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Annual to Inter-Decadal Variability in Surface Air Temperature Along the Coast of Tanzania

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Keywords: Surface temperature, low frequency oscillations, climatic systems, Tanzanian coast

Abstract — Patterns in atmospheric surface temperature along the coast of Tanzania were investigated for variability and trends over the last 50 years (1960-2009). Various statistical tools were employed in the study, including non-parametric models as well as trend, spectral and wavelet analyses. The results revealed that the ENSO was generally the most important climate phenomenon affecting the inter-annual surface temperature variations. Seasonally, the influence of the ENSO was most prominent around equinoxes, and was also significant around solstices as well as during October-December. At the decadal timescale, surface temperatures were generally composed of two low frequency oscillations at about 24-year and 50-year periodicities. Each of these oscillations had alternate epochs of low and high temperatures which were directly related to decadal oscillations in the IOD. A key finding of this study was the revelation of significant warming trends in surface temperatures along the coast. The increases per decade were consistent with global trends, being generally greater in minimum temperature (0.14-0.72°C) than in maximum temperature (0.07-0.13°C). Shifts in minimum surface temperature generally coincided with cool phases of the 50-year oscillations at the beginning of the record, and with warm phases at the end of the record. An increase in cloud cover over the coast of Tanzania during the observation period may have contributed to this disparity. Within the last half century, the warmest years in minimum temperature differed slightly between stations but all fell within the last decade (2000-2009). The last decade, which generally coincided with warm phases of the decadal oscillations in surface temperature and the IOD, was also the warmest.

INTRODUCTION

Global average surface temperatures have increased by about 0.074°C per decade over the period 1901 to 2010 (Morice *et al.*, 2012). Over the last three decades (1979-2010), the

rate of warming has more than doubled to about 0.169° C per decade. According to Trenberth *et al.* (2007), the global rise in minimum temperature per decade during the last half

Corresponding author: SBM Email: shigalla@tafiri.go.tz century (1950 to 2004) was 0.20°C, much higher than that of maximum temperature which was only 0.14°C. The decade 1991-2000 was the warmest of the previous 150 years, and the warmest 22 years have occurred since 1980, while 1998 and 2005 were the two warmest years on record (Ehrhart & Twena, 2006; Trenberth et al., 2007). It has also been observed that eleven of the last twelve years between 1995 and 2006 rank among the 12 warmest years in the instrumental record of global surface temperatures since 1850 (Trenberth et al., 2007). The consensus is that this warming trend has been triggered by anthropogenic emissions of greenhouse gases. Some of the global rates have recently been updated in the IPCC AR5 reports, extending the period of observations up to 2012 (Hartmann et al. 2013).

The warming trend, however, has not been continuous but has been interspersed by cooling periods due to natural climate variability such as the El Niño - La Niña cycle in tropical ocean temperature (Hansen et al., 2010). During the period of instrumental records, episodes of cooling included an abrupt drop in sea surface temperature around 1970 (Thompson et al., 2010) when both the Atlantic Multidecadal Oscillation (AMO) and the Pacific Decadal Oscillation (PDO) were in their cool phases (Obeysekera et al., 2007). The recent hiatus in the rate of global warming has prompted much discussion. The increase in global mean surface temperatures was lower between 1997 and 2013 (0.07±0.08°C per decade) than over the last 50 years (0.16±0.02°C per decade) (Schmidt et al., 2014). This phenomenon has been attributed to natural variability in the climate system, whereby a short period of cooling (about a decade or two) is superimposed on the longer-term warming trend (Easterling & Wehner, 2009).

Other oceanographic parameters such as the well-known El Niño Southern Oscillation (ENSO) also play a role in global climate. The strength of ENSO events is measured by the Niño-3 index (McPhaden *et al.*, 2006), which is defined as the SST anomaly averaged over the eastern equatorial Pacific region (5°N-5°S and 150°W-90°W). The ENSO is near global in extent but it appears to wax and wane on decadal to multi-decadal timescales (Allan, 1993). The Indian Ocean Diploe (IOD) constitutes the difference between an SST anomaly in the western equatorial Indian Ocean (50°E-70°E and 10°S-10°N) relative to the south eastern equatorial Indian Ocean (90°E-110E and 10°S-0°N). This difference is named the Dipole Mode Index (DMI; Saji et al., 1999). A positive IOD event is marked by a drop in SST in the south-eastern part of the Indian Ocean, counteracted by an SST increase in the western equatorial Indian Ocean, i.e. off the eastern coast of Africa from the northern part of Madagascar to the northern edge of Somalia, and vice versa for a negative IOD event (Marchant et al., 2006). The DMI index is archived at the Japan Agency for Marine-Earth Science and Technology (JAMSTEC) (http://www.jamstec. go.jp/frcgc/research/d1/iod/). The Pacific Decadal Oscillation (PDO) Index (Mantua et al., 1997) is the leading principal component of North Pacific monthly SST anomalies poleward of 20°N. Monthly mean global average SST anomalies are removed from the PDO Index so as to separate it from any "global warming" signal that may be present in the data.

The climate of East Africa is regulated by a number of factors, including the Inter-Tropical Convergence Zone (ITCZ), subtropical anticyclones, tropical cyclones, monsoon wind systems, the African jet streams, easterly-westerly wave perturbations, and teleconnections between regional and large-scale quasi-periodic climate systems like the quasi-biennial oscillation, intra-seasonal waves, the ENSO and the IOD, among others (King'uyu et al., 2000). The teleconnection between the ENSO and the Western Indian Ocean is well documented in analyses of instrumental sea surface temperature (SST) and East African rainfall records (e.g. Hastenrath et al., 1993). ENSO events have usually occurred with an average return period of about 2-7 years (McPhaden et al., 2006).

Generally, the dominant variability in surface air temperature is assumed to come from slowly varying SSTs (Chelliah & Bell, 2004). However, low frequency decadal to multi-decadal fluctuations in the climate system are often related to large scale ocean-atmosphere exchanges involving changes in mass water transport, the oceanic thermohaline circulation, and deep water formation (Allan *et al.*, 1995).

One of the key studies on trends in mean surface air temperatures over eastern Africa was undertaken by King'uyu et al. (2000). These authors used daily and monthly minimum and maximum temperature records from 71 locations (both coastal and inland) covering the period between 1939 and 1992. Their investigation encompassed two of the four stations included in the present study (Dar es Salaam and Tanga). Another key investigation was that of Christy et al. (2009) who used several global datasets to investigate trends in maximum and minimum temperatures from 118 coastal and inland locations in East Africa over a 100-year period (1904-2004). In the earlier study, the results revealed an increase in both maximum and minimum temperatures. In the later study, the maximum temperatures were relatively unchanged, but there was evidence of an accelerated rise in minimum temperatures.

The objectives of the present study were to determine the annual to decadal variability and trends in surface air temperatures along the coast of Tanzania. The investigation was undertaken using temperature data recorded in the last half century.

METHODS

Monthly maximum and minimum temperature data were obtained from the Tanzania Meteorological Agency (TMA), which is the custodian of all meteorological data in the United Republic of Tanzania. The data were collected from the key meteorological stations of Tanga, Dar es Salaam and Mtwara along the mainland coast, and from the major offshore island of Zanzibar (Fig. 1). The data covered 50 years, extending from 1960 to 2009. Table 1 presents geographical information on the meteorological stations used in the study. They are all installed sufficiently distant from physical obstructions, despite the Dar es Salaam station being located in an urban setting, making the data uniform in quality and comparable. The instruments are also serviced and calibrated annually to ensure reliability in the data collected.

Although the coastal topography and the micro-climatic conditions may differ slightly between land and water surfaces, the land-based stations were considered representative of the temperature field in the near-shore coastal domain. This is an assumption which poses a possible limitation in the study given the strong diurnal cycle (land-sea breezes) along the coast of Tanzania (Summer, 1982).

The first analysis involved simple averaging of the monthly means of maximum and minimum temperatures at each station to obtain annual series in each. The annual means could not be calculated for years with missing monthly data (which were few). Trends in the series were then computed from the annual means. Many statistical tests are available to detect trends in time series but the trend magnitudes can often be determined reliably using combinations of parametric and nonparametric techniques (Partal & Kahya, 2006).

Trend analyses were thus undertaken employing a variety of techniques including the least-squares linear regression, Kendall's τ statistic and the Spearman's rank correlation test. Kendall's τ statistic is a non-parametric test which can be used to test for the presence of a

Table 1. Geographic information on the Tanzanian coastal meteorological stations.

Station	Latitude	Longitude	Altitude above sea level (m)	Urban/Exposed
Tanga	05.05°S	39.04°E	49	Exposed
Zanzibar	06.13°S	39.13°E	18	Exposed
Dar es Salaam	06.53°S	39.12°E	53	Urban
Mtwara	10.21°S	40.11°E	113	Exposed

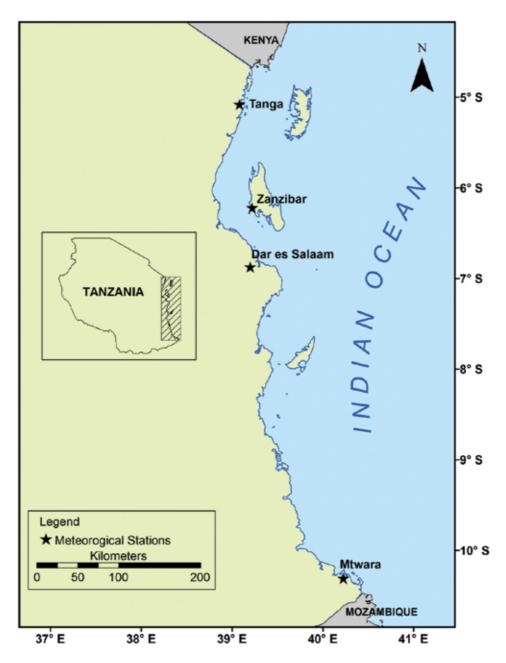


Figure 1. Map of coastal Tanzania showing the sites of the meteorological stations.

linear trend, while the Spearman's test validates the result (Mitchell *et al.*, 1969). Kendall's τ statistic has been widely used in particular to test for randomness in trends in climatology and hydrology (Partal & Kahya, 2006). A disadvantage of a simple linear regression approach is that it may fail to detect trends that are nonlinear but still monotonic and unidirectional. The Kendall's τ test and the Spearman rank correlation can detect trends that are monotonic but not necessarily linear, and only indicate the direction, and not the magnitude, of the trends. Time series spectra of the monthly means were thus estimated using Fast Fourier Transform (FFT) in the STATISTICA software package to determine the significant spectral peaks. The Parzen window (Oppenheim & Schafer, 1999) was used to smooth the raw data sets in preference to other approaches as it provided better interpretation of the results.

Wavelet analysis was used to further test for the presence of low frequency oscillations and temporal peaks in the monthly maximum and minimum temperatures as it constitutes the best tool to detect relatively slow changes in the frequency content of non-stationary series. While the time series may contain dominant periodic signals, the oscillations can vary in both amplitude and frequency over a longer time period. This technique therefore permits decomposition of the time series into time-frequency space, revealing the evolution in relative strength of the dominant modes with time. The analysis (Torrence & Compo, 1998) was undertaken using MATLAB to determine continuous wavelet transformation in the time series.

The relationship between local surface temperatures and the large scale climatic systems was explored in partial correlations. The Ninō-3 index was obtained from the US National Oceanic and Atmospheric Administration (NOAA) Climate Prediction Center (http://www.cpc.ncep.noaa.gov/data/ indices). The PDO index was obtained from the Joint Institute for the Study of the Atmosphere and Ocean (JISAO) (http://jisao.washington. edu/pdo/PDO.latest). Partial correlation of local temperatures with Niño-3 was computed by isolating the effects of the DMI and PDO. Likewise, the partial correlation of maximum and minimum temperatures with the DMI (PDO) was determined by isolating the effects of the Niño-3 (DMI) and PDO (Niño-3), respectively. All computation of partial correlations was performed using STATISTICA software. Prior to analysis, missing data were interpolated from adjacent points.

RESULTS

The average monthly maximum and minimum air temperatures along the coast of Tanzania were about 30.5°C and 21.5°C respectively (Table 2). Temperatures generally increased northwards along the coast towards the equator. The coolest temperatures ranged from 12.8°C to 16.7°C during the southeast monsoon. The warmest monthly maximum temperatures were between 32.7°C and 34.5°C during the northeast monsoon.

The mean temperature in the coolest year at each station was about 20°C except at Zanzibar where it was only 17°C. The annual mean temperatures in the warmest years at each station were between 31°C and 32°C in 2003 at Zanzibar and Dar es Salaam, and at Tanga and Mtwara in 1983 and 1961 respectively. The warmest minimum temperatures were all recorded during the last decade, between 2003 and 2007.

Table 2. Mean and peak maximum and minimum temperatures (°C) recorded on the Tanzanian coast during 1960-2009.

Station	Mean monthly max temp	Mean min temp	Warmest monthly max temp	Coldest monthly min temp	Warmest monthly annua max temp	Coldest al annual min temp	Warmest annual min temp
Tanga	30.6	22.2	34.5	16.4	31.2	20.2	23.3
(Period)			(Mar 1987)	(Sep 1973)	(1983)	(1973)	(2006)
Zanzibar	30.6	21.7	34.1	12.8	31.4	16.6	23.3
(Period)			(Feb 1982)	(Aug 1966)	(2003)	(1966)	(2003)
D' Salaan	1 30.8	21.1	34.1	16.7	32.0	20.0	22.3
(Period)			(Mar 2003)	(Jul 1981)	(2003)	(1980)	(2003)
Mtwara	30.1	21.0	32.7	16.7	30.9	19.9	22.1
(Period)			(Dec 1960	(Aug 1971)	(1961)	(1971)	(2007)

Time series of maximum and minimum temperatures clearly revealed a progressive northward increase in the amplitude of maximum temperatures along the coast (Fig. 2). Conversely, corresponding variations in the amplitude of minimum temperature increased southwards. All the sites manifested an increasing trend in both the maximum (daytime) and minimum (night-time) temperatures according to the Loess fit to the data. This also showed that the rises in minimum temperature were generally higher than that in maximum temperature. There was a large drop in minimum temperatures at Zanzibar between 1965 and 1970, and at Tanga between 1970 and 1975 (Fig. 2).

Linear regressions of the annual maximum and minimum temperature time series yielded warming trends at all stations (Table 3). Increases in minimum temperature were greater than that in maximum temperature. The greatest change in maximum temperature occurred at Dar es Salaam (0.65°C) while the smallest was recorded at Zanzibar (0.35°C). The greatest change in minimum temperature occurred at Zanzibar (3.59°C) and the smallest at Mtwara (0.7°C). The trends in both maximum and minimum temperatures were found to be statistically significant using Kendall's τ statistic and the Spearman rank test. The corresponding maximum and minimum temperature changes per decade averaged 0.07-0.13°C and 0.14-0.72°C respectively.

Decadal means of both maximum and minimum temperatures (Table 4) were highest during the last decade (2000-2009). The highest decadal maximum and minimum temperatures of 31.2°C and 23°C were recorded at Dar es Salaam and Zanzibar respectively. The corresponding lowest maximum and minimum temperatures of 30.0°C and 20.0°C were recorded at Mtwara

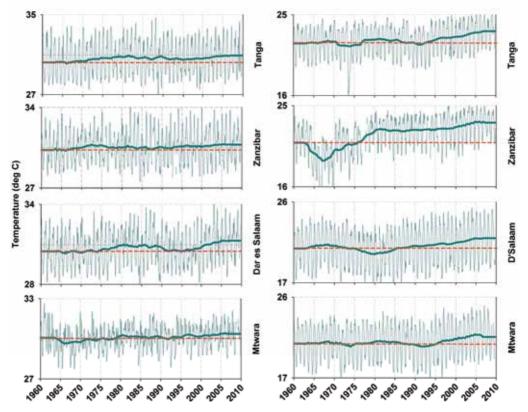


Figure 2. Monthly variation in maximum (left) and minimum (right) temperatures at the four study sites. Bold lines represent the Loess fit and red dashed lines correspond to the mean 1960 level.

Station	Parameter	Regression coefficient	Kendall τ	Spearman's R	Total change (°C)	Change decade (°C.decade ⁻¹)
Tanga	Max temp	0.01	0.33	0.47	0.50	0.10
	Min temp	0.02	0.44	0.62	1.15	0.23
Zanzibar	Max temp	0.01	0.23	0.32	0.35	0.07
	Min temp	0.07	0.68	0.87	3.59	0.72
Dar es Salaam	Max temp	0.01	0.32	0.45	0.65	0.13
	Min temp	0.02	0.39	0.55	1.05	0.21
Mtwara	Max temp	0.01	0.21	0.30	0.40	0.08
	Min temp	0.01	0.29	0.41	0.70	0.14
7°30S, 39°30E	SST	0.01	0.10	0.15	0.62	0.12

Table 3. Regressions and trends in surface temperatures (°C) for the Tanzanian coast during 1960 to 2009. All correlations were significant at the 95% level.

(1960-1969 and 1970-1979) and Zanzibar (1960-1969) respectively.

The time series spectra (Fig. 3) indicated that the annual cycle was the dominant mode of oscillation at all the stations. A small semi-annual signal was also prominent in the maximum temperature at Mtwara, which was expected because, in equatorial regions, the sun crosses its zenith twice a year, leading to weak double maxima in the air temperature cycle (Legates & Willmott, 1990). A semiannual signal is also believed to be associated with the position of the rising branch of the Hadley circulation twice a year (Van Loon & Jenne, 1970). The maximum temperature at Mtwara and the minimum temperature at Zanzibar were also indicative of the existence of relatively small non-stationary signals in the time series spectra.

Wavelet analysis of the monthly time series indicated that the strength of the annual cycle varied throughout the record, clearly showing the presence of warm and cold spells in different periods at each site (Figs 4 and 5). An abnormally cold spell was discernible in the annual minimum temperature cycle at Zanzibar during the period 1976-1978. A weak, semi-annual signal was also apparent in both the maximum and minimum temperatures and, as in the spectral analyses, the signal was

		1960-1969	1970-1979	1980-1989	1990-1999	2000-2009
Tanga	Max temp	30.3	30.6	30.7	30.6	30.9
	Min temp	21.9	21.8	22.1	22.2	22.9
Zanzibar	Max temp	30.4	30.6	30.4	30.6	30.7
	Min temp	20.0	21.1	22.3	22.5	23.0
Dar es Salaam	Max temp	30.5	30.6	30.9	30.6	31.2
	Min temp	21.1	20.7	20.7	21.3	21.8
Mtwara	Max temp	30.0	30.0	30.2	30.2	30.3
	Min temp	21.0	20.8	21.0	20.8	21.6
7°30S, 39°30E	SST	27.0	27.3	27.4	27.45	27.51

Table 4. Mean decadal surface temperatures (°C) recorded on the Tanzanian coast during 1960-2009.

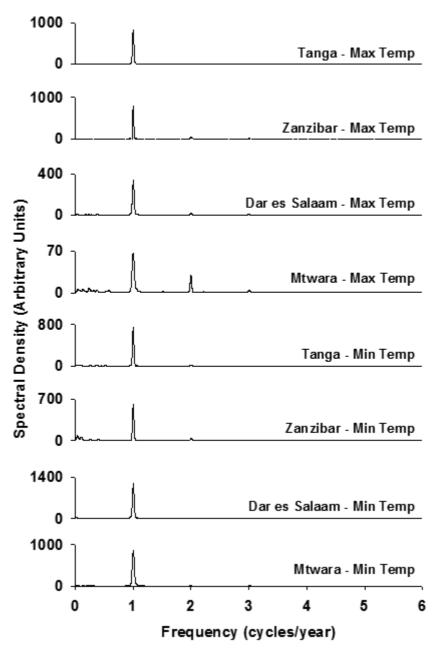


Figure 3. Time series spectra of annual cycles in maximum and minimum temperatures at each station.

only prominent in the maximum temperature records for Mtwara. Although the Zanzibar and Dar es Salaam stations are only about 35 km apart, the wavelet spectra for these two stations differed slightly, possibly due to different degrees of exposure to the land and ocean. This consequently appeared to lead to somewhat different surface temperature regimes. At the inter-annual timescale (Figs 6 and 7), spectral analysis revealed significant energy at an ENSO interval of 2-8 yrs (see e.g. D'Arrigo *et al.*, 2005), especially in the maximum temperatures. Strong La Niña events (1984/85) and El Niño (1987/88) were clearly evident in the wavelet spectra of maximum temperatures at each of the sites.

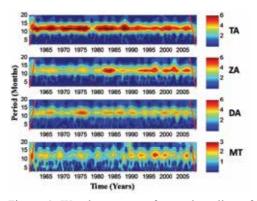


Figure 4. Wavelet spectra of annual cycling of maximum temperatures at Tanga (TA), Zanzibar (ZA), Dar es Salaam (DA) and Mtwara (MT). Red solid lines represent the Cone-of-Influence. Colour scales = standard deviations.

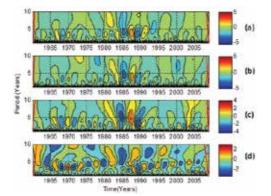


Figure 6. Wavelet spectra of ENSO timescale signals for maximum temperatures at a) Tanga, b) Zanzibar, c) Dar es Salaam and d) Mtwara. Red solid lines represent the Cone-of-Influence. Colour scales = standard deviations.

Strong and alternating La Niña and El Niño episodes were also evident in the minimum temperatures at Tanga between 1971 and 1976. There were no prominent peaks at the ENSO timescale in the minimum temperature records at the other sites.

At the decadal timescale, there was a prominent signal in the minimum temperatures at each station, as well as in the maximum temperatures at Mtwara, with a period of about 50 years (Figs 8 and 9). The signal had alternate epochs of warm and cool temperatures, each with a period of about 25 years. The decadal signal was directly related to the IOD low

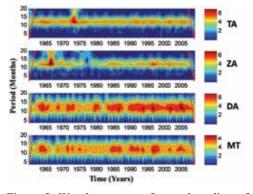


Figure 5. Wavelet spectra of annual cycling of minimum temperatures at Tanga (TA), Zanzibar (ZA), Dar es Salaam (DA) and Mtwara (MT). Red solid lines represent the Cone-of-Influence. Colour scales = standard deviations.

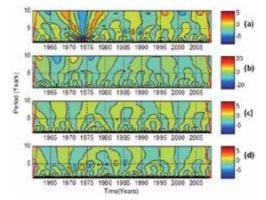


Figure 7. Wavelet spectra of ENSO timescale signals for minimum temperatures at a) Tanga, b) Zanzibar, c) Dar es Salaam and d) Mtwara. Red solid lines represent the Cone-of-Influence. Colour scales = standard deviations.

frequency oscillation which was also revealed through wavelet analysis (Fig. 10). Generally, cold phases prevailed in the 50-year periodicity during the first half of the records, and warm phases in the second half.

The maximum and minimum temperatures also revealed prominent peaks with a periodicity of about 24 years at most stations and an inter-annual timescale signal in the minimum temperatures at Dar es Salaam alone (Figs 8 and 9). Alternating phases of low and high temperatures occurred during the 24-year periodicity, closely related to the bi-decadal signal of the IOD in Figure 10.

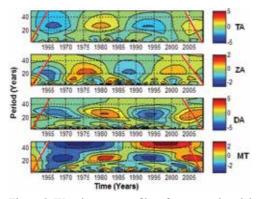


Figure 8. Wavelet spectra of low frequency decadal oscillations in maximum temperature at Tanga (TA), Zanzibar (ZA), Dar es Salaam (DA) and Mtwara (MT). Red solid lines represent the Cone-of-Influence. Colour scales = standard deviations.

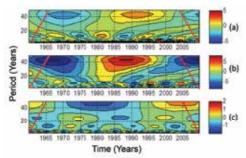


Figure 10. Wavelet spectra of low frequency (decadal) oscillations of a) the ENSO, b) the PDO and c) the IOD. Red solid lines represent the Cone-of-Influence. Colour scales = standard deviations.

Partial correlation analysis between surface temperatures and the large-scale climatic systems resulted only in weak and unsystematic relations in the monthly data (Table 5). The partial correlations were also generally weak during the northeast and southeast monsoons as well as in the long rainfall season of March-May. However, significant partial correlations were found between minimum temperatures and the ENSO during October-December, but these relationships were much stronger around equinoxes (Feb-Apr and Aug-Oct). Generally, the surface temperatures were directly influenced by ENSO at equinoxes, and appeared indirectly influenced by the IOD and the PDO. Conversely, the maximum temperatures were indirectly influenced by the ENSO at solstices (May-Jul and Nov-Jan).

