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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 m^3s^{-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),

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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^3s^{-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; Sætre & 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

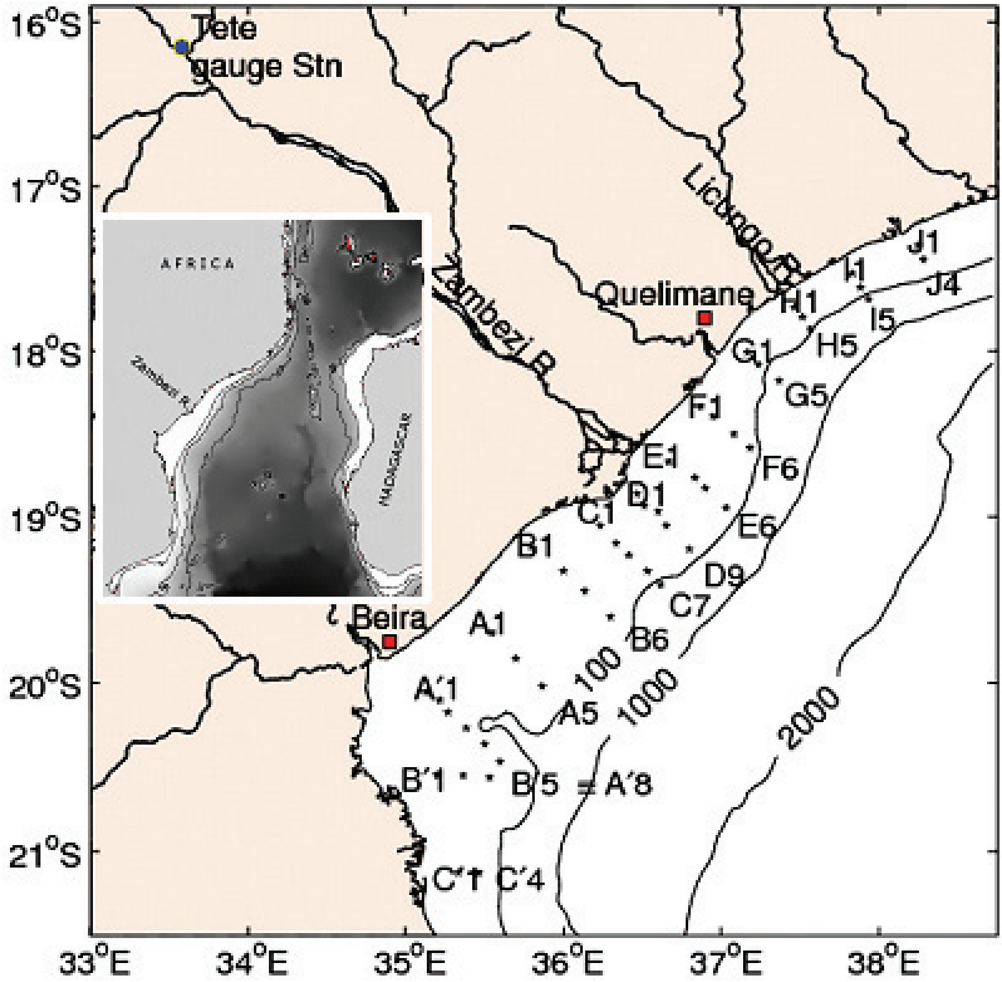

Figure 1. Hydrographic transects and stations in the vicinity of the Zambezi River delta.

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.

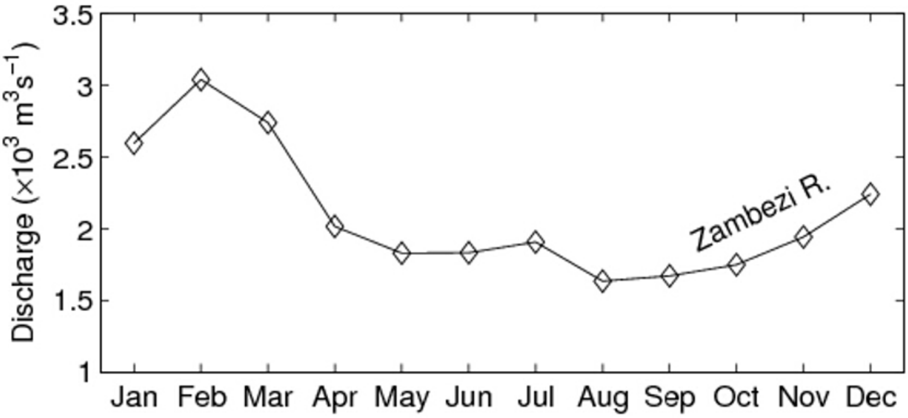

Figure 2. Seasonal variation in Zambezi River discharge based on 1976-2007 data from the Mozambique National Water Directorate.

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

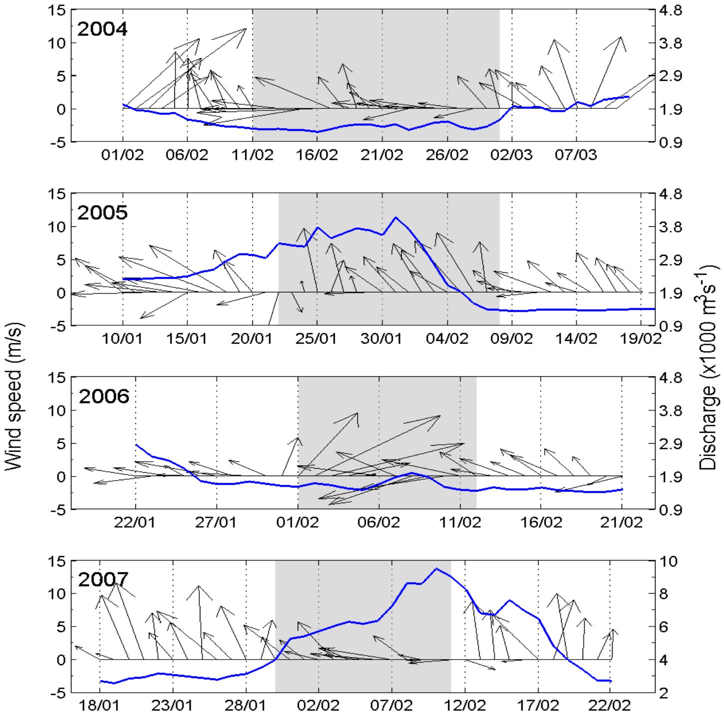

Figure 3. Zambezi River discharge data (solid line) derived from the Tete gauge station and QuikSCAT wind data (arrow vectors) for 2004-2007. Shaded areas correspond to periods of plume observation.

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

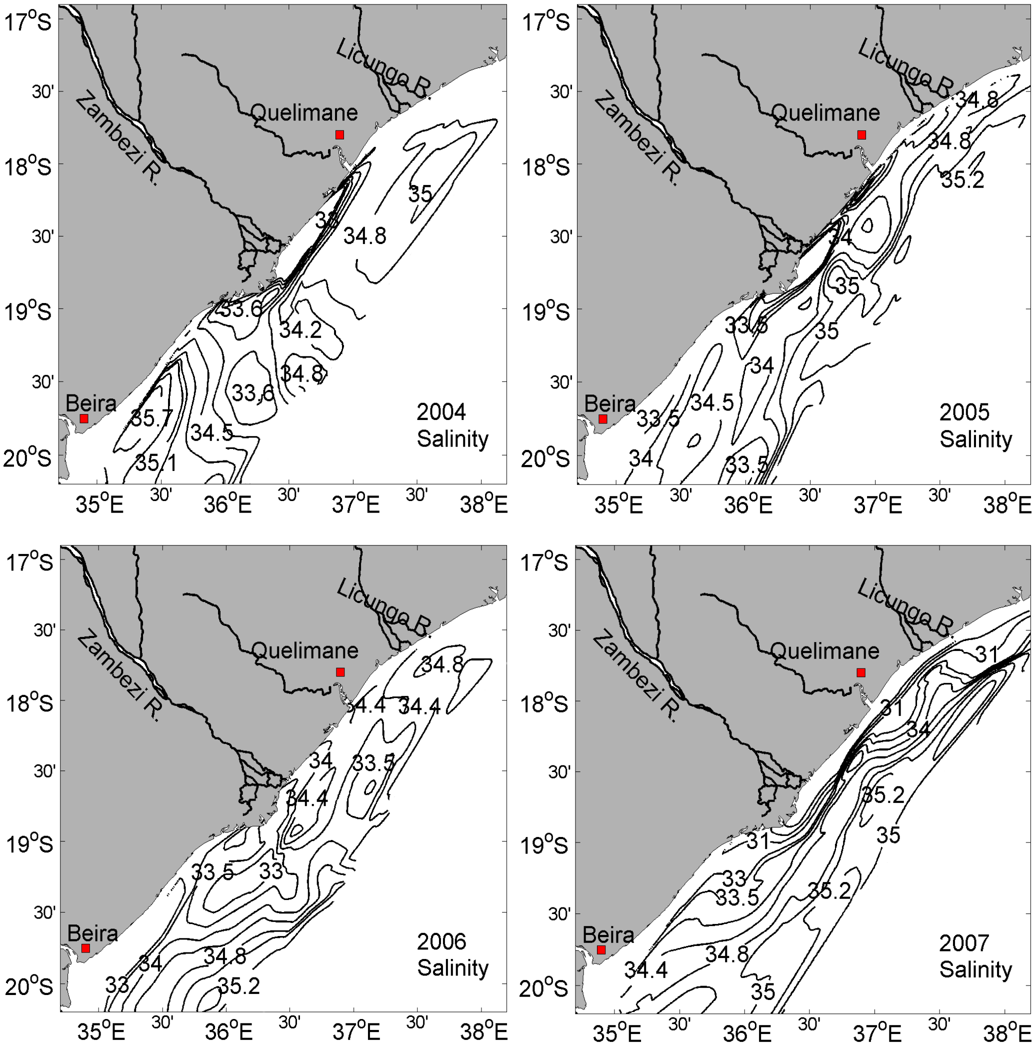

Figure 4. Near-surface salinity derived from CTD data collected in 2004-2007.

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

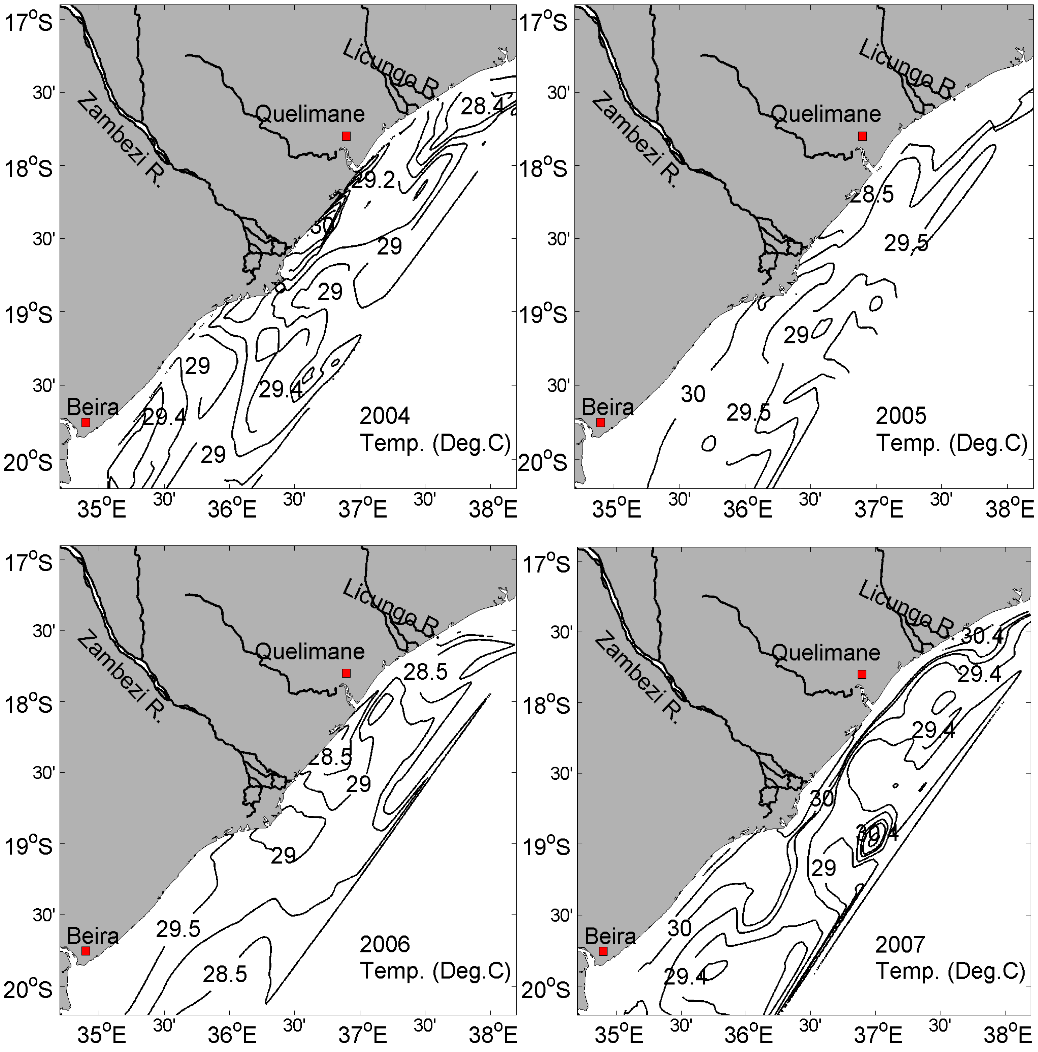

Figure 5. Near-surface temperatures derived from CTD data collected in 2004-2007.

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

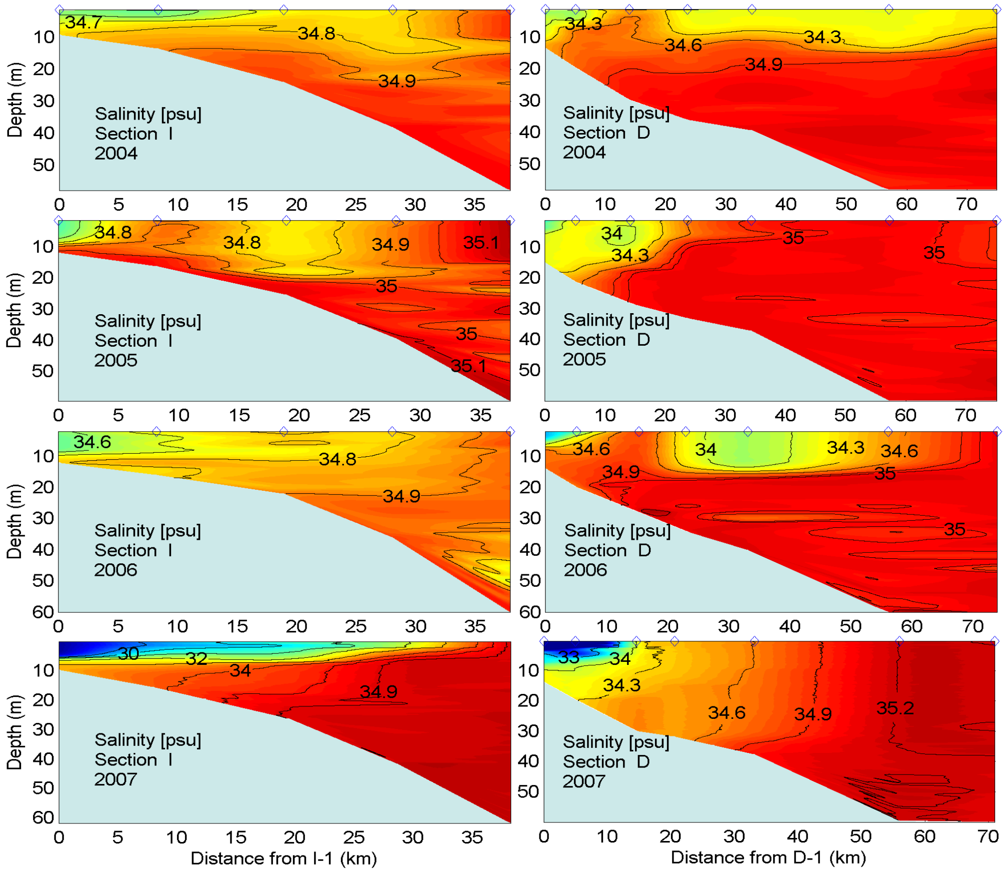

Figure 6. Vertical profiles of salinity recorded in Transects D (at the Zambezi River delta) and I (located north of the delta).

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^3s^{-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^3s^{-1}, and bottom-advected under larger discharges.

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References

Beilfuss R, dos Santos D (2001) Patterns of hydrological change in the Zambezi Delta, Mozambique. Program for the Sustainable management of Cahora Bassa dam and the lower Zambezi valley. Working Paper #2, 159 pp

Brakel WH (1984) Seasonal dynamics of suspended-sediment plumes from the Tana and Sabaki Rivers, Kenya: Analysis of Landsat Imagery. Remote Sensing of Environment 16: 165-173

Chao S-Y (1988) River-forced estuarine plume. Journal of Physical Oceanography 18: 72–88

Chapman DC, & Lentz SJ (1994) Trapping of a coastal density front by the bottom boundary layer. Journal of Physical Oceanography 24: 1464–1479

Fong DA, Stacey MT (2003) Horizontal dispersion of a near bed coastal plume. Journal of Fluid Mechanics 489: 239–267

Gammelsrød T (1992) Variation in shrimp abundance on the Sofala Bank, Mozambique, and its relation to the Zambezi River runoff. Estuarine, Coastal and Shelf Science 35: 91–103

Garvine RW (1999) Penetration of buoyant coastal discharge onto the continental shelf: A numerical model experiment. Journal of Physical Oceanography 29: 1892–1909

Hoguane AM (1997) Shrimp abundance and river runoff in Sofala Bank - The role of Zambezi. In: Workshop on The Sustainable Utilisation of the Cahora Bassa Dam and the Valley of the Lower Zambezi, Songo, September 29 – October 02, 1997, 16 pp

IMR (1977) Cruise report No. 1 of R/V DR. FRIDTJOF NANSEN. Joint NORAD/Moçambique/FAO project to investigate the fish resources of the coast of Mozambique. Institute of Marine Research, 31 pp

IMR (1978a) Cruise report No. 3 of R/V DR. FRIDTJOF NANSEN, January-March 1978. Joint NORAD/Moçambique/FAO project to investigate the fish resources of the coast of Mozambique. Institute of Marine Research, 38 pp

IMR (1978b) Cruise report No. 4 of R/V DR. FRIDTJOF NANSEN, April-June 1978. Joint NORAD/Moçambique/FAO project to investigate the fish resources o# the coast of Mozambique. Institute of Marine Research, 40 pp

Kourafalou VH, Oey L-Y, Wang JD, Lee TN (1996) The fate of river discharge on the continental shelf. 1: Modelling the river plume and the inner shelf coastal current. Journal of Geophysical Research 101(C2): 3415–3434

Lutjeharms J (2006) The coastal oceans of south-eastern Africa. In: Robinson AR, Brink KH (eds) The Sea, volume 14B, Harvard University Press, Cambridge, MA., USA, pp 783–834

Magome S, Isobe A (2003) Current structure and behavior of the river plume in Suo-Nada. Journal of Oceanography 59: 833–843

Mann KH, Lazier JRN (2013) Dynamics of marine ecosystems: Biological-physical interactions in the oceans. Blackwell Scientific Publications, Boston, USA, 512 pp

Mavume AF, Rydberg L, Rouault M, Lutjeharms JRE (2009) Climatology and landfall of tropical cyclones in the South-West Indian Ocean. Western Indian Ocean Journal of Marine Science 8: 15–36

Nehama FPJ (2012) Modelling the Zambezi River plume using the Regional Oceanic Modelling System. PhD thesis. University of Cape Town, 177 pp

Nezlin NP, DiGiacomo PM, Stein ED, Ackerman D (2005) Stormwater runoff plumes observed by SeaWiFS radiometer in the Southern California Bight. Remote Sensing of Environment 98: 494–510

Sætre R, da Silva AJ (1984) The circulation of the Mozambique Channel. Deep-Sea Research 31: 485–508

Schumann EH (1998) The coastal ocean off southeast Africa, including Madagascar. In: Robinson AR, Brink KH (eds) The Sea, Volume 11, John Wiley & Sons, New York, USA, pp 557–58

Scodanibbio L, Mañez G (2005) The World Commission on Dams: A fundamental step towards integrated water resources management and poverty reduction? A pilot case in the lower Zambezi, Mozambique. Physics and Chemistry of the Earth 30: 976–983

Siddorn JR, Bowers DG, Hoguane AM (2001) Detecting the Zambezi River plume using observed optical properties. Marine Pollution Bulletin 42: 942–950

Walford H, White N, Sydow J (2005) Solid sediment load history of the Zambezi Delta. Earth and Planetary Science Letters 238: 4-63

Yankovsky AE, Chapman DC (1997) A simple theory for the fate of buoyant coastal discharges. Journal of Physical Oceanography 27: 1386–1401

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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

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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 1km 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

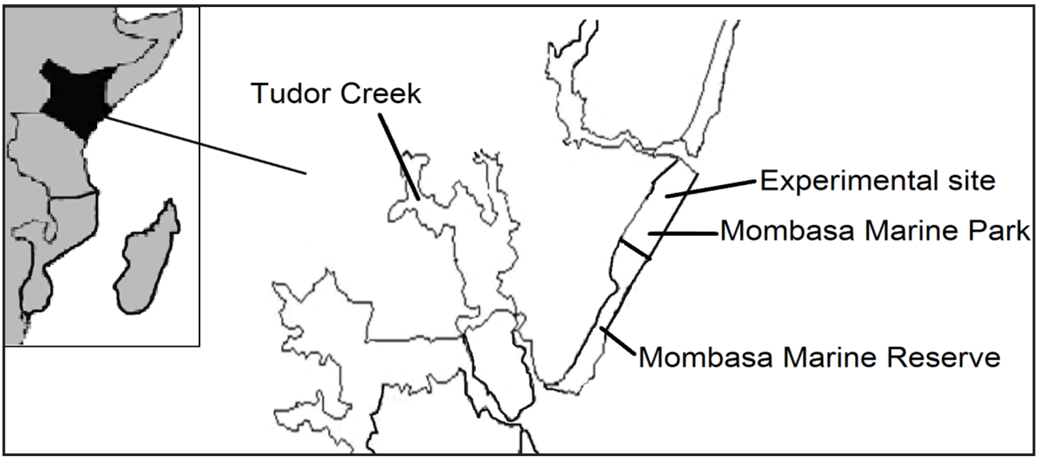

Figure 1. Location of the experimental site within Mombasa Marine Park.

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

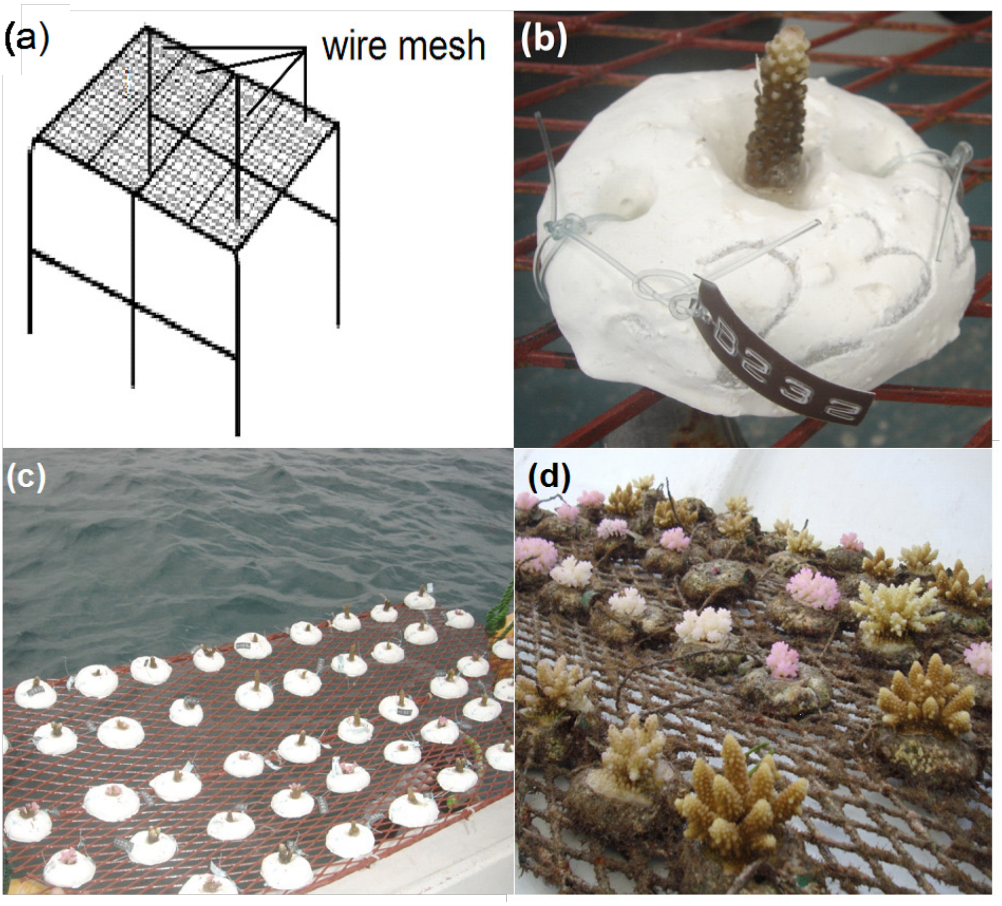

Figure 2. a) Diagram of a culture table, b) coral fragment attached to a labelled cement disk and secured to the wire mesh grid with nylon monofilament, c) fragments prior to deployment and d) at the end of the experiment.

