several difficulties associated with the observation of turtles underwater, including adequate access to the study subject, variable underwater visibility and sea conditions, and depth-related SCUBA limitations (Hooker & Baird, 2001; von Brandis et al., 2010). Furthermore, because animals are unmarked, pseudoreplication involving repeat observations of the same subject, may present bias in quantitative studies such as this. However, despite these constraints (Booth & Peters, 1972; Houghton et al., 2000; Houghton et al., 2003; Schofield et al., 2006; Dunbar et al., 2008; Blumenthal et al., 2009; von Brandis et al., 2010), in-water observation is, in many ways, a superior technique to determine diet composition and selectivity. Not only are the limitations associated with gut content and lavage analysis eliminated, but related behavioural data can also be collected and individual subjects can be re-observed in subsequent surveys (von Brandis et al., 2010). Immature hawksbill turtles are especially suitable for in-water studies because they commonly forage in shallow, near-shore environments (Musick & Limpus, 1997), have small home ranges (van Dam & Diez, 1998) and, when feeding, often remain unaffected by observers (von Brandis et al., 2010).

Despite the wide geo-spatial distribution of our sampling sites in Seychelles, diet determination was only conducted in relatively shallow nearshore foraging grounds inhabited primarily by immature turtles. Although the scarcity of adults at nearshore foraging sites could be an artifact of past exploitation (Leon & Diez 1999), this does not appear to be the case in Seychelles where it is better explained by developmental migration, that is, migration from shallower juvenile feeding grounds to progressively deeper adult foraging grounds (Carr & Caldwell, 1956; Limpus, 1992, Mortimer & Donnelly, 2008), and by migration of adults between nearshore reproductive habitats and distant foraging grounds (Mortimer, 1984). In support of this, five post-nesting, satellite-tracked females moved from the Inner Islands in 1998 (Mortimer & Balazs 1999) and seven from D’Arros Island in 2014 (von Brandis & Mortimer unpublished data) to deeper (>40 m) off-shore foraging grounds (>100 km from land) on the Seychelles Bank (Figure 1) where different dietary material may well occur. Turtles may also make use of deeper foraging habitats along the verges of the Seychelles and Amirantes Banks and the mid-oceanic islands (Mortimer, 1984). Our study, although limited to relatively shallow nearshore habitats is, nevertheless, the first of its kind in the Western Indian Ocean and provides a list of hawksbill turtle dietary species representative of that environment.

The Government of Seychelles passed legislation in 1994 and implemented social programmes to eliminate all trade in hawksbill
shell (Mortimer, 2000). Conservation and monitoring programmes currently underway at more than 20 hawksbill breeding sites nationwide have demonstrated population increases at protected nesting sites (Mortimer, 2006) and increased numbers of foraging turtles in Seychelles waters. It follows that the future of habitats rich in hawksbill forage need to be protected, and such sites ought to be identified and prioritised during the planning of new MPAs currently underway in Seychelles.

Taking evidence into account that the majority of post-nesting hawksbill turtles from beaches in the inner islands and D’Arros forage within Seychelles territory (Mortimer & Balazs, 1999; von Brandis & Mortimer, unpublished data), further research is needed to locate and describe heretofore undocumented foraging habitats on the Seychelles and Amirantes Banks, and on other deeper reefs in the region. Basic ecosystem mapping of most of these deeper sites has yet to be conducted. Further research entailing satellite telemetry to track turtles to their foraging grounds is also needed.