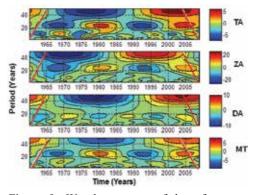


Figure 9. Wavelet spectra of low frequency decadal oscillations in minimum temperature at Tanga (TA), Zanzibar (ZA), Dar es Salaam (DA) and Mtwara (MT). Red solid lines represent the Cone-of-Influence. Colour scales = standard deviations.

The partial correlations of surface temperature with the ENSO were the most significant, making it the most important climate phenomenon that affects inter-annual surface temperatures along the coast of Tanzania.

DISCUSSION

Changes in air temperature have implications on the coastal environment such as an increase in the thermal expansion of the ocean and, hence, changes in mean sea level which affect coastal and marine ecosystems. An assessment of air temperature variability and trends in the coastal climate is thus important in elucidating local and regional climatic systems.

The results of this study indicate that variations in inter-annual surface temperature are modified by low frequency oscillations at decadal timescales which are superimposed on the annual signal. For instance, the cool episode in the minimum temperature record at Zanzibar during the late 1960s (Figs 2 and 5) resulted from a co-occurrence of cool epochs in both the 24-year and 50-year periodicities which emerged from the data (Fig. 9). This notable finding concurs with global observations, which indicate the presence of a weak worldwide cooling from the 1960s to the early 1970s (Baines & Folland, 2007). Inter-annual oscillations have also been

Table 5. Partial correlations of temperature with Niño-3 (r_a), DMI (r_a) and PDO (r_p), after isolating the effects of the DMI and PDO, Niño-3 and PDO, and Niño-3 and DMI respectively for monthly data and for the period October-December (OND), the equinoxes (Feb-Apr & Aug-Oct), the solstices (May-Jul & Nov-Jan), MAM (Mar-Apr-May) and regional SST in each season. Partial correlation coefficients significant at the 95% level are in bold.

]	OND											
		Max tem	ıp .	Mi	n temp		Max	temp		Ν	1in tem	ıp		
Station	<i>r</i> _n	r_d	r_p	<i>r</i> _n	r_d	r _p	r _n	r _d	r_p	r_n	r_d	r_p		
Tanga	0.25	-0.02	0.06	0.41	0.06	0.10	0.05	-0.15	0.11	0.29	0.16	0.13		
Zanzibar	0.07	-0.05	0.03	0.42	0.04	0.22	-0.09	-0.21	0.13	0.24	0.16	0.14		
Dar es Salaam	-0.2 1	0.00	0.03	0.02	0.06	-0.07	0.09	-0.15	0.21	0.18	0.18	-0.03		
Mtwara	-0.12	0.09	0.02	0.01	0.03	-0.04	0.03	0.03	0.00	0.21	0.07	0.12		
	Equinoxes						Solstices							
Tanga	0.64	-0.19	-0.17	0.74	-0.12	-0.07	-0.28	0.07	0.09	-0.08	0.08	0.06		
Zanzibar	0.39	0.07	0.15	0.62	-0.14	0.09	-0.29	0.05	0.05	0.05	0.03	0.18		
Dar es Salaam	-0.12	-0.14	-0.22	0.55	-0.14	-0.03	-0.38	0.12	0.13	-0.38	0.19	0.03		
Mtwara	0.55	-0.01	-0.22	0.50	-0.06	-0.17	-0.37	0.17	0.10	-0.37	0.16	0.05		
			MAM						Monthl	у				
	Ν	Aax temp	2		Min te	emp				SST				
Station	r _n	r_d	r_p	r _n	r_d	r_p	Sease	on	r _n	r_d	1	p		
Tanga	0.15	0.01	0.11	0.23	0.00	0.21	Montl	ıly	0.49	0.01	0.	12		
Zanzibar	0.13	0.01	0.08	0.24	-0.09	0.40	Equino	oxes	0.80	-0.3	0 -0.	28		
Dar es Salaam	0.22	0.02	0.20	0.16	-0.04	0.03	Solsti	ces	-0.03	0.05	0 .	05		
Mtwara	0.13	0.04	0.14	0.13	-0.09	0.04	MAN	M	0.35	0.00) 0.	22		

observed to be associated with the solar passage (equinoxes and solstices). This may be attributable to the fact that solar radiation in equatorial regions tends to increase close to the equinoxes when the sun crosses the equator northwards in March, and southwards in September (Ashkenazy *et al.*, 2010).

Decadal oscillations with a 24-year periodicity in the surface temperatures under consideration are comparable to those in East African coral oxygen isotope records, which were found to fluctuate at 18-25-year decadal timescales (Zinke *et al.*, 2009). The results also concur with SST observations by Royer (1989), who detected prominent peaks at 20 to 30-year cycles in the northeast Pacific.

One lingering question is whether the observed oscillations over coastal Tanzania are related to natural internal oscillations of the Indian or Pacific Ocean climate systems. Warm (positive) SST anomalies are associated with El Niño events, while La Niña events are typically associated with cold (negative) SST anomalies. According to Ware & Thomson (2000), the decadal oscillations in the northeast Pacific are probably caused by natural internal oscillations of the north Pacific climate system. During this century, the PDO was predominantly negative (cool conditions) between 1947 and 1976, positive (warm conditions) between 1977 and 1998, and has been negative since 1999 (Mantua et al., 1997, Mantua & Hare, 2002). The timing of these PDO shifts is in agreement with the results of wavelet analysis of the PDO in this study (Fig. 10), confirming that our wavelet analysis method was effective in extracting low frequency oscillations from the surface temperature time series.

Wavelet analysis revealed that the decadal oscillations in minimum surface temperatures at 50-year and 24-year periodicities, as well as in the maximum surface temperature at Mtwara (Figs 8 and 9), coincided with similar cycles in the Indian Ocean Dipole (Fig. 10). This coincidence clearly suggests that these decadal oscillations and the IOD are strongly linked. It follows, therefore, that the decadal oscillations in surface temperature along the coast of Tanzania are probably caused by natural internal oscillations in the Indian Ocean. Similar decadal and multi-decadal peaks of the IOD were found by Ashok *et al.* (2004) in data from 1950 to 1999.

There was a mismatch between the decadal surface temperature oscillations (Figs 8 and 9) and those of the decadal ENSO and PDO indices (Fig. 10) in our data. The decadal oscillation period of surface temperature was, for instance, about 50 years, while that of ENSO events, which co-occurred with the PDO, was only about 40 years. Nevertheless, the decadal oscillation periodicity of 24 years in surface temperatures was shorter than that of the ENSO and PDO decadal timescale signal. This implies that the PDO and ENSO decadal oscillations have little influence on variations in the decadal surface temperatures. The fact that the decadal oscillations in surface temperature are in turn related to those of the IOD is in agreement with the findings of Ashok et al. (2004), who found no consistent phase relationship of the IOD with the Niño-3 index of the ENSO.

The existence of decadal variability in the IOD was first investigated by Ashok et al. (2004), who revealed decadal IOD peaks at 8 to 13-year and 8 to 32-year oscillations that were associated with decadal modulations of the inter-annual IOD. Accordingly, the decadal oscillations of surface temperatures along the coast of Tanzania found in this study may also be related to decadal modulations in interannual surface temperature variability and the IOD, due to a strong association between decadal variability in surface temperature and decadal IOD cycles. According to Ashok et al. (2004), the decadal signal of the IOD index is related to the 20°C isotherm depth anomaly, indicating that ocean dynamics is involved in decadal IOD fluctuations.

Decadal signals with about a 60-80 year period such as those observed by Ware & Thomson (2000) in the Northeast Pacific were not considered in this investigation. The record was too short (50 years) and could not resolve such lower frequency components. In the Northeast Pacific, the 60-80-year decadal signal has been the dominant mode of oscillation during the past four centuries (Ware & Thomson, 2000).

It would be of interest to show that changes in surface air temperatures in the study area follow that of SSTs. This was assessed by extracting SSTs from monthly gridded global temperature data (Rayner et al., 2003) from the UK Hadley Centre's Sea-Ice and Sea Surface Temperature record (HadISST1) at a location centred around 7°30 S and 39°30 E. Sea surface temperatures increased by about 0.12°C per decade during the period 1960-2009 (Table 3) and, as with the surface air temperatures, have risen consistently over the last five decades (Table 4). Partial correlations of SST with the large scale climatic systems (Table 5) also revealed that, in the study area, they were significantly correlated with ENSO events, and indirectly with the IOD and PDO, especially during equinoxes (R = 0.80, -0.30 and -0.28 at p<0.05, respectively). The relationships of SSTs with large scale climatic systems were thus similar to those observed with surface air temperature.

Records for the months of January to March were extracted and wavelet spectra were plotted (results not shown) for comparison with plots of 21-year epochs of SST in the wider Indian Ocean described by Allan et al. (1995). The resulting spectra for coastal Tanzania were not remarkably different from those shown in Figures 8 and 9. In their investigation, Allan et al. (1995) showed graphically that the epoch of 1963-1983 was relatively warmer than the preceding epoch (1942-1962) along the coast of Tanzania. It must be noted, however, that the timing of epochs described by Allan et al. (1995) does not match with the decadal timescale oscillations observed in this study. In the case of minimum temperatures, for instance, the period 1963-1983 almost coincided with cold phases in the decadal timescale signal (Fig. 9). The same was also true for the maximum temperatures at Mtwara (Fig. 8).

The changes in surface air temperature detected in this study agree closely with global observations of warming trends in

both maximum and minimum temperatures (Trenberth *et al.*, 2007). The warming rates for the maximum and minimum temperatures on the Tanzanian coast of 0.07-0.13 °C and 0.14-0.72 °C per decade respectively over the period 1960-2009, were generally similar to the global increases of 0.12 °C and 0.20 °C per decade over the period 1950-2004 (Trenberth *et al.*, 2007). The present results are also similar to other observations in the region, such as those in South Africa and Ethiopia, where warming trends in both maximum and minimum temperatures have been recorded (Conway *et al.*, 2004; Kruger & Shongwe, 2004).

Forster et al. (2007) have suggested that minimum temperatures are warming faster than maximum temperature, presumably as a result of the 'urban heat island' effect. This emanates partly from physical properties of the urban landscape and partly from the anthropogenic release of heat into the environment from the use of energy in appliances and vehicles. Solar radiation heat stored during the day is slowly released at night as long-wave terrestrial radiation which keeps the minimum temperature higher than in rural areas. In the recent past, Tanzania has experienced a massive construction boom and the import of numerous vehicles as a result of rapid economic growth. All the study sites are located in cities, the largest being Dar es Salaam followed by Zanzibar, Tanga and Mtwara.

According to Trenberth et al. (2007), however, the urban heat island effect is localized and has negligible overall influence. At the global level, it contributes >0.006°C per decade to warming over land and zero over the ocean (Forster et al., 2007). The extent of urbanization does not necessarily match with the rate of warming along the coast of Tanzania. For instance, the city of Dar es Salaam has expanded extensively over the recent past, more than any other city in Tanzania, but the rate of change in the minimum temperature per decade at Dar es Salaam was lower than that at Zanzibar and Tanga. King'uyu et al. (2000) similarly found no differences in the inter-annual temperature patterns between rural and urban locations in East Africa. It therefore seems plausible

that factors other than urbanization must be considered in explaining the anomaly in the rates of increase of surface temperatures.

Christy et al. (2009) suggested that the relatively recent and rapid rise in minimum temperature may be attributable to changes in the surface characteristics and the boundary laver atmosphere. Normally, maximum temperatures occur during daytime when the surface is vertically connected to a mixed layer 1.5-2.5 km in depth. In contrast, minimum temperatures occur during the night, through early morning, characterising temperature in a thin boundary layer of air (Pielke Sr. et al., 2007). The minimum temperature is therefore sensitive to local land surface properties due to strong vertical gradients and its determination on measurement heights. Nevertheless, the horizontal footprint of minimum temperatures is smaller than that of maximum temperature since the former is more localised than the latter (Christy et al., 2009).

The results of this study strongly suggest that the faster rate of increase in minimum temperatures over maximum temperatures along the coast of Tanzania are most probably associated with natural decadal oscillations in the climate system. It is notable that cool epochs in the 50-year oscillations occurred during the first half of the record and warm epochs during the second half of the records, both in minimum temperatures at each site as well as in the maximum temperature at Mtwara. Correspondingly, warm epochs in both the 24-year and 50-year periodicities cooccurred during the last decade (Fig. 9).

Apart from decadal oscillations, changes in cloudy conditions are another factor worth considering for the accelerated rise in minimum temperatures. This is evident in the ship-based Extended Edited Cloud Reports Archive (EECRA), which indicate that there was an increase in cloud cover over Tanzania during the period 1954–2008 (Bellomo *et al.*, 2014). These authors also showed that there has been an increase in cloud cover, mainly in the northern sector of the country, according to the Coupled Model Intercomparison Project (CMIP5). Cloud cover during the night prevents heat from being radiated from the earth's surface into the upper atmosphere. The minimum temperature, which is generally recorded before the sunrise, thus goes up. Similarly, cloudy conditions do not allow the sun's rays to enter the earth surface, leading to drop in the daytime temperature.

In conclusion, the warmest years in terms of minimum temperature along the coast of Tanzania differed slightly between stations but occurred within the last decade. These results are similar to those observed in other parts of the region. For example, the warmest years in terms of SST fell within the last decade (2003 and 2004) at Pointe des Galets at Reunion Island (François et al., 2007). Surface temperatures appeared to be largely influenced by ENSO events at the inter-annual timescale, as well as by the IOD at the decadal timescale. Seasonally, a combination of the large scale climatic systems (the ENSO, PDO and IOD) as well as solar intensity was the main driver of inter-annual variations in surface temperature. A greater increase in minimum temperature over maximum temperature during the last half century was associated with warm epochs in 50-year oscillations at the end of the records, and with the increase in cloud cover during the study period. In view of the changing global climate, the rise in surface temperatures is likely to continue and this must be taken into consideration in terms of coastal resilience, adaptation and mitigation strategies.

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Meiofaunal Responses to Leaf Litter Added to Azoic Sediments in a Kenyan Mangrove Forest

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Keywords: *Rhizophora mucronata,* seagrass, leaf litter, meiofauna, nematodes, re-colonisation, mangrove sediment, Gazi Bay, Kenya

Abstract — Replicate azoic and organic-free sediments from a natural *Rhizophora mucronata* mangrove were enriched with similar amounts of mangrove and seagrass leaf litter to the natural organic concentration to establish which sources of litter most influence meiofaunal re-colonisation of reforested *R. mucronata* mangrove sediments in Gazi Bay. Sediments were incubated in 70 cc syringes with screened openings on the sides, allowing meiofaunal colonisation from the natural mangrove sediment. The syringes were retrieved on days 1, 14, 30 and 60 days post-placement. Replicate cores were taken on the first day of the experiment to provide baseline data on the meiofaunal densities and community composition. Recolonisation occurred one day post-placement and meiofaunal densities by the end of the experiment. ANOVA revealed a significant (p <0.05) litter source effect between mangrove and seagrass leaf litter, especially 30 days post-placement.

INTRODUCTION

Meiofauna, particularly nematodes, occur on all substrata in the marine environment. Detritus is a major energy source in many marine benthic systems and supports a high abundance and diversity of these meiofauna (Findlay & Tenore, 1982). In this regard, the phytal meiofaunal assemblages on mangrove leaf litter have been shown to be dynamic (Gee & Sommerfield, 1997; Zhou, 2001; Gwyther,

2003). Although the nitrogen content of detrital material may be the best measure of its nutritional quality, factors such as polyphenols (tannins) in mangrove leaf litter may lead to complex interactions between the tannins, the nitrogen content and age of the detritus (Tietjen & Alongi, 1990). This influences the utilisation of mangrove detritus by meiofauna, in particular nematodes. Mangrove leaves

initially undergo rapid leaching of dissolved organic matter (DOM) on the forest floor (Fell et al., 1975). This is followed by slow decomposition of the remaining particulate organic matter (POM), facilitated by bacterial and fungal communities which condition the leaf litter for various invertebrate groups that utilise it as food. Gwyther (2003) indicated that the food value for meiofauna in leaf litterderived particulate comprises the surface biofilm of bacteria, microalgae, protozoa and fungi. These are fed on by nematodes, in particular (Krishnamurthy et al., 1984). Gee and Sommerfield (1997) showed that the initial chemical composition of leaves from different mangrove species is responsible for observed differences in meiofaunal communities during the decomposition process under similar conditions (sediment composition, salinity and tidal inundation). They also showed that a succession of meiofaunal communities occurs during the decomposition process.

Several meiofaunal colonisation studies have been published on mangrove leaf litter, including work by Zhou (2001) who investigated the responses of meiofauna in general and nematodes in particular to decaying mangrove leaf litter; Sommerfield et al. (1998) who investigated the relationship between meiofaunal communities and leaf litter from different mangrove species; and Gee and Sommerfield (1997) who investigated the effects of mangrove diversity and leaf litter decay on meiofaunal diversity. However, no study has investigated the effect of leaf litter of other origin on the meiofaunal re-colonisation of mangrove sediments. While mangrove leaves are naturally shed in this environment, seagrass leaves are also introduced to mangroves by tidal flooding in Kenya. This study was thus undertaken to elucidate the effect that different types of leaf litter have on meiofaunal re-colonisation of reforested Rhizophora mucronata mangrove sediments in Gazi Bay. Such information is needed to design restoration programmes for mangrove ecosystems after deforestation. The study thus focused on whether the availability of leaf litter or the origin of the leaf litter (mangrove or seagrass) affects meiofaunal recolonisation of mangrove sediments.

METHODS

The meiofaunal colonisation experiments were undertaken in a natural Rhizophora mucronata forest in Gazi Bay (4° 25'S; 39° 30'E; Fig. 1), located on the southern part of the Kenyan coast about 50 km from Mombasa. An area of approximately 50 m² was demarcated for the experiment.

Mangrove and seagrass leaf litter was used in the experiments for four incubation periods with two sets of controls. The latter comprised three cores from the experimental site as well as three azoic sediment samples, prepared as described below, which received no further treatment. Mangrove or seagrass leaf litter was added to the treated samples. Colonisation rates by meiofauna at different stages of the leaf litter decomposition were determined by sampling the experimental treatments at time intervals of 1, 14, 30 and 60 days post-placement. Each treatment was replicated four times.

Surface sediments were collected to a depth of 5 cm from the natural R. mucronata site for the preparation of the azoic, organic-free sediment. After collection the sediments were air-dried for two days and combusted in an oven at 600°C for six hours to obtain azoic and organic-free sediment. The total organic matter (TOM) of the natural mangrove sediment at the experimental site was determined in three replicate, dried (80°C for 24 h), similarly combusted, sediment samples (20 g). The TOM was calculated as the difference in dry weight of the sediment before and after combustion (Buchanan & Kain, 1971). This value was used to calculate the amount of leaf litter to be added to the experimental sediment.

Yellowish, senescent and ready to fall *R. mucronata* leaves were picked in the natural forest while seagrass leaves were collected along the beach in Gazi Bay. Senescent mangrove leaves were used instead of fresh green leaves because these are naturally shed on the forest floor. Seagrass leaves were collected from the beach since these are washed into the mangrove during tidal flooding. The leaves were air-dried for one week and granulated using an electric grinder. The C:N ratio of the mangrove and seagrass

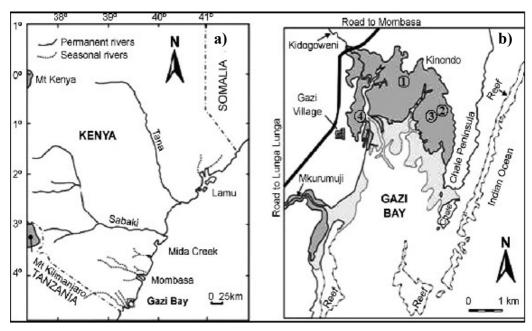


Figure 1. a) Map of the Kenyan coast and b) Gazi Bay showing the location of the experimental site (adapted from Bosire et al., 2004).

leaf litter was determined by first eliminating inorganic carbon from subsamples with dilute hydrochloric acid. The amounts of carbon and nitrogen were then analysed using a Carlo Erba element analyser, type NA-1500 (Nieuwenhuize & Mass, 1993-2002).

Plastic 70 ml (3 cm in diameter, 13.5 cm long) syringes were used as experimental vessels. Circular windows 2.5 cm in diameter were cut on opposite sides of each syringe and screened with plastic 2 mm mesh netting (Fig. 2) to allow water exchange with the surrounding natural sediment. The windows also enabled meiofauna to colonise the experimental sediments by horizontal migration, in addition to vertical movement from the overlying water column through each syringe top. The azoic, organic-free experimental sediments were put into the syringes and leaf litter was added on top. The syringes were labelled and randomly embedded in the sediment flush with its surface, covering a surface area of 7 cm^2 . They were fastened onto nearby roots or seedlings using nylon thread to avoid being washed away by tidal currents. Upon retrieval on days 1, 14, 30 and 60, they were immediately fixed in the field with 5% formalin.

In the laboratory, the meiofauna were rinsed from the samples with tap water through a 1 mm sieve to exclude macrofauna and debris, and retained on a 38 μ m sieve. They were then centrifuged three times at 6000 rpm with MgSO₄ (specific density 1.28) for 10 minutes. After centrifuging, the supernatant was poured onto a 38 μ m sieve, rinsed in tap water and stained with Rose Bengal. Meiofauna were identified under a dissecting microscope using Higgins and Thiel (1992) and enumerated.

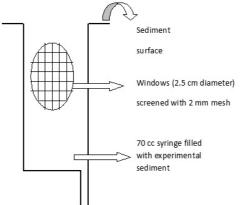


Figure 2. Diagram of the experimental sediment holders made from syringes (adapted from Zhou, 2001).

RESULTS

Thirteen meiofauna taxa were recorded; seven taxa in the seagrass leaf treatments, and four and five taxa were recorded in the mangrove leaf and control treatments respectively. Nine taxa were recorded in the field control treatments. Nematoda were the most abundant fauna and accounted for 99% of the meiofaunal densities in the field control, 95% in the experimental control and 93% in both the seagrass and mangrove leaf litter treatments. Oligochaeta comprised the second most abundant taxon, accounting for 5% of the total densities in the seagrass leaf litter treatments, 3% in the experimental control and mangrove leaf litter treatments and 1% in the field control. Halacaroidea occurred in relatively high numbers in the mangrove leaf litter treatment, accounting for 2% of the total meiofauna. The abundance of copepods was very low in the field control (<1%), and only comprised1% of the meiofauna in the experimental control, seagrass and mangrove leaf litter treatments. Figure 3 depicts the re-colonisation trends of the meiofauna, nematodes in particular, in the leaf litter treatments and revealed that meiofaunal re-colonisation commenced in all the experimental treatments one day postplacement.

control $(1209 \pm 198 \text{ individuals.7 cm}^2)$ on day one. The meiofaunal densities continued to increase during the course of the experiment, especially in the mangrove leaf litter. In fact, they surpassed those in the field control on day 30 (2071 \pm 958 individuals.7 cm⁻²), and remained higher than the field control to the end of the experiment, although they declined between days 30 and 60. As stated, nematodes accounted for most of this increase in the mangrove leaf litter treatment, attaining 2017 \pm 966 individuals.7 cm⁻² on day 30, surpassing that of the field control and remaining higher to the end of the experiment, although they reflected the aforementioned decline between days 30 and 60. The above trends in meiofaunal and nematode densities in the mangrove leaf litter treatment coincided with a low C:N ratio recorded on days 30 and 60 (Fig. 4).

A meiofaunal increase occurred in the experimental control up to day 14, after which they remained more or less constant. Meiofaunal densities in the seagrass treatment remained below those of the field control throughout the experiment.

The differences in the meiofaunal densities, particularly of nematodes, were significant (ANOVA df=2, F=19.511, p<0.05 and df = 2, F = 14.712, p<0.05 respectively).

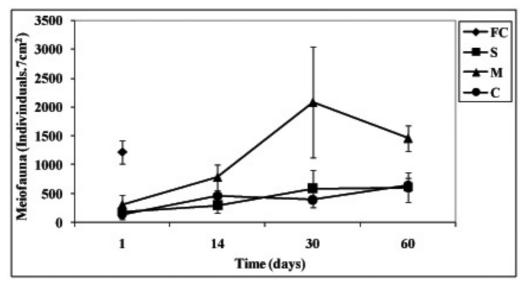


Figure 3. Colonisation rates expressed as densities (mean \pm SD) of a) meiofauna and b) nematodes during the experimental period (days). FC = field control, C = experimental control, S = seagrass leaf litter and M = mangrove leaf litter.

