Western Indian Ocean JOURNAL OF Marine Science

Volume 19 | Issue 2 | Jul – Dec 2020 | ISSN: 0856-860X

Western Indian Ocean JOURNAL OF Marine Science

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Published biannually

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ISSN 0856-860X

Cover image: Ngalawa (traditional dugout, outrigger canoe) being readied for a boat race in the 2018-2019 Kraken cup, Kilwa, Tanzania. © Rahim Saggaf

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JOURNAL OF
Marine Science

Volume 19 | Issue 2 | Jul – Dec 2020

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The influence of habitat preference on longitudinal population composition and distribution of Groupers (Serranidae) in Chumbe Island Coral Park, Zanzibar, Tanzania

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Abstract

A survey of six common grouper (Serranidae) species was conducted on both the western protected and eastern unprotected reefs around Chumbe Island, Zanzibar. Species, estimated maturity, and habitat were recorded using standardized categories. Fundamental niche and general habitat preference were extrapolated based on observed realized niche and qualified based on substrate, depth, slope position, and general reef region. Taking habitat preference into account, abundance and biomass density of serranid populations were compared between locations on the reef in order to best account for how habitat influences distribution and population health. The results of this study provide depth to previous research on the protected reef and indicate noteworthy shifts in population composition between 2014 and 2018 that favour species with less specified habitat preference, such as *Aethaloperca rogaa* and *Cephalopholis argus*. Surveys of Chumbe's nearby unprotected eastern reef indicate low levels of species abundance, which this study hypothesizes is the result of inappropriate habitat structure, increased fishing pressure, and decreased population health within the MPA. Ultimately, this study suggests that MPAs do not protect all species equally, and habitat preference must be taken into account when assessing MPA effectiveness at protecting different species. Indeed, especially as serranid habitat faces continued degradation, serranid conservation will depend even more on protection of each species' preferred habitat in coral systems. As such, assessing serranid populations as a whole fails to capture the changes in population distribution and composition that is occurring between species, which may be more indicative of shifts and disturbances in the ecosystem.

Keywords: marine protected areas, habitat preference, phase shift, groupers, Chumbe Island, Western Indian Ocean

Introduction

Coral reefs offer many ecosystem services, many of which operate in a synergistic relationship with one another. For example, a reef's capacity to support a biodiverse aquatic community is contingent, in part, on the degree to and manner in which it is fished by coastal communities, and vice versa. In Zanzibar, the rapid growth of coastal populations has resulted in unsustainable exploitation of the productive fishing grounds offered by nearby coral reefs. This overexploitation has not only diminished reef biodiversity, but also sapped these systems of the bountiful fisheries that attracted coastal populations to fish them in the first place.

Coral reefs are sensitive ecosystems, and many of the services they offer and much of the marine life that occupy them are contingent on a high standard of health (Richmond, 2011). Groupers (Serranidae) are apex predators that exhibit strong habitat preferences to structurally complex and healthy reefs and therefore are often regarded as an indicator of overall reef health (Hackradt *et al*., 2014). The presence of groupers on a reef indicates (1) that the reef is not overexploited, (2) that the coral is healthy and complex, (3) that lower trophic levels are being balanced by natural predation (Hackradt *et al*., 2014; Kelly and Ruhl, 2011), and (4) that the reef likely supports high abundances and biodiversity of marine life and offers noteworthy, stable

http://dx.doi.org/10.4314/wiojms.v19i2.1

ecosystem services to the surrounding area (Hackradt *et al.*, 2014; Worm *et al.*, 2006). However, serranids are especially vulnerable to overfishing and ecosystem degradation due to their site fidelity and highly specific habitat preferences (Chiappone et al., 2000; Kelly and Ruhl, 2011; Zeller, 1997, 2002); tendency to form spawning aggregates (Sadovy and Coiin, 1995); and long life, slow growth rate, and delayed sexual maturity (Hackradt et al., 2014; Sadovy and Coiin, 1995), all of which result in low resilience to disturbances in population and habitat (Sadovy de Mitcheson *et al.*, 2013).

While the aforementioned qualities situate serranids as an indicator of reef health, in the face of coral degradation due to global climate change and ocean acidification, they also contribute to the vulnerability of Zanzibar's reef dwelling serranid populations. Additionally, in a burgeoning tourist economy like that of Zanzibar, groupers often generate a high market price, and their populations have suffered as a result. Moreover, in a reality in which comprehensive studies of grouper spawning aggregations, larval export, and population dynamics are lacking worldwide, longitudinal research into the persistence of grouper populations in the western Indian Ocean has fallen relatively by the wayside. While these factors contribute to groupers' vulnerability, they also render groupers an ideal case study for comprehensively assessing the effectiveness of Chumbe Island Coral Park Limited (CHICOP) at protecting serranids and restoring reef biodiversity, as well as promoting spillover and restoring fisheries in neighboring unprotected areas.

In order to best account for the rapid changes occurring on coral reefs in the face of climate change, this study aims to identify habitat preferences of six common species of grouper in order to inform best management strategies in the face of external pressures that cannot be eliminated by the boundaries of a no-take area (NTA). Habitat health and type have been shown to significantly influence not only the distribution, but also abundance and biomass of groupers (Hackradt *et al.*, 2014). Thus, defining the habitat preferences of these apex predators is of the utmost importance in order to appropriately attune management strategies in response to environmental change and to best ensure continued conservation of serranids under present and future threats (Berger and Possingham, 2008; Friedlander *et al.*, 2003). Comparisons between fundamental niche, or the habitat that a species is expected to occupy based on known preferences, and realized niche, the habitat that a species actually occupies within CHICOP, serve as a foundation for discussion of the variables at play that might cause these two areas to be different, and an assessment of overall reef health (Buxton *et al.*, 2014). Accurate definitions of a species' fundamental niche allow for efficient and effective conservation of their habitat, if the population of that species is found to be in decline. Likewise, by methodically observing changes in a species realized range, one is able to extrapolate changes in overall ecosystem and reef health and better understand phenomena such as regime shifts and spillover effect (Rowly, 1994). Thus, a sound understanding of the relationship between a species and the habitat it occupies is foundational to their effective and long-term conservation.

CHICOP is a privately-owned marine protected area (MPA) off the western coast of central Unguja, Zanzibar, safeguarding ecological ecosystem services offered by coral reefs, which include buffering coastlines from wave action, sequestering carbon dioxide, and supporting the biodiversity of marine species that depend upon them (Richmond, 2011). Indeed, even small scale MPAs like CHICOP have been shown to consistently support higher abundance, biodiversity, and biomass of groupers and other predatory and commercially fished species than surrounding unprotected areas (Edgar *et al.*, 2014; Fenberg *et al.*, 2012; Hackradt *et al.*, 2014). In order to better understand the effectiveness of CHICOP in adequately meeting the needs of the reef – both in terms of ecological health and the aesthetics necessary to generate income from tourism to fuel management and research - and those of local fishermen, this study aimed to systematically assess serranid populations on the protected and unprotected areas and serves as an initial foray into a study of localized population dynamics around Chumbe Island (Francis *et al.*, 2002).

This report uses data gathered by Catherine Nesbitt in 2014 to compare population composition and biodiversity before and after a significant disturbance in coral reef health (2016 mass coral bleaching event). Nesbitt's study contextualizes the findings of this study and provides a basis for predicting the system's response to future threats. It is important to consider that this study draws its analytical power from the fact that it takes each species' habitat appropriateness into account when considering its respective abundance and biomass density. Moreover, focused investigation into realized niche offers amendment to current understanding of each species' fundamental niche. Overall health of the reef is measured based on the abundance of groupers it currently supports and both the quality and type of habitat they occupy. By conducting research within an NTA that adheres to four out of the five features shown by Edgar *et al*. (2014) to exponentially benefit conservation success (no-take, effective enforcement, isolation by deep water or sand, and more than 10 years of existence), changes in serranid populations may largely be attributed to the anthropogenic degradation of coral reefs via sea level and temperature rise, which unfortunately cannot be kept at bay by the boundaries of an MPA (Edgar *et al*., 2014). Ultimately, this study intends to lay a foundation for continued monitoring and research on population dynamics on and between protected and unprotected reefs and to generate an understanding of how grouper habitat might be better managed to maximize the benefit to reef health and local fishers.

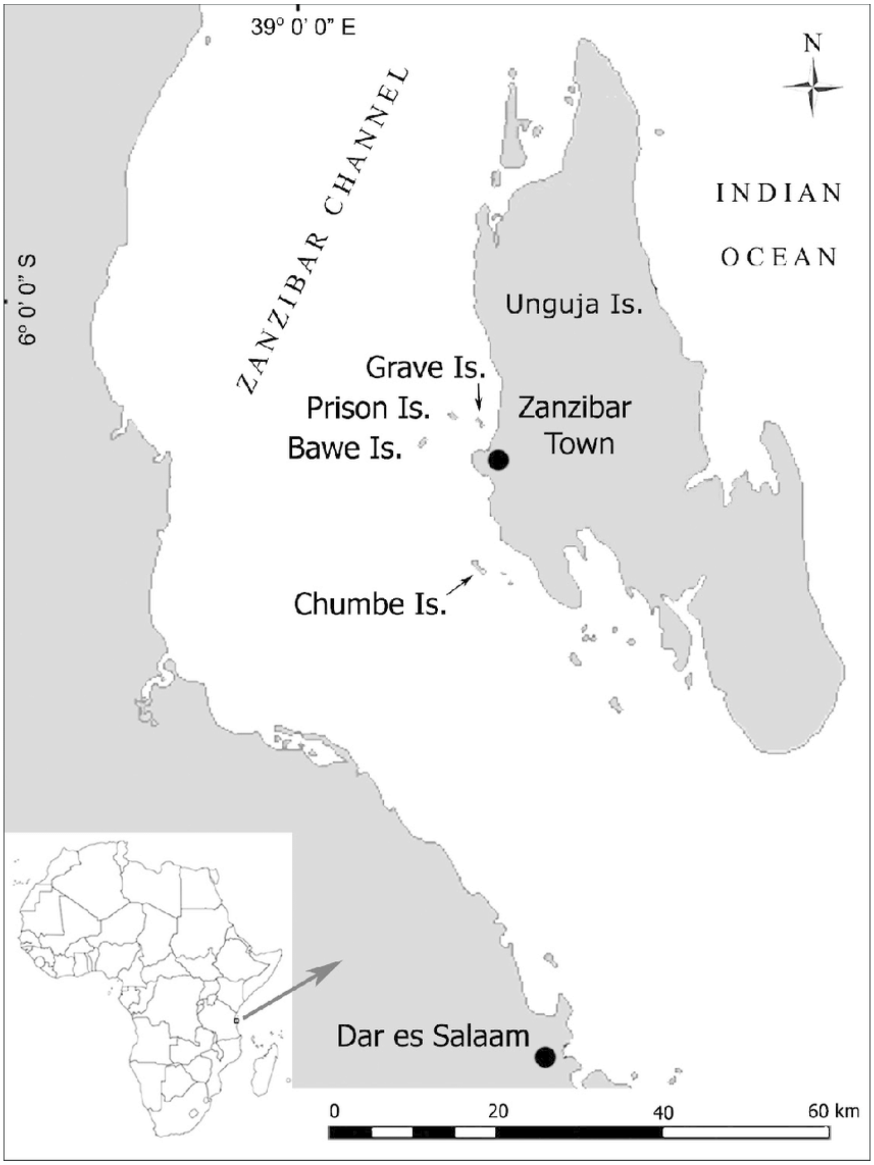


Figure 1. Map of Chumbe Island in relation to Zanzibar and mainland Africa (adapted from Nesbitt and Richmond 2015).

Materials and methods

Study Site

Chumbe Island is located 6 km off the western coast of Zanzibar and 33 km off the eastern coast of Tanzania in the Zanzibar Channel. It measures a maximum of 1 km running north to south and is characterized by a fringing coral reefs on both sides.

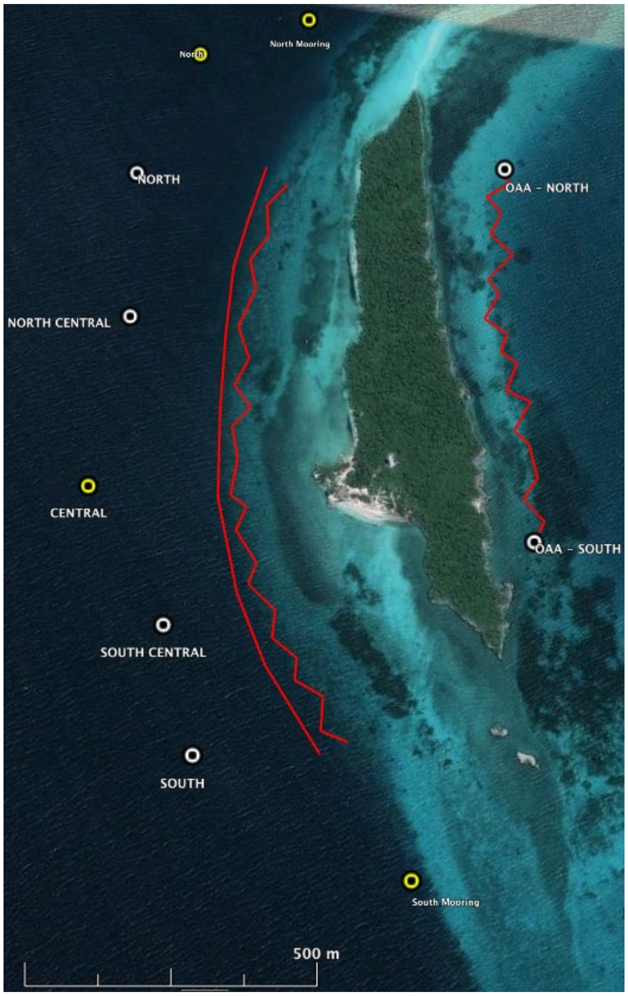
Table 1. Description of focus species and respective fundamental niche (Debelius, 1999; Hiatt and Strasburg, 1960; Lieske and Myers, 1996; Kelly and Ruhl, 2011; Nesbit, 2014; Nesbit and Richmond, 2015; Unsworth *et al*., 2007, IUCN.org).

Species	Description	Distinction of Maturity	Substrate	Depth	Reef Slope	IUCN Status	Notes
Aethaloperca rogaa (Redmouth Grouper)	Dark body, red inside mouth; juveniles distinguished by white margin at end of tail and variable white bar on side	Reaches 34 cm Maximum length: 60 cm	Sparse coral Deep coral Deep sand	1 – 54 m	On and around reef slope and backreef	Data Deficient (Unknown trend)	Uncommon; not caught by fishermen; wide range
Anyperodon leucogrammicus (Slender Grouper)	Elongated body with flat, long snout and round tailfin; pink-brown with pale stripes; juveniles distinguished by white and yellow stripes	Reaches 30 cm and/or Color change Maximum length: 65 cm	Sparse coral Dense coral	1 – 50 m	Top of reef slope and backreef	Least Concern (Unknown trend)	Associates with table corals in shallow reefs; uncommon with generally low abundance
Cephalopholis argus (Peacock Grouper)	Dark brown or red with blue rimmed black spot and lighter bands toward tail	Reaches 22 cm Maximum length: 60 cm	Dense coral Deep sand	< 6 m	On and around reef slope	Least Concern (Stable)	Common on coral reefs
Cephalopholis miniata (Coral Grouper)	Orange-red body with small, blue spots with brown boarders; juveniles distinguished by orange coloration with widely scattered blue spots	Reaches 26 cm Maximum length: 50 cm	Dense coral Deep sand	4 – 150 m	On and around reef slope; concentrated where steepest	Least Concern (Decreasing)	Common; caught in artisanal fisheries
Epinephelus fuscoguttatus (Brown Marbled Grouper)	Dark brown with light brown mottling	Reaches 50 cm Maximum length: 120 cm	Dense coral Deep sand	1 – 60 m	On and around reef slope	Near Threatened (Unknown trend)	Uncommon and wary; caught in artisanal fisheries
Plectropomus laevis (Black Saddled Grouper)	Red-brown, dark spots and white belly; five light bands on back and flanks; juveniles distinguished by yellow fins and five black bands across back	Color change Maximum length: 125 cm	Sparse coral Dense coral Deep sand	4 – 90 m	Bottom of reef slope	Vulnerable (Decreasing)	Strong habitat preference; wary

In accordance to Tanzania's commitment to protect 10 % of its marine ecosystems by 2012, Chumbe Island Coral Park Limited - which includes mangrove forests and other terrestrial ecosystems, as well as 55 hectares of the western fringing reef and associated backreef, seagrass beds, and coast – was established in 1994 by the semi-autonomous government of Zanzibar (Nordlund *et al*., 2012). Chumbe's western fringing reef and abutting backreef and seagrass beds fall within the NTA, providing extensive research opportunities and vigilant protection by CHICOP. Even before the Park's inception in 2006, the western fringing reef supported a grouper population that was 300 % larger than that of the eastern unprotected reef (CHICOP, 2017). Chumbe's unprotected eastern fringing reef, however, has no protection, and, as a result, is vulnerable to over-exploitive and sometimes destructive fishing practices.

Focus Species

Table 1 includes brief descriptions of the six serranid species included in this study. These species are informally regarded as the most commonly observed within CHICOP. Fundamental niche and general habitat preference are informed both by external species profiles and Nesbitt's survey of these same species in the MPA in 2014, thereby attuning the descriptions to the populations specific to Chumbe's western reef. Other species were observed within the MPA, but were not included in this survey for the sake of continuity between this and Nesbitt's study. An understanding of general fundamental niche contextualizes and corroborates the validity of the realized niches of each species observed in this study.



	Zone	Latitude	Longitude
MPA	NORTH	6° 16.509'S	39° 10.483'E
	NORTH CENTRAL	6° 16.664'S	39° 10.453'E
	CENTRAL	6° 16.837'S	39° 10.456'E
	SOUTH CENTRAL	6° 16.971'S	39° 10.494'E
	SOUTH	6° 17.096'S	39° 10.571'E
OAA	NORTH	6° 16.505'S	39° 10.730'E
	SOUTH	6° 16.892'S	39° 10.771'E

Figure 2. Map of Chumbe Island and estimated transects and zones. Red lines represent estimated transects. Yellow markers indicate buoys present at time of survey, white markers indicate imaginary points of differentiations. Capitalized labels indicate differentiation between zones, estimated latitude and longitude included in above table. Estimations of area surveyed were calculated based on these coordinates.

Survey Methods

Visual under-water censuses were conducted on both the slope and backreef of the western no-take zone and the reef of the eastern open access area on either side of Chumbe Island, Zanzibar during the month of November 2018. The western reef was surveyed within the MPA between points at which coral becomes notably sparse and the slope disappears. Start and end locations in the southern- and northern-most reaches of the MPA were replicated relative to landmarks on the island and were approximated at 6°17.096'S, 39°10.571'E and 6°16.509'S, 39°10.483'E, respectively. Both the slope and the backreef were surveyed between these two points from south to north within prescribed zones approximated by visual landmarks on the island (Fig. 2). The slope was surveyed linearly from south to north, thereby representing an informal transect. The reef slope was defined as the area of steepest bathymetric decline between dense coral and deep sand and was characterized by dense coral cover. The backreef was surveyed in a serpentine swim parallel to the slope at a minimum perpendicular distance of approximately 10 m (English *et al*., 1997). Backreef was defined as the area adjacent to the slope with no significant incline and was characterized by sparse to dense coral cover. The eastern reef was surveyed north to south in a serpentine swim parallel to Chumbe's coast and the area surveyed was bounded by landmarks on the island that corresponded to where coral begins and ends at the northern and southern ends of the informal transect, and were approximated at 6°16.505'S, 39°10.730'E and 6°16.892'S, 39°10.771'E, respectively. The western slope and backreef (hitherto, in addition to the east reef, referred to as 'regions') were divided into four 'zones' (north, north central, south central, and south) according to landmarks in order to compare serranid populations between eight distinct 'locations' (e.g. south central backreef). Southern zones were surveyed at low to mid tide, northern zones were surveyed at mid to high tide, and the eastern reef was surveyed exclusively at low tide.

Differentiation of 'zones' is explained in greater detail in Fig. 2. Yellow markers represent physical buoys that were present at the time of survey, and white markers represent markers that were approximated based on position relative to specified on-land markers. Markers with capitalized labels indicate differentiations between zones. The red lines represent approximate transects, the straight line represents slope surveys while the serpentine lines represent backreef swims.

The entire slope, backreef, and eastern slope were surveyed a total of three times, and the north and south-central zones were surveyed an additional three and two times respectively due to the importance of slope to serranid habitat. All individuals within 5 m of either side of the transect were included in the survey. Species and estimated length and/or maturity for each individual as well as habitat parameters such as depth, substrate, position on slope, and general notes for each sighting were recorded using a waterproof audio recorder attached to a floating ring. In addition to the time at which each species was sighted, time at which each zone was entered and exited, region surveyed, tide, and ambient weather conditions were recorded. Maturity was determined post-survey based on the information in Fig. 1, unless species maturity is indicated by color change (e.g. Plectropomus laevis), in which case it was determined in-field (Debelius, 1999; Nesbitt, 2014).

Results

Population distribution, composition, and diversity

A total of 362 individuals were observed around Chumbe Island, the majority of which were recorded within the MPA. Nearly twice as many individuals were observed on the slope compared to the backreef. There were 700 % more individuals on the protected backreef than the unprotected eastern reef, and the protected backreef supported a biomass density of 93.43 kg/ha compared to the eastern reef's 2.3 kg/ha (Table 3). Across all study locations, *Aethaloperca rogaa* dominated the population and was observed more frequently than *Plectropomus laevis*, *Epinephelus fuscogutattus*, *Cephalopholis miniata*, and *Anyperodon leucogrammicus* (Kruskal-Wallis, Dunn posthoc, $p < 0.0001$ for all species). There was no statistically significant difference observed between populations of *A. rogaa* and *C. argus*, though *C. argus* was also observed more frequently than the aforementioned four species (Kruskal-Wallis, Dunn posthoc, $p = 0.0013$, $p = 0.0005$, $p = 0.0008$, $p = 0.0013$, respectively). *A. rogaa* also exhibited a total biomass that is significantly higher than all study species except *C. argus* (Kruskal-Wallis, Dunn posthoc, $p = 0.0026$, $p = 0.0192$, $p = 0.0003$, $p = 0.0009$, respectively). Similar to abundance, no statistically significant difference in biomass between *A. rogaa* and *C. argus* was observed, and the population biomass of *C. argus* was significantly higher than that of *P. laevis*, *C. miniata*, and *A. leucogrammicus* (Kruskal-Wallis, Dunn posthoc, $p = 0.0247$, $p = 0.0052$, $p = 0.0115$, respectively). Slope and backreef regions were dominated by *A. rogaa*, both in relative species abundance and biomass density (Tables 2 and 3). *A. rogaa* was only exceeded in biomass density in the north slope by *E. fuscogutattus* (Fig. 4). With a relative abundance that was still less than half that of *A. rogaa*, *C. argus* was observed to have the second highest relative abundance in both protected regions, and like *A. rogaa*, its biomass density also fell behind that of *E. fuscoguttatus* (Fig. 4). The relative abundance and biomass density of *C. argus* remained relatively constant across locations, whereas both relative abundance and biomass density for populations of *A. rogaa* spike in central sloping regions (Fig. 3 and 4). High relative abundances and biomass densities were shown on both central slopes across all species (Fig. 3 and 4). In keeping with their distribution within the population and across regions, relative species abundances of *P. laevis, E. fuscoguttatus*, *C. miniata*, and *A. leucogrammicus* were consistently lower than those of *A. rogaa* and *C. argus*.

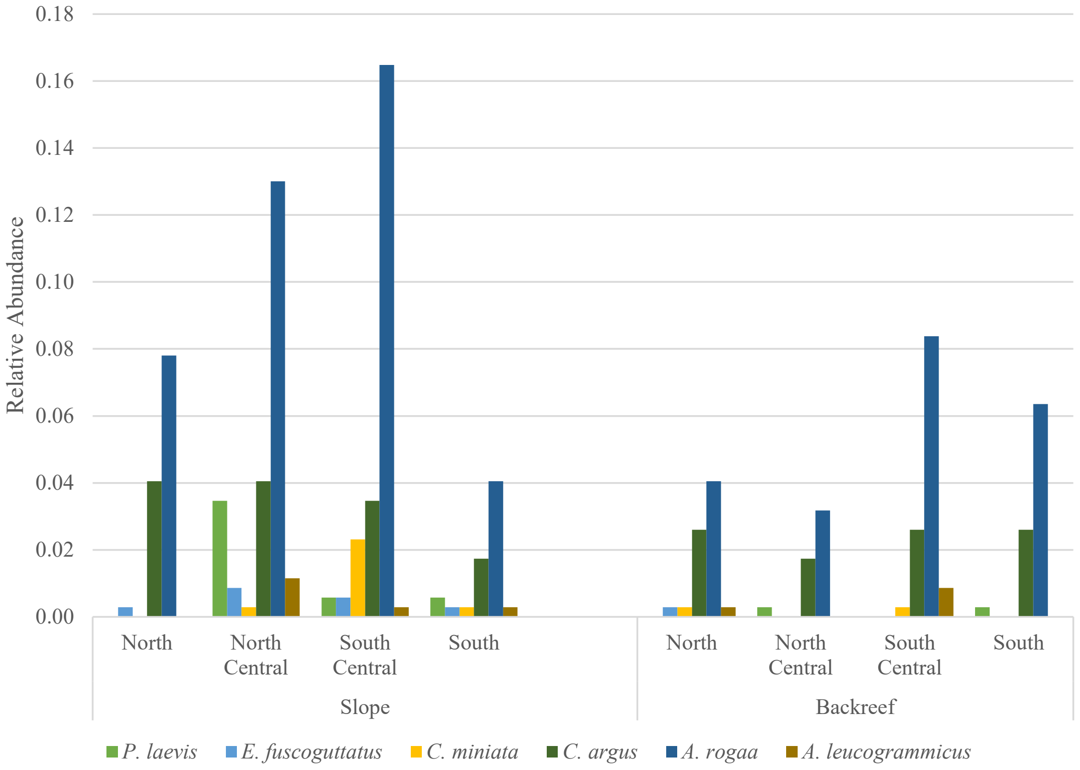


Figure 3. Total species abundance and relative abundance of six focus Serranidae species between regions and locations in Chumbe Island's MPA. Table 3a. Relative species abundance calculated between regions out of region total population counts. East reef not included in "TOTAL" MPA species abundance and relative species abundance. Figure 3b. Relative species abundance calculated between 'locations' out of total reef population count. East reef not included.

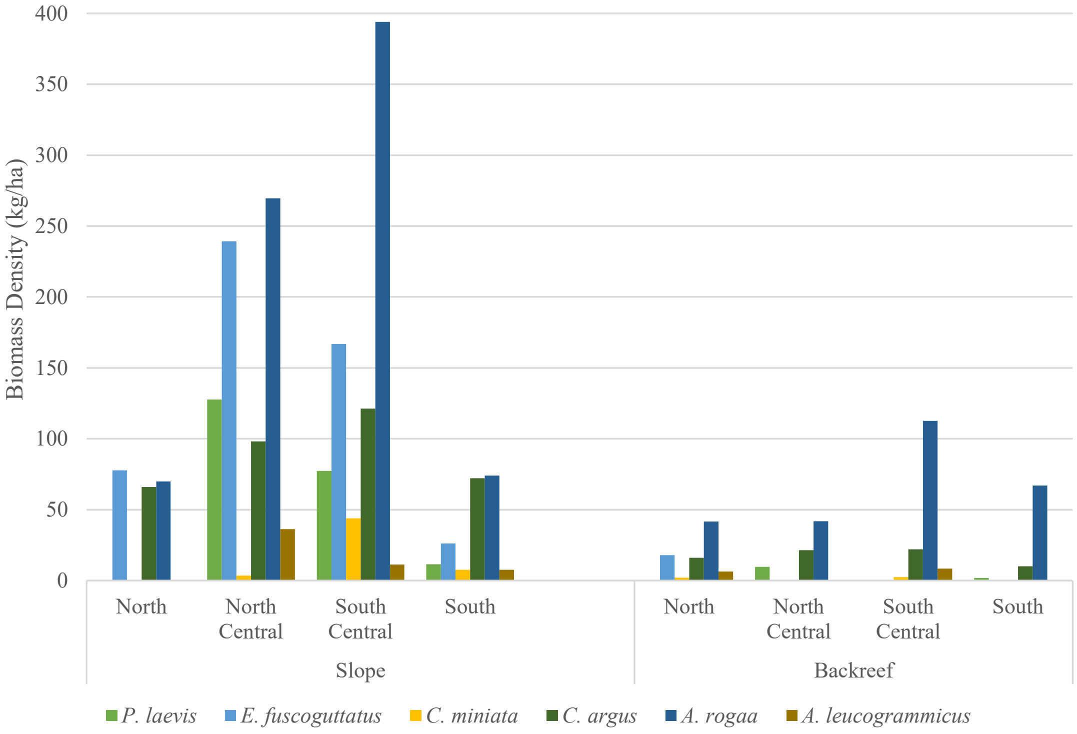


Figure 4. Total biomass density (kg/ha) of six focus Serranidae species between regions and locations in Chumbe Island's MPA. Total hectares surveyed estimated by multiplying total transect length for each region by perpendicular width of area surveyed. Individual fish masses calculated according to length-weight relationships offered in "Biomass Calculator" Excel sheet available at Chumbe Office, Stonetown, Zanzibar. Table 3. Species biomass density calculated between regions out of total region hectarage. East reef not included in "TOTAL" MPA biomass density. Figure 4b. Species biomass density calculated between 'locations' out of total reef hectarage.

Table 2.

	Total Abundance (Relative Abundance)			
	Slope	**Backreef**	**Total**	**East Reef**
P. laevis	16 (0.07)	2 (0.02)	**18 (0.05)**	0 (0)
E. fuscoguttatus	7 (0.03)	1 (0.01)	**8 (0.02)**	0 (0)
C. miniata	10 (0.04)	2(0.02)	**12 (0.03)**	1 (0.06)
C. argus	46 (0.20)	33 (0.28)	**79 (0.23)**	13 (0.81)
A. rogaa	143 (0.63)	76 (0.63)	**219 (0.63)**	1 (0.06)
A. leucogrammicus	6 (0.03)	4 (0.03)	**10 (0.03)**	1 (0.06)
Total	**228**	**118**	**346**	**16**

Table 3.

	Biomass Density (kg/ha)			
	Slope	**Backreef**	**Total**	**East Reef**
P. laevis	54.09	3.17	**27.29**	0.00
E. fuscoguttatus	128.01	4.68	**63.10**	0.00
C. miniata	12.57	1.10	**6.55**	0.05
C. argus	88.38	17.51	**51.83**	1.94
A. rogaa	196.18	63.42	**126.37**	0.17
A. leucogrammicus	14.09	3.54	**8.59**	0.14
Total	**493.31**	**93.43**	**283.74**	**2.30**

Reef slope exhibited higher diversity than the backreef within the MPA, except in the northern zone (Table 4). The north central zones exhibited the highest diversity and the other three zones displayed diversity comparable to one another. In terms of both the Shannon-Weiner Index and general species richness, the lowest diversity occurred in the southern backreef and northern slope. Diversity in the eastern open access area (OAA) was comparable to the southern backreef and northern slope, despite the fact that the total abundance and biomass density of the eastern reef were lower than these two locations. Overall, the western MPA exhibited a Shannon-Weiner Index of 1.09 and a species richness of 6.

Table 4. Shannon-Wiener Index of diversity and (species richness) by location on both protected and unprotected reefs around Chumbe Island.

MPA - West Reef	**North**	**N. Central**	**S. Central**	**South**	
Backreef	1.08 (5)	0.83 (3)	0.86 (4)	0.72 (3)	0.93 (6)
Slope	0.65 (3)	1.24 (6)	1.00 (6)	1.26 (6)	1.14 (6)
	0.90 (4)	1.20 (6)	0.99 (6)	1.01 (6)	
OAA - East Reef	**0.69 (4)**				

Figure 5. Habitat preferences of juvenile and mature individuals of each species according to the relative abundance of each age class observed in each qualifier. X-axis represents abundance relative to total population count on both the western and eastern reef. Distinctions between juvenile and mature individuals made according to parameters listed in Figure 1.

Habitat Preference

Significant relationships between maturity and habitat preference existed in *C. argus* and *A. rogaa*. There was a significant relationship between maturity of *A. rogaa* and slope and depth (Chi Squared Test, $p < 0.001$ and $p < 0.001$, respectively). Mature individuals favoured the bottom of the reef slope, and juvenile individuals favoured the middle of slope. Juvenile individuals were observed more frequently at depths of less than 5 meters, while mature individuals were observed most often at depths between 5 to 10 meters. There was also a significant relationship between maturity of *C. argus* and depth and slope, as well as region observed (Chi Squared, $p = 0.021$, $p < 0.001$, $p = 0.001$, respectively). Both mature individuals favoured non-sloping environments and the bottom of slopes, and juvenile individuals exhibited a strong preference to non-sloping environments. Both juveniles and mature individuals were observed more frequently at depths between 5 to 10 meters. Juvenile *C. argus* exhibited a preference to reef slopes, while mature individuals preferred backreef environments. No significant relationship between age and substrate existed for either *A. rogaa* or *C. argus* (Fig. 5).

C. argus and *A. leucogrammicus* were present in almost equal relative abundance in the slope and non-sloping environments. Only *A. rogaa* and *C. miniata* were observed at depths greater than 10 meters, and these two species were observed in all habitat categories. Out of all focus species, *A. rogaa* exhibited the largest relative abundance at depths greater than 10 meters (Fig. 5). *P. laevis* was observed in all habitats except at depths greater than 10 meters and on the OAA eastern reef. *A. rogaa* and *C. argus* were observed in all habitat categories. *E. fuscoguttatus* was not observed in 3 habitat categories, with no sightings on the eastern backreef, at depths greater than 10 meters, and at the bottom of the reef slope.

Age Distribution

Very few mature *P. laevis* and very few juvenile *A. leucogrammicus and C. miniata* were recorded, and no juvenile *E. fuscoguttatus* were observed (Fig. 6). Theis small sample size renders it difficult to determine whether differences in habitat preference exist between age groups in these species. Comparatively, populations of *A. rogaa* and *C. argus* were more evenly distributed across maturities, and juvenile habitat preference mirrored that of the adult individuals. More juvenile *P. laevis* were observed than mature individuals, which is an age distribution unique to this species.

Abundance, biomass, and biodiversity between 2014 and 2018

A comparison between 2014 and 2018 survey data indicated a change in population composition over the four years. Relative species abundance decreased for all species, except *A. rogaa*, which exhibited an almost 100 % increase in relative abundance between 2014 and 2018 (Fig. 6). In conjunction with a spike in relative abundance, biomass of *A. rogaa* increased as well. Relative abundance of *C. miniata*, *A. leucogrammicus*, and *E. fuscoguttatus* all decreased minimally and

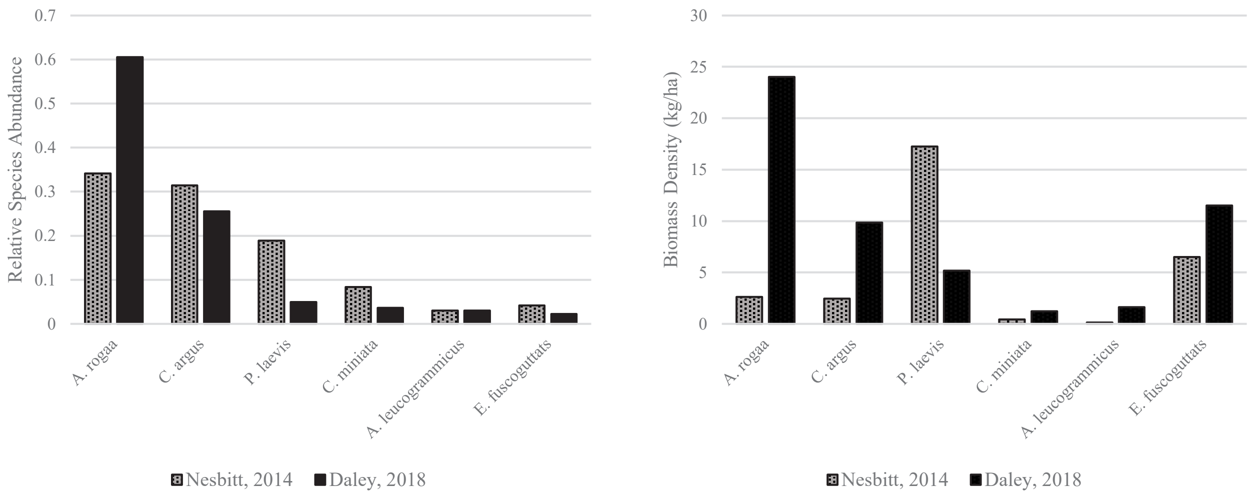


Figure 6. Comparison of relative species abundance and biomass density between serranid surveys conducted in 2014 and 2018 around Chumbe Island. Biomass density calculated over 12.5 hectares of coral reef within the NTA. The 2014 biomass calculated based on averaged weight categories.

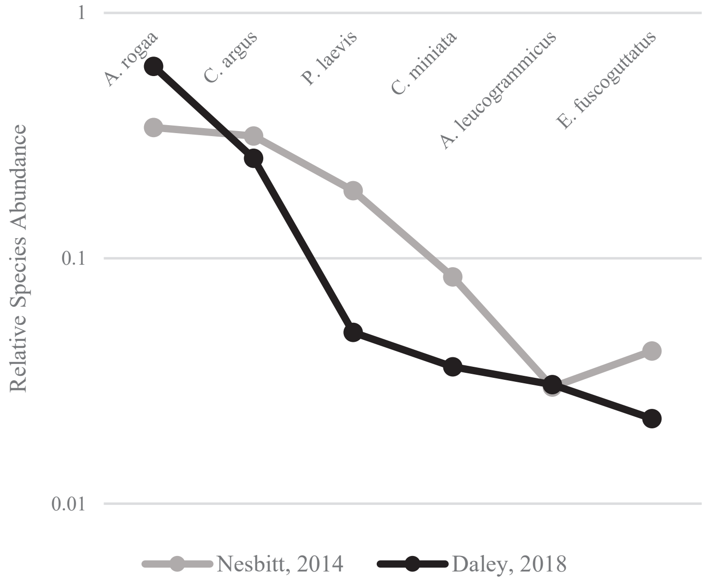


Figure 7. Comparison of average biomass per individual (kg) within the MPA between CHICOP's general long-term monitoring programme and Nesbitt's (2014) and Daley's (2018) focused surveys.

stayed below 0.1, but biomass density of all three species increased since 2014. *C. argus* experienced minimal decreases in relative abundance and an increase in biomass.

There was a 75 % decline in the already relatively low abundance of *P. laevis*, and a 66 % decline in biomass density (Fig. 7). These shifts in abundance are reflected in the decrease in serranid biodiversity from 1.49 in 2014 to 1.09 in 2018. All species except *A. rogaa* experienced a decrease in relative abundance, and therefore the population experienced losses in both evenness and biodiversity. Though all species were represented in both years, this decrease in evenness is corroborated by the steep and concave appearance of the Whittaker plot in 2018 compared to the 2014 trendline (Fig. 7).

Discussion

Population distribution and composition

All six species exhibited lower abundance on the backreef than the slope, and a lower abundance and biomass density on the OAA than the protected backreef. This phenomenon was also observed by Nesbitt (2014) and suggests that most serranid species prefer deeper reef slopes to shallower, non-sloping environments (Chiappone *et al*., 2000; Nesbitt and Richmond, 2015). Relative abundance and biomass density were generally higher for all species on the north and south central slopes, indicating that the continuity and complex reef structure of the central slopes attracted more and larger individuals than other locations (García-Charton *et al*., 2001). This pattern was not reflected in the central backreef locations. This is potentially due to the fact that while the central slopes are differentiated from the northern and southern slopes by steeper slope and higher structural complexity, there is less preference given to location on the more structurally homogeneous backreef.

A. rogaa dominated the serranid population both in terms of abundance and biomass density, exhibiting significantly higher abundance and biomass density than all species except *C. argus*. The high biomass density of these two species is especially noteworthy considering A. rogaa and C. argus share the second smallest maximum length (60cm) of the six focus species. *A. rogaa* had the highest relative species abundance across all locations, with noteworthy increases on the central sloping locations. This increase in relative abundance suggests that while *A. rogaa* thrives in a variety of habitat types, like all species observed, it prefers deeper sloping reefs. Thus, the fact that the biomass of *A. rogaa* exceeded that of both *P. laevis* and *E. fuscoguttatus* (except on the northern slope) despite its relatively small maximum length speaks to the scale of its relative abundance (63 %) across all eight locations. Unlike many serranid species, *A. rogaa* is known to have a wide fundamental niche and low site fidelity. Therefore, it is not surprising that a species with less distinct habitat preference dominates Chumbe's MPA and was most frequently observed pelagically on deep reef slopes.

C. argus exhibited the second highest abundance, with a more consistent relative abundance and biomass across locations. The biomass density of *C. argus* was surprisingly high given its small maximum length, which is likely attributable to the fact that its relative abundance is consistently second to that of *A. rogaa*. The low abundances and biomass densities of *E. fuscoguttatus*, *P. laevis*, *C. miniata*, and *A. leucogrammicus* reflect a patchy distribution and highly specified fundamental niche that was likely not adequately assessed by the survey methods employed by this study (Unsworth *et al*., 2007). Despite this, potentially due to its large maximum size, *E. fuscoguttatus* surpassed *A. rogaa* in biomass density, but not relative abundance on the north slope. *E. fuscgotuttatus* and *P. laevis* exhibited specific preference to the central slope, and *E. fuscoguttatus* displayed particular preference to the north central slope where coral begins to become sparse (Nesbitt, 2015).

Serranid diversity

A. rogaa dominated both Chumbe's western backreef and slope, and, as a result, the distribution of these six species was not even, which is attributable overarchingly to the fact that small MPAs do not protect all species equally. Although Chumbe meets four of the five qualifications for successful conservation via an MPA as listed by Edgar *et al.* (2014), it does not meet the minimum size (100 km^2) cited to maximize marine park benefits. Small NTAs fail to adequately protect large serranid species and species that participate in spawning aggregations (Unsworth *et al*., 2007). Moreover, small NTAs render rare species with specific habitat preferences especially vulnerable to density dependent intra and interspecific competition compared to more robust species that are able to thrive in more than one habitat or microhabitat (Donaldson, 2002).

As a region, the backreef supported a lower level of diversity than the slope. This finding was congruent with the decreased biomass density and relative abundance of all species in that region. The northern zone was the only zone in which the diversity of the slope exceeded that of the backreef. This discrepancy was likely due to the fact that the northern backreef extends further north than the slope, thereby providing a larger area of potential habitat. The central zones of each region exhibited higher levels of diversity according to the Shannon-Wiener Index than adjacent locations in the same region, which substantiates the hypothesis that all six *Serranid* species favor the complex central slope (García-Charton *et al*., 2001).

Habitat preference and age distribution

The abundance of *A. rogaa* in all locations implies a broad fundamental niche (Nesbitt, 2015). The distribution of *A. rogaa* and *C. argus* revealed specific habitat preferences between species. While *A. rogaa* was observed in all habitat categories, the species indicated preference to the bottom of the slope and non-sloping environments and depths between 0 and 9 m. These preferences reflect a unique willingness to venture away from the structure of continuous reef, and *A. rogaa* was frequently observed swimming pelagically more than 10 m away from reef slope structure. Juveniles were observed in all habitat categories (except at depths greater than 10 m) in relative abundance proportionate to the mature population, indicating that the reef within the NTA was suitable to this species at all life stages and that the age distribution of this species was healthy.

The only other species that exhibited a healthy age distribution is *C. argus*, though there was a more distinct difference in preferred habitat between juvenile and mature individuals. Juvenile *C. argus* were more frequently observed on the backreef, non-sloping environments and mid reef slope. This population's apparent lack of preference for substrate and region and noticeable preference to depths less than 10 m allows it to exhibit high abundance and biomass density within the MPA, which is characterized by a dense reef slope and a sparse, shallow backreef.

P. laevis, E. fuscoguttatus, and *C. miniata* displayed high relative abundances on the slope and areas of dense coral cover, corroborating Nesbitt's observations that their habitat and range are limited and specific (Nesbitt, 2015). Their preference for these qualities explains the spike in relative abundance and biomass density in central sloping regions and on the slope in general. Indeed, the central slopes possess increased coral complexity and density as well as a wealth of vertical niches not offered by more shallow and non-sloping locations. This richness and variety predispose the north and south-central slopes to support higher abundances and biodiversity, and the presence of species with more specific niches in these regions reflects their complexity and health (García-Charton *et al*., 2001).

Few to no juvenile *E. fuscoguttatus, C. miniata,* and *A. leucogrammicus* were observed, and therefore, no representative conclusions regarding difference in habitat preference and age can be drawn. It is not surprising that few *A. leucogrammicus* were identified in surveys conducted by both Nesbitt and in the present study because they are notoriously furtive and generally uncommon (Hiatt and Strasburg, 1960; Nesbitt, 2015; Unsworth *et al*., 2007). However, the absence of juveniles of all three species suggests an imbalance in age distribution. It is possible that larval import and juvenile migration into the MPA have been compromised either by these species' contribution to exploited spawning aggregations (Friedlander *et al*., 2003; Sadovy de Mitcheson *et al*., 2013), lack of connectivity between appropriate habitat (Fenberg *et al*. 2012), or the absence of other healthy ecosystems to contribute to larval export and from which developed individuals might migrate (García-Charton *et al*., 2001). Additionally, the MPA may simply not include enough appropriate habitat to support high abundances of these species. These imbalances in maturity and population abundance as a whole have the potential to negatively impact reproductive health and generate a positive feedback loop that ultimately results in population collapse (Hackradt *et al*., 2014). Thus, populations of *E. fuscoguttatus*, *C. miniata*, and *A. leucogrammicus* are especially at risk due to the fact that these reproductive stressors are exacerbated in small populations with limited and specific habitat niches (Hiatt and Stasburg, 1960).

The population of *P. laevis* was composed of fewer adults than juveniles, which exhibit a broad realized niche. Too few mature individuals were observed to determine representative differences in habitat preference between age groups. While the habitat preference of juvenile *P. laevis* was apparently broad, mature individuals most likely favour more specific habitats due to their large maximum size (Nesbitt, 2015). Their scarcity, as well as that of *E. fuscoguttatus*, may be attributed to the slow growth rate and limited spawning period of large species (Sadovy and Coiin, 1995). The population as a whole was still relatively small compared to those of *A. rogaa* and *C. argus* and exhibited a decrease in relative abundance and biomass densities since 2014. The scarcity of mature *P. laevis* and the general decline in population health is especially significant considering the species' status as "vulnerable" according to the IUCN and warrants further attention.

Regime shift between 2014 and 2018

Nesbitt (2015) conducted a foundational serranid survey within the MPA in order to establish long term monitoring efforts for these important species. This study adopted her six species of focus and modified and expanded the methods slightly in order to compare serranid population composition and distribution before and after a mass coral beaching event that occurred within CHICOP in 2016. Between 2014 and 2018, the biomass density for all species except *P. laevis* increased, and in 2014, the population of *P. laevis* was divided evenly between juvenile and mature individuals. These changes in the population of *P. laevis*, in conjunction with a decrease in relative species abundance, suggest that fewer individuals are reaching maturity and that the population as a whole is in decline. Indeed, *P. laevis* exhibited the highest biomass density of all species in 2014, making its decline all the more alarming. While it is difficult to fully attribute the decline in *P. laevis* to changes in coral structure and complexity caused by the bleaching event, it is likely that they contribute in some way. The increase in biomass density within the MPA for all species except *P. laevis* further emphasizes the need to specifically investigate population composition and distribution of this species in order to best attune management toward conserving this vulnerable species both on Chumbe and other reefs in the Zanzibar archipelago.

While species' biomass density generally increased between 2014 and 2018, relative abundance of all species except *A. rogaa* decreased in the same time interval. *A. rogaa* held the highest relative abundance in 2014 by only 0.03 and supported only the third highest biomass density. Moreover, the decrease both in population biodiversity and evenness, in conjunction with *A. rogaa*'s increase in relative abundance and biomass density, suggest that an ecological regime shift may have occurred on Chumbe's western reef between 2014 and 2018. The coral bleaching event may have caused a disturbance large enough to alter not only the health of the coral, but the populations of grouper that depend heavily on specific coral habitats (Cheal *et al*., 2008; Hackradt *et al*., 2014). The surge in abundance and biomass density of serranid species with broader fundamental niches and less specific habitat preferences (*A. rogaa* and *C. argus*) and decline of species with narrower habitat niches between 2014 and 2018 is in keeping with this hypothesis (Russ and Alaca, 2011).

Indeed, the shift to complete dominance by *A. rogaa*, a species shown to exhibit generalist habitat preference and low site fidelity, reflects that change is occurring not only within the serranid population, but also in the coral reef that supports it (Nesbitt, 2015). In the face of global climate change, even populations of coral dwelling groupers protected within MPAs are vulnerable to decline as their highly specialized and delicate habitat collapses (Berger and Possingham, 2008; Hackradt *et al*., 2014). Thus, a comprehensive understanding of each species fundamental niche is paramount to successful management of serranids and other reef dwelling species as the static protection of even immensely successful MPAs like CHICOP proves insufficient (Berger and Possingham, 2008; Friendlander *et al*., 2003).

Conclusion

Between 2014 and 2018, Chumbe's MPA has experienced a regime shift from a more even and biodiverse serranid population to one dominated by *A. rogaa* and *C. argus.* The dominance of *A. rogaa* and *C. argus* might be attributable to the fact that their fundamental niche was less specific than that of the other four species. Both this study and that conducted by Nesbitt (2015) noted that *C. miniata*, *A. fuscoguttatus*, *P. laevis*, and *A. leucogrammicus* exhibited highly specific habitat preferences. Overarchingly, in keeping with Nesbitt's findings, all species exhibited preference to the slope where it is most steep and complex in the central zones (Richmond and Nesbitt, 2015). The age distribution of *A. rogaa* was balanced and indicated healthy reproductive capacity, while populations of *C. miniata, A. fuscoguttatus*, and *A. leucogrammicus* consisted of mostly adults and those of *P. laevis* were composed primarily of juvenile individuals (Claudet *et al*., 2008; Fenberg *et al*., 2012; García-Charton *et al*., 2008; Lester *et al*., 2009). High abundance and biomass across locations, wide range and unspecified realized niche, and balanced age composition suggest that populations of *A. rogaa* and *C. argus* are healthy and thriving. Decreased abundance and biomass, high site fidelity and specified habitat, and unstable age composition of the remaining four species suggest that these populations are at risk in the face of continued degradation to their coral habitat despite the protection of the MPA.

The relationship between wide habitat range, relatively small maximum size, and high relative abundance and biomass density of *A. rogaa* and *C. argus* further emphasizes the inequity in protection generated by small MPAs. These findings suggest that populations of species with restricted habitat preferences benefit minimally from small protected areas, and this unfortunate reality is compounded by the fact that many rare species must compete not only amongst each other for resources and habitat, but also with dominant species that are able to inhabit less specialized niches. The overall health of the reef within CHICOP can be extrapolated based on the composition and distribution of groupers on the reef. Similarly, it can be deduced that declines in coral health will result in declines in the health of grouper populations, and vice versa. With this relationship in mind, the degrative impact of a bleaching event in addition to consistent destruction of coral ecosystems by global climate change, it should not be surprising that compositions of serranid populations are experiencing regime shifts in favor of species that are able to adapt and accommodate intense habitat disturbances.

Assessment of serranid populations within the context of their preferred habitat promotes more detailed understanding of the localized reasons behind population composition and distribution. Interestingly, many of the backreef locations resemble the eastern OAA with regard to biodiversity, but the OAA's comparatively low population and biomass density indicates that the shallow, discontinuous, and fished reef exhibits poor grouper population health compared to the NTA. Thus, the relatively small serranid populations on nearby open access reefs suggest that the ecosystems are unable to sustain healthy populations due to the stress of extractive fishing practices, the unsuitable coral reef structure, or to the fact the MPA might not support a healthy or large enough population to result in spillover into adjacent open access fishing areas.

Acknowledgements

I would like to thank Dr Narriman Jiddawi and Dr Richard Walz for their guidance, Chumbe Island Coral Park staff for their hospitality and friendship, and Kenna Kuhn for her support in and out of the field.

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The trophic structure of fish in seaweed farms, and adjacent seagrass and coral habitats in Zanzibar, Tanzania

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Abstract

Coral reefs, seagrasses and seaweed farms (*Eucheuma denticulatum*) are characteristic habitats in many parts of the coast of Zanzibar, Tanzania. However, information on trophic interactions, movements of fish, and variation in fish diet specialization between these habitats are scarce. The present study determined the trophic structure and the variation in diet composition of fish caught in (floating) seaweed farms, and in adjacent seagrass and coral reef habitats in Pongwe, Zanzibar. Fish were caught using traditional basket traps (*dema*) and gut contents of 392 fish were analyzed. A one-way Analysis of Similarities (ANOSIM) showed that there was a significant difference in the composition of prey items eaten by invertivores in different habitats (Global R = 0.109, p = 0.002). There was no significant difference in the composition of prey items eaten by herbivores, invertivore-piscivores and omnivores ($p > 0.05$), likely due to movement of fish between these habitats for foraging. There was no significant difference in the relative proportion of trophic groups between the habitats ($p > 0.05$) except for herbivores ($p < 0.05$). Floating seaweed farms attract invertebrates and smaller fish, thus providing feeding grounds for predatory fish, and should be considered as ecologically important habitats as are coral reefs and seagrass beds.

Keywords: trophic structure, seaweed farm, seagrass, coral, habitats

Introduction

Determining the ecosystem state and connectivity of biomass between ecological groups or trophic levels is vital to understanding ecosystem function (Christensen and Pauly, 2004). The understanding of fish trophic networks is important in establishing ecologically based management programmes (Kulbicki *et al*., 2005). Gut content analyses are used in studies related to fish composition and abundance of wild fish assemblages (Arechavala-Lopez *et al*., 2011; Fernandez-Jover *et al*., 2011). They provide information of the most recent meal and can be used to track changes in feeding habits of captured fish (Fernandez-Jover *et al*., 2008), and trophic relationships (Berkstrom *et al*., 2012).

Connectivity of organisms is known to occur between seagrass beds and coral reefs (Berkstrom *et al*., 2013). Fish belonging to trophic groups such as planktivores, piscivores and motile invertebrate feeders that eat high protein and energy-rich food with high assimilation rates (Bowen *et al*., 1995) form the most diverse trophic groups worldwide (Jones *et al*., 1991; Ferreira *et al*., 2004). In many tropical regions, shallow water habitats are strongly connected through ontogenetic or foraging migration of fish (Krumme, 2009). Large piscivores and invertebrate feeders are known to migrate from coral reefs to feed in adjacent seagrass and sandy areas (Appeldoorn *et al*., 2009). Meyer *et al*. (1983) reported at least 15 fish families that leave coral reefs to forage in neighboring areas. Seagrass beds provide high abundance of food and suitable refuge, thus functioning as a complementary or supplementary resource for many multi-habitat species (Pittman *et al*., 2004; 2007). Furthermore, studies from tropical and subtropical marine waters have shown that seasonal changes in resource availability and environmental conditions influence fish feeding patterns and variation in food composition (Harrigan *et al.,* 1989; Layman and Silliman, 2002). Dietary ecology and

http://dx.doi.org/10.4314/wiojms.v19i2.2

feeding habits can be explored by quantifying variations in resource use and feeding intensity. Individual species are predicted to shift resource use in response to food availability in the environment (Stephens and Krebs, 1986). Therefore, studying how the diet of species from different trophic groups varies within a multihabitat may help to provide knowledge about the nature of interactions that exist between individuals and habitats (Heng *et al*., 2018).

Seaweed farming is being practiced in a number of coastal villages in Zanzibar (Eklund and Pettersson, 1992). While the seaweeds provide income and livelihood to thousands of artisanal farmers, it has been suggested that macroalgal habitats like seaweed farms provide benefits in terms of recruitment, provision of food, shelter and refuge for fish (Bergman *et al*., 2001; Eklöf *et al*., 2006). Seaweeds are used as a source of food for herbivorous reef fish such as the Siganidae as well as foraging sites for invertebrate feeders and omnivores which predate on the associated epifauna (Bergman *et al*., 2001).

There is little information on trophic regimes of fish in seagrass and coral reefs in the Western Indian Ocean (WIO) region (de Troch *et al*., 1998; Almeida *et al*., 2001; de Boer *et al*., 2001; de la Torre-Castro *et al*., 2008). Foraging fish that migrate daily are known to move between a few hundred meters to a few kilometers, often between coral reefs and seagrass beds (Nagelkerken *et al*., 2000; Berkstrom *et al*., 2013), yet information on trophic interactions and movements of fish between seaweed farms, seagrass and coral reefs is scarce and variation in fish diet specialization has not yet been well reported (de Carvalho *et al*., 2015). Thus, the aim of this study was to determine the trophic structure and variation in dietary composition of fish caught in seaweed (*Eucheuma denticulatum*) farms, and adjacent seagrass and coral reef areas.

Methodology

Study area

The study was conducted in Pongwe Village on the mid-eastern coast of Unguja Island, Zanzibar (Fig. 1) from April 2018 to April 2019. The area is located in the equatorial belt of the WIO and experiences two types of seasonal wind patterns annually; the South East Monsoon, which lasts from April to September, and the North East Monsoon, lasting from November to February. The average rainfall is 1,560 mm and the average atmospheric temperature is about 26°C. Pongwe beach is protected by an offshore reef which keeps the inner waters calm and safe. It has a large intertidal area covered by seagrass. The substratum consists of coral rubble and sand. Agriculture, fisheries and seaweed farming form the basic occupations for livelihood sustenance and food security in the area. In this study the seaweed stations were located on deep-water floating farms either over sand or seagrass.

Sampling and data collection

Sampling of fish was carried out during neap tides at intervals of 15 days from planting to harvesting for every seaweed cultivation period (45 days) in each habitat. A fixed basket trap known as "*dema*" was set to capture fish in each seaweed, seagrass, coral reef and sand site. The "*dema*" traps are traditional hexagonal traps measuring 1.04×1.32×0.24 m^3, with a mesh size of 3 cm. Two traps were placed in each station. Each trap was anchored by two stones attached to its sides and fish were lured into a narrow funnel by bait comprising of macroalgae, seagrass leaves, sea stars and brittle stars (after Jiddawi and Öhman, 2002). The respective position of the traps was marked by buoys to allow retrieval and removal of the caught fish. After retrieval the traps were re-baited and re-deployed in a different location within the same habitat.

Processing of fish samples

Fish catch from the traps was harvested and stored in an ice box immediately after capture and preserved to reduce post-capture digestion that could result in loss of dietary information (Bowen, 1996). The samples were transported to the Institute of Marine Sciences (IMS) laboratory in Zanzibar town for sorting into species and analysis of gut contents. Fish were sorted and identified using standard taxonomic keys and guides (Bianchi, 1985; Allen and Steene, 1987; Lieske and Myers, 1994; Richmond, 2011). Fish guts were removed from each individual and food items in each stomach were visually identified to the lowest taxonomic group possible using a stereo microscope. The number of stomach samples including those with and without food items and the types of food categories were recorded. The schemes used by Froese and Pauly (2019) and Berkstrom *et al.* (2012) were adopted to determine the trophic groups of fish according to the types of food categories contained in their stomachs. Fish were classified as (i) herbivores (feeding mainly on seagrass, detritus and algae), (ii) invertivores-piscivores (preying on bivalves, crabs, shrimps, detritus and fishes), (iii) omnivores which had mixed contents of plant material, animal (except fish) and detritus, (iv) invertivores (feeding specifically on bivalves, crabs and shrimps), and (v) piscivores that fed on fishes. However, in this study only one piscivorous fish (*Conger cinereus*) was caught during sampling and therefore this category was not considered for further analysis.

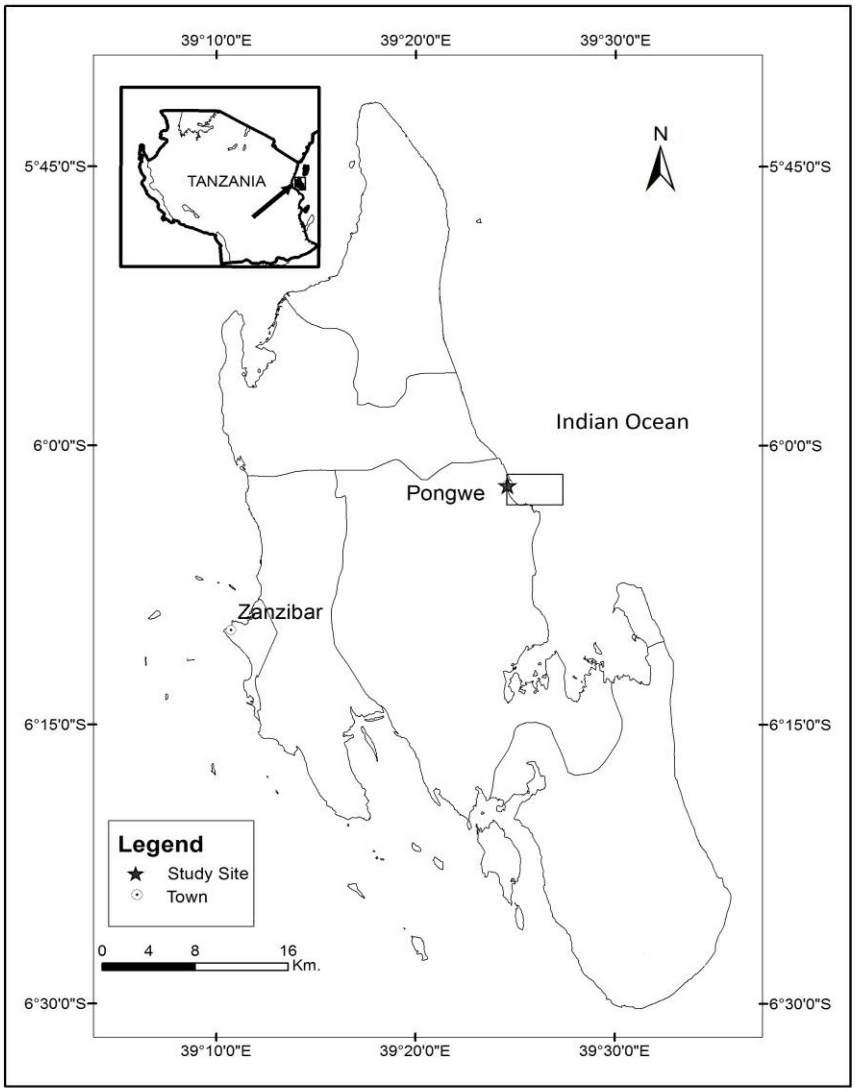

Figure 1. Map of Unguja Island showing the study site.