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

Table 1.The number of coral fragments used during the SEM and NEM phases of the study.

Coral species	SEM	NEM
Acropora humilis	133	43
Acropora selago	36	46
Acropora verwei	197	48
Pocillopora damicornis	161	46
Pocillopora eydouxi	17	8
Pocillopora verrucosa	46	0
Porites rus	10	9
	600	200

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. verwe*i, *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).

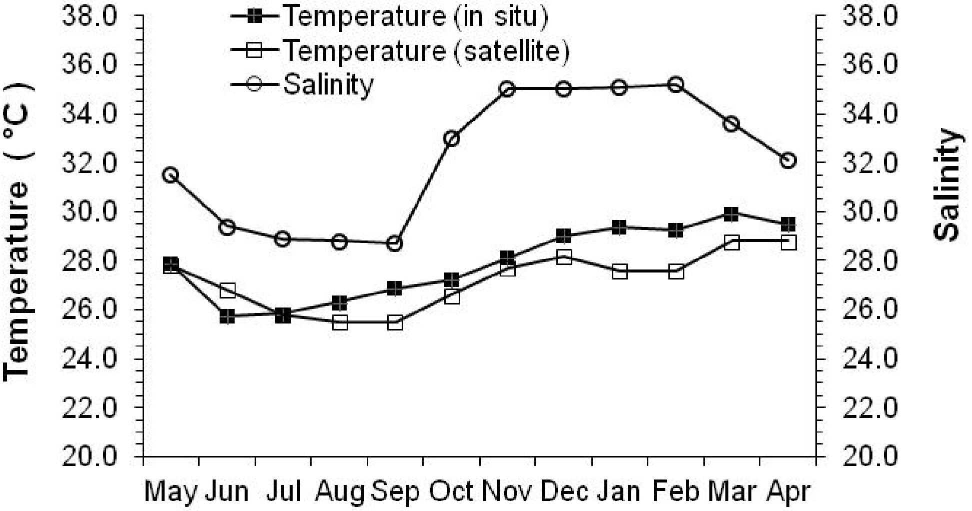

Figure 3.Mean monthly variation of temperature and salinity measured at the coral culture site and remotely sensed monthly sea surface temperature for Bamburi, Kenya (www.worldseatemp.com/en/Kenya/Bamburi).

Influence of initial fragment size on survival

The survival of fragments >2 cm (87.1%) was higher than that of fragments <2cm (73.4%). When grouped by size class (Fig. 4), fragments <1cm 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.

Environmental Factors	SEM	NEM	Test Statistic	P	Annual mean
Temperature	27.0±1.39	29.1±1.25	Z=6.30	<<0.05	28.2±1.65
Salinity	30.5±3.73	33.9±4.55	Z=2.65	<0.007	32.4±4.53
Total suspended matter	0.07±0.017	0.04±0.047	Z=3.79	<<0.05	0.061±0.039

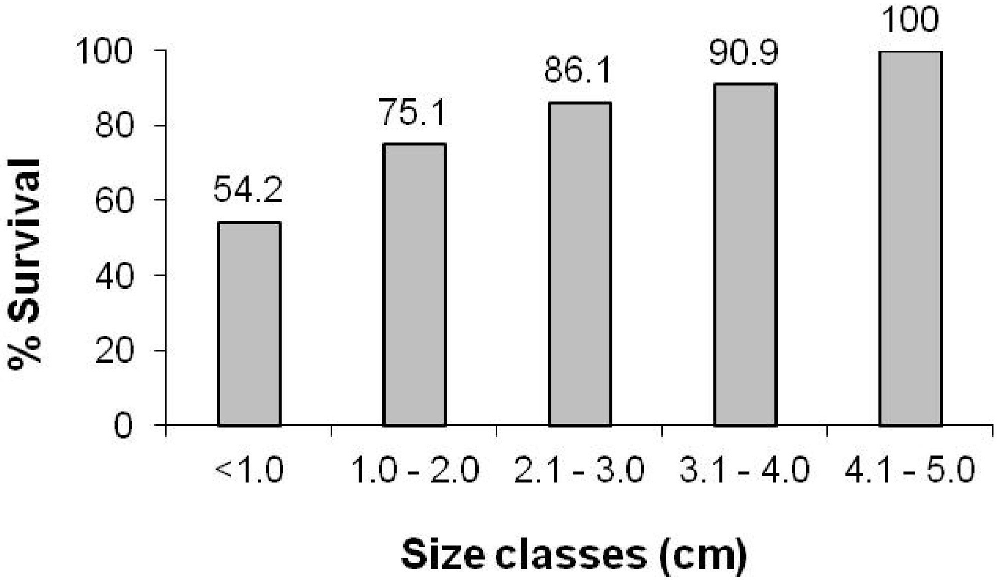

Figure 4. Percentage survival of the size classes of coral fragments grown out in the Mombasa Marine Park.

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.

Species	Regression formula	R	DF	p
Acropora humilis	W=28.9+0.915L	0.618	90	>0.001
Acropora selago	W=23.6+1.220L	0.730	20	>0.001
Acropora verwei	W=35.8+0.823L	0.579	63	>0.001
Pocillopora verrucosa	W=12.1+0.822L	0.607	5	0.147
Pocillopora damicornis	W=10.7+0.402L	0.723	55	>0.001

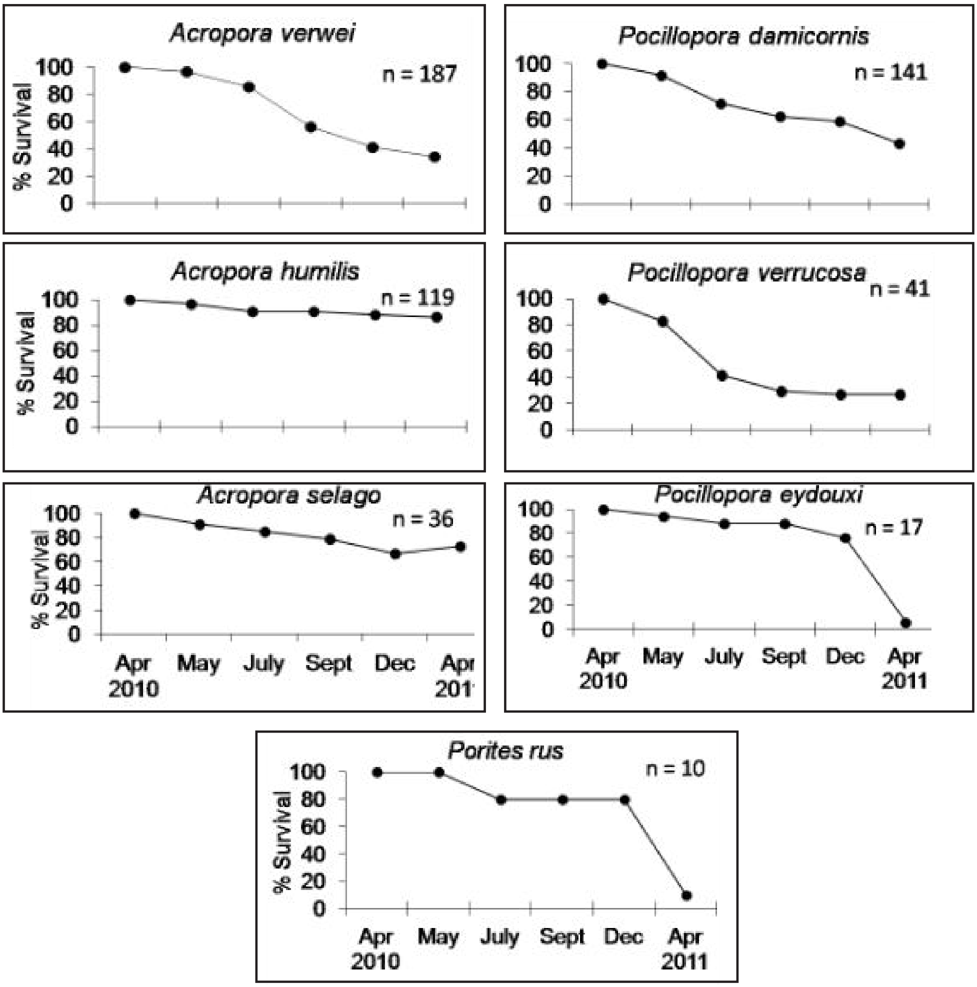

Figure 5. Percentage survival of seven species of corals transplanted to the experimental culture tables for grow-out in the Mombasa Marine Park during April 2010-April 2011. N = the initial number of fragments that were transplanted.

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).

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

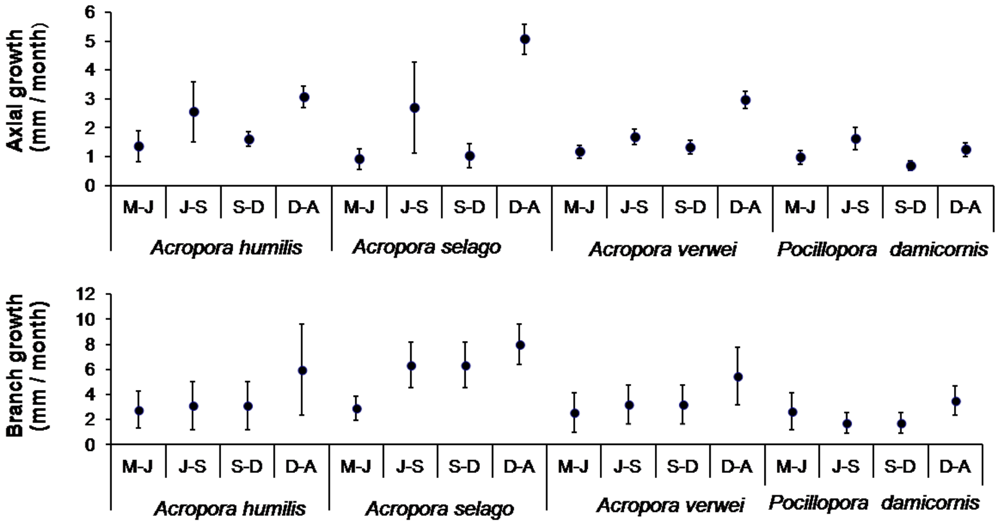

Figure 6. Mean axial and branch width growth in *Acropora humilis*, *A. selago*, *A. verwei* and *Pocillopora damicornis* during the measurement intervals of May-July, July-September, September-December and December-April.

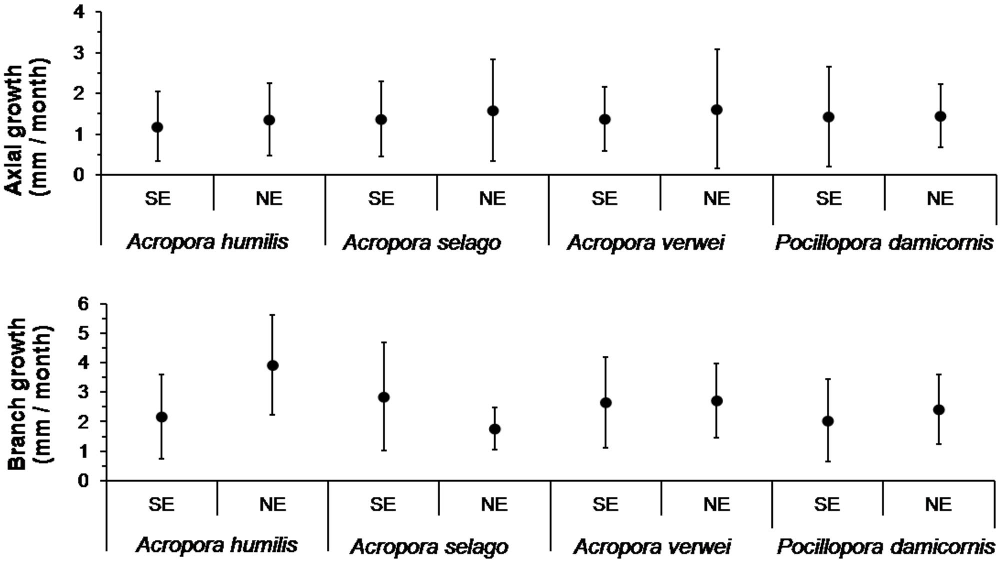

Figure 7. Mean monthly axial and branch width growth in *Acropora humilis*, *A. selago*, *A. verwei* and *P. damicornis* during the NEM and SEM.

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^2 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.

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References

Arvedlund M, Craggs J, Pecorelli J (2003) Coral culture – possible future trends and directions. In:Cato JC, Brown CL (eds) Marine ornamental species collection, culture and conservation. Iowa State Press, Iowa, USA, pp 233-248

Clark S, Edwards AJ (1995) Coral transplantation as an aid to reef rehabilitation: Evaluation of a case study in the Maldive Islands. Coral Reefs 14: 201-213

Cros A, McClanahan T (2003) Coral transplant damage under various management conditions in the Mombasa Marine National Park, Kenya. Western Indian Ocean Journal of Marine Science 2: 127–136

Delbeek JC (2001) Coral farming: Past, present and future trends. Aquarium Sciences and Conservation 3: 171-181

Edwards AJ, Clark S (1998) Coral transplantation: A useful management tool or misguided meddling? Marine Pollution Bulletin 37: 8-12

Forsman ZH, Rinkevich B, Hunter CL (2006) Investigating fragment size for culturing reef-building corals (Porites lobata and P. compressa) in *ex-situ* nurseries. Aquaculture 261: 89-97

Franklin H, Muhando CA, Lindahl U (1998) Coral culturing and temporal recruitment patterns in Zanzibar, Tanzania. Ambio 27: 651-655

Grey M, Blais AM, Vincent ACJ (2005) Magnitude and trends of marine fish curio imports to the USA. Oryx 39: 413-420

Guzman HM, Cortes J (1989) Growth rates of eight species of scleractinian corals in the eastern Pacific (Costa Rica). Bulletin of Marine Science 44: 1186 -1194

Harriott VJ (1999) Coral growth in subtropical eastern Australia. Coral Reefs 18: 281-291

Herlan J, Lirman D (2008) Development of a coral nursery program for the threatened coral *Acropora cervicornis* in Florida. Proceedings of the 11th International Coral Reef Symposium, Ft Lauderdale, Florida, 7 -11 July 2008, pp 1244-1247

Jones R (2008) CITES, corals and customs: A review of the international trade in wild coral. In: Leewis RJ, Janse M (eds) Advances in coral husbandry in public aquariums. Burgers' Zoo, Arnhem, The Netherlands, pp351-361

Kirugara D, Cederlof U, Rydberg L (1998) Wave induced net circulation in ringed lagoon: Bamburi, Kenya. Ambio 27: 752-757

Lal P, Kinch J (2005) Financial assessment of the marine trade of corals in Solomon Islands. Foundation of the People of the South Pacific International, Suva, Fiji and the South Pacific Regional Environment Programs, Apia, Samoa, 32 pp

Lindahl U (1998) Low-tech restoration of degraded coral reefs through transplantation of staghorn corals. Ambio 27: 645-650

Lindsay SRE, Stanley LJ (2004). Regional assessment of the commercial viability for marine ornamental aquaculture within the Pacific Islands (giant clam, hard and soft coral, finfish, live rock and marine shrimp). SPC Aquaculture Technical Papers, Noumea, New Caledonia, 99pp

Moothien Pillay R, Bacha Gian S, Bhoyroo V, Curpen S (2011) Adapting coral culture to climate change: The Mauritian experience. Western Indian Ocean Journal of Marine Science 10: 155-167

McClanahan TR, Kaunda-Arara B (1996) Fishery recovery in a coral-reef marine park and its effect on the adjacent fishery. Conservation Biology 10: 1187-1199

Okemwa G, Fulanda B, Ochiewo J, Kimani E (2009). Exploitation of coral reef fishes for the marine ornamental trade in Kenya: In: Hoorweg J, Muthiga NA (eds) Advances in Coastal Ecology, African Studies Centre, Leiden,The Netherlands, pp 28-42

Paletta M (1999) Coral farming. Seascope, Spring Volume: 1-2

Putchim L, Thongtham N, Hewett A, Chansang H (2008) Survival and growth of *Acropora* spp. in mid-water nursery and after transplantation at Phi Phi Islands, Andaman Sea, Thailand. Proceeding of the 11thInternational Coral Reef Symposium, Ft Lauderdale, Florida, 7-11 July 2008 pp 1268-1261

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

Soong K, Chen T (2003) Coral transplantation: Regeneration and Growth of *Acropora* fragments in a nursery. Restoration Ecology 11: 1-10

Suresh VR, Mathew KJ (1995) Growth of staghorn coral *Acropora* (Dana) (Scleractinia: Acroporidae) in relation to environmental factors at Kavaratti Atoll (Lakshadweep Islands), India. Indian Journal of Marine Science 24: 175-17

Suresh VR, Mathew KJ (1993) Skeletal extension of staghorn coral A*cropora formosa* in relation to environment at Kavaratti Atoll (Lakshadweep). Indian Journal of Marine Science 22:176-179

Tamelander J, Visram S, Obura D (2000) Prospects for coral recovery through transplantation and natural recruitment, Kenya. Proceedings of the 9th International Coral Reef Symposium, 2: 991-926

Wabnitz C, Taylor M, Green E, Razak T (2003) From ocean to aquarium. UNEP-WCMC, Cambridge, UK, 66 pp

Wells SM, Barzdo JG (1991) International trade in marine species: Is CITES a useful control mechanism? *Coastal Management* 19: 135-154

Yap HT, Gomez ED (1981) Growth of *Acropora pulchra* (Brook) in Bolinao, Pngasinan, Phillipines. Proceedings of the 4th International Coral Reef Symposium, 2: 207-213

Yap HT, Gomez ED (1985) Growth of *Acropora pulchra*. III Preliminary observations on the effects of transplantation and sediment on the growth and survival of transplants. Marine Biology 8: 203-209

Yap HT, Alvarez ARM., Custodio HM, Dizon RM (1998) Physiological and ecological aspects of coral transplantation. Journal of Experimental Marine Biology and Ecology 229: 69-84

Yap HT, Molina RV (2003) Comparison of coral growth and survival under enclosed, semi-natural conditions and in the field. Marine Pollution Bulletin 46: 858-864

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Short Note

A First Inventory of Echinodermata at Juan de Nova (Iles Eparses, France) in the Mozambique Channel

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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 km^2, 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 km^2 in area and its coral reefs are 206.69 km^2 in extent, comprising 163.22 km^2 of reef flats and lagoon and 43.47 km^2 of barrier reef (Andréfouët *et*

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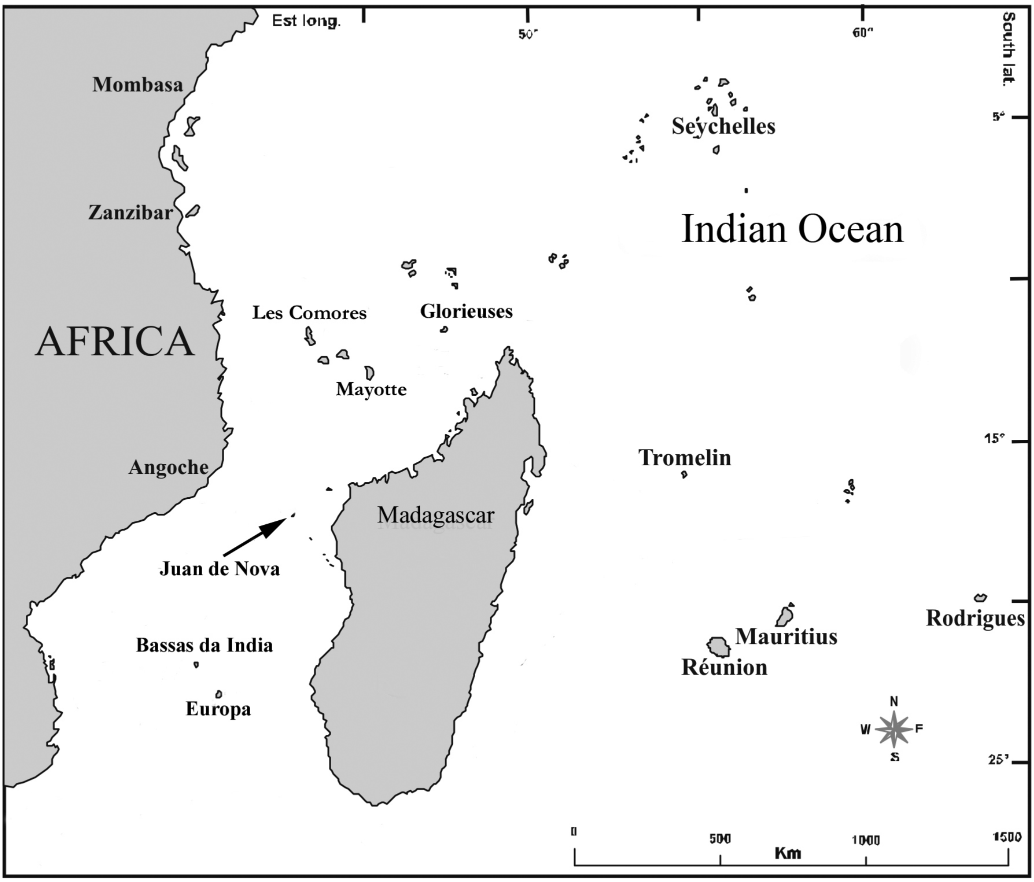

Figure 1. Map of the south-west Indian Ocean with the location of Juan de Nova.

al., 2009). The EEZ around Juan de Nova is 61 050 km^2 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.

Site code	Reef geomorphology	Date	Lattitude	Longitude	Depth (m)
2	Reef flat	08/12/2013	-17.06136	42.71416	0.2
3	Reef flat	09/12/2013	-17.07019	42.71046	0.5
8	Reef flat	12/12/2013	-17.05806	42.69461	0.5
15	Reef flat	15/12/2013	-17.04192	42.71683	1
17	Reef flat	16/12/2013	-17.04783	42.68040	1
20	Lagoonal reef patch	07/12/2013	-17.03259	42.73574	10
25	Lagoonal reef patch	10/12/2013	-16.95350	42.75982	15-18
27	Outer reef slope	11/12/2013	-17.08177	42.72536	13-16
28	Lagoonal reef patch	12/12/2013	-17.01960	42.68127	14
29	Outer reef slope	12/12/2013	-17.05418	42.67435	16-18
30	Lagoonal reef patch	13/12/2013	-16.96562	42.69472	16
31	Lagoonal reef patch	13/12/2013	-16.94298	42.70940	18-19
33	Outer reef slope	14/12/2013	-17.01507	42.65688	20-22
34	Subtidal reef flat	15/12/2013	-17.01076	42.80413	17
35	Outer reef slope	15/12/2013	-17.07472	42.76651	14-20
36	Reef flat	16/12/2013	-17.03337	42.72390	1
37	Reef flat	16/12/2013	-17.03573	42.68453	2
38	Lagoonal reef patch	17/12/2013	-17.03507	42.77117	10
52	Reef flat	07/12/2013	-17.03712	42.72429	3
86	Lagoonal reef patch	09/12/2013	-17.01781	42.71705	15
117	Lagoonal reef patch	11/12/2013	-17.02772	42.72481	16
140	Outer reef slope	14/12/2013	-17.01493	42.65645	28
144	Reef flat	14/12/2013	-17.02939	42.68913	3
165	Reef flat	15/12/2013	-17.05728	42.77669	2
196	Lagoonal reef patch	17/12/2013	-17.03056	42.75651	10

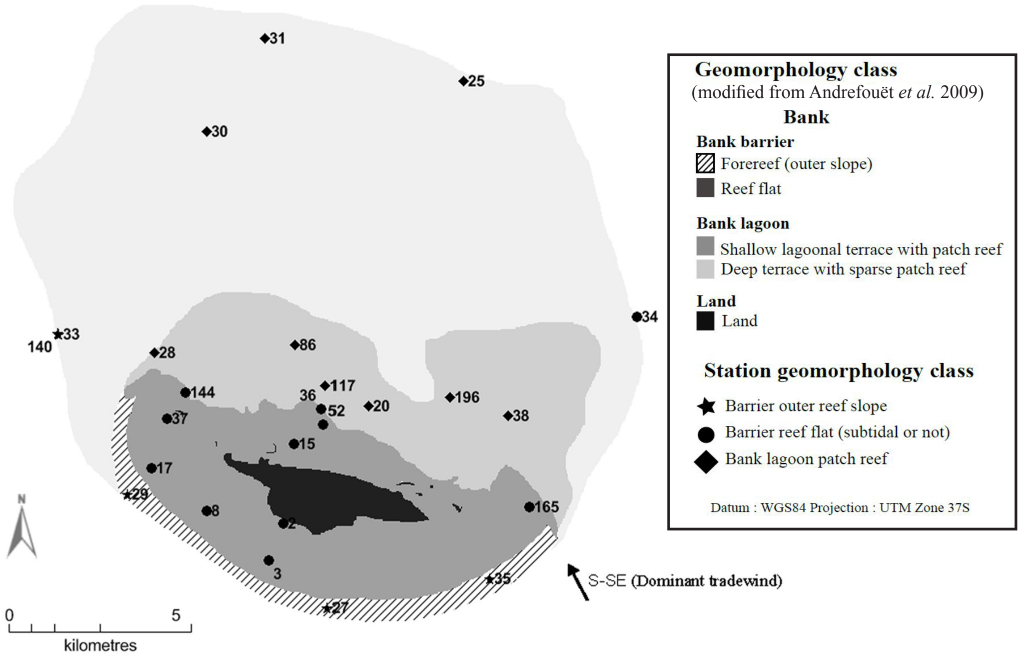

Figure 2. Sampling sites surveyed at Juan de Nova in 2013.