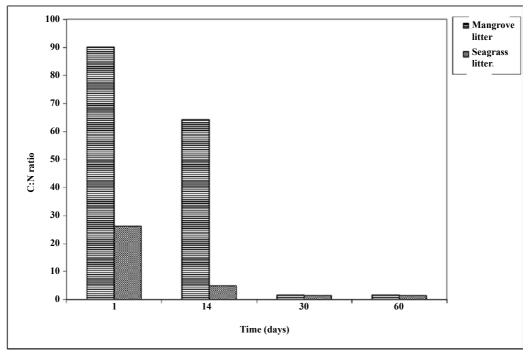


Figure 4. Variation in the C:N ratio over time (days) in the mangrove and seagrass leaf litter.

The re-colonisation rate on day one was higher in the organically enriched treatments (maximum 307 ± 160 individuals.7 cm²) compared to the organic-free control (128 ± 75 individuals.7 cm⁻²), the highest recolonisation being in mangrove leaf litter (307 ± 160 individuals.7 cm⁻²), which was nevertheless much less than the densities in the field

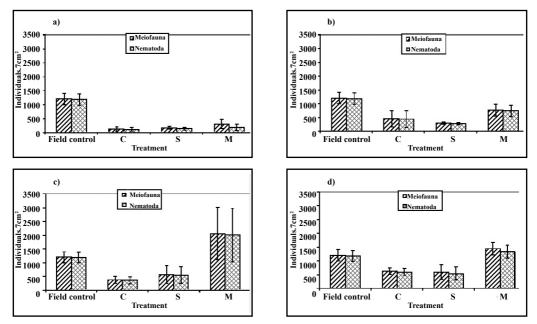


Figure 5. Densities of meiofauna and nematodes (mean \pm SD, n = 3) on a) day 1, b) day 14, c) day 30 and d) day 60 in the different treatments. FC = field controls, C = experimental controls, S = seagrass leaf litter and M = mangrove leaf litter.

between the leaf litter sources. A Tukey HSD test revealed no significant differences between the litter sources on day one (Fig. 5a) but, on days 14, 30 and 60 (Figs. 5b, 5c & 5d), the mangrove leaf litter treatment yielded significantly higher meiofaunal and nematode densities than the seagrass leaf litter and the controls (p < 0.05).

DISCUSSION

As outlined in the introduction, there is a paucity of information on the influence of different detrital sources on meiofaunal abundance and community composition in mangrove benthic ecosystems and no literature was found on field experiments examining the meiofaunal re-colonisation of such detritus. This field experiment was thus the first to investigate the influence of different sources of detritus on meiofauna within mangrove ecosystems. The results show that meiofaunal re-colonisation of mangrove sediments is affected by the availability of leaf litter since much higher densities were attained in its presence compared to the experimental controls. Additionally, meiofaunal re-colonisation within the Gazi mangrove was affected by the source of the leaf litter since mangrove leaves yielded higher recolonisation than seagrass leaves. Indeed, the meiofaunal densities became almost constant after day 14 within the control and seagrass leaf litter treatments

The fact that meiofauna re-colonised the experimental controls devoid of organic matter one day post-placement indicates that meiofauna will occupy any available space, even in the absence of a food source. However, meiofaunal densities in the experimental controls remained low throughout the experiment.

The meiofaunal densities in the experimental treatments increased with time, which is possibly related to the decomposition process and the associated microflora. This implies that decomposition enhanced the nutritional value of the mangrove detritus, thereby attracting more meiofauna, especially nematodes. Macrophyte decomposition and detritus recycling have been shown to be important in mangrove ecosystems (Lugo & Snedaker, 1974; Lee, 1995) and contribute much of the nutrition needed by grazers and filter feeders, while providing habitat for benthic fauna.

Although meiofaunal colonisation was observed one day after commencement of the experiment, the rate of colonisation of mangrove leaf litter was initially low, showing that there was a time lag before meiofauna could colonise the mangrove leaf litter and attain densities similar to the field controls. Alongi (1987) showed that the concentration of polyphenic acids in mangrove leaf litter, mainly tannins, is negatively correlated with the associated meiofauna densities as these substances reduce the palatability of mangrove detritus. According to Zucker (1983) and Robbins et al. (1987), hydrolysable tannins impart a noxious taste to detritus, increasing the acidity of the plant material, and precipitating the plant proteins and the gastrointestinal enzymes of the meiofauna. Thus, these substances interfere with the feeding of benthic herbivores and detritivores. However, the tannins appear to be rapidly lost during the initial days of mangrove litter decay (Robertson, 1988; Tietjen & Alongi, 1990). Similarly, Gee and Sommerfield (1997) showed that meiofaunal proliferation may be affected and controlled by changes in leaf litter chemistry during its decomposition, influencing the subsequent successional development of the microbial community. Thus, while tannins may have been responsible for the slow initial colonisation of the leaf litter in the present study, their disappearance may have increased the palatability of the detritus, promoting meiofaunal colonisation, particularly by nematodes. This increased attractiveness is supported by the decrease in the C:N ratio in the mangrove leaf litter, implying that the nutritional value of the detritus improved as the nitrogen content increased (Skov & Hartnoll, 2002).

Nematodes were preponderant in the meiofauanl community that colonised the experimental sediment and leaf litter. According to Riemann and Helmke (2002), nematodes are believed to release hydrolytic enzymes in mucus which, together with bacterial enzymes,

assist in the breakdown of the detritus. The hydrolysed products can be directly consumed by the nematodes, garnering nutrition from the detritus. This, together with a decrease in tannin concentration and the stimulation of microbial growth probably accounts for the observed increase in meiofaunal and nematode densities within the experiment, most notably in the mangrove leaf litter.

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Macrofauna Associated with the Sponge Neopetrosia exigua (Kirkpatrick, 1900) in Mauritius

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Keywords: *Neopetrosia exigua*, sponge, associated-fauna, species richness, Mauritius, Indian Ocean

Abstract — The macrofaunal community associated with the sponge *Neopetrosia exigua* (Kirkpatrick, 1900) was studied across a Mauritian lagoon. A total of 191 macrofauna belonging to 18 macro-invertebrate species were found in association with host sponges collected at depths of 1.4-2.7 m. Polychaetes and amphipods mostly inhabited the sponge canals whereas crabs and brittle stars were found at the base of the sponges. The most speciose taxon comprised Crustacea (61%, 11 spp.), followed by Polychaeta (33%, 6 spp.) and Echinodermata (6%, 1 sp.). The most dominant species was the polychaete *Haplosyllis djiboutiensis* (Gravier, 1900), comprising 71% of the specimens collected. There was, at best, moderately significant evidence that the number of macrofaunal species and individuals and their diversity index values were related to sponge volume and water depth. This sponge contributes to the maintenance of biodiversity in the lagoon by providing shelter and food for a number of invertebrates.

INTRODUCTION

Once described as "living hotels" by Pearse (1932), sponges are known to act as hosts for a number of micro and macro benthic organisms. They are an important source of biogenic structure for the settlement of epi-faunal and endo-faunal invertebrates in the marine ecosystem (Greene, 2008). According to Bascescu (1971), sponges constitute one of the richest and most interesting biotopes apart from tropical reefs.

The relationships between sponges and their endobionts can be of several types, including commensalism, predation, competition for space, mutualism and parasitism (Wulff, 2006). Past studies indicated that the most common macroinvertebrates associated with sponges included polychaetes, amphipods, decapods and molluscs (Wendt *et al.*, 1985; Çinar *et al.*, 2002; Schejter *et al.*, 2012). Other studies also indicated the high dominance of brittle stars (Ophiuroidae) on marine sponges (Çinar *et al.*, 2002; Henkel & Pawlik, 2011). Most of these organisms either live within the complex sponge canal system as endobionts or directly on the sponge surface as epibionts (Voultsiadou-Koukoura *et al.*, 1987; Ribeiro *et al.*, 2003). Sponges also provide reproduction sites for their endobionts, as well as nurseries for juvenile specimens, providing refuge from predators and a food supply for their associates (Westinga and Hoetjes, 1981; Wulff, 2006).

The endofaunal species composition and abundance can vary greatly relative to the characteristics of the host's environment (Greene, 2008). Klitgaard (1995) suggested that the majority of the fauna associated with sponges in temperate waters is composed of facultative species, while those in warm tropical waters are mostly obligate sponge associates. Size (Pearse, 1932), morphology (Koukouras et al., 1992), volume (Çinar et al., 2002; Ozcan & Katagan, 2011) and geographic location (Klitgaard, 1995) of the hosts can significantly influence the composition, diversity and abundance of their associated invertebrate fauna. Furthermore, environmental parameters such as depth (Pearse, 1950) and the habitat near sponges (Westinga and Hoetjes, 1981) can also affect the species composition of their associates.

Sponge-associated endofauna have been relatively well studied in temperate regions, e.g. in the Mediterranean Sea (Koukouras et al., 1985; Voultsiadou-Koukoura et al., 1987; Çinar et al., 2002), northeast Atlantic Ocean (Klitgaard, 1995) and northeast Pacific Ocean (Beaulieu, 2001). Fewer studies have been conducted to date in the tropical and subtropical regions, e.g. the Red Sea (Fishelson, 1962), the Caribbean region (Pearse, 1950; Westinga & Hoetjes, 1981) and the Great Barrier Reef (Skilleter et al., 2005). In the Indian Ocean, Abdo (2007) recorded some macrofaunal species on sponges in southwest Australia but these fauna have not been studied thus far in Mauritius

Previously known as *Xestospongia exigua*, *Neopetrosia exigua* (Kirkpatrick, 1900) is a branched, chocolate brown sponge commonly distributed in the Indo-Pacific region (Levi, 1998). The present study aimed to evaluate macrofauna inhabiting this sponge in a northern lagoon of Mauritius and to assess the relationship between this community, host size and depth.

METHODS

Study Site

The lagoon of Trou aux Biches is located on the north-west coast of Mauritius and is known for its recreational activities. It is one of the biggest lagoons in the country and has discontinuous fringing reefs. Its shoreline is partially rocky but it has an elongated sandy beach about 3 km long. The depth in the lagoon varies from 1.5-6 m at low tide and is shallowest in the south. The sponge *Neopetrosia exigua* is widely distributed within the lagoon and even dominates the benthos at some locations (Appadoo *et al.*, 2011).

Sampling and sorting

Ten sponge samples were collected by free diving at ten stations within the lagoon at 1-2.7 m depth (Table 1). GPS coordinates as well as the depths of stations were recorded. A zip-lock bag was carefully placed over targeted sponges to avoid escape of motile macrofauna, closed and the sponge was detached from its base with a knife. Samples were kept in their respective bags for a few hours to allow the associates to emerge with the progressive reduction of oxygen levels. The sponges were then cut into small sections of about 1-2 cm along the sponge canals and the fauna remaining inside were removed and sieved through a mesh of 1.0 mm. Water from the zip-lock bags was also filtered. Sponge volumes were determined using the water displacement method described by Scheiter et al. (2012). The endobionts were fixed in 10% formal-saline, sorted under a stereomicroscope and preserved in 70% ethanol. All endobionts were identified to the lowest taxonomic level possible and counted.

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Station	Latitude (S)	Longitude (E)	Depth (m)	Sponge volume (ml)	Total species (N)	Shannon Diversity Index (H')	Pielou's evenness (J')
1	20°02'10.8"	57°32'36.9"	1.40	55	2	0,5623	0,8113
2	20°02'08.3"	57°32'37.5"	1.70	30	2	0,5297	0,7642
3	20°02'05.7"	57°32'37.6"	1.70	47	3	0,3805	0,3464
4	20°02'03.4"	57°32'39.0"	1.60	28	3	0,2771	0,2522
5	20°01'59.6"	57°32'38.8"	1.50	33	2	0,6365	0,9183
6	20°01'52.8"	57°32'39.8"	2.00	65	2	0,1391	0,2006
7	20°01'48.2"	57°32'41.4"	1.80	10	4	1,3210	0,9528
8	20°01'44.8"	57°32'41.5"	2.10	30	3	0,3944	0,3590
9	20°01'42.0"	57°32'42.4"	2.30	60	6	1,6430	0,9172
10	20°01'37.4"	57°32'43.8"	2.70	70	11	1,2870	0,5367

Table 1. Location of sampling sites (Stations) for *Neopetrosia exigua* (Kirkpatrick, 1900) in Trou aux Biches, Mauritius, and the Shannon Diversity Index (H'), Pielou's evenness index (J') and total number of the associated macrofaunal species (N) obtained from the samples.

Data analysis

Statistical analyses were performed using STATISTICA 10 and PRIMER 6. Shapiro-Wilk tests were performed to ensure that all raw data were normally or near to normally distributed. Non-normal data were log(x)-transformed prior to parametric analyses. Shannon-Weaver's (H')Diversity and Pielou's (J') Evenness indices were estimated to assess the level of species diversity in the samples. The relationship between the macrofaunal communities (number of individuals and species, and the diversity and evenness indices) and sponge volume and depth were assessed using Pearson's correlation analysis. Multiple regressions (quadratic polynomial fit) were performed to assess the combined influence of depth and volume on the number of associates (species and individuals). Species associations in the area were determined using Bray-Curtis similarity analysis. Multi-Dimensional Scaling was performed to assess the macrofaunal species similarity between stations relative to environmental parameters (depth and sponge volume).

RESULTS

Faunistic analysis macrofaunal associates of *Neopetrosia exigua* in Trou aux Biches yielded a total of 191 specimens, belonging to 18 species in three taxa (Table 2). The most speciose taxon comprised Crustacea (11 species), followed by Polychaeta (six species) and Echinodermata (one species). The diversity and evenness indices of all samples irrespective of station were H'=1.29 and J'=0.44.

Polychaeta were the most individuals to the macrofauna (79%), followed by the Crustacea (16.3%) and Echinodermata (4.7%). The most abundant species was *Haplosyllis djiboutiensis* (Gravier, 1900), accounting for 71% of all the macrofauna collected. The other dominant species were a *Balanus* sp. and *Ophiactis savignyi* (Müller & Troschel, 1842).

The canal networks of the host sponges were inhabited by various organisms. Polychaetes (mostly *H. djiboutiensis*) were densely abundant in small canals, whereas the larger canals were mostly inhabited by Crustacea (several *Maera* spp.). Crabs (*Dromia dormia* and *Thalamitoides tridens*) and a brittle star (*O. savignyi*) were prevalent in the bases of the sponges.

The number of macrofaunal species and individuals associated with *N. exigua* were positively but weakly correlated (r = 0.45, p = 0.187 and r = 0.48, p = 0.160) with sponge volume (Fig. 1A, B) but the macrofaunal diversity and evenness indices were very weakly correlated (r = 0.10, p = 0.775 and r = -0.23, p = 0.518) with this parameter (Fig. 1C, D). The number of macrofaunal species yielded a relatively strong positive correlation (r = 0.85, p = 0.002) with water depth, and the number of macrofaunal individuals a

Table 2. Species associated with the Neopetrosia exigua and their abundance on this sponge in Trou aux Biches, Mauritius. ND – Not determined.

Taxa/Station No	1	2	3	4	5	6	7	8	9	10
Crustacea										
Maera serratipalma (Nagata, 1965)	-	-	-	-	-	-	-	-	1	-
Ampithoe sp.	-	-	1	-	-	-	-	-	-	1
Maera sp. 1	-	-	-	-	-	-	-	-	-	1
Maera sp. 2	-	-	-	-	-	-	3	-	-	1
Elasmopus sp.	-	-	-	-	-	-	-	1	-	-
Copepoda ND	-	-	-	-	-	-	-	-	-	1
Leptochelidae ND	-	2	-	-	-	-	2	-	1	-
Balanus sp.	2	7	-	-	2	-	-	1	-	-
Thalamitoides tridens (A Milne Edwards, 1869) (D)	-	-	-	-	-	1	-	-	-	1
Dromia dormia (Linnaeus, 1763)	-	2	-	-	-	-	2	-	1	-
Diogenes sp.	-	-	-	-	-	-	-	-	-	1
Polychaeta										
Polynoidae sp.	-	-	-	1	-	-	-	-	1	-
Haplosyllis djiboutiensis (Gravier, 1900)	-	-	19	30	4	31	1	18	3	3
Opisthosyllis brunnea (Langerhans, 1879)	-	-	1	-	-	-	2	-	-	2
Eunice sp.	-	-	-	-	-	-	-	-	-	1
Eunice antennata (Savigny in Lamark, 1818)	-	-	-	1	-	-	-	-	-	4
Dorvilleidae ND	-	-	-	-	-	-	-	-	-	1
Echinodermata										
Ophiactis savignyi (Müller and Troschel, 1842)	6	-	-	-	-	-	-	-	3	-
Total	8	9	21	32	6	32	8	20	10	4

moderately positive correlation (r = 0.57, p = 0.075) with this parameter (Fig. 1E, F). The macrofaunal diversity index was positively and moderately correlated (r = 0.54, p = 0.109) with water depth but the evenness index showed a very weak negative correlation (r = -0.15, p = 0.688) with this parameter (Fig. 1G, H).

The quadratic polynomial fit based on multiple regressions (Fig. 2) revealed a degree of interaction between the number of macrofaunal species and individuals with sponge depth and volume. The number of species was very variable at low depths where fewer species, on average, were present but their number was clearly higher in the larger sponges at greater depth. Conversely, small sponges (below 30-40 ml, irrespective of depth) and those at shallow depths (below ~1.6 m, irrespective of sponge size) had fewer associated fauna and these were less diverse. Thus, depth seemed more important than sponge volume in the regulation of the number of sponge-associated species.

Cluster analysis revealed that three major species associations occur in the area (Fig. 3). The first group comprised Stations 1 and 2 were not significantly distinguishable from each other but were characterised by a high abundance of the brittle star Ophiactis savignyi and the barnacle Balanus sp. The second group comprised five stations (3, 4, 5, 5)6 and 8) which manifested a high abundance of the polychaete Haplosyllis djiboutiensis. The last group comprised Stations 7 and 10 and was characterized by the presence of the crab Dromia dormia and the amphipod Maera sp. 2. MDS analysis (Fig. 4) revealed no influence of host size or depth on the groups of species associated with the host sponge. Thus, in spite of some evidence that total number of species and total number of individuals were influenced by sponge size and depth, the taxonomic composition of the associated communities did not appear to be related to these variables

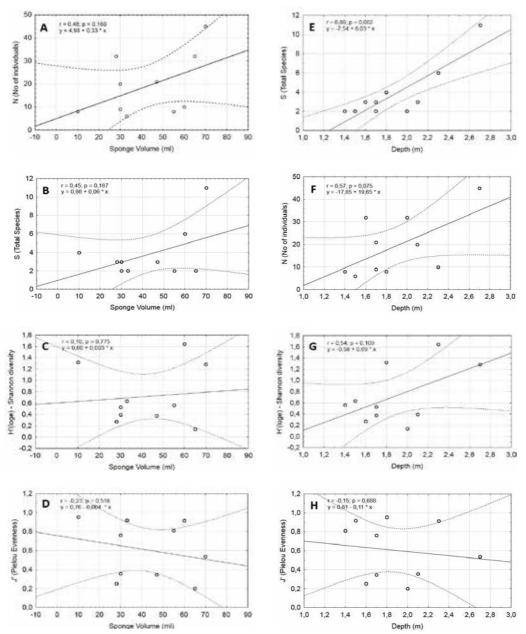


Figure 1. Correlations between the number of associated macrofaunal species, individuals, and their diversity and evenness indices versus *Neopetrosia exigua* size (A, B, C and D) and depth (E, F, G and H) in Trou aux Biches, Mauritius.

DISCUSSION

The sponge *Neopetrosia exigua* hosts a relatively low number of species of associated macrofauna in Trou aux Biches; only 18 species belonging to three invertebrate taxa were recorded. The endofauna associated with

sponges in the family Petrosiidae are known to be impoverished (Koukouras *et al.*, 1992) and a relatively low number of species were recorded associated with the sponge *Petrosia ficiformis* (Poirel, 1789). Crustaceans and polycheates were the most abundant groups associated with *N. exigua* in the present study.

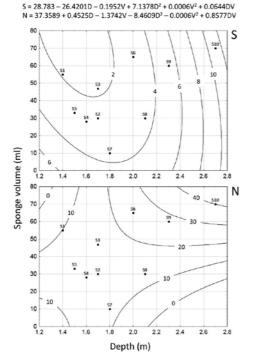


Figure 2. Response contours of quadratic polynomial fits of the number of associated macrofaunal species (S) and number of individuals (N) relative to *Neopetrosia exigua* size and depth. Collecting stations in Trou aux Biches, Mauritius, are marked as S1 - S10.

This observation is corroborated by several similar studies, since these taxa are known to be dominant associates in several sponge species, for example Mycale microsigmatosa (Ribeiro et al., 2003), Sarcotragus foetidus (Çinar et al., 2002), M. magellanica (Schejter et al., 2012) and Spheciospongia vesparia (Westinga & Hoetjes, 1981). Both crustaceans and polychaetes appear to favour the internal canals of sponges as refugia (Wulff, 2006) and detritus accumulated within the base of sponges provide these organisms with a source of food (Westinga & Hoetjes, 1981). The diversity of endofauna in sponges has been reported to be influenced by the host morphology (Koukouras et al., 1985; Skilleter et al., 2005). For instance, the small sponge *Clathria* (Thalysias) schoemus (de Laubenfels, 1936) harboured only five species in the Bahamas (Pearse, 1950), whereas large sponges with a complex canal system, such as Sarcotragus

foetidus (Schmidt, 1862) (cited as *S.muscarum*; Çinar *et al.*, 2002) and *Mycale (Aegogropila) magellanica* (Ridley, 1881) (Schejter *et al.*, 2012) were reported to have a rich associated fauna. *Neopetrosia exigua* has mostly small oscules <0.2 cm in diameter (Levi, 1998) and thus its morphological structure enables the ingress of only small organisms.

There was evidence that the number of species and individuals associated with the sponge was, to a degree, positively correlated with sponge volume, a finding that parallels those of Koukouras *et al.* (1992), Çinar *et al.* (2002) and Ribeiro *et al.* (2003). The volume of an individual sponge is generally an indication of the amount of space available within its canal systems, an important factor for its occupation by associated organisms (Duarte & Nalesso, 1996). A larger sponge thus usually has more space for these fauna.

Sponges are reported to have higher endobiont richness in shallow and warm water (Schejter et al., 2012). However, the number of species and individuals associated with N. exigua was found to be slightly higher at increased depth. This observation may be due to the greater size (Appadoo et al., 2011) and complexity of the sponges within the depths of the lagoon as they are known to exhibit more complex morphology in deeper environments (Bell et al., 2013). Moreover, the presence of corals and seagrasses (Daby, 2003) in slightly deeper water in the lagoon may also enhance the abundance and diversity of the associated macrofauna. Lower and more variable numbers of associated macrofauna at shallow depths in Trou aux Biches may reflect marginal and more stochastic settlement by these fauna in a less stable environment.

The high abundance of *Haplosyllis djiboutiensis* associated with the host sponge is notable as this species has been described as a parasite by Magino and Gaino (1998). With regard to the other polychaetes, previous work has suggested that those in the family Syllidae prefer cryptic habitats, creeping actively through canals and crevices of sponges and corals (Uebelacker, 1978). Syllids have also been reported to be the most diverse and abundant

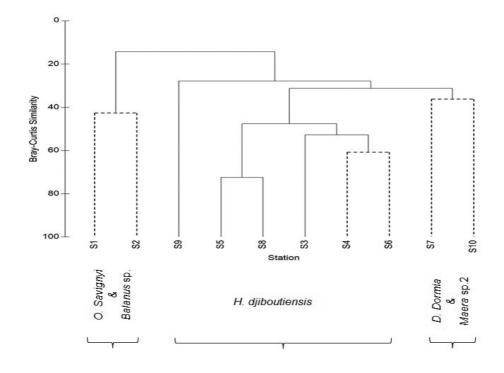


Figure 3. Similarity dendrogram of macrofaunal communities associated with *Neopetrosia exigua* at the sampling stations in Trou aux Biches, Mauritius (dashed lines indicate significantly similar groups).