Data analysis

Comparisons of fish diet composition were tested by one-way Analysis of Similarities (ANOSIM) with 999 permutations (Clarke and Warwick, 1994). Similarity percentage analysis (SIMPER) was used to identify the proportional contribution of individual species to average similarity/dissimilarity (Warwick *et al*., 1990). Prior to the multivariate analysis, the data were square root transformed to reduce the weight of dominant values. Data on trophic groups was analyzed in the SPSS software package. All data were checked for normality and homogeneity of variance. Since much of the data on biological parameters did not meet the criteria for normality and homogeneity of variances, a non-parametric Kruskal-Wallis test was used to test for differences in proportion of trophic groups between habitats.

Gut content analysis

Data for gut content composition was obtained from specimens caught by traps at all sampling stations and used for the determination of the feeding trophic level.

Stomach content indices were calculated as:

i. SCIs (%) = (Number of fish stomachs with specific food type per habitat/Number of fish stomachs with variety of food per habitat) x 100

Relative Trophic Composition (RTC) of fish species per site was calculated as:

ii. RTC (%) = (Number of fish specimens belonging to one trophic group per habitat/ Number of fish specimens belonging to all trophic groups per habitat) x 100

Results

Stomach content indices

Gut contents of 392 fish caught by basket traps were analyzed; 159 from coral reefs, 98 from seagrass beds, 69 from sandy habitat, 44 from a floating seaweed farm placed over sand, and 22 from a floating seaweed farm placed over seagrass.

Herbivores

For herbivorous fish caught in coral reefs, results indicated a higher percentage contribution of brown algae (42 %), followed by seagrass, while green and red algae were found only in a few stomachs and in lower percentages. For those caught in seagrasses, the dominant prey item was seagrass with a percentage contribution of 48 %, followed by brown algae, green algae and animals. In the sand area, brown algae had the highest percentage contribution (43 %), followed by seagrass, whereas green and red algae were rarely found. In seaweed farms, both over sand and seagrass, the dominant food item was brown algae (60 % and 50 % respectively) followed by red algae, while seagrass and green algae were rarely observed (Fig. 2). Animals like annelids, nematodes and sipunculids were only observed in stomach contents of fish caught in coral reef, seagrass and sand habitats. A one-way Analysis of Similarities (ANOSIM) showed that there was no significant difference in prey items eaten by herbivorous fish in different habitats (Global R= 0.017, p = 0.191). Similarity percentages (SIMPER) analysis showed that the main contributors for the observed similarities were seagrass ranging from 50-59 % and brown algae (31-100 %).

Invertivore-piscivores

The diet of invertivore-piscivores caught in both coral reefs and seagrasses was dominated by crabs with percentage contribution of 41 % and 33 % respectively, followed by shrimps. Fish, gastropods and bivalves contributed the least. In the sand area bivalves had the highest contribution (36 %) followed by shrimps, gastropods and crabs. Crabs were the dominant prey for fish caught in seaweed farms over sand, with a percentage contribution of 44 % followed by shrimps, while in seaweed farms over seagrass, gastropods contributed highest (43 %), followed by crabs. Sea urchin remains were only observed in samples caught in coral reef habitat and the seaweed farm over seagrasses (Fig. 3). The ANOSIM test showed that there was no significant difference in prey items eaten by invertivore-piscivores in different habitats (Global R= 0.008, p = 0.316.). The SIMPER analysis showed that the prey items contributing most to similarities between habitats were crabs (46-75 %) and shrimps (11-37 %).

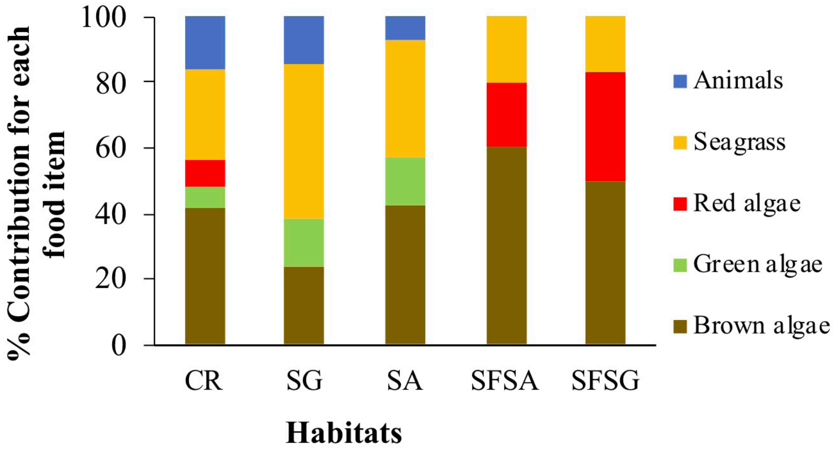

Figure 2. Stomach Content Indices for herbivorous fishes in all habitats. CR = Coral reef, SG = Seagrass, SA = Sand, SFSA = Seaweed farm over sand and SFSG = Seaweed farm over seagrass.

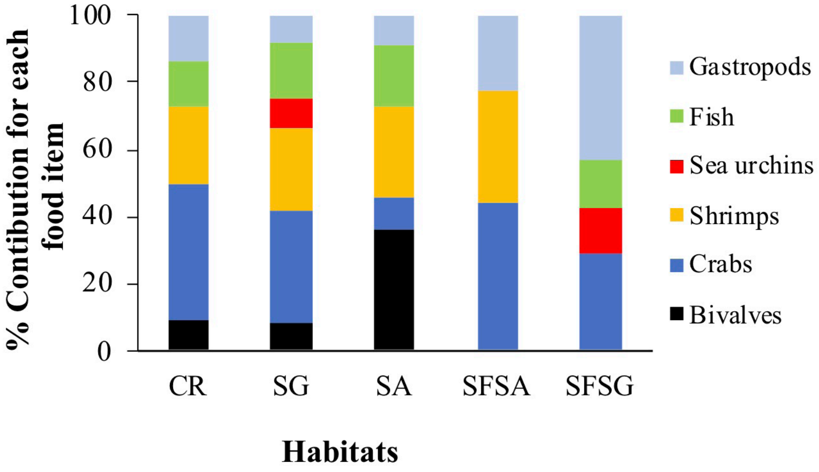

Figure 3. Stomach Content Indices for invertivore-piscivores in all habitats. CR = Coral reef, SG = Seagrass, SA = Sand, SFSA = Seaweed farm over sand and SFSG = Seaweed farm over seagrass.

Invertivores

For invertivores, results indicated a highest percentage contribution of crabs in the diet of fish caught in coral reefs (53 %), seagrasses (50%) and sand (42%), followed by shrimps with a contribution of 30 %, 29 % and 25 % respectively. Gastropods, brittle stars and calcareous algae also contributed to the diet of fishes in each habitat. For fish samples from the seaweed farm over sand, the dominant prey was crabs (50 %), followed by gastropods (33 %), while the diet of invertivores in the seaweed farm over seagrass was composed of only crabs (Fig. 4). ANOSIM showed a significant difference in the composition of prey items eaten by invertivores in different habitats (Global R = 0.109, p = 0.002). Pairwise comparison showed a significant difference in prey item composition between fish caught in coral reefs and the seaweed farm over seagrass (R = 0.252, p = 0.003), and between those in seagrass and the floating farm over sand (R = 0.356, p = 0.001). SIMPER analysis showed that the highest contributors to dissimilarities were crabs (52 %), shrimps (33 %) and gastropods (10 %).

Omnivores

The diet of omnivores was dominated by gastropods for coral reef (42 %) and seagrass (47 %) fish. The dominant prey on samples from sand was gastropods (50 %), followed by polychaetes (21 %) while bivalves

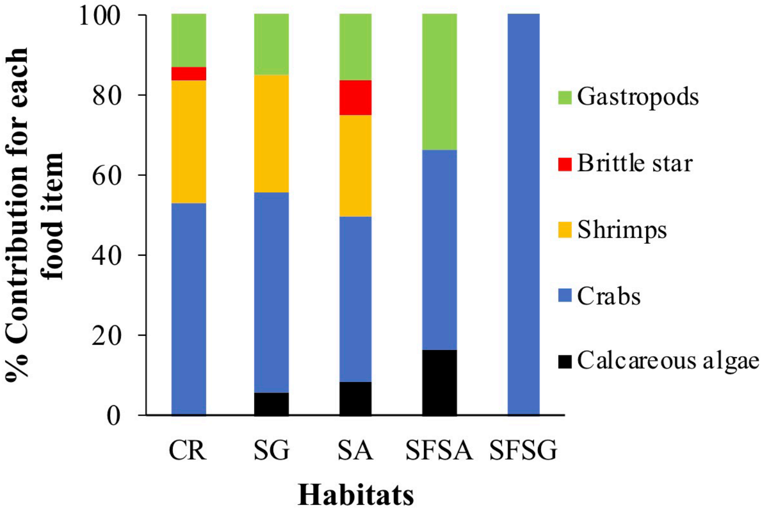

Figure 4. Stomach Content Indices for invertivores in all habitats. CR = Coral reef, SG = Seagrass, SA = Sand, SFSA = Seaweed farm over sand and SFSG = Seaweed farm over seagrass.

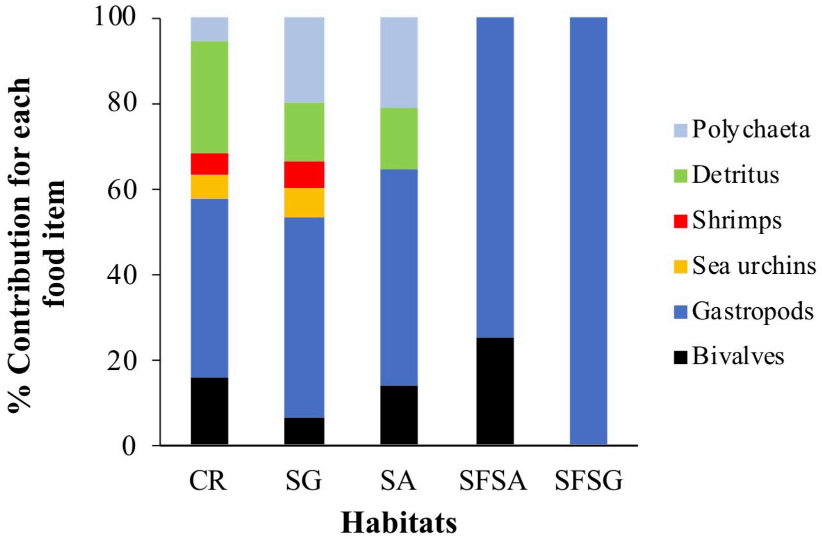

Figure 5. Stomach Content Indices for omnivores in all habitats. CR = Coral reef, SG = Seagrass, SA = Sand, SFSA = Seaweed farm over sand and SFSG = Seaweed farm over seagrass.

featured least in samples from these habitats. For fish caught in the seaweed farm over sand, gastropods contributed 75 % followed by bivalves (25%), while samples from the seaweed farm over seagrass had gastropods only in their stomachs (Fig. 5). The ANOSIM test showed a weak difference in prey items eaten by omnivores between the habitats (Global R =0.020, p=0.011). Similarity percentages (SIMPER) analysis showed that the food item contributing most to dissimilarities were gastropods (40 %), polychaetes (36 %) and detritus (11 %).

Trophic groups and relative trophic composition

In terms of trophic groups, coral reef habitat had the highest numbers of herbivores (66), invertivore-piscivores (28) and omnivores (23). Seagrasses had the highest number of invertivores (46), while the seaweed farm over seagrass had the lowest number of individuals from all four trophic groups (Table 1).

The Relative Trophic Composition (RTC %) indicated that all trophic groups identified were present in all the sites. Fish species belonging to all trophic groups were caught on coral reefs, where unexpectedly, herbivores (represented mostly by Siganids) had the highest RTC % (Table 1). Invertivores had the highest RTC % on seagrass, invertivores and omnivores on sand and invertivore-piscivores on seaweed farms (both over sand and seagrass) (Table 1). Differences in the relative proportion of trophic groups between the habitats were not significant ($\chi^2 = 5.76$, df = 4, $p > 0.05$). A significant difference was observed in the proportions of herbivores between habitats ($p<0.05$), while there was no significant

Table 1. Number of individuals from four trophic groups and Relative Trophic Composition (RTC %) of fish caught at different habitats.

	Herbivores		**Invertivore-piscivores**		**Invertivores**		**Omnivores**	
Sites	**Number**	**RTC%**	**Number**	**RTC%**	**Number**	**RTC %**	**Number**	**RTC %**
Coral reef	66	41.5	28	17.61	42	26.41	23	14.46
Seagrass	26	26.53	15	15.3	46	46.93	11	11.22
Sand	17	24.63	13	18.84	20	28.98	19	27.53
Seaweed farm over sand	8	18.18	15	34.88	11	25.58	10	23.25
Seaweed farm over seagrass	7	31.81	12	54.54	2	9.09	1	4.54

difference for invertivore-piscivores, invertivores and omnivores (p > 0.05).

Discussion

Analysis of stomach content indices (SCIs) showed that herbivorous fish preferred a variety of macroalgae. The higher abundance of brown algae and seagrass in the diet of herbivorous fish caught in these habitats is likely due to the availability of these food groups locally all year round. Furthermore, various species of the brown algae *Sargassum* were the dominant food item and were mainly ingested by herbivorous fish. Similarly, a study by Yatsuya *et al.* (2015) on seasonal changes of diet of *Kyphosus bigibbus*, found that brown algae was the dominant dietary component in all seasons. Contrary to expectations, the red algae *Eucheuma* sp. and green algae *Ulva* and *Enteromorpha* spp. were found in insignificant amounts in most herbivorous fish stomachs except for those caught in seaweed farms, even though *Eucheuma* sp., was available year round and is reported to be a potential food source for herbivores like Siganids. The higher ocurrence of *Eucheuma* sp. in the diet of fish caught in seaweed farms suggests that the farms act as both shelter and a source of food. Comparatively, Anyango *et al.* (2017) also found significant amounts of red algae in the stomachs of herbivorous fish caught in seaweed farms in the coastal waters of Kibuyuni, Kenya. However, Ojeda *et al*. (1999) concluded that green macroalgae were better food items than red macroalgae, and red macroalgae were better than brown macroalgae in terms of their greater protein, calories and digestibility values. Stomach content indices also showed a high occurrence of undigested annelids, nematodes and sipunculids in the stomachs of herbivorous fishes, although it was difficult to determine if these burrowing animals were ingested intentionally or incidentally. There are a few studies which suggest that juveniles of several species of herbivorous fishes consume significant amounts of animal items (Horn, 1989), or in small amounts as adults (Noda *et al*., 2002). The lack of a significant difference in the type of food eaten by herbivores in different habitats could be due to availability of these resources in the area. Macroalgae and seagrasses occur year round in the region, with peaks during the monsoon period (McClanahan, 1988).

For invertivore-piscivores and invertivores, there was a high percentage contribution of *Portunus* crabs and penaeid shrimps in their diet, which was observed in almost all stomachs of the fishes caught in the coral reef, seagrass habitats and seaweed farms throughout the year. This study showed that crustaceans are a potential food source and are mainly ingested by invertivore-piscivores and invertivores in the area. This could be due to their availability in habitats like segrass beds (Unsworth *et al*., 2007) and in seaweed farms as observed in the present study. Kulbicki *et al*. (2005) also reported that crustaceans are a major food items in nearshore, soft bottom and reef habitats and are among the most important item in pelagic fish stomachs. The high pecentages of crabs and shrimps was moslty observed from fish samples caught between December and July, probably due to an increase in abundance after spawning, which is reported to occur between late October to November (Svane and Hooper, 2004). In addition it has been reported that the onset of the wet season (March to May) triggers an offshore migration of juvenile shrimps (Teikwa and Mgaya, 2003). Bivalves were found mostly in the diet of invertivore-piscivore fishes caught in the sandy area, possibly due to the preference of bivalves to such habitats. There are often a very large number of bivalves and other invertebrates living beneath the surface of the sand (Christian, 2007). Gastropods also featured highly in the diet of invertivores caught in seaweed farms. These invertebrates are usually found attached on seaweed fronds.

The presence of crabs and shrimps at higher percentages in fish stomachs contributed to the lack of significant difference in type of food eaten by invertivore-piscivores in these habitats. The observed differences in the type of prey item consumed by invertivores between coral reefs, seagrasses and seaweed farms could be due to higher abundance of epifauna on seaweeds. Moreover, changes in seasonal assemblage, abundance and composition of epifaunal communities associated with seaweeds frequently occurs in tropical areas (Ateweberhan *et al*., 2005), which may contribute to variation in diet composition of fish.

Omnivorous fish were found to prefer a variety of gastropods in their diet. Specifically, the Littorinidae, Trochidae and Strombidae dominated stomach contents of fish collected between October and November. This is a period when they are commonly found attached to seagrasses, coral reef and seaweeds (B. Yahya, pers. obs.). This inter-tropical monsoon period is also a time when spawning activity is typically high in the WIO region (Robinson *et al*., 2008). Polychaetes and detritus were observed in high percentages in most fishes, contributing to the lack of significant difference in type of food eaten by omnivores in these habitats.

Analysis of stomach contents showed four main trophic groups in different habitats. Piscivores were relatively scarce in the samples as were planktivores such as the Pomacentridae, the latter likely due to gear type limitations. The herbivores dominated catch caught in all habitats, with highest RTC % in coral reefs followed by seagrasses, and the lowest in seaweed farms. This could be due to the fact that fish use coral reefs and seagrass beds either as feeding, breeding, nursery or hiding grounds (Beck *et al*., 2001). These habitats also play an important role in the regulation of foraging patterns (Erlandsson *et al*., 1999). Studies indicate that the evolution and development of modern reefs has been dependent on the presence of herbivores, controlling growth of algae and thus creating the space for development and evolution of corals (Bellwood and Wainwright, 2002; Arosemena, 2005). The herbivores may greatly depend on the physical structure of the coral reef and the distribution of the associated benthic organisms (Ferreira *et al*., 1998). An important part of the diet of some herbivores (e.g. Scaridae) is detritus and/or calcified materials (Arosemena, 2005). The lower RTC % of herbivores in seaweed farms could be because they avoid the areas of macroalgal dominance and prefer coral reef areas. According to Hehre *et al*. (2016), Siganidae tend to avoid areas of high macroalgal biomass even though seaweed farms potentially provide them with food subsidies.

The high RTCs % of invertivores and invertivore-piscivores in the coral reef area was likely because most species that belong to these trophic groups use coral reefs as their main habitats, thus making up a substantial proportion of the coral reef fish population (Berkstrom *et al*., 2012), although in this study they were also recorded in seagrasses, seaweed farms and on sand. These results are consistent with earlier findings (Dorenbosch *et al*., 2005; Berkstrom *et al*., 2012) where it was found that although these trophic groups use coral reefs as their main habitats, they are also recorded in other habitats like seagrass and sandy areas where they migrate for feeding. Invertivores dominated on seagrass because seagrass habitats generally produce an abundant invertebrate fauna (Randall *et al*., 2009) and offer important feeding sites for fish (Nakamura and Sano, 2005). The higher RTC % of invertivores and omnivores in sand areas may be due to their food requirements. Omnivores feed on a variety of organisms, including animals (such as small fish and invertebrates common in sand areas), plants and detritus materials and, for example, have been found to be more abundant in zones of rubble and sand (Arosemena, 2005). Seaweed habitats (both over sand and seagrass) were dominated by invertivore-piscivores. Floating seaweed farms may act as fish aggregating devices, whereby they attract smaller fish and invertebrates, thus providing feeding grounds for predatory fish. Further studies are recommended on the cross-boundary movement of fish between seaweed farms and adjacent seagrass and coral reef habitats.

Conclusion

The findings of this study show that fish used food resources variably depending on availability in their environment and also feeding preference. It was unclear why annelids, nematodes and sipunculids were also observed in the stomachs of herbivorous fishes during the period March to October. Further studies are needed to confirm if these animals are eaten accidentally or intentionally and their importance in the herbivores' diet. Studies on trophic structure where seaweed farming occurs may further reveal the importance of this artificial habitat in tropical waters.

Acknowledgements

This study was fully funded by the Sida Bilateral Marine Science Program. We would like to express our sincere gratitude to the staff of the Institute of Marine Sciences, University of Dar es Salaam, fishers and seaweed farmers at Pongwe Village, Zanzibar for their cooperation and assistance.

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A socio-ecological system perspective on trade interactions within artisanal fisheries in coastal Kenya

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Abstract

Assessments of coastal artisanal fisheries are progressively adopting a social-ecological system (SES) approach as an effective means to accumulate knowledge and integrate findings on different aspects of the fisheries. Ostrom's SES framework was used to guide assessment of interactions between and within the harvesting and supply-chain processes and the effect of external drivers, seasonal monsoons and tourism, on both processes in a coastal artisanal fishery system in Gazi Bay, Kenya. Specific analyses focused on seasonal catch composition, key resource user groups involved in the fish trade and the resource units traded by each user group. The snowball method was used to identify key resource user groups within the fishery sector, who were then interviewed using semi-structured questionnaires (n = 60). Additionally, existing annual shore-based catch assessment and monthly fish landings data for the years 2014 and 2015 were incorporated for analysis of artisanal catch properties (species composition and weight). Comparison of seasonal catch composition was carried out using sample-based rarefaction curves. Higher fish landings and higher species diversity were recorded during the North-East Monsoon season. Further, a simple fish harvesting-supply network comprising of six key resource user groups (i.e. hotels, fish processing companies, dealers, small-scale fish processors (mama karanga), fish mongers and fishers) was outlined. The tourism industry, through hotels, creates a high demand for fish coinciding with a higher catchability and supply during the calm North-East Monsoon season and consequently, dealers hire migrant fishermen to target pelagic fish. Evidence of interactions within and between different fishery sub-systems, as well as the effect of monsoon seasons and tourism on the exploitation and market dynamics of the multispecies fishery, highlight the need for comprehensive management plans to strengthen self-organization among resource users and to increase adaptive capacity within the fishery system.

Keywords: artisanal fishery, socio-ecological system, Gazi, south coast Kenya

Introduction

Coastal artisanal fisheries (CAFs) are an important source of food and livelihood to millions of people globally (Barnes-Mauthe *et al.*, 2013). CAFs are characterized by a diversity of activities both in the catch harvesting and supply/processing chain processes. Fishing in this sub-sector is commonly characterized by the use of small-sized fishing crafts coupled with low technology investment, the application of multiple fishing gears and landing of multiple species (Nagelkerken, 2009; Balogun *et al.*, 2011). On the other hand, the supply/processing chain activities show a distinct differentiation of roles (for example between gender), with different intensity in labour and subsistence operations both in fish processing and selling (Béné *et al.*, 2010).

Previous studies on CAFs have often focused on the harvesting and supply chain processes as two independent entities, leaving a crucial knowledge gap on attributes and implications of the interactions between the two processes (Garcia, 2007; Garcia *et al.*,

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2008). CAFs are however increasingly being perceived as complex and highly interlinked social-ecological systems (SESs), based on their multiple biophysical and social properties, structural organization, role partitioning and types of problems they face (Basurto *et al.*, 2013). Various SES frameworks have been proposed to integrate harvesting and supply chain studies of CAFs, however, the Ostrom (2009) framework is often conveniently used to describe and characterize SESs in an integrated manner, giving ecological and social systems a near-equal weight (Johnson *et al.*, 2019). It was decided to adopt the Ostrom framework (Fig. 1) since it fits the nature and objectives of the study as: (i) it integrates social and ecological aspects and their interactions; (ii) it is applicable to CAFs and; (iii) it includes qualitative and quantitative data.

The Ostrom SES framework conceptualizes the two-way relationship between social and ecological systems from an anthropogenic perspective while guiding an approach to analyse relationships between individual variables in an SES quantitatively (Virapongse *et al.*, 2016). The framework has four primary sub-systems of an SES that interact with and affect each other (Fig.1): (i) the resource system (i.e. the CAF itself); (ii) the resource units (i.e. different fish species/sizes landed and traded within the CAF); (iii) the governance systems (e.g., the national and county governments, self-organizing groups such as Beach Management Units (BMUs) and other organizations that manage the fishery); and (iv) the resource user groups (e.g., individuals who fish and sell the fish). The Ostrom framework further proposes a set of 53 second-level variables, building on the main attributes of each subsystem, while providing the option to choose other second-level variables or add a deeper level of variables according to the particularities of the analyzed SES (McGinnis and Ostrom, 2014; Ostrom, 2009).

Social-ecological studies have outlined the potential of ecological, economic and institutional processes to influence the relationship between market demand and ecosystem health (Armsworth *et al.*, 2010). For instance, considering the supply chain processes of a CAF, a trader who buys from a fisher may also

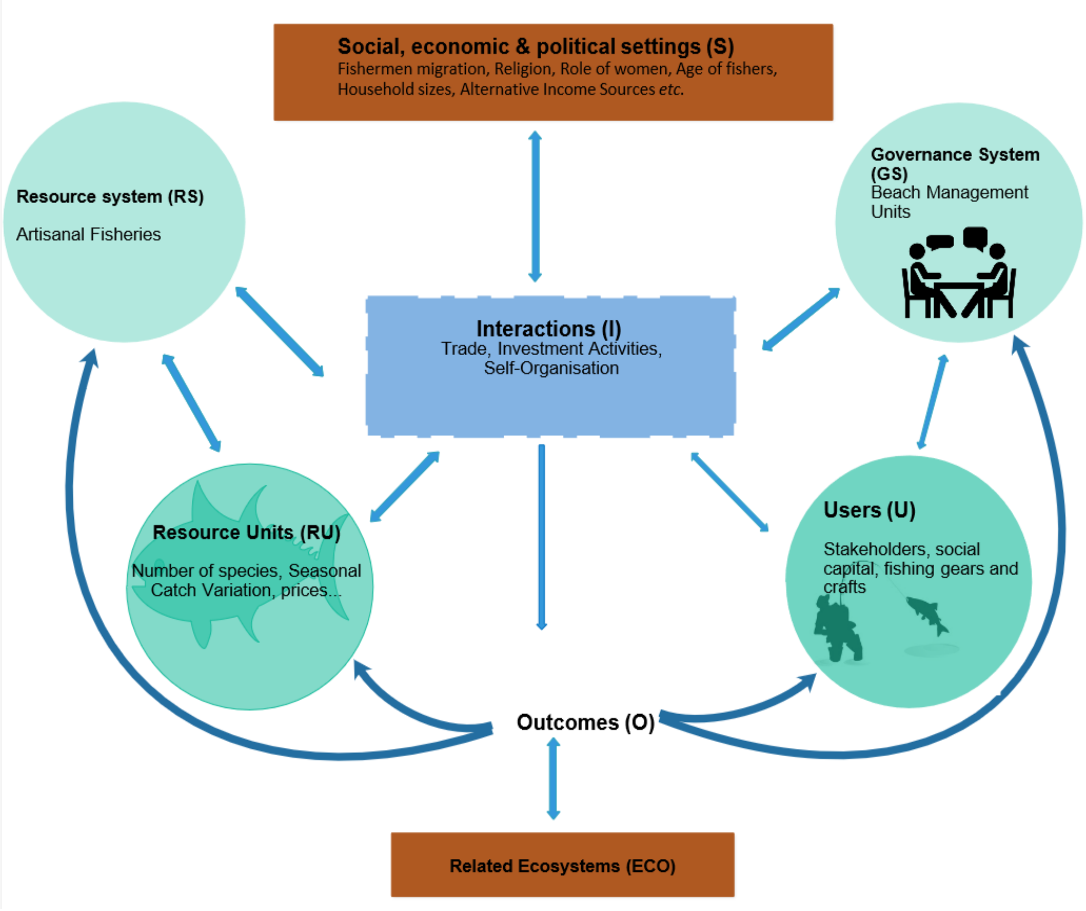


Figure 1. Artisanal fisheries as an SES: On the left is the revised SES framework, with multiple-tier components fitted in the context of coastal artisanal fisheries. On the right are the 53 subsections of the SES. This study focuses across the subsections highlighted in green (adopted from Ostrom, 2009).

provide capital for fuel, ice for storage/preservation, fishing gears and even finance the boat and demand specific types of fish (based on species, size or geographical location) from the fishers. The nature of the market demand in turn impels the fishers to fish selectively, leading to dramatic changes in aquatic ecosystems such as a change of the mean size of individuals within populations, general change in trophic interactions and loss of certain fish species (Jennings and Kaiser, 1998; Pauly *et al*., 1998; Myers and Worm, 2003; Kinnison *et al*., 2009; Shackell *et al*., 2010). For example, in La Paz, Mexico, increase in market supply of medium-sized Pacific red snapper (*Lutjanus peru*), due to tourism-driven demand, was shown to result in a reduced supply and price of large fish species (Reddy *et al*., 2013).

In Kenya, where coastal fisheries are largely artisanal, both the catch harvesting, and supply/processing chain activities have been studied but mostly in a piecemeal, non-integrated manner. Catch harvesting is heavily influenced by climatic seasons, with higher fishing effort and catches during the calm, dry North-East Monsoon (NEM) season, from October to March than during the rough and cool South-East Monsoon (SEM) season between April and September (McClanahan, 1988; Van der Elst *et al*., 2005). Moreover, catch harvesting is mainly restricted to the inshore lagoons along the continuous fringing reef, and mangrove creeks (Munga *et al*., 2012). Further, several studies on post-harvest processes such as the role of women in fish trade (Matsue *et al*., 2014), the change in fish transport culture (Gerlach, 1963), the involvement of middlemen in fish trade (Crona *et al*., 2010; Crona and Rosendo, 2011), value addition and fish marketing by traders in local markets (Wamukota, 2009) have been conducted separately along the Kenyan coast.

This study uses Ostrom's framework (Fig.1) to steer the integrative assessment of the processes between and within the harvesting and supply-chain processes (including catch processing) in Kenyan artisanal fisheries. Although the Ostrom framework provides for the four aforementioned dimensions, the focus in this study is on generating knowledge about the outcomes resulting from interactions (investment/trade (I5) and self-organizing (I7) activities) between two key dimensions, resource units and resource user groups, as well as the impact of external factors such as climatic seasonality (which describes the environmental conditions where the resources are located) and market forces influencing trade in order to postulate the outcome. Within each of the two dimensions, a subset of second-level variables have been further highlighted, which are readily measurable or have been proposed by existing literature to directly influence the harvesting and supply-chain processes in a CAF (Basurto *et al*., 2013; Ostrom, 2009). Within the resource units, the second-level variables focused on include economic value (RU4), number of units (RU5), and spatial and temporal distribution (RU7). For the resource user groups the number of users (U1), social economic attributes of users (U2), norms/social capital (U6) and technology used (U9) (Fig.1), are considered.

Materials and methods

Study area

The study was conducted in Gazi village, on the south coast of Kenya, near the townships of Msambweni and Ukunda, and about 50 km from the city of Mombasa (Fig. 2). The site was selected since it is an active research area with substantial existing scientific information, covered by the Kenya Marine and Fisheries Research Institute's Gazi field station. Research at Gazi is mainly concentrated on mangroves, seagrass and coral, and on the human interactions associated with these.

Gazi is a coastal fishing village with about 4000 inhabitants, according to the 2009 Kenya population census. The village is adjacent to Gazi Bay, which comprises a shallow channel of approximately 4 km long fringed by mangrove forest dominated by the species *Sonneratia alba* and *Rhizophora mucronata* (Bosire *et al*., 2003). Gazi Bay, fronting the channel, is approximately 1.5 km^2 and is protected by the Chale Peninsula to the east and a coast-fringing reef to the south (Kimani *et al*., 1996). The coral reefs largely contribute to the fish communities of adjacent seagrass and mangroves (Okechi and Polovina, 1995; Bennett *et al*., 2001).

The Gazi fishing area, fish landing site and public beach are managed by the Gazi Beach Management Unit (BMU). BMUs were developed under the Fisheries Beach Management Legislation 2007, which aims at promoting stewardship and sustainable exploitation of fisheries resources by all stakeholders in collaboration with the national and county governments. BMUs have jurisdiction over a beach, the geographical area that constitutes a fish-landing station and is adjacent to the local fishing grounds (Oluoch *et al*., 2008). Fish is locally traded in Gazi village with external markets for excess fish found in the nearby townships of Msambweni and Ukunda as well as the city of Mombasa.

In the past four decades, there has been a substantial immigration of fishermen, both permanent and seasonal, especially from Pemba Island in Tanzania, who continually transform Gazi's fishery sub-sector with their relatively efficient fishing capability (Ochiewo, 2004). However, other than small scale artisanal fisheries trade, which is the main source of income, there are relatively few alternative livelihood opportunities in the village (Richard and Stephen, 2012).

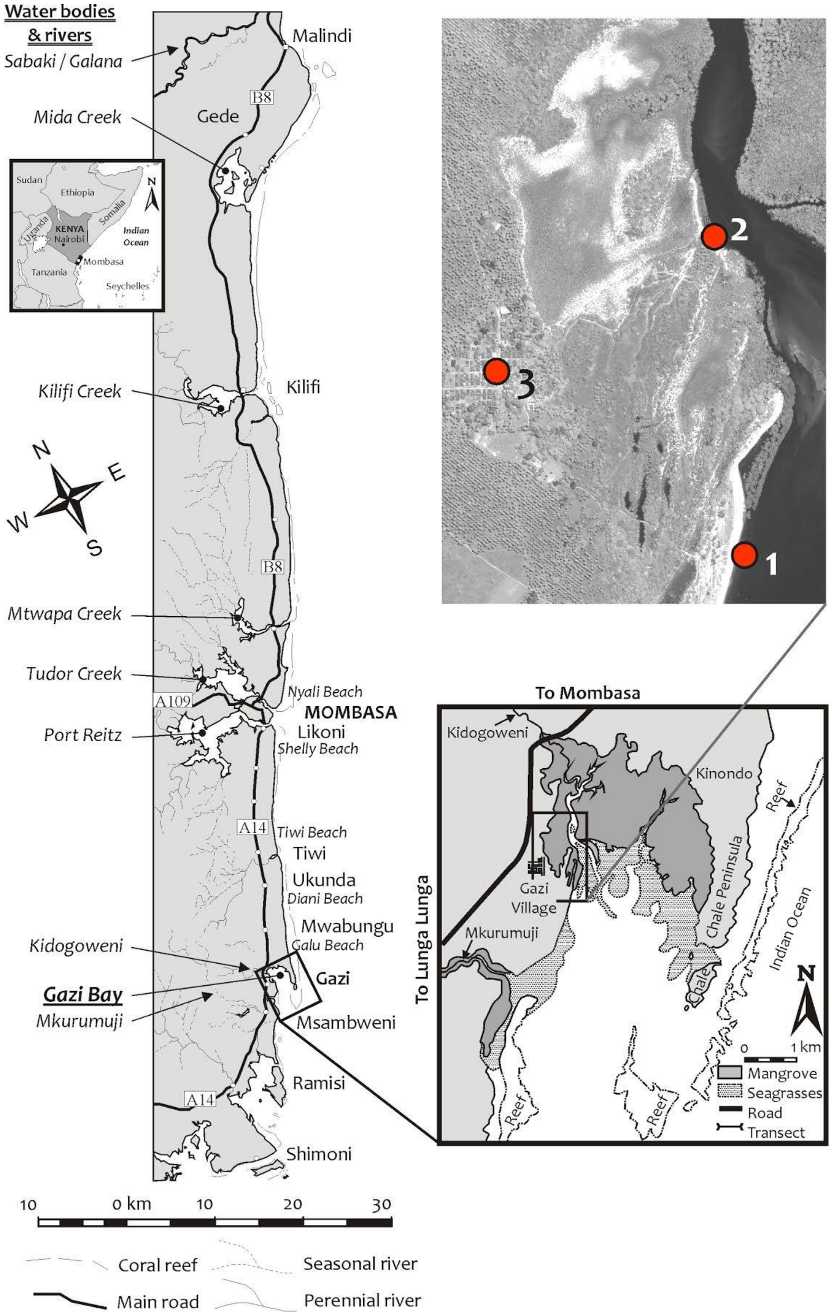


Figure 2. Map showing the study sites. Sites 1 and 2 are the main and alternative landing sites respectively in Gazi. The alternative landing site 2 is mostly used during the NEM. Number 3 is Gazi village (Adapted from Bosire et al. (2003)).

Data collection

Three data sets were collected and used to identify and quantify the resource units and the resource user groups. In the first set, the snowball method, which involves interviewing individuals from initial resource user groups, who in turn identify new stakeholder categories and contacts (Reed *et al*., 2009), was used to identify key resource user groups in the trade chain. The initial respondents of the interviews were identified using key informants from Gazi BMU and the Kenya Marine and Fisheries Research Institute (KMFRI). Resource user group semi-structured questionnaires (Hay, 2000; Young *et al*., 2018) were employed for data collection. Two sets of questionnaires were developed – for the fishers and the trader groups. The questionnaires were developed using split and funneling questions, which were brainstormed beforehand with guidance of experienced researchers from KMFRI and fishery officers from the Kenya State Department of Fisheries. The respondents were informed about the aim of the study and were requested to give consent before being interviewed. Data recorded included the respondent's fish suppliers and /or customers, amount and type of fish traded, fish processing methods, challenges faced in their trade, and cost of doing the trade. Additional demographic information including age, gender, alternative income-generating activities, amongst others, were recorded where applicable. The questionnaires were written in English but administered in Kiswahili, the national language, when appropriate. In total, the questionnaires were administered to 60 respondents across the different resource user groups. Additional information was collected through non-participant observations and telephone surveys (when impossible to physically reach the respondents) using the same questionnaires.

The second dataset comprised of existing shore-based catch assessment data from January 2013 to April 2014 for the Gazi fishing area that was obtained from KMFRI, was used for analysis of resource units, i.e. catch composition (species and weight). Additional data captured (but not presented in this study) included fishing craft and gear types (technology), and fishing grounds (resource system) accessed.

The final dataset on resource units included existing catch data (from January 2011 to June 2016), obtained from the Gazi BMU and the Kwale County Fisheries Department (KCFD). The data included aggregated total monthly weights (in kg) of sharks and rays, crustaceans, mollusks (octopuses, sea cucumbers and squids), and major demersal and pelagic fishes from the fish markets, listed against their respective prices per kg for Gazi and the entire Msambweni area. This data set compliments the second one, since BMU catch records are obtained from a wide pool of fishermen over a long period, given that BMUs, through the Beach Management Units Regulations, 2007 of the Management and Development Act, have the primary rights over fish landing sites and are required to provide data on catches in order to ensure sustainable fisheries.

Data analysis

Responses to the questionnaire sections surveying catch acquisition practices, i.e. fishing method, fishing effort, composition and weight of the catch (among fishermen), and amount of fish stock purchased per trading day (among different trader categories) was used to estimate how much fish was traded by each resource user groups. This was done by finding the median of the fish amount respondents indicated they purchased or sold per day in each season. The median was preferred as the measure for central tendency due to the skewed nature of the data obtained from each respondent group.

Sample-based rarefaction curves analyses were applied to the second dataset, to assess for variation in catch by season. This analysis is based on the observation that species richness obtained from a sample (*n*) of plots increases with sampling efforts (Gotelli and Colwell, 2001). As the curve approaches an asymptote it shows that few or no new species may occur in additional sampling units (Bacaro *et al*., 2012). The curves are interpreted by checking the expected number of species at a given sampling effort (number of samples). This was followed by the SIMPER analysis, to calculate the contribution of each species (%) to the dissimilarity between each season. SIMPER analysis is calculated from the Bray-Curtiss dissimilarity matrix, with the last two columns showing the contributions for each species in descendant order, and it is accumulative (Gibert and Escarguel, 2019).

Finally, the third dataset was visualized for monthly variations in total catch weight amounts using trend lines, whereas pie charts were used to indicate the percentage weight contribution of each catch group to the total catch for the Gazi landing site between 2011 and 2015.

Results

Seasonal variation of resource units

Based on the catch data (dataset 2), higher landings were observed during the NEM season compared to the SEM season in all years (Fig. 3). In total, 73 species belonging to 36 families were identified from the total number of 889 and 839 individuals sampled during the SEM and NEM seasons, respectively. Landings

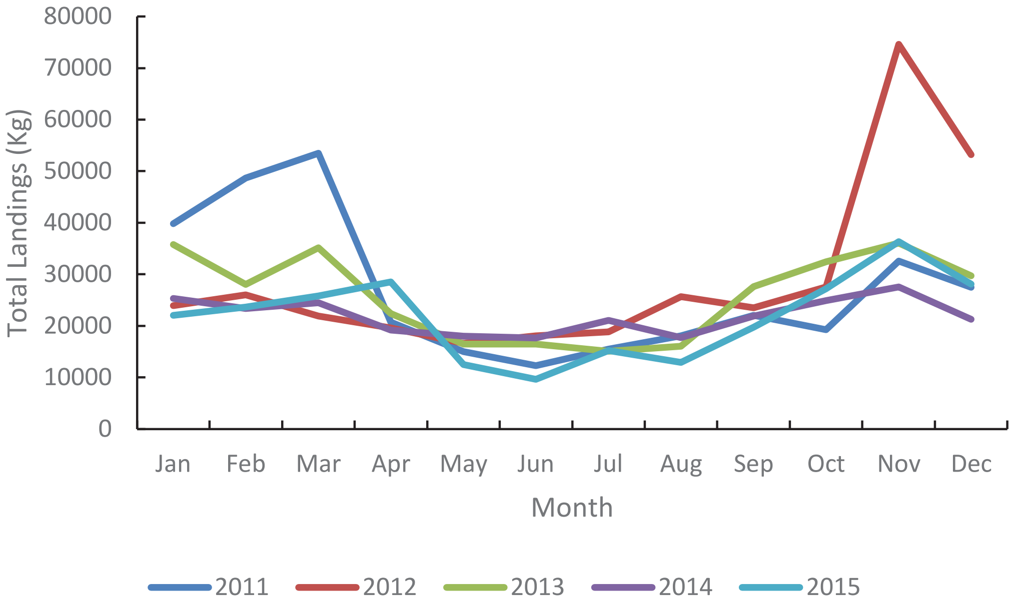


Figure 3. Total monthly landings (kg) for the period between 2011 and 2015 showing high quantities in NEM (October to March) and relatively low SEM landings (April to September) for Gazi landing site.

were dominated by bony fishes (92 %), mollusks (4 %), sharks and rays (2 %), and decapod crustaceans (2 %) (Fig. 4). Rarefaction curves analysis indicated more species were available during the NEM than SEM season (Fig. 5). A dissimilarity of 86.1 % between the two seasons was mainly caused by 16 species (summarized in Table 1) which were more abundant in the SEM than NEM.

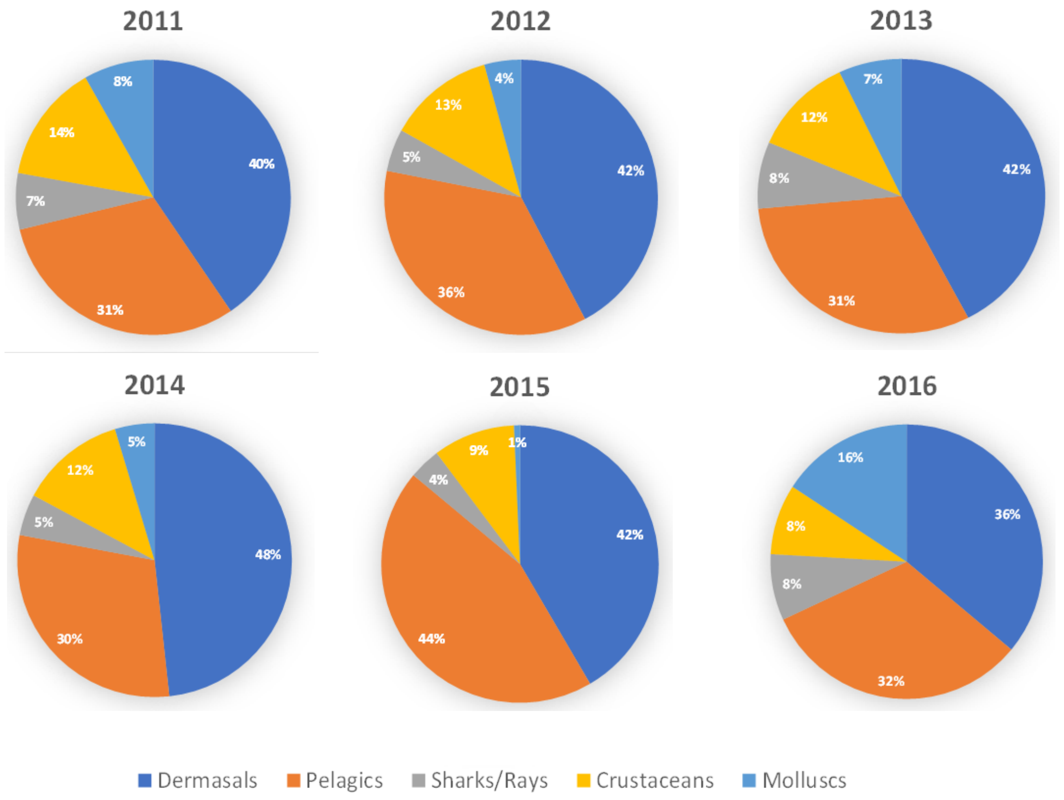


Figure 4. Proportion (%) of different catch groups between year 2011 and 2016 for Gazi fishing area on the south coast of Kenya based on existing catch data (source: Kwale County Fisheries Department).

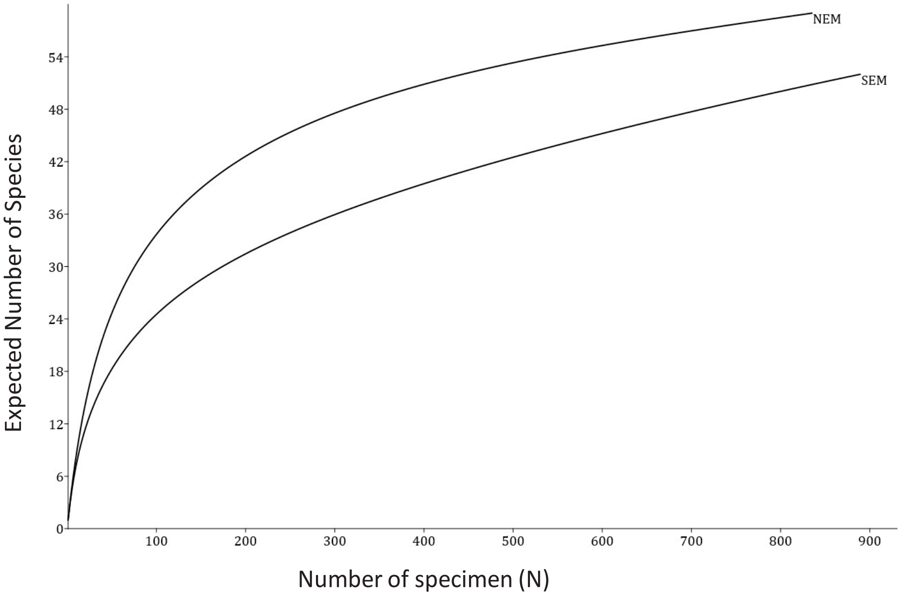


Figure 5. Rarefaction curves comparing expected species per number of individuals sampled during the NEM versus the SEM at Gazi landing site, Kenya.

Table 1. SIMPER results showing a seasonal dissimilarity of 86.1 %, based on catch composition, between the NEM and SEM at Gazi landing site, Kenya. The dissimilarity was caused by the 16 most abundant species listed herein.

	NEM	SEM			
Species	**Av. Abundance (%)**	**Av. Abundance (%)**	**Av. Dissimilarity**	**Contribution (%)**	**Cumulative (%)**
Hyporhamphus affinis	0.33	1.22	11.20	0.67	13.32
Calotomus carolinus	0.62	1.19	10.97	0.87	13.04
Katsuwonus pelamis	0.22	1.05	9.24	0.58	10.99
Carangoides ferdau	0.34	0.20	6.96	0.73	8.27
Anampses caeruleopunctatu	0.54	0.51	5.65	0.81	6.71
Himantura uarnak	0.19	0.61	5.15	0.82	6.12
Aphareus furca	0.22	0.17	3.66	0.51	4.36
Kyphosus cinerascens	0.08	0.58	3.63	0.72	4.31
Caranx melampygus	0.29	0.59	3.24	0.58	3.85
Istiompax indica	0.23	0.87	3.03	0.47	3.60
Lutjanus sp.	0.28	0.24	2.59	0.44	3.08
Cephalopholis argus	0.24	0.18	2.57	0.59	3.05
Carcharhinus melanopterus	0.08	0.55	2.14	0.53	2.54
Aetobatus narinari	0.10	0.04	2.08	0.40	2.48
Lethrinus harak	0.18	0.18	1.85	0.47	2.19
Lutjanus argentimaculatus	0.10	0.30	1.53	0.50	1.82
Chanos chanos	0.23	0.12	1.40	0.35	1.66

Further, analysis of dataset 3 indicate higher catch proportions of pelagic fish from 2011 to 2014 and demersals for year 2015 and 2016 (Fig. 3)

Resource user groups operations

In total, 6 key resource user groups, comprising of 32 fishermen, 16 retailers, 5 major fish dealers, 1 representative of a Fish Processing Company (FPC) and representatives of 6 hotels were identified and interviewed (Fig. 6). The retailers were further classified into two groups: fish mongers (selling unprocessed fish) and mama karanga (women who process and cook the fish before selling it). Figure 6 (b) provides a description of each actor category.

Nearly all the interviewed fishermen had prior agreements or preferred traders to whom they sell their catch, with 50 % of them preferring to sell to middlemen (dealers), 27 % to fish mongers, and 23 % to small-scale fish processors (mama karanga). No fishermen were recorded selling their catch directly to consumer markets, hotels or FPCs. Dealers on the other hand, hire or employ fishermen and possess fishing gears and crafts which they lend to the hired fishermen. All the interviewed dealers responded that they hired fishermen specifically from Pemba in Tanzania, during the NEM season. Remuneration and sharing of profits between the dealers and fishermen are catch percentage-based. For instance, one dealer reported buying the fish from the fishermen at $1/kg and selling it at $1.45/kg. The fishermen further give an additional 20 % of their revenue ($1) to the dealer as a gear-hiring fee and shared the remaining amongst themselves.

Although dealers mainly supply the hotels and Fish Processing Companies (FPC), they also supply to other traders including small-scale fish processors and fish mongers, especially during the low-landings SEM season (Fig. 7). Thus, dealers play an integral role in the trade; directly financing the fishermen, providing key links between fishermen and others, facilitating acquisition of fish by other resource user groups, and hence smoothing the trade.

Both small-scale fish processors and fish mongers purchase fish directly from the fishermen. However, none of them reported directly hiring fishermen; instead, most of these traders extend loans to the fishermen by means of cash, boat fuel and lighting to those who fish at night (Fig.7). None of the hoteliers interviewed had direct investments in the fishery trade. However, the FPC reported that they owned three fishing boats on different parts of the coast which were lent out to fishermen.

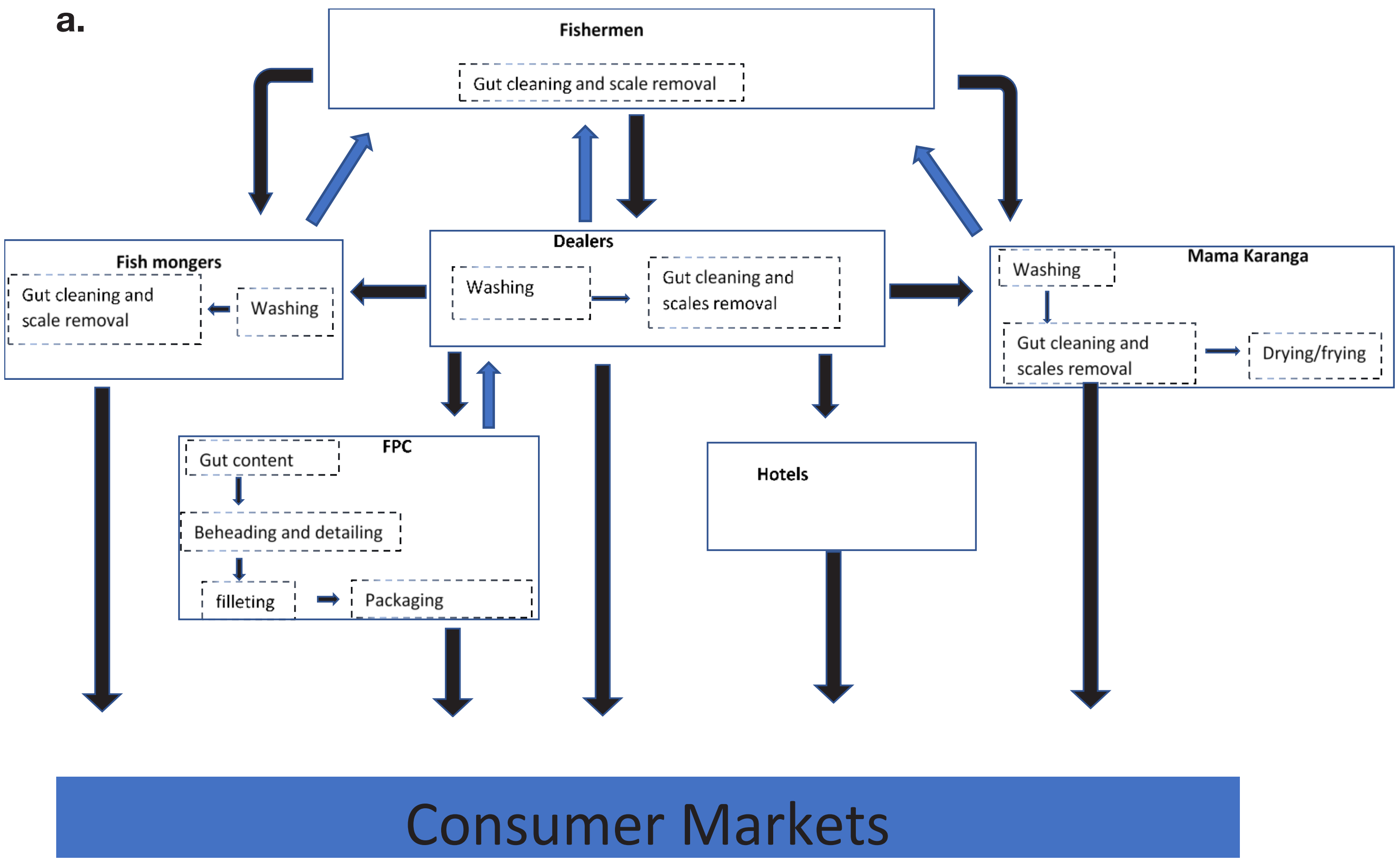
Resource units traded within actor groups

On average, fish dealers purchase more fish (between 100 and 700 kg per day depending on season) than small-scale fish processors and fish mongers with a range of between 10 and 30 kg per day each. The three categories of traders are not highly selective with regard to the type of fish as neither listed preference to any specific fish size or species. Hoteliers on the other hand buy the fish depending on demand, which is higher during the peak tourism period that is between July and December, coinciding with the NEM season (Fig. 7). For instance, one of the hoteliers indicated they buy between 8 and 60 kg per week depending on season. In addition, they have a higher preference for the pricey high trophic level fish species that are large and fleshy such as tuna and kingfishes (Scombridae), red snappers (Lutjanidae), and mullets (Mugilidae).

Finally, the FPCs trade in relatively large amounts of fish compared to the other resource user groups and are supplied with fish by many dealers from Gazi and other fishing areas. During the NEM season, procuring is more oriented towards finfish, amounting to between 5 and 15 tons of fish per day and shifts towards crustaceans and mollusks in the SEM which reduces the catch to between 3 and 8 tons per day.

Catch processing

Catch processing varied with the form of catch, individual catch size or the agreement between the resource user groups. For instance, de-gutting by fishermen is restricted to the large fish species such as *Coryphaena hippurus* (Coryphaenidae) and to some elasmobranchs species (sharks and rays). Fishermen removed the claws of crustaceans (lobsters and crabs) on a case-by-case basis before weighing and selling to the traders. The rest of the catch is sold unprocessed to the other traders (Fig. 6). Dealers also hire workers to process (mostly cleaning and removing scales) the catch that is sold to hotels and FPCs but not when selling it to the small-scale fish processors and fish mongers. Processing by FPCs is more comprehensive and normally involves scaling and de-gutting, filleting, and beheading (Fig. 6). It is also tailored to suit the customer or market demand; for instance, fish destined for South African markets is processed to fillet form whereas thise for the Saudi Arabian market could be filleted or frozen whole.



b.

Fishermen	✓ Involved in capture and landing of fish
Dealers	✓ Buys fish in large amounts (>5okg/day) ✓ Hires fishermen, owns many fishing gears and boats ✓ Transports fish in relatively large amounts ✓ Own freezing facility and permanent-structured fish shops
Fish Mongers	✓ Trade in <5okg fish/day ✓ Include individuals vending along roads, open air markets and in temporally sheds
Mama Karanga	✓ Sell in small quantities ✓ Fry fish prior to selling it
Fish Processing Companies (FPC)	✓ Highly selective in species and size ✓ Conduct Advanced processing of fish e.g. produce fish fillets ✓ May be involved in exporting

Figure 6 (a). Schematic representation of the catch supply chain on the south coast of Kenya, showing the main resource users (block boxes) and processing within each resource user group (dashed boxes). The flow direction of fish / products is shown by the black arrows, whereas direct investments, which include fishing gear, boats and credit are indicated by the blue arrows. The key users (U) are briefly defined and described in Table (b).

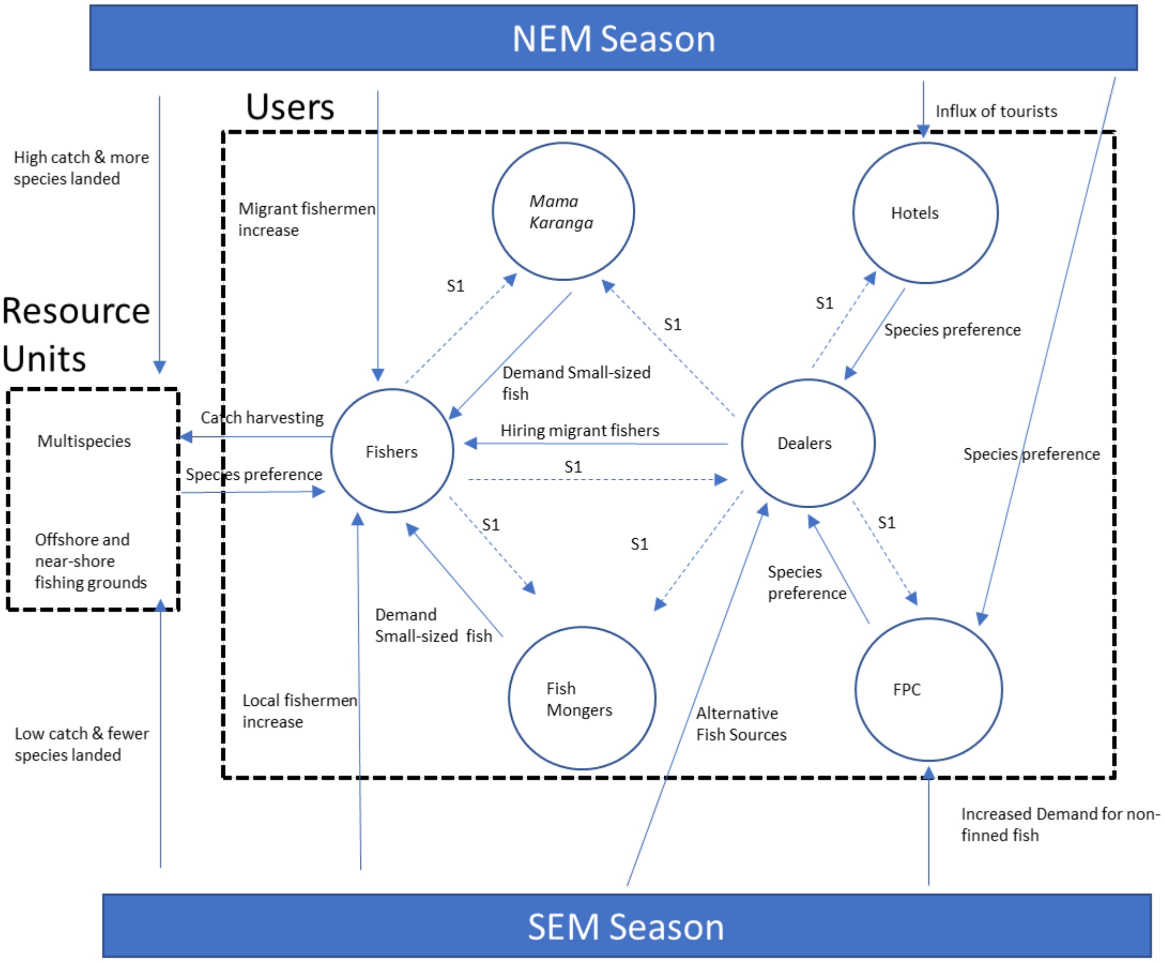


Figure 7. Interactions (dashed arrows) and implications (block arrows) between Resource Units (RU) and Users (U) components in the Gazi CAF system. S1 indicates supply chain direction among users as elaborated in Figure 6. The top and bottom block boxes are the contrasting calm NEM and rough SEM seasons respectively. NEM season coincides with the peak tourism season, which results in high fish demand from hotels. FPCs also demand large pelagic fish during the NEM and finance the dealers to secure their supply. The dealers in turn hire migrant fishermen during the NEM, increasing fishing effort which in turn results to landing of more species (see Fig. 3). In contrast, low tourism and rough sea conditions during the SEM results in low fishing effort with low catch and fewer species landed.

Discussion

Resource units

Previous studies have indicated distinct seasonal variation in finfish catches along the Kenyan coast. Lower catches during the wet SEM season was attributed to low fishing effort owing to the rough sea conditions hampering artisanal fishing activities (McClanahan, 1988; Agembe *et al.*, 2010). Furthermore, during the calm NEM season, fishermen access a wider variety of fishing grounds, operate in larger areas, across a wider range of habitats while using a variety of fishing gears and methods, hence landing higher catches. Contrasting studies however report that more species are landed during the SEM than NEM season, attributing this to fishermen concentrating their efforts around the inner reef, with a higher habitat complexity (McClanahan, 1988; Van der Elst *et al.*, 2005; Wamukota, 2009; Agembe *et al.*, 2010; Munga *et al.*, 2012).

Organization of resource user groups

According to the Government of Kenya (2016), there were about 13,000 artisanal fishermen along the Kenyan coastline, each playing a key role in sustaining a fish trade network for suppliers, processors and traders. The documented fishermen-trader agreements are important as they provide means for fishermen to secure income and fish market access during the surplus NEM season. Similarly, traders are assured of stock and labour especially from the migrant Pemba fishermen (Wamukota *et al.*, 2015). These localized social and economic networks remain important to the economy and social components of the communities even as other sectors of the country's economy such as mining, agriculture and tourism experience rapid growth.

Since low quantities of fish are landed and sourced locally among different resource user groups during the SEM season, some users have means of sourcing fish stocks externally during this season (Fig. 7). For instance, the dealers reported operating fish retail shops which outsource imported Chinese fish from the fish market in Mombasa, at an even lower cost. Fish mongers and small-scale fish processors in turn source this fish from these retail shops. Other studies Crona, 2006; Bodin and Crona, 2008; Cinner *et al*., 2010); Daw *et al*., 2011) documented various alternative income-generating activities that different users engage in to supplement their income during this low season.