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.

Class	Reef flat and lagoon	Outer reef slope	Total
Holothuroidea	20	10	21
Ophiuroidea	14	4	16
Echinoidea	8	5	10
Asteroidea	7	2	7
Crinoidea	2	4	6
Total	51	22	60

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).

		Occurrence		
Species	N of sites	Total	rf	os
Holothuria nobilis	7	0.28	0.37	0
Thelenota ananas	10	0.4	0.26	0.83
Stichopus chloronotus	10	0.4	0.37	0.33
Holothuria atra	12	0.48	0.53	0.33
Bohadschia subrubra	10	0.4	0.42	0.33
Bohadschia atra	9	0.36	0.37	0.33
Pearsonothuria graeffei	5	0.2	0.16	0.33
Stichopus herrmanni	1	0.04	0.05	0
Holothuria impatiens	2	0.08	0.1	0
Actinopyga cf.*miliaris*	3	0.12	0.1	0.17
Actinopyga cf.*obesa*	5	0.2	0.05	0.5
Actinopyga mauritiana	4	0.16	0.21	0
Holothuria hilla	2	0.08	0.1	0
Holothuria pardalis	1	0.04	0.05	0
Actinopyga echinites	1	0.04	0.05	0
Thelenota anax	1	0.04	0.05	0
Holothuria fuscogilva	2	0.08	0.05	0.17
Holothuria difficilis	1	0.04	0.05	0
Holothuria sp. 1	1	0.04	0.05	0
Holothuria sp. 2	1	0.04	0	0.17
Holothuria cf.*fuscocinerea*	1	0.04	0.05	0

CLASS OPHIUROIDEA

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).

	No. of sites/sp	total occ.	occ. rf	occ. os
Macrophiothrix longipeda	5	0.2	0.26	0
Ophiocoma erinaceus	3	0.12	0.16	0
Ophiocoma (breviturma) brevipes	6	0.24	0.26	0.17
Ophiomastix venosa	1	0.04	0.05	0
Ophiocoma cynthiae	3	0.12	0.16	0
Ophionereis dubia	1	0.04	0	0.17
Ophiarachnella gorgonia	1	0.04	0.05	0
Ophionereis sp.	1	0.04	0.05	0
Ophionereis porrecta	3	0.12	0.1	0.17
Ophiopeza fallax	1	0.04	0	0.17
Ophiactis savignyi	1	0.04	0.05	0
cf. *Ophiactis*	1	0.04	0.05	0
cf. *Ophiolepis* (juv)	1	0.04	0.05	0
Ophiura cf. *kinbergi*	1	0.04	0.05	0
Ophiocoma pusilla	1	0.04	0.05	0
cf. *Ophiothela*	1	0.04	0.05	0

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 Asreroidea 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).

	No. of sites/sp	total occ.	occ. rf	occ. os
Acanthaster planci	4	0.16	0.16	0.17
Culcita schmideliana	5	0.2	0.26	0
Linckia laevigata	5	0.2	0.26	0
Asteropsis carinifera	1	0.04	0.05	0
Neoferdina offreti	3	0.12	0.05	0.33
Dactylosaster cf.*cylindricus*	1	0.04	0.05	0
Linckia multifora	1	0.04	0.05	0

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*, *Eucidaria 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).

	No. of sites/sp	total occ.	occ. rf	occ. os
Echinothrix calamaris	9	0.36	0.42	0.17
Echinothrix diadema	2	0.08	0.1	0
Echinostrephus molaris	14	0.56	0.37	1
Echinometra mathaei	1	0.04	0.05	0
Stomopneustes variolaris	2	0.08	0.1	0
Plococidaris verticillata	1	0.04	0.05	0
Eucidaris metularia	3	0.12	0.1	0.17
Prionocidaris cf. *pistillaris*	1	0.04	0	0.17
Heterocentrotus mammillatus	1	0.04	0	0.17
Metalia spatagus	1	0.04	0.05	0

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).

	No. of sites/sp	total occ.	occ. rf	occ. os
Stephanometra indica	1	0.04	0	0.17
Antedonidae	1	0.04	0	0.17
Tropiometra carinata	1	0.04	0.05	0
Cenometra bella	1	0.04	0	0.17
Crinoidea sp. 1	1	0.04	0.05	0
Crinoidea sp. 2	1	0.04	0	0.17

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.

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References

Andréfouët S, Chagnaud N, Kranenburg CJ (2009) Atlas of Western Indian Ocean coral reefs. Centre IRD de Nouméa, New-Caledonia, 157 pp

Baird AH, Pratchett MS, Hoey AS, Herdiana Y, Campbell SJ (2013) *Acanthaster planci* is a major cause of coral mortality in Indonesia. Coral reefs 32: 803-812

Boxshall GA, Mees J, Costello MJ, Hernandez F, Gofas S, *et al*. (2014) World Register of Marine Species. Available at http://www.marinespecies.org at VLIZ. Date accessed 2014.

Caceres S (2003) Etude préalable pour le classement en réserve naturelle des îles Eparses. Mémoire de DESS Sciences et Gestion de l'Environnement tropical. DIREN Réunion, Laboratoire d'écologie marine de l'Université de La Réunion, Saint-Denis, 195 pp

Chabanet P, Bigot L, Nicet J-B, Andrefouët S, Bourmaud AF, Conand C, Durville P, Fricke R, Gravier-Bonnet N, Le Pape O, Mulochau T, Magalon H, Obura D, Poupin J, Quod J-P, Tessier E, Zubia M (2012) Multi-disciplinary approaches for coral reef management in Eparses Islands (SWIO). 12th International Coral Reef Symposium, Cairns, Australia, 9-13 July 2012, abstract

Chabanet P, Bigot L, Bourmaud A-F, Cavailles G, Durville P, Gravier-Bonnet N, Magalon H, Mattio L, Mulochau T, Nicet J-B, Obura D, Poupin J, Zubia M (2013) Assessing coral reef biodiversity at Glorieuses islands Marine Park (Scattered Islands, SW Indian Ocean) with identification for priority zones for conservation. 8th Western Indian Ocean Marine Science Association Conference, Maputo, Mozambique, 28 October – 2 November 2013, abstract

Chabanet P, Andrefouet S, Bigot L, Bourmaud A-F, Conand C, Durville P, Fricke R, Gravier-Bonnet N, Mattio L, Mulochau T, Magalon H, Nicet J-B, Obura D, Poupin J, Russo C, Tessier E, Zubia M (2014) Biodiversité, ressources et conservation des récifs coralliens des Iles Eparses. Colloque Iles Eparses, Campus Gérard-MEGIE du CNRS, Paris, 28-29 April 2014, abstract

Conand C (2008) Population status, fisheries and trade of sea cucumbers in Africa and Indian Ocean In: Toral-Granda V, Lovatelli A, Vasconcellos M (eds) Sea cucumbers. A global review on fishery and trade. FAO Fisheries Technical Paper No. 516. Rome, FAO, pp 153-205

Conand C, Stöhr S, Eléaume M, Magalon H, Chabanet P (2013a) The echinoderm fauna of Europa, Eparses Island, (Scattered Islands) in the Mozambique Channel (South Western Indian Ocean). Cahiers de Biologie Marine 54: 499-504

Conand C, Mulochau T, Chabanet P (2013b) Holothurian (Echinodermata) diversity in the Glorieuses Archipelago (Eparses Islands, France, Mozambique Channel). Western Indian Ocean Journal Marine Science 12: 71-78

Conand C, Polidoro BA, Mercier A, Gamboa RU, Hamel J-F, Purcell SW (2014) The IUCN Red List assessment of aspidochirotid sea cucumbers and its implications. Bêche-de-mer Information Bulletin, 34: 3-7

Eriksson H, Conand C, Lovatelli A, Muthiga N, Purcell S (2015) Governance structures and sustainability in Indian Ocean sea cucumber fisheries. Marine Policy 56: 16–22

FAO (2013) Report on the FAO Workshop on sea cucumber fisheries: An ecosystem approach to management in the Indian Ocean (SCEAM Indian Ocean). FAO Fisheries and Aquaculture Report No. 1038, 92 pp

Fell HB (1966) The ecology of ophiurids. In: Boolootian RA (ed) Physiology of Echinodermata. John Wiley, New York, pp 129-145

Gabrié C. 1998. L'état des récifs coralliens en France Outre-Mer. ICRI. Doc. Secrétariat d'Etat à l'Outre-Mer et Ministère de l'Aménagement du Territoire et de l'Environnement, 136 pp

Hemery LG, Eléaume M, Roux M, Améziane N (2013) High resolution crinoid phyletic inter-relationships: A preliminary study. Cahiers de Biologie Marine 54: 511-523

Mulochau T, Conand C (2008) Holothurians and other echinoderms of the Glorieuses Islands (Scattered Islands of the Indian Ocean). SPC Bêche-de-mer Information Bulletin 28: 34-39

Muthiga N, Conand C (2014) Sea cucumbers in the western Indian Ocean: Improving management of an important but poorly understood resource. WIOMSA Book Series No. 14, 74 pp

Purcell SW, Mercier A, Conand C, Hamel J-F, Toral-Ganda V, Lovatelli A, Uthicke S (2013) Sea cucumber fisheries: Global analysis of stocks, management measures and drivers of overfishing. Fish and Fisheries 14: 34–59

Torrence KG, Correia MD, Hoffman EA (2012) Divergent sympatric lineages of the Atlantic and Indian Ocean crinoid *Tropiometra carinata*. Invertebrate Biology 131: 355-365

Vergonzanne G (1977) Etude sur les mollusques et les echinodermes récifaux des Iles Glorieuses (nord-ouest de Madagascar). Bionomie et évaluations quantitatives. Thèse de 3ème cycle d'Océanographie, Université de Bretagne occidentale, Brest, 159 pp

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

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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 km^2 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; Mutagyera, 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 2º 30'S - 3º 30'S and 40º 000'E - 41º 000'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 km^2 (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

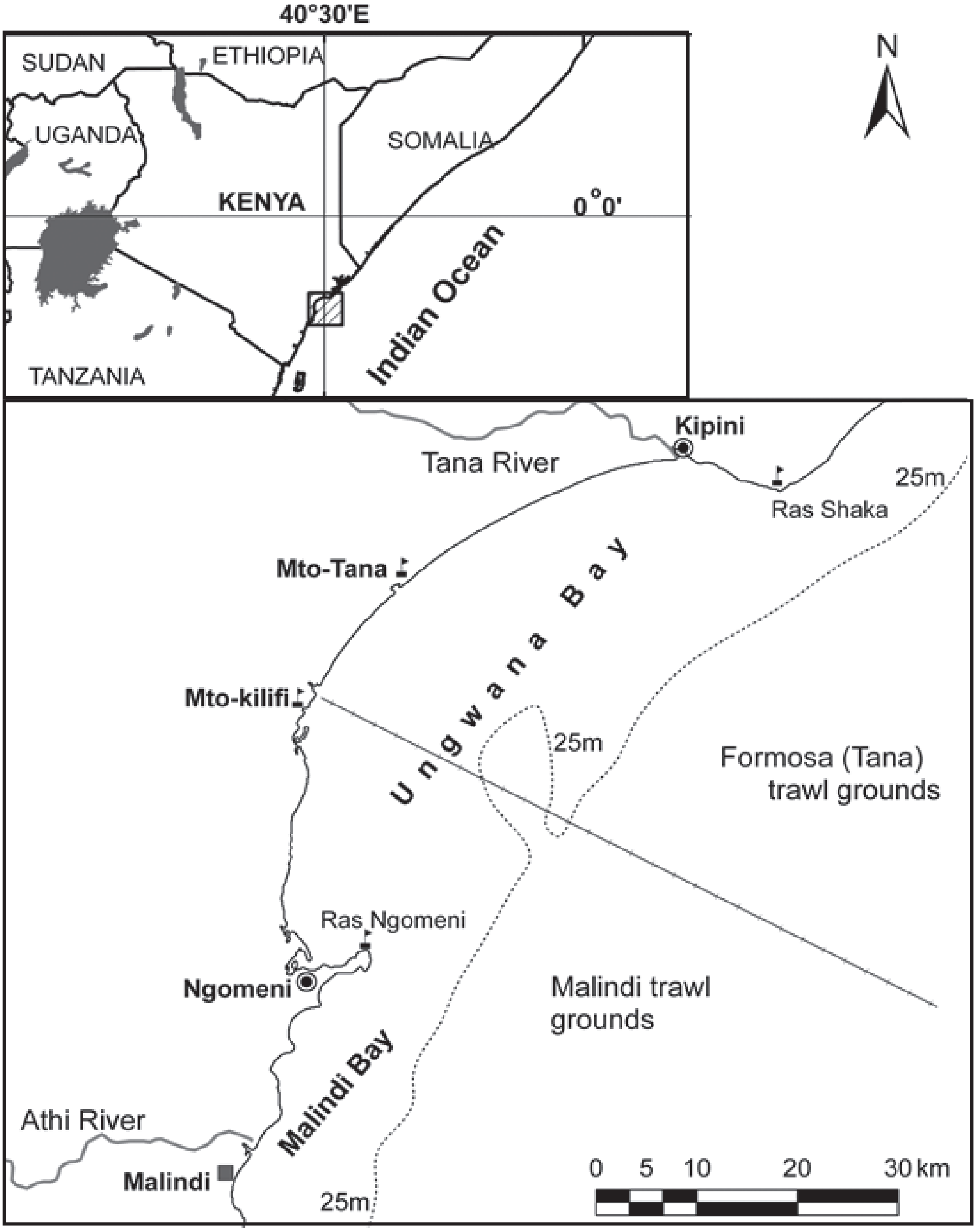

Figure 1. Map of the Malindi–Ungwana Bay area showing the discharge point of the Athi and Tana Rivers into the bay and the demarcation of the Formosa and Malindi commercial fishing (Source: Munga *et al.*, 2012).

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 km^2 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:

$$D=60*Sqrt((Lat1-Lat2)^2+(Lon1-Lon2)^2*\cos^2(0.5*(Lat1+Lat2))) \quad \text{......(1)}$$

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, nm^2), with a correction factor of 0.5 for the net configuration (Pauly, 1980):

$$\text{Swept Area } (A) = D * 22.5 * 0.5 \quad \text{......(2)}$$

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 = density x A / X1 ....(3)

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):

$$H' = - \Sigma i \; pi \log (pi)$$

Where pi is the proportion of the total count arising from the ith 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).

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.

Species	%	NEM	%	SEM
Penaeidae				
Fenneropenaeus indicus	57.6	8318 ± 4132	41.5	12151 ± 3329
Marsupenaeus japonicus	0.9	149 ± 35	0.6	418 ± 135
Metapenaeus monoceros	12.5	1489 ± 688.8	27.0	6790 ± 1580
Penaeus monodon	8.9	1008 ± 439.3	5.9	1233 ± 294
Penaeus semisulcatus	9.8	1069 ± 414.6	10.3	3777 ± 1784
Portunidae				
Portunus sanguinolentus	9.3	347± 156.1	9.7	331 ±106
Thalamita crenata	0.1	19	0.05	20
Charybdis feriata	-	-	0.6	38 ±7
Charybdis hellerii	-	-	0.8	144 ± 124
Charybdis natator	-	-	0.2	81
Charybdis smithii	-	-	0.5	172
Podophthalmus vigil	-	-	0.05	21
Portunus pelegicus	-	-	0.05	21
Scylla serrata	-	-	0.3	33 ± 13
Calappidae				
Calappa calappa	0.3	40	-	-
Calappa sp.	0.1	21	0.4	168
Matutidae				
Ashtoret lunaris	0.7	97	1.0	91 ± 17
Majidae				
Majid sp.	-	-	0.2	31 ± 11
Scyllidae				
Thenus orientalis	0.4	20 ± 0.4	0.7	58 ± 24
Palinuridae				
Panulirus ornatus	0.3	-	0.1	21± 0.3

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

Table 2. Seasonal distribution and abundance (individuals.Km^2 ± SE) of decapod crustaceans within depth zones during a) the northeast monsoon (NEM) and b) southeast monsoon (SEM) in Malindi-Ungwana Bay. Values without standard errors indicate that species appeared in only one transect; (-) indicates absence of catch.

Species	Depth Strata			
	Zone 1 (0-10 m)	Zone 2 (10-20 m)	Zone 3 (20-40 m)	Zone 4 (40-100 m)
a) NEM				
Fenneropenaeus indicus	11265 ± 5383	458 ±386	-	-
Marsupenaeus japonicus	248	116 ± 16	-	-
Metapenaeus monoceros	1918 ± 953	735	367 ±320	-
Penaeus monodon	1239 ±539	199 ± 74	-	-
Penaeus semisulcatus	-	564 ±544	1405 ± 577	-
Portunus sanguinolentus	576± 201	117 ± 12	-	-
Thalamita crenata	19	-	-	-
Charybdis feriata	-	-	-	-
Charybdis hellerii	-	-	-	-
Charybdis natator	-	-	-	-
Charybdis smithii	-	-	-	-
Podophthalmus vigil	-	-	-	-
Portunus pelagicus	-	-	-	-
Scylla serrata	-	-	-	-
Calappa calappa	40	-	-	-
Calappa sp.	-	21	-	-
Ashtoret lunaris	97	-	-	-
Majidae sp.	-	-	-	-
Thenus orientalis	20	21	20	-
Panulirus ornatus	-	-	-	-
b) SEM				
Fenneropenaeus indicus	15437± 4217	8208± 5210	-	-
Marsupenaeus japonicus	520 ± 294	350± 161	-	-
Metapenaeus monoceros	7003± 2046	7024±3141	4342	-
Penaeus monodon	1127 ± 428.2	1799 ± 250	632	-
Penaeus semisulcatus	1799 ± 250	6680 ± 3144	461± 234.0	-
Portunus sanguinolentus	486 ±168	176 ±59	21	-
Thalamita crenata	20	-	-	-
Charybdis feriata	41±1.0	41±12	21	-
Charybdis hellerii	-	20	-	268
Charybdis natator	-	81	-	-
Charybdis smithii	-	-	-	172
Podophthalmus vigil	-	-	21	-
Portunus pelagicus	-	21	-	-
Scylla serrata	20	39±19	-	-
Calappa calappa	-	-	-	-
Calappa sp.	-	-	167	-
Ashtoret lunaris	90 ± 24	98	-	-
Majidae sp.	20	42	-	-
Thenus orientalis	20 ± 0.2	54±34	145	-
Panulirus ornatus	20	21	-	-

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

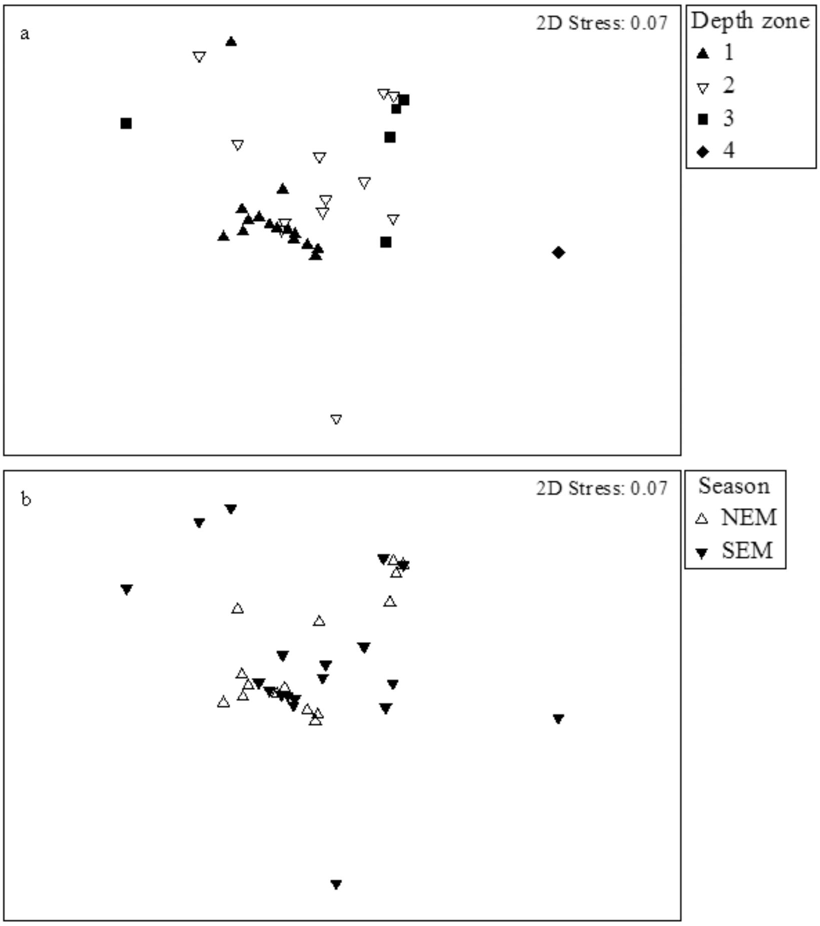

Fig. 2. Non-metric MDS plots showing decapod crustacean abundance according to a) depth zones and b) season in Malindi-Ungwana Bay, Kenya, based on combined northeast (NEM) and southeast monsoon (SEM) data.

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 pair-wise 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 ≤0.05 in bold.

Depth zones	R statistic	p-value	Possible permutations	Actual permutations	Number ≥observed
1, 2	0.232	**0.013**	3185325	999	12
1, 3	0.806	**0.001**	54450	999	0
1, 4	0.952	0.125	8	8	1
2, 3	0.083	0.271	17325	999	270
2, 4	0.638	0.111	9	9	1
3, 4	0.5	0.400	5	5	2

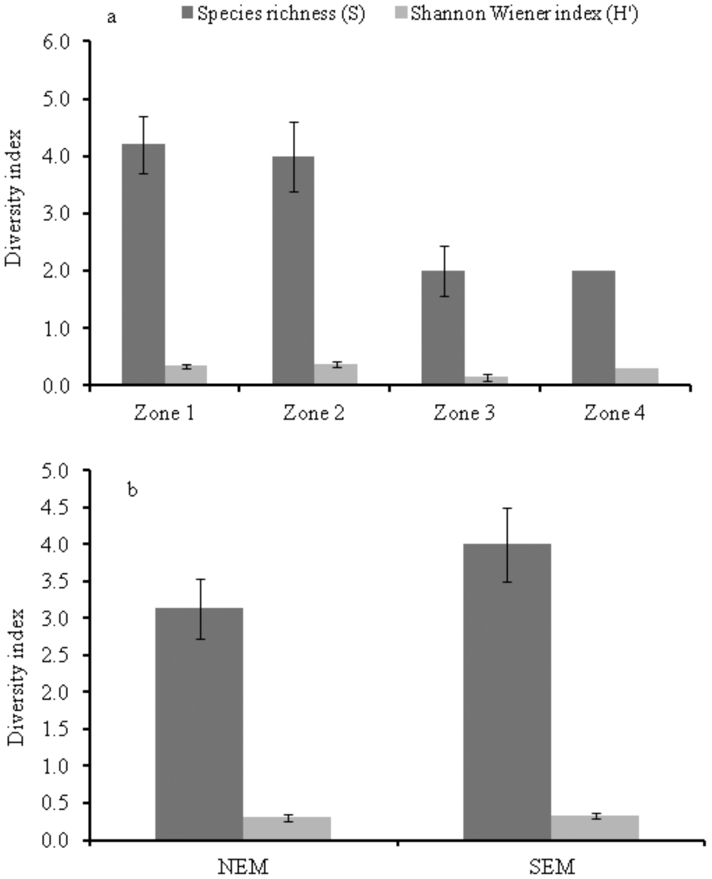

Fig. 3. Bathymetric variation of diversity measures (S ± SE and H' ± SE) of decapod crustacean species according to a) depth and b) season in Malindi-Ungwana Bay, Kenya.

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

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.

Species	Depth zone 1 Average abundance (%)	Depth zone 2 Average abundance (%)	Average dissimilarity	Contribution (%)
Fenneropeneaus indicus	**58.11**	22.89	19.35	29.63
Penaeus semisulcatus	1.32	**29.05**	14.47	22.15
Metapenaeus monoceros	22.26	18.65	10.89	16.67
Portunus sanguinolentus	7.13	6.95	7.07	10.81
Penaeus monodon	9.43	5.45	4.43	6.78
Charybdis natator	0.00	**6.67**	3.18	4.87

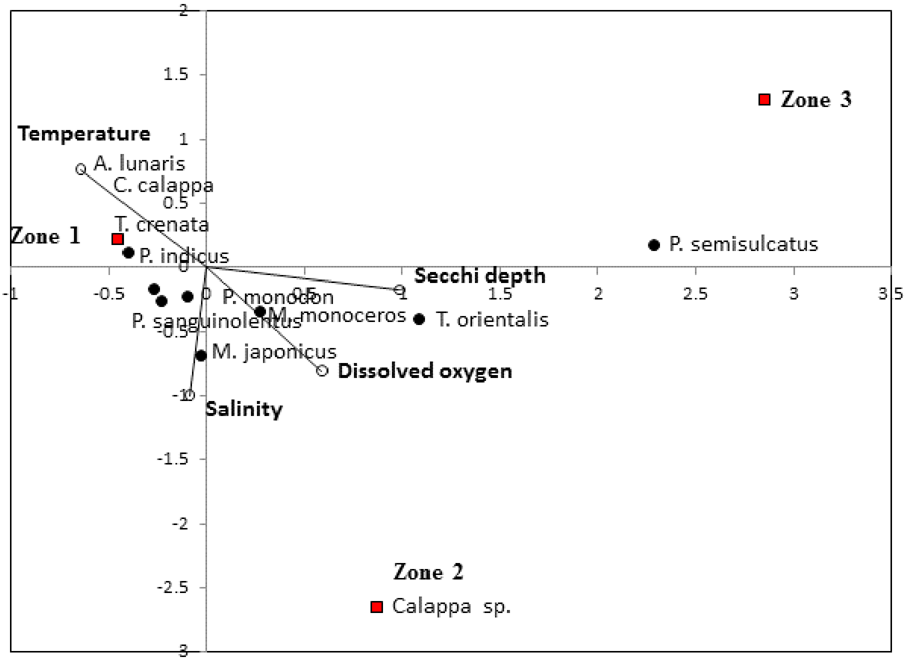

Fig. 4. Canonical Correspondence Analysis (CCA) showing the influence of physico-chemical factors on crustacean species abundance in the three shallower depth zones within Malindi-Ungwana Bay during the NEM. Species names are as shown on Table 1.

in bottom water samples collected from the different depth strata in the NEM (Table 6). 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 5. Two-Way SIMPER Analysis of decapod crustacean species contribution to dissimilarity in terms of abundance (%) between depth zones 1 and 3 in Malindi-Ungwana Bay. The average dissimilarity was 91.7%, notable contributors to this being highlighted in bold.