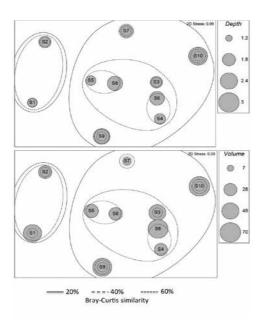


Figure 4. MDS of the macrofaunal communities associated with *Neopetrosia exigua* at the sampling stations in Trou aux Biches, Mauritius, relative to sponge size (volume, ml) and depth (m).

polychaetes in association with marine hosts such as sponges and corals (Çinar & Ergen, 1998). However, predation by the brittle star *Ophiactis savignyi* may explain the absence of polychaetes (including *H. djiboutiensis*) and amphipods at Station 1; despite it being detritivorous, many brittle stars usually feed on small organisms including polychaetes and crustaceans (Çinar *et al.*, 2002). It is a common associate of marine sponges (Mladenov & Emson, 1988) and has also been found within the sponges *S. foetidus* (Cinar *et al.*, 2002) and *M. microsigmatosa* (Ribeiro *et al.*, 2003). It usually occupies sponges for shelter, feeding and reproduction (Mladenov & Emson, 1988).

Similarly, the crab *Dromia dormia* may feed on polychaetes within sponges at Station 2, resulting in the absence of any polychaetes at this station. The same observation was made at Station 7, where only a few polychaetes were present in the sample containing *D*. *dormia*. This crab, also known as the sponge crab, usually carries sponges on its carapace for camouflage (McLay, 1993) and the relationship between the two organisms can be considered mutualistic.

A relatively low number of polychaetes and crustaceans were recorded in sponges containing specimens of the *Balanus* sp. (Stations 1, 2 and 5). All these barnacles were located at the external pores of the sponge canals, blocking internal access to the hosts. Westinga and Hoejtes (1981) suggested the likelihood that they use the waterflow in the sponge as a feeding aid, being filter feeders.

No clearly significant relationships emerged between the sponge macrofaunal asociations and the environmental variables measured in this study, i.e. sponge size and depth. Other factors must therefore also contribute to the heterogeneity of associated communities. Current patterns in the lagoon may influence the settlement of these organisms, as well as other factors such as the distribution of the different sediment types, detritus and the surrounding biodiversity. Notwithstanding the relatively low macrofaunal diversity found associated with N. exigua in the study, this sponge does contribute to the maintenance of some species such as the H. djiboutiensis within the region and constitutes an important benthic community within the lagoon of Trou aux Biches.

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Review

A Review on Kenyan Fisheries Research: 1970-2009

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Keywords: Marine fish resources; fisheries management; Kenya, artisanal fisheries, fishing methods

Abstract — Fish resources in Kenya have been exploited for centuries, mostly by artisanal fishers in inshore lagoons, on reefs and, occasionally, in deeper waters. Fish in Kenya, as in many other tropical coastal countries, constitute an important source of food and livelihood. Artisanal fisheries thus play a key role in food security and employment, and are seen as a means to poverty alleviation. We review research on the fisheries in Kenya and the usefulness of the results in fisheries management, considering information from 135 peer-reviewed publications, reports and grey literature on research undertaken over the past 40 years. Subjects covered ranged from fish surveys, species diversity and composition to marine protected areas. The research has been useful in guiding management for the sustainable use of these resources. Research gaps have been identified, emphasising the need for integrated management of Kenya's marine and coastal resources.

INTRODUCTION

Fishing in Kenya has been carried out for centuries and has been an important economic sector (Fisheries Department, 2012). Fish resources, especially reef fishes, have been exploited for many years, mostly by artisanal fishers, and constitute an important source of food and livelihood. The Fisheries Department of Kenya is vested with the management of fisheries resources in the country. The fisheries sector plays a major role in the economy of the country by providing food security, a source of employment and, hence, poverty alleviation (Fisheries Department, 2012). The annual marine fisheries production in Kenya is estimated at 7 000 tonnes, representing approximately 5% of the total catch in the country, but over 60% of the coastal and marine landings (Fisheries Department, 2012).

Information recording and reporting on marine fish resources in Kenya commenced in the 1950s (Martin, 1973) and research has, in more recent years, been conducted by various local and international research institutions and organizations. 'Frame Surveys' were conducted along the Kenyan coast by the Fisheries Department in 2004, 2006, 2008 and 2012 and are census-based, data being collected on all fishing vessels and gear (at all homeports and fishing sites) operating within a chosen context or stratum. They gather information on the number of fishers, landing sites, fishing gear and vessels, and further provide an opportunity to record supplementary information useful for management planning and implementation (e.g. fishing patterns and the seasonal use of fishing gear). They can also be used to

provide information on the socio-economics and demography of fishing communities (Stamatopoulos, 2002). Marine fisheries in Kenya are mainly artisanal, currently comprising an estimated 13 706 participants (Fisheries Department, 2012). There are 160 fish landing sites and about 3 090 fishing craft operating within the marine artisanal fisheries sector (Fisheries Department, 2012).

While fisheries research has been ongoing in Kenya for many years, more intensive research has only been conducted in recent years. The objective of this review was to assemble this information from publications and grey literature as a baseline for future reference. Apart from serving as a one-stop source on Kenyan fisheries, it is hoped that it will be used by researchers and students to identify areas for future research, and provide information on past trends for the purposes of comparison and emphasis.

METHODS

Information for the review was gathered from the Kenya Marine and Fisheries Research Institute (KMFRI) This included peer-reviewed publications, reports and grey literature accessioned in the KMFRI Library from 1970 to 2009 on or related to the marine fish resources in Kenya. Information on the Frame Surveys conducted by the Kenya Fisheries Department was also used. Several steps were involved in compiling the review, the first involving searching for the relevant records using the following keywords: fish resources; fish surveys; impacts of fishing; overfishing and overexploitation; fish yields and catches; catch per unit effort; fish species diversity and composition; fishing methods and destructive gear; Marine Protected Areas (MPAs); predation; fish seasonality; ornamental fisheries; by-catch; fishery and habitat degradation; reproductive biology of fish species; general biology of selected fish species; age and growth; diets; spawning aggregations and homing; pollution; threatened species: genetic studies: and fisheries management. A number of records were also identified through the Internet or other sources (grey literature, books, etc.). The second step involved screening and retrieving the relevant publications and reports for review. These were then assessed for eligibility and the various topics considered were rated from those most investigated to those least studied.

REVIEW

Overview

The amount of research undertaken on Kenyan fisheries within the topics searched is reflected in the number of references on these topics (Fig. 1). Most of the research has focused on fish species diversity and composition (40 references), followed by fishing gear and fish resources in MPAs (both with 28 references), then management and yields (both with 22 references). Areas least studied included ornamental fisheries (1), habitat degradation (2), and spawning aggregations and homing (3).

A total of 207 publications were sourced from the various databases but, after screening for duplication or relevance, these were reduced to 135. The relevant publications were then reviewed under the 18 topics that follow. Note that some of the publications and reports fall under more than one topic.

Fish surveys

A number of fish resource surveys have been conducted in Kenyan waters, mainly within Food and Agriculture Organization of United Nations (FAO) projects. The first FAO survey off Malindi Bay was undertaken in 1958 and this was repeated in 1966. From these, the FAO reported that the annual catch was about 5 000 tonnes and recommended mechanization of the inshore craft with their gradual replacement by small seagoing vessels which could operate outside the reef (Martin, 1973). Bottom trawl surveys in inshore waters were conducted in the 1960s using the Kenyan research vessels Shakwe, Menika II and Manihine and, in 1964 and 1965, with commercial trawlers. Nansen surveys conducted in 1980-83 (Mbuga, 1984) between 10-700 m investigated the abundance and distribution of fish acoustically and by trawling. The biomass estimate was 18 000-

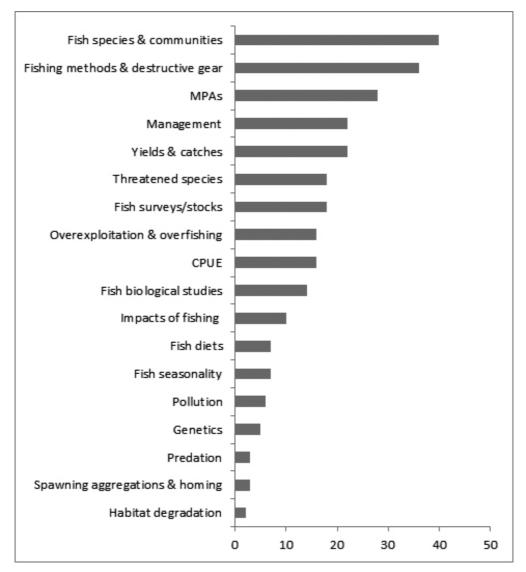


Figure 1. Research topics and the number of references on these topics considered in this review.

32 000 tonnes (Mbuga, 1984; Iversen, 1984), with a potential offshore yield of 10 000 tonnes (Mbuga, 1984). The total potential of marine fish production was estimated to be 150 000 tonnes yr^{1} (Iversen & Myklevoll, 1984).

The Frame Surveys (2004, 2006, 2008, 2012) have also been useful in providing an overview of fisheries activities along the Kenyan coast and future surveys will be important for the management of the Kenyan marine fisheries. They have generated data and information on the status of the marine

fisheries. The surveys by research vessels yielded the aforementioned potential marine fish production and yield (Iversen & Myklevoll, 1984), and form a good reference point for ongoing regional fish surveys and stock assessments. Both the Frame and fish surveys, if conducted regularly, will be important in tracking changes in the marine fisheries and provide indicators for management actions and options. Changes in fishing gear and fishing areas can be traced over time and will be crucial in future management.

Yields and catches

Annual marine catches in Kenya have fluctuated between 4 000 and 10 000 tonnes over the last two decades, with some areas reporting overfishing (Kamau et al., 2009). Some estimates of the fish landed annually have been greater, viz. 16 000 tonnes (Tuda et al., 2008). The status of fish catches and landings in Kenva has been assessed (Oduor, 1984) and analysis of long-term trends in coral reef fish catches have revealed that Kenyan reefs yield an estimated 2-4 tonnes km⁻² yr⁻¹ of demersal fish (Kaunda-Arara et al., 2003). The fish yield on Kilifi reef during 1982–1984, which is about 4 km2 in extent, was found to be 5.07-12.9 tonnes km⁻², the mean catch being 8.8 tonnes km-2 yr⁻¹ (Nzioka, 1990). Studies have indicated that habitat protection in reserves can underpin fish productivity and, depending on its effects on fish movements, augment catches (Rodwell et al., 2003).

Catch-per-unit-effort

Catch-per-unit-effort (CPUE) - also called catch rate - is considered the single most useful index for long-term monitoring of a fishery (Stamatopoulos, 2002). Various studies have incorporated it in the assessment of fisheries and it was demonstrated that the CPUE of most species improved in traditional basket (Dema) trap fisheries adjacent to protected reefs in Kenya's coastal National Parks (Kaunda-Arara & Rose, 2004). A study on the influence of the 1998 coral bleaching and mortality event on coral reef ecosystems and fisheries in southern Kenya revealed a decline in total fish catches and CPUE, combined with an increase in effort, suggestive of overexploitation (McClanahan et al., 2002a; Maina et al., 2008a). It has also been observed in other studies that sites where illegal beach seining was excluded through active gear management, yielded increased catches and CPUE (McClanahan et al., 2008). For example, two landing sites at Diani where beach seining was prohibited for over 20 years yielded the highest per fisher catches, these being 13% greater than at sites where such fishing is allowed (McClanahan

& Mangi, 2001). CPUE data collected and analysed in other studies (Mwatha & Orembo, 1998, Munywoki *et al.*, 2008; Okemwa *et al.*, 2008) have provided valuable results for the management of fisheries, especially in gear and effort regulation (Stamatopoulos, 2002).

Species diversity and composition

Of the 736 marine fish species recorded in Kenva according to FishBase (www.fishbase. org), 121 species are exploited commercially (pers. comm. Fisheries Department), 193 for ornamental aquaria (Okemwa et al., 2009) and 26 are threatened. The earliest fish checklists were compiled on the south bank of Kilifi Creek (Bock, 1975) and in the lagoon of Diani (Bock, 1972). In a fisheries survey of Kilifi Creek, the major fish groups that were harvested were Siganidae, Scaridae, Plectorhynchidae, Scombridae, Lutjanidae, Serranidae, Carangidae, Sphyraenidae and Caesionidae (Nzioka, 1990). A more recent survey of the fish fauna in the creek yielded 63 finfish species (Sigana et al., 2009).

An assessment of Kenyan coral reef lagoon fishes has revealed a consistent and considerable reduction in the population density and species richness of five families (Acanthuridae, Balistidae, Chaetodontidae, Pomacanthidae, and Scaridae; McClanahan, 1994a). However, protected areas have a higher abundance and species richness of commercially important triggerfish, surgeonfish, and parrotfish (McClanahan & Arthur, 2001). Studies on spillover effects have shown that this is greatest for the dominant fisheries species, viz. moderately active species like rabbitfish (Siganidae; herbivores), emperors (Lethrinidae; carnivores) and surgeonfish (Acanthuridae; herbivores) which had instantaneous emigration rates from the protected area to the fishing grounds of approximately 0.5 (McClanahan & Mangi, 2000).

Studies on the different Kenyan marine habitats have been useful to identify the fish species and communities inhabiting them (McClanahan *et al.*, 1999a, 2002b; Huxham *et al.*, 2008). Five taxa accounted for approximately 70% of the total fish abundance amongst juvenile fish communities associated with natural, degraded and replanted Sonneratia alba mangroves in Gazi Bay, the majority (65%) being reef associates, and the Gobidae and Gerres oyena being dominant (Crona & Rönnbäck, 2007). A total of 128 teleost fish species belonging to 50 families were identified in an earlier study of the bay (Kimani et al., 1996). Then the families Gerreidae. Atherinidae and Clupeidae accounted for 78.5% of the fish population and, of the species found, 44% were associated with coral reefs (Kimani et al., 1996). In another study, a total of 3601 fishes (>95% juveniles) were caught, comprising 75 species in 40 families (Little et al., 1988).

In Mida Creek further north, the most common fish landed included Siganidae, Lethrinidae, Lutjanidae, Scaridae and Nemipteridae, comprising ~80% of the catch (Mwatha & Orembo, 1998). In the mangrove area of Tudor Creek at Mombasa, 83 species of teleost fish were collected and ~90% of these were juveniles (Little *et al.*, 1988).

Approximately 70% of the fish caught for the marine aquarium industry belong to four families, viz. the Pomacentridae (damselfish), Labridae (wrasses), Acanthuridae (surgeonfish) and Gobiidae (gobies) (Okemwa *et al.*, 2009). Ten species made up 58% of the harvest, of which two species, *Amphiprion allardi* (10%) and *Centropyge acanthops* (9%), were the most important (Okemwa *et al.*, 2009). Overall, these results show that the Kenyan coast is rich in fish species, particularly in protected areas.

Seasonality

Higher fish catches are recorded during the dry and calm northeast monsoon season along the Kenyan coast (Nzioka, 1990; Sigana *et al.*, 2009; Okemwa *et al.*, 2008) and it has been established that fishing activities follow the lunar cycle which affects tidal fluctuations that determine the daily fishing times (Otieno *et al.*, 2001). Fishing activities are limited during the southeast monsoon period when sea conditions are rough (Nzioka, 1990).

Spawning aggregations and homing

About 24 fish species have been reported to form spawning aggregations in Kenya (Jan et al., 2008) and these have been studied in some species including: Siganus sutor; Lutjanus sanguineus, L. gibbus, L. bohar, L. argentimaculatus, Epinephelus fuscoguttatus, Mulloidichthyes vanicolensis and Plectorhinchus spp. (Maina et al., 2008b). Other studies that have investigated reef fish spawning aggregations have been conducted by Nzioka (1981b), Ntiba and Jaccarini (1990) and Jan et al., (2008). Reef fishes spawn during the north-east monsoon period (Novemebr-April) (Jan et al., 2008), while other species spawn in the two monsoon seasons (Nzioka, 1979; Ntiba & Jaccarini, 1990). The status of these spawning aggregations is poorly known and they have not been properly monitored in Kenya (Jan et al, 2008). Very few occur in MPAs (Jan et al., 2008) and, because of this, they are not adequately protected and their management should be complemented by catch and effort regulations (Jan et al., 2008). Marine protected areas have particular conservation potential for species (e.g. groupers) that have homing behaviour and establish home ranges (Kaunda-Arara & Rose, 2003). However, homing and site fidelity has only been studied in the greasy grouper, Epinephelus tauvina (Kaunda-Arara & Rose, 2003). Home ranges were found to be negatively correlated with size in this species, suggesting an ontogenetic shift in home range development (Kaunda-Arara & Rose, 2003).

Biological studies

A total of 45 species of marine fish have been studied in terms of their biology in Kenya (Table 1). These studies have included: estimates of the growth and mortality of the grunt (*Pomadasys opercularis*), thumbprint monocle bream (*Scolopsis bimaculatus*), spotted sicklefish (*Drepane punctatus*) and rabbitfish (*Siganus sutor*) (de Souza, 1986); the ecology and exploitation of yellowfin Tuna, Thunnus albacares (Hemphill, 1995);

Species/Genera	Biology	Diet	Behaviour
1. Lutjanus fulviflamma			
2. Pomadasys opercularis			
3. Scolopsis bimaculatus			
4. Drepane punctata			
5. Siganus sutor			
6. Lethrinus harak			
7. Thunnus albacares			
8. Plectorhincus spp.			
9. Sphaeramia orbicularis			
10. Istiophorus platypterus			
11. Anyperodon			
12. Cephalopholis			
13. Dermatolepis			
14. Epinephelus			
15. Plectropomus			
16. Variola			
17. Leptoscarus vaigiensis			
18. Epinephelus tauvina			
19. Sardinella gibbosa			
20. Atherinomorous lacunosus			
21. Pellona ditchella			
22. Spratelloides delicatilus			
23. Gerres oyena			
24. Secutor insidiator			
25. Leiognathus equula			
26. Selar crumenopthalmus			
27. Herklotsichthys quadrimaculatus			
28. Stolephorus indicus			
29. Atherinomorus duodecimalis			
30. Apogon thermalis			
31. Fowleria aurita			
32. Paramonacanthus barnardi			
33. Mulloides flavolineatus			
34. Lutjanus argentimaculatus			
35. Gerres acinaces			
36. Bothus myriaster			
37. Fistularia commersonii			
38. Sphyraena barracuda			
39. Plotosus lineatus			
40. Cheilio inermis			
41. Apogon fragilis			
42. Apogon nigripes			
43. Lethrinus nebulosus			
44. Parascorpaena mossambica			
45. Scarus sordidus			

Table 1. List of marine fish species/genera studied in Kenyan coastal waters and the aspects considered.

the biology and fishery of *Plectorhinchus* spp. (Murage & Mavuti, 2001); aspects of the biology and feeding ecology of the orbiculate cardinal fish, Sphaeramia orbicularis (Mees et al., 1999), the reef fish, Scolopsis bimaculatus (Nzioka, 1981a, 1988); the sailfish, Istiophorus platypterus (Williams, 1970); some aspects of the biology and fishery of six genera of groupers (Teleostei: Serranidae), viz. Anyperodon, Cephalopholis, Dermatolepis, Epinephelus, Plectropomus and Variola (Agembe, 2008); and the morphometric relationship and condition factor of Siganus stellatus, S. canaliculatus and S. sutor (Wambiji et al., 2008).

The reproductive biology of some fish species has also been covered in several studies, including Lutjanus fulviflamma (Kaunda-Arara & Ntiba, 1997), Lethrinus harak (Kulmiye, 2002) and S. sutor (de Souza, 1988; Ntiba & Jaccarini, 1990, 1992). Other biological studies include the age and growth of S. sutor (Ntiba & Jaccarini, 1988), and the growth and survival rates of exploited coral reef fishes: the whitespotted rabbitfish, S. sutor, emperors (Lethrinus spp.), the orangestriped triggerfish, Balistapus undulates, sky emperor, Lethrinus the mahsena (Kaunda-Arara & Rose, 2006) and Scolopsis bimaculatus (Nzioka, 1988).

Diet

Information on the diets of fish is important in bionomic studies and in investigations of ecosystem energetics (Mavuti et al, 2004) and, for example, that of Sardinella gibbosa and Atherinomorous lacunosus has been elaborated (Nyunja et al., 2002). Eight common fish species in Mtwapa Creek, S. gibbosa, Pellona ditchella, Spratelloides delicatilus, Atherinomorous lacunosus, Gerres oyena, Secutor insidiator, Leiognathus equula, were shown to consume mostly copepods (Mavuti et al., 2004). Their feeding niches overlapped, revealing flexibility in their diets (Mavuti et al., 2004). The diets of various juvenile fish in Kenya have been revealed to comprise mainly plankton and benthos (Nyunja & Mavuti, 2001; De Troch, 1998; Wakwabi, 1996).

investigation of the trophic An organisation of the fish fauna in Gazi Bay revealed that they fall into four guilds: omnivores, piscivores, zooplanktivores and benthic carnivores (Wakwabi, 1999). Fourteen fish species abundant in beach seine catches from seagrass beds in the area (Herklotsichthys quadrimaculatus, **Stolephorus** indicus. Atherinomorus duodecimalis, Apogon thermalis, Fowleria aurita, Paramonacanthus barmardi, Mulloides flavolineatus, Lutjanus fulviflamma, L. argentimaculatus, Gerres acinaces, Bothus myriaster, Fistularia commersonii, Sphyraena barracuda and Plotosus lineatus) fell into only three trophic guilds: planktivores, benthivores and piscivores, and benthivores were dominant (De Troch, 1998).

Genetics

Molecular genetic techniques offer the ability to identify and delineate fish stock structure where it may not be apparent from phenotypic or behavioural characteristics. However, genetic studies on Kenyan marine fishes have been very limited, focusing mostly on freshwater species (Abila et al., 2004). The few genetic studies on marine fishes include the population genetic structure of Lutjanus fulviflamma (Dorenbosch et al., 2006), in which no clear relationship between genetic distance and geographic distance between populations was found (Dorenbosch et al., 2006). This suggests that populations of Lutjanus fulviflamma have an open structure and are possibly genetically connected on a larger geographic scale in the western Indian Ocean (Dorenbosch et al., 2006). The genetics of coelacanths have also been considered (Okada et al., 2007), revealing that the Kenyan coelacanth may be a member of an undiscovered population between Tanzania and Kenya (Okada et al., 2007).

Fishing methods and destructive fishing gear

Various types of fishing gear are used to fish along the Kenyan coast. These include longlines, hand-lines, trolling lines, traps (fence and basket), mono- and multi-filament gill nets (mesh size ranging from <63 to >250 mm), seine nets, beach seines, cast nets, trawl nets, ring nets, scoop nets, trammel nets prawn seines, spearguns/harpoons (Fisheries Department, 2012; Mbuga, 1984) and some traditional gear (Mwatha & Orembo 1998; Ochiewo 2004, 2008). The different fishing methods used on the Kenyan coast and the targeted catch are listed in Table 2.

The use of these gear, fishing techniques and destructive gear have been extensively studied by Crabbe and McClanahan (2003), Crona (2006), Cros and McClanahan (2003), Fulanda *et al.* (2009), Glaesel (2000), Kiszka *et al.* (2009), Mangi (2006), Mangi *et al.* (2007), McClanahan (2007), McClanahan *et al.* (1997, 2008,2005), McClanahan and Mangi (2001), McClanahan and Obura (1996), Mwaura *et al.* (2001), Tunje and Hoorweg (2003) and Samoilys (1988). Some of these studies (Glaesel 2000; Mangi 2006; Mangi *et al.*, 2007) suggest that high levels of fishing effort coupled with the use of destructive gear types intensify the effects of overfishing.

Despite these studies, more are needed to ascertain the effects of each gear (especially those that are prohibited e.g. spearguns and beach seines which are still used in some areas), as well as the effects of new fishing techniques which need investigation before they are introduced. Management action is also needed based on recommendations proposed in some of the studies such as:

- 1. The need for enabling and enforcement by managers to achieve high user compliance (McClanahan *et al.* 2005, 2007).
- 2. Redress of poverty and the issue of phasing out destructive fishing gear use (McClanahan *et al.*, 2005)
- 3. Investment geared towards the previous point should be combined with support for and enhancement of existing local ecological knowledge (Crona, 2006).
- 4. The provision of credit facilities for fishers to purchase authorized gear and compensation for gear that has been declared illegal, allied with facilitation and strengthening of Fishers' cooperative societies or Community Based Organizations (Mangi *et al.* 2007).

