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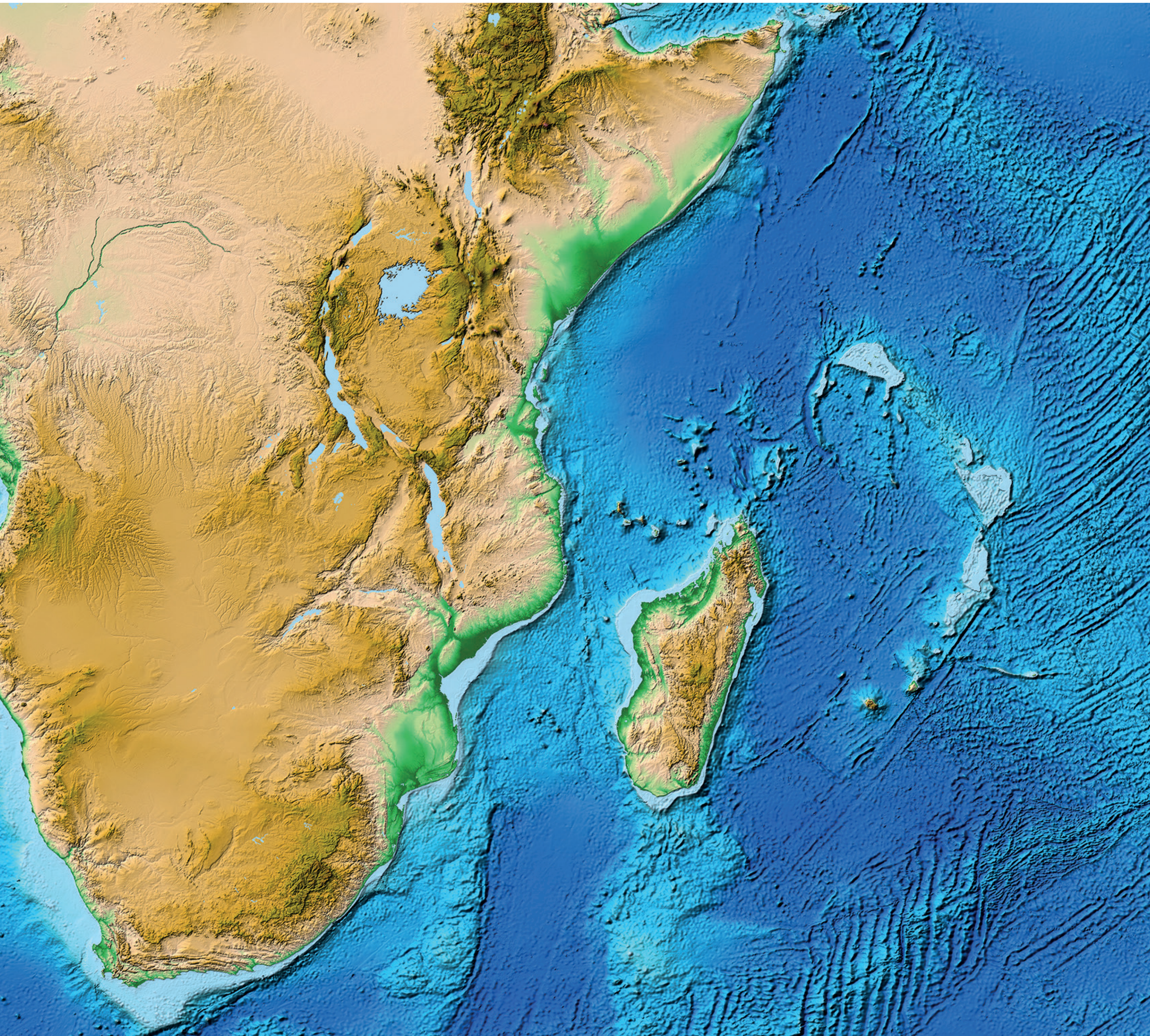

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Cover image: Relief model of the WIO surface that integrates land topography and ocean bathymetry. Amante and Eakins / National Geophysical Data Center, NOAA (2009)

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Seasonal fluctuations in photochemical efficiency of *Symbiodinium* harbored by three reef-building corals that differ in bleaching susceptibility

Leonard J. Chauka[1*], Nsajigwa E. Mbije[2], Simon J. Kangwe[3]

[1] Institute of Marine Sciences,
University of Dar es Salaam,
P. O. Box 668, Zanzibar,
Tanzania.

[2] Sokoine University of Agriculture,
Faculty of Forestry and Nature
Conservation, P.O. Box 3073,
Morogoro, Tanzania.

[3] Tanzania Fisheries Research
Institute, Dar es Salaam centre,
P. O. Box 78850, Dar es Salaam,
Tanzania.

* Corresponding author:
leonard@ims.udsm.ac.tz

Abstract

Coral reefs are amongst the most vulnerable ecosystems to climate change. This study was conducted to evaluate the fluxes in the adaptations of reef-building corals to climate change. In order to explore this, chlorophyll *a* fluorescence, *Symbiodinium* abundance and types were monitored in nursery-reared corals for two years in three species that differ in bleaching susceptibility. The species were *Pocillopora verrucosa*, *Porites cylindrica* and *Acropora formosa.* Internal transcribed spacer two (ITS-2) region of nuclear ribosomal DNA genes (rDNA) was used in monitoring the *Symbiodinium* types associated with the studied coral species. Pulse Amplitude Modulated (PAM) fluorometry was used to determine seasonal changes in chlorophyll *a* fluorescence. In this study, it was found that *A. formosa*, *P. verrucosa* and *P. cylindrica* maintained their *Symbiodinium* types; C3u, C1h, and C15 respectively throughout the seasons. *A. formosa* and *P. verrucosa* responded significantly to seasonal fluctuation in both solar radiation and sea surface temperature by regulating their *Symbiodinium* cell density and photochemical efficiency whereas *P. cylindrica* did not. However, such seasonal fluctuations in these environmental parameters are not accompanied by acquisition of foreign *Symbiodinium* types from the environmental pool. It is concluded that seasonal fluctuations in both solar radiations and sea surface temperatures are not intense enough to effect acquisition of foreign *Symbiodinium* types by reef building corals in Zanzibar waters.

Keywords: Coral Reefs, Chlorophyll *a* fluorescence, *Symbiodinium*, PAM fluorometry, Photosynthesis, Resilience

Introduction

Coral reefs, often referred to as 'the rain forests of the ocean' (Reaka-Kudla, 1995), play a key role in the functioning of tropical coastal ecosystems by sheltering a huge diversity of sessile and free-living organisms. They are also economically important because of their ability to provide critically important goods and services to over 500 million people worldwide through fisheries and tourism industries (Moberg and Folke, 1999). The ecological success of the coral reef ecosystem is primarily driven by a mutualistic endosymbiosis between corals and photosynthetic dinoflagellates in the genus *Symbiodinium* (Muscatine, 1990). Unfortunately, the past few decades have witnessed an increase in coral bleaching events (Hoegh-Guldberg, 1999; Baker *et al*., 2004). Bleaching in this study is defined as the whitening, or paling of corals and other invertebrate taxa, resulting from the loss of symbiotic zooxantheallae and/or a reduction in photosynthetic pigment concentrations in zooxanthellae residing within scleractinian corals.

Coral bleaching has become one of the greatest threats to the survival of coral reef ecosystems (Hughes *et al*., 2003; Wilkinson, 2002; Hoegh-Guldberg, 2004). Many of the reef systems in the Western Indian Ocean region have remained severely damaged following the 1997/1998 El-Niño that caused massive coral mortality (Obura, 2005; McClanahan *et al*., 2007; Mbije *et al*., 2010). In most cases, coral bleaching events result from a sustained increase in SST (Fitt and Warner, 1995; Berkelmans and Willis, 1999; Winters *et al*., 2003;

Jokiel and Brown, 2004). Seasonal fluctuations in sea surface temperatures may result in localized seasonal bleaching events (Chen *et al.*, 2005). Such bleaching events have been accompanied with seasonal fluctuations in *Symbiodinium* cell abundance in some coral species (Fitt *et al.*, 2000, Mwaura *et al.*, 2009), photosynthetic capacities (Warner *et al.*, 2002), and change in *Symbiodinium* types (Chen *et al.*, 2005). Moreover, fluctuation in photochemical efficiency of *Symbiodinium* was found in corals that occur in higher latitudes where seasonal fluctuations in both solar radiation and SST are very high (Fitt *et al.*, 2000, Warner *et al.*, 2002). Very little is known about seasonal fluctuations in photochemical efficiency of *Symbiodinium* cells in corals in lower latitude areas closer to the equator, where seasonal fluctuation in both SST and solar radiation is low. A study by Mwaura *et al.* (2009) showed significant seasonal fluctuations in *Symbiodinium* density in most corals species growing in low latitudes environments. However, few coral species maintained their *Symbiodinium density* throughout the year (Mwaura *et al.*, 2009), although it is not known whether seasonal fluctuation in cell *density* correlates to its changes in type and photochemical efficiencies.

Coral reef monitoring programmes in Tanzania showed seasonal bleaching events to occur from February to May (Mohammed *et al.*, 2000; 2002). Based on these observations, this study aimed at establishing the relationship between the seasonal fluctuations in photosynthetic efficiency and *Symbiodinium* types hosted by young nursery-farmed coral species. To accomplish this, monitoring of *Symbiodinium* density and types, photosynthetic pigment concentration and maximum quantum yield (F_v/F_m) was monitored monthly in a mid-water coral nursery (Mbije *et al.*, 2010). *Pocillopora verrucosa*, *Porites cylindrica* and *Acropora formosa* were studied at Chumbe Island in Zanzibar, from September 2008 to August 2010.

Materials and Methods

Sampling site and experimental design

The study was conducted in Chumbe Island Marine Park (39010'32.20"E, 6016'39.67"S) (Figure 1), which was chosen as it is a no-take marine protected area thus offering a protected experimental setting. Chumbe is located about 12 km from the main Zanzibar urban area, and the coral reef sanctuary receives little land based pollution as compared to other reefs close to the city centre. Information related to solar radiation was gathered from the Zanzibar Meteorological Agency whereas SST data were obtained by converting data from temperature data loggers located below the established hanging coral nurseries. These temperature loggers were set to record at 15 minute intervals. From the 15 minute interval data, the mean daily temperature was calculated.

A. formosa, *P. verrucosa* and *P. cylindrica* were selected for this study because of their differences in bleaching susceptibilities and *Symbiodinium* types they host (Marshall and Baird, 2000). While the 1997/98 warming in East Africa resulted into massive mortality of many coral reef species, the most severely affected were the Acroporids (Wilkinson *et al.*, 1999; Lindahl *et al.*, 2001). Subsequently, many reefs have remained barren without Acroporids signifying that they are very susceptible to environmental perturbations (Garpe and Öhman, 2003). On the other hand, *Porites* has been found to be bleaching-tolerant compared to other species (Marshall and Baird, 2000; Sampayo *et al.*, 2008). The selection of the three species considered these differences and the data were collected from the established coral nursery located at Chumbe coral sanctuary. The coral nursery was established as per Shafir and Rinkevich (2010). Basically, the nurseries were situated in mid-water, above the substrate to

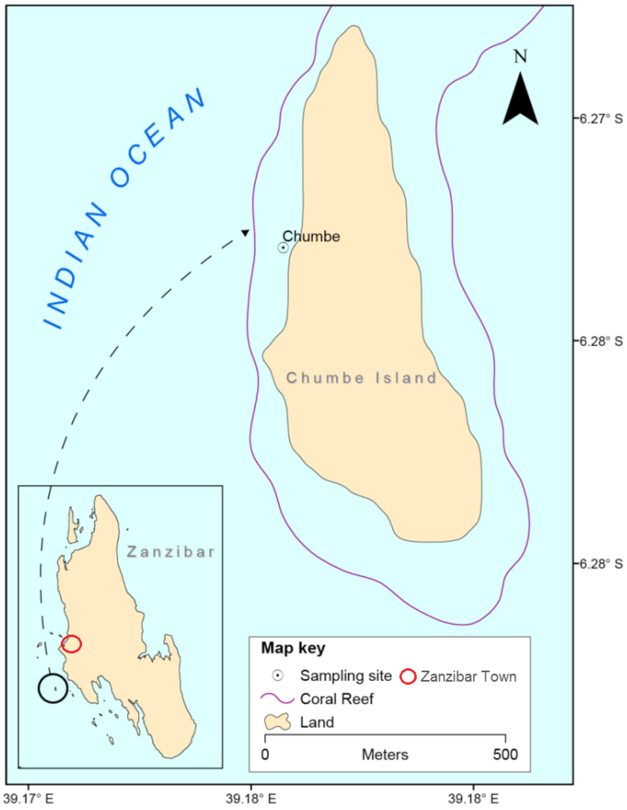

Figure 1. Map of Zanzibar (Unguja Island) showing the location of Chumbe Island Coral Park where *in-situ* experiments to investigate seasonal fluctuations in photochemical efficiency of coral species that differ in bleaching susceptibilities was conducted. [IMS base Maps]

avoid sedimentation; far from the reef to avoid corallivorous species; in an area sheltered from storms and wave action but sufficiently shallow (5 m below sea level during low tide) to provide good light conditions for fast growth and easy maintenance. The nurseries remained in place for two years from August 2008 to July 2010 with monthly monitoring surveys during the second week of each month. To make sure that all coral branches received similar solar radiation, the nursery was established at 5m depth during the lowest tide. Each coral species was represented by 200 branches.

Fluorescence measurements

In situ measurements of maximum quantum yields (F_v/F_m) were calculated for the transplants of *A. formosa*, *P. verrucosa* and *P. cylindrica* by using a diving Pulse Amplitude Modulated Fluorometer (Diving PAM, Walz, Germany) (Hoegh-Guldberg and Jones, 1999; Winters *et al.*, 2003). *In situ* chlorophyll fluorescence signatures provide insight into the daily homeostasis and stress response of the symbiotic algae (Winters *et al.*, 2003). PAM fluorometry induced chlorophyll fluorescences were measured *in vivo* in order to estimate the potential quantum yield of photosystem II during photosynthesis, a parameter that correlates with more traditional measures of photosynthetic rate such as CO_2 uptake and O_2 evolution (Beer *et al.*, 1998). During the use of the fluorometer, an opaque plastic fiber-optics holder was used to maintain equal distances between the fiber-optics tip and the coral surface (10 mm) in each sampling. In order to allow dark adaptation of coral fragments all sampling was done in the evening, about 15 minutes after sunset. According to Winters *et al.* (2003), this period is sufficient to maximize the frequency of open-reaction centres in PSII so as to record maximum quantum yield of photosystem II (F_v/F_m), where F_v = variable fluorescence and F_m = maximum fluorescence for the dark-adapted sample.

Monitoring *Symbiodinium* abundance and Chlorophyll *a* concentration

During each sampling session, small (2-3 cm) coral branches (n=5 for each species) were randomly taken for both analysis of *Symbiodinium* cell abundance and chlorophyll *a* concentration. Upon detachment, the branches were immediately put in plastic bags that were kept in a cool box at a temperature of 4-5°C ready for transportation to the Institute of Marine Science, where analysis of *Symbiodinium* abundance and chlorophyll *a* concentration was done. By using filtered seawater (0.45 µm mesh) through a water pick, coral tissues was extracted. To ensure the majority of algae and tissue were extracted, the coral fragment samples were washed until the coral skeletons were completely white. Each tissue sample was then homogenized for 30 seconds in 10 ml of filtered seawater in a blender. To separate *Symbiodinium* cells from the host tissues, the resulting slurry from homogenized tissue was centrifuged for 5 min at 6000 rpm at 4°C. After centrifugation, an aliquot containing *Symbiodinium* and another containing host tissue were obtained.

To determine the *Symbiodinium* cell density, 1 ml of *Symbiodinium*-containing aliquots were preserved with 10% formalin. Such aliquots were later loaded into a haemocytometer. *Symbiodinium* cells in 10 random quadrants in the haemocytometer were counted from each replicate (n = 5) using a light microscope at 400 X magnification. The surface area of the coral skeleton was determined by using the aluminum foil method (Naumann *et al.*, 2009). In this technique, aluminum foil was wrapped over and fitted to the surface of each coral fragment; the foil was then removed, and its area determined. Thus, *Symbiodinium* density was expressed in terms of number of cells divided by the surface area of the coral tissue estimated by using the aluminum foil method.

To determine the chlorophyll *a* concentration, 2 ml of the *Symbiodinium* -containing aliquots was re-suspended in 8 ml of 100% acetone and incubated at 2°C for 24 h for extraction of photosynthetic pigments. On the following day, the sample was centrifuged again for 10 minutes at 2000 rpm. The supernatant was transferred to a quartz cuvette and its absorbance was determined at 750, 663, 630, 480 and 510 nm using a Genesys 5 spectrophotometer™ (Spectronic Instruments, Rochester, NY, USA). The coral surface area, obtained as explained above, together with the estimated coral mass were used to determine the concentration of chlorophyll *a*. The concentration of Chl *a* ($\mu g cm^{-2}$) was calculated using equation presented by Jeffrey and Humphrey (1975):

$$[Cl\text{-}a\ (mg\ Ml^{-1})] = 11.43 * (E664 - E750) - 0.64 *(E630 - E750)$$

Where; 11.43 and 0.64 are constants, while E630, E663, and E750 are spectrophotometric readings at 630, 663 and 750, respectively.

Determination of seasonal change in *Symbiodinium* type

In order to determine whether seasonal fluctuation in photochemical efficiency can cause changes in *Symbiodinium* type as an adaptation strategy, coral fragment samples were collected and analysed during the months that differ in terms of temperature and solar radiation. The months included January 2008, April 2008, August 2008, June 2009, October 2009 and December 2009 (Table 2). Both SST and solar radiation data in Zanzibar showed the mentioned months to differ. In order to analyse the *Symbiodinium* types in the coral tissue, total DNA was extracted from the collected coral fragments using a protocol adopted from LaJeunesse *et al.* (2003). Amplification of the extracted DNA was done by targeting the ITS-2 region of ribosomal DNA (rDNA) genes as these genes have been successfully used in the analysis of *Symbiodinium* types. PCR was performed by using forward primer ITSintfor2, 5'GAATTGCAGA ACTCCGTG 3' with a GC clamp and the reverse ITSintrev2, 5' GGGATCCAT ATGCTTAAGTT CAGCGGGT 3' designed by LaJeunesse and Trench (2000). The PCR cycling conditions were as follows: denaturing step of 4 minutes at 94°C, 30 cycles at 60 seconds at 94°C, 60 seconds at 57°C, and 60 seconds at 72°C, with extension of 5 minutes at 72°C. The PCR products were checked on 1.5% agarose gels stained with ethidium bromide.

Successful PCR products were subjected to DGGE as described in Chauka (2012). All dominant bands in DGGE gel profiles were carefully cut and diluted overnight in 500 µl dH2O and re-amplified on the following day using ITS-2 with no GC clamp. The products of the re-amplified excised bands were purified using the UltraClean PCR purification Kit (Molecular Biology Laboratories, USA). Purified PCR products were sent for sequencing using the forward (ITSintfor2) or reverse (ITS2reverse) primers in separate runs at the Pennsylvania State University Science Facility. The obtained sequences were identified from the Genbank by using the Basic Local Alignment Search Tool (BLAST).

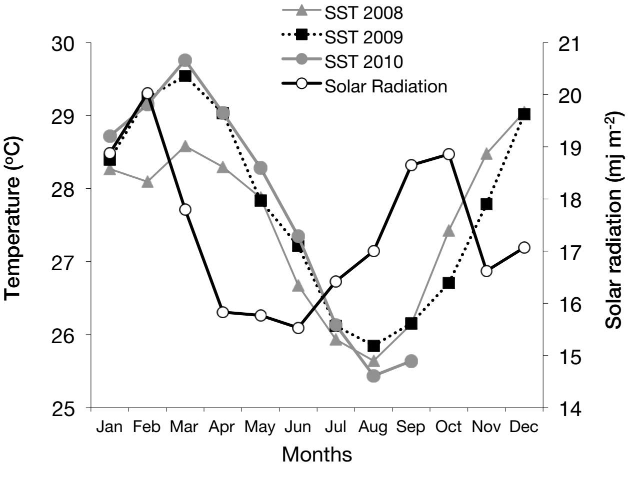

Figure 2. Mean measured sea surface temperature and solar radiation in Chumbe Island Coral Park where in-situ experiments to investigate seasonal fluctuations in photochemical efficiency of coral species that differ in bleaching susceptibilities was conducted.

Data analysis

The R – Statistic package was employed in analysis where Two-way Analysis of Variance (ANOVA) was used to examine the influence of sampling date and coral species on photosynthetic efficiencies of photosystem II of *Symbiodinium* cells. In these analyses, *Symbiodinium* density, maximum quantum yields and chlorophyll *a* concentrations were independently analysed. In addition, the Tukey HSD test was used to find specific difference among the months and species. Before analysis, the normality of data was tested.

Results

Monthly fluctuation in temperature and solar radiation

SST data presented were collected for two years (between August 2008 and September 2010). The data show monthly SST in Chumbe Island Marine Park ranged from 25.8°C in July to 30.0°C in March. Highest SST occurs during the Northeast monsoon season while the lowest occurs during the southeast monsoon season (Figure 2). The difference in SST between the two seasons is about 4°C. In addition to the measured SST, data obtained from the Tanzania Meteorological Agency shows solar radiation in Zanzibar to range from 15.5 (mj m^{-2}) in June to 20.03 (mj m^{-2}) in February (Figure 2).

Seasonal fluctuation in *Symbiodinium* density, types and photosynthetic pigments

Except in *P. cylindrica,* paling in most colonies of *P. verrucosa* and *A. formosa* were observed in March and April; probably due to decreased *Symbiodinium* densities and/or photosynthetic pigments as shown in Figure 3. In those corals colonies that exhibited signs of bleaching, paling was homogeneous, especially on the sides that were directly exposed to solar radiations. *Symbiodinium* densities ranged from 1.84 ± 0.015 million cells cm^{-2} sampled in *P. verrucosa* in April to 3.188 ± 0.021 million cells cm^{-2} sampled in *A. formosa* sampled in July (Figure 3). Chlorophyll *a* concentration ranged from 1.958 recorded in *P. verrucosa* in February to 3.313 ± 0.065422 in *A. formosa* recorded in July (Figure 3). After subjecting the data to a one-way ANOVA test, it was revealed that both chlorophyll *a* concentrations and *Symbiodinium* densities significantly fluctuated over time in all species (Table 1). However, *P. cylindrica* was less affected by seasonal fluctuation in both SST and solar radiation when compared with other species (Figure 3). A seasonal fluctuation in *Symbiodinium* types was also investigated and

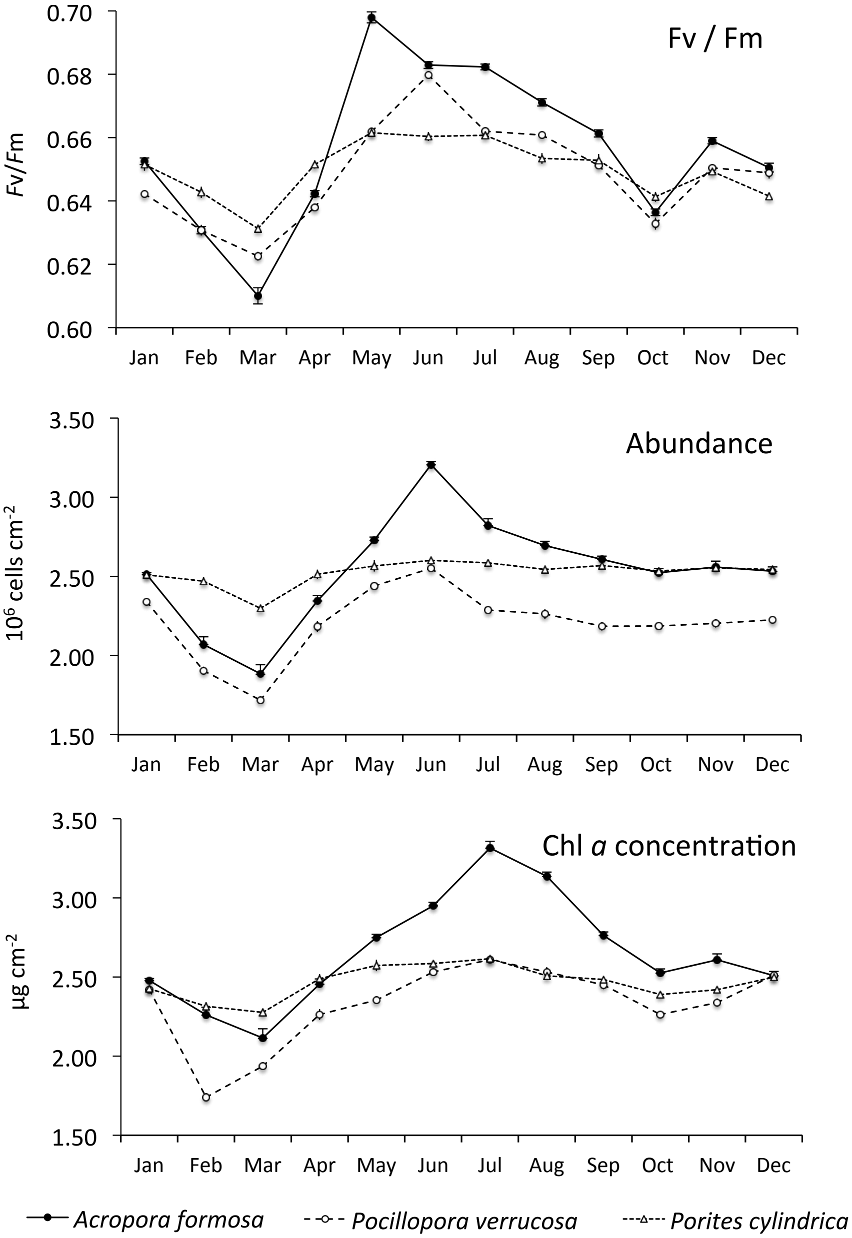

Figure 3. Seasonal variation in maximum quantum yield (F_v/F_m), zooxanthellae abundance and chlorophyll *a* concentrations in corals *Pocillopora verrucosa* (PV), *Porites cylindrica* (PC) and *Acropora formosa* (AF) found in Zanzibar reefs as recorded from September 2008 to August 2010 in coral nursery established in Chumbe Island Coral Park (±SE).

it was found that coral-*Symbiodinium* symbioses were stable throughout the year in all species (Table 2).

Seasonal fluctuation in F_v/F_m of studied coral species

Generally, maximum quantum yield as expressed in F_v/F_m fluctuated seasonally in all species (Figure 3). A mean F_v/F_m of 0.6966 ± 0.008649 was the highest recorded, in *A. formosa* in July, the coldest month when solar radiation was also relatively low compared with other months (Figure 3). Moreover, the lowest mean F_v/F_m value (0. 0.6176 ± 0.0273) was recorded in *A. formosa* in April, which was amongst the hotter months indicating the influence of temperature on photosynthetic efficiency of *Symbiodinium* harbored by corals. This has also been noted in other studies (Winters *et al*., 2003). When the data were subjected to two-way ANOVA, sampling date was found to have significant effects on F_v/F_m values (Table 1). After subjecting the data to the Tukey HSD test for specific differences, it was found that only F_v/F_m values of *A. formosa* and *P. verrucos*a were significantly affected by sampling date ($p < 0.05$). By using the same test, it was found that *P. cylindrica* was not significantly affected by sampling date ($p = 0.096375$).

Table 1. Two-way ANOVAs of photosynthetic parameters of transplants of **corals** *P. verrucosa, P. cylindrica* **and** *A. formosa* after 24 months kept in Chumbe Island Coral Park, Zanzibar.

	DF	Sum Sq	Mean Sq	F value	Pr(>F)
Fv/Fm					
Month	11	0.05238	0.004762	307.8	<2e-16 ***
Species	2	0.00265	0.001323	85.5	<2e-16 ***
Month x Species	22	0.01113	0.000506	32.7	<2e-16 ***
Residuals	180	0.00278	0.000015		
Zoozanthellae abundance					
Month	11	8.522	0.7747	189.63	<2e-16 ***
Species	2	5.078	2.5391	621.5	<2e-16 ***
Month x Species	22	2.743	0.1247	30.52	<2e-16 ***
Residuals	180	0.735	0.0041		
Chlorophyll *a* concentration					
Month	11	9.841	0.8946	387.57	<2e-16 ***
Species	2	3.863	1.9315	836.79	<2e-16 ***
Month x Species	22	3.263	0.1483	64.25	<2e-16 ***
Residuals	180	0.415	0.0023		

Table 2. Influence of seasonality on the diversity and distribution of *Symbiodinium.* The clade type is denoted by letters in uppercase; the ITS-2 DGGE fingerprint type is shown by a number followed by letters in lower case. The number of samples analysed and found to have a particular *Symbiodinium* type is shown in parenthesis.

Species / Sampling	Jan-08	Apr-08	Jun-09	Aug-08	Oct-09	Dec-09
Pocillopora verrucosa	C1h (4)	C1h (4)	C1h (4)	C1h (4)	C1h (4)	C1h (4)
Porites cylindrica	C15 (4)	C15 (4)	C15 (4)	C15 (4)	C15 (4)	C15 (4)
Acropora formosa	C3u (4)	C3u (4)	C3u (4)	C3u (4)	C3u (4)	C3u (4)

Discussion

The current observations on seasonal fluctuation in both chlorophyll *a* concentration and *Symbiodinium* densities concur with previous studies (Fitt *et al.*, 2000; Warner *et al.*, 2002; Mwaura *et al.*, 2009) in the sense that photochemical efficiencies of corals responded to seasonal change in both SST and solar radiation. However, our data deviate from the data presented by Mwaura *et al.* (2009) in that statistically significant low values of *Symbiodinium* density were recorded during the hotter months with higher solar radiation. This might be attributed to the slight differences in temperature and solar radiation patterns between Mwaura's study in Mombasa, and Zanzibar (see Mwaura *et al.*, 2009 figures compare with Figure 2). Significantly low *Symbiodinium* density and chlorophyll *a* concentrations in the hotter months with higher solar radiation in all species studied indicate that they have similar bleaching strategies (Douglas, 2003). Thus, *A. formosa*, *P. verrucosa* and *P. cylindrica* bleach by losing both *Symbiodinium* cells and/or the degradation of photosynthetic pigments. Some coral species (e.g., *Montipora capitata*) do not exhibit these characteristics as they bleach by losing only photosynthetic pigments. Such species might be resilient to bleaching inducers as they maintain their algal cells during the episodes of high temperatures. However, the data from the current study excludes *P. verrucosa*, *A. formosa* and *P. cylindrica* from the category of species that bleach by losing only photosynthetic pigments.

Seasonal change in coral colouration and its relation to photochemical efficiency of coral transplants

Paling of transplants of studied coral species that was observed in the months of March and April reflect the seasonal variations in sea surface temperature (Figure 1). These signs of bleaching are suggested to be attributed to photoinhibition as they were accompanied by reduction in F_v/F_m (Winters *et al.*, 2003). Although signs of bleaching were observed in March and April, the *Symbiodinium* abundances in bleached colonies were above the suggested level of 0.5×10^6 cells cm^{-2} (Fitt *et al.*, 2000). It is possible that visual signs of bleaching are subjective and can vary from one species to another. In this study, a 40% and 25% decrease in *Symbiodinium* density was enough to cause the appearance of signs of bleaching in *A. formosa* and *P. verucosa* respectively.

An interesting trend was found in *P. cylidrica* where sampling date was found to significantly affect *Symbiodinium* density and chlorophyll *a* concentration, but not the maximum quantum yield of *Symbiodinium* cells harbored by *P. cylindrica* (Table 1). The results of this study therefore support the findings of Fitt *et al.* (2009) who suggest a special mechanism is employed by *P. cylindrica* to maximize photosynthetic efficiency during high temperatures and solar radiation. In their study, Fitt *et al.* (2009) observed low light-induced excitation pressure on the C15 *Symbiodinium* hosted by *P. cylindrica* and therefore relatively high quantum yield of PSII fluorescence at noon ($\Delta F/Fm'$) was maintained. It is possible therefore that the ability of *P. cylindrica* to maintain high F_v/F_m throughout the year regardless of temperature and solar radiation change is attributed to its ability to synthesize high concentrations of heat-stress protein (HSP) 70 and superoxide dismutase (SOD) as reported by Fitt *et al.* (2009). This ability, which is influenced by both the host (*P. cylindrica*) and the symbiont (*Symbiodinium* C15), is responsible for bleaching resistance of *P. cylindrica.*

Seasonal change in *Symbiodinium* types in coral tissue

Reef building corals can acquire foreign *Symbiodinium* types when the populations of the resident *Symbiodinium* types are very low (Brown *et al.,* 1995; Hoegh-Guldberg and Smith, 1989; Fautin and Buddemeier, 2004; Baker *et al.*, 2004). However, significant reduction in populations of dominant resident *Symbiodinium* types is required to either induce proliferation of background resident populations or for secondary acquisition from the environmental pool (Fautin and Buddemeier, 2004; Baker *et al.*, 2004). This is probably why Chen *et al.* (2005) were able to detect clade D *Symbiodinium* type in *Acropora palifera* during the hotter months while *Symbiodinium* clade C type dominated colonies of the same species during the colder seasons. Existence of a similar pattern of seasonal distribution was not found in Zanzibar, even in coral species which harbour more than one *Symbiodinium* type, as these coral species maintained their *Symbiodinium* types as previously found by LaJeunesse *et al.* (2010) and Chauka (2012).

Secondary acquisition of *Symbiodinium* types is complex. When secondary acquisition occurs following a bleaching event, the foreign *Symbiodinium* types exist for shorter periods of time (usually 1-3 years after the bleaching event) (Thornhill *et al.*, 2006; LaJeunesse *et al.*, 2009). Since the well-known and documented bleaching event took place ten years prior to the present study, and while reef building corals need only about two years to return to their original symbionts (Thornhill *et al.*, 2006), it is possible that coral species in Zanzibar have reverted to their original *Symbiodinium* type and established stable symbioses. Thus, seasonal bleaching events that have occurred are likely to not have been intense enough to cause secondary acquisition of *Symbiodinium* type.

In conclusion, this is the first study to use the PAM fluorometry method in determining coral health in Zanzibar waters. This study shows that Zanzibar corals respond to seasonal fluctuation in both solar radiation and sea surface temperature by regulating their *Symbiodinium* density and chlorophyll *a* concentrations. However, such seasonal fluctuations in these environmental parameters are not accompanied by acquisition of foreign *Symbiodinium* types from the environmental pool. Therefore, it is concluded that seasonal fluctuations in both solar radiation and sea surface temperature are not intense enough to effect acquisition of foreign *Symbiodinium* types by reef building corals in Zanzibar waters.

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Mangrove transformation in the Incomati Estuary, Maputo Bay, Mozambique

Célia C. F. Macamo[1*], Henriques Balidy[2], Salomão O. Bandeira[3], James G. Kairo[4]

[1] Departamento de Ciências Biológicas, Universidade Eduardo Mondlane, CP 257 Maputo, Moçambique

[2] Centro para o Desenvolvimento Sustentável das Zonas Costeiras (CDS-ZC), Xai-Xai, Moçambique

[3] Departamento de Ciências Biológicas, Universidade Eduardo Mondlane, CP 257 Maputo, Moçambique

[4] Kenya Marine and Fisheries Research Institute, P.O. Box 81651-80100, Mombasa, Kenya

* Corresponding author:
celia.macamo@uem.mz
celiamacamo@yahoo.com

Abstract

The mangroves around Maputo city in Maputo Bay were studied to assess changes in forest cover area and the effect of cutting pressure on the forest structure and conservation condition, by using GIS techniques and ground-truthing. On site, the forest was classified into semi-intact (predominantly intact trees), degraded (with many cut trees), degraded with reed invasion, dwarf mangrove, and new mangrove area. The results showed a 5% increase in forest area in 2003 as compared to 1991, with 64% of the total forest consisting of degraded mangroves. Deforestation took place at a mean rate of 17 ha year^{-1} between 1991 and 2003. *Avicennia marina* dominated over the other 5 species. Overall, the forest was composed of small trees (mean height 2.6 m; mean DBH 7.45 cm); height and DBH varied significantly when comparing species and communities ($p < 0.05$ for both). In terms of forest conservation condition, only the semi-intact community had the structural characteristics of a healthy forest. Selective tree cutting targeted *A. marina* trunks with diameter of 6 - 12 cm. The regeneration potential of the forest was 181 individuals ha^{-1}; the new mangrove area had the highest density of juveniles (671 individuals ha^{-1}). By identifying the most critical areas of the Incomati Estuary and describing forest condition, this study shows the poor condition of peri-urban mangroves at locations such as this in eastern Africa, and highlights the need for further understanding of estuary regimes that may influence mangrove community changes, other that deforestation.

Keywords: peri-urban mangrove, deforestation, mapping, Incomati Estuary, Mozambique

Introduction

Mangroves are woody intertidal plants that grow on protected coasts in tropical and sub-tropical areas (FAO, 1997). They are ecologically important and provide numerous goods and services to the coastal community, ranging from habitat for fish and other wildlife (Laegdsgaard and Johson, 2001), exporting organic matter (de Boer, 2000; Dorenbosh *et al.*, 2004; Mumby, 2006), shoreline protection (Thampanya *et al.*, 2006), control of water quality (Twilley *et al.*, 1997; Ye *et al.*, 2001) and carbon sequestration (Kristensen *et al.*, 2008; Komiyana *et al.*, 2008). From a socio-economic perspective, mangroves are important sources of livelihood for communities, providing firewood, building poles as well as being sites for the development of economic activities, such as bee keeping, fishing, aquaculture and ecotourism (Taylor *et al.*, 2003; Walters *et al.*, 2008).

Despite their importance, mangrove ecosystems are under pressure worldwide. Major causes of loss and transformation of mangrove ecosystems include over-exploitation, conversion of mangrove areas to other land uses (particularly aquaculture, mining and urban development) and pollution effects (Hogarth, 1999). Other threats include erosion and sedimentation (Alongi, 2002; FAO, 2007; Rakotomavo and

Fromard, 2010) often related to poor agriculture practices upland, and climate change.

In developing countries, peri-urban mangroves (growing within or close to an urban area) are particularly vulnerable to degradation, because the population density is high, and local communities still have a high level of dependency on coastal natural resources. Some of the threats that occur more frequently in peri-urban forests include insufficient treatment of waste-water, urban expansion and overexploitation due to the dependence of peri-urban populations on resources such as fuelwood (Krutilla *et al.*, 1995). This has been seen in many countries in Asia, South America and Africa (Gomes *et al.*, 2008; Wickramasinghe *et al.*, 2009; UNEP/Nairobi Convention Secretariat, 2009). In Mozambique, the massive rural exodus that occurred during the 16 years of civil war overcrowded coastal cities, exceeding their capacities and heightening the exploitation of surrounding natural resources, mangrove forests included. Maputo and Beira cities are the most critical cases (UNEP/Nairobi Convention Secretariat, 2009). Although the situation is probably replicated in other parts of the country, very few studies in Mozambique have focused on mangrove forest transformations.

Remote sensing techniques are a powerful tool in monitoring the area and condition of mangrove forests (Blasco *et al.*, 2001, Kairo *et al.*, 2002a; Alonso-Pérez *et al.*, 2003). When combined with intensive ground-truthing, the use of remote sensed data with GIS is cost- and time-effective, and efficient in quantifying changes in forest structure and dynamics in the past and in real time (Jupiter *et al.*, 2007). Remote sensing has already been used to map mangrove distribution, determine species composition (Neukermans, 2005; Neukermans and Koedam, 2014), assess stand density (Verheyden *et al.*, 2002), and monitor these parameters over periods of time (Daudouh-Guebas *et al.*, 2004). Commonly, satellite imagery used in forestry include SPOT, LandSat Thematic Mapper and Enhanced Thematic Mapper (ETM) (Jupiter *et al.*, 2007). For higher resolution surveys, other types of imagery that have been used in mangroves include Quickbird (Neukermans *et al.*, 2007; Neukermans and Koedam, 2014), IKONOS (Kovacs *et al.*, 2005), and CASI hyper spectral images (Held *et al.*, 2001).

In Mozambique the application of remote sensing techniques for studying mangroves started relatively recently. Saket and Matusse (1994) estimated the total mangrove area of the country as 3.960,8 km^2 in 1990; a figure that was revised to 2.909 km^2 in 2002 by Fatoyinbo et al (2008). Using aerial photographs, de Boer (2002) studied changes in the mangroves of Maputo Bay between 1958 and 1991. In a similar study, LeMarie *et al.* (2006) used LandSat7 TM imagery to assess changes in the mangroves of Xefina Pequena and Benguelene Islands (Maputo Bay) between 1984 and 2003. More recently Ferreira *et al.* (2009) mapped the mangrove forests in the northern trans-boundary area between Mozambique and Tanzania, also using LandSat5 TM imagery. In all these studies, the general trend has been of decreasing forest cover, particularly in the densely populated areas of Maputo Bay. In the remote and accreting areas in the north of the country, mangroves have been seen to expand. None of the above mentioned studies looked at forest conservation condition.

The main objective of this study was to assess changes in forest cover, structure and conservation condition in the mangroves of the Incomati Estuary, a peri--urban forest around Maputo city. The forest comprises 22.3% of the total mangrove area of Maputo Bay (de Boer, 2002), and threats come from several sources, including pollution, urban expansion and wood exploitation by the local communities. The information generated constitutes an important tool for management of the peri-urban mangroves, and will aid in the implementation of a reforestation program for the degraded areas.

Material and methods

Description of study site

The Incomati Estuary is located in north western Maputo Bay, and includes 3 main islands (Benguelene, Xefina Grande and Xefina Pequena), with well established mangrove forests extending up to 7 km inland (Figure 1). The climate of the Bay is subtropical, with a cool dry season from April to October, and a warm wet season for the rest of the year. Mean annual rainfall is 837 mm. Water temperature varies between 17°C and 39°C, and salinity varies between 30-39ppt (mean 35ppt). The tides are semi-diurnal, and tidal range at the river mouth is about 3 m (Hoguane, 1998; UNEP/Nairobi Convention Secretariat, 2009). The estuary is located close to the major urban centre of the country, with an estimated population of about 1.5 million people in 2003 (Instituto Nacional de Estatistica, 2007). Agriculture and fisheries are two of the most important economic activities. Industry (cement, furniture, rubber, food industry, aluminium smelting, tourism, etc.) is flourishing in Maputo and its satellite

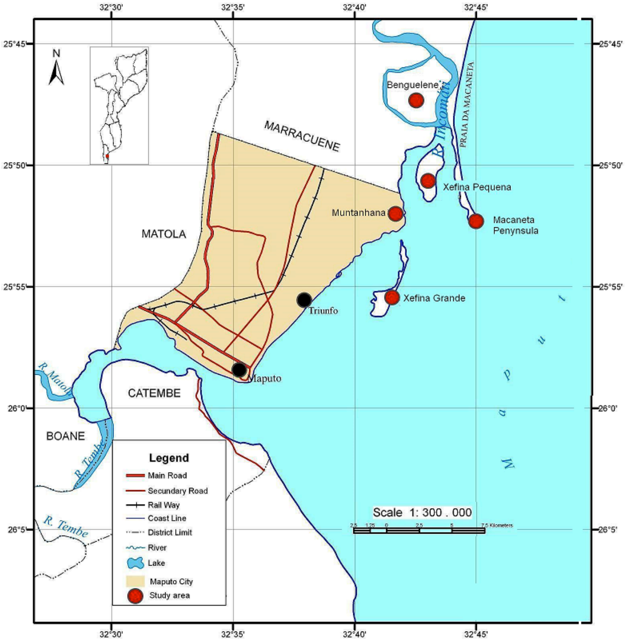

Figure 1. Geographic location of the Incomati Estuary, close to Maputo city and other large human settlements.

city Matola. Mangroves around Maputo (peri-urban) are exploited for wood, fuelwood and charcoal, mainly for domestic purposes. Brower and Falcão (2004) described markets dedicated to mangrove fuelwood in this area.

Methods

Mangrove change detection

Quantification of mangrove area and change detection was made over a timespan of 12 years, combining remote sensing techniques and intensive ground-truthing. Satellite images (Landsat TM 1991, and Landsat TM7+ 2000 and 2003) with a resolution of 30 m were obtained from CENACARTA, already ortho-rectified and cleared for noise. After performing band combination tests, the combination 4, 3, 2 was chosen. Analysis on ArcGIS3.2 (Image Analysis Extension) was performed (e.g. Ramirez-Garcia *et al.*, 1998). The changes in cover area where detected by comparing the results from mapping in different years. Mangrove tree communities were classified according to species composition and land use. Three categories were used for classification of mangrove communities when analyzing Land Sat images: 'Degraded mangrove', with many trees cut in different levels, and dwarf trees present; 'Degraded mangrove with reed (*Phragmites australis*) invasion', where reeds and mangrove trees were present; and 'Healthy mangrove', including regenerating communities and new mangrove areas.

Mangrove forest structure, conservation condition and regeneration status

Five mangrove forest communities were identified on the ground in the study area: semi-intact community, which was composed predominantly of intact trees; degraded community, where many trees were completely, severely or partially cut; dwarf mangrove, composed of very small adult trees or shrubs; and new mangrove area, where, after accretion, new mangroves were establishing just prior to or during the study. Mangrove forest structure and conservation condition were assessed using the quadrat methods elaborated in Kairo *et al.* (2002b) and Bandeira *et al.* (2009). Quadrats of 10x10 m were set in the upper, middle and lower parts of the mangrove forest, following transects that were set perpendicular to the coast line. A total of 60 plots were sampled. Sampled areas in the estuary included Xefina Grande and Xefina Pequena Islands, Benguelene Island, Ponta Macaneta and Muntanhana (Figure 1). All individuals inside the quadrats were counted and identified to species level. Diameter at breast height (DBH) was measured with a calliper, while height was estimated with a 5 m graduated stick. This data allowed the calculation of structural parameters of the forest, such as species density and frequency, basal area, and mean height and diameter (Cintron and Schaeffer-Novelli, 1984; Kairo *et al.*, 2002b; Bandeira *et al.*, 2009). It also allowed a height vs diameter distribution scatter graph to be generated for each community, which was useful to identify transformations in the structure of the forest (Kairo *et al.*, 2002). The ecological importance value (IV) of the species and the complexity index of the communities were calculated as described by Cintron and Schaeffer-Novelli (1984) and Holdridge *et al.* (1971). Measuring height and DBH also allowed classification of individuals in the quadrat as adults or juveniles, as described by Bandeira *et al.* (2009); those up to 1.5 m high and 2.5 cm wide (DBH) were classified as adults, and those below these figures were juveniles. This classification was useful to assess forest regeneration status.

To assess mangrove conservation condition, adult individuals in the quadrat were counted and grouped into four categories. These were: Intact, for trees with no sign of being cut; Partially cut, for those with one or more branches which had been cut, but the main trunk was intact; Severely cut, with most branches cut; and Stump, for those whose main trunk had been cut (Bandeira *et al.*, 2009). The diameter of stumps was measured to estimate preferred sizes for cutting.