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Co-variation of Cholera with Climatic and Environmental Parameters in Coastal Regions of Tanzania

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Keywords: cholera, climate, environment, coastal regions, mainland Tanzania

Abstract — The bacterium causing cholera, *Vibrio cholerae*, is essentially a marine organism and its ecological dynamics have been linked to oceanographic conditions and climate. We used autoregressive models with external inputs to identify potential relationships between the number of cholera cases in the coastal regions of mainland Tanzania with climatic and environmental indices (maximum air temperature, sea surface temperature, wind speed and chlorophyll *a*). Results revealed that, between 2004 and 2010, coastal regions of mainland Tanzania inhabited by approximately 21% of the total population accounted for approximately 50% of the cholera cases and 40% of the total mortality. Significant co-variations were found between seasonally adjusted cholera cases and coastal ocean chlorophyll *a* and, to some degree, sea surface temperature, the outbreaks lagging behind by one to four months. Cholera cases in Dar es Salaam were also weakly related to the Indian Ocean Dipole Mode Index, lagging by five months, suggesting that it may be possible to predict cholera outbreaks for Dar es Salaam this period ahead. The results also suggest that the severity of cholera in coastal regions can be predicted by ocean conditions and that longer-term environmental and climate parameters may be used to predict cholera outbreaks along the coastal regions.

INTRODUCTION

*Vibrio cholerae*, which causes the acute enteric infection of cholera, is essentially a marine bacterium, with coastal waters acting as an important reservoir (Colwell *et al.*, 1981). The bacterium has been found in coastal environments around the world, both in areas where cholera is endemic and in cholera disease-free areas (Karunasagar *et al.*, 2003). It is now well known that cholera occurs in regions with natural aquatic reservoirs...
where the bacteria can persist in a free-living state, or in association with phytoplankton, zooplankton and detritus (Nelson et al., 2009). These environmental reservoirs may play a significant role in cholera epidemiology by favouring persistence of the pathogen in periods between epidemics (Vezulli et al., 2010). Indeed, the dynamics of cholera outbreaks have been linked to climate and environmental variables, such as air and water temperature, rainfall, wind direction (e.g. Paz and Broza, 2007; Jutla et al., 2011). The dynamics of environmental V. cholerae have been linked, for example, to water salinity, nutrients and plankton biomass (Vezulli et al., 2010). Water temperature, in particular, has been shown to be an important factor governing the seasonal and geographical variation in V. cholerae (Igbinosa & Okoh, 2008). Evidently the ecology of V. cholerae is important, as are the socio-economic factors for endemic and epidemic cholera. Studies have shown that the cumulative incidence of cholera is strongly correlated with low scores on several socio-economic development indices (Ackers et al., 1998), including lack of adequate water and sanitation infrastructure in densely populated areas and ineffective cholera management (Mhalu et al., 1984; Sedas, 2007; Sow et al., 2011). Inadequate and leaking sanitation provides opportunities for transmission of the virulent forms of the pathogen into environmental reservoirs (Vezulli et al., 2010) where it may survive and propagate depending on environmental and climatic conditions.

Studies on the relationship between cholera outbreaks and climatic or seasonal variables in Tanzania are few (Trærup et al., 2011) and mainly limited to the Lake Victoria Basin and the islands of Zanzibar (e.g. Nkoko et al., 2011; Reyburn et al., 2011). Furthermore, demonstrated relationships between cholera outbreaks and weather and climate in mainland Tanzania are scarce (Trærup et al., 2011). There has, for example, been no analysis of data for the mainland coastal regions connected to the marine environment. Given the potential importance of such relationships for the prediction of cholera outbreaks in a country like Tanzania, we sought to analyse the relationship between cholera cases and climate in the coastal regions of mainland Tanzania, focusing on the years 2004 to 2010. We also aimed to establish whether any identified co-variations of cholera with seasonal or climatic cues would be useful in predicting outbreaks in coastal Tanzania regions ahead of time.