The resources user chains, (Fig. 6) in this CAF system are relatively short and poorly organized compared to similar systems elsewhere. For instance, around Lake Victoria in Kenya, fishermen are registered within cooperatives which are used as channels for selling fish to FPCs; while the FPCs may have arrangements for directly hiring fishermen (Abila and Jansen, 2007). Furthermore, it is apparent that the fish-processing methods as well as the processing links are very basic, hence a large proportion of fish reaches target markets in an unprocessed state. This contrasts with other tropical CAFs in areas such as Ghana, Sierra Leone, and Cameroon where a range of processing methods such as smoking, fermenting, sun-drying, grilling and frying are applied prior to transporting fish to different markets (Essuman, 1992; Nfotabong *et al.* 2009; Kallon *et al.* 2017).

Interactions between the resource units and user groups within the CAF system

CAFs, just like other socio-ecological systems, are characterized by numerous, complex vertical and lateral interactions between and within the four key components proposed by Ostrom (2009): resource user groups, resource units, resource system, governance systems and expected outcomes (see Fig. 1). The interactions, which have multiple stable states, comprise the catch harvesting and supply processes as well as management procedures. In Kenya, transition between the multiple stable states is normally initiated by seasonal change in accessibility of fishing grounds, market availability as well as change in fishing technology (see Fig. 7). Thus, notwithstanding the socio-economic importance attached to CAFs by the country, their operations and stability are usually characterized by a high degree of uncertainty due to their heavy dependency on the external forces of tourism and climatic seasonality (Fulton *et al*., 2011).

The demand, supply and catchability of fish are highest during the NEM season and relatively lower during the SEM (See Fig. 7). As such, hotels and FPCs buy more fish during the NEM season; FPCs due to abundant supply, and hotels due to increased demand created by the tourism influx between December and March. Both users have a preference for the high-priced, large pelagic finfish and lobsters, which mostly occur in offshore fishing grounds (Crona *et al*., 2010). Therefore, seasonal demand created by the two user groups may directly influence the type of fish that is sought as well as the fishing effort variation within the CAF (Fig. 7). This is reflected by the dealers who hire migrant fishermen from Pemba during the NEM season, with better offshore fishing skills. Increase in fishing effort as well as a wider variety of fishing habitats accessed during NEM in turn results in more fish species landed during this season (Fig. 7). Notwithstanding the costs of importing migrant fishermen's labour, dealers consider these fishers to be easily available and more efficient compared to the local fishermen, especially during the NEM season, who in most cases are less competent compared to the more effective migrant fishermen (Samoilys *et al*., 2017).

Although patterns in numbers of migrant fishermen in Kenya have been well documented, details on the variation in number of local fishers during the overlapping NEM-peak tourism season are contrasting. For instance, Daw *et al.* (2011) stated that the number of fishermen increases as more people take advantage of the calm sea hence engaging in fishing activities, whereas Tuda *et al.* (2008) observed that the number of fishermen decreases since local communities may prefer to be employed in tourist-related work which is better paying.

While both hoteliers and representatives of FPCs reported preference of certain species of fish, size of catch has previously been described as the main factor determining the market to which the fish is shipped or brought (Crona *et al*., 2010). The small and medium-sized catch, for both the high and low-priced species, are mainly purchased by the small-scale fish processors and fish mongers. These categories of fish are destined for the local markets and have a special relevance to local food security since they are the easiest to access and the most affordable source of animal protein for the majority of people in the local communities (Creel, 2003). However, the small-sized fish are often caught from lagoons and inshore fishing grounds using mainly unselective and destructive fishing gears such as beach seines. With the growing human population in these areas, the demand for these unsustainably harvested fish continues to grow, hence compromising the state of fish stocks and the integrity of the shallow coastal habitats which serve as fishing grounds.

On the other hand, increased demand for large pelagic species in the market can result in an increase of their market price and can encourage more fishermen to overexploit these species. For instance, there are records of increased use of spearguns, an illegal traditional fishing gear, in Gazi during the NEM season, as fishermen target highly priced parrotfishes (Scaridae), grouper (Serranidae), snappers (Lutjanidae), rabbitfishes (Siganidae), octopus (Octopodidae) and lobsters (Nephropidae) (Fonteneau *et al*., 2013; Tuda *et al*., 2016). If uncontrolled, the selective harvesting of large species can cause a change in trophic composition, where overexploitation of such species results in their decrease, and eventually fishermen end up targeting other less valuable species from lower trophic levels (Pauly *et al*., 1998).

Conclusion

The socio-ecological system framework (Fig. 7) provides a structured and systematic way to describe and analyze coastal artisanal fisheries in Kenya – showing the composition and interactions between and among the multiple elements in this sectoral system. Moreover, both the socio-economic and ecological sub-systems of a coastal artisanal fishery are dynamic and co-evolve because of their interaction and in response to common external drivers such as season and tourism. Knowledge of how resource user groups organize within the supply chains and how this organization influences harvesting preferences and behavior can be important in strengthening both the socio-economic and ecological resilience within a coastal artisanal fishery through management of their adaptive cycles, with an aim of sustaining the resource units and ecosystem services at multiple scales. Moreover, such information can enable coastal artisanal fishery managers to anticipate more accurately how relationships and feedbacks within their system, intended or unintended, affect the achievement of management objectives. Secondly, both the demand and supply or availability of the resource units (fish) increase simultaneously during the meteorologically calm, high-tourism NEM season. When both demand and supply increase, there is an increase in the equilibrium output which determines the general market price where fish tend to be more expensive during the SEM season (Fig.7). Combining this fact with the common property nature of the fishery resource, there is a risk of overexploitation of the resource units as well as a dissipation of the income yielded from these resources. To avoid a collapse of the coastal artisanal fishery, management plans taking into consideration the interactive nature of catch harvest and market dynamics should be formulated and implemented in close collaboration with all key resource users.

Finally, this study tracked two key sub-systems (resource user groups and resource units) plus their second-level variables (the amount and type of catch, the number of resource users etc.) and the outcomes of their interactions (Fig. 1 and Fig. 7). The choice of sub-systems and variables to study was guided by the key research question, "How is the artisanal fisheries trade organized in a coastal artisanal fishery like that on the Kenyan coast?" However, this still leaves a knowledge gap on interactions and outcomes between other sub-systems and key variables within this socio-ecological system. Therefore, this study recommends further, complementary studies on the same topic, based on Ostrom's SES model.

Acknowledgements

This study was made possible through the financial support of VLIR UOS and the laboratory of Systems Ecology and Resource Management at ULB. The authors further acknowledge the support from the Belgian Fund for Scientific Research (F.R.S.-FNRS), through the SASES project'. We are also grateful to Kwale County Fisheries Department for provision of fish landings data, Mr Evans Nyachonka from KMFRI Gazi, for his undivided dedication during the data collection phase, members of the Gazi Beach Management Unit, especially the chairman, Mr Juma for his guidance and help in mobilizing his group members. We thank the Flemish Inter-University Council - University Development Cooperation (VLIR UOS) for its financial support to the TRANSCOAST project and to the Global Minds Programme of the Vrije Universiteit Brussel.

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Movement patterns and growth rate of cavebass *Dinoperca petersi* (Pisces: Dinopercidae) in the iSimangaliso Marine Protected Area, South Africa

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Abstract

Dinoperca petersi is a relatively common fish species caught in the line-fishery in KwaZulu-Natal (KZN), South Africa. Yet, little is known about the biology and ecology of this species. Movement patterns and growth rate of this species were studied based on data obtained from a long-term tag-recapture study conducted in the iSimangaliso Marine Protected Area in northern KZN between 2001-2019. Results showed that *D. petersi* is a highly resident species with a linear home-range size of 290-405 m. While most fish showed high site fidelity, 8.8 % of the tagged fish showed wider ranging movements of 2.4-90 km. However, only 5 fish showed movements out of no-take zones into adjacent exploited areas, suggesting limited adult spillover. Growth rate of tagged fish was found to be reasonably slow compared to other sympatric predatory reef fish with an average growth rate of 61.76 mm y^{-1} for smaller fish (g_α = 300) and 9.58 mm y^{-1} for larger fish (g_β = 550). Based on these life history characteristics, options for the future conservation and management of this species are discussed.

Keywords: tag-recapture, station-keeping, ranging, no-take area

Introduction

Dinoperca petersi, known locally as cavebass or lampfish, has a patchy, coastal distribution throughout the Western Indian Ocean including Pakistan, southern Oman, Kenya, Mozambique and the eastern seaboard of South Africa, extending south to Mossel Bay (Heemstra and Heemstra, 2004, Froese and Pauly, 2019). They inhabit high profile rocky and coral reefs to depths of 75 m. While often found in caves and under ledges during the day, they are generally more active nocturnally. They feed on a variety of reef invertebrates such as shrimps, crabs, octopus, as well as small fish (van der Elst, 1993). *D. petersi* can reach a maximum size of 75 cm total length (TL) and a weight of 5.8 kg (van der Elst, 1993). Although fairly common in KwaZulu-Natal (KZN), they form a relatively minor component of catches in the line-fishery contributing 0.07 % to the shore fishery (Dunlop and Mann, 2012), 1.5 % to the recreational ski-boat fishery, and 0.33 % to catches of the commercial line-fishery, by number (Dunlop and Mann, 2013). They are also occasionally taken by spearfishers (Lloyd *et al*., 2012, Fennessy and Mann, 2013). Despite an extensive literature review, there is very little published information on catches of this species elsewhere within its distribution range.

Considering their local abundance in KZN waters, surprisingly little is known about the biology and ecology of this species (van der Elst, 1993, Heemstra and Heemstra, 2004). *D. petersi* comprise an important component of the catch in the surf-zone within the iSimangaliso Marine Protected Area (MPA) in northern KZN (Mann *et al*., 2015), providing an ideal opportunity to learn more about this species. A surf-zone fish monitoring and tagging project has been undertaken in the iSimangaliso MPA by the Oceanographic Research Institute (ORI) since 2001 (Mann *et al*., 2015, 2016a, 2016b, 2016c, 2018) and a substantial amount of data have been collected on *D. petersi* over the past 19 years. More specifically, the tagging project has enabled the collection

http://dx.doi.org/10.4314/wiojms.v19i2.4

of data on both movement patterns (Mann *et al.*, 2015) and growth rates (Mann *et al.*, 2016c) of focal species. The primary aim of this study was therefore to use the available tag-recapture data that have been collected on *D. petersi* to describe their movement patterns and estimate their growth rate. This study also provided the opportunity to comment on the effectiveness of the iSimangaliso MPA in providing protection for this species.

Materials and Methods

Research line-fishing, using standardised shore fishing gear, has been undertaken by teams of trained anglers on a quarterly basis within the iSimangaliso MPA since 2001 (see detailed description of the methods used in Mann *et al.*, 2015, 2016a, 2018). Research catch-and-release fishing was conducted in zoned no-take and exploited areas in four accessible parts of the MPA. These included (from north to south): Bhanga Nek, Sodwana, Cape Vidal and Maphelane (Fig. 1). Research fishing normally took place during approaching spring tides so that low tide was in the early morning and evening. This enabled fishing teams to reach the designated sampling areas by driving a 4x4 vehicle on the hard sand at low tide. Most fishing days were therefore at least 12 hours in duration (depending on prevailing weather conditions). Use of barbless hooks was strictly enforced (the barb on the hook being crimped using long-nose pliers) as this inflicted less damage on the fish and made their release considerably quicker and easier (Casselman, 2005). If a fish was 'gut-hooked' (i.e. with the hook lodged in the oesophagus) no attempt was made to remove the hook and the snood was simply cut off near to the eye of the hook (Schaeffer and Hoffman, 2002; Butcher *et al.* 2010). Use of circle hooks was encouraged (Cooke and Suski, 2004) but not enforced due to the higher price of these hooks and the gear preferences of some anglers.

All fish caught were immediately placed into a bucket of fresh seawater before being carried to the tagging station. Once removed from the bucket, they were covered with a wet cloth and quickly measured (total length [TL] in mm) on a wet plastic stretcher with a ruler down the centre, before being returned to the water. Emphasis was placed on keeping the fish out of the water for as short a time as possible and all surfaces were kept moist to reduce injury and stress (Cooke and Wilde, 2007). All fish >300 mm TL were tagged using plastic dart tags (Hallprint©) supplied by ORI's Cooperative Fish Tagging Project (ORI-CFTP) (Dunlop *et al.*, 2013). Only D-tags (85 mm in length and 1.6 mm in diameter) were used to tag *D. petersi*. Each time a fish was tagged or recaptured, the tag number, species, length (mm TL), date, time and GPS locality was recorded. The GPS position was linked to markers placed every 100 m for the length of all four sampling areas so that fish movement could be determined with an accuracy of 50 m. A note was made if there was a tagging scar present on the fish, indicating that it had been previously tagged but the tag had been shed. Aside from fish recaptured by the research team, members of the angling public also reported recaptures from adjacent exploited areas north and south of the study area. Fish recaptured by members of the angling public were reported through the ORI-CFTP, which uses locality codes that corresponded to a coastal location such as a town, estuary, and/or popular fishing site along the coast with a resolution of approximately one kilometre (Dunlop *et al.*, 2013).

Data analysis

Movement patterns

Movement was categorised as station-keeping (generally refers to movements within a home range and is usually linked to foraging) or ranging (an exploratory movement that takes an individual permanently beyond its home range to settle eventually into a new one) as defined by Dingle (1996) and Dingle and Drake (2007). In this study, because of the relatively small size of the original sampling areas (see Mann *et al.*, 2015), a fish was considered to be station-keeping if it was recaptured within 2 km of its release site. If a fish moved >2 km and did not return to its original tagging location, it was considered to be displaying ranging behaviour. Station-keeping is a good indicator of the potential for fish to remain within a protected area and was used to quantify the degree of residency. Ranging behaviour on the other hand indicates the potential for export of fish to adjacent fisheries out of a no-take area.

Station-keeping

In the current study, station-keeping behaviour was quantified for each species by taking the 95th percentile of intra-study site movement distances only (Maggs *et al.*, 2013) and excluded all long-distance (>2 km) movements (Attwood and Cowley 2005). The resulting value is referred to as 'single linear distance' (SLD) in the current study. Assuming that a fish is randomly drawn from within the boundaries of its home range at first capture (tag-release) and then redrawn from that same home range at a later stage (recapture), the Euclidean distance between the two points (SLD) can be considered to represent some unknown proportion of the length of the home range. Repeating this several times, with different individuals of the same species, provides a good reflection of the degree of residency for that species. To prevent pseudo-replication, the calculation of SLD used only the distance between the original tagging site and the first recapture location.

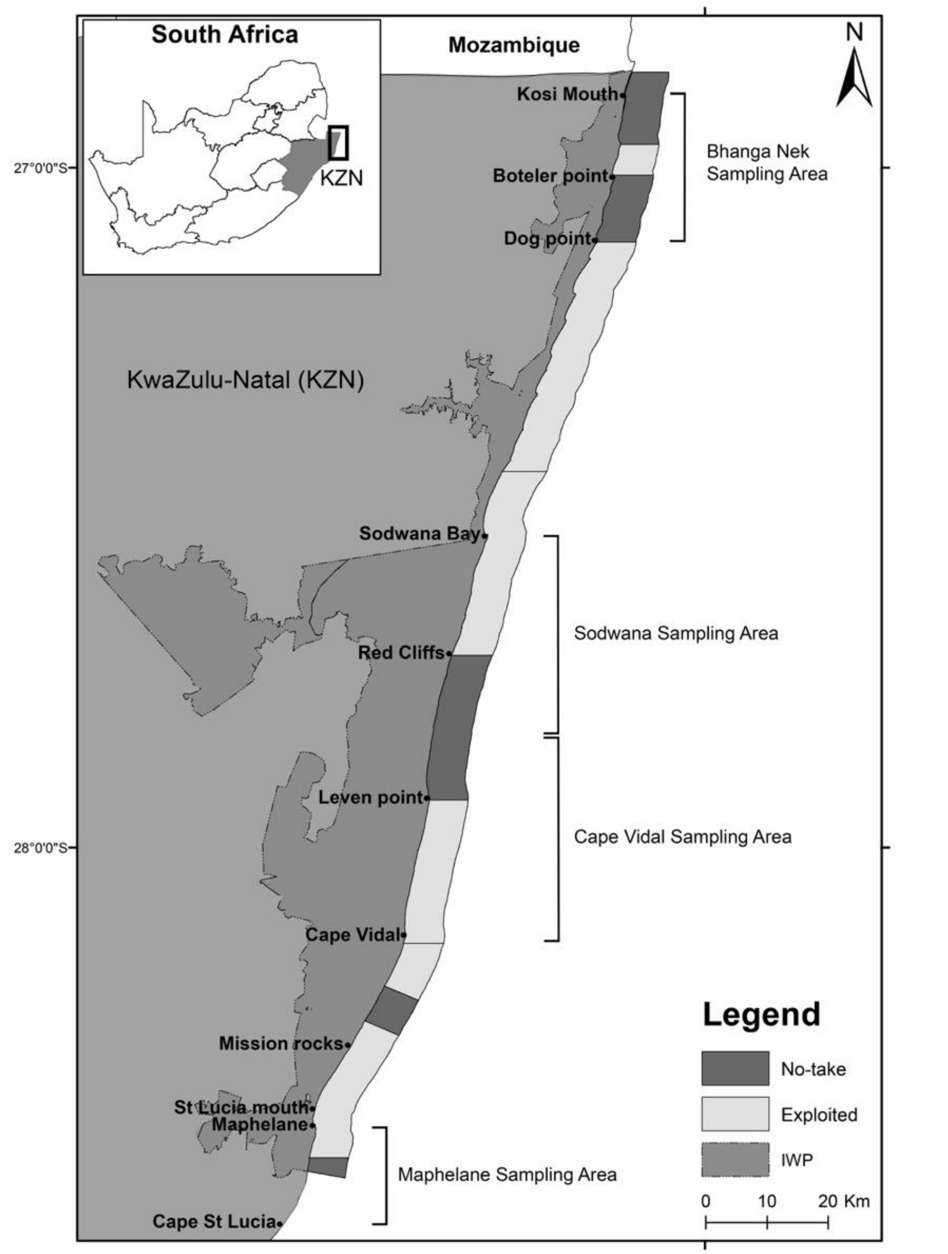

Figure 1. Map of the iSimangaliso Wetland Park (IWP) showing the zonation and areas sampled in this study. Note that this map does not show the new inshore and offshore zonation plan or the southern extension of the MPA that was implemented in August 2019 (see https://www.saambr.org.za/new-mpas-for-anglers/ for further information).

Multiple recaptures (three or more capture points) provide stronger evidence of area utilisation by an individual fish. In this case, an alternative method for quantifying station-keeping behaviour was applied by taking the 'greatest linear distance' (GLD) between all the recapture locations from the original tagging location (provided that all recaptures were within 2 km of the original tagging location). The resulting estimate was used to validate the SLD calculated above. Note that the GLD could be less than the SLD as only multiple recaptures were used to calculate the GLD.

Ranging

The potential of the no-take zones to export fish was evaluated using records of long-distance movements (i.e. tagged fish leaving the no-take zones). Most of the recaptures of ranging fish were recorded by the research team, but some recaptures were also reported by members of the angling public through the ORI-CFTP. Although relatively few long-distance movements were reported by members of the public, there was potential for non-reporting (Dunlop *et al.*, 2013), particularly if fish were recaptured by local subsistence fishermen who did not possess means of communication (i.e. a cell phone) to report the recapture.

Capture time was plotted as a rose diagram using the statistical software Oriana (Version 4, Kovach Computing Services). A Chi-square test was used to determine if the number of fish moving north or south was significantly different. A two-sample *t* test assuming unequal variances was used to determine if the distance moved north or south was significantly different. Time at liberty was compared to distance moved using a linear regression. Similarly, fish length was compared with distance moved.

Growth rate

Tag-recapture length data were initially filtered to remove all recaptures where length was not reported or where there were obvious measurement discrepancies. The tag-recapture data were represented by T_1, T_2, L_1 and L_2 where T denotes time (date) and L length (mm, TL). The subscripts 1 and 2 refer to the dates of tagging and recapture, respectively. Increments in length and time are given as ΔL and ΔT, respectively. Growth rates were modelled from the tag-recapture data using the maximum-likelihood approach described by Francis (1988a, 1988b) in the statistical package “R” (R Core Development Team, 2020), running the function (grotag) from the R-Package ‘fishmethods’ (Nelson, 2019). The usual form of the von Bertalanffy growth function, as used with tag-recapture data, may be written as:

$$\Delta L = (L_\infty - L_1)(1 - e^{-K(t_2 - t_1)}) \tag{1}$$

Francis (1988a) described a re-parameterisation and extension of the Faben’s (1965) growth model for tag-recapture data that incorporates seasonal growth:

$$\Delta L = \left[\frac{\beta g_a - \alpha g_\beta}{g_a - g_\beta} - L_1\right]\left[1 - \left(1 - \frac{g_a - g_\beta}{a - \beta}\right)^{\Delta T + (\varphi_2 - \varphi_1)}\right] \tag{2}$$

where

$$\varphi_i = u\frac{\sin[2\pi(T_i - w)]}{2\pi} \text{ for } i = 1, 2 \tag{3}$$

The parameters g_α and g_β are the estimated mean annual growth (mm y^{-1}) of fish of initial lengths α mm and β mm, respectively, where α<β. The reference lengths α (300 mm) and β (550 mm) were chosen such that the majority of values of L_1, the length at tagging, fell between them. Seasonal growth is parameterised as w (reflecting the portion of the year in relation to 1 January when growth is at its maximum) and u (with u = 0 indicating no seasonal growth through to u = 1 indicating maximum seasonal growth effect).

The measured growth increment of the *i*th fish, ΔL_i, has a corresponding expected mean growth increment u_i, where u_i is normally distributed with standard deviation σ_i. In this study, σ_i was assumed to be a function of the expected growth increment u_i:

$$\sigma_i = \nu\mu_i \tag{4}$$

where v is estimated as a scaling factor of individual growth variability.

The model was fitted by minimizing the negative log-likelihood function λ for each dataset, made up of i=1 to n growth increments:

$$\lambda = \sum_i \ln\left[(1 - p)\lambda_i + \frac{p}{R}\right] \tag{5}$$

where

$$\lambda_i = e\frac{-\frac{1}{2}(\Delta L_i - u_i - m)^2 / (\sigma_i^2 + s^2)}{[2\pi(\sigma_i^2 + s^2)]^{\frac{1}{2}}} \tag{6}$$

When the model is fully parameterised, the likelihood function estimates the population measurement error in ΔL as being normally distributed, with a mean m and standard deviation s. The proportion of outliers was identified by the parameter p, the probability that the growth increment for any individual could exist erroneously in the dataset as any value, within the observed range of growth increments R.

The optimal model parameterisation was determined by following a stepwise fitting procedure. Initially, a simple 3-parameter model was fitted and then parameters were added in the order determined by selecting

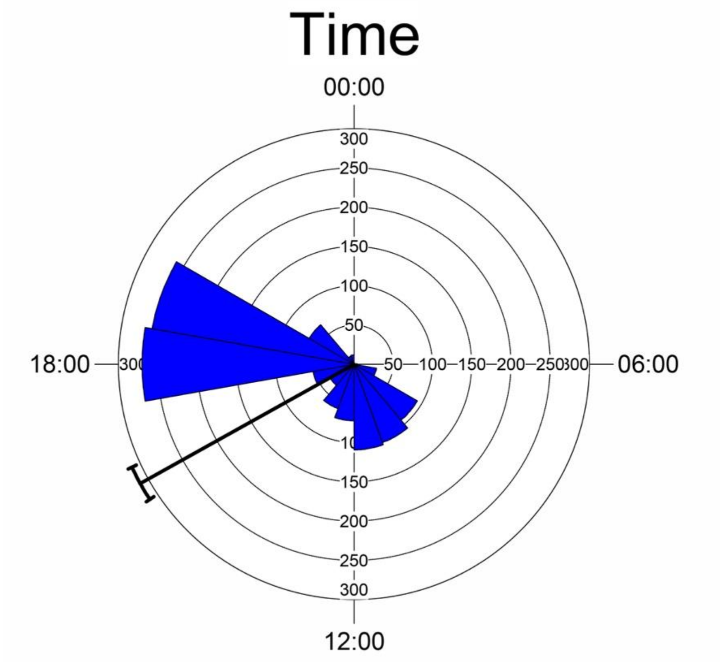

Figure 2. A rose diagram showing the time of capture of 1173 *Dinoperca petersi* caught during research fishing in the iSimangaliso MPA between 2001 and 2019. Note that on most days, fishing seldom took place beyond 21:00, except on a few occasions when fishing occurred later due to logistical reasons. The dark line represents mean capture time and capped line represents 95 % confidence interval.

the parameter that gave the greatest reduction in the Akaike Information Criterion (AIC) value, with unfitted parameters held at zero. When the introduction of an additional parameter did not result in a significantly better model fit, these results were excluded from the analyses. The final model was bootstrapped 1 000 times and 95% confidence intervals were calculated for parameter estimates.

Results

From November 2001 to November 2019 a total of 83 field trips was conducted, during which 1 173 *D. petersi* were caught. Time of capture for each fish is shown in Fig. 2 highlighting the number of fish caught at dusk and during the first few hours of darkness. Of the *D. petersi* caught, 775 were tagged and released and 111 were recaptured at least once (the remainder being

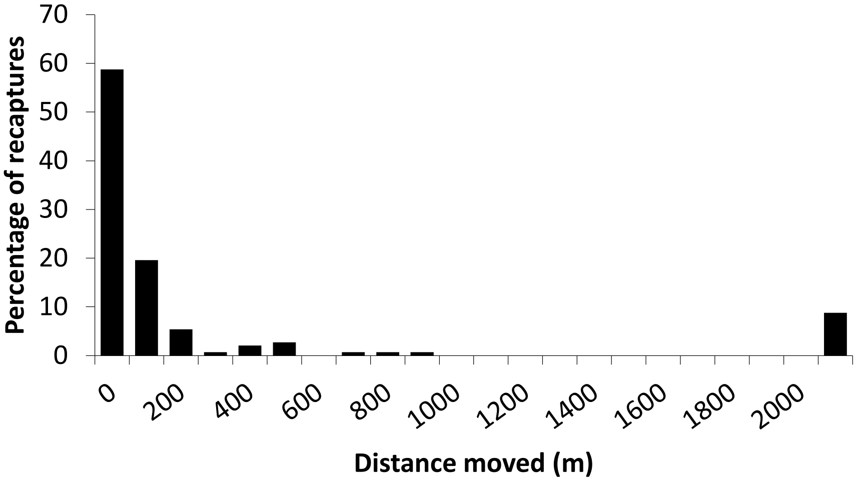

Figure 3. Movement displayed by 148 *Dinoperca petersi* recaptured in the iSimangaliso Marine Protected Area between 2001 and 2019. Note that the last column of the graph cluster all the individuals that moved > 2 000 m.

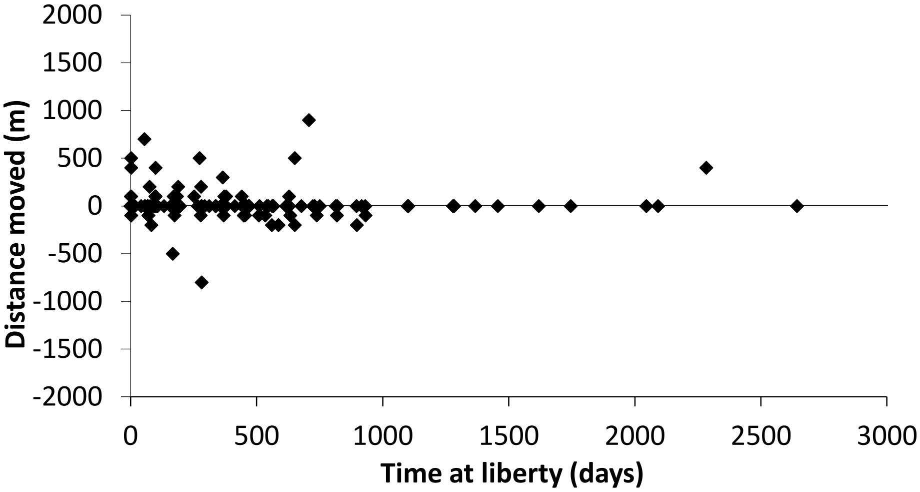

Figure 4. Distance and direction of movement and time at liberty displayed by 148 *Dinoperca petersi* recaptured in the iSimangaliso Marine Protected Area between 2001 and 2019. Positive values indicate northward movement while negative values indicate southward movement. Note that 13 fish which moved >2 km are not displayed.

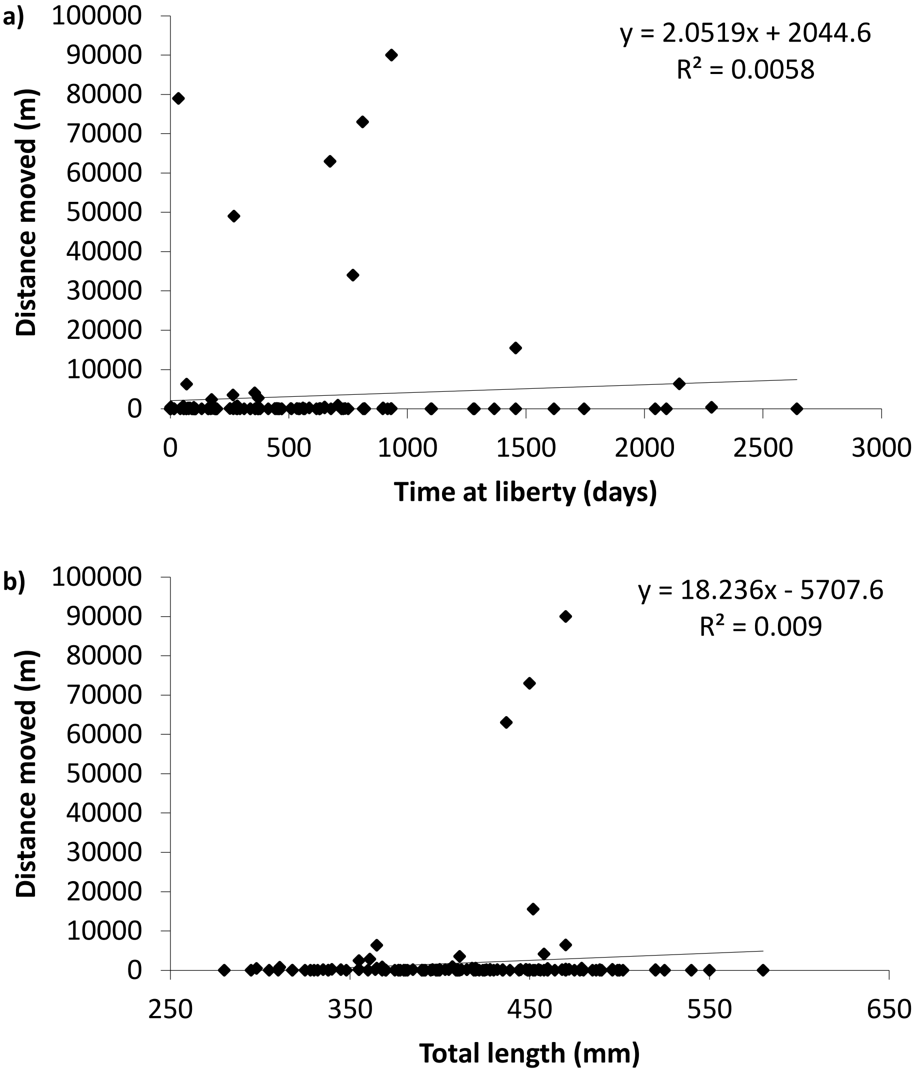

Figure 5. a) A correlation between time at liberty and distance moved (n=148); and b) a correlation between total length and distance moved (n=145) by *Dinoperca petersi* recaptured in the iSimangaliso MPA (note that 3 fish recaptured by members of the public were not measured).

<300 mm TL and thus too small to tag). A further 37 multiple recaptures (fish having three or more capture points) and six fish with tag scars (i.e. tag had been shed) were also recorded. Of the 37 multiple recaptures, 24 fish were recaptured twice, 6 were recaptured thrice, 4 were recaptured 4 times, 2 were recaptured 5 times and 1 fish was recaptured 6 times.

Movement patterns

Of all the recaptures (including multiple recaptures) 83.1 % were recaptured within 200 m of their original tagging locality, thereby predominantly displaying station-keeping behaviour. Only 13 recaptures (8.8 %) were from fish recorded moving distances greater than 2 km, thereby displaying ranging movement behaviour (Fig. 3).

In terms of direction moved, there was no significant difference ($\chi^2 = 0.41$, $p > 0.05$) between the number of fish that moved in a northerly or southerly direction (Fig. 4). However, the distance that fish travelled in a northerly direction was significantly greater ($t = -2.32$, df = 33, $p < 0.05$) than those that travelled in a southerly direction. The greatest movement recorded was by a fish that moved 90 km in a northerly direction. Time at liberty ranged from 0 – 2643 days (7.2 years) (Fig. 4). There was no significant correlation ($p > 0.05$, $R^2 = 0.006$) between time at liberty and distance moved (Fig. 5a) or between fish length and distance moved ($p > 0.05$, $R^2 = 0.009$) (Fig. 5b).

The home range size (linear distance) of *D. petersi* was calculated to be 405 m based on the SLD (95th percentile) of 100 recaptures that moved less than 2 km. Using movements of 35 multiple recaptures that moved less than 2 km, the GLD (95th percentile) was calculated to be 290 m.

In terms of movement between zoned areas within the iSimangaliso MPA (Table 1), 5 tagged *D. petersi* moved out of a zoned no-take area, 3 moved directly through a no-take area, 1 moved into a no-take area and the remaining 102 fish stayed in the same zone that they were originally tagged in (n=111). No fish were recaptured outside of the MPA and no fish were recorded moving out of their home range and then moving back later.

Growth

Of the 148 recaptures obtained during the 19-year study period, 109 had suitable length data that could be used in the growth study following filtering out of unrealistic data. The length frequency of fish lengths at tagging and at recapture are shown in Fig. 6 and ranged between 300-600 mm TL.

To understand the importance of interpretation of the different parameters, a stepwise fitting procedure was followed, starting with the simplest 3-parameter model. Successive parameters were included for all the combinations that improved the fitted model best (Table 2).

Table 1. A summary of the movements of 111 *Dinoperca petersi* tagged and recaptured in the iSimangaliso MPA between 2001 and 2019.

	Number	%	Mean distance moved (km + SD)
No. tagged	775		-
No. recaptured	148	19.1	2.97 ± 13.37
No. of single recaptures	111	14.3	3.46 ± 14.71
No. of multiple recaptures	37	4.8	1.49 ± 8.06
No. of fish caught with tag scars	6	0.8	-
No. tagged and recaptured in an exploited zone	55	49.5	0.34 ± 1.22
No. tagged and recaptured in a no-take zone	47	42.3	0.1 ± 0.21
No. that moved out of a no-take zone	5	4.5	41.2 ± 35.32
No. that moved into a no-take zone	1	0.9	2.80
No. that moved right through a no-take zone	3	2.7	67.0 ± 15.87
No. recaptured outside the MPA	0	0	0

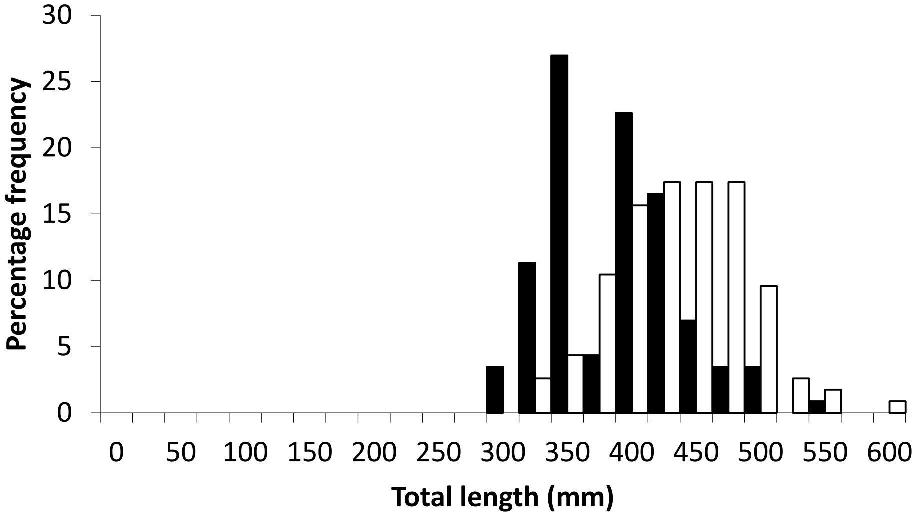

Figure 6. Length of *Dinoperca petersi* at tagging (solid bars) and recapture (clear bars) in the iSimangaliso MPA between 2001 and 2019 (n=109).

The remaining combinations that did not improve the model were excluded. The best fit model (Model 5, Table 2) consisted of the following parameters:

- g_α – the mean annual growth rate of fish at length α (300 mm TL was selected as this reflected the smaller size range of the sample).
- g_β – the mean annual growth rate of fish at length β (550 mm TL was selected as this reflected the larger size range of sampled fish).
- *s* – the root mean square error, which comprises possible measurement error during sampling, individual growth variability and lack of fit of the model.
- *v* – the growth variability parameter. The addition of this resulted in the slight increase of both the L_∞ and *k* values.
- *m* – the combined mean measurement error (mm) at tagging and recapture.
- *p* – the probability that the growth increment for any individual could exist erroneously in the dataset as any value within the observed range of growth increments *R*.
- *u* (year) - based on 0 reflecting no seasonal variability and 1 indicating strong seasonal variability. The resultant value (0.23) indicated that there is weak seasonal variation in growth for *D. petersi*.
- *w* (year) – a value reflecting time (data) as a fraction of the year when growth rate is at its maximum. The value 0.52 indicated that the growth peaked in June/July.

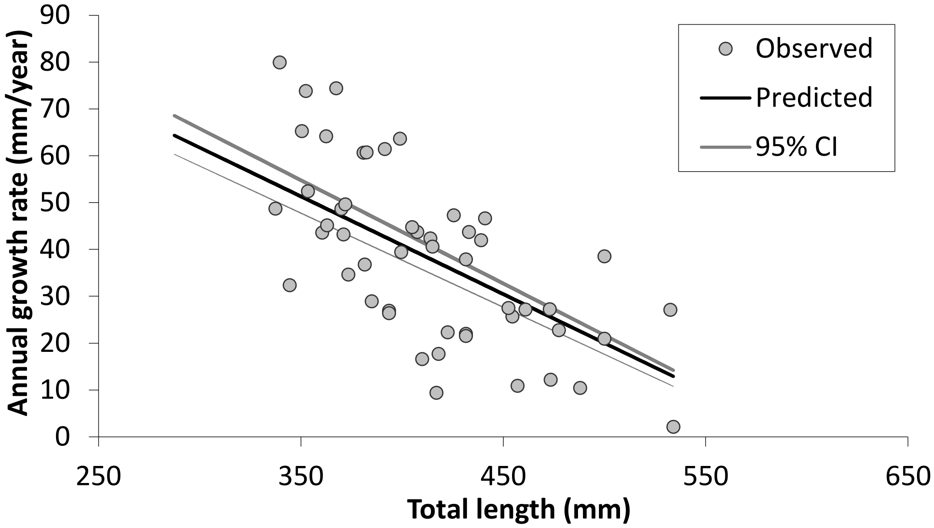

Figure 7. Observed and predicted growth rate for *Dinoperca petersi* tagged and recaptured in the iSimangaliso MPA between 2001 and 2019 (n=109). (Note: observed data points for recaptures <1 year-at-liberty (n = 59) were excluded from the figure for clarity).

Table 2. Parameters estimated for the growth rate of *Dinoperca petersi* in the iSimangaliso MPA between 2001 and 2019 using five different tag-recapture growth models (following Francis 1988a, b). The final and best estimates are shown in bold. See the methods section for an explanation of the parameters.

Parameter	Symbol (unit)	Model									
		1		2		3		4		5	
		Estimate	Error	Estimate	Error	Estimate	Error	Estimate	Error	Estimate	Error
Mean growth rates	g300 (mm/y)	54.840	3.630	57.330	3.850	56.620	3.320	64.420	3.880	**61.760**	**3.860**
Mean growth rates	g550 (mm/y)	9.580	3.320	9.580	4.900	9.580	4.190	9.580	4.040	**9.580**	**4.030**
Seasonal variation	*u* (year)	*0	0.000	*0	0.000	*0	0.000	*0	0.000	**0.231**	**0.142**
	w (year)	*0	0.000	*0	0.000	*0	0.000	*0	0.000	**0.523**	**0.134**
Growth variability	*v*	*0	0.000	0.393	0.050	0.284	0.041	0.270	0.038	**0.271**	**0.037**
Measurement error	*s* (mm)	20.233	1.683	6.484	1.065	6.805	0.922	6.308	0.907	**6.079**	**0.892**
	m (mm)	*0	0.000	*0	0.000	*0	*0	-2.808	1.220	**-2.947**	**1.186**
Outliers	*p*	*0	0.000	*0	0.000	0.031	0.022	0.031	0.022	**0.031**	**0.022**
Negative log likelihood		482.50		449.20		442.10		439.60		**438.200**	
AIC		970.90		906.30		894.10		891.10		**892.400**	
Parameters											
Maximum theoretical length	L_∞	-602.32		-600.15		-600.91		-596.20		**-595.893**	
Growth rate parameter	k	0.200		0.212		0.208		0.232		**0.234124**	

*0 parameter held fixed (see explanation in text)

As with most reef fish species, growth rate declined with increase in length, although there was a high degree of variability in individual growth rates (Fig. 7). Relatively fast growth (61.76 $mm.y^{-1}$ ± 3.86) was recorded in smaller fish compared to larger fish (9.58 $mm.y^{-1}$ ± 4.03) (Table 2). There was a weak seasonal influence (0.23 ± 0.14) with fastest growth rate recorded in June/July. The mean measurement error in ΔL was low and estimated at -2.95 mm ($\pm$ 1.19). The probability of outliers detected in the model fit was also relatively low (0.031 $\pm$ 0.022), although 59 recaptures were caught after being at liberty for less than one year which increased the number of outliers.

Discussion

Movement patterns

Station-keeping

The results of this study showed that *D. petersi* is a highly resident reef fish with a home range size of between 290-405 m. Most of the movements undertaken by recaptured fish were relatively small (mean = 83 $\pm$ 100 m, n=100) inferring station-keeping behaviour. With its large eyes and nocturnal habits, it is likely that *D. petersi* remains in caves or under ledges during the day and moves out to forage at night. This nocturnal foraging behaviour was confirmed by examining the time when most of the fish were caught. As shown in Fig. 2, although some fish were caught during the day, especially on the pushing tide between 09:00 and 12:00, most fish were caught at dusk and into the evening between 18:00 and 20:00. Another interesting observation to support this theory was that the tags of most recaptured *D. petersi* were remarkably clean and not covered with biofouling as observed with many other fish species tagged in this project. This suggests that the fish are remaining out of direct sunlight during the day thereby limiting growth of photosynthetic algae on the tags.

As *D. petersi* is found on both inshore and offshore reefs down to depths of 75 m (van der Elst, 1993), there is scope for ontogenetic movement offshore, which would not have been observed in this study as sampling was confined to the surf-zone. However, the fact that fish were caught throughout their adult size range in the surf-zone (estimated size at maturity is ~30 cm TL), suggests that they are not only using surf-zone reefs as juvenile nursery areas as found with some other sympatric species in this habitat (e.g. *Epinephelus tukula* and *E. marginatus*) (Mann *et al.*, 2015).

High levels of site fidelity (i.e. station-keeping) as observed in *D. petersi* can lead to localised depletion in exploited areas but can be of benefit in no-take areas. All the inshore no-take zones sampled in the iSimangaliso MPA during this study were longer than 2 km in coastline length (range = 2.5-25 km, Fig. 1). This suggests that retention of fishes within the no-take zones is likely to be high. This is supported by the observed movements of *D. petersi* where only 5 recaptured fish (9.6 %) were recorded moving out of a no-take zone, whereas the remaining 47 (90.4 %) recaptures remained resident in the no-take zone that they were originally tagged in (Table 1). No-take areas of suitable size and habitat therefore undoubtedly provide some insurance against fishing pressure in adjacent fished areas by acting as a refuge for *D. petersi*. Based on the methodology used by Mann *et al.* (2016b), it is estimated that the minimum size of a no-take area with suitable surf-zone reef habitat required to protect a resident population of *D. petersi* should be at least 1.5 km in length. There is also the potential for these resident fish to spawn within a no-take zone and provide a source of eggs and larvae that could be dispersed to adjacent fished areas (Brouwer *et al*., 2003; Harrison *et al*., 2012), however this aspect was beyond the scope of this study.

Ranging

Only 13 fish were observed undertaking longer distance, ranging-type movements of between 2.4 and 90 km (mean = 33 $\pm$ 13 km, n=13). These fish clearly abandoned their home range and moved elsewhere to find better habitat, which fits well with Dingle's (1996) definition for ranging, described as 'exploratory movements over wide areas in search of resources'. None of the tagged fish were recorded displaying homing behaviour (i.e. moving out of their home range and then coming back to it later). There are several possible reasons why a normally resident reef fish would undertake long-distance movements of this nature. These include inter- or intra-species competition for food, displacement because of territorial aggression, deterioration in habitat quality and/or movement to a spawning site, amongst others. Within the surf-zone of the iSimangaliso MPA, frequent sanding events were observed where reef patches would occasionally get covered with sand while others would be scoured out. With a sanding event taking place, it is likely that resident fish would move away to find better reef habitat. While these phenomena could explain movements of a few hundred metres to a few kilometres in extent, it does not explain why some fish would move distances of up to 90 km away from their original home range. However, this type of extensive movement behaviour is not unique to *D. petersi* and has been observed to take place in a large variety of different reef fish species including species such as *Dichistius capensis* (Attwood and Cowley, 2005), *Epinephelus marginatus* (Maggs *et al*., 2013), *Lutjanus rivulatus* (Mann *et al*., 2015) and many others (see review by Maggs *et al*., 2019).

Attwood and Cowley (2005) suggested two models to explain similar movement behaviour (i.e. station-keeping and ranging) of *Dichistius capensis*, a warm-temperate surf-zone fish in South Africa. Firstly, these authors proposed polymorphism to explain that within a species, some individuals remain resident whereas others are nomadic and may move continuously (Attwood and Bennett, 1994). Reasons for the differentiation may be either genetic or dependent on social or environmental cues (Swingland, 1984; Dingle, 1996) and the variation could be used as a hedge against inbreeding in geographically isolated reef fish populations. Their other alternative, the "tourist" model (Craig and Hulley, 1994), predicts that individuals of a given species will spend part of their time exhibiting resident behaviour, but will temporarily abandon their home range to feed elsewhere before returning later. Despite the relatively large number of multiple recaptures, this latter behaviour was not observed in *D. petersi*. Based on these observations, it was predicted that polymorphism is the more likely model to explain the movement behaviour in *D. petersi*, but on-going monitoring and/or an acoustic telemetry study would be necessary to test this. The movement behaviour observed would also discount the possibility of seasonal movements for reproductive purposes unless this took place offshore.

The relevance of these two models to no-take MPAs is that in the case of polymorphism, only certain individuals may become available to an adjacent fishery, whereas in the tourist model all individuals may at some time become available to the fishery (Attwood and Cowley, 2005; Maggs *et al*., 2013). The possibility of both behaviours being present in a population should also not be discounted; some individuals could be highly resident, with some ranging, whereas others might maintain temporary home ranges. Should the differentiation be due to polymorphism, the effect of differential selection on different movement behaviours could pose an ecological problem for the population (Attwood, 2002, Parsons *et al*., 2010). In addition to removing resident fishes, fishing in an exploited area would also opportunistically remove nomadic (or ranging) individuals that leave a no-take area. This would select for residency in the no-take area, which, although potentially important from a conservation perspective, may have unforeseen ecological consequences for the population. With the tourist model, in which all individuals move, the population should not suffer from differential selection in the same way (Maggs *et al*., 2013; Mann *et al*., 2015).

In this study, movements of ranging fish were undoubtedly under-sampled because very little shore angling takes place in remote areas far from beach access points in the MPA (Mann *et al*., 2016a; Mann and Mann-Lang, 2020). In addition, Dunlop *et al*. (2013) estimated a non-reporting rate of 42 % by members of the angling public, which would further hamper data collection on ranging fishes that had been recaptured. Despite these biases, it can be concluded that exploited areas adjacent to no-take areas were supplied with a limited number of adult fishes, which had been under temporary protection within no-take areas.

Many studies have failed to discriminate between spillover and variability in individual movement patterns (Zeller *et al*., 2003). Spillover, which is the net export of adult fish from a no-take area (Abesamis and Russ, 2005), implies that fishes will move from a no-take area where there is a high concentration of individuals, to areas where fishing has reduced the number and size of fish (Kramer and Chapman, 1999; Kerwath *et al*., 2013). While there may be some true density-dependent spillover of *D. petersi* from the no-take zones into the adjacent exploited zones within the iSimangaliso MPA, the remoteness of many of the areas and the low fishing effort adjacent to the no-take zones, especially since the implementation of the beach vehicle ban in 2002 (Mann *et al*., 2016a; Mann and Mann-Lang, 2020), has likely reduced the gradient in fish density between the zones (Mann *et al*., 2016a), with the result that much of the dispersal observed in this study is more likely to have been as a consequence of variability in individual movement patterns. This observation is supported by the fact that ranging movements were undertaken by 4 fish tagged in an exploited zone, 1 of which moved into a no-take zone and the other 3 swam right through a no-take zone and were recaptured in an exploited zone on the other side (Table 1). A further contributing factor is because there is no offshore (i.e. boat-based) exploitation of reef fish allowed throughout the iSimangaliso MPA, meaning that the *D. petersi* population beyond the surf-zone remains largely unexploited.

Table 3. Published growth parameters of 5 sympatric reef fish species based on the median record of phi-prime (Ø) obtained from FishBase (Froese and Pauly, 2019).

Species	L_∞	K	Ø	Region	References
Dinoperca petersi	59.6 cm TL	0.23	2.92	South Africa	This study
Epinephelus marginatus	135.9 cm TL	0.1	3.17	France	Bouchereau *et al.* (1999)
E. tukula	115 cm TL	0.1	3.24	Seychelles	Grandcourt (2005)
Lutjanus argentimaculatus	105 cm TL	0.19	3.32	Malaysia	Ambak *et al.* (1986)
L. rivulatus	91.8 cm FL	0.06	2.69	South Africa	Mann *et al.* (2016c)

Growth

The high recapture rate of *D. petersi* (19.1 % including multiple recaptures) can be ascribed to a combination of factors including good fish handling and tagging, suitability of the species for tagging, and the high level of residency and site fidelity displayed by this species (Mann *et al.*, 2015). The low number of fish observed with tag scars (n=6) also suggests that this species takes and retains the tag well. Although some tagged fish had swallowed the hook, which may affect growth rate (Aalbers *et al.*, 2003), there were too few to enable a comparison of growth to be made. Despite the effects on growth rate of the tagging procedure, the physiological burden of carrying the tag (Attwood and Swart, 2000) and/or swallowing the hook could not be assessed, *D. petersi* appeared to be a suitable species for calculation of growth rate using tag-recapture methods.

The L_∞ parameter derived from tag-recapture data has a fundamentally different meaning to the L_∞ parameter obtained from length-at-age data (Francis, 1988b). Consequently, due to the correlation between L_∞ and K, the K parameter also has a different meaning/interpretation (Mann *et al.*, 2016c). The L_∞ value obtained in this study (L_∞ = 596 mm TL) was smaller than the maximum size recorded for this species i.e. 750 mm TL (van der Elst, 1993) but this can be explained by the fact that the largest fish captured only measured 580 mm TL. This may also suggest that fish living in the surf-zone with its higher energetic requirements do not reach as large a size as those living on deeper offshore reefs. Tag-recapture growth modelling primarily solves two parameters, namely g_α and g_β (i.e. annual growth rate at length α and β). These parameters are also easily obtained from growth models derived from length-at-age data (including the von Bertalanffy Growth Function) and have been shown to be mathematically comparable (Francis, 1995). Therefore, the results of growth studies utilising these different types of data are comparable, highlighting the value of growth information that can be extracted from tag-recapture datasets.

Acknowledging the above limitations, the present results suggest that *D. petersi* is a relatively slow-growing species with an average growth rate of 61.76 mm.y^{-1} for smaller fish (g_α = 300) and 9.58 mm.y^{-1} for larger fish (g_β = 550). Growth rate at 300 mm TL was significantly faster compared to that of larger fish at 550 mm TL. In order to compare this growth rate to other sympatric reef fish species, the index phi-prime (Ø), developed for this purpose by Pauly and Munro (1984), was used. This suggests that the growth rate of *D. petersi* is comparatively slower than that estimated for several other sympatric reef fish species, except for *Lutjanus rivulatus* (Table 3).

The growth model suggested relatively low seasonal differences (0.23) in the growth rate of *D. petersi* with fastest growth in June/July (0.52). This period is associated with cooler seawater temperatures in the iSimangaliso MPA, averaging around 22 °C (BQM unpublished data). Considering that Connell (2012) reported the highest frequency of *D. petersi* eggs during summer (December to April) on the KZN south coast, it may be that somatic growth is faster during the winter months when adult fish are not investing energy into reproduction.

Conclusion

Life-history parameters such as slow growth and high residency result in fish species being more vulnerable to overexploitation (Smale and Punt, 1991; Buxton, 1993). *D. petersi* displays both these characteristics and a conservative approach is thus required for its management. Although this study has shown that *D. petersi* receives protection from fishing within no-take zones in the iSimangaliso MPA, it is not currently listed in the suite of fish species regulated by species-specific minimum size and bag limits in South African fisheries legislation (RSA, 2005). As such, and based on the results of this study, a minimum size limit of 300 mm TL based on the estimated size-at-maturity (van der Elst, 1993) and a daily bag limit of 5 fish per person per day is recommended as a precautionary approach for the future management of this species in South African waters. This would then make the bag limit the same as the current limit for other related "rockcod" species (Family Serranidae).

Acknowledgements

Thank you to the South African Association for Marine Biological Research and the iSimangaliso Wetland Park Authority for providing funding for this project. Ezemvelo KwaZulu-Natal Wildlife is thanked for providing logistical support. Thank you to the 129 anglers that have voluntarily assisted on this project and especially Mike Tyldesley, Stuart Dunlop and Rob Kyle for helping to lead the teams.

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Conservation of cultural heritage for community socio-economic prosperity: The case of Lamu East and West Sub-Counties, Lamu County, Kenya

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Abstract

Worldwide, cultural heritage has become both an element and a tool for achieving socio-economic prosperity. This study assessed the contribution of conservation of cultural heritage as a resource for the development of Lamu County. A descriptive survey design was used to conduct the study. Proportionate and systematic random sampling procedures were used to sample key informants and households selected from a sampling frame obtained from Lamu West and East Sub-Counties. An interview schedule and a semi-structured questionnaire were used to collect data from key informants and households respectively. Data were analysed using descriptive statistics and narratives. The results revealed that cultural heritage conservation contributes to job creation both directly and indirectly. However, cultural barriers contributed to observed exclusivity in benefitting from income generated from tangible and non-tangible activities. Revenue gains from the cultural heritage are also limited by the poor state of sites such as Pate and Ishakani ruins. The study recommends development and implementation of training programmes in cultural heritage conservation activities to ensure the community is educated and empowered to utilize cultural heritage for socio-economic development. The Government should also institute proper revenue sharing mechanisms to enhance socio-economic development of the Lamu County community.

Keywords: community, cultural heritage conservation, socio economic prosperity

Introduction

Worldwide, cultural heritage has become both an element and a tool for achieving goals of social inclusion and cohesion (Loulanski, 2006). Cultural heritage preservation is becoming recognized as an inherent dimension of development in both 'developed' and 'developing' countries (European Union, 2014). Preserving and promoting cultural heritage is directly linked to job creation and growth, through the positive externalities and spill-over effects in areas such as tourism, construction or real estate. Consequently, the integration and transformation of cultural heritage as a "leading partner and a driving force" in development is advised (Rodwell, 2003). More specifically, in a new developmental context, cultural heritage is both an engine and a catalyst of promoting diverse livelihood activities to support better standards of living.

The potential contribution of cultural heritage to community development throughout the world is evidently very significant (Baycan and Girard, 2011). More specifically, at a global scale, it represents an estimated 7% of employment and Gross Domestic Product (GDP), with an estimated average annual growth rate of 10 Cultural heritage is both an engine and a catalyst for promoting diverse livelihood activities to support better standards of living and can be an important asset for the community (Kakiuchi, 2000). Rehabilitation of cultural heritage such as old buildings and monuments for re-use has the potential to provide work opportunities as it is a labour-intensive activity. According to UNESCO (2012) and Hasan et al. (2008), rehabilitation costs constitute 60 % for labour and 40 % for materials. Further, rehabilitation of historic buildings creates more jobs that new construction projects. Jobs related to restoration and

http://dx.doi.org/10.4314/wiojms.v19i2.5

conservation are often highly skilled and require rare skills, which are usually well paid.

The conservation of cultural heritage has been given major attention globally through development of legal frameworks to ensure local community participation (UNESCO, 2010). The legal framework for promoting and protecting cultural heritage comprises International Covenants on Civil and Political Rights (ICCPR), Economic, Social and Cultural Rights (ESCR), as well as the United Nations (UN) declaration on the rights of indigenous communities, as well as local legislation such as the National Museums and Heritage Act 2006 (The Constitution of Kenya (CK), 2010). These instruments are in turn executed globally by institutions such as the United Nations System (UN), International Council on Monuments and Sites (ICOMOS), The World Bank (WB) Group as well as the European Union (EU). Regionally they are regulated by the African Union (AU), East African Community (EAC) and international delegations, and locally by line ministries. In Kenya for example, the institutions working in the area of heritage conservation in promoting and protecting heritage sites is guided by Kenya's Vision 2030, Kenya Coastal Development Project (KCDP) and County Integrated Development Plans (CIDPs) (UNESCO, 2012).

The developmental role of cultural heritage is explained further by Graham and Ashworth (2000) who suggested a theoretical framework, based on three main economic dimensions. First, they identify heritage as "an economic sector in itself" - often referred to as "the heritage industry" - "using resources, producing products, and generating returns in profits, [incomes] and jobs." Second, it is also considered "one element in economic development alongside others, frequently exercising a catalytic or integrating role in development projects" due to its capacity to attract economic activities and accommodate economic functions. Finally, it is looked upon as "an instrument in the management of economies at various spatial scales from the international to the local (UNESCO, 2012).

The 1972 World Heritage Convention, called for "a general policy aimed at giving the cultural and natural heritage a function in the life of the community and to integrate the protection of that heritage into comprehensive planning programs" in order to constitute a vital ingredient of sustainable local development (Grimwade and Carter, 2000). According to Grimwade and Carter (2000), the World Heritage Committee has also been encouraging greater community involvement in the identification and management of heritage properties since the 1990s. However, studies around Africa have revealed that the application of participatory management in the field of cultural heritage conservation and its contribution to community development has had varied success depending on the context in which it has been applied. Most of the goals, particularly those aimed at involving local communities in decision making in heritage resources, still remain unfulfilled (Chirikure and Pwiti, 2008).

However, it is prudent to note that conservation is one of the major debates in the modern world which is occasioned by the observed rapid deterioration of physical and social environments. Scholars have endeavoured to tackle the problem of the destruction of cultural environments after the realization that human beings are the chief agents of the destruction owing to their socio-economic activities such as tourism, agriculture, mining and fishing (UNESCO, 2012).

In Kenya, South Africa and Zimbabwe, where there were large populations of Europeans settlers, heritage management developed as the preserve of the few. It was pursued as a highly academic subject not meant for popular consumption. Management of archaeological sites was the responsibility of museums and universities. These institutions existed in order to research and apply scientific principles. In carrying out these studies very little was done in the way of linking up with local communities, who were themselves seen as objects of study (Ndoro, 2001). The rich cultural heritage that Kenya is endowed with in various parts of the country was majorly used for academic purposes and as tourist destinations. This cultural heritage which includes sites and monuments have played a major role in contributing to socio-economic development by serving as tourist destinations and sources of employment; and is recognised as an economic pillar in the Country's Vision 2030 (Adam, 2012).

Lamu County is rich in cultural heritage and is unique for its aesthetic cultural heritage collection and the old town that was inhabited by the Arabs and other immigrant groups, and has remained largely unchanged over the centuries. Lamu County is recognised for its tangible cultural heritage and was designated as a World Cultural Heritage Site by UNESCO in 2001. It is a tourist destination and serves as a source of livelihood for the community (Abungu and Abungu, 2009; UNESCO, 2012). However, it is not

Table 1. Proportionate distribution of sample size of households.

Sub county	Households	Proportionate percentage	Sample size (n)
Lamu East	3,562	0.16	16
Lamu West	18,622	0.84	84
Total	**22,184**	**100%**	**100**

clear to what extent Lamu County has fully utilized its assets to transform the community's economic status, despite the devolved management of most of the services initially carried out by the central government. The inscription of Lamu as a UNESCO World Heritage Site in December 2001 has failed to bring significant economic benefit to the area due to lack of proper promotion and of a concrete Management Plan. Lamu Old Town, a typical predominant Swahili settlement that thrived on marine resources, faces an uncertain future. Development projects have added to the effects of changes that might impact on Lamu's culture and consequently influence the community's livelihoods (Wanderi, 2019). The purpose of this study was to establish to what extent the tangible cultural heritage of Lamu County contributes to socio-economic development.

Methodology

Research design

A descriptive survey research design was used in this study. The design was suitable because it allows for not only the collection of descriptive data but also the use of qualitative and quantitative methods in data collection (Kothari, 2004). The design was appropriate for the study's intention as it allowed for observation of the environment in its natural setting. It also allowed the use of an interview schedule suitable for probing, as well as a questionnaire to collect information. The design was also useful in that it allowed for analysis of data using descriptive statistics. Randomised sample selection was used to overcome the problem of chance differences that are known to give biased results, and increased the validity and reliability of collected information.

Study site

The research was carried out in Lamu County. The County has a total area covering 6497.7 km^2 and a population of 101,539 residents (Kenya National Bureau of Statistics (KNBS), 2009). Lamu County has been able to maintain its social and cultural fabric for over 700 years with more than five hundred stone buildings standing within its boundaries, representing 30 % of the total number of structures in the town (KNBS, 2009). Lamu Old Town is part and parcel of the community and houses over one third of Lamu's population. Indigenous culture forms part of the cultural heritage as outlined in the cultural criteria of values/influences and associations. The main livelihoods for the community living in Lamu are agriculture and fishing. Lamu County, through the Department of Tourism and Culture, is playing a vital role in creating awareness in the community on the need to conserve cultural heritage as a resource for socio-economic development (Lamu County, 2013).