Capture method	Resources targeted				
Basket traps	Siganidae, Scaridae, Lethrinidae				
Fence traps	Clupeidae, and other shore swimming fish				
Handlines/Hook and line	Lethrinidae, Lutjanidae, Serranidae, Carangidae, Scombridae				
Trolling	Scombridae, Sphyraenidae, Coryphaenidae, Istiophoridae				
Longlining	Scombridae, Carcharhinidae, Xiphiidae, Istiophoridae				
Spearguns	Scaridae, Lutjanidae, Serranidae, Siganidae,				
Spears and harpoons	Octopoda, Myliobatidae, Muraenidae				
Gillnets (stationary)	Carangidae, Scombridae, Belonidae, Hemiramphidae,				
	Lethrinidae, Siganidae, Myliobatidae, Panulirus				
Gillnets (drifting)	Carcharhinidae, Scombridae,				
Monofilament gillnets	Hemiramphidae, Mugilidae				
Ringnets	Carangidae, Scombridae, Sphyraenidae, Lutjanidae, Clupeidae,				
-	Engraulidae				
Prawn seines	Penaeid prawns				
Cast nets	Clupeidae, Engraulidae, Gerreidae, Penaeid prawns				
Beach seines	Scaridae, Siganidae, Lethrinidae, Atherinidae, Hemiramphidae				
Reef seines	Scaridae, Siganidae, Lethrinidae, Atherinidae, Hemiramphidae				
Scoopnets/handnets	Mugilidae, Clupeidae, Penaeid, Panulirus				
Mosquito nets	Clupeidae, Engraulidae, Labridae, Lethrinidae, Lutjanidae				
Trawling	Penaeid prawns				

Table 2. Table 2. Fishing methods used on the Kenyan coast and the resources targeted (adapted from Samoilys *et al.*, 2010)

5. The inclusion of local fishermen in decision making on fisheries management and the provision of information on the benefits of appropriate conservation and management that result in higher fish yields (Tunje & Hoorweg, 2003).

Impacts of fishing

The effects of fishing relative to levels of protection and substratum complexity have been investigated on coral reef lagoon fish (McClanahan, 1994a, 1997a; McClanahan et al., 1999b; Watson & Ormond, 1994), as well as the effects of fishing and overfishing, mainly on reef fishes (Jennings & Polunin, 1996; McClanahan, 1995a; McClanahan et al., 1994; Watson & Ormond, 1994), and the factors that influence fish catches on Kenya's coral reefs (Mangi & Roberts, 2007). Several factors, including levels of fishing, protection from fishing and characteristics of reef habitat, were examined to determine the effect of these factors on the ecology of fish communities (McClanahan & Arthur, 2001). The number of fishers and live coral cover proved to be the strongest factors that determine total catches (Mangi & Roberts,

2007). The findings also showed that heavy fishing results in increased sea urchin abundance and algal turf cover, and reduced hard coral and coralline algal cover (McClanahan & Arthur, 2001). Furthermore, protected areas had greater species richness and higher abundances of some commercially important fish (ibid.).

Goñi (1998) provided an overview of the wide ecosystem effects of fishing, and the potential direct and indirect effects of the main fisheries of the world. The consequences of fishing on reef areas are reductions in coral cover, habitat and refuge for both fish and their food, and reef productivity (McClanahan, 1996). The study revealed the need for protected areas, as well as the areas that need protection, with continuous monitoring, to improve fish yields. Changes in fish populations affect reefs, since fish play important roles in reef ecology, and overfished reefs have fewer fish that are smaller. Areas which have become degraded may require restoration to achieve recovery but there have been few studies on the recovery of fish populations from heavy fishing (e.g. McClanahan, 1997b).

Habitat degradation

Loss of biodiversity, habitat degradation and the modification of mangrove and coral reef ecosystems have been identified as major concerns in Kenyan coastal areas. Anthropogenic pressures arise from overfishing and fishing-related damage, urbanization and tourism development, agriculture and industry, and damming for hydropower (Matlock, 2008). These activities alter and destroy coastal habitats with implications for marine fisheries (Brakel, 1981). Marine habitats are also damaged by natural catastrophes but, if this happens, they almost always recover (Palumbi et al., 2008). However, anthropogenic impacts are often the cause of permanent damage (Palumbi et al., 2008). Regulation of development in coastal areas and in habitat use plays an important role in the protection of fish spawning and breeding areas, their nursery grounds, and refugia (Bilkovic & Roggero, 2008). A clean environment is also important for a healthy fishery (Government of Kenya, 2009). An integrated approach to management is necessary to introduce improvements in the system with minimal and gradual changes to the activities of the human users (Government of Kenya, 2009).

Pollution

The marine environment in East Africa does not seem to be severely polluted and may be considered 'clean' when compared with the seas receiving wastes from more industrialized societies (Bliss-Guest, 1983). However, other studies have concluded that East African coral reefs are presently heavily used by fishermen and tourists, and that they experience pollution (McClanahan & Obura, 1996). Several sectors contribute to this pollution in Kenya, including coastal development, agriculture, processing industries, mining, transportation and energy (Government of Kenya, 2009). Oil spills from shipping accidents and hazardous waste from petroleum refineries and shipping activities also pose threats to the coastal and marine environment (Government of Kenya, 2009). Studies on heavy metal distribution

and enrichment in Port Reitz Creek, Mombasa (Kamau, 2002) showed that fluvial input to it introduced Cd, Cu, Fe and Zn, but some Cd and Zn were also of anthropogenic origin. Other surveys have been conducted on heavy metal pollutants in sediments and fish in Port Reitz, Mtwapa and Shirazi (Muohi *et al.*, 2001), and on Cd and Pb in water, sediments and selected fish species in Mombasa (Mwashote, 2002). These revealed that the levels of Pb and Cd were elevated in sediments and in some fish species, especially during the rainy season, but were generally within acceptable limits according to the FAO standards in the fish species that were analysed (Mwashote, 2002).

Such pollution studies are important in identifying hot spots and areas prone to pollution. They are important in fisheries management, especially when considering that the fish resources are harvested for human consumption, some for export.

Marine Protected Areas

Various studies related to fisheries have been conducted in Kenyan Marine Protected Areas (MPAs). They have focused largely on the role of the MPAs in enhancing local fisheries through the emigration or spill-over of recruits, the recovery of reef fish populations, and comparisons between protected and unprotected areas (Cros & McClanahan, 2003; Eklöfl et al., 2009; Kaunda-Arara et al., 2009; McClanahan, 2007, 2008b; McClanahan et al., 1999b 2002b, 2006, 2007; McClanahan & Arthur, 2001; McClanahan & Graham, 2005; McClanahan & Kaunda-Arara 1996; McClanahan & Mangi, 2000, 2001; McClanahan & Shaffir, 1990; Mwatha & Orembo, 1998; Munga et al., 2010; Rodwell et al., 2003; Watson et al., 1997; Watson & Ormond, 1994).

Results of this research suggest that MPAs provide refugia for fish (Rodwell *et al.*, 2003) and potentially protect and increase fish stocks for spawning, leading to the aforementioned spill-over. For example, the Mombasa MPA increased the catch per unit effort and per unit area adjacent to the park, decreased variation in the catches, and provided some spill-over of adults to the adjacent fishing ground (McClanahan & Kaunda-Arara 1996; McClanahan & Mangi, 2000). The catch per fisher increased by up to 75% (McClanahan & Mangi, 2000) and unfished sites had up to ten times more fish than fished areas (Watson & Ormond, 1994). However, it was suggested that reserves needed to be older than ten years before they sustained the full diversity of fishes (McClanahan & Arthur, 2001).

Threatened species

The Kenyan coast, being rich in biodiversity, has some fish resources that have become threatened, including species such as the whale shark. Conservation efforts and studies on the distribution and abundance of the latter were undertaken by the East African Whale Shark Trust in Kenya (Bassen, 2007). Rare fish such as the coelacanth may also be threatened. An inventory of all known specimens of Latimeria chalumnae has thus been compiled (Bruton & Coutouvidis, 1991), as well as a bibliography (Bruton et al., 1991), but the first specimen was only captured in Kenya in 2001 (De Vos and Oyugi, 2002). The genetic variation between individuals from different locations was studied to determine relatedness among east African coelacanths, and it was shown that this is unexpectedly low (Schartl et al., 2005). There has been little research on threatened species beyond this and more studies are needed

Management

Open-access fishing has been practiced since time immemorial in Kenya and is currently causing excessive fishing effort. The Kenyan fisheries and their management have been described by various authors, with management proposals aimed at maximizing fish production at a sustainable level, a reduction in post-harvest losses and support for local fisheries management (Allela, 1984; Barabara *et al.*, 2008; Brakel, 1981; Crabbe & McClanahan, 2005; Gitonga & Achoki, 2003; Mangi, 2006; McClanahan *et al.*, 1997, 1999, 2006, 2008, 2009; Munywoki *et al.*, 2008; Omondi, 1995; Oluoch & Obura, 2008; Samoilys, 1988; SWIOFC, 2006). Some of the strategies and proposals for sustainable management of the fish resources in Kenya include collaborative fisheries management (Gitonga & Achoki, 2003) coupled with large, permanent closed areas to sustain ecosystem function and the associated fisheries, and protect sensitive species from overfishing (McClanahan *et al.* 2006).

DISCUSSION

This review covers the period from 1960 to 2009. Several regional and national projects were undertaken subsequent to this period or were ongoing at the time of writing, e.g. the South West Indian Ocean Fisheries Project (SWIOFP) and Kenya Coastal Development Project (KCDP); these have further addressed fisheries-related issues. While it is possible that more studies have been undertaken than those reviewed here, this article nevertheless provides a general picture of the status of Kenyan fisheries research.

Regular frame and fish surveys are proving important in tracking changes in the Kenyan marine fisheries and providing indicators for management actions and options. Changes in fishing gear and fishing areas are being tracked through these surveys, matters crucial for the management of the fisheries. Studies on fish yields have focused on different areas of the Kenyan coast, reporting varying vields depending on area, season and fishing pressure. It must be noted that estimates of Maximum Sustainable Yield (MSY) are lacking, even though they are important in fisheries management as they provide a means of establishing sustainable targets (Garcia et al., 1989). Fish catch rates according to boat and gear categories, often combined with data on fish size at capture, permit a large number of analyses related to gear selectivity, provide indices of exploitation and monitor economic efficiency (Stamatopoulos, 2002), all these being important indicators of fisheries management.

It is important that research plays a role in informing management regarding the various strategies for the management of marine resources. Different departments are involved in fisheries planning and management (e.g. fishing, tourism, MPAs, the port and maritime authorities, development) and need to liaise in accomplishing their task. Changes in management should be done in a manner that results in improvements to the system with minimal or gradual changes in the activities of the human users. These changes in management involve the temporal and spatial regulation of fishing, using different fishing gear and, possibly, the provision of alternatives to fishing. Such changes should increase the economic returns from fishing without damaging the ecosystem. In this regard, co-management would give people more control over their resources for a more secure living (Barabara et al., 2008), an approach that needs to be strengthened on the Kenyan coast. It is also essential that fisheries managers plan for change in today's rapidly changing environment rather than attempt to regulate or prevent such change.

Studies on fish species diversity, community structure and general biology have been conducted in a number of areas along the Kenyan coast, but only on a fraction of the number of marine species (736) reported in FishBase. Investigations of fish diets are also needed to understand the trophic dynamics and fisheries interactions in the ecosystem. Only one study has been undertaken on homing behaviour (Kaunda-Arara & Rose, 2003), even though such research is important to determine the likelihood of sustaining locally reproducing populations to restock adjacent areas (Kaunda-Arara & Rose, 2003); in addition such studies can be used to guide management on areas in need of protection.

Some studies have been conducted on destructive fishing gear (Crabbe & McClanahan, 2005; Crona, 2006; Cros & McClanahan, 2003; Fulanda *et al.*, 2009; Glaesel, 2000; Kiszka *et al.*, 2009; Mangi, 2006; Mangi *et al.*, 2007; McClanahan, 2007; McClanahan *et al.*, 1997, 2008, 2005; McClanahan & Mangi, 2001; McClanahan & Obura, 1996; Mwaura et al., 2001; Tunje & Hoorweg, 2003; Samoilys, 1988), but more studies are needed to ascertain the deleterious effects of each type of gear. Overfishing and overexploitation and the effects these have on local communities and the ecosystem have been reported in several areas (e.g. Hoorweg et al. 2009; McClanahan, 1994b; McClanahan et al., 2000; Mörk et al., 2009) and reveal the need for protected areas. The latter can vary from zonation to integrated management or closure to promote sustainability and health in the protected ecosystems. They are important in achieving sustainability in fisheries, since they allow enough fish to grow to maturity and produce larvae that will recruit to areas outside the MPAs. They also provide baseline information on what an unfished area should be like, and demonstrate the fishery benefits of MPAs to local communities. While they provide a useful management option, they should not be used in isolation (Jan et al., 2008; Munga et al., 2010); local communities must be included in the planning, design, establishment and management of MPAs to improve their likelihood of success in the long term (Munga et al., 2010; Tunje & Hoorweg, 2003).

In conclusion, most of the research reviewed here focused on specific habitats, sites or species and therefore did not cover the whole Kenyan coast. Many studies were undertaken in inshore areas and offshore studies were very few. There is evidence to suggest that overexploitation and destructive fishing have led to a decline in Kenyan marine fisheries and, in some cases, habitat degradation, especially of coral reefs. Innovative methods, incorporating the use of biomarkers, population genetics, acoustic telemetry, underwater videography and highresolution sonic recordings, will open up opportunities to test new hypotheses on the fish resources in Kenya and in the Western Indian Ocean region. However, such research is limited in Kenya by inadequate financial and technological resources as well as expertise, and efforts must be made to meet these shortfalls

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The Distribution, Biological Characteristics and Vulnerability of the Giant Sea Catfish, *Arius thalassinus* (Rüppell, 1837), to Fishing at Mafia Island, Tanzania

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Keywords: *Arius thalassinus*, reproduction, vulnerability, artisanal fisheries, Rufiji Delta, western Indian Ocean

Abstract — The distribution and some biological characteristics of commercially important giant sea catfish, Arius thalassinus (Rüppell, 1837) were studied at Mafia Island. Artisanal fishing catches were sampled, caught mainly with longlines, shark nets and ring nets. These yielded a total of 2 723 kg of A. thalassinus, comprising 756 individuals, the largest measuring 1 000 mm TL. Arius thalassinus occurred only on the western coast of Mafia Island and the highest catch rate was 19.3 kg.fisher⁻¹.day⁻¹ in March when murky water was predominant. The reproductive biology of A. thalassinus was investigated to assess its vulnerability to fishing. Arius thalassinus reached a size at first maturity (L_{M50}) of 520 mm TL and exhibited a low mean (\pm SE) fecundity of 65.6 \pm 3.37 eggs per female within the size range of 605-970 mm TL. The hydrated oocytes were large (mean diameter \pm SE = 15.2 \pm 0.12 mm). Arius thalassinus spawned once in the study year during February and April, during heavy precipitation (124-499 mm). We therefore conclude that its restricted distribution, large size, low fecundity, late maturation and its reported high trophic level indicate that it would be vulnerable to fishing pressure. It is therefore recommended that fishing for A. thalassinus be restricted during its spawning season to ensure its sustainability.

INTRODUCTION

Catfishes (Order Siluriformes) are mostly freshwater fishes but two families (the Ariidae and Plotosidae) inhabit murky marine or brackish waters (Moyle & Cech Jr, 2004). These two families of sea catfish are regarded as unusual in that they live primarily in tropical

and subtropical seawater, unlike the majority of catfish families that have little tolerance for brackish or marine conditions (Moyle & Cech Jr, 2004). The giant sea catfish, *Arius thalassinus* (Rüppell, 1837), is among 23 species of sea catfish that are mostly confined

Corresponding author: ATK Email: kamukuru@udsm.ac.tz to murky coastal waters in the western Indian Ocean, within a depth range from 10 to 195 m (Fischer & Bianchi, 1984), and it is native to Tanzania (Bianchi, 1985).

Studies on the distribution and biology of sea catfishes in Tanzanian coastal waters are still sparse. Bianchi (1985) recorded five species of the genus Arius (Family Ariidae) and two species of the genus Plotosus (Family Plotosidae) along the Tanzanian coast. All were found in shallow coastal waters, predominantly brackish, around major river mouths. Arius spp. are of high economic value and are caught using mainly hook and line, shore seines, shark nets and fixed traps (Fischer & Bianchi, 1984; Bianchi, 1985). Catch statistics have revealed the high value of ariid catfishes as they constitute 7% of the total fish caught in the Rufiji Delta, compared to Mafia Island where their contribution is significantly lower at 0.6% (MLFD, 2007).

Ariid catfishes furthermore are carnivorous. feeding predominantly on crabs, prawns, mantis shrimps, fishes and molluscs (Taylor, 1986). They inhabit murky water, foraging by using one to four pairs of barbels (Moyle & Cech Jr., 2004), a characteristic of catfishes. Their ecological and reproductive characteristics include gonochorism, characterised by large-sized oocytes (Etchevers, 1978; Yáñez-Arancibia & Lara-Domínguez, 1988), and low fecundity (Bruton, 1995), with the males being oral incubators (Shadashiv & Vivekanandan, 2008). Studies have confirmed that parental care is exhibited by A. thalassinus, as the fertilised eggs are carried in the buccal cavity of males for a month (Mojumder, 1978; Menon, 1991). Furthermore, giant sea catfish males refrain from feeding while carrying eggs, embryos or fry (Menon, 1991).

O'Malley (2010) defined vulnerability as the intrinsic aspects in a species' biology, such as its life history or ecological variables, which increases its sensitivity to or inhibits its recovery from an external threat. Morphological characteristics, life history and ecological traits such as area occupancy and rarity (Hawkins *et al.*, 2000) and large body size, slow growth, late maturity, low reproductive output and high trophic level (Jennings *et al.*, 1999), have been used to predict the vulnerability of marine fishes to fishing. The sex ratio in a species and evidence of parental care, spawning aggregations or sex change have also been considered predictors of vulnerability of marine fishes to fishing (Reynolds *et al.*, 2001).

Following the collapse of some fish stocks (Hutchings & Myers, 1996; Roberts & Hawkins, 1999; Hutchings & Reynolds 2004) and fishing threats to existing stocks (Sadovy & Cheung, 2003; Cheung, 2007), overfishing has remained the most pervasive threat to commercial marine fishes (Pitcher, 1998). Other threats to wild fish stocks include loss of essential habitats critical to complete their life cycle (Watling & Norse, 1998), climate change (Brander, 2010) and pollution (Sindermann, 1994). Currently, about 75% of wild fish stocks have been determined to be fully exploited (52%), overexploited (16%) or depleted (7%) (Botsford *et al.*, 1997).

Published information on the distribution and biological characteristics of *A. thalassinus* at Mafia Island is meagre. This study aimed to provide preliminary observations on the occurrence and some biological aspects of *A. thalassinus* at Mafia Island, especially those likely to predispose it to high fishing mortality.

METHODS

Study area

The Mafia District comprises a chain of small islets, with the main island centred at 7°50'S and 39°45'E some 20 km off the Tanzanian coastline east of the Rufiji Delta (Fig. 1). Mafia Island is one of 169 administrative districts in Tanzania, with a population of 46 438 inhabitants living in 20 villages (URT, 2013). The island consists of Pleistocene reef covered by a sandy, loam soil. It experiences two monsoon seasons with an annual precipitation of 1 655 mm (Kamukuru, 2003), this figure being derived from rainfall data for Mafia Island obtained from a 1937-1973 dataset (Greenway *et al.*, 1988) and the Agriculture Office, Mafia District Council for 1979-2010.

People depend largely on agriculture, notably coconut cultivation, and artisanal fishing on Mafia, the latter being restricted to inshore waters due to a lack of capital to purchase larger fishing vessels to engage in deep sea fishing (McClanahan et al., 2009). Two sites were studied, Kilindoni and Mfuruni, which lie within the most intensively fished area at Mafia Island (Kamukuru et al., 2005) at which one incident of dynamite fishing is reported per month (Horrill & Ngoile, 1992). The fishing grounds are dominated by sand, bare rock and rubble (Kamukuru et al., 2004) and occasional murky water (Roitenbeek et al., 2005), probably originating from the Rufiji Delta which has the largest single mangrove ecosystem in East Africa (UNEP, 2001).

Data collection

A survey was launched at all fish landing sites around Mafia Island in October 2010 to determine the occurrence of ariid catfish in the catches. It was evident that they were familiar to fishers on the western side of Mafia Island between the Kitoni and Tumbuju fish landing sites (Fig. 1). Giant sea catfish specimens were landed on roughly seven days each month at the Kilindoni and Mfuruni fish landing sites by fishers using longlines, seine nets and shark nets. These were sampled between November 2010 and October 2011. Information on the number of fishers per boat, gear used and locality caught was recorded. The total length (TL) of the giant sea catfish was measured to the nearest millimetre, the total and eviscerated weight (TW and EW) to the nearest gram using a suspended digital balance, and the paired gonads (GW) to the nearest 0.1 g using a toploading digital balance. Macroscopic gonadal maturation staging was undertaken following the key by Kaunda-Arrara and Ntiba (1997). Ovaries at maturity stage IV were preserved in plastic bottles containing Gilson's fluid for fecundity estimates and mean ova diameter determination. These were kept at room temperature for three months and regularly, vigorously agitated to release the eggs from the ovarian tissues. Mature, hydrated intraovarian oocytes were counted for individual fecundity estimates. The diameters of 20 randomly selected, hydrated oocytes from ten mature females were measured to the nearest 0.01 mm using a digital calliper.

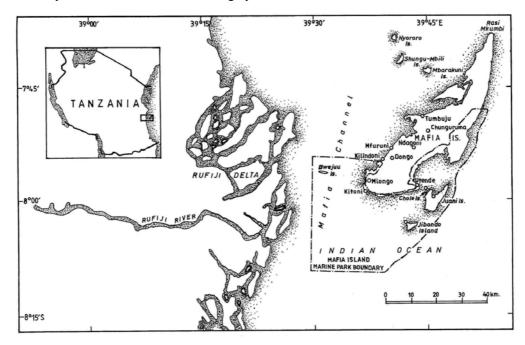


Figure 1. Map showing Mafia Island and position of the Rufiji Delta in Tanzania.

Data analysis

Relationships between TL and TW, and TL and fecundity (F), were estimated using least squares regression analysis and were derived from the equations:

TW = a x TL^b and F = aTL \pm b, respectively, where a is the intercept and b is the slope of the relationship (Le Cren, 1951). The monthly variation in gonadosomatic index (GSI), relative condition factor (*Kn*) and gonadal maturity stages were used to predict spawning periodicity in *Arius thalassinus*. The GSI was determined using the equation:

$$GSI = \frac{Paired GW}{EW} \times 100 . Kn$$

was determined using the equation:

$$Kn = \frac{TW}{aTL^b}$$

where, a and b are constants in the lengthweight relationship (Le Cren, 1951). The length at which 50% of the fish were sexually mature was considered the size at first maturity (L_{M50}). This was estimated by fitting the percentage of mature individuals per 30 mm TL interval to an ogive function (Duponchelle

& Panfili, 1998):
%MF =
$$\frac{1}{1 + e^{(-a(L - L_{MS0}))}}$$

where, %MF is the percentage of mature fish by size class, L is the mid-length of each size class, and a is a constant. Monthly variation in CPUE was analysed using single factor ANOVA and the post-hoc test followed the Tukey honestly significant difference (HSD) test. The sex ratio was analysed using the Chisquare test.

RESULTS

A total of 2 723.14 kg and 381.2 kg of *Arius thalassinus* and *Arius venosus*, comprising 758 and 152 individuals respectively, were measured at the Kilindoni and Mfuruni fish landing sites. Longlines contributed 85.9% to the total catch, with ring nets and shark nets contributing 7.2% and 6.9% respectively (Fig.

2a). The monthly variation in the giant sea catfish CPUE was not significant statistically (ANOVA: df = 11; F = 1.734; p = 0.078). The mean (\pm SE) CPUE peaked at 19.3 \pm 6.92 kg.fisher¹.day⁻¹ in March with a minor peak at 10.1 \pm 1.22 kg.fisher¹.day⁻¹ in December, coinciding with heavy (March/May) and light (November/December) rainy seasons, respectively (Fig. 2b).