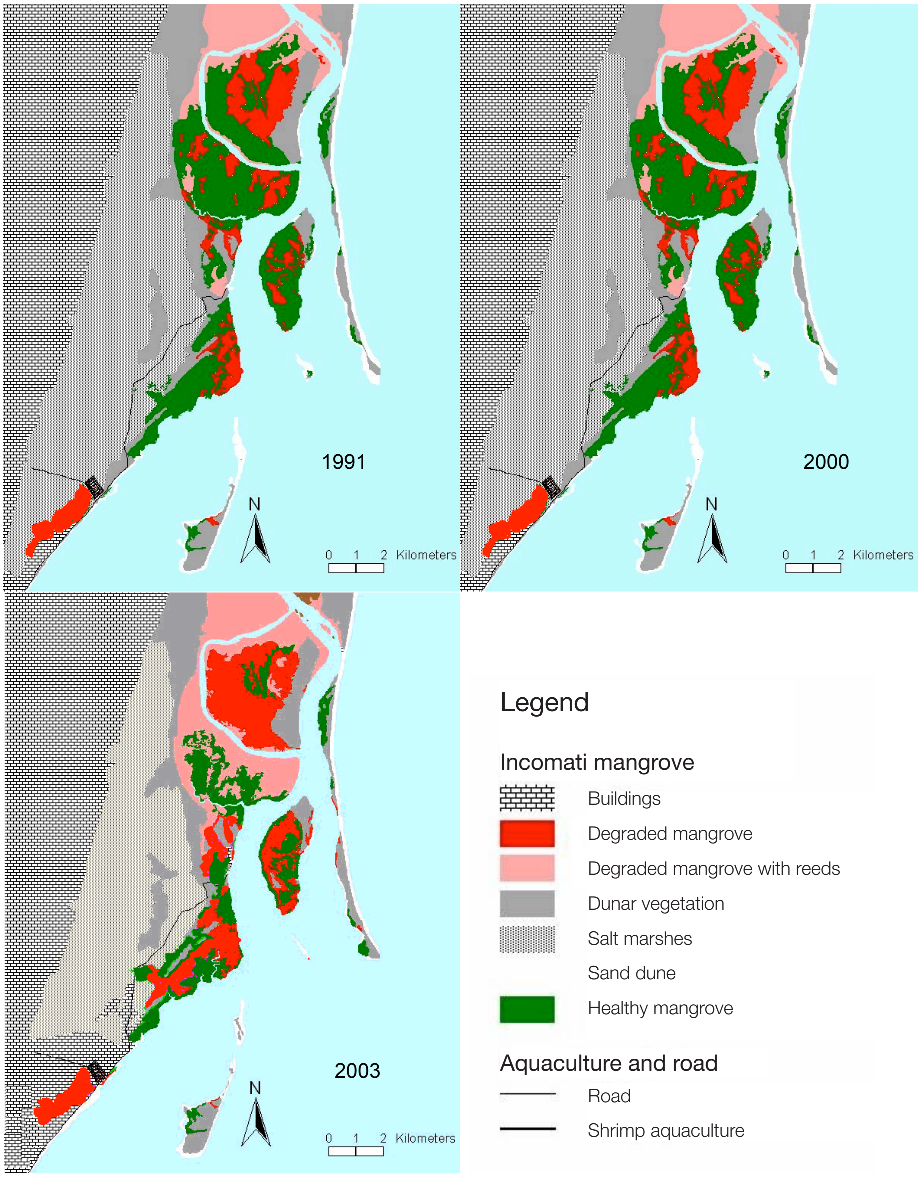

Figure 2. Mangrove area variation between 1991 and 2003. Healthy forest includes recovering mangrove and new mangrove area, while dwarf communities were considered degraded.

All juveniles within the quadrat were identified and counted to assess regeneration status of the forest.

Data on mangrove structure were subject to normality and homogeneity of variances tests. Multifactorial ANOVA was conducted to assess significant differences in parametric data, while Kruskal-Wallis was used for non-parametric data. All tests were performed at 0.05 probability level.

Results

Mangrove change detection

The total mangrove area in the Incomati Estuary increased from 4,231 ha in 1991 to 4,451 ha in 2003; an increase of 18 ha per year (Figure 2). However, the rates of change varied over this period. From 1991 to 2000, the 'Degraded area' increased by 113 ha, and 'Degraded with reeds' expanded by 218 ha into previous mangrove areas. 'Healthy' area decreased, but this change was compensated by an increase of 174 ha of new mangrove (also considered 'Healthy'). From 2000 to 2003, the 'Degraded' area increased by 91 ha and reeds took over a larger area (520 ha). The area of 'Healthy mangrove' decreased, but the total mangrove area increased by 46 ha. When comparing 1991 and 2003, 'Degraded mangrove' increased at a rate of 17 ha/year, while reeds gained 62 ha each year and the total area increased by 18 ha each year. In 2003, 'Total Degraded mangrove' (with and without reed invasion) made up 63.8% of the total forest area.

A rapid increase in degradation rate after 2000 was apparent. It is probable that the deforestation rate increased gradually between 1991 and 2000, with a mean value of 12 ha/year. Similarly, degradation rate for the whole period 1991-2003 was 17 ha/year, lower than that of the 2000-2003 period (Table 1).

Most changes occurred in Benguelene and Xefina Pequena Islands, while in Muntanhana changes were marked by reed invasion.

Forest structure

A total of 2,334 individuals of 6 species were sampled in the Incomati forest. *Avicennia marina* was the dominant species (71.46%), being present in all communities. *Rhizophora mucronata* and *Ceriops tagal* represented 17.15% and 6.56% of the total number of individuals respectively, while the other tree species (*Bruguiera gymnorhiza*, *Xylocarpus granatum* and *Lumnitzera racemosa*) accounted for less than 3% each. These figures where reflected in the ecological importance value of the species (Table 2). Mean stand density in the forest was 4,024 ind ha^{-1}. There were significant differences when comparing stand densities in the communities ($p < 0.05$), with the densest communities being 'New mangrove' (7833 ind ha^{-1}) and 'Semi-intact mangrove' (5646 ind ha^{-1}). 'Semi-intact mangrove' was also the most complex community (Table 3).

Structurally, this forest was composed of small trees (as defined by Cole *et al.*, 1999; Kairo *et al.*, 2002b; Kairo *et al.*, 2008). The mean height of the forest was 2.62 ± 0.03 m and mean DBH 7.45 ± 0.25 cm. A large majority of adult trees had DBH between 2.5 and 6 cm (Figure 3). Mean height varied significantly when comparing species ($p < 0.05$) and communities ($p < 0.05$), with *A. marina* being the tallest species, and 'New mangrove' the tallest community.

Lumnitzera racemosa had the highest mean DBH, while the greatest basal (proportional to DBH) area was found in the 'Semi-intact' community. Statistical analyses showed significant differences when comparing DBH among species and communities ($p < 0.05$).

Only 'Semi-intact' mangrove kept a size distribution (Height vs. DBH) typical of a healthy forest; that is having individuals in all size classes, but the majority had narrow stems (Figure 4). Structural differences between 'Degraded mangrove' and 'Degraded mangrove with reeds' were also apparent. In the 'Degraded with reeds' community, all diameters were very similar

Table 1. Mangrove area (ha) and dynamics between 1991 and 2003 in the Incomati Estuary.

Mangrove community	1991	2000	Change	Rate/year
Degraded	1,007.28	1,120.79	113.51	12.61
Degraded with reeds	889.20	1,107.66	218.46	24.27
Semi-intact	2,334.75	2,176.85	-157.89	-17.54
Total area	4,231.23	4,405.30	174.08	19.34
	2000	**2003**	**Change**	**Rate/year**
Degraded	1,120.79	1,211.56	90.77	30.26
Degraded with reeds	1,107.66	1,627.37	519.71	173.24
Semi-intact	2,176.85	1,612.29	-564.56	-188.19
Total area	4,405.30	4,451.22	45.92	15.31
	1991	**2003**	**Change**	**Rate/year**
Degraded	1,007.28	1,211.56	204.28	17.02
Degraded with reeds	889.20	1,627.37	738.17	61.51
Semi-intact	2,334.75	1,612.99	-722.46	-60.21
Total area	4,231.23	4,451.22	219.99	18.33

Table 2. Ecological importance of species in the Incomati Estuary. IV represents the importance value of species, which is obtained by summing the relative dominance, density and frequency (Cintron and Schaeffer-Novelli, 1984). Mean DBH and mean height ± standard error.

Species	Mean height (m)	Mean DBH (cm)	Relative values			IV
			Dominance	Density	Frequency	
A. marina	2.85± 0.03	6.85±0.29	71.46	77.72	52.22	201.4
B. gymnorhiza	1.82±0.09	6.29±1.31	1,16	1.37	5.56	8.09
C. tagal	1.63±0.04	5.23±0.27	6,56	9.34	13.33	29.23
L. racemosa	1.71±0.11	14.54±1.66	2,17	1.11	2.22	5.5
R. mucronata	1.95±0.09	13.62±0.94	17,15	9.38	15.56	42.09
X. granatum	2.49±0.2	10.47±1.94	1,50	1.07	11.11	13.68

Table 3. Structural parameters of the Incomati Estuary communities. Complexity index is the product of number of species, basal area, maximum tree height and stem density (Holdridge *et al.*, 1971).

	Semi-intact	Dwarf	Degraded	Degraded with reeds	New mangrove	Whole forest
Number of species	5	4	5	2	2	6
Density (ind ha^{-1})	5,646.15	3,893.33	1,460.00	1,533.33	7,833.33	4,024.14
Mean height (m)	2.61	2.02	1.60	2.55	3.44	2.62
Basal area (m^{2}ha^{-1})	3.6	0.67	0.97	0.32	1.30	3.75
Complexity index	9.15	0.41	0.43	0.04	1.33	3.26

and below 20 cm, whilst in the 'Degraded' community, sizes varied more and were greater than 20 cm.

Forest structure and conservation condition

Data analysis showed that this forest was subject to deforestation pressure. Cut trees (stumps) had different sizes, but preference was for those with a trunk diameter of 6 – 12 cm. However, the forest was composed mostly of intact individuals (Table 4). *A. marina* was the preferred species, while *B. gymnorhiza* was almost never cut.

Each community was composed of different proportions of tree categories. Intact trees were found mostly in 'Dwarf', 'New mangrove', and 'Degraded with reeds' areas (Figure 5).

The regeneration potential of the forest was low (181 juveniles ha-1). A. marina had the highest density of juveniles (178 ind ha-1) and dominated the forest in all communities, though with low densities in 'Degraded mangrove' and 'Degraded with reeds' areas. Other species had less than 4 juveniles ha-1. The highest regeneration was seen in the 'New mangrove' areas (Figure 6), with 671 juveniles ha-1, and in the 'Semi-intact mangrove' areas, with 422 juveniles ha-1.

Discussion

Forest transformation and conservation condition

The Incomati Estuary supplies the local community with forestry resources, mostly domestic fuel, wood and poles (local community, personal communication). In 1995 it was estimated that 9200 tonnes of mangrove firewood was extracted from Benguelene Island alone, for sale and domestic consumption (Hatton, 1995). It is thus an area of considerable importance as a source of livelihood for the local communities. Apart from wood resources, the Incomati forest and its surroundings are important for other income generating activities, such as the fish and shrimp fishery, and invertebrate collection (Barbosa *et al.*, 2001).

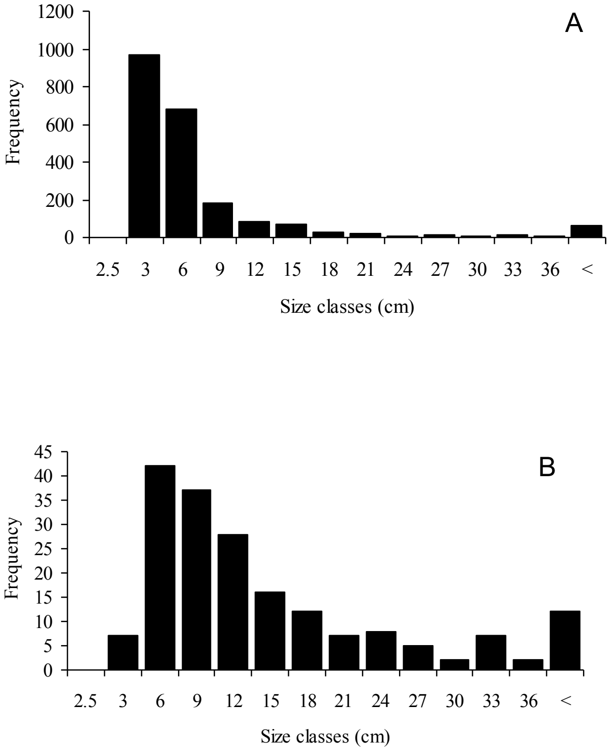

Figure 3. DBH size class distribution for live trees (A) indicates the presence of human disturbance; while the diameter size distribution for stumps (B) indicates clear preferences for 6-12 cm poles.

The results of this study show an increase of about 5% in total mangrove area over the study period. This trend of an increase in total forest cover has previously been recorded in other parts of the country such as Inhaca, Machangulo, Xefina and Benguelene Island in Maputo Bay (17% between 1958-1991), Maputo Province (6 km² between 1990-2002) , and the Rovuma-Quiterajo-Ibo-Pemba area in northern Mozambique (3% between 1995-2005) (de Boer, 2002; Fatoyinbo *et al.*, 2008; Ferreira *et al.*, 2009). Slight increases have also been recorded in other parts of the world, such as in the Sundarbans (India/Bangladesh) and Madagascar (Giri *et al.*, 2007; Rakotomavo and Fromand, 2010). However, the general global trend is one of decrease (Valiela *et al.*, 2001). Among African countries, Liberia and Mauritius were listed as the countries with the highest rates of mangrove loss. According to FAO (2007), they lost 6.1% and 5.9% of the total mangrove area in the period 2000-2005, respectively. In eastern Africa, Madagascar lost the largest mangrove area (3000 ha) in the same period, although this corresponds to only 1% of its total mangrove area.

Most mangrove studies are limited to a description of changes in cover area, while others combine it with structural aspects (Simard *et al.*, 2006; Krausse *et al.*, 2004),

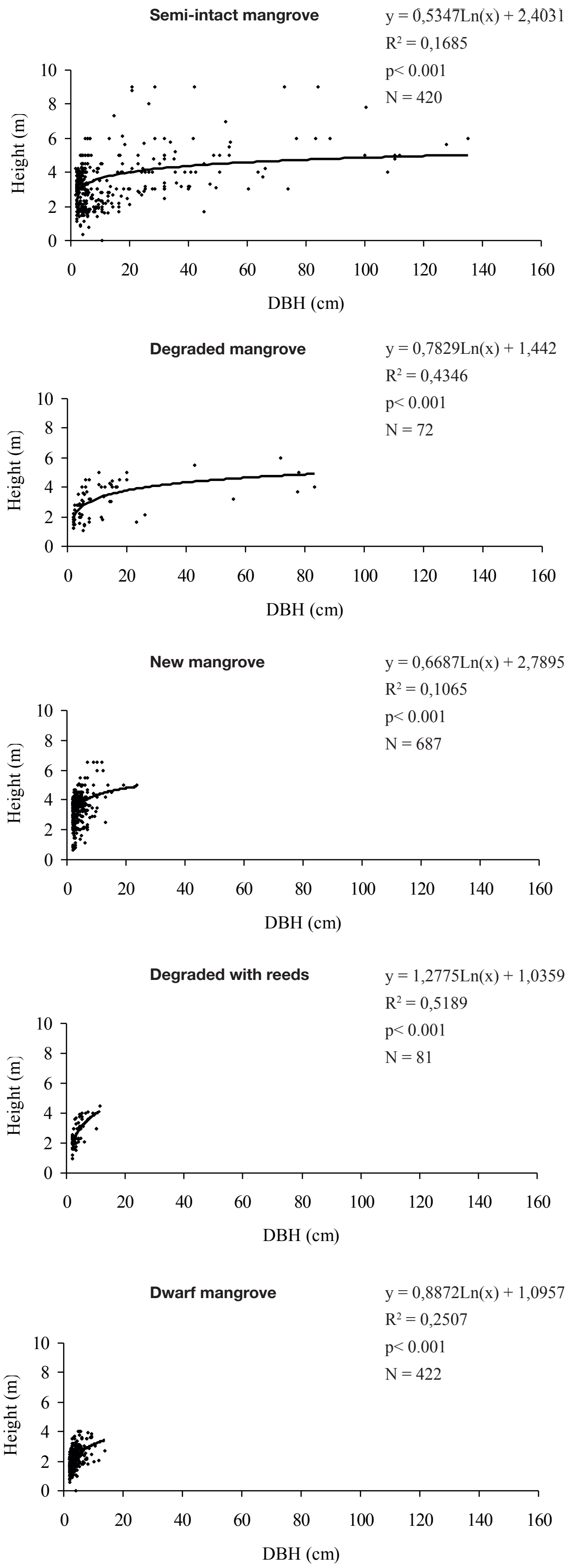

Figure 4. Height-diameter distribution of *Avicennia marina*, the dominant species in the Incomati Estuary. Structural differences can be seen in each community.

Table 4. Conservation per species

Species	**Density (ind ha^{-1})**			
	Intact	**Partially cut**	**Severely cut**	**Stump**
A. marina	2,301	287	305	232
B. gymnorhiza	51	1	1	0
C. tagal	322	13	15	24
L. racemosa	31	6	3	3
R. mucronata	181	72	65	58
X. granatum	25	8	8	0
Whole forest	**2,913**	**391**	**400**	**319**

but very few look at forest conservation condition. The combination of the three aspects as in this study provides more expansive information on the forest, and a more robust basis for informed decision-making. For instance, this study showed that a small increase in the area of mangrove cover is largely offset by a dramatic increase in degraded area (50% of the forest is degraded through cutting and reed invasion) and decrease in forest health. The presence of the reed *Phragmites australis* within a mangrove forest is often perceived as a sign of instability (Walters, 2005; Granek and Ruttenberg, 2008), and it can be an indicator of the presence of hydrological-related stresses (Vasquez *et al.*, 2005; Katering *et al.*, 2010), such as increased runoff and freshwater seepage. In the case of the Incomati Estuary, both phenomena occurred after the year 2000, when massive floods impacted the area, providing an explanation for the accelerated rate of colonization by the reed after 2000. Prior to this period, the hydrological regime of this estuary had reportedly being altered by water abstractions upstream (agriculture, urban and industrial consumption, dam construction, etc.) and increased salt intrusion downstream (Sengo *et al.*, 2005; Brockway *et al.*, 2006; LeMarie *et al.*, 2006; UNEP/Nairobi Convention, 2009). The overall effect of the floods, water abstraction and salt intrusion, and their influence on reed invasion in the estuary, is poorly understood and requires further study.

The comparison of community structural parameters reveals several interesting differences between the categories. For instance, the 'Degraded with reeds' community is composed mostly of intact trees, indicating that reed invasion does not only occur in cleared areas. In addition the presence of dwarf *A. marina* indicates stress, which can be related to nutrient shortage or high salinity (Naidoo, 2009). The influence of all these factors on forest health condition has not yet been assessed.

The regeneration potential of this forest is low. Other healthy forests in Mozambique (Saco, Sangala, Ibo, Pemba, Luchete) had more than 6000 recruits ha^{-1}

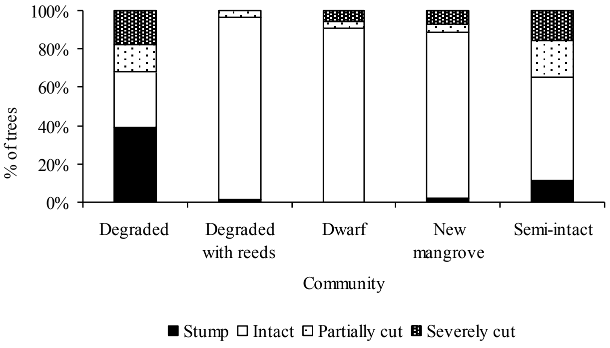

Figure 5. Conservation status of the different mangrove communities in the Incomati estuary.

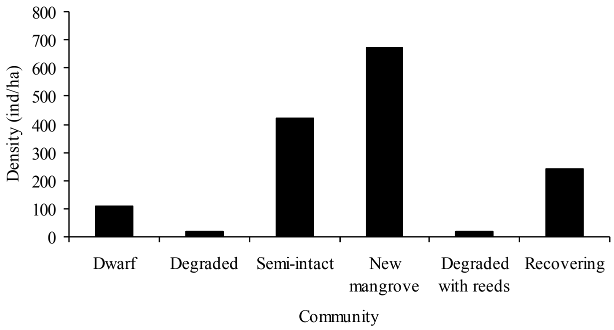

Figure 6. Regeneration per mangrove community in the Incomati estuary.

(Bandeira *et al.*, 2009). Similarly in Kenya, on less impacted and recovering replanted sites, the density of recruits per species varies between 700-5400 ind ha^{-1} (Kairo *et al.*, 2002b; Bosire *et al.*, 2003; Kairo *et al.*, 2008). The recruit density in the Incomati Estuary was comparable to other heavily deforested sites, such as Sematan in Malaysia and Mngoji in Tanzania (500 and 1000 ind ha^{-1}, respectively) (Ashton and Macintosh, 2002; Bandeira *et al.*, 2009). *A. marina* is the dominant adult species, and this explains why it has the best regenerative success. Additionally this species is vigorous and capable of adapting to changing environmental conditions such as changes in salinity; more so than other species (Bentjee and Bandeira, 2007).

Incomati Estuary: Is restoration possible?

Degraded areas can recover through natural processes. Sherman *et al.* (2000) reported that the creation of gaps may increase sapling density and growth rate of some species in forests with low cutting intensity, because competition for light and space is reduced. However, intensive forest cutting can decrease forest regeneration potential, by reducing the number of reproductive individuals and changing optimum environmental conditions (Hogarth, 1999, Granek and Ruttenberg, 2008).

Natural recovery in the Xefina and Benguelene Islands mangrove forest was reported by LeMarie *et al.* (2006). The authors verified that about 54 ha of degraded forest recovered to non-degraded forest between 1984 and 2003. In the present study, recovering mangrove and new mangrove areas were identified during ground-truthing, suggesting that the system can recover. However, human intervention may be helpful, as replantation could boost forest recovery and re-colonization of invaded areas. Mozambique has experienced at least one demonstration programme on mangrove replantation (in Lumbo, Northern Mozambique), where the local communities were trained in mangrove replanting techniques and alternative income-generating activities such as integrated aquaculture, ecotourism and silviculture (Veronica Dove, personal communication).

Some positive actions for restoration in the Incomati Estuary could include raising the level of education and awareness of local communities around sustainable harvesting of mangrove products. Mangrove replantation in severely degraded areas might also contribute to the process. The use of conservation practices (such as establishment of no-cut zones, regulation of harvesting, and diversification of mangrove uses like ecotourism, bee-keeping etc.) and resource management initiatives are required in order to make sustainable use of mangrove resources in the future. *A. marina* could be considered as a suitable pioneer species in any replantation programme (Bentjee and Bandeira, 2007; Lang'at, 2010).

This research shows the history of mangrove vegetation change in the Incomati Estuary during the period from 1991 to 2003. Although the forest area increased during the study period, the area of healthy forest decreased, while 'Degraded' areas expanded (63.8% of the total forest area). Structural differences were found in different forest communities, and only the semi-intact community had a structure that was similar to that of healthy forests. Although the regeneration potential of the forest is low, recovery is possible, as demonstrated by the presence of recruits and colonization of new mangrove areas. Efforts towards forest restoration should be accompanied by education and awareness of the user communities, mangrove replantation, and the introduction of management and conservation practices.

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Feasibility of extensive, small-scale mud crab (*Scylla serrata*) farming in East Africa

Per-Olav Moksnes[1*], David Mirera[2], Razack Lokina[3], Jacob Ochiewo[2],
Humphrey Mahudi[4], Narriman Jiddawi[5], Muumin Hamad[5], Max Troell[6]

[1] Department of Marine Sciences, University of Gothenburg, Box 461, Sweden

[2] Kenya Marine and Fisheries Research Institute (KMFRI), Box 81651, Mombasa, Kenya

[3] Department of Economics, University of Dar es Salaam, Box 35045, Dar es Salaam, Tanzania

[4] Mafia Island Marine Park (MIMP), Box 74, Tanzania

[5] Institute of Marine Sciences, Zanzibar, University of Dar es Salaam, Tanzania

[6] Beijer Institute, KVA and Stockholm Resilience Centre, Stockholm University,

* Corresponding author:
per.moksnes@marine.gu.se

Abstract

Small-scale farming of mud crabs (*Scylla serrata*) has been suggested as a low investment alternative for generating incomes to resource-poor coastal communities in East Africa. However, it is unclear if the present culture methods are profitable and ecologically sustainable. Here we assess the two dominant culture methods, extensive 'crab-fattening' in cages (cage culture) and grow-out farming of small juveniles in ponds (pond culture) using economic and ecological analyses in Kenya and Tanzania.

Cost-revenue analyses of cage culture showed negative results at all scales in both countries. High labor costs and poor survival and growth make cage culture an unprofitable and unsustainable livelihood in its present form. Pond culture showed a positive return at prices above $US 3.4 kg^{-1}, which is achievable in Kenya and Mozambique, but not in Tanzania. Analyses also showed that larger ponds and selling crabs at a smaller size improved profitability. However, the availability of seed-crabs and local feed sources limit the size of sustainable crab farms in a coastal community to approximately 500 commercial crabs per year. Before crab farming in ponds can become a profitable alternative income in East Africa, survival rates need to be improved, market conditions and profits to local crab farmers enhanced, and potential negative impacts on mangroves evaluated.

Keywords: Feasibility, livelihoods, cost-revenue, grow-out farming, crab-fattening, pond, cage culture

Introduction

The populations in coastal areas of East Africa have increased dramatically in the last decades, contributing to increased pressure and degradation of coastal resources. Examples include declining fish catches, deteriorating conditions of coral reefs, and reduction of mangroves (van der Elst *et al*., 2005). Various management responses are being undertaken to halt the deterioration of coastal resources, including restriction on fishing and extraction through MPAs, introduction of community-based management practices and regulation of harvest practices. However, these measures, in combination with decreasing coastal resources, increase the need for additional livelihoods for the large number of impoverished people that directly depend on coastal resources for their survival. Due to unproductive soils for agriculture, coastal residents usually have few alternative livelihood options, and intensified competition for coastal resources increases conflicts between stakeholders within the increasingly crowded coastal zone (Hecht, 2006). In the last decade, small-scale farming of mud crabs has been suggested as a viable alternative income for resource poor coastal communities in East Africa (ACDI/VOCA, 2005; Shipton and Hecht, 2007; Mirera, 2009; Mirera, 2014).

Mud crabs (*Scylla* spp.) are large portunid crabs that inhabit coastal mangrove habitats in the Indian Ocean. Four species of mud crabs are recognized (*S. serrata,* *S. paramamosain, S. tranquebarica* and *S. olivacea*), but only one species (*S. serrata*) is found in East Africa (Keenan *et al.*, 1998). All mud crab species have good taste and generate high prices on domestic and international markets, and are fished by artisanal and commercial fishers throughout the region. The unique ability of mud crabs to stay alive out of water for 4-5 days enables cost effective transport from remote coastal areas to national and international markets without the need for cooling (Keenan, 2003).

Mud crabs can survive and grow well in captivity and they have for the last 40 years been farmed throughout Southeast Asia and Southern China (FAO, 2015). In Southeast Asia, there are two basic forms of mud crab aquaculture: 'fattening' of adult crabs with a low meat content, and 'grow-out' of juveniles to market size. Fattening has been the dominating form, primarily conducted in ponds or small bamboo enclosures placed in the intertidal, where adult crabs with low meat content (and low market value) are fed for a short period (<1 month) to gain weight and higher market price. Generally, the fattening is completed prior to molting since mortality otherwise reduces production (Keenan, 2003). However, a growing part of the fattening industry now produce crabs that have recently molted, so called "soft shelled crabs", as these fetch a higher price and are in great demand in Southeast Asia. Grow-out farming of crabs is usually carried out in intertidal ponds or pens (net-fence systems) with or without mangroves, where juvenile crabs (10-100 g) are farmed through several molts until they reach market size. High growth rates have been reported from Asia for all systems, with production of commercial-sized crabs (200-400 g) 3-6 months after stocking with seed crabs (Keenan, 2003; Shelley and Lovatelli, 2011; Moksnes *et al.*, 2015).

Aquaculture of mud crabs in Asia consists of both small-scale farms and large industrial system of >100 hectares (Trino and Rodriguez, 2002; Keenan, 2003; Shelley and Lovatelli, 2011). Because of an increasing demand for mud crabs, the aquaculture industry has expanded very rapidly in the last 10 years and in 2014 global production reached 185 000 tons (valued at US$ 565 million), with most of the production taking place in China (FAO, 2016). For example, in Myanmar, the second largest crab producer, intensive farming is carried out with floating cages (up to a million cages in just one farm) where all seed crabs are collected from the wild.

The rapid expansion of cultured crabs has been possible due to an increasing market for soft-shell crabs in Asia, ready access to feed fish and vast areas of mangroves providing a steady supply of juvenile crabs, although seed supply now seems to be decreasing (Nicolini, 2013). Mud crab farming throughout Asia has historically been based on collection of wild seed crabs, but an unmet demand for mud crabs has led to over-exploitation of both adult and juvenile seed crabs, which has led to decreasing stocks in many countries (Keenan, 2003). Difficulties in obtaining juveniles from the wild for farming operations, plus concerns of further over-exploitation, has led to development of larval hatchery techniques, and today, for example, both Vietnam and China have industrial production of juvenile seed crabs for *S. serrata* and *S. paramamosain* (Shelley and Lovatelli, 2011) and development is under way also in other countries.

With the increasing industrial production of mud crabs based on seed crabs from hatcheries, feed is perceived as the next major bottleneck to mud crab aquaculture. Formulated diets to replace 'trash fish' are being developed, but the demand for low value fish resources is still high (Shelley and Lovatelli, 2011). Parallel to the development of industrial scale mud crab farming, the development of more extensive farming methods has also continued. In the Philippines and Malaysia such technologies have been transferred to resource-poor fishing villages for adoption as sustainable alternative livelihoods. These are low investment, small-scale grow-out farms in ponds or pens located within natural mangrove habitats and designed to maintain the integrity of the mangrove ecosystem. These farms show high survival and growth rates of crabs, with a high cost return (Wei Say and Ikhwanuddin, 1999; Trino and Rodriguez, 2002). These more extensive farming systems can also be found in Indonesia and Vietnam, for example, where mangroves forests are integrated with different species including mud crabs (Joffre and Bosma, 2009).

Mud crab farming in East Africa

East Africa has substantial populations of mud crabs (*S. serrata*) that are fished mainly by artisanal fishers using traditional capture methods such as hook, sticks, traps, and seine nets (Muthiga, 1986; Mirera *et al.*, 2013). This fishery is minor in comparison to Southeast Asia, but the local demand for mud crabs is increasing, as well as an increasing demand from the Asian market (ACDI-VOCA, 2005, Shipton and Hecht, 2007; Mirera, 2011); as indicated by the increasing number of Chinese traders becoming active in the region. The fishery is to a large extent unregulated and there are indications that some local crab populations in East Africa have decreased significantly as a result of increased fishing effort (Francis and Bryceson, 2001; Mahika *et al*., 2005; Mirera *et al.,* 2013).

In contrast to Southeast Asia, there is little tradition of aquaculture in East Africa, and especially marine farming is still in its infancy (Bryceson, 2002; Troell *et al.,* 2011). Research on mud crab farming was initiated in Kenya in the late 1990s assessing the use of mangrove pens, but with limited success (Mwaluma, 2002). Recent studies have assessed different methods for crab culture with the aim of involving local communities as a participatory management tool for mangrove forests (Mirera, 2009; Mirera and Mtile, 2009). These culture practices are based on collection of wild seed crabs as no larval hatcheries for mud crabs yet exist in East Africa.

In the last decades, developmental projects have been undertaken by various NGOs in East Africa to develop small-scale crab farming in local communities (e.g in Tanga, Rufiji, Kilwa, Mtwara and Mafia in Tanzania, and in the Mombasa, Kwale and Malindi areas in Kenya (Shipton and Hecht, 2007; Mirera, 2011). These projects have all focused on a method referred to as 'crab-fattening' that use small (0.30 x 0.30 m) individual cages with lids, built of local material (usually mangrove sticks or bamboo), that are placed in the intertidal zone within the mangroves, without cutting any trees. The cages are stocked with sub-adult crabs (one 150-300 g crab per cage) collected from the wild and farmed through several molts (many months) until they reach 500-1000 g. These 'extended' crab-fattening farms (referred to as 'cage culture' in this text) are presented as an alternative source of income for the local communities where the crabs are sold as a cash crop to local hotels or middlemen for export markets (ACDI-VOCA, 2005; Mahika *et al*., 2005; Shipton and Hecht, 2007).

These initiatives are all in a more or less developmental stage, and only negligible quantities of mud crabs are today produced in Tanzania and Kenya (Shipton and Hecht, 2007; UNEP-Nairobi Convention and WIOMSA, 2015). Still, as interest is growing for this activity the development of mud crab farming may now be at a critical cross-road. A demand-driven rapid expansion of cage culture could result in overexploitation of seed crabs with subsequent collapse of local mud crab stocks, and negative ecological and social impacts, similar to the situation in several Southeast Asian countries (Allan and Fielder, 2004). Lack of fishery data and basic information on reproductive biology and ecology of small juvenile mud crabs in East Africa make it difficult to assess sustainable limits for a seed crab fishery. It is possible that the pressure on crab populations may already be too high from fisheries that target the consumer market directly. Moreover, the present cage culture activities in East Africa rely to a large extent on mangrove snails (*Terebralia palustris*) as a feed resource, which are also consumed by the poorest segment of coastal communities, and there is a potential risk that further expansion of crab aquaculture may have negative effects on local food sources for humans (Hamad, 2012). There is therefore a need to assess alternative feed sources, not used for human consumption, which could be used to support an expansion of mud crab aquaculture.

Importantly, farming crabs in cages for extended periods may not be the best aquaculture method for the sustainable development of mud crab farming in East Africa. Recent studies suggest that growth in these culture systems is very slow compared to natural growth of *S. serrata* in East Africa (Moksnes *et al*., 2015), and that the mortality rates in captivity may be higher than in nature (Mirera, 2014). Moreover, it is also unclear if this farming system is sustainable from an economic perspective. A value-chain and profitability analysis of cage culture in the Tanga region, Tanzania, showed that farmers could not make a net profit due to low prices, and suggested that the farms need to increase in size to increase profitability (ACDI-VOCA, 2005). In contrast, profitability analyses of an experimental cage culture system in Kenya showed a high return on capital investment (Mirera, 2009). However, the cost of labour in maintaining cage culture farms were not included in these analyses, and it is therefore not clear if this activity is rational from an economic perspective.

Grow-out aquaculture of mud crabs using small juvenile crabs (<10 g) in pond or pen systems, compared to using sub-adult crabs, may constitute a more sustainable alternative for East Africa, both from an ecological and economic context. Small-scale pond and pen systems in Southeast Asia show high survival and growth rates with high profitability (Trino and Rodriguez, 2002). In the absence of hatcheries, recent field studies in East Africa demonstrated that small juvenile seed crabs can be efficiently collected along mangrove fringes (Mirera, 2014), and studies of grow-out culture methods in pond and pen systems in Kenya show high growth rates for such seed crabs (Mirera and Moksnes, 2015). However, it is not clear if this form of aquaculture could constitute a profitable activity since cost-revenue analyses are missing, and it is unclear how prices of mud crabs vary between different markets and countries in East Africa. It is also not clear if and how the profitability in cage and pond systems will increase with scale, and how seed crabs and feed limit the maximum scale of a sustainable farm in a coastal community setting, as such analyses are lacking.

Here we assess the profitability of small-scale aquaculture of mud crabs in cage and pond systems in Kenya and Tanzania using cost-revenue analyses based on realistic growth rates of crabs, and on realistic costs (including labour costs) and prices in the two countries, obtained through culture studies and market surveys in East Africa. Specific aims of the study were (1) to compare the profitability and identify the major costs in the two culture systems, (2) to assess how prices and profitability differ between markets and countries, (3) to assess how market size for crab affects profitability in pond culture, and (4) to assess the economy of scale in the two systems, and how seed and feed resources may limit the maximum size of a sustainable crab culture operation in a coastal community.

Material and Methods

The present study was part of a larger research project financed by MASMA-WIOMSA to assess if small-scale aquaculture of mud crabs could be developed into a sustainable alternative livelihood for coastal communities in East Africa. Using a multidisciplinary approach, parallel field studies and surveys were carried out in Kenya and Tanzania to assess opportunities and constraints of this activity from both an ecological and economic perspective.

Markets and prices for mud crabs

To assess markets and price ranges available to mud crab farmers in East Africa, informal interviews were carried out with crab fishers, crab farmers, middlemen, exporters, market salesmen and hotels in the Mombasa and Malindi areas in Kenya, in Dar es Salaam, Mafia and Zanzibar in Tanzania, and in Maputo in Mozambique. The prices were compared to earlier studies in East Africa and South East Asia obtained from the literature.

Cost-revenue analyses of cage and pond culture in East Africa

To compare the cost and profit margins of pond and cage culture of mud crabs in Kenya and Tanzania, cost-revenue analyses were carried out assessing the total cost to produce 450 commercially sized crabs (i.e. 500 g). For pond culture, the estimates were based on farming 0.5 and 2.0 g small juvenile seed crabs, stocked at approximately 5 crabs m^{-2} in 15x15 m earthen ponds, for 11.6 and 10.9 months, in Tanzania and Kenya, respectively (Table 2). The difference in culture periods was due to smaller seed crabs dominating in Tanzania (see below) requiring slightly longer time to reach commercial size. For cage culture, the estimates were based on 3 consecutive 3-month culture periods, growing 300 g seed crabs in cages with 200 individual compartments.

To estimate the growth period to commercial size for different sizes of seed crabs, a von Bertalanffy growth function of natural growth of *S. serrata* in East Africa was used:

$$L_t = 310*(1- e^{-0.57*(t-0.019)})$$

where L_t is the size (carapace width) at time (t) since settlement (Moksnes *et al.*, 2015). A growth model was used since existing studies of mud crab culture in East Africa have not raised crabs to commercial size. In pond culture, the growth rate was similar to the modeled growth (99%; Mirera and Moksnes, 2015), whereas in cage culture the growth rate was substantially lower (on average 39% of the modeled growth; Moksnes *et al.*, 2015). To partly adjust for this difference, a growth rate in cage culture that was approximately 75% of the modeled growth was used, simulating an improvement of the present growing conditions by approximately 50%. This was done to assess if cage culture could become profitable if growth rates improved. The same growth rates were used in both countries.

In both culture systems, the mortality rate was assumed to be 10% month^{-1}, which is similar to what is obtained in mud crab cultures in Southeast Asia (Baliao *et al.*, 1999, Trino *et al.,* 1999, Trino and Rodrigues, 2002). However, in East Africa, reported mortality rates have been substantially higher, ranging from on average 20-60% month^{-1} in different culture systems (Mwaluma, 2002; Mirera, 2009; Mirera and Mtile, 2009; *see* Mirera and Moksnes, 2015 *for review*). Thus, it is important to note that the cost-revenue analyses assumed a substantial improvement of survival rates in the East African cultures, something that may be feasible under better management.

All cost estimates were based on data from experimental cage culture studies in Mtwapa Creek, north of Mombasa, Kenya, in 2005 (Mirera, 2009) and from experimental grow-out pond studies in Mtwapa Creek (Mirera and Moksnes, 2015) and on Mafia Island, Tanzania (H. Mahudi unpubl. data), in 2010-2011. Realistic estimates of all costs, including initial construction of the pond and all labour costs were made so that this activity could be compared to other established income generating activities. The labour (person-hours) for construction and maintenance were standardized between the two countries to make them comparable, while local costs for material and labour were included. Labour costs for construction and farm maintenance were based on estimated daily salaries in coastal communities in Tanzania (5000 Tsh day^{-1} = 2.9 \$US day^{-1}) and Kenya (350 Ksh day^{-1} = 3.8 \$US day^{-1}) and converted to monthly costs assuming a person working 6 h per day, 26 d per month. The costs of night guards were based on a monthly salary of 65 000 Tsh (37 \$US) and 4500 Ksh (49 \$US) in Tanzania, and Kenya respectively, working 8 h per day, 7 d per week. Conversions of currencies to US dollars were based on the exchange rate in Jan, 2015 (1 \$US = 1733 Tsh and 92 Ksh; www.oanda.com).

For pond culture, the initial costs of construction consisted of manual digging of the pond, building a mud levy around the pond and installing water pipes (10 persons working for 10 days). Yearly labour costs consisted of building a net fence around the pond (3 persons working 2 days), and yearly maintenance and repair of the pond (10 persons working for a total of 2 days). Life expectancy was assumed to be 10 years for the pond itself and 1 to 10 years for tools and material. Cost of seed crab collection for ponds were based on the average number of crabs collected per hour on Mafia Island, Tanzania (13 crabs h^{-1}), and in Mtwapa Creek, Kenya (7 crabs h^{-1}) during recruitment season (April to October in Mafia; Mirera, 2014). On Mafia Island, where collection can only be carried out at night (Moksnes *et al*., unpubl. data) the cost of flashlight and batteries was added (9 \$US per growth cycle). The daily labour costs for a pond consisted of collecting and preparing feed (*Terrebralia* snails, fish offal, etc.) and feeding the crabs (on average 2 person-hours per day). The labour cost of guards was based on 1 person working 7 nights (8 h/night) per week for the last 2.5 months of the growth cycle (when crabs had reached a market size of 300 g). Cost of harvesting crabs and selling them on the local market was based on one person fishing crabs with drop-traps once a week for a month, and two persons draining the pond and harvesting all remaining crabs at the end of the harvest cycle (in total 20 person-hours).

For cage culture, the initial costs consisted of building the 200 individual cages out of mangrove sticks (a total of 80 person-hours). Life expectancy was assumed to be 4-8 years for tools, and 4 growing cycles for the cage material. Cost of seed crabs were based on purchasing 250-300 g crabs from local fishermen for 0.12 \$US in Tanzania (ASDI/VOCA, 2005) and 0.20 \$US per individual in Kenya (Mirera, 2009). The average daily labour costs for a 200-compartment cage farm consisted of collecting and preparing feed, and feeding each crab individually, and repair of the cages (in total 8 person-hours per day). The cost of guards was assumed to be the same as for pond culture (1 person working 7 nights per week), but for the whole culture period (3 months). Cost of collecting commercially sized crabs from the cages and selling was estimated to 12 person-hours in total. The revenue from both forms of culture was estimated based on the prices of market sized mud crabs (>500 g) at tourist hotels on Mafia Island and Dar es Salaam, Tanzania (2.5 \$US per kg) and Mombasa, Kenya (5.4 \$US per kg; Table 1).

Effect of market size of crabs on costs in pond culture

A major difference between the Southeast Asian and East African markets, in particular Tanzania, is that smaller mud crabs (300 g) obtain good prices in the former market (Table 1). Because the inter-molt period increases exponentially with the size of a mud crab (Moksnes *et al.,* 2015), and larger crabs need more feed than smaller crabs, the cost and the need for feed increases exponentially for each additional molt that the crab must pass through. Because the risk of theft is high mainly for commercial size crabs, the cost of preventing theft at the culture site (e.g. night guard) makes up a larger proportion of the total culture cost the longer the commercial sized crabs are kept. Thus, it may be more profitable to harvest and sell crabs smaller than the present market size in Tanzania (>500 g).

To assess how the cost may change with size of the crabs at harvest in pond culture, the total number of seed crabs and amount of feed required (using a feeding rate of 10% of the biomass of crabs per day), and the total cost of seed crabs, feed and theft prevention (employing a night guard one month before the crabs reach 300 g and thereafter) to produce 100 kg of mud crabs harvested at either 300, 500, 700 or 1000 g body weight, using the same methods as in the cost-revenue analyses, were estimated. In these analyses, seed crabs of 15 mm Carapace Width (CW), an average mortality of 10% per month, and a 10x10 m pond for all size-classes were used, resulting in stocking densities between 4 and 7 crabs m^{-2} for the 4 size-classes (assuming no density-dependent mortality) to achieve the same total production of crabs.

Economy and sustainability of scale for grow-out pond farms

One possible way to increase the profitability of crab cultures would be to increase the size of the culture system since the cost per produced crab may decrease with the scale of the operation (i.e. economy of scale). For example, if the size of a pond increases from 10x10 m to 20x20 m, the area of the pond (and available space for crabs) increases 400%, whereas the circumference (and the cost of building a wall and fence) only increases by 200%, and the cost of transportation and distributing feed in the pond increase only a little. However, for crab culture based on collection of wild seed crabs and local feed sources there are issues of sustainability if the farms are too large due to limitations of the local ecosystem (i.e. mangrove forest for placing the farm and for extraction of feed and seed resources). To study these questions, we assessed the economy of scale of pond culture on Mafia Island in Tanzania, and how feed and seed resources limit the maximum size and the profitability of a sustainable farm. Mafia Island was chosen as an example because empiric data on seed and feed limitations are available (Nyqvist, 2010; Hamad, 2012).

The total cost of the required seed crabs and feed, and revenue was estimated for pond culture systems ranging from 50 to 500 m^2 in size, using the same methods as in the cost-revenue analyses (Table 2). The cost per crab was assumed to decrease in larger ponds due to: (1) no increase in cost for tools and pipes for pond construction, (2) little increase in labour costs for daily transportation of feed and feeding, and guarding the farm, (3) only a small increase in the cost of building the fence around the pond, and (4) the labour cost in collecting and preparing the feed (these costs were assumed to increase with area of the pond as the circumference increases with the area ($y = 4x^{0.5}$; where y is the circumference and x is the area). The labour cost of digging the pond and levies, and harvesting the crabs were assumed to increase proportionally with the area of the pond. Two price-scenarios of $US 2.5 and 5.0, representing the high end of prices offered by hotels on Mafia Island and in Dar es Salaam respectively, were assessed (Table 1).

Based on a field survey of alternative mud crab feed sources that were not used for human consumption on Mafia Island, it was estimated that approximately 20 kg of different feed sources (fish offal, maize bran and dried anchovy waste) should be available per day in an average village on Mafia Island. It was assumed that a total of 10 kg of maize bran and unwanted dried anchovies could be collected from 5 households and 5 kiosks in the village, and that 10 kg fish offal could be collected at the village landing site for fisherman every day (Hamad, 2012). These resources were assumed available for free, but competing alternative uses may exist. Based on an impact study of the collection of small juvenile mud crabs on Mafia Island, it was estimated that no more than 1200 small juvenile seed crabs could be fished from the same local area per recruitment season without negative effects on the local population (Nyqvist, 2010).

No attempt was made to analyze the economy of scale of cage culture because the cost-revenue analysis showed that the cost per crab decreased very little with the size of the culture system. This was due to the fact that the crabs were kept in individual cages that had to be constructed, repaired, and opened and closed at each feeding for each crab. Only the cost of guarding and tools decreased with the size of the cage culture.

Results

Markets and prices for mud crabs

In all markets, the best prices were obtained for live crabs, full of meat with both chelipeds (claws) intact. The market size and prices for mud crabs showed large variation both within and between countries and regions (Table 1). The commercial market size in Tanzania and Kenya (500-1000 g in most areas) is substantially higher than the general market size in Southeast Asia (150-400 g). Still, the price ranges per kg in Southeast Asia (US$ 3.0-13.6 kg^{-1}), most of which were based on information >10 years old, were similar to the highest prices presently found in East Africa (i.e. in Kenya; Table 1), indicating higher profit margins in Southeast Asia. In Kenya, there are indications that market sizes have decreased during the last decade, as good prices were also currently obtained for

Table 1. Market sizes and prices for mud crabs in Southeast Asia and East Africa. All prices are in $US based on exchange rates on 01-07-2012. References: (1) Cholik, 1999, (2) Wei Say and Ikhwanuddin, 1999, (3) Trino *et al.*, 1999; Trino and Rodrigues 2002 (4) Johnston and Keenan, 1999, (5) Cann and Shelley, 1999 (6) This study, (7) Mirera, 2011, (8) ACDI/VOCA, 2005, (9) Richmond *et al.*, 2006.