**METHODS**

The study focused on the coastal regions of mainland Tanzania, East Africa using retrospective climatic and health data. The regions were Mtwara and Lindi in the south, Pwani and Dar es Salaam in the centre, and Tanga in the north (Fig. 1). We reviewed the national data on the number of cholera cases and deaths, and climatic cues (rainfall, air temperature and wind speed) recorded on a monthly basis from the years 2004 to 2010. In addition, we compared cholera cases and selected socio-economic health indicators (access to safe water and access to latrines) in the studied regions. The data for the number of cholera cases and deaths, as well as the socio-economic data, were obtained from the Ministry of Health and Social Welfare (MoHSW), United Republic of Tanzania. The cholera surveillance records were reported according to recommended WHO guidelines (Global Task Force On Cholera Outbreak, 2004). Case Fatality Rates (CFR) were calculated using the number of cases and mortality (i.e. deaths/cases x 100 = CFR). Demographic data were obtained from the National Bureau of Statistics (NBS) (Ministry of Planning, Economy and Empowerment, United Republic of Tanzania, 2008), while the monthly average data for rainfall and maximum air temperatures were obtained from the Tanzania Meteorology Agency (TMA). This study obtained ethical approval from the National Institute of Medical Research (NIMR/HQ/R.8a/Vol.IX/1155), Dar es Salaam, Tanzania.

Remotely sensed data for sea surface temperature (SST), chlorophyll (Chl a in mg m$^{-3}$) and wind stress (Wind, N m$^{-2}$)
were obtained from the United States of America National Oceanic and Atmospheric Administration Coastwatch website (http://coastwatch.pfeg.noaa.gov). The following datasets were used: SST (Aqua MODIS, NPP, Global, Daytime, Science Quality, 8-day Composite), Chl a (Aqua MODIS, NPP, Global, Science Quality and Monthly Composite) and wind (NOAA/NCDC Blended Monthly 0.25° Sea Surface Wind Stress). Data files covering 4.5-11°S to 38.5-42°E were extracted from the databases for 2004 to 2010. SST and Chl a data were extracted for the study regions from bands 0.208° wide (i.e. 5 pixel in width) along the coast. Wind data were similarly extracted from bands 0.5° longitude wide (2 pixels in width). Monthly averages were calculated from the 8-day SST data using simple averaging.

The number of cholera cases was compared between the different regions and seasons using non-parametric ANOVA (Kruskal Wallis) and the Mann Whitney U test, respectively. Time series analysis was performed using Matlab (2012a, The MathWorks, Natick, Ma., USA.). A Jarque-Bera test (jbtest) was used to test for normality of the data. An augmented Dickey-Fuller test (adftest) was used to assess the null hypothesis of a unit root in the data. All model estimation was carried out using the Matlab System Identification toolbox that is based on Ljung (1999). Autoregressive models with ARX (Box and Jenkins, 1970) external inputs were used to study the relationships between the incidence of cholera in the coastal regions and environmental parameters. Data from the two most populous regions, Dar es Salaam and Tanga, were subjected to time series analysis.
Numbers of case in other regions were insufficient for this type of analysis. The case and environmental data were transformed to obtain stationary time series. Before exploring the model, collinearity between predictor variables was studied. Significant collinearity was observed, firstly between transformed temperature anomalies and transformed rain anomalies for Dar es Salaam, and secondly between transformed temperature anomalies and SST anomalies, also for Dar es Salaam, with respective $r^2$ values of 0.30 and 0.37. Collinearity for Tanga predictive variables was only found between transformed temperature anomalies and transformed SST anomalies, with an $r^2$ of 0.18. Belsley collinearity diagnostics were used to determine if these exceeded tolerance levels. This was not the case; condition indices were $<2$ in all cases.

The cholera case data were not normally distributed and varied seasonally, i.e. the data were non-stationary. Seasonality in the data was removed by normalizing data by monthly means. A square root transformation did not achieve normal distribution in the case data ($jbtest: p < 0.001$). This, however, was achieved using a log-transformation ($jbtest: p = 0.2$). Since values of zero are undefined when using a log-transformation, uniformly distributed pseudorandom values ranging from 0.2 to 4 were added to all cases data. This procedure was carried out 100 times and the resultant time series was subjected to statistical analysis. The augmented Dickey-Fuller test rejected the presence of a unit root in the transformed case data (adftest, model ‘ar’, 6 lags), suggesting that undifferentiated data could be used for the regression analysis. All data were further normalised by their mean and standard deviation ($zscore$). Box-Jenkins type autoregressions were fitted to the data with external inputs in an ARX model ($na$, $nb$, $nk$). Regressions of monthly data on the number of cholera cases for Dar es Salaam and Tanga against monthly values of the Indian Ocean Dipole Mode Index (DMI; Saji et al., 1999) were used to examine the influence of climate on cholera outbreaks.