Length-frequency distribution data revealed that the size of the giant sea catfish ranged between 390 and 1 000 mm TL, with an overall mean size (±SE) of 720.6±3.57 mm TL (Fig. 3a). Females (726.8±5.22 mm TL) grew to a similar size as males $(714.1\pm4.91 \text{ mm TL})$ (t = 1.963; df = 756; p = 0.077). The length-weight relationship of A. thalassinus was significant (r = 0.92; F =4227.8; df = 659; p < 0.001), the equation being $TW = 2E - 05 \text{ x} TL^{2.976}$ (Fig. 3b). The Student t-test for the length-weight relationship indicated that A. thalassinus exhibited isometric growth (t = -1.287; df = 657; p > 0.05) with a length exponent of 2.976±0.045.

The overall sex ratio of A. thalassinus (F:M) was 0.99:1, conforming to unity (χ^2 = 0.05; df = 1; p > 0.05). There was no significant evidence of size-dependent sex ratios but there were monthly differences in the sex ratio, with males being significantly fewer than females in April and May (Table 1). The species exhibited a single spawning season during February-April. This was inferred from peaking GSI and Kn values in females in February, and in males in March. A sharp decrease in the GSI and Kn for both sexes during May and June, presumably when the fish had released their gametes, indicated that they had concluded their reproductive cycle (Fig. 4). Evidence of this spawning season was further supported by the occurrence of a high proportion of fish with ripe and running gonads (stage IV) in February (Fig. 5). The sizes at first maturity of male and female A. thalassinus were 527.7 and 564.3 mm TL respectively (Fig. 6), with an overall L_{M50} of 520 mm TL.

Mature hydrated oocyte diameters ranged between 10 to 20 mm, the mean (\pm SE) being 15.2 \pm 0.12 mm, and their size

Table 1. Size and monthly variation in sex ratios of *Arius thalassinus* sampled at the Kilindoni and Mfuruni fish landing sites on Mafia Island between November 2010 and October 2011 (F = female; M = male; NS = not significant; df = 1; ** = p < 0.01; *** = p < 0.001).

TL (mm)	F	Μ	χ²	Month	F	М	χ^2
350 - 400	1	0	1.00 NS	Jan	16	24	1.60 NS
400 - 450	1	1	0.00 NS	Feb	17	14	0.29 NS
450 - 500	1	3	1.00 NS	Mar	121	132	0.48 NS
500 - 550	15	16	0.03 NS	Apr	63	30	11.71***
550 - 600	25	34	1.37 NS	May	20	7	6.26**
600 - 650	30	40	1.43 NS	Jun	7	15	2.91 NS
650 - 700	65	71	0.26 NS	Jul	17	20	0.24 NS
700 - 750	110	109	0.00 NS	Aug	13	22	2.31 NS
750 - 800	65	55	0.83 NS	Sep	15	18	0.27 NS
800 - 850	21	15	1.00 NS	Oct	40	46	0.42 NS
850 - 900	20	28	1.33 NS	Nov	22	26	0.33 NS
900 - 950	13	6	2.58 NS	Dec	25	28	0.71 NS
950 - 1000	9	4	1.92 NS	TOTAL	376	382	0.05 NS
TOTAL	376	382	0.01 NS				

frequency distribution was unimodal at 16.5 mm (Fig. 7a). The number of hydrated oocytes per female ranged between 25 to 101, the mean count (\pm SE) being 65.6 \pm 3.37 ova per female in fish between 605-970 mm TL. The length-fecundity relationship was linear (F= 0.1216TL - 30.653) with a significant, positive correlation coefficient (r = 0.61; F = 17.39; df = 29, p < 0.001) (Fig. 7b).

DISCUSSION

Two species of sea catfishes, viz. *Arius thalassinus* and *A. venosus*, were found on the western side of Mafia Island, with the former constituting 86% by weight of the catch. The preponderance of *A. thalassinus* at Mafia Island was probably due to its reported wider depth range (10-195 m), while *A. venosus* is restricted in coastal waters to a depth of 10 m (Fischer and Bianchi, 1984). Giant sea catfish were caught throughout the year, mostly during the rainy season, conforming to its preferred habitat of murky marine or brackish water which prevails in the Mafia Channel (Roitenbeek *et al.*, 2005). This habitat has been described as ideal for carnivorous catfishes which forage using their

barbels (Moyle & Cech Jr, 2004). Other parts of Mafia Island were devoid of ariid catfishes, partly due to the predominance of clear oceanic water that favours the development of coral reefs (Darwall & Guard, 2000) and other factors such as deeper waters devoid of soft bottoms.

A. thalassinus is a large-bodied fish which makes it a favoured catch and therefore vulnerable to fishing. It has been hypothesized that body size is negatively correlated to the intrinsic rate of natural increase in a species, and large-bodied fish thus generally have little ability to recuperate from high mortality events (Jennings & Reynolds, 2007). Furthermore, fishing activities target larger-bodied species more often, and receive disproportionately more fishing effort, than species of smaller body size (Reynolds *et al.*, 2002).

Our results indicated that *A. thalassinus* spawned once per year during February-April in the northeast monsoon following the onset of the heavy rainy season. Similar findings were reported for the species in the Arabian Sea (Dmitrenko, 1970; Naama & Yousif, 1987) and India (Mojumder, 1978), with spawning lasting for two months during the

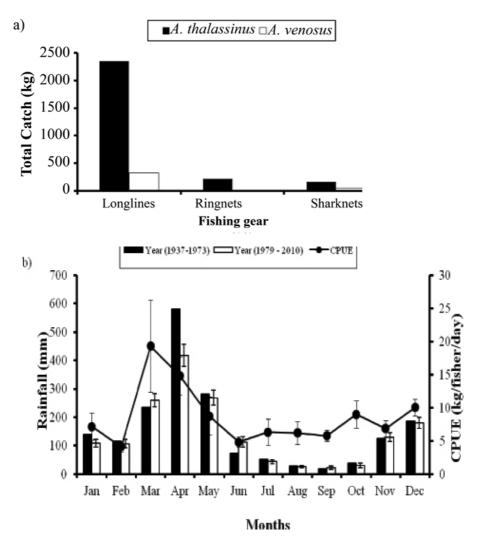


Figure 2. a) Total catch of ariid catfishes by fishing gear and b) monthly variations in rainfall during 1937-1973 (solid bars) and 1979-2010 (open bars) with mean CPUE (solid circle) of *Arius thalassinus* (error bar \pm SE).

northeast monsoon. *Arius thalassinus* becomes sexually mature at a large size, and is a late maturer that produces relatively few eggs. Fecundity alone has been widely criticized as a measure of vulnerability (Sadovy, 2001; Sadovy & Cheung, 2003; Dulvy *et al.*, 2005) but workers on elasmobranchs consider fecundity to be an important predictor of vulnerability (Brander, 1981; Stevens, 1999). After spawning, male sea catfishes assume the role of oral incubation (Dmitrenko, 1970; Mendoza-Carranza & Hernández-Franyutti, 2005; Shadashiv & Vivekanandan, 2008) and are believed to move from the fishing grounds (Mendoza-Carranza, 2003). This hypothesis is supported by our study in which a significant reduction in the number of males occurred in April-May, accompanied by the low GSI and *Kn* values associated with the post-spawning period.

Ariid catfishes have large oocytes compared to other teleosts, and mouthbrooders tend to have larger ova and therefore lower fecundity (Etchevers, 1978; Yáñez-Arancibia & Lara-Domínguez, 1988). *A. thalassinus* has large ova, the mature eggs

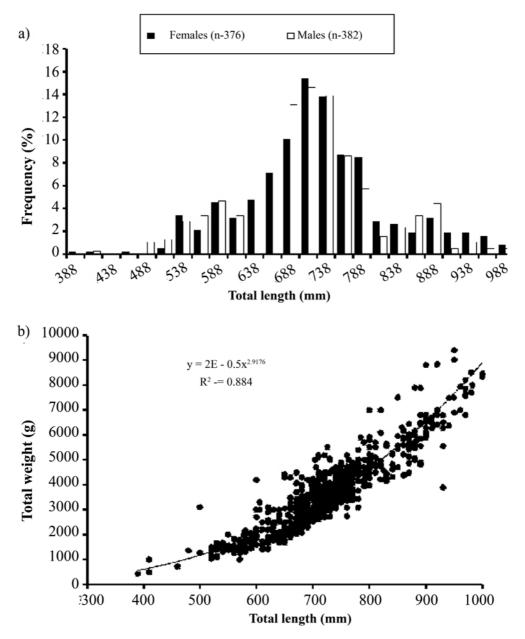


Figure 3. a) Length-frequency distribution of females (solid bar) and males (open bar) and b) length-weight relationship of *Arius thalassinus* (n = 758).

having a modal diameter of 16 mm which is typical of this group (Mojumder, 1978). The shortcomings of large ova and lower fecundity are, however, likely to be compensated by a low rate of egg and larval predation due to parental care rendered by male oral incubation (Menon, 1991). This strategy might well give this species an advantage in colonising suitable habitats and increasing its survival. However, drawbacks in the strategy include the fact that the size of the buccal capacity limits the number of eggs that can be incubated and are forced to lose a portion of the eggs when dealing with threats such as fishing gear

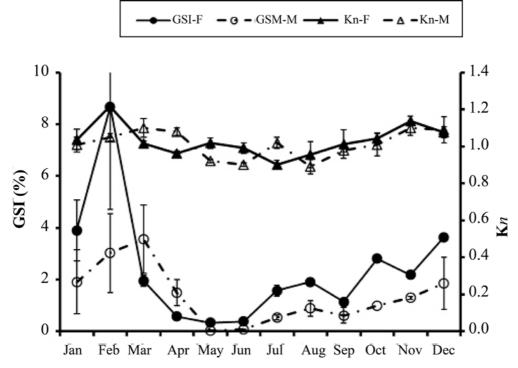


Figure 4. Monthly changes in GSI and Kn of female (solid line) and male (dashed line) Arius thalassinus.

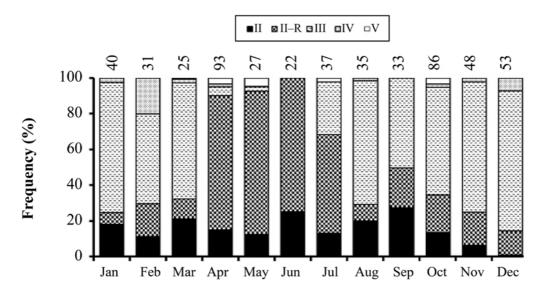


Figure 5. Monthly variations in gonadal maturity stages of *Arius thalassinus*: II = maturing; II-R = resting and recovering; III = active; IV = ripe and running; V = spent (sample N is indicated above the bars).

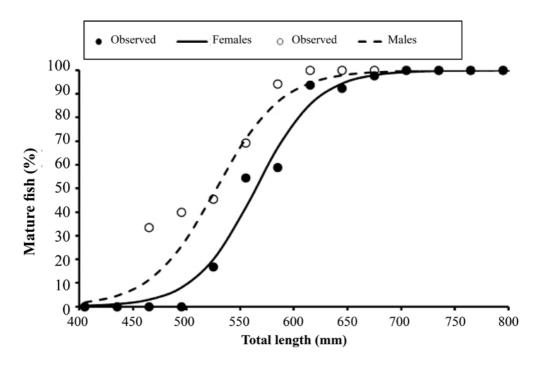


Figure 6. Size at first maturity of female ($L_{M50} = 564.3 \text{ mm TL}$) and male ($L_{M50} = 527.7 \text{ mm TL}$) Arius thalassinus.

(Shadashiv & Vivekanandan, 2008). Studies have also indicated that males feed on embryos to avoid starvation, and 'gestating males' have decreased condition, making them vulnerable to fishing and predation (Menon, 1991; Mendoza-Carranza & Hernández-Franyutti, 2005). This could not be confirmed in the present study as gestating males refrain from feeding (Mendoza-Carranza & Hernández-Franyutti, 2005; Shadashiv & Vivekanandan, 2008) and hence were not caught on baited longlines. The current exploitation of *A. thalassinus* stocks seemed sustainable at Mafia Island, considering that the mean landed size was larger than the size at first maturity. However, the restricted distribution of this giant sea catfish, its rarity, low fecundity, late maturation and large size make it potentially vulnerable to overfishing. Moreover, little or nothing is known about the current status of *A. thalassinus* stocks at Mafia Island and a precautionary approach to its fisheries management is advisable.

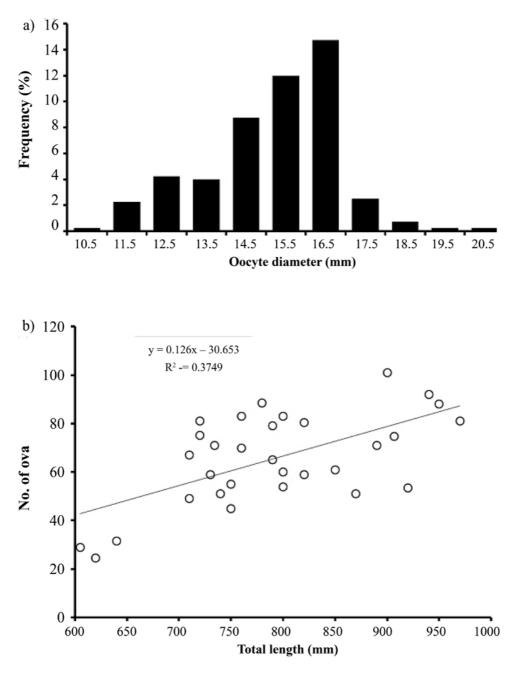


Figure 7. a) Mature hydrated oocyte size frequency distribution (n = 200) and b) length-fecundity relationship of *Arius thalassinus* (N = 31).

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Fish Catch Composition of Artisanal and Bottom Trawl Fisheries in Malindi-Ungwana Bay, Kenya: A Cause for Conflict?

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Keywords: Trawl bycatch, artisanal catch, catch composition, resource user conflict, Malindi-Ungwana Bay, Kenya

Abstract — Artisanal and shrimp bottom trawl fisheries in Ungwana Bay compete for fish resources and this has resulted in unresolved conflict over several decades. Landings of artisanal fishers (2009-2011) and bottom trawl catches (2011) were sampled to compare fish species composition and abundance according to area (inshore; offshore) and season (northeast monsoon - NEM, southeast monsoon -SEM) and identify the species contributing most to catch overlap. The diversity of fish catches was greater in trawl (223 species) than artisanal samples (177) in both seasons. The diversity and catch rates were greater in artisanal samples during the NEM, when most fishing occurs. The diversity was greater in trawl samples during the SEM, when productivity is higher. The offshore trawl catch composition differed from the inshore trawl and artisanal samples; the shared species in the latter two categories were Galeichthys feliceps, Pellona ditchela, Johnius amblycephalus, Leiognathus equulus, Pomadasys maculatus, Lobotes surinamensis and Otolithes ruber. Trawl samples contained smaller-sized fish of the shared species than artisanal samples. A shrimp fishery management plan (2010) bans trawling closer than three nautical miles from the coast, and introduces closed fishing seasons and gear modifications, but has not been fully implemented. The artisanal fishery is expected to grow and active management is crucial to reduce resource user conflict.

INTRODUCTION

Malindi-Ungwana Bay in Kenya (hereafter called Ungwana Bay) is a species-rich ecosystem in the tropical Western Indian Ocean where fisheries exploit a variety of crustacean, teleost, elasmobranch and mollusc species. An artisanal fishery in the bay dates back to the 9th century, coinciding with the rise of East African Indian Ocean trade with Arabia, Persia and India (Fulanda, 2003). Artisanal fishers use traditional and more modern fishing techniques such as collecting by hand and the use of hand and long lines with baited hooks, seine, cast and gillnets, and traps of various designs (Munga et al., 2014). Recent estimates place the number of fishers in the bay at >3000, with around 1000 fishing craft ranging from dugout canoes used near the shore to large dhows for open sea fishing (Government of Kenya, 2014). The number of artisanal fishers in Ungwana Bay is expected to increase as a result of population growth (Government of Kenya, 2014). Catches of the fishery comprise a multi-species mix of demersal fishes (50% by weight), pelagic fishes (28%), sharks and rays, octopus and squid, shrimps, lobsters and crabs (Government of Kenya, 2010a; Munga et al., 2012, 2014). This species mix is typical of artisanal fisheries in the south west Indian Ocean (SWIO) (Jiddawi & Ohman, 2002; van der Elst et al., 2005).

Ungwana Bay also supports an industrial bottom trawl fishery for penaeid shrimps, active since the early 1970s (Fulanda et al., 2011; Munga et al., 2012), and similar to the trawl fisheries on Sofala Bank (Mozambique) and Tugela Bank (eastern South Africa), and in the Rufiji Delta (Tanzania) and western Madagascar (Fennessy & Everett, 2015). Fulanda et al. (2011) describe the Ungwana Bay trawl fleet and fishing gear in detail. Briefly, they comprise steel double rig or outrigger trawl vessels (12-41 m long), towing otter nets and beam trawls, and fitted with blast freezers and freezing holds. Trawl catches include shrimps and a large bycatch of fish, sharks, rays, crustaceans and other invertebrates (Fennessy et al., 2004, 2008). Although some of the bycatch is retained and sold, most has low commercial value and is discarded overboard. Discarded fish are mostly dead or damaged by barotrauma, exposure to air or being crushed in the trawl net.

The shrimp trawl bycatch in the SWIO has been estimated at 80 000 to 120 000 t annually (Fennessy *et al.*, 2004; Keleher, 2005). Fish discards in Ungwana Bay weighed 1.5 to 7 times more than the retained shrimp (Fulanda et al., 2011; Munga et al., 2012). Mwatha (2005) recorded more than 90 fish species in catches retained by Ungwana Bay shrimp trawlers, of which the Sciaenidae, Sillaginidae, Mullidae and Pomatomidae (all demersal), Sphyraenidae and Scombridae (pelagic) represented the highest biomass. In the same study, the Leiognathidae and Dasyatidae (demersal), Clupeidae and Carcharhinidae (pelagic) contributed more than 43% to the discarded fishes. Juveniles of Otolithes ruber, Johnius sp. (both Sciaenidae), and Pomadasys sp. (Haemulidae) made up 25% of trawl discards by mass; these are important demersal species in the artisanal fishery (Munga et al., 2012).

Shared fishing grounds, catch composition and gear interaction in artisanal and trawl fisheries has given rise to resource user conflict since the early 1990s, despite a regulation that trawlers may only operate beyond three nautical miles (nm) from the shore (formerly five nm; Government of Kenya, 2010a; Munga et al., 2012). This conflict is exacerbated by factors such as weakly defined harvest strategies, an increasing number of artisanal fishers, entanglement of fishing gear and trawl discard practices (Fennessy et al., 2004; Fulanda et al., 2009, 2011). Biodiversity and conservationbased indicators show Ungwana Bay to be ecologically degraded, with a reduced biomass across trophic levels, including shrimps and fish (Swaleh et al., 2015). Reduced artisanal catches and escalating human reliance on the sea for food security led to a commercial trawl ban in 2006 (Munga et al., 2012). The trawl fishery resumed in 2012 but the spatiotemporal management strategy of Ungwana Bay remains under review.

Initiatives to reduce bycatch have been limited or sporadic in the region, and poorly enforced (see Fennessy *et al.*, 2004, 2008). In Kenya, trawl companies are encouraged to land (instead of discard) fish bycatch to satisfy the demand for fish in local markets (FAO, 2007). The overall objective of this study was to evaluate the conflict between the artisanal and bottom trawl fisheries in terms of overlapping fish species composition, and the key commercial species captured by the two sectors. Specific aims were: a) to compare the species composition of artisanal and bottom trawl catches according to area (inshore, offshore) and season (northeast monsoon - NEM, southeast monsoon - SEM); and b) to identify key species that result in the conflict between the two fishing sectors.

METHODS

Study area and field sampling

Ungwana Bay (2°30'- 3°30'S; 40°- 41°E) extends about 200 km along the shoreline of Kenya and has a total trawlable area of about 11 000 km² (Fig. 1). Fisheries are centered around

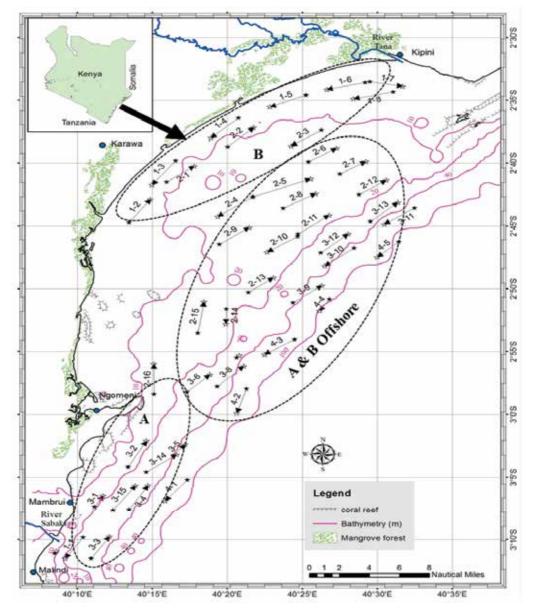


Figure 1. Map of Ungwana Bay, Kenya, showing the groupings of trawl transects in the Sabaki (A) and Tana (B) inshore area, and the offshore area (A & B offshore). Figures on the map indicate the transect number and depth stratum respectively, e.g. 1-2 means transect number 1 in depth stratum 2. Transect 1-1 was incomplete and hence excluded from the survey data. Artisanal catches were sampled at Malindi, Ngomeni and Kipini.

the Tana and Sabaki River estuaries and their shallow offshore banks (see Kitheka, 2013; Kitheka *et al.*, 2005). Mangrove forests, patchy reefs, islets, sandy shores and tidal flats are important habitats in the bay. Weather patterns are dominated by large scale pressure systems of the western Indian Ocean, and the dry northeast monsoon (NEM; October to March) and wet southeast monsoon seasons (SEM; April to September) (McClanahan, 1988).

Shore-based catch assessments of artisanal fisheries were conducted in 2009 (June, November, December), 2010 (March, June, September), and 2011 (March, July, September) at Malindi, Ngomeni and Kipini (Fig. 1). Fortynine visits were made and 84 random day-time catches were sampled. All fish in the samples were identified and measured.

Shrimp bottom trawl surveys were undertaken in January and February (13 days) and May and June (11 days) in 2011, using a leased shrimp trawler (25 m length, 146 t gross register displacement) and trawl net (44.3 m length; 70 mm mesh size in the body and 45 mm in the cod-end; 22.5 m head rope length). Trawls were dragged roughly parallel to the shore, for 1 h at 2.5 knots. The position and depth was recorded at the start and end of each trawl. Totals of 36 (NEM, covering 507.7 nm²) and 41 (SEM, covering 546.4 nm²) trawls were sampled during the two surveys.

Samples of catches were treated in a manner similar to shore-based samples but, if large, the catch was randomly subsampled. The total catch of each species was calculated by multiplying the subsample by a factor needed to arrive at the total catch weight (see Stobutzki *et al.*, 2001; Tonks *et al.*, 2008).

Data analyses

Measures of diversity (species richness, S; Shannon-Wiener diversity index, H') were compared between samples of the artisanal and trawl catches (inshore and offshore areas) for the NEM and SEM seasons using ANOVA. Multivariate, non-metric, multi-dimensional scaling (MDS) was used to identify whether area or season affected the composition of the trawl and artisanal catches based on their BrayCurtis similarity using PRIMER v6 (Clarke & Warwick, 2001). Two-way ANOSIM was used to further assess their spatial and seasonal similarity. The species that contributed most towards dissimilarity were identified using two-way SIMPER analysis. The body size of shared fish species was compared using two-way ANOVA or Kruskal-Wallis in STATISTICA v. 7 to assess whether artisanal and trawl fisheries catch similar life stages.

The swept area (a, nm²) of each trawl was calculated as:

$a = D \square h \square X$

where *D* is the distance covered in nm: $D = 60 \times \sqrt{(Lat1 - Lat2)^2 + (Lon1 + Lon2)^2 \cos 0.5^2 (Lat1 + Lat2)}, h$ is the head-rope length (m) and X the fraction of head-rope length equal to the swept path-width (set at 0.5; Pauly, 1980; Sparre & Venema, 1998).

Bycatch rates were calculated as catch (C, kg) divided by the time spent trawling (t, hours) and converted to catch-per-unit-area (CPUA, kg.nm⁻²) by dividing by the swept area: (C/t) / (a/t) = C/a)

Total biomass (B, kg) was calculated from:

$$B = \frac{(\overline{C/a}) \Box A}{X_1}$$

where C/a is the CPUA of all trawls, A is the overall area under investigation and X = 0.5.