Country	Seed size (g)	Seed price US$ kg^{-1}	Market size (g)	Price/kg US$	Buyer	Ref
Southeast Asia						
Indonesia	350		>400	3.1[1]	-	1
Malaysia	100	1.2	150-300	3.0	Middlemen	2
Philippines	10		>300	8.9-9.5	Middlemen	3
Vietnam	25-100	2.0-4.0	>300	8.0-12.0	Middlemen	4
Australia		0.5-2.9	-	8.7-13.6	-	5
Kenya						
Mombasa			>500	4.7-6.5	Hotels	6
			250-500	2.9	Hotels	6
			>1000	15.0	Exporter	7
			>500	8.0	Exporter	6
Malindi			>500	4.1-5.2	Middlemen	6
			250-500	2.9-4.7	Middlemen	6
Tanzania						
Tanga	250	0.5	700-1000	0.8-1.4	Middlemen	8
Rufiji	-	-	500	1.0	Middlemen	9
Mafia Island	-	-	500	1.3-2.6	Hotels	6
Zanzibar	-	-	500	3.8[2]	Restaurant	6
Dar es Salaam	-	-	500	2.5-5.1	Hotels	6
Dar es Salaam	-	-	500	1.9-3.2	Exporter	9
Dar es Salaam	-	-	700-1000	2.6-7.0	Exporter	6, 8
Mozambique						
Maputo	-	-	200	2.0-3.7[3]	*Market*	6
			400	3.0-5.5[3]	*Market*	6

[1] *Price in 1994*

[2] *Market food-stands selling cooked seafood products to tourist.*

[3] *Prices paid by customers at fish market or to private vendors*

250-500 g crabs. In contrast, the market size in Tanzania is still large (>500 g), and the prices (US$ 0.8-7.0) are several times lower than in the other countries. A large variation was also found within the country. In northern Tanzania, in the Tanga region, the middlemen demanded large sizes (700-1000 g) and paid low prices (US$ 0.8-1.4, ACDI/VOCA, 2005) whereas middlemen in southern Tanzania (Rufiji) accepted smaller crabs (500 g) at similar prices (Richmond *et al.*, 2006). Hotels in Tanzania generally offered higher prices for crabs (US$ 1.3-5.2) than middlemen, and appeared to be more flexible in also accepting smaller crabs (300-500 g). In Kenya, the prices offered by middlemen and hotels were similar (US$ 2.9-6.5), and on average twice as high as in Tanzania. Highest prices in both Tanzania and Kenya were offered by exporters buying large, live crabs (700-1000 g) for the Asian market (Table 1). In Tanzania, there is also a small market for frozen crabs that are exported to the European market. This market accepts smaller crabs (350-700 g), but the prices are lower (US$ 3.0; Richmond *et al.*, 2006).

In Maputo, Mozambique, mud crabs are an important ingredient in traditional dishes, and mainly sold on the local market, and the market size is smaller than in other East African countries (200-400 g). However, the prices on the local markets in Maputo are almost two times higher than in Tanzania (Table 2). In both Tanzania and Kenya, different sources gave very different information regarding size classes and prices for the same market section, indicating an unstructured and dynamic market.

Cost-revenue analyses of cage and pond culture in East Africa

From a cost perspective, the two culture methods differ strongly in the initial investment, and the amount of labour needed during the growth period (Table 2). For ponds, a large initial investment is needed for the construction of the pond, including tools and labour, and the material costs are high, in particular for the fencing around the pond to prevent crabs from escaping. In the first year, the total cost for the construction of a 15 x 15 m pond was estimated to be $US 998 in Tanzania and $US 1051 in Kenya (not including the costs of supervision). The larger costs in Kenya were due to the approximately 30% higher prices of material and labour in Kenya. Since the ponds with levees are expected to last for approximately 10 years (with minor yearly repairs), only the net fence needs to be replaced on a yearly basis over the following 9 years. To estimate the total cost per 11-month growth cycle and harvest, the investment cost in the pond was split with the number of years that the construction, tools and material were expected to last. This resulted in a yearly investment cost of $US 289 and $US 360, and a total cost per harvest of $US 773 and $US 989 in Tanzania and Kenya, respectively, to grow 450 small juvenile seed crabs to commercial size (Table 2). The construction costs represented 36-37% of the total cost per harvest, whereas the costs of daily labour maintaining the culture (on average 2.4 h per day) constituted approximately 41-42% in both countries. Since theft of crabs appears to constitute a major problem, the cost of a night watch for the last 2.5 months of the culture period was included, constituting about 12% of the total cost. Seed crab collection represented 12% and 8% of the total cost in Kenya and Tanzania, respectively.

In contrast, the cost in cage culture involves a smaller initial investment to construct the cages ($US 38 and $US 48 in material and tools, and $US 79 and $US 104 in labour in Tanzania and in Kenya, respectively), but a very high labour costs per growth cycle for maintenance. The total labour costs to maintain the crabs in 200 individual cages for three 3-month growth-cycles was $US 1464 and $US 1109 in Kenya and Tanzania, respectively, representing approximately 68% and 69% of the total cost per harvest. In addition to this, the need for guards during the whole production cycle to prevent theft of the easily accessible crabs constitute a major cost ($US 441 and $US 339 in Kenya and Tanzania) constituting approximately 21% of the total cost per harvest. In comparison, the total cost of crab seeds and cage construction was small (9-11% in total; Table 2). The high labour cost in cage culture is a result of the time consuming labour of opening and closing the lid of individual cages each day to feed, and the high amount of labour required to repair the cages (in total approximately 8 h per day).

The cost-revenue analyses showed that profit margins were low in both systems, particularly in cage culture when using realistic costs of labour. Pond culture showed a $US 226 profit in Kenya in this scenario, but a net loss in Tanzania. The difference between the countries was explained by the more than 2x higher prices paid for market sized crabs in Kenya compared to Tanzania, on average, which more than compensated for the 30% higher labour and material costs in Kenya (Table 2). The break-even price to make a profit in Tanzania in this scenario was $US 3.5 kg^{-1}, which is presently only obtained when selling directly to some hotels and restaurants in Dar es Salaam and Zanzibar (Table 1), a market presently handled by middlemen. If the high initial investment cost of constructing the pond could be avoided, for example through support by an NGO or government, pond culture would be profitable also in Tanzania. However, the economic activity may then not be sustainable once the funding ends and the ponds need to be reconstructed. In contrast to pond culture, cage culture at this scale (450 crabs per year) showed large net losses in both Kenya and in Tanzania, mainly due to high labour cost of daily maintenance, which on its own was higher than the revenue obtained in both countries (Table 2).

Table 2. Cost-revenue of mud crab aquaculture in East Africa. Culture data and cost-revenue estimates assessing the total cost to produce 450 commercially sized crabs (i.e. 500 g) in ponds (15x15 m pond) and cages (200 compartment drive-in cages) in Tanzania and Kenya. To compare profit, 9-month growth-cycles in the pond systems were compared to 3 consecutive 3-month culture periods in cage fattening system. All cost estimates are per harvest cycle of 450 commercial crabs, and are in $US.

	Pond culture		Cage culture	
	Tanzania	Kenya	Tanzania	Kenya
A. Culture data				
Average seed-crab size (g)	0.5	2	300	300
No. seed-crabs	1170	1100	618	618
Stocking density	5.2	4.9	-	-
Culture duration (months)	9.2	8.6	3x3	3x3
Mortality per month	10%	10%	10%	10%
Mortality per harvest	62%	59%	27%	27%
Harvest density	2.0	2.0	-	-
Harvest (no. >500 g crabs)	450	450	450	450
B. Culture costs ($US)				
1. Culture construction	**289**	**360**	**84**	**111**
Labour costs/harvest	140	169	59	78
Material/harvest	149	191	25	33
2. Crab-seed costs	**65**	**102**	**71**	**121**
3. Daily maintenance	**325**	**405**	**1109**	**1464**
Labour costs	316	391	1107	1461
Material	9	14	2	3
4. Security against theft	**94**	**122**	**339**	**441**
TOTAL COSTS	773	989	1607	2141
C. Culture revenue ($US)				
Harvest (kg)	225	225	245	245
Price per kg	2.5	5.4	2.5	5.4
Revenue	**563**	**1215**	**638**	**1324**
D. Harvest profit ($US)	**-211**	**226**	**-970**	**-816**

Effect of market size of crabs on costs in pond culture

The results show that the culture time varied from 9.1 month to produce 300 g crabs to 11.6 and 16.4 months to produce a 500 g and 1000 g crab, respectively. The number of seed crabs needed to produce 100 kg of crabs decreased from around 700 seeds for crabs harvested at 300 g, to around 400 seeds to produce 100 kg of 1000 g crabs (Fig. 1a). Thus, although the total mortality was higher during the longer culture time needed to raise the larger crabs, their large final size still meant that fewer seed crabs were needed compared to raising smaller commercial crabs. In contrast, the total amount of feed needed for the whole culture period increased 2.6 times with the size of the harvested crabs, from 644 kg feed to produce 100 kg

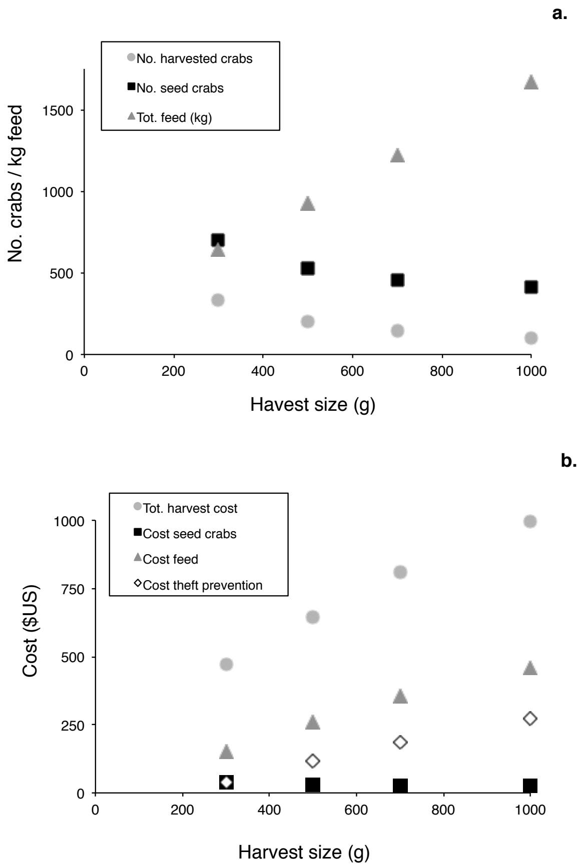

Figure 1. Pond culture of mud crabs. Relationship between the size of mud crabs at harvest (300, 500, 700 and 1000 g) and (a) the total number harvested crabs, total number seed-crabs, and total amount of feed needed to produce 100 kg of mud crabs, and (b) the cost of seed crabs, feed, theft protection (night guard) and the total cost to produce 100 kg of mud crabs at different harvest size.

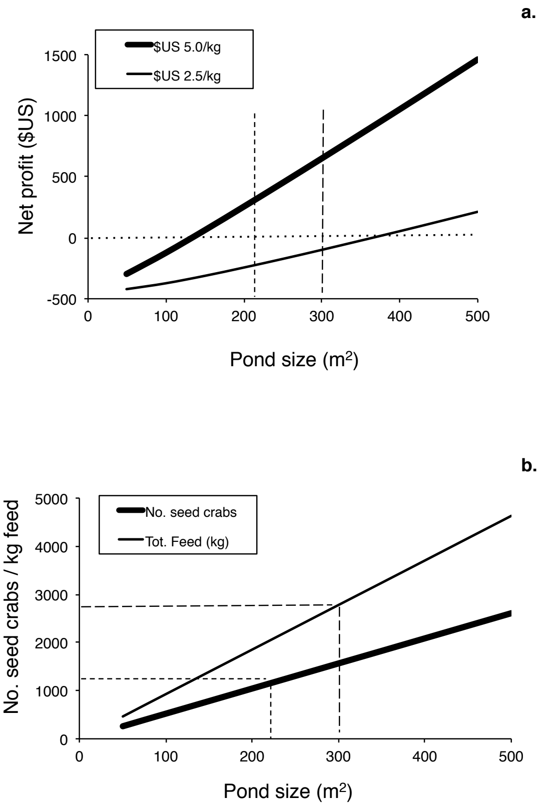

Figure 2. Pond culture of mud crabs. Relationship between the size of aquaculture pond and (a) the profit of the aquaculture at two different price scenarios for 500 g crabs, and (b) the total number seed-crabs, and total amount of feed needed to produce two 500 g mud crabs m^{-2}. Dashed lines indicate the suggested maximum sustainable level of seed crabs and feed that can be collected at an average village on Mafia Island.

of 300 g crabs, to 1668 kg feed to produce the same biomass of 1000 g crabs. Because small seed crabs are relatively inexpensive to collect, feed is costly, and the cost of theft prevention is 3 times higher for the largest crabs, the total cost per harvest increased by over 100% with the size of the produced crabs, from $US 473 for 300 g crabs, to $US 996 to produce 100 kg of 1000 g crabs (Fig. 1b).

Economy and sustainability of scale for pond culture

The results show that as the size of the pond increases from 50 to 500 m², the profit in the $US 5 price-scenario increases rapidly from minus values at a pond size of 50 m², breaking even at a pond size of 133 m² (11.5 x 11.5 m), and making a profit of almost $US 1500 at a pond size of 500 m² (Fig. 2a). At the price-scenario of $US 2.5, the increase in profit is much slower, and the farm does not break-even until the pond is 365 m², making a profit of $US 213 at the 500 m² pond size (Fig. 2a). However, as the pond size increases, the total number of seed crabs needed increases from 260 to over 2600 crabs, and the total amount of required feed increases from 463 to over 4630 kg (Fig. 2b).

For crab feed, the limiting factor was assumed to be the amount of feed needed per day during the last inter-molt period (2.6 months) at the end of the growth period when the crabs are largest. Based on the maximum sustainable amount of feed that could be obtained per day from a village on Mafia (20 kg), a maximum of approximately 770 crabs with an average size around 270 g could be fed per village. This would result in a total amount of crab feed needed during the growth cycle of approximately 2800 kg and limit the maximum size of the pond to around 300 m² (Fig. 2b), which in turn limits the maximum profit at a price $US 5 per kg to approximately $US 650 per harvest. However, at a price of $US 2.5, a pond of this size is too small to yield any profit (Fig. 2a).

In addition, the availability of crab seed further limits the maximum pond size. The maximum sustainable number of seed crabs that could be collected per month (1200 crabs) limits the maximum size of a pond to approximately 230 m^2, in which a maximum of 460 market size crabs can be raised (assuming 10% mortality per month). This in turn limits the maximum profit of the $US 5 price-scenario to approximately $US 374 per harvest, and prevents the aquaculture operation realizing a profit if the price is $US 2.5 per kg. At this pond size, the break-even price is $US 3.4 per kg.

Discussion

Cage culture

In the last decades, various NGOs in East Africa have tried to develop small-scale aquaculture of mud crabs as an alternative livelihood for coastal communities. The method promoted is based on collection of subadult mud crabs (80-110 mm CW) from the wild that are farmed in individual cage-systems through several molts until they reach market size (Rice *et al*., 2006; Shipton and Hetch, 2007; Mirera, 2011). However, recent studies suggest that this culture method has several limitations, obtaining growth rates of <40% of those in the wild for *S. serrata* in East Africa (Moksnes *et al.,* 2015). In addition, the high mortality rates in these culture practices (on average 19% month^{-1}; Mirera, 2009, Mirera and Mtile, 2009) appear to be several times higher than natural mortality for this size-class of crabs (approximately 4% month^{-1}; Mirera, 2014) suggesting that this type aquaculture is in fact decreasing the overall local production of crabs. The present study adds to this critique by demonstrating that these culture activities also provide very low profits when taking into account the cost of labour.

Although we simulated much higher growth and survival rates than what is presently obtained in these forms of culture (75% of natural growth and 10% mortality month^{-1}, respectively) cage culture resulted in net losses (equivalent to $US 323 and 272 per 3-month growth cycle of 150 crabs, respectively in Tanzania and Kenya). The low profit was mainly due to the high cost of daily labour for maintenance, which is time consuming because each individual cage has to be opened and closed at feeding, and the need of almost daily repair. Excluding this labour cost in the cost-revenue analysis resulted in a profit equivalent to a salary of $US 0.28 and $US 0.03 per hour, approximately only 45% and 6% of the average salary in coastal communities in Kenya and Tanzania, respectively. Thus, the present form of cage culture does not appear to constitute an attractive source of income for coastal communities, at least not for persons that have other alternatives. If more realistic (lower) growth and survival rates had been used in the analyses the profitability of this culture method would have been even lower.

The results indicating low profit obtained by cage culture of crabs differs from analyses of an experimental cage culture system in Kenya, which showed a high return on capital investment (Mirera 2009). However, in that analysis the cost of labour for daily maintenance was not included. The present results are consistent with cost-revenue analyses from the Tanga region that also showed a net loss (ACDI/VOCA, 2005). In that study it was suggested that profit would increase for larger cage culture farms. However, in the present study we assessed farms that were many times larger than the farms presently in use in East Africa (10-100 crabs per farm; ACDI/VOCA, 2005; this study), and we found that profit increased very little with the size of the fattening operation.

In combination, the poor growth, survival, and profitability of mud crabs farmed through several molts in individual cages demonstrated that this culture method does not constitute a sustainable or profitable alternative livelihood in its present form. These issues must be solved before cage farming is promoted to coastal communities in East Africa. The poor survival rates in the cages, despite the fact the crabs are kept separately to prevent cannibalism, indicate that the intertidal cage environment where crabs only have access to water during high tides is a poor environment for completion of the molt processes. For aquaculture requiring molts, culture systems that allow crabs permanent access to water, such as pond or pen systems, appear to perform much better.

In Southeast Asia, mud crab fattening has been described as a profitable enterprise, but it differs in an important aspect from the fattening operation in East Africa, i.e. crabs are only fattened for a short period of time (<1 month), and are sold prior to molt, to decrease mortality (Keenan, 2003). Mud crab fattening in East Africa could possibly become profitable if farmers adopted the same strategy, and only fattened adult crabs with low meat content for a short period of time. Studies to investigate this possibility from practical, environmental and economic perspectives are encouraged.

Grow-out culture in ponds and pens

Grow-out aquaculture of small juvenile mud crabs in ponds or pens shows better potential to develop into a sustainable and profitable livelihood in East Africa compared to current cage farming practices. Recent studies demonstrated that small juvenile mud crabs can be efficiently collected at low tides with minimal negative environmental impact, and indicated high growth rates in both pond and pen cultures. However, high mortality rates and low market price and profitability are issues that need to be resolved for this farming to be profitable in East Africa.

Progress and challenges of pond and pen culture methods in East Africa

Recent studies have identified mangrove fringes and back-flats as important habitats for small juvenile mud crabs in East Africa where high numbers of small seed crabs (up to 40 crabs person^{-1} h^{-1}) can be collected at low tide by hand with no by-catch and minimal impact on the environment (Karlsson, 2009; Mirera, 2014). The studies also suggest that natural mortality of small juvenile mud crabs (<20 mm CW) in East Africa is very high (>50% month^{-1}), but decreases strongly with size indicating that small juvenile stages represent a bottleneck in the life-history of mud crabs where most crabs perish due to high predation mortality (Mirera, 2014; P-O Moksnes, unpubl. data). These results suggest that negative impacts of a seed crab fishery on local populations would be minimized if small juvenile stages were used as seeds, and that the aquaculture operation could increase the local production of crabs if survival in the culture were higher than in nature. In South East Asia, small-scale, grow-out farms for *S. serrata* using small juvenile seed crabs (12-50 mm CW) in pond or pens obtain mortality rates <10% month^{-1} (Baliao *et al.*, 1999; Trino *et al.*, 1999; Trino and Rodrigues, 2002), suggesting that grow-out culture based on collection on small juvenile crabs has the potential of increasing the local production of mud crabs and be more sustainable than culture based on collection of large crabs.

Experimental pond and pen studies in East Africa using small juvenile seed crabs show high growth rates (93-112% of natural growth rates) when shelter is provided in the culture systems (Mirera and Moksnes, 2015). However, mortality rates during the first 2-3 months of culture in these studies have been very high (on average 41-58% month^{-1}), likely due to high rates of cannibalism (Mirera and Moksnes, 2015), a problem that needs to be resolved before the culture could be profitable. Recent studies in East Africa demonstrate that juvenile cannibalism could be minimized by separating small and large juvenile seed crabs to keep the size-ratio below 50%, and by providing shelter to the juveniles in the culture system (Mirera and Moksnes, 2013; 2015). Studies in Southeast Asia also indicate that cannibalism is lower at lower stocking densities (Trino *et al.*, 1999; Trino and Rodriguez, 2002). Further studies assessing how mortality can be decreased in East African grow-out culture in ponds and pens are needed.

Profitability and sustainability of grow-out culture in East Africa

In the Philippines, small-scale, grow-out culture of *S. serrata* in 200 m^2 pens integrated in mangrove forests was found to be profitable with a high return on capital investment (49-68%) even after including the cost of labour (Trino and Rodriguez, 2002). In the current cost-revenue analysis of similarly sized pond culture operations (225 m^2) in East Africa, simulating survival rates presently obtained in Southeast Asia (90% month^{-1}), but using growth rates, cost and market prices presently obtained in East Africa, showed a much smaller profit margin. At this size of operation, a positive return of the investment could only be obtained with prices above $US 3.4 per kg for market sized crabs, which is currently achievable in Kenya and Mozambique, but difficult in Tanzania. Market analyses showed that prices for mud crabs were over 50% lower in Tanzania than in other East African countries, and that most of the profit appears to go to middlemen and exporters (Table 1).

In Southeast Asia, the market size of mud crabs (>300 g) is smaller than the size in most markets in East Africa (>500-1000 g). Still, the prices for mud crabs available to farmers in South East Asia are much higher compared to East Africa (Table 1). Thus, there appear to be room to improve the prices obtained by crab farmers and fishers in East Africa, particularly in Tanzania. Studies investigating ways to develop new markets and market-chains for crab farmers to improve the prices and the profitability of the culture activity in East Africa are needed.

The present study showed that farming crabs to 300 g would require 25% and 75% less time, 48% and 159% less feed, resulting in 36% and 111% lower total costs compared to farming the same total biomass of crabs to 500 g and 1000 g, respectively. In addition to having lower costs, the shorter culture time of farming crabs to 300 g would allow more harvests in the same amount of time, and decrease the risk for unpredictable events (e.g. heat shocks, storms, theft, diseases, etc.) that may ruin the crop and subsequent profit. Thus, farming crabs to 300 g would be more sustainable from a feed perspective, less risky, and possibly also more profitable than farming larger crabs, if there was a market for this size class of crabs. In Kenya, a market for smaller crabs appears to be developing as both middlemen and hotels pay high prices (US$ 2.9-4.7) for crabs as small as 250 g, although larger crabs still obtain a higher price, particularly for the export market (Table 1). In Tanzania, most middlemen and hotels still want crabs of 500 g or larger, but some hotel are starting to accept smaller crabs because of increasing demand. There are also reports that middlemen in the Rufiji area, and exporters in Dar es Salaam are showing interest in 300 g crabs, particularly for the market of frozen mud crabs destined for Europe, which obtain a relatively high price (US$ 3.0; Richmond *et al.*, 2006). In Tanzania, the break-even price for farming crabs to 300 g in a 225 m^2 pond would be $US 2.2 per kg, and at a price of $US 3.0 per kg, the farm would make a net profit of $US 180 per 9-month cycle (assuming 10% mortality $month^{-1}$). Promoting a market for 300 g mud crabs in East Africa could thus be one way to assist the development of pond aquaculture in the region. However, since a larger number of seed crabs are needed to farm the same biomass of 300 g crabs compared to e.g., 500 g crabs (at 10% mortality $month^{-1}$), the availability of seed crabs may limit the size of a sustainable pond, and therefore its profitability. Since *S. serrata* in East Africa becomes sexually mature at around 300 g (Roberson and Kruger, 1994) care must also be taken not to promote a market for even smaller crabs. If fishers start to exploit immature crabs before they have a chance to reproduce it may have negative effect on wild populations.

Another way to increase profitability would be to increase the size of the mud crab farm. The present study showed that the profit of a pond culture operation increased rapidly with the size of the pond, making a profit of almost $US 1500 at a pond size of 500 m^2 in the $US 5 price-scenario, and breaking-even at a pond size 365 m^2 in the $US 2.5 price-scenario. However, both the availability of small juvenile seed crabs and sustainable crab feed limit the maximum size of pond culture systems in a coastal community to approximately 460 and 770 market size crabs per 11-month growth cycle, respectively. This in turn limits the maximum profit to approximately $US 374 per harvest at the $US 5 price-scenario, and prevents the aquaculture operation from realizing a profit if the price is $US 2.5 per kg.

The sustainable limit of 1200 seed crabs per village area (ca 5 km of mangrove shore line) is a rough estimate based on mark-recapture studies on Mafia Island. These studies showed limited dispersal of juveniles (Björkvik, 2010) and no detectable effects on local juvenile populations by removing ca 330 small juvenile mud crabs (5-15 mm CW) from a 50 m area of the shore in 2 weeks of intensive sampling (Nyqvist, 2011). However, this is only based on one studies from one location, and more studies are needed to assess the sustainable levels of seed crab fisheries in different areas of East Africa. Since the fishery of mud crabs is unregulated in Kenya and Tanzania, and there are indications of overfishing in several areas (Francis and Bryceson, 2001; Mirera, 2012), an unregulated fishery for juvenile seed crabs may enhance the overexploitation and result in declining stocks, as have been reported in Southeast Asia (Keenan, 2003). A fishery for juveniles may also lead to competition with local traditional fisheries for adult crabs. Even if juvenile seed crabs are fished in a sustainable way, the difficulty of collecting high numbers of juveniles may inhibit larger culture operations. The experience from intensive sampling of small juvenile crabs during a two year period at multiple sites in Tanzania, Kenya and in Mozambique suggest that it would be very difficult to obtain more than 1000 small juvenile mud crabs (<40 mm CW) within one month, from any mangrove area in East Africa due to the low densities of juveniles (Mirera, 2014; P-O Moksnes unpubld. data). Thus, natural availability of seed crabs put strong limitations on the scale of mud crab culture in East Africa.

In Southeast Asia, larval hatchery techniques have been developed for several species of mud crabs for production of juvenile seed crabs to industrial scale mud crab farms (Shelley and Lovatelli, 2011). Using seed crabs from hatcheries would clearly be more sustainable than collecting crabs from the wild, and could be a long-term solution to meet an increasing demand in East Africa. However, larval hatcheries require advanced laboratories and are sensitive operations. For example, in Australia, despite considerable efforts, larval hatchery methods for *S. serrata* have proved difficult to develop (Allan and Fielder, 2004). It is therefore not realistic to expect high-technology hatcheries to provide a dependent and low priced supply of seed crabs to local farmers in East Africa in near future.

Furthermore, cost and transportation issues may prevent the effectiveness of such hatcheries in remote resource-poor coastal communities.

Even if hatchery-produced seed crabs become available in East Africa, the availability of sustainable crab feed also limits the maximum size of pond and pen culture possible in coastal communities. To find acceptable and sustainable sources of feed for aquacultures is critical in many developing countries where low valued fish resources constitute important protein sources for human consumption (Funge-Smith *et al.*, 2005; Camber, 2008; Beveridge *et al.*, 2013). Most cage culture farms in East Africa use mangrove snails (*T. palustris*) as a feed. However, these snails are also consumed by humans, and recent field studies on Mafia Island indicate that intense collection to feed small cage culture farms can have negative effects on local snail populations (Hamad, 2012). Thus, mud crab farms using mangrove snails as feed can compete with food for humans if performed at a large scale. In the present study, we assessed how the availability of alternative crab feed resources, which were not used for human consumption, could affect the scaling-up of the farming operation. Hamad (2012) showed that alternative feed sources for mud crabs that were not used for human consumption (fish offal, maize bran and dried anchovy wastes), as well as mangrove snails, resulted in high growth rates in small juvenile mud crabs. On Mafia Island, it was estimated that approximately 20 kg of these feed sources should be available per day in an average sized village (Hamad, 2012), which would limit the maximum size of a pond culture to approximately 300 m^2 and 770 market size crabs (500 g) per village per year, and preventing a profit at the prices presently obtainable on the island. The size of the culture and the production could possibly increase by collecting mangrove snails as a complement. However, considering the large amount needed per day, it would be very time consuming and costly, affecting profitability, and importantly, will likely not be sustainable.

On Mafia Island there is a fish processing plant that produces over 100 kg of byproducts per day that could possibly be used as feed, if made available to crab farmers (Hamad, 2012). If the limitation of seed crabs was solved, villages with access to such or similar food sources could possibly increase the size of the total pond area and the production of mud crabs by approximately 6 times. It is important to note that even a 1800 m^2 pond is very small compared to the industrial grow-out farms for mud crabs in Southeast Asia and China that are often 10-100 times larger (Table 1). Even if all available byproducts on Mafia Island were used as feed there would not be enough feed resources on the island to support a commercial farm of that scale. A commercial-scale mud crab farm would therefore result in competition for food resources with humans and other cultured animals, unless commercial feeds or feed resources were imported. In addition, large-scale industrial mud crab farms would likely result in the clearing of mangroves and destruction of coastal environments, similar to what has occurred as a result of the development of penaeid shrimp farms (Naylor *et al.,* 2000).

In summary, grow-out pond culture of mud crabs could potentially be developed into a sustainable alternative source of income for coastal communities in East Africa. Methods to collect small juvenile seed crabs and farm them in ponds and pens are currently available in East Africa (Mirera and Moksnes, 2015; Mirera, 2014) and local sources of feed appear available in coastal villages. However, mud crab farming based on wild seed crabs and locally available feed can only be sustainable on a very small scale. Moreover, before this activity should be recommended there is a need to solve problems related to high mortality rates in the pond culture systems, and to improve markets and market-chains to increase profits for farmers. Decreasing the market size to 300 g crabs may be one way to improve profit margins. For expansion of these systems to larger scales, interactions with local ecosystems need to be carefully evaluated and hatcheries and formulated feeds need to be developed.

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Gear-based species selectivity and potential interactions between artisanal and aquarium fisheries in coastal Kenya: implications for reef fisheries management

*Gladys M. Okemwa[1, 2], Boaz Kaunda-Arara[2], Edward N. Kimani[1], Benrick Ogutu[3],
Harrison Ong'anda[1], Clay Obota[1], Mary Ontomwa[1]

[1] Kenya Marine and Fisheries
Research Institute,
P.O. Box 81651-80100,
Mombasa, Kenya

[2] University of Eldoret,
P.O. Box 1125-30100,
Eldoret, Kenya

[3] State Department of Fisheries,
P.O. Box 90423-80100,
Mombasa, Kenya

* Corresponding author:
gokemwa@kmfri.co.ke

Abstract

Multivariate and ecological approaches were used to investigate potential interactions in species selectivity between artisanal and aquarium fisheries on the south coast of Kenya. Aquarium fishery landings were monitored from September 2010 to March 2013, while artisanal landings were monitored over 1 year from January to December 2014. Target aquarium species constituted approximately 12% of the artisanal catches by weight and 8% by relative abundance, and was comprised of 17 fish families and 58 species dominated by wrasses. Handlines and spearguns had the highest potential interaction with the aquarium fishery. Pair-wise comparisons of Pianka's overlap index revealed basket traps and monofilament gillnets as having the strongest overlap. The index further showed that aquarium snorkel fishers had a higher overlap in species selectivity with artisanal gears; while DCA ordination also showed a high overlap in the shared fishing grounds. DCA ordination further revealed the ornamental angelfishes, *Pomacanthus imperata* and *Pomacanthus semicirculatus* as strongly associated with spearguns, while the wrasses *Halichoeres hortulanus* and *Thalassoma hebraicum*, and the surgeonfish *Acanthurus leucosternon* were strongly associated with handlines. Spatial regulation of fishing effort will be most appropriate in minimizing the cumulative effects of fishing on vulnerable species resulting from interactions between the two fisheries.

Keywords: catch composition, resource overlap, Shimoni, Western Indian Ocean

Introduction

Coral reef fisheries are multi-species and multi-gear in nature, and provide an important source of protein as well as livelihoods for coastal communities worldwide (Davies *et al*., 2009). Over 55% of the world's coral reefs have been estimated to be under threat from unsustainable fishing practices caused by unregulated fishing effort and the use of destructive fishing methods (Jennings and Keiser, 1998; Burke *et al.,* 2011) including beach seines (Mangi and Roberts, 2006) and dynamite fishing (Wells, 2009). Nearly 95% of Southeast Asian reefs are affected by overfishing compared to 65% of reefs in the Indian Ocean (Burke *et al*., 2011). In Kenya, an estimated 163 reef fish species belonging to 38 families are captured in artisanal food fisheries (McClanahan and Mangi, 2004; Tuda *et al*., 2016), while the aquarium fishery targets over 220 reef fish species and continues to expand in the diversity of species targeted and extent of fishing grounds (Okemwa *et al*., 2016). Artisanal fishers mainly use passive non-selective fishing methods such as basket traps, gillnets and handlines, but even methods which may seem to be selective such as spearguns also capture fish opportunistically and are thus non-selective in practice (Fenner, 2012). Artisanal gears also capture a high volume of juvenile reef fish with estimates averaging at about 50% of the total catches (Mangi and Roberts, 2006). On the other hand, aquarium fishers selectively target juveniles of specific species and sizes which are strongly associated with corals (Wood, 2001; Sadovy and Vincent, 2002).

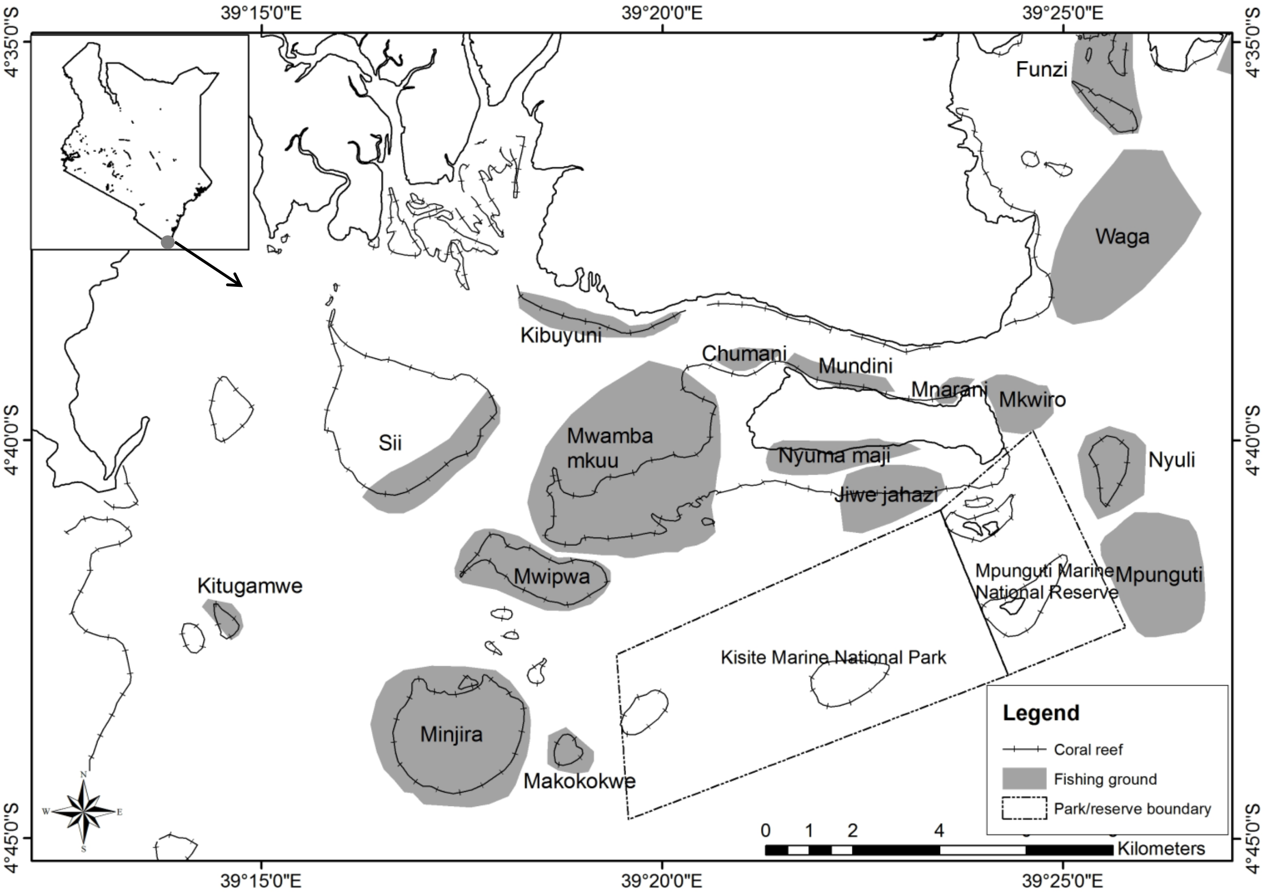


Figure 1. Map showing the location of key artisanal and aquarium fishing grounds in the Shimoni area of coastal Kenya.

Management of multi-species and multi-gear reef fisheries is typically challenging and requires a good understanding of the technical interactions, whether direct or sequential, between co-occurring fishing gears and fisheries (Hoggarth *et al.*, 2006). Such interactions can have significant impacts on fisheries yields, biodiversity and habitat quality especially where fishing effort is concentrated within restricted areas. In shared fishing grounds, different gear types and fishing methods can interact resulting in different life stages of the same stocks suffering fishing mortalities due to variations in the selectivity of the fishing methods used. Various studies have assessed interactions in species selectivity among artisanal gears (McClanahan and Mangi, 2004; Nunes *et al.*, 2009; Stergio *et al.*, 2002; Tuda *et al.*, 2016), between artisanal and industrial fisheries (e.g. Leroy *et al.*, 2016; Munga *et al.*, 2014), and between recreational and commercial fisheries (Cooke and Cowxs, 2006). However, similar studies within small spatial-scales are limited, especially in the western Indian Ocean (WIO). Regular collection of site-specific information on fishing pressure, gear use and selectivity can be useful in assisting managers to make informed decisions about adaptively managing gear (Cinner *et al.*, 2012). In this context, this study aimed to investigate potential interactions in species selectivity between artisanal fishing gears and commercial aquarium fisheries in coastal Kenya and further discusses the implications for reef fisheries management.

Materials and Methods

Study area

The study was carried out on the south coast of Kenya in the Shimoni area near the Tanzanian border (Fig. 1). The Shimoni area is fringed with an extensive cover of mangrove forests, and contains intertidal areas covered with seagrass beds and a complex of patchy and submerged lagoonal reefs. Water depth in the fishing grounds varies but is generally shallow (up to 12 metres) during spring low tide. The area contains the Kisite Marine National Park (KMNP) (Fig. 1), a no-take zone where all fishing activities are prohibited, and the Mpunguti Marine National Reserve (MMNR) which serves as a buffer zone adjacent to KMNP where the use of traditional fishing methods such as basket traps

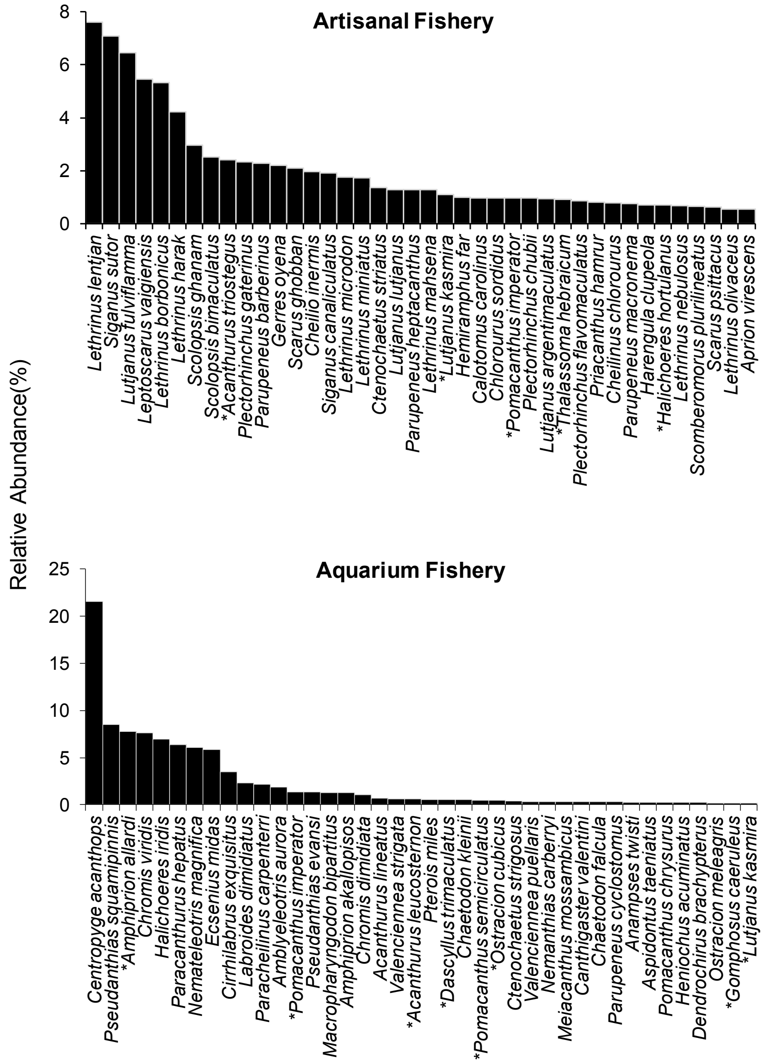


Figure 2. Composition of the 40 most abundant reef fish species landed by (a) artisanal and (b) aquarium fisheries in the Shimoni area, Kenya. Species that overlapped between the two fisheries are marked with an asterisk.

and handlines is allowed. Artisanal fishers mainly use traditional non-motorized vessels which limits fishing effort to nearshore shallow areas within coral reefs, mangrove creeks, and seagrass beds (McClanahan and Mangi, 2000). Shimoni is also notably among the most important fishing grounds for the marine aquarium fishery in Kenya (Okemwa *et al.*, 2016). Aquarium fishers use scoop and barrier nets by either snorkel or SCUBA diving and fish in small distinct groups targeting different species influenced by depth distributions (Okemwa *et al.*, 2016). Generally, fishing activities in the area are influenced by monsoon seasonality with more intense fishing effort being exerted during the northeast monsoon season (NEM) when the sea is calm (Ochiewo, 2004).

Data collection

Artisanal fisher catches were monitored for 5 - 7 days monthly from January to December 2014. The landings were sampled randomly as fishers landed the catches for weighing. For each fishing operation, the fishing gear used, boat type, fishing grounds, and number of fishers was recorded. The total weight (kg) of the entire catch for each fisher was measured and recorded. The catch was then sorted and the landed fish identified to species using identification guides (Lieske and Myers, 2001; Anam and Mostarda, 2012). Digital photos were taken for fish that were not immediately identifiable and a photo identification number was recorded as a reference for later identification purposes. The individual weight of the fish was measured using a hand-held electronic spring

Table 1. The number of species (S), Margalef's species richness (d), Shannon diversity index (*H'*) and Pielou's evenness (*J'*) for the artisanal and aquarium fishery in Shimoni, Kenya by gear type and fishing method (SCUBA fishing vs. snorkeling)

Fishery	Gears / Methods	Average length of fish (cm)	S	(D)	(*J'*)	(*H'*)	Avg. nº of species day $^{-1}$ vessel $^{-1}$
Artisanal fishery	Handlines	22	145	18.37	0.73	3.62	13
	Basket traps	20	104	13.81	0.70	3.25	11
	Spearguns	23	88	12.78	0.68	3.07	8
	Monofilament nets	23	45	8.10	0.77	2.93	18
	Reef seines	20	47	7.04	0.68	2.60	6
	Gillnets	27	38	6.20	0.71	2.59	4
	Cast nets	11	3	0.31	0.46	0.51	2
	Ringnets	58	2	0.25	0.94	0.65	1
Aquarium fishery	SCUBA fishing	-	106	10.65	0.58	2.71	8
	Snorkeling	-	122	12.4	0.55	2.67	10

balance (to the nearest gram), while total length (TL) was taken using a measuring board to the nearest 0.1 cm. In cases where the catches were large (e.g. schooling fish), a representative sample of approximately 10-20 % of the total catch was taken and measured as above.

For the aquarium fishery, the fish catch data was collected for 5-10 days monthly from September 2010 to March 2013. Vessel captains were requested to record the species and numbers collected, total number of fishers and fishing method used, and the fishing grounds visited for each fishing trip. The data recorded by the captains was validated on landing before the fish were loaded into vehicles for transportation to holding facilities. In addition, secondary data officially reported by aquarium dealers was obtained from the State Department of Fisheries (SDF) for the period January - December 2014 detailing species and numbers collected from the Shimoni area.

Data analysis

Artisanal fishing effort was estimated as the summation of number of fishers recorded daily (number of fisher days) for each gear type. The fish species landed were categorized by commercial use as: C (artisanal commercial) or A (Aquarium). Categorization of aquarium species was based on published species lists (Okemwa *et al.*, 2016) and data compiled by the SDF. To estimate the proportion of juvenile fish caught by each gear, the total lengths for each species caught were compared against published estimates of length at 50% maturity extracted from Fishbase (Froese and Pauly, 2015) and published literature (Mangi and Roberts, 2006). The fish were then categorized as either juvenile or mature and the relative percent abundance of juveniles for each gear calculated.

Histograms were generated for the 40 most abundant species for the main gear types in order to compare catch composition between gear types within a fishery, and between fisheries (Artisanal and Aquarium).

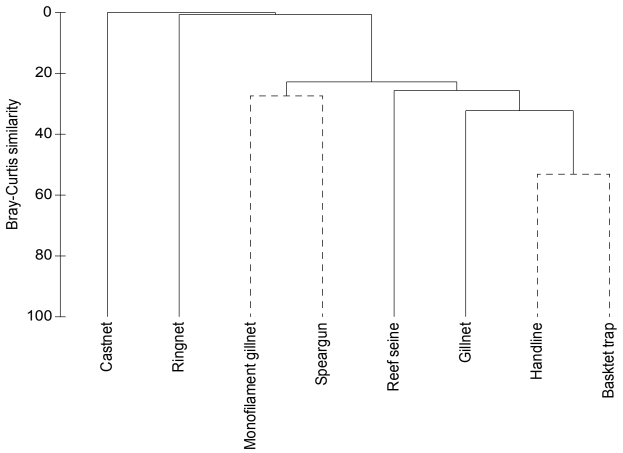


Figure 3. Cluster analysis dendrogram showing the similarity in species composition of 8 gear types used in the Shimoni area, Kenya. The dashed lines indicate sub-clusters that were not detected as significant by the similarity profile (SIMPROF) test (at P<0.5).

Table 2. A pairwise matrix showing interactions in species selectivity among the main artisanal fishing gear types and aquarium fishing methods in Shimoni, Kenya, based on Pianka's niche overlap (*Oi*) index which ranges between 0 (total separation) and 1 (total overlap)

	Handline	Basket trap	Speargun	Reefseine	Gillnet	Monofilament gillnet	Aquarium SCUBA fishing	Aquarium snorkel fishing
Handline		0.545	0.233	0.392	0.453	0.334	0.002	0.039
Basket trap			0.415	0.469	0.549	0.722	0.0001	0.005
Speargun				0.326	0.176	0.418	0.012	0.017
Reef seine					0.368	0.351	0.001	0.009
Gillnet						0.403	0.0001	0.002
Monofilament gillnet							0.0003	0.003
Aquarium SCUBA fishing								0.016

Three community indices (species richness S, Shannon-Wiener H' and Pielou's evenness J') as described by Magurran (1988) were used to characterize the diversity of the catches. Hierarchical agglomerative cluster analysis (Clarke and Warwick, 2001) was used to confirm the degree of similarity in species selectivity among the artisanal gear types. Prior to the cluster analysis, Bray-Curtis similarity index was applied on square-root transformed data to down-weigh the influence of rare and extremely abundant species. The Similarity Profile (SIMPROF) analysis test (Clarke *et al.*, 2008) was then used to detect the presence of a statistically significant structure in identified clusters. Further, Pianka's index (Pianka, 1973) was used to characterize overlap in species selectivity, calculated as follows:

$$O_{kl} = = \frac{\sum_i^n p_{il} p_{ik}}{\sqrt{\sum_i^n p_{il}^2 \sum_i^n p_{ik}^2}}$$

Where, O_{kl} = Pianka's index of niche overlap between gear k and gear l, p_{il} = the proportion of the ith species in gear l, p_{ik} = the proportion of the ith species in gear k, and n = the total number of species. The index ranges from 0 (no species in common) to 1 (complete overlap). There was a basic assumption in using the index that all species were equally accessible to all the gears. Detrended Correspondence Analysis (DCA, Hill and Gauch, 1980), which ordinates associations between paired groups in a two-dimensional space, was applied to test for associations in species selectivity among artisanal fishing gears based on the composition of aquarium species captured, and for associations with fishing grounds. In addition, the dominance of aquarium species captured in the artisanal gears was assessed by plotting K-Dominance Curves (Clarke and Warwick, 2001) of the catches for the main gear types. The data analyses were done using PRIMER version 6.1.5 (Clarke and Gorley, 2006) and STATISTICA version 7 Software (StatSoft, Inc., 2007). EcoSim v. 7.0 (Gotelli and Entsminger, 2001) was used to calculate niche overlaps.