**RESULTS**

On average, cholera cases in Tanzanian coastal regions occurred every month between 2004 to 2010 (Fig. 2a). The highest number of cholera cases was recorded in 2006, while the least number of cases occurred in 2008. The North East Monsoon (NEM) period (December – April) had significantly ($U = 382; p = 0.0069$) more cases of cholera compared to the South East Monsoon (SEM) period (June – October). The number of cases was also high during the inter-monsoon period (May and November). During the study period, a total of 43 560 cholera cases were reported on mainland Tanzania (Fig. 2b). Although the coastal regions are only inhabited by ~21% of the total population of mainland Tanzania (Table 1), approximately 50% of the cases (21 760) occurred in these regions. The most populated coastal regions, Dar es Salaam and Tanga, had higher rates of cholera cases on average (5.5 and 3.3 cases per one hundred thousand people respectively) compared to the less populated regions Lindi, Mtwara and Pwani (2.0, 1.5 and 1.0 cases per one hundred thousand people respectively).

Deaths attributable to cholera on mainland Tanzania totalled 902 during the study period (Table 1); of these 357 (40%) occurred in the coastal regions. The Case Fatality Rate (CFR) varied between years, the average being 2.1%. In the coastal regions, the highest mortality due to cholera was recorded in 2006 (120 deaths), while the lowest was recorded in 2008 (23 deaths). The total mortality differed between regions during 2004-2010, with Tanga and Dar es Salaam reporting the highest numbers of 148 (41.5%) and 128 (35.9%) respectively. Lindi, Pwani and Mtwara reported lower numbers of 49 (13.7%), 26 (7.3%) and 6 (1.7%) respectively.

In general, 60% of the coastal population had access to safe water, compared to 46% in the inland regions and 53% overall in mainland Tanzania in 2006 (Table 1). The population in Dar es Salaam had the best access to safe water, followed by Pwani Region, whilst the population in Mtwara Region had the lowest
access. Similarly, coastal populations had better access to latrines (70%) compared to inland populations (60%). Dar es Salaam had a higher provision of latrines, indicating better sanitation, followed by Tanga Region, while Pwani Region had the lowest. Country wide, the provision of latrines was 65% in 2006 and, according to the Ministry of Health and Social Welfare (Tanzania), this increases annually by ~1%.

Air temperature and SST values in all coastal regions were highest from December to March (Fig. 3a, b) and significantly higher during the NEM period compared to the SEM (t = 7.528, p = 0.0001; U' = 625, p = 0.0001 respectively), with June to August being the coldest. Although there was weak evidence for differences between the regions, these were not significant for air temperature or

Figure 2. The total number of cholera cases during 2004-2010 in a) the coastal regions of mainland Tanzania and b) a comparison between the coastal regions and interior.
Rainfall was on average lowest from June to September and highest from March to May (Fig. 3c), with no significant differences between the five regions ($f = 0.098$, $p = 0.983$). Significantly higher rainfall was recorded during the NEM compared to the SEM ($U' = 574$, $p = 0.0001$). Wind speed was high in Mtwara and Lindi compared to Pwani, Dar es Salaam and Tanga (Figure 3d; $KW = 51.78$, $p < 0.0001$). However, average monthly wind speeds in all the coastal regions of Tanzania (pooled data) did not differ significantly between the NEM and SEM ($U' = 339$, $p = 0.614$). Coastal chlorophyll $a$ (Chl $a$) concentrations differed significantly between the coastal regions ($KW = 37.45$, $p < 0.0001$; Fig. 3e); the Pwani Region had significantly higher levels compared to the others. Chl $a$ concentrations were on average higher during the months of January to May but were not significantly different between the NEM and SEM ($U = 314$, $p = 0.985$).