Two-way ANOVA, followed by the post hoc Tukey HSD test, was used to test for differences in trawl bycatch rates (kg.h⁻¹) according to area and season. Artisanal fishery catch rates (kg.fisher⁻¹.h⁻¹) were compared between seasons using ANOVA.

RESULTS

Catch composition in the trawl and artisanal samples

Trawl samples contained 223 species; 158 in the NEM and 161 in the SEM. Artisanal catches comprised 177 species; 148 in the NEM and 90 in the SEM samples. Species

richness (S) of artisanal catches was higher in NEM (avg. 12 per sample) than SEM (9) samples. For trawls, S was higher for the SEM (18 inshore; 20 offshore) than the NEM (17 and 15) samples (Fig. 2a). The Shannon-Wiener diversity index (H') for the artisanal catches was higher for the NEM (avg. 1.7 per sample) than the SEM (1.6), while the H' for inshore and offshore trawls was higher for the SEM (2.3 in both cases) than the NEM (1.7 and 1.8) samples (Fig. 2b). *S* differed significantly between the artisanal and bottom trawl samples (two-way ANOVA: p < 0.05) but not between seasons, nor was the fishing sector × season interaction significant (p > 0.05, Table 1). *H'* differed significantly between the fishing sector × season interaction (p < 0.05, Table 1). Post hoc pairwise comparisons confirmed higher *S* and *H'* for the trawl than the artisanal samples in both seasons (p < 0.05).

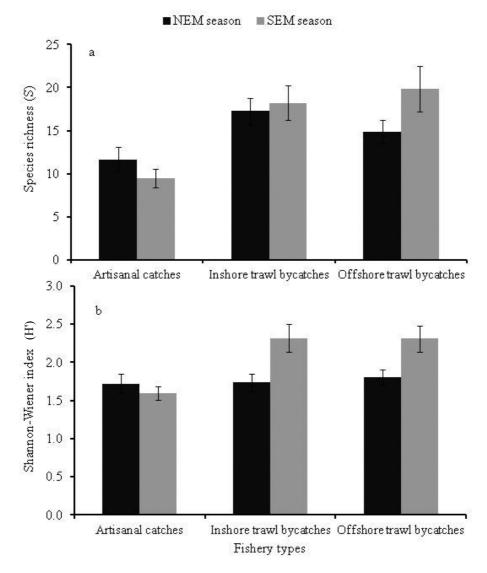


Figure 2. Comparison of a) mean species richness (\pm SE) and b) and Shannon-Wiener diversity index for artisanal, inshore and offshore trawl bycatches during the northeast and southeast monsoon seasons in Ungwana Bay.

			Species richness (S)		Shannon-Wiener diversity index (H')		
Factors	Df	Error Df	F	p-value	F	p-value	
Fishing sector	2	149	14.718	<0.001	6.794	0.002	
Season	1	149	0.834	0.363	8.178	0.005	
Fishing sector \times Season	3	149	2.726	0.069	5.089	0.007	

Table 1. Two-way ANOVA comparing fish species richness and Shannon-Wiener diversity for fishing bycatches (artisanal versus trawl), season and interactions (sector \times season) in Ungwana Bay (p-values in bold are significant).

The non-metric MDS plots distinguished a difference between the species composition of artisanal and trawl samples (Fig. 3a) and suggested a seasonal effect (Fig. 3b) (two-way ANOSIM: R = 0.317, p = 0.001 and R = 0.088, p = 0.003, respectively). Pair-wise comparisons confirmed that inshore trawl samples differed from those harvested offshore (R = 0.631, p = 0.001), but not from artisanal samples (R = 0.066, p = 0.09). Offshore trawl samples also differed from artisanal samples (R = 0.460, p = 0.001). The dissimilarity was attributed to abundant Bothus mancus, Trachinocephalus myops, Callionymus gardineri and Leiognathus lineolatus in offshore samples, versus abundant Lobotes surinamensis, Lutjanus fulviflamma, Galeichthys feliceps, Psettodes erumei and Pellona ditchela in artisanal samples (two-way SIMPER, Table 2). A seasonal dissimilarity between the artisanal and trawl samples was attributable to an abundance of G. feliceps, P. ditchela, B. mancus, Thryssa vitrirostris and T. myops in the NEM, and an abundance of P. erumei in the SEM samples.

Table 2. Two-way SIMPER analysis of species contributing most to the dissimilarity (bold values) in the abundance of bycatches (%) in offshore trawl versus artisanal catches in Ungwana Bay, Kenya, showing the percentage contribution of bycatch fish species that yielded an average dissimilarity of 99.0%.

	Average abundance		Average dissimilarity	Contribution (%)	
Species	Offshore trawl bycatches	Artisanal catches			
Bothus mancus	11.96	0.10	5.62	5.67	
Trachinocephalus myops	11.91	0.00	5.49	5.54	
Lobotes surinamensis	0.00	7.52	3.79	3.83	
Lutjanus fulviflamma	0.02	5.85	3.05	3.08	
Callionymus gardineri	7.34	0.00	2.96	2.99	
Galeichthys feliceps	0.08	5.20	2.87	2.90	
Psettodes erumei	0.06	6.41	2.86	2.89	
Pellona ditchela	0.66	4.09	2.71	2.74	
Peocilopseta natalensis	4.94	0.00	2.63	2.66	
Otolithes ruber	0.29	3.90	2.31	2.33	
Leiognathus lineolatus	5.18	0.03	2.25	2.27	

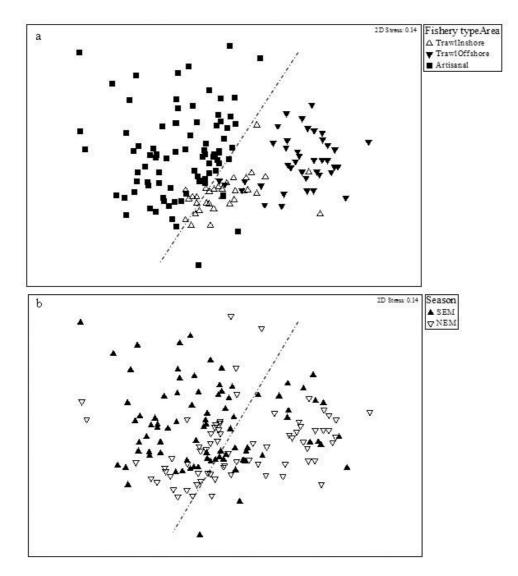


Figure 3. Non-metric MDS plots showing the composition of fish catches in Ungwana Bay a) for the artisanal, inshore and offshore trawl fishing sectors and b) per season (NEM and SEM) in combined artisanal and trawl bycatches. Dotted lines separate artisanal from trawl bycatches.

Seven common species explained the similarity between artisanal and inshore trawl samples (Table 3). Six out of the seven species had a smaller mean body size in trawl than in artisanal samples (p < 0.05, Table 4). *Lobotes surinamensis* and *Leiognathus equulus* were larger in NEM than SEM samples (p < 0.05, Table 4).

Catch rates and biomass

Trawl bycatch rates and biomass were significantly higher in inshore than offshore samples, and were also higher during the SEM than the NEM (Table 5). Although not significant (ANOVA, p = 0.103), artisanal catch rates were marginally higher in the NEM than the SEM (1.3 versus 0.9 kg.fisher⁻¹.h⁻¹).

Species	Average abundance	Average similarity % contrib	
Inshore trawl bycatches			
Galeichthys feliceps	14.65	5.27	22.59
Pellona ditchela	9.12	2.79	11.97
Johnius amblycephalus	6.68	1.95	8.35
Leiognathus equulus	3.54	1.30	5.57
Pomadasys maculatus	4.05	1.10	4.71
Otolithes ruber	2.36	0.84	3.61
Lobotes surinamensis	0.95	0.22	0.96
Artisanal catches			
Lobotes surinamensis	7.52	1.40	14.98
Galeichthys feliceps	5.20	0.80	8.61
Pellona ditchela	4.09	0.70	7.45
Otolithes ruber	3.90	0.58	6.23
Pomadasys maculatus	2.50	0.30	3.17
Leiognathus equulus	1.24	0.13	1.44
Johnius amblycephalus	1.15	0.12	1.33

Table 3. Two-way SIMPER analysis of species contributing most to the similarity in bycatch abundance (%) between inshore trawl (within a similarity of 23.3%) and artisanal catches (within a similarity of 9.3%) in Ungwana Bay, Kenya.

Table 4. a) Mean total lengths ($cm \pm SE$) of the most abundant shared fish species in artisanal and trawl samples in Ungwana Bay (pooled data per gear type, irrespective of season) and b) seasonal comparison of fish size (pooled data per season, irrespective of gear type). P-values in bold are significant.

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a) Species	Artisanal	Trawl	N/Error Df	Statistic	p-value
Galeichthys feliceps	39.8 ± 1.3	20.5 ± 0.3	357	227.171	<0.001
Johnius amblycephalus	14.4 ± 1.8	11.4 ± 2.2	228	51.819	<0.001
Pellona ditchela	14.8 ± 0.4	13.6 ± 0.1	787	8.272	0.004
Lobotes surinamensis	56.2 ± 0.9	55.1 ± 1.7	298	3.045	0.082
Otolithes ruber	24.3 ± 0.3	18.9 ± 0.2	380	165.400	<0.001
Leiognathus equulus	12.5 ± 0.2	13.3 ± 0.1	448	19.218	<0.001
Pomadasys maculatus	21.9 ± 0.6	12.9 ± 0.1	289	299.596	<0.001
b) Species	NEM	SEM			
Galeichthys feliceps	25.8 ± 0.7	24.4 ± 0.7	357	0.129	0.719
Johnius amblycephalus	11.9 ± 2.5	11.8 ± 2.2	228	0.960	0.328
Pellona ditchela	14.4 ± 0.4	14.0 ± 0.1	787	0.002	0.968
Lobotes surinamensis	59.4 ± 1.3	53.2 ± 1.0	298	12.823	<0.001
Otolithes ruber	21.4 ± 0.3	20.9 ± 0.3	380	1.093	0.296
Leiognathus equulus	13.4 ± 0.2	12.7 ± 0.1	448	13.349	<0.001
Pomadasys maculatus	17.1 ± 0.4	16.6 ± 0.5	289	2.857	0.910

Table 5. Mean (\pm SE) fish bycatch rates (kg.h⁻¹) and biomass (kg.nm⁻²) per trawled area (inshore and offshore) and season (NEM and SEM) in Ungwana Bay. Bycatch rates differed according to area (p <0.001) and season (p = 0.042). Biomass differed according to area (p <0.001) and season (p = 0.044) (Kruskal-Wallis test).

Area	Season	Bycatch rate kg.h ⁻¹	Biomass kg.nm ⁻²
Inshore	NEM	123.5 ± 54.5	8,565.9 ± 3,781.5
Inshore	SEM	106.5 ± 17.5	$7,\!427.5\pm1,\!221.6$
Offshore	NEM	6.2 ± 1.9	631.3 ± 210.0
Offshore	SEM	56.9 ± 19.3	$4,\!067.4 \pm 1,\!306.7$

DISCUSSION

The objectives of this study were to evaluate the conflict between the Kenyan artisanal and bottom trawl fisheries in terms of overlapping species composition, and to identify the key shared species of commercial importance. A priori assumptions were that trawling would be less selective than artisanal gear (i.e. higher S and H' values), that biomass would be lower offshore than inshore, near the productive Tana and Sabaki River estuaries (see Munga et al. 2013), and that season would affect species diversity in catches of both fisheries because of fluctuations in sea conditions and biological productivity (McClanahan, 1988; Fulanda et al., 2009). We also assumed that species composition of offshore trawl catches would differ significantly from those in trawls in inshore waters and artisanal catches, because of depth and habitat preferences, and different exploitation levels.

We obtained higher *S* and *H'* values for trawl (223 fish species) than artisanal samples (177) in both seasons, thus confirming that trawling was less selective than artisanal gear. Trawl nets can catch most organisms in their path, whereas some artisanal gear, such as hook and line, seine or gillnets, are more likely to select specific species or size classes (Gobert, 1994; McClanahan & Mangi, 2004). In this study, trawl catches were sampled onboard fishing vessels immediately after emptying the trawl net onto the deck, and therefore all species were taken into account. Artisanal fishers prefer certain species, but only a few species are considered inedible (Davies et al., 2009; Mangi & Roberts, 2006). Most of the catch would therefore have been retained and sampled at landing sites. Nevertheless, some sorting and discarding may have occurred at sea, potentially biasing the S and H' downwards. Even though the sampling method may thus have introduced some bias (i.e. comparing unsorted trawl samples with sorted artisanal samples), our results manifested a highly diverse catch composition typical of tropical shrimp trawl fisheries. This nonselective nature of shrimp trawling has been widely criticized (Jones, 1992; Hall, 1996; Kelleher, 2005).

Both the S and H' were higher during the NEM in the artisanal fishery when most fishing takes place (Fulanda et al., 2009). Artisanal catch rates were also higher during the NEM. This reflects the effect of adverse sea conditions during the SEM on fishing activities that rely on small craft. Conversely, the fish bycatch of trawlers was more diverse during the SEM, and this confirms trends from long term catch data for Ungwana Bay (Mwatha, 2005; Munga et al., 2012). Increased nutrient input and productivity in the bay, resulting from elevated discharge of the Tana and Sabaki Rivers during the rainy SEM, are the most likely factors driving the increase in species composition during the SEM (Kitheka, et al., 2005; Kitheka, 2013). The trawl catch rates and total biomass were also higher during the SEM, signifying seasonally increased abundance or higher catchability (see Fulanda et al., 2011; Mwatha, 2005).

Trawl bycatch rates and biomass were lower offshore than inshore where productivity is higher near the Tana and Sabaki River estuaries (see Kitheka, 2013; Kitheka *et al.*, 2005). It is unlikely that the offshore biomass was lower due to depletions caused by trawling, because most trawling occurs inshore, near the river outflows, where shrimps are more abundant (Munga *et al.*, 2013). The most common fish bycatch species in offshore samples were *Bothus mancus, Trachinocephalus myops, Callionymus gardineri* and *Leiognathus lineolatus*; this differed significantly from the most common species in the artisanal and inshore samples (see Table 2). Similarity in the artisanal and inshore trawl fish composition was attributable mainly to their common abundance of *Galeichthys feliceps*, *Pellona ditchela*, *Johnius amblycephalus*, *Leiognathus equulus*, *Pomadysis maculatus*, *Lobotes surinamensis* and *Otolithes ruber*. This similarity was indicative of overlap in resource use patterns, such as targeting similar fishing areas, depths or habitats. These species are commercially important to artisanal fishers and are also, on occasion, retained and landed by the trawl fishery.

The average size of the above species in trawl bycatches was mostly smaller than in artisanal catches. This trend appears to be a result of gear selectivity, rather than a seasonal effect (see Table 4). The hypothesis that juveniles are more abundant during the SEM, when they are caught in large numbers by trawlers, was not be supported by the seasonal size comparison (except for *L. surinamensis* and *L. equulus*). Rather, it is more likely that trawl nets (mesh size 45-70 mm) retain smaller fish than those regularly caught by artisanal fishing gear.

The seven fish species most exploited in Ungwana Bay are G. feliceps, P. ditchela, J. amblycephalus, L. equulus, P. maculatus, L. surinamensis and O. ruber, with demonstratable resource user overlap. Therefore they are the most likely subject of conflict between the artisanal and trawl fishing sectors. Fennessy et al. (2008) reviewed initiatives to reduce the prawn trawl bycatch in Kenya; these initiatives included a combination of turtle excluder devices (TEDs) for shrimp trawlers, a minimum inshore trawling distance (set at five nm), closed seasons, restrictions on nocturnal trawling, and the closure of the Ungwana Bay shrimp trawling grounds for several years. These measures have been introduced at various times, either as legislation or, intermittently, as permit conditions. Compliance has generally been poor and, thus, management initiatives have largely been ineffective in preventing conflict.

A new shrimp fishery management plan (Government of Kenya, 2010b) limits shrimp trawling to further than three nm from the shore (previously five nm). The management plan further incorporates a closed season for the trawl fishery (November to April) which coincides with the recruitment of shrimps onto offshore banks, and with spawning of fish species caught as trawl bycatch (Mwatha, 2005; Munga et al. 2013; Nzioka, 1979). The trawl closure also falls within the main artisanal fishing season during the NEM, and will reduce some physical conflicts such as gear entanglement and market competition. Bycatch reduction devices (BRD) fitted to trawl nets that allow the escape of smallsized and juvenile fishes have not been given sufficient attention, and their testing and successful deployment may further mitigate conflict. The direct benefits of BRDs to users may include reduced catch processing times, improved product quality, improved catch rates and reduced fuel consumption (e.g. Broadhurst 2000; Broadhurst & Kennelly 1997; Salini et al., 2000). Artisanal fishing effort is expected to increase in Ungwana Bay (Government of Kenya, 2014) and the implementation and enforcement of the existing management plans are therefore crucial if conflict is to be reduced.

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Confirmed Sighting of a Spawning Aggregation of the Brown-marbled Grouper, *Epinephelus fuscoguttatus*, in Kenya

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Keywords: *Epinephelus fuscoguttatus*, grouper, spawning aggregations, Kenya, fisheries management, reproductive behaviour

Abstract — The occurrence of spawning aggregations at fixed sites and times is well documented for several species of reef fish. These aggregations are known to attract fishers and such species may therefore be vulnerable to overfishing. This is particularly true in the case of groupers which have intrinsically vulnerable life history traits. The brown-marbled grouper, Epinephelus fuscoguttatus, distributed throughout the Indo-Pacific region and classified by IUCN as Near Threatened, is reported to form spawning aggregations but little is known about its spawning behaviour; in the Western Indian Ocean this has only been reported for the Seychelles. This study confirmed spawning aggregation behaviour in E. fuscoguttatus in Kenya based on underwater observations and fishers' knowledge of the phenomenon. We showed that *E. fuscoguttatus* forms short aggregations for ~5 days linked to the new moon for a 3-4 month period during the northeast monsoon (austral summer). The numbers of aggregating fish appear to be low, however, and the species is currently not managed in Kenya. Considering the fact that only small areas of the Kenyan coastline are under total protection (8.6% of the country's coral reefs), these factors suggest that there is an urgent need for additional management of E. fuscoguttatus if it is to survive in Kenya.

INTRODUCTION

The brown-marbled grouper, *Epinephelus fuscoguttatus* (Epinephelidae) (Forsskål 1775), is widely distributed throughout the Indo-Pacific region (Heemstra & Randall, 1993) and is known to form spawning aggregations (Johannes *et al.*, 1999; Pet *et al.*, 2005; Robinson *et al.*, 2008a; Rhodes *et al.*, 2012). In the western Indian Ocean, *E. fuscoguttatus*

has been reported by fishers to form spawning aggregations in Kenya (Samoilys *et al.*, 2006; Robinson *et al.*, 2013) but little is known about their spatio-temporal formation. The reproductive biology of this species remains unstudied in eastern Africa, with the exception of reports of spawning in the northeast monsoon (October to March) period (Nzioka, 1979).

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Epinephelus fuscoguttatus is not considered an abundant grouper (Pears *et al.*, 2006) and, in Kenya, it is rare in artisanal catches, with only 24 individuals recorded in southern Kenya over a six-month period in 2007 (Agembe *et al.*, 2010). Due to its large size, it comprises a relatively important proportion of the biomass of reef fishes captured. In Kenya, it is targeted by speargun and handline, however catches are so small that they are not reported separately (WIOFish database (www.wiofish.org); McClanahan & Mangi, 2004).

Global concern over the status of E. fuscoguttatus populations led to its Near Threatened Redlist classification by the IUCN Groupers and Wrasses Specialist Group in 2007 (IUCN, 2015). Concerns over the status of the species in Kenya have arisen due to our awareness of two spawning aggregations within the Diani-Chale Reserve on the south coast of Kenya, an area not under active management and which does not include notake zones (Robinson et al., 2008a). There are anecdotal reports of targeted fishing of these aggregations for the local tourism market and catches of E. fuscoguttatus have been observed with running ripe gonads (MS pers. obs), suggesting aggregation fishing.

Epinephelus fuscoguttatus inhabits depths of up to 60 m (Heemstra & Randall, 1993) and may therefore be partially protected within a natural depth refuge (Tyler et al., 2009; Mangubhai et al., 2011; Rhodes et al., 2012) since fishers in Kenya have less access to the seaward reef slopes where these fish occur. Boats are still largely not mechanised (Samoilys et al., 2011), preventing easy access to these sites, and the winds of the south-eastern monsoon (4-5 months) are prohibitively strong. However, with technological developments, notably the growing use of outboard engines, increasing effort by new fishers within an open access fishery (Samoilys et al., in review), and the intrinsic vulnerability of E. fuscoguttatus due to its life history characteristics (Robinson & Samoilys, 2013a), this species is probably highly vulnerable to overexploitation in Kenya.

Fisher interviews were undertaken regarding *E. fuscoguttatus* spawning aggregations on the south coast of Kenya as part of a larger fisher knowledge survey of spawning aggregations in key fishery species (Samoilys *et al.* 2006; Maina *et al.*, 2013; Samoilys *et al.* 2013). Key informants and experienced fishers known

to target *E. fuscoguttatus* were questioned on their knowledge of spawning aggregation sites, behaviour and timing, based on established indicators defined by Colin *et al.* (2003). Fishers' descriptions considered reliable were assessed against established indicators, such as increased fish abundances (at least four-fold), courtship, territoriality, reproductive colouration, gravid females and gamete release. They reported that aggregations formed between January and April but were less knowledgeable concerning spawning behaviour or lunar timing (Samoilys *et al.* 2013).

There is strong evidence that targeted spawning aggregation fishing is rarely sustainable (Sadovy & Domeier, 2005). This fact, combined with the life history characteristics of *E. fuscoguttatus*, viz. slow growth, late maturity and long life (Pears et al., 2007), highlight the need to identify the management requirements of this species both at and apart from spawning sites vulnerable to fishing. This study was designed to verify a previously reported aggregation site in the Diani-Chale Reserve on the south coast of Kenya, describe the spawning behaviour of the species and determine the seasonal and lunar periodicity of aggregation formation. Aspects of the work presented in this paper were published (Samoilys et al., 2013) in an integrated and multi-disciplinary study of groupers in Kenya, Seychelles and Zanzibar (Robinson & Samoilys, 2013b). The purpose of the present publication is to report the behaviour of E. fuscoguttatus in spawning aggregations to a wider audience and highlight the continuing lack of fisheries management of this species in East Africa, despite its vulnerable status.

METHODS

Study site

The study area was approximately 25 km south of Mombasa, and extended from Tiwi (4°12'36"S; 39°37.06"E) in the north to Chale Island off Gazi Bay (04°27'807"S; 39°32.158E) in the south, in the region of Diani that encompasses the Diani Chale Marine Reserve (Fig. 1). A linear fringing reef characterises this coastline, broken by the Tiwi River in the north and Gazi Bay to the south. The fringing reef has a spur and groove structure accentuated in places to form

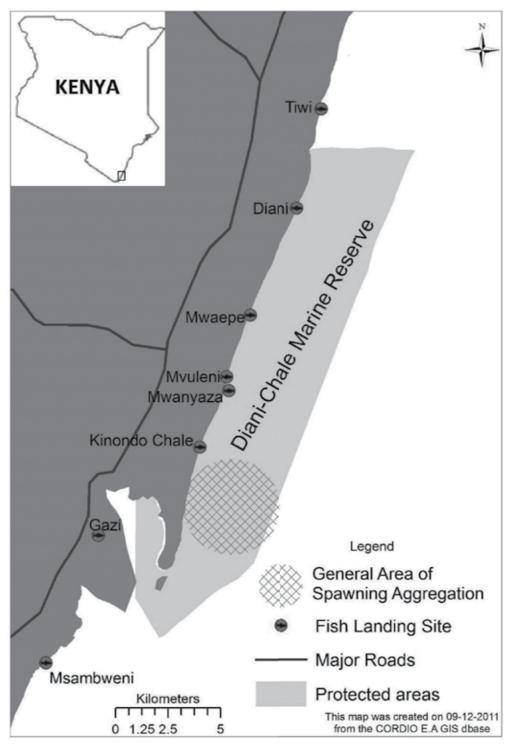


Figure 1. Study area and approximate location of the spawning aggregation site of *Epinephelus fuscoguttatus* in the Diani-Chale Marine Reserve.

promontories, and is broken by reef passages, all known and named by fishers.