	Depth zone 1	Depth zone 3		
Species	Average abundance (%)	Average abundance (%)	Average dissimilarity (%)	Contribution (%)
Penaeus semisulcatus	1.32	**69.90**	35.15	38.32
Fenneropeneaus indicus	**58.11**	0.00	28.59	31.16
Metapenaeus monoceros	22.26	14.28	12.25	13.35
Calappa sp.	0.00	**10.39**	4.90	5.34
Penaeus monodon	9.43	1.54	4.58	4.99

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 run-off 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

Table 6. Environmental variables (mean ± SE) in the different depth zones measured during the northeast monsoon (NEM) in Malindi-Ungwana Bay, Kenya. Df = 3; p-values in bold are significant at P <0.05.

Environmental variables	0-10 m	10-20 m	20-40 m	40-100 m	ANOVA F	P
Temperature (°C)	27.7 ± 0.2	27.2 ± 0.3	27.7 ± 0.2	27.3 ± 0.2	1.000	0.408
Salinity	36.3 ± 0.2	36.4 ± 0.2	36.2 ± 0.1	37.0 ± 0.6	1.900	0.151
Secchi depth (m)	1.5 ± 0.2	8.6 ± 0.7	12.7 ± 1.2	14.0 ± 1.2	19.22	**0.000**
Dissolved Oxygen (mg/l)	5.5 ± 0.1	5.7 ± 0.0	5.4 ± 0.1	5.7 ± 0.2	3.050	**0.043**
Chlorophyll-*a* (µg/l)	0.2 ± 0.0	0.3 ± 0.1	0.3 ± 0.1	0.3 ± 0.1	0.557	0.647
(Nitrate + Nitrite) - N (µM)	1.8 ± 0.4	1.3 ± 0.1	1.2 ± 0.2	0.8 ± 0.2	1.084	0.370
Phosphates - P (µM)	1.1± 0.2	0.9 ± 0.1	1.1 ± 0.1	1.2 ± 0.6	0.839	0.482
BOD_{5days} (mg/l)	4.7 ± 0.2	4.6 ± 0.1	4.1 ± 0.2	3.5 ± 0.1	5.885	**0.003**

(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.

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References

Branch GM, Beckley LE, Branch ML, Griffiths CL (2007) Two Oceans: A guide to the marine life of Southern Africa. Struik Publishers, South Africa, 368 pp

Can MF, Mazlum Y, Demirci A, Akta M (2004) The catch composition and catch per unit of swept area (CPUE) of penaeid shrimps in the bottom trawls from İskenderun Bay, Turkey. Turkish Journal of Fisheries and Aquatic Sciences 4: 87-91

Clark KR, Warwick RM (2001) Change in marine communities: An approach to statistical analysis and interpretation, 2nd edition. PRIMER-E: Plymouth

de Freitas AJ (2011) The Penaeoidea of South Africa IV- The Family Penaeidae: Genus *Penaeus*. Oceanographic Research Institute Investigational Report (59): 1-125

De Grave S, Fransen CHJM (2011) *Carideorum catalogus*: The recent species of the dendrobranchiate, stenopodidean, procarididean and caridean shrimps (Crustacea: Decapoda). Zoologische Mededelingen, Leiden 85: 195-589

de Juan S, Cartes JE (2011) Influence of environmental factors on the dynamics of macrobenthic crustaceans on soft-bottoms of the Ebro Delta continental shelf (northwestern Mediterranean). Scientia Marina 75: 691-700

Fanelli E, Colloca F, Ardizzone G (2007) Decapod crustacean assemblages off the West coast of central Italy (western Mediterranean). Scientia Marina 71:19-28

FAO (1984) FAO Species identification sheets for fishery purposes, Western Indian Ocean Fishing Area 51, Volume VI

FAO (2008) The state of world fisheries and aquaculture. FAO Fisheries and Aquaculture Department, 176 pp

FAO (2010) The state of world fisheries and aquaculture. FAO Fisheries and Aquaculture Department, 197 pp

FAO (2011) Yearbook of fishery statistics summary tables. FAO, 120 pp

FAO (2012) The state of world fisheries and aquaculture. FAO Fisheries and Aquaculture Department, 209 pp

Follesa MC, Porcu C, Gastoni A, Mulas A, Sabatini A, Cau A (2009) Community structure of bathyal decapod crustaceans off South-Eastern Sardinian deep-waters (Central-Western Mediterranean). Marine Ecology 30: 188–199

Gillett R (2008) Global study of shrimp fisheries, FAO fisheries technical paper 475. Food and Agriculture Organization of the United Nation, Rome. 331 pp

Groeneveld JC (2000) Stock assessment, ecology and economics as criteria for choosing between trap and trawl fisheries for spiny lobster *Palinurus delagoae*. Fisheries Research 48: 141-155

Groeneveld JC, Melville-Smith R (1995) Spatial and temporal variability in the multispecies crustacean trawl fishery along the East Coast of South Africa and Southern Mozambique,1988-1993. South Africa Journal of Marine Science 15: 123-136

Iversen SA (1984) Kenyan marine fish resources in waters deeper than 10 m investigated by R/V *"Dr. fridtjof Nansen."* The Proceedings of NORAD-Kenya seminar to review the marine fish stocks and fisheries in Kenya, Mombasa, Kenya, 13-15 March 1984

Jackson JBC, Kirby M X, Berger WH, Bjorndal KA, Botsford LW, Bourque BJ, Bradbury RH, Cooke R, Erlandson J, Estes JA, Hughes TP, Kidwell S, Lange CB, Lenihan HS, Pandolfi JM, Peterson CH, Steneck RS, Tegner MJ, Warner RR (2001) Historical overfishing and the recent collapse of coastal ecosystems. Science 293: 629-637

Jennings S, Kaiser MJ (1998) The effects of fishing on marine ecosystems. Advances in Marine

Biology 34: 201–351

Lavrado HP, Falcao AP, Carvalho-Cunha P, Silva SHG (2000) Composition and distribution of Decapoda in Guanamara Bay, RJ. Nauplius 8: 15-23

Leibold MA (1996) A graphical model of keystone predators in food webs: Trophic regulation of abundance, incidence and diversity patterns in communities. The American Naturalist 147: 784-812

Magurran AE (1988) Ecological diversity and its measurement. Chapman and Hall, London, 172 pp

McClanahan TR (1988) Seasonality in East Africa's coastal waters. Marine Ecology Progress Series 44: 191-199

Meager JJ, Vance DJ, Williamson I, Loneragen NR (2003) Seasonal variation, and environmental influences on juvenile banana prawn (*Penaeus merguiensis*) abundance in a subtropical estuary (Logan River) of eastern Australia. Estuarine Coastal and Shelf Science, 56: 1-8

Mueni EM (2006) A trophic model for the Ungwana Bay Fishery, Kenya: Linking fisheries toecosystem management. MSc Thesis, UNESCO-IHE Institute for Water Education, Delft, The Netherlands

Munga C, Fulanda B, Manyala J, Kimani E, Ohtomi J, Vanreusel A (2012) Bottom shrimp trawling impacts on species distribution and fishery dynamics: Ungwana Bay fishery Kenya before and after the 2006 trawl ban. Fisheries Science 78: 209-219

Munoz JEG, Manjón-Cabeza ME, Raso JEG (2008) Decapod crustacean assemblages from littoral bottoms of the Alborán Sea (Spain, west Mediterranean Sea): Spatial and temporal variability. Scientia Marina 72: 437-449

Mutagyera WB (1984) Distribution of some deep water prawn and lobster species in Kenya's waters. Proceedings of NORAD-Kenya seminar to review the marine fish stocks and fisheries in Kenya, Mombasa, Kenya, 13-15 March 1984

Mwatha, G. (2005). Stock assessment and population dynamics of penaeid prawns in the prawn trawling grounds of Malindi-Ungwana bay: The challenges of managing the prawn fishery in Kenya. WIOMSA MARG 1 Project report no: WIOMSA/MARG-I/2005 – 06

Ng PKL, Guinot D, Davie PJF (2008) Systema Brachyorum: Part I. An annotated checklist of extant brachyuran crabs of the world. Raffles Bulletin of Zoology Suppl. 17: 1-286

Nzioka RM (1981) The evaluation of marine fisheries resources of Kenya. Proceedings of the workshop of KMFRI on aquatic resources of Kenya, 32 pp

Papiol V, Cartes JE, Fanelli E, Maynou F (2012) Influence of environmental variables on the spatio-temporal dynamics of bentho-pelagic assemblages in the middle slope of the Balearic Basin (NW Mediterranean). Deep-Sea Research 61: 84–99

Pauly D (1980) A selection of simple methods for the assessment of tropical fish stocks. FAO Fisheries Circular No. 729, 54 pp

Richmond MD (ed) (2011) Field guide to the seashores of Eastern Africa and the Western Indian Ocean Islands. SIDA, 464 pp

Sparre P, Venema SC (1998) Introduction to tropical fish stock assessment: Part 1 manual; FAO Fisheries Technical Paper 306/1, 376 pp

Staples J, Vance DJ (1986) Emigration of juvenile banana prawns *Penaeus merguiensis* from a mangrove estuary and recruitment to offshore areas in the wet-dry tropics of the Gulf of Carpentaria, Australia. Marine Ecology Progress Series 27: 239-252

Stephenson TA (1948) The constitution of the intertidal fauna and flora of South Africa. Part 3. Annals of the Natal Museum 11: 207-324

Teikwa ED, Mgaya YD (2003) Abundance and reproductive biology of the penaeid prawns of Bagamoyo coastal waters, Tanzania. Western Indian Ocean Journal of Marine Science 2: 117–126

Tychsen J (ed) (2006) KenSea. Environmental sensitivity atlas for the coastal area of Kenya. Geological Survey of Denmark and Greenland (GEUS), Copenhagen, 76 pp

Vance DJ, Stapples DJ, Kerr JD (1985) Factors affecting year to year variation in the catch of banana prawns in the Gulf of Canpentaria, Australia. Journal du Conseil International pour l'Exploration de la Mer 47: 83-97

Wakwabi EO, Jaccarini V (1993) The distribution and abundance of planktonic penaeid larvae in Tudor creek, Mombasa, Kenya. Hydrobiologia 264: 185-192

Wakwabi EO (1996) Recruitment of giant (Jumbo) tiger prawn in the backwaters of Tudor Creek, Mombasa, Kenya. IOC/UNESCO/SAREC/WIOMSA MARG I report, Contract no. SC. 298010.5

Wienner EL, Read TH (1982) Seasonal composition and abundance of decapod crustacean assemblages from the south Atlantic bight. USA Bulletin of Marine Science 32: 181-206

Worm B, Barbier EB, Beumont N, Duffy JE, Folke C, Halpern BS, Jackson JBC, Lotze HK, Micheli F, Palumbi SR, Sala E, Selkoe KA, Stachowicz J, Watson R (2006) Impacts of biodiversity loss on ocean ecosystem services. Science 5800: 787-790

Ye Y, Mohammed HM, Bishop JM (1999) Depth, salinity and temperature preferences of newly recruited penaeid shrimp in Kuwait waters. Fisheries Oceanography 8: 128-138

Yilmaz ZS, Ozvarol AB, Ozvarol Y (2009) Fisheries and shrimps economy, some biological properties of the shrimp *Metapenaeus monoceros* (Fabricus 1798) in the Gulf of Antalya (Turkey). Journal of Animal and Veterinary Advances 8: 2530-2536.

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

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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 ($DML_{50\%}$) 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).

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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 soci0-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.

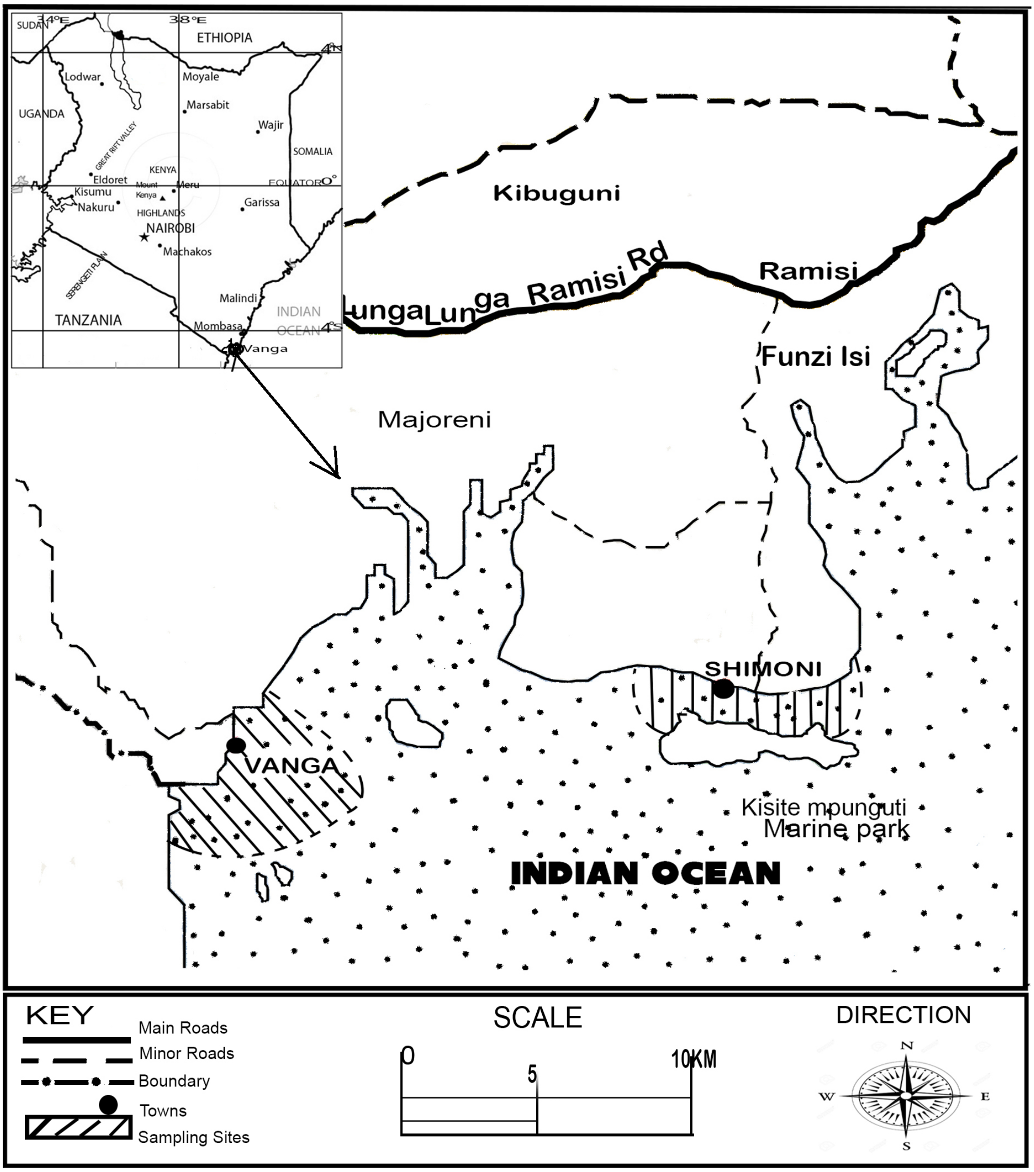


Figure 1. The location of the study areas, Shimoni and Vanga, on the south coast of Kenya.

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 (χ^2) test.

$$\chi^2 = \sum (f-F)^2/F$$

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 ($DML_{50\%}$) was estimated by fitting the length-frequency distribution of the proportion (P_i) of mature females to a logistic model, $P_i = 1/(1+\exp[-a + bDML_i])$, where $DML_{50\%} = -a/b$, using nonlinear methods, and deriving the regression line by the least squares method using the Gauss-Newton algorithm (Quinn & Keough, 2002).

Here:

P_i = represents the relative frequencies of fully mature individuals in length class DML_i

'a' and 'b' = are the regression constants, and

$DML_{50\%}$ = 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.

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

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

Stage	Description
Stage I: Immature	Ovary small, generally weighing <3 g with no follicles and a thick outer wall; small white oviducal glands located mid-way down very narrow proximal and distal oviducts.
Stage II: Maturing	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.
Stage III: Mature	Ovary very large (>20 g), packed tightly with elongated, striated but unstalked eggs; oviducal glands large and dark in colour and positioned high up the proximal oviduct.
Stage IV:Pre-spawning	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.
Stage V: Post-spawning	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.

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).

$$GSI_m = (\text{Testis weight/ Total Tissue Weight}) \times 100$$

$$GSI_f = (\text{Ovary weight/ Total Tissue Weight}) \times 100$$

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):

$$F = (V/V_i)\, n \times (W/W_i)$$

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

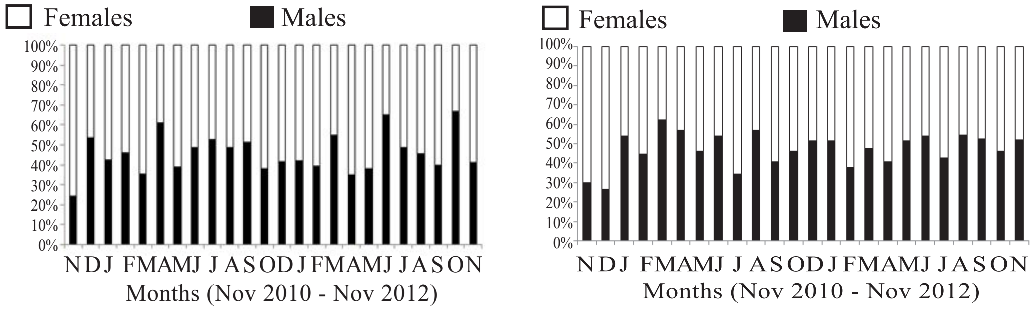
While the sex ratio (M:F) of common octopus at Shimoni was 1:1.2, at Vanga it was 1:1. The monthly ratios were variable (Figure 2) but a chi-squared test (Shimoni: $\chi^2 = 6.2$, df = 1, $p > 0.75$; Vanga: $\chi^2 = 1.7$, df = 1, $p > 0.05$) revealed no significant differences in the monthly or annual 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

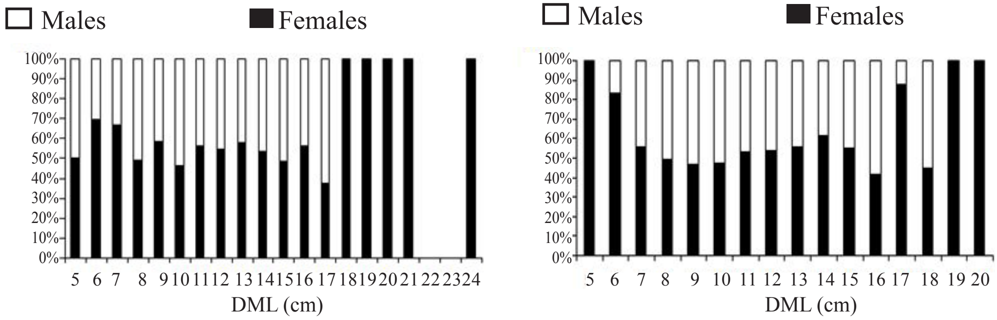
Analysis of the length at first maturity revealed that the female size at first maturity ($DML_{50\%}$) was 10.8 cm and that of males was 10.5 cm (Fig. 4).



a) Shimoni

b) Vanga

Figure 2. Variation in monthly sex ratios of common octopus at a) Shimoni and b) Vanga.



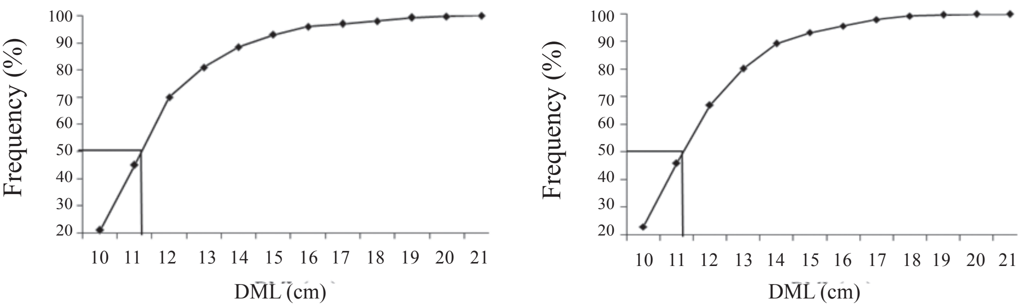
a) Shimoni

b) Vanga

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

a) Females - Shimoni

b) Females - Vanga



c) Males - Shimoni

d) Males - Vanga

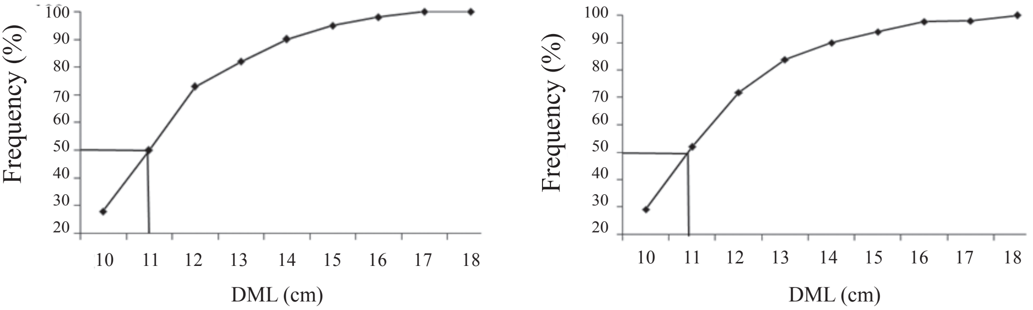
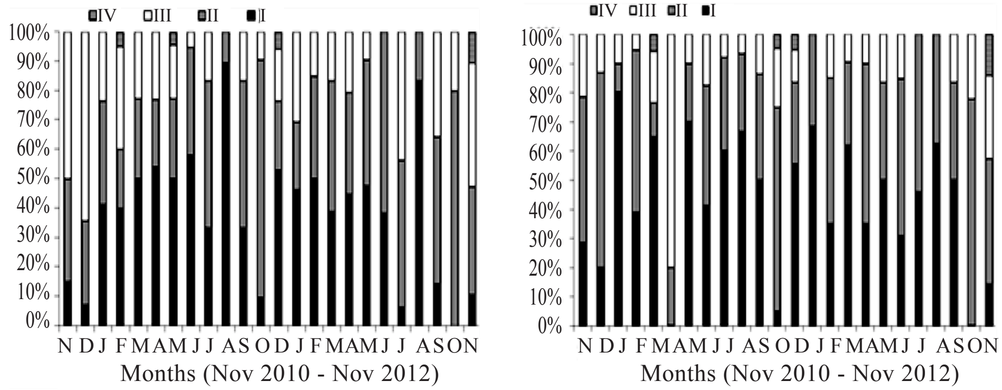


Figure 4. Cumulative frequency curves of length of maturity stages II, III and IV in common octopus in southern Kenya: a) females at Shimoni, b) females at Vanga, c) males at Shimoni and d) males at Vanga.

a) Female maturity stages - Shimoni

b) Female maturity stages - Vanga



c) Male maturity stages - Shimoni

d) Male maturity stages - Vanga

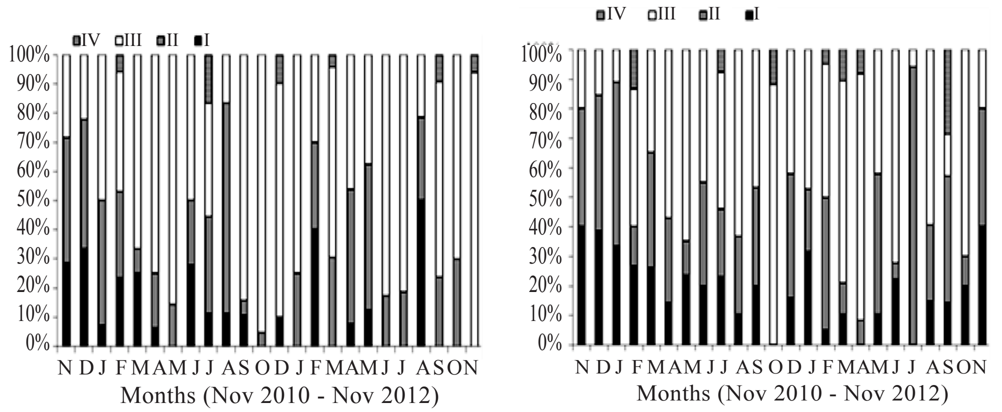


Figure 5. Monthly percentages of common octopus at different stages of maturity in southern Kenya: a) females at Shimoni, b) females at Vanga, c) males at Shimoni and d) males at Vanga.