Sample size and sampling procedure

The sample size was selected from the accessible population of 18,622 and 3,562 households from Lamu West and Lamu East Sub-County, respectively. A sample of 10 key informants and 100 households was used in the study. According to Roscoe (1975) a sample of 100 or more is appropriate for a survey study. The unit of analysis for the study was a household, while the unit of observation was the head of the household. The households' sample size for the selected sub-counties was proportionately distributed to each sub-county as shown in Table 1.

Proportionate random sampling, systematic random and purposive sampling were used to select the sample size. First, proportionate random sampling was used to select households from Lamu West and East sub-counties. After the proportionate assignment of households, systematic random sampling was used to select the household respondents from a sample frame obtained from the Lamu County Government for the two sub-counties. The sample was obtained by picking every nth individual after a random start (Bordens and Abbot, 2011). Purposive sampling was then used to select the key informants. The latter were people with extensive knowledge on cultural heritage, community participation and conservation in Lamu County.

Data collection instruments

Data collection was carried out using semi-structured questionnaires, an interview and observation schedule, and document analysis. One set of semi-structured questionnaires was administered to the households in Lamu East and Lamu West Sub-Counties. The questionnaire was used to collect information that pertained to the demographic characteristics of the respondents. An interview schedule was administered to the key informants who were mainly professionals in the Cultural Heritage field, employees of the National Museums of Kenya, officers in the department of Tourism and Culture in Lamu County, and the old men and women in Lamu County. The interview schedule allowed the interviewer to probe further and gave greater freedom to ask supplementary questions, or at times omit certain questions if the situation so required, and allow for change in the sequence of questions and greater freedom in recording the responses to include some aspects and exclude others (Kothari, 2004). Documentation was used in the collection of secondary data that complemented primary data and to supplement information collected through the social survey and in-depth interviews (Cohen *et al.*, 2007). Sources of secondary data included national population census records, demographic and health survey reports, books, theses, dissertations, journals, web-based publications as well as private records of government. An observation schedule was used to help in gaining insights and validation of information collected using other tools and methods of data collection.

Validity and reliability of the instruments

The determination of validity of the instruments in terms of content and construct which was carried out before being used for data collection in the field was undertaken by experts in the field of social sciences. Internal consistency and reliability of the questionnaire was determined prior to its administration for data collection through use of the Cronbach Alpha Coefficient. The calculated coefficient for inter-item correlation that was used as the acceptance threshold was 0.87.

Data analysis and presentation

The collected qualitative data were coded according to emerging themes. The coding started from the onset of data collection since the analysis of qualitative data was a continuous process which started when entering the field (Mugenda and Mugenda, 2003). The type of data collected comprised of categorical nominal and ordinal statements. With the help of Minitab software, the collected quantitative data were analysed using descriptive statistics which included frequency distributions. Findings for all the objectives were presented using charts, graphs, percentage frequency tables and narratives from the respondents.

Results and discussion

Demographic characteristics of the households

Data on the characteristics of households was collected using a semi-structured questionnaire. The collection of data was guided by the need to know how their socio-economic characteristics influence the extent of their participation and benefits that may be accrued from cultural heritage conservation. Table 2 presents the results of the study on age and gender of respondents, level of education, and their occupations.

Results in Table 2 reveal that over half (55 %) of the primary respondents were aged between 18 and 37 years. The age of the respondents may have an impact on the knowledge of cultural heritage in that the older people have a lot of experience and knowledge of history. However, over one half of the respondents, who were within the middle age category, could potentially benefit from capacity development around cultural heritage and contribute to related economic activities (Organization for Economic Co-operation and Development (OECD), 2016). The results also show that over 72 % of the respondents were male. This high percentage is probably explained by the fact that the study targeted household heads that are predominantly male as is usual in African culture. This implied that more men are engaged in cultural activities than women. Women may engage in intangible cultural heritage such as henna painting, dances and songs but may not engage as much in activities such as restoration of historical sites and tourism. Women have to do all the domestic and child-caring work and they have little time for relaxation or rest, or to participate in community activities (Tuyet, 2007).

Table 2 further shows that over one third (47 %) of the respondents reported to have attained primary level of education. This low level of education reflects the situation among the majority of residents in the Republic of Kenya (H Shauri, pers. comm., April 19, 2016). According to Chimombo (2005), education is the route to participation in social, economic and technological development. Important for this study is that the finding on low levels of education may not have implications on the community's understanding and participation in cultural heritage conservation

Table 2. Socio-economic characteristics of the primary respondents.

Variable	Category	Frequency	Percent (%)
	18-37	55	55
Age	38-52	39	39
	Above 52	6	6
Gender	Female	28	28
	Male	72	72
Level of Education	Not gone to school	12	12
	Tertiary	9	9
	Primary education	47	47
	Secondary Education	32	32
Occupation	Tour guide	5	5
	Wood curving	6	6
	Fishing	11	11
	Formal sector	16	16
	Farmer	26	26
	Boat business	7	7

activities in Lamu County. Informal education on cultural heritage has been passed down from the elderly since days immemorial. Accordingly, the low level of education was not considered to have an influence on knowledge of cultural heritage and conservation.

Table 2 also shows that over one quarter (29 %) and (26 %) of the 100 respondents were working in small-scale business and farming, respectively. More critical for this study is the observation that there is no mention of respondents working in the conservation of cultural heritage among the sampled residents. This finding is not surprising as the cultural industry has not been given prominence in Kenya and most people working in this industry are likely to wrongly identify themselves with other industries, especially tourism, than to the cultural heritage industry *per se*.

Status of existing cultural heritage

The study sought to find out the status of cultural heritage in Lamu. Information with regard to respondents' awareness of cultural heritage, types of cultural heritage and different conservation activities was collected using an interview schedule.

Awareness on tangible cultural heritage

To establish awareness of the tangible cultural heritage in Lamu County, the questionnaire and interview schedule were administered to heads of household and key informants, respectively. The respondents were asked questions pertaining to the extent of awareness of individuals to the existence of different tangible cultural heritage, types of cultural heritage conservation methods used in the study site. These findings are captured in Table 3.

Table 3. Extent of awareness on the existence of cultural heritage among the residents.

Variable	Strongly Agree (%)	Agree (%)	Neutral (%)	Disagree (%)	Strongly Disagree (%)
Awareness on the existence of cultural heritage	42	50	8	0	0

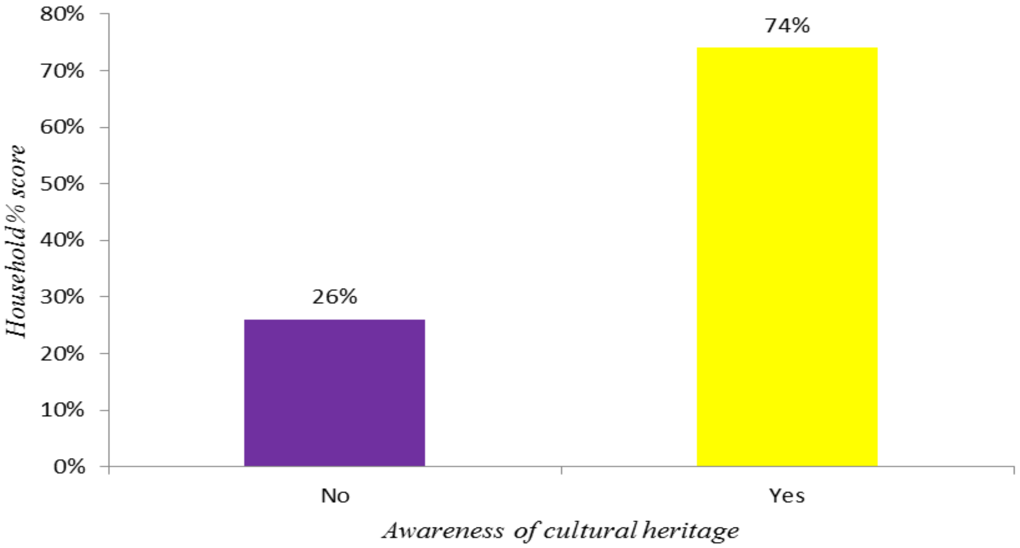

Figure 1. Awareness of existing cultural heritage.

From Table 3 it is clear that half (50 %) of the respondents agreed with the statement that many residents of Lamu County were aware of the existence of cultural heritage, with over one third (42 %) strongly agreeing to the statement. The implication of this finding is that most (92 %) of the respondents were aware of the existence of cultural heritage. This overwhelming level of awareness may be attributed to the importance of cultural heritage, manifested by the annual cultural festival that is celebrated by community which is given much recognition by the Lamu residents, as it is during this period that they showcase their rich heritage. The fact that Lamu is a world cultural heritage site has allowed many residents to survive on promotion and sale of cultural heritage as a means of living.

When the respondents were asked whether they knew about the status of cultural heritage in the county, the responses were overwhelmingly favorable as shown in Fig. 1. Almost three quarters (74 %) of the respondents were aware of the of tangible cultural heritage that exists, such as the existence of old buildings and monuments and the unique Lamu carved doors. One of the key informants attributed the community awareness of the existing cultural heritage to the cultural festivals and the 'Maulid' festival that are held annually. The implication of this finding is that the community is well informed on the cultural heritage conservation in Lamu despite not listing them among their respective occupations. However, findings by Wiggins (2010) during informal discussions and formal interviews, established

Table 4. Tangible cultural heritage in Lamu.

Tangible
Siyu Fort
Lamu Fort
Lamu curved doors
Lamu Museum
Tawa ruins
Lamu Old town
Pate ruins
Old Mosque
Archaeological sites
Wood carvings

that most of the residents lacked an understanding of what it meant for Lamu to be a World Heritage Site. Whether this was due to lack of effort on their part, or whether it was due to a lack of promotion of community awareness by the County Council and the National Museums of Kenya is unclear. What is clear however, is that effective community involvement in cultural heritage management is necessary for the integrity and authenticity of the site to be maintained.

Types of tangible cultural heritage in Lamu County
The study also sought to establish the diversity of cultural heritage in Lamu County. From the responses given, the analysis listed the diversity of tangible cultural heritage in Lamu as shown in Table 4.

Tangible heritage ranged from archaeological sites to pathways, drainage systems, mangroves, to Lamu carved doors. Explanation from one of the respondents revealed that "*Some of the archaeological sites are sold to foreigners who are renovating them using modern technology and materials that are destroying the cultural heritage valued by tourists. The ancient buildings should be protected from vandalism and dynamics of today's developers*". This indicates that the study area is rich in cultural heritage, although this is being destroyed by developers. The results are in agreement with what UNESCO (2004) found that Lamu Town has inherent values and an almost undisturbed authenticity, and made it possible for Lamu to be declared a world cultural heritage site. The narrative is supported by the findings of Abungu and Abungu (2009), cited in Wanderi (2019) who established that the use of modern technologies such as replacing the use of lime with cement has negatively impacted livelihoods and cultural heritage.

Contribution of cultural heritage to community development

Respondents were asked whether they were aware of any benefits the community accrued directly and indirectly from conservation of cultural heritage, and to name some of these A Likert scale was further used to achieve the study objective.

Benefits of cultural heritage conservation to community development

Respondents were asked whether they were aware of benefits accrued from cultural heritage conservation. The results are shown in Fig. 2. It is evident that the majority (63 %) of the respondents were not aware of the contribution of cultural heritage. This may be attributed to the community not being conversant with how to utilize the existing heritage to spur development, especially if they are not fully involved as observed in the findings of this study.

It was important to establish the extent to which cultural heritage has been of benefit to the community. Findings are captured in Table 5 which show that contribution of cultural heritage to community development is still low in Lamu County. Sixty-one percent of the respondents disagreed with the statement that 'the existing cultural heritage has benefitted the community as a source of employment', while 13 % agreed with the statement and 10 % strongly agreed. When asked about the statement that 'cultural heritage has not brought development to the community', 54 % of the respondents agreed, 21 % strongly agreed, while 9 % disagreed. When the respondents were asked to give their responses on the statement that 'cultural heritage brings about social cohesion and cultural integration, over half (55 % and 53 %) strongly agreed, and over two fifths (42 % and 40 %) agreed. The implication

Figure 2. Awareness of the contribution of cultural heritage conservation.

Table 5. Contribution of cultural heritage to community development.

Statements	**Strongly agree**	**Agree**	**neutral**	**Disagree**	**Strongly disagree**
	f (%)	*f* (%)	*f* (%)	*f* (%)	*f* (%)
The existing cultural heritage has benefitted the community as a source of employment	10 (10)	13 (13)	16 (16)	61 (61)	0(0)
Cultural heritage has not brought development to the community.	21(21)	54(54)	16(16)	9(9)	0(0)
Cultural heritage brings about social cohesion	55(55)	42(42)	0(0)	3(3)	0(0)
Cultural heritage bring about cultural integration	53(55)	40(42)	2(0)	5(3)	0(0)

of this finding is that cultural heritage has not fully contributed to the economic development of Lamu community. This could be attributed to the residents not being aware of the different activities related to cultural heritage such as the repair and restoration of historical monuments. According to Wiggins (2010), Lamu residents have been unable to reap benefits from tourism and the designation of Lamu as a World Heritage Site. In order to improve the economic prospects in the area, the government of Kenya plans to develop a new mega port within the district (now County) bringing the possibility for alternative employment and economic prosperity.

Indirect benefits of cultural heritage to community development

Respondents were further asked whether they were aware of any revenue accrued indirectly from cultural heritage conservation in Lamu County. From the results shown in Fig. 3 it is clear that the majority (60 %) of the respondents were aware of the revenue accrued from cultural heritage. This implies that the community is informed of the extent to which cultural heritage in Lamu contributes to national revenue.

It was observed that the revenue from cultural heritage was from gate fees collected at the cultural sites and monuments in Lamu town. On further probing to establish the source of revenue, the respondents stated various sources. The results in Table 6 reveal that most (40 %) of the respondents are not aware of any indirect revenue from conservation of cultural heritage. However, 26 % of the respondents indicated that there is indirect revenue for the museum from conservation activities related to cultural heritage in Lamu. This implies that the community indirectly benefits from these activities. A study by Barillet *et al.* (2005) found that heritage has today become a powerful instrument in the economic and territorial development of a community, when properly valorized and promoted, often in the context of tourism related activities.

Figure 3. Community awareness of revenue accrued indirectly from cultural heritage conservation in Lamu.

Table 6. Sources of indirect benefits from cultural heritage in Lamu County.

Sources of Indirect Benefits	Frequency	Percent (%)
Revenue from Tourism	34	34
Revenue for museum	26	26
None	40	40
Total	**100**	**100**

These authors assert that the development of tourism is a potential source of many types of financial gain including the entrance fees to sites and museums, guided tours and visits, sales of handcrafts, documents and photos, and the development of the craft industry. It is also a source of more important financial repercussions in areas such as the hospitality industry, transportation and restaurant services. For local governments, tourism is also a potential source of revenues through taxes.

Intervention strategies for utilization of cultural heritage

This study sought to establish appropriate intervention strategies for enhanced utilization of cultural heritage in Lamu County. The assumption was that enhanced community participation through the utilization of cultural heritage can spur livelihood diversification and community development. The respondents provided several suggestions as explained in the subsequent subsections on community participation and utilization.

Strategies to promote participation in conservation of cultural heritage

The respondents were asked about strategies that can promote participation in conservation of cultural heritage in Lamu County. Findings shown in Fig. 4 indicate clearly that over half (51 %) of the respondents were of the view that there is a need to involve the community more in conservation. In fact, field observations showed that the community want the government to engage them actively on matters of heritage preservation. This finding is supported by that of the National Museums of Kenya (1993) where they noted that a carefully designed approach for public relations should be a shared concern with the local community on matters of heritage conservation.

The results also show that over one fifth (24 %) of the respondents stated that there should be more emphasis on the promotion of cultural festivals. Additionally, 13 % of the respondents wanted the government to engage the youth more in cultural activities as a way of creating employment, while 7 % asserted that the

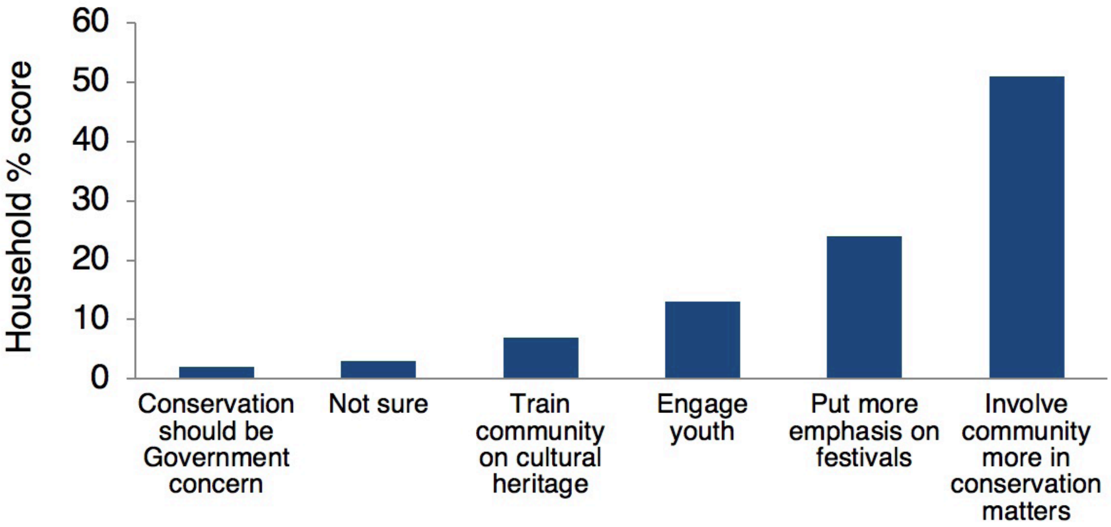

Figure 4. Strategies to promote participation in conservation of cultural heritage.

government needs to train the community in heritage preservation. Only 2 % reported that conservation matters should be entirely a government affair, with 3 % stating that they were not sure.

Community empowerment is observed by various authors (Burns *et al.*, 1994; Wilson and Wilde, 2003) as one of the main ingredients to effective participation. In fact, the community must be able to influence decisions, and have the capacity and a communications network created by partners to ensure its voice is incorporated in heritage conservation. This study revealed that local community members lacked skills and adequate knowledge on World Heritage Site management. As expressed by one respondent (a 29-year-old male) *"Lack of commitment from the locals is due to the challenge of non-involvement by heritage managers, lack of empowerment and inadequate capacity building on importance of cultural heritage".*

The findings further indicate that the respondents recommended training the community on cultural heritage. On further probing to establish the specific group that would require training, it was suggested that the focus should be on women. The study revealed that lack of empowerment varied with gender. More precisely, it is higher among women than it is in men. Field observation showed that all (women interviewed were 28 % of the total sample) of the women interviewed did indeed lack capacity to be empowered. One respondent stated that *"women lagged behind on matters of heritage conservation because of the limitation from their local beliefs and traditions".*

Furthermore, the study indicated that the community traditions restrained women from speaking to strangers or attending events without their husband's consent. It is for this reason, as reported by one key informant, that the Museum delivered a tailor-made sensitization programme targeting women empowerment on issues of heritage conservation. The programme was reported to have been initiated by one of the staff members in the Museum but became moribund after the staff member got transferred. This problem is further expounded by a 43-year-old woman key informant who narrated that:
"The museum has failed especially in involving women, long time ago education officers used to go door to door to educate or even bring awareness to the locals on issues to do with heritage conservation. That initiative is forgotten because the pioneer is no longer with them. Nevertheless, women in this community are so conservative due to their cultures and so without the museum or the stakeholders support they will continue lagging behind in development. This is unfortunate situation as the women have so much information on the heritage and they would play a great part in transferring knowledge to their children. This would help fill in the gaps created by institutions especially on youths training. It is very sad however these women do not enjoy any involvement because of the limitations set by their cultures".

The narrative implies that the conservative nature of the women encourages them not to be actively involved in cultural conservation activities. Lack of, or passive, participation may hamper the economic benefits they could accrue to women from activities or services related to conservation of cultural heritage.

Table 7. Intervention measures for utilization of cultural heritage.

Themes	Frequency	Percent (%)
Formation of new heritage management body	3	3%
More emphasis on traditional craft	4	4%
Training and community board	5	5%
Introduction of home stay for visitors	6	6%
Creation of awareness on importance of cultural heritage	7	7%
Provide scholarship and bursaries for community education in conservation studies	8	8%
Involve youth and women in heritage matters	10	10%
Community training on importance of heritage conservation	20	20%
Actively involve community in matters of conservation	37	37%
Total	**100**	**100%**

Although culture is recognised as a powerful instrument for economic development and social inclusion in the United Nations Sustainable Development Goals of 2015, it can also lead to exclusion from decision-making and representation in heritage Serageldin and Martin-Brown (1999).

Intervention measures for utilization of cultural heritage

This study sought to determine the intervention measures for cultural heritage conservation. Table 7 presents the results where it is clear that over one third (37 %) of the respondents suggested that community involvement should be improved for better utilization of cultural heritage as a community development strategy. This suggestion is supported by the recommendation of the National Museums of Kenya (1986), that each restoration or rehabilitation of project should start with a targeted programme of community development activities, such as discussions in meetings, interviews and surveys. They further recommended that community participation should be considered in order to involve and commit the community.

In addition, 20 % of the respondents were of the opinion that community training on heritage conservation should be a key strategy for utilization of cultural heritage. Other strategies suggested by the respondents included: youth and women involvement (10 %); revenue collected to remain in Lamu for education in heritage conservation (8 %); awareness creation on the importance of cultural heritage (7 %); and introduction of home stays (6%) for visitors instead of hotels so that the community benefits directly from heritage as indicated in Table 5. One key informant stated that *"Investment in festivals and cultural programmes should be done so as to maintain the intangible heritage and promote the welfare of the community".*

In addition, a female respondent said that *"Our people should be allowed to organize and plan for the cultural activities without interference by outsiders and maybe this will change the mindset of members of the community towards preservation of the heritage".*

Another 44 year old key informant stated that:
"I think heritage conservation should be included in the curriculum starting probably from primary level because the young generation is not aware of their heritage and they are the leaders of tomorrow. Nevertheless, the youth should be empowered more by either training them or creating jobs for them and specific beneficial roles in the management. This will not only improve their living standards, but will foster responsibility and enable them to focus on the participation process".

The results further show that there is a need to establish a management body as an intervention measure to ensure effective utilization of cultural heritage. Field observations further revealed that there was no management body in charge of cultural heritage conservation in Lamu County, even though Lamu hosts a World Heritage Site and is very rich in cultural heritage. When the respondents were probed on what the situation was like before the coming of the recent county governments, it was reported that there used to be a body called the Local Planning Commission (LPC). The LPC was established by the then District Physical Planning Liaison Committee (DPPLC) to make legally binding decisions on the management of World Heritage property in Lamu. District. The LPC's main mandate was to give advice to the local authority on salient issues pertaining to the protection and preservation of Lamu as a cultural heritage and to review proposals for the alteration, extension and construction of new buildings within the protected area of Lamu town and its buffer zones, with a view to maintaining its authenticity. However, the LPC has ceased to operate creating a gap in cultural heritage management in the area. This creates a gap explaining the confusion witnessed during field work with regard to cultural heritage conservation in the county. Further field observation revealed that some of the residents have actually participated in these activities in one way or the another but did not know that what they are doing actually constituted heritage conservation. It emerged from all these findings that appropriate intervention measures are needed for utilization of cultural heritage to enhance community development. According to Wiggins (2010), the inscription of Lamu town as a UNESCO World Heritage Site in December 2001 has failed to bring significant economic benefit due to the lack of proper promotion and the lack of a concrete Management Plan. Wiggins asserts that the current state of the town combined with the impact of the proposed port upon the county could further marginalize the local population and serve as a barrier to overall prosperity.

The process of community education in Lamu had begun in earnest in the past where, for example, community education specialists working under a Ford

Foundation Programme were involved in a campaign of community education in 1984 (National Museums of Kenya, 1993). According to the National Museums of Kenya (NMK), the results of these campaigns were encouraging and the message of the Museum's goodwill reached the community to such an extent that house owners went to the Museum to seek for financial assistance to restore their houses. NMK further records that a conservation week was held with lectures, audio-visuals, round tours, brochures and cultural activities in 1988. Later, in 1992 the discussion on community development was given more priority. After sensitizing the NMK staff, a consultant was selected to assist with the setting up of a community development programme based on heritage.

According to ICCROM (2009), universities as training institutions of higher learning need to play a direct role in capacity building and knowledge production in heritage matters. However, ICCROM notes that even though universities have played significant roles in a number of African countries in training and executing research in cultural heritage, many African countries still lack local experts in archaeology, museum training, architectural conservation, and management planning, among others. ICCROM further notes that the absence of such professional and expertise further hampers cultural conservation efforts not only in Lamu County, but for the entire nation. This may be the reason for the poor state of cultural heritage in the country. In fact, this poor state of assets has seen a number of heritage sites acquiring a new label of 'ruins' such as Pate and Ishakani ruins, to mention but a few.

Conclusions

The value of a cultural heritage conservation strategy largely depends on the strength of its links to the local economy and involvement of the community. These linkages are important for the longer-term sustainability of the heritage programme and of the asset itself. A good heritage conservation strategy should contribute to overall developmental goals such as poverty reduction and job creation or income generation. The goal of job creation is particularly important, either directly in the cultural heritage programme itself in terms of activities such as construction or archaeological work, or indirectly through support services in shops, restaurants and hotels for visitors. Job creation can be tourism-related; for example, hospitality and transportation, creation of handicraft and in the marketing of handicraft items or other types of jobs. However, the exclusion of women due to cultural barriers can hamper community inclusiveness in access to benefits such as income from handcrafts, festive activities such as dances, the tourism industry, and in the holding of management positions. Also, the poor state of assets such as at Pate and Ishakani, affects their contribution as a source of revenue for the development of the County. Appropriate intervention measures to ensure enhanced revenue for socio-economic benefits which are currently not adequately in place in Lamu County are necessary for full utilization of cultural heritage for community development.

Policy recommendations

It is recommended from this study that:
County government and other stakeholders such as the NMK should sensitize the community members on the importance of conservation of cultural heritage so that community members can own and take responsibility of their tangible cultural heritage and thus participate in conservation of Lamu cultural heritage.

The study recommends that aappropriate intervention measures necessary for utilization of cultural heritage be developed and implemented to ensure enhanced socio-economic gains and full contribution to Lamu County's community development. The interventions should include community empowerment through capacity building in cultural heritage conservation activities. Further, it is recommended that proper revenue sharing (benefit sharing) should be instituted in order to enhance socio-economic development for the community. The community must be at the centre of this new paradigm to ensure measures taken are successful and sustainable. Benefits of Lamu cultural heritage conservation depends very much on the acceptance and positive response of the local people. Accordingly, efforts need to be made to explain the benefits and responsibilities associated with the idea of natural heritage conservation.

Acknowledgements

This research was funded by the Kenya Coastal Development Project (KCDP) which is acknowledged for providing financial support throughout the study.

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Microplastic pollution in the surface waters of creeks along the Kenyan coast, Western Indian Ocean (WIO)

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Abstract

Microplastic pollution has been recognized as a global threat in marine environments and a danger to prey, predators and humans. Yet there have been limited studies in the Western Indian Ocean (WIO) and along the Kenyan coast making it difficult to estimate the extent of such pollution. This is the first study on microplastics (MPs) in the surface waters within creeks (Tudor, Port-Reitz and Mida creeks) in Kenya. Sampling was done in January/February and September 2018 to collect microplastics from surface water. Neuston nets of 500 µm (large) and 250 µm (medium) size were towed for ten minutes and 50 litres of seawater sieved through a 20 µm net (small) in three replicates. The samples were digested in 10 % Potassium Hydroxide, sieved, and then filtered with cellulose nitrate membrane microfilters. Concentrations of total microplastics, different shapes and colours were established under a microscope. High concentrations of small size (20-250 µm) MPs were encountered and Tudor and Port Reitz had higher concentrations compared to Mida Creek. The study provides data on microplastic concentrations within the creeks and recommends focussing on small size microplastics for monitoring purposes, which due to their high concentrations can be hazardous to organisms.

Keywords: microplastics, marine, Kenya coast, Western Indian Ocean

Introduction

Microplastics (MPs) are defined as tiny plastic particles measuring between 0.1 µm and 5000 µm (Andrady, 2011), although there is still no universally accepted definition of MPs (Frias and Nash, 2019). In this study, microplastics ranging from 20 to 5000 µm were considered. Plastics are a major pollutant to marine environments that have been recognized as a global threat (Sharma and Chatterjee, 2017). Plastics have now joined other marine stressors like habitat destruction, overfishing, ocean acidification and climate change (Amaral-Zettler *et al*., 2015). Most of the plastics manufactured are for single-use and it was estimated that between 4.8×10^9 – 12.7×10^9 kg of plastics entered the ocean in 2010 (Jambeck *et al*., 2014). Of these, an estimated 2.7×10^8 kg was in surface waters (Eriksen *et al*., 2014). It is estimated that by 2050 plastic production will hit 33 billion tons (Zalasiewicz *et al*., 2016) which may result in a considerable amount of plastics reaching the oceans, hence the need to investigate the extent of MPs pollution along the Kenyan coast to inform policy formulation on plastic waste management and disposal.

Microplastics in the environment occur in either the primary (originally manufactured to be that size and

http://dx.doi.org/10.4314/wiojms.v19i2.6

entering directly as nurdles; fibres, pellets or granules), secondary (if they originate from the breakdown of macroplastics forming fragments; small irregular shaped particles), or film form (Andrady, 2015; Frere *et al.*, 2014; Lusher *et al.*, 2013). Gradual degradation of plastics through biological and chemical processes adds MPs into the water thereby increasing their concentration (Halle *et al.*, 2016). Microplastics sorb many Persistent Organic Pollutants (POPs) due to their large surface to volume ratio and hydrophobic nature (Cauwenberghe *et al.*, 2015). The water column is a habitat to many key species in an aquatic environment and if ingested in considerable quantities, MPs may affect the biota therein (Halle *et al.*, 2016). Owing to their small size (0.1 µm-5 mm) MPs are bioavailable to a great diversity of organisms since they mimic prey particles and sediment grains, causing some animals to mistake them for prey while filter feeders may incorporate them as prey (Botterell *et al.*, 2019). Microplastics transport POPs to biota from the environment and even at low levels could harm or kill organisms, ultimately causing a decrease in biodiversity (Invar do Sul and Costa, 2014). Bioaccumulation and biomagnification of MPs to higher trophic levels has also been observed where copepods and polychaete larvae ingesting 10 µm of polystyrene transfer the particles to mysid shrimps (Setälä *et al.*, 2014). Earlier research found that MPs concentrations of > 12.5 µg/L decrease survival and fecundity in *Tigriopus japonicas* Mori 1938 (Lee *et al.*, 2013), and concentrations of 0.25 mg/L cause analogous embryonic development in the sea urchin *Lytechinus variegatus* Lamark 1938 (Nobre *et al.*, 2015).

Most coastal cities in the world are the source of plastics through manufacturing, packaging, building and construction, textile, food processing industries, fishing and tourist activities (Frere *et al.*, 2017). Some industries in some parts of the world release their effluents into the sea, major contributors being coastal cities of China, Indonesia, Philippines and Africa (Ocean Conservancy Report, 2017). Industrial effluents together with discarded plastics (Okuku *et al.*, 2011) introduce MPs into the oceans. On the Kenyan coast for example, Mombasa City is a busy coastal port with dense human settlement, many industrial plants, fishing and tourist activities and produces vast quantities of waste, including plastic waste. Research studies documenting the presence of MPs in the surface waters along the Kenyan coast are virtually non-existent, resulting in a severe deficit of information on the extent of microplastic pollution in the area. A study in the central part of Kenya's Exclusive Economic Zone (EEZ) found 33-275 particles m^{-3} (Kosore *et al.*, 2018); a concentration that is lower than that of some of the most polluted waters of the world such as Geoje Island, South Korea where 16000 ± 14000 items m^{-3} were found (Song *et al.*, 2014), China sea with 4137.3 ± 2461.5 items m^{-3} (Zhao *et al.*, 2014), and the west coast of Sweden with 150-2400 items m^{-3} (Noren, 2007). The microplastic concentrations in the EEZ were similar to those detected in the North Sea and East Pacific (275 ± 255 m^{-3}) (Desforges *et al.*, 2014). Following the report by Kenya's National Environmental Management Agency (NEMA) in conjunction with the United Nations Environmental Programme (UNEP), and the Kenya Institute of Public Policy Research and Analysis (KIPPA), that showed that supermarkets alone contribute tens of millions of plastic bags into the environment annually, the Kenya Government effected a ban in February 2017 on the use of low weight plastic bags.

This study aimed at providing an assessment of the presence of MPs in the surface waters in Tudor and Port-Reitz creeks in Mombasa City, and Mida Creek within a less urban environment near Watamu. Mida Creek, being within a marine National Reserve (KWS, 1997), was the control. The data and information generated will allow an evaluation of the effect of the Kenya Government ban on low weight plastic bag production and use effected in February 2017, and provide a baseline for future monitoring as there are no previous estimates of MPs levels available (NEMA, 2017). It will also provide data and information for the formulation of plastic waste management policies to protect the ecosystem which is rich in both terrestrial and marine biodiversity (Rochman, 2016).

Materials and methods

The study was carried out in two creeks in Mombasa County (Tudor and Port-Reitz) and one creek in Kilifi County (Mida) along the Kenyan coast (Fig. 1). The creeks are enclosed, with limited water flow, low currents, and are surrounded by informal settlements, villages and manufacturing industries (Okuku *et al.*, 2011) making them prone to plastic pollution. The Coastal Region of Kenya has two rainy seasons with maxima in May and October, and a mean annual rainfall of 1204 mm (Obiero and Onyando, 2013). The region experiences fairly high average temperatures ranging between 26 and 32 ^{0}C, with a small diurnal range of between 7 and 9 ^{0}C (Obeiro and Onyando, 2013). The creeks are subjected to semi-diurnal patterns of tides averaging between 0.6 and 1.0 m during neap tide and 2.5 and 4.5 m during spring tide (Nguli *et al.*, 2006). Highly populated villages surround the creeks, such as Mushomoroni and Mikindani around Tudor Creek, Dongo Kaya, Dunga Nusa and Ngala around Port-Reitz Creek, and Kirepwe and Dabaso around Mida Creek (Maritim *et al.*, 2016). Rapid urbanization and high population growth have led to the development of informal settlements around the Coast General Hospital and Kenya Meat Commission near Tudor Creek (Okuku *et al.*, 2011).

Port-Reitz Creek receives freshwater from the Mwache, Cha Shimba, and Mwambone rivers while Tudor Creek is fed by two main seasonal rivers, Kombeni and Tsalu, which arise from around Mariakani town, 32 km northwest of Mombasa (Kitheka *et al.*, 1999). Tudor Creek passes under Nyali Bridge and is bordered by Makupa causeway which dissects it into Tudor Creek to the east and Port-Reitz to the west (Kitheka *et al.*, 1999). The Kibarani dumpsite at Makupa station lies within Port-Reitz. The channels are fringed by mangrove forests, mainly *Rhizophora mucronata* Lam and *Avicennia marina* Vierh.

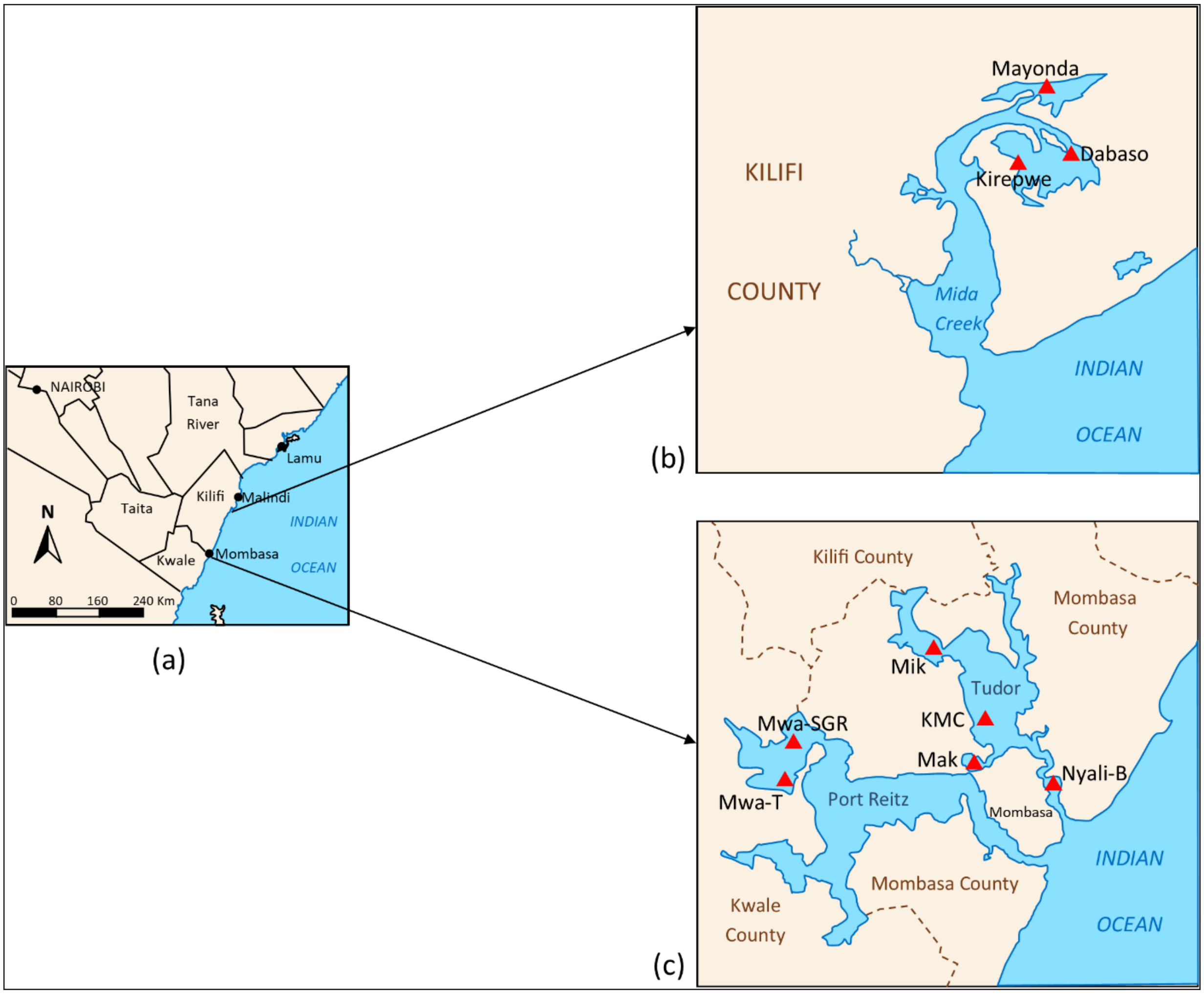

Figure 1. Map of Kenya showing the sampling sites and stations (Table 1). a) Kenya Coastal region; b) Mida Creek; c) Mombasa Island with Tudor and Port-Reitz creeks.

Mida creek, located on the Kenyan north coast, generally has gentle tidal currents (Kitheka, 1998). The constricted narrow entrance, sills and rough bottom generate modified currents that show significant spatial–temporal variations (Kitheka, 1998). The speed of currents at the entrance can be high, reaching 2.0 ms^{-1} during spring tide. At low tide, currents are barotropic with minor deviations with changing tidal elevation. In the main creek channel, the flow is flood-dominated compared to the backwater region (Kitheka, 1998). Next to Sudi Island the tides are asymmetrical

Table 1. Sampling sites and GPS locations of sampling sites and stations.

Site	Station	Southing	Easting
Tudor	Mikindani (Mik)	4° 41´´ 51´	39° 21´´ 12´
	Nyali Bridge (Nyali-B)	4° 2´´48.1´	39° 40´´ 27.4´
	Kenya Meat Commission (KMC)	4° 1´´34.7´	39° 38´´47.5´
Port-Reitz	Makupa (Mak)	4° 2´´16.5´	39° 38´´ 50.1´
	Mwache Tsunza (Mwa-T)	4° 2´´ 47´	39° 40´´26.7´
	Mwache SGR (Mwa-SGR)	4° 1´´53.6´	39° 48´´ 47´
Mida	Kirepwe (Kir)	4° 3´´23.5´	39° 48´´ 47´
	Mayonda (May)	3° 19´´ 33.2’	39° 59´´47´
	Dabaso (Dab)	3° 20´´ 39.8´	39° 59´´ 12.8´

with ebb flow being dominant compared to flood flow (Kitheka 1998). Water conductivity is highest in August (53 µS cm^{-1}) during the dry spell and low during the rainy season (Kitheka, 1998).

Sampling strategy

At each of the three sites (Tudor, Port-Reitz, and Mida creeks) three stations were identified for sampling (Table 1). Sampling was done in January/February 2018 during a dry period and in September 2018 during the short rains to collect sea surface water for microplastic analysis. At each station, GPS coordinates were recorded (Table 1) using a handheld GPS (version Mitac mio168) and various physico-chemical parameters (water conductivity (µS cm^{-1}), salinity (PSU) and temperature (°C)) were measured using a multi parameter meter (YSI ProDSS).

Surface water sampling

The microplastics were categorized into three different sizes (large size - 500-4999 µm; medium size - 249-500 µm; and small size - 20-249 µm). For the large and medium sizes, samples were collected from the surface water by towing neuston nets (500 and 250 µm pore sizes) fitted with a flowmeter for 10 min per tow according to Hidalgo-Ruz *et al.* (2012). Surface water was sampled in triplicate for each station keeping nets as close to the surface as possible in order to capture any MPs in the water surface. The large size net mouth area was 0.2 m^2 while that of the medium size was 0.07 m^2. The boat moved at a speed between 0.5-1.5 knots, sampling between 525.5– 1329.2 m^3 of water for the large net size and 177.1– 550.2 m^3 for the medium net size. For the small size MPs, 50 litres of seawater was drawn with a metal bucket and filtered through a 20 µm neuston net. All the sampling was replicated three times for each station. Material on the net was rinsed into glass sample bottles using sieved seawater and the bottles were corked with aluminium foil-lined lids. The samples were transferred to the laboratory and stored in a refrigerator at - 6 °C awaiting processing. To minimize contamination in the field, hand gloves were worn throughout, glass or metal equipment used, and sample bottles covered with aluminium lined lids immediately after filling. Samples of towing gear material were examined under a microscope at 40x magnification for microplastics, and any similar microplastics in the water samples were not included in the total counts.

Laboratory analysis

Quality control check

Sample processing and analysis were done in a clean room with negative air flow and limited foot traffic. Microplastic contamination through exposure to air was reduced by covering samples with aluminium foil and glass covers, the use of distilled water-rinsed glassware and metal equipment (Liebezeit and Liebezeit, 2014). The working surface was thoroughly cleaned with 70 % ethanol on non-shedding paper three times and allowed to dry before use (Cole *et al.*, 2014). A cotton laboratory coat was worn over natural or synthetic fibre clothes throughout. Hand gloves were used throughout the sample processing and analysis period. Sample fibres from clothing, and any potential contaminants from ropes and mesh screens were analysed alongside the surface water samples by setting up blanks (1 blank per three samples analysed). A dampened filter paper (30 mm diameter, Whatman No. 1) (Courtene–Jones *et al.*,

2017) was placed in a petri dish and left exposed during the processing and analysis period. The counts per blank were subtracted from the total count in each sample to correct ground contamination.

Microplastic extraction process

Sieving: The samples of the large size were sieved through 5000 µm (to remove MPs sizes larger than 5 mm) and collected on 500 µm sieves to obtain microplastics between 500 and 4999 µm. Materials on the 500 µm sieve were retained for further analysis. The samples for the medium size were sieved through 500 µm and collected onto a 250 µm sieve to remove particles above 500 µm. The material on the 250 µm sieve was retained for further analysis. The 20 µm samples were sieved using the 250 µm and collected onto a 20 µm sieve. The material from the 250 µm sieve was discarded while that on 20 µm sieve was retained for further analysis.

Digestion: The sieved samples of different size categories were digested in 50 ml 10 % Potassium Hydroxide (KOH) at 60 °C for fourteen hours to remove organic matter (Lusher *et al.*, 2017, modified protocol). After 14 hours, the digested samples were then sieved through the respective sieve sizes (500, 250 and 20 µm), thoroughly rinsed with distilled water, and transferred to individual glass beakers using distilled water. The samples were then filtered through a vacuum pump fitted with a cellulose nitrate membrane (millipore HA of 0.8 µm). The membrane filters were placed in a membrane dish-holder, covered and dried at 40 °C for 12 hours (modified protocol) after which the samples were ready for microplastic enumeration and characterisation.

Microplastic enumeration and characterisation

The membrane filters were examined under a dissecting microscope at 40 x magnification as described by Hidalgo-Ruz *et al.* (2012) and microplastics confirmed using the hot needle test as outlined by Devriese *et al.* (2015). Further confirmation was done by observing particles under a stereomicroscope while prodding them with tweezers. Plastic particles sprung on prodding while non-plastic particles broke. Sand and salt crystals broke with a glass sound when prodded and were pushed aside. Under a stereomicroscope, the MPs were characterised as fibre (thread-like, microfibers, filaments or strands), fragments (irregular shaped particles, crystals, fluffs or granules) and films (sheet-like soft fragments) according to Hidalgo-Ruz *et al.* (2012), and their colour noted.

Data analyses

Data was processed using the Statistics and Data (STATA) version 15. The data was checked for normality using the Shapiro-Wilk W test for normality. Since all the three sets of data were not normally distributed, the data was log transformed. Both the large size and small size microplastic data became normally distributed while the medium size did not achieve normality. Thus, for testing for significant differences, ANOVA was used for the data on large and small size, while a non-parametric test (Kruskal-Wallis) was used for the data on the medium size microplastics. The total mean concentration and the concentrations of the different shapes and colours were assessed between sites (Tudor, Port-Reitz and Mida creeks) and between stations in each of the sites. The tests were considered significant at $p < 0.05$.

Results

Physical factors

The physical factors of the surface water within the creeks did not vary significantly between seasons and sites (p > 0.05). Surface water temperature was relatively low with Tudor having a mean of 23.6 ± 0.7 °C, Port-Reitz 21.9 ± 0.8 °C and Mida 22.2 ± 0.9 °C. Salinity was almost similar in all the sites with Tudor recording a mean of 34.7 ± 0.1 PSU, Port-Reitz 34.5 ± 0.1 PSU and Mida 34.4 ± 0.1 PSU. Similarly, conductivity was almost the same across sites with Tudor having 55810.1µS cm^{-1}, Port-Reitz 55985.1 µS cm^{-1}, and Mida 55682.1 µS cm^{-1}.

Small Size (20-249 µm) microplastics category

The overall (±SE) mean MPs concentration of the small size was 2897.7 ± 232 microplastic particles per cubic meter (mp m^{-3}) of water. Mean MPs concentrations were 3364 ± 431 mp m^{-3} in the first sampling campaign and 2534 ± 223 mp m^{-3} in the second, but were not significantly different (p> 0.05). The mean concentrations were high across sites averaging 3161.3 ± 363.7 mp m^{-3} in Tudor, 2883.3 ± 485.4 mp m^{-3} in Port-Reitz, and 2523.3 ± 211.8 mp m^{-3} in Mida, but the difference between sites was not significant (ANOVA: $F_{2,45} = 0.52$; p-value = 0.6).

There was no significant difference in the concentrations between stations (ANOVA: $F_{8,39} = 1.8$; p-value = 0.1). Mikindani in Tudor averaged 4520 ± 425.7 mp m^{-3}, Makupa in Port-Reitz averaged 3736.7 ± 893 mp m^{-3}, Mwache-Tsunza in Port Reitz averaged 2040 ± 311.7 mp m^{-3}, and Dabaso in Mida averaged 2100 ± 177.8 mp m^{-3} (Table 2).

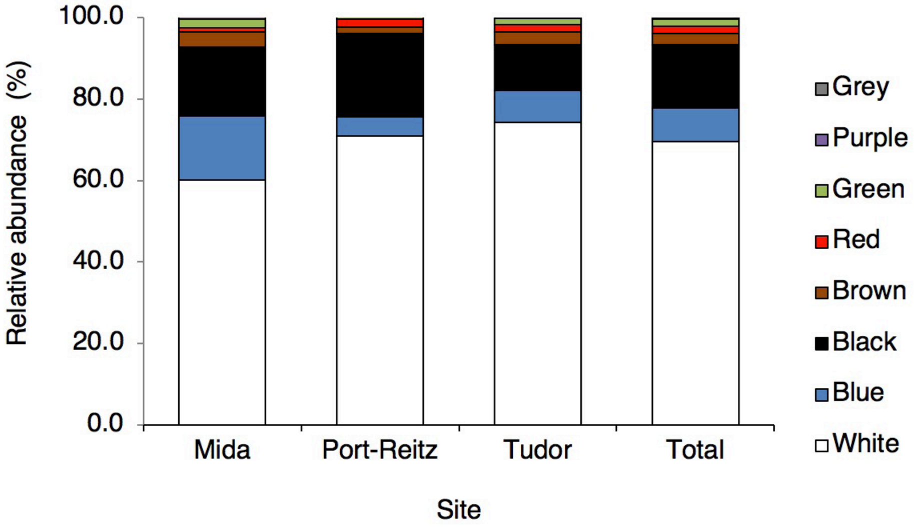

Figure 2. Mean percentage proportions of microplastic particles of different colours in the small size category in different sites.

Three categories of MPs based on shape were encountered in the surface water identified as fibres, fragments and films. Generally, in the small size MPs category, fibres were the most abundant (2703 ± 226 mp m^{-3}) accounting for 93 %, followed by fragments (164.6 ± 20.4 mp m^{-3}) accounting for 6 %, then films (33.5 ± 9.2 mp m^{-3}) accounting for only 1 %, and the differences were statistically significant (ANOVA: $F_{2,45} = 5.61$; p-value = 0.01).

There was no significant difference (p> 0.05) in the concentration of MPs categories between sites. In Tudor fibres averaged 2931.7 ± 358.5 mp m^{-3}, Port-Reitz averaged 2716 ± 474.4 pm m^{-3} and Mida averaged 2340.8 ± 186.1 mp m^{-3}. Fragments in Tudor averaged 197.8 ± 31.9 pm m^{-3}, Mida averaged 176.7 ± 39.8 pm m^{-3} and Port-Reitz averaged 123.3 ± 146.3 pm m^{-3}). The mean concentration of films was significantly higher (Chisq.$_{2,41}$ = 8.5, p-value = 0.01) in Port-Reitz (53.3 ±

Table 2. Mean concentration (m^{-3}) of the different microplastics of the small size in different stations.

Site	Station	Total MPs	Fiber	Fragment	Film
	Dabaso	2100 ± 177.8	1966.7 ± 225.2	126.7 ± 67.7	6.7 ± 6.7
Mida	Kirepwe	2776.7 ± 391.3	2515 ± 342.4	253.3 ± 58.3	8.3 ± 8.3
	Mayonda	2440 ± 180.4	2366.7 ± 155.1	73.3 ± 29.1	0 ± 0
	Makupa	3736.7 ± 893	3575 ± 867.7	146.6 ± 81.6	25 ± 8.9
Port Reitz	Mwache-SGR	2873.3 ± 1105	2758 ± 1081	131.6 ± 47.2	3.3 ± 3.3
	Mwache-Tsunza	2040 ± 311.7	1816 ± 255	91.7 ± 53.9	131.3 ± 57
	KMC	2328.3 ± 658	2180 ± 651.9	113.3 ± 68.4	35 ± 13.6
Tudor	Mikindani	4520 ± 425.7	4245 ± 439.1	245 ± 33.8	30 ±11
	Nyali-Bridge	2636.7 ± 415.1	2370 ± 414.6	235 ± 49.0	31.7 ± 8.7
	Total	2897.7 ± 232	2703.3 ± 226	164.6 ± 20.4	33.5 ± 9.2
	F	1.81	1.81	0.94	1.93
	Df	8	8	8	8
	p-value	0.1038	0.103	0.5	0.09

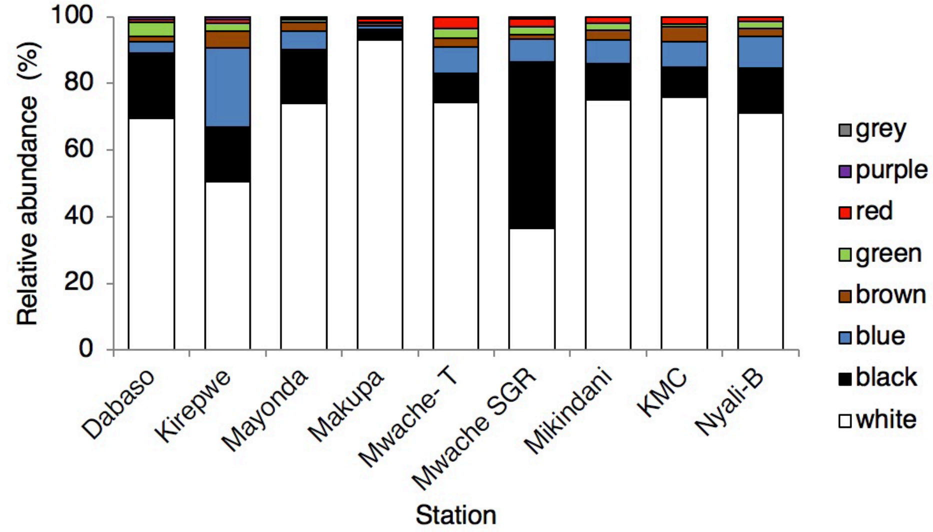

Figure 3. Mean percentage proportions of microplastic particles of different colours in the small size category in different stations.

22.8 mp m^{-3}) compared to Tudor (32.2 ± 6.1 mp m^{-3}), and Mida (5.8 ± 4.4 mp m^{-3}) (Table 2).

The mean concentration of MPs categories did no vary significantly ($p > 0.05$) between stations (Table 2). Mikindani averaged 4245 ± 437.1 pm m^{-3} fibres, Makupa averaged 3575 ± 867.7 pm m^{-3}, while Dabaso averaged 1966.7 ± 225.2 mp m^{-3}, and Mwache-Tsunza averaged 1816 ± 255.6 pm m^{-3}. On the other hand, fragments were most abundant in Kirepwe averaging 253.3 ± 58.3 mp m^{-3}, Mikindani averaged 245 ± 33.8 mp m^{-3} and Nyali-Bridge averaged 235 ± 49.0 mp m^{-3}, while films were most abundant in Mwache-Tsunza averaging 131.7 ± 57.5 mp m^{-3} (Table 2).

Eight colours of MPs were encountered among the small size MPs. Overall, the concentrations were significantly different ($p < 0.05$) and white colour was predominant (2015.2 ± 203.6 mp m^{-3}) accounting for 69.6 %, followed by black (453.5 ± 159.7 mp m^{-3}) 15.6 %, blue (239.6 ± 35.6 mp m^{-3}) 8.2 %, brown (76.9 ± 15.2 mp m^{-3}) 2.7 %, green (53.3 ± 10.2 mp m^{-3}) 1.8 %, red (48.5 ± 9.6 mp m^{-3}) 1.7 %, purple (6.3± 3.4 mp m^{-3}) 0.2 %, and finally grey (4.4 ± 2.1 mp m^{-3}) 0.2 % . By site, the mean concentration of MPs colours did not differ significantly ($p < 0.05$) but white in Tudor averaged 2348.3 ± 312 mp m^{-3}, accounting for 74 %, Port-Reitz averaged 2012 ± 424 mp m^{-3} (71 %), and Mida averaged 1519 ± 169.7 mp m^{-3} (60 %) (Fig. 2). The mean concentration of MPs of black colour averaged 348 ± 81.1 mp m^{-3} (20.2 %) in Port-Reitz, while blue averaged (250.6 ± 36.4 mp m^{-3} (17 %) in Mida (Fig. 2).

By station, the mean concentrations for white and blue were significantly different ($p < 0.05$). Makupa (3475 ± 934 mp m^{-3}) had the highest mean concentration for white accounting for 93 %, while Mwache-SGR (1050 ± 468.3 mp m^{-3}) had the lowest accounting for 36.5 %. Blue MPs were most abundant in Kirepwe (660 ± 160.7 mp m^{-3}) accounting for 23.8 %. Mwache-SGR recorded a mean concentration of 1431.7 ± 1256.4 mp m^{-3} for black MPs accounting for 49.9 %, while Makupa recorded a low concentration accounting for 3.2 % (Fig. 3).

Medium size (250- 449µm) microplastics category

The overall mean concentration of the medium microplastics was generally low at 3.1 ± 0.4 mp m^{-3} of water, compared to the small size category. The mean MPs concentrations were significantly different (Chisq $_{1}$= 29.3, p-value < 0.01) between the two sampling campaigns, at 1.1 ± 0.2 mp m^{-3} in the first sampling campaign and 4.5 ± 0.4 mp m^{-3} during the second. Mida recorded the highest mean concentration (4.2 ± 0.58 mp m^{-3}), followed by Port-Reitz (2.7 ± .71 mp m^{-3}) and finally Tudor (2.6 ± .45 mp m^{-3}). There was a significant difference (Chisq $_{2,45}$ = 6.4, p-value = 0.041) in mean MPs concentration between sites. Post hoc analysis showed that the mean concentration for Mida differed significantly from that of Tudor and Port-Reitz while the latter two sites were not different. By station, the mean concentration of microplastics was highest in Dabaso (6.2 ± 0.53 mp m^{-3}), while the lowest mean concentration was recorded in Mwache-Tsunza (1.0 ± 0.2 mp m^{-3}) (Table 3). The Kruskal Wallis test showed a

Table 3. Mean concentration (m^{-3}) of the different microplastics of medium size in the different stations.

Site	Station	Total MPs	Fiber	Fragment	Film
	Dabaso	6.2 ± 0.5a	5.8 ± 0.5	0.2 ± 0.1	0.14 ± 0.1
Mida Creek	Kirepwe	2.7 ± 0.6bcd	2.5 ± 0.6	0.1 ± 0.1	0.09 ± 0
	Mayonda	5.5 ± 0.3a	5.2 ± 0.3	0.1 ± 0.0	0.22 ± 0.1
	Makupa	1.8 ± 0.6bcd	1.6 ± 0.5	0.2 ± 0.1	0.05 ± 0.0
Port Reitz	Mwache-Tsunza	1.0 ± 0.2cd	0.9 ± 0.2	0.1 ± 0.0	0 ± 0
	Mwache-SGR	5.4 ± 1.6a	4.5 ± 1.4	0.8 ± 0.2	0.07 ± 0.0
	KMC	2.3 ± 0.7bcd	2.1 ± 0.7	0.1 ± 0.1	0.1 ± 0.0
Tudor Creek	Mikindani	3.6 ± 1abc	2.9 ± 0.8	0.7 ± 0.3	0.09 ± 0.1
	Nyali-bridge	1.7 ± 0.4bcd	1.5 ± 0.3	0.2 ± 0.1	0.04 ± 0.0
	Total	3.1 ± 0.4	2.7 ± 0.3	0.3 ± 0.1	0.08 ± 0.0
	F	20.866	20.686	17.953	18.912
	Df	8	8	8	8
	p-value	0.008	0.008	0.02	0.02

Mean within columns followed by the same letters are not statistically different (Tukey test, $p \leq 0.05$)

statistically significant difference in mean microplastic concentration between stations (ANOVA: Chisq $_{8,41}$ = 20.87; p = 0.008) (Table 3).

The mean concentration of medium size microplastic fibres was higher (2.7 ± 0.3 mp m^{-3}) compared to fragments (0.3 ± 0.1 mp m^{-3}) and films (0.1 ± 0.01 mp m^{-3}). The mean concentration of fibres was significantly different (Chisq$_{2,45}$ = 7.7, p-value = 0.02; Chisq$_{2,39}$, = 11.8, p-value = 0.002, respectively), and higher in Mida Creek (4 ± 0.6 mp m^{-3}) compared to Port-Reitz (2.3 ± 0.6 mp m^{-3}) and Tudor (2.2 ± 0.4 mp m^{-3}) creeks where the latter sites were not significantly different. The mean concentration of fragments was higher in Port-Reitz (0.4 ± 0.4 mp m^{-3}) and Tudor creeks (0.3 ± 0.1 m^{-3}) compared to Mida Creek (0.1 ± 0 mp m^{-3}) and the difference was significant (Chisq$_{2,45}$ = 7.7, p-value = 0.02; Chisq$_{2,39}$, = 11.8, p-value = 0.002, respectively). The mean concentration of films was relatively low across sites and did not show significant differences (p> 0.05).

Within the stations, fibres were most abundant in Dabaso (5.8 ± 0.1 mp m^{-3}), Mayonda (5.2 ± 0.3 mp m^{-3}) and Mwache SGR (5.4 ± 1.6 mp m^{-3}) and lowest in Mwache-Tsunza (0.9 ± 0.2 mp m^{-3}). Fragments were most abundant in Mwache-SGR (0.8 ± 0.2 mp m^{-3}) and lowest in Kirepwe, Mayonda, Mwache-Tsunza and KMC, at 0.1 ± 0.03 mp m^{-3}, while films were highest in Mayonda (0.2 ± 0.1 mp m^{-3}) and none were encountered in Mwache-Tsunza (0 mp m^{-3}). The differences in the mean concentrations of fibres, fragments and films between stations were significant (ANOVA: Chisq$_{8,39}$ = 20.69, p-value = 0.008; Chisq$_{8,29}$ = 17.95, p-value = 0.02; Chisq$_{2,29}$ = 18.9, p-value = 0.02) respectively (Table 3).

Unlike the small sized MPs, only six colours were encountered in this size with purple and grey totally missing. Overall, white colour was most abundant (2.1 ± 0.3 mp m^{-3}) followed by black (0.5 ± 0.1 mp m^{-3}) and blue (0.3 ± 0.1 mp m^{-3}). By site, the percentage proportion of the white MPs was almost the same across the sites at 70 % (Fig. 4) with that of MPs of other colours being only 30 %. Green colour was encountered in small proportions in Mida Creek while it was nearly missing in the other two sites (Fig. 4).

Large size (500 µm- < 5 mm) microplastics category

The concentrations of the large size MPs category were generally less than 1 MPs particle per m^3 in all the sites. Overall, mean concentration of the large size MPs was 0.6 ± 0.1 mp m^{-3} of water. There was a significant difference ($F_{1,46}$ = 41.82, p< 0.05) in the MPs concentrations between sampling periods. During the first sampling campaign the overall concentration was

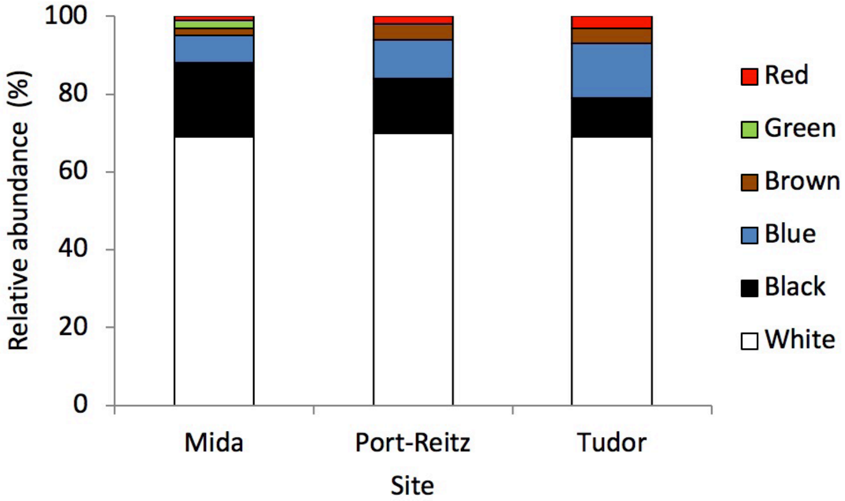

Figure 4. Mean percentage proportions of microplastic particles of different colours in the medium size category in different sites.