Partial autocorrelation of the cholera case time series with environmental parameters for Dar es Salaam and Tanga, the regions with the highest numbers of cholera cases, suggested that the time series could be modeled using an

<table>
<thead>
<tr>
<th>Region</th>
<th>Mortality (number of deaths)</th>
<th>Population (n)</th>
<th>Access to infrastructure (2006)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>2004 2005 2006 2007 2008 2009</td>
<td>2010</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>2004 (x10$^6$)</td>
<td>2010 (x10$^6$)  Safe  Sanitation</td>
</tr>
<tr>
<td>Dar es Salaam</td>
<td>4 0 101 1 1 3 18</td>
<td>2.64 3.118</td>
<td>90 81</td>
</tr>
<tr>
<td>Mtwara</td>
<td>2 0 1 0 0 0 3</td>
<td>1.17 1.324</td>
<td>36 66</td>
</tr>
<tr>
<td>Lindi</td>
<td>15 0 0 13 14 0 7</td>
<td>0.82 0.924</td>
<td>54 63</td>
</tr>
<tr>
<td>Tanga</td>
<td>35 48 6 11 6 35 7</td>
<td>1.71 1.967</td>
<td>59 77</td>
</tr>
<tr>
<td>Pwani</td>
<td>7 0 12 1 2 4 0</td>
<td>0.92 1.063</td>
<td>61 62</td>
</tr>
<tr>
<td>Coastal Regions</td>
<td>63 48 120 26 23 42 35</td>
<td>7.26 8.396</td>
<td>60 70</td>
</tr>
<tr>
<td>Inland Regions</td>
<td>179 60 134 44 27 39 60</td>
<td>27.6 33.52</td>
<td>46 60</td>
</tr>
<tr>
<td>Tanzania mainland</td>
<td>242 108 254 70 50 81 95</td>
<td>34.9 41.91</td>
<td>53 65</td>
</tr>
<tr>
<td>CFR</td>
<td>2.4 3.3 1.3 2.1 2.5 1.0 2.0</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>

Table 1. Cholera mortality (number of deaths), human population, access to infrastructure (safe water and sanitation expressed as a percentage of total population) in the coastal regions of Tanzania (CFR = Case Fatality Rates).

<table>
<thead>
<tr>
<th>Region</th>
<th>Variable</th>
<th>Lag 1</th>
<th>Lag 2</th>
<th>Lag 3</th>
<th>Lag 4</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dar es Salaam</td>
<td>SST</td>
<td>0.093 ± 0.062</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Dar es Salaam</td>
<td>Wind</td>
<td>0.089 ± 0.067</td>
<td>-0.066 ± 0.068</td>
<td>-0.120 ± 0.064</td>
<td>-</td>
</tr>
<tr>
<td>Dar es Salaam</td>
<td>Chl. $a$</td>
<td>0.132 ± 0.063*</td>
<td>0.162 ± 0.066*</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Tanga</td>
<td>SST</td>
<td>-</td>
<td>-</td>
<td>0.192 ± 0.098</td>
<td>+0.177 ± 0.099</td>
</tr>
<tr>
<td>Tanga</td>
<td>Wind</td>
<td>-</td>
<td>-0.084 ± 0.094</td>
<td>--</td>
<td>-</td>
</tr>
<tr>
<td>Tanga</td>
<td>Chl. $a$</td>
<td>-0.162 ± 0.090*</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>