Our study focused on a single *Epinephelus fuscoguttatus* spawning aggregation site reported by fishermen on the outer reef slope in the Diani area. It was subsequently identified as a potential spawning site during SCUBA observations and through further discussions with fishers. The site coordinates are not provided on the map for reasons of confidentiality.

Once numbers of *E. fuscoguttatus* were found at the aggregation site, the extent of the aggregation area, as defined by the presence of the groupers, was mapped by divers, including its depth and habitat features. The map was incorporated in the underwater datasheet for recording of fish numbers and their behaviour (Fig. 2). Co-ordinates delineating the perimeter of the aggregation site were obtained using GPS while swimming at the surface.

Underwater visual census surveys

Initial underwater visual census (UVC) counts of E. fuscoguttatus at the site were made during the new moon period (lunar days, LD, 25-3) of 11-18 November 2009. The new moon was selected for this, based on previous fishers' reports of lunar periodicity in the spawning of this species in Kenya and Seychelles (Samoilys et al., 2006; Robinson et al., 2008b). UVC counts and behavioural observations of E. fuscoguttatus were repeated each month to February 2010, the period reported as the spawning season by fishers. UVC counts were also recorded during the purported non-spawning season in July-August 2010. In both seasons, censuses were always undertaken during a seven-day period over the new moon (LD 27-3, where 1=new moon). One full moon period (LD 17-18) was also surveyed (31 Jan-1 Feb 2010). We calculated the non-spawning density of E. fuscoguttatus from surveys conducted in July and August (winter), based on the fact that fishers reported that spawning aggregations occur only in summer months and studies of this species in the Pacific have revealed strong seasonality in its reproductive pattern, with a peak aggregation abundance over 3-4 months (Hamilton *et al.*, 2012; Rhodes *et al.*, 2012). We used criteria provided by Colin *et al.*, (2003) and Domeier (2012) to confirm the presence of spawning aggregations, considered to be fish abundances at least four times that of non-reproductive periods.

Abundances were estimated from counts made by a single diver along a set path around the site during a 30-min swim on SCUBA. Counts started along the deeper ledges (maximum depth 25 m) and finished in shallower areas closer to the reef crest (minimum depth 10 m). Swims consistently covered the same route and area, and were undertaken by one of two trained observers (MS, DM) to minimise observer bias. Although fish were sometimes mobile and visibility was often poor (around 10 m), biases caused by double counting were assumed to be consistent between counts. Fish location and size (in 5 cm size classes) were recorded on the datasheet map.

The presence of E. fuscoguttatus and spawning-related behaviour were recorded during all surveys, based on established criteria: a distinct reproductive colouration in males, courtship, swollen abdomens in females, male-to-male aggression and fish suspended unusually high in the water column (Samoilys, 1997; Johannes et al., 1999; Colin et al., 2003; Robinson et al., 2008b), bearing in mind that sexing this species underwater is uncertain. Following abundance counts, fish behaviour was recorded over a 10 min period to estimate the frequency of occurrence of the above events. Visual estimates of the size of fish engaging in spawning-related behaviour were also recorded. Still digital photographs of behaviour were recorded using a Nikon Coolpix camera (Nikon Inc., Melville, NY).

RESULTS

Spawning aggregation site

Spawning aggregations of *Epinephelus fuscoguttatus* were verified at the site, based on a combination of their increase in abundance above non-reproductive levels and observations of spawning-related behaviour. The area of the site was estimated to be 2744 m². It was

characterised by abundant soft corals on the upper slope (*ca* 10 m depth), which shelved gently (*ca* 25°) to the reef edge at 15-16 m depth (Fig. 2), where it dropped steeply to >30 m. The reef slope was high in relief with ledges, caves and overhangs. The site was bounded by a reef

passage to the north and a continuous reef slope to the south. *E. fuscoguttatus* were observed aggregating along the upper reef edge near the overhangs and caves, and also on the upper, more open reef slope at depths of 12-18 m.

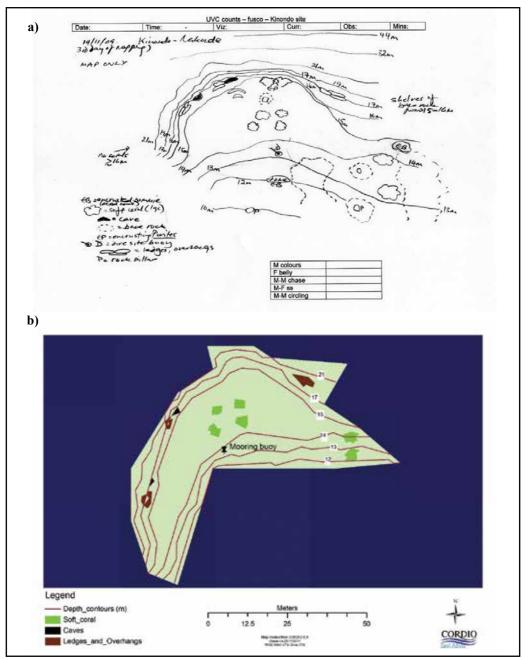


Figure 2. Epinephelus fuscoguttatus spawning aggregation site: a) diagrammatic map used as datasheet to record numbers and behaviour of fish and b) GIS map from GPS co-ordinates of the site perimeter, contours and features.

Size and periodicity of spawning aggregations

Relatively high numbers of E. fuscoguttatus were observed at the site from November 2009 to February 2010 with maximum monthly estimates ranging from 16 to 32 (Fig. 3). Numbers of E. fuscoguttatus in July and August, the putative non-spawning winter months, were lower, particularly in August when only three fish were observed. In contrast, a maximum of 13 fish were recorded in July (Fig. 3). We calculated the mean non-spawning density to be 6.0 fish (± 2.5) SE) during these winter months, though the sample size was limited (n=4 counts). Based on the published criteria of an at least fourfold increase in numbers (Domeier, 2012), 24 fish would therefore constitute a spawning aggregation of E. fuscoguttatus. Counts from November to February (LD 28-2) ranged from 10 to 32 (n=9), with a mean of 21.3 (± 2.6 SE), indicating that only some aggregations in December-February could be defined as spawning aggregations, while some densities were no different from those in July (Fig. 3).

Daily counts relative to lunar period indicated that the *E. fuscoguttatus* aggregations formed around the new moon (Fig. 4). A gradual increase in the numbers at the site was observed just prior to the new moon (LD 29) with peak numbers observed on LD 1. Exploratory surveys beyond the southern boundary of the site at new moon in

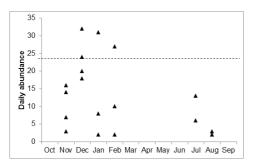


Figure 3. Seasonal pattern in abundance of *Epinephelus fuscoguttatus* at the spawning aggregation site (*ca* 2 744 m²). Data are total counts from daily UVC surveys. The dashed line represents the minimum abundance (24 fish) that constitutes an aggregation based on the criterion of at least a four-fold increase in fish density.

February 2010 yielded three *E. fuscoguttatus* (two males and one female). Aggregation numbers decreased abruptly on LD 2 and 3, suggesting fish had departed from the site. Unfortunately it was not possible to conduct surveys throughout a lunar cycle, but lower numbers of fish were observed during the full moon period (Fig. 4). Diel changes in aggregation abundance during LD 28-2 in December-February were not apparent. Diurnally, aggregation numbers were high (>25) by 0900 hr and throughout the day, though data were few.

Verification of spawning behaviour

Fish behaviour indicative of spawning was observed providing strong evidence for reproductive aggregations of *E. fuscoguttatus*. All five behavioural indicators were observed repeatedly during the new moon periods of December, January and February. These are described in Table 1 and their frequency presented in Table 2. However, spawning rushes and gamete release were never observed.

Males did not appear to defend territories but rather moved within small areas that seemed to be close to or overlapping that of other males. For example, in December 2009 (LD 1) we observed two males and two females together in a small area, approximately 5x5 m. Male-male aggression appeared in two forms (behaviour 4, Table 1), though chasing was more frequent (Table 2).

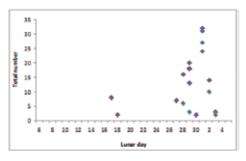


Figure 4. Lunar periodicity in numbers of *Epinephelus fuscoguttatus* at the spawning aggregation site during the reported spawning season (November-February).

Table 1. Spawning-related behaviour observed amongst *Epinephelus fuscoguttatus* at the aggregation site during the new moon period based on known criteria (Colin *et al.*, 2003). The timing and frequency of these behaviours are provided in Table 2. The normal colour of *Epinephelus fuscoguttatus* is shown for comparison (behaviour 1).

Behaviour and appearance	Description
1. Normal colour	Normal colour of male and female <i>Epinephelus fuscoguttatus</i> – black splodges on pale brown background.
2. Male colouration	The usual brown-and-black marbled colour pattern (see 1) disappears completely; fish display white ventrally, on the opercula and the dorsal, caudal and anal fins. Fin edges darken to black, and dorsal half of body darken. When in this colour pattern, males swim slowly around and above the coral. Also court in this colour pattern (see 5). Assumed to be dominant males displaying to females within their territory. Possibly not all males display this colouration.
3. Female swollen with eggs	Female with clearly swollen abdomen, probably due to hydrating eggs expanding the gonad; normal colouration.
4. Male aggression	 Fish assumed to be males based on behaviour but not in male colouration. Two behaviours were observed: a) An individual chases another away from its area, swimming rapidly and following opponent for up to <i>ca</i> 10 m. Assumed to be males contesting territories. b) Two individuals circling tightly head to tail, moving very slowly; as one moves away (possibly a submissive response), the other uses its lips to audibly hit opponent on the caudal peduncle area. Some individuals were scarred with superficial wounds, while others were more severely injured. For example, one fish had a badly torn upper lip. These injuries were assumed to be from malemale aggression.
5. Courtship	Male in spawning colours (see 2) swims slowly, close to a female (see 3) and turns sideways towards her, then shakes his body while swimming slowly past her. This display lasts <2 min and was sometimes repeated to the same female within 10 to 15 minutes of the first encounter.
6. Suspended in the water column	Fish stationary, or moving slowly, at least 1 m above the substratum. Individuals hovered over the same area where other fish were aggregating. This behaviour continued for 5-10 minutes. The fish were assumed to be males, but were not displaying male courtship colours (behaviour 2). This was assumed to be pre-spawning behaviour.

Table 2. Frequency of *Epinephelus fuscoguttatus* spawning-related behaviour at the spawning site in spawning (December-February) and non-spawning months (July-August). Data comprise the number of individuals observed exhibiting a behaviour within the census period (30 min counts followed by 10 min observations). Numbers in parentheses refer to behaviour described in Table 1; an asterisk denotes pairs of fish. NM=new moon; FM=full moon.

Month & lunar stage	Colour change (2)	Gravid female (3)	Male-male chase (4a)*	Male-male, head to tail (4b)*	Courting (5)*	Suspended in water column (6)
Dec NM	31	11	7	1	3	5
Jan NM	7	5	2	0	5	0
Feb NM	7	6	2	0	3	0
Jan-Feb FM	2	2	0	0	1	0
Jul-Aug	0	0	0	0	0	0

Courtship behaviour was performed by the male with the female stationary on the reef bed (behaviour 5, Table 1). Observed courtship acts involved a male swimming slowly past a female, turning sideways to her and quivering his body. Males either engaged in multiple courtship acts with the same female, or with several females. Courtship behaviour ceased if divers approached too close. Females were observed hidden within the reef topography or lying close to the substratum; in one instance, a male was observed courting a female that was hidden within the reef.

Fish size and sex ratios in spawning aggregations

Twelve pairs of E. fuscoguttatus were observed courting and, in all but one case, the male was larger than the female. The modal size class of courting fish was 81-85 cm TL for males and 71-75 cm TL for females. Since it is possible to determine the sex of males when they are in courtship colouration or showing male-male aggression (Table 1), the approximate proportion of males in an aggregation could be calculated. This ranged from 7 to 64%, the mean being 35% (±7.3% SE). Consistently higher proportions of males in aggregations (mean = 46%) were observed during the December new moon when most spawning-related behaviour was recorded (Table 2). Size frequency plots of the aggregations revealed that the minimum size of aggregating fish was 56-60 cm TL (December) and the maximum size was 96100 cm TL (November; Fig. 5). Monthly size frequencies showed that the largest fish were present only during the months of November, December and January.

DISCUSSION

Observations of spawning-related behaviour at the aggregations site, increased densities of fish and fishers' knowledge all combined to provide strong evidence for the occurrence of *Epinephelus fuscoguttatus* spawning aggregations at a site on the south coast of Kenya. A likely second spawning aggregation site approximately 23 km north of the study site has also been reported (Samoilys *et al.*, 2013), providing some indication of the geographic scale at which these aggregations might occur.

behaviour The spawning of Ε. fuscoguttatus observed in Kenya is typical of many groupers that spawn in pairs within aggregations (Samoilys & Squire, 1994; Samoilys, 1997; Johannes et al., 1999; Robinson et al., 2008b). The distinct colour changes and swimming high in the water column by males have been previously described in E. fuscoguttatus spawning aggregations in Palau and the Seychelles (Johannes et al., 1999; Robinson et al., 2008b). Strong territorial behaviour by males at aggregation sites, such as that observed in the smaller, more mobile grouper, Plectropomus leopardus (Samoilys, 1997), was not apparent. Although aggressive encounters between males occurred, the demarcation of territories was not apparent. A lack of male aggression

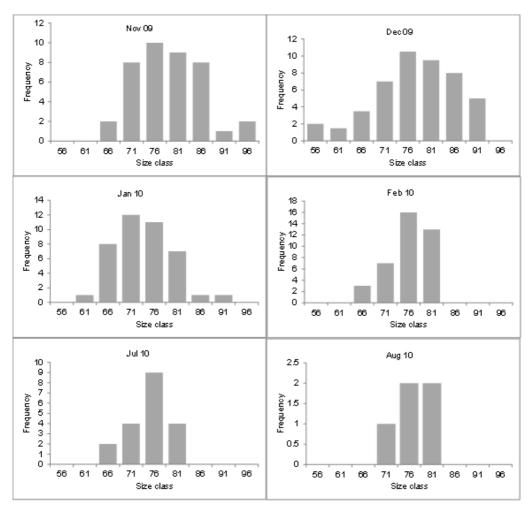


Figure 5.Size structure of the *Epinephelus fuscoguttatus* population at the spawning aggregation site during the spawning (November-February) and non-spawning months (July-August), based on underwater estimates of fish sizes to 5 cm. Samples comprise pooled data for each month (total numbers of fish are shown in Fig. 3).

in this species during the development of a spawning aggregation has been documented in the Seychelles, where the level of aggression increased with aggregation density (Robinson *et al.*, 2008b). Clear demarcation of territories occurred in the high density aggregations at Farquhar Atoll, with males regularly chasing other males (Robinson *et al.*, 2008b). The lack of territorial behaviour in males at the Kenyan site may reflect the low densities that characterised these aggregations.

Spawning rushes and the release of gametes, direct evidence that aggregations have formed for the purpose of spawning,

were not observed. This may be due to the SCUBA observations being limited to between 0900 and 1700 for safety reasons, since the sites were seaward of the fringing reef. However, courtship behaviour was observed as late as 1650, suggesting that spawning occurred after that, as appeared to be the case in the Seychelles (Robinson *et al.*, 2008b). Other grouper species are known to spawn during a narrow window before, during and after sunset (Colin *et al.*, 1987; Samoilys, 1997; Domeier & Colin, 1997; Heyman *et al.*, 2005; Rhodes & Sadovy, 2002). The proportion of males in aggregations, 45% during December, is high for a protogynous grouper in which the sex ratios are normally female-biased (Pears *et al.*, 2007). This may be due to females remaining hidden in the reef and, therefore, undetectable during the UVC surveys. An observation of a male courting a female hidden deep within the reef supports this. Alternatively, sex ratios in aggregations may not mirror the overall population sex ratio, especially if females do not attend every aggregation (Rhodes *et al.*, 2012).

Our UVC surveys did not provide conclusive evidence of reproductive seasonality because counts were not continued throughout the year or the lunar month. However, the survey estimates of a three-month season (December-February) partially overlap fisher reports of a four month period (January-April, Samoilys et al., 2006). Monitoring of acoustically tagged E. fuscoguttatus in the Seychelles identified a 2-3 month aggregation period, with a reduced fish abundance in the final month. There, the spawning period started as early as November and finished as late as March (Bijoux et al., 2013). Pears et al. (2007) found that E. fuscoguttatus spawns for three months (November-January) on the Great Barrier Reef, while Hamilton et al. (2012) reported that it spawned over 4-5 months (between December and March) in the Solomon Islands. The winter density at the Diani spawning site was relatively high in July, suggesting that reproduction may also occur in winter, a fact unknown by local fishers. However, this is not supported by studies in the Indo-pacific region in which E. fuscoguttatus was found to have a 3-5 month spawning season during the Austral summer.

In Kenya we found spawning aggregations occurred around the new moon (LD 28-2), which was also reported for the Seychelles (Robinson *et al.*, 2008b), Palau (Johannes *et al.*, 1999), Komodo in Indonesia (Pet *et al.*, 2005; Mangubhai *et al.*, 2011), the Solomon Islands (Hamilton *et al.*, 2012) and in captivity (Rimmer *et al.*, 2013). In contrast, the species appears to spawn just after full moon in Pohnpei, Micronesia (Rhodes *et al.*, 2012). *Epinephelus fuscoguttatus* aggregations usually develop gradually, 1-3 weeks in advance of

actual spawning. During these periods, females arrive later and stay for shorter periods than the males (Robinson *et al.*, 2008b, Nemeth, 2012; Rhodes *et al.*, 2012).

The mean number of E. fuscoguttatus at the aggregation site was 21.3 fish, corresponding to a density of 7.6 fish.1000 m⁻². When compared with the non-spawning count of 6.0 fish, equivalent to a density of 2.2 fish.1000 m⁻², the Kenyan aggregations of E. fuscoguttatus represent a 3.5-fold increase above the normal fish density. This does not strictly satisfy the Domeier (2012) definition of a four-fold increase in fishes in a spawning aggregation, and only some aggregations in December-February would comply with this requirement. Although our sample size was small, our estimate of the non-spawning density (2.2 fish.1000 m-2) was comparable to those of UVC surveys conducted elsewhere in the East African region where densities ranged from 0.8 (Mozambique) to a maximum of 3.2 (Tanzania) fish.1000 m⁻²; the mean density at three surveys sites was $1.8 (\pm 0.73 \text{ SE})$ fish.1000 m⁻² and zero sightings were recorded at a further 69 sites (Samoilys, unpubl. data). E. fuscoguttatus aggregation sizes in Kenya thus appear small and most closely resemble those at Komodo in Indonesia, where high aggregation fishing pressure is reported (Pet et al., 2005; Mangubhai et al., 2011). Densities at the Kenyan site were four- to ten-fold less than those at the Solomon Islands, Palau, Micronesia and the Seychelles (Johannes et al., 1999; Robinson et al., 2008b; Hamilton et al., 2012; Rhodes et al., 2012). Fishing pressure has possibly been sufficiently intense to deplete numbers at this site. However, it is not strictly valid to assess the status of an aggregation through comparison with different sites, as aggregation size may vary substantially within the same reef system and may be inversely related or correlated to fishing pressure (Johannes et al., 1999; Robinson et al., 2008b; Mangubhai et al., 2011). For example, at the Farquhar Atoll in the Seychelles, E. fuscoguttatus forms aggregations ranging in size from tens to hundreds of individuals at different sites, with the larger aggregations (68 fish.1000 m⁻²) the most heavily exploited (Robinson et al., 2008b; Bijoux et al., 2013).

Recent studies of groupers have demonstrated complex dynamics at aggregation sites, with the actual spawning or core site being small and nested within a larger courtship area, which is further nested within a staging area (Nemeth, 2012). This has been reported for E. polyphekadion and E. fuscoguttatus in the Seychelles (Robinson et al., 2008b). Our surveys in Kenya did not determine these zones but it is likely that the aggregation site area of 2744 m² included the core area and most of the courtship area. Aggregation densities may thus vary, depending on whether the core area alone is surveyed or the fish catchment area is included. Kenya may be characterised by small aggregations of this species, but larger aggregations of E. fuscoguttatus may form elsewhere in southern Kenya, particularly if located on deeper fringing or submerged reefs where fishing effort is reduced (Samoilys et al., 2011). Nevertheless, the relatively low numbers encountered in the study's aggregation raises cause for concern for this Near Threatened species in Kenya.

The sizes of E. fuscoguttatus individuals in the aggregating study aggregation conform to those of reproductively active E. fuscoguttatus on the Great Barrier Reef (GBR), Australia (Pears et al. (2006). These authors reported that this species is a longlived protogynous hermaphrodite, with males ranging in size from 68.3 to 92.5 cm TL and mature females from 32.0 to 85.5 cm TL. No fish smaller than 56-60 cm TL were observed in the Kenyan aggregations. The change in size frequency distribution at the aggregation sites between the summer spawning and winter non-spawning periods, with fish greater than 90 cm TL being observed only during November-January, suggests that the largest males migrate to the aggregation site to spawn. These may be the males that dominate access to females, as seen in other groupers (Samoilys & Squire, 1994; Samoilys, 1997; Robinson et al., 2008b).

Management implications

The long life of *E. fuscoguttatus* (\geq 40 years), the late onset of sexual maturity in females (nine years) and increasing female fecundity with age

over a \geq 30 year reproductive lifespan (Pears *et* al., 2006) does not confer it resilience to fishing. In fact, such life history traits are closely correlated with vulnerability to extinction (Mace & Hudson, 1999; Reynolds et al., 2003; Dulvy et al., 2003). These demographic factors, coupled with heavy fishing pressure and the many unmanaged fisheries for this grouper, led to it being classified by the IUCN Groupers and Wrasses Specialist Group in 2007 as Near Threatened on the Red List (IUCN, 2015). The fact that E. fuscoguttatus also forms spawning aggregations that appear to be spatio-temporally predictable increases its vulnerability (Sadovy de Mitcheson et al., 2008). This is particularly so in Kenya where coastal fishing is not regulated by size class (both minimum and maximum size class fishery restrictions would be beneficial for this species). Additionally, the fully-protected marine areas (nationally gazetted Marine Parks) are small, protecting only 8.6% of the country's coral reef area (Spalding, 2001; Wells, 2006) in contrast with global recommendations in the order of 30% (Fernandes et al., 2005). Recent reports of reproductive movements by E. fuscoguttatus and estimates of its catchment area suggest that large-scale marine parks are needed to protect populations of this species (Rhodes et al., 2012).

A vulnerability analysis of spawning aggregations of this species revealed that they have relatively high intrinsic vulnerability (Robinson & Samoilys, 2013a). Local artisanal catches of *E. fuscoguttatus* have dwindled in recent years (Samoilys *et al.*, in review), reflected by our inability to collect adequate gonads for reproductive assessment, or to assess population abundance through catch rate analysis. Population abundance surveys on eastern African reefs using SCUBA to 30 m have also shown that this species is now rare (Samoilys, unpubl. data), possibly because of targeted fishing of aggregations of this species.

Considering the reproductive life history and small size of the *E. fuscoguttatus* aggregation we encountered, together with the small area of the Kenyan coastline under protection, there is clearly a need for additional management measures for the conservation of this species if it is to survive along the southern Kenyan coast. The aggregation site documented here was neither managed nor protected, despite occurring within the nationally gazetted Diani-Chale Reserve. Compliance in this Reserve is not enforced due to strong local opposition by fishers. Furthermore, we know from studies in Australia (Pears et al., 2006, 2007) that E. fuscoguttatus females need to breed for \geq 30 years to reach their full reproductive potential and studies on spawning in this species suggest that aggregation sites are important for reproduction. We therefore recommend that management of this spawning aggregation site be discussed as a matter of urgency with all stakeholders, including local fishing communities, the hotel and dive tourism industry, and the Kenya Wildlife Service (KWS) which has authority over the Diani-Chale Reserve. Conflict between different users in this area has been ongoing for many years; however, a neighbouring fishing community in Msambweni has recently established a no-take zone to protect a spawning aggregation of the rabbitfish, Siganus sutor (CORDIO, unpubl. data), which provides a useful precedent. Now is the time to discuss management options, including permanent no-take zones, to protect the valuable and threatened brown-marbled grouper.

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