0.33 ± 0.04 mp m^{-3} while during the second the concentration was 0.80 ± 0.05 mp m^{-3} of water. Mida had the highest mean concentration (0.8 ± 0.1 mp m^{-3}), followed by Port-Reitz (0.6 ± 0.1 mp m^{-3}), then Tudor (0.5 ± 0.1 mp m^{-3}). The Kruskal Wallis test showed significant difference ($F_{2,45}$ = 4.97, p-value = 0.01) in mean microplastic concentration between sites. The Post hoc test showed that the mean concentration in Mida was different from that in Port-Reitz and Tudor but the latter two were not different.

Discussion

The presence of MPs in marine surface waters along the Kenyan Coast clearly provides evidence for widespread MPs pollution in these waters. Seasonal changes affect MPs distribution in surface water differently. The average monthly rainfall in the January/February sampling period was low (6.1-9.8 mm), and relatively high (36.3 mm) in September 2018 (Kenya Meteorological Department, 2018). Mean concentrations of 3365.1 ± 431.2 and 2539.3 ± 223.5 mp m^{-3} were encountered in the first and second sampling seasons respectively, but the concentrations were not significantly different (p> 0.05). The lack of significant difference between the sampling campaigns may mean that land-based sources may not be the major sources of MPs in the creeks with little new input through runoff or wind (Veerasingam *et al.*, 2016). This could be attributed to the calm ocean conditions with low wind, wave intensity and similarity in physico-chemical factors (Maes *et al.*, 2017) that prevailed during the sampling seasons leading to uniform distribution of MPs in the sites. High salinity of 34.2 ppt during sampling periods could have increased water density making MPs buoyant and resulting in high concentrations in the surface waters.

Microplastics recovery from different studies are different due to varied sampling protocols adopted. Lusher *et al.* (2015) recovered between 0.02 and 100 particles m^{-3} from the Northeast Atlantic Ocean by pumping and sieving surface water with a 250 µm sieve. Lucia *et al.* (2014) recovered 0.11-119 MPs particles m^{-2} from surface water in the Mediterranean Sea using a 333µm manta net. Kosore *et al.* (2018) recovered an average of 110 MPs particles m^{-3} in the Indian Ocean along the Kenyan Coast in the central EEZ by sieving water samples through a 250 µm stainless steel mesh. In this study, an estimated average of 2897 MPs particles m^{-3} of the small size MPs were recovered by sieving surface water samples through a 20 µm net. These levels are high as expected due to the high population densities and the many anthropogenic activities around the creeks. The recoveries of MPs from 250 µm and 500 µm neuston nets were very low estimated at 3.1 MPs and <1 MPs particle m^{-3} of water respectively. This points to the possibility of there being much lower concentrations of large and medium MPs particles in the water surface compared to the small size MPs. Thus, the manta trawl with 300 µm mesh size that has been proposed for sampling of MPs in the water column (Viršek *et al.*, 2016) and used in many studies (Tamminga *et al.*, 2018) may be underestimating the MPs in the water column (Dai *et al.*, 2018). On the other hand, there is the possibility that the effect of currents generated by towing the nets could be causing the MPs to be pushed out of the nets through the large mesh size. Kang *et al.* (2015) found that MPs less than 2 mm were two orders of magnitude higher in concentration in a hand net compared to the trawl.

In this study MPs concentrations of three size categories (large, medium and small MPs) were estimated using different net mesh sizes and sampling strategies. Although the small size MPs samples were collected by scooping water using a bucket, the concentrations were several orders of magnitude higher compared to the medium and large sizes. The medium and large size MPs samples were collected by towing plankton nets for ten minutes where less than 10 MPs and less than 1 MPs particles per cubic meter were recovered, respectively. However, owing to the heterogeneous distribution of MPs on the sea surface (Eriksen *et al.*, 2018) towing nets on the sea surface helps to overcome the heterogeneity. Owing to the great contrast in mean concentrations of MPs between the small size and the others, it may be critical to test the efficiency of bulk sampling vis-a-vis use of towed plankton or manta trawl nets for all sizes of MPs and compare the recovery. The challenge of heterogeneity of MPs distribution can be overcome by taking several replicate samples at different points. It is also worth noting that bulk sampling can take much less time compared to towing of nets and thus is less costly in terms of sea time.

Some of the risks associated with marine microplanktons is the incorporation of the particles and the adsorbed chemicals into the food web through trophic transfer (Setälä *et al.*, 2018). The smaller the MPs particle the more the likelihood of being ingested by marine animals and being transferred in food webs (Botterell *et al.*, 2019). It is therefore prudent that assessment of MPs considers those less than 300μm (normal size of the manta trawl net mesh size) as well. Small MPs have a large surface area and can thus adsorb much more POPs which accumulate on the MPs and are transferred to many marine organisms (Hermabessiere *et al.*, 2017) where they could become toxic at high levels.

Microplastic categories by shape were similar to those found in other regions of the world with fibres being the most dominant category (>90%) (Dai *et al.*, 2018). This could be as a result of release from fishing nets and ropes or washing of synthetic textiles (Napper and Thompson, 2016), while few were fragments and films from packaging material (Kowalski *et al.*, 2016).

A greater proportion of MPs in this study were white, followed by coloured MPs. This is in line with earlier research findings in the Hawaii islands (Alan and James, 2016), the North Pacific Ocean and Bering Sea (Boerger *et al.*, 2010). Colour is used for preliminary identification of MPs. Plastic pellets and polypropylene (PP) pellets are transparent (Ismail *et al.*, 2009), high density polyethylene (PE) pellets white, low density PE opaque, while ethyl venyl acetate corresponds to clear and almost transparent pellets (Ismail *et al.*, 2009). However, MPs colour inherited from their plastic products can change due to weathering. Currently, there is no scheme for colour designation for plastic litter hindering its use in identifying the source of plastics in the marine environment. The results from this study imply that plastics in the Indian Ocean waters along the Kenyan coast are from sea-based activities such as fishing and tourist activities and could be transported from distant areas.

Microplastics were found in all the sites including Mida Creek, a National Marine Reserve thought to be safe from pollution by industrial effluents, sewage disposal and fishing activities. The relatively high concentration of MPs in this site suggests that the source may not necessarily only be from activities on the adjacent land. The higher concentration of the large size microplastics category in Mida compared to Tudor and Port-Reitz suggests that the microplastics were entering the system close to their source and could mainly originate from the tourists to the Marine National Park, and the inhabitants of Dabaso village and Kirepwe Island, backing up findings from earlier research linking human population density and plastic pollution (Dai *et al.*, 2018). The human inhabitants release domestic effluent into the ocean and dispose off plastic waste which could be seen floating on the water surface (personal observation) thereby contributing to the pollution. This also suggests that plastic debris has not stayed within the creek waters for long as little degradation has occurred, probably due to the regular cleaning done to remove anthropogenic litter from the creek waters (personal observation). The trend of MPs distribution is similar to those observed for the Mediterranean Sea, the Northeast Pacific Ocean and the open ocean waters (Goldstein *et al.*, 2013; Cozar *et al.*, 2015). Extensive boat and dhow fishing activities go on in the creek waters (personal observation) which could be contributing to the high concentration of MPs in the waters.

Makupa in Port-Reitz had a high MPs concentration compared to other stations within the site. This could be attributed to the fact that Kibarani dumpsite is near Makupa where municipal waste has been dumped for many years (Eriksen *et al.*, 2014). Water flow within the station is limited hence MPs are not carried away by ocean currents. High MPs levels have been linked to anthropogenic activities like aquaculture, fishing and coastal tourism in other parts of the world (Frere *et al.*, 2017; Dai *et al.*, 2018). Population density and the level of urbanization and waste infrastructure have also been linked to high accumulation of MPs in different regions of the world (Lebreton *et al.*, 2012; Pedrotti *et al.*, 2016). This could be the case with Port-Reitz Creek which is adjacent to suburban areas on the mainland which host oil refineries and housing estates and are surrounded by densely populated villages such as Dongo Kaya, Dunga Nusa, and Ngala (IAME, 2018). The relatively high concentration of MPs of small and medium size categories in Mwache-SGR in Port-Reitz could be attributed to Port activities as well as high population density. Mwache-Tsunza, also in Port-Reitz, has a high population density (IAME, 2018) but low MPs concentrations, probably because of flushing by the many channels such as the Mwache, Cha Shimba and Mwambone rivers, and frequent ocean waves and currents (Kitheka *et al.*, 1999).

Mikindani in Tudor is an outlying township on the mainland along the Nairobi highway within the heavy industrial areas at Changamwe and accommodates the working population who work in the Port of Mombasa, town centre and in the industries (IAME, 2018). Tudor creek is fed by two major seasonal rivers; Kombeni and Tsalu, which arise near the town of Mariakani (Kitheka *et al.*, 1999). The rivers collect surface runoff with plastic and other waste debris from the mainland and discharge them into the creek. Rapid urbanization has led to the development of informal settlements near the Coast General Hospital and Kenya Meat Commission (Okuku *et al.*, 2011) that may be adding to the MPs brought in by the seasonal rivers and ocean currents through the release of raw domestic waste contributing to the high MPs concentrations observed.

Conclusion

The creeks along the Kenyan coast are highly polluted with microplastics of the 20 µm - 250 µm size range. Microplastics of the 250µm – 5000µm size range occur in low concentrations. Tudor Creek is more polluted with microplastics compared to Port-Reitz and Mida creeks. Makupa in Port-Reitz was the most polluted station, perhaps due to the Kibarani dumping site in the vicinity. Mida Creek which is located within a Marine National Park, is a protected environment considered as a control, but was also contaminated with microplastics. Microplastics fibres were the most abundant in the creek surface waters accounting for over 90 %, followed by fragments and films accounting for around 10 %. The bulk of the microplastics recovered were white, suggesting that gear from fishing activities may be one of the main sources of MPs in the coastal waters.

The results of this study provide a baseline for future monitoring of the effect of the Kenya Government ban on single use plastic carriers of February 2017. Future assessments can be compared with these results to establish whether the ban is making a difference to the extent of MPs pollution in the coastal waters. Countries bordering the WIO and neighbouring Kenya are likely to be polluted with microplastics and together with other governments in the world should join and support the fight against plastic pollution in the oceans.

There is a need for a critical evaluation of plastic waste disposal policies in Kenya to curb the problem. The Kenyan Government should protect the ocean through legislation on plastic waste management; encourage the development of plastic recycling industries by availing capital to investors. Manufacturers should produce alternative packaging materials to plastics such as sisal bags. The Kenyan Government should also conduct mass education to create awareness on the dangers of MPs to marine ecosystems as well as human health and conduct frequent massive beach cleaning. Recycling of plastics could lead to a closed-loop system where plastics are continuously reused.

It is recommended that the recovery of MPs of all three sizes using the bulk sampling method be tested. Microplastic pollution along the Kenyan coast needs to be monitored to establish the effect of the 2017 ban on the production and use of light plastics. Finally, monitoring during the Northeast and Southeast Monsoon, when fishing activities are different along the Kenyan coast, needs to be conducted.

Acknowledgements

This study was funded by NRF, to which we are very grateful. The Director of the Kenya Marine and Fisheries Research Institute (KMFRI) for allowing the use of institutional facilities, Agnes Muthumbi, John Onyari and Dr Deborah Robertson-Andersson for mentorship and developing sampling methodologies, co-authors for ensuring quality manuscript production, George Ong'amo and David Gitahi for guiding in data analysis, and the UON and KMFRI technical staff for fieldwork assistance that was vital in executing the study, are all appreciated.

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Morphological and meristic characters of six rabbitfish species (Family: Siganidae) in Kenya

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Abstract

Siganus species (rabbitfishes) are caught by artisanal fishers in Kenyan marine waters. The identification of recently captured rabbitfish species is based on colour patterns, but colours fade after death or during preservation, making species identification more difficult. Morphometric measurements and meristics are then useful in differentiating between species. Twenty-four morphological and twelve meristic characteristics of rabbitfish were obtained from samples collected at six landing sites along the Kenyan coast. Principal Component Analysis (PCA) and Mann-Whitney U-tests were used to evaluate variability among the species. Four of six rabbitfish species showed similar body morphometry and could not be distinguished using PCA analysis, but *Siganus stellatus* and *S. luridus* differed from the other species and each other. No clear morphological evidence of separate stocks of individual rabbitfish species was found, apart from *S. rivulatus* for which the sample size was small. It is recommended that existing taxonomic descriptions are updated to include additional distinctive characters documented in this study.

Keywords: taxonomy, Siganidae, morpho-meristic, length-weight, body condition

Introduction

The Siganidae (rabbitfishes or spine foots) are widely distributed throughout tropical and subtropical Indo-Pacific regions, primarily in shallow waters less than 15 m deep. They also occur in the eastern Mediterranean basin, having invaded that water body through the Red Sea and Suez Canal which has been open since 1869 (Renanel *et al*., 2018). Tharwat and Al-Owfeir (2003) reported *Siganus rivulatus* as one of the first siganids to enter the Mediterranean basin, where it is now common. Most rabbitfish species are exclusively marine, apart from *Siganus vermiculatus* which is estuarine and has successfully been introduced to freshwater habitats (Tharwat and Al-Owfeir, 2003). Rabbitfishes are valuable commercial species in many parts of the world (Woodland, 1990).

Rabbitfishes in the Western Indian Ocean (WIO) region are harvested by artisanal fishers using a popular local basket trap (*malema*) (Wambiji *et al*., 2016; 2008; Kamukuru, 2009), gill nets, intertidal wiers (*uzio*) and hand-lines (*mishipi*). In Kenya, they are among the most common species in landings of marine artisanal fisheries (39% of landings by weight; Robinson and Samoilys, 2013).

The Siganidae comprises of two genera: *Siganus* and *Lo,* with 29 known species. *Siganus* is distinguished by a deep compressed body, a snout resembling that of a rabbit, 13 dorsal, seven anal and two strong ventral fin spines. They possess a leathery skin, smooth, small and closely adherent scales, and are frequently mistaken to be scaleless. *Lo* comprises of five species, with extended snouts and prominent face stripes earning them the name of "foxface fishes". Snout shapes, caudal fins, body depths and shapes have been useful in distinguishing the members of these two genera (Woodland, 1990).

Rabbitfish graze on algae, seaweeds and sea grasses and are important to reef ecosystems because their grazing prevent corals from being smothered by mats of

http://dx.doi.org/10.4314/wiojms.v19i2.7

filamentous and leafy algae. Their faeces in reef crevices promote growth and diversity of corals (Duray, 1998). Siganids show lunar synchronized spawning activity, similar to other reef fish species (Harahap *et al*., 2001; Robinson and Samoilys, 2013).

Siganids exhibit few morphological differences, making them difficult to differentiate from each other. Descriptions currently used for their identification are based on colouration of live specimens (Woodland and Randall, 1979). However, colours change with age, after death and in preserved specimens (Masuda *et al*., 1980; Randall and Kulbicki, 2005). Fisheries studies depend mainly on landed (dead) and preserved specimens, hence other identification features (apart from colour) are useful in species identification. Morphometric and meristic characteristics are two powerful tools for fish identification. Morphometric characteristics describe aspects of body form, whereas meristic characteristics are related to discrete numbers (counts) that are repeated. Morphological plasticity is an adaptive response to complex ecological conditions under which fish species live. A mixture of environmental factors, such as temperature, salinity, dissolved oxygen, radiation, water depth and current flow may induce morphological variations between fishes (Brraich and Akhter, 2015). Other factors, such as reproduction and gonad development may also influence fish morphology (Fakunmoju *et al*., 2014; Kashefi *et al.,* 2012).

Accurate identification to species level is an essential step in fisheries research and management, and formulation of conservation strategies. The aim of this study was to compare morphometric and meristic characteristics of six rabbitfish species known from Kenya.

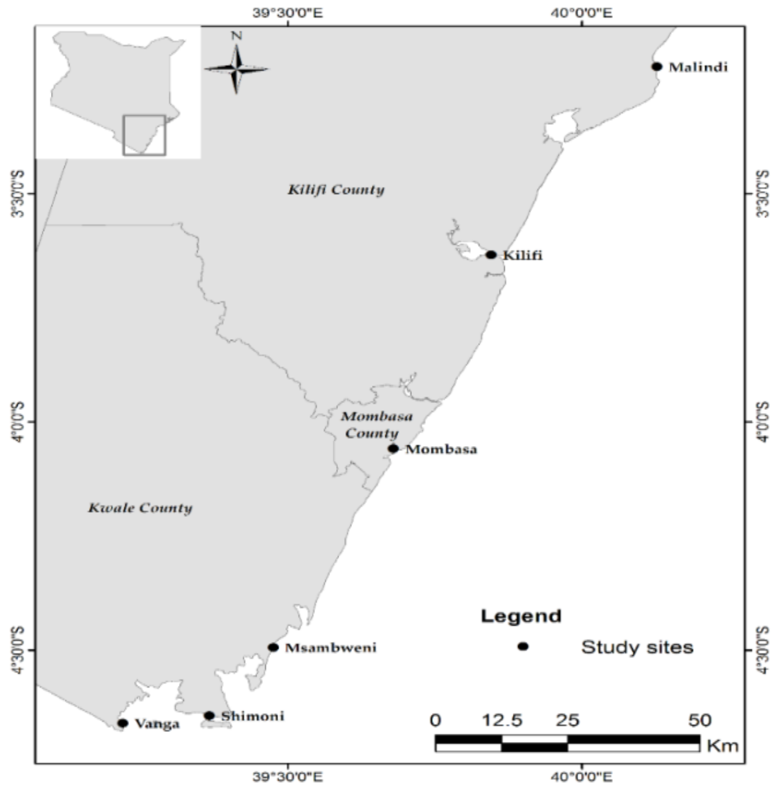

Figure 1. Map of Kenya (inset) showing the Kenyan coast and locations of the study sites.

Materials and methods

Study Sites

This study was conducted at six landing sites in Kenya: Vanga, Shimoni and Msambweni in the south, and Mombasa, Kilifi and Malindi in the north (Fig. 1). Vanga is located within a mangrove area, with fishing occurring in a complex mangrove ecosystem, estuaries and creeks, near patch and island reefs interspersed with sea grass beds. Shimoni borders on a Marine National Reserve (Agembe *et al*., 2010) with fishing taking place on patch and fringing coral reefs, sea-grass beds, reef flats and sand bars. Msambweni has complex mangrove bays, estuaries and creeks close to the shore near patch and island reefs and is also a popular tourist resort (Koornhof, 1997). In Mombasa, inshore fishing take place year round in shallow lagoons (<5m deep), on sea grass beds with narrow channels opening into the open sea (Malleret-King *et al.*, 2002), with some limitations in the marine protected areas (MPA; e.g. Bamburi Marine Reserve; Marsh *et al.*, 2002). Fishing in Kilifi is mainly in Kilifi Creek (part of the Goshi River estuary; Weiss and Heinrich, 2006), shallow lagoons, sea grass beds and narrow channels opening into the open sea (Malleret-King *et al.*, 2002). The Malindi fish landing site is located on Malindi Bay, adjacent to the Athi-Sabaki-Galana river system, with fringing reef and high coral diversity, and includes Mida Creek with shallow mangrove and sea grass habitats (Malleret-King *et al.*, 2002). The Malindi and Watamu National Parks restrict fishing in some areas (Kaunda-Arara and Rose, 2006).

Data collection

Field sampling was conducted for three consecutive days per month at each landing site between November 2013 and September 2015. Freshly landed rabbitfish were selected from artisanal catches and sorted to species level based on distinctive features such as caudal fin shapes, and colour patterns on body and fins (Anam and Mostarda 2012) (Table S1). During field sampling, standard length (SL) and total length (TL) of 1554 specimen was measured on a measuring board (±0.1 cm) from the tip of the snout (mouth closed) to the caudal peduncle base and tip of the longest caudal fin respectively, according to Fischer and Bianchi (1984) and Anam and Mostarda (2012). Body weight (BW, g ± 0.1g) was recorded on a top loading balance (Ashton Meyers, model 7765).

A total of 234 specimens of the six species were purchased for morpho-meristic studies, chilled in ice and taken to KMFRI laboratories where they were deep frozen at -20° C for at least one week before undertaking morphometric and meristic measurements.

Frozen specimens were thawed at room temperature and dried with soft tissue paper to remove excess water. Identification features were recorded on these specimens, as well as additional specimens obtained from the National Museum of Kenya, and preserved in formalin and 70% alcohol. Measurements of 24 morphometric characters were taken with Vernier calipers from the left lateral aspect of each specimen (Table S2) and twelve meristic characters were counted on each specimen (Table S 3) (Fischer and Bianchi, 1984).

Data Analysis

Morphometric data were expressed as a percentage of standard length to remove size effect, and a Principal Component Analysis (PCA) was used to identify components accounting for variance in multi-dimensional data. Identified variables were linear combinations of original variables (Davies, 1986; Harper, 1999). The non-parametric Mann-Whitney U-test was used as a post-hoc test for the differences discerned from PCA analysis at $\alpha \leq 0.05$. Meristic data were analyzed for dorsal spines and rays, anal spines and rays, pectoral rays and branched and un-branched caudal fin rays.

Regressions of the form $W = aL^b W$ where W = weight (g), L = total length (cm), and a and b = regression constants were fitted to length and weight data using a least squares method. Data were log-transformed ($\text{Log } W = \log a + b\log L$) for comparisons among species. Condition factors were calculated employing the formula: $K = 100\ W/L^{b:}$ (Fulton, 1904; Wootton, 1990).

Results

All six rabbitfish species were recorded at Msambweni, five at Shimoni and Malindi respectively, four at Kilifi, and three at Mombasa and Vanga (Table 1). *S. canaliculatus* and *S. sutor* occurred at all sites. *S. canaliculatus*, *S. sutor*, *S. stellatus*, *S. luridus* and *S. rivulatus* were landed in all seasons, while *S. argenteus* were landed seasonally during the South East Monsoon only, although the sample size for this species was small (n = 9) (Fig. 2). Most *S. canaliculatus*, *S. sutor* and *S. stellatus* were landed during the North East Monsoon, but landings of *S. luridus* and *S. rivulatus* were roughly equal between seasons.

Morphometric measurements of the six rabbitfish species (Table 2) indicated that the mean length was largest for *S. stellatus* and smallest for *S. luridus*. Meristic counts of the six species (Table 3) were comparable for most species except for *S. stellatus* caudal fin rays that differed from those of other species. Gill raker counts also differed between *S. luridus* and *S. argenteus* and from counts of the other species. Raw meristic data were therefore not analyzed with PCA.

The PCA of standardized morphometric data showed significant variation in morphometric characters of *S. stellatus* and *S. luridus*, but the mean values of most morphometric characteristics were similar between the other four species (Fig. 3). The first principal component accounted for 64.3 % of total variation and the second for 19.9 %. Factor loadings showed that the first

Table 1. Numbers of rabbitfish of each of six species recorded per landing site.

Species	**Site**						**Sub-total**
	Vanga	Shimoni	Msambweni	Mombasa	Kilifi	Malindi	
S. canaliculatus	75	104	118	67	76	93	553
S. sutor	98	103	94	62	91	78	526
S. luridus	0	43	126	86	92	10	357
S. stellatus	5	26	34	0	8	37	119
S. rivulatus	0	0	5	0	0	4	9
S. argenteus	0	2	7	0	0	0	9
Grand total							1554

component was defined by snout length (SnL), pre-pectoral distance (PPD) and pre-ventral distance (PVD), while the second component was defined by pre-pectoral distance (PPD), pre-anal distance (PVD), pectoral-anal fin distance (PtAFD), ventral-anal fin distance (VtAFD) and caudal peduncle width (CPW) (Table 4). Mann-Whitney U-test results (Table S4) confirmed significant differences ($p< 0.05$) between *S. stellatus* and *S. luridus* in head depth (HD), SnL, eye diameter (ED), body depth (BD), PVD, dorsal fin base length (DFbL) and ventral fin length (VFL). *S. luridus* and *S. argenteus* differed in ED, PPD, VtAFD, DFbL, dorsal fin ray length (DFL), dorsal spine length (GDspL), pectoral fin length (PFL), VFL, ventral spine length (VspL) and caudal peduncle length (CPL). *S. canaliculatus* and *S. sutor* differed only in ED and anal spine length (GAspL).

The morphometry of *S. rivulatus* differed between two collection sites at Msambweni and Malindi based on a small sample size (n = 9). The first principal component explained 54.7 % of total variation and the second explained 19.6 % (Fig. 4), and factor loadings are shown in (Table S5). Subsequent Mann-Whitney U-tests showed significant difference in ED and GDspL at $p \leq 0.05$.

The length-weight relationships of six rabbitfish species (n=1554; Table 5) resulted in b-values between 2.554 and 3.537, within an expected range of 2.3 to 3.5 proposed by Bagenal and Tesch (1978). Rabbitfish species collected from most landing sites exhibited mixed growth patterns: *S. sutor*, *S. luridus* and *S. stellatus* displayed isometric growth, however, *S. luridus* from Msambweni showed positive allometric growth. *S. canaliculatus* data exhibited isometric growth at all sites except at Malindi where it showed negative allometric growth. *S. argenteus* and *S. rivulatus* also displayed negative allometetric growth, but in both cases sample sizes were small with a weak fit for *S. rivulatus* (r^2= 0.378).

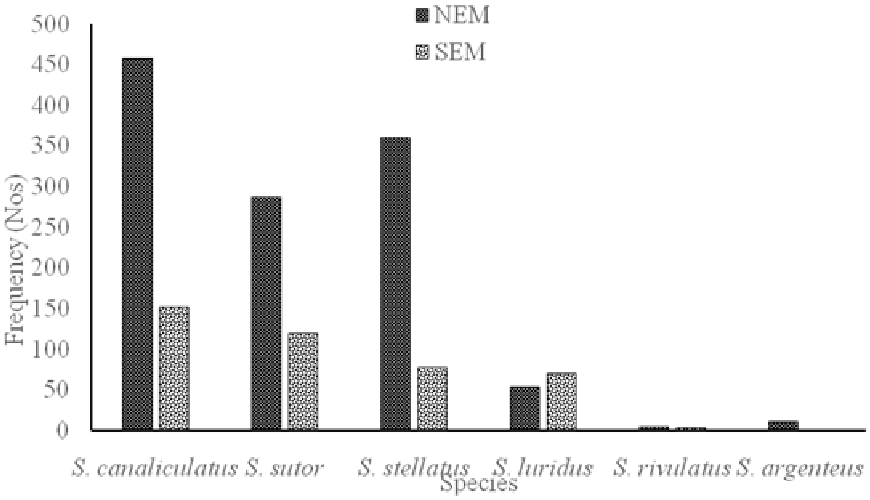

Figure 2. Seasonal distribution of rabbitfish samples in the present study.

Table 2. Descriptive statistics for the morphometric characters (Mean ± SD) of rabbitfish specimens recorded during the study. Abbreviations are summarized in Table S2.

	***Siganus canaliculatus* (n=60) Mean±SD**	***Siganus rivulatus* (n=9) Mean±SD**	***Siganus sutor* (n=62) Mean±SD**	***Siganus argenteus* (n=9) Mean±SD**	***Siganus stellatus* (n=39) Mean±SD**	***Siganus luridus* (n=55) Mean±SD**
SL	20.2±2	18.9±2.5	20.1±1.7	18.9±2.4	22.0±1.8	14.1±1.4
HD	25.3±3	23.5±3.0	20.0±1.9	25.2±1.8	25.6±21.6	26.7±2.0
Sn L	9.2±0.6	8.2±0.3	9.4±0.6	9.3±1.0	11.6±0.9	8.5±0.6
ED	6.0±0.7	6.9±1.7	6.1±0.7	7.7±0.3	5.8±0.7	7.1±0.9
BD	38.5±2.8	35.5±1.4	38.4±2.0	36.7±2.2	46.1±2.3	34.0±2.2
PDD	23.9±2	23.0±1.6	24.1±1.3	22.7±1.5	26.3±1.2	23.5±1.2
PPD	22.3±1.2	21.5±1.4	21.8±1.1	21.7±1.5	22.5±1.7	21.0±1.4
PVD	30.3±2	29.5±1.4	30.3±1.5	31.1±2.0	33.9±1.1	27.8±1.9
PAD	46.6±3.6	47.5±3.3	48.1±2.4	48.5±2.8	52.0±3.8	48.2±2.3
PtAFD	26.9±2	25.4±1.3	25.7±2.4	26.9±1.7	28.4±2.1	27.4±2.2
VtAFD	19.9±2	19.1±1.0	18.9±1.6	19.8±1.4	20.7±1.7	22.0±1.8
DFbL	64.4±1.7	68.1±1.9	65.8±2.5	68.6±1.4	67.9±1.2	56.0±1.7
DFL	36.3±2.5	38.5±2.3	38.4±2.1	39.5±2.1	38.5±2.0	37.6±2.2
GDspL	10.2±1.0	9.8±2.2	10.3±1.7	11.2±1.5	13.3±1.0	13.6±1.7
PFL	18.0 ±1.0	15.6±0.8	18.6±1.2	6.9±1.1	20.3±1.1	19.0±2.0
VFL	13.9 ±1.4	14.5±1.6	14.1±1.0	14.0±0.8	17.9±1.3	18.0±1.3
VspL	10.6±0.8	10.2±0.8	10.5±1.2	10.2±0.6	13.8±0.9	12.4±1.9
AFbL	41.7 ±1.8	44.4±1.5	41.9±2.0	43.6±1.9	43.0±1.9	42.5±1.4
AFL	30.3±1.0	34.6±1.0	29.9±2.0	34.2±1.3	34.1±1.5	31.1±2.1
GAspL	9.5±1.1	11.6±1.2	10.2±1.1	11.0±0.9	14.0±1.0	13.1±1.1
LwJL	5.2±0.2	5.1±0.67	5.2±0.4	4.6±0.4	5.7±0.5	5.4±0.3
LwJW	2.5±0.2	1.9±0.3	2.8±0.3	2.2±0.2	2.7±0.4	2.6±0.6
CPL	10.6 ±0.8	11.3±1.0	10.7±1.1	11.9±1.2	10.0±1.1	10.8±1.0
CPW	5.2±0.4	4.8±0.4	5.2±0.4	5.1±0.6	6.3±0.1	5.5±0.4

The mean body condition of the six rabbitfish species was lowest for *S. luridus* and highest for *S. argenteus*. Condition factor-values of all six species ranged from 0.46 to 3.53. Condition factor-values of most species were > 1, indicating a good body condition. At the extremes, mean body condition values of 2.64 ± 0.08 were estimated for *S. argenteus* and 1.22 ± 0.37 for *S. canaliculatus* (Table 6).

Discussion

Relatively more rabbitfish species and specimens (as part of landings) were recorded at sites along the south coast compared to the north coast, plausibly attributed to differences in coral reef and sea grass cover (estimated at 19.5 % on the south coast and 11.1% on the north coast; Obura *et al*., 2002). Fringing reefs along the Kenya coast extend for a distance of about 200

Table 3. Counts of meristic characters for six rabbitfish species analyzed during the study. Abbreviations are summarized in Table S3.

Abbreviation	*S. canaliculatus*	*S. sutor*	*S. stellatus*	*S. luridus*	*S. rivulatus*	*S. argenteus*
Dspine	XIII	XIII	XIII	XIII	XIII	XIII
Dray	10	10	10	10	10	10
Aspine	VII	VII	VII	VII	VII	VII
Aray	9	9	9	9	9	9
Pectray	17 (17-18)	17(17-18)	17(17-18)	17 (17-18)	17 (17-18)	17 (17-18)
Crays	18	18	20	18	18	18
ULSCray	5	5	5	5	5	5
BCray	10	10	10	10	10	10
LLCray	4	4	5	4	4	4
ULGr	10	10	10	10	10	10
LLGr	VII	VII	VII	VII	VII	VII
TGr	6-7+(17-18)	6-7+(17-18)	6-7+(17-18)	5-7+(15-17)	6-7+(17-18)	4-6+(17-18)

km between Malindi and Vanga, and are more prominent on the south coast. Coral reef and sea grass cover are patchy along the north coast (Obura *et al.*, 2002) as a result of river discharge and the proximity of the Somali current which brings cooler (17 - 22°C) nutrient rich (5 - 20 µm of nutrient) waters to the northern coast. This creates productive ecosystems in the north but with a higher silt load which may reduce coral reef and sea grass growth and cover. Habitat suitability can therefore explain the greater numbers and species of rabbitfishes along the south coast.

The PCA showed no morphological variation among *S. canaliculatus*, *S. sutor*, *S. rivulatus* and *S. argenteus* suggesting that they have similar body morphometry. However, Mann-Whitney U-tests revealed significant

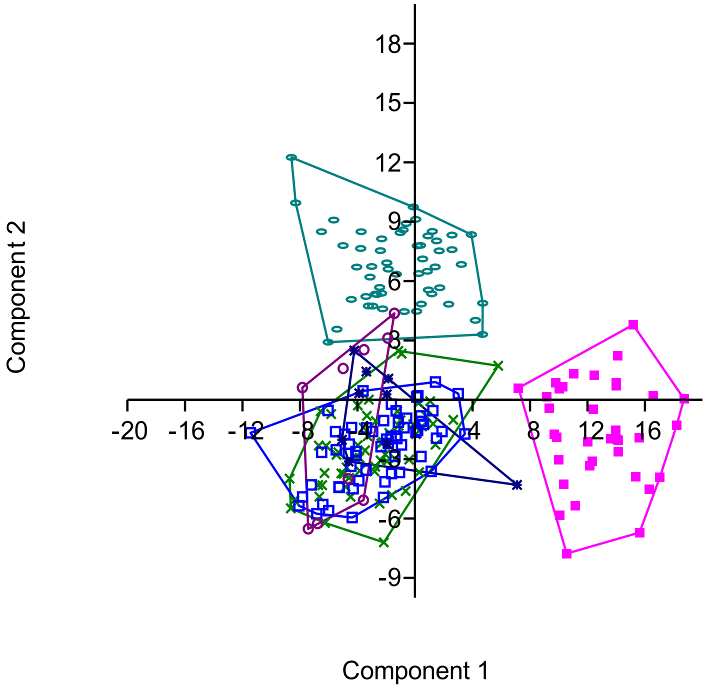

Figure 3. Plot of individual scores on first and second components of morphometric as a percentage of standard length of *S. canaliculatus* (Cross), *S. sutor* (Open Square), *S. luridus* (Oval), *S. stellatus*(Filled Square), *S. rivulatus*(Circle) and *S. argenteus* (Diamond).

Table 4. Loading of percentage standard metrics of morphometric measurements for *S. stellatus* (n = 36) and *S. luridus* (n = 25) specimens from Kenya coast. Values in bold indicate significant difference.

Morphometric Characters	Abbreviations	PC 1	PC 2	Morphometric Characters	Abbreviations	PC 1	PC 2
Head depth	HD	0.169	0.015	Dorsal spine length	GDspL	0.084	0.193
Eye depth	ED	-0.071	0.050	Pectoral fin length	PFL	-0.028	0.109
Snout length	SnL	0.494	-0.048	Ventral fin length	VFL	0.096	0.182
Body depth	BD	0.153	0.002	Ventral spine length	VspL	0.039	0.235
Pre-dorsal distance	PDD	0.088	0.162	Anal fin base length	AFbL	0.165	0.037
Pre-pectoral distance	PPD	0.398	0.314	Anal fin ray length	AFL	0.045	0.024
Pre-ventral distance	PVD	0.249	0.002	Anal spine length	GAspL	0.014	0.030
Pre-anal distance	PAD	0.117	0.279	Lower jaw length	LwJL	0.008	0.007
Pectoral-anal fin distance	PtAFD	-0.027	0.319	Lower jaw width	LwJW	0.007	0.039
Ventral-anal fin distance	VtAFD	0.142	0.477	Caudal peduncle length	CPL	0.104	0.012
Dorsal fin base length	DFbL	0.076	0.104	Caudal peduncle width	CPW	0.067	0.319
Dorsal fin ray length	DFL	-0.025	0.244				

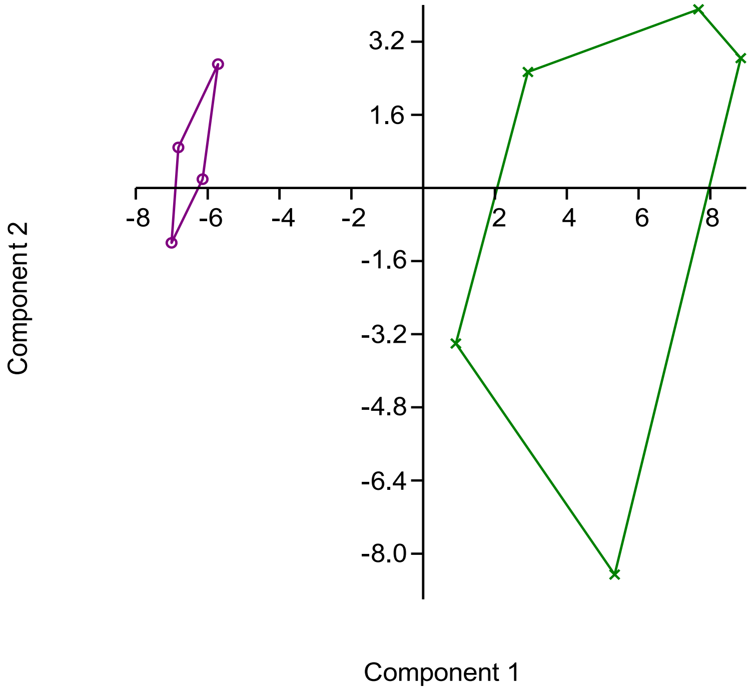

Figure 4. Plots of individual scores on first and second principal components as a percentage of standard length for *S. rivulatus* collected from Msambweni (Cross) and Malindi (Open Circle) along the Kenyan coast.

Table 5. Length-weight relationship of six rabbitfish species recorded along the Kenyan coast. (n = sample size; a = regression intercept; b = length exponent; r^2 = coefficient of determination).

Species	Site	Parameters			
		n	*a*	*b*	r^2
S. canaliculatus	Vanga	65	0.372	2.725	0.908
	Shimoni	90	0.248	2.625	0.948
	Msambweni	108	0.353	2.831	0.963
	Mombasa	57	0.530	2.898	0.906
	Kilifi	65	0.221	2.681	0.614
	Malindi	83	0.542	0.736	0.983
S. sutor	Vanga	93	0.199	2.554	0.948
	Shimoni	83	0.302	2.700	0.973
	Msambweni	87	0.221	2.681	0.788
	Mombasa	52	0.857	3.045	0.957
	Kilifi	82	0.627	2.947	0.957
	Malindi	30	0.018	3.370	0.814
S. luridus	Shimoni	114	0.358	2.855	0.585
	Msambweni	76	0.022	3.537	0.878
	Mombasa	82	0.957	3.194	0.955
	Kilifi	82	0.627	2.947	0.957
	Malindi	16	0.505	2.958	0.972
S. stellatus	Shimoni	38	0.460	2.914	0.992
	Msambweni	27	0.434	2.855	0.964
	Malindi	65	0.372	2.725	0.908
S. rivulatus	Malindi	4	0.030	1.967	0.378
	Msambweni	5	0.131	2.339	0.988
S. argenteus	Msambweni	7	0.055	1.904	0.982

Table 6. Estimated mean values of condition factor (K), range and sample size (n) of rabbitfish specimens examined during the study.

Species	n	Range	Mean±SD
S. canaliculatus	468	0.88-2.86	1.22±0.37
S. sutor	465	1.26-3.53	2.08±0.43
S. luridus	302	0.46-2.87	1.24±0.56
S. stellatus	81	1.66-2.33	2.07±0.19
S. rivulatus	9	1.46-1.75	1.57±0.03
S. argenteus	9	2.26-2.98	2.64±0.08

character differences in several individual parameters such as eye diameter, body depth and lower jaw length, among others (see Table S4). Difference in lower jaw length may be related to variation in the habitat characteristics of the area where the fish lives. Morphological variations such as these could be an adaptive response to factors such as temperature, salinity, dissolved oxygen, radiation, water depth, current flow and food type (Turan, 2000; Tharwat and Al-Owfeir, 2003).

S. stellatus and *S. luridus* differed morphometrically from each other and from the other four species. The Mann-Whitney U-test results confirmed significant differences in HD, SnL, ED, BD, PVD, PtAFD, DFbL, DFL and VFL (Table S4). The two species also differed in the number of their caudal fin rays (Crays) and gill rakers (TGr), implying that they can easily be distinguished on the basis of their body morphometric characters. PCA outputs indicated no clear separation of *S. canaliculatus*, *S. sutor* and *S. stellatus* from Vanga and Malindi, and could also not separate *S. argenteus* from Shimoni and Msambweni, or *S. luridus* from Shimoni and Malindi. The five rabbitfish species therefore have similar body morphometry regardless of their geographical locations along Kenya coast. Conversely, the body morphometry of *S. rivulatus* from Msambweni differed from those at Malindi, resulting in a clear separation in the PCA. Although based on a small sample size, the implication is that geographical isolation may have given rise to differentiation attributed to variations in physico-chemical conditions.

Previous studies by Murta (2000), Poulet *et al.* (2004) and Turan (2004) suggested that morphological differences can also occur within species due to genetic and environmental factors during the early stages of fish growth. Mann-Whitney U-test results (Table S4) confirmed that the *S. rivulatus* specimens from the two localities differed significantly in two of their morphometric characters, ED and GAspL; therefore, the two morphometric characters are useful in differentiating *S. rivulatus* species from the two sites.

The meristic counts of all the six rabbitfish species examined in the present study were similar in most species. The only differences found were in the number of caudal-fin ray counts for *S. stellatus*. Furthermore, gill raker counts differed between *S. luridus* and *S. argenteus* as well as with the counts for the rest of the species. Variations in meristic and morphometric traits within a species or among closely related species has been attributed to a combination of environmental and genetic factors interacting on the developing embryos (Fowler, 1970), although this has not yet been tested for rabbitfishes.

This study established key morphometric and meristic characteristics of six rabbitfish species from Kenya and found that the *b* exponents of the length-weight relationships of most species were close to 3, indicative of an isometric growth pattern. Similar values of *b* were reported for siganids in Kenya by Wambiji *et al*. (2008; 2010) and De Souza (1998) while *b* values varied slightly from those reported by Mbaru *et al*. (2011). However, *b*-values for *S. canaliculatus* from Malindi, *S. argenteus* and *S. rivulatus* exhibited negative allometric growth patterns. Biological parameters in fishes, including length-weight relationships, are affected to factors such as prevailing environmental conditions, ecosystem health, season, food, sex, time of year, stage of maturity, population differences, shape and fatness of the species (Mousavi-Sabet*et al*., 2014; Olapade and Tarawallie, 2014). The condition factors (K) obtained from this study suggested that the specimens were in a good condition, but the influences of season and specific environmental conditions still need to be evaluated.

Conclusions

Four of the six rabbitfish species showed similar body morphometry and could not be distinguished using PCA analysis. Two species (S. *stellatus* and *S. luridus*) differed from each other and from the other species. While existing species descriptions are useful in identifying live specimens, morpho-meristic characters become more useful in differentiating landed and preserved specimens that have lost their colours. No clear morphological evidence of separate stocks of individual rabbitfish species was found, apart from *S. rivulatus* for which the sample size was small. Meristic counts were similar for most species except *S. stellatus* and *S. luridus*, which differed in caudal-fin rays and gill-raker counts. All six species showed mixed growth patterns and their physiological condition factors were >1.

It is recommended that existing taxonomic descriptions are revised to include the additional distinctive characters documented in this study, particularly for the accurate identification of landed and preserved specimens that have lost characteristic colour patterns and markings.

Acknowledgements

We sincerely thank the Kenya Coastal Development Project (KCDP), and the National Commission for Science and Technology (NACOSTI) for providing funds for this study. We wish to express our profound gratitude to the Kenya Marine and Fisheries Research Institute (KMFRI) for providing laboratory space and equipment.

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Appendix

Table S1. Features used to identify dead or preserved rabbitfish specimens, based on personal observations.

Morphometric Character	*Siganus canaliculatus*	*Siganus sutor*	*Siganus luridus*	*Siganus argenteus*	*Siganus rivulatus*	*Siganus stellatus*
Caudal fin shape	Moderately lunate	Slightly forked	Truncate	Deeply forked with pointed lobes	Moderately forked	Emarginate in young, deeply forked in old
Caudal fin colour	Dark	Dark	Dark	Light or Silvery	Light or Silvery	Paler to dark lilac
Caudal fin lobe tip shape	Sharply pointed	Moderately pointed		Sharply pointed	Sharply pointed	
Caudal fin lobe lengths	Nearly equal	Unequal		Equal	Equal	Unequal
On lateral line origin	Dark patch or blotch					Dark patch or blotch
On caudal fin	4-5 dark, 3-4 light bars		6-7 dark, 6 light bars	Light bars		
On dorsal fin base	Dark spots	Dark spots	Dark spots	Light spots		
On anal fin base	Dark spots	Dark spots	Dark spots		Dark spots	
Stripes on dorsal fin base					Dark	
Anal and dorsal fin rays			3-4 dark bars			Paler to dark lilac
On caudal peduncle base	Broad vertical dark bars			Broad vertical dark bars	Narrow vertical dark bars	
On each caudal lobe		3 light vertical stripes		3-4 dark/light vertical stripes	4 dark vertical stripes	
On operculum edge				Dark vertical bar		
On pelvic fin		Dark spots				
On pelvic fin				4-5 light/ 4 dark bars		
Pectoral fin colour					Olive green	
On dorsal part of head					Dark patch	
Above lateral line		7-9 dark patches				
Caudal fin perimeter/caudal peduncle saddle						Paler
On upper part of caudal peduncle		Silvery patch				
Spawning			Usually gravid ~ 8 months a year			

Table S2. Morphometric characters measured on each rabbitfish specimen examined in this study.

Characters	Abbreviations	Description
Standard length	SL	Tip of upper jaw to tail base
Head depth	HD	Vertical measurement across anterior end of gill opening
Snout length	SnL	Tip of upper jaw to anterior border of eye
Eye diameter	ED	Greatest bony diameter of orbit
Body depth	BD	Maximum depth measured from base of dorsal spine
Pre-dorsal distance	PDD	Tip of upper jaw to anterior base of dorsal fin
Pre-pectoral distance	PPD	Tip of upper jaw to anterior base of pectoral fin
Pre-ventral distance	PVD	Tip of upper jaw to anterior base of ventral (pelvic) fin
Pre-anal distance	PAD	Tip of snout (upper jaw) to anterior base of anal fin
Pectoral-anal fin distance	PtAFD	Distance from anterior base of pectoral fin to anterior base of anal fin
Ventral-anal fin distance	VtAFD	Distance from anterior base of ventral fin to anterior base of anal fin
Dorsal fin base length	DFbL	Distance from anterior to posterior base end of dorsal fin
Dorsal fin ray length	DFL	Longest dorsal fin length
Dorsal spine length	GDspL	Longest dorsal spine (5th or 8th) length
Pectoral fin length	PFL	Distance from anterior to posterior end of the pectoral fin
Ventral fin length	VFL	Distance from anterior to posterior end of ventral fin
Ventral spine length	VspL	Longest (1st) ventral spine length
Anal fin base length	AFbL	Distance from anterior to posterior base end of the anal fin
Anal fin ray length	AFL	Longest anal fin length
Spine length Anal	GAspL	Longest anal spine (3rd or 4th) length
Lower jaw length	LwJL	Straight line between the snout tip and posterior edge of mandible
Lower jaw width	LwJW	Distance between the posterior ends of the mandible
Caudal peduncle length	CPL	Distance from posterior end of dorsal/anal fin to base of column
Caudal peduncle width	CPW	Depth of caudal peduncle taken in middle of its length

Table S3. Meristic characters examined on each rabbitfish specimen.

Characters	Abbreviations	Description
Dorsal fin spines	Dspine	Number of spines
Dorsal fin rays	Dray	Number of branched rays on
Anal fin spines	Aspine	Number of spines
Anal fin rays	Aray	Number of branched rays
Pectoral fin rays	Pectray	Number of rays
Caudal fin rays	Crays	Number of single and branched rays
	ULSCray	Number of single rays in upper lobe
	BCray	Number of branched rays
	LLCray	Number of single rays in lower lobe
Gill rakers	ULGr	Number of gill rakers on upper gill arch limb
	LLGr	Number of gill rakers on lower gill arch limb
	TGr	Number of gill rakers on both limbs

Table S4. Mann-Whitney U-test confirmed significant morphological differences between species.

Morphometric characters	Abbreviation	Morphometric characters	Abbreviation
S. stellatus* and *S. Luridus			
Head depth	HD	Snout length	SnL
Eye diameter	ED	Body depth	BD
Pre-ventral distance	PVD	Dorsal fin base length	DFbL
Ventral fin length	VFL		
S. luridus* and *S. Argenteus			
Eye diameter	ED	Pre-dorsal distance	PDD
Ventral-anal fin distance	VtAFD	Dorsal fin base length	DFbL
Dorsal fin ray length	DFL	Dorsal spine length	GDspL
Pectoral fin length	PFL	Ventral fin length	VFL
Ventral spine length	VspL	Caudal peduncle length	CPL
S. canaliculatus*, *S. sutor, S. rivulatus* and *S. argenteus			
Eye diameter	ED		
Body depth	BD		
Lower jaw length	LwJL		
S. canaliculatus* and *S. sutor			
Eye diameter	ED		
Spine length Anal	GAspL		
***S. rivulatus* from Msambweni and Malindi**			
Eye diameter	ED		
Spine length Anal	GAspL		

Table S5. Loading of percentage standard metrics of morphometric measurements on PC1 and PC2 for *S. rivulatus* specimens collected from Msambweni and Malindi along the Kenyan coast. Values in bold show characters that differ significantly and can be used to distinguish the two species.

Morphometric characters	Abbreviations	PC 1	PC 2
Head depth	HD	0.224	0.625
Eye depth	SnL	0.134	0.124
Snout length	ED	0.096	0.072
Body depth	BD	0.229	0.041
Pre-dorsal distance	PDD	0.235	0.063
Pre-pectoral distance	PPD	0.196	0.022
Pre-ventral distance	PVD	0.125	0.089
Pre-anal distance	PAD	0.396	0.312
Pectoral-anal fin distance	PtAFD	0.121	0.157
Ventral-anal fin distance	VtAFD	0.020	0.087
Dorsal fin base length	DFbL	0.099	0.389
Dorsal fin ray length	DFL	0.027	0.371
Dorsal spine length	GDspL	0.219	0.198
Pectoral fin length	PFL	0.080	0.100
Ventral fin length	VFL	0.105	0.185
Ventral spine length	VspL	0.083	0.047
Anal fin base length	AFbL	0.136	0.207
Anal fin ray length	AFL	0.050	0.089
Anal spine length	GAspL	0.204	0.068
Lower jaw length	LwJL	0.087	0.037
Lower jaw width	LwJW	0.001	0.021
Caudal peduncle length	CPL	0.001	0.112
Caudal peduncle width	CPW	0.046	0.003

Valuation of harvested goods in Mida Creek with application of the TESSA approach

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Abstract

Mangroves are considered a highly productive blue forests resource providing services that are important to the community both locally and globally. In recent times there has been an increase in studies on valuation of ecosystem services provided by mangroves. However, there is need to provide a simplified approach to identify, assess and quantify ecosystem services. In this study the Toolkit for Ecosystem Services Site-based Assessment (TESSA) was used to assess the value of harvested goods provided by the mangroves of Mida Creek in the current state and under plausible alternative scenarios. Spatial methods (GIS) were used to collect data for the period 1985-2019, and household interviews were used to collect data on harvested goods. Descriptive statistics were used to summarize quantitative data. Results show that the estimated current annual value of harvested goods in Mida Creek is US$ 11.2 million. This value increased to US$ 14.3 million under the conservation scenario and reduced to US$ 10.9 million under the business as usual scenario (BAU). These findings add to the growing literature on ecosystem service valuation and the need to use site-specific non-modelling tools like TESSA.

Keywords: current scenario, ecosystem services, plausible alternative scenario, mangrove

Introduction

Mangroves are important coastal ecosystem providing numerous ecosystem services and critical ecological functions (Kauffman and Donato, 2012). These services include: provisioning services including wood products, medicine, honey and fish; regulating services such as climate regulation, coastal protection and air quality regulation (Millennium Ecosystem Assessment, 2005; Bosire *et al.*, 2008; Donato *et al.*, 2011); supporting services including primary production, nutrient cycling, and breeding and nursery grounds for marine and pelagic species (Millennium Ecosystem Assessment, 2005; UNEP, 2014); and cultural services such as recreation, spiritual enrichment and aesthetic features (TEEB, 2010; Anam and Thomas, 2017). The sustainable provision of these ecosystem services is essential for human wellbeing (Hooper *et al.*, 2012). However, approximately 60 % of the world's ecosystem services have been degraded or unsustainably used (Millennium Ecosystem Assessment, 2005). Globally, mangrove cover has declined by 30 – 50 % over the past decades (Donato *et al.*, 2011) because of anthropogenic activities (Halpern *et al.*, 2008; Butchart *et al.*, 2010; Malik *et al.*, 2016). This degradation has led to loss of coastal protection services thus increasing coastal vulnerability to natural disasters (Alongi, 2002; Barbier *et al.*, 2008; Bosire *et al.*, 2008). With many competing uses of marine and coastal ecosystem and their services, there is need to formulate and implement policies that will inform effective management of natural resources in order to reduce the continued degradation of these important ecosystems (Owuor *et al.*, 2017).

Economic valuation of ecosystem services allows policy makers to appreciate the value of ecosystem services to society, and the cost of their imminent loss (Ruckelshaus *et al.*, 2013; Laurans *et al.*, 2013), enabling them to integrate ecosystem services into policy and decision-making processes (Fisher *et al.*, 2008; Fisher *et al.*, 2010). Valuation also contributes

http://dx.doi.org/10.4314/wiojms.v19i2.8

to sustainable use of natural resources which in turn leads to poverty alleviation and conservation of natural resources (Owuor *et al.,* 2017).

Although Mida Creek is globally recognized as an Important Bird Area (IBA) and is part of Watamu Marine Park and Reserve (Owuor *et al.*, 2017; Birdlife International, 2020), increasing human population and an increase in demand for natural resources has led to continued degradation and loss of the mangrove forest and associated ecosystem services (Alemayehu, 2016). Undervaluation of the benefits provided by mangrove forests has led to them being rarely considered when resource management decisions are made (Huxham *et al.*, 2015). This hampers awareness creation and policy formulation processes aimed at protecting mangroves. Many studies fail to value ecosystem services that would be lost or gained under plausible alternative scenarios (Peh *et al.*, 2017).

This study was designed to assess the types, quantities and values of goods harvested from Mida Creek in the current state and how these values will change under plausible alternative states. This study adopted the TESSA toolkit because it emphasizes the importance of comparing estimates for alternative states of a site. This enables decision makers to assess the net consequences of such a change, and hence the benefits of human wellbeing that may be lost through the change, or gained through conservation (Peh *et al.,* 2017). For example, the study done by Muoria *et al.* (2015) in Yala swamp recommended that the land use and management policies and plan adopt a balance between development and conservation, to improve the socioeconomic wellbeing of the local residents while protecting biodiversity.

This study will provide decision makers and community members with data on how changes in mangrove cover would affect the provision of ecosystem services under current and future scenarios. It will also add to the growing literature on ecosystem services.

Materials and methods

Study area

Mida Creek is in Kilifi County on the Kenyan coast (Fig. 1). It lies at $3^{0}22^{1}0^{11}$S and $39^{0}58^{1}0^{11}$E. The Creek lies at an altitude of between 0-10 m above sea level. The total mangrove cover in Mida Creek is estimated at 1,746 ha and is dominated by *Rhizophora-Ceriops* type forest (Government of Kenya, 2017). Seven mangrove species have been identified including *Avicennia marina, Bruguiera gymnorrhiza, Ceriops tagal*, *Rhizophora mucronata, Sonneratia alba, Xylocarpus granatum* and *Lumnitzera racemosa* (Gang and Agatsiva, 1992; Kairo *et al*., 2002).

Mida Creek is an important passage and wintering area for Palearctic migrant waders. The populations of *Charadrius leschenaultii*, *Charadrius mongolus* and *Dromas ardeola* in Mida Creek are internationally important, and many other species use the site; up to 6 000 waders may be present in the Creek at any one time (BirdLife International, 2020). It is also an important spawning ground for many fish species, for example, *Spratelloides delicatulus* and *Ambassis natalensis*.

The mangrove forest ecosystem is surrounded by human settlements living in seven villages: Dabaso, Kirepwe, Uyombo, Sita, Gede, Matsangoni and Mida with approximately 4838 households (Kenya National Bureau of Statistics, 2010). The main economic activities of the people living around Mida Creek are fishing, crop farming, business activities and tourism-related ventures (Owuor *et al*., 2019). The major drivers of change include overexploitation of some mangrove species, overfishing, residential and commercial development, conservation action, climate change, lack of management plans and pollution (Alemayehu, 2016; Government of Kenya, 2017)

Methods

Land use land cover changes

To determine plausible alternative scenarios, mangrove cover changes were obtained from Landsat imagery to assess the changes in the land use characteristics of the study area for the years 1985, 2000, 2015 and 2019. The images were on the Landsat path 166 and row 062 and at a resolution of 30 m. The data was downloaded from the USGS (United States Geological Survey) Earth Explorer website and processed using remote sensing software (ArcMap 10.8).

Quantification of harvested goods

A detailed questionnaire was used to collect data for estimating amount of harvested goods. The number of households around Mida Creek was estimated from the 2009 Kenyan Population and Housing Census. The total number of people in Mida Creek in 2009 was estimated to be 30 300 occupying 4838 households. The number of people per household was estimated to be 6.26 persons with a growth rate of 2.9 % (Kenya National Bureau of Statistics, 2010). From these figures the total population currently living around Mida

Creek was estimated to be 40,327 persons. This translated to 6442 households. The sample size was then obtained by the formula:

$$n_o = \frac{Z^2pq}{e^2}$$

Where: n0 is the sample size; e is the margin of error; p is the estimated proportion of the population which has the attribute in question; q is 1 – p; and Z is the desired confidence level (Israel, 2013). The sample size was found to be 95 households at 95 % confidence level and a margin of error of 10 %. This number was then rounded off to 100 for easier computations. Heads of the families in the 100 households sampled were interviewed. The interviews were conducted in villages adjacent to Mida Creek including Uyombo, Dabaso, Dongo Kundu, Kirepwe Island and Mida.

Systematic sampling was used to select households. The main path, track or road in each village was used as sampling transects to standardize participant selection. The first household was then selected randomly, followed by selection of every fifth homestead along transects.

The data collected included the type and quantity of harvested goods, the unit of measurement, whether the product is harvested for domestic consumption, price of the commodity per unit, and production cost. Production cost comprised of annual costs of labour, tools, and marketing costs.

Data analysis

Supervised classification was conducted with the maximum likelihood algorithm (Otukei, 2010). High-resolution imagery from RapidEye was used to run the accuracy assessment for the recent years (2015 and 2019), while Google Earth imagery was used in the accuracy assessment of the years 1985 and 2000. For accuracy assessment, 100 random points were selected for the mangrove classified areas, while 25 sampling points were selected for the non-mangrove terrestrial areas (Miettinen, 2012). The random points were then used to verify the classified land cover in comparison to RapidEye and Google Earth.

The rate of change of mangrove cover was then quantitatively estimated based on procedures used by Peng *et al.* (2008) and the following formula:

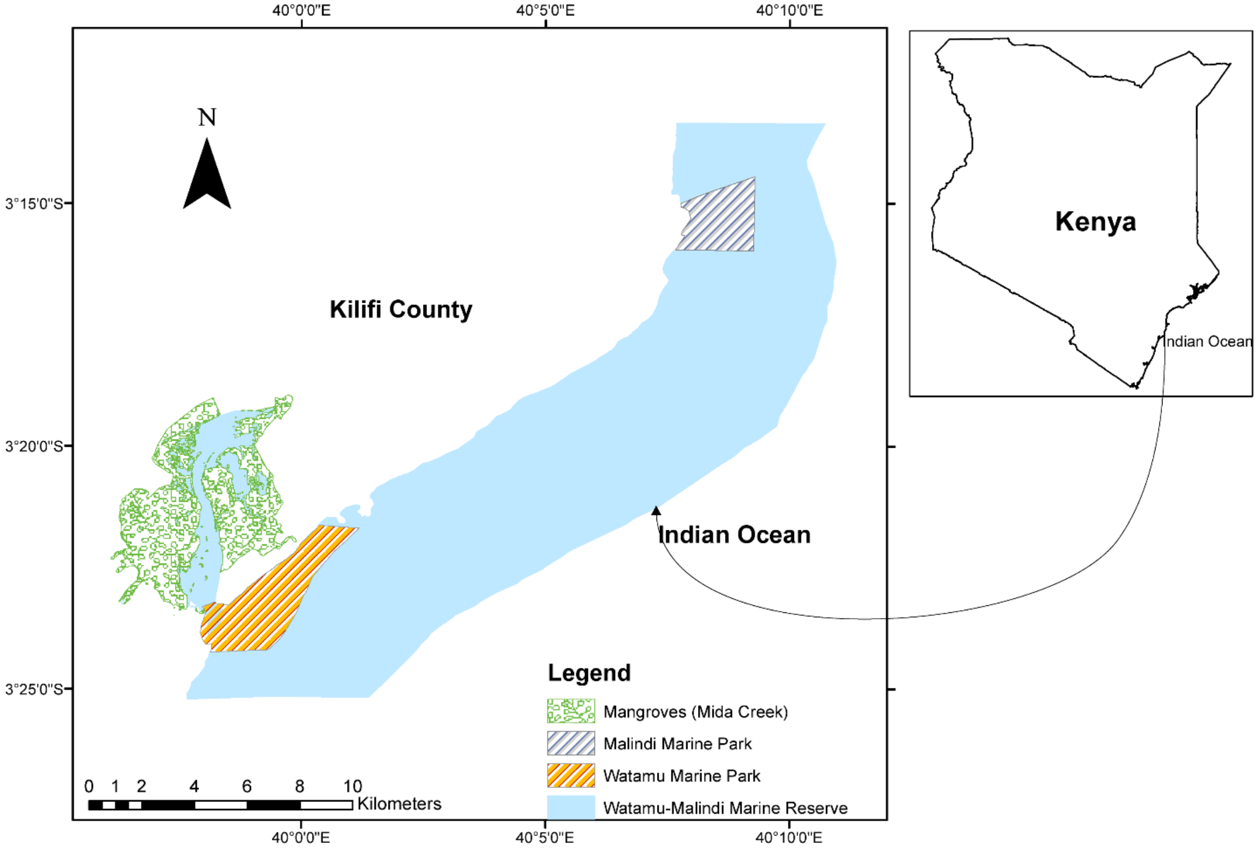

Figure 1. Location of the study area (Mida Creek) in Watamu – Malindi Reserve complex (from Owuor *et al.*, 2017).

$$K1 = \frac{Ub-Ua}{Ua} \times \frac{1}{T} \times 100\%$$

Where: K1 is land use dynamic degree; Ua and Ub are the areas of the target land use at the beginning and end of the study period respectively; and T is Study period.