Table 2. Regression coefficients ($±SE$) derived from autoregression models of monthly cholera case numbers for Dar es Salaam and Tanga and corresponding data for sea surface temperature (SST), wind speed (wind) and concentration of chlorophyll $a$ (Chl $a$), for lags of 1-4 months. Significance levels are 5%* or 10%+. 
autoregressive process with a lag of one month, i.e. AR(1). This result was confirmed during the system identification step when fitting the data to an ARX model, resulting in an autoregression coefficient of $0.79 \pm 0.06$ (95% confidence interval) for the Dar es Salaam time series. The environmental parameter with the highest predictive value for cholera was Chl \(a\) in the Dar es Salaam Region (Table 2). The relationship between cholera cases and this parameter in the Dar es Salaam dataset was positive and significant at the 5% level for lags.
of one and two months. The other parameters which were potentially correlated with the incidence of cholera were SST and wind speed. Weak predictions of cholera cases one or two months ahead of time became possible when combined with results of the other variables. The relationships between cholera cases and these parameters were similar in the Tanga

Figure 4. Co-variation between monthly (2004 – 2010) average number of cholera cases in the five Tanzanian coastal regions relative to a) air temperature, b) sea surface temperature, c) rainfall, d) wind speed and e) chlorophyll a concentration.
Table 3. Regression coefficients (±SE) derived from autoregression models of the number of cholera cases in Dar es Salaam and Tanga and Indian Ocean Dipole Mode Index data, for lags of 3-6 months.

<table>
<thead>
<tr>
<th>Location</th>
<th>Lag 3</th>
<th>Lag 4</th>
<th>Lag 5</th>
<th>Lag 6</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dar es Salaam</td>
<td>-</td>
<td>-0.061 ± 0.096</td>
<td>-0.179 ± 0.121</td>
<td>-0.025 ± 0.1</td>
</tr>
<tr>
<td>Tanga</td>
<td>-0.146 ±0.135</td>
<td>0.203 ± 0.179</td>
<td>-0.042 ± 0.140</td>
<td>-</td>
</tr>
</tbody>
</table>

Region, however, whereas Chl a at a lag of one month was positively correlated with the incidence of cholera in the Dar es Salaam Region, the results were negative in the Tanga Region. Wind had a weak negative effect at a lag of two months in the Tanga Region and SST had a significant effect at the 10% confidence level at lags of three and four months, which contrasts with the Dar es Salaam Region where it had a weak effect at a lag of one month.

When monthly numbers of cholera cases for Dar es Salaam and Tanga were regressed against monthly values of the Indian Ocean Dipole Mode Index (DMI) using an ARX model, weak relationships were found between the number of cholera cases at Dar es Salaam and the DMI data at a lag of five months (Table 3). The relationship between the numbers of cases in Tanga and the DMI was even weaker (Table 3).

DISCUSSION

A higher number of cholera cases were recorded along the Tanzanian coast compared to its inland regions during this study. This is probably due to the close proximity of the coastal regions to the natural reservoir of *Vibrio cholerae*, the marine environment (Dalusi et al., 2015). Previous studies elsewhere have shown that cholera usually strikes villages in coastal regions before it occurs inland (Colwell et al., 1981; Karunasagar et al., 2003; Julta et al., 2010). The Tanzanian coast also has rivers and estuaries that provide an environmental niche for *V. cholerae*, as it associates with organic material such as detritus or biofilms and plankton (Colwell et al., 1981; Dalusi et al., 2015; Vezzulli et al., 2010). These riverine corridors and networks, which undergo tidal flux, may allow the passage of the free-living or attached bacterium inland through a combination of different hydroclimatic macroscale drivers and less well described active and passive transport mechanisms (Paz & Broza, 2007; Akanda et al., 2011). Once humans have ingested the pathogen, asymptomatic infections and a pre-epidemic build-up may occur before the index case of cholera emerges (Faruque et al., 2004). In densely populated areas, as is the case in Dar es Salaam and Tanga, cholera may then rapidly spread among the population (Mhalu et al., 1984) via contaminated water or human interactions.