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 north-western 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, wher 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.

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References

Anderson RC, Wood JB, Byrne RA (2003) Octopus senescence: the beginning of the end. Journal of Applied Animal Welfare Science 5: 275–283

Bagenal TB, Erich B (1978) Eggs and early life history. In: B. Timothy (ed.) Methods for assessment of fish production in freshwater. Blackwell Scientific Publications, London, Oxford, pp 165-201

Carson F (1992) Histotechnology: A Self-Instructional Text. American Society for Clinical Pathology (ASCP) Press, Chicago, 19 pp

Caverivière A (1990) Étude de la pêche du poulpe (*Octopus vulgaris*) dans les eaux côtières de la Gambie et du Sénégal. L’explosion démographique de l’été 1986. Centre Rech. Océanogr. Dakar-Thiaroye, Doc. Scient. 116: 1–42

Caverivière A, Thiam M, Jouffre D (2002) The common octopus *Octopus vulgaris*: Senegal and northwestern coasts African. IRD Editions, Paris, 385 pp

Dia MA (1988) Biologie et exploitation du poulpe *Octopus vulgaris* des côtes mauritaniennes. PhD thesis, University of West Brittany, France, 146 pp

Gonçalves JMA (1993) *Octopus vulgaris* Cuvier, 1797 (the common octopus): Synopsis of the biology and exploitation. Synthesis for access to the category of Assistant Career University Lecturer, University of Azores, 470 pp

Gonzalez M, Barcala E, Pérez-Gil JL, Carrasco MN, Garcia-martnez MC (2011) Fisheries and reproductive biology of *Octopus vulgaris* (Mollusca: Cephalopoda) in the Gulf of Alicante (Northwestern Mediterranean). Mediterranean Marine Science 12: 369-389

Guerra A (1975) Determination of the different stages of sexual development of *Octopus vulgaris* Lamarck, using an index of maturity. Fisheries Research 39: 397-416

Guerra A (1979) Fitting a von Bertalanffy`s expression to *Octopus vulgaris* growth. Investigation Pesquera 43 : 319-326

Hanlon RT, Messenger JB (1996) Cephalopod Behaviour. Cambridge University Press, Cambridge, UK, 232 pp

Hatanaka H (1979) Spawning season of common octopus, *Octopus vulgaris* Cuvier, of the northwestern coasts of Africa. In: Rapport du groupe de travail ad hoc sur l'évaluation des stocks des céphalopodes. COPACE/PACE séries 78/11 (Fr.), pp 121–132

Hernández-Garcia V, Hernandez-Lopez JL, Castro-Hdez JJ (2002) On the reproduction of *Octopus vulgaris* off the coast of the Canary Islands. Fisheries Research 57: 197-203

Inejih CA (2000) Spatiotemporal dynamics and biology of octopus (*Octopus vulgaris*) in Mauritanian waters: Modeling of abundance and fisheries management. PhD thesis, University of Western Britain, 155 pp

Isshiki Y, Tsuchiya K, Kohno H, Segawa S (2012) The embryonic development of *Octopus vulgaris* and O. ocellatus. Cephalopod International Advisory Council Symposium 2012, Majestic Palace Hotel, Florianópolis, Santa Catarina, Brazil, 53 pp.

Katsanevakis S, Verriopoulos G (2005) Seasonal population dynamics of *Octopus vulgaris* in the eastern Mediterranean. International Council for the Exploitation of the Sea (ICES) Journal of Marine Sciences 63: 151-160

Kume S, Joseph H (1969) Size composition and sexual maturity of bill-fish caught by the Japanese longline fishery in Pacific Ocean east of 130° degrees. Bulletin of the National Research Institute of Far Seas Fisheries 2: 115-162

Mangold K (1983) *Octopus vulgaris*. In Boyle PR (ed.) Cephalopod life cycles. Species Accounts, Academic Press, London, UK, pp 335-364

Mangold-Wirz K (1963) Biology of benthic cephalopods nektonic of the Catalan sea. Life and Environment, 13 (Suppl.): 1-285

McClanahan TR, Mangi S (2001) The effect of a closed area and beach seine exclusion on coral reef fish catches. Fisheries Management and Ecology 8: 107–121

Oosthuizen A (2003) A development and management framework for a new *Octopus vulgaris* fishery in South Africa. PhD thesis, Rhodes University, 203 pp

Oosthuizen A, Smale MJ (2003) Population biology of *Octopus vulgaris* on the temperate south-eastern coast of South Africa. Journal of the Marine Biological Association of the United Kingdom 83: 535-541

Otero J, Gonźalez AF, Pilar-Sieiro M, Guerra A (2007) Reproductive cycle and energy allocation of *Octopus vulgaris* in Galician waters, NE Atlantic. Fisheries Research 85: 122-129

Quinn GP, Keough MJ (2002) Experimental design and data analysis for biologists. Cambridge University Press, UK, 527 pp

Sánchez P, Obarti R (1993) The biology and fishery of *Octopus vulgaris* caught with clay pots on the Spanish Mediterranean coast. In: Okutani T, O'Dor RK, Kubodera T (eds) Recent advances in cephalopod fisheries biology. Tokai University Press, Tokyo, Japan, pp 477-487

Scheel D (2002) Characteristics of habitats used by *Enteroctopus dofleini* in Prince William Sound and Cook Inlet, Alaska. Marine Ecology 23: 185-206

Silva L, Sobrino I, Ramos F (2002) Reproductive biology of the common octopus *Octopus vulgaris* Cuvier, 1797 (Cephalopoda: Octopodidae) in the Gulf of Cadiz (SW Spain) Bulletin of Marine Science 71: 837-850

Simpson AC (1951). The fecundity of the plaice. Fishery Investigations, London, Series 17, 27 pp

Zguidi W (2002) Ecobiologie et exploitation du poulpe commun *Octopus vulgaris* Cuvier, 1797 (Cephalopoda, Octopoda) dans le golfe de Gabès (Tunisie, Méditerranée centrale). Thesis 3rd cycle, University of Tunis, 165 pp

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

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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 m^2 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

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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 km^2 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 m^2 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

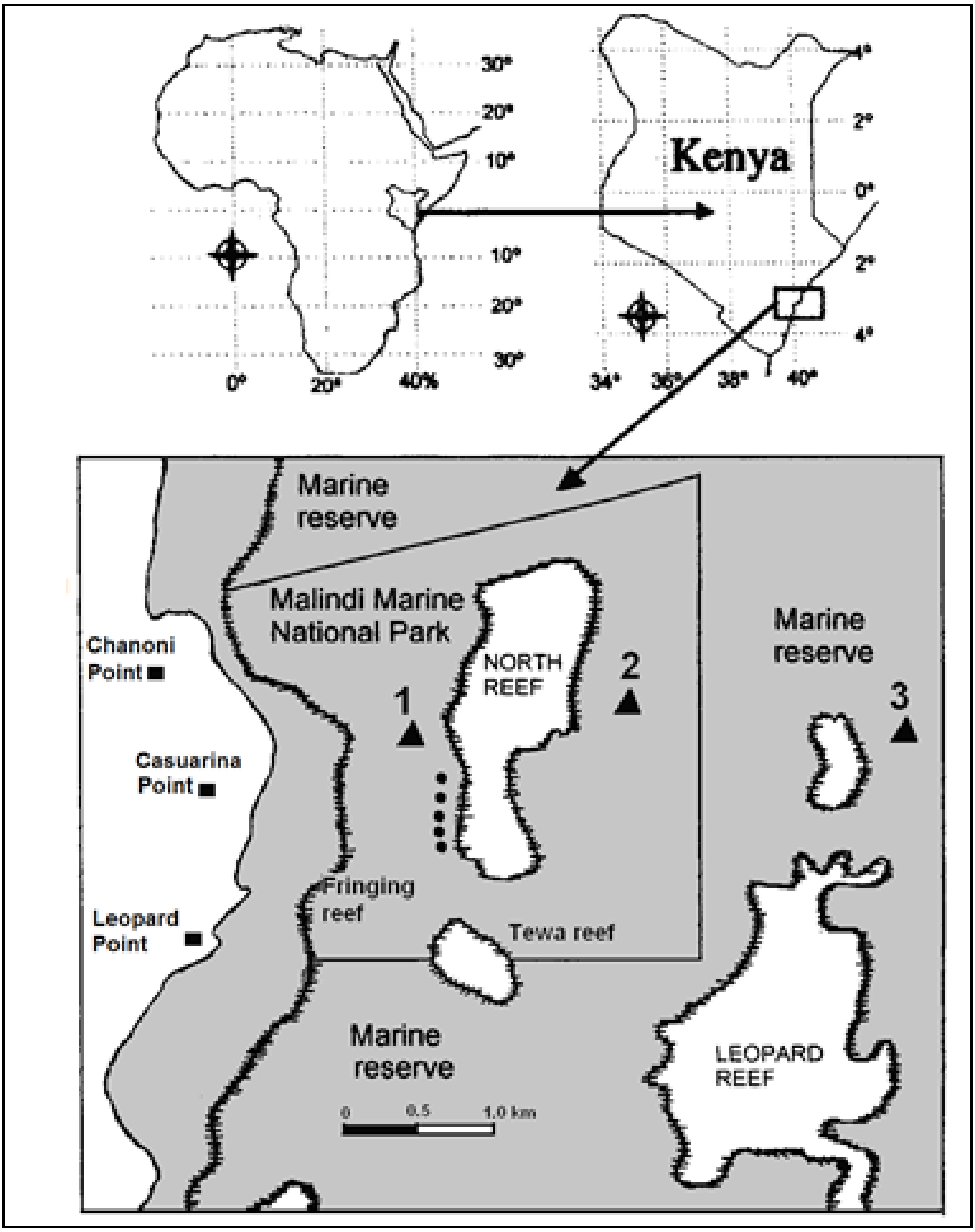

Figure 1. Map of Malindi Marine National Park, Kenya, showing the stations (1-3) sampled monthly for fish larvae and the location of transects for the 24-hr sampling sessions (●).

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).

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.

Taxa	Stage	Spring tide		Neap tide		t-test	
		Mean abundance	Total larvae	Mean abundance	Total larvae	t	p
Acanthuridae							
Acanthurus sp.	pr	10 ± 10	50	-	-	-	-
Apogonidae							
Archamia sp.	pr	20 ± 20	100	-	-	-	-
Apogon sp.	pr	8 ± 8	40	28 ± 9	142	-0.66	0.52
Balistidae							
Balistid sp.	pr	1 ± 1	7	-	-	-	-
Blenniidae							
Blenniidae n.d.	pr,fl,po	131 ± 41	465	46 ± 25	230	0.53	0.60
Parablennius sp.		-	-	96 ± 48	482	-	-
Bothidae							
Bothus pantherinus	pr	-	-	4 ± 4	20	-	-
Caesionidae							
Pterocaesio sp.	pr	-	-	6 ± 4	30	-	-
Carangidae							
Caranx sp.	pr	-	-	2 ± 2	4	-	-
Scomberoides sp	fl	-	-	2 ± 2	11	-	-
Dactylopteridae							
Dactyloptena sp.	pr	-	-	2 ± 2	2	-	-
Engraulidae							
Stolephorus commersonii	pr,fl,po	360 ± 252	1802	117 ± 84	533	0.71	0.49
Gerreidae							
Gerres sp.	pr	1 ± 1	4	-	-	-	-
Gobiidae							
Amblygobius sphynx	po	1 ± 1	7	7 ± 7	33	-1.43	0.17
Gobiidae n.d.	pr,fl,po	31 ± 18	157	18 ± 14	73	-0.17	0.87
Haemulidae							
Pomadysis maculatum	pr,fl	5 ± 5	25	-	-	-	-
Labridae							
Labridae n.d.	pr,fl,po	215 ± 215	1075	1 ± 1	6	-	-
Lethrinidae							
Lethrinus sp.	pr	2 ± 2	8	7 ± 7	33	-1.36	0.19
Lutjanidae							
Lutjanus argentimaculatus	pr	2 ± 2	8	1 ± 1	5	-0.66	0.51
Monocanthidae							
Monacanthus ciliatus	pr	1 ± 1	7	4 ± 4	20	1.13	0.27
Aluterus scriptus	pr	2 ± 2	8	-	-	-	-
Nemipteridae							
Nemipteridae n.d.	pr	-	-	3 ± 3	13	-	-
Platycephalidae							
Thysanophyrs arenicola	fl	1 ± 1	2	-	-	-	-
Platycephalidae n.d.	fl	-	-	1 ± 1	7	-	-
Pomacentridae							
Chromis sp.	pr	5 ± 5	25	-	-	-	-
Abudefduf sp.	pr,fl	-	-	22 ± 20	108	-	-
Pomacanthidae							
Pomacanthidae n.d.	pr	2 ± 2	8	-	-	-	-
Scaridae							
Leptoscarus vaigiensis	pf,fl,po	100 ± 100	500	-	-	-	-
Calotomus sp.	pr	3 ± 3	13	-	-	-	-
Scaridae n.d.	pr	-	-	6 ± 5	30	-	-
Siganidae							
Siganus sutor	pr	20 ± 20	100	-	-	-	-
Siganus canaliculatus	pr,po	7 ± 7	33	4 ± 4	20	0.64	0.53
Sparidae							
Sparidae n.d.	pr	-	-	4 ± 4	20	-	-
Sphyraenidae							
Sphyraena barracuda	po	11 ±10	57	-		-	-
Sphyraena jello	fl,po	10 ± 10	50	2 ± 2	4	1.93	0.07
Sygnathidae							
Coryoichthys sp.	pr	1 ± 1	3	1 ± 1	4	-	-
Sygnathidae n.d.	fl	-		9 ± 3	47	-	-
Tetraodontidae							
Arothron sp.	pr	2 ± 2	8	-	-	-	-
Totals		951 ± 408	4562	394 ± 260	1890	2.10	0.03

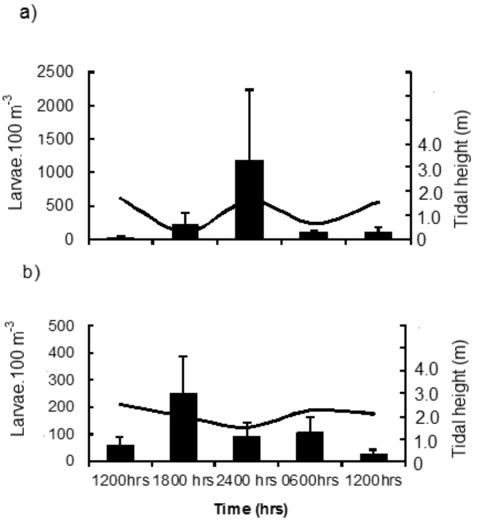

Figure 2. Diel variation in mean fish larval abundance (vertical bars represent the SE) with tidal heights for six 24-hr sampling sessions during a) spring tides and b) neap tides in Malindi Marine Park, Kenya.

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).

The numbers of larvae collected in the 24-hour sampling regime were also standardised (number of larvae.100 m^{-3}). The data were Log$_{10}$ (x+1) transformed to stabilise the variance caused by zero values and the unpredictable occurrence of rare species. The data were grouped according to season (NE and SE monsoon) and time of day (day or night) and a two-factor ANOVA was used to examine for seasonal or diel variation. Factor analysis was used to describe the relationship between tidal height and larval abundance. Statistical analyses followed Zar (1999).

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

Species	Season		Time of day		Season and time of day	
	F	p	F	p	F	p
Total catch	0.575	0.455	1.771	0.195	2.003	0.169
Stolephorus commersonii	2.014	0.168	2.504	0.126	2.341	0.138
Blenniidae n.d.	3.520	0.124	0.801	0.378	1.198	0.283
Gobiidae n.d.	0.06	0.806	2.41	0.132	0.03	0.851

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. 2 b). 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 ($p = .195$) 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

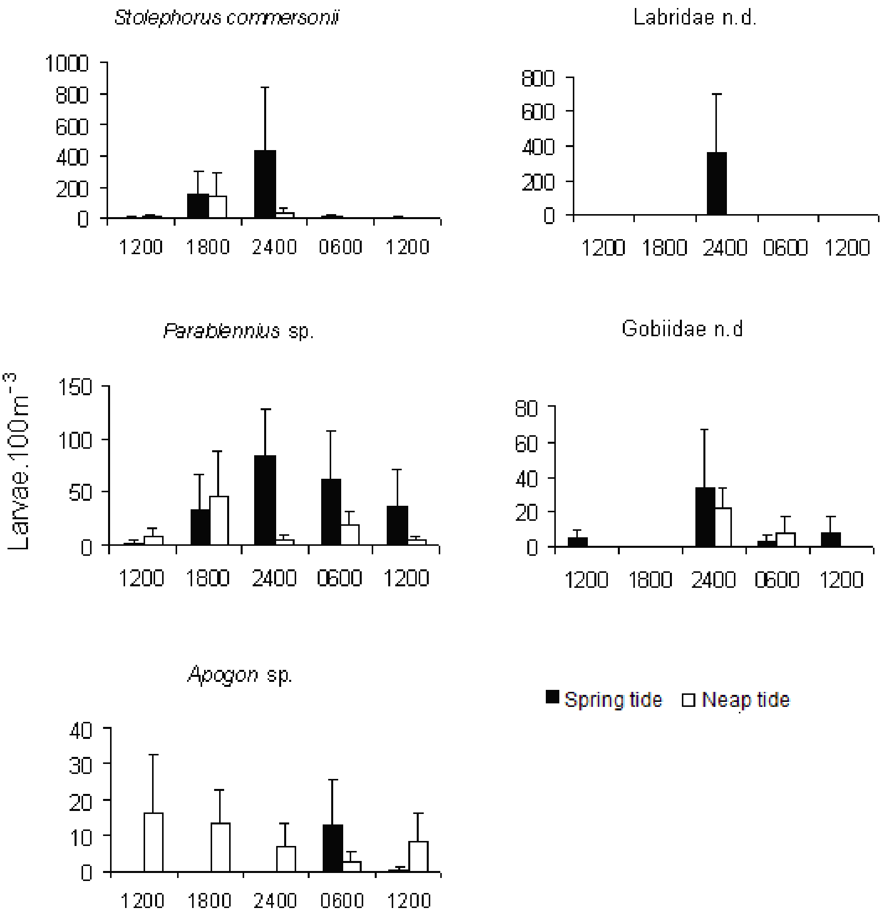

Figure 3. Diel variation in abundance (vertical bars represent the SE) of the dominant fish larval species collected during six 24-hr sampling sessions in Malindi Marine Park, Kenya.

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 periodiogram (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 AFC 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).

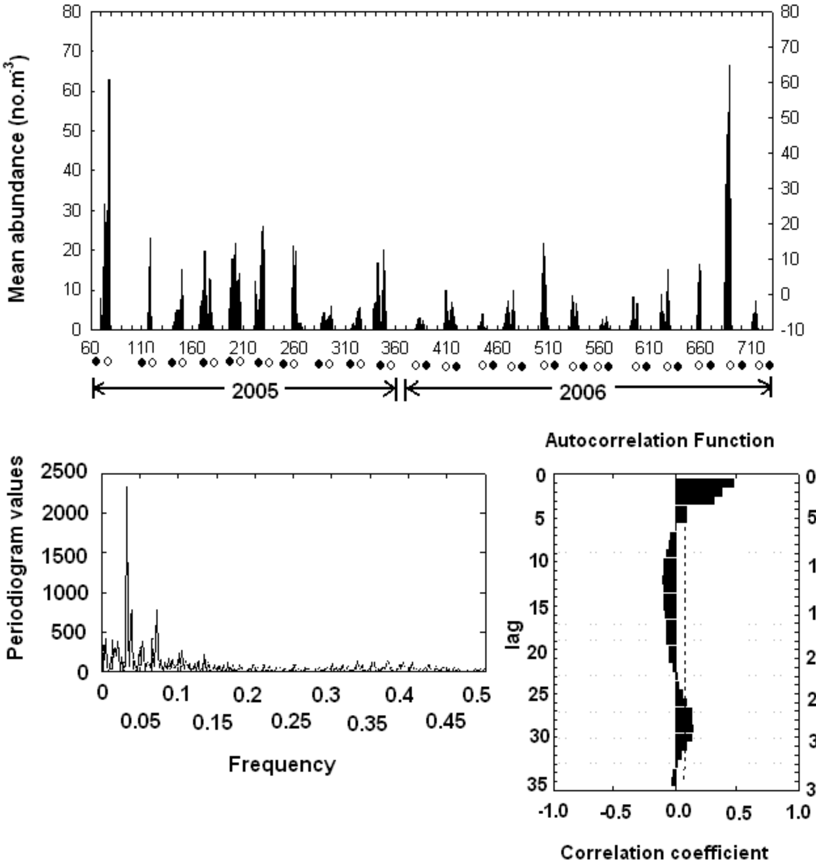

Figure 4. Time-series of mean total fish larval abundance from March 2005 to December 2006 in Malindi Marine Park, Kenya (upper graph; = full moon and = new moon). The lower left spectral density plot shows the cyclical peaks within the time series (period in days) of larvae confirmed by the Autocorrelation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

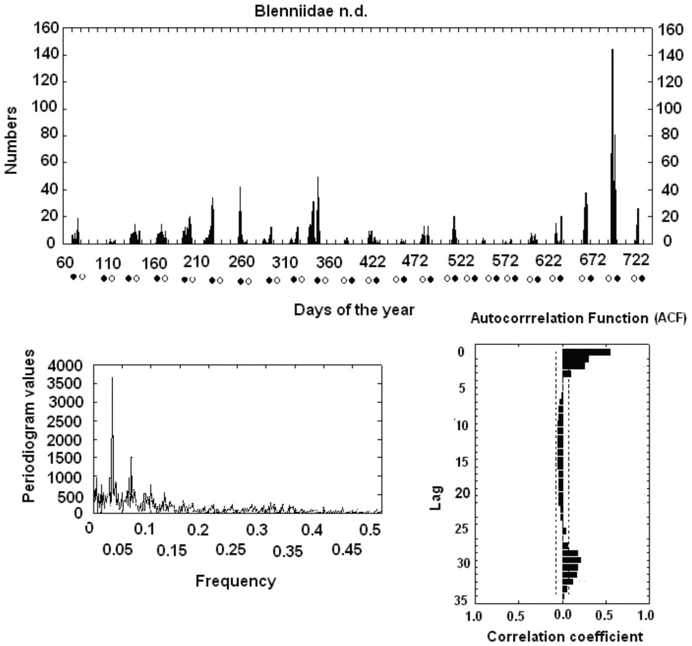

Figure 5. Time-series of larval abundance of a *blenniid* sp. from March 2005 to December 2006 in Malindi Marine Park, Kenya (upper graph;   = full moon and   = new moon). The lower left spectral density plot shows the cyclical peaks within the time series (period in days) of larvae confirmed by the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

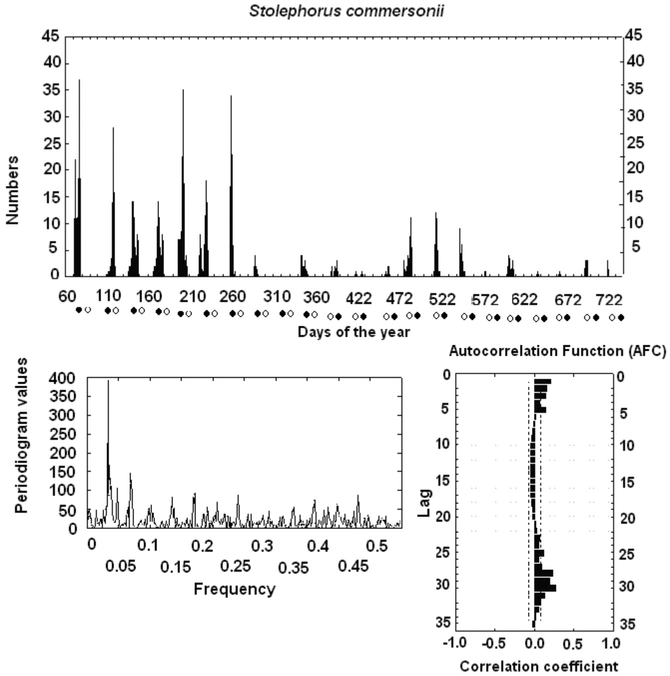

Figure 6. Time-series of larval abundance of *Stolephorus commersonii* from March 2005 to December 2006 in Malindi Marine Park, Kenya (upper graph;   = full moon and   = new moon). The lower left spectral density plot shows the cyclical peaks within the time series (period in days) of larvae confirmed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

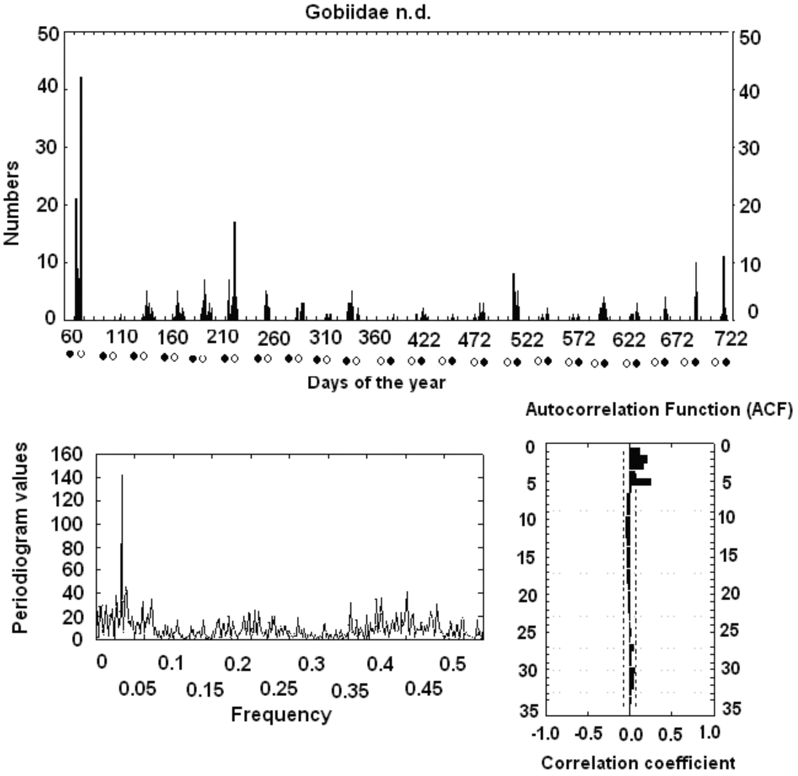

Figure 7. Time-series of larval abundance of a *gobiid* sp. from March 2005 to December 2006 in Malindi Marine Park, Kenya (upper graph; = full moon and = new moon). The lower left spectral density plot shows the cyclical peaks within the time series (period in days) of larvae confirmed by the Autocorrelation Function plot (lower right) of the raw data, where the horizontal bars represent 2x the SE.