From the land use dynamic degree, the rate of mangrove cover change over 15 years was estimated and the mangrove cover area under future scenarios was projected assuming that all factors remain constant.
Data on harvested goods collected using questionnaires was summarized into percentages and means. Since the total number of households was estimated to be 6 442 and the sample size was 100 households, the total value of harvested goods was obtained by multiplying the values obtained from the 100 respondents by a figure of 64.42. The value of harvested goods that would be gained or lost was obtained from extrapolation of the future states based on the changes in the land cover of mangroves.

Results

Land use land cover changes

The land use changes for the 34-year period were quantified to show changes in land use and the area covered by the mangroves. Results as summarized in

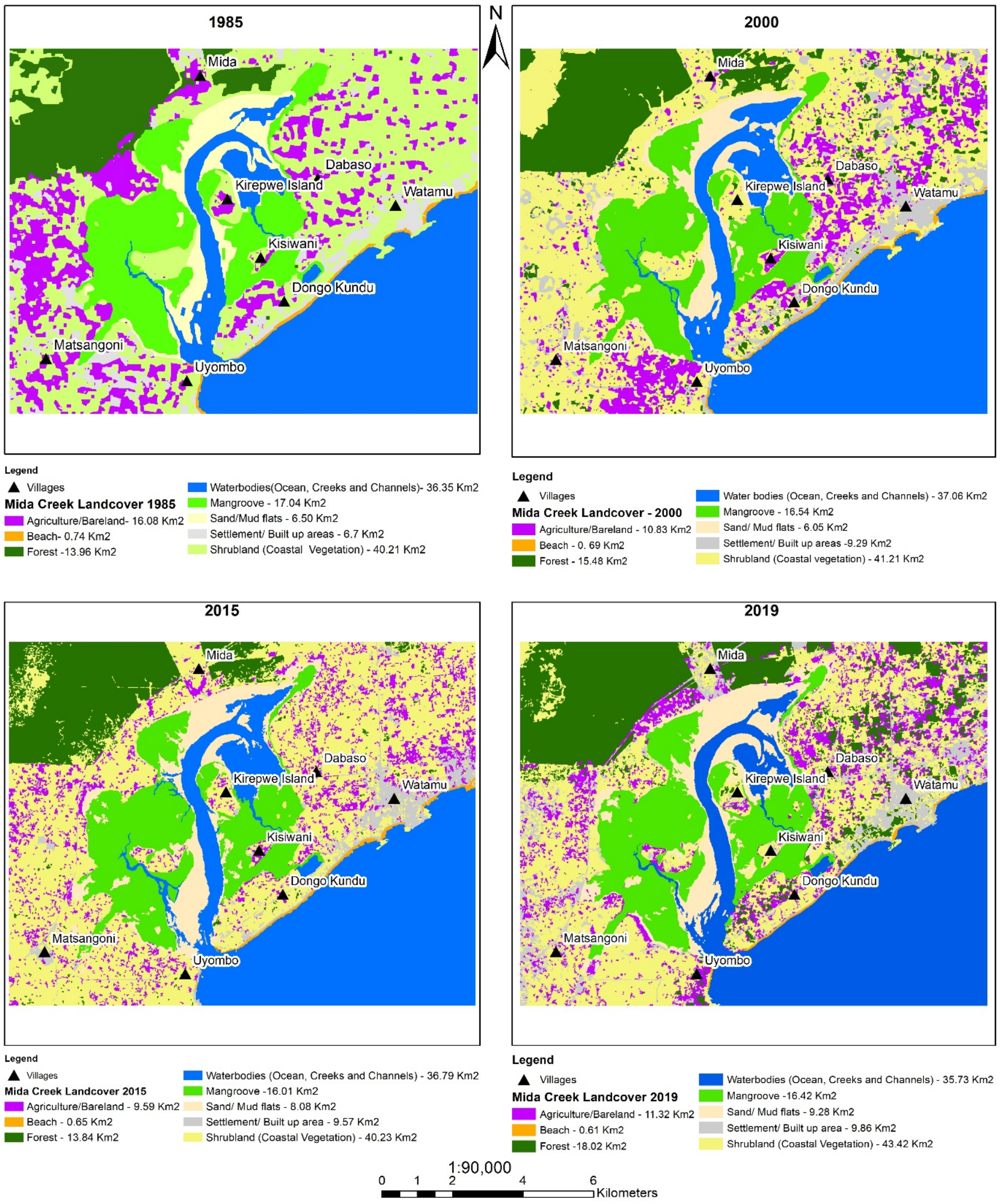

Figure 2. Maps showing mangrove cover changes for the years 1985, 2000, 2015 and 2019.

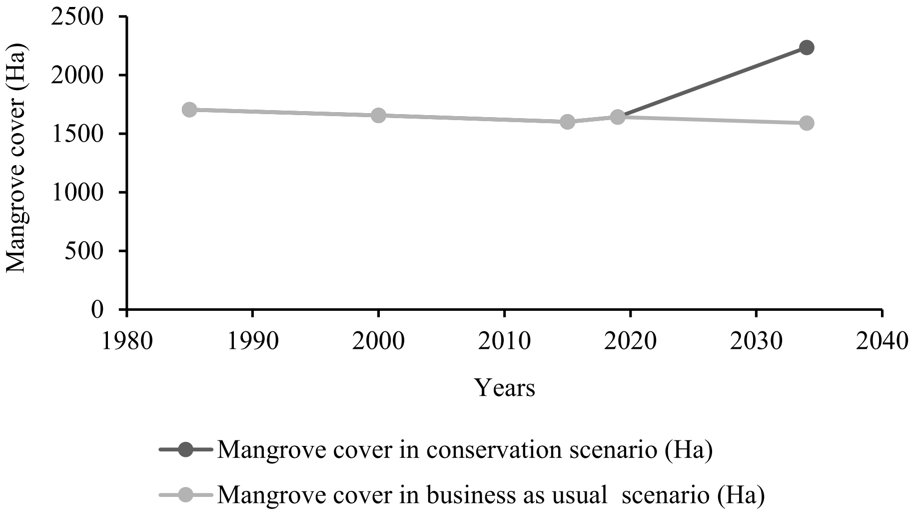

Figure 3. Mangrove cover in previous years and the projected cover in future scenarios.

Figure 2 show that the land cover for mangroves in the years 1985, 2000, 2015 and 2019 were estimated to be 1 704 ha, 1 654 ha, 1 601 ha and 1 642 ha, respectively. Based on these results, two possible future scenarios were assumed: the business as usual scenario (BAU) where the threats facing mangroves were not mitigated and mangrove cover continued to decrease; and a conservation scenario where conservation efforts are in place and mangrove cover increased.

The degree of change dynamic of mangrove cover between the periods of 1985 – 2000 was calculated to be -0.2 % while that of the periods between the years 2000 – 2015 was calculated to be -0.22 %. The average change dynamic for a period of 15 years (a period when the mangrove cover was found to be decreasing) was therefore estimated to be -0.21 %. It was then estimated that if the BAU scenario continues to take place and no measures are put in place to curb degradation, the mangrove cover area in 2034 would be 1 590.3 ha.

The degree of change dynamic between the periods of 2015-2019 was estimated to be 0.64 %. This was the period when mangrove cover was found to have increased. The degree of change dynamic in fifteen years was then calculated to be 2.4 %. This was with an assumption that all factors remained constant and the conservation efforts continued to take place. The mangrove cover area in Mida Creek in 2034 in the conservation scenario was then projected to be 2 233.2 ha. Figure 3 shows the mangrove cover in the previous years and the projected cover under the plausible alternative scenarios.

Harvested goods from mangrove forest in the current state

Demographic characteristics of the respondents of the household questionnaires

The age of the respondents ranged from 20 to 70 years with a mean age of 38.8 years (Standard Deviation [SD] = 12.0614 years). 60 % of the respondents were men while 40 % were women. Only 19 % of the respondents had no formal education. The percentage of the respondents who were members of various environmental groups within Mida Creek was 54 % while 46 % did not belong to any environmental group. The primary source of income for the respondents included fishing (32 %), business activities (29 %) and crop farming (25 %).

Types, quantities and values of harvested goods in Mida Creek in the current state

The respondents interviewed mainly harvested fish, honey, firewood and poles. Other goods like oysters, crabs and medicinal plants were harvested by very few respondents (1 %) and were excluded from further analysis. Fish was the most valuable good harvested from the Creek with an annual net value of US$ 4 892.12 / ha. It was found that most households harvested two or three goods from the mangroves.

Fish

Results as summarized in Table 1 show that 54 % of the households harvested fish with an assumption that the mangroves play a role in the fish caught from the Creek by providing breeding sites for the fish. The mean annual fish catch was estimated at 1 746.2 kg (SD = 934.23; range 155 kg to 4 320 kg) per

Table 1. Types, quantities and values of harvested goods in the current scenario (2019).

Attributes	**Description**				
Types of goods		**Fish**	**Honey**	**Firewood**	**Poles**
No. harvesting	N	54	25	35	24
Annual quantity harvested	Total	98615	4516	19296	7680
	Min	155	80	24.12	200
	Max	4320	432	1800	500
	Mean	1746.2	180.64	551.3	320
	SD	934.23	89.96	590.84	113.29
Unit price (US$)	Mean	2.31	9.09	1.03	0.97
	SD	0.19	0.924	0.43	0
Annual cost of production (US$)	Mean	1724.55	501.26	134.93	31.14
	SD	181.9	225.76	20.03	7.46
Annual gross value (US$)	Mean	4,033.72	1,642.00	565.7	310.62
	SD	1984.21	822.93	228.43	100.8
Annual net value (US$)	Mean	2,309.17	1,140.74	430.77	279.48
	SD	1,860.22	683.02	129.03	107.65
	Total	8,032,863.00	1,843,535.49	971,257.12	432,098.44
	per ha	4,892.12	1,122.74	591.51	263.15

1 United State Dollar (US $) =103.02 Kenya Shillings

respondent. The annual total amount of fish harvested by the respondents was found to be 98 615 kg out of which 20.5% was used for domestic consumption while the rest was sold. The mean market price of fish per kg as quoted by the respondents was estimated to be US$ 2.31 per kg (SD = 0.19; range US$ 1.94 to US$ 2.91 per kg). The difference in price might be due to the type of fish caught. The cost of harvesting included the annual cost of buying a canoe, fishing nets, labour, fishing lines and bait.

The cost of buying a canoe ranged from US$ 242.67 to US$ 582.41 and the canoe was expected to last for a period of at least three years. Hence the annual cost of buying a canoe was estimated to be US$ 137.52. The average annual cost of fishing nets was US$ 72.8 (range US$ 48.53 to US$ 97.07). If two people work in a canoe at a cost of US$ 5.82 per day and they are working on an average of 5 days in a week, the mean annual cost of labour per respondent was estimated to be US$ 1 514.23. The mean annual cost of harvesting fish per respondents was estimated to be US$ 1 724.55. The mean annual net value of fish was therefore estimated to be US $2 309.17 per respondent. The total net value for the 100 respondents was therefore estimated to be US$ 124 695.18 per annum. From the estimated total number of household (6 442) around Mida Creek and the land coverage of mangroves in 2019 (1 642 ha), the annual current net value of fish for the whole population was estimated to be US$ 8 032 863.00, or US$ 4 892.12 per hectare per year.

Honey

Twenty five percent of the households harvested honey as summarized in Table 1. The mean annual quantity of honey harvested per year was found to be 180.64 kg (SD = 89.96; range 80kg to 432 kg) per respondent. The total annual quantity harvested by the respondents was estimated to be 4 516 kg. Nine percent of the honey produced was domestically consumed while the remainder was sold.

The mean market price of honey per kg was estimated to be US$ 9.09 (SD = 0.924; range US$ 7.77 to 9.71) per kilogram. The cost of production included the annual cost of hives, the bee suit, and annual cost of labour, a smoker and a torch. The annual cost of equipment that lasted more than a year was obtained by dividing the buying price by the number of years the equipment was expected to last. The mean annual cost of harvesting honey was estimated to be US$ 501.26 (SD = 225.76; range US$ 184.11 to US$ 1 118.23).

The cost of production varied mainly due to the number of hives present per household; the minimum number of hives was 4 and maximum 12. This meant that the initial cost of buying the hives and the cost of maintaining each hive varied from one household to another based on the number of hives present in each household. The annual mean gross value of honey per respondent was estimated to be US$ 1 642 (range US$ 706.66 to US$ 4193.36) while the annual mean net value of honey was estimated to be US$ 1 140.74 (range US$ 452.90 to US. 3 293.5) per respondent. The total net value for 100 respondents was estimated to be US$ 28 617.44 per annum. The wide range of the value was mainly due to the number of hives per household which ranged from between 4 and 12, and the amount of honey harvested per hive which ranged from between 13 kg to 45 kg per hive per harvest.

This study also established that honey was harvested approximately 3 times year. The current net annual value of honey for the whole population was estimated to be US$ 1 843 535.49 or US$ 1 122.74 per hectare per year.

Firewood

Thirty five percent of the respondents harvested a total of 19 296 bundles of firewood annually with a mean annual quantity of 551.30 bundles (SD = 590.84; range 24.12 bundles to 1800 bundles) per respondent. Most of the firewood collected (71.41 %) was used for domestic consumption while the excess was sold. The annual cost of harvesting firewood per respondent was estimated to be US$ 134.93 which included annual cost of the tools used (axe and machete) and labour. The price of a bundle of firewood was estimated from the 28.59 % of the respondents who sold firewood and was found to be US$ 1.03 (SD = 0.43).

The annual gross value of firewood per respondent was therefore estimated to be US$ 565.70 while the annual net value of firewood per respondent was estimated to be US$ 430.77, or US$ 15 076.95 for 100 respondents. The current net value for the whole population was therefore estimated to be US$ 971 257.12 or US$ 591.51 per hectare per year.

Poles

Finally, Table 1 shows that 24 % of the respondents harvested poles. The poles were mainly harvested when there was need to construct a house. The mean annual quantity of poles harvested per respondent was estimated to be 320 pieces (SD = 113.29; range 200 to 500 pieces). The total number of pieces harvested by the respondents was estimated to be 7 680 with each piece estimated to be worth US$ 0.97. The annual mean gross value of poles was therefore estimated at US$ 310.62.

The mean annual cost of harvesting poles was estimated to be US$ 31.14 and it included annual labour paid and the cost of buying a machete. The mean annual net value of poles per respondent was estimated to be US$ 279.48 or US$ 6 707.52 for 100 respondents. Therefore, the annual net value of poles for the whole population was estimated to be US$ 432 098.44 or US$ 263.15 per hectare per year.

Table 2. Annual net value of harvested goods in 2019 and in future scenarios.

Attribute	Annual Net Value (US $)		
	Current (2019)	Business as Usual Scenario (2034)	Conservation Scenario (2034)
Fish	8,032,863	7,743,680	10,924,694
Honey	1,843,535	1,777,168	2,507,208
Firewood	971,257	1,006,222	621,605
Poles	432,098	447,654	276,543
Total	11,279,754	10,974,725	14,330,050

Value of harvested goods in the future alternative scenarios

From the projected mangrove cover in 2034, it was found that in the BAU scenario mangrove cover would decrease by 3.6 %, while in the conservation scenario the cover would increase by 36.0 %. The values of harvested goods in the future scenarios have been summarized in Table 2. In the BAU scenario, the value of fish and honey were projected to decrease to US$ 7.7 million and US$ 1.8 million respectively, while that of firewood and poles were projected to increase to US$ 1 million and US$ 447 654, respectively. The overall value of harvested goods in the BAU scenario was expected to decrease from US$ 11.3 million to US$ 11.0 million annually.

In the conservation scenario, the net value of fish and honey were expected to increase to US$ 10.9 million and US$ 2.5 million respectively, while that of firewood and poles were expected to decrease to US$ 621 605 and US$ 276 543, respectively. The overall net value of harvested goods was therefore projected to increase to US$ 14.3 million per annum in the conservation scenario.

Discussion

Change in mangrove cover

The spatial analysis found that the area coverage of mangroves decreased from the years 1985 to 2015 by about 103 ha and then increased from the year 2015 to 2019 by 41 ha. Mangrove coverage area reduced in the earlier years mainly due to conversion from one land use to another. Between the years 1969 to 2010 there was the emergence of urban centers, expansion of settlements, and increase in private holiday houses and hotels (Alemayehu, 2016).

Kirui *et al.* (2013) also found that the highest loss of mangroves in Kenya occurred between 1992 and 2000 during which mangroves in Kilifi County where Mida Creek is found experienced the highest loss of approximately 76 %. The lowest rate of loss was witnessed between 2000 to 2010 which coincided with the presidential ban on harvesting mangroves for domestic markets (Kirui *et al.*, 2013). Various conservation groups (Government of Kenya, 2017) attribute the increase in mangrove cover between 2015 and 2019 to conservation efforts initiated on the Creek.

The slight variation in the results of the mangrove cover area in this study to those of other studies, for example, Alemayehu (2016), may be attributed to the tidal variation during the capture of satellite imagery. Findings of Xia *et al.* (2018) show that only high stands of mangroves will be captured by satellite imagery during high tides, while the low stands will be submerged.

Value of harvested goods in the current state and future scenarios

Locals harvest several products from the mangroves which are of great economic value. According to this study, fish was the most valuable good harvested from the Creek. Mukherjee *et al.* (2014) also established that fisheries were the highest ranked in terms of provisional services. Consultation with the local fishermen indicated that fishing is carried out both in the Creek and the open sea.

The annual net value of fish was found to be US$ 8 million (US$ 4 892 per hectare per year). This value is within the range of the value of fish in similar ecosystems. A review on the role of mangroves in fisheries enhancement by Hutchison *et al.* (2014) found that the mean value of fish in similar wetland to this study was US$ 3 114.8 per hectare per year. The slight difference in the value might be due to time differences between the periods of study. In addition, the cost of production varied from one fisherman to another due to the types of fishing vessels used.

The respondents who used canoes and nets for fishing had a higher cost of production and a larger catch as compared to those who used fishing lines and bait, and realized more proceeds from fishing. The value of fishing was expected to increase in the conservation scenario due to increased area for breeding and feeding for fish, while the value was expected to decrease in the BAU scenario due to the continued destruction of the breeding and feeding grounds of the fish. Assuming that all factors remain constant, it was projected that the value of fish will increase by the same percentage (36 %) that the mangrove cover would increase in the conservation scenario, and decrease by the same percentage (3.6 %) that the mangrove cover would decrease in the BAU scenario.

Honey was the second most valuable harvested good at US$ 1.8 million (US$ 1 123 ha per year). This value is higher than that reported by UNEP (2011) in Gazi Bay, Kenya, which recorded a value of US$ 14.7 ha per year.

The quantity of honey harvested by each respondent depended on the number of hives an individual owns. There is a potential increase in the value of honey in the conservation scenario since there would be controlled cutting of mangroves and increased breeding and feeding grounds for the bees. Since beekeeping is considered a conservation-friendly activity and requires minimum labour and financial inputs (Field *et al*., 2018), the locals should be encouraged to engage in apiculture. Where beekeeping is practiced, the forest ecosystem will be conserved as the beekeepers will discourage cutting down of mangroves for timber and poles. People will also be afraid of frequenting areas close to the hives for fear of being stung. The beekeepers should therefore be supported financially and technologically to fully exploit the potential of beekeeping in forest conservation to contribute to sustainability. The value of honey was expected to increase in the conservation scenario but decrease in the BAU scenario.

Harvesting of firewood and building poles is expected to increase in the BAU scenario as the human population around the Creek increases. However, this increase is temporary as the land cover of mangroves continues to decline. The value of firewood was higher than that of poles because the frequency of harvesting the firewood was greater than that of poles which were only harvested when there was a need to construct a house.

The number of respondents harvesting firewood was also higher than those harvesting poles. The total value of both firewood and poles was estimated to be US$ 855 ha per year which is within the range reported by Spalding *et al.* (2010) for global timber and wood fuel of US$ 10 - 1093 ha per year. The value of poles and firewood obtained in this study might not be very accurate since some respondents were not willing to give details on wood harvesting for fear of being arrested owing to the ban on harvesting of mangroves by the Kenyan government. The value of both poles and firewood in the conservation scenario is expected to decrease as there would be controlled cutting of mangroves.

The total overall value of harvested goods was expected to increase in the conservation scenario since the mangrove cover is expected to increase, and reduce in the BAU scenario as the mangrove cover was expected to decrease. Muoria *et al.* (2015) projected a decline in the amount of harvested goods from Yala swamp if development continued, as opposed to a scenario where there was a balance between development and conservation. Additionally, Field *et al.* (2018) reported an increase in the value of goods in a scenario where conservation and development coexist as opposed to a scenario where commercial development was allowed.

Conclusions

The value of harvested goods was projected to decline from US$ 11.3 million to US$11.0 million annually in the BAU scenario due to a decrease in mangrove cover, while conservation efforts in the conservation scenario would lead to an increase in the value of harvested goods to US$ 14.3 per annum by the year 2034. This shows that Mida Creek has a high realized and potential monetary value, emphasizing the need for an effective resource management plan to ensure sustainability.

There is also a need to develop a Land Use Plan for Mida Creek accompanied by a Strategic Environmental Assessment to ensure that all ecosystem services provided by the creek are adequately recognized and protected.

It is recommended that a detailed assessment on the value of other ecosystem services such as carbon sequestration and tourism in the current and future states be carried out on Mida Creek to establish the full value of the Creek under future scenarios.

Acknowledgements

The authors thank the Kenya Wildlife Service for allowing the research to be carried out in a forest reserve. Special thanks to the people of Mida Creek for their time and cooperation during the survey. Thanks to Benjamin Karisa, John Khonde, David Fondo, Ali Kibwana and Dickson Mizinga of Dabaso Creek conservation group for their assistance with data gathering. Thanks to Ben Mwangi for his assistance with the GIS analysis.

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Nematodes as bio-indicators of physical disturbance of marine sediments following polychaete bait harvesting

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Abstract

Sediment disturbance in marine environments is caused by activities including polychaete bait harvesting, trawling, dredging, sediment erosion and treading. These activities affect the benthic communities by changing the densities, community assemblage and diversity. The aim of this study was to evaluate the potential of nematodes as indicators of sediments disturbance following polychaete bait harvesting. The study was conducted in three sites experiencing different bait harvesting intensities in Mida Creek, Kenya. Sediment samples were collected from the mudflats during low tide, preserved in 5% formalin and transported to the laboratory for processing and identification of nematodes. The highly disturbed site recorded the lowest nematode genus richness while the less disturbed sites had the highest. Overall, the most abundant nematode genera in the non-disturbed (Dabaso) and less disturbed sites (Kirepwe) were selective deposit feeders (*Spirinia* and *Terschellingia)*, while most disturbed sites (e.g. Mayonda) had predators/omnivores (*Pheronus, Aporcelaimellus*) and selected members of the genus *Spirinia*. The disturbed site was characterised by low nematode diversity (H') and low dominance (D) while the non-disturbed and less disturbed sites had higher diversity and dominance. Clearly, nematode community assemblage, diversity and feeding guilds changed following disturbance to a low diversity that favoured higher proportions of predator/omnivore taxa.

Keywords: bait harvesting, meiofauna, nematodes, biomonitoring, Mida Creek, Kenya

Introduction

Mangrove forests occur within the intertidal zones and are economically and ecologically important ecosystems especially to coastal communities in developing countries. The forests provide building materials, fuel wood, herbal medicines, carbon sequestration, coastal protection and reduce sediment erosion (Lee *et al,* 2014). Ecologically, the ecosystem is important as nursery (Gajdzik *et al.,* 2014; Sheaves *et al,* 2015) and feeding grounds for many offshore fish (Lugendo *et al.,* 2007; Fry and Ewel, 2010). Mangrove ecosystems are also important fishing grounds (Kihia *et al.,* 2015), especially for artisanal fishers as the forest provides food and shelter for fish (Hutchison *et al.,* 2014). However, being close to the shoreline and easily accessible to humans, the ecosystem is rendered vulnerable to anthropogenic impacts such as poor harvesting methods and overexploitation of these coastal resources (Glaser *et al.,* 2003). In addition, no regulations exist on the harvesting of non-woody products such as crabs, shrimps, fishing baits, ornamental fish etc. (Linneweber, 2002).

Harvesting fishing bait from the mangrove forests and the adjacent mudflats is a common practice among artisanal hook and line and trap fishers that provides cheap and readily available bait. Bait harvesting, though very important and prevalent in coastal

http://dx.doi.org/10.4314/wiojms.v19i2.9

areas, is unregulated and uncontrolled (Watson *et al.,* 2016). Most fishery stakeholders consider the bait fishery as less harmful compared to net fishing (personal observation). Nevertheless, bait harvesting that involves collection of invertebrates such as gastropods and crabs from the mangrove forest floor or digging of various polychaete worms from sediments may be equally harmful because of its effects on target and non-target organisms (Watson *et al.,* 2007). Digging for worms using a stave (*jembe*) within the intertidal mud flats causes continuous disturbance of the sediments and the benthic fauna community. Due to a lack of studies elucidating impacts of the practice on benthic epi- and in-fauna and the consequence to the coastal ecosystem integrity, regulations controlling the bait fishery are difficult to develop. Thus, the focus of this study was to collect data and information that could inform policy development on this type of fishery and in particular polychaete bait harvesting.

Meiobenthos are normally very diverse and abundant in mangrove sediments due to the complexity of the habitat (Pinto *et al.,* 2013) and the densities can reach up to 2000 ind.10cm^{-2} (Xuan *et al.,* 2007). Physical disturbance of the sediments is known to interfere with the assemblages because of the permanent association of the community with the substrate (Sun *et al.,* 2014). Nematodes are normally the most abundant meiofauna taxon and have been recognised as the best candidate for ecological health assessment (Semprucci *et al.,* 2015). Schratzberger and Warwick (1998) demonstrated that nematodes are sensitive to physical disturbance where diversity varied depending on level of disturbance. This study was carried out to investigate the potential of nematodes as an indicator of disturbance following polychaete bait harvesting on an intertidal mud flat. The information will inform policy development related to the bait fishery and in particular harvesting of polychaetes from the sediments.

Mida Creek in Kenya was selected for the study because the fishery (bait collection and fishing) was intense. The creek supports the local human communities by providing a livelihood in the form of the fishery, building material, medicine, and fuel wood, among other mangrove forest resources. The creek and the larger Watamu Marine National Park are an important tourist destination for local and international tourists due to the rich biodiversity, wonderful beaches and warm temperatures. This rich biodiversity is however threatened by the excessive bait collection from the forest floor and the mud flat. Bait in the form of hermit crabs (*Clibanarius spp*) and gastropods (*Terebralia palustris*) are collected from the mangrove forest while polychaetes (*Marphysa mosambica*) are dug out from the mud flats (Kihia *et al.,* 2015, 2016). Digging of polychaetes entails churning of sediments continuously and thus interfering with the benthic fauna including nematodes.

Materials and methods

Study area

The study was carried out at Mida Creek in Kilifi County, Kenya. The creek is located 100 km north east of Mombasa and about 15 km from Malindi town. It is a mangrove-forested creek covering an area of 32 km^2 bordered by Arabuko Sokoke forest landwards and Watamu Marine Park towards the sea. The area is gazetted as a nature reserve and a UNESCO-MAB reserve managed as a national reserve by the local communities. The creek has mangrove forests composed majorly of *Rhizophora mucronata* and *Ceriops tagal* (Alemayehu *et al.,* 2014) and other species in lower abundances. Where mangrove zonation is present, the landward species is mainly *Avicennia marina* followed by a mixed *Ceriops tagal*, a mixed *Rhizophora mucronata* and *Bruguiera gymnorrhiza* zone, and finally *R. mucronata* and *Sonneratia alba* zones of pure stands (Dahdouh-Guebas *et al.*, 2002). The creek is one of the most important bird areas in Kenya supporting at least 60 % of the total numbers of birds along the Kenya Coast (Seys *et al.*, 1995). There is also high diversity of crabs associated with the diversity of mangrove species (Dahdouh-Guebas *et al.*, 2002). Benthic fauna such as crabs and molluscs form the major diet of birds in this area and a resource for the local human community either as food or fishing bait.

Three sampling sites (Dabaso, Kirepwe, Mayonda) were identified for this study based on the level of bait harvesting as a proxy of disturbance; that is, low, moderate and high harvesting effort coinciding with low, moderate and high disturbance (Fig. 1).

Dabaso, considered low disturbance (low harvest), is located on the eastern edge of the creek (S 15°03 20.53´: E 039°59.23´). It has a zone with large mature mangrove forest of *Rhizophora mucronata* next to a zone of mixed forest of *R. mucronata*, *C. tagal* and *B. gymnorrhiza*. There was bait (hermit crabs and mangrove whelks) collection on the forest floor but no digging for polychaetes on the mudflat was observed. This zone enjoys some form of Participatory Forest

Management (Frank *et al.*, 2017) which helps in the control of the activities that take place in the mangrove, unlike the other two sites. Therefore, the station was selected as a control site and sampling was done on the mudflat next to the mixed forest.

Kirepwe, considered moderately disturbed (moderate harvesting), is an island within the creek off Dabaso (S03*°27.28': E039°58.490').* It is characterized by a narrow fringe of mangrove forest mainly *C. targal* on the eastern side, and an extended mixed forest (*R. mucronata*, *C. tagal* and *B. gymnorrhiza*) on the northern side. There are single species forest stands of *R. mucronata* and *S. alba* on the southern side of the Island. The site selected for this study was the mudflat adjacent to *C. targal* mangrove forest on the eastern side. The site had bait harvesting going on within the mudflat but by only a few (2-3) fishermen per day.

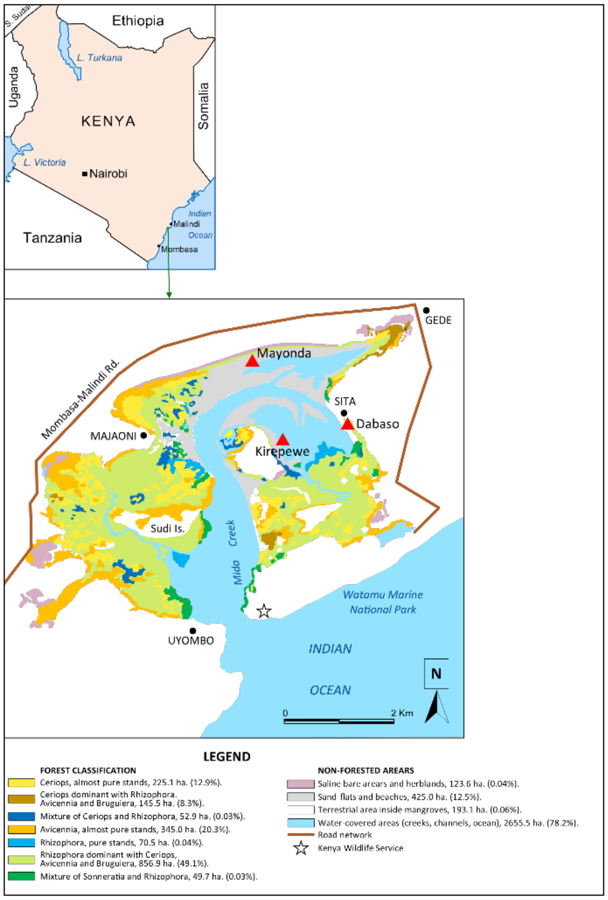

Figure 1. The Kenyan coast and Mida Creek showing the sampling sites of Kirepwe, Dabaso, and Mayonda.

Mayonda, considered high disturbance (high rate of harvesting), is located on the northern side of the creek (S03°19.274': E039°59.098'). In Mayonda the mangrove forest is limited to the high intertidal zone and mainly composed of large trees of *A. marina.* The intertidal mudflat zone was at least 60 m in length and many bait harvesters (7-10 fishermen) could be spotted during the low tide period each day.

Sampling design

Sampling was conducted during spring low tide in November, 2013. Sediment samples were collected from the intertidal mudflat between the mangrove forest and the low water mark during spring low tide for nematodes, grain size and organic matter analysis. Two replicate samples for each parameter were collected from a quadrat along a transect from the mangrove-mudflat zone and every 10 m down towards the low water mark. Due to the difference in the length of the mudflat different number of quadrats were sampled in the different sites. Kirepwe had 2 quadrats (QC to QD), Dabaso had 4 quadrats (QC to QF) and Mayonda had 5 quadrats (QC to QG).

Sample collection

Two replicate sediment samples were collected using a perspex hand corer of 3.6 cm diameter to a depth of 10 cm for each analysis (nematodes, grain size and organic matter). Samples for nematode analysis were immediately preserved in 5 % formaldehyde solution. Samples for sediment organic matter were placed in ziplock bags, carried in a cooler box and put in the freezer on arrival in the laboratory. Samples for sediment grain size analysis were carried in plastic bottles without preservation. All samples were clearly labelled with the date, station, transect and replicate.

Sediment grain analysis

Sediment samples were dried in the oven at 70 °C until no further loss of weight was recorded. The dried samples were gently crushed to loosen the particles and a sub-sample of 100 g from each replicate weighed out for grain size analysis. The samples were sieved using a mechanical shaker through a series of sieves as follows: very coarse sand (2.00 mm); coarse sand (1.00 mm); medium sand (0.5 mm); fine sand (0.25 mm); very fine sand (0.125 mm); and silt (0.063 mm). The proportion of sediment collected on each sieve was weighed and calculated as a percentage of the total sub-sample sieved.

Determination of sediment organic matter

Sediment samples for organic matter analysis were dried in the oven at 70 °C. A sub-sample of 10 g was weighed and burned at 600 °C using a muffle furnace for six hours. The ash-free dry weight was used to calculate the percentage proportion of sediment organic matter in each sample.

Nematode analysis

Sediment samples for nematode analysis were rinsed with tap water over a 1 mm sieve to exclude macrofauna and any other debris, and collected on a 38 µm sieve. The samples were centrifuged three times at 6000 rpms using Magnesium Sulphate ($MgSO_4$) (1.28 g/cm^3 specific density). The supernatant was then rinsed thoroughly with water and put back into labelled sample bottles using 4 % formaldehyde solution and stained with Rose Bengal overnight before sorting. The nematodes were counted with a dissecting microscope at 10 X magnification and 100-200 individuals picked out for identification to genus level. The selected nematodes were processed through step-wise transfer into anhydrous glycerol in order to make permanent slides of the specimens. Identification of the nematodes to the genus level was carried out under a stereo microscope using the key by Platt and Warwick (1988) and Warwick *et al.* (1998). Genera composition and diversity was compared between sites. Nematode feeding guilds by Wieser (1953) that identifies four feeding guilds as selective (1A) and non-selective (1B) deposit feeders, epistrate feeders (2A) and predator-omnivore feeders (2B) were used to analyse the nematode trophic distribution.

Nematode community analysis was carried out using PRIMER version 5 to produce the cluster and MDS for nematode assemblages. The species richness S, Simpson's reciprocal for dominance (1/D), Shannon-Wiener (H') and Pielou's evenness (J) were derived from PRIMER which was also used for community analysis. Analysis of Variance (ANOVA) was carried out using STATA version 15 to check for differences in densities and diversities between sites. Significant difference was considered at $p<0.05$.

Results

Grain size (granulometric) analysis and sediment organic matter

Six sediment grain size categories were encountered in the three sites. The most common sediment grain size was fine sand in all three sites. The median grain size was medium sand in Dabaso and Kirepwe while it was coarse sand in Mayonda. The largest proportion (35 %) of medium sand and the lowest proportion of very fine sand and silt (<5 %) was recorded in Mayonda. Kirepwe had 29 % medium sand, 5 % of very fine sand and silt while Dabaso had the lowest proportion of medium sand (22 %) and the highest proportion of very fine sand and silt (10 %). Consequently, the proportion of the finer grain size (fine sand, very fine sand and silt) was highest in Dabaso (57 %), followed by Kirepwe (53 %), and was much lower in Mayonda (43 %) (Fig. 2).

Sediment organic matter was highest in Dabaso (8.1±7.01 %) followed by Kirepwe 4.1±2.48 % and Mayonda which had 2.6±0.64 %, but the differences were not significant ($F_{2,23}$=4.00 P=0.13) between the sites.

Nematode density

Nematode densities (Fig. 3) ranged between 900±250 ind.10cm^{-2} in Dabaso, 710±210 ind.10cm^{-2} in Mayonda and Kirepwe with 680±240 ind.10cm^{-2}. Although the nematode mean density was slightly higher in Dabaso compared to the other sites the difference was not significant ($F_{2,23}$ = 1.15; p=0.33).

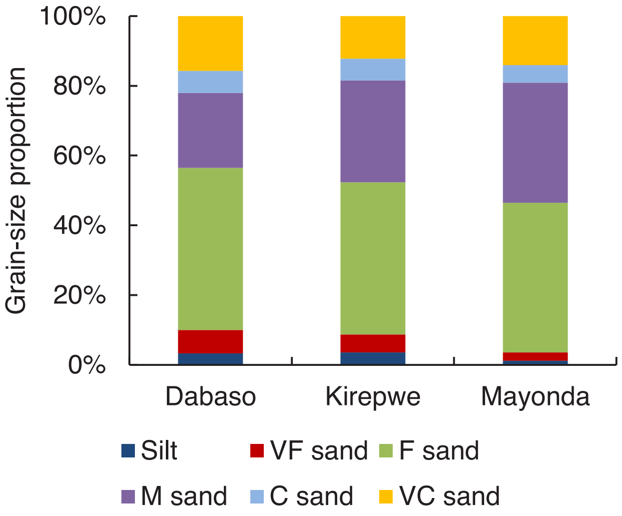

Figure 2. Grain size composition (%) at sites (Kirepwe, Dabaso, and Mayonda) in Mida Creek, Kenya.

Nematode family distribution

A total of 3985 nematode individuals identified yielded 31 families from Mida Creek (Table1). Seven of the families (Comesomatidae, Chromadoridae, Cyatholaimidae, Desmodoridae, Linhomoeiidae, Selachinematidae and Xyalidae) were represented by more than two genera and were present in all the three sites (Dabaso, Kirepwe and Mayonda). The remaining families were represented by one or two genera and were encountered in either one or two sites but not all three, except Anoplostomatidae, Ethmolaimidae, Enchelididae, Haliplectidae and Oncholaimidae. Thus, there were 12 families that were common in all three sites and four to five families that were restricted to only one site. Most of the families represented by a single genus and restricted to only one site had low abundances except Aporcelaimidae in Mayonda that was the second most abundant family in that site.

Nematode genera distribution

A total of 83 putative nematode genera were encountered in Mida Creek. The distribution of nematode genera differed across the stations with Kirepwe (58) having the highest number, followed by Dabaso (46) and lastly Mayonda (34) (Table 1). Only a few genera had relative abundances above 1 % in any of the sites with 12 genera in Kirepwe, 16 genera in Dabaso and 18 genera in Mayonda (Table 1).

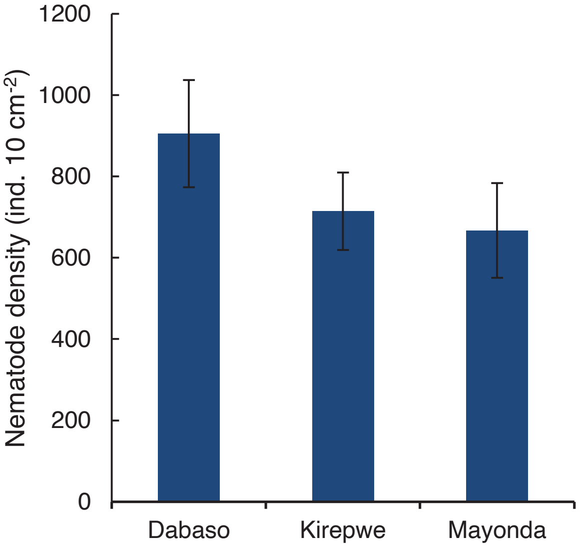

Figure 3. Nematode densities (ind. 10cm^{-2}) at sites in Mida Creek.

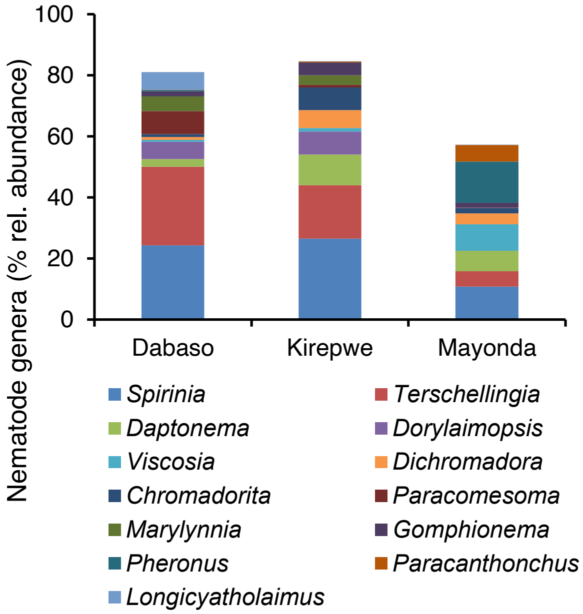

Figure 4. Distribution of the overall most dominant nematode genera in Mida Creek.

The thirteen most abundant nematode genera across all the three stations contributed to 80 % of the total nematode population in Kirepwe and Dabaso and less than 60 % in Mayonda (Fig. 4) indicating a low nematode dominance in Mayonda. Both Dabaso and Kirepwe were characterised by relatively high abundances (>18 %) of the two overall most common mangrove nematode genera (*Spirinia* and *Terschellingia*) and *Dorylaimopsis* at 7.6 % and 5.7 % respectively (Fig. 4). Dabaso however, differed from Kirepwe in having high proportions of *Paracomesoma* (7.5 %) and *Paralongicyatholaimus* (5.8 %). Kirepwe had high proportions of *Daptonema* (10 %) *Dichromadora* (5.9 %) and *Chromadorita* (7.5 %). Mayonda on the other hand, had relatively lower abundances of the overall most common genera, that is, *Spirinia* (10.7 %) and *Terschellingia* (5 %), but high relative abundances of *Daptonema* (6.7 %), similar to Kirepwe (10 %). Clearly, the overall most abundant genera at Dabaso and Kirepwe were relatively lower in Mayonda (Fig. 4).

A comparison of the most abundant genera in each site independent of the other sites showed that Mayonda was dominated by a unique combination of nematode genera; *Pheronus* (13 %) and *Aporcelaimellus* (11.2 %) (Table 1). *Spirinia* (10.7 %) that was highly abundant in the other two sites was only third most abundant in Mayonda. *Aporcelaimellus* (11.2 %) *Pontonema* (8.8 %), *Viscosia* (8.7 %), *Synonchium* (7.4 %), *Haliplectus* (6.8 %) and *Parachanthochus* (5.4 %) had relatively high abundances in Mayonda while they were either totally missing in the other two sites (Dabaso and Kirepwe) or were in very low abundances. Dabaso and Kirepwe were not only similar in having high relative abundance of the overall most abundant genera (*Terschellingia* and *Spirinia*) but they also shared many other genera in common, though at different relative abundances, demonstrating high similarity between the sites (Table 1).

Cluster analysis showed a low similarity (20 %) between nematode communities in the lower intertidal zone in Mayonda (quadrats QE, QF and QG) on one the hand and that in Dabaso and Kirepwe on the other (Fig. 5a). The nematode community in Dabaso and Kirepwe had between 50 % and 70 % similarity. The nematode community from the high intertidal zone (quadrats QC and QD) in Mayonda had a slightly higher similarity (40 %) with the community from Dabaso and Kirepwe. In general, nematode communities from Dabaso and Kirepwe had higher similarity between them (50 % and 70 %) compared to their similarity with Mayonda, at 20 % for the low intertidal zone community and 40 % for the high intertidal zone (Fig. 5a). Among the nematode community in Mayonda high dissimilarity was observed between the different intertidal zones sampled but also between the replicates as they are placed far from each in the nMDS (Fig. 5b). This confirms the relationship observed in the TWINSPAN analysis.

Table 1. Relative abundances (%) and feeding guilds of nematodes at Mida Creek.

Family	Genus	Feeding guild	Dabaso (Low)	Kirepwe (Medium)	Mayonda (Heavy)
Anoplostomatidae	*Anoplostoma*	1B	0.6	0.1	1.3
Anticomidae	*Paranticoma*	1B	-	0.1	-
Aporcelaimidae	*Aporcelaimellus*	2B	-	-	**11.2**
Comesomatidae	*Dorylaimopsis*	2A	**5.7**	**7.6**	-
	Paracomesoma	2A	**7.5**	0.8	0.1
	Sabatieria	1B	0.4	3.4	-
	Pierrickia	1A	0.1	1.3	-
	Comesoma	1B	-	0.9	0.3
	Metacomesoma	2A	-	0.3	-
	Actarjania	2A	-	0.1	-
	Laimella	1B	-	0.1	-
	Hopperia	2A	-	0.1	-
	Paramesonchium	2A	-	0.1	-
Chromadoridae	*Dichromadora*	2A	0.9	**5.9**	**3.6**
	Chromadorita	2A	1.0	7.5	1.7
	Spilophorella	2A	1.7	0.8	1.0
	Chromadorella	2A	-	-	1.0
	Chromadorina	2A	-	0.3	-
	Neochromadora	2A	-	0.2	-
	Chromadora	2A	-	0.1	-
	Graphonema	2A	-	0.1	-
	Trochamus	2A	-	0.1	-
Cyatholaimidae	*Marylynnia*	2A	**4.9**	3.1	-
	Paracanthonchus	2A	0.1	0.3	**5.4**
	Longicyatholaimus	2A	**5.8**	0.1	0.1
	Paralongicytholaimus	2A	-	0.9	-
	Metacyatholaimus	2A	0.5	0.2	-
	Cyatholaimus	2A	0.3	-	-
	Paracyatholaimus	2A	-	0.1	-
	Pomponema	2B	-	0.1	-
Desmodoridae	*Spirinia*	1A	**24.3**	**26.5**	**10.7**
	Desmodora	2A	0.6	0.4	1.1
	Chromaspirina	2A	0.2	-	0.5
	Molgolaimus	2A	0.1	-	-
	Stygodesmodora	2A	-	0.1	-
	Eubostrichus	1A	0.1	-	-
Diplopeltidae	*Campylaimus*	1A	-	0.1	-
Desmoscolecidae	*Desmoscolecidae*	1A	-	-	0.2
Draconematidae	*Draconema*	1A	-	-	0.2
Ethmolaimidae	*Gomphionema*	2A	1.6	4.2	1.5
	Comesa	2A	-	0.4	-

Family	**Genus**	**Feeding guild**	**Dabaso (Low)**	**Kirepwe (Medium)**	**Mayonda (Heavy)**
Enchelidiidae	*Eurystomina*	2A	0.4	-	1.0
	Pareurystomina	2B	0.5	0.1	0.1
Haliplectidae	*Haliplectus*	1A	0.2	0.1	**6.8**
Ironidae	*Pheronus*	2B	0.5	-	**13.5**
	Dolicholaimus	2B	0.1	-	-
Linhomoeidae	***Terschellingia***	1A	25.8	17.5	5.0
	Megadesmolaimus	2A	3.4	-	0.2
	Paralinhomoeus	1B	1.8	0.7	0.1
	Metalinhomoeus	1B	0.1	0.3	-
	Desmolaimus	1B	0.1	-	-
	Didelta	1B	-	0.1	-
	Eleutherolaimus	1B	-	0.1	-
Leptosomatidae	*Metacylicolaimus*	2B	0.3	-	-
Leptolaimidae	*Procamacolaimus*	2A	-	-	0.3
	Cricolaimus	2A	0.1	-	-
Microlaimidae	*Microlaimus*	2A	-	-	0.2
Monoposthiidae	*Monoposthia*	2A	-	0.1	-
	Nudora	2A	-	-	0.1
Monhysteridae	*Monhystera*	1B	-	1.5	-
Oncholaimidae	*Viscosia*	2B	0.7	1.1	**8.7**
	Pontonema	2B	-	-	**8.8**
Oxystomatidae	*Oxystomina*	1A	-	0.2	-
Pandolaimidae	*Pandolaimus*	1B	0.1	-	-
Pharnodermatidae	*Crenopharynx*	2B	0.1	0.1	-
Rhabdonemaniidae	*Rhabdodemania*	2A	0.1	-	-
Selachnematidae	*Synonchium*	2B	0.3	0.1	**7.4**
	Demonema	2B	0.2	-	-
	Gammanema	2B	-	-	0.1
	Halichoanolaimus	2B	-	0.1	-
Siphonolaimidae	*Siphonolaimus*	1A	0.1	-	-
Tripyloididae	*Bathylaimus*	2B	1.3	0.1	-
	Tripyloides	2B	1.1	0.1	-
Trefusiidae	*Rhabdocoma*	1A	-	0.2	-
Tarvaiidae	*Tarvaia*	1A	-	-	0.1
Xyalidae	*Daptonema*	1B	2.5	**10.0**	**6.7**
	Stylotheristus	1B	2.8	0.1	0.8
	Promonhystera	1B	1.0	0.4	-
	Theristus	1B	0.1	0.8	-
	Linhystera	1A	0.1	0.3	-
	Paramonohystera	1B	0.3	0.1	0.1
	Valvaelaimus	2A	-	0.1	-
No. of Genera	Total: 83		46	57	34
No. of Families	Total: 31		20	20	20

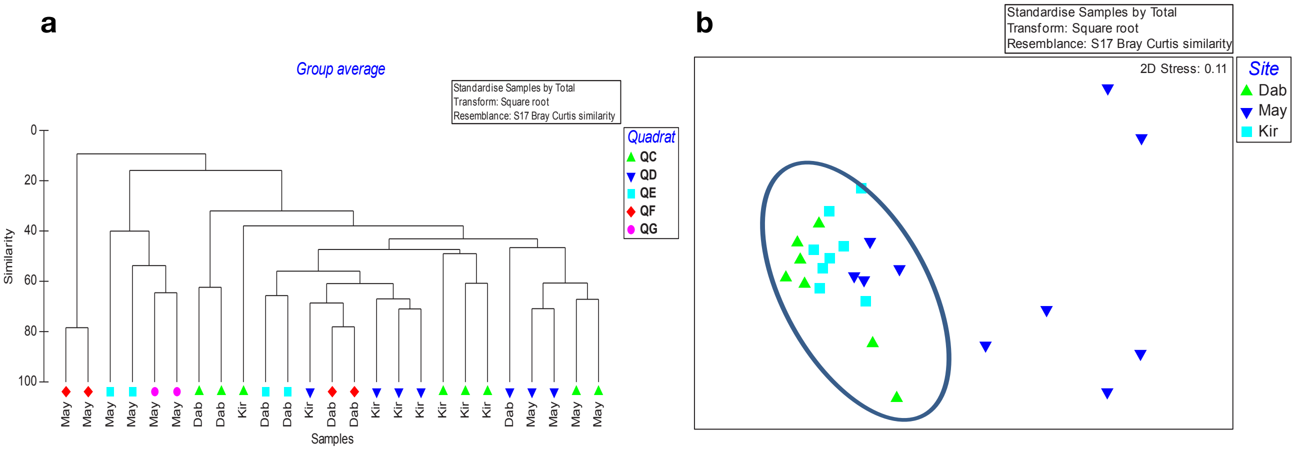

Figure 5. a) Cluster analysis b) nMDS for nematodes showing community assemblages in Mida Creek, Kenya.

Nematode diversity

Nematode diversity based on average number of genera (S) was significantly different between sites ($F_{2,\ 22}$= 6.97, P<0.01) being highest in Kirepwe (17.8±2.2) followed by Dabaso (16.9±1.5) and finally Mayonda (9.8±1.3). The average number of genera in Mayonda was significantly different from that in Dabaso (P=0.022) and Kirepwe (P=0.007). Similarly, Shannon diversity H' was also significantly different between sites ($F_{2,\ 22}$= 6.91, P=0.01). It was significantly lower in Mayonda compared to Dabaso (P=0.017) and Kirepwe (P=0.009). Equally, species dominance was also significantly different between sites ($F_{2,\ 22}$= 7.70, P<0.01) being lower in Mayonda compared to Dabaso (P=0.015) and Kirepwe (P=0.005). On the other hand, the nematode genus evenness was not different between the three sites ($F_{2,\ 22}$= 0.17, P=0.8427) (Table 2). Mayonda displayed generally lower nematode genus diversity compared to Dabaso and Kirepwe.

Nematode feeding guilds

The nematode feeding guilds distribution in Mida Creek was more or less similar in Dabaso and Kirepwe (Fig. 6). The feeding type was dominated by selective deposit feeders at 50 % and 44 %, (in Dabaso and Kirepwe respectively) that was composed mainly of the genus *Terschellingia* and *Spirinia* (Table 1). The epistrate feeders were the next most abundant being 27.4 % and 29.5 % of the community in Dabaso and Kirepwe, respectively, being contributed by the families Comesomatidae (*Dorylaimopsis* and *Paracomesoma*), Chromadoridae (*Dichromadora*) and Cyatholaimiade (*Longicyatholaimus* and *Marylynnia*). The non-selective deposit feeders contributed 2.9 % and 10 % in Dabaso and Kirepwe respectively, with the main genus being *Daptonema* in the family Xyalidae. The predator-omnivores were very low at 1.1 % and 1.2% of the nematode community, respectively. In Mayonda the distribution was different with predator-omnivores being the most dominant feeding guild at 49.8 % of the community and represented by the families Ironidae (*Pheronus)*, Selachnematidae (*Synonchium*), Aporcelaimidae (*Aporcelaimellus*) and Oncholaimidae (*Pontonema* and *Viscosia*). The epistrate feeders composed of 17.8 % of the nematode community being represented by the families Cyatholaimidae (*Paracanthochus*) and Chromadoridae (*Dichromadora*). The non-selective deposit feeders contributed 23.1 % of the community being represented mainly by the family Xyalidae (*Daptonema*). Selective deposit feeders had the lowest proportion of 9.3 % in this site being made up of the families Desmodoridae (*Sprinia*), Haliplectidae *Haliplectus*) and Linhomoeidae (*Terschellingia*) (Table 1).

Table 2. Nematode diversity indices among the sites in Mida Creek.

Indices	**S**	**H'**	**D**	**J**
Dabaso	16.9±1.5	2.6±010	4.5±0.40	0.91±0.01
Kirepwe	17.8±2.2	2.6±0.11	4.7±0.60	0.91±0.01
Mayonda	9.8±1.3	2.0±0.15	2.7±0.34	0.91±0.01

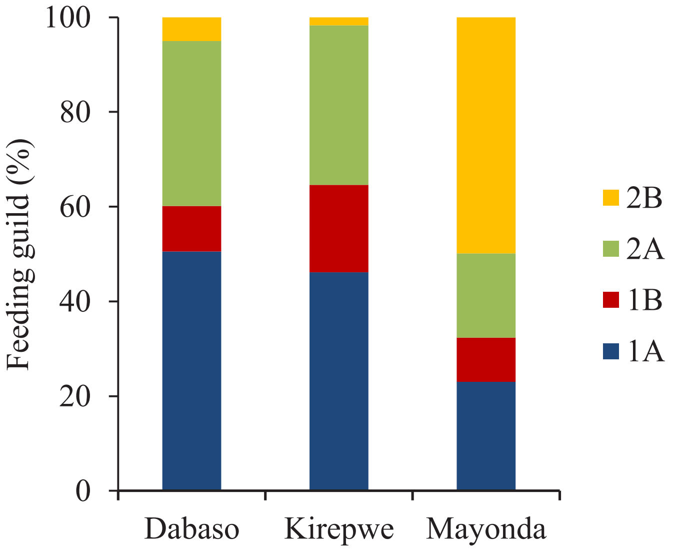

Figure 6. Nematode feeding guilds in Mida Creek.

Discussion

Sediment grain size distribution is a reflection of sedimentary activity that is prone to either erosion or deposition of fine sediments (Yang *et al.,* 2008). Fine sediments tend to get eroded through natural activity like wave action influenced by the set-up of the coastline, or due to human interference involving sediment disturbance (Paik *et al.,* 2008). Presence of cover such as mangrove forest or seagrass bed helps to reduce the sediment erosion by water. A relatively higher proportion of medium sand grain observed in the highly disturbed site, could be an indication of sediment erosion as a consequence of disturbance. Mutua *et al.* (2013) observed that natural and reforested sites in Gazi Bay were rich in silt and clay compared to the degraded site that had higher levels of larger grain sizes. The continuous churning of sediments in the highly disturbed site may have led to continuous removal of very fine sand and silt and retention of medium sand grains. In the moderately disturbed site, there was a lower proportion of medium sand and a higher proportion of very fine sand and silt, while in the low disturbed site there was a high proportion of very fine sand and silt sediments and the lowest proportion of coarse sand recorded. It can be concluded therefore, that disturbance of sediment through bait harvesting has led to change of sediment grain size distribution that favours larger sediment grain size (medium sand, coarse sand and very coarse sand) over the finer grain size (very fine sand and silt).

Although the area under study was a mudflat adjacent to mangrove forests, the lowest sediment organic matter was observed in Mayonda and the highest in Dabaso, while Kirepwe had intermediate values. Continuous sediment disturbance leads to exposure of sediments to oxygen leading to mineralization of organic matter from the sediments. In nature, bioturbation and bio-irrigation by benthic organisms has been shown to cause organic matter mineralization and nutrient recycling (Martinez-Garcia *et al.*, 2015), thus reducing the sediment organic matter. Secrieru and Oaie (2009) modelled total organic carbon (TOC) against grain size and found that presence of TOC was dependent on the presence of fine sediments (very fine sand, silt and clay). It follows therefore, that the presence of a high proportion of large sediment grain size (medium sand) that was observed in the highly disturbed site was associated with low sediment organic matter, perhaps as a result of a high organic matter (OM) mineralization rate. The high rate of mineralization may be influenced by the fact that the highest proportion of sediment organic carbon is found in the top 5 cm of sediment (Chaikaew and Chavanich, 2017) which is being churned continuously and exposing the OM to the air. The high rate of OM mineralization compromises the capacity of the sediments to retain sequestered carbon (Lee *et al.*, 2014). This has serious implications in the face of climate change and associated ocean acidification in the long run.

Nematode densities vary widely in mangrove ecosystems in the world as a response to ecosystem status and other physico-chemical conditions. In a tropical mangrove forest, Netto and Galucci (2003) recorded between 196 ind. 10cm^{-2} and 810 ind. 10cm^{-2} in Brazil, while Xuan *et al.* (2007) recorded between 960 ind 10cm^{-2} and 1758 ind10cm^{-2} in Vietnam. In Gazi Bay, Kenya, Mutua *et al.* (2013) recorded between 800 and 1320 ind 10cm^{-2} in a natural forest and reforested site while the degraded site recorded only 320 ind 10cm^{-2}. In Mida Creek the densities of between 666 and 905 ind 10cm^{-2} observed were slightly lower than the densities observed in the natural forest in Gazi Bay but higher than the densities in the degraded forest (Mutua *et al.*, 2013). This suggests that nematode densities were not significantly affected by physical disturbance of the sediment and that nematode density changes may not be a good indicator of sediment physical disturbance.

Nematode families and genera encountered in most habitats range between 20 and 30 and between 70 and 90 genera in most mangrove environments. Xuan *et al* (2007) recorded 24 families and 80 genera from an intertidal mudflat in a mangrove forest in Vietnam. Netto and Gallucci (2003) recorded 28 families and 86 genera in a mangrove forest in Southern Brazil. In a Northern Brazil mangrove forest Pinto *et al.* (2013) recorded 25 families and 73 genera. Mutua (2016) recorded 24 families and 76 nematode genera from a mangrove forest in Gazi Bay. In this study 31 nematode families and 83 genera were encountered from the three sites with an average number of 20 families per site. The number of families per site was lower than the number encountered in other studies while the total number was slightly higher, perhaps because a total of three spatially separated sites were studied. The total number of genera encountered from the study was within the range of the number encountered in other mangrove sites. However, the highly disturbed site, Mayonda, had less than half (34) the average number of genera from the mangrove environments and this could indicate sensitivity of most genera to sediment disturbance. Indeed, Schratzberger and Warwick (1998) demonstrated that nematode community changed following disturbance.

The potential of nematode as a bioindicator of environmental disturbance is based on the high genus diversity where different assemblages are encountered depending on the prevailing environmental conditions. In nature, nematode community assemblages are driven mainly by nature and availability of food and sediment granulometry (van der Heijden *et al.*, 2018). *Terschellingia* has been encountered in biotopes characterised by the presence of fine sediments (Nanajker *et al.*, 2011) but they easily disappear where there is physical disturbance (Schratzberger and Warwick, 1998). Biological disturbance due to macrofauna activity in the sediments resulted in reduction of both *Terschellingia* and *Spirinia* (Austen *et al.*, 1998). In degraded mangrove sites (deforested), *Haliplectus* and *Terschellingia* were almost absent, but increased in natural and reforested sites (Mutua *et al.*, 2013). In the current study the abundances of selective deposit feeders, *Terschellingia* and *Spirinia,* reduced in the highly disturbed site, while that of *Haliplectus* increased relative to the other sites. In organically enriched muddy sediments *Terschellingia* increased in relative abundances (Moreno *et al.*, 2008) while *Spirinia* has been observed to dominate sediments with high sediment organic matter (Hourston *et al.*, 2009). This suggests that the two genera may be sensitive to sediment disturbance (which resulted in high levels of medium grain size relative to fine sand and silt) while *Haliplectus* may be adapted to physical sediment disturbance but not to ecosystem alteration such as the clear-cutting of the mangrove forest. For the low disturbed and medium disturbed sites, the presence of very fine sand and silt may explain the presence of the two selective deposit feeders in relatively high abundance.