We found that cases of cholera and climatic variables co-vary on a seasonal basis in coastal regions of Tanzania (Fig. 4), hot months typically having high numbers of cholera cases. Nevertheless, our analyses did not reveal significant relationships between cholera cases and maximum air temperatures or rainfall but rather between cholera and ocean and ocean-related climate conditions, i.e. sea surface temperature, wind and phytoplankton biomass. The incidence of cholera lagged behind peaks in these variables by a month or months in relationships that ranged in strength. Some results were contradictory and this may reflect the complex aetiology of cholera. Seasonally changing air temperature and rainfall may nevertheless provide the necessary, but insufficient, conditions for the outbreak and severity of cholera. During strong rains and monsoon flooding, the salinity in coastal environments is reduced, potentially affecting the physiological state of *V. cholera* and its association with zooplankton, which are important for its survival (Thomas et al., 2006). On the other hand, if salinities drop too far, this can have a negative effect on *V.*
cholera abundance and survival (e.g. see Hashizume et al., 2011), particularly the free-living cells.

The lag effects we encountered could, for example, be attributable to strong rainfall increasing the riverine discharge of inorganic nutrients and organic material into estuaries, resulting in turn in phytoplankton and zooplankton blooms, indicated by an increase in Chl a (Jutla et al., 2011). As environmental conditions become optimal for zooplankton, this may be benefit the physiological state of V. cholera as it is associated with plankton (Colwell et al., 1981). Such a change in physiological state might not be sufficient for a cholera outbreak if the bacteria are low in number, insufficient become virulent, or the mechanisms for their transport into human populations are absent. It is also possible that, during the wet season, storm-water overflow may enter sewage systems, introducing faecal-contaminated water into rivers. Indeed, heavy rainfall and flooding is known to facilitate outbreaks of diarrhoeal disease in low-income countries (McMichael and Hales, 2006).

Conditions which promote the growth and virulence of the pathogen, or those, that facilitate its transfer from the marine environment to human populations, might thus constitute sufficient conditions for a cholera outbreak. Significantly higher number of cholera cases occur in Tanzanian coastal regions during the NEM with its high temperatures, low wind speeds and calm seas, and this could be due to several factors, including increased plankton biomass along the Western Indian Ocean during this period (Lugomela et al., 2002). Plankton and other organic particles provide a surface area for the attachment of V. cholera (Colwell et al., 1981). In addition, inorganic particles and the chitin of zooplankton provide nutritional substrates for the pathogen, and induce natural competence (Meibom et al., 2005), important for environmental adaptation and survival.

Our regression analyses suggested that sufficient conditions for cholera outbreaks are indicated by elevated sea surface temperatures, phytoplankton biomass and wind but this does not suggest that there are direct causal relationships between these parameters: they should be viewed as proxies. For example, Chl a co-varies with sea surface temperature, zooplankton biomass, total particulate matter etc., and thus serves as a proxy for all these. Other studies have similarly linked cholera to environmental and oceanographic conditions (plankton biomass, sea surface temperature, winds and season; De Magny et al., 2008; Igbinosa & Okoh, 2008; Koelle et al., 2005; Vezzulli et al., 2010, Jutla et al., 2011). The exact nature of these interactions is unknown. However, the advantage of using such proxies is that they can be remotely sensed, and thus could be used to predict cholera caseloads months ahead of time.

The observed seasonal patterns in cholera outbreaks relative to rainfall and temperature, in conjunction with the regression analyses on the seasonally adjusted data, suggest that the severity of cholera outbreaks may not depend on how much it rains or how hot it is. Rather, wet or hot conditions must occur before other factors can trigger an outbreak. The ephemeral nature of cholera outbreaks in Tanzania – it is always hot and wet during the NEM but cholera epidemics do not always occur – supports this hypothesis. The functional relationship between cholera cases, air temperature and rain is thus not a simple monotonic relationship (e.g. linear or quadratic) but might be a step-function. This implies that, once the wet and or hot season has advanced sufficiently, the conditions necessary for a cholera outbreak occur, but not necessarily at the required intensity. Our results thus suggest a complex relationship between cholera outbreaks and climatic conditions.

We also found a relationship between the number of cholera cases and a five-month lag in the Indian Ocean Dipole. The DMI is based on the temperature difference between the eastern and western tropical Indian Ocean and reflects the Indian Ocean Dipole Mode Index, which has been shown to be a predictor of East African rainfall (Saji et al., 1999). This suggests that it may be possible to predict cholera outbreaks for Dar es Salaam five months ahead of time. These results
corroborate similar findings on the subject in Bangladesh (Hashizume et al., 2011). Luo et al. (2007) also suggested that it may be possible to predict the severity of cholera outbreaks months in advance using climate indices. Inter-relationships between climate indices and cholera outbreaks have been used to assess the effects of global climate change on the incidence of cholera in Tanzania (Trærup et al., 2011).

Insufficient sanitary conditions and health care are factors that exacerbate outbreaks; however, these do not vary strongly on a seasonal basis or from year to year. The lower mortality from cholera in Tanzanian coastal regions compared to the interior may be due to improved socio-economic conditions. Here, improved awareness, the availability of and access to better health care facilities, and cholera management in coastal regions may also reduce outbreaks. However, the Dar es Salaam and Tanga Regions have the highest levels of sanitation, yet had a higher incidence of cholera, suggesting the importance of the environmental reservoir. Generally, the access to clean and safe water in Tanzania was only 53% in 2006 and the access to latrines was 65%. Despite this, the Case Fatality Rate (CFR) in Tanzania has decreased from 11.7% in the 1970s to 2% in 2010, a reduction similar to the global trend (WHO, 2010). Nonetheless, endemic outbreaks remain a major health problem in Tanzania. Their successful prevention in cholera-endemic countries must include developing an awareness of the relationship between the outbreaks, the environmental reservoir and climate.

In summary, our results have shown that the coastal regions of Tanzania are more prone to cholera outbreaks than the interior, probably due to their proximity to the marine environment, the natural reservoir of \( V.\) cholerae. It is evident that climate indices show promise in predicting these outbreaks and studies of this nature will become increasingly important in managing the disease and developing early warning systems of outbreaks in this era of climate change.

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Observations of Acropora Spawning in the Mozambique Channel

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Figure 1. An Acropora colony spawning on 25 September 2013.

Thirteen Acropora species were monitored at 4-6 m depth at high tide on a reef at Andavadoaka in SW Madagascar. Although this genus is common throughout the western Indian Ocean, there is sparse information in the literature about its spawning pattern. Acropora oocytes are large (>300 um diameter; Harrison & Wallace, 1990) and visible to the naked eye (Mangubhai, 2007).

The reproductive stage and oocyte colour of 53 coral fragments collected from 19 tagged colonies was determined from August to September 2013. The oocyte size increased and colour changed from white to cream, then to an intense pink or orange in most of the species during the monitoring period. Small, immature white to cream-coloured oocytes were observed in A. appresa, A. formosa and A. tenuis but no spawning was witnessed. No oocyte development or spawning was detected in A. pinguis or A. roseni. Spawning of three species (A. arabensis, A. divaricata and A. nasuta) was observed during night-time observations of a 30 m x 30 m lagoonal reef patch dominated by Acropora spp. on 9 September 2013, four nights after the September new moon. On the fifth night after full moon two A. ocellata colonies spawned on 24 September 2013, and on the sixth night a major spawning event involving four species (A. clathrata, A. squarrosa and two unidentified Acropora species) was observed. Setting of the pink or orange-coloured gamete bundles (3 mm in diameter) began approximately 3 h after sunset; spawning occurred shortly after setting. Approximately 80% of Acropora colonies spawned that night, causing a noticeable spawn slick on the water surface.

These observations constitute the first documented in situ observations of coral spawning for Madagascar and the Mozambique Channel, close to the southernmost range in the global distribution of these Acropora species.

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References


WESTERN INDIAN OCEAN JOURNAL OF MARINE SCIENCE

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