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; Pattrick & 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 (McIIwain, 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.

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References

Botsford LW, Coffroth MA, Jones GP, Paris CB, Planes S, Shearer TL, Thorrold SR, White JW (2009) Measuring connectivity and estimating resilience of coral reef metapopulations in MPAs: matching empirical efforts to modelling needs. Coral Reefs 28: 327-337

Cushing DH (1987) Population biology and the management of fisheries. Trends Ecological Evolution 2: 138-139

D'Alessandro E, Sponaugle S, Lee T (2007) Patterns and processes of larval fish supply to the coral reefs of the upper Florida Keys. Marine Ecology Progress Series 331: 85-100

Doherty PJ (1987) Light - traps: selective but useful devises for quantifying the distributions and abundances of larval fishes. Bulletin of Marine Science 41: 423-431

Dufour V, Galzin R (1993) Colonisation patterns of reef fish larvae to the lagoon at Moorea Island, French Polynesia. Marine Ecology Progress Series 102: 143-152

Jenkins GP, Welsford DC, Keough M, Hamer PA (1998) Diurnal and tidal vertical migration of pre-settlement King George whiting *Sillaginodes punctuate* in relation to feeding and vertical distribution of prey in a temperate bay. Marine Ecology Progress Series 170: 239-248

Johannes RE (1978) Reproductive strategies of coastal marine fishes in the tropics. Environmental Biology of Fishes 3: 65-84

Kaunda-Arara B, Mwaluma J, Gamoe A, Oresland V, Osore M (2009) Temporal variability in fish larvae supply to Malindi Marine Park, coastal Kenya. Aquatic Conservation: Marine and Freshwater Ecosystems 19: S10-S18

Kingsford MJ, Leis JM, Shanks A, Lindeman KC, Morgan SG, Pineda J (2002) Sensory environments, larval abilities and local self-recruitment. Bulletin of Marine Science 70: 309-340

Leis J M, Rennis DS (1983) The larvae of Indo-Pacific coral reef fishes. New South Wales University Press, Kensington, Australia, 268 pp

Leis J M, Trnski T (1989) The Larvae of Indo-Pacific Shore fishes. New South Wales University Press, Kensington, Australia, 372 pp

Leis JM (1993) Larval fish assemblages near indo-Pacific coral reefs. Bulletin of Marine Science 53: 362-392

Leis JM, Carson-Ewart BM (2000) The larvae of Indo-Pacific coastal fishes. An identification guide to marine fish larvae. Fauna Malesiana Handbooks 2, EJ Brill, Leiden, 870 pp

McClanahan TR (1988) Seasonality in East Africa's coastal waters. Marine Ecology Progress Series 44: 191-199

McIlwain JL (2003) Fine-scale temporal and spatial patterns of larval supply to fringing reef in Western Australia. Marine Ecology Progress Series 252: 207-222

Mwaluma JM, Kaunda-Arara B, Rasowo J, Osore MK, Øresland V (2011) Seasonality in fish larval assemblage structure within marine reef National Parks in coastal Kenya. Environmental Biology of Fishes 90: 393-404

Pattrick P, Strydom NA (2008) Composition, abundance, distribution and seasonality of larval fishes in the shallow nearshore of the proposed Greater Addo Marine Reserve, Algoa Bay, South Africa. Estuarine, Coastal and Shelf Science 79: 251-262

Platt T, Denman KL (1975) Spectral analysis in ecology. Annual Review of Ecology, Evolution and Systematics 6: 189-210

Richards WJ, Lindeman KC (1987) Recruitment dynamics of reef fishes: Planktonic processes, settlement and demersal ecologies, and fishery analysis. Bulletin of Marine Science 41: 392- 410

Robertson DR (1991) The role of adult biology in the timing of spawning of tropical reef fishes. In: Sale PF (eds) The ecology of fishes on coral reefs. Academic Press, San Diego, CA, USA, pp 356-386

Sinclair M (1988) Marine populations: An essay on population regulation and speciation. University of Washington Press, Seattle, Washington, 252 pp

Taylor MC (1984) Lunar synchronization of fish reproduction. Transactions of the American Fisheries Society 113: 484-493

Thorrold SR, Shenker JM, Mojica R, Maddox ED, Wishinski E (1994) Temporal patterns in the larval supply of summer-recruitment reef fishes to Lee stocking Island, Bahamas. Marine Ecology Progress Series 112: 75-86

Valles H, Sponaugle S, Oxenford HA (2001) Larval supply to a marine reserve and adjacent fished area in the Soufriere Marine Management Area, St Lucia,West Indies. Journal of Fish Biology 59: 152-177

Wright KJ, Higgs DM, Belanger AJ, Leis JM (2005) Auditory and olfactory abilities of pre-settlement larvae and post-settlement juveniles of a coral reef damselfish (Pisces: Pomacentridae). Marine Biology 147: 1425-1434

Zar JH (1999) Biostatistical analysis. 4th Edition, Prentice Hall Inc., Upper Saddle River, NJ, USA, 931 pp

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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

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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 (Rijnsdorp, 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.

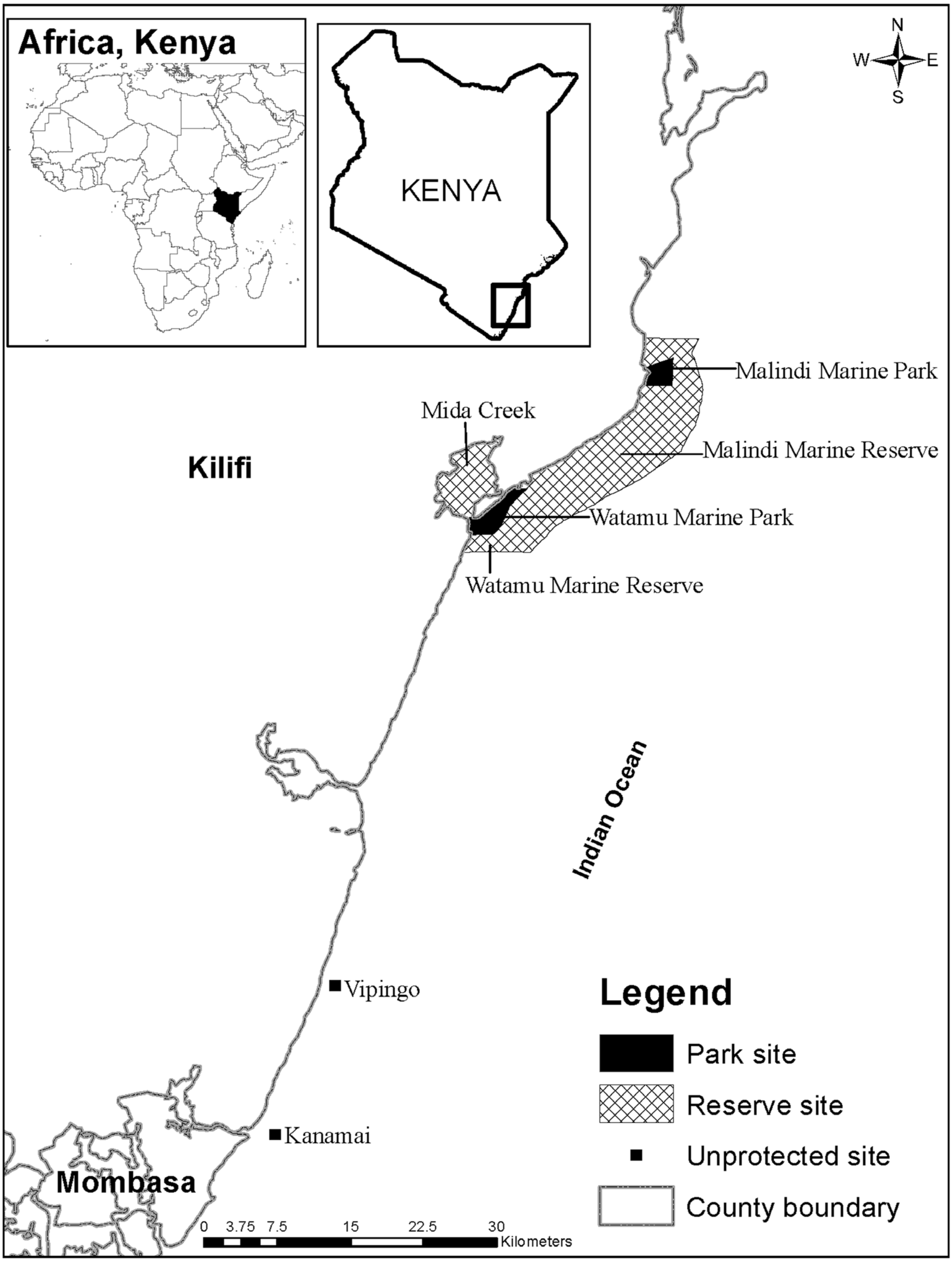

Figure 1. Map of Kenya showing the sites sampled for marbled parrotfish, *Leptoscarus vaigiensis*.

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:

$F = V/V_1 N \times W/W_1$.......................... Equation 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:

$F = aSL^b$..Equation 2

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:

$P(L) = 1/1+e^{-(a+bL)}$ ....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 L50 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 (χ^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 ≈ 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 1. Numbers of *Leptoscarus vaigiensis* caught during the north-east (NEM) and south-east monsoons (SEM) at reef sites with different levels of protection in coastal Kenya.

Sites	NEM			SEM			Total
	M	F	Immature	M	F	Immature	
Malindi Marine Park	39	27	0	87	28	0	181
Watamu Marine Park	34	12	1	48	29	2	126
Watamu Reserve	3	5	0	7	6	0	21
Malindi Reserve	58	56	0	134	90	0	338
Kanamai	28	28	2	99	112	16	285
Vipingo	67	53	8	80	106	16	330
Overall sex ratio (M:F)	1.28:1						
χ^2	12.723						
P	0.364						

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.

Sites	Mean fecundity (oocytes)	N
Watamu MarinePark	137 669 ± 88 048	9
Malindi Marine Park	108 655 ± 64 314	14
Watamu Reserve	106 610 ± 67 289	3
Malindi Reserve	156 456 ± 99 233*	46
Vipingo (unprotected)	92 299 ± 53 647	27
Kanamai (unprotected)	77 459 ± 62 275	18
ANOVA F	3.742	
p	0.004	
df	5	

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

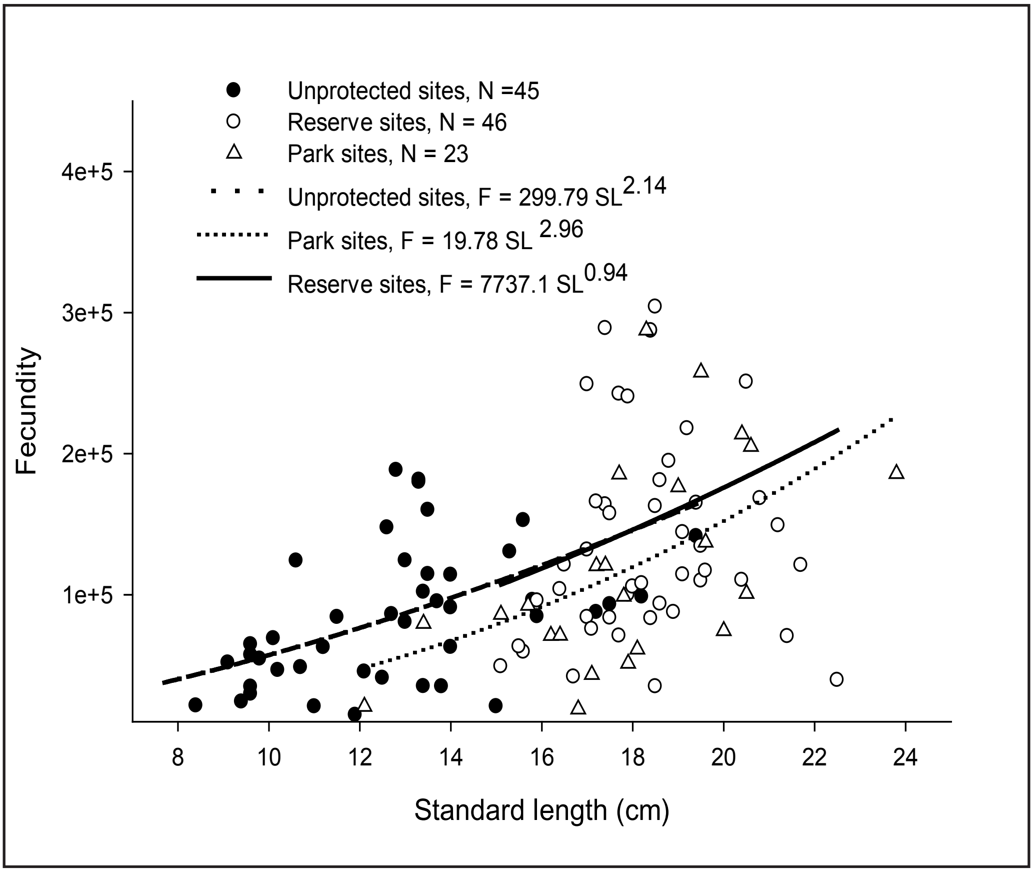

Figure 2. Relationships between fecundity (F) and standard length (SL) in *Leptoscarus vaigiensis* at reef sites with different levels of protection in coastal Kenya. N denotes number of ovaries examined at sites.

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.

Source	*SS*	*df*	*MS*	*F*	*P*
Corrected model	2.519E11	11	2.290E10	4.173	0.000
Sites	1.388E10	5	2.776E9	0.506	0.771
SL	4.048E10	1	4.048E10	7.376	0.008
Sites×SL	1.174E10	5	2.347E9	0.428	0.828
Error	5.763E11	105	5.488E9		

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

Sites		Mean size (mm)	Modal size (mm)	Size range (mm)	N
Kanamai		0.17 ± 0.07	0.20	0.06-0.28	1 209
Vipingo		0.19 ± 0.06	0.20	0.10-0.28	632
Malindi Marine Park		0.23 ± 0.08	0.20	0.10-0.36	3 363
Malindi Reserve		0.19 ± 0.07	0.20	0.08-0.30	14 714
Watamu Marine Park		0.18 ± 0.07	0.20	0.08-0.28	2 295
Watamu Reserve		0.18 ± 0.07	0.20	0.08-0.28	537
ANOVA	F	1.147			
	p	0.345			
	df	5			

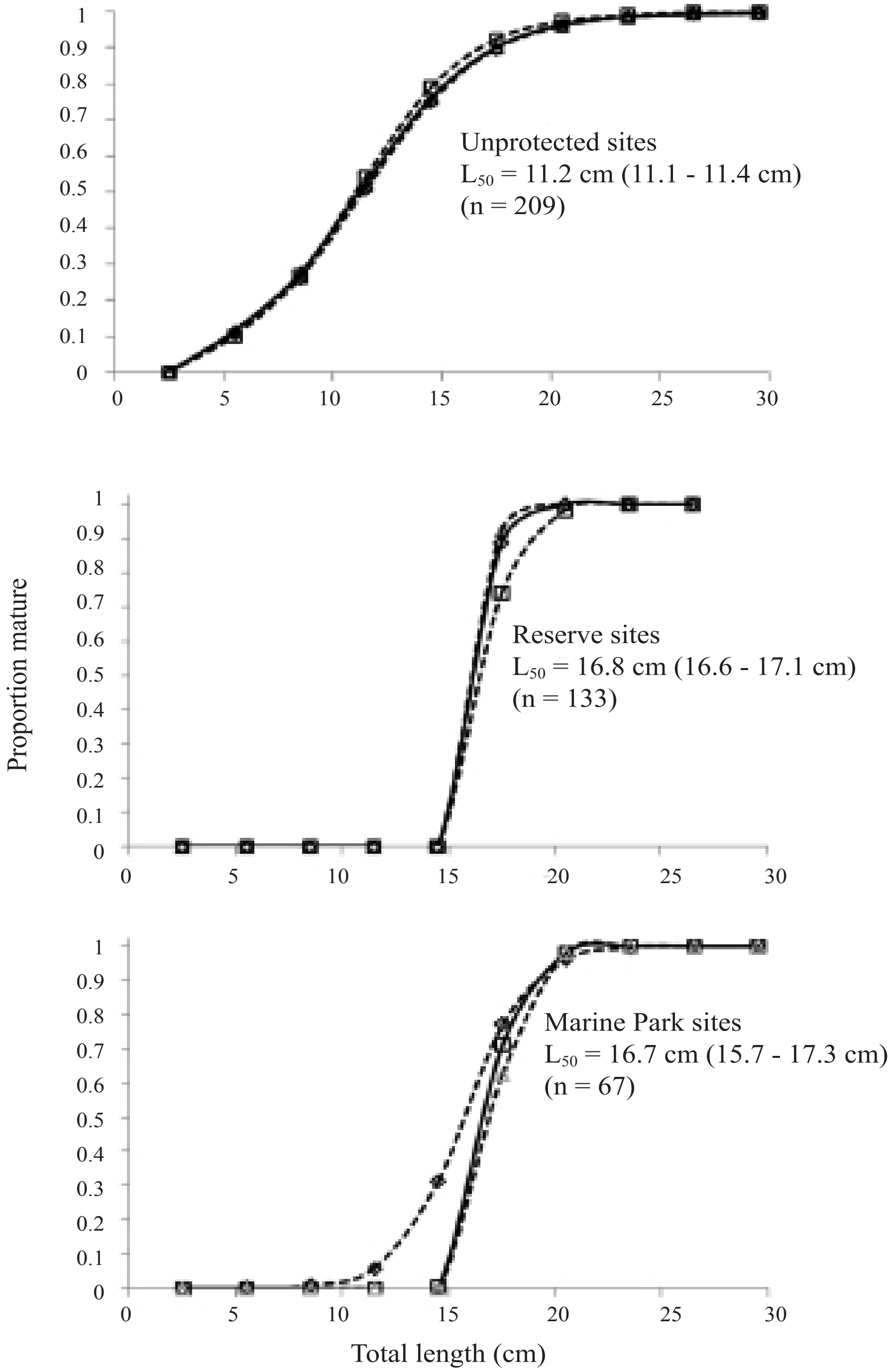

Figure 3. Length at first maturity ogives (solid lines) of female *Leptoscarus vaigiensis* caught at sites with different levels of protection in coastal Kenya; confidence intervals of the estimates are given in parentheses. The dashed lines represent the 95% confidence intervals for lengths at first sexual maturity (L_{50}).

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_{50})

A comparison of the estimates of length at first maturity (L_{50}) indicated that the lowest L50 for female *L. vaigiensis* occurred at unprotected sites (mean 11.2 cm, range 11.1-11.4 cm, 95% CI), whereas the highest L_{50} occurred at reserve sites (mean 16.8 cm, range 16.6-17.1 cm, 95% CI; Fig. 3). The L_{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.

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References

Bagenal TB (1978) Aspects of fish fecundity. In: Gerking SD (ed) Ecology of freshwater fish production. 3rd edition. FBA Windermere Laboratory, Ambleside, UK, pp 75-101

Candolin U (2009) Population responses to anthropogenic disturbance: Lessons from three-spined sticklebacks *Gasterosteus aculeatus* in eutrophic habitats. Journal of Fish Biology 75: 2108-2121

Dieckmann U, Heino M (2007) Probabilistic maturation reaction norms: Their history, strengths, and limitations. Marine Ecology Progress Series 225: 253-269

Efron B, Tibshirani RJ (1993) An introduction to the bootstrap. Chapman & Hall, New York, USA, 436 pp

Einum S, Fleming IA (2000) Highly fecund mothers sacrifice offspring survival to maximize fitness. Nature 405: 565-567

Gomes JL, Monteiro LR (2007) Size and fecundity variation in populations of *Poecilia vivipara* Block & Schneider (Teleostei; Poeciliidae) inhabiting an environmental gradient. Journal of Fish Biology 71: 1799-1809

Haug R, Tjemsland J (1986) Changes in size- and age-distributions and age at sexual maturity in Atlantic halibut, *Hippoglossus hippoglossus*, caught in North Norwegian waters. Fisheries Research 4: 145-155

Heath DD, Hearh JW, Bryden CA, Johnson RM, Fox CW (2003) Rapid evolution of egg size in captive salmon. Science 299: 1738-1740

Heino M, Godo O (2002) Estimating reaction norms for age and size at maturation with reconstructed immature size distributions: A new technique illustrated by application to Northeast Arctic cod. ICES Journal of Marine Science 59: 562-575

Hicks CC, McClanahan TR (2012) Assessing gear modification needed to optimize yields in heavily exploited, multi-species, seagrass and coral reef fishery. PLoS One 7: e36022. doi:10.1371/journal.pone.003602236022

Hutchings J, Baum J (2005) Measuring marine fish biodiversity: Temporal changes in abundance, life history and demography. Philosophical Transactions of the Royal Society B: Biological Sciences 360: 315-338

Jennings S, Kaiser MJ (1998) The effects of fishing on marine ecosystems. Advances in Marine Biology 68: 201-352

Jennings S, Reynolds JD, Mills SC (1998) Life history correlates of responses to fisheries exploitation. Proceedings of the Royal Society of London B 265: 333-339

Jennings MJ, Phillips DP (1992) Reproductive investment and somatic growth rates in longear sunfish. Environmental Biology of Fishes 35: 257-271

Kaunda-Arara B, Rose GA (2006) Growth and survival rates of exploited coral reef fishes in Kenyan marine parks derived from tagging and length–frequency data. Western Indian Ocean Journal of Marine Science 5: 17-26

Kaunda-Arara B, Rose GA (2004) Effects of marine reef national parks on fishery CPUE in coastal Kenya. Biological Conservation 118: 1-13

Kaunda-Arara B, Rose GA (2004) Out-migration of tagged fishes from marine reef National Parks to fisheries in coastal Kenya. Environmental Biology of Fishes 70: 363-372

Kaunda-Arara B, Ntiba MJ (1997) The reproductive biology of *Lutjanus fulviflamma* (Forsskål, 1775) (Pisces: Lutjanidae) in Kenyan inshore marine waters. Hydrobiologia 353: 153-160

King M (1995) Fisheries biology, assessment and management. Fishing News Books, Blackwell Science, Oxford, UK, 342 pp

Kuparinen A, Merila J (2007) Detecting and managing fisheries-induced evolution. Trends in Ecology and Evolution 22: 652-659

Law R (2000) Fishing, selection, and phenotypic evolution. ICES Journal of Marine Science 57: 659-668

Law R, Grey DR (1989) Evolution of yields from populations with age-specific cropping. Evolutionary Ecology 3: 343-359

Marteinsdóttir G, Pardoe H (2008) Effects of fishing on inter and intra stock diversity of Marine resources. Fisheries for Global Welfare and Environment, Memorial book of the 5th World Fisheries congress. Terrapub, Tokyo, Japan, pp 27-43

McClanahan TR (1988) Seasonality in East Africa's coastal waters. Marine Ecology Progress Series 44: 191-199

McClanahan TR, Kaunda-Arara B (1996) Fishery recovery in a coral-reef marine park and its effect on the adjacent fishery. Conservation Biology 10: 1187-1199

McClanahan TR, Obura D (1995) Status of Kenyan coral reefs. Coastal Management 23: 57-76

Morita K, Morita S (2002) Rule of age and size at maturity. Individual variation in the maturation history of resident white-spotted charr. Journal of Fish Biology 61: 1230- 1238

Mumby, PJ (2006) The impact of exploiting grazers (Scaridae) on the dynamics of Caribbean coral reefs. Ecological Applications 16: 747-769

Olsen EM, Heino M, Lilly GR, Morgan MJ, Brattey J, Ernande B, Dieckmann U (2004) Maturation trends indicative of rapid evolution preceded the collapse of northern cod. Nature 428: 932-935

Pitcher TJ, Hart PJ (1993) Fisheries Ecology. Chapman and Hall, UK, 414 pp

Policansky D (1993) Fishing as a cause of evolution in fishes. In Stokes T, McGlade J, Law R (eds) The Exploitation of Evolving Resources, Springer-Verlag, Berlin, pp 8-18

Raventos N, Macpherson E (2005) Effect of pelagic larval growth and size-at-hatching on post-settlement survivorship in two temperate labrid fish of the genus *Symphodus*. Marine Ecology Progress Series 285: 205-211

Rijnsdorp AD (1993) Fisheries as a large-scale experiment on life-history evolution: disentangling phenotypic and genetic effects in changes in maturation and reproduction of North Sea plaice, *Pleuronectes platessa* L. Oecologia 96: 391-401

Sale PF (2002) The ecology of fishes on coral reefs: What has the last decade taught us? Fisheries Science 1: 113-118

Sharpe DM, Hendry AP (2009) Life history change in commercially exploited fish stocks: An analysis of trends among studies. Evolutionary Applications 2: 260-275

Taylor L, Stefa´nsson G (1999) Growth and maturation of haddock (*Melanogrammus aeglefinus*) in Icelandic waters. Journal of Northwest Atlantic Fisheries Sciences 25: 101-114

Trippel EA (1995) Age at maturity as a stress indicator in fisheries. BioScience 45: 759-771

Tomkiewicz J, Morgan MJ, Burnett J, Saborido-Rey F (2003) Available information for estimating reproductive potential of Northwest Atlantic groundfish stocks. Journal of Northwest Atlantic Fisheries Sciences 33: 55-70

Wilson SK, Fisher R, Pratchett MS, Graham NA, Dulvy NK, Turner RA, Cakacaka A, Polunin NV (2010) Habitat degradation and fishing effects on the size structure of coral reef communities. Ecological Applications 20: 442-451

Zar JH (1999) Biostatistical analysis, 4th ed. Prentice-Hall, Upper Saddle River, New Jersey, 662 pp

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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

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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 km^2). D'Arros Island is a small sand cay located on the Amirantes Bank (depth range 10-60 m; area ~3 500 km^2). 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:

$$\%\ \text{occurrence of species x} = \frac{\text{number of samples in which species x occurred}}{\text{total number of samples}} * 100$$

$$\%\ \text{weight of species x} = \frac{\text{combined weight of species x in the samples}}{\text{total weight of all samples}} * 100$$

$$\text{IRI of species x} = \frac{\%\ \text{occurrence} * \%\ \text{weight}}{100}$$

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.

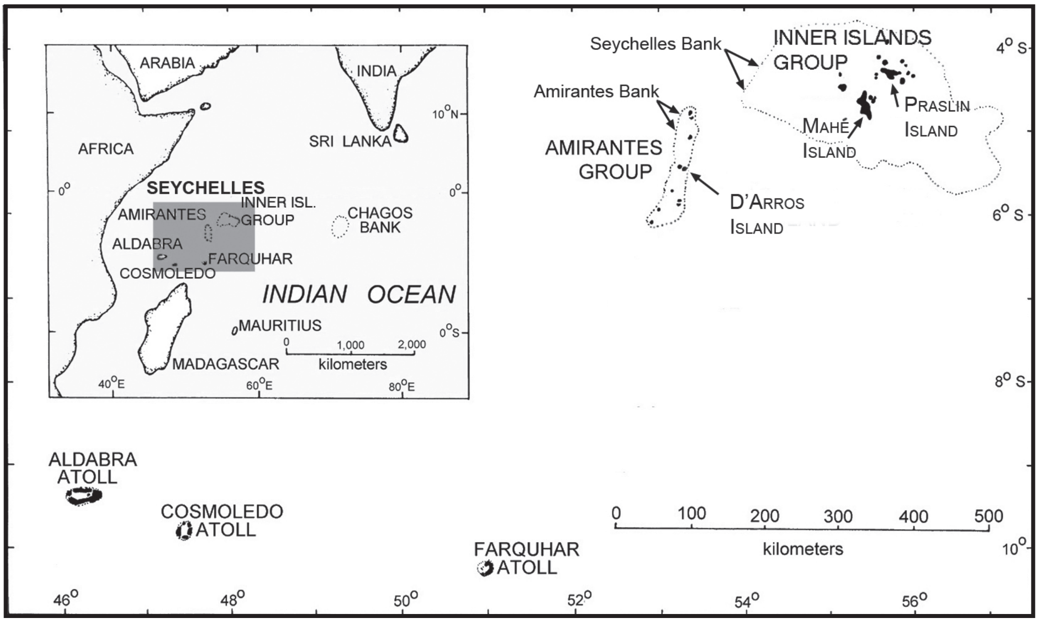

Figure 1. Map of Seychelles indicating locations where hawksbill diet samples were collected.

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:

$$\text{IRI} = \frac{\text{number of feeding events in which species x was ingested}}{\text{total number of feeding events}} * 100$$

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 Ascidiacea) 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 hemprichi* 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

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.

Kingdom	Phylum	Class	Order	Family	Genus	Species	Inner Islands	D'Arros Island		Aldabra Atoll		Cosmo.	Farqu.
Diet determination method (G = Gut contents; L = Oesophageal lavage; I = In-water observation)							G n=17	L n=20	I n=501	L n=19	G n=1	G n=26	G n=2
Animalia	Chordata	Ascidiaceae	-	-	-	-	<1					<1	9
	Cnidaria	Anthozoa	Alcyonacea	Alcyoniidae	*Dendronephthya*	-			<1				
			Corallimorpharia	Discosomatidae	*Discosoma*	-			3				
			Scleractinia	Caryophylliidae	*Physogyra*	*lichtensteinii*			<1				
			Zoantharia	Zoanthidae	*Zoanthus*	*sansibaricus*		24		<1			29
	Mollusca	Gastropoda	Neotaenioglossa	Ranellidae	*Charonia*	-						<1	
	Porifera	Demospongiae	Astrophorida	Ancorinidae	*Ecionemia*	*acervus*				3		10	
					Rhabdastrella	*rowi*	<1						
					Stelletta	-	17		45	<1	48	2	
			Chondrosida	Chondrillidae	*Chondrilla*	*australiensis*	12		6				
					Chondrosia	-	5						
			Hadromerida	Suberitidae	*Aaptos*	*suberitoides*	<1						9
				Clionaidae	*Spheciospongia*	-		43		13	23	23	
				Tethyidae	*Tethya*	-	10					<1	
			Haplosclerida	Chalinidae	*Haliclona*	*cymaeformis*	<1			<1		6	
			Verongida	Pseudoceratinidae	*Pseudoceratina*	*purpurea*			13				
Plantae	Magnoliophyta	Monocotyledon	Hydrocharitales	Hydrocharitaceae	*Thalassia*	*hemprichii*	<1	<1		1		1	3
	Phaeophyta	Phaeophyceae	Fucales	Sargassaceae	*Turbinaria*	-	2			<1			
	Rhodophyta	Florideophyceae	Gigartinales	Solieraceae	*Eucheuma*	*denticulatum*		<1		<1		<1	
				Cystocloniaceae	*Hypnea*	*cornuta*	<1			17	29	<1	

= 7.8) and turtles consumed 0-3 diet species per feeding event. 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.

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).

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; Acevedo, 1984; Meylan, 1988; Vicente & Carballeira, 1992; Vincente 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 (*Stelletta*, *Rhabdastrella*, *Haliclona* 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 lichtensteinii* (bubble coral) and *Dendronephthya* sp. (thistle coral). Obura *et al*. (2010) observed hawksbill turtles eating *P. lichtensteinii* 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 respectively). Irrespective 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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References

Acevedo M (1984) Alimentación de tres especies de quelonios marinos en la plataforma suroccidental De Cuba. Revista De Investigaciones Marinas 5: 29-35

Alcala AC (1980) Observations on the ecology of the pacific hawksbill turtle in the central visayas, Philippines. Fisheries Research Journal of The Philippines 5: 42-52

Allen GR, Steene R (1996) Indo-Pacific coral reef guide. Tropical Reef Research, Singapore, 401 pp

Anderes BL, Uchida I (1994) Study of hawksbill turtle (*Eretmochelys imbricata*) stomach content in Cuban waters. In: Study of the hawksbill turtle in Cuba (I). Cuba: Ministry Of Fishing Industry, pp 27-40

Balazs GH (1978) A hawksbill in Kaneohe Bay, Ohau. Elapaio 38: 128

Balazs GH (1980) Field methods for sampling the dietary components of green turtles Chelonia mydas. Herpetological Review 11: 5-6

Berube M, Dunbar SG, Rützler K, Hayes WK (2012) Home range and foraging ecology of juvenile hawksbill sea turtles (*Eretmochelys imbricata*) on inshore reefs of Honduras. Chelonian Conservation and Biology 11: 33-43

Bjorndal KA (1997) Foraging ecology and nutrition in sea turtles. In: Lutz PL, Musick JA (eds) The biology of sea turtles. CRC Press, Boca Raton, pp 199-231

Bjorndal KA, Jackson JBC (2003) Roles of sea turtles in marine ecosystems: Reconstructing the past. In: Lutz PL, Musick JA, Wyneken J (eds) The biology of sea turtles. CRC Press, Boca Raton, pp 259-273

Blumenthal JM, Austin TJ, Bell CDL, Bothwell JB, Broderick AC, Ebanks-Petrie G, Gibb JA, Luke KE, Olynik JR, Orr MF, Solomon JL, Godley BJ (2009) Ecology of hawksbill turtles *Eretmochelys imbricata* on a western Caribbean foraging ground. Chelonian Conservation and Biology 8: 1-10

Booth J, Peters JA (1972) Behavioural studies on the green turtle (*Chelonia mydas*) in the sea. Animal Behaviour 20: 808-812

Carr AF (1952) Handbook of turtles. New York, Cornell University Press, 321 pp

Carr AF, Caldwell DK (1956) The ecology and migration of sea turtles. Results of field work in Florida, 1955. American Museum Novitates 1793: 1-23

Carr AF, Stancyk S (1975) Observations on the ecology and survival outlook of the hawksbill turtle. Biology Conservation 8: 161-172

Debelius H (2001) Indian Ocean reef guide. Frankfurt, Ikan Unterwasser-Archiv, 205 pp

Den Hartog JC (1980) Notes on the food of sea turtles: *Eretmochelys imbricata* and *Dermochelys coriacea*. Netherlands Journal of Zoology 30: 595

Dunbar SG, Salinas L, Stevenson L (2008) In-water observations of recently released juvenile hawksbills (*Eretmochelys imbricata*). Marine Turtle Newsletter 121: 5-9

Flores EC, Liceaga-Correa MA, Garduno-Andrade M (2003) Mapping and characterizing foraging habitat of immature hawksbill turtles in front of the Ria Lagartos Biosphere Reserve, Yucatan, Mexico. In: Pilcher NJ (ed) Proceedings of the 23rd annual symposium on marine turtle biology and conservation. NOAA Technical Memorandum NMFS-SEFSC-536: 178-181

Forbes GA (1999) Diet sampling and diet component analysis. In: Eckert KL, Bjorndal KA Abreu-Grobois FA, Donnelly M (eds) Research and management techniques for the conservation of sea turtles. 4th Pub. IUCN/SSC Marine Turtle Specialist Group, pp 144-148

Forbes GA, Limpus CJ (1993) A non-lethal method for retrieving stomach contents from sea turtles. Wildlife Research 20: 339-343

Frazier J (1985) Marine turtles in the Comores Archipelago. Verhandeling Der Koninklijke Nederlandse Akademie Van Wetenschappen. Afdeling Natuurkunde 2: 84

Gosliner TM, Behrens DW, Williams GC (1996) Coral reef animals of the indo-pacific. Sea Challengers, Monterey, California, 609 pp

Green D (1996) Sea turtles of north Yemen. In: Keinath JA, Barnard DE, Musick JA, Bell BA (eds) Proceedings of the 15th annual symposium on sea turtle biology and conservation. NOAA Technical Memorandum NMFS-SEFSC-387: 116-118

Hill MS (1998) Spongivory on Caribbean reefs releases corals from competition with sponges. Oecologia 117: 143-150

Hooker SK, Baird RW (2001) Diving and ranging behaviour of odontocetes: A methodological review and critique. Mammal Review 31: 81-105

Hooper JNA, Van Soest RWM (2002) Systema Porifera: A guide to the classification of sponges. Kluwer Academic / Plenum Publishers, New York, 1810 pp

Houghton JDR, Callows MJ, Hays GC (2000) Sea turtle diving and foraging behaviour around the Greek island of Kefalonia. Journal of the Marine Biological Association UK 80: 761-762

Houghton JDR, Callows MJ, Hays GC (2003) Habitat utilisation by juvenile turtles (*Eretmochelys imbricata*) around a shallow water coral reef. Journal of Natural History 37: 1269-1280

Lazara B, Anderes A (1998) Hawksbill turtle feeding habits in Cuban waters. In: Abreu-Grobois FA, Briseño-Dueñas R, Márquez-Millán R, Sarti-Martínez L (eds) Proceedings of 18th annual symposium on marine turtle biology and conservation. NOAA Technical Memorandum MFS-SEFSC-436: 65-66

León YM, Bjorndal KA (2002) Selective feeding in the hawksbill turtle, an important predator in coral reef ecosystems. Marine Ecology Progressive Series 245: 249-258

León YM, Diez CE (1999) Population structure of hawksbill turtles on a foraging ground in the Dominican Republic. Chelonian Conservation and Biology 3: 230-236

Limpus CJ (1992) The hawksbill turtle (*Eretmochelys imbricata*) in Queensland: Population structure within a southern Great Barrier Reef feeding ground. Wildlife Research 19: 489-506

Limpus CJ, Reed PC (1985) The green turtle (*Chelonia mydas*) in Queensland: A preliminary description of the population structure on a coral reef feeding ground. In: Grigg G, Shine R, Ehmann H (eds) Biology of Australasian frogs and reptiles. Sydney: Royal Zoological Society of New South Wales, pp 47-52

Martinez C, Fallabrino A, Carrillo D, Escudero A, Guada H (2002) Analysis of stomach contents of a hawksbill turtle entangled in a net in the Peninsula De Paria, Sucre State, Venezuela. Poster Presentation: Feeding and growth. In: Seminoff JA (eds) Proceedings of the 22nd annual symposium on sea turtle biology and conservation. NOAA Technical Memorandum NMFS-SEFSC-503: 203-204

Mayor PA, Phillips B, Hillis-Star Z (1998) Results of the stomach content analysis on the juvenile hawksbill turtles of Buck Island Reef National Monument, U.S. Virgin Islands. In: Sheryan P. Epperly SP, Braun J (eds) Proceedings of the 17th annual symposium on marine turtle biology and conservation. NOAA Technical Memorandum NMFS-SEFSC-415: 244-246

Meylan AB (1988) Spongivory in hawksbill turtles: A diet of glass. Science 239: 393-395

Mortimer JA (1984) Marine turtles in the Republic of Seychelles: Status and management. Publication of the IUCN Conservation Library: Gland, Switzerland, 80 pp

Mortimer JA (2000) Conservation of hawksbill turtles (*Eretmochelys imbricata*) in the Republic of Seychelles. In: Pilcher N, Ismail G. (eds) Sea Turtles of the Indo-Pacific: Research management and conservation. Proceedings of the second ASEAN symposium and workshop on sea turtle biology and conservation. ASEAN Academic Press Ltd, London, 361 pp

Mortimer JA (2006) Simple, yet effective: Protection at the nesting beach. SWoT State of the World's Sea Turtles Report, 1: 8

Mortimer JA, Balazs GH (1999) Post-nesting migrations of hawksbill turtles in the Granitic Seychelles and implications for conservation. In: Kalb H, Wibbels T (eds). Proceedings of the 19th annual symposium on sea turtle biology and conservation. NOAA Technical Memorandum NMFS-SEFSC-443: 22-26

Mortimer JA, Bresson R (1999) Temporal distribution and periodicity in hawksbill turtles (*Eretmochelys imbricata*) nesting at Cousin Island, Republic of Seychelles, 1971-1997. Chelonian Conservation and Biology 3: 318-325

Mortimer JA, Donnelly M (2008) Marine turtle specialist group IUCN red list status assessment: Hawksbill turtle (*Eretmochelys imbricata*). Available at: http://www.iucnredlist.org/documents/attach/8005.pdf

Musick JA, Limpus CJ (1997) Habitat utilization and migration in juvenile sea turtles. In: Lutz PL, Musick JA (eds) The biology of sea turtles. Boca Raton, CRC Press, pp 137-164

Obura DO, Harvey A, Young T, Eltayeb MM, von Brandis RG (2010) Hawksbill turtles as significant predators on hard coral. Coral Reefs 29: 759-759

Pemberton R, Coyne M, Musick JA, Phillips B, Hillis-Starr Z (2000) Habitat utilization of hawksbill sea turtles at Buck Island Reef National Monument: The Zoanthid question. In: Mosier M, Foley A, Brost B (eds) Proceedings of the 20th annual symposium on marine turtle biology and conservation. NOAA Technical Memorandum NMFS-SEFSC-477: 69-70

Richmond MD (2002) A field guide to the seashores of eastern Africa and the western Indian Ocean islands. 2nd Ed. Sida, Dar Es Salaam, 461 pp

Ross JP (1981) Hawksbill Turtle (*Eretmochelys imbricata*) in the Sultanate of Oman. Biological Conservation 19:99

Schofield G, Katselidis KA, Dimopoulos P, Pantis JD, Hays GC (2006) Behaviour analysis of the loggerhead sea turtle (*Caretta caretta*) from direct in-water observation. Endangered Species Research 2: 71-79

Stampar SN, Da Silva PF, Luiz OJ (2007) Predation on the zoanthid *Palythoa caribaeorum* (Anthozoa, Cnidaria) by a hawksbill turtle in south-eastern Brazil. Marine Turtle Newsletter 117: 3-5

Valeris C, Barrios-Garrido H, Montiel-Villalobos MG (2002) Analysis of the stomach and intestinal contents of a hawksbill turtle (*Eretmochelys imbricata*) captured in Porshoure, Zulia State, Venezuela. In: Seminiff JA (ed) Proceedings of the 22nd annual symposium on marine turtle biology and conservation. NOAA Technical Memorandum NMFS-SEFSC-503: 234

Van Dam RP, Diez CE (1997) Predation by hawksbill turtles on sponges at Mona Island, Puerto Rico. In: Schroeder BA (ed) Proceedings of the 8th international coral reef symposium 2: 1421-1426

Van Dam RP, Diez CE (1998) Home range of immature hawksbill turtles (*Eretmochelys imbricata*) at two Caribbean Islands. Journal of Experimental Marine Biology And Ecology 220: 15-24

Vicente VP, Carballeira NM (1992) Studies on the feeding ecology of the hawksbill turtle (*Eretmochelys imbricata*) In Puerto Rico. In: Salmon M, Wyneken J (eds) Proceedings of the 11th annual symposium on marine turtle biology and conservation. NOAA Technical Memorandum NMFS 302: 117-119

Vicente VP (1993) Spongivory in Caribbean hawksbill turtles, *Eretmochelys imbricata*: Data from stranded specimens. In: Schroeder BA, Witherington BE (eds) Proceedings of the 13th annual symposium on marine turtle biology and conservation. NOAA Technical Memorandum NMFS-SEFSC-302: 185-188

von Brandis RG (2011) Foraging ecology of hawksbill turtles at D'Arros Island, Republic Of Seychelles. Doctorate Technologiae Thesis, Tshwane University of Technology, 241 pp

von Brandis RG, Mortimer JA, Reilly BK (2010) In-water observations of the diving behaviour of immature hawksbill turtles (*Eretmochelys imbricata*) on a coral reef at D'Arros Island, Republic of Seychelles. Chelonian Conservation and Biology 9: 26-32

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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

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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})

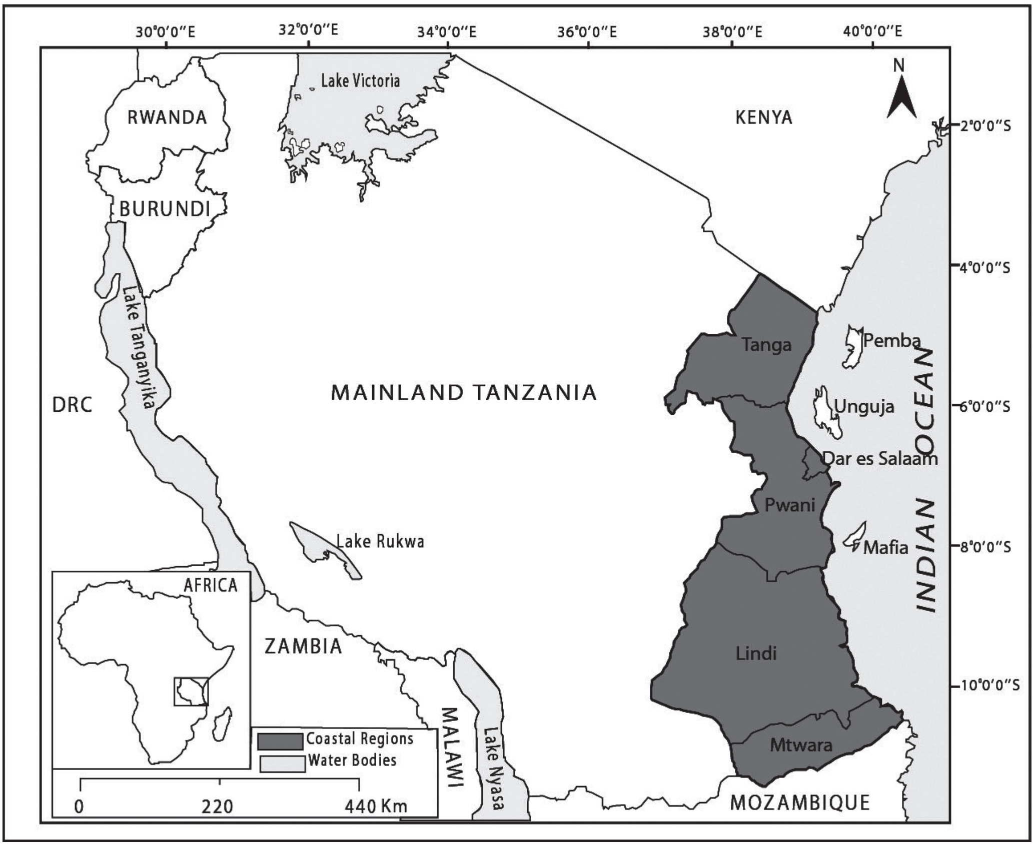

Figure 1. Map of Tanzania showing its five coastal regions: Tanga, Pwani, Dar es Salaam, Lindi and Mtwara.

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

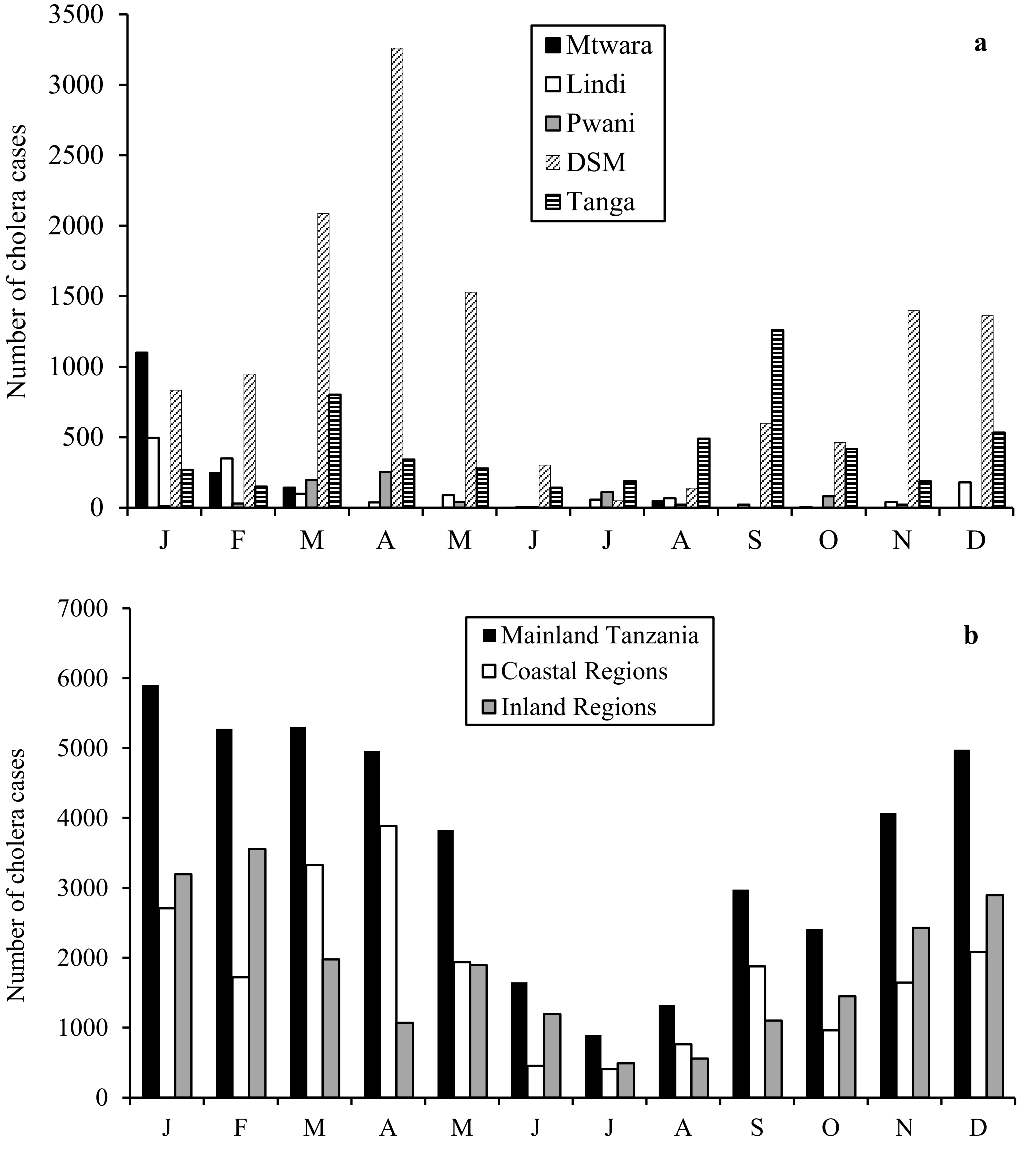

Figure 2. The total number of cholera cases during 2004-2010 in a) the coastal regions of mainland Tanzania and b) a comparison between the coastal regions and interior.

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

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).

Region	Mortality (number of deaths) and CFR (%)							Population (n)		Access to infrastructure (2006)	
	2004	2005	2006	2007	2008	2009	2010	2004 ($\times10^6$)	2010 ($\times10^6$)	Safe water	Sanitation
Dar es Salaam	4	0	101	1	1	3	18	2.64	3.118	90	81
Mtwara	2	0	1	0	0	0	3	1.17	1.324	36	66
Lindi	15	0	0	13	14	0	7	0.82	0.924	54	63
Tanga	35	48	6	11	6	35	7	1.71	1.967	59	77
Pwani	7	0	12	1	2	4	0	0.92	1.063	61	62
Coastal Regions	63	48	120	26	23	42	35	7.26	8.396	60	70
Inland Regions	179	60	134	44	27	39	60	27.6	33.52	46	60
Tanzania mainland	242	108	254	70	50	81	95	34.9	41.91	53	65
CFR	2.4	3.3	1.3	2.1	2.5	1.0	2.0	-	-	-	-

SST, (f = 2.262, p = 0.074; f = 0.083, p = 0.983 respectively). 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 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%$^+$.

Location	Variable	Lag 1	Lag 2	Lag 3	Lag 4
Dar es Salaam	SST	0.093 ± 0.062	-	-	-
Dar es Salaam	Wind	0.089 ± 0.067	-0.066 ± 0.068	-0.120 ± 0.064$^+$	-
Dar es Salaam	Chl. *a*	0.132 ± 0.063*	0.162 ± 0.066*	-	-
Tanga	SST	-	-	0.192 ± 0.098 +	-0.177 ± 0.099
Tanga	Wind	-	-0.084 ± 0.094	-	-
Tanga	Chl. *a*	-0.162 ± 0.090 +	-	-	-

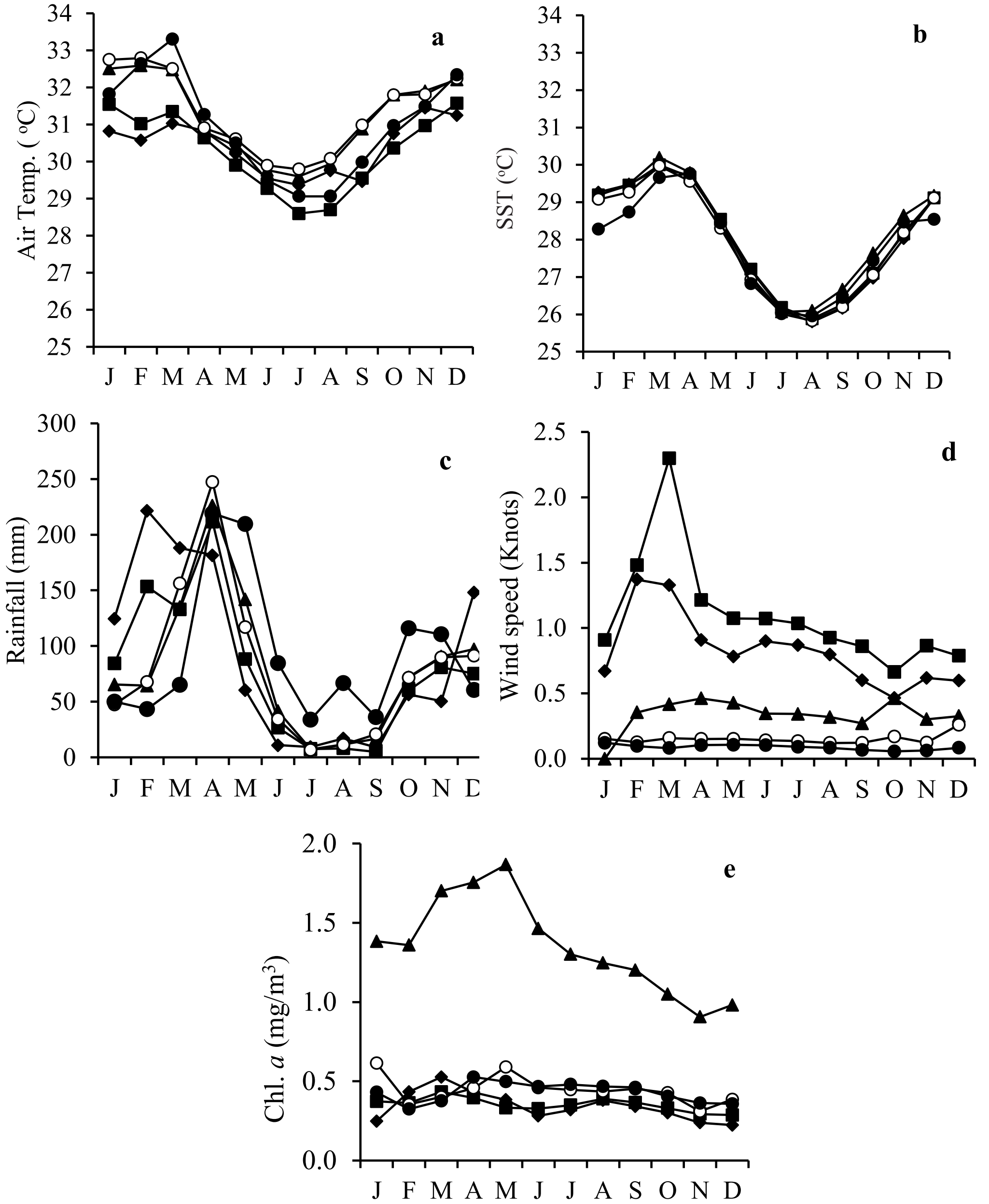

Figure 3. Average a) maximum air temperature, b) sea surface temperature, c) rainfall, d) wind speed and e) chlorophyll *a* in Mtwara (♦), Lindi (■), Pwani (▲), Dar es Salaam (○) and Tanga (●) during 2004 – 2010.

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 ± 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

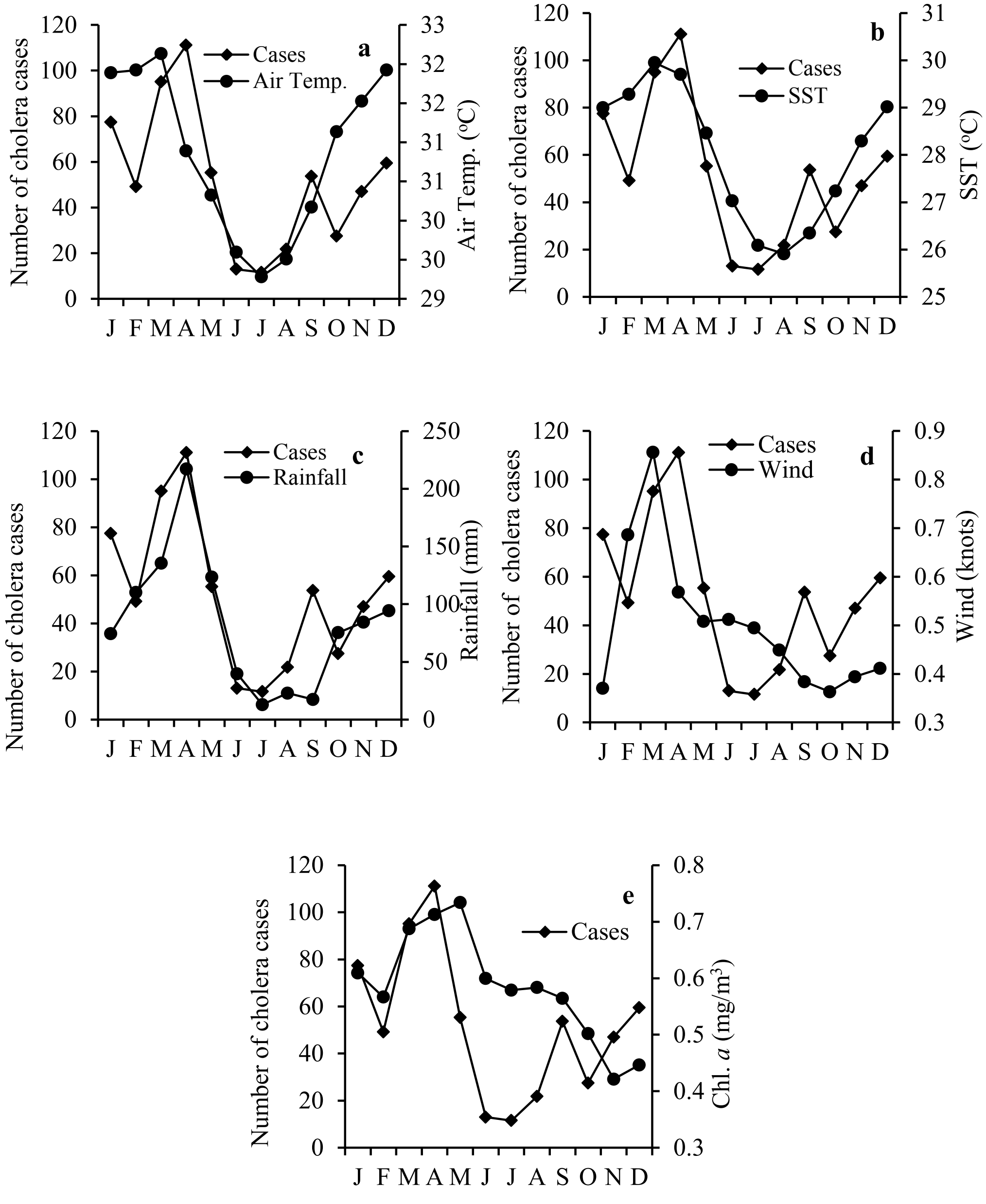

Figure 4. Co-variation between monthly (2004 – 2010) average number of cholera cases in the five Tanzanian coastal regions relative to a) air temperature, b) sea surface temperature, c) rainfall, d) wind speed and e) chlorophyll a concentration.

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.

Location	Lag 3	Lag 4	Lag 5	Lag 6
Dar es Salaam	-	-0.061 ± 0.096	-0.179 ± 0.121	-0.025 ± 0.1
Tanga	-0.146 ±0.135	0.203 ± 0.179	-0.042 ± 0.140	-

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 macro-scale 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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References

Ackers ML, Quick RE, Drasbek CJ, Hutwagner L, Tauxe RV (1998) Are there national risk factors for epidemic cholera? The correlation between socioeconomic and demographic indices and cholera incidence in Latin America. International Journal of Epidemiology 27: 330-334

Akanda AS, Jutla AS, Alam M, de Magny GC, Siddique AK, Sack RB, Huq A, Colwell RR, Islam S (2011) Hydroclimatic influences on seasonal and spatial cholera transmission cycles: Implications for public health intervention in the Bengal Delta, Water Resource Research 47, W00H07

Box G, Jenkins G (1970) Time series analysis: Forecasting and control. Holden-Day, San Francisco, USA, 575 pp

Colwell RR, Seidler RJ, Kaper J, Joseph SW, Garges S, Lockman H, Maneval D, Bradford H, Roberts N, Remmers E, Huq I, Huq A (1981) Occurrence of *Vibrio cholerae* serotype O1 in Maryland and Louisiana estuaries. Applied Environmental Microbiology 41: 555-558

Dalusi L, Lyimo TJ, Lugomela C, Hosea KMM, Sjöling S (2015) Toxigenic *Vibrio cholerae* identified in estuaries of Tanzania using PCR techniques. FEMS Microbiology Letters, doi: 10.1093/femsle/fnv009 de Magny GC, Murtuguddeb R, Sapianob MRP, Nizamc A, Brown CW, Busalacchi AJ, Yunus M, Nair GB, Gil AI, Lanata CF, Calkins J, Manna B, Rajendran K, Bhattacharya MK, Huq A, Sack RB, Colwell RR (2008) Environmental signatures associated with cholera epidemics. Proceedings of the National Academy of Sciences of the USA 105: 17676-17681

Faruque SM, Chowdhury N, Kamruzzaman M, Dziekman M, Rahman MH, Sack DA, Nair GB, Mekalanos JJ (2004) Genetic diversity and virulence potential of environmental *Vibrio cholerae* population in a cholera-endemic area. Procedings of the National Academy of Science 101: 2123-2128

Hashizume M, Faruque ASG, Terao T, Yunus M, Streatfield K, Yamamoto T, Moji K (2011) The Indian Ocean Dipole and cholera incidence in Bangladesh: A time-series analysis. Environmental Health Perspectives 119: 239-244

Igbinosa EO, Okoh AI (2008) Emerging *Vibrio* species: An unending threat to public health in developing countries. Research in Microbiology 159: 495-506

Jutla AS, Akanda AS, Griffiths JK, Colwell R, Islam S (2011) Warming oceans, phytoplankton, and river discharge: Implications for cholera outbreaks. American Journal of Tropical Medicine and Hygiene 85: 303-308

Karunasagar I, Rivera I, Joseph B, Kennedy B, Shetty VR, Huq A, Karunasagar I, Colwell RR (2003) OmpU genes in non-toxigenic *Vibrio cholerae* associated with aquaculture. Journal of Applied Microbiology 95: 338-343

Koelle K, Xavier Rodó X, Pascual M, Yunus M, Mostafa G (2005) Refractory periods and climate forcing in cholera dynamics. Nature 436: 696-700

Ljung L (1999) System identification: Theory for the user. PTR Prentice-Hall, Upper Saddle River, New Jersey, USA, 238 pp

Lugomela C, Lyimo TJ, Bryceson I, Semesi AK, Bergman B (2002) *Trichodesmium* in coastal waters of Tanzania: diversity, seasonality, nitrogen and carbon fixation. Hydrobiologia 477: 1-13

Luo JJ, Masson S, Behera S, Yamagata T (2007) Experimental forecasts of the Indian Ocean dipole using a coupled OAGCM. Journal of Climate 20: 2178-2190

McMichael AWR, Hales S (2006) Climate change and human health: present and future risks. Lancet 367: 859-869

Meibom K, Blokesch M, Dolganov NA, Wu CY, Schoolnik GK (2005) Chitin induces natural competence in *Vibrio cholerae*. Science 310: 1824-1827

Mhalu FS, Mtango FD, Msengi AE (1984) Hospital outbreaks of cholera transmitted through close person-to-person contact. Lancet 2: 82-84

Nelson EJ, Harris JB, Morris JG, Calderwood SB, Camili A (2009) Cholera transmission: The host, pathogen and bacteriophage dynamic. Nature Reviews 7: 693-702

Nkoko DB, Giraudoux P, Plisnier PD, Tinda AM, Piarroux M, Sudre B, Horion S, Tamfum JJM, Ilunga BK, Piarroux R (2011) Dynamics of cholera outbreaks in Great Lakes Region of Africa, 1978–2008. Emerging Infectious Diseases, Vol. 17, No. 11, http://dx.doi.org/10.3201

Olago D, Marshall M, Wandiga SO, Opondo M, Yanda PZ, Kanalawe R, Githeko AK, Downs T, Opere A, Kavumvuli R, Kirumira E, Ogallo L, Mugambi P, Apindi E, Githui F, Kathuri J, Olaka L, Sigalla R, Nanyunja R, Baguma T, Achola P (2007) Climatic, socio-economic, and health factors affecting human vulnerability to cholera in the Lake Victoria basin, East Africa. Ambio 36: 350-358

Paz S, Broza M (2007) Wind direction and its linkage with *Vibrio cholerae* dissemination. Environmental Health Perspectives 115: 195-200

Reyburn R, Kim DR., Emch M, Khatib A, von Seidlein L, Ali M (2011) climate variability and the outbreaks of cholera in Zanzibar, East Africa: A time series analysis. American Journal of Tropical Medicine and Hygiene 84: 862-869

Rodo X, Pascual M, Fuchs G, Faruque ASG (2002) ENSO and cholera: a nonstationary link related to climate changes? Procedings of the National Academy of Science 99: 12901-12906

Saji NH, Goswami BN, Vinayachandran PN, Yamagata T (1999) A dipole mode in the tropical Indian Ocean. Nature 401: 360-363

Sedas VTP (2007) Influence of environmental factors on the presence of *Vibrio cholerae* in the marine environment: A climate link. Journal of Infection in Developing Countries 1: 224-241

Sow S Antonio M, Oundo JO, Mandomando I, Ramamurthy T (2011) Endemic and epidemic cholera in Africa. In: Ramamurthy T, Bhattacharya SK (eds) Epidemiological and molecular aspects on cholera. Springer Science, New York, USA, pp 31-50.

Thomas KU, Joseph N, Raveendran O, Nair S (2006) Salinity-induced survival strategy of Vibrio cholerae associated with copepods in Cochin backwaters. Marine Pollution Bulletin 52: 1425-1430

Trærup SLM, Ortiz RA, Markandya A (2011) The costs of climate change: A study of cholera in Tanzania. International Journal of Environmental Research and Public Health 8: 4386-4405

Vezzulli L, Pruzzo C, Huq A, Colwell RR (2010) Environmental reservoirs of *Vibrio cholerae* and their role in cholera. Environmental Microbiology Reports 2: 27-33

Global Task Force on Cholera Outbreak (2004) Cholera outbreak: assessing the outbreak response and improving preparedness. WHO, Geneva, Switzerland, 87 pp

WHO (2010) World Health Statistics. WHO, Geneva, Switzerland, 177 pp

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Field Note

Observations of *Acropora* Spawning in the Mozambique Channel

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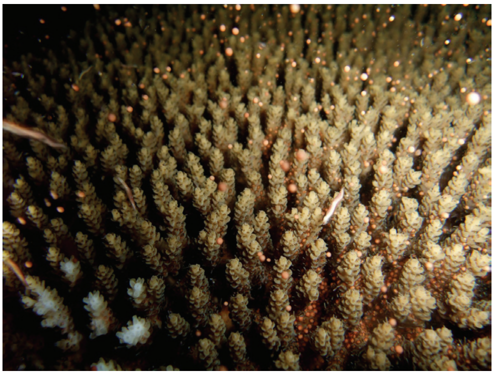

Figure 1. An *Acropora* colony spawning on 25 September 2013.

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

Harrison PL, Wallace CC (1990) Reproduction, dispersal and recruitment of scleractinian corals. In Dubinsky Z (Ed) Ecosystems of the World: Coral Reefs. Elsevier, Amsterdam, pp 133-207

Mangubhai, S. (2007) Reproduction and recruitment of scleractinian corals on equatorial reefs in Mombasa, Kenya. PhD thesis. Southern Cross University, Lismore, NSW, 283 pp

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Instructions for Authors

Editorial Policy

The Western Indian Ocean Journal of Marine Sciences is the research publication of the Western Indian Ocean Marine Science Association (WIOMSA). It publishes original research papers or other relevant information in all aspects of marine science and coastal management as articles, reviews, short communications and field notes. While submissions on tropical and subtropical waters of the western Indian Ocean and the Red Sea will be given primary consideration, articles from other regions of direct interest to the western Indian Ocean will also be considered for publication.

All manuscripts submitted to the Western Indian Ocean Journal of Marine Sciences are accepted for consideration on the understanding that their content has not been published elsewhere and is not under consideration by any other journal. Manuscripts and all illustrations should be prepared according to the instructions provided below and submitted online at http://www.ajol.info/index.php/wiojms/. Submissions will be subject to a pre-review by the Chief Editor or a member of the Editorial Board and those that fall within the remit of the journal, make a substantial contribution to the field of research, and are in the correct style and format will be sent for review. Manuscripts that do not meet these criteria will be rejected. Every manuscript will be reviewed by at least two referees competent in the field of interest. The choice of reviewers is made by the Chief Editor or the Editorial Board.

The Manuscript

1. Contributions must be written in UK English. If English is not your first language we suggest that the text is edited, before submission, by an English speaker.
2. The manuscript must be typed in Times Roman, font size 12 and double-spacing. The total number of pages, including all illustrations (graphs, tables, photos etc.), should not exceed 20 pages. Short communications must not exceed 8 pages.
3. Species names must be in italics; the genus is written in full at the first mention in the Abstract, again in the main text and the figure and table legends, and abbreviated thereafter.
4. Illustrations (figures, tables) can be placed in the text or at the end of the manuscript. Originals of all figures should be in black and white; the lettering should be of a size readable after reduction for the final layout. Legends must incorporate all the information needed and placed on the same page as the figure or table. Authors are requested to indicate the recommended position of illustrations in the left-hand margin if not placed in the text.
5. The international system of units (SI Units) must be used throughout; abbreviations and acronyms should be identified where they first appear; mathematical symbols and formulae should be used only when absolutely necessary and should be clearly defined in the text.
6. A complete manuscript must include the following: title page, abstract, keywords, introduction, materials and methods, results, discussion, acknowledgements, references, tables and illustrations (with figure legends) in that order.
    a. ***Title Page:*** This should contain a concise title and the names of authors followed by affiliations and their complete postal addresses. The contact author and email address must be indicated.
    b. ***Abstract:*** The abstract should not exceed 200 words, and should be on a separate page. It should briefly describe the main points of the manuscript, i.e. the topic, the main findings and the conclusions.
    c. ***Keywords*** - four to six key words are required for indexing purposes.

d. ***Introduction:*** A brief survey of relevant literature and objectives of the work should be given in this section. Thus, the introduction should largely be limited to the scope, purpose and rationale of the study.

e. ***Materials and Methods:*** In this section, the methodology used should be clearly explained, including relevant references, such that another person can repeat the procedures. It should provide the framework to gain answers to the questions or problems identified. Sampling methods must be elaborated as well as analytical frameworks and model specifications.

f. ***Results:*** Make the text as objective and descriptive as possible. Only material pertinent to the subject should be included. Avoid presenting the same information in both graphical and tabular form.

g. ***Discussion:*** This section could be combined with the above to present "Results and Discussion". It should interpret the results in view of the problems identified in the introduction, as well as in relation to other published work. The final paragraph of this section could include concluding remarks and recommendations for future work.

h. ***Citations:*** Authors should be cited using their surnames, followed by the year of publication. Two authors should be separated by an ampersand. If there are more than two authors, only the first author, followed by "*et al.*", should be given. This and other Latin or foreign terms should be italicized.

i. ***Acknowledgement/s:*** This section should be brief. Authors are advised to limit acknowledgements to substantial contributions to the scientific and technical aspects of the paper, financial support or improvements in the quality of the manuscript.

j. ***References:*** The reference section must contain an alphabetical list of all references mentioned in the text of the manuscript. Limit punctuation and special fonts as indicated and give all journal names in full. Examples for citations from periodicals, books and composite works are given below:

- *Periodicals*. Here the following should be sequentially listed: author's name/s, initials, year of publication, full title of paper, periodical (in full), volume, first and last page numbers.

  Examples: Richardson K, Beardall J, Raven J (1983) Adaptation of unicellular algae to irradiance: An analysis of strategies. The New Phytologist 93: 157-191

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- *Books*. The following should be listed: author's or editor's name, initials, year of publication, full title, publisher, place of publication, total pages.

  Example: Kirk TJO (1983) Light and photosynthesis in aquatic ecosystems. Cambridge University Press, Cambridge, 401 pp

- Composite works or serials. The sequence should be as above, but also should include full title of paper followed by In: editor(s) if any, full title of publication, publisher, etc., and the first and last page numbers. *Examples*: Moothien Pillay R, Terashima H, Kawasaki H, Chineah H (2006) Recovery of massive poritid corals from bleaching at Albion, Mauritius. Proceedings of 10th International Coral Reef Symposium, Okinawa, Japan, pp 617-623

  Sathyendranath S, Platt T (1993a) Remote sensing of water-column primary production. In: Li WKW, Maestrini SY (eds) Measurement of primary production from the molecular to the global Scale. ICES Marine Science Symposia, Vol. 97, Copenhagen, pp 236-243

- *Articles with a Digital Object Identifier* (DOI) *Examples*: Gooseff MN, McKnight DM, Lyons HJ, Blum RJ (2002) Weathering reactions and hyporheic exchange controls on stream water chemistry in a glacial meltwater stream in the McMurdo Dry Valleys. Water Resources Bulletin 38 [doi: 10.1029/2001WR000834]

  Guest JR, Baird AH, Maynard JA, Muttaqin E, Edwards AJ, Campbell SJ, Yewdall K, Affendi YA, Chou LM (2012) Contrasting patterns of coral bleaching susceptibility in 2010 suggest an adaptive response to thermal stress. PLoS ONE 7: e33353 [doi:10.1371/journal.pone.0033353]

k. ***Tables and illustrations:*** Each figure/table/photograph should be numbered consecutively, accompanied by a complete caption, and must be cited in the text. Figures should be of high quality to allow reproduction and reduction without loss of information. Photographs should be of excellent quality to avoid loss of contrast during printing.

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