In the sediment disturbed site, the selective deposit feeding nematode community was replaced by omnivore/predator genera that included *Aporcelaimellus*, *Pheronus*, *Viscosia*, *Pontonema* and *Synonchium*. *Pheronus* is in the order Enoplida, and family Ironidae. It is characterized by having two large dorsal teeth and two smaller sub-ventral ones (Smol *et al.*, 2014) that qualify it as a predator known to depend on other nematodes and other small organisms for food (Yeates *et al.*, 1993). The genus *Aporcelaimellus* is in the order Dorylaimida and Family Aporcelaimidae (Santiago *et al.,* 2014). The genus is characterized by a short, thick odontostyle with a wide aperture and feeds on algae, nematodes, nematode eggs, and rotifers (Wood, 1973), and is thus categorized as a predator/omnivore (Yeates *et al.,* 1993). The other genera (*Pontonema*, *Viscosia* and *Synonchium*) are categorized as predators based on buccal morphology and the presence of large teeth. It seems therefore that the nematode community in the disturbed site was characterized by a shift to more predator/ominivore genera (and less selective deposit feeders like *Spirinia*) than the less disturbed and non-disturbed sites. The genus *Viscosia* has been shown to increase in abundance in environments with continuous physical disturbance (Schratzberger and Warwick, 1998), which may be comparable to the continuous disturbance experienced as a result of bait harvesting in this study. It is however, not clear what the driving force may be that caused the increase of the predator/omnivore feeding guild in the disturbed site. The presence and high abundance of an otherwise terrestrial nematode, *Aporcelaimellus*, is also not clear.

The epistrate, non-selective and selective deposit feeders had much lower relative abundance in the highly disturbed site. Schratzberger and Warwick (1999) observed that mud dwelling nematodes tend to be more affected by physical disturbance than the sand dwelling nematodes. Disturbance in this case led to the reduction of the fine sediment and organic matter which may be the reason why deposit feeders were reduced in abundance in the disturbed site. Disturbance which leads to continuous churning of sediments is likely to interfere with growth of benthic algae and diatoms, the main food source for epistrate feeders, and thus leading to their lower abundance. It is however, not clear how predators survived in such high abundances while the likely source of their food (lower trophic feeding nematodes) was in lower abundances. This needs to be researched further.

The nematode community changed from a high number of taxa and high dominance in the less disturbed site to a low number of taxa, low dominance and low taxa diversity in the disturbed sites. The less disturbed site had the highest number of taxa. Intermediate disturbance hypothesis suggests that medium disturbance promotes high diversity as opposed to a relatively stable or highly disturbed community (Weithoff *et al.*, 2001) where refugia exist within a disturbed area and recolonization is faster and diversity is improved (Townsend and Scarsbrook, 1997). Schratzberger and Warwick (1998) observed that intermediate physical disturbance on nematode communities resulted in the highest diversity. This could explain why the site with intermediate disturbance had the highest nematode genus richness. However, increased physical disturbance led to generally low diversity as was observed in the most disturbed site.

Conclusion

Bait harvesting and continuous disturbance of the sediment led to changes in sediment grain size distribution where the proportion of larger grain size increased over the finer ones. Sediment organic matter also reduced in the disturbed station relative to the undisturbed station and a consequent change in the nematode community was observed. There was no difference in the total meiofauna community distribution between the stations suggesting that total meiofauna may not be a good indicator of sediment disturbance.

In terms of nematode community, not only did the diversity differ between the stations but also the assemblage of the genera. Low diversity was observed in the disturbed station that also recorded a different nematode community; thus, nematode community structure can be used as an indicator of sediment disturbance.

It is recommended that the impacts of bait harvesting are investigated further (different baits, different sites) in order to obtain data that can inform policy development to guide coastal resource management.

Acknowledgements

The funding for this research was provided by the Kenyan Ministry of Education, Science and Technology through the National Research Fund.

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Fine-scale habitat use by humpback whales (*Megaptera novaeangliae*) in Zavora Bay, Mozambique

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Abstract

Little is known about the humpback whales (*Megaptera novaeangliae*) of the East-African Coast genetic sub-unit (C1). With an estimated population size of 7000 whales, they demonstrate the resilience of the species after commercial whaling caused population numbers to decline drastically. Zavora Bay, Mozambique offers an ideal observation point of the passage of the whales during their annual migration towards the breeding ground of southern Africa and serves as an operating base to monitor this population. This study aimed at identifying the importance of Zavora Bay as part of this breeding ground and the core regions for humpback whale use within the study area. Results showed the waters off the coast of Zavora are actively used for breeding and do not merely serve as passage towards the wintering habitats. A mother-calf pair separation with a preference for shallower waters closer to shore was observed. Besides depth and distance to shore, slope also proved to have a significant influence on the distribution of adult humpback whales. Increased survey effort and more detailed investigation of the threats to humpback whales within the waters of Zavora are recommended.

Keywords: occupancy, breeding ground, geospatial, GIS, modelling probabilities, habitat use

Introduction

The humpback whale (*Megaptera novaeangliae*) is a cosmopolitan species, found in all oceans except the Arctic (Clapham *et al*., 1999; Smith *et al*., 1999; Andriolo *et al*., 2010). It has one of the largest geographical ranges in the animal kingdom, coupled with a strong annual cycle; summering in prey-abundant high latitude waters, then migrating to tropical and subtropical waters in the winter to breed and give birth (Smith *et al*., 1999; Rasmussen *et al*., 2007; Ryan *et al*., 2013). There are currently 14 different distinct populations of humpback whales worldwide (NOAA, 2018). Individuals observed in the western Indian Ocean belong to the Breeding Stock C (Rosenbaum *et al*. 2009) and in Mozambique, the East-African Coast genetic sub-unit (C1) has an estimated population size of 7000 individuals (Pereira *et al*., 2014).

Up until a moratorium agreed upon by the IWC (International Whaling Commission) in 1982, commercial whaling caused the population of humpback whales to decline to <10% of its estimated original size (Clapham *et al*., 1999; Tulloch *et al*., 2018). The present status of the species is difficult to determine given its wide-ranging nature and the difficulty of providing adequate sampling coverage across ocean basins (Smith *et al*., 1999; Bettridge *et al*., 2015; Gabriele *et al*., 2017). However, humpback whales are proving to be a resilient species showing strong recovery in multiple areas across the globe (Clapham *et al*., 1999; Smith *et al*., 1999; Stevick *et al*., 2003; Gabriele *et al*., 2017; Pavanato *et al*., 2017). Despite these recoveries, humpback whales still face a wide range of threats such as direct killing (Clapham *et al*., 1999; Ryan *et al*., 2013), vessel strikes (Garcia-Cegarra *et al*., 2018),

http://dx.doi.org/10.4314/wiojms.v19i2.10

entanglement (Johnson *et al*., 2005), and vessel-based harassment (Corkeron, 1995; Clapham *et al*., 1999; Andriolo *et al*., 2010; Ryan *et al*., 2013), resulting in lowered genetic diversity. Further, an increase in anthropogenic underwater noise can interrupt normal behaviour, driving them away from areas important to their survival (Au and Green, 2000), impede proper communication between individuals (Fournet *et al*. 2018) and cause permanent damage to their hearing (Ketten *et al*., 1993; Maybaum, 1993).

Identifying ecologically and biologically significant areas is crucial in implementing proper marine spatial planning that facilitates economic activity and combats the degradation of marine habitats or species (Ardron *et al*., 2008; Douvere, 2008; Agardi *et al*., 2011). For large transient marine mammals such as humpback whales, protection of migratory corridors that link breeding and foraging grounds should be a high priority (Berger *et al*., 2008; Douvere 2008; Pendoley *et al*., 2013).

Abundance is a measure often used to assess species' distribution in time and space, but data to estimate abundance can be difficult to collect, require a lot of time and effort and carry a large bias in observational experience (Guillera-Arroita *et al*., 2010; Guillera-Arroita *et al*., 2011, MacKenzie *et al*., 2017). Moreover, data collection for ecological research is prone to a substantial number of challenges, for example, influence of the focus species' behaviour on the data, disruptive methodologies or unpredictable weather events limiting the data collection (Barry and Elith, 2006; Guillera-Arroita *et al*., 2011; Ruiz-Gutierrez *et al*., 2016). Occupancy models that use presence/absence data can assess a population without the need of abundance estimates (Hall *et al*., 2010; Sadoti *et al*., 2013). This is done by analysing the proportion of area, patches, or sample units occupied (Guillera-Arroita *et al*., 2010; Mackenzie *et al*., 2003) and can be used for a wide range of purposes, such as extensive monitoring programmes, distribution, habitat selection, meta-population dynamics, species richness and interactions (MacKenzie *et al*., 2002; Currie *et al*., 2018).

The aim of this study was to investigate the movement of humpback whales (from the C1 population) to and from the wintering habitats of southern Africa and identify specific areas of importance within Zavora Bay. In this context, the objectives were to (i) determine the functionality of Zavora as part of a known breeding ground, (ii) assess which areas were more prone to be visited by the whales, and (iii) identify the different factors driving the absence/presence of the humpback whales within their local distribution by making use of an occupancy model. Identifying habitat preference, as well as the factors influencing their behaviour and choice of habitat, will help to improve long-term conservation and management strategies within Mozambique and along the eastern African coastline.

Material and methods

Study area

The study area is part of the continental shelf, located in Zavora Bay, Inhambane Province, Mozambique (Fig. 1). The survey area was approximately 35 km long and 20 km wide with a maximum water depth of 53 m. The bay has a shallow reef (10–20 m) and a deep reef system (35–65 m) parallel to shore with a predominant sand depression area (15–53 m) between these two reef systems. Yearly sea surface temperature ranges from 21°C to 27°C (Amone-Mabuto *et al*., 2017).

Data collection

Data (i.e. number of individuals and groups, distribution and behaviour) were collected from 2010 to 2018, from June to October by trained volunteers. Land-based observations were made from a dune top ('whale station'), 20 m above sea level, immediately adjacent to and overlooking the study area. The maximum study area and land references were determined by collecting the GPS coordinates of the position of a 9 m long boat when this was just visible from the 'whale station'. Visual surveys were conducted from 07h00 to 17h30. Every half hour, a thorough scan from left to right of the study area was undertaken systematically, using binoculars (NIKON Aculon A211 10x50) to search for visual cues of humpback whale presence.

When a sighting occurred, the time was recorded, as well as the group size (minimum, maximum and best estimate, where the latter was further used for analysis), geographical position on a hand drawn map (based on African east coast Mozambique, 1993), primary behaviour, presence/absence of a calf, and dispersion. To identify between groups, individuals that were >100 m apart were assumed to be from different focal groups. During the sightings, environmental variables were also noted (e. g. wind speed and direction, swell, sea state, cloud cover). If whales were observed outside of the search time, it was recorded as a 'watch' rather than a 'scan' and included all the above listed variables.

Underwater temperature data were collected using two temperature sensors (STAR ODDI – Starmon mini), one on a deep reef at 32 m depth (24°33.944'S 35°16.899E) and one on a shallow reef at 16 m depth (24°28.931'S 35°14.346'E) (Fig. 1). Temperature was recorded throughout the year, with one-hour intervals.

Data analysis

All sighting data from 2010–2018 were used to determine effort. Due to inconsistency in visual surveys (e.g. incomplete coverage of the whale season), only data from 2017 and 2018 (June to October) were used for temporal relative abundance, habitat suitability and occupancy modelling.

For statistical analyses, R 1.1.463 was used (R development Core Team, 2010). All statistical tests were performed at the 0,05 significance level. The 'dunn.test' package was used for non-parametric post hoc tests.

Digitization of drawings

Location of each whale sighting was captured by the observers by plotting their location onto paper maps referenced with land markers. Maps were digitized, georeferenced and analysed using GIS. The JPEG output files were loaded into ArcMAP for georeferencing using GCS_WGS_1984.

Geospatial analysis

Sightings were mapped with ArcMap 10.4.1 and projected onto the UTM zone 36S coordinate system and the study area was divided into 1km x 1km grid cells. Sightings were stratified for mothers with calves and categorized according to presence of a mother with a calf, with or without escorts, and plotted correspondingly in order to identify areas of particular importance for the whales, especially for mother-calf pairs.

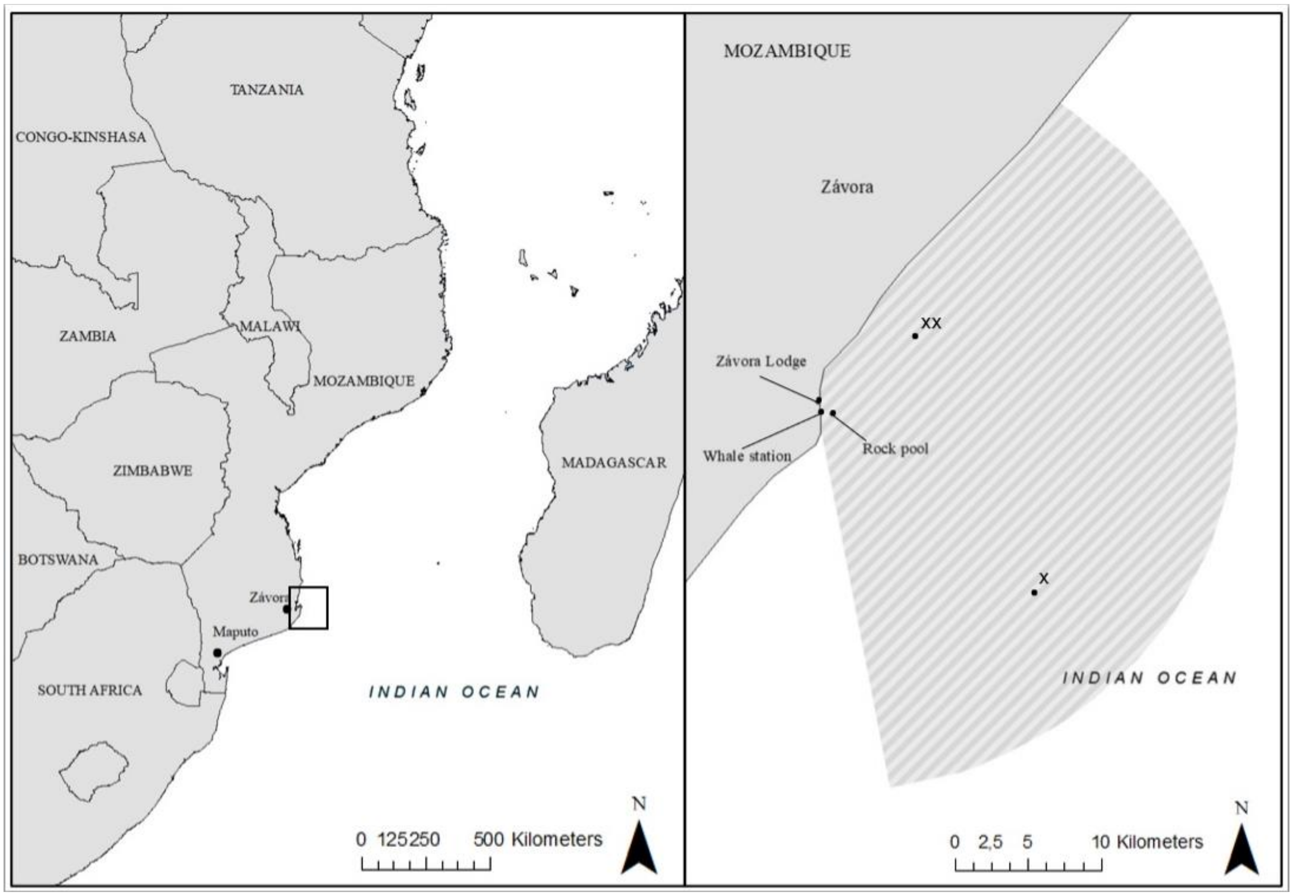

Figure 1. (a) Map of the study area located in the southern part of Mozambique. (b) Close up view of the study area, where the patterned segment highlights the area observed from the 'whale station' (observation point). The total surface covered by this study has a size of 389 km². The south-east border of the area is an approximation as the observations are limited by vegetation and land obstructions. Included are the locations of the temperature sensors (X, deep (> 30 m) and XX, shallow (< 30 m)).

Occupancy model for habitat suitability

Habitat suitability was determined by applying occupancy modelling, which allows for the correction of biases inherent in opportunistic data collection, without requiring distance sampling techniques (Sadoti *et al.*, 2013). The methodology of MacKenzie (2012), MacKenzie *et al.* (2017) and Currie *et al.* (2018) was followed and adapted to the present data.

A standard single species, single season occupancy model was used to allow for the inclusion of multiple covariates and dependent surveys. Assumptions for this model were met and addressed (Table 1).

For the occupancy model, two components were defined as following:

1. Site occupancy (ψ_i) – the probability that a species occupies the sampling site *i*
2. Detectability (p_i) – the probability that a species is detected during survey *j* at site *i*

Both of these were estimated using the logit-link function (Mackenzie, 2006; MacKenzie, 2012; Currie *et al.*, 2018).

Occupancy (probability of whale use) = logit (ψ_i) = ln (ψ_i /1− ψ_i) = $\alpha_0 + \alpha_1 x_{1,i} + \alpha_{2,i} x_{2,i}$

Detection probability = logit (p_{ij}) = ln ($p_{i,j}$ /1− $p_{i,j}$) = $\beta_0 + \beta_1 x_{1,i} + \beta_2, x_{2,i} + \beta_3 y_{1,ij} + \beta_4 y_{2,ij}$

Where: ln is the natural logarithm, x represents site-specific covariates, y represents survey-specific covariates, α and β are the estimated regression coefficients.

Model input was subdivided into survey-specific and site-specific covariates. Each grid cell within the survey area as defined in the geospatial analysis was given a unique ID number, to which these variables were linked. The sequence of these values per survey, per site is called the detection history (h) (MacKenzie and Bailey, 2004; MacKenzie, 2012).

Site-specific covariates

Each grid cell, for future reference referred to as 'site', was characterized by a specific depth. Bathymetry data of the survey area originated from GEBCO, sheet G.08 compiled by the Lamont-Doherty Earth Observatory (LDEO) of Colombia University and was extracted from the GEBCO Digital Atlas published by the British Oceanography Data Centre on behalf of the IOC and IHO (2014). For each site the mean slope, distance from shore, latitude and longitude were included as site covariates.

Survey-specific covariates

Data from 2017 and 2018 were grouped as one single season and the 'year' was included as an additional survey covariate. This allowed for the variance between different years to be accounted for, without addressing the change of occupancy between the two years. Other survey covariates included month of the year and temperature (°C), where temperature was split into a deep (>25 m) and a shallow (<25 m) category.

A Shapiro-Wilk test was used to test for normality of the data. Correlation between variables was assessed

Table 1. Occupancy associated assumptions and measures that were taken to meet these assumptions.

Assumption	Addressed by
The system is closed to changes in occupancy	Output was interpreted as the probability of whale 'use' rather than actual occupancy
Assumption of independence (i.e. the outcome of one survey does not depend on the outcome of another survey)	Inclusion of survey-specific covariates, which account for a so-called 'trap-response' (i.e. species is easier to detect at a site where it has already been detected) (Hines *et al.*, 2010)
Misidentification of humpback whales as a species	Excluded due to the size, nature and known distribution of humpback whales in the area
Assumption of no false positives and (site occupancy) and *p* (detectability) are constant or a function of covariates.*	Modelling was performed with finite mixture (Royle and Link, 2006)

using the Pearson correlation. In cases of non-normality in covariates, the Spearman rank correlation coefficient was used instead.

PRESENCE (Version 2.12.17) (Hines, 2006) was used to develop a candidate set of models to fit the data. First, the procedure was followed for all sightings. Secondly, only sightings with calves were tested to assess mother-calf pair separation.

The best-fit model was chosen based on the AIC criterion (MacKenzie, 2012). The estimated beta parameters from the output were used for completion of the logistic regression equations for both occupancy and detection probabilities. The final outcome displays the factors influencing both detection and occupancy of whales, in this case translated as the suitability for a site to be visited by this species.

Goodness Of Fit (GOF) of the models was assessed using a Pearson's Chi Square test (MacKenzie and Bailey, 2004).

Results

Evidence for Zavora Bay as a humpback whale breeding ground

Summary of effort and whale sightings

A total of 230 surveys were carried out between 2010 and 2018 (Table 2). Sightings were corrected and displayed in sightings per unit effort (SPUE) over time for further use. Higher sightings were found from 2012 to 2014, with 2018 having the lowest SPUE. The highest abundance of mother-calf pairs was recorded in 2013. During all years, the majority of the sightings with a calf were unescorted by adults other than the mother. Detection of pods without calves was highest in the season of 2011 and highest for pods with calves in 2013. However, relative to the observed number of groups, lowest calf abundance was recorded in 2010, followed by 2011.

Relative abundance

Relative abundance varied from a minimum average of 1.6 ± 1.5 animals/hour on the 22 October to the maximum of 25.2 ± 9.5 on 4 August during 2018. In both 2017 and 2018, whale abundance increased early/mid-July and mid/late July, respectively, and decreased at the beginning of September (Fig. 2).

Group size

To calculate group size and number of individuals, each group was only taken into account once per survey to exclude resightings and avoid overestimation of the number of whales present. During the 2017 whale season, a total of 655 groups were sighted, accounting for 1157 individual whales. The mean group size (± SD) was 1.9 (± 1.02) over the entire duration of the season. Within

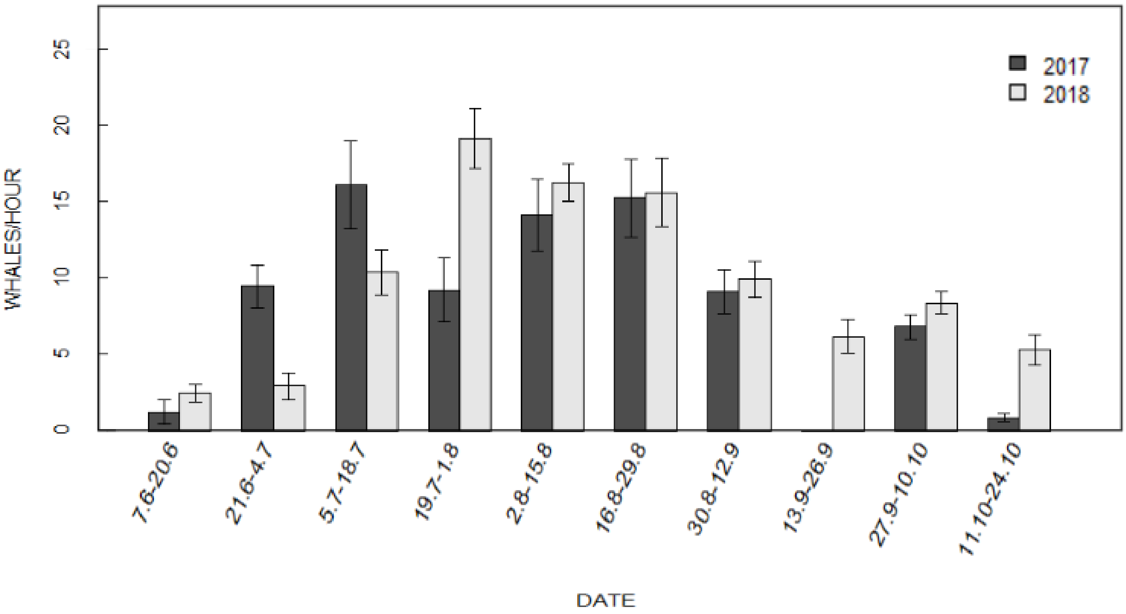

Figure 2. Seasonal changes in relative abundance of humpback whales throughout the 2017 and 2018 season. Relative abundance is represented by the average number of whales seen per hour in each two-week period (error bars represent SD, data corrected for re-sightings of the same individuals within the same hour). The two-week periodicity was chosen in the function of the survey dates, as these were inconsistent throughout the season and a two-week periodicity allowed for a nearly equal distribution of surveys. The alternative (i.e. relative abundance displayed per month), might mask potential patterns over time.

Table 2. Summary of shore-based observation effort for humpback whales at Zavora Bay, Mozambique from 2010 to 2018. Sightings were displayed in absolute numbers within brackets the number of sightings per hour spent surveying (SPUE).

	2010	2011	2012	2013	2014	2015	2016	2017	2018	Total
Effort										
No. of obs. days	14	59	37	23	17	12	17	17	34	230
No. of scans	112	1 347	755	495	339	196	311	284	676	4 515
No. of watches	19	855	666	414	293	71	211	174	146	2 849
First day of effort	4 July	29 June	7 June	3 July	4 August	18 June	4 July	9 June	7 June	
Last day of effort	27 October	30 October	26 October	28 September	27 October	22 August	18 September	29 October	30 October	
Sightings (SPUE)										
No. of whales	347 (5.69)	3 555 (4.80)	4 207 (9.89)	3 626 (13.71)	2 813 (14.39)	707 (6.37)	1 068 (6.40)	1 157 (7.92)	1 059 (3.39)	18 539 (7.65)
No. of groups (n>1)	104 (1.70)	971 (1.31)	1 459 (3.43)	1 260 (4.76)	861 (4.40)	225 (2.03)	304 (1.82)	297 (2.03)	348 (1.11)	5 829 (2.41)
No. of single whales	92 (1.51)	1074 (1.45)	566 (1.33)	492 (1.86)	627 (3.21)	119 (1.07)	337 (2.02)	358 (2.45)	220 (0.70)	3 885 (1.60)
Total	196 (3.21)	2045 (2.76)	2 025 (4.76)	1 752 (6.62)	1 488 (7.61)	344 (3.10)	641 (3.84)	655 (4.49)	568 (1.82)	9 714 (4.01)
No. groups with calf										
Unescorted cow-calf	0.00	67 (0.09)	33 (0.08)	238 (0.90)	177 (0.91)	35 (0.32)	48 (0.29)	90 (0.62)	63 (0.20)	751 (0.31)
Cow-calf pair escorted by one adult	0.00	13 (0.02)	6 (0.01)	114 (0.43)	37 (0.19)	13 (0.12)	12 (0.07)	16 (0.11)	18 (0.06)	229 (0.09)
Cow-calf pair escorted by two or more adults	0.00	7 (0.01)	1 (0.00)	20 (0.08)	8 (0.04)	6 (0.06)	4 (0.02)	5 (0.03)	10 (0.03)	61 (0.03)
Total	0.00	87 (0.12)	40 (0.09)	372 (1.41)	222 (1.14)	54 (0.50)	64 (0.38)	111 (0.76)	91 (0.29)	1 041 (0.43)

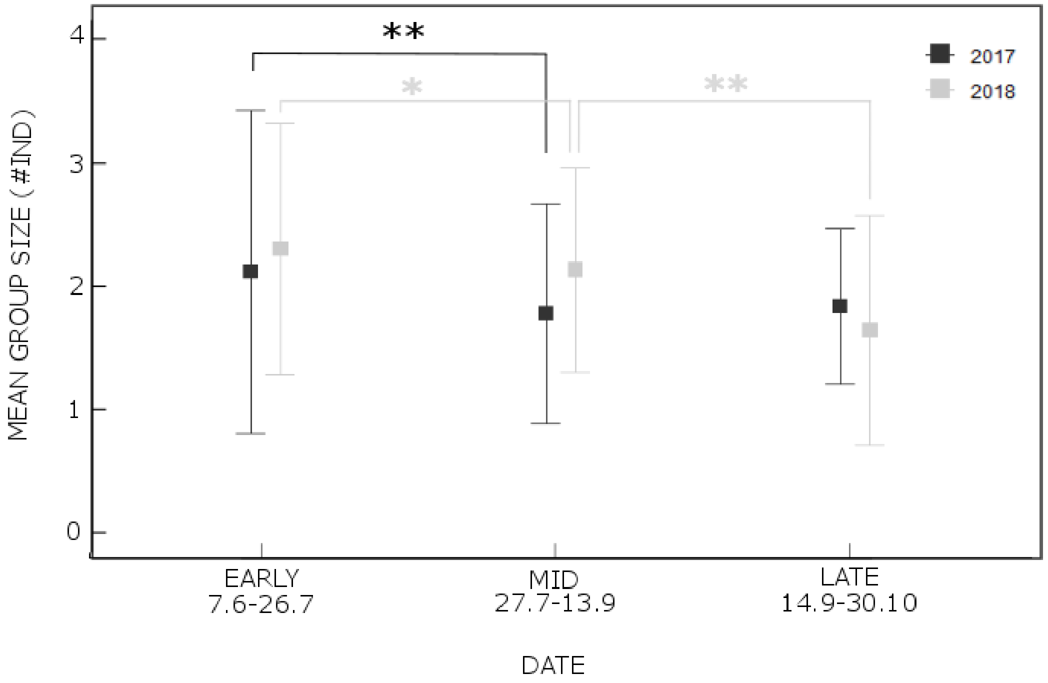

Figure 3. Seasonal changes in mean group size (±SD) for both the 2017 and the 2018 humpback whale season in Zavora, Mozambique. * indicates a significance level of 0.05, and ** indicates a significance level of 0.01.

the year, the mean group size decreased from 2.2 (± 1.3) at the beginning of the season to 1.8 (± 0.9) mid-season (Fig. 3). The mean group size at the beginning of the season was significantly higher than the group size mid-season (Kruskal-Wallis, $p < 0.05$, post hoc = Dunn Test). The difference between mid- and late season showed no significance (Kruskal-Wallis, $p > 0.05$).

In 2018, a total of 568 groups were sighted, accounting for 1059 individual whales. The mean group size was 2.1 (± 0.9) and significantly decreased from 2.3 (±1.0) in early season to 2.1 (± 0.8) mid-season and again to 1.6 (± 0.9) at the end of the season (Kruskal-Wallis, $p < 0.05$, post hoc = Dunn Test) (Fig. 3).

Modal pod size during both 2017 and 2018 was two. Sightings varied from a single individual to a maximum pod size of 10.

Presence of calves

In 2017, a total of 76.84 % of the sightings had 'undetermined' listed for calf presence. Of the remaining 23.16 % of sightings, the calf observations increased from 41.03 % in early season, to 58.82 % mid-season and again to 75.14 % late in the season. For pods with calves, a group of two signifies a mother-calf pair alone. Larger-sized pods indicate that other adult whales known as 'escorts' (Clapham, 2000) were accompanying the mother-calf pair. In the same year, 15.49 % of all sightings consisted of three or more animals. Of all sightings with calves, the most common comprised mother-calf pairs without observed escort presence (81.82 %).

Regrettably, calve presence was not recorded in a standardized manner over the years. For 2018, calf presence was recorded, however calf absence was not. Only 'undetermined' was used when no calf was sighted and thus no percentage of absence of calves could be displayed.

Identification of core areas

In the combined seasons of 2017 and 2018, both from June to October, a total of 52 surveys were conducted. Surveys were split into searches and watches, and since the effort was only consistent within and equal over all 'searches', these were the only sightings used to display the relative distribution of humpback whales (Fig. 4). The searches accounted for a total of 126.66 hours of surveying.

When SPUE included all whales (adults and calves), a north-south gradient indicating passage of the whales through the bay, as well as east-west differences showing increased abundance in areas characterized

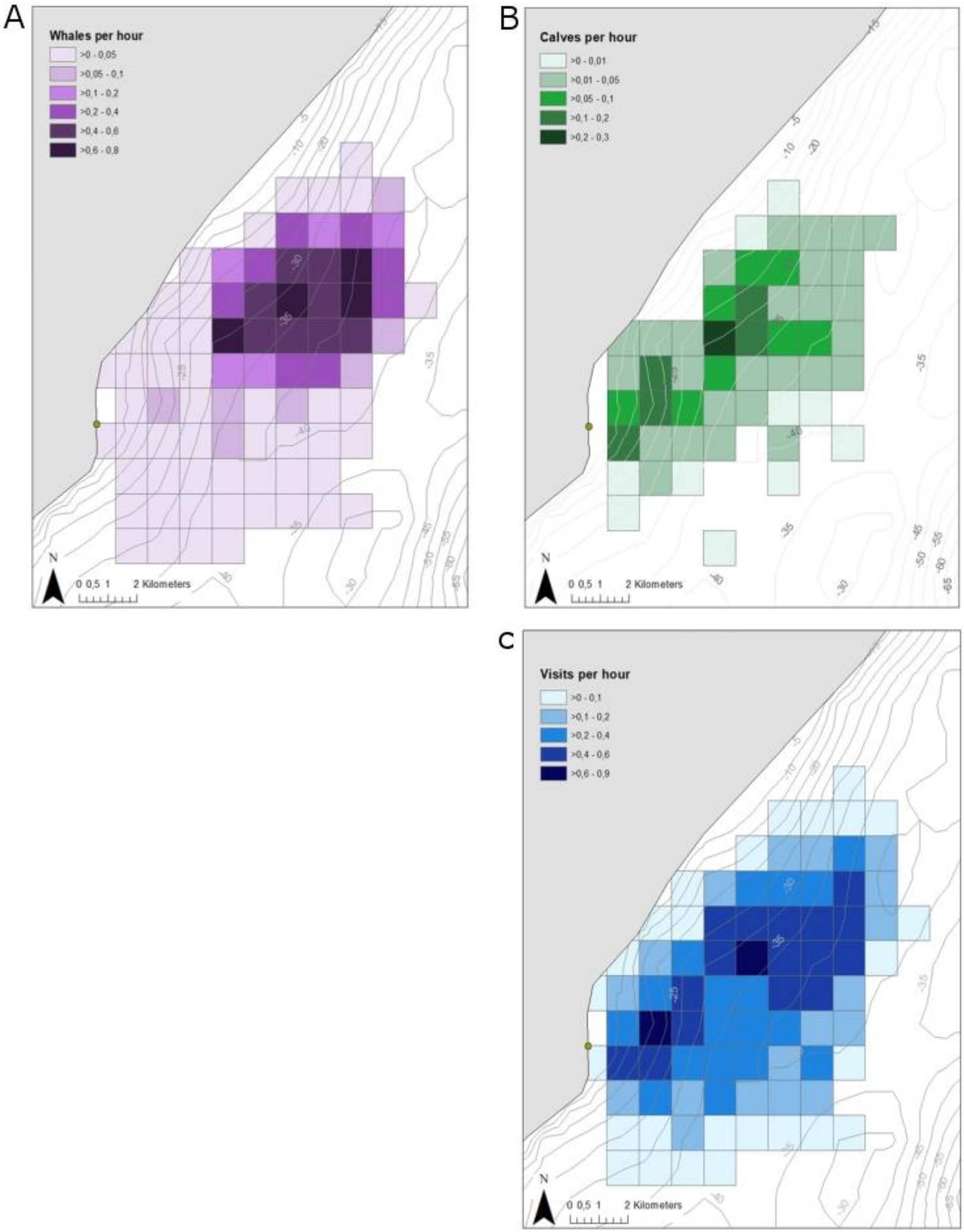

Figure 4. Relative abundance and distribution of humpback whales, with adults and calves combined (a), calves with accompanied mother only (b), and number of visits (presence/absence) per square kilometre per hour of adults and calves (c) in Zavora, Mozambique from June to October 2017 and 2018 combined. White areas lay within the survey area, but no sightings were registered in those parts of the water. The whale station is highlighted with a green dot for reference.

Table 3. Model selection results of detection probability for all humpback whale pods regardless of group size or calf presence/absence; i.e. visits of humpback whales in Zavora Bay in the combined seasons of 2017 and 2018 (June to October). Table values represent model, the change in AIC for the best model (ΔAIC), the Akaike weights (AIC_{wt}) and the number of parameters (K).

Model	K	*AIC*	*ΔAIC*	AIC_{wt}
p(month + year + temp)	5	5115.04	0.00	0.6142
p(year + temp)	4	5115.97	0.93	0.3858
p(month + temp)	4	5140.82	25.78	0.0000
p(temp)	3	5143.74	28.70	0.0000
p(year)	3	5152.25	37.21	0.0000
p(year + month)	4	5153.68	38.64	0.0000
p(.)	2	5185.71	70.67	0.0000
p(month)	3	5186.32	71.28	0.0000

by a depth of 20 to 35 meters was observed (Fig. 4a). When looking at SPUE that only included calf presence, shallower areas and those closer to the shore where of higher importance (Fig. 4b). As the observational experience was not equal over all surveys, bias is decreased by displaying the presence/absence of whales per site (Fig. 4c), instead of abundance over time. This shows that regardless the group size, the whales tend to use parts of the bay within a 10 km radius from shore, within the 35 m depth range.

Drivers of area suitability

All individuals

For the use of the occupancy model, all 2017 and 2018 sightings were grouped together, including those with calves. For all pods considered together, the model including month, year and temperature is ranked highest (Table 3). However, including month only marginally reduced ΔAIC (0.93). To ensure the most parsimonious model was used, the final model included only the survey covariates month and temperature.

The model output can be summarized as follows:

$$\text{logit}\ (All\_whales\ p) = 0.83 + 0.41_{year} - 0.25_{temp}$$

Whereby probability of detection decreases with increasing temperature and progression from 2017 to 2018 increases the detection probability.

Since depth and longitude were correlated (Pearson's product-moment correlation, $p < 0.05$, $r = 0.725$), depth was retained as the biologically most relevant variable for humpback whale distribution modelling and longitude was excluded from the model (Currie *et al.*, 2018).

The model including depth, slope, latitude and distance to shore was ranked highest (Table 4). Including latitude only marginally reduced ΔAIC (0.65). Therefore, the final model selected included covariates for depth, slope and distance to shore.

$$\text{logit}\ (All\_whales\ \psi i) = 1.12 + 0.05_{depth} - 2.31_{slope} - 22.58_{distance\ to\ shore}$$

Distance proved to be the most important variable for determining humpback whale use. Slope also showed a negative relationship in this model, where on the contrary, probability of whale use increased with increasing depth.

Given the output, the individual site estimates of the probability of use (psi per site), standard error and 95 % confidence intervals were provided as a measure of the relative suitability of the site given the model predictions.

To assess the lack of fit of the model, a significance level of 0.05 was used, whereby $p < 0.05$ was evidence of lack of fit (MacKenzie and Bailey, 2004; MacKenzie *et al.*, 2017). The Pearson's Chi-Square Goodness of Fit test showed no lack of fit for the chosen model ($p = 0.9901$). The overdispersion parameter $\hat{c}$ (0.6806) approached the value of one, which confirms the model is an adequate description of the data (MacKenzie and Bailey, 2004).

Table 4. AIC values for occupancy models describing the influence of environmental factors on the occurrence of humpback whale pods regardless of group size or calf presence/absence; i.e. visits of humpback whales in Zavora Bay in the combined seasons of 2017 and 2018 (June to October). Table values represent model , the change in AIC for the best model (ΔAIC), the Akaike weights (AIC_{wt}) and the number of parameters (K).

Model	K	*AIC*	*ΔAIC*	AIC_{wt}
p(year + temp), ψ(depth + slope + distance + latitude)	8	5092.60	0.00	0.3554
p(year + temp), ψ(depth+ slope + distance)	7	5092.71	0.65	0.2568
p(year + temp), ψ(slope + distance)	6	5094.31	2.25	0.1154
p(year + temp), ψ(slope + distance + latitude)	7	5094.50	2.44	0.1049
p(year + temp), ψ(slope)	5	5095.08	3.02	0.0785
p(year + temp), ψ(slope + latitude)	6	5096.63	4.57	0.0362
p(year + temp), ψ(slope + depth)	6	5096.79	4.73	0.0334
p(year + temp), ψ(slope + depth + latitude)	7	5098.46	6.40	0.0145
p(year + temp), ψ(distance + depth + latitude)	7	5101.08	9.02	0.0039
p(year + temp), ψ(depth + distance)	6	5103.90	11.84	0.0010
p(year + temp), ψ(distance)	5	5112.23	20.17	0.0000
p(year + temp), ψ(distance + latitude)	6	5112.45	20.39	0.0000
p(year + temp), ψ(depth)	5	5116.93	24.87	0.0000
p(year + temp), ψ(latitude)	5	5117.85	25.79	0.0000
p(year + temp), ψ(depth + latitude)	6	5118.90	26.84	0.0000
p(.), ψ(.)	2	5185.71	93.65	0.0000

Pods with calves

The model including calf sightings showed that all survey specific covariates (i.e. month, year and temperature) affected the detectability of the whales (Table 5), however including temperature only marginally reduced ΔAIC (0.64 < 1). Therefore, including only month and year gives the most parsimonious model to explain humpback whale calf habitat use.

$$\text{logit}\ (Calf\,p) = -\,0.12 + 0.27_{month} - 0.67_{year}$$

Probability of detection increased from early whale season (June) to late whale season (October). Calf detection is characterized by a negative relationship with progression towards 2018.

The conditional models after model selection of detection probability (Table 6) show that the model including 'depth' and 'distance to shore' is best for explaining the variation in distribution of the calves (ΔAIC = 0.00).

$$\text{logit}\ (Calf\,\psi_i) = -\,0.69 + 0.08_{depth} - 46.16_{distance\ to\ shore}$$

Probability of whale use from calves with pods is characterized by a negative relationship with distance to the shore; the further away from shore, the lower the probability of humpback whale use. This same probability of whale use however increases with depth.

The coefficient of 'distance to shore' for the calf model (46.16) is larger than the one for all sightings combined (22.58) and though the first model also includes calf sightings, this shows a stronger preference of the calves for waters closer to shore.

A Pearson's Chi-Square Goodness of Fit test showed evidence for a lack of fit ($p < 0.05$). There is also more variation in the observed data than expected by the model, as confirmed by the overdispersion parameter ($\hat{c}$ = 5.2281).

Table 5. Model selection results of detection probability for humpback whale pod sightings that include calves in Zavora Bay in the combined seasons of 2017 and 2018 (June to October). Table values represent model , the change in AIC for the best model (ΔAIC), the Akaike weights (AIC_{wt}) and the number of parameters (K).

Model	K	*AIC*	*ΔAIC*	AIC_{wt}
p(month + year + temp)	5	1720.30	0.00	0.5720
p(year + month)	4	1720.88	0.58	0.4280
p(temp + year)	4	1741.30	21.00	0.0000
p(month)	3	1741.77	21.47	0.0000
p(month + temp)	4	1742.25	21.95	0.0000
p(year)	3	1744.50	24.20	0.0000
p(temp)	3	1768.08	47.78	0.0000
p(.)	2	1769.21	48.91	0.0000

Table 6. AIC values for occupancy models describing the influence of environmental factors on the occurrence of humpback whale pod sightings with caves in Zavora Bay in the combined seasons of 2017 and 2018 (June to October). Table values represent model , the change in AIC for the best model (ΔAIC), the Akaike weights (AIC_{wt}) and the number of parameters (K).

Model	K	*AIC*	*ΔAIC*	AIC_{wt}
p(month + year), ψ(depth + distance)	6	1707.78	0.00	0.2827
p(month + year), ψ(depth+ slope + distance)	7	1707.98	0.20	0.2558
p(month + year), ψ(depth + distance + latitude)	7	1708.07	0.29	0.2446
p(month + year), ψ(depth + slope + distance + latitude)	8	1708.83	1.05	0.1673
p(month + year), ψ(slope + distance)	6	1712.89	5.11	0.0220
p(month + year), ψ(slope + latitude + distance)	7	1714.80	7.02	0.0085
p(month + year), ψ(slope)	5	1715.02	7.24	0.0076
p(month + year), ψ(slope + latitude)	6	1716.81	9.03	0.0031
p(month + year), ψ(slope + depth)	6	1716.86	9.08	0.0030
p(month + year), ψ(distance)	5	1717.09	9.31	0.0027
p(month + year), ψ(depth + slope + latitude)	7	1718.58	10.80	0.0013
p(month + year), ψ(distance + latitude)	6	1718.94	11.16	0.0011
p(month + year), ψ(depth)	5	1722.41	14.63	0.0002
p(month + year), ψ(latitude)	5	1722.58	14.80	0.0002
p(month + year), ψ(depth + latitude)	6	1723.96	16.18	0.0001
p(.), ψ(.)	2	1769.21	61.43	0.0000

Discussion

Bias and study limitation

Long-term monitoring programs are critical for understanding population trends to allow effective management measures for conservation. Nevertheless, it is particularly challenging in developing countries and even more in remote locations, where resources and experts are limited. As a result, many small organizations rely on trained volunteers to collect data which may enhance inconsistency in the data. Biases on data collection were mitigated by choosing a simple methodology, in-person training of volunteers prior to surveys, and use of a survey protocol (Lewandowski and Specht, 2014). Nevertheless, sample efforts were variable depending on the availability of volunteers. To calibrate this, for a general view of whale sightings over the years SPUE was applied, while for the determinate occupancy model only data from 2017 and 2018 was used.

Functionality as part of known breeding ground

The results from this study show that the relative abundance of humpback whales in Zavora Bay displays a pattern typical for a breeding ground (Stern, 2009), with an increase in abundance just after the arrival in June, a peak in July, followed by a decrease in September which coincides with the southern migration of the whales. A similar breeding pattern has been observed in known humpback whale breeding grounds in the South Pacific Ocean (Scheidat *et al.*, 2000), the Southern Atlantic (Martins *et al.*, 2001) and the North Atlantic (Mattila *et al.*, 1994). If the study area was merely a location along the migration route and not actively used as a breeding ground, the patterns would have displayed a bimodal distribution with a high number of whales during the migration periods, i.e. June and September (Best *et al.*, 1995; Scheidat *et al.*, 2000).

According to Craig *et al.* (2003), immature animals and late-pregnant females are the first to arrive at the breeding grounds, followed by mature males and non-pregnant females. This induces an increase of modal pod size to two and even three towards the end of the season (Scheidat *et al.*, 2000). This increase in group size is explained by mature males who seek access to reproductively active females and at the same time provide protection against predators, such as killer whales (*Orcinus orca*) (Whitehead and Glass, 1985; Pitman *et al.*, 2015). The observed decrease in mean group size from beginning to mid-season and again towards the end of the season is in contradiction with these patterns. This can partially be explained by the limitations of the 2018 calf data where no distinction between ‘absent’ or ‘undetermined’ was made, likely causing an underestimation of calves. However, the mean group size ranged from 1.6 (± 0.9) to 2.2 (± 1.3) individuals, so whether or not a statistically significant decrease in these values is biologically meaningful is debatable. It is more likely that the group size stagnated to a modal size of 2 individuals and considering that there were groups with up to 10 individuals, the presence of escorts accompanying the mother-calf pairs is patent. Available data on calf presence from 2017 show an increase in calf numbers towards the end of the season. Non-standardized data from 2014 and 2015 also support this finding.

Competitive groups, often associated with breeding seasons and ovulating females, arise due to males seeking access to single mature females (Tyack and Whitehead, 1982; Oña *et al.*, 2017), leading to aggressive surface-active behaviour (Tyack, 1981; Clapham *et al.*, 1992; Kavanagh *et al.*, 2017). Likewise, escorts accompanying a mother-calf pair display a similar array of behavioural events (i.e. breaching, repetitive slapping of the pectoral fins and flukes) in an attempt to protect the rest of the focal group. This form of close-range communication within and between groups (Kavanagh *et al.*, 2017) was observed in Zavora every year.

Additionally, singing was heard on almost every SCUBA dive throughout the season (Cullain, *pers. comm.*). Humpback whale singing is traditionally heard in breeding areas (Oña *et al.*, 2017), although some vocalization patterns have been observed in feeding areas (Vu *et al.*, 2012). Though systematic acoustic research was not conducted, the presence of singers further exemplifies the area as an important reproduction ground, but a further understanding of the song production within the study area is recommended.

Areas of preference and driving factors for habitat suitability

Models are an attempt to simplify complex distributional patterns with a reduced set of predictor variables and contain a degree of bias and mismatch between the predictions and the reality they describe (Barry and Elith, 2006). The occupancy model as described by MacKenzie (2003) is designed to model distributional patterns and accounts for a large part of this mismatch, by allowing for imperfect detection (MacKenzie, 2006). This method provides a flexible modelling framework for the incorporation of both covariate information and missing observations (MacKenzie, 2006).

Detection probabilities were slightly influenced by temperature. This lends support to the hypothesis that humpback whale seasonal migration is driven by energetic demands (Burns, 2010). Calves are born in warmer waters so that they are able to conserve more energy, which can then be used for growth and development, leading to higher reproductive success than if they were born in colder waters (Clapham, 2001; Burns, 2010). Additionally, the year of the survey influenced the detection rate of the whales, which can be explained by the survey effort that was twice as high in 2018 compared to 2017. Though corrected for in the relative distribution maps, this was not accounted for in the model and must be remembered when interpreting the results. Further studies applying a multi-annual approach, with the use of a multi-season occupancy model are recommended and would enable the estimation of colonization, extinction and persistence (MacKenzie *et al.*, 2003). The increased calf sightings with progression towards the end of the whale season (the covariate 'month' is positively related to increased calf observations), can be related to the fact that as the breeding season progresses, more mothers will have birthed their calves, demonstrating temporal segregation (Scheidat *et al.*, 2000; Pack *et al.*, 2017; Trudelle *et al.*, 2018).

Continuing with the model that best explains the detectability of the humpback whales, the probability of occupancy (probability of whale use in this case) was predicted. These results confirm the observations from the distribution maps, where the whales are more or less equally distributed throughout the continental shelf waters. This conforms to what is observed in other breeding grounds (Félix and Botero-Acosta, 2011; Bortolotto *et al.*, 2017; Gonçalves *et al.*, 2018; Trudelle *et al.*, 2018). Areas most often visited by the whales have two parameters in common, namely depth and distance to shore, which are undoubtedly connected to each other (Ersts and Rosenbaum, 2003; Burns, 2010) and have shown to be driving factors for humpback whale distribution (Ersts and Rosenbaum, 2003; Currie *et al.*, 2018; Gonçalves *et al.*, 2018). The limited role of the depth of the bay might be explained by the fact that the bathymetry within Zavora Bay region is not highly complex and only consists of two reef systems with different depths, with no steep gradient separating these areas from each other. This helps to understand why on a fine scale depth plays a rather limited role, but distance to shore has a greater influence, though both variables cannot completely be interpreted independently from each other (Ersts and Rosenbaum, 2003; Burns, 2010). Incorrect recordings of calf sightings might explain the results of the GOF test, in which the overall model including all sightings proved a good fit for the data, where the calf model was not. However, in combination with the mapped distribution, both models identified key trends. One of them being the mother-calf pair separation. The distribution of mother-calf pairs is usually much higher in shallow waters, and simultaneously much closer to shore (Bruce *et al.*, 2014; Mattila *et al.*, 1994; Smultea, 1994; Félix and Botero-Acosta, 2011). This might be biased due to the distance between the observer and the deeper reefs associated with rough sea conditions which might hinder their occupancy and detection due to the size of the calves (Ryan *et al.*, 2013); nevertheless anecdotal boat observation in Zavora does suggest a higher abundance of mother-calf pairs closer to shore. Their distribution might be a strategy to avoid interactions with competitive groups (Martins *et al.*, 2001) or potential predators such as sharks or killer whales (Chittleborough, 1953; Smultea, 1994). At fine spatial scale, this avoidance strategy ensures energetically expensive associations with multiple male groups are minimized. Calves are then protected from accidental injury (Trudelle *et al.*, 2018) in these calm sea conditions and provided with shelter from strong ocean currents (Trudelle *et al.*, 2018). Females have also been shown to decrease their active swimming speed in these sheltering areas characterized by a lower current speed (Trudelle *et al.*, 2016), which allows them to make more localized movements related to the breeding activity (i.e. searching, pairing, mating and resting). The distribution of whales can also be related to the bottom topography (Hastie *et al.*, 2003) since courting males seek deeper waters to avoid collision with the sea floor or reef structures (Mattila *et al.*, 1989), explaining why the slope of the ocean floor influenced occupancy by adult whales in this study. The preference of courting whales for deeper waters explains why escorted mother-calf groups can be found further away from shore compared to unescorted mother-calf pairs as male escorts are assumed to be prospecting for potential mating opportunities (Trudelle *et al.*, 2018).

Preference of mother-calf pairs for near-shore, shallow regions makes them more vulnerable to human related disturbances (Ersts and Rosenbaum, 2003; Félix and Botero-Acosta, 2011; Pack *et al.*, 2017) and the progression of coastal development forces these whales to expand their range to new habitats (Andriolo, 2010). Management should aim to avoid critical human-animal conflicts and protect the habitat important for successful calf rearing (Smultea, 1994). Several action plans for the conservation of marine systems and fisheries of the southwestern Indian Ocean, including Zavora, have been developed in order to establish regional marine protected areas and to implement sustainable coastal management measures (Trudelle *et al.*, 2018). Therefore, the data and conclusions from this research can provide important information on the distribution and habitat patterns of humpback whales in Mozambique and further assist with future regional coastal management plans.

Latitude and longitude were included as site specific covariates, as they are characteristic for each predetermined site and might identify importance of areas based on hidden covariates or variables which were not recorded. Cloud cover, sea state and swell were factors that initially were expected to impact the detection probability of the whales (Findlay *et al.*, 2011), however, earlier research in Zavora (Allen, 2016) shows that environmental variables did not affect the ability to survey whales when sea state is below Beaufort Scale 4, except for the effect of glare – a confounding factor in the ability to detect cetaceans. Therefore, these environmental variables were discarded from the occupancy model. Marine vessel presence was not recorded in a standardized way and therefore not included in the model. It is recommended that data on marine vessel presence as described in Bas *et al.* (2017) is included in future surveys.

Further, investigating different uses of the bay, as well as anthropogenically induced mortalities of the whales could be mapped to identify areas of concern where anthropogenic use conflicts with the humpback whale habitat use. Results from this study show the significance of the area for humpback whales and can be used as a baseline to determine the habitat suitability of regions along the Mozambican coastline for these whales.

Conclusions and future implications

This study attempted to collate all of the existing survey data on humpback whales passing through Zavora Bay, Mozambique, and, for the first time, provide clarification of their habitat choice in these waters. Both reproductive behaviour and the observation of young calves, as well as the pattern of relative abundance throughout the season, provide evidence that the area off the coast of Zavora serves as a reproductive area for humpback whales as part of the larger scale breeding ground of southern Africa. Remaining uncertainties concerning population estimates and breeding ground affinity can be reduced by an increased effort in photo-identification processes and the comparison of catalogues of different sites and regions along the coastline. This is necessary in order to raise understanding of the migration routes and the distribution of breeding grounds throughout the region. For the humpback whales in the Zavora Bay area, a new photo-identification catalog was created (Fluke Matcher V.4.21) using photos assembled through the open resource platform called www.mozwhales.org. However, the current effort in photo-identification remains low and more data is needed to draw adequate conclusions about this population.

Areas characterized by a depth no greater than 35 m, within 10 km from shore are most probable to be used by the whales visiting Zavora Bay. A mother-calf pair separation from other adult pods was observed, with a preference for waters closer to the shore. Model outcomes predict the detection rates to be determined by temperature of the water, year and month. Considering the possibility of imperfect detection, depth and distance from shore were identified as main factors determining the suitability of the sites in the bay. After optimization of the model, these findings can be used to project to surrounding areas and further map the distribution of humpback whales. This macroecological study is the first to provide baseline information on the spatial distribution and habitat preferences of humpback whales in Zavora Bay. Further research to enhance our knowledge on priority areas for protection, management and conservation measures is recommended.

Acknowledgements

We thank Zavora Marine Lab and all their volunteers, interns and research assistants who dedicated their time to collect data for this manuscript. Gratitude goes out to the IMBRSea for granting the opportunity of performing this research as part of their educational program. We thank S Elwen, associated with the Namibian Dolphin Project for providing helpful tools and support in the initial phase of statistical analysis. Thank you to A Hanusch for her helpful remarks on the manuscript.

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Stock assessment of the Tigertooth croaker, *Otolithes ruber* (Bloch & Schneider, 1801) from the commercial prawn trawl fishery by-catch in coastal Kenya

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Abstract

Commercial bottom prawn trawling has been reported to generate a higher proportion of by-catch of up to 70% in Kenya. The Tigertooth croaker, *Otolithes ruber* is one of the species caught in large quantities as commercial by-catch and also by artisanal fishers. This has led to growing concern that the species could be at risk of over-exploitation. The purpose of this study was to carry out a stock assessment of *O. ruber*. Stock assessment parameters were estimated using ELEFAN with the generic algorithm as included in the R package TropFishR. The length-converted catch curve and the length-based yield per recruit model were employed. The exploitation rate (F/Z = 0.71) indicates that the stock is overfished based on the length-converted catch curve. The current fishing mortality (F = 2.3) based on the catch curve is larger than the reference level (= 1.1) based on the yield per recruit analysis and also indicates that the stock is overfished (= 2.09). To reverse the current trend of exploitation, improved management of the stock is required, which should include further studies on other by-catch species and the generation of data to capture the whole fishery for a better estimation of stock status.

Keywords: *Otolithes ruber*, data-limited, Malindi-Ungwana bay, Kenya, exploitation

Introduction

The Tigertooth croaker, *Otolithes ruber* (Bloch & Schneider, 1801), is a demersal fish species belonging to the family Sciaenidae and is widely distributed throughout the Indian Ocean along the east coast of Africa and the west Pacific ocean (Brash and Fennessy, 2005; Froese and Pauly, 2019). They inhabit warmer (26 °C – 29 °C) marine and brackish waters and are found over sandy and muddy substrates and river mouths at depths of 10 – 40 m (Eskandari *et al.*, 2012; Farkhondeh *et al.*, 2018). Previous studies have reported on some aspects of the biology of *O.ruber*, reporting a maximum and common length of 90 cm and 40 cm (TL), respectively (Froese and Pauly, 2019; Sousa and Dias, 1981). Length at first maturity of *O. ruber* was estimated to range from about 22 cm to 40 cm (TL) (Fennessy, 2000). Studies by Eskandari *et al.* (2012), from the Northwest Persian Gulf in the south of Iran, reported a size at maturity range of between 30 to 40 cm (TL). In both India and South Africa, the species has been reported to mature at a comparatively smaller size, ranging between 22-24 cm (Brash and Fennessy, 2005). Mature females have been found to occur throughout the year, suggesting prolonged and continuous spawning activity (Santhoshkumar *et al.*, 2017; Velip and Rivonker, 2018). *O. ruber* are mainly carnivores with adults feeding on fishes, prawns and other invertebrates (Froese and Pauly, 2019).

In most of the southwest Indian ocean countries, for example, South Africa, Mozambique and Tanzania, *O.ruber* is caught as by-catch from Panaeid prawn

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trawlers (Fennessy, 2000; Schultz, 1992). In addition, the fish is also targeted by recreational hook and line fishers in South Africa and by gillnet and beach seine artisanal fishers in Mozambique and Tanzania (Olbers and Fennessy, 2007). Similarly, in Kenya, *O. ruber* is mainly caught as by-catch on prawn trawlers (Munga *et al.*, 2014), and by artisanal fishers using gillnets, prawn seines and handlines (Mwatha, 2002; Omukoto *et al.*, 2017).

It is well known that *O. ruber* is caught in large numbers, but since it is rarely studied, very little is known about the status of the species. This raises the question of whether the stock is being overexploited or being sustainably fished. Studies by Olbers and Fennessy (2007) have shown that though the species is not a principal target for most fisheries, the vast quantities of small individuals discarded due to its low economic value makes it particularly vulnerable to overexploitation. Similar observations have been found off Malindi-Ungwana Bay in Kenya where juveniles of *O. ruber*, *Johnius sp.* (both Sciaenidae), and *Pomadasys sp.* made up to 25 % of the by-catch by mass (Munga *et al.*, 2014). This implies that the local artisanal fisheries, which rely on the resource as a source of livelihood, are impacted.

Information on the status of exploited fish stocks is vital for making fisheries management decisions (Melnychuk *et al.*, 2017). Traditionally, such information is derived from stock assessment models, which are often data-intensive and complex, rendering them unsuitable for data-limited fisheries (Prince and Hordyk, 2019; Wang *et al.*, 2020). Even in the presence of a routine data collection system, often there is a lack of long time-series data, and often, the data is aggregated, limiting the use of stock assessment models (Chrysafi and Kuparinen, 2015). Over the past decade, a number of data-limited assessment methods (DLMs) have been developed to assess data-limited stock status (Dowling *et al.*, 2019). Given that for most data-limited fisheries length-frequency data from commercial catches tend to be the primary data type available, most of the DLMs are length-based, which has made it possible to assess the population parameters of exploited fish stocks in tropical waters (Chong *et al.*, 2019; Rudd and Thorson, 2017).

The present study is the first attempt to assess the stock status of *O.ruber*, a by-catch species from the prawn trawl fishery in Malindi-Ungwana Bay. Most studies have predominantly focused on the assessment of target and commercially important species, but the assessment of by-catch species is mostly ignored, and as a result, very little is known about their status (Cook and Heath, 2018). In this study, we explore the use of the most widely used non-parametric length based approach, the Electronic Length Frequency Analysis (ELEFAN) (Pauly, 1987; Pauly and David, 1981), to estimate growth and mortality parameters of *O. ruber* to provide management advice for their sustainable exploitation in the fishery.

Materials and methods

Study area

The prawn trawling fishery in Kenya is carried out in Malindi-Ungwana Bay, between latitudes 3°30'S and 2°30'S and longitudes 40°00'N and 41°00'N (Fig. 1). The area is considered one of the most productive fishing grounds along the coast due to its wide continental shelf (extending between 15 and 60 km offshore) relative to other parts of the Kenyan coastline. In addition, the bay is influenced by the inflow of the rivers Tana and Sabaki, which carry sediments resulting in a vast stretch of sandy beaches and dunes made up of terrigenous sediments. The bay is shallow with a mean depth of 12 m during high spring tide at 1.5 nm and 18.0 m at 6.0 nm offshore, respectively. The depth increases rapidly to 100 m after 7 nm and generally decreases northwards. Due to its bathymetry, environmental characteristics and topography, Malindi-Ungwana Bay has the highest concentrations of shallow water prawns on the Kenyan coast with several semi-industrial prawns trawling in the area.

The bay is influenced by two dominant offshore current regimes: the Northeast Monsoon (NEM) and the Southeast Monsoon (SEM). During the SEM, which occurs between April and October, the current circulation is dominated by the northward flow of the East African Coastal Current (EACC). During this season, the bay also receives the most substantial river discharge from the rivers Tana and Sabaki (Kitheka *et al.*, 2005). During the NEM, between November and March, the northward-flowing EACC meets the southward flowing Somali Current to form the Equatorial Counter Current, which flows away from the coast of the Indian Ocean (Jacobs et al., 2020). During the NEM, the ocean waters in nearshore areas have higher salinities than during the SEM due to low precipitation and reduced river discharge compared to the SEM period. Prawn fishing and production are higher during the SEM.