Results

Species composition

A total of 7,786 individuals caught in the artisanal gears were identified to species and consisted of 52 families and 230 species. The artisanal catch was dominated by Lethrinidae (20%), Atherinidae (10.3%), Siganidae (9%), Scaridae (9%), Lutjanidae (8.2%) and Labridae (6%) by weight. The most abundant species included *Lethrinus lentjan* (7.6%), *Siganus sutor* (7.1%), *Lutjanus fulviflamma* (6.5%), *Leptoscarus vaigiensis* (5.5%), *Lethrinus borbonius* (5.3%) and *Lethrinus harak* (4.2%) respectively (Fig. 2a). For the aquarium fishery, a total of 2,033 fish were recorded constituting 183 species of which 90% was composed of 23 species (Fig. 2b). Aquarium fisher catches were dominated by small sized species including the angelfish *Centropyge acanthops* (21%) and the anthias, *Pseudanthias squamippinnis* (9%).

Gear use and selectivity

Artisanal fishers mainly used handlines, spearguns, basket traps, reef seines and gillnets which constituted 89% of total landed catch by weight (2795 kg),

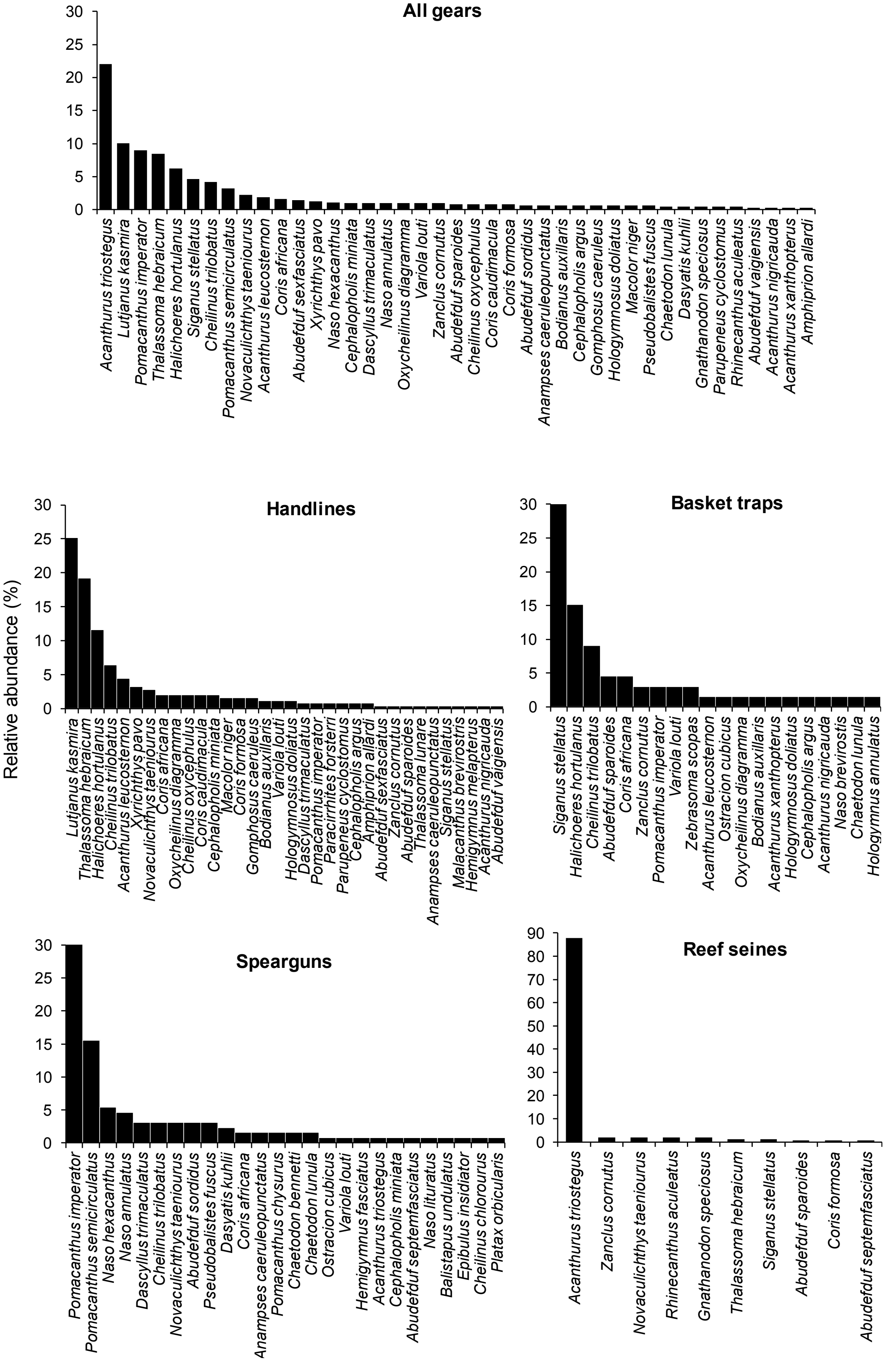


Figure 4. The relative abundance of aquarium species captured by the four main artisanal gear types used in the Shimoni area, Kenya.

Table 3. The diversity of aquarium species captured by artisanal fishers from major fishing grounds in the Shimoni area, Kenya indicating number of species, S; number of fishing units sampled, N, and proportional abundance; Margalef's species richness D; Pielou's evenness, *J'*; and Shannon diversity index, *H'*; during January to December 2014. Refer to Fig. 1 for locations.

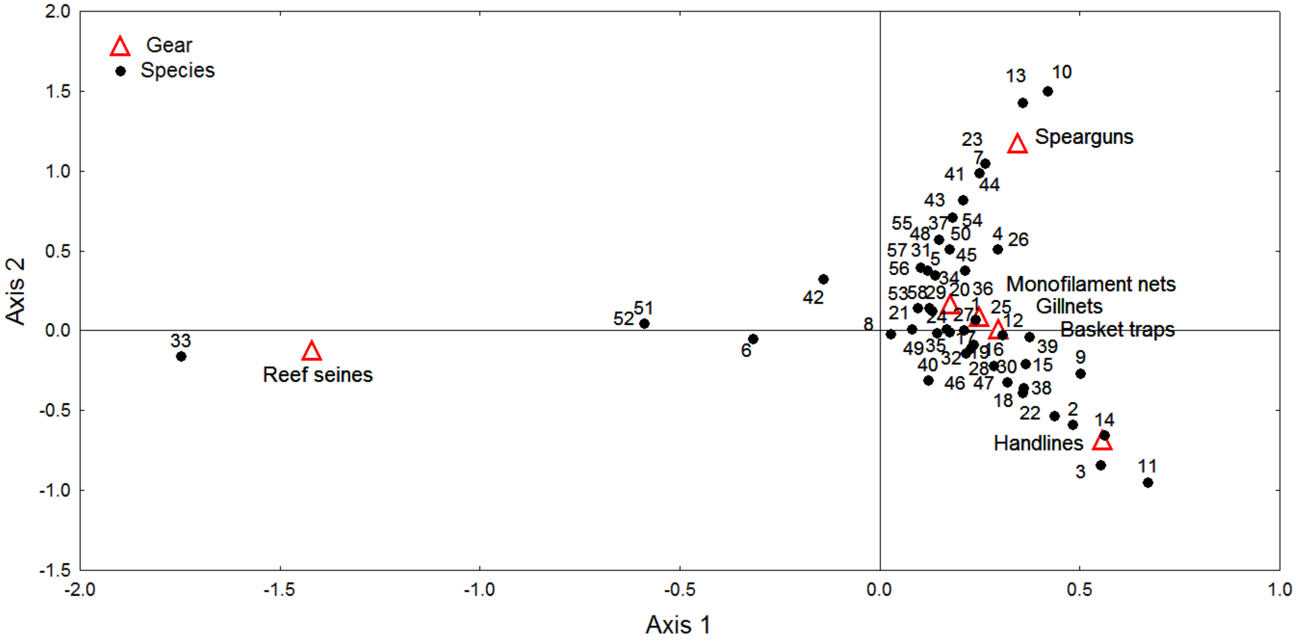
Fishing grounds	S	N	Proportional abundance (%)	D	*J'*	*H'*
Mpunguti	39	194	30.1	7.21	0.80	2.92
Mkwiro	17	170	26.4	3.12	0.34	0.96
Kitugamwe	11	73	11.3	2.33	0.70	1.68
Nyuli	20	72	11.2	4.44	0.86	2.58
Waga	19	47	7.3	4.68	0.87	2.55
Mwamba mkuu	15	43	6.7	3.72	0.83	2.25
Mwipwa	7	12	1.9	2.42	0.96	1.86
Sii Island	2	3	0.5	0.91	0.92	0.64
Mijira	1	2	0.3	-	-	-
Mnarani	2	9	1.4	0.46	0.50	0.35
Kibuyuni	5	7	1.1	2.06	0.96	1.55
Nyuma ya maji	5	9	1.4	1.82	0.89	1.43
Jiwe jahazi	3	4	0.6	1.44	0.95	1.04

and 95% of the total fishing effort (n = 4367 fisher days). Handline fishers contributed the highest fishing effort (1 265 fisher days, 29%) followed by speargun fishers (1 040 fisher days, 24%) and basket trap fishers (1 015 fisher days, 23%). However, by weight, basket trap fishers contributed the highest catches (743 kg, 27%), followed by speargun (655 kg, 23%) and handline fishers (622 kg, 22%). Handline fishers cumulatively captured the highest number of species (n = 145), the highest average number of species per day (13 species) and the highest diversity of species (*H'* = 3.62). This was followed by basket traps (104 species, 11 species/day, *H'= 3.25*) and spearguns (88 species, 8 species/day, *H'=3.07*); while cast nets and ringnets had the lowest (Table 1). On average, the Pielou's evenness (*J'*) index was about 0.71, with ringnets having the highest (*J'* = 0.94) and cast nets having the lowest (*J'* = 0.46) (Table 1). In comparison, a total of 153 aquarium fish species (*H'* = 3.33) were collected from Shimoni during January to December 2014 based on officially reported statistics. The catch monitoring done between September 2010 and March 2013 showed that aquarium snorkel fishers collected more species compared to SCUBA fishers, however the species diversity between the two fishing methods was relatively similar (Table 1).

Cluster analysis of the main artisanal gear types used, based on the species composition of the catches, revealed 3 distinct clusters at 20% similarity (Fig. 3). The first cluster (cluster 1) was characterized by basket traps, handlines, gillnets, spearguns, monofilament gillnets and reef seines. The second cluster was characterized by castnets, and the third cluster by ringnets. Within cluster 1, the SIMPROF test further revealed no significant ($p < 0.05$) statistical evidence of a sub-structure for the grouping of handlines with basket traps, and spearguns with monofilament gillnets. Pair-wise comparisons using Pianka's niche overlap index for the gears grouped in cluster 1 showed that basket traps and monofilament gillnets had the strongest overlap in species selectivity (*O* = 0.722) followed by basket traps and gillnets (*O* = 0.549) and basket traps and handlines (*O* = 0.545), while the lowest niche overlap was between spearguns and gillnets (*O* = 0.176) (Table 2).

Potential interactions between aquarium and artisanal fisheries

A total of 660 (8%) fish categorized as aquarium species were recorded from the sampled artisanal catches. The fish constituted of 58 species and 17 families (see Appendix 1) of which 80% were adult sized individuals. Labridae dominated the catches constituting 31% by relative abundance and 19 species, followed by



1 *Abudefduf sexfasciatus*
2 *Acanthurus leucosternon*
3 *Thalassoma hebraicum*
4 *Dascyllus trimaculatus*
5 *Ostracion cubicus*
6 *Zanclus cornutus*
7 *Naso annulatus*
8 *Abudefduf sparoides*
9 *Cheilinus trilobatus*
10 *Pomacanthus imperator*
11 *Lutjanus kasmira*
12 *Coris africana*
13 *Pomacanthus semicirculatus*
14 *Halichoeres hortulanus*
15 *Oxycheilinus diagramma*
16 *Bodianus auxillaris*
17 *Paracirrhites forsterri*
18 *Cheilinus oxycephulus*
19 *Parupeneus cyclostomus*
20 *Acanthurus xanthopterus*
21 *Novaculichthys taeniourus*
22 *Xyrichthys pavo*
23 *Naso hexacanthus*
24 *Thalassoma lunare*
25 *Variola louti*
26 *Anampses caeruleopunctatus*
27 *Siganus stellatus*
28 *Hologymnosus doliatus*
29 *Malacanthus brevirostris*
30 *Macolor niger*
31 *Hemigymnus fasciatus*
32 *Cephalopholis argus*
33 *Acanthurus triostegus*
34 *Hemigymnus melapterus*
35 *Acanthurus nigricauda*
36 *Zebrasoma scopas*
37 *Pomacanthus chysurus*
38 *Coris caudimacula*
39 *Cephalopholis miniata*
40 *Coris formosa*
41 *Abudefduf sordidus*
42 *Abudefduf septemfasciatus*
43 *Dasyatis kuhlii*
44 *Pseudobalistes fuscus*
45 *Naso lituratus*
46 *Amphiprion allardi*
47 *Gomphosus caeruleus*
48 *Balistapus undulatus*
49 *Abudefduf vaigiensis*
50 *Epibulus insidiator*
51 *Rhinecanthus aculeatus*
52 *Gnathanodon speciosus*
53 *Naso brevirostis*
54 *Chaetodon bennetti*
55 *Chaetodon lunula*
56 *Cheilinus chlorourus*
57 *Platax orbicularis*
58 *Hologymnus annulatus*

Figure 5. Results of Detrended Correspondence Analysis (DCA) of artisanal fishery catches indicating similarity in the composition of aquarium species captured by the main key gear types used in the Shimoni area, Kenya.

Acanthuridae (28%, 9 species), Pomacanthidae (12%, 3 species), Lutjanidae (11%, 2 species), and Pomacentridae (5%, 7 species). Handlines, basket traps, spearguns and reef seines interacted most in species selectivity with the aquarium fishery (Fig. 4). Pairwise comparison of Pianka's niche overlap between the artisanal gears and the aquarium fishing methods (SCUBA vs snorkeling) showed that handlines and spearguns had the highest overlap with the aquarium fishery respectively, and more so with snorkel fishers (Table 2). The most abundant aquarium species captured included *Acanthurus triostegus* (reef seines), *Lutjanus kasmira* (handlines), *Pomacanthus imperator* (spearguns) and *Thalassoma hebraicum* (handlines and reef seines) (Fig. 4).

The DCA ordination showed the angelfishes, *Pomacanthus imperata* and *Pomacanthus semicirculatus* as strongly associated with spearguns, while the wrasses *Halichoeres hortulanus* and *Thalassoma hebraicum*, and the surgeonfish, *Acanthurus leucosternon* were strongly associated with handlines in the artisanal fisheries (Fig. 5). DCA ordination further showed that the composition of aquarium species in reef seine catches was distinctly different from all the other gear types. Although the other gear types generally grouped together, handlines remained distinctly separated from spearguns; while gillnets, monofilament gillnets and basket traps grouped together indicating high overlaps in the selectivity for aquarium species among the three gears.

Results of the *K*-dominance curves showed a high dominance of aquarium species captured in reef seines, gillnets and monofilament gillnets, likely due to the capture of schooling surgeonfishes *Acanthurus triostegus* and the snapper, *Lutjanus kasmira* (Fig. 6a).

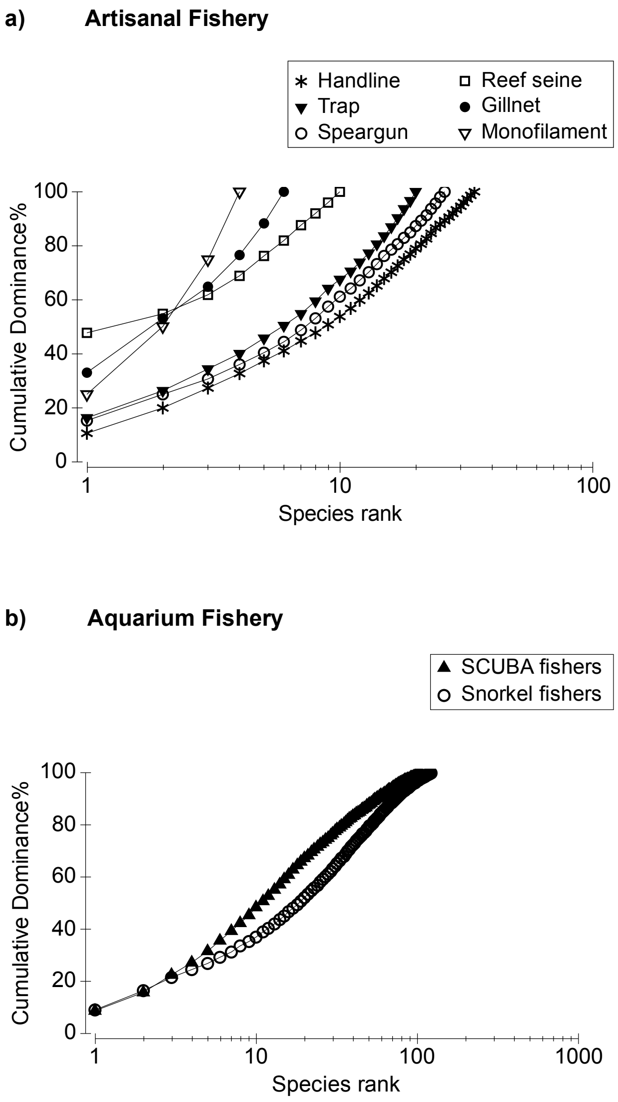


Figure 6. *K*-Dominance curves of (a) artisanal fishing gears based on the composition of aquarium species captured and (b) aquarium fishing methods in the Shimoni area, Kenya.

Dominance was also higher for aquarium SCUBA fishers compared to snorkel fishers (Fig. 6b).

On a spatial scale, 93% of the aquarium fish were captured from 6 fishing grounds: Mpunguti, Mkwiro, Kitugamwe, Nyuli, Waga and Mwamba mkuu (Table 3, see Fig. 1 for locations). The highest diversity of aquarium species was captured from the Mpunguti area while the lowest was from Mnarani. DCA ordination associated handlines, basket traps, and speargun with the Mpunguti area (including the adjacent reserve), Mkwiro, Waga, Jiwe jahazi and Kibuyuni (Fig. 7), while reef seines and cast nets were mainly associated with Mwamba mkuu, Sii Island and Chumani fishing grounds. The DCA also associated aquarium snorkel fishers with more diverse fishing grounds compared to SCUBA fishers who mainly concentrated their fishing effort in Nyuli (Fig. 7). Aquarium snorkel fishers are thus more likely to have technical interactions with artisanal fishing gears both in terms of species selectivity as well as spatially in the sharing of fishing grounds.

Discussion and Conclusion

This is the first study in the WIO region to examine interactions between artisanal fishing gears and the aquarium fishery. A limitation of the study was the time lag in the sampling periods as gear selectivity can vary depending on the fishing effort, fishing time, season and even the area fished (Azovsky, 2011). Nonetheless, the study provides strong evidence of potential interactions between the two fisheries. A major finding of the study was that handlines, basket traps and speargun had the highest potential to interact with the aquarium fishery. The study estimated that approximately 8% of the artisanal catch by abundance consisted of species of value to the aquarium fishery. In comparison, Cinner *et al.* (2009) estimated that <6% of artisanal fish catches by abundance constituted species that were strongly associated with corals, many of which are most likely targeted by aquarium fishers. Artisanal fishers preferentially target the largest sized individuals and there was evidence that large sized adults of the angelfishes *Pomacanthus imperator* and *Pomacanthus semicirculatus* were selectively targeted by speargun fishers. Selective targeting of angelfishes by speargun fishers has also been observed elsewhere in Belize (Babcock *et al.,* 2013) and is an issue of concern as these species are highly valued, heavily fished and highly vulnerable to localized population declines due to their life history (Okemwa *et al.*, 2016). Further research is needed to assess how such selective fishing practices affect recruitment dynamics of affected populations in the area.

The study showed that certain fishing grounds were preferred by both fisheries. Aquarium snorkel fishers were observed to be more likely to interact with artisanal fishing gears compared to SCUBA fishers both in terms of species selectivity as well as the diversity of shared fishing grounds. Various studies have demonstrated that allocation of fishing effort is essentially not random as fishers will tend to concentrate in areas where they are likely to experience higher catch rates to maximize on returns (Johannes *et al.*, 2001; Pet-Soede *et al.,* 2001; Wiyono *et al.*, 2006; Daw, 2008). As observed by Micheli *et al.* (2014), multiple fisheries are more likely to cause local depletion of fish stocks

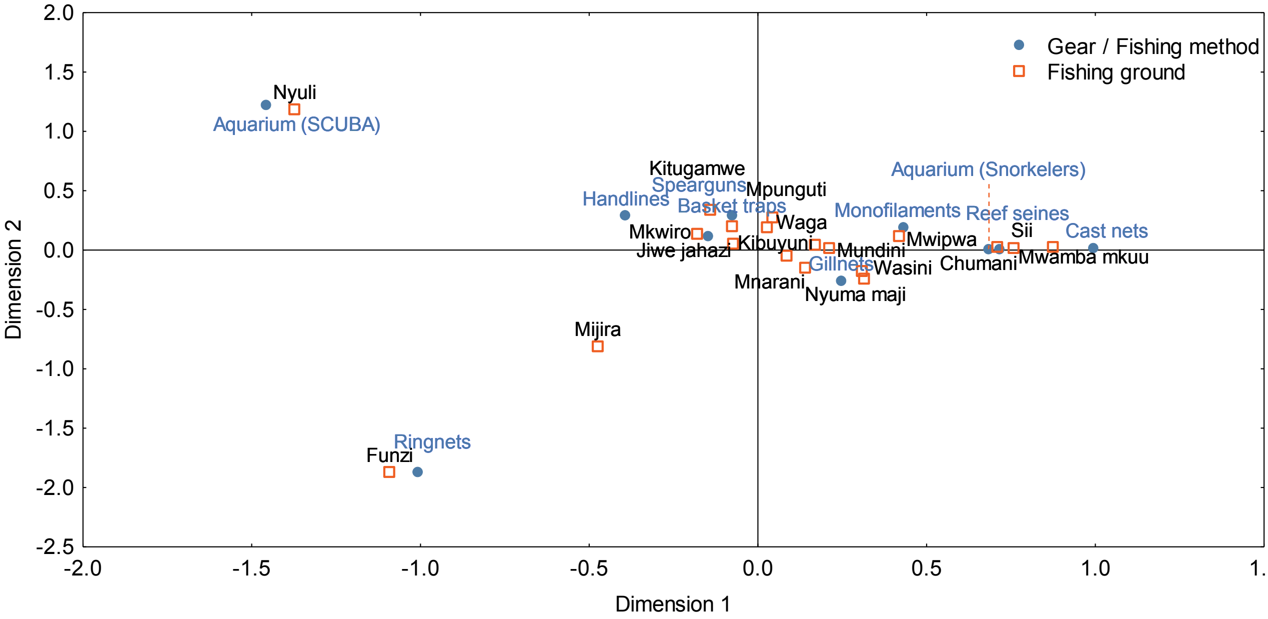


Figure 7. Detrended correspondence analysis plot showing the spatial association of artisanal gear types and aquarium fishing methods with fishing grounds in the Shimoni area, Kenya.

compared to individual fisheries. Thus, local scale ecosystem based management interventions such as spatial closures are likely to be the most effective in sustaining the affected fish populations. The Kisite Marine National Park provides an important replenishment zone for the study area. This is further complemented by a number of Community Conservation Areas (CCAs) which have increasingly gained local support by resource managers and fisher communities (Rockliffe *et al.*, 2014). However, the existing spatial controls need to be further augmented with gear-based interventions including improved enforcement of the ban on speargun s and adoption of modified gears that are more selective in minimizing the capture of juveniles and low-value food species. Trials on basket traps modified with escape gaps have yielded promising results in Kenya (see Mbaru and McClanahan, 2013; Gomes *et al.*, 2014); however, similar trials to establish optimum mesh and hook sizes for gillnets and handlines are also recommended. In conclusion, an important consideration for fisheries managers will be to closely monitor fishery interactions at small spatial scales as demonstrated in this study to assist in developing effective strategies so as to minimize the cumulative impacts from both fisheries on vulnerable species that may be at risk of depletion.

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Appendix 1. The full list of 58 species that overlapped between the artisanal and aquarium fishery in Shimoni area during January to December 2014, categorized by the gear type and commercial use (C: artisanal commercial vs A: Aquarium)

Family	Scientific Name	Handline	Reefseine	Gillnet	Basket traps	Mono-filament	Speargun	Value Use
Pomacentridae	*Abudefduf sexfasciatus*	x		x				A
	Abudefduf sordidus						x	A
	Abudefduf sparoides	x	x		x			A
	Abudefduf vaigiensis	x		x				A
	Amphiprion allardi	x						A
	Dascyllus trimaculatus	x					x	A
Acanthuridae	*Acanthurus leucosternon*	x			x			A
	Acanthurus triostegus		x			x	x	C/A
	Acanthurus xanthopterus			x	x			C/A
	Naso annulatus						x	C/A
	Naso brachycentron		x					C/A
	Naso brevirostis				x			C/A
	Naso hexacanthus						x	C/A
	Naso lituratus						x	C/A
	Naso vlamingi		x					C/A
	Zebrasoma scopas				x			A
Carangidae	*Gnathanodon speciosus*		x				x	C/A
Chaetodontidae	*Chaetodon bennetti*						x	A
	Chaetodon lineolatus	x						A
	Chaetodon lunula				x		x	A
	Chaetodon trifasciatus					x		A

Labridae	*Anampses caeruleopunctatus*		x				x	x	C/A
	Bodianus auxillaris		x			x			A
	Cheilinus chlorourus		x			x	x	x	C/A
	Cheilinus trilobatus		x			x		x	C/A
	Coris africana		x			x		x	C/A
	Coris caudimacula		x						C/A
	Coris formosa		x	x					C/A
	Epibulus insidiator							x	C/A
	Halichoeres hortulanus		x			x			C/A
	Halichoeres scapularis		x						C/A
	Hemigymnus fasciatus						x	x	C/A
	Hologymnosus doliatus		x			x			C/A
	Hologymnus annulatus				x				C/A
	Labroides dimidiatus	x							A
	Novaculichthys taeniourus	x	x				x		A
	Thalassoma hebraicum	x	x	x					C/A
	Thalassoma lunare	x							C/A
	Xyrichthys pavo	x							C/A
Ostraciidae	*Ostracion cubicus*				x		x		A
Cirrhitidae	*Paracirrhites forsterri*	x							A
Zanclidae	*Zanclus cornutus*	x	x		x				A
Malacanthidae	*Malacanthus brevirostris*	x							A
Serranidae	*Cephalopholis argus*	x			x	x	x		C/A
	Cephalopholis miniata	x				x	x		C/A
	Variola louti	x			x		x		C/A
Dasyatidae	*Dasyatis kuhlii*						x		C/A
Lutjanidae	*Lutjanus kasmira*	x			x				C/A
	Macolor niger	x							C/A
Mullidae	*Parupeneus cyclostomus*	x		x	x				C/A
Plotosidae	*Platax orbicularis*						x		C/A
Pomacanthidae	*Pomacanthus chysurus*						x		C/A
	Pomacanthus imperator	x			x		x		C/A
	Pomacanthus semicirculatus						x		C/A
Balistidae	*Balistapus undulatus*						x		C/A
	Pseudobalistes fuscus						x		C/A
	Rhinecanthus aculeatus		x						C/A
Siganidae	*Siganus stellatus*	x	x	x	x	x			C/A

Micro-tidal dependent micro-phytoplankton C-biomass dynamics of two shallow tropical coral reefs

Shamimtaz B. Sadally[1], Nawsheen Taleb-Hossenkhan[1], Beatriz Casareto[2], Yoshimi Suzuki[2], Ranjeet Bhagooli[3]*

[1] Department of Biosciences,
Faculty of Science,
University of Mauritius,
Réduit 80837, Mauritius

[2] Graduate School of Science
and Technology, Shizuoka
University, 836 Ohya,
Suruga-ku, Shizuoka,
422-8529, Japan

[3] Department of Marine
and Ocean Science,
Fisheries and Mariculture,
Faculty of Ocean Studies,
University of Mauritius,
Réduit 80837, Mauritius

*Corresponding author:
r.bhagooli@uom.ac.mu

Abstract

This study investigates micro-tidally induced variations in micro-phytoplankton carbon biomass (C-biomass), concentrations of chlorophyll *a*, nitrate, phosphate and silicate, temperature, salinity and pH at three zones (near-coast, lagoon and reef) at two sites (Flic-en-Flac and Belle Mare) on two consecutive days covering two high and low tides in August (winter) and in November (summer) 2011. At Flic-en-Flac, 36 different genera of micro-phytoplankton were recorded, including 29 bacillariophyceae, 5 dinophyceae and 2 cyanophyceae. At Belle Mare, 34 different genera of micro-phytoplankton were recorded, including 31 bacillariophyceae, 3 dinophyceae and 2 cyanophyceae. At low tides the total micro-phytoplankton C-biomass (TMPB) and nutrient levels were significantly higher compared to those at high tides. At both sites, zonal variation in TMPB was evident with significantly higher C-biomass closer to the coast. Only bacillariophyceae and dinophyceae C-biomass along with nutrient levels exhibited seasonal variation with higher values in summer. Bacillariophyceae was dominant, followed by cyanophyceae and dinophyceae, irrespective of micro-tidal changes, indicating their ability to tolerate a wide range of micro-tidally induced environmental changes. These findings provide insights on the effect of micro-tidal cycles on micro-phytoplankton dynamics and might have implications for carbon cycling over shallow tropical coral reefs and other inter-connected coastal ecosystems.

Keywords: C-biomass, chlorophyll *a*, environmental factors, micro-phytoplankton, micro-tides

Introduction

Phytoplankton form the basis of marine food chains and food webs (Ersanli and Gönülol, 2003; Gameiro *et al.*, 2007; Zhou *et al.*, 2009) and they play an important role in the cycling of greenhouse gases since they participate in the biological pump of carbon dioxide (Tréguer and Pondaven, 2000), as well as in biogeochemical cycling (Khenari *et al.*, 2010). Pure physical forcing mechanisms mainly control the ratio between euphotic and mixing depth, which in turn determines net primary production (Falkowski and Raven, 1997). In coral reef-lagoons, the physical mechanisms that contribute to circulation can also influence the transport, dispersal, and retention of several organisms, including phytoplankton (Hench *et al.*, 2008). Environmental forcing by tidal cycle is one of the factors that has been found to govern variability in phytoplankton abundance, biomass and growth in coastal waters (Cloern, 1991; Torréton *et al.*, 2010; Blauw *et al.*, 2012). Tides have a crucial role to play in many coastal systems' functioning, by contributing to variations in both biotic and abiotic characteristics in these systems (Davies and Ugwumba, 2013). For example, tidal movements have been found to be partly responsible for variation in nutrient concentrations in coral reef areas (Torréton *et al.*, 2007), whilst tidal height and amplitude can influence light penetration, temperature, salinity and pH (Blauw *et al.*, 2012).

In shallow coastal waters, tide plays an important role in short-term variability in phytoplankton biomass

(Cloern *et al.*, 1989; Cloern, 1991; Villate, 1997), such that vertical mixing intensity generated by wind action and tidal motion contribute to either settling or resuspension of coastal phytoplankton (Blauw *et al.*, 2012). Increase in phytoplankton biomass is usually a result of temporary phenomena, including variation in vertical mixing rate, brought about by the effect of tidal mixing, wind-driven mixing and thermal mixing/stratification (Jin *et al.*, 2006). In addition, non-linear internal waves have also been found to considerably affect biogeochemical fluxes and distribution of phytoplankton in coastal areas (Cuypers *et al.*, 2011).

Carbon is the principal structural component of heterotrophic and phototrophic organisms; it can be used for comparing biomass and bioenergetics for community-wide and group-specific planktonic organisms. In fact, the carbon biomass of phytoplankton is considered to be an essential parameter in ecosystems models and biogeochemical carbon budgets (Menden-Deuer and Lessard, 2000). Few studies have focused on short-term variation of micro-phytoplankton and made use of C-biomass for the study of micro-phytoplankton. This process involves measuring the size of the different groups of micro-phytoplankton, converting these to cell volumes and finally to carbon biomass through existing formulae and equations. Knowledge on the carbon content of major planktonic organisms, including bacillariophytes, dinophytes and cyanophytes, can help in predicting and in quantifying the temporal and spatial variability in total and export primary production. However, to-date most of the studies carried out on phytoplankton comprise the enumeration and quantification of the density, and diversity, and limited C-biomass data sets for micro-phytoplankton are available, especially in tropical lagoons dominated by coral reefs.

Short-term temporal (hourly) and long-term (seasonal) variations are of great importance in assessing plankton processes (Torréton *et al.*, 2010). However, studies have put more emphasis on the long-term (seasonal and weekly) variations in phytoplankton (Lucas and Cloern, 2002; Bresnan *et al.*, 2009; Drake *et al.*, 2010) despite the fact that short-term variations, such as those observed on an hourly basis, have been found to be equally significant. These short-term variations may be due to physical and biological forces, including internal current and wind-driven re-suspension of benthic microalgae (Cloern *et al.*, 1989). To-date limited studies have reported the tidal influence on both nutrients and phytoplankton community, and this study therefore provides important information about the variation of phytoplankton C-biomass, chlorophyll *a*, distribution and diversity in response to micro-tidal changes.

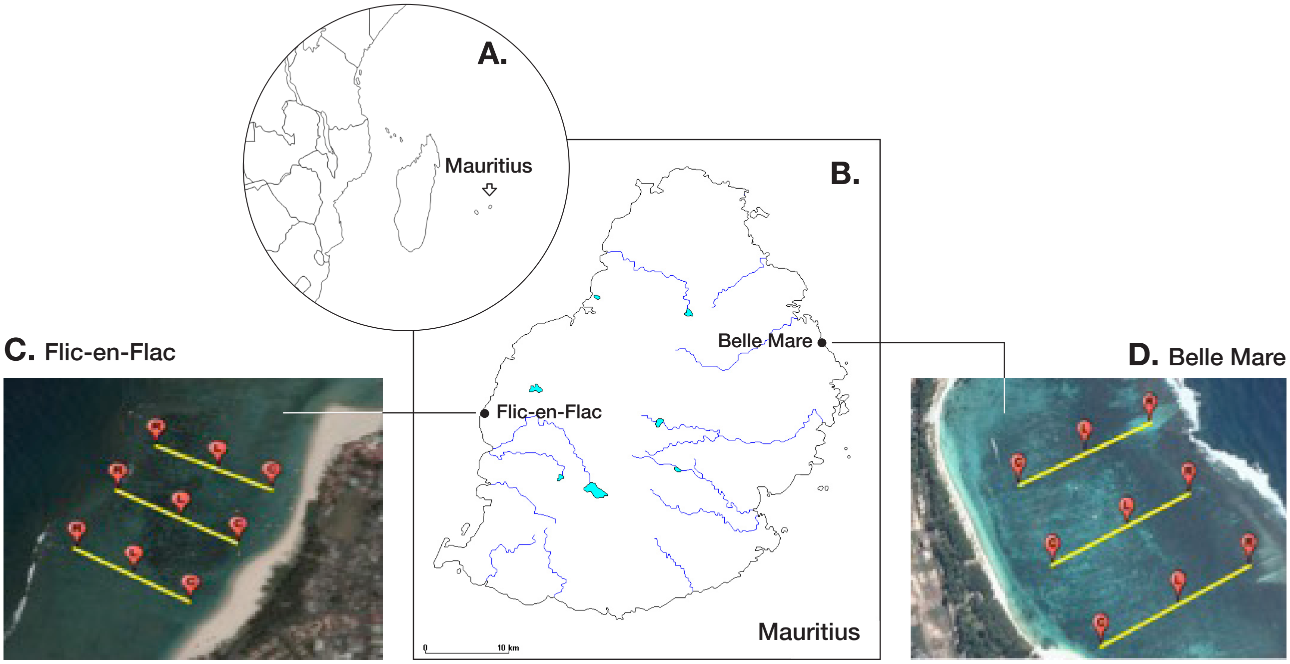


Figure 1. Maps showing the location of Mauritius in the Indian Ocean (A) (Source: https://sites.google.com/site/indianoceancommunity1/geo-politics) and the sampling sites in Mauritius (B) (Source: http://www.hmsmauritius.co.uk/pageone.htm), namely Flic-en-Flac (C) and Belle Mare (D) (Source: Google Earth).

Material and Methods

Study sites

Mauritius is situated in the South West Indian Ocean and the tidal cycle comprises two high and two low tides in each lunar cycle (Turner *et al.*, 2000). Tidal characteristics around Mauritius include micro-tides (Magori, 2009) of 0.3-0.8 m changes (Baird and Associates, 2003).

Micro-phytoplankton sampling was carried out at Flic-en-Flac (FEF) and Belle Mare (BM), which are situated on the western and eastern coasts of Mauritius Island respectively (Fig. 1a, b). Micro-phytoplankton samples were collected in three zones; namely shore, lagoon, and reef, at both FEF and BM (Fig. 1c, d).

The two sites were chosen because they differ in terms of percentage coral cover, coral diversity, topography, lagoonal area, level of coastal development and anthropogenic input, and wind intensity. The percentage of live coral cover was higher at BM (45%) than at FEF and this is evenly distributed throughout the lagoon compared to FEF, where live corals are mostly concentrated near the coral reef area, which is around 500 m from the shore. BM has a larger lagoonal area compared to FEF, with a distance of 850 m from the shore to the reef (MoE, 2004). Water depth is also greater at BM than at FEF. FEF is among the Mauritian beaches with extensive coastal development, and where the coastline has been artificially modified to accommodate new developments. Meethoo (2010) recorded higher building density, including hotels, near the coast of FEF compared to BM. However, although BM is less developed than FEF, anthropogenic inputs in the form of fertilisers and sewage discharge are a major problem, especially during periods of heavy rainfall, when these pollutants are washed into the nearby lagoon. These run-off events in turn promote growth of algae and may even lead to algal blooms. BM, being situated on the eastern coast of the island, is more exposed to the South East Trade Winds and wind intensity is higher there than at FEF.

Micro-phytoplankton and seawater sampling

Micro-phytoplankton sampling was carried out twice a day over a period of 24 hours covering two low tides and two high tides in the months of August and November 2011. For micro-phytoplankton and chlorophyll *a* samples, 10 L of seawater was collected at a depth not exceeding 1 m. The seawater was filtered and concentrated (Chowdhury *et al.*, 2007) using a 5 µm plankton net (Rigosha and Co. Ltd, Japan) and the concentrate was collected in 250 ml opaque plastic bottles. Triplicate water samples for nitrate, phosphate, silicate and chlorophyll *a* analysis were collected in 500 ml plastic bottles at a depth not exceeding 1 m.

All sampling bottles were kept in the dark and at low temperature in isotherm boxes during transportation to the laboratory. Samples for chlorophyll *a* and micro-phytoplankton were processed on the day of collection while samples collected for nutrient analysis were kept at -20°C for later analyses.

Measurement of physico-chemical parameters

In-situ temperature (Comark 314 thermometer), salinity (Erma) and pH (Hanna H1 9024C) were measured. Nitrate, phosphate and silicate concentrations were estimated using the cadmium reduction method, ascorbic acid method, and the molybdenum blue method, respectively (Greenberg *et al.*, 1992).

Measurement of biological parameters: Chlorophyll a, micro-phytoplankton identification and C-biomass

Chlorophyll *a* samples were filtered through a Glass-fibre filter (0.45 µm pore size) (Whatman Paper Limited) and chlorophyll *a* pigment was extracted using 90% acetone for 24 hrs at 4°C. Concentration of chlorophyll *a* was determined using a spectrophotometer (Spectronic® Genesys™ 8 spectrophotometer) (Jeffrey and Humphrey, 1975).

Prior to identification and counting, the collected samples were centrifuged (Häder, 1995) at 3000 rpm for 5 minutes (Khenari *et al.*, 2010) and the concentrate was fixed with Lugol's solution (Meesukko *et al.*, 2007) and kept in the dark at 4°C. One millilitre of sample was placed in a Sedgewick-Rafter Counting chamber (Sidik *et al.*, 2008) and micro-phytoplankton was identified and counted using a light microscope at magnifications X100, X200 and X400 (Smith and Johnson, 1996; Tomas, 1997; Dhargalkar and Ingole, 2004). Micro-phytoplankton were grouped into Bacillariophyceae, Dinophyceae and Cyanophyceae. Biovolumes of the different micro-phytoplankton classes were calculated and these were in turn converted to C-biomass according to Jun and Dongyan (2003).

Statistical analyses

Statistica 10.0 software was used for computing data and statistical analyses. Two-way analysis of variance (ANOVA) was carried out to test the tidal differences within measured parameters and different stations at the study sites, followed by Tukey's Post hoc analysis for comparison of means. C-biomass data was $\log_{10}$ transformed while temperature, salinity, pH, chlorophyll *a*, nitrate, phosphate and silicate data were arcsin (square root) transformed prior to ANOVA analyses. Correlations between physico-chemical and biological parameters, namely pH, temperature, salinity, dissolved oxygen, chlorophyll *a* concentrations, nitrate, phosphate and silicate concentrations, with the total C-biomass of micro-phytoplankton at the different study sites were tested using Pearson correlation with SPSS software (version 14). Shannon's diversity Index at the sampling sites (BM and FEF), seasons (summer and winter) and tides (both high and low) were calculated using Primer software (version 6). Further Simpson's diversity was used to test for correlation among the different tested parameters.

Results

Physico-chemical parameters

Table 1 summarises the variations in temperature, pH and salinity recorded at FEF and BM at high and low tides during both summer and winter. Temperature and pH were slightly higher during summer compared to winter but these were not significantly different. Variations in pH at the different zones at both sampling sites were not significant. Furthermore, salinity did not show significant variability between low and high tide, and during summer and winter seasons.

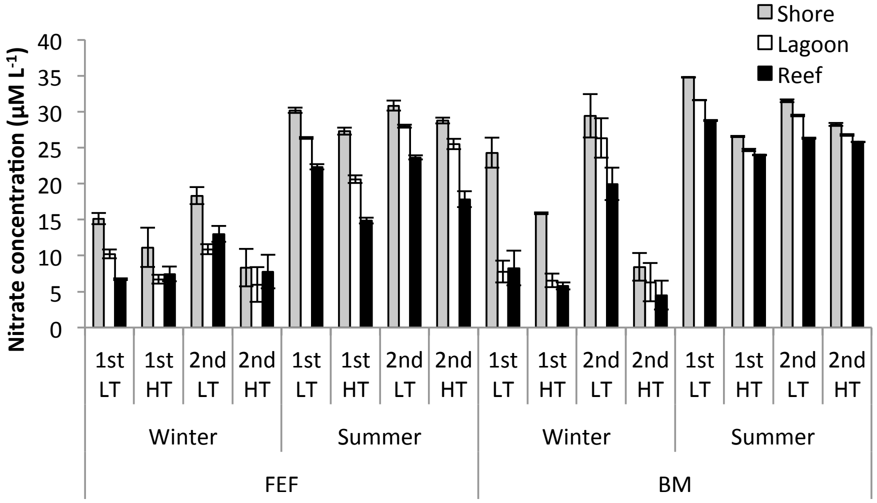
Nitrate and phosphate concentrations exhibited spatial variation in term of sites, with higher concentration recorded at BM, while no significant differences were observed among the different zones (Two-way ANOVA) (Fig. 2a, b). Silicate concentrations showed spatial variation both in terms of sites (higher concentrations at FEF) and zones (higher near the shore and lagoon of FEF) (Fig. 2c). Only nitrate and silicate concentrations exhibited seasonal variations with higher concentrations in summer. No clear tidal effect was recorded for nitrate and silicate at the study sites, but higher concentrations were obtained at several occasions at low tide. Phosphate at FEF was not influenced by tidal changes, but at BM, phosphate concentration was higher at high tides during winter, while the contrary was observed during summer (Fig. 2b).

No significant seasonal variation in chlorophyll *a* concentration was recorded at both FEF and BM. Chlorophyll *a* concentration exhibited spatial variation, in terms of sites, with higher values recorded at BM. Significant spatial variation within the different zones at each site was also observed. Significantly higher concentrations were recorded near the shore and in the lagoon

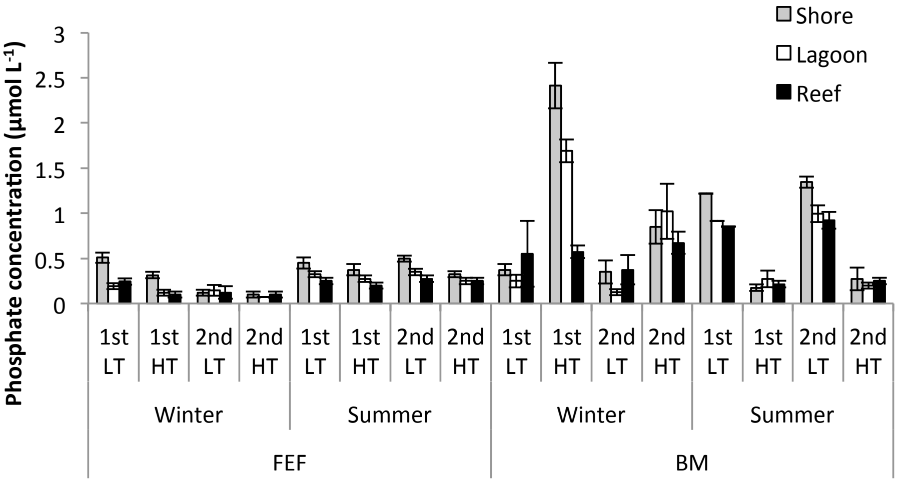
Table 1. *In-situ* measurement of temperature (°C), pH and salinity (ppt). Data represent mean ± SD (n = 3). LT: low tide; HT: High tide; Temp.: Temperature; S: Shore; L: lagoon; and R: reef.

Season	Tide	Station	Flic-en-Flac (FEF)			Belle Mare (BM)		
			Temp (°C)	pH	Salinity (ppt)	Temp (°C)	pH	Salinity (ppt)
Winter	LT	S	25.62±0.21	8.23±0.02	35.42±0.45	25.18±1.34	7.88±0.33	35.33±0.24
		L	25.08±0.34	8.42±0.24	35.50±0.41	24.05±0.44	7.92±0.15	35.33±0.37
		R	25.00±0.50	8.34±0.20	35.42±0.61	23.58±0.12	7.94±0.08	35.25±0.25
	HT	S	25.92±0.30	8.27±0.02	35.42±0.34	23.63±0.37	8.00±0.08	35.50±0.41
		L	24.32±1.51	8.26±0.05	35.50±0.41	23.92±0.43	7.95±0.12	35.75±0.69
		R	24.22±1.27	8.29±0.01	35.08±0.45	24.22±0.17	7.92±0.19	35.83±0.62
Summer	LT	S	26.93±0.24	8.44±0.10	34.33±1.11	27.73±0.94	8.54±0.10	34.92±0.34
		L	26.95±0.45	8.45±0.10	35.00±0.58	27.22±0.58	8.51±0.14	35.42±0.45
		R	26.87±0.27	8.47±0.02	35.00±0.29	27.00±0.84	8.51±0.06	35.00±0.29
	HT	S	27.23±0.35	8.38±0.14	34.50±0.76	27.57±0.76	8.55±0.05	35.25±0.38
		L	27.45±0.55	8.44±0.13	35.00±0.58	27.10±0.45	8.51±0.15	35.25±0.38
		R	26.97±0.62	8.51±0.06	35.33±0.47	26.87±0.36	8.50±0.04	35.25±0.25

a. Nitrate concentration



b. Phosphate concentration



c. Silicate concentration

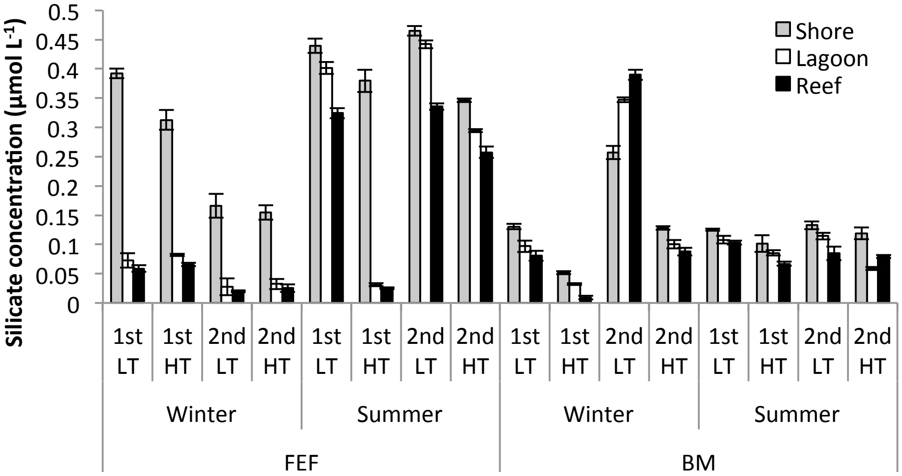


Figure 2. Nitrate (a), Phosphate (b) and silicate (c) concentrations at Flic-en-Flac (FEF) and Belle Mare (BM).

of FEF (Fig. 3A). At BM, chlorophyll *a* concentrations increased from the shore to the reef area (Fig. 3b).

The overall effect of tides on chlorophyll *a*, irrespective of sampling sites, was significantly different during the sampling period. However, analysis of the effect of tides at each study site, showed no significant effect on chlorophyll *a* at FEF (Two-way ANOVA), while higher concentrations were recorded during low tides at BM. As the water level increased during periods of high tide, the concentration of chlorophyll *a* was found to decrease, and this corresponded to episodes of increase in total micro-phytoplankton C-biomass.

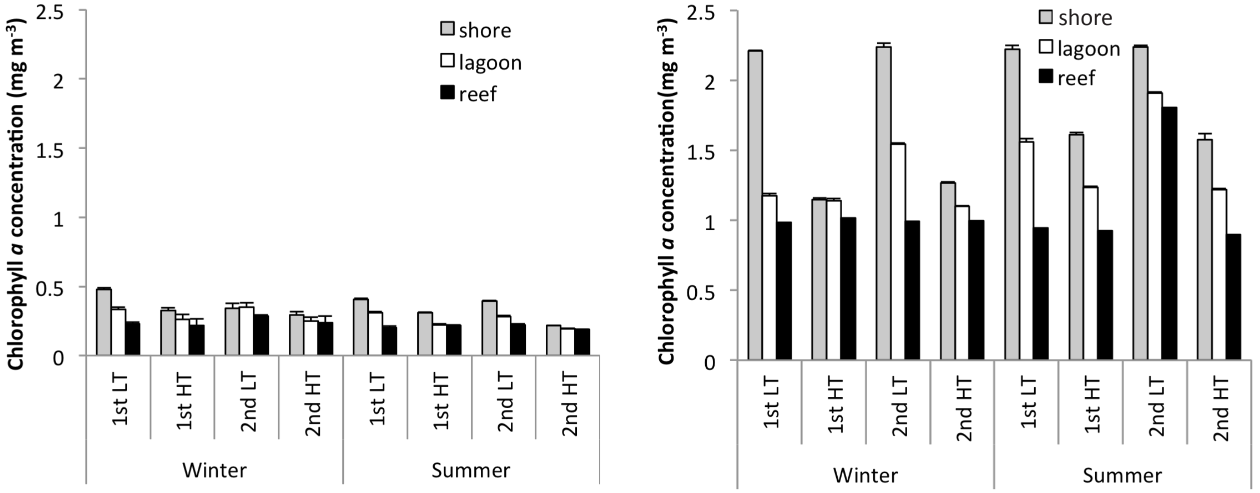
Micro-phytoplankton density, C-biomass and diversity

Tides and zones had significant effects on the overall total C-biomass of total micro-phytoplankton and bacillariophytes, and concentrations of chlorophyll *a*, nitrate, phosphate and silicate (Table 2).

There was no significant difference in C-biomass of micro-phytoplankton between the two sites. C-biomass of total micro-phytoplankton, bacillariophytes and dinophytes, nitrate, silicate and chlorophyll *a* exhibited significant spatial variations in terms of zones (shore, lagoon and reef) within each site. Tides had no effect on C-biomass of dinophytes and

a. Chlorophyll a concentration at FEF

b. Chlorophyll a concentration at BM



c. Total micro-phytoplankton density

d. Total micro-phytoplankton C-biomass

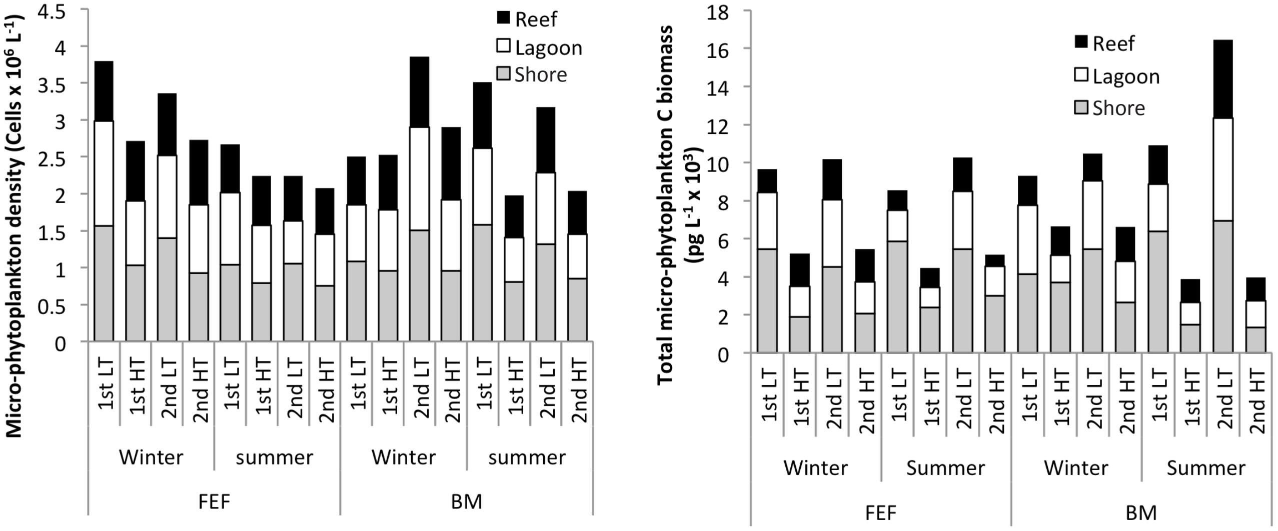


Figure 3. Total micro-phytoplankton density and carbon biomass (pg L^{-1}) at Flic-en-Flac (FEF) and Belle Mare (BM) at low tide (LT) and high tide (HT) during summer and winter. Data represent mean (n=9 at each zone for micro-phytoplankton C-biomass and density; n=3 at each zone for chlorophyll a) at both sites.

Table 2. Two-Way ANOVA comparison of the tidal cycles, in terms of C-biomass (pg L^{-1}) of total micro-phytoplankton, micro-phytoplankton groups (bacillariophyceae, dinophyceae and cyanophyceae) and physico-chemical parameters at the different stations within and across the two sites (FEF and BM). Asterisks indicate significant differences at 5% level. (* = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$; NS = not significant).

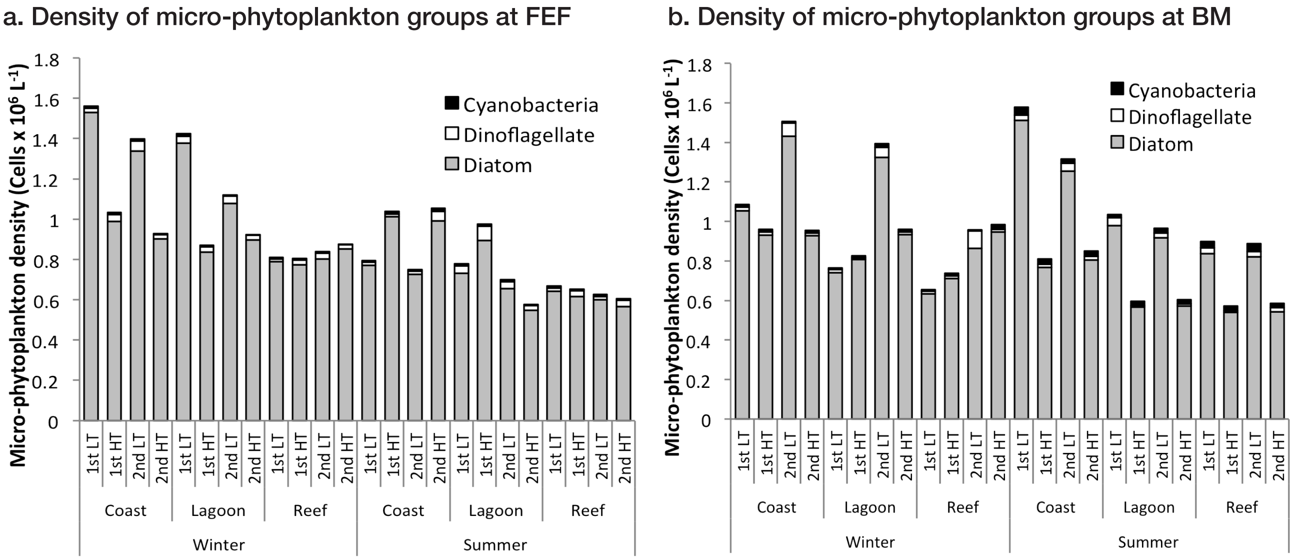
Parameters		DF	MS	F	p
Total micro-phytoplankton C-biomass (pg L^{-1})	Site	1	0.04	3.73	NS
	Season	1	0.04	3.08	NS
	Tide	2	0.53	44.3	***
	Zone	1	0.98	82.1	***
	Site*Tide	1	0.02	1.60	NS
	Site*Season*Tide	1	0.07	5.97	*
C-biomass of Bacillariophyceae (pg L^{-1})	Site	1	0.05	3.70	NS
	Season	1	0.06	4.55	*
	Tide	2	0.65	51.6	***
	Zone	1	1.04	82.5	***
	Site*Tide	1	0.04	3.39	NS
	Site*Season*Tide	1	0.07	5.65	*
C-biomass of Dinophyceae (pg L^{-1})	Site	1	0.01	0.02	NS
	Season	1	1.18	5.05	*
	Tide	2	0.06	0.24	NS
	Zone	1	1.36	5.81	*
	Site*Tide	1	0.44	1.87	NS
	Site*Season*Tide	1	0.01	0.023	NS
Chlorophyll *a* (mg m^{-3})	**Site**	1	0.55	1087	***
	Season	1	0.00	1.5	NS
	Tide	2	0.02	39.7	***
	Zone	1	0.02	45.0	***
	Site*Tide	1	0.01	11.0	**
	Site*Season*Tide	1	0.00	0.32	NS
Nitrate (Um L^{-1})	Site	1	0.02	7.21	*
	Season	1	0.47	163	***
	Tide	2	0.04	12.8	***
	Zone	1	0.09	29.9	***
	Site*Tide	1	0.01	2.05	NS
	Site*Season*Tide	2	0.01	1.78	NS
Phosphate (Um L^{-1})	Site	1	0.12	62.8	***
	Season	1	0.00	1.23	NS
	Tide	2	0.01	4.75	*
	Zone	1	0.00	1.82	NS
	Site*Tide	1	0.00	0.72	NS
	Site*Season*Tide	1	0.09	49.6	***
Silicate (Um L^{-1})	Site	1	0.20	8.54	**
	Season	1	0.19	8.11	**
	Tide	2	0.16	6.65	**
	Zone	1	0.27	11.4	**
	Site*Tide	1	0.00	0.02	NS
	Site*Season*Tide	1	0.17	7.25	*

cyanophytes. Nutrient (nitrate, phosphate and silicate) levels were significantly different in terms of sites and season and among the three zones.

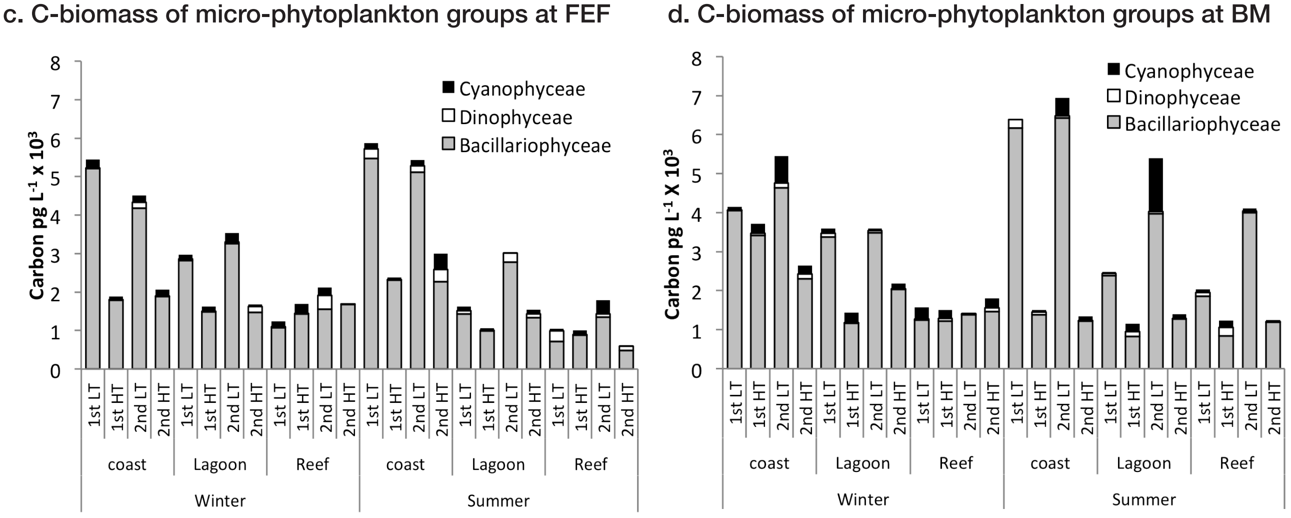
During winter, at both FEF and BM, there was no significant difference in total micro-phytoplankton density (TPD) near the shore and the lagoon, but lower TPD was recorded near the reef area. During summer, FEF had higher TPD near the shore, with no difference between lagoon and reef, while at BM, TPD was higher near the shore followed by the lagoon and the reef area. The C-biomass of total micro-phytoplankton exhibited short-term variations in response to tidal changes throughout the sampling periods, with higher biomass during low tides (Fig. 3). TPD C-biomass varied over the tidal cycle, and also showed spatial variations, with significantly higher biomass being recorded near the shore at both sites (Fig. 3).

At both sites, bacillariophytes, in terms of densities and C-biomass (Fig. 4a-d), were the dominant micro-phytoplankton group as compared to dinophytes and cyanophytes. Although the correlation coefficients were generally very low, there was a positive correlation between bacillariophytes and nutrient concentrations (Table 3). Bacillariphytes C-biomass showed seasonal and spatial (in terms of zones) variation at both sites. Higher C-biomass was recorded near the shore, followed by lagoon and reef. Although no distinct tidal-related variations were observed during summer, higher micro-phytoplankton C-biomass was recorded mostly at low tides (Fig. 4c). However, diatom C-biomass at BM showed a clear trend and exhibited short episodes of rapid increase during low tides (Fig. 4d).

At BM, the distinct tidal-associated difference in diatom C-biomass is a result of changes in silicate


a. Density of micro-phytoplankton groups at FEF

b. Density of micro-phytoplankton groups at BM


c. C-biomass of micro-phytoplankton groups at FEF

d. C-biomass of micro-phytoplankton groups at BM

Figure 4. Density (cells L^{-1}) and carbon biomass (pg L^{-1}) of micro-phytoplankton groups at FEF (a and c) and BM (b and d). Data represent mean ± SD (n=9 at each zone for micro-phytoplankton C-biomass) at both sites.

Table 3. Shannon's Diversity Indices (H') for micro-phytoplankton genera at Flic-en-Flac (FEF) and Belle Mare (BM).

		FEF	BM
Site		3.007	3.093
Season	Winter	2.841	3.052
	Summer	3.013	3.073
Tide	Low tide	2.979	3.086
	High tide	2.959	3.060

concentrations since it was significantly correlated with diatom C-biomass (Table 3). It must be noted that marked tidal-induced differences in micro-phytoplankton was more apparent near the shore and in the lagoon, compared to the reef area (Fig. 4c, d).

Dinophytes and cyanophytes were the least observed during the study. Dinophytes showed seasonal variation with higher C-biomass in the summer season and spatial variation in terms of zones. No spatial variation between the two sites was observed. At FEF, dinophytes C-biomass was generally higher near the shore and the lagoon, while lower C-biomass was recorded near the reef. There was no spatial variation among the three zones at BM.

Cyanophytes exhibited no seasonal and spatial (both in terms of sites and zones) variation at both sites. However, C-biomass of cyanobacteria was higher than that of dinophytes. Moreover, higher C-biomass of cyanobacteria was recorded on several occasions and this corresponded to periods of low tides and was mostly near the shore and lagoon (Figs. 4C, D).

A total of 36 micro-phytoplankton genera were identified at FEF while 34 genera were sampled at BM. Among the 36 micro-phytoplankton genera sampled at FEF, 29 bacillariophytes genera, 5 dinophytes and 2 cyanophytes genera were identified (Appendix A). At BM, 31 bacillariophytes genera, 3 dinophytes and 2 cyanophytes genera were recorded (Appendix B). Shannon's diversity at BM was slightly higher than at FEF, during summer and at low tide (Table 3).

Correlation of biological parameters (micro-phytoplankton and chlorophyll a) with nutrient variability

Positive Pearson's correlation was obtained between parameters tested (C-biomass of total micro-phytoplankton, bacillariophytes, dinophytes and concentration of chlorophyll *a*) and nutrient concentrations, but these were not always significant. At FEF, total

Table 4. Pearson's correlation coefficient, *r* value, tested at Flic-en-Flac (FEF) and Belle Mare (BM). TMP= Total Micro-Phytoplankton. Asterisks indicate significant correlation at 5% level. (* = $P< 0.05$; ** = $P< 0.01$; ***= $P<0.001$).

Site	Parameters	Nitrate	Phosphate	Silicate	Temperature	pH	Salinity
FEF	TMP C-biomass	0.359	0.542**	0.456*	0.031	-0.264	-0.084
	Bacillariophyceae C-biomass	0.328	0.544**	0.441*	0.022	-0.254	-0.096
	Dinophyceae C-biomass	0.484*	0.155	0.317	0.318	-0.213	0.192
	Cyanophyceae C-biomass	0.107	0.062	0.085	-0.198	-0.051	-0.079
	Chlorophyll *a*	0.127	0.509*	0.361	-0.070	-0.111	-0.135
BM	TMP C-biomass	0.415*	0.361	0.221	0.223	-0.285	0.044
	Bacillariophyceae C-biomass	0.425*	0.355	0.240	0.221	-0.309	0.042
	Dinophyceae C-biomass	0.194	0.041	0.033	0.141	-0.208	0.165
	Cyanophyceae C-biomass	0.078	0.195	0.009	0.078	-0.062	0.001
	Chlorophyll *a*	0.605**	0.086	0.240	0.458*	-0.349	0.200

micro-phytoplankton and bacillariophytes C-biomass were significantly (positively) correlated with phosphate and silicate concentrations, while at BM, total micro-phytoplankton and bacillariophytes were significantly (positively) correlated with nitrate (Table 3). Similarly, significant positive correlation was obtained between chlorophyll *a* concentration and phosphate at FEF while at BM chlorophyll *a* was positively correlated with nitrate only. Although positive correlations were found between physical parameters and micro-phytoplankton C-biomass, these were not significant.

Discussion

Short-term variations of micro-phytoplankton biomass can be as significant as long-term ones, governed either by high frequency physical forcing (such as vertical displacement of chlorophyll gradients caused by internal waves, re-suspension of benthic microalgae by wind-driven waves, and re-distribution of phytoplankton biomass by wind-driven surface currents) or biological processes (such as diel vertical migrations of dinoflagellates, diel periodicity of grazing by zooplankton, high frequency periodicity of chlorophyll *a*, among others) (Cloern *et al.*, 1989). However, although studies on short- and long-term variation of micro-phytoplankton diversity, biomass and distribution pattern, as well as factors and processes influencing them, are of great importance, they have received little consideration, with almost no data available on how these physico-chemical and biological factors interact at temporal scales in the Mauritian lagoons. In this study, we investigated the variations of micro-phytoplankton C-biomass, including different micro-phytoplankton groups (Bacillariophyceae, Dinophyceae and Cyanophyceae), chlorophyll *a* and nutrient (nitrate, phosphate and silicate) concentrations at short (in response to tide) and long (seasonal) time frames. Therefore, this study attempts to generate novel information by investigating the effect of tide in governing short-term variations in micro-phytoplankton density, distribution, diversity and carbon biomass (C-biomass) in two coral reef lagoons in Mauritius, in an effort to better understand the mechanisms and strategies adopted by micro-phytoplankton, including behavioural and physiological responses, and migration in the water column, during their response to micro-tidal changes.

Micro-phytoplankton composition and nutrients

Tides had no clear effect on nutrient status at both BM and FEF, but higher concentrations of nitrate and phosphate were recorded on several occasions at BM during periods of low tides; probably as a result of internal waves leading to upwelling of nutrients. This may suggest that mineralisation is taking place in the sediment, releasing nitrite and phosphate as first by-products to the overlying water, which has been found to affect the water column mainly at low tides (Morales-Zamorano *et al.*, 1991).

Nutrients, mainly nitrate and phosphate, showed spatial variation with higher concentration being recorded at BM. The effect of the South East Trade Winds are more significant at BM due to its geographical location and according to Lowe *et al.* (2005) this particular wind stress forcing can stay stable for extended periods in exposed reef regions. Given that wind and tide-induced currents play an important role in enhancing vertical circulation (Arfi *et al.*, 1993), their coupling effect might have contributed to the enhanced sediment re-suspension and release of trapped nutrients at this site, leading to nutrient loading in the lagoon of BM. The intrusion of sub-marine ground water inputs at FEF may also contribute to inputs of nutrients in the coastal water as reported by Ramessur *et al.* (2011), which could also explain the low salinity recorded at both sites during summer, as well as explain the higher silicate concentration at FEF. In addition, BM also appears to experience run-off events due to the presence of nearby agricultural fields (Bhagooli and Taleb-Hossenkhan, 2012), which likely added to the nutrient regime in its coastal water.

Further comparison within the two sites showed that variation in nitrate and phosphate concentrations were not significant among the different zones at BM and FEF, however, variation could be seen at the seasonal level, with higher nitrate and phosphate concentrations during summer. Although this is a snapshot study and does not provide sufficient data to extrapolate on variations in nutrient concentrations at the seasonal and spatial levels, the long-term seasonal and spatial variations in the study of Sadally *et al.* (2014) showed that nutrient concentrations exhibited clear pattern of seasonal and spatial variations, with higher concentration being recorded at BM and near the shore and lagoon compared to the reef area.

A lower N:P ratio as compared with the normal Redfield ratio was also recorded during this study, implying that nitrate was limiting at both study sites. This result is usual for coral reef waters and is in agreement with the study of Jacquet *et al.* (2006) in the New Caledonian's SW lagoon. Moreover, the lower Si:N ratio observed during this study showed that silicate concentration was below the normal range, suggesting its rapid uptake by the dominant diatoms (bacillariophytes) at both sites.

Micro-phytoplankton composition changes with nutrient fluxes since individual taxa have different requirements (Davies and Ugwumba, 2013). In the present study the possible correlation between micro-phytoplankton groups and nutrient concentration (Spearman's Correlation) was also tested. It was found that the community composition of micro-phytoplankton at both sites respond differently to varying levels of nutrients since correlation between the latter and C-biomass of micro-phytoplankton showed the differential response of micro-phytoplankton groups (Bacillariophyceae, Dinophyceae and Cyanophyceae) to nutrient inputs at each study site, thus conforming with the result of Jacquet *et al.* (2006).

Micro-phytoplankton density, C-biomass and distribution in response to micro-tidal changes

Tropical ecosystems can experience rapid changes in physical and meteorological variables, which can in turn induce short-term variations in biological processes (Torréton *et al.*, 2010). The present study indeed showed that tidal forcing contributes to short-term variability in micro-phytoplankton density, C-biomass and chlorophyll *a* concentration in the lagoons of Mauritius. The semi-diurnal tidal system in Mauritius accounts for the short-term fluctuation of micro-phytoplankton over a 6-hour periodicity through alternating sinking and re-suspension brought about by tidal mixing, tidal current and the effect of wind (Blauw *et al.*, 2012). These semi-diurnal tidal-generated internal waves could have contributed to enhancing phytoplankton productivity and dynamics at the study sites by moving nutrients to shallower depths, whereby solar irradiance is higher at the surface, corresponding to the results of Neveux *et al.* (2010).

The higher density and C-biomass of micro-phytoplankton during low tides corroborates the results of Melo and Huszar (2000) and could have been a result of wind-induced vertical mixing of the water column leading to sediment re-suspension, or advection (Torréton *et al.*, 2010). The higher C-biomass and density of micro-phytoplankton with the receding tide could be a result of increased photosynthetic rate and rapid phytoplankton growth occurring during periods of low tidal energy as reported by Davies and Ugwumba (2013) and Winter *et al.* (1975). The lower C-biomass of micro-phytoplankton during high tide could be due to the effect of water currents derived from semi-diurnal tide and wind-induced advection, coupled with the South East Trade Winds inducing rapid renewal of lagoon water by oceanic water. Thus the incoming tide may entrain oceanic waters, causing a diluting effect in the lagoon.

The higher micro-phytoplankton biomass and density at low tide may further be explained by the stability of the water column, inhibiting vertical mixing such that the rate of micro-phytoplankton biomass production in the euphotic zone is faster than the rate at which it is being transported to the lower aphotic zone, or to benthic grazers (Cloern, 1991). Indeed, a study by Lucas and Cloern (2002) showed that net phytoplankton growth decreases with increasing tidal range in a shallow, clear water column with strong benthic grazing, which might have contributed to the observed result at both sites.

In-phase dynamics of chlorophyll *a* can partly be explained in terms of the alternating sinking and vertical mixing of phytoplankton driven by the tidal cycle (Blauw *et al.*, 2012). Despite the fact that there was no significant difference in terms of total micro-phytoplankton biomass between the two sites, a significantly higher chlorophyll *a* concentration was recorded at BM compared to FEF, which might be due to the presence of other photosynthetic microorganisms such as nano- and pico-plankton, that were not taken into account in this study. However, it is also probable that the more nutrient-rich water at BM, coupled with its more significant exposure to the effect of the South East Trade Winds, contributed to a higher chlorophyll *a* concentration (Neveux *et al.*, 2010).

Micro-phytoplankton diversity and tidal change

Tide had varied effects on the nutrient status and phytoplankton community (in terms of genera composition, diversity, abundance, and distribution). Bacillariophytes were the dominant micro-phytoplankton group and contributed more towards total micro-phytoplankton C-biomass during the study period, which is in accordance with the study of Chakraborty *et al.* (2015). Furthermore, it is common that re-suspended benthic diatoms contribute temporarily to enhancing phytoplankton populations (Lucas, 2003). Indeed, the higher C-biomass contribution and dominance over the other micro-phytoplankton groups at both low and high tide during the study, might be due to the re-suspension of several benthic and attached (epilithic, epiphytic) bacillariophytes such as *Navicula, Licmophora*, *Biddulphia*, among others (Appendix A and B). Moreover, their capacity for rapid cell division (Davies and Ugwumba, 2013) with higher growth rate (Cermeño *et al.*, 2005; Wilkerson *et al.*, 2006), their ability to thrive in conditions of high mixing (Pikaitytė and Razinkovas, 2007), as well as their resilience to high turbidity at high tide (Davies and Ugwumba, 2013), might have contributed to the observed result.

The various micro-phytoplankton groups also appeared to be differentially influenced by tidal effects, such that only bacillariophytes showed significant variations in response to tides at both sites, with higher biomass during periods of low tides. Temporal variation in the micro-phytoplankton community may result from temporal variation in turbulent mixing (Blauw *et al.*, 2012). Many species migrate vertically in sediments and these migrational periodicities have been found to be strongly correlated with tidal and diurnal cycles (Admiraal *et al.*, 1982). Moreover, several epilithic diatoms migrate in an upward direction during low tide and downwards with the incoming tide (Pinkney and Zingmark, 1991) and certain of these epilithic diatoms were encountered in the current study. This upward and downward migration in response to tide, as well as the re-suspension of benthic micro-phytoplankton, could explain the higher biomass of bacillariophytes at low tides. Therefore, the fact that they contributed to the higher C-biomass at the sampling sites implies that they are the main contributor to primary productivity and thus play an important role in increasing the C-biomass of micro-phytoplankton in these tropical lagoons as reported by Jacquet *et al.* (2006).

Little contribution of dinophytes and cyanophytes to the total micro-phytoplankton C-biomass in both lagoons in Mauritius was recorded during this study, which could be attributed to their behavioural and physiological response. The fact that dinophytes have a lower growth rate compared to bacillariophytes (Camacho *et al.*, 2007; Davies and Ugwumba, 2013) and can regulate their position in the water column in response to environmental parameters (Hackett *et al.*, 2004), could have contributed to their lower densities and C-biomass during the study period. Similarly the low irradiance preference of cyanophytes (Jones and Gowen, 1990) and their comparatively lower growth rate as compared to many other algal species (WHO, 1999), also accounted for their low biomass.

In fact, planktonic unicellular cyanobacteria, such as *Synechococcus* and *Prochlorococcus*, have also been found to dominate oligotrophic waters surrounding coral reef ecosystems and lagoons (Charpy *et al.*, 2012) with abundances ranging from 10 × 10^3 to 500 × 10^3 cells mL^{-1} and 10 × 10^3 to 400 × 10^3 cells mL^{-1}, respectively. The role of cyanobacteria as an important source of dissolved organic carbon (DOC) in reef ecosystems was also not investigated during this study. Indeed, any change in their abundance may alter the quantity and chemical composition of organic materials being provided to the reef environment, as well as long-term impacts on reef communities (Brocke *et al.*, 2015). Moreover, given that several species of cyanobacteria are less than 5µm, including both *Synechococcus* (size 0.8 µm) and *Prochlorococcus* (size 0.6 µm), this important contributor to primary production (Ribes *et al.*, 2003; Patten *et al.*, 2011) and to DOC were not taken into account since a size range corresponding to micro-phytoplankton only was focused on, and thus requires future attention. Therefore, C-biomass production in Mauritian coral reef lagoons seems primarily supported by bacillariophytes primary production.

Shannon's Diversity Indices (H') for micro-phytoplankton genera at FEF and BM were not significantly different in this study. The presence of almost the same micro-phytoplankton genera at both high and low tides was recorded, indicating that these genera were true species (permanent residents) at these sites. According to Blauw *et al.* (2012), a periodicity of 6 hours results in rapid environmental fluctuations that will be faster than the generation time of most phytoplankton species, leading mainly to a vertical re-distribution of existing populations. Indeed, the present study showed that the semi-diurnal system comprising of 6 hour periodicities in Mauritius, is not sufficient to cause a shift in micro-phytoplankton diversity but rather caused a re-distribution of the same species.

Spatial (sites and zones) and seasonal variation of micro-phytoplankton C-biomass

Although in this study seasonal trends were weak using August and November 2014 data, probably as a result of limited sampling, the long-term study of Sadally *et al.* (2014) clearly showed how nutrients, chlorophyll *a*, as well as the different micro-phytoplankton groups and genera, exhibited temporal and spatial variations over a three-year period. In the current study, only bacillariophytes exhibited spatial and seasonal variations at both sites, which may be attributed to their sensitivity to a wide range of limnological and environmental conditions (Verma *et al.*, 2011), and the rapid response of their community structure to variations in physical, chemical, and biological conditions in the immediate environment (Davies and Ugwumba, 2013). However, their higher C-biomass in summer is due to the combination of higher solar radiation and increased frequency of heavy rainfall, which causes run-off events and nutrient loading in the coastal waters.

The high C-biomass of bacillariophyes in summer was due to the high concentration of silicate during this season because bacillariophytes showed rapid development with increasing silicate concentrations (Lasternas *et al.*, 2008). Bacillariophytes were positively correlated with silicate and their higher biomass in summer corresponded to higher silicate concentrations. Higher C-biomass of dinophytes was also recorded in summer and could be due to the higher nutrient levels and because their preference to warmer waters (Lasternas *et al.,* 2008).

No site-specific variation in total micro-phytoplankton C-biomass was recorded between the two sites but significant spatial differences among the different zones were observed, with higher biomass near the shore, compared to the lagoon and the reef areas. This spatial variation in terms of zones is in accordance with previous studies (Sadally *et al.*, 2011; Sadally *et al.*, 2014) and might be attributed to several factors, including nutrient availability. Nutrient concentration near the shore was higher at both sites and this may account for the higher micro-phytoplankton C-biomass near the shore by increasing their growth rate, as reported by Fu *et al.* (2009).

Conclusion

This study showed that micro-phytoplankton biomass exhibited short-term variability in response to micro-tidal effects, with higher biomass recorded during periods of low tides. This tidal oscillation of micro-phytoplankton biomass with higher and lower C-biomass at low and high tides, respectively, may be a result of micro-tidally-induced water movement and water stability during low tides and increased micro-phytoplankton growth rate and high grazing pressure at high tide. No seasonal variation was apparent in total micro-phytoplankton C-biomass, chlorophyll *a* and cyanophytes. However, the bacillariophytes and dinophytes showed seasonal variation with higher C-biomass in summer and this was mainly attributed to seasonal changes in nutrients. Spatial variation of C-biomass of micro-phytoplankton was significant in terms of zones within the sites but was not significant across the sites. Higher biomass of micro-phytoplankton was recorded near the shore, possibly as a result of higher nutrient concentrations there. Therefore, micro-tide has varied effects on the nutrient status and phytoplankton community (in terms of micro-phytoplankton groups) and this study also demonstrated the importance of episodic micro-tidal forcing in determining the primary productivity in coral reef lagoon systems. This study provides baseline information on the short-term variability of micro-phytoplankton biomass in response to micro-tidal changes. Continuous monitoring is warranted in predicting long-term response of coastal micro-phytoplankton C-biomass, and thus primary productivity, to changing environmental conditions in coral reef ecosystems.

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Appendix A. Micro-phytoplankton diversity at FEF. Data represents percentage of the different micro-phytoplankton genera sampled during the study. S: Shore, L: lagoon, R: reef.

		Winter (August 2011)												Summer (November 2011)											
		1st LT			1st HT			2nd LT			2nd HT			1st LT			1st HT			2nd LT			2nd HT		
	Genera	S	L	R	S	L	R	S	L	R	S	L	R	S	L	R	S	L	R	S	L	R	S	L	R
Class Bacillariophyceae	*Achnanthes*	0.0	4.4	0.0	0.0	0.0	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Asterionellopsis	1.3	2.2	0.0	1.9	0.0	1.8	2.5	6.1	0.0	0.0	0.0	0.0	0.0	15.7	6.1	11.3	1.5	1.5	0.0	0.0	2.5	0.0	28.9	2.7
	Biddulphia	3.4	3.3	0.0	0.0	0.0	0.0	1.3	4.0	0.0	0.0	0.0	2.9	6.5	0.0	0.0	1.4	0.0	1.5	11.3	0.0	0.0	5.4	0.0	8.1
	Cavinula	4.7	5.6	1.5	5.7	2.6	1.8	8.8	8.1	0.9	3.5	4.3	1.9	3.3	2.9	12.2	2.8	10.6	9.1	7.3	6.8	2.5	8.1	4.4	2.7
	Climacodium	5.4	3.3	0.0	1.9	0.0	1.8	0.6	3.0	3.5	3.5	5.7	1.0	1.6	2.9	0.0	1.4	0.0	0.0	1.7	3.4	0.0	0.0	4.4	2.7
	Cocconeis	14.8	12.2	12.1	13.2	6.6	12.5	30.6	10.1	6.1	8.8	7.1	17.1	9.8	7.1	8.2	7.0	16.7	13.6	5.1	10.2	25.0	8.1	11.1	10.8
	Coscinodiscus	0.0	2.2	3.0	3.8	1.3	5.4	1.9	1.0	0.9	0.9	1.4	3.8	0.0	1.4	2.0	5.6	1.5	3.0	1.7	3.4	2.5	2.7	2.2	2.7
	Cyclotella	4.0	0.0	3.0	3.8	0.0	10.7	1.9	0.0	1.8	0.0	2.9	4.8	3.3	2.9	0.0	5.6	3.0	3.0	0.0	3.4	2.5	2.7	2.2	2.7
	Cylindrotheca	3.4	3.3	1.5	3.8	2.6	0.0	8.1	3.0	1.8	1.8	1.4	0.0	3.3	0.0	0.0	0.0	1.5	3.0	1.7	0.0	0.0	5.4	2.2	0.0
	Diatoma	0.0	1.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Diploneis	6.0	4.4	10.6	7.5	7.9	7.1	2.5	6.1	13.2	14.2	7.1	1.0	1.6	1.4	2.0	0.0	3.0	1.5	3.4	3.4	2.5	2.7	2.2	2.7
	Ditylum	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Fragilaria	2.7	2.2	4.5	1.9	0.0	0.0	1.3	2.0	2.6	0.9	1.4	0.0	8.1	0.0	0.0	0.0	1.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Haslea	0.0	4.4	3.0	1.9	3.9	1.8	1.9	2.0	0.9	2.7	1.4	1.0	0.0	0.0	0.0	0.0	1.5	0.0	1.7	0.0	0.0	2.7	0.0	0.0
	Licmophora	0.0	3.3	0.0	1.9	3.9	0.0	0.6	4.0	0.9	1.8	1.4	0.0	4.9	1.4	2.0	5.6	0.0	1.5	3.4	6.8	5.0	5.4	2.2	8.1
	Lyrella	6.7	3.3	4.5	3.8	22.4	1.8	0.6	7.1	7.9	8.0	5.7	1.9	1.6	1.4	2.0	0.0	6.1	7.6	5.1	0.0	10.0	5.4	2.2	0.0
	Manguinea	2.0	6.7	0.0	0.0	1.3	0.0	0.0	6.1	0.0	3.5	0.0	0.0	1.6	1.4	0.0	1.4	3.0	4.5	0.0	0.0	0.0	0.0	2.2	0.0
	Melosira	0.0	1.1	6.1	0.0	13.2	10.7	0.0	2.0	4.4	4.4	15.7	12.4	3.3	12.9	0.0	8.5	6.1	6.1	5.1	3.4	10.0	0.0	8.9	2.7
	Navicula	23.5	13.3	28.8	28.3	13.2	25.0	20.6	15.2	34.2	18.6	12.9	42.9	29.3	8.6	14.3	18.3	22.7	21.2	20.9	23.7	7.5	10.8	11.1	10.8
	Nitzschia	1.3	2.2	0.0	0.0	1.3	0.0	0.0	2.0	0.0	0.9	1.4	0.0	1.6	0.0	0.0	0.0	1.5	3.0	0.0	0.0	0.0	0.0	0.0	0.0
	Odontella	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.6	8.8	0.0	0.0	0.0	0.0	0.0	15.5	0.0	0.0	5.6	0.0	0.0	0.0	0.0	0.0
	Pinnularia	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.9	0.0	0.0	2.8	4.5	3.0	5.1	0.0	2.5	16.2	0.0	0.0
	Pleurosigma	1.3	2.2	1.5	1.9	1.3	1.8	0.6	2.0	0.0	0.9	1.4	0.0	0.0	0.0	0.0	0.0	1.5	3.0	0.0	0.0	0.0	0.0	0.0	0.0
	Pseudo-nitzschia	6.7	7.8	6.1	5.7	6.6	5.4	2.5	5.1	4.4	7.1	4.3	3.8	4.9	2.9	2.0	4.2	3.0	4.5	1.7	10.2	10.0	8.1	6.7	2.7
	Stauroneis	3.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Striatella	2.7	0.0	1.5	0.0	1.3	0.0	1.3	2.0	0.9	0.9	1.4	1.0	0.0	1.4	2.0	2.8	1.5	3.0	0.0	6.8	2.5	2.7	0.0	0.0
	Thalassionema	1.3	1.1	9.1	7.5	6.6	8.9	0.6	4.0	8.8	2.7	4.3	2.9	1.6	2.9	4.1	1.4	3.0	1.5	1.7	6.8	2.5	2.7	2.2	2.7
	Thalassiosira	0.0	3.3	0.0	0.0	0.0	0.0	0.6	1.0	1.8	2.7	10.0	0.0	0.0	1.4	2.0	0.0	1.5	1.5	1.7	3.4	5.0	2.7	2.2	5.4
	Thalassiothrix	1.3	1.1	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	1.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

		Winter (August 2011)												Summer (November 2011)											
		1st LT			1st HT			2nd LT			2nd HT			1st LT			1st HT			2nd LT			2nd HT		
	Genera	**S**	**L**	**R**	**S**	**L**	**R**	**S**	**L**	**R**	**S**	**L**	**R**	**S**	**L**	**R**	**S**	**L**	**R**	**S**	**L**	**R**	**S**	**L**	**R**
Class Dinophyceae	***Ceratium***	0.0	0.0	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Gymnodinium	1.3	2.2	1.5	0.0	1.3	1.8	1.9	2.0	1.8	2.7	4.3	0.0	1.6	1.4	2.0	1.4	3.0	3.0	3.4	3.4	2.5	2.7	2.2	2.7
	Prorocentrum	2.0	1.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.4	1.0	1.6	0.0	0.0	1.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Protoperidinium	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.3	0.0	36.7	0.0	0.0	0.0	11.3	3.4	2.5	2.7	0.0	2.7
	Symbiodinium	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	24.3
Class Cyanophyceae	***Oscillatoria***	0.7	2.2	1.5	3.8	2.6	1.8	1.3	1.0	0.9	0.9	1.4	1.0	1.0	30.0	2.0	1.4	1.5	0.0	1.1	1.7	2.5	2.7	2.2	2.7
	Phormidium	0.0	0.0	0.0	0.0	0.0	0.0	6.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

Appendix B. Micro-phytoplankton diversity at BM. Data represents percentage of the different micro-phytoplankton genera sampled during the study. S: Shore, L: lagoon, R: reef.

		Winter (August 2011)												Summer (November 2011)											
		1st LT			1st HT			2nd LT			2nd HT			1st LT			1st HT			2nd LT			2nd HT		
	Genera	S	L	R	S	L	R	S	L	R	S	L	R	S	L	R	S	L	R	S	L	R	S	L	R
Class Bacillariophyceae	*Achnanthes*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Asterionellopsis	3.6	0.0	3.2	0.0	2.0	0.0	7.8	1.2	3.8	0.0	3.9	5.5	4.1	6.3	3.0	6.2	6.8	2.4	1.5	2.8	2.8	2.4	2.1	2.6
	Biddulphia	0.0	0.0	0.0	0.0	0.0	2.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Cavinula	4.6	4.9	0.0	5.2	2.0	7.5	3.4	4.7	3.8	11.5	11.7	16.5	5.3	4.2	3.0	3.1	6.8	4.7	21.9	8.3	12.3	7.3	16.7	7.9
	Climacodium	1.5	2.5	6.5	0.0	0.0	0.0	4.5	2.4	0.0	5.8	0.0	2.8	1.8	2.1	0.0	3.1	3.4	0.0	1.5	0.0	0.0	0.0	0.0	0.0
	Cocconeis	4.6	7.4	16.1	12.9	26.5	17.5	24.0	12.9	15.0	5.8	3.9	8.3	5.3	4.2	11.9	6.2	6.8	25.9	4.4	8.3	2.8	7.3	6.3	7.9
	Coscinodiscus	3.0	2.5	3.2	5.2	2.0	5.0	1.7	2.4	0.0	0.0	7.8	2.8	3.6	2.1	3.0	3.1	3.4	2.4	8.8	8.3	2.8	0.0	0.0	0.0
	Cyclotella	0.0	0.0	0.0	5.2	4.1	2.5	0.0	0.0	0.0	2.9	0.0	0.0	0.0	0.0	3.0	0.0	0.0	2.4	1.5	0.0	5.7	0.0	0.0	0.0
	Cylindrotheca	4.6	4.9	3.2	0.0	0.0	0.0	5.0	2.4	0.0	0.0	0.0	0.0	5.3	6.3	3.0	3.1	3.4	2.4	7.3	11.0	5.7	9.8	10.4	7.9
	Diatoma	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Diploneis	3.0	2.5	3.2	5.2	4.1	5.0	5.0	2.4	0.0	2.9	3.9	0.0	3.6	2.1	3.0	3.1	6.8	4.7	1.5	2.8	0.0	2.4	2.1	5.3
	Ditylum	0.0	2.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	5.7	0.0	0.0	0.0
	Fragilaria	1.5	0.0	3.2	2.6	2.0	0.0	6.7	0.0	0.0	2.9	0.0	0.0	1.8	10.5	0.0	15.4	0.0	0.0	1.5	2.8	0.0	0.0	0.0	0.0
	Haslea	1.5	2.5	0.0	2.6	0.0	0.0	0.0	1.2	3.8	0.0	0.0	4.6	1.8	4.2	0.0	3.1	3.4	0.0	1.5	2.8	0.0	2.4	2.1	2.6
	Licmophora	11.7	7.4	9.7	2.6	2.0	10.0	1.7	3.5	16.3	5.8	7.8	2.8	13.6	6.3	11.9	6.2	10.2	11.8	4.4	8.3	5.7	9.8	8.3	10.5
	Lyrella	0.0	2.5	0.0	2.6	0.0	2.5	0.0	0.0	0.0	2.9	3.9	0.0	0.0	0.0	9.0	0.0	0.0	4.7	2.9	0.0	5.7	2.4	2.1	2.6
	Manguinea	0.0	0.0	6.5	2.6	0.0	2.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.0	0.0	0.0	4.7	0.0	2.8	0.0	2.4	2.1	2.6
	Melosira	0.0	0.0	0.0	7.8	14.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.4	0.0	0.0	5.7	0.0	0.0	0.0
	Navicula	11.7	19.8	19.4	10.3	16.3	10.0	16.8	23.5	15.0	19.2	11.7	8.3	13.6	8.4	26.9	9.2	13.6	18.8	7.3	13.8	16.0	9.8	10.4	7.9
	Nitzschia	3.0	4.9	9.7	2.6	0.0	2.5	3.4	2.4	3.8	5.8	3.9	5.5	3.6	4.2	0.0	0.0	3.4	0.0	8.8	2.8	0.0	0.0	0.0	0.0
	Odontella	13.7	9.9	0.0	11.2	0.0	12.5	0.0	17.6	0.0	0.0	19.5	9.2	16.0	0.0	0.0	0.0	0.0	0.0	4.4	0.0	4.7	24.4	22.9	21.1
	Pinnularia	6.1	2.5	3.2	0.0	2.0	0.0	0.0	3.5	3.8	2.9	3.9	2.8	7.1	0.0	0.0	0.0	6.8	0.0	0.0	0.0	2.8	0.0	0.0	0.0
	Pleurosigma	0.0	4.9	0.0	0.0	0.0	2.5	0.0	3.5	0.0	0.0	0.0	2.8	0.0	4.2	0.0	6.2	0.0	0.0	1.5	0.0	0.0	0.0	0.0	0.0
	Podocystis	0.0	2.5	0.0	2.6	0.0	0.0	0.0	4.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Pseudo-nitzschia	1.5	4.9	0.0	5.2	4.1	7.5	8.4	3.5	3.8	4.8	3.9	8.3	1.8	6.3	3.0	6.2	3.4	0.0	7.3	2.8	2.8	4.9	4.2	7.9

		Winter (August 2011)												Summer (November 2011)											
		1st LT			1st HT			2nd LT			2nd HT			1st LT			1st HT			2nd LT			2nd HT		
	Genera	**S**	**L**	**R**	**S**	**L**	**R**	**S**	**L**	**R**	**S**	**L**	**R**	**S**	**L**	**R**	**S**	**L**	**R**	**S**	**L**	**R**	**S**	**L**	**R**
Class Bacillariophyceae	***Stauroneis***	1.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	7.7	0.0	0.0	1.8	2.1	0.0	0.0	3.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Striatella	0.0	2.5	0.0	5.2	4.1	0.0	3.4	3.5	3.8	5.8	0.0	2.8	0.0	4.2	0.0	3.1	0.0	0.0	4.4	0.0	2.8	0.0	0.0	0.0
	Thalassionema	1.5	4.9	3.2	5.2	6.1	2.5	3.4	2.4	3.8	2.9	0.0	5.5	1.8	14.7	6.0	12.3	3.4	4.7	1.5	2.8	5.7	2.4	2.1	2.6
	Thalassiosira	1.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	7.5	2.9	3.9	0.0	1.8	0.0	3.0	0.0	3.4	2.4	0.0	5.5	2.8	2.4	2.1	2.6
	Thalassiothrix	0.0	0.0	3.2	0.0	2.0	0.0	0.0	0.0	3.8	0.0	3.9	2.8	0.0	2.1	0.0	3.1	0.0	0.0	1.5	0.0	0.0	2.4	2.1	2.6
Class Dinophyceae	***Ceratium***	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Gymnodinium	1.5	2.5	0.0	2.6	2.0	2.5	1.7	1.2	3.8	2.9	0.0	2.8	1.8	0.0	3.0	0.0	3.4	2.4	1.5	0.0	2.8	2.4	2.1	2.6
	Prorocentrum	1.5	0.0	3.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.8	4.2	0.0	6.2	3.4	0.0	1.5	2.8	0.0	0.0	0.0	0.0
	Protoperidinium	1.5	0.0	0.0	0.0	2.0	2.5	1.7	0.0	3.8	2.9	3.9	2.8	1.8	0.0	0.0	0.0	3.4	2.4	1.5	5.5	0.0	2.4	0.0	0.0
Class Cyanophyceae	***Gomphosphaeria***	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.8	2.8	0.0	0.0	0.0
	Lyngbya	0.0	0.0	0.0	0.0	0.0	0.0	0.6	0.0	2.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Oscillatoria	15.2	1.2	3.2	0.9	2.0	2.5	1.1	1.2	2.5	1.9	2.6	0.9	1.2	1.1	1.5	1.5	1.7	1.2	0.7	3.7	1.9	2.4	2.1	2.6
	Phormidium	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

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Demersal trawl surveys show ecological gradients in Southwest Indian Ocean slope fauna

Bernadine Everett[1*], Johan C. Groeneveld[1], Sean Fennessy[1], Sean Porter[1], Cosmas N. Munga[2,3], Nilza Dias[4], Osvaldo Filipe[4], Lourenço Zacarias[4], Mathias Igulu[5], Baraka Kuguru[5], Edward Kimani[2], Guy Rabarison[6], Herimamy Razafindrakoto[7]

[1] Oceanographic Research Institute, Durban, South Africa

[2] Kenya Marine and Fisheries Research Institute, Mombasa, Kenya

[3] Department of Environment and Health Sciences, Marine Sciences Section, Technical University of Mombasa, Mombasa, Kenya

[4] Instituto de Investigação Pesqueira, Maputo, Mozambique

[5] Tanzania Fisheries Research Institute, Dar es Salaam, Tanzania

[6] Centre National de Recherche sur l'Environment, Antananarivo, Madagascar

[7] Centre d'Etudes et de Développement des Pêches, Mahajanga, Madagascar

* corresponding author: bernadine@ori.org.za

Abstract

We assessed the richness, diversity and community structure of demersal fish and benthic invertebrates caught by trawl nets along the deep shelf and upper continental slope of the Southwest (SW) Indian Ocean. Four depth-stratified surveys were undertaken in 2011-2012, in Kenya, Tanzania, Mozambique and southwestern Madagascar. The effects of region (north vs south), country (proxy for latitude) and depth stratum on catch composition were considered. Of 243 genera identified from 206 trawls, the majority were teleosts (55%), followed by crustaceans (18%), elasmobranchs (12%) molluscs (10%), and other invertebrates (5%). Species richness was highest in Mozambique, and in the 300-399 m depth stratum. Shannon's diversity was greatest at 200-299 m depth in Kenya, decreasing southwards along a latitudinal gradient. Genera contributing most to the dissimilarity between the north and south were greeneye fishes, *Chlorophthalmus*, and knife prawns, *Haliporoides.* By country, Madagascar and Tanzania were most dissimilar, with blackchin fishes, *Neoscopelus*, greeneye fishes, and nylon shrimps, *Heterocarpus*, the main drivers. By depth, the 200-299 m and 500-599 m strata were most dissimilar, based on blackchin fishes, knife prawns and greeneye fishes. Our study shows a clear difference in community structure of slope fauna across the Mozambique Channel, reflecting sampling of two ecologically different soft-sediment communities. The information provided is new to the SW Indian Ocean region, and an important step towards understanding diversity trends, for the prioritization of conservation needs and development of deep-water fisheries management strategies in the region.

Keywords: Marine biodiversity, Benthic environment, Soft-sediment

Introduction

The Southwest (SW) Indian Ocean is a low-latitude, mainly tropical region that extends along the East African coast, from the equator to eastern South Africa, and around the island states of Madagascar, Mauritius, Comoros and Seychelles. It is analogous to the Western Indian Ocean province of Spalding *et al.* (2007), which comprises several ecoregions defined as areas of relatively homogenous species composition, clearly distinct from adjacent systems. In the global context, the Western Indian Ocean hosts a peak of species richness, comparable to Southeast Asia (western Pacific) and the Caribbean (Atlantic), and this pattern is mostly driven by the high diversity of coastal fishes (Tittensor *et al.*, 2010). A large variety of habitats and favourable oceanographic conditions support the high overall richness and biodiversity (van der Elst *et al.*, 2005; Obura *et al.*, 2012; Everett and van der Elst, 2015; Schleyer, 2015), but at a local scale, abundance and biodiversity tend to be more patchy, influenced by the distribution of habitats in a heterogenous marine environment (Mackas and Boyd, 1979; Kirkman *et al.*, 2013).

As in other oceans, anthropogenic activities have a large impact on marine habitats and biodiversity of the SW Indian Ocean (Schleyer, 2015). Coastal states in the region are some of the poorest in the world, with low United Nations development indices (UNDP, 2013) and all face severe socio-economic challenges. Hence, rapidly-growing coastal communities rely heavily on fishing as a source of food and economic activity (van der Elst *et al.*, 2005; Groeneveld, 2015). Overfishing and habitat deterioration are serious concerns, especially in nearshore areas, because the numbers of fishers, harvest methods and offtake are infrequently controlled. Industrial trawl fisheries for crustaceans on shallow mudbanks and on deep trawl grounds yield high bycatches of many different species, most of which are discarded overboard and do not survive (Fennessy and Everett, 2015). Apart from direct removals through fishing and related damage to habitats, the conservation of biodiversity in the SW Indian Ocean is also affected by maritime activities (Jackson, 2015), oil and gas exploration (Richmond, 2015), coastal mining (Barwell, 2015), tourism and recreation (Ragoonaden, 2015), and urbanization and coastal development, sometimes stretching far inland to catchment areas (Celliers and Ntombela, 2015).

An important motivation for understanding geographic diversity patterns is concern over biodiversity threats being concentrated in areas of high richness and thus affecting large numbers of species (Myers *et al.*, 2000). At the level of the SW Indian Ocean, there is a need for systematic conservation planning, to accommodate multiple user-groups while conserving the environments and biological diversity on which ecosystem functioning relies (Obura *et al.*, 2012; Schleyer, 2015). While reef communities have been a particular focus (Obura, 2015a), soft sediment habitats predominate spatially, yet their biota remain poorly known (Fennessy and Green, 2015). This is a concern for governments in the region, which have limited capacity particularly for deep-sea research, with consequent limits to their abilities to plan and manage exploitation of resources in this environment (Obura, 2015b). Despite the presence of deep-water trawl fisheries in some parts of the region (Groeneveld and Everett, 2015), existing knowledge of SW Indian Ocean soft-sediment biota is mostly confined to shelf waters, and is mainly based on crustacean trawl fisheries associated with muddy substrata, as well as from research trawl surveys (Fennessy and Green, 2015).

The latitudinal decline of species richness from the tropics to the poles is the best known generalized spatial gradient in biological diversity, and was already known to early naturalists nearly two centuries ago (Humboldt, 1828; Hawkins, 2001). The trend has since been described for many taxa, but with some notable exceptions (Hillebrand, 2004). In the marine realm, the strength and slope of the gradient is subject to regional, habitat and organismal features (Hillebrand, 2004). By region, coastal species reach maximum richness in the western Pacific, whereas oceanic groups peak across a broad mid-latitudinal range (Tittensor *et al.*, 2010). By depth, it is commonly found that richness increases away from the coast and tends towards a unimodal pattern, with a peak at intermediate depths (1500-2500 m) and depressed diversity at upper bathyal and abyssal depths (Rex *et al.*, 1993; 2000; Gray, 1997). This pattern however, does not appear to be universal (Gray, 2001), and may be attributed to varied environmental gradients. For example, Levin *et al.* (2001) related deep-sea diversity patterns to the regional-scale phenomena of geographic boundary effects, sediment grain size, productivity gradients, oxygen minimum zones, current regimes, and catastrophic disturbances.

A recent analysis of trawl survey data from the SW Indian Ocean focussed on deep-water crustacean species with potential for fisheries (Everett *et al.*, 2015). In summary, this analysis found that about 70% of catches by weight comprised teleosts, the proportion of crustaceans increased with depth between 300 and 700 m, species composition differed by country along a latitudinal gradient, and the proportions of crustaceans with commercial potential in the catch differed markedly across the Mozambique Channel (i.e. in southern Mozambique versus southwestern Madagascar). We extend the above analysis by investigating the species richness, diversity and community structure of benthic (demersal) taxa caught during trawl surveys. All the genera that could be identified are listed in the supplementary material (Table S1), and gradients by region (north versus south), latitude (using country as a proxy), longitude (across the Mozambique Channel), and depth are investigated, relative to generalized gradients. The information provided is new to the region, and is an important step towards understanding diversity trends, for purposes ranging from the prioritization of conservation needs to fisheries management of deep-water resources in the areas investigated.

Materials and Methods

Study area

The study area covers the deep shelf and upper continental slope of eastern Africa and southwestern Madagascar (Fig. 1). Everett *et al.* (2015) provide a detailed description of the study area, survey methods and data collection protocols. In brief, the shelf is generally narrow, widening in bights or near river deltas, while the shelf edge is frequently rocky and unsuitable for trawling (Fennessy and Green, 2015). Trawlable grounds on the steep upper continental slope likely comprise sand, mud, hardened sediment accretions, foraminifera and spicules (Berry, 1969). Sea surface temperatures are 26-33°C near the equator and 22-27°C further south (NOAA, 2016), and bottom temperatures of 8-12°C have been reported from 200-700 m depths (Berry, 1969; Pripp *et al.*, 2014). Large-scale circulation patterns include the nutrient-rich Somali Current (Schott and McCreary, 2001), the East Africa Coastal Current (EACC) off Kenya and Tanzania, and the Mozambique Channel circulation. The latter region is mostly oligotrophic, characterised by recurring mesoscale cyclonic and anti-cyclonic cells and eddies (Lutjeharms, 2006; Ternon *et al.*, 2014). The Agulhas Current off south-east Africa originates near the southern end of the channel (Lutjeharms, 2006).

Data collection

Demersal trawl surveys were conducted in Kenya, Tanzania, southern Mozambique and southwestern Madagascar, between October 2011 and March 2012 (Fig. 1) using two commercial fishing vessels. The FV Roberto (23 m length; 117 t GRT; 295 hp) towed an otter trawl net from the stern (net length 26 m; footrope length 26 m; mesh in codend 38 mm stretched), and was used in Tanzania and Kenya. The FV Caroline (40 m length; 313 t GRT; 745 hp) also towed a single otter trawl net deployed from the stern (net length 75 m; footrope length 60 m; mesh in codend 50 mm stretched), and was used in Mozambique and Madagascar. Survey

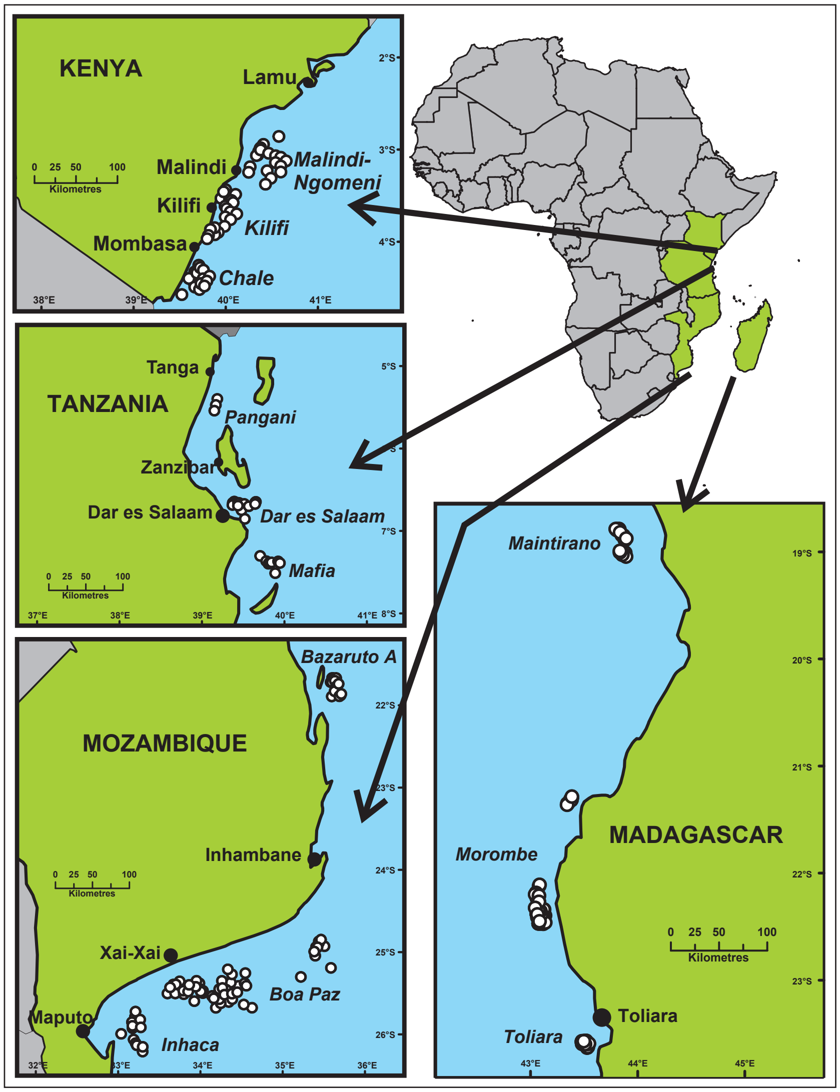

Figure 1. Areas trawled during the South West Indian Ocean Fisheries Project deep-water crustacean surveys. Symbols indicate actual positions where nets were set, trawl area names in italics.

areas were defined based on knowledge of existing fishing grounds (Mozambique), information from historical research surveys (Saetersdal *et al.*, 1999), or anecdotal information obtained from fishing companies (Madagascar, Tanzania, Kenya). Criteria used to select trawling sites within the survey areas were trawlability and depth range (100-699 m), and sites were stratified by depth and latitude. The entire catch per trawl was sorted, and species or groups were identified, weighed and counted. Regrettably, voucher specimens were not retained for confirmation of identities.

Data sorting and vetting

All species records were validated by comparing their occurrence in the trawl catches with known distribution and depth ranges given in the World Register of Marine Species (WoRMS Editorial Board, 2015), Fishbase (Froese and Pauly, 2015) and SeaLifeBase (Palomares and Pauly, 2015). Where mismatches occurred (trawled species beyond known depth and/or latitudinal ranges) species records were eliminated for the purposes of this analysis. To account for potential misidentification, analyses were conducted at genus, rather than species level.

Two survey vessels with unequal fishing power were used, therefore catches were standardised using the raising method described by Everett *et al.* (2015). To convert from densities (the output of the swept area method) to count data (as required for the present study), an average swept area per trawl was determined for each vessel, and the ratio of these was used as a multiplication factor to raise catches made by the smaller net of the FV Roberto to the equivalent of those made by the FV Caroline. Night-trawls and trawls in shallow (<200 m depth) and very deep (>599 m) water were sparse and inconsistently distributed across the sampling domain, and therefore only catches made during the day and between 200 and 599 m were analysed.

Data analysis

Data matrices with the frequency of occurrence of each genus per station were analysed. Species richness indices and accumulation plots were calculated per country and 100 m depth stratum using EstimateS9 (Colwell, 2013). While species counts can be used to determine species richness, there is consensus that this is not the best estimate of true richness (Palmer, 1990; Nichols *et al.*, 1998; Reese *et al.*, 2014), because it is affected by sampling effort. Therefore we also used the Chao2 non-parametric estimator (Chao; 1987; 2005), based on the incidence or frequency of encounters, to estimate total species richness. The species richness indices were analysed using one-way ANOVA to test for significant differences by country and depth. Shannon's diversity and Pielou's index were calculated to respectively determine the diversity and evenness of genera in trawls. Shannon's diversity quantifies the unevenness of the probability distribution by taking both abundance and evenness of the species present into account (Lesne, 2014), while Pielou's index is a measure of equitability, i.e., a measure of how evenly the individuals are distributed among the different species (Clark and Gorley, 2006).

Multivariate, non-metric, multi-dimensional scaling (MDS) was used to graphically identify whether communities differed among geographical areas, categorized as individual countries, north (Kenya and Tanzania) versus south (southern Mozambique and southwest Madagascar), or depth strata. The MDS plots were based on Bray-Curtis similarities using untransformed count data. The data were not transformed prior to analysis as (i) the count data used precluded the manifestation of any large biases due to body size differences among taxa (which is often the case when using biomass data), and (ii) the aim of the analyses were to describe communities in a manner that allowed for the dominant (in frequency), and thus characteristic taxa, to drive patterns in multivariate community structure.

Differences among geographical areas and depths were tested using a three-factor permutational multivariate analysis of variance (PERMANOVA) (Anderson, 2001). Region (with two levels – north versus south), country (with four levels), and depth strata (with four levels), were all treated as fixed factors. Region was included as a factor due to the large geographical divide between the Kenya and Tanzania sites in the north, and the southern Mozambique and southwest Madagascar sites in the south (Fig. 1). Country was nested within region and depth strata treated as orthogonal with country and region. The analysis was based on the Bray-Curtis similarity distance measure, run using 9999 permutations of the residuals under a reduced model with type III partial sums of squares employed due to the unbalanced nature of the design. Post hoc tests using the same model were conducted when relevant. The PERMANOVA analysis was supplemented with several permutational analyses of multivariate dispersions (PERMDISP) to assess whether significant differences found by the PERMANOVA were due to location or dispersion (or both) effects (Anderson,

Table 1. Number of trawls set per country and depth stratum, total catch in tons and the numbers of families and genera identified.

Country	**Trawls at depth (m)** **200-299**	**300-399**	**400-499**	**500-599**	**Total trawls**	**Total catch (t)**	**No. of families**	**No. of genera**
Kenya	13	14	12	5	44	5.5	105	148
Tanzania	9	11	4	3	27	1.3	82	100
Mozambique	12	34	25	6	77	29.2	109	153
Madagascar	9	13	15	21	58	19	106	142
TOTAL	**43**	**72**	**56**	**35**	**206**	**55**	**154**	**243**

2006). One and two-way SIMPER analyses identified which genera were most influential in characterising and discriminating between assemblages. All multivariate analyses were conducted using PRIMER (Clarke and Gorley, 2006) and PERMANOVA+ for PRIMER (Anderson *et al*., 2008).

Results

A total of 206 trawls were available for use in the analyses, mostly from Mozambique (37%) and Madagascar (28%), and mostly (62%) concentrated in the 300-399 m depth stratum (Table 1). Catch weight of all taxa combined was 29.2 t in Mozambique, 19.0 t in Madagascar, 5.5 t in Kenya and 1.3 t in Tanzania. The highest catch weight (17.7 t) came from the 300 to 399 m depth stratum, consistent with the high effort level at that depth.

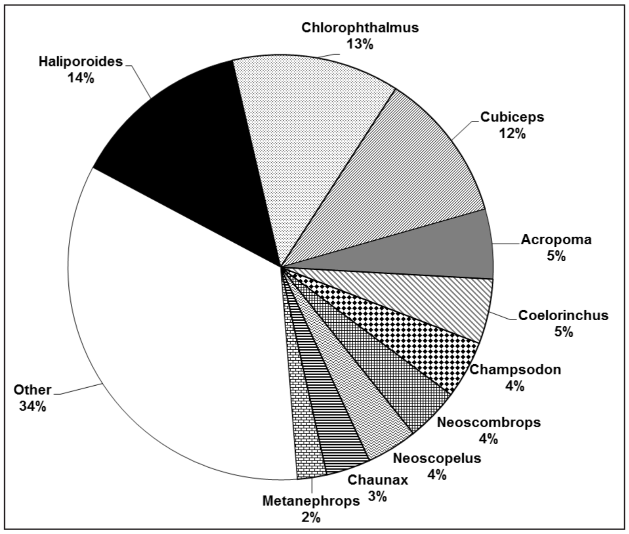

Figure 2. Proportions by frequency of occurrence of the 10 most abundant genera in trawl samples across the SW Indian Ocean region. *Haliporoides* and *Metanephrops* are commercially important crustaceans. All other genera are fish.

A total of 243 genera were identified after validation, during which 8 taxa were eliminated due to likely identification error. These were *Caesio xanthonota, Halichoeres iridis* and *Leiognathus equulus* (all shallow coastal species with no similar deep-water species with which they could have been confused), records of *Hymenocephalus natalensis*, *Psisychilus* sp., *Rassis* sp. (not found in any of the species guides), and "Coelenterata" and "Pleuronectiformes" (not possible to assign to known genera). The 8 eliminated taxa combined made up 0.2% of the total catch numbers and were therefore considered to have minimal influence on the analyses. Of the 243 genera, 55% were teleosts, 18% were crustaceans, 12% were elasmobranchs, 10% were molluscs and 5% were other invertebrates. The genera identified in this study, and the countries in which they were recorded, are provided as supplementary material (Table S1).

Across the region, the most common genera in trawl catches (by frequency of occurrence) were knife prawns *Haliporoides* (14%), greeneye fishes, *Chlorophthalmus* (13%), and drift-fishes, *Cubiceps* (12%) (Fig. 2). *Haliporoides* was completely absent from catches in Kenya, and rare in Tanzania. The clawed lobster genus, *Metanephrops*, was the only other crustacean present in the 10 most frequently caught genera – all the others were fish species. These most frequently caught genera were found at all depths surveyed but *Neoscopelus* was more rare than the other genera in the 200-299 and 300-399 m depth strata.

Species richness and evenness

Consistent with sampling effort, species richness was highest in Mozambique (77 trawls; 152 genera in total with a mean of 35.1 ± 7.3 per trawl) and lowest in Tanzania (27 trawls; 100 genera with a mean of 21.7 ± 5.5) (Table 2).

Table 2. Number of specimens recorded (N), observed species richness, mean richness per variable, Chao2 and Pielou's parameters and Shannon's diversity. SD values are shown in parenthesis.

Variable	N	Observed species richness	Richness (Mean observed species)	Chao2	Evenness (Mean Pielou's index)	Shannon's diversity
Kenya	174 119	148	31.5 (7.3)	191.2	0.6 (0.1)	3.4
Tanzania	11 006	100	21.7 (5.5)	128.9	0.8 (0.1)	3.4
Mozambique	593 693	152	35.1 (7.3)	175.3	0.6 (0.2)	2.9
Madagascar	186 112	143	28.6 (6.1)	169.5	0.7 (0.1)	3.3
200-299 m	138 696	177	27.7 (8.8)	229.5	0.7 (0.1)	3. 7
300-399 m	362 204	174	33.1 (8.7)	194.4	0.7 (0.2)	3.3
400-499 m	312 928	161	29.8 (6.6)	202.7	0.6 (0.2)	2.9
500-599 m	151 102	130	31.1 (6.3)	166.7	0.6 (0.1)	3.0

The Chao2 non-parametric estimator and the estimated species accumulation (S) plots showed significant differences in species richness between all the countries (Chao2 ANOVA: P <0.0001; S ANOVA: P <0.0001) (Fig. 3, Table 2). When the Chao2 estimator was used, Tanzania still had the lowest species richness but Kenya emerged as having the highest. The country with the highest evenness was Tanzania followed by Madagascar, Kenya and Mozambique respectively. Shannon's diversity (i.e. abundance and evenness taken into account) returned the highest diversity in Kenya and the lowest in Mozambique.

Similarly, the Chao2 estimator and species accumulation plots showed significant differences in species richness between all depth strata (Chao2 ANOVA: P <0.0001; S ANOVA: P <0.0001) (Fig. 4). The number of genera declined from 177 at 200-299 m to 130 at 500-599 m. Chao2 estimated that species richness was highest at 200-299 m and lowest at 500-599 m (Table 2). The two shallower depth zones showed slightly higher evenness than the two deeper zones while diversity was highest at 200-299 m and lowest at 400-499 m (Table 2).

Most of the estimated species accumulation and Chao2 non-parametric estimator plots did not reach an asymptote (Fig. 3; Fig. 4). This indicates that sampling effort should have been increased to improve species coverage, particularly in Tanzania and in the 500-599 m depth stratum. The Chao2 non-parametric estimator plots for Mozambique, Madagascar and the 300-399 m depth stratum did, however, approach an asymptote and indicated that sampling was adequate when taking into account rarer species. The initial spike in the Chao2 plots (Fig. 3; Fig. 4) indicates little or no overlap in species composition in the first few stations (Herzog *et al*., 2002).

Community assemblages

The MDS plots derived from all four surveys showed geographical separations of species assemblages for stations grouped according to various factors. The regional plot of north versus south indicated some overlap between several stations, but the majority were distinct (Fig. 5). PERMANOVA detected that these two regions were significantly different (Table 3), whilst PERMDISP found no significant difference (F = 2.041; P_{perm} = 0.1912), thus indicating a location effect only.

The MDS ordination of stations grouped according to country showed a clear distinction between Mozambique and Tanzania (Fig. 6). Other countries showed relatively less distinction but in general showed separation with only some overlap among stations. PERMANOVA found a significant difference between countries nested within each region (Table 3), and post hoc comparisons detected differences between

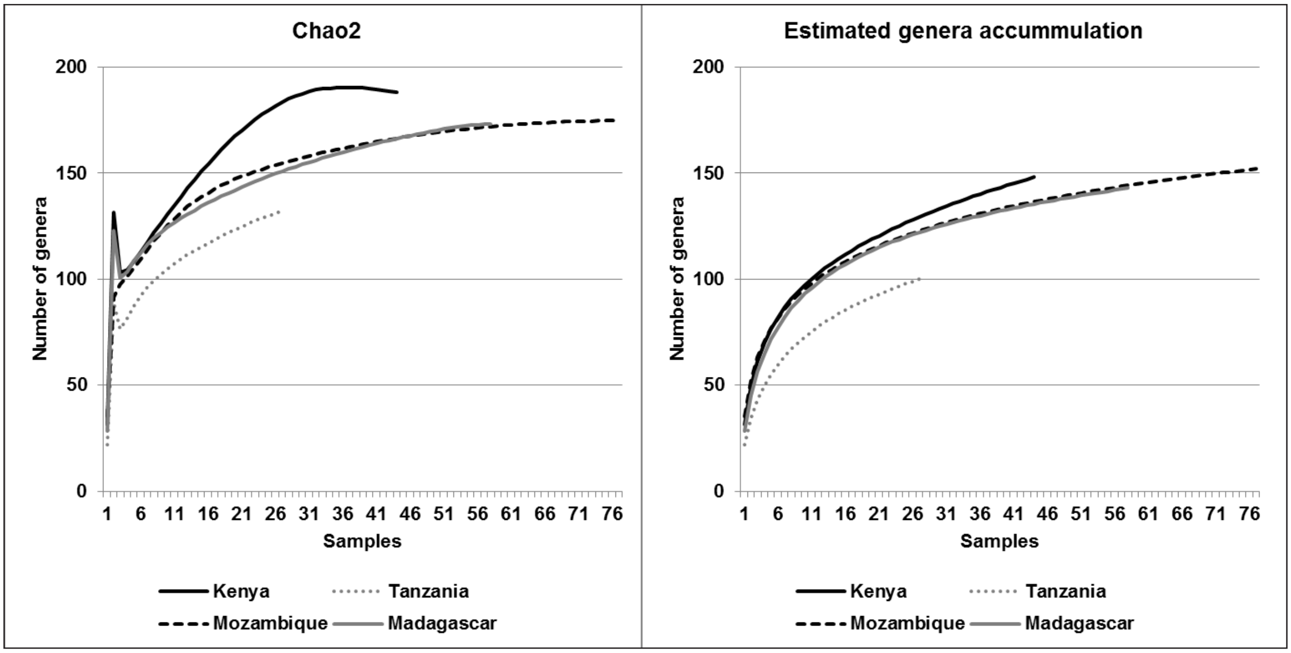

Figure 3. Chao2 non-parametric estimator and estimated species accumulation plots for each country. The initial spike in the Chao 2 plot indicates little or no overlap in species composition in the first couple of stations.

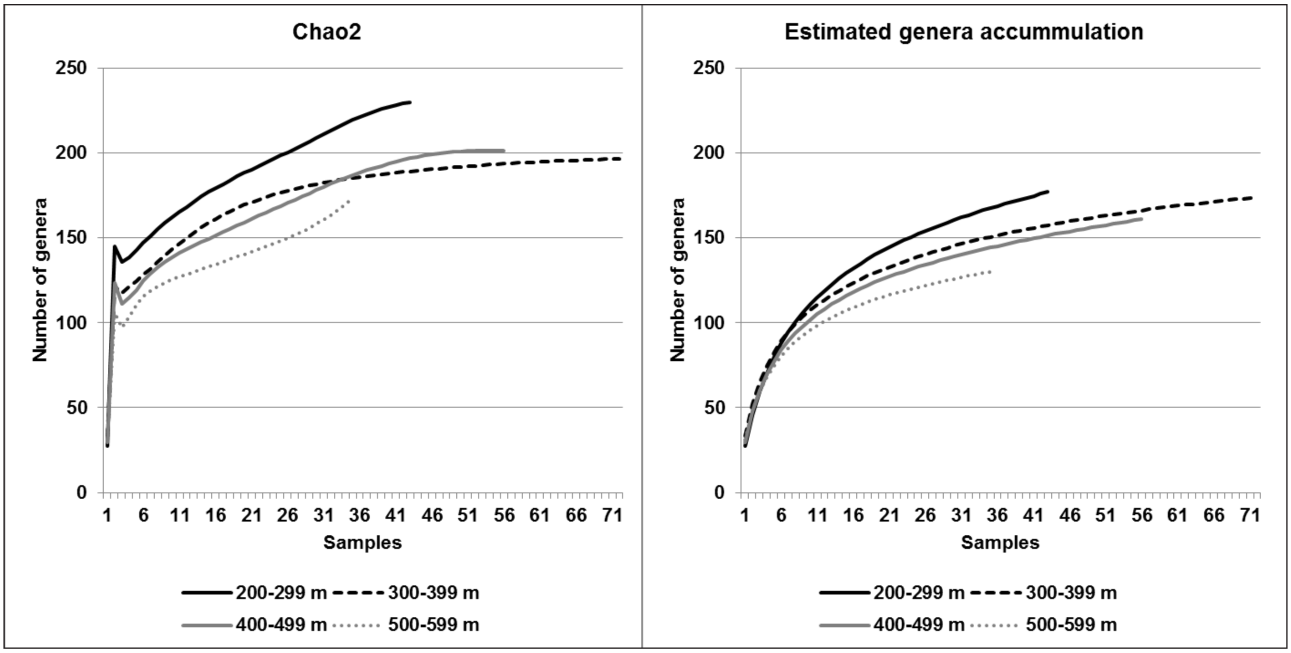

Figure 4. Chao2 non-parametric estimator and estimated species accumulation plots for each depth stratum. The initial spike in the Chao 2 plot indicates little or no overlap in species composition in the first couple of stations.

Kenya and Tanzania (t = 3.274; P_{perm} = 0.0001), and between Mozambique and Madagascar (t = 4.428; P_{perm} = 0.0001). PERMDISP analyses indicated a significant difference in dispersion between Mozambique and Madagascar (t = 2.745; P_{perm} = 0.0094), but not between Kenya and Tanzania (t = 1.592; P_{perm} = 0.1607). Thus differences between the former are likely due to both location and dispersion effects.

The ordination of stations grouped according to depth stratum showed greater levels of separation among the shallower zones and relatively more overlap among the deeper depths (Fig. 7). PERMANOVA found a significant difference among depth strata (Table 3), and post-hoc pairwise comparisons revealed significant differences between all combinations of these strata (P_{perm} < 0.001). PERMDISP analyses determined that

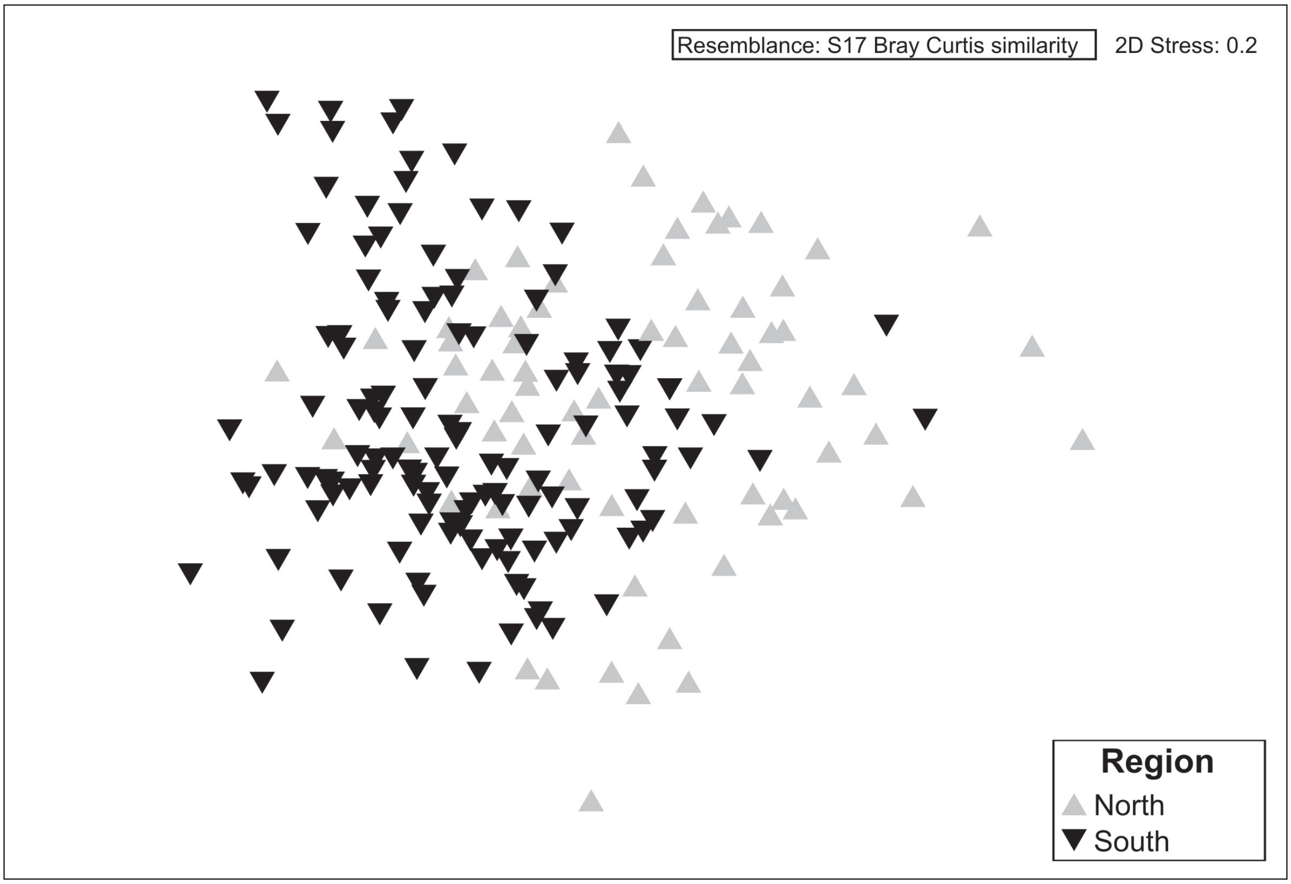

Figure 5. Non-metric MDS plot showing clusters formed by the communities of each region.

for the majority of these pairwise comparisons, there were significant differences in dispersion ($P < 0.05$); exceptions were between the two most shallow depth strata (200-299 and 300-399 m), and between the 300-399 and 400-499 m strata.

Overall dissimilarity between the north and south regions was 90%. *Chlorophthalmus*, *Haliporoides* and *Acropoma* were responsible for this dissimilarity; of these, *Chlorophthalmus* and *Haliporoides* were more abundant in the south, while *Acropoma* was relatively more abundant in the north (Fig. 8). The main genera responsible for the dissimilarity between Mozambique and Tanzania were *Haliporoides* and *Chlorophthalmus* (Fig. 9). While these two genera were found in both countries, catches were much greater in Mozambique. The dissimilarity between Madagascar and Tanzania was explained by the greater abundance of three genera in Madagascar: *Neoscopelus*, *Chlorophthalmus* and *Heterocarpus* (Fig. 9). When comparing Mozambique with Madagascar, *Haliporoides*, *Chlorophthalmus* and *Cubiceps* drove dissimilarity (Fig. 9). Overall, *Chlorophthalmus* was the most discriminating species in accounting for dissimilarities between all group comparisons, reflected in the consistently high Dissimilarity/Standard Deviation ratios for this genus.

By depth stratum, the greatest dissimilarity was seen between 200-299 and 500-599 m (Fig. 10). The genera driving the dissimilarity were *Neoscopelus*, *Haliporoides* and *Chlorophthalmus*. *Haliporoides* and *Chlorophthalmus* were also responsible for most of the dissimilarity between the 200-299 and 400-499 m strata. Other dissimilarity levels and genera contributing to them are provided in Fig. 10.

Discussion

Analysis of trawl data showed marked differences in species richness, diversity and community structure by region, country and depth stratum. Whereas these trends emerge quite clearly from the analyses, the potential effects of sampling artefacts, such as reliance on two different survey vessels, using separate trawl gears, or inconsistent identification of poorly-known deep-water taxa, require some attention. To accommodate the vessel and gear effects, we calculated a standardized catch per swept area (a proxy for vessel power). Based on this, comparable abundance measures (numbers caught per trawl station) could be obtained for most taxa. Axelsen and Johnson (2015) emphasized that even minor modifications in gear and fishing techniques can have profound effects on trawl performance. Ideally, comparative trawling trials to calibrate catchability coefficients should be undertaken, but given the large geographical scale of this study, with one vessel surveying in the north (Kenya and Tanzania) and the other in the south (Mozambique and Madagascar), this was not possible. Hence, some gear-related bias in the estimators may remain, particularly between northern and southern sampling areas. A greater number of trawl samples were available for Mozambique and Madagascar, and were collected by the same vessel, gear and crew, so these datasets were considered to be more representative than those from Tanzania and Kenya.

Species identification guides for deep-water taxa in the SW Indian Ocean are incomplete, with the result that many specimens, particularly invertebrates, were difficult to identify to species level on these surveys. This was compounded by the infrequency of deep-water surveys in the region, particularly north of Mozambique, and the absence of voucher specimens for verification of identities. These problems are not unique to the region – Bianchi *et al*. (2000) also note the difficulties they impose on analyses and interpretation, particularly in diverse, tropical regions. While there is greater confidence in the identification to species level of taxa encountered in the more regularly sampled shelf waters, we were less certain about species level identification of deep-water taxa, so we adopted a conservative approach by analysing the data at genus instead of species level. Use of higher taxa as a surrogate measure of species richness is not unreasonable (Reid, 1998), particularly when lower taxonomic ranks are used (Balmford *et al*., 1996).

The four surveys undertaken in this study were exploratory in nature, especially in Kenya, Tanzania and Madagascar. In these countries, there is scant information on bottom fish resources at depths greater than 200 m. Occasional bottom trawl surveys were undertaken mainly by the Norwegian *RV Dr Fridtjof Nansen* programme during the early 1980s (Kenya, Tanzania and Madagascar; Saetersdal *et al*., 1999), and more recently (2008 and 2009) in Madagascar. Surveys have been much more regularly undertaken in Mozambique, gradually shifting from exploratory purposes to monitoring the temporal changes in abundance of commercially important deep-water crustaceans (see Groeneveld and Everett, 2015). More is therefore known of the soft-sediment demersal taxa in Mozambique than in the other countries sampled, albeit not always formally published.

The commitment to distribute sampling effort across four countries in a regional project, combined with a very long coastline along a north-south axis (from 2 – 27°S), resulted in relatively small spatial coverage per country, with large unsampled stretches in between. The consequent patchy distribution of samples along a latitudinal axis necessitated the grouping of samples by country, as a proxy for latitude. This strategy was also followed by Everett *et al*., (2015), to circumvent similar data limitations, and gave plausible results. In the present case, samples grouped by country still allowed for inferences based on latitude because of their north-south distribution, without attempting to redress the unbalanced sampling design. Another practical reason for grouping samples by country, instead of using latitude only, was that information on species diversity and community structure remains important at a country level, for the development of national conservation strategies and fisheries management.

Table 3. Three-factor PERMANOVA to investigate variation in the community structure among stations according to region, country and depth strata.

Source of variation	df	SS	Pseudo-F	P_{perm}
Region	1	33475	13.424	0.0001
Country(Region)	2	75742	15.187	0.0001
Depth	3	44949	6.009	0.0001
Region x Depth	3	29333	3.921	0.0001
Country(Region) x Depth	6	55764	3.727	0.0001
Residual	190	473800		
Total	205	776300		

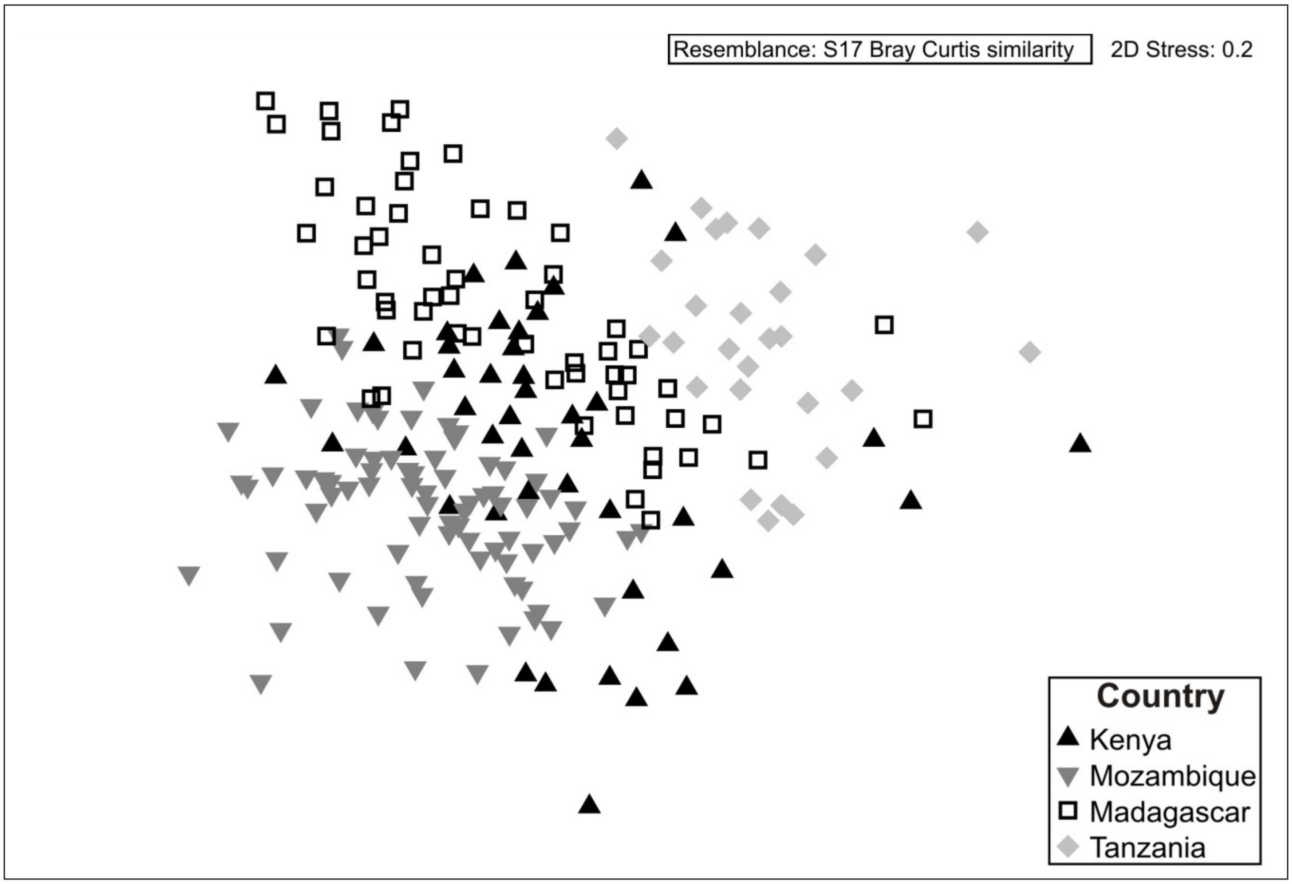

Figure 6. Non-metric MDS plot showing clusters formed by the communities of each country.

The most marked differences in community structure were recorded between Tanzania and Mozambique, and Tanzania and Madagascar, but this was most likely because of disparities in the scale of sampling between the countries. There was also a marked difference between communities from Madagascar and Mozambique, but this must be interpreted with caution, as there were differences in levels of sampling effort per depth stratum between these countries (see below).

Comparing the species composition of catches made in this study with those identified from previous surveys in the region at similar depths (listed by Groeneveld and Everett, 2015) showed that catches were dominated by *Chlorophthalmus*, *Haliporoides* and *Saurida* in both historical and recent surveys. While all the key genera in recent surveys were reported in the historical data, catches in recent surveys were in some cases much lower, particularly for *Cubiceps*, *Neoscopelus* and *Acropoma*. A further observation was that, in the recent surveys, several species, for example *Argentina sphyraena* and *Bythaelurus alcockii*, were captured outside of their depth/distribution ranges reported in Fishbase (Froese and Pauly, 2015). *Argentina sphyraena* and *B. alcockii* are deep-water bycatch species which are commonly discarded by South African deep-water crustacean trawl fisheries without being reported (ORI unpubl. data). That they have escaped scientific notice prior to this, either in historical surveys or in industrial fisheries catches in Kenya, Tanzania and Madagascar, is indicative of how little is known of deep-water trawlable areas in these countries. Our study therefore also highlights the importance of collecting voucher specimens, and lodging them in national or regional collections where they are accessible to researchers.

Information on demersal, soft-bottom, slope communities from equivalent depths and latitudes in other regions is limited, and is mainly focussed on fishes. The review by Longhurst and Pauly (1987) identifies several prominent taxa from the Atlantic and eastern Indian Oceans which were also commonly found in our study, namely *Chlorophthalmus* (which appears particularly widely distributed), *Chaunax*, *Acropoma* and members of the decapod family Solenoceridae (represented by *Haliporoides* in our study). The upper slope (~200 m) off Angola is also dominated by *Chlorophthalmus*, with several Macrouridae genera

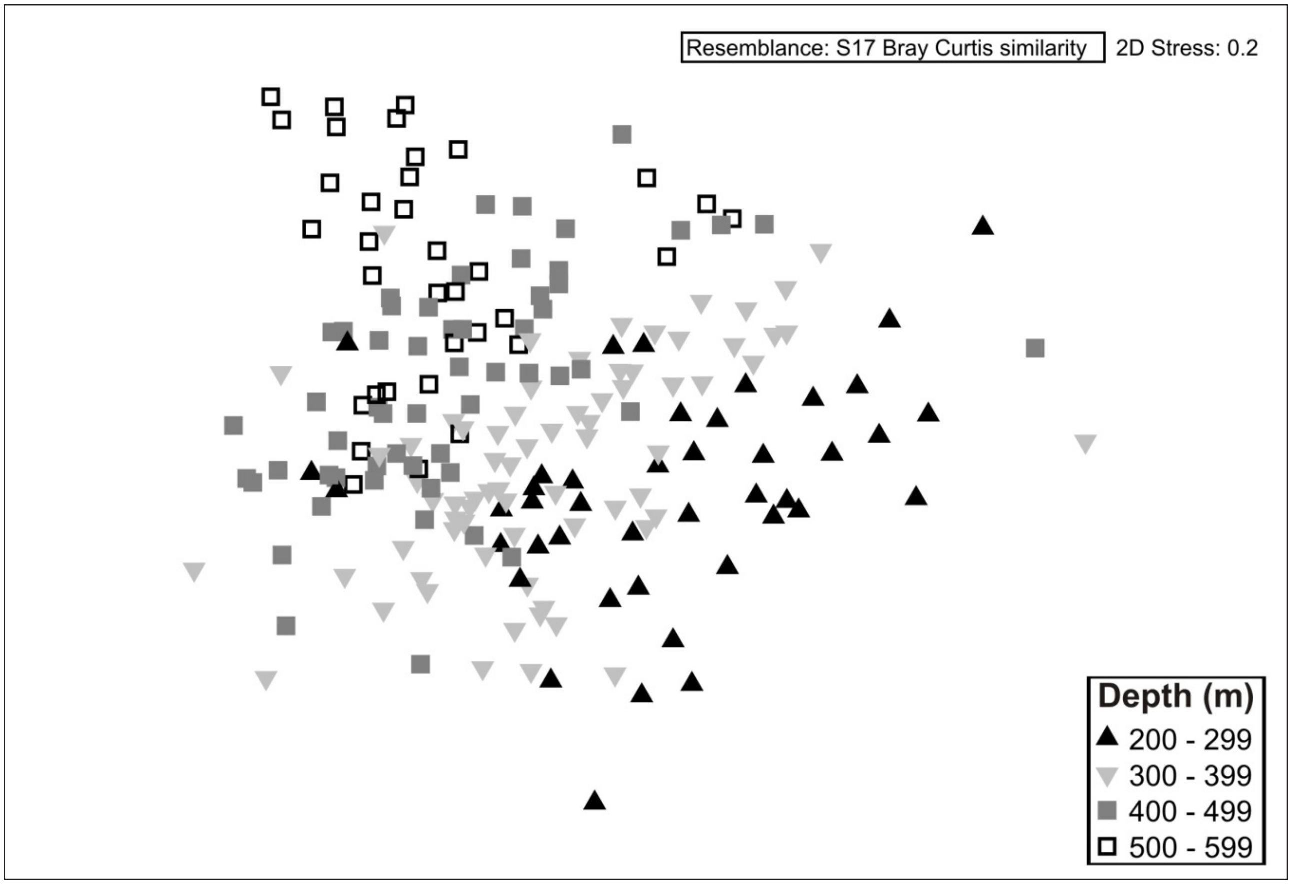

Figure 7. Non-metric MDS plot showing clusters formed by the communities at each depth stratum (in metres).

prominent over the deeper slope, between 300 and 550 m (Bianchi, 1992a), in common with our findings. There were also commonalities between our communities and western Australian communities, where members of the Acropomatidae, Chlorophthalmidae and Macrouridae dominated at the shelf break and upper slope from 200 to 600 m depth (Williams *et al.*, 2001).

The latitudinal gradient of species richness, as a general spatial pattern of diversity in the marine environment (see Hillebrand, 2004), was supported by our study, with Shannon's diversity showing the highest diversity in Kenya (samples collected between 3 and 5°S), followed by Tanzania (5 to 8°S), Madagascar (19 to 24°S) and Mozambique (21 to 27°S) (Table 2). Richness based on counts alone did not replicate this trend, however, because far fewer trawls were undertaken in Tanzania and Kenya than in Mozambique and Madagascar, thus resulting in fewer genera. Investigating the factors responsible for the latitudinal gradient was beyond the scope of this study. Willig *et al.* (2003) provide a thorough review of hypotheses accounting for the general trend of declining diversity with increasing latitude. Productivity, temperature and sediment grain size in particular have been cited as determinants of regional-scale species richness of marine soft sediments (Levin *et al.*, 2001; Gray, 2002), but measurements of these parameters are not available for the depths sampled in this study. Notwithstanding the disparity in sampling effort and potential differential effect of the trawl gears used, it is apparent that there is considerable latitudinal change in the demersal fauna of slope communities adjoining the African mainland. Further studies are required to establish whether these are ecological differences which can be ascribed to latitude changes *per se*, or habitat differences, or a combination thereof.

Our study covered a narrow depth range (200-599 m), in which a general decline in species diversity was detected as depth increased. Given the narrow depth range sampled, we could not replicate the reported generalized pattern of an increase in richness from ca. 200 m to 2500 m depths, followed by a decrease with increasing depth to 5000 m (Rex *et al.*, 1993; 2000; Gray *et al.*, 1997). There remains some doubt over the generality of this pattern, as it is not always consistent,

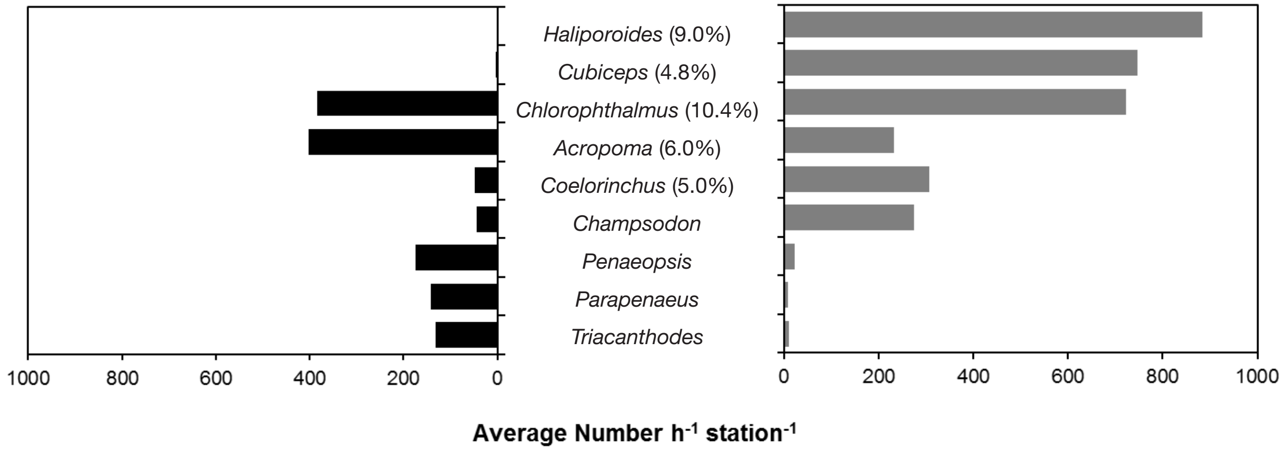

Figure 8. SIMPER results for the regional comparison between the north and the south showing the frequency of the top five most abundant genera per region. Percentages show the contribution to dissimilarity each of the most discriminating genera make to overall dissimilarity between the two regions.

or it corresponds with other environmental factors such as temperature, pressure and oxygen, i.e. depth is a proxy for these factors (Bianchi, 1992b; Levin *et al.*, 2001). Fennessy (2016) also found an increase in diversity with depth in trawled fauna off the east coast of South Africa some 350 km to the south of the southernmost Mozambican trawl localities, but that survey was also confined to depths < 600 m.

An interesting result of our study was the clear difference in community structure between southern Mozambique and southwestern Madagascar. Two alternative explanations are forwarded to explain the observed difference in community structure across the Mozambique Channel. The first is that the trawl surveys covered different bottom types and habitats, thus sampling two ecologically different deep-water

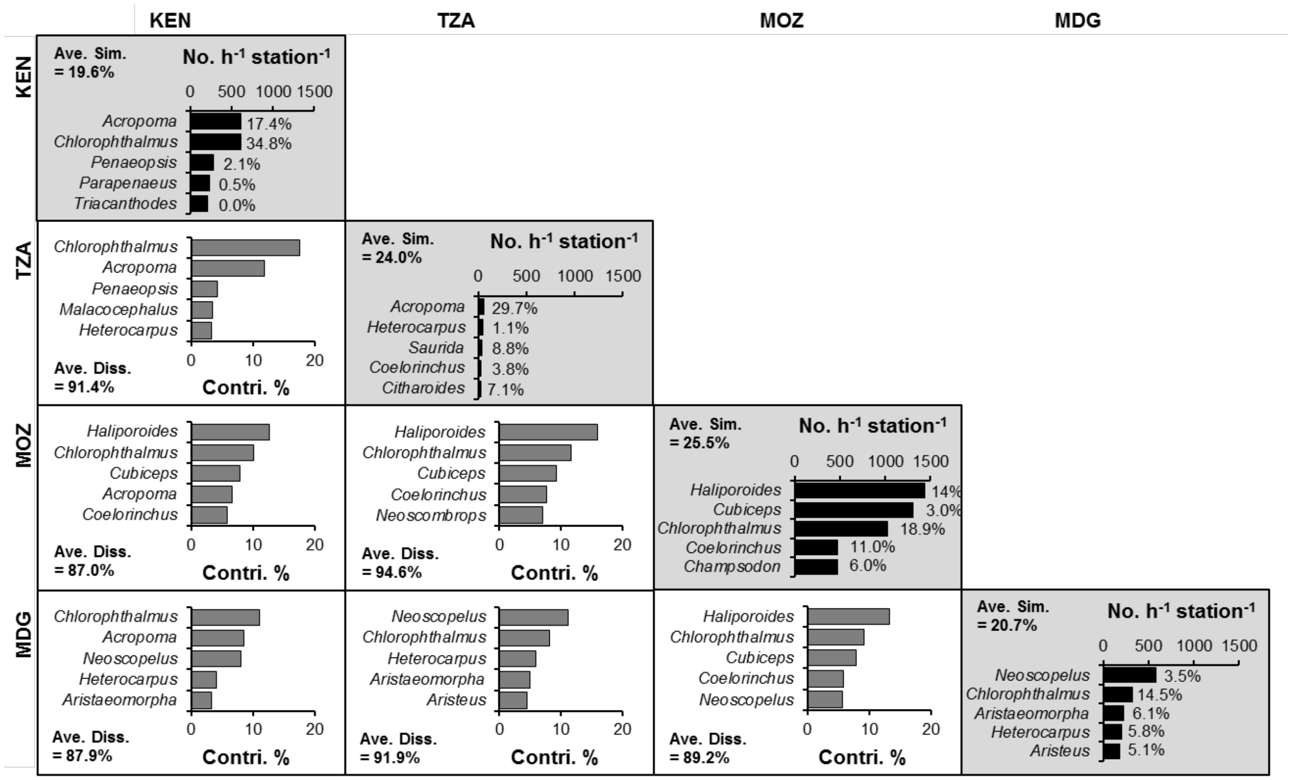

Figure 9. SIMPER results for the country contrasts (Kenya = KEN; Tanzania = TZA; Mozambique = MOZ; Madagascar = MDG). Grey cells indicate the top five most characteristic genera for each country (based on average number per hour per station) along with the % contribution of that genus to the within-country average similarity (Ave. Sim.). White cells indicate the % contribution of each of the top five most distinguishing genera to average dissimilarity (Ave. Diss.) according to orthogonal comparisons between countries.

soft-sediment communities. This explanation is supported by the expectation that regular bottom trawling on commercial fishing grounds may have altered benthic habitats and hence the composition of communities in Mozambique, relative to infrequently trawled grounds in Madagascar. Tillen *et al.* (2006) demonstrated that chronic bottom trawling can lead to large scale shifts in the functional composition of benthic communities, with likely effects on the functioning of coastal ecosystems.

Alternatively, the Mozambique Channel forms a physical barrier to connectivity of biota between the two localities – and this putative barrier must have endured for long enough to allow for different communities to evolve in parallel. This theory follows the model developed for terrestrial biota of Madagascar, which separated from the African mainland around 120 million years ago, and evolved into startlingly different life forms and communities compared to those present along the eastern coast of Africa (Goodman and Benstead, 2003).

Additional support that the separation also applies to marine species is provided by recent population genetic studies of several marine taxa, which suggest that the Mozambique Channel forms a barrier to larval dispersal between western Madagascar and the African mainland. Species that show low, or no genetic connectivity across the channel include spiny lobster *Panulirus homarus rubellus* (Reddy *et al.*, 2014), crown-of-thorn starfish *Acanthaster planci* (Volger *et al.*, 2012), several ophiuroid brittle stars (Hoareau *et al.*, 2013), and the reef fish *Myripristis berndti* (Muths *et al.*, 2011). Most of these species have drifting early life history phases, with eggs or larvae that can disperse widely in ocean currents. In combination, the apparent failure of these species to propagate across the Mozambique Channel suggest that the channel forms a physical or oceanographic barrier to gene flow to at least some species, and by extension to communities occurring on opposite sides of the channel. However, these genetic studies are mostly based on shelf organisms, and the evidence is not unequivocal. Other studies indicate that there is cross-channel connectivity (Visram *et al.*, 2010). In another study, Muths *et al.* (2015) conclude that the Mozambique Channel is "a complex and fluctuating system of mixing and retention that generates a patchy pattern of connectivity depending [on] species life history traits."

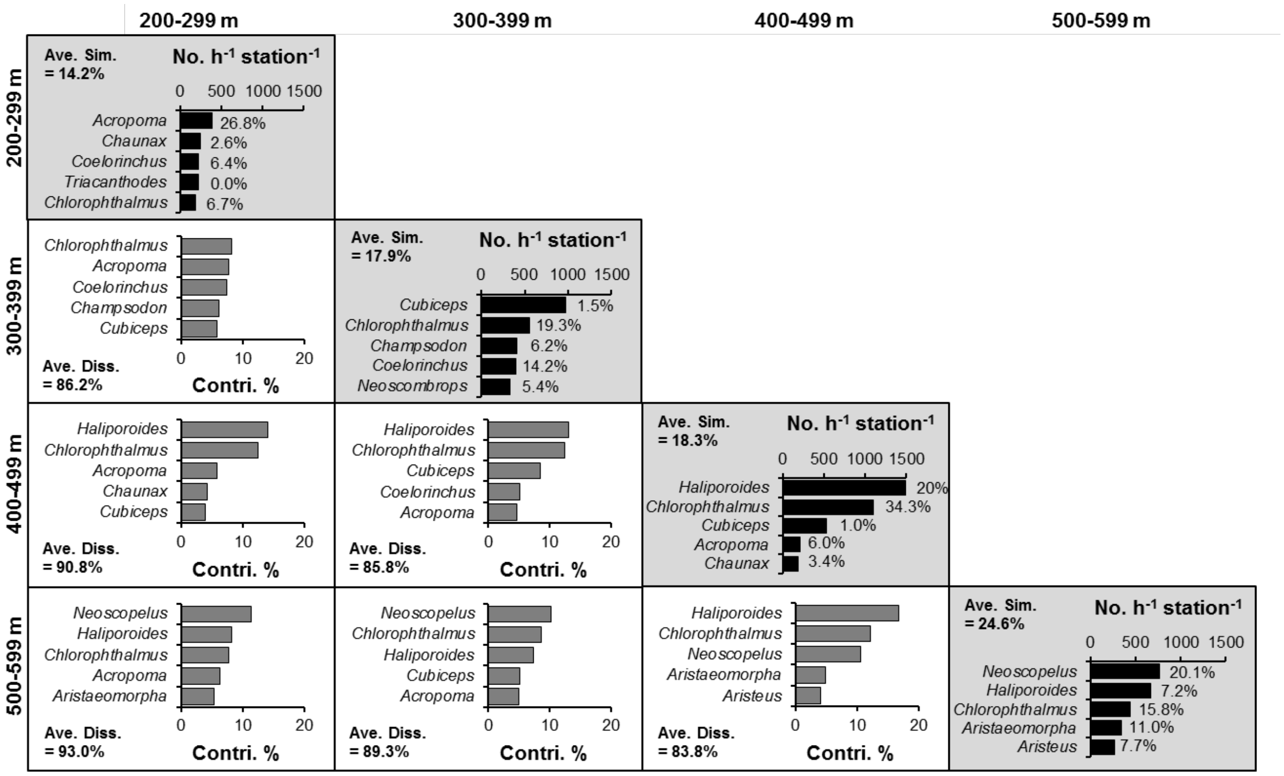

Figure 10. SIMPER results for the depth stratum comparisons. Grey cells indicate the top five most characteristic genera for each depth stratum (based on average number per hour per station) along with the % contribution of that genus to the within-depth stratum average similarity (Ave. Sim.). White cells indicate the % contribution of each of the top five most distinguishing genera to average dissimilarity (Ave. Diss.) according to orthogonal comparisons between depth strata.

To conclude, we identified a total of 243 genera from 206 demersal trawls undertaken along the deep shelf and upper continental slope of the SW Indian Ocean. Diversity decreased southwards along a latitudinal gradient – consistent with generalized spatial patterns shown in several other studies in marine environments (see Hillebrand, 2004). Marked community differences were observed between northern (Kenya and Tanzania) and southern (Mozambique and Madagascar) sites, between each of the countries and also in depth-wise comparisons, notably between the shallowest and deepest strata. Whereas the data used for this study suffered from several limitations incurred during field sampling (i.e. collected by different vessels with different size trawl gear; inconsistent species identification; unbalanced survey design), these could be partially redressed after surveys, so that broad trends in community structure and species diversity could be confidently identified. The information provided by this study is new to the SW Indian Ocean region, and an important step towards understanding diversity trends, a key consideration in prioritization of conservation needs. Offshore/slope habitats are seldom included in Marine Protected Areas in the region. Our study has contributed to the gradually building global body of knowledge which is pointing to the necessity to protect deep-water habitats which are increasingly being surveyed for potentially extractable resources as part of the development of so-called Blue Economies.

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Supplementary material

Table S1. List of genera used in the analyses. The shaded blocks indicate the countries in which the genera were caught (K=Kenya, T=Tanzania, Mo= Mozambique, Ma=Madagascar; Type: E = Elasmobranch, T = Teleost, Cr = Crustacean, M = Mollusc, OI = Other invertebrate).

Species	Type	K	T	Mo	Ma	Species	Type	K	T	Mo	Ma
Acanthobatis	E			■		*Munida*	Cr				■
Acropoma	T	■	■	■	■	*Mursia*	Cr	■	■	■	■
Aetobatus	E			■		*Mustelus*	E	■	■		■
Agononida	Cr	■	■	■	■	*Nansenia*	T	■		■	■
Amblyrhynchotes	T			■		*Nematopalaemon*	Cr	■			
Antigonia	T	■	■	■	■	*Neobythites*	T	■	■	■	■
Antipatharia	OI			■		*Neoepinnula*	T		■	■	■
Apristurus	E				■	*Neoscombrops*	T			■	■
Argentina	T	■	■	■	■	*Neoscopelus*	T	■	■		■
Ariomma	T	■				*Nephropsis*	Cr	■	■	■	■
Aristaeomorpha	Cr	■		■	■	*Nettastoma*	T	■	■	■	■
Aristaeopsis	Cr			■		*Nototodarus*	M	■	■	■	■
Aristeus	Cr			■	■	*Ommatocarcinus*	Cr			■	
Ateleopus	T	■	■	■	■	*Ophidiidae*	T	■			■
Atrobucca	T	■	■		■	*Opisthoteuthis*	M	■	■	■	■
Aulostomus	T			■		*Ornithoteuthis*	M			■	■
Bathycongrus	T	■	■	■	■	*Ostracion*	T			■	
Bathynomus	Cr				■	*Ostracoberyx*	T	■			■
Bathyraja	E		■			*Ovalipes*	Cr	■			■
Bathysquilla	Cr	■			■	*Owstonia*	T	■	■		
Bembrops	T	■	■	■	■	*Palinurus*	Cr		■	■	
Benthodesmus	T			■		*Pandalus*	Cr	■			
Beryx	T			■	■	*Parabathynomus*	Cr			■	■
Bohadschia	OI	■				*Parabembras*	T	■	■	■	

Species	**Type**	**K**	**T**	**Mo**	**Ma**	**Species**	**Type**	**K**	**T**	**Mo**	**Ma**
Bothus	T	■				*Parapenaeus*	Cr	■	■	■	■
Branchiostegus	T		■	■	■	*Parapercis*	T		■		
Brotula	T	■				*Paraplagusia ?*	T	■			
Bythaelurus	E	■				*Parascolopsis*	T	■			
Calliaster	OI	■		■		*Parascorpaena*	T	■			
Callionymus	T	■	■			*Paratriacanthodes*	T	■	■		■
Carcharhinus	E			■		*Parazen*	T	■	■	■	■
Carcinoplax	Cr			■	■	*Parthenope*	Cr			■	
Caryophyllia	OI			■		*Penaeopsis*	Cr	■	■	■	■
Centrophorus	E	■	■	■		*Penaeus*	Cr	■	■		
Cephaloscyllium	E	■	■	■	■	*Pennatulacea*	OI		■		
Chaceon	Cr	■	■	■	■	*Pentaceros*	T		■	■	■
Champsodon	T	■	■	■	■	*Peristedion*	T	■	■	■	■
Charybdis	Cr	■			■	*Philine*	M			■	
Chascanopsetta	T	■	■	■	■	*Phormosoma*	OI	■	■	■	■
Chaunax	T	■	■	■	■	*Phosichthys*	T			■	
Chelidonichthys	T	■	■	■	■	*Physiculus*	T	■	■	■	■
Chlorophthalmus	T	■	■	■	■	*Platepistoma*	Cr	■		■	
Cirrhigaleus	E			■		*Platymaia*	Cr	■	■	■	■
Citharoides	T	■	■	■	■	*Pleistacantha*	Cr	■	■	■	■
Clypeaster	OI	■	■			*Plesiobatis*	E	■		■	
Cnidaria1	OI			■		*Plesionika*	Cr	■	■	■	■
Coelorinchus	T	■	■	■	■	*Pleuroscopus*	T	■			
Coloconger	T		■	■	■	*Pliotrema*	E	■	■	■	■
Coluzea	M			■		*Poecilopsetta*	T	■	■		■
Conus	M				■	*Polycheles*	Cr	■		■	■
Cruriraja	E		■	■		*Polyipnus*	T	■	■	■	
Cryptopenaeus	Cr	■		■		*Polymetme*	T	■	■	■	■
Cubiceps	T	■		■	■	*Polymixia*	T	■	■	■	■
Cynoglossus	T	■	■	■	■	*Polysteganus*	T	■	■	■	■
Cyttopsis	T				■	*Priacanthus*	T	■		■	■
Dalatias	E	■		■	■	*Pristigenys*	T				■
Deania	E	■			■	*Pristipomoides*	T				■
Decapterus	T	■			■	*Propeamussium*	M	■		■	
Diaphus	T	■		■	■	*Psenes*	T			■	
Dipturus	E	■			■	*Pseudarchaster*	OI	■	■	■	■
Emmelichthys	T		■			*Pseudocaranx*	T		■		
Epetriodus	T	■		■	■	*Pseudoginglymostoma*	E	■			
Epinephelus	T				■	*Pseudorhombus*	T	■			
Eridacnis	E	■		■		*Pteroeides*	OI				■
Etelis	T				■	*Pterygotrigla*	T			■	

Species	Type	K	T	Mo	Ma	Species	Type	K	T	Mo	Ma
Etmopterus	E			■	■	*Puerulus*	Cr	■	■		■
Euciroa	M			■	■	*Raja*	E	■	■	■	
Eudolium	M			■		*Ranella*	M		■	■	
Ficus	M		■			*Rexea*	T				■
Fistularia	T				■	*Rhinobatos*	E	■			■
Fusivoluta	M			■		*Rhizoprionodon*	E	■			
Gemmula	M			■	■	*Rochinia*	Cr	■		■	
Gempylus	T			■		*Rossia*	M	■	■	■	■
Gephyroberyx	T	■		■	■	*Rossiinae*	M			■	
Glyphocrangon	Cr	■		■	■	*Ruvettus*	T			■	
Glyptophidium	T	■		■	■	*Satyrichthys*	T	■	■	■	■
Gonorynchus	T			■		*Saurida*	T	■	■	■	■
Gymnothorax	T	■				*Scammarctus*	Cr	■			■
Halaelurus	E				■	*Scombridae*	T				■
Halieutaea	T	■		■	■	*Scombrops*	T				■
Haliporoides	Cr		■	■	■	*Scorpaena*	T	■		■	
Heptranchias	E			■	■	*Scyllarides*	Cr		■	■	■
Heterocarpus	Cr	■	■	■	■	*Scyllarus*	Cr	■	■		
Heteronarce	E			■		*Sebastes*	T	■			
Heteropriacanthus	T				■	*Selachophidium*	T			■	■
Histiopterus	T				■	*Selar*	T				■
Histioteuthis	M	■			■	*Semicassis*	M			■	
Holohalaelurus	E	■		■	■	*Sepia*	M	■	■	■	■
Holothuria	OI				■	*Setarches*	T	■	■	■	■
Homola	Cr	■	■			*Solea ?*	T		■		
Hoplichthys	T	■	■	■	■	*Solenocera*	Cr	■		■	
Hoplobrotula	T	■		■		*Solocisquama*	T			■	
Hoplostethus	T	■	■	■	■	*Sphoeroides*	T	■		■	■
Hymenocephalus	T	■			■	*Squalus*	E	■	■	■	■
Ibacus	Cr	■		■	■	*Squatina*	E	■			■
Inquisitor	M		■			*Stephanolepis*	T				■
Kentrocapros	T	■				*Stolephorus*	T				■
Laeops	T	■	■	■	■	*Synapturichthys*	T	■			
Lagocephalus	T	■				*Synchiropus*	T	■		■	■
Lepidopus	T	■			■	*Thunnus*	T			■	
Lepidotrigla	T	■	■	■	■	*Thyrsitoides*	T	■		■	■
Leptoconus	M				■	*Todarodes*	M			■	
Leptomelanosoma ?	T		■			*Torpedo*	E	■	■	■	
Lestrolepis	T	■	■	■		*Tosarhombus*	T	■			
Leucoraja	E	■	■	■		*Trachysalambria*	Cr	■			
Linuparus	Cr	■	■			*Triacanthodes*	T	■			

Species	Type	K	T	Mo	Ma	Species	Type	K	T	Mo	Ma
Lithodes	Cr				■	*Triacanthus*	T		■		
Loligo	M			■		*Trichiurus*	T	■	■	■	■
Lophiodes	T	■	■	■	■	*Tydemania*	T	■			
Lophius	T			■		*Tylerius*	T				■
Luthulenchelys	T	■				*Upeneus*	T				■
Lyreidus	Cr	■		■	■	*Uranoscopus*	T		■	■	■
Macroramphosidae	T				■	*Uroteuthis*	M	■	■		■
Macroramphosus	T	■	■	■	■	*Velodona*	M	■	■	■	■
Macrorhamphosodes	T	■				*Ventrifossa*	T	■	■	■	■
Malacocephalus	T	■	■	■	■	*Vinciguerria*	T			■	
Malthopsis	T	■	■	■	■	*Xenolepidichthys*	T	■		■	■
Megalops	T		■			*Xenophora*	M	■	■	■	■
Mene	T			■		*Zenion*	T	■		■	■
Merluccius	T			■	■	*Zenopsis*	T	■		■	
Metanephrops	Cr	■	■	■	■	*Zeus*	T		■	■	

Mechanisms of trophic partitioning within two fish communities associated with a tropical oceanic island

Clément Trystram[1*], David Roos[2], David Guyomard[3], Sébastien Jaquemet[1]

[1] UMR 9220 Entropie (Université de La Réunion-IRD-CNRS), Avenue René Cassin CS 92003, 97744 Saint-Denis Cedex 9, Ile de La Réunion, France.

[2] Ifremer Délégation Océan Indien, Rue Jean Bertho - BP 60 - 97822 Le Port Cedex, Ile de La Réunion, France

[3] Comité Régional des Pêches Maritimes et des Elevages Marins, 47 rue Evariste de Parny, 97827 Le Port Cedex, Ile de La Réunion, France

*corresponding author: clement.trsytram@gmail.com

Abstract

Understanding drivers of trophic partitioning at the community level is an essential prerequisite to the establishment of ecosystem-based management of fisheries. In this study, we identify drivers of trophic partitioning within a community of epipelagic fish and a community of deep-water fishes off Reunion Island. Effects of intrinsic (species identity, etc.) and environmental variables (fishing zone, month) on stomach content composition and stable isotope ratios were tested using regression trees and linear models respectively. Our results demonstrated firstly an independence of both communities, with very few common prey although they occurred in similar localities, and secondly, very different patterns of resources partitioning among each community. The community of epipelagic fish segregated into three trophic guilds composed of species foraging on a limited range of prey. This observation is not consistent with the general view that these high trophic level species are opportunistic and generalist. The habitat seems to be the main driver of deep-water fishes feeding partitioning, which is in accordance with the sound-scattering layer interception hypothesis. Deep-water fishes would distribute in the water column at different depths and all species would feed on the same resources at each depth. The results of this study suggest that fisheries management should be very different for epipelagic (more species-centred) and deep-water fish (more habitat-centred).

Keywords Trophic partitioning, Deep-sea, Epipelagic, Predator, Stable isotopes, Stomach contents

Introduction

In the context of increasing demand for marine-derived food (Msangi *et al.*, 2013), fisheries have extended both down the marine food web (decrease in the mean trophic level – TL – of catches of 0.1 TL.decade^{-1}; Pauly *et al.*, 1998) and into the depths (increase in the mean depth of fishing of 62.5 m.decade^{-1}; Watson and Morato, 2013). This rapid development of fisheries led to drastic declines of numerous fish stocks, with 58% of known stocks being overfished or already collapsed (Froese *et al.*, 2012). Moreover, fisheries can extend their effects beyond targeted species by affecting habitats or non-target species, and fish communities, thereby changing the structure and function of ecosystems (Jackson *et al.*, 2001; Hsieh *et al.*, 2006; Myers *et al.*, 2007). In order to understand the impacts of fisheries on ecosystems, it is nowadays acknowledged that the implementation of model-based ecosystem fisheries management is necessary (Garcia *et al.*, 2003; Pikitch *et al.*, 2004; Cury *et al.*, 2008). Such models are useful to evaluate and predict the impacts of resource overexploitation and climate change on ecosystems and to propose measures to make fisheries more sustainable.

Prior to the development of such models, information on biological interactions, energy transfer, consumption and production at the different trophic levels is required (Pauly *et al.*, 2002; Christensen and Walters, 2004), but such information is usually lacking. In particular, the influence of biotic and abiotic parameters on trophic habits still requires clarification. Predator species, ontogeny and distance to shore have been demonstrated to have significant influence

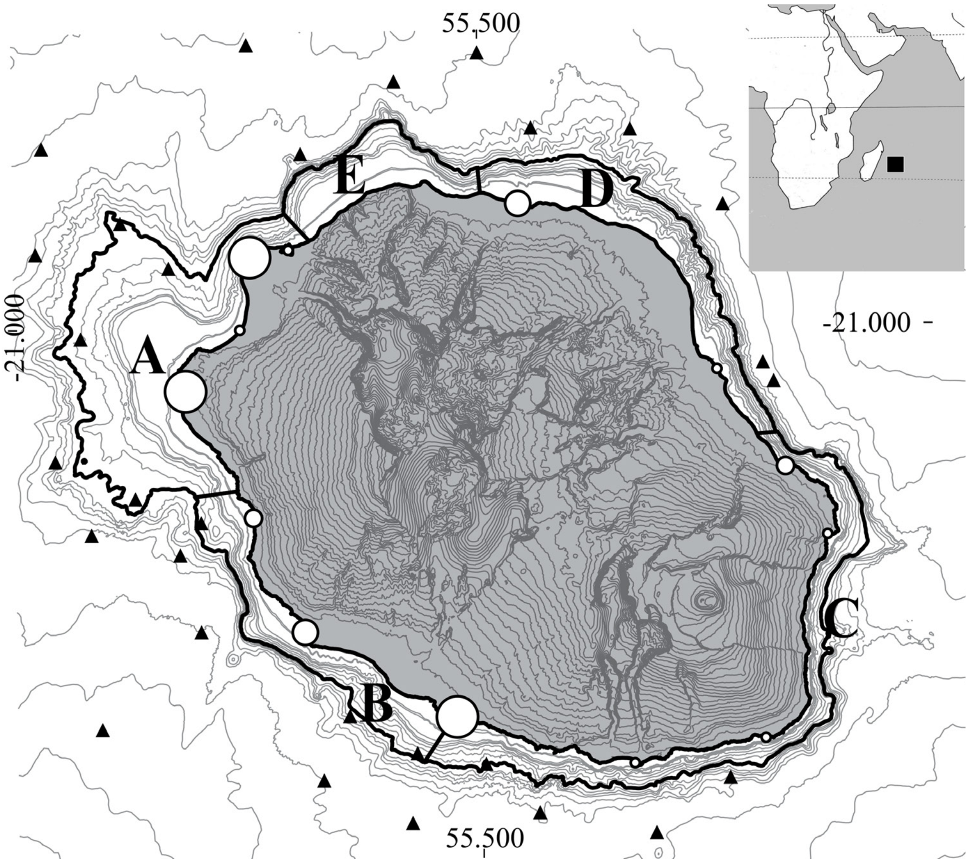

Figure 1. Map of Reunion Island representing deep-water fish fishing zones in bold letters, limited by the 600 m isobath, and anchored fishing aggregating devices in black triangles. White circles represent harbours with size proportional to the number of fishermen, from 2 (smallest circles) to 42 (largest circles).

on predator diet and community structure (Haight, 1993; Lowe *et al.*, 1996; Jaquemet *et al.*, 2011, Allain *et al.*, 2012). Nevertheless, some regional or temporal diet variations suggest various degrees of dietary specialisation according to parameters that remain undetermined for many species, including both oceanic (eg *Coryphaena hippurus* and *Thunnus albacares*; Buckley and Miller, 1994; Taquet, 2004; Graham *et al.*, 2007; Tripp-Valdez *et al.*, 2010) and deep-water predators (eg *Beryx decadactylus* and *Etelis coruscans*; Haight, 1993; Dürr and González, 2002; Trystram *et al.*, in revision).

The present study aims to investigate the drivers of diet variability in communities of predatory fish. For this purpose, we analysed the trophic ecology of several species in two exploited communities of fish around Reunion Island. This small volcanic island located in the Western Indian Ocean has a limited island shelf that naturally enhances the connectivity between coastal, oceanic and deep-sea ecosystems. In recent years a significant decrease in the landings of both epipelagic and deep-water predatory fishes exploited by the local artisanal fisheries was reported (Fleury *et al.*, 2012; Guyomard *et al.*, 2012; Le Manach *et al.*, 2015). Although they are economically important for the artisanal fishing sector, knowledge of the ecology of these fish species remains very limited. Jaquemet *et al.* (2011) showed that yellowfin (*Thunnus albacares*) and skipjack (*Katsuwanus pelamis*) tuna feed upon diverse assemblages of coastal fish and crustacean larvae and juveniles off Reunion Island around anchored fish aggregating devices,. The trophic habits of eight deep-water species were very recently described around Reunion Island and recorded a surprising diversity of dietary patterns among species (Trystram *et al.*, in revision). The factors driving these diet variations among deep-water fishes remain unclear, while individual length within each species appeared to affect dietary pattern, as both δ^{13}C and δ^{15}N increased with length (Trystram *et al.*, in revision).

The present study investigated the effects of multiple exploratory variables (depth, fishing zone and month, species, length, sex and maturity) on stomach content composition and stable isotope ratios of the two communities. Carbon and nitrogen stable isotope ratios measured in fish muscle give long-term information on the organic matter sources they depend upon, and their trophic level, respectively (Peterson and Fry, 1987).

Materials and Methods

Sampling

Study area

The study was conducted off Reunion Island, a small (60 km diameter) oceanic island of volcanic origin, situated in the southwestern Indian Ocean (Fig. 1). The mountainous central part of the island (3070 m maximum) creates a clear distinction between the wet windward east coast and the dry leeward west coast, where a small discontinuous fringing coral reef has developed. The island's volcanic cone topography results in steep slopes of up to 60° and a limited shallow island shelf (maximum 5 km wide) that leads to offshore ecosystems directly adjacent to coastal ecosystems. As such, physico-chemical gradients in the vicinity of the island are strong and most likely represent major structuring factors for ecological communities.

Biological models

The study focused on eight deep-water and eight epipelagic fish species. Deep-water species were sampled during a directed stock assessment effort, whereas six of the eight epipelagic species were caught by local fishermen in the vicinity of anchored fishing aggregative devices (aFAD), and two coastal shark species were caught during culling programmes coordinated by local authorities to control species involved in shark attacks along the shore. The deep-water species considered were the red bream (*Beryx decadactylus*), the oblique-banded grouper (*Epinephelus radiatus*), the deep-sea red snapper (*Etelis carbunculus*), the deep-sea long-tail red snapper (*E. coruscans*), the brilliant pomfret (*Eumegistus illustris*), the ornate jobfish (*Pristipomoides argyrogrammicus*), the goldbanded jobfish (*P. multidens*) and the shortnose spurdog (*Squalus megalops*), which represented 64% of the 2680 fishes collected during the sampling effort. Epipelagic species considered were the yellowfin tuna (*Thunnus albacares*), the skipjack tuna (*Katsuwonus pelamis*), the dolphinfish (*Coryphaena hippurus*), the wahoo (*Acanthocybium solandri*), the great barracuda (*Sphyraena barracuda*), and the giant trevally (*Caranx ignobilis*), which constitute ~90% of the artisanal fishery landings in Reunion (SIH, 2013). Tiger shark (*Galeocerdo cuvier*) and bull shark (*Carcharhinus leucas*) have not been targeted by artisanal fishermen for over 15 years (Le Manach *et al.*, 2015) therefore samples were collected during specific culling programmes.

Sample collection

Epipelagic fishes were sampled between January 2012 and December 2014 off the west coast, whereas deep-water fishes were sampled all around the island between April and December 2014 at depth ranging from 100 m to 600 m. Each fresh fish was weighed and measured (total length) on board. Deep-water fishes were kept whole in a coolbox and then stored at -20°C in the laboratory. In the laboratory, each fish was dissected to collect the gut contents and to sample dorsal white muscle for stable isotopes analysis. In addition, the sex and sexual maturity of deep-water fishes were determined. The maturity was determined based on gonad dissection and translated into a qualitative variable with six stages (from 0 - juveniles, to 5 - spawning adult). Epipelagic fishes were gutted on board by the fishermen. Their stomachs were stored in coolboxes in labelled plastic bags and a sample of white dorsal muscle was collected for the stable isotopes ratio measurements. All samples were then stored in the laboratory at -20°C until further analysis. Finally, sharks were dissected in a cold room, the stomach contents and a sample of dorsal muscle were kept and stored at -20°C in the laboratory.

Laboratory processing

Prey identification

Stomach content samples were thawed and weighed in the laboratory. Prey items found were counted, weighted to an accuracy of 0.01 g and identified to the lowest possible taxonomic level using identification keys adapted to taxonomic groups and/or to anatomical parts (cephalopod beaks, teleosts, otoliths, etc) (Clarke, 1986; Smith and Heemstra, 1986; Smale *et al.*, 1995) and then compared to Reunion species lists (Letourneur *et al.*, 2004; Durville *et al.*, 2009; Poupin, 2009) and to our own collection. Given the difficulties with identifying digested prey items, they were pooled into functional groups for some of the analyses (Table S1). Prey importance found in the stomach was expressed as the relative numerical abundance.

Stable isotope measurement

Frozen white dorsal muscle samples were freeze-dried at <0.5 mBar and <-40 °C for 48h using a Labconco freeze-drier coupled with a Vacuubrand 2.5 pump, then ground into a fine and homogeneous powder using an automated Retsch MM301 grinder.

Table 1. Description of observed and exploratory variables used in this study.

	Specificity	Name	Description	Unity	Type
Observed variables	All species	$\delta^{13}C$	Chemical tracer of organic matter sources	‰	quantitative
		$\delta^{15}N$	Chemical proxy of trophic level	‰	quantitative
		Stomach composition	Identity of each single prey	Ecological functioning group	qualitative
Exploratory variables	All species	Species	Identity of each predator	Species (16 modalities)	qualitative
		TL	Total length	cm	quantitative
		Month	Sampling month	Month (12 modalities)	qualitative
		Zone	Sampling zone		qualitative
	Deep-water	Depth	Sampling depth	m	quantitative
		Sex	Gender of predatory fishes	3 modalities (male, female, immature)	qualitative
		Maturity	Reproductive stage, from immature to spawning adult	6 modalities	qualitative
	Epipelagic	DistShore	Sampling distance from shore	m	quantitative

Low fish C/N ratio (<3.5, Table S2) suggested low lipid content, which reduces the need to perform lipid extraction or analytical corrections (Post *et al.*, 2007). For tropical tuna, Sardenne *et al.* (2015) showed that the white muscle was low in lipids and consequently no lipid extraction was necessary. We assumed that the same was true for other large epipelagic species. For the deep-water shark *S. megalops,* which are enriched in urea, De Lecea and De Charmoy (2015) showed that chemical treatments did not modify muscle isotopic ratios, and that treatment was not required for this species. Prior to stable isotope measurements, all samples were weighed (0.5 mg) and packed into tin capsules in duplicate. Isotopic composition and %C and %N content were measured at the National Stable Isotope Laboratory, GNS Science, Lower Hutt, New Zealand, the IsoEnvironmental, Rhodes University, Grahamstown, South-Africa, or at the Stable Isotope Facility, LIENSs laboratory, La Rochelle, France, using an isotope ratio mass spectrometer, interfaced to an elemental analyser in continuous-flow mode (EA-IRMS). Standard reference materials were used to ensure accuracy and precision between laboratories. Results were expressed in conventional delta notation (δ), defined as parts per thousand (‰), according to Peterson and Fry (1987).

Factors driving diet composition

The potential effects of explanatory variables (described in Table 1) on prey composition (expressed in term of functional group, Table S1) in predator diet were investigated using the classification and regression tree (CART) approach (Breiman *et al.*, 1984). This non-parametric method uses a partitioning algorithm to estimate a series of binary decision rules that divide the data into smaller homogeneous subgroups in an optimal way. All data are represented by a single node at the top of the tree. The tree is then built by repeatedly splitting the data. Each split is defined by a simple rule based on a single explanatory variable. Splits are chosen to maximize the homogeneity of the resulting two nodes. However, the splitting procedure grows an overlarge tree with a very low predictive power. To keep the tree reasonably small (i.e. keep the predictive power high), a prune back procedure is applied. Following Kuhnert *et al.* (2012), we predicted the composition of prey (expressed in term of functional group) consumed by the predators, given the explanatory variables. Unidentified prey were not taken into account in the analysis. Analyses were conducted using the 'rpart' package of the statistical open source R software.

Trophic structure of the communities

Epipelagic and deep-water community-wide aspects of the trophic structure were compared using Layman's metrics (Layman *et al.*, 2007) based on carbon and nitrogen stable isotope ratios, and calculated using each species isotopic averages as measurement units.

The degree of trophic level diversity and basal resource diversity of the food web were assessed with the $\delta^{15}N$ (NR) and $\delta^{13}C$ (CR) range of values respectively. The isotopic niche occupied by each community was represented by the area of the smallest convex hull (TA) including all species of each community in the isotopic space ($\delta^{13}C$-$\delta^{15}N$ bi-plot). The mean distance to centroid (CD), calculated as the mean Euclidian distance between each species isotopic values and the mean $\delta^{15}N$ and $\delta^{13}C$ values of the community, was used as a proxy for the global degree of trophic diversity. Mean nearest neighbour distance (MNND) and its standard deviation (SDNND) among all species pairs are measures of species packing and its evenness within a trophic niche. Small MNND express a high trophic redundancy among species comprising each community.

Factors driving the isotopic composition of white muscle

The potential effects of explanatory variables on $\delta^{13}C$ and $\delta^{15}N$ (Table 1) were investigated using linear models followed by ANOVA. This procedure allowed the identification of explanatory variables that significantly affect $\delta^{13}C$ and $\delta^{15}N$ ratios. For these variables univariate procedures were used to explore the direction and amplitude of each effect.

Data were first tested for normality and homoscedasticity using a Jarque-Bera test (Thadewald and Bünin, 2007) and a Levene test, respectively. For qualitative variables statistical differences between two modalities were tested using either a Student t test or a Mann-Whitney U test, depending on the normality and homoscedasticity of the data. Statistical differences between more than two modalities were tested using a one-way variance analysis (ANOVA) test (followed by Tukey's multiple comparison), or a Kruskal-Wallis H test, followed by multiple pairwise comparison using the kruskalmc procedure, depending on the normality and homoscedasticity. Monotonic direction (increasing or decreasing) and amplitude effects of quantitative variables on stable isotopic ratios were tested using either the Pearson or Spearman ρ correlation test, depending on the normality and homoscedasticity of variables. Statistical significance was established at 5% for all statistical tests. All statistics were performed using R.

Results

Factors driving diet composition

The classification tree applied to diet composition expressed in terms of prey functional groups presented very different pictures for deep-water and epipelagic fish (Fig. 2). Indeed, among all exploratory variables, depth, location (zone), and fish species, had a significant influence on the diet of deep-water fish only when the identity of the predator allowed separating the epipelagic community into 3 homogeneous groups (Fig. 2).

T. albacares and *K. pelamis* fed mostly on Stomotopoda (28%), Brachyoura (megalopa stage, 21%) and squid (21%), while *A. solandri* and *C. hippurus* fed on the juvenile stage of reef-associated species (46%), and the four other species (*G. cuvier, C. leucas, C. ignobilis* and *S. barracuda*) fed on demersal coastal fish (29%) and squid (20%, Fig. 2). For these species no effect of month, fishing zone, distance from shore, and predator length was detected on diet composition. This result suggests that epipelagic predators partitioned available prey between groups of specialised species, while their feeding habits appeared homogeneous within each species.

On the other hand, CART analysis emphasized the importance of predator species, depth and fishing area, on deep-water fish trophic habits, segregating the studied species in four groups. This analysis predicted a high dietary overlap between *B. decadactylus* and *E. radiatus* (feeding chiefly on Caridea, which composed 77% of their prey) on the one hand, and between the six remaining species on the other hand (Fig. 2). Only the fishing depth and area allowed prediction of the dietary habits of *S. megalops, E. illustris, E. carbunculus, E. coruscans, P. multidens* and *P. argyrogrammicus*. Thus, all predators present in a given area and at a given depth would consume the same prey, irrespective of the predator species. Above 345 m depth, all predators fed on shrimps (42%) all around Reunion Island, whereas there was a distinction between the East and West coasts in the feeding habits of predators caught below 345 m depth. Below 345m on the East coast, all predators seem to rely mainly on mesopelagic prey (lantern fish – Mytophiliformes, 64%), whereas on the West coast, they fed on a mix of Caridea (36%) and mesopelagic prey (30%). The month, fish length, sex and maturity had no significant effect on the deep-water fish diet composition.

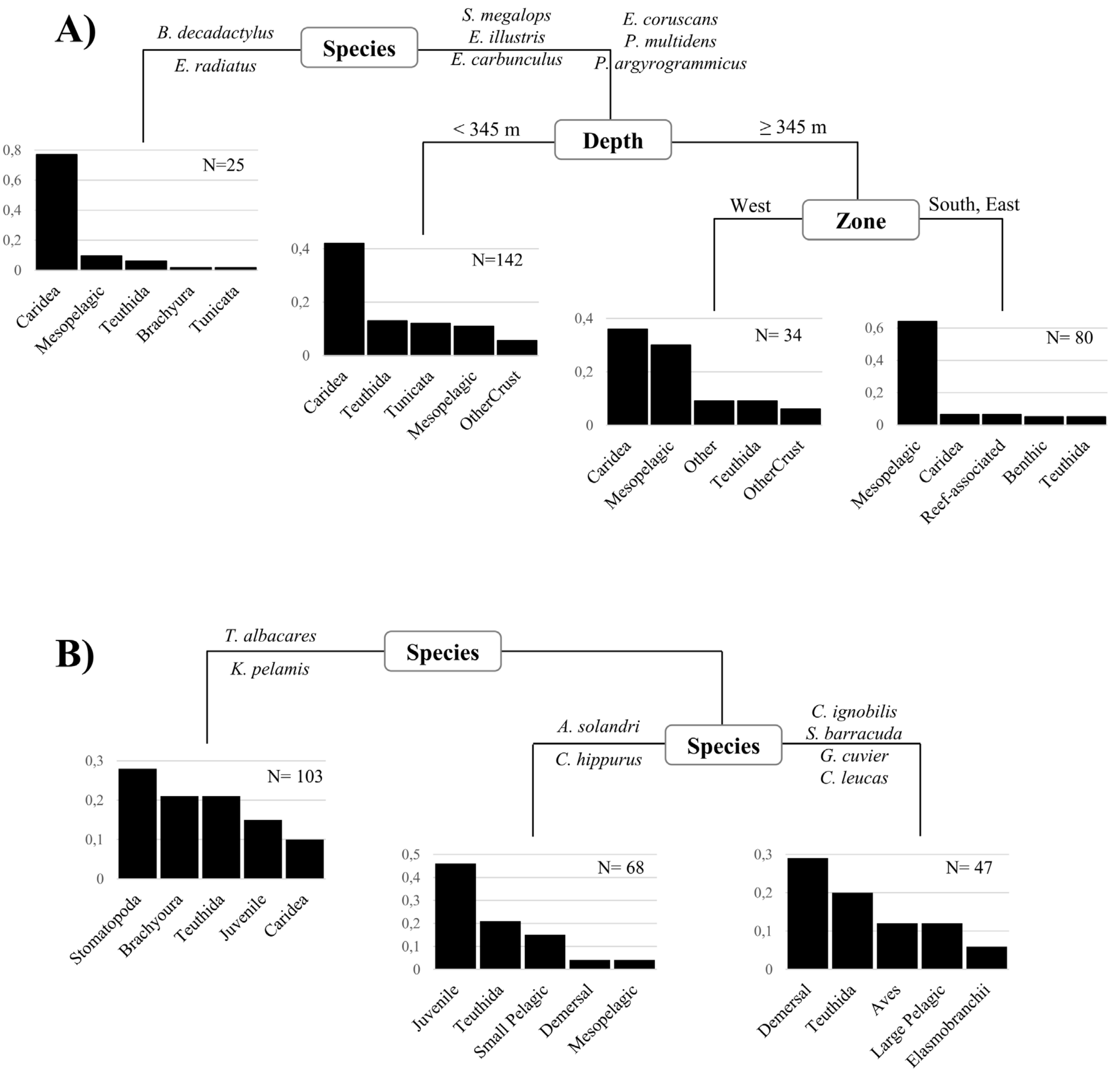

Figure 2. Pruned regression tree predicting diet composition of A) eight deep-water predators and B) eight epipelagic predators. The exploratory variables are represented in Table 1. N represent the number of predatory fish individuals composing each trophic groups.

Structure of the community of deep-water and epipelagic fish

Stable isotope based metrics of trophic structure were very similar between demersal and epipelagic fish communities (Table 2). Both communities exhibited similar degrees of trophic level diversity, basal resource diversity and isotopic niche (assessed by NR, CR and TA respectively Table 2, Fig. 3). Their global degree of trophic diversity and species packing were not statistically different (assessed by CD and MNND respectively, Table 2). However, the epipelagic fish community exhibited a significantly lower species packing evenness (SDNND = 0.08) than the deep-water fish community (SDNND = 0.29, Fisher test: F^{7}_{7} =10,304, p=0.006) (Table 2). To sum up, the two communities presented similar isotopic niches but a different species distribution within each niche, with epipelagic species being more evenly distributed than deep-water species (Fig. 3).

Factors driving the isotopic composition of the species

While the models analysing the variance of the stable isotope ratios in fish were statistically significant for both communities (all models $p < 0.001$), it explained more of the variance for deep-water fish (explaining 74% of $\delta^{13}C$ variability and 70% of $\delta^{15}N$ variability,

Table 3) than for epipelagic fish (explaining 34% of $\delta^{13}C$ variability and 25% of $\delta^{15}N$ variability, Table 4). Among the five considered variables only species identity significantly affects the isotopic ratios for the epipelagic fishes (Table 4), while six and seven of the nine exploratory variables (seven main variables and two interaction terms) significantly influenced the $\delta^{13}C$ and $\delta^{15}N$ ratio in deep-water fishes (Table 3).

The average $\delta^{13}C$ values in epipelagic fishes ranged from -17.7 to -15.8 ‰ and $\delta^{15}N$ values ranged from 10.7 to 12.5 ‰ (Table S2). Both $\delta^{13}C$ and $\delta^{15}N$ were significantly different between species (Kruskal-Wallis: $H_{df=7} = 129$, $p < 0.001$ and $H_{df=7} = 68$, $p < 0.001$). The highest and the lowest carbon and nitrogen values were found in *C. leucas* (-15.8 ± 0.6 ‰) and *K. pelamis* (-17.7 ± 0.4 ‰) respectively. The isotopic values of *C. leucas* were not significantly different from those of *C. ignobilis* ($\delta^{15}N$= 12.5 ± 0.6 ‰ and 12.0 ± 0.3 ‰; $\delta^{13}C$= -15.8 ± 0.6 ‰ and -16.0 ± 0.5 ‰ respectively) and were isotopically enriched compared to all other species. *K. pelamis* and *T. albacares* fed at the lowest trophic level ($\delta^{13}N$ = 10.7 ± 0.5 ‰ and 11.0 ± 1.0 ‰ respectively) but seemed to depend on similar carbon sources as *C. hippurus* and *A. solandri* ($\delta^{13}C$ = -17.7 ± 0.4, -17.5 ± 0.5, -17.7 ± 0.9 and -17.7 ± 1.7 respectively). In fact, these four species were significantly ^{13}C-depleted compared to the four other epipelagic species. *G. cuvier* and *S. barracuda* had intermediate nitrogen and carbon isotope values ($\delta^{15}N$= 12.0 ± 0.7 ‰ and 11.6 ± 0.8 ‰; $\delta^{13}C$= -16.9 ± 0.7 ‰ and -16.6 ± 0.4 ‰ respectively).

For the deep-water species, the month had no effect on both $\delta^{13}C$ and $\delta^{15}N$, and in addition the sex of the predator had not effect on $\delta^{13}C$ (Table 3). The stage of maturity of fish affected both $\delta^{13}C$ (Kruskal-Wallis: $H_{df=5} = 52$, $p < 0.001$) and $\delta^{15}N$ ($H_{df=5} = 99$, $p < 0.001$). Both isotopic tracers significantly increased with the fish maturity, from an average $\delta^{13}C$ of -18.3 ± 0.2 ‰ and $\delta^{15}N$ of 11.4 ± 0.6 ‰ for juveniles, to an average $\delta^{13}C$ of -17.4 ± 0.6 ‰ and $\delta^{15}N$ of 12.7 ± 0.7 ‰ for spawning adults. The $\delta^{15}N$ significantly increased with depth (Spearman's rank correlation: S=17404130, $p < 0.001$, ρ = 23 %), from 11.1 ± 0.3 ‰ above 100 m, to 12.9 ± 0.3 ‰ below 500 m, whereas $\delta^{13}C$ values were not affected by depth (S = 22369470, p = 0.79, ρ = 1.2 %).

Finally, the fishing zone only significantly influenced the $\delta^{13}C$ and $\delta^{15}N$ values for *E. illustris* and *E. carbunculus* (Kruskal-Wallis tests, $p < 0.05$), with enrichment in heavy isotopes increasing from West (zone A) to East (zone D, Fig. 4).

Discussion

In a context of a global rise in concern about the sustainability of fishing activities and the need to adopt an ecosystem-based management approach to fisheries, improving our understanding of the factors driving variations in fish feeding habits is a crucial prerequisite. The novelty of the present study is that it combines both stable isotopes and stomach content analysis to identify the factors that structure two fish communities in the same location. Our results demonstrated firstly, an independence of both communities, with very few common prey items, although caught in similar localities, and secondly, a very different pattern of resource partitioning among each community, with the species feeding habits being the main driver for the epipelagic species, and the habitats for the deep-water fishes. Overall these results support our hypothesis that different factors structure the two communities, though they exist in similar localities. It should be noted however that epipelagic fishes were sampled over a two-year period whereas deep-water fishes were sampled during nine months only, potentially affecting interpretations.

Table 2. Layman's metric for the two studied fish communities: d15N and d13C ranges (NR and CR); convex hull total area (TA); distance to centroid (CD); nearest neighbor distance mean and standard deviation (MNND and SDNND).

Metric	Demersal	Pelagic	Statistics
NR	1.85	1.8	
CR	1.31	2	
TA	1.5	1.7	
CD	0.63 ± 0.34	0.86 ± 0.38	U = 20, p = 0.23
MNND	0.48	0.49	U = 32, p=0.98
SDNND	0.29	0.08	F^{7}_{7} = 10,304, p=0.006

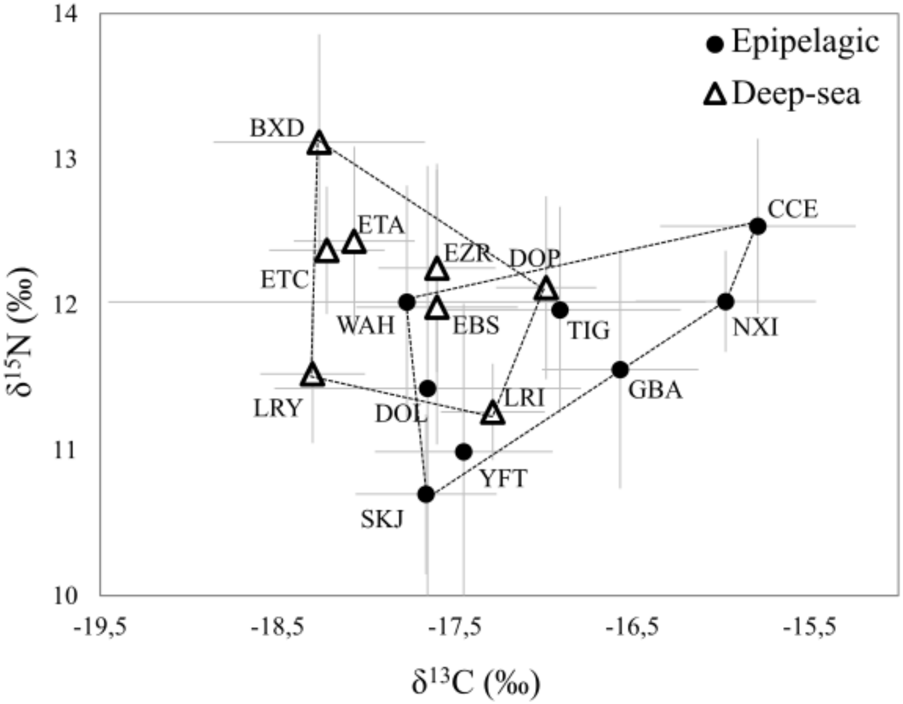

Figure 3. Isotopic structures of the deep-water and epipelagic studied fish communities. Deep-water species are: BXD, *Beryx decadactylus*; ETA, *Etelis coruscans*; ETC, *Etelis carbunculus*; LRY, *Pristipomoides argyrogrammicus*; LRI, *Pristipomoides multidens*; EBS, *Eumegistrus illustris*; EZR, *Epinephelus radiatus* and DOP, *Squalus megalops*. Epipelagic species are: YFT, *Thunnus albacares*; SKJ, *Katsuwonus pelamis*; WAH, *Acanthocybium solandri*; DOL, *Coryphaena hippurus*; GBA, *Sphyraena barracuda*; NXI, *Caranx ignobilis*; TIG, *Galeocerdo cuvier* and CCE, *Carcharhinus leucas*.

Trophic independence of epipelagic and deep-water fish communities

According to the analyses of the major functional groups of prey consumed by the studied species, the epipelagic and deep-water fish communities rely on different resources. Considering the geomorphology of the island, which results in close proximity between coastal and oceanic ecosystems, one could expect a greater trophic similarity between these two communities. It seems that even in similar localities, they remain independent in their functioning. Interestingly, for both communities, the analyses of the isotopic niche suggested that they exploit a limited number of carbon sources, probably because these sources are limited both in surface and deeper waters around Reunion Island.

The main prey found in surface predators were larval stage Stomatopoda, juveniles of reef-associated species, and coastal shallow benthic species, typical of surface waters, whereas the main prey found in deep-water predators were mesopelagic species such as Myctophids and large shrimps. Some studies previously reported a significant proportion of Myctophids consumed by surface predators such as *C. hippurus* (Castriota *et al.*, 2007), *A. solandri* (Iversen and Yoshida, 1957), *T. albacares* and *K. pelamis* (Jaquemet *et al.*, 2011) in different locations, including Reunion Island. Most Myctophid species belong to the sound-scattering layer community that engages in vertical migrations at night to access biomass produced in surface waters during the day. This migration can move horizontally in addition to vertically in areas close to seamounts or oceanic islands, becoming available to surface coastal predators during the night (Benoit-Bird and Au, 2006). In the present study, the high abundance of Myctophids in deep-water fishes and their absence in the stomach of surface predators could reflect local particularities such as a deep thermocline (Manola et al. 2015), which could limit the vertical movement of mesopelagic prey, or be a consequent of sampling bias (low sample size, sampling not heterogeneous through time for some species). The timing of the foraging activity of the surface predators might also prevent these species accessing the vertically migrating Myctophids. Further investigations on the distribution, abundance and movement of mesopelagic organisms in relation to the structure of the water masses are required to understand the local availability of such prey to surface predators.

Table 3. Results of an ANOVA applied on linear models assessing the effect of exploratory variables on the stable isotopic ratios of the deep-water fish species.

		δ13C				δ15N			
	Df	**Sum Sq**	**Mean Sq**	**F value**	**Pr(>F)**	**Sum Sq**	**Mean Sq**	**F value**	**Pr(>F)**
Depth	1	0.004	0.004	0.04	0.84	20.00	20.00	88.23	< __0.001***__
TL	1	57.49	57.49	597.77	< __0.001***__	12.44	12.44	54.87	< __0.001***__
Zone	4	5.99	1.50	15.56	< __0.001***__	38.05	9.51	41.97	< __0.001***__
Species	7	50.79	7.26	75.45	< __0.001***__	112.19	16.03	70.72	< __0.001***__
Month	1	0.09	0.09	0.95	0.33	0.02	0.02	0.075	0.78
Sex	2	0.17	0.08	0.86	0.42	3.90	1.95	8.60	< __0.001***__
Maturity	4	2.43	0.61	6.32	< __0.001***__	17.31	4.33	19.10	< __0.001***__
TL*species	7	4.32	0.62	7.29	< __0.001***__	19.92	2.85	15.42	< __0.001***__
Area*species	18	3.46	0.19	2.27	__0.002**__	4.97	0.28	1.49	0.08
Residuals	467	39.54	0.08			86.61	0.19		
P-val model			< 0.001***				< 0.001***		
R^2			74%				70%		

The observed dietary difference between the two studied fish communities was result of a difference in the resource use among species. The surface community gathered in 3 homogeneous dietary groups based on predator species identity only, while within the deep-water community, the depth and the geographical location were also important factors explaining the trophic variability. In other words, for the epipelagic community, all individuals of a given species seem to have similar diets wherever and whenever they are caught, independent of their size. On the contrary, all deep-water predators caught in a given area and depth seem to consume the same prey, independent of species. The fact that such morphologically different species fed on the same prey in a given area likely reflects a low prey availability that would force fishes to exploit the same resources. This similarity in the diet is also observed in the isotopic space, where the

Table 4. Results of an ANOVA applied on linear models assessing the effect of exploratory variables on the stable isotopic ratios of the epipelagic fish species.

		δ13C				δ15N			
	Df	**Sum Sq**	**Mean Sq**	**F value**	**Pr(>F)**	**Sum Sq**	**Mean Sq**	**F value**	**Pr(>F)**
Species	7	67.168	9.5954	14.2740	<__0.001***__	46.446	6.6351	8.5721	<__0.001***__
TL	1	0.837	0.8375	1.2458	0.27	0.289	0.2894	0.3739	0.54
Month	1	0.109	0.1086	0.1615	0.69	4.550	4.5500	5.8783	__0.02*__
Zone	19	10.992	0.5785	0.8606	0.63	13.615	0.7166	0.9257	0.55
DistShore	1	1.850	1.8498	2.7518	0.10	1.835	1.8346	2.3702	0.12
Residuals	141	94.784	0.6722			109.139	0.7740		
P-val model			< 0.001***				<0.001***		
R^2			35%				25%		

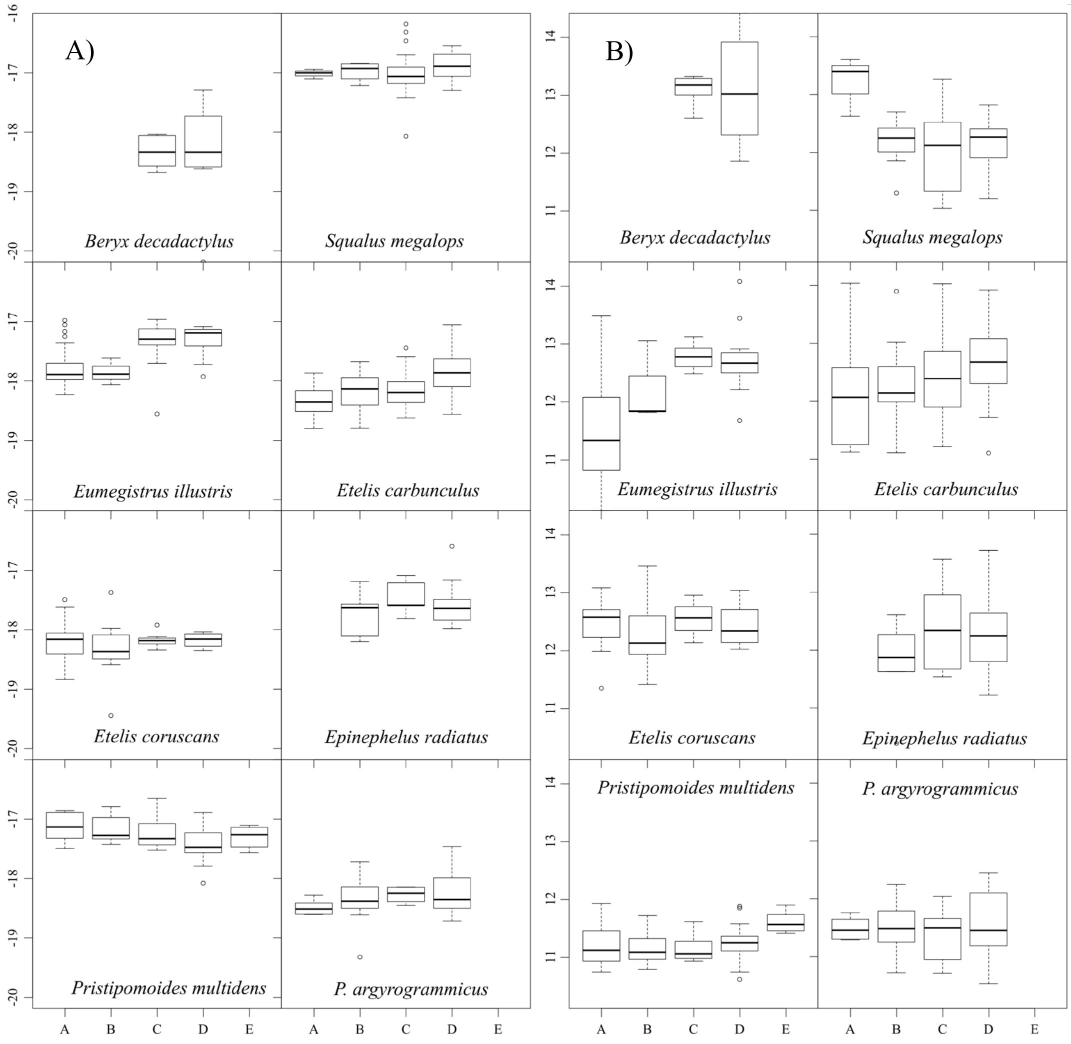

Figure 4. Variations of A) $\delta^{13}C$ and B) $\delta^{15}N$ with fishing zone (see Figure 1) of eight deep-water fish species.

distribution of the deep-water fishes is more packed than for the epipelagic species. Such an observation is in accordance with the fact that deep-water ecosystems are considered as highly food-limited (Iken *et al.*, 2001). This segregation of the two communities can be related to the structure of the water masses. In tropical areas, surface waters are usually well stratified, exhibiting a deep thermocline (Manola *et al.*, 2015), as observed around Reunion Island, where the temperature is homogeneous in the first 100 meters before decreasing gradually from 24°C to 12°C at 500 meter depth (Leroy and Barbaroux, 1980).

Factors structuring the surface and the deep-water fish communities

To explore the diet and stable isotope variability between species within the epipelagic community, five exploratory variables were considered: predator species, total length, month, fishing zone and distance from shore. Among these variables, only the species was identified to have a statistically significant effect. The absence of effect from the other exploratory variables is surprising given the information on their feeding ecology contained in the existing literature. Both size and distance from shore were demonstrated as important factors for tuna diet (Allain *et al.*, 2012; Ménard *et al.*, 2013), even in the Western Indian Ocean (Jaquemet *et al.*, 2011). The studied species are highly mobile predators, meaning that the distance from the shore should not be a limiting factor in the context of the present study (most distant catch was ~15km offshore). In addition, some of the species caught at the same place during the same periods exhibited differences in their diet composition and stable isotope ratios. This suggests that the trophic segregation among species is mostly driven by intrinsic factors rather than environmental ones. The swimming characteristics, the diving capability, the prey detection and catching ability are all likely major structuring factors for this community of epipelagic predators. In this community, the species seem rather specialized in their feeding habits, which could be a mechanism to reduce competition for resources, which are often considered in low abundant and patchy in tropical surface waters (Weimerskirch, 2007). The presence of the coastal ecosystems of the island also has to be considered in the foraging behaviour of the large pelagic fish. Indeed Jaquemet *et al.* (2011) in a comparison of the diet of tuna caught in the vicinity of the island and far offshore, showed clear differences in the diet composition, with offshore tuna feeding more on deep prey species whereas tuna in the vicinity of the island feed mostly on coastal species, as found in the present study. It seems that inshore-offshore transfers of organic matter is a key factor affecting the epipelagic fish around Reunion Island.

Deep-water demersal fish diet variability was explored in the light of seven exploratory variables. For this community, fishing zone and depth had significant effects on individual stomach contents in addition to the species identity. Moreover, both intrinsic (predator species, total length, sex and maturity) and environmental (fishing zone and depth) factors affected the deep-water fish isotopic ratio. Both carbon and nitrogen isotopic ratios increased with individual length for all deep-water demersal fish species (Trystram *et al.*, in revision). These results are in accordance with previous studies on the diet and distribution of deep-water fishes around oceanic islands and seamounts, which reported high habitat-dependence and trophic shifts associated with the length of the individuals (Fock *et al.*, 2002; Misa *et al.*, 2013). The feeding of these species is highly constrained by abiotic conditions, which limit prey availability. In these conditions, it is not surprising that variables characterising habitat determine the structure of the community of deep-water fishes. Their main feeding opportunity seems to be the interception of mesopelagic organisms that undertake diel migration to feed in the upper layers of the water column. These results support the sound scattering layer interception hypothesis for deep-water fish diet (Fock *et al.*, 2002; Trystram *et al.*, in revision). Depth and other abiotic conditions act on these migrating organisms, rendering them more or less available to the fish. The effects of sex and length on the stable isotope ratios suggest ontogenetic changes in trophic ecology and differences related to reproduction. All these mechanisms could reveal adaptations of the species to limited resources, with an overall strategy toward a reduction of the overlap between the diet of the different species and stages of development.

The difference observed in the stomach contents according to the depth of fish collection, and between the West and East coasts, could reflect differences in the distribution of mesopelagic organisms. Carid shrimps would be more abundant in the upper layer compared to Myctophids (see Fig. 2A). At first, this result seems surprising as it is in opposition with observations made in Hawaii, where Myctophids were more abundant in the upper layer. This difference can be explained by the fact that in this study fishes were caught mostly below 150m, a depth at which Myctophids are still abundant in Hawaii, but less so than in upper layers (Benoit-Bird and Au, 2006). In these conditions, feeding on large shrimps could be advantageous for the fish, as they could be easier to catch and could provide more energy. The difference between the West and East coasts follows the same pattern as with depth, suggesting that shrimps are more abundant on the West coast. This observation could be the consequence of an island effect as Reunion Island lies in the path of the south-equatorial current (Pous *et al.*, 2014). The obstruction of the island could create a sheltered zone behind the island, such as the situation described for Tome Island, where a complex flow pattern forms downstream of the island (Bakun, 2006). Upstream the island a local high in the sea surface topography is created, which would tend to accelerate the down-gradient flow skirting either side of the island obstruction, creating bands of swift flow downstream north and south of the island; these last features providing lateral torques that drive counter-rotating eddies behind the island, with upwelled waters in their core. As a consequence, on the West coast, the upwelled waters could raise deep waters and favour the presence of mesopelagic shrimps close to the surface, whereas the accumulation of water on the East coast would favour downwelling, which would lead to an increase of the upper layer the water column, which would render the Myctophids that migrate to the upper layers more accessible to the fishes (Benoit-Bird and Au, 2006).

Conclusion

In this study we propose that the factors underlying the trophic structure of two communities of fish that are spatially closely located and exploited by artisanal fishermen in Reunion Island are different. The community of surface predatory fishes exploits different functional groups of prey and this seems to be mostly related to intrinsic factors rather than being controlled by the environment. This specialization of the different species might be a response to both a low biomass and a high diversity of resources that the predators can exploit. On the other hand, the community of deep-water fishes seems to be mostly structured by environmental factors, which control the distribution of the prey in the water column, though there seem to be within-species mechanisms to reduce the competition between sex and age classes. As a consequence, all species at a given depth exploit the same resources, while individuals of the same species do not necessary feed on the same prey in different habitats (i.e. depth). This situation is related to the fact that resources are rare below the euphotic zone and that the main feeding opportunity seems to be the deep scattering layer, composed of mesopelagic prey that undergo diel vertical migrations. Interestingly, the two communities seem to function independently from each other, although both have evolved in the vicinity of Reunion Island. This suggests that surface species do not dive deep to forage and deep-water species do not forage in the epipelagic zone, or that the species in each community do not forage at the same time. This apparent independence of each community is counterbalanced however by the fact that all species rely mostly on the pelagic primary production of the euphotic zone. More precisely, the epipelagic community may primarily depend on inshore-offshore transfer of biomass, with export of coastal material to the oceanic realm, and the deep-water community depending on the export of surface materiel to deeper waters; all these transfers depending on the movements of prey (passive drifting of fish larvae or active movement of mesopelagic micronektonic animals). Further investigations should be conducted to better understand the patterns of predator and prey distribution in space and time and the role of each species in the transfer of biomass and energy between ecosystems. The results presented in this study suggest that fisheries management should be very different for epipelagic and deep-water fishes. For epipelagic fisheries management should be more species-centred (restriction by size or season for example, for one particular species all around the island), whereas deep-water fisheries management should be more habitat-centred (with restricted zones, deep marine protected areas for example).

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Supplementary materials

Table S1. Correspondence between prey species or families and ecological functional group. NI: unidentified.

Predator	Functional Group	Family	Species
Deep-sea fish	Bathydemersal	Berycidae	
		Scorpaenidae	
		Serranidae	
		Trachichthyidae	
	Benthic	Bembridae	*Parabembras robinsoni*
		Bothidae	
		Congridae	
		Lophiidae	
		Muraenidae	*Muraenesox baggio*
		Peristediidae	*Satyrichthys sp*
	Brachyura	CrabNI	
		Majidae	
		Portunidae	*Chrybdis sp*
	Caridea	Caridea	*Heterocarpus laevigatus*
		Panaeoidea	*Aristaeomorpha foliacea*
		Peneidae	
		ShrimpNI	
	Epipelagic	Carangidae	
	Pelagic Tunicata		
	Mesopelagic	Bregmacerotidae	
		Carapidae	
		Epigonidae	*Sphyraenops bairdianus*
		Gempylidae	NI
			Thyrsitoides marleyi
		Gonostomatidae	
		Macroramphosidae	
		Myctophidae	*Benthosema sp*
			Ceratoscopelus warmingii
			Diaphus effulgens
			Diaphus lucidus
			Lampanyctus vadulus
			NI
			Pseudoscopelus sp
		Nemichthyidae	
		Sternoptychidae	*Argyropelecus aculeatus*
			NI
			Polyipnus indicus
		Stomiiformes	
	Octopoda	Octopoda	
	Other	Algae	
		Annelida	
		Bivalvia	
		Echinoidea	

Predator	Functional Group	Family	Species
		Gasteropoda	
		Gravel	
		Sipuncula	
		Taeniidae	
	OtherCeph	Sepiolidae	
	OtherCrust	Aegidae	
		Amphipoda	
		Cirripedia	
		Enoplometopidae	*Enoplometopus sp*
		Isopoda	
		Lysiosquillidae	*Lysiosquilla sp*
			Lysiosquilla tredecimdentata
		Munididae	*Munida shaula*
		Odontodactylidae	
		Palinura	
		Scyllaridae	
		Squillidae	
	Reef-associated	Acanthuridae	
		Chaetodontidae	
		Holocentridae	NI
			Sargocentron sp
		Menidae	*Mene maculata*
		Monacanthidae	
		Mullidae	NI
			Upeneus sp
		Ostraciidae	*Lactoria sp*
		Pomacentridae	
		Syngnathidae	
		Tetraodontidae	NI
			Sphoeroides pachygaster
	Teuthida	Bathyteuthidae	
		Histioteuthidae	*Histioteuthis sp*
		Lepidoteuthidae	*Lepidoteuthis sp*
		Loliginidae	
		Lycoteutidae	
		Onychoteutidae	
		OtherTeuthida	
Epipelagic fish	Aves	Phasianidae	*Gallus gallus*
		Sternidae	*Anous sp*
			NI
	Coastal.Fish	Acanthuridae	*Brachycentron sp*
			NI
		Balistidae	
		Batrachoïdidae	
		Diodontidae	
		Fistulariidae	
		Holocentridae	*Myripristis sp*

Predator	Functional Group	Family	Species
			Sargocentron sp
		Lutjanidae	*Aprion viriscens*
			Lutjanus sp
		Monacanthidae	
		Mullidae	*Parapeneus sp*
		Muraenidae	
		Ostraciidae	
		Polynemidae	*Polydactylus sp*
		Scaridae	
		Scorpaenidae	NI
			Scorpaena scrofa
		Tetraodontidae	
	Crust.Benthic	Paguroidea	
		Raninidae	*Ranina ranina*
	Crust.Epipelagic	Amphipoda	NI
			Phrosina semilunata
		Isopoda	
		Lysiosquillidae	*Lysiosquilla tredecimdentata*
		NI	
		Odontodactylidae	*Odontodactylus scyllarus*
		Ostracoda	
		Palinuridae	
		Squillidae	*Neoanchisquilla tuberculata*
	Elasmobranchii	NI	
		Sphyrnidae	
		Torpedinidae	
	Gaster.Meso	Cavoliniidae	*Cavolinia sp*
	Juvenile	Acanthuridae	*Acanthurus sp*
			Naso sp
			NI
		Antennaridae	*Histrio histrio*
		Balistidae	*Cantherhinus sp*
			NI
			Rhinecanthus sp
		Blennidae	
		Carangidae	
		Carapidae	
		Chaetodontidae	
		Dactylopteridae	*Dactyloptena orientalis*
		Diodontidae	
		Holocentridae	*Myripristis sp*
			NI
			Sargocentron sp
		Labridae	
		Monacanthidae	
		Mullidae	
		NI	

Predator	Functional Group	Family	Species
		Ostraciidae	
		Pomacentridae	
		Scorpaenidae	
		Serranidae	
		Sphyraenidae	
		Synodontidae	
		Tetraodontidae	*Lagocephalus sp*
			NI
		Zanclidae	*Zanclus canescens*
	Large.Pelagic.Fish	Carangidae	*Carangoïdes sp*
			Caranx ignobilis
			Caranx sexifaciatus
		Coryphaenidae	*Coryphaena hippurus*
		Istiophoridae	
		Scombridae	*Gymnocerda unicolor*
			Katsuwonus pelamis
			NI
			Thunnus albacares
	Mesopelagic	Bramidae	NI
			Pteraclis sp
		Gempylidae	*Nealotus tripes*
			NI
		Nomeidae	
		Paralepididae	*Lestrolepis sp*
		Trachichthyidae	*Gephyroberyx darwini*
	Octopoda	NI	
		Octopodidae	
	Shrimp.Epipelagic	Caridae	
		NI	
	Small.Pel.Fish	Carangidae	*Decapterus macarellus*
			Decapterus sp
			Selar crumenophtalmus
		Chanidae	*Chanos chanos*
		Clupeidae	*Sardinella gibbosa*
		Exocoetidae	*Exocoetus sp*
			Exocoetus volitans
			NI
		Nomeidae	*Cubiceps sp*
		Scombridae	
	Teuthida	Chirotheuthidae	
		Histioteuthidae	
		NI	
		Ommastrephidae	*Stenotheuthis oulaniensis*

Table S2. Characteristics of data used to explore factors influencing stomach contents and stable isotope composition. Ndis: number of dissected stomachs; Nfood: number of stomachs containing food; %empt: percentage of empty stomachs; TL: total length (cm); N: number of samples; C/N: atomic ratio of carbon to nitrogen composition.

Species	**Stomach contents**					**Stable isotopes**				
	Depth	**Ndis**	**Nfood**	**%empt**	**Mean TL [min-max]**	**N**	**Mean TL [min-max]**	**Mean $\delta^{13}C$ ±SD**	**Mean $\delta^{15}N$ ±SD**	**C/N**
Acanthocybium solandri	0	28	25	10.7	107 [64-142]	21	109 [97-142]	-17.7 ±1.7	12.0 ±0.8	3,4 ±0,4
Caranx ignobilis	0	13	9	30.8	104 [83-135]	15	99 [83-135]	-16.0 ±0.5	12.0 ±0.3	3,4 ±0,1
Carcharhinus leucas	0	24	16	33.3	227 [178-267]	27	224 [171-275]	-15.8 ±0.6	12.5 ±0.6	3.0 ±0.1
Coryphaena hippurus	0	53	49	7.5	96 [58-128]	34	96 [69-120]	-17.7 ±0.9	11.4 ±1.5	3,5 ±0,5
Galeocerdo cuvier	0	58	30	48.3	280 [206-336]	56	276 [206-336]	-16.9 ±0.7	12.0 ±0.7	2.9 ±0.1
Katsuwonus pelamis	0	23	16	30.4	61 [47-92]	18	60 [39-90]	-17.7 ±0.4	10.7 ±0.5	3,2 ±0,1
Sphyraena barracuda	0	14	8	42.9	116 [103-138]	10	110 [64-138]	-16.6 ±0.4	11.6 ±0.8	3,2 ±0,1
Thunnus albacares	0	97	91	6.2	72 [45-145]	34	77 [49-145]	-17.5 ±0.5	11.0 ±1.0	3,3 ±0,2
Beryx decadactylus	404 ±73	27	19	29.6	50 [39-58]	23	49 [35-60]	-18.3 ±0.6	13.1 ±0.7	3.3 ±0.6
Epinephelus radiatus	202 ±41	43	6	86.0	37 [30-46]	33	37 [12-62]	-17.6 ±0.3	12.3 ±0.7	3.1 ±0.1
Etelis carbunculus	298 ±49	791	60	92.4	28 [16-48]	158	29 [16-98]	-18.1 ±0.3	12.4 ±0.7	3.2 ±0.1
Etelis coruscans	314 ±27	94	15	84.0	43 [27-112]	47	52 [21-112]	-18.2 ±0.3	12.4 ±0.4	3.2 ±0.2
Eumegistrus illustris	432 ±65	89	18	79.8	67 [50-85]	73	67 [45-87]	-17.6 ±0.5	12.0 ±0.9	3.2 ±0.1
Pristipomoides argyrogrammicus	279 ±48	273	50	81.7	24 [16-29]	71	23 [16-29]	-18.3 ±0.3	11.5 ±0.5	3.2 ±0.1
Pristipomoides multidens	115 ±35	109	11	89.9	54 [35-70]	46	54 [34-86]	-17.3 ±0.3	11.3 ±0.3	3.2 ±0.1
Squalus megalops	384 ±40	289	107	63.0	57 [35-78]	63	57 [31-80]	-17.0 ±0.3	12.1 ±0.6	2.5 ±0.1

A preliminary assessment of the status and habitat preference of the grouper (Serranidae) population of Chumbe Island Coral Park, Zanzibar, Tanzania

Kimberly D. Nesbitt[1] , Matthew D. Richmond[2]

[1] University of Denver,
School for International Training
99 Rose Laurel Ct., Pawleys Island,
SC, 29585 USA
(Kim.Nesbitt@du.edu)

[2] Samaki Consultants Ltd.,
PO Box 77143, Dar es Salaam,
Tanzania
(matt@samaki.net)

Abstract

A census of the six most commonly occurring grouper (Serranidae) species was conducted on Chumbe Island off the coast of Unguja, Zanzibar, Tanzania in late 2014. The species were *Plectropomus laevis*, *Cephalopholis argus*, *Cephalopholis miniata*, *Epinephelus fuscoguttatus*, *Aethaloperca rogaa* and *Anyperodon leucogrammicus*. Results showed that, in general, larger individuals and species inhabit the deeper waters of the reef slope, while smaller species (and juveniles) inhabit the shallower back reef. The combined mean biomass recorded, derived from the mean biomass of all six species, was 43.96 kg over 12.5 ha, highly concentrated at the reef slope.

Keywords Grouper, Serranidae, Fringing Reef, Indian Ocean, Zanzibar

Introduction

Chumbe Island is located approximately 5 km off the western shores of Unguja Island, the principle island among the Zanzibar archipelago (Fig. 1). It is a small, 1 km long, rocky island of 22 ha size, covered in semi-arid coral-rag forest. On the western shores it is bordered by a fringing coral reef with an adjacent shallow back-reef. The island and reef gained protected status in 1991 and the western coral reef area was designated as the Chumbe Reef Sanctuary in 1994 (Gössling, 2003), and became known as the Chumbe Island Coral Park (CHICOP) (Fig. 1). The coral reef has been closed to all fishing and extractive activities, anchoring, and recreational scuba diving for over twenty years, complying with the criteria of a no-take-area (Nordlund *et al*., 2013), and making it one of the Marine Protected Areas (MPAs) in Tanzania with the longest history of no fishing within a coral reef habitat.

Initial studies in 1994 reported 343 fish species from 49 families within CHICOP (Fiebig, 1994), including the six species evaluated in this study. The current CHICOP fish species list now includes a total of ten grouper species. Unfortunately, no previous fish investigations documented the numbers of individuals of each grouper species, thus historic biomass estimates are also lacking. Among the groupers of CHICOP, *P. laevis* (black-saddled grouper) is classified as Vulnerable (IUCN Red–List). The aim of this study was to establish an inventory of the larger groupers on the CHICOP coral reef that will serve as a baseline for future monitoring of these apex predators.

Materials and Methods

Surveys were conducted during October and November 2014, with a single survey defined as an underwater visual census swim either along the entire reef slope (1,000 m length) or a serpentine swim through the shallow back reef, at depths from 0-10m. The north end of the survey was at 6° 16' 31" S, 39 °10' 30" N, and the south end of the survey was at 6° 17' 01" S, 39 °10' 31" N, covering approximately 12.5 ha (Fig. 2). The prevailing currents (mainly tidal) were used to aid surveys; being north to south on the ebb, and south to

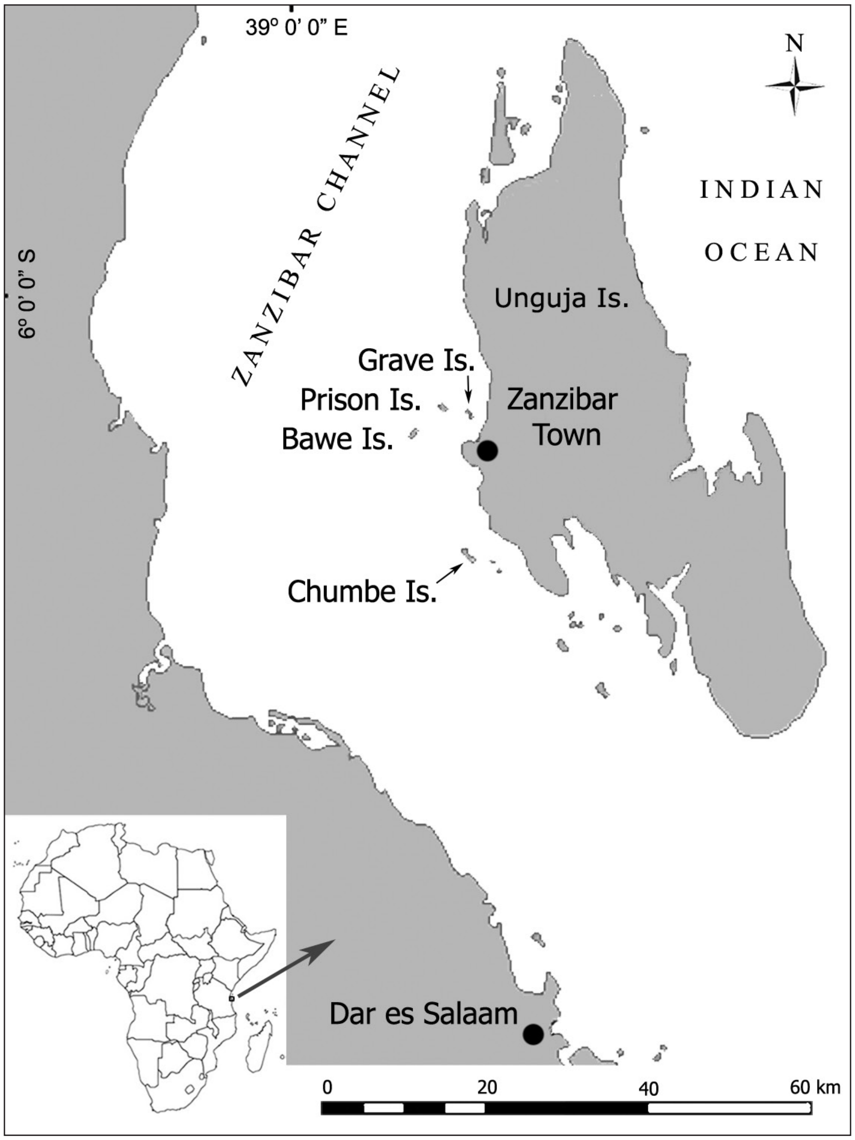

Figure 1. Location of Chumbe Island in relation to Unguja Island and mainland Tanzania.

north during the flood. Length was determined based on visual estimation, and biomass calculated using a series of length/weight categories for each species using data from Fishbase.org. Surveys were timed, ranging from 1.25 to 1.5 hours, conducted during the day between 0800 and 1600 hours. Notes were taken on individual habitat preferences for each species.

Results and Discussion

The western reef slope was surveyed thirteen times, and the inner back reef was surveyed four times. A total of 318 individual sightings were recorded from the reef slope with 60 from the back reef (Table 1). From the combined total of 378 individual sightings of groupers, overall most species were found among higher densities of coral, closer to, or on, the reef slope (Fig. 2).

The *P. laevis* population showed a strong habitat preference, with large adults inhabiting the bottom of the reef slope, approximately 6-8 m deep, with juveniles in shallower water, approximately 2-5 m deep. *C. argus* were more concentrated on and around the reef slope, and were not seen at depths below 6 m. This species had a specific concentration at the southernmost point of the Chumbe reef (Fig. 2), yet adults were observed all around the reef, in both reef slope and back reef areas. *C. miniata* were always recorded in water deeper than 4 m, close to the edge of the reef slope, especially concentrated where the slope was steepest (Fig. 2), but not seen in the back reef area (Table 1). *E. fuscoguttatus* was also absent from the back reef and seen to favour specific areas of the reef, with the highest concentration being the northernmost extent of the reef, where the coral becomes sparse (Fig. 2). *A. rogaa* had a wide

Table 1. Details of grouper species sighted and their distribution in Chumbe Island Coral Park (reef slope n = 13 back reef n = 4); mean sighting values = mean number seen per survey.

Species	Common English name	IUCN Red List Category	Total sightings			Biomass (kg/12.5 ha)	
			Reef Slope (mean)	Back Reef (mean)	Maximum count (times recorded)	Reef Slope (mean)	Back Reef (mean)
Plectropomus laevis	Blacksaddled	Vulnerable	71 (5)	4 (1)	12 (2)	23.8	0.34
Cephalopholis argus	Peacock	Least Concern	117 (8)	22 (5)	19 (1)	2.76	1.43
Epinephelus fuscoguttatus	Brown marbled	Near Threatened	20 (1)	0	4 (1)	9.05	0
Aethaloperca rogaa	Redmouth	Data Deficient	84 (9)	24 (6)	14 (2)	3.66	1.94
Cephalopholis miniata	Coral	Least Concern	26 (3)	0	8 (1)	0.61	0
Anyperodon leucogrammius	Slender	Least Concern	0	10 (2)	2 (1)	0	0.37
		Total	318 (24)	60 (14)	59	39.88	4.08

distribution that covered both the reef slope as well as the back reef where larger individuals and smaller ones were observed, respectively. They were generally concentrated in the middle of the reef, more along the dense coral of the reef slope than the sparse coral of the back reef. *A. leucogrammicus* was only observed in the back reef areas, always associated with table corals, and not seen on the reef slope.

The overall impression on the distribution of adults and juveniles for four species was that larger individuals were more common on the reef slope and smaller individuals the shallower back reef. The absence of adult *P. laevis* or *E. fuscoguttatus* in the back reef further confirms that mature individuals exclusively inhabit the reef slope. Once the large individuals reach a certain size, they can no longer seek refuge in shallow water to ambush prey, so must move to deeper water where larger coral formations occur. The combined mean biomass density of the six grouper species was 43.96 kg, with a biomass density of 39.88 kg on the reef slope and 4.08 kg on the back reef (Table 1).

The finding of this survey presents a baseline on the abundance, size, habitat distribution, and biomass of the six principle grouper species, for the main coral reef area (12.5 ha) within CHICOP. This also demonstrates that CHICOP has succeeded in protecting a small section of fringing reef to the extent that after 20 years a number of apex predators are now commonly observed, at a time when neighbouring coral reefs are witnessing significant declines in diversity and standing stock (Muthiga *et al.*, 2008). The relatively small, 1 km-long, western reef of CHICOP at present supports a population of at least twelve *P. laevis* individuals among a total grouper population of 59 individuals, and a mean standing stock estimated at

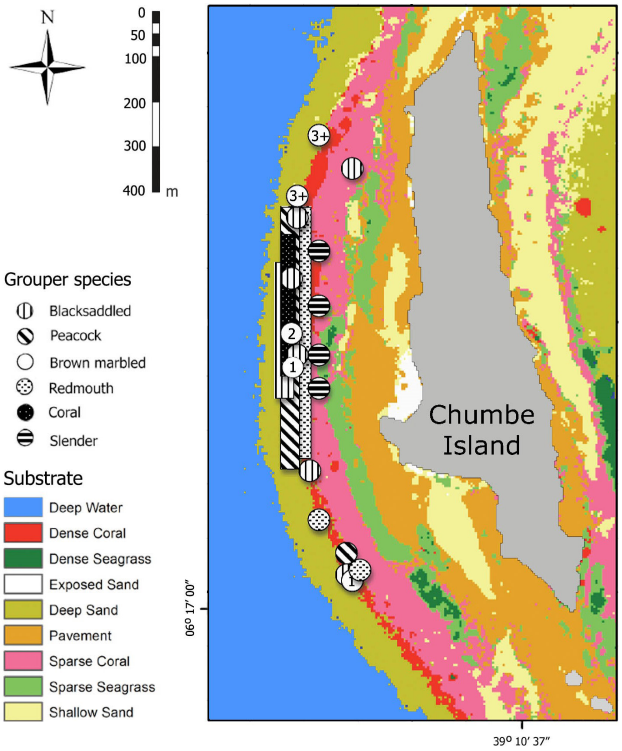

Figure 2. Marine habitats of Chumbe Island's western reef area (CHICOP) showing location of grouper species sighted in the present study (circles are areas of high or regular occurrence; rectangle indicates the broader territory of a species; and numbers in circles indicate the number of individual Brown marbled groupers (*E. fuscoguttatus*) observed at each location).

43.96 kg. This is an important contribution to grouper stocks, not only for Zanzibar and Tanzania, but for the region as a whole.

Further understanding of the movements of these large fish would also be beneficial, particularly combined with photo-identification of individuals to help better establish the precise territories of individual fish. Understanding the egg production capacities of each species within CHICOP, in terms of larvae export, would contribute to the debate on how MPAs replenish fish stocks outside their boundaries.

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