Sampling

Length data for *O. ruber* was collected by trained scientific observers on-board 3 shallow water (5 – 40 m) prawn trawlers during the trawling season of April - October for 2016, 2017 and 2018. Data collection followed documented trip instructions and designated sampling protocols adopted from the Southwest Indian Ocean Fisheries Project (SWIOFP) Observer Program Data Collection Guide, 2012. Specifically, the trip instructions included: Capturing vessel and trip information, recording of the gear characteristics, collecting and recording the catch and fishing effort information which entails start and end time of haul, positions, depth, target catch, by-catch, discards, catch composition, mitigation measures and environmental interactions (TEDs, PETs, large by-catch, e.g. sharks and fate of these species). The sampling protocols used for catch composition determination was as follows: First, large-sized fish samples were stored before being processed and the catch divided virtually into random sample portions of 30% to a maximum of 20 kg from the catch (1 portion). Samples were then sorted to species/family level, total weight and numbers for each species/family observed in the sample was recorded,

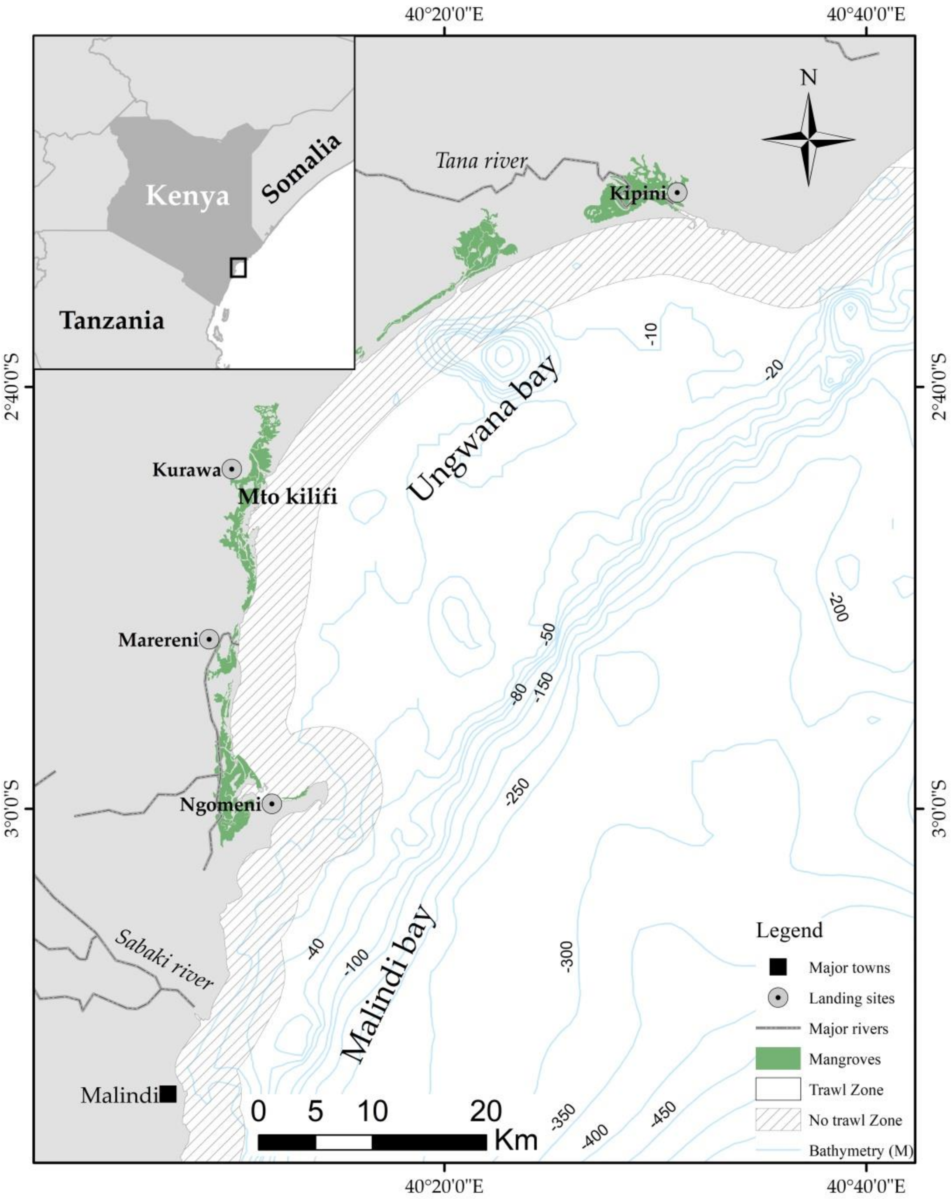

Figure 1. Map of Kenya (inset) and the Kenyan coastline showing the location of Malindi and Ungwana Bays and the Sabaki and Tana rivers.

and individual total length was measured to the nearest mm using a standard measuring board.

This data collection was part of the annual observer deployment programme that commenced in 2016 to contribute to fisheries management of panaeid prawns and associated by-catch.

Data Analysis

Length frequency catch data (LFCD) of *O.ruber* from 2016 to 2018 was pooled and converted to quarterly catches with the assumption that the samples were representative of the total catch of the month (Abobi *et al*., 2019). The ShinyTropFish (version 0.9.1) based on the TropFishR package (version 1.7.0; Mildenberger *et al*., 2017) was used to assess the status of the species by estimating the growth and mortality parameters from modal progression and catch curve analysis using the ELEFAN_GA function (Taylor and Mildenberger, 2017).

To generate a confidence interval around the estimated growth parameters, the updated version of the TropFishR with bootstrap functionality was used to fit the growth curve to the length-frequency catch data (LFCD) (Pauly, 1987; Pauly and David, 1981; Schwamborn *et al*., 2019).

Estimation of Growth Parameters

The Von Bertalanffy's growth parameters (VBGP) (von Bertalanffy, 1938), that is, asymptotic length (L∞) and growth constant (K), were estimated using the length-frequency catch data (LFCD) in TropFish. This was done by applying the seasonalised von Bertalanffy's growth function (VBGF) to the length-frequency catch data (LFCD) (Somers, 1988).

An updated version of the Electronic Length frequency Analysis (ELEFAN) (Pauly, 1987; Pauly and David, 1981; Schwamborn *et al*., 2019) was used to fit the growth curve to the length-frequency catch data (LFCD). For optimum search and improvement in the accuracy of the growth parameters L∞ and K estimation, the LFCD was binned according to the maximum body length observed for the fish species (Wang *et al*., 2020).

$$\text{Optimum bin size (OBS)} = 0.23 * \text{Lmax}^{0.6}$$

An initial seed value of L∞ was estimated based on the mean of the 1 % of the largest observed individual in the sample (Lmax) following the formula by Pauly (1984):

$$\text{where } L\infty = \text{Lmax}/0.95$$

The growth performance index (Φ') (Pauly, 1984), was used to compare growth parameters.

The estimated potential longevity $t_{\max}$ of *O.ruber* was computed from the formula (Pauly, 1980; Taylor, 1958):

$$t_{\max} = 3/K$$

Mortality Parameters

The instantaneous total mortality rate (Z) was computed from the LFCD based on the linearized length-converted catch curve (LCC) (Pauly, 1983).

Given the importance yet difficulty in reliably estimating the natural mortality (M) (Jørgensen and Holt, 2013), an updated version of the Pauly (1980) growth-based method was applied (Then *et al*., 2015):

$$M = 4.118K^{0.73}L\infty^{-0.33}$$

This approach is preferred over other empirical formula used to estimate natural mortality (M) given that it resulted in better prediction power from meta-analyses of more than 200 fish species of different life histories (Then *et al*., 2014). The rates of fishing mortality (F) and exploitation rates (E) were calculated based on the relationship:

$$F = Z - M \text{ and } E = \frac{F}{Z}$$

where Z is the total mortality, F the fishing mortality, and M is the natural mortality.

Probability of capture

The probability of capture was estimated based on the ascending left arm of the length-converted catch curve (Pauly and Munro, 1984). Primarily, the method entails the backward extrapolation of the right, descending left arm of the catch curve in each length class. The probability of capture is obtained by dividing, for each length-class, the numbers caught (N) by the numbers available (N/P), resulting in a curve from which the length at first capture Lc can be estimated (Pauly, 1987).

Yield per recruit

The length-based yield per recruit model (YPR) by Thompson and Bell (1934) was used to evaluate the exploitation levels of O.ruber, which would result in optimum yield. With the growth parameters as the

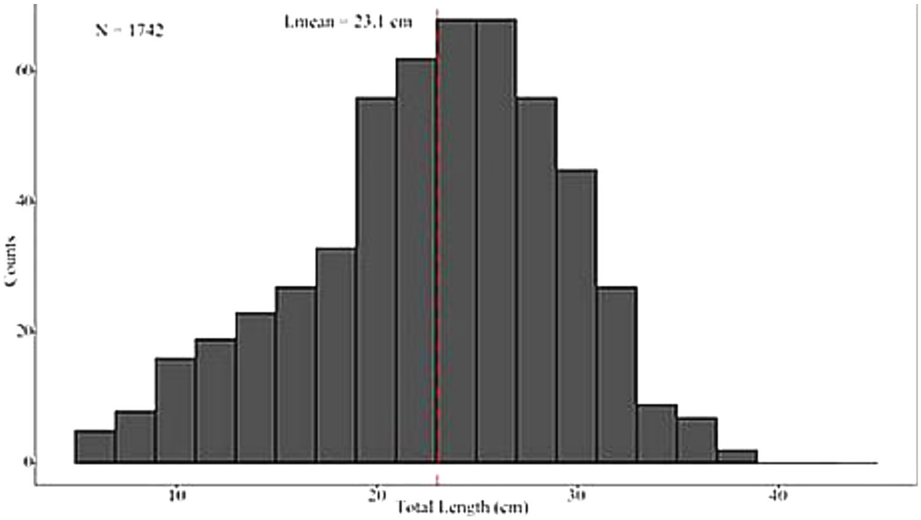

Figure 2. Length frequencies of *O. ruber* collected from commercial prawn trawlers as by-catch samples from Malindi-Ungwana Bay, 2016-2018.

input, the reference levels F_{max} (the fishing mortality, which produces the highest yield per recruit), $F_{0.5}$ (the fishing mortality that results in a 50 % reduction of the biomass compared to the unexploited population), and $F_{0.1}$ (the fishing mortality that corresponds to 10 % of the slope of the yield per recruit curve at the origin) were estimated. The impacts of varying fishing mortality and selectivity (Lc/ L∞) were assessed using the yield isopleths diagramme.

Results

Size distributions of the stock

The length frequency distribution of the 1742 individuals of *O. ruber* revealed a unimodal distribution and was negatively skewed (Fig. 2). The total length (TL) ranged between 5 and 38.4 cm, with a mean size of 23.1 cm (Fig. 2). The majority of the *O.ruber* individuals caught (53.1 %) had a TL larger than the mean size. The mean size of the individuals caught was generally lower in 2016 (22.04 ± 7.6 cm) and 2017 (22.9 ± 5.5 cm) compared to 2018 (24.4 ± 4.9 cm; Table 1).

The results of the Kruskal-Wallis rank-sum test revealed that there was a significant difference between the mean length across the years (chi-squared = 10.123, df = 2, p-value = 0.006337). A pairwise comparisons using the Wilcoxon rank-sum test showed that the mean length in 2018 was significantly different ($p < 0.05$) from the year 2016 and 2017 (Table 2).

Estimation of growth parameters

The length frequency (LFQ) data spans 3 years (2016, 2017, 2018) and comprises of 1742 length measurements, which are aggregated over 9 sampling times (Fig. 3). The figure shows the raw LFQ data (Fig. 3a) and after restructuring with a moving average of 5 (Fig. 3b).

The analysis of the pooled length-frequency data of the *O.ruber* gave an initial L∞ value of 39.2 cm estimated from the mean of the 1 % largest fish in the sample (Table 3). Using L∞ = 39.2 cm as a seed value and an MA of 5, the ELEFAN_GA routine in TropFishR yielded L∞ estimates of 41.7 cm and a K of 0.70 yr^{-1} (Fig. 3c). The bootstrapped ELEFAN routine in TropFishR yielded L∞ estimates of 41. 7 cm, (CI=33.1- 44.6 cm) and a K of 0.79 yr^{-1} (CI = 0.23-0.89).

The value of mode of the distribution (maximum density result after 500 resamples = 0.79) was slightly higher than the GA estimate (Appendix, Figure A).

Table 1. Summary statistics of the size distribution of the *Otolithes ruber* in the commercial prawn by-catch sample.

Year	N	Min (cm)	Max (cm)	Mean size (cm) ± SD
2016	526	5.0	38.4	22.0 ± 7.6
2017	630	10.0	34.0	22.9 ± 5.5
2018	586	9.0	36.0	24.4 ± 4.9

Table 2. Pairwise comparisons of the mean length between the years in *Otolithes ruber* using Wilcoxon rank-sum test.

	2016	**2017**
2017	0.435	
2018	0.013	0.013

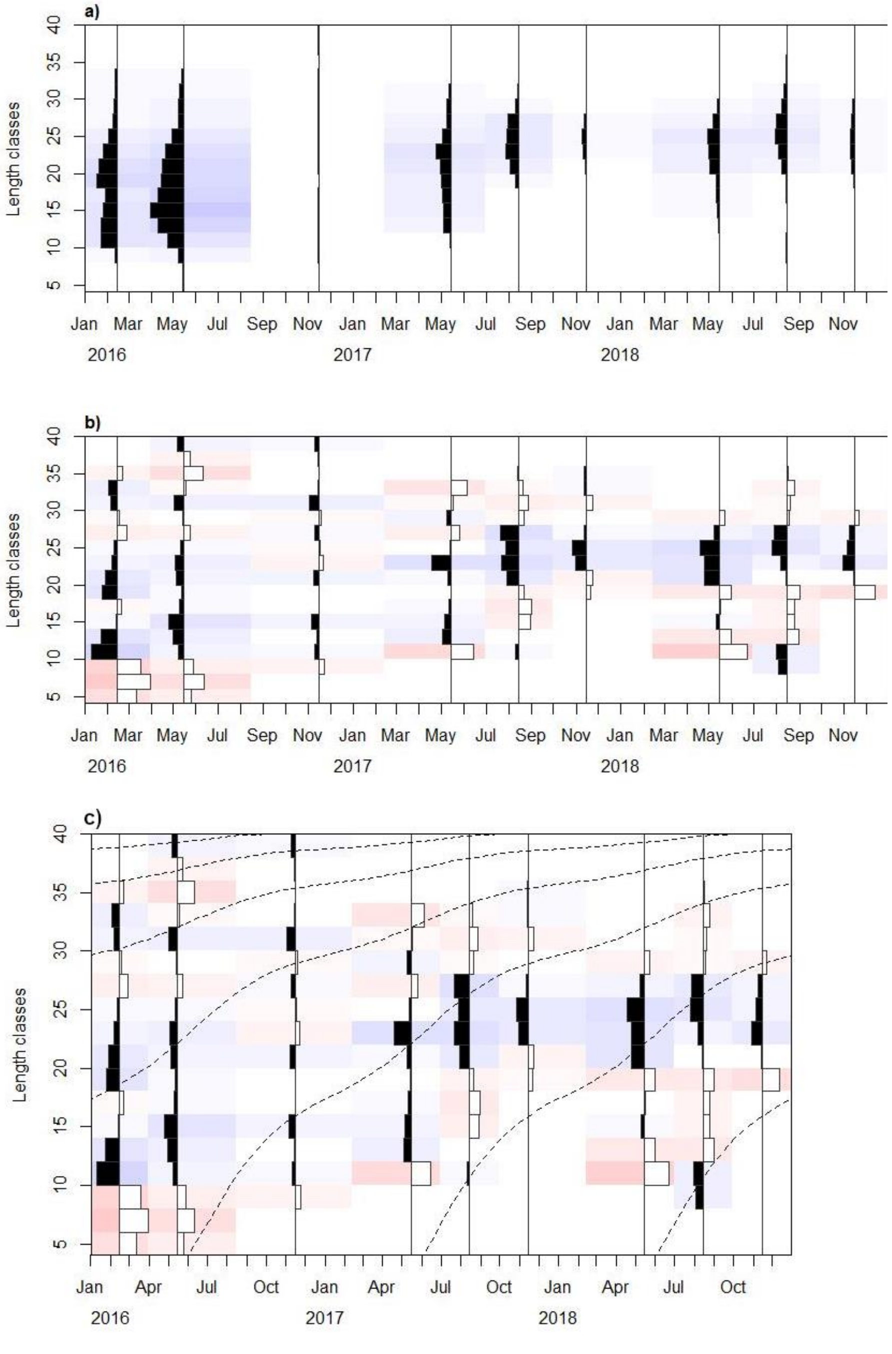

Figure 3. Raw (a) restructured (b) length frequency data of *O. ruber* from Malindi-Ungwana Bay, 2016-2018; (c) restructured length-frequency distribution with superimposed growth curves of *O. ruber* obtained through the ELEFAN_GA function (with the settings MA = 5, Linf = 41.7, K = 0.79, C = 0.43).

Table 3. Comparison of growth parameters of *Otolithes ruber* in this study with those from other studies.

Study	Methods	L∞ (cm)	K (year^{-1}	Φ'	Reference
FishLife	Aggregated	43.9	0.38	2.86	(Thorson *et al.*, 2017)
This study	Length- based	41.7	0.70	3.087	
KwaZulu-Natal, South Africa	Age-based	41.9	0.31	2.74	(Brash and Fennessy, 2007)
KwaZulu-Natal, South Africa	Length-based	51.1	0.6	3.19	(Fennessy, 2000)
Kuwait	Length- based	59.0	0.39	3.13	(Almatar, 1993)
Sofala Bank, Mozambique	Length- based	42.9	0.14	2.42	Gislason (1985)
San Miguel Bay, Philippines	Length- based	29.5	0.455	2.60	Navaluna (1982)

The growth performance index (Φ') and the longevity (tmax) estimated for *O.ruber* was 3.087 and 4.28 years, respectively.

Mortality and selectivity

The instantaneous total mortality (Z) of *O.ruber* derived from the computed VBGP values was 3.23 (Fig. 4), with natural mortality of 0.931 estimated by the Then *et al.* (2015) approach. The estimated instantaneous rate of fishing mortality (F) was 2.30 per year, with an exploitation ratio of 0.71 (Table 4) which suggests that the *O.ruber* stock in Malindi-Ungwana Bay could be overexploited (E > 0.5). Applying the bootstrap routine resulted in a comparatively lower Z estimate of 1.02 for the maximum density value but with a wide confidence interval (Z = 0.57-3.69). With this procedure, the estimated range of the exploitation rate also varied widely (E = 0.28-0.70) (Appendix, Table A). With the above values, the backward projection of the descending arm of the catch curve resulted in a mean size at first capture (Lc) of 23.8 cm, assuming a trawl-like gear selectivity (Fig. 5).

Recruitment and yield per recruit

Given the growth parameters, the LFQ data can be extrapolated backwards onto the time axis to indicate the relative recruitment pattern (Fig. 6). The pattern exhibited by the size distribution of the *O.ruber*

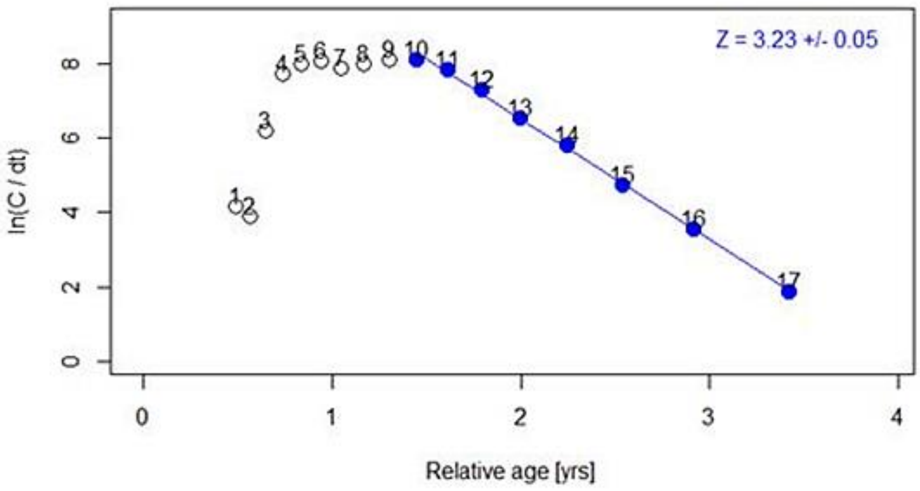

Figure 4. Length converted catch curve showing total mortality (Z) of *O.ruber* in the prawn trawl fishery.

Table 4. Computed mortality, exploitation rates and the selectivity of *Otolithes ruber*.

Z	M	F	E	L50	L75
3.23	0.931	2.302	0.71	23.8 cm	25.3 cm

indicated two unequal recruitment pulses with the major peak occurring during the eighth month (Fig. 6).

The estimation of the biological references are presented in Table 5 and Fig. 7. The optimal exploitation and fishing rate E_{max} (0.542) and F_{max} (2.32) values were well below the actual values of the current exploitation of 0.7 and fishing mortality of 2.3 year^{-1}, respectively and is an indication that the species appears to be overexploited.

The yield and biomass per recruit isopleth diagrammes are represented in Figs. 8 and 9, respectively. The solid black lines are the isopleths indicating different areas of the same yield and biomass, with the dotted lines indicating the current fishing mortality

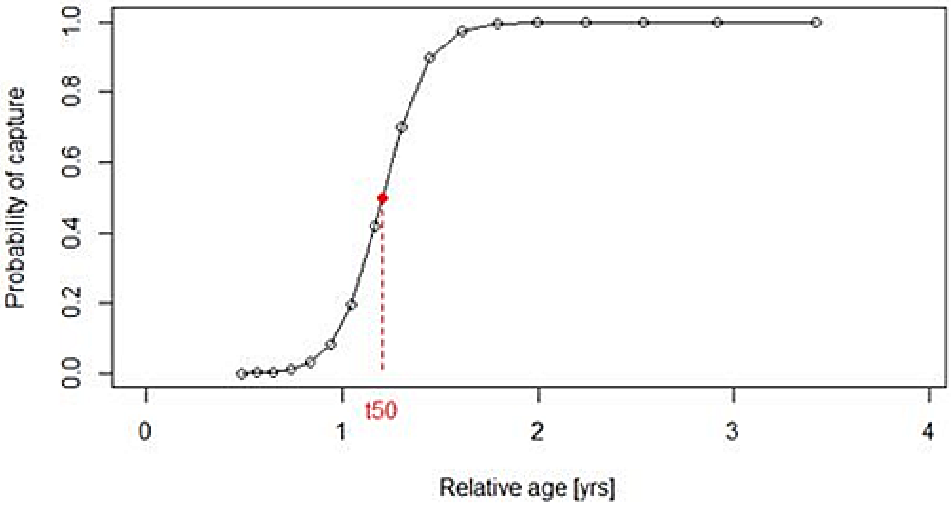

Figure 5. Probability of capture of *O.ruber* as estimated from the backward extrapolation of the descending arm of the catch curve. The dotted line indicates the relative age corresponding to the size at first capture (L50 = 23.8 cm).

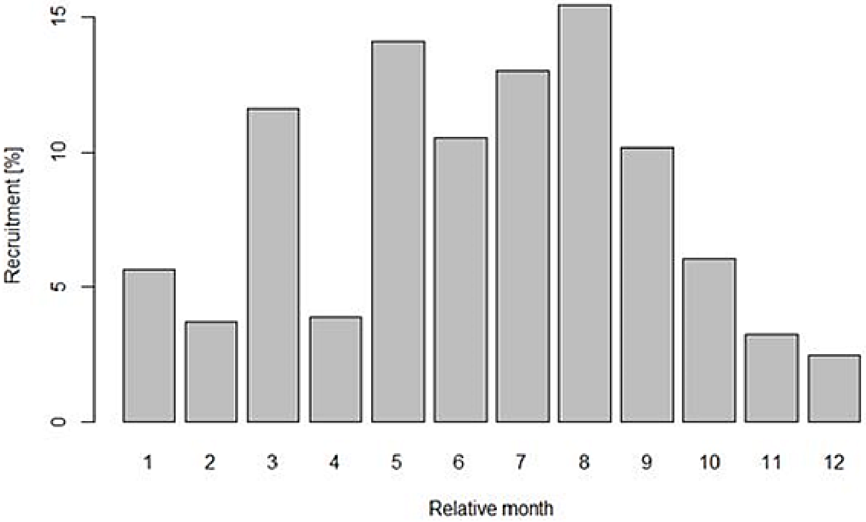

Figure 6. Recruitment pattern of *O. ruber* of the Malind-Ungwana Bay estimated from the restructured length–frequency data onto an arbitrary 1-year timescale. The species exhibits two peaks of unequal magnitude.

Table 5. The estimated biological reference levels from the length-based yield per recruit model (Thompson and Bell, 1934).

F01	Fmax	F05	E01	Emax	E05
1.102	3.306	0.918	0.542	0.78	0.497

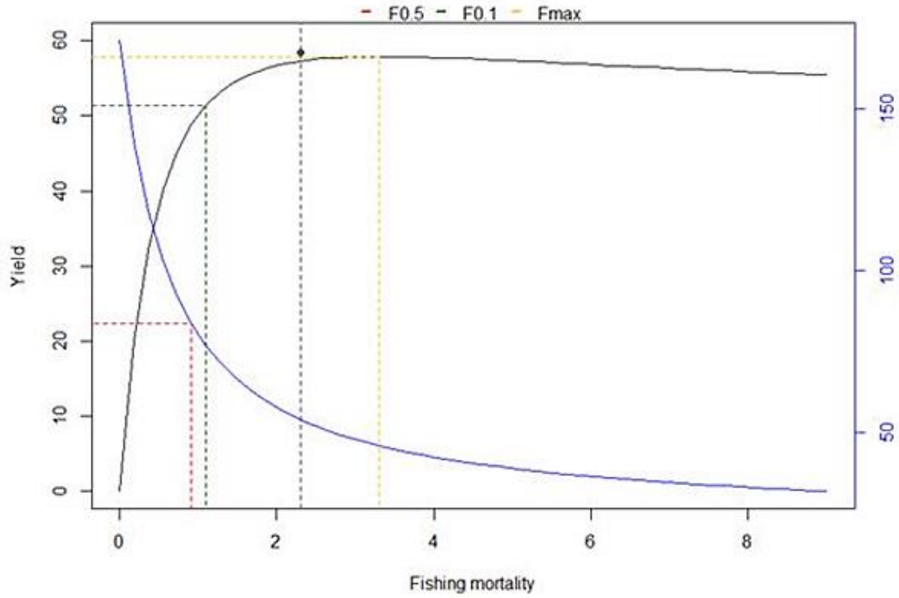

Figure 7. Relative yield per recruit curve for *O.ruber* indicating the yield and biomass per recruit for a range of fishing mortality values, respectively. The dashed lines show the reference levels F0.1, F0.5, Fmax and the current fishing mortality based on the catch curve analysis.

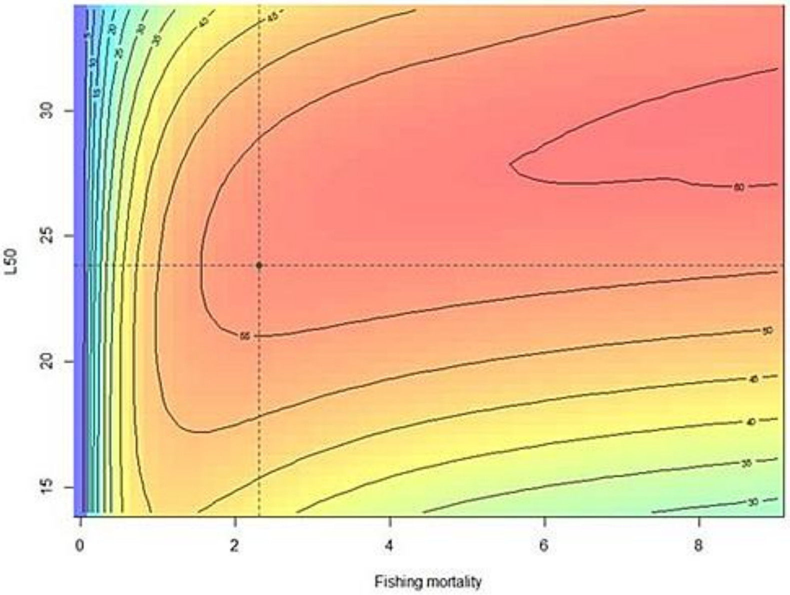

Figure 8. Isopleth diagrammes of the relative yield per recruit as a function of relative size at first capture (Lc/Linf) and fishing mortality for *O. ruber*. The solid black lines are the isopleths indicating different areas of the same yield, while the dashed line indicates the current fishing mortality and selectivity based on the catch curve analysis.

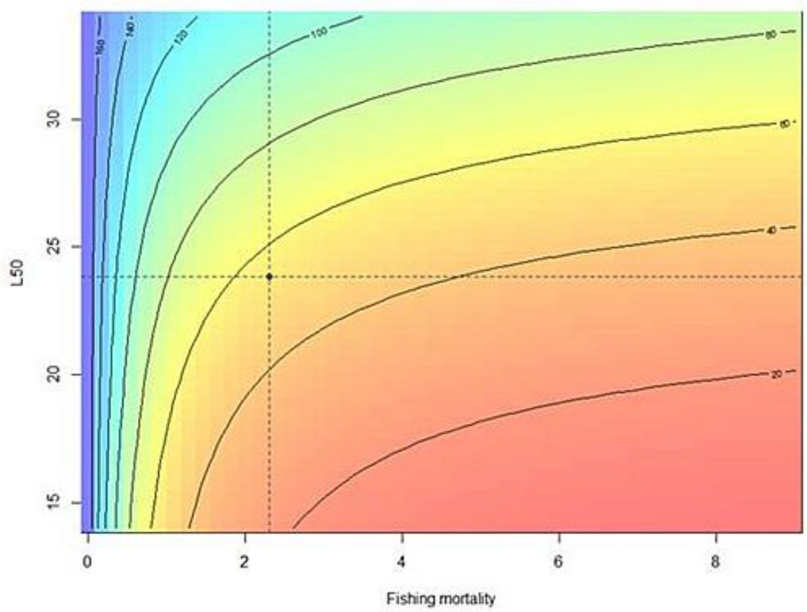

Figure 9. The biomass per recruit isopleth graph as a function of the fishing mortality and the relative size at first capture (L50). The black solid lines are the isopleths indicating different areas of the same biomass, and the dashed line indicates the current fishing mortality and selectivity based on the catch curve analysis.

and selectivity based on the catch curve analysis. The ratio between the Lc and the L∞ represents different scenarios typical to changes in mesh size. At the fishing effort and selectivity found in this study, *O.ruber* stocks are mostly exploited at a smaller size and at a much higher fishing effort. The Lc/L∞ ratio for the fishery was estimated at Lc/L∞ = 0.57.

Discussion

O. ruber commonly occurs as by-catch in prawn trawl fisheries in the western Indian Ocean region and many tropical fisheries of the world (Fennessy, 2000; Munga *et al.*, 2014; Olbers and Fennessy, 2007). on the east African coast, the contribution of *O. ruber* to the overall by-catch landed is substantial (Munga *et al.*, 2014). Nevertheless, their commercial importance is low compared to other demersal species of comparable size. Studies from the region suggest that industrial fleets discard a high proportion of *O. ruber*, the majority being juveniles, (< 20 cm) (Mwatha, 2002; Olbers and Fennessy, 2007). Moreover, relatively little is known regarding their status, and that of other by-catch species, which compromises the management and sustainability of these fisheries. One of the primary goals of fisheries management is to conserve sufficient reproductive potential in stock to allow sustainable exploitation, which requires knowledge of the species' life history (Komoroske and Lewison, 2015). However, the challenge of inadequate data (type, amount and quality) limits the proper assessment and management of these fisheries (Dowling *et al.*, 2008).

This study is the first attempt on the Kenyan coast to assess the status of *O. ruber,* from Malindi-Ungwana Bay, making use of the length-frequency data from catch obtained from non-selective prawn trawl fishing nets. Validation of stock status from length-at-age data provides a more precise and unbiased estimate compared to length-frequency analysis, which strongly affects sample bias. The application of both methods offers the most robust results (Pauly, 1987). Nevertheless, given the cost implications of sampling and the difficulty in the ageing of tropical fish from otoliths, the length-based approaches have become more popular for tropical data-limited fisheries, where length-frequency data is easily collected.

In the absence of time series data on catch or catch-at-age data, the non-parametric ELEFAN routine in TropFishR (Mildenberger *et al.*, 2017) was used to estimate the growth parameters of *O. ruber* based on 1742 length measurements over the period from February 15, 2016, to November 15, 2018. The sample size (n = >1500) and the period over which the sample was collected (> 6 consecutive months) met the requirements for the appropriate sample size for assessing length data for growth studies (Hoenig *et al.*, 1987; Pauly, 1987). Besides, the graphical representation of both the raw and restructured length-frequency data revealed clearly defined modal groups with shifts in the modal length over time, a criterion for assessing the suitability of length-frequency data for the estimation of growth parameters (Wolff, 1989).

The size distribution of the caught individuals from this study demonstrates that *O. ruber* is being caught at relatively larger sizes with more than 53.1 % larger than the mean size at maturity (23.8 cm). Other studies on *O. ruber* have reported the length at first maturity (L50) as 22.6 cm (Froese and Pauly, 2019) and ranging from 22.1 cm in the Arabian Gulf (Lee and Al-Baz, 1989) and between 22-24 cm and 23.8 cm in India and South Africa, respectively (Brash and Fennessy, 2005). Thus, using an approximate value of 23 cm as the length at maturity, which compares to the length at first capture obtained in this study (Lc = 23.8 cm), it is clear that the current exploitation of *O. ruber* with regards to size is slightly above the size at first capture and size at maturity, but falls short of the optimum target (% mature fish in catch = 100%) (Froese, 2004). According to Munga *et al*. (2014), the average sizes of the individuals caught in trawl by-catches was significantly smaller than in artisanal catches. Nevertheless, both fisheries operate within the same area but with the artisanal fleets operating less than 3 nm from shore. The difference in sizes of individuals caught is attributed to the selectivity of the trawl nets, which retain much smaller individuals than those regularly caught by artisanal fishing gears due to the smaller mesh size (mesh size of trawl gear; 45-70 mm). The maximum reported size of *O.ruber* in this study (Lmax 38.4 cm) is much smaller than individuals observed in the northern waters of the Persian Gulf, which reported much higher estimates (Lmax = 67.57 cm; Eskandari *et al*., 2012).

Table 3 compares the growth parameters obtained in this study with those obtained from other studies. The results indicate that the values of $L\infty$ compare well with estimates from Mozambique and South Africa, although not with the estimates of K, which is more than double that obtained in these studies (Brash and Fennessy, 2007; Gislason, 1985). The potential longevity of *O. ruber* was estimated at 4.3 years, which indicates that the species is short-lived. In contrast, the estimated longevity of the species varied widely from other studies (Brash and Fennessy, 2005), which indicated that *O. ruber* and most species of family Sciaenidae are generally slow-growing and long-lived (mean K = 0.32 ± 0.05).

Munro and Pauly (1983) proposed the phi prime (φ) as a suitable indicator for interspecific comparison of growth performance of different species of fish stocks given that the index is more or less constant for a family or similar taxa. The estimated phi prime with current estimates of K and $L\infty$ is 3.08, which compares well with the estimates from Kuwait (φ = 3.19) and South Africa (φ = 3.13) and is within the range of estimates reported in the FishBase (φ = 2.41-3.39) (Froese and Pauly, 2019). The differences in the φ index can be attributed to the differences in the estimation of growth parameters related to the bias in the size distribution of the specimens analyzed here due to the absence of juveniles and larger individuals (Lmax = 90 cm), which may have been missed.

Based on estimated growth parameters, two dependent stock status indicators were estimated employing the length-converted catch curve and the length-based yield per recruit model. The estimated natural mortality (M) was 0.931 year^{-1} leading to fishing mortality of 2.302 year^{-1} and an exploitation rate (F/Z) of 0.71 for the fully exploited part of the stock, indicating that *O. ruber* in the Malindi-Ungwana Bay stock is experiencing excessive fishing pressure ($E > 0.5$). However, the confidence interval estimated from the bootstrapping routine of the TropFishR gives a wide range of estimates for both the growth parameters and the exploitation rate (E = 0.28-0.70). The wide range of confidence interval around the exploitation rate may be due to the biased sample from the commercial trawl fishery. According to Beare *et al*. (2005), data from commercial sources are likely to be biased due to levels of misreporting and discarding and lack spatial detail, which can result in biased estimates of growth parameters. The estimate of fishing mortality in the current study(F = 2.3) based on the catch curve is larger than the reference level (= 1.1) based on the yield per recruit analysis, further strengthening the evidence of overexploitation (= 2.09). Similar results have been reported in Mozambique and the Philippines, where *O. ruber* has been overfished by the prawn trawlers (Brash and Fennessy 2005). Also, the estimated Z/K ratio (Z/K = 4.6) is high, further highlighting that the population of *O. ruber* is mortality-dominated (Z/K>2) and is experiencing excessive fishing pressure (Etim *et al*., 1999).

Pauly and Soriano (1986) proposed an extension to the length structured yield per recruit model applied to tropical fisheries for species associated with high M/K values and E> 0.5. Based on the Lc/ $L\infty$ ratio (a proxy for mesh size) and fishing effort, four quadrants are proposed, each with distinct properties. Under the current fishing scenario, the estimate of Lc/ L∞ of 0.57 and an exploitation rate (E) of 0.71 falls within quadrant D (Pauly and Soriano, 1986). The implication is that small fish are caught at a higher fishing effort requiring a reduction in effort and an increase in mesh size as a management intervention. The recruitment pattern of the *O. ruber* conforms to the general pattern exhibited by most tropical fish species, which have double recruitment pulses (Pauly, 1982). The recruitment pattern was estimated by the backward extrapolation of the LFQ data onto the time axis to indicate the relative recruitment pattern (Fig. 7). However, the pattern can not be interpreted in absolute terms as information about the length at age 0 is lacking and cannot be estimated from length frequency data alone (Pauly, 1987). Nevertheless, based on the length-frequency data used (Appendix, Table B), the observed peak for smaller sized individuals is between the fifth and seventh months, with the possibility that the young join the adults as recruits in the eighth month. The bimodal peak observed for *O. ruber* in this study is consistent with the results reported for the species in the northwest Arabian Gulf (Mohamed *et al.*, 2002). Thus, a better understanding of the recruitment pattern of the *O.ruber* is critical in formulating better management practices such as in the determination of the seasonal closure for prawn trawling, which is currently from November to March annually (Munga *et al.*, 2016). However, to infer an informed management recommendation, there is a need to augment the current studies with biological, catch and effort data and biomass estimates to capture the variability and changes in population structure. Comparison of biomass and catch-based methods will give a true picture of the fishery, as some studies have reported significantly different results when the two methods were employed (Branch *et al.*, 2011).

Management implications

O. ruber constitutes the highest by-catch species in the commercial prawn trawl fishery in Malindi- Ungwana Bay in Kenya, and is also common among artisanal landings. Previous studies have documented resource-use conflict between the artisanal fishers and the trawlers arising from resource-use overlap, which resulted in the trawling ban in 2006 (Munga *et al.*, 2012). Among the critical issues highlighted included the infringement of the trawlers into the artisanal fishers fishing zones and the incidental capture and discarding of the fisher's target species, of which *O. ruber* is a crucial component. Thus, the Prawn Fisheries Management Plan (PFMP-2010) was instituted to guide fisheries management decision and reduce conflict with artisanal fishers (Thoya *et al.*, 2019). The management plan is due for a review, but the lack of routine monitoring and appropriate data makes it challenging to assess the effectiveness of the management plan. This study highlights the importance of describing and assessing by-catch in specific fisheries to determine whether there are problems in the fishery (Kennelly, 1995; Munga *et al.*, 2012).

This study has assessed the stocks of *O.ruber,* a common by-catch species in the Malindi-Ungwana Bay prawn fishery, and has found that the stocks are being over-exploited (based on a data-limited situation). This calls for stringent measures for the management of the Malindi-Ungwana Bay fishery. However, for practical management recommendations, there is a need for further studies on other by-catch species, and complement these with independent surveys. The current sample is biased towards specific sizes, which might be an artefact of the spatial preference by the commercial prawn trawl. It is suggested that data from the artisanal fishery is included in future assessments to capture the whole fishery for a better estimation of the stocks. Further attempts should be made towards the collection of biological data to provide improved estimates of the reference points, which can be used to complement the current study and thereby contribute to more informed decision making. These efforts should be complemented by the ongoing seasonal closure and gear adjustments to reduce by-catch and juvenile capture.

Conclusions

Given the fact that *O. ruber* is the highest by-catch species in catches of the commercial prawn trawlers in Malindi-Ungwana Bay, it can be expected that their stocks could be at risk. This study has proven that the stocks of *O.ruber* are being overexploited. Further studies are, however, required across all gears and methods, for comparison. It is strongly recommended that stocks of *O.ruber* need proper management to ensure sustainable exploitation and to avoid collapse.

Acknowledgements

We express our gratitude to Kenya Marine and Fisheries Research Institute (KMFRI), Kenya Fisheries Service (KeFS) and the fishing industry (East African Sea Foods Ltd and Ittica Ltd) for logistical support and funding of all the shallow water prawn trawling observer programme surveys. The cooperation and support of the captains of the fishing vessels and the entire fishing crew provided the scientific observers with the support needed to collect data and samples. The help, cooperation and commitment of the KMFRI fishery observer team during the field and laboratory work is appreciated.

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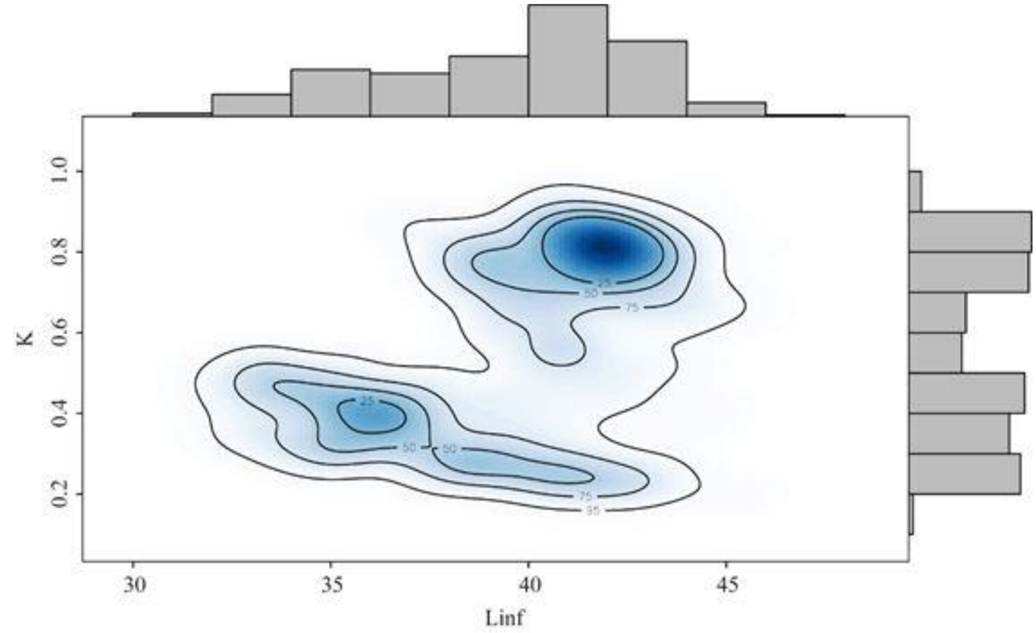
Appendices

Table A. Pooled length frequency of *Otolithes ruber* from 2016 to 2018 (constant interval of 2 cm).

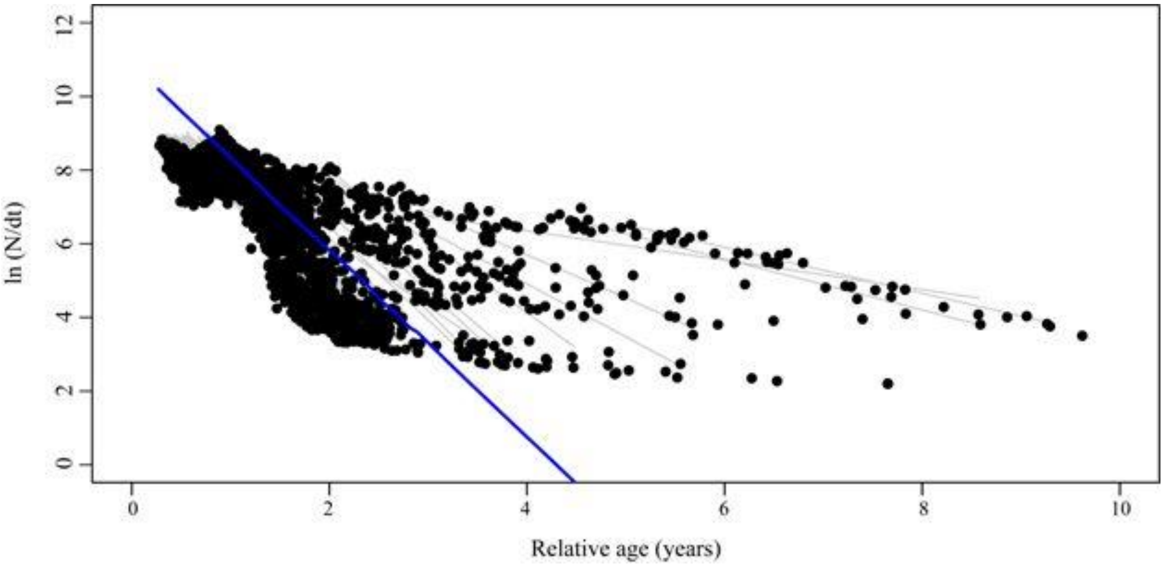
	2016					2017						2018				
ML	**Jun**	**Jul**	**Aug**	**Sep**	**Oct**	**May**	**Jun**	**Jul**	**Aug**	**Sep**	**Oct**	**May**	**Jun**	**Jul**	**Sep**	**Oct**
5		1														
7																
9		1		1	1									3		
11	15	28		3	5	5			1				1	3		
13	27	15		29	5	25							4	1		
15	20	10	2	32	7	24	1		2				10	2		
17	24	15	2	24	4	27	3		5				18	5		
19	11	26	10	16		10	15	1	11	2	4	1	19	6		2
21	7	21	13	15	2	16	27	10	23	13	6	7	36	24	4	16
23	6	11	8	10	1	18	39	11	34	21	19	9	27	27	13	19
25	2	9	6	5	3	12	20	6	27	24	26	20	21	32	20	26
27	4	2	5	5	3	4	15	1	28	24	14	19	8	21	38	22
29	11	2	1	2	2	2	8	2	7	10		13	1	6	25	14
31	11	4	1	3	3	2	4		5	4	2	5		7	12	4
33	6				3		2		1	3	1			3	5	1
35	1						1		1		1			2	1	
37			1		1									3		
39			1		1											

Table B. Growth parameter estimates resulting from the bootstrapping routine of the TropFishR indicating the confidence interval.

Species	Parameter	Mod	Lower	Upper
Otolithes ruber	L∞	41.7	33.1	44.6
	K	0.79	0.23	0.89
	t_{anchor}	0.43	0.12	0.87
	C	0.54	0.19	0.88
	t_s	0.68	0.17	0.86
	Φ	3.14	2.39	3.25



Appendix, Figure A. Scatter histogram of bootstrapped ELFFAN for *O. ruber* using TropFishR. The points represent the individual combinations of L_∞ and K estimates, while the contours represent the density of the combinations.



Appendix, Figure B. The bootstrapped linearized length-converted catch curve based on pooled length frequency catch data for *O. ruber*.

New strandings of True's beaked whale, *Mesoplodon mirus*, in Mozambique and their destiny as marine bushmeat

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Abstract

True's beaked whales have a uniquely fragmented distribution of sightings recorded, mostly from stranding reports. The species is assumed to be associated with deep oceanic waters, occurring in both the northern and southern hemispheres. A hotspot for strandings in the southern hemisphere is South Africa. The third and fourth reported stranding of True's beaked whales for Mozambique is presented, and the first for Tofo Beach, Inhambane Province. This stranding event resulted in the carcasses being butchered and the bushmeat taken for human consumption. This report develops and discusses strategies for mitigation of future risk to public health from aquatic bushmeat consumption in Mozambique.

Keywords: *Mesoplodon mirus*, Mozambique, beaked whale, stranding, bushmeat, IMMA

Introduction

The beaked whales (family: Ziphiidae) are among the least known mammalian groups (Dalebout, 1998). There are 22 described species in the group (Aguilar de Soto *et al*., 2017), and most are rarely seen at sea due to their affinity to deep oceanic waters and possible low abundance (Mead, 1989). All species of beaked whale are incompletely described, missing information such as basic life-history, behaviour and distribution, and variations in morphology. At least 14 species of beaked whale are known to occur in the southern hemisphere, although misidentification is common, especially within the genus *Mesoplodon*, even with the whole animal available for examination, as they are very similar in overall appearance (Kitchener and Herman, 1995). The True's beaked whale *Mesoplodon mirus* was originally thought to be a solely northern hemisphere species until a stranding in South Africa greatly expanded the known range (Talbot, 1960). Other countries which have reported strandings of True's beaked whales in the southern hemisphere include New Zealand (Constantine *et al.,* 2014), Brazil (Souza *et al.,* 2005), and Tristan da Cunha (Best *et al.,* 2009). True's, like other beaked whales, are thought to feed mainly on squid which they hunt off the continental shelf, making sightings and strandings relatively rare (Kitchener *et al.,* 2020). Only two beaked whale species have previously been recorded in Mozambique; one Cuvier's beaked whale *Ziphius cavirostris* (Bachara and Deffontaines, 2016), one True's beaked whale in Ponta do Ouro and another in Pomene (Bachara and Gullan, 2016) (see Fig. 1).

The first known stranding record of True's beaked whales on Tofo Beach in Inhambane Province, a national hotspot for tourism, and the third and fourth recorded strandings of True's beaked whales in Mozambique is reported here. While this is a rare stranding event, it demonstrates that the area is not only within their range but that the species may be more common to the waters of Mozambique than previously recorded, with the potential for further

http://dx.doi.org/10.4314/wiojms.v19i2.12

unreported stranding events resulting in rapid disposal of the carcass by consumption as bushmeat.

Several Mozambican laws refer or apply to marine (or aquatic) bushmeat. Under Mozambican law, beached or stranded live wild marine mammals may not be killed or inflicted any injury (General Regulation of Maritime Fisheries – Decree no. 43/2003). The Regulation of Law of Forestry and Wildlife also covers some aspects regarding their destiny once deceased and while trophies are state property, bushmeat can be freely distributed for consumption to communities if safe to human health as certified by a Veterinary authority (Regulation of Law of forestry and wildlife – Decree no. 12/2002). The regulation of animal sanitation also deals with health and consumption of livestock and animals generally, which includes bushmeat. It declares that consumption can be allowed if certified by a Veterinary authority as harmless and not posing a threat of dissemination of diseases to humans or domestic animals. Otherwise, by law bushmeat must be confiscated to be incinerated or buried (Diploma Ministerial – Decree no. 219/2002).

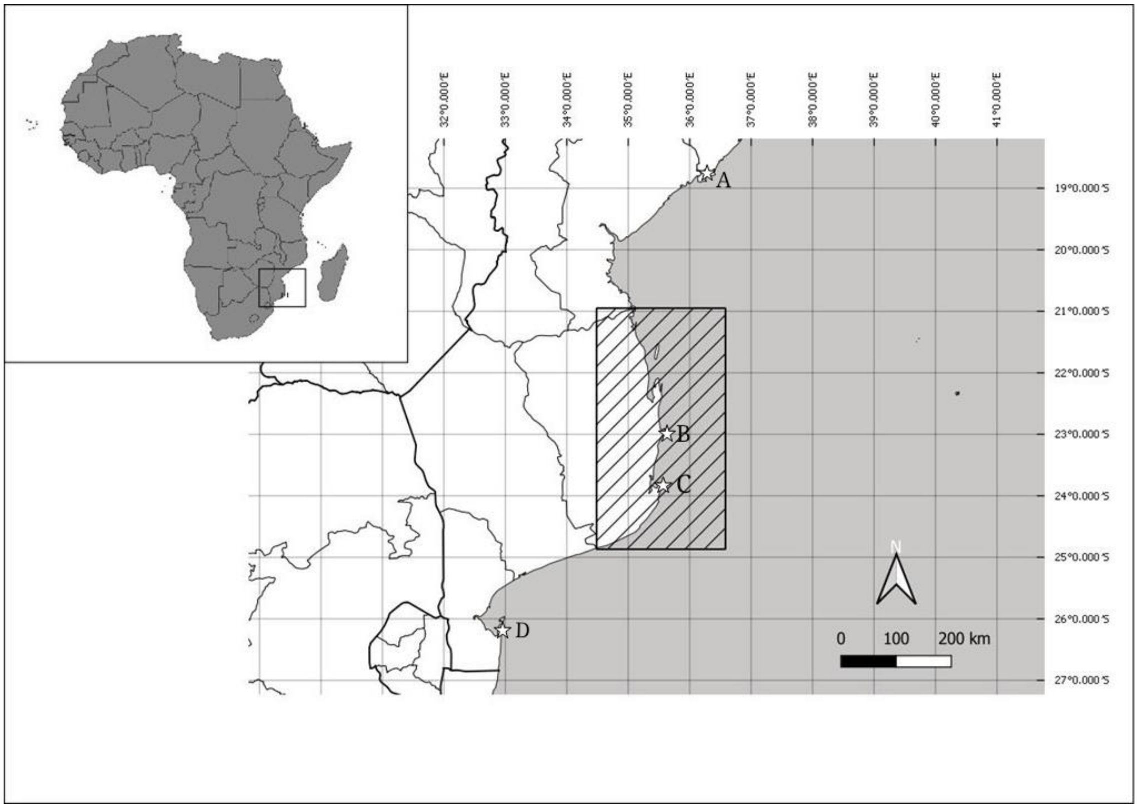

Figure 1. Oceanic region of the cross-hatch region indicates the designated Important Marine Mammal Area (IMMA). Stars indicate all reported stranding sites of beaked whales in Mozambique. (C) indicates stranding site (35°5.33 E, -23°8.57 S) of the two True's beaked whales (*Mesoplodon mirus)* in this report. (A) indicates the stranding site of a Cuvier's beaked whale on Mafamede Island, (B & D) indicates the stranding sites of True's beaked whales at Pomene and Ponta do Ouro, respectively.

Materials and Methods

Two True's beaked whales stranded at approximately 2 am on 8th April 2019 on Tofo Beach, Mozambique (S23°51' E35°32') (Fig. 1). Upon discovery within the breaking shore waves, the animals were confirmed dead at 2:10 am and remained under constant supervision by the local police from that point onwards. The only evident injury at this time was a 10 cm cut under the mandible of one animal from which fresh blood was emanating. It cannot be ruled out that this injury may have been inflicted during the beaching incident. A tractor was used to pull them fully out of the surf-zone at 5:30 am. At 5:35 am the animals were assigned field numbers and photographs, measurements and other observations as per the stranding data sheet from the Center of Dolphin Studies in South Africa, by staff from All Out Africa (https://www.alloutafrica.org/marine.html). Further minor injuries to both carcasses were evident, largely bruising and skin abrasions. As these injuries were not present three hours earlier, they were likely a result of abrasions from sand during the prolonged post-mortem beaching, and removal from the surf and boat launch zone by a tractor, pulled along the sand using rope tied around the tailstock of each carcass.

Local government officials and maritime authorities were contacted and attended the scene. Twelve hours after the beaching event, the skulls and several vertebrae were collected, and samples of blubber were taken and labelled for donation to the Natural History Museum in Maputo. Both carcasses were butchered and eaten by the local community.

Results

The two beaked whales were sexed and measured (Table 1); the male to 471 cm (Fig. 2a), and the female to 491 cm in length (Fig. 2b; further measurements and the skulls are available from Museu de Historia Natural, Maputo, from A. Guissamulo). Both animals displayed a dark grey dorsal surface, with darker circular patches surrounding the eyes and a paler grey ventral surface from the lower jaw extending posteriorly towards the pectoral fins and the belly. The ventral surface then darkened slightly before again lightening at the ano-genital region (Fig. 2c). Based on the relative location of ano-genital openings, Whale 1 was identified as male (Fig. 2d) and Whale 2 as female (Fig. 2e). A large white elliptical from the anal to genital slit was present, which was larger and whiter on the male (Fig. 2d) than the female (Fig. 2e). Light grey colouration was also noted around the base of the dorsal fins on both whales, which also appeared lighter and more pronounced in the male in contrast to the female. This colouration is thought to be typical of the Southern Hemisphere True's beaked whale (Baker, 1983; Jefferson *et al.,* 2015). However, a lighter colouration on the body, matching the pectoral fin contour, was not obvious, as was observed in Brazil (Souza *et al.,* 2005). Several scars and wounds were seen on the flanks of both specimens, similar to those caused by the cookie-cutter shark *Isistius* spp. (Fig. 2d).

Teeth were not evident in the lower mandibles, which is indicative of either juvenile male or female True's beaked whales (Mead, 1989) (Fig. 2f). There was no opportunity to investigate whether teeth were concealed under the skin prior to the burial of the heads in a soft sand and loose soil pit. After excavation there was sign in the skulls of vestigial teeth cavities or tooth alveoli (Fig. 2g). However, in both whales the tooth cavities were very small, suggesting both whales were potentially immature (Best, 2007). The skulls of both whales are now held at the Natural History Museum in Maputo (catalogue numbers: MHNM.MAM.2019.0002 and MHNM.MAM.2019.0003).

Table 1. Measured lengths of fresh carcasses in centimetres (cm).

	Whale 1 (male)	Whale 2 (female)
Tip upper jaw to deepest part of notch on flukes	471	491
Tip upper jaw to apex of melon	19	21
Tip upper jaw to angle of gape	30	30
Tip upper jaw to centre of eye	50	62
Centre of eye to angle of gape	29	29
Length of eye	4	3
Projection of lower jaw beyond upper jaw	2	2
Length of mammary slit (Left, Right)	8, 6	10.5, 9
Length of genital slit	11	21
Length of anal opening	1	2
Width of blowhole	11	12
Height of dorsal fin	14.5	26
Pectoral fin anterior length (length of fin base)	44	49
Fluke width tip to tip	120	153

Figure 2. a) Whale 1 – Male, 4.71 m total length. **b)** Whale 2 – Female, 4.91 m total length, with absence of erupted teeth shown. **c)** Dark eye patch. Darker grey dorsal and light grey ventral colouration. Abrasions to the face suspected from movement of dragging by tractor along the beach (Whale 2). **d)** White elliptical around the genitalia, scars and lesions consistent with cookie cutter (*Isistius* spp.) bites. Relative location of ano-genital openings further apart identified this whale, Whale 1, as male. **e)** Relative location of ano-genital openings and mammary slits close together were used to identify this whale, Whale 2, as female. **f)** No teeth were evident protruding from the mandibles of the fresh carcasses (Left - Whale 1 Male, Right - Whale 2 Female). **g)** Skulls and mandibles of both whales. Mandibles of both showing small tooth cavities visible (unfortunately burial was performed without record of relation to field identification). **h)** Presence of the police from 2:30 am and keen interest of the local community from 5.30 am through to the butchering of the carcasses at 4:30 pm (Whale 1).

Discussion

With the True's beaked whale listed as Data Deficient by the IUCN red list (Taylor *et al.,* 2008), all new information gathered on this species adds to the understanding of its life history and conservation status. Indeed, so little is known about them that new information can still serve to improve knowledge of the Ziphiidae family as a whole.

Africa is recognised as a global hotspot for cetacean diversity (Pompa *et al.,* 2011). Cetacean stranding records, however, are extremely scarce in Mozambique. Dedicated offshore surveys are required to determine the distribution and abundance of cetacean species in Mozambique and along the southern Africa coastline. With increasing demands on the coastal waters of Mozambique from commercial fishing and tourism as well as resource exploration and exploitation, it is critical to gather further data and increase scientific understanding of the area to advise sustainable management and conservation. Megafauna species, such as beaked whales and other cetaceans, dugongs and turtles, are impacted by increased ocean traffic and elevated noise that accompanies coastal resource prospecting and extraction (Weilgart, 2007; Nelms *et al.*, 2016). The identification of the Inhambane coastline, where Tofo Beach is found, as an Important Marine Mammal Area (IMMA) recognises the unique, well preserved habitat this area has to offer and its value to the endangered species found there (IUCN-MMPATF, 2020) (Fig. 1). As this, the first report of True's beaked whales from Tofo Beach, Inhambane, shows, there is still much to learn about the region's wildlife, with data collection and reporting essential. The fact that there have now been three separate True's beaked whale stranding incidents recorded along the Mozambican coastline suggests that this species is likely using these waters more commonly than had previously been recognised.

This report highlights the demand for marine mammal meat, or aquatic bushmeat as it is known, within Mozambique. While use of landed and stranded cetaceans as marine bushmeat has been previously documented in coastal regions of many other African countries, including North and West Africa (Clapham and Van Waerebeek, 2007; Segniagbeto *et al.*, 2019), a scarcity of literature exists regarding both marine strandings and bushmeat consumption in Mozambique (Guissamulo, 2008). In this case, harvest occurred despite the unknown cause of death, undefined public health status of the carcasses and police presence (Fig. 2h).

A key management issue, also highlighted by this report, is the lack of clear protocol regarding stranding events, covering the correct handling and disposal of such remains. Preservatives, freezer space and autopsy equipment are limited and there is no clear delegation of responsibility, which results in confusion and delay or inaction by authorities. It is suggested that the better dissemination of procedural information, sampling and necropsy equipment and expertise is essential in order to support the upholding of legislation and avoid spread of illness derived from unsafe carcasses. This improved management approach could serve to reduce related negative outcomes, such as the recent tragic deaths of several citizens of the Memba district of Nampula after consuming contaminated sea turtle meat (as reported by the media: 'Rádio Moçambique' from 12 July 2020 and 'Jornal Notícias' from 27 July 2020).

Several stranded beaked whale carcasses have been shown to be infected with diseases, ranging from herpesvirus (Arbelo *et al.*, 2012; Saliki *et al.* 2006) and a novel beaked whale circovirus (Landrau-Giovannetti *et al.*, 2019) to mortality and stranding-related dolphin morbillivirus (Centelleghe *et al.*, 2017) all of which could pose threats to the survival and health of these marine mammals. With the diseases of beaked whales still poorly studied, more commonly studied cetacean species can give an indication of future directions for beaked whale research in their findings. Recently, three novel coronaviruses of marine mammals have been identified. BdCoV HKU22 was identified in Indo-Pacific bottlenose dolphins *Tursiops aduncus*, and US BdCoV in Atlantic bottlenose dolphins *T. truncatus*, in addition to BWCoV SW1 already identified in Beluga whales *Delphinapterus leucas* (Woo *et al.*, 2014; Wang *et al.*, 2020). Infectious diseases, such as brucellosis and toxoplasmosis, have been isolated from marine mammals which may pose a transmission threat to humans via contact or ingestion (Van Bressem *et al*., 2009; Waltzek *et al.*, 2012). These zoonoses range in severity from localised skin infections to life-threatening diseases of public health risk. Reports from more widely studied coastal areas indicate a risk of zoonotic disease development and transmission at the aquatic animal-human interface (Bogomolni *et al.,* 2008). Anthropogenic alteration of these environments, particularly through introduction of pollutants or release of ship ballast water, could potentially drive the spread and development of disease in marine wildlife populations (Van Bressem *et al*., 2009). Aquatic reservoirs of zoonotic diseases are understudied in Mozambique.

The primary issue with marine mammal bushmeat in Mozambique, evident in the specific case of these True's beaked whale carcasses, is that consumption takes place before any assessment and certification of risk has been carried out. Defining the process, with accompanying education and training, should serve to improve reporting, sampling and testing of stranded marine mammals in Mozambique. This will increase understanding to advise conservation management and mitigate risks to public health from stranded aquatic bushmeat consumption.

Acknowledgements

We would like to thank the Natural History Museum in Maputo for their invaluable assistance regarding the acquisition, housing and display of the skulls. In addition, we would like to thank All Out Africa LDA Mozambique who provided the staff-hours necessary for this